Movement of fishes in a network of streams and implications for persistence.

Brett Albanese

Dissertation submitted to the Faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Fisheries and Wildlife Sciences

Paul Angermeier, Chairman
Charles Gowan
Carola Haas
Andrew Dolloff
Donald Orth

10 December 2001

Blacksburg, Virginia 24061-0321

Key Words: *Rhinichthys atratulus, Semotilus corporalis, Nocomis leptocephalus, Thoburnia rhothoeca*, drought, James River drainage

Movement of fishes in a network of streams and implications for persistence.

Brett Albanese

(ABSTRACT)

Mark-recapture studies sample unevenly over distance and generate biased or "distance-weighted" movement data, where short distances are sampled more frequently than long distances. I examined how study design affects the degree of distance-weighted sampling and observed movement distributions of stream fish. A modeling study illustrated how distance-weighting increases with the number of mark sites and decreases with the length of stream sampled during recapture. Sub-sampled empirical data sets indicated that longer movements can be detected by increasing the length of the recapture section and that a substantial proportion of fish may move long distances outside of study areas.

I also examined factors that were associated with movement in a network of streams. The probability of emigrating from a site was positively related to intermittency and body size and negatively related to distance from the mainstem creek and habitat complexity. Movement rates, measured as the number of fish moving upstream through a trap per day, were positively related to increases in flow, daylength, and water temperature. Distance moved was greater for fish that were initially marked within intermittent reaches. Overall, some species moved in association with several of these factors but others did not respond to any factors.

Finally, I identified species-level attributes that were associated with colonization rates after experimental defaunation. Movement rate and abundance explained the most interspecific variation in colonization rates when compared to competing predictors (spatial distribution, body size, and family). Recovery occurred slowly and several species had not restored more than half of their pre-defaunation abundance within a year. Despite slow recovery for some species, defaunation had only a short-term (i.e., < 3 months) effect on relative abundance patterns.

This study has important implications for conservation. Improvements in study design will allow detection of longer movements that may be a key component of species invasions, demographic rescue, and colonization. Species that move in association with multiple factors

may be better colonists than species that do not. Finally, species that are rare and less-mobile will recover their populations slowly and will be vulnerable to extirpation in systems impacted by frequent pulse disturbances.

Acknowledgements

Table of Contents

List of Tables

List of Figures

Chapter 1. Using mark-recapture techniques to estimate movement distance distributions for stream-fishes: strategies to reduce bias, increase recapture rates, and detect longer movements.

INTRODUCTION

Movement links fishes to habitats over a broad range of spatial scales (e.g., adjacent microhabitats to entire drainage networks) and allows fishes to track spatio-temporally variable resources, emigrate from unsuitable habitats, avoid competition, escape predation, reproduce, and colonize after extinction (Fausch and Young 1995; Schlosser and Angermeier 1995; Fraser et al. 1995; Ensign et al. 1997; Labbe and Fausch 2000). Accurate information on movement is thus necessary for managing and understanding stream-fish populations. Mark-recapture is often the most feasible approach to study movement because of its applicability to large numbers of animals, small-bodied species, and limited research budgets (Stenseth and Lidicker 1992). Unfortunately, the interpretability of mark-recapture studies is challenged by methodological problems that decrease recapture rates and bias movement distance distributions. This paper is primarily concerned with factors that bias movement distance distributions, but has implications for recapture rates as well.

Study design may distort empirical movement distance distributions and terrestrial ecologists have long recognized a bias toward detecting short movement distances when study areas are small (Barrowclough 1978; Matthysen et al. 1995; Koenig et al. 1996). The bias occurs because short movements are sampled more frequently than longer movements when animals move outside of the study area (Baker et al. 1995). Thus mark-recapture studies on unbounded animal populations sample unevenly over distance, a problem that is formally referred to as distance-weighted sampling (Stenseth and Lidicker 1992; Porter and Dooley 1993). The effect of distance weighting on observed distributions has been reduced in terrestrial studies by increasing study area size or applying correction factors that adjust the observed number of movements to under-sampled distances upwards and over-sampled distances downwards (Porter and Dooley 1993; Baker et al. 1995; Koenig et al. 1996).

Gerking (1959) recognized the influence of study area size on estimates of home range size in fishes, but few of the many mark-recapture studies conducted since his time have utilized

1

large study areas or acknowledged that observed movement distributions may be biased. Gowan et al. (1994) brought new attention to the problem and highlighted the difficulties of estimating movement when recapture efforts are primarily directed at sites where marked fishes were released. Gowan and Fausch (1996) acknowledged that distances between mark sites and recapture sites can bias observed movement distributions of stream fish. More recently, Skalski and Gilliam (2000) corrected empirical stream-fish movement distributions to account for this bias and concluded that corrected and uncorrected distributions were not distinguishable.

While Skalski and Gilliam's findings suggest that distance-weighted sampling may not seriously bias stream-fish movement distributions, it may not be appropriate to extend this inference beyond the specific characteristics of their design. The location of mark sites, the length of stream sampled during recapture events, and the number of movement pathways leading out of the recapture section could all influence distance weighting and observed movement distributions. The primary objective of this study was to evaluate how these attributes of study design affect the degree of distance weighting and observed movement distributions. First, I performed a simple modeling exercise to determine the degree of distance-weighted sampling occurring under alternative study designs. I then examined the effect of study design on observed movement distributions for three stream-fish species. More specifically, I addressed the following questions:

1). Can more extensive movements be detected for stream fishes by increasing the length of stream sampled during recapture?

2). Are "corrected" movement distributions similar to distributions resulting from more spatially extensive sampling efforts?

3). Can movement be accurately described when there are multiple pathways (i.e., tributaries) leading out of the recapture section?

MATERIALS AND METHODS

Alternative study designs

I determined the degree of distance-weighted sampling under 16 alternative study designs. Although a broad range of designs has been used in past studies, I selected designs to bracket parameters in "typical" mark-recapture studies (e.g., Hill and Grossman 1987; Mundahl

and Ingersoll 1989; Freeman 1995; Goforth and Foltz 1998; Aparicio and Sostoa 1999; Grant and Maslin 1999; Smithson and Johnston 1999). The first eight designs considered a 1000-m section of stream divided into twenty 50-m sites. All 20 sites were considered part of the recapture section, but the location and number of mark sites differed among designs. The first design considered a single mark site located in the center of the recapture section. In subsequent designs, contiguous mark sites were added sequentially toward recapture section boundaries. These additional mark sites extended equal distances upstream and downstream of the recapture section's central mark site. The same mark sites were selected in the remaining eight designs, but were embedded within a 2000-m section of stream divided into forty 50-m sites.

I determined the proportion of total possible movements sampled for each distance under each of the alternative study designs. For example, mark sites always occurred within recapture sections, so 100% of the total possible movements of 0 m were sampled and the number of fish moving this distance could be estimated without bias. It is more difficult to calculate the proportion of total possible movements sampled for other distances, because fish leaving mark sites could follow one of two movement pathways (upstream or downstream; hereafter "tracks") that extended outside of the recapture section.

For each track x mark-site combination, I classified each 50-m distance bin as sampled, unsampled, or not possible (see Table 1.1 for example). To identify sampled distances, I measured distances from the midpoint of each mark site to the midpoint of each recapture site (see Table 1.2 for example). Distances were recorded as negative (downstream of mark site) or positive (upstream of mark site). Distances were recorded as not possible if they were not encountered along a track. For example, all upstream distances were recorded as not possible for the downstream track (this distinction seems trivial now but is very important for more complex study designs). Distances that occurred outside of the recapture section but were otherwise possible were recorded as unsampled.

The number of times that each distance (d) was sampled was calculated for each mark site (s) by summing the number of times distances were recorded as sampled across all tracks (S_{ds}; see Table 1.1 for example). The number of times that each distance was possible was calculated for each mark site by summing the number of times distances were recorded as sampled and unsampled across all tracks (P_{ds}; See Table 1.1 for an example). The total number

of times that each distance was sampled or possible was then calculated from the following formulas:

$$TS_d = \sum_{s=1}^{z} S_{ds} \times M_s \quad \text{and}$$

$$TP_d = \sum_{s=1}^{z} P_{ds} \times M_s$$

where TS_d is the total number of times that distance d is sampled, z is the total number of mark sites, M_s is the number of fish marked in site s, and TP_d is the total number of times that distance d is possible. The proportion of total possible movements sampled for each distance (PS_d) was then obtained by dividing TS_d by TP_d. I set all M_s values = 1, so PS_d values reflect sampling effort at each distance when the same number of fish are marked in each site. Following the example illustrated in Tables 1.1 and 1.2, PS_{-250} and PS_{250} = 0.50 and all other PS_d values = 1

Ideally, PS_d values would be 1 (i.e., 100%) for all distances sampled under each design, indicating that all possible distances were sampled and that sampling effort did not vary with distance. I plotted PS_d x 100 values across all distances to visually represent the degree of distance weighting imposed by each design. Following Porter and Dooley (1993), I also calculated coefficients of variation (CV) for PS_d values to compare the degree of distance weighting among designs. Finally, I determined the maximum detectable movement distance and the length of stream sampled with uniform effort for each design.

Mark-recapture study

Data for the observed movement distributions comes from a spatially extensive mark-recapture study conducted during 1999. The study area consisted of a network of streams tributary to Johns Creek (James River drainage) in Craig County, Virginia (Figure 1.1). The study area was divided into 88 contiguous sites, averaging ca. 50 m in length (Figure 1.1). Site boundaries were determined by pulling a measuring tape 50 m along a stream and finding the

closest logical endpoint (e.g, habitat unit boundary, culvert, tributary confluence etc.,) for the site. An additional criterion was that each site contained riffle, run, and pool habitats. This site design allowed me to compare movements among sites of similar length and ensure that fishes moving within a single habitat unit did not appear to change sites.

Fifteen sites were selected for marking during spring 1999. (Figure 1.2 left). Fishes captured at two weir traps (see below) during spring 1999 were also marked. Several mark sites were strategically selected near tributary-mainstem confluences to facilitate detection of movements between mainstem and tributary sites. The remaining mark sites were chosen by dividing streams into two or three equal-sized sections and then randomly selecting one mark site from each section. This procedure allowed me to distribute mark sites throughout the study area without subjectively selecting individual sites.

Fishes were sampled by completing three passes with a backpack electrofishing unit through each mark site and stunned fishes were collected with 4.8-mm-mesh dipnets. *Nocomis leptocephalus* (bluehead chub), and *Thoburnia rhothoeca* (torrent sucker) >/= 60 mm total length (TL) and *Rhinichthys atratulus* (blacknose dace) >/= 45 mm TL were given a site-specific batch mark by injecting photonic tags (New West Technologies, Inc.) into two different body locations. *Nocomis leptocephalus* and *T. rhothoeca* >/= 80 mm TL were also injected with passive integrated transponder (PIT) tags. The results of mark-retention experiments are given in Appendix A. After marking, fishes were placed into aerated buckets containing clean stream water and aquarium salt. Their behavior was monitored for at least 30 minutes before they were released back into their original site of capture. The ecology of focal species is reviewed in Jenkins and Burkhead (1993).

Recapture sampling took place during August 1999 using the same protocol as described for the mark sites except that only two passes were completed in each site. The recapture event included all sites upstream of a series of beaver ponds in lower Dicks Creek that were too deep to sample. Two additional sites located between these ponds and the confluence with Johns Creek were also sampled (Figure 1.1). The total length of the recapture section was 4459 m.

Distance distributions and estimates of distance weighting

Movement distance distributions were developed for each species. Distances were calculated between mark site and recapture site midpoints, but were not signed as positive

5

(upstream) or negative (downstream) to indicate the direction of movement. The presence of multiple tributaries within the recapture section permitted fishes to change direction during movement, making comparisons between upstream and downstream movements meaningless. Distances for fishes recaptured within their original mark site were recorded as zero and all other distances were grouped into 100-m bins for the construction of frequency distributions. I used a wider distance interval than in the modeling exercise because variation in site length decreased the resolution of distance estimates.

Sequential observations of dispersing individuals could lead to overestimation of short-distance movements relative to long-distance movements (Porter and Dooley 1993). The use of continuously sampling weirs (see *Recapture section closure* below) increased opportunities for sequential observations of individuals and many of the fishes captured at weirs were later recaptured at more distant sites. Thus, to account for the sequential observation bias, I omitted weir recaptures from all movement distributions. As in any study using batch marked individuals, however, there were still opportunities to unknowingly capture individual fish multiple times during a recapture event. Analysis of PIT-tagged recaptures suggests that very few fish were caught more than once during a single recapture event. For example, only one of 72 recaptured *N. leptocephalus* was caught more than once during the August 1999 recapture event and zero of 44 PIT-tagged *T. rhothoeca* exhibited multiple recaptures during this period.

I calculated separate PS_d values for each species because of variation in the number of fishes marked in each site. The same formulas were used, but calculations were more tedious than in the modeling exercise because of the large number of movement tracks. For example, a fish marked in lower Dicks Creek could move upstream into Little Oregon Creek (1), Middle Creek (2), Mudlick Branch (3), upper Dicks Creek (4), or White Branch (5), move downstream into Johns Creek (6), move upstream into an unnamed tributary after moving 1000 m downstream into Johns Creek (7), move upstream into Johns Creek (8), or move upstream into Laurel Branch after moving 1500 m upstream into Johns Creek (9). There were also more opportunities to record distances as "not possible" because dams blocked movement tracks (see Table 1.3 for an example of movement tracks).

Study section length simulation

To assess the effect of study section length on distance weighting and observed movement distributions, I re-calculated PS_d values and re-created movement distributions after reducing the length of stream sampled during the recapture event (Figure 1.2). I reduced the study section length to 1978 m; smaller study section lengths would have imposed more severe distance weighting but would not have included all of the original mark sites. Movement distance distributions for the full and reduced data sets were compared with one-sided (i.e., Ha: median distance of reduced data set < median distance of full data set) Mann-Whitney U tests (Sokal and Rohlf 1995).

I then used PS_d values to adjust the full and reduced distributions for distance weighting using the following formula:

$$C_d = 1/PS_d$$

$$A_d = (O_d*C_d)/(\Sigma O_d*C_d/\Sigma O_d)$$

Where C_d is the correction factor for distance d, A_d is the adjusted number of movements of distance d after accounting for distance weighting, and O_d is the observed number of movements of distance d (adapted from Porter and Dooley 1993). This procedure adjusts movements to under-sampled distances upwards while the opposite is true for distances sampled with relatively high effort; the denominator in the lower equation ensures that the adjusted number of fish will be equal to the observed number of fish (Porter 1998; Porter and Dooley 1993). Adjusted and observed distributions were visually compared within each study design to estimate the degree to which observed data were distorted by distance weighting (Porter and Dooley 1993). I also compared adjusted data from the reduced design to unadjusted data from the full design to determine if adjusted distributions more closely resembled distributions from the more spatially extensive sampling effort. I did not compare unadjusted and adjusted frequency distributions statistically because expected values for cell counts were too low (Sokal and Rohlf 1995).

Recapture section closure

A significant shortcoming of mark-recapture studies is that animals can leave recapture sections without detection, biasing movement distance distributions toward short distances (see Introduction). I installed three bi-directional fish traps (weirs) to assess the importance of this

bias. These weirs effectively closed off a 1752-m section of the study area and allowed me to estimate the proportion of marked fish that "escaped" this section. Since I actually sampled beyond weirs, I also examined attributes of movement for fish that would have otherwise escaped the recapture section. Weirs were checked each morning between 26 May and 19 August 1999. Fishes caught within traps were identified, measured, checked for tags, and released in their direction of travel. Trap design and results of escapement trials are given in Chapter 2.

Two mark sites located in the upper reaches of Middle Creek were not within the section of the study area closed off by weirs and were excluded from calculations. Short movements by fishes in sites located adjacent to weirs (but inside closed recapture section) might overemphasize the importance of study site emigration on movement distributions, so I also excluded these sites from calculations. After excluding these sites, marked fishes had to move at least 225 m to reach any of the weirs.

My study design was somewhat unique because most of the tracks leading out of the recapture section were blocked by dams (Figure 1.1). White Branch was also closed to emigration because this first-order spring emerged from the ground within the recapture section. Thus, fishes could only escape the recapture section by moving downstream through lower Dicks Creek and into Johns Creek. Removing barriers to dispersal would have increased the number of possible movements for all but the shortest distances and would have decreased the proportion of movements sampled for longer distances. Thus, it may be very difficult to accurately measure movement in more natural systems where dispersal pathways are not blocked by dams.

To gauge the difficulty of estimating movement in more open systems, I recalculated PS_d values after simulating removal of two dams. I selected the dams on Little Oregon Creek and upper Dicks Creek because they occur lower in the drainage on these two streams compared to dams on Middle Creek and Mudlick Branch. Thus, removing these dams would more realistically increase the number of possible movements. Dam removal was simulated by re-classifying distances that were formerly considered not possible (i.e., 0 in Table 1.3) to unsampled (i.e., 2 in Table 1.3). I maintained a 4459-m recapture section to allow comparisons of PS_d values among the "closed" and "open" designs.

Alternative study designs

No distance weighting was imposed when a single mark site was located in the center of the 1000-m recapture section; PS_d values were uniform across all distances sampled (Figure 1.3). Because the mark site was located in the center of the recapture section, it was not possible to detect movements beyond 500 m with this design. Distance weighting and the maximum detectable movement distance increase while the length of stream sampled with uniform effort decreases as contiguous mark sites are added to designs (Table 1.4; Figures 1.3 and 1.4; only 2 additional PS_d distributions are shown because they illustrate the pattern of change as mark sites are added). Extreme distance weighting occurs when all 20 sites are selected for marking (Figure 1.3; Table 1.4). The greatest effort is allocated to sampling movements of 0m and sampling effort declines gradually with increasing distance. Placement of mark sites on the upstream and downstream ends of the recapture section allows sampling for movements up to 950 m, but these distances are sampled with much lower effort than shorter movement distances.

Similar patterns emerge when mark sites are embedded within a 2000-m recapture section: distance weighting and the maximum detectable movement distance increase while the length of stream sampled with uniform effort decreases as more mark sites are incorporated into designs (Table 1.4). However, for a fixed number of mark sites, the degree of distance weighting is consistently lower for the longer recapture section. Similarly, the maximum detectable movement distance and the length of stream sampled with uniform effort are consistently longer when mark sites are embedded in the longer recapture section (Table 1.4; Figure 1.4).

Study section length simulation

The length of stream sampled during the recapture event had a strong effect on estimates of distance weighting. PS_d values rapidly declined with distance for each species under the reduced design, but were uniformly high for distances up to and exceeding 1000 m for the full design (Figure 1.5). However, PS_d values for *T. rhothoeca* actually increased after their initial decline. Quantitative estimates of distance weighting paralleled these results (Table 1.5). Variation in sampling effort (i.e., CV of PS_d) increased 31-58% and average sampling effort (i.e., mean PS_d) decreased 38-41% after decreasing the length of the recapture section. However,

increases in CV values are not as pronounced if the CV is calculated over the longer range of distances sampled under the full design.

More extensive movements were detected under the full study design. Median distances moved were longer for each species and this difference was significant for *N. leptocephalus* (P=0.0210; Mann-Whitney Test). Maximum movement distances doubled for *R. atratulus* and increased by more than 400 m for *N. leptocephalus* (Table 1.6). Shapes of observed distributions were similar under full and reduced designs for *R. atratulus* and *T. rhothoeca*, but were markedly different for *N. leptocephalus* (Figure 1.6). In particular, the proportion of fish that moved short distances (100-300 m) or not at all (0m) was lower under the full design. These decreases were driven largely by detection of comparatively long movements (> 600 m); the proportion of fish moving intermediate distances changed little between designs.

Adjustments for distance weighting had a slight (*N. leptocephalus*) to moderate effect (*T. rhothoeca*) on observed movement distributions under the reduced design, but no discernible effect under the full design (Figure 1.6). The adjustment procedure reduced the proportion of *N. leptocephalus* that did not move and slightly increased the proportion of fishes moving longer distances. However, no adjustments could be made to the four longest distance categories because no fish were captured at these distances under the reduced design and the overall distributions were still markedly different after adjustment. The adjustment procedure appeared to distort the observed distribution for *T. rhothoeca* under the reduced design. The largest changes occurred for 0 and 500-m distance bins and the adjusted proportion of fish moving these distances was less similar to the full design than the unadjusted proportion of fish moving these distances under the reduced design.

Recapture section closure

A substantial proportion (10.5%) of marked *N. leptocephalus* emigrated from the section enclosed by weirs. Many of these fish (13/20) were captured again and had moved relatively long distances (range 666- 1144 m) from their original mark sites (Figure 1.7). The distance moved by the remaining emigrants is unknown, but these fish had already moved 514-646 m when they were last captured in weirs. Only one *R. atratulus* emigrated from the section enclosed by the weirs and this fish was later captured over 1000 m away from its original mark site. Only ten *T. rhothoeca* were marked within the section enclosed by weirs and all five of the

recaptures were detected within the enclosed section during August. However, one of these fish moved upstream and then back downstream through the Middle Creek weir during late July. This fish moved the longest distance (759 m) recorded for this species during the 1999 mark-recapture study.

Opening the recapture section to emigration through the upper Dicks Creek and Little Oregon Creek dams increased distance weighting and decreased mean sampling effort over distance (Table 1.5). However, opening the recapture section to emigration did not change these quantities as much as reducing the length of stream sampled during recapture (Table 1.5). Sampling effort began to noticeably decline after 100 m in *R. atratulus* (not shown*)* and *N. leptocephalus*, but did not noticeably decline for *T. rhothoeca* until after 400 m (Figure 1.8).

DISCUSSION

All mark-recapture studies of unbounded animals result in biased, distance-weighted movement data (Stenseth and Lidicker 1992; Porter and Dooley 1993). This bias manifests in two inter-related ways: the true number of animals moving a given distance is underestimated because movements outside of the recapture section are not detected (i.e., $PS_d < 1$), and the overall distribution is distorted because the probability of detecting a movement varies with distance (i.e., CV of PS_d's > 0). My results suggest some general strategies to reduce bias and detect longer movements in future mark-recapture studies on stream fish. Higher recapture rates are a fortuitous by-product of adopting these strategies.

Number and location of mark sites

First, mark sites should be positioned in the center of the recapture section. As mark sites are positioned closer to the upstream or downstream boundary of the recapture section, shorter movement distances between mark sites and recapture section boundary sites are over-sampled relative to the longer distances between more centrally located mark sites and recapture section boundary sites. Additionally, fishes marked near recapture section boundaries are more likely to move out of the recapture section without detection and reduce recapture rates.

Positioning mark sites in the center of the recapture section will not eliminate distance weighting. In the modeling exercise, variance in sampling effort increased as additional mark

sites were incorporated into designs. Thus, my second suggestion is to select as few mark sites as possible. The largest increases in sampling effort variance occurred as the first few mark sites were added, so the total number of mark sites incorporated into designs should be determined very carefully. While a single mark site results in uniform sampling effort across all distances, it is unlikely that a suitable number of fish can be marked from a single site. Preliminary sampling can help identify areas where focal species are abundant and ensure that a large number of fishes can be marked from a limited number of centrally located sites.

Admittedly, certain research questions may constrain adoption of this strategy. An additional objective of my study was to characterize movement throughout a network of streams (see Appendix B). Locating mark sites exclusively within the mainstem (Little Oregon Creek) would have reduced bias, but would have also prevented me from examining movements between tributary streams. Other strategies to reduce bias (e.g., increase length of recapture section) should be emphasized when study objectives preclude centering of mark sites.

Length of recapture section

My results underscore the importance of making recapture sections as long as possible. Given a fixed number of mark sites, the overall (i.e., over the entire range of distances sampled by the design) degree of distance weighting can be reduced by increasing the length of the recapture section. Doubling the length of the recapture section reduced the CV by 4.6-11.1% over the range of mark sites that I modeled. An approximate doubling of the recapture section in the field study reduced the CV 1.8-10.1% across the three focal species. Decreases in the CV for the field study were accompanied by large increases in the magnitude of PS_d values. Thus, increasing recapture length will not only decrease distance weighting but may also result in higher recapture rates.

An obvious benefit of longer recapture sections is the ability to detect more extensive movements. Substantially longer maximum movements were detected for two species and medians were longer for all three species under the full design. Furthermore, the longer maximum distance detected for *N. leptocephalus* did not reflect a rare dispersal event. Eleven fish (10.8% of recaptures) moved longer than the maximum distance detected under the reduced design. More extensive movements can also be detected by positioning mark sites closer to recapture section boundaries, but this strategy comes at the expense of greater distance

weighting. It is also unlikely that any movements to these maximum detectable distances would actually be detected because they are sampled with such low effort. For example, movements up to 1500 m could be detected under the reduced design, but PS_d values did not exceed 3.2% for this distance.

Despite the relatively long recapture section in the field study, variation in sampling effort was still high when the entire range of sampled distances is considered. However, there was a zone of relatively uniform sampling effort apparent in the modeling exercise and in the field study. In the modeling exercise, the length of this zone increased with recapture section length and decreased as more mark sites were added. In the field study, the zone only existed for the longer recapture section and became truncated when this section was opened to more emigration.

The zone of uniform sampling effort is an area where fish movement distances can be detected with little or no bias. If the zone is large relative to length of the recapture section, it may be desirable to focus interpretation of movement data on distances detected within this zone. I do not suggest, however, that distances detected outside of the zone be ignored. Rather, the frequency of fishes moving these distances will be underestimated unless efforts are made to close the recapture section or correct for bias.

Recapture section closure

Despite the best efforts to improve study design, mark-recapture studies can only estimate movement distances over limited spatial scales because fishes can escape recapture sections. The subset of the recapture section considered in the analysis of escapement rates was relatively long (1752 m) compared to many studies, but a substantial proportion of *N. leptocephalus* left this section. Emigration from recapture sections will lower recapture rates (from 44.5 % to 34.0% in *N. leptocephalus*) and weaken inferences about population–level movement patterns. Perhaps more importantly, fishes that escape recapture sections may go on to move exceptional distances that will not be detected—as several *N. leptocephalus* and one *R. atratulus* did in the sub-sampled data set.

Bias resulting from study site emigration is particularly acute in stream networks where there are multiple pathways leading out of the recapture section. I mitigated for this problem by selecting a study area that was partially closed off by dams—other physical barriers to dispersal

(e.g., waterfalls) can also be used to reduce emigration from recapture sections. I also recommend the use of bi-directional fish traps (weirs) that intercept fishes moving past a certain point in the stream (e.g., Hall 1972;Gowan and Fausch 1996; see Chapter 2). These traps can be positioned at recapture section boundaries or points beyond to estimate the proportion of fish moving distances that are not detectable within the primary recapture section. However, it is not appropriate to directly combine distances detected by continuously sampling fish traps with those detected by a discrete recapture event because distances to traps are sampled with much higher effort (Gowan and Fausch 1996). Weirs also provide information about the timing of dispersal events (see Chapter 2).

<center><i>Correction factors</i></center>

It is tempting to rely on correction factors to adjust observed movement distributions for distance weighting. Increasing the length of the recapture section and operating weirs requires a considerable investment of time and money and study objectives may preclude centering of mark sites. However, my results suggest that correction factors cannot mitigate for flawed study design.

The reduced study design illustrates a fundamental weakness of the adjustment procedure: adjustments can be made only to distances that are detected. Thus, it is not surprising that the corrected distance distribution for *N. leptocephalus* under the reduced design did not resemble the distribution revealed by the more spatially extensive sampling effort. Movements were detected only at distances with high PS_d values (min = 39.8) under both designs, so no adjustments could be made to distances with low PS_d values. Thus, the adjustment procedure is likely to fail where it is needed most; severely biased designs almost guarantee that no movements will be detected at distances with low PS_d values.

Correction factors could also distort observed movement patterns, particularly for severely weighted designs. The distribution of PS_d values was highly irregular for *T. rhothoeca* under the reduced design; PS_d values did not decrease gradually but actually increased after their initial decline. Adjusted proportions mirrored this irregular pattern and were less similar to the full design than the unadjusted proportions under the reduced design. Severely weighted designs also risk over-adjustment when a few or even a single fish happens to be captured at a distance

<center>14</center>

sampled with relatively low effort. The same problem occurs in habitat selection studies when animals are captured in extremely rare habitats (Charles Gowan, pers. comm.).

Despite these limitations, correction factors still have an important role—they can be used to assess the degree to which observed movement patterns are distorted by distance weighting. Adjusted frequencies change little when PS_d values are uniformly high and similarities between adjusted and unadjusted distributions may reflect a good study design (Porter and Dooley 1993). Adjusted and unadjusted distributions were virtually identical under the full design and in the study by Skalski and Gilliam (2000). But there is a caveat. Adjusted and unadjusted distributions will also appear similar when movements are only detected at distances sampled with high effort. Thus, large changes after adjustment will always indicate severe bias, but similarity can reflect a good study design or sparse data.

Assumptions underlying estimates of bias

Given the limitations of correction factors, it is more appropriate to use PS_d values to improve design a priori. The method used to calculate PS_d values incorporates all possible pathways of movement and can be used to evaluate any study design where these pathways are known. Distribution and abundance patterns of focal species can have strong effects on estimates of distance weighting (e.g., *T. rhothoeca*) and can be incorporated into calculations after conducting preliminary surveys. Before PS_d values are interpreted, however, it is important to discuss the assumptions underlying their calculation.

The first assumption is that there is no bias in movement direction. Consider the following scenario where 12 fish are marked in a single site and each fish can achieve a 1000-m movement by moving along one of four different tracks. Two of these tracks lie within the recapture section, so $PS_{1000} = .50$. Thus, if an equal number of fish move along each track and each fish moves 1000 m, then six movements of 1000 m will be detected and PS_d will accurately reflect the degree of bias in estimating this movement distance. However, if there is a bias toward tracks falling outside of the recapture section, then fewer movements of 1000 m will be detected and PS_d will underestimate bias. Alternatively, a bias toward tracks falling within the recapture section will result in a higher proportion of actual movements detected and overestimation of bias. This assumption does not have to be met when $PS_d = 1$; all possible movements to this distance are sampled regardless of the direction in which marked fishes travel.

The second assumption is that the probability of capturing marked fish <u>that do not leave the recapture section</u> does not depend upon where the fish are marked or captured. Calculation of PS_d values involves weighting values of S_{ds} and P_{ds} by the number of fish marked in each site. This is appropriate because sites with large numbers of marked fish will influence observed movement distributions more than sites where only a few fish are marked (Gowan and Fausch 1996). Thus, differences in tag retention or survival among mark sites will lead to inaccurate calculation of PS_d values. Suppose a large number of fish are marked at a site near the boundary of the recapture section, but they all lose their tags. Weighting by the number of fish marked in this site pulls PS_d values down for longer distances and increases the overall estimate of bias (i.e., CV value) for the study design. Since none of these fish will be captured, however, this mark site does not influence the degree of distance weighting. The assumption is also violated when sampling efficiency varies across recapture sites; PS_d values for distances sampled with less effort than other distances will underestimate bias.

Are these assumptions met for the observed data set? The first assumption is probably not met; it seems unlikely that an equal number of marked fish would follow each movement pathway given the high spatial variation in habitat characteristics in the recapture section (see Chapter 2). This assumption would be clearly violated in other studies if fish move downstream to over-wintering habitats and drought refugia, or upstream to spawning habitats (Hall 1972; Schlosser and Angermeier 1995) However, PS_d values would underestimate bias only if a disproportionate number of fish followed movement tracks <u>outside</u> of the recapture section. I recalculated the proportion of fishes that escaped the recapture section after including all of the mark sites upstream of the lower Dicks Creek weir (recall that only a subset of mark sites was included in the recapture section closure simulation) and excluding all of the fish that were recaptured after moving through this weir. Only 1.4% of the *R. atratulus* and 1.2 % of the *N. leptocephalus* escaped the recapture section; no *T. rhothoeca* escaped. The low proportion of escapees indicates that very few fishes moved along the only track leading out of the recapture section. Although this assumption is probably not met, the PS_d values reported here are more likely to overestimate than underestimate bias. Thus, the observed distributions under the full design should be little affected by distance weighting.

The second assumption is difficult to address directly without estimates of survival, mark retention, and capture probability for each species x site combination, which are not available for

batch-marked fish in this study. This assumption will also be difficult to address in other studies and cannot be addressed a priori. Thus, efforts used to increase tag retention (e.g, double marking scheme), minimize handling stress, and sample efficiently over all distances (e.g., use of block nets) in this study should also be used to reduce the importance of this assumption in other studies. Violation of this assumption will lead to greater underestimates of distance weighting when relatively large numbers of fish are marked near the center of the recapture section and exhibit substantially lower mark retention or survival than fishes marked in sites located near recapture section boundaries.

Mobility of stream fishes

I detected longer movements compared to other mark-recapture studies on small stream-fishes (Table 1.6). Hill and Grossman (1987) did not detect movements beyond 100 m for *Clinostomus funduloides*, *Rhinichthys cataractae* (longnose dace), or *Cottus bairdi* (mottled sculpin) in a fourth-order mountain stream in North Carolina. Mundahl and Ingersoll (1989) detected movements up to 135 m for *Campostoma anomalum* (central stoneroller) in a second-order stream in Ohio. In a fifth-order coastal-plain stream in Georgia, Freeman (1995) detected movements up to 200 m for *Lepomis auritus (*redbreast sunfish*)* and up to 420 m for *Percina nigrofasciata* (blackbanded darter). Fuselier and Edds (1994) detected movements up to 225 m for *Noturus placidus* (Neosho madtom), in a low gradient fourth-order stream in Kansas. The longest movement detected for *Notropis lutipinnis* (yellowfin shiner) in a small stream in South Carolina was 521 m (Goforth and Foltz 1998). Skalski and Gilliam (2000) detected movements up to 225 m for *N. leptocephalus* in a piedmont stream in North Carolina (G.T. Skalski, pers. comm.). I am aware of no studies that have measured movement distances for *R. atratulus or T. rhothoeca.*

Shorter distances detected during past movement studies reflects real variation in movement behavior but is probably related to study design as well (Gowan and Fausch 1996). The length of stream sampled during all of these studies was relatively short compared to the length of stream sampled in this study [<900 m vs. 4459 m]. Many investigators in past studies have acknowledged that longer movements probably went undetected (e.g., Freeman 1995; Goforth and Foltz 1999; Skalski and Gilliam 2000) and studies that have sampled longer sections of stream have detected longer distances. For example, Means and Johnson (1995) detected a

906-m movement by *Amblyopsis rosae* (Ozark cavefish) after sampling a 1280-m section of stream. Harvey (1998) observed movements up to 1970 m for *Oncorhynchus clarki clarki* (coastal cutthroat trout) after sampling a 3850-m study reach. Gatz and Adams (1994) detected movements > 17.0 km for three centrarchid species [*L. auritus*, *L. macrochirus* (bluegill sunfish), and *Micropterus salmoides* (largemouth bass)] by allocating recapture efforts to non-contiguous sites that were 800-2300 m in length. Such an approach (see also Funk 1957; Zeng and Brown 1987; Haas 1995) clearly allows detection of long distance movements, but may complicate efforts to estimate distance distributions without bias (because fish can move into unsampled gaps—Gatz and Adams (1994) addressed this problem by conducting additional sampling between non-contiguous recapture sites). It may be impossible to sample enough continuous stream to detect all long distance movements, but future studies that sample longer sections of stream will likely result in the detection of more extensive movement patterns. Given the importance of long distance movements to colonization and the spread of invasive species (Wiens 1996; Lewis 1997; Dunham and Rieman 1999; Angermeier et al. 2001; Scott and Helfman 2001), the increase in sampling effort is clearly justified.

Gerking's (1959) view that stream fishes are sedentary has been repeatedly challenged (Funk 1957; Linfield 1985;Gowan et al.1994) and the spatial extent of movements documented in this study also call the "restricted movement paradigm" into question. Nonetheless, a large proportion of fishes were captured in their original mark sites despite relatively uniform sampling over movement distances exceeding 1000 m. Similarly, correcting for distance weighting did not change the leptokurtic patterns documented for *S. atromaculatus*, *N. leptocephalus*, and *L. auritus* by Skalski and Gilliam (2000). Thus, high site fidelity documented in past studies (see review in Matthews 1998) is a real phenomenon in stream fishes and is not purely an artifact of study design. While fishes may move extensive distances or make routine exploratory movements outside of their home sites (e.g., Gatz and Adams 1994; Smithson and Johnston 1999), characterizing fishes as completely mobile (sensu Linfield 1985) may be unwarranted in many cases. Furthermore, the interspecific differences in movement attributes documented in this study suggest that a single concept cannot be used to define the movements of stream fishes (see also Appendix B, Chapters 2 and 3).

Implications for study design

The degree of distance-weighted sampling varies considerably with study design parameters that are typical of most mark-recapture studies on stream fish. The implication is that observed distributions may poorly reflect true distributions in many studies. Study design affected observed distributions for all three species in this study, but the effect was extreme for a highly mobile species (*N. leptocephalus*). The unique aspects of my study design (e.g, long recapture section, use of weirs) enabled me to estimate the effect of study design on observed distributions, but this approach may not be practical in other studies. Instead, the degree to which observed distributions might be biased can be estimated from attributes of the study design.

I developed a procedure to estimate the degree of distance weighting for mark-recapture studies on stream fish. This procedure may be used to adjust observed distributions for distance weighting but cannot make adjustments to distances that are not detected. A better use for this procedure is to evaluate bias in future studies before data are collected and it can be easily modified to incorporate the specific characteristics of any stream system. While it is impossible to design a completely unbiased mark-recapture study in an open stream system, this procedure can be used to identify the spatial scale over which distances are estimated with minimal or no bias.

I have also presented some general strategies that will reduce bias, increase recapture rates and enable detection of longer distances in future fish movement studies. The ideal study would include: centrally located mark sites, a long recapture section, and weirs that would estimate the number of fish moving distances outside of the primary recapture section. These strategies will be especially important when tributary streams provide multiple pathways leading out of the recapture section. I realize that practical constraints may preclude adoption of some of these strategies under certain conditions (e.g., weirs during high flow periods) and that other techniques (e.g., radio telemetry, turnover analysis) may be more appropriate for certain species or research questions (Stenseth and Lidicker 1992; Matheny and Rabeni 1995; Gowan and Fausch 1996; Hughes 1998). Nonetheless, mark-recapture studies that implement these strategies have the potential to contribute to the conceptual understanding of stream-fish movement and allow for better conservation and management of stream-fish populations.

Table 1.1 Example of distance-bin classification table used to calculate the proportion of total possible movements sampled for each distance when two centrally located mark sites are embedded within a 500-m section of stream (see Table 1.2). Zeros indicate distances that are not possible, 1s indicate sampled distances that fall within the recapture section, and 2s indicate unsampled distances that fall outside of the recapture section. Stay = track of fish that do not leave original mark site, up = upstream track, down = downstream track, S_{ds} = the number of sampled movements of distance d from site s (= number of cells with values =1), and P_{ds} is the number of possible movements of distance d from site s (= number of cells with values > 0).

	Site 225					Site 275				
Distance	Stay	Up	Down	S_{ds}	P_{ds}	Stay	Up	Down	S_{ds}	P_{ds}
-250	0	0	2	0	1	0	0	1	1	1
-200	0	0	1	1	1	0	0	1	1	1
-150	0	0	1	1	1	0	0	1	1	1
-100	0	0	1	1	1	0	0	1	1	1
-50	0	0	1	1	1	0	0	1	1	1
0	1	0	0	1	1	1	0	0	1	1
50	0	1	0	1	1	0	1	0	1	1
100	0	1	0	1	1	0	1	0	1	1
150	0	1	0	1	1	0	1	0	1	1
200	0	1	0	1	1	0	1	0	1	1
250	0	1	0	1	1	0	2	0	0	1

Table 1.2 Example of matrix used to generate the magnitude and frequency of distances sampled when two centrally located mark-sites are embedded within a 500-m section of stream. Distances are calculated between site midpoints and can be either negative (downstream of mark site) or positive (upstream of mark site). All sites are identified by their midpoint distance from the downstream boundary of the study section. The study design used in this example is illustrated below the distance matrix. The boxes indicate the ten different 50-m sites within the recapture section; mark sites are shown in gray.

Mark Sites	Recapture Sites									
	25	75	125	175	225	275	325	375	425	475
225	-200	-150	-100	-50	0	50	100	150	200	250
275	-250	-200	-150	-100	-50	0	50	100	150	200

0 m   500 m

downstream   upstream
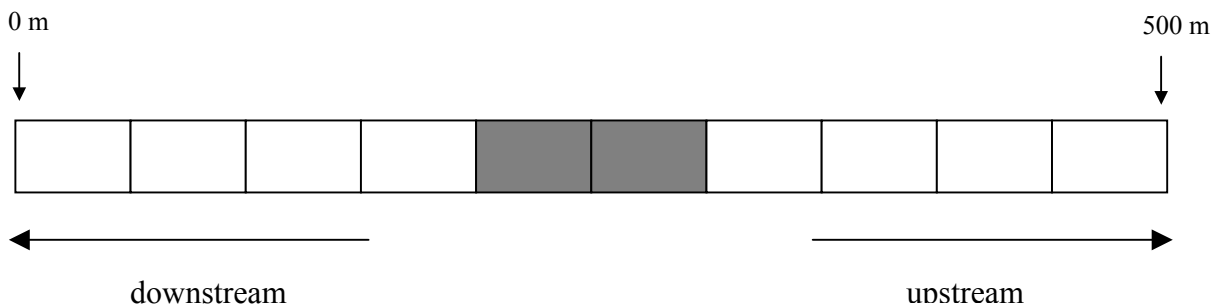
Table 1.3 Example of a distance-bin classification table used to calculate the proportion of total possible movements sampled for each distance during the mark-recapture study. Tracks correspond to alternative movement pathways from a single mark site located in lower Dicks Creek. Stay represents the track of fishes that do not leave the original mark site. Zeros indicate distances that are not possible, 1s indicate sampled distances that fall within recapture section, and 2s indicate unsampled distances that fall outside of the recapture section. The number of possible movements for each distance was determined by counting the number of cells with values > 0 across all movement tracks. The number of sampled movements of each distance was determined by counting the number of cells with values = 1 across all movement tracks. See text for description of each track.

Distance	Stay	Track 1	Track 2	Track 3	Track 4	Track 5	Track 6	Track 7	Track 8	Track 9	Possible	Sampled
0	1	0	0	0	0	0	0	0	0	0	1	1
100	0	1	0	0	0	0	1	0	0	0	2	2
200	0	1	0	0	0	0	1	0	0	0	2	2
300	0	1	0	0	0	0	1	0	0	0	2	2
400	0	1	0	0	1	0	1	0	0	0	3	3
500	0	1	0	0	1	0	2	0	0	0	3	2
600	0	1	0	0	1	0	1	0	0	0	3	3
700	0	1	0	1	1	0	1	0	0	0	4	4
800	0	1	0	0	1	0	2	0	2	0	4	2
900	0	1	1	1	1	0	2	0	2	0	6	4
1000	0	1	1	1	1	0	2	0	2	0	6	4
1100	0	0	1	0	0	0	2	0	2	0	3	1
1200	0	0	1	0	1	0	2	0	2	0	4	2
1300	0	0	1	0	0	0	2	0	2	0	3	1
1400	0	0	1	0	0	0	2	0	2	0	3	1
1500	0	0	1	0	0	0	2	0	2	0	3	1
1600	0	0	1	0	0	0	2	0	2	0	3	1
1700	0	0	1	0	0	0	2	0	2	0	3	1
1800	0	0	1	0	0	1	2	2	2	0	5	2
1900	0	0	1	0	0	1	2	2	2	0	5	2
2000	0	0	1	0	0	1	2	2	2	0	5	2
2100	0	0	1	0	0	0	2	2	2	0	4	1
2200	0	0	1	0	0	0	2	2	2	0	4	1
2300	0	0	1	0	0	0	2	2	2	2	5	1
2400	0	0	0	0	0	0	2	2	2	2	4	0
2500	0	0	0	0	0	0	2	2	2	2	4	0
2600	0	0	0	0	0	0	2	2	2	2	4	0
2700	0	0	0	0	0	0	2	2	2	2	4	0
2800	0	0	0	0	0	0	2	2	2	2	4	0
2900	0	0	0	0	0	0	2	2	2	2	4	0
3000	0	0	0	0	0	0	2	2	2	2	4	0

Table 1.4 Coefficient of variation (CV) of the proportion of total possible movements sampled (PS_d), maximum detectable movement distance (Max D), and length of stream sampled with uniform effort (Uniform) under alternative mark-recapture study designs. Contiguous mark sites were added sequentially from the center of the recapture section toward recapture section boundaries. Recapture sections were divided into 20 (1000-m study section) and 40 (2000-m study section) 50-m sites.

No. Mark Sites	1000-m Recapture Section			2000-m Recapture Section		
	CV	Max D	Uniform	CV	Max D	Uniform
1	0.0	500	1000	0.0	1000	2000
2	15.8	500	950	11.2	1000	1950
3	23.1	550	900	16.5	1050	1900
4	28.6	550	850	20.6	1050	1850
5	32.9	600	800	23.9	1100	1800
10	46.7	700	550	35.6	1200	1550
15	53.4	850	300	43.1	1350	1300
20	55.6	950	0	48.3	1450	1050

Table 1.5 Mean and coefficient of variation (CV) of the proportion of total possible movements sampled (PS_d) under the reduced (1978-m recapture section), full-closed (4459-m recapture section), and full-open (4459-m recapture section) study designs. Statistics were calculated over the same subset of distances (0- 1500 m) to facilitate comparisons of designs. However, longer distances could be detected for the full designs, so CV values calculated over the entire range of sampled distances (0-2400 m) are also reported. Higher means indicate greater sampling effort over all distances. Higher CVs indicate greater variability in sampling effort over all distances.

| Species | Reduced Design | | Full Design-Closed | | | Full Design-Open | | |
	Mean	CV_{0-1500}	Mean	CV_{0-1500}	CV_{0-2400}	Mean	CV_{0-1500}	CV_{0-2400}
Rhinichthys atratulus	55.4	55.0	96.4	7.6	50.3	80.6	17.5	59.7
Nocomis leptocephalus	51.1	70.0	93.7	12.0	59.9	76.2	20.4	67.8
Thoburnia rhothoeca	55.0	41.1	93.0	10.5	39.3	79.1	26.1	53.9

Table 1.6 Summary statistics for movement distances (meters) measured under the reduced (R; 1978-m recapture section) and full (F; 4459-m recapture section) study designs. The median distance moved by *N. leptocephalus* was significantly higher under the full design (Mann-Whitney U-Test, P = 0.0210), but other medians were not significantly different.   The number of fish marked and the proportion of marked fish recaptured (Recap.) are also reported. SD = standard deviation.

Species	Design	Marked	Recap	Mean (SD)	Median	Max
Rhinichthys atratulus	R	130	27.7	58 (106)	0	500
Rhinichthys atratulus	F	130	29.2	88 (189)	19	1029
Nocomis leptocephalus	R	257	31.5	153 (189)	60	708
Nocomis leptocephalus	F	257	39.7	275 (328)	133	1144
Thoburnia rhothoeca	R	49	57.1	117 (179)	0	669
Thoburnia rhothoeca	F	49	63.3	119 (171)	40	669
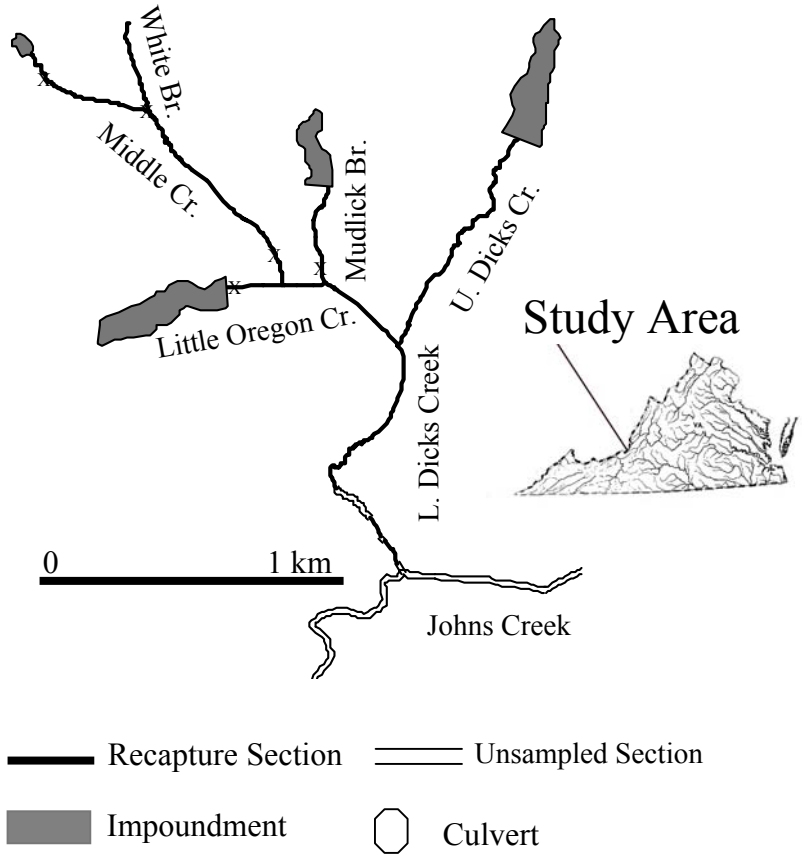
Figure 1.1 Network of streams in the James drainage, Craig County, Virginia that was sampled during the mark-recapture study in 1999. The unsampled section of stream that was not contiguous with Johns Creek coincided with a series of beaver dams that were too deep to sample effectively. Abbreviations are U. = upper, L. = lower, Cr. = Creek, and Br. = Branch.
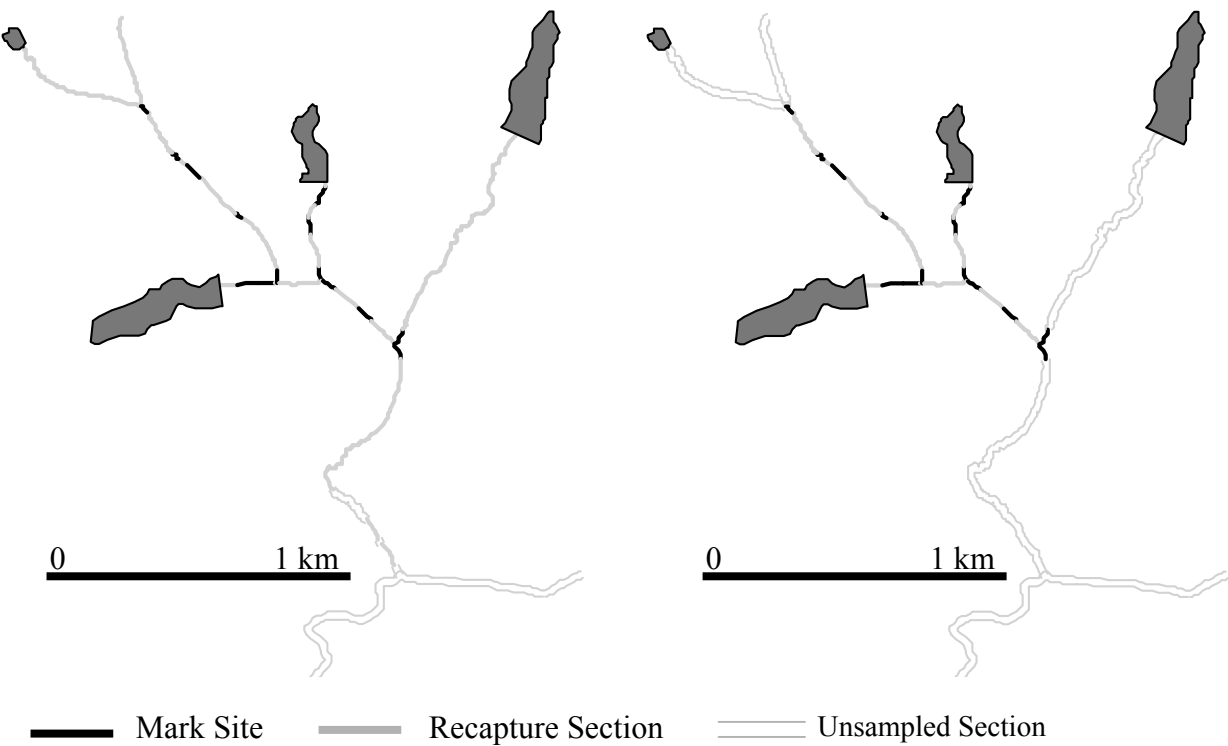
Figure 1.2 Location of mark sites and section of stream sampled for recaptures under the full (4458-m; left) and reduced (1978-m; right) study designs. Fishes were marked during May-June 1999 and the recapture event took place during August 1999.
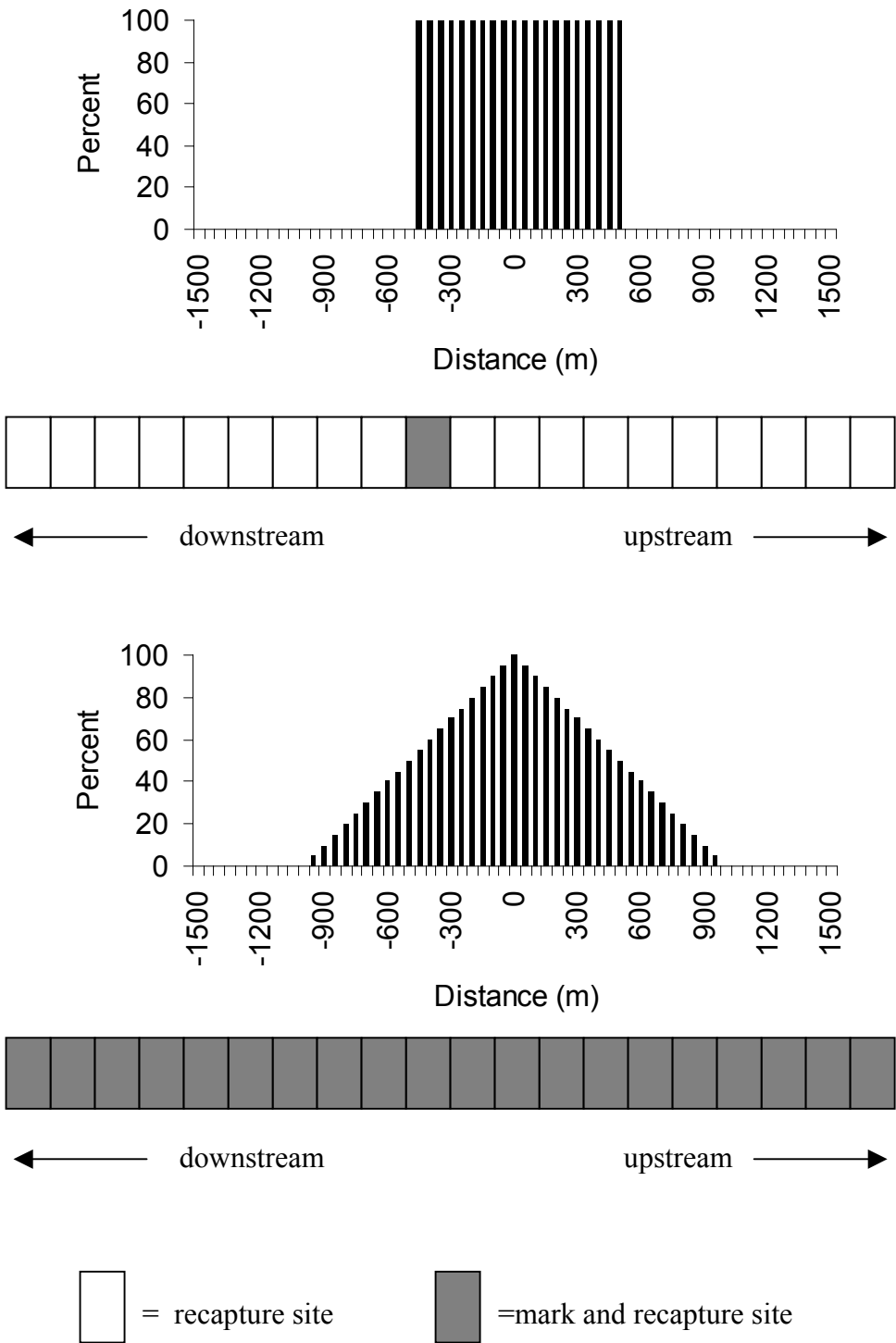
Figure 1.3 Proportion of total possible movements sampled for each distance under alternative mark-recapture study designs. One centrally located site was selected for marking in the upper graph and all sites were selected for marking in the lower graph. Both designs considered a 1000-m section of stream divided into twenty 50-m sites that were each sampled during recapture.
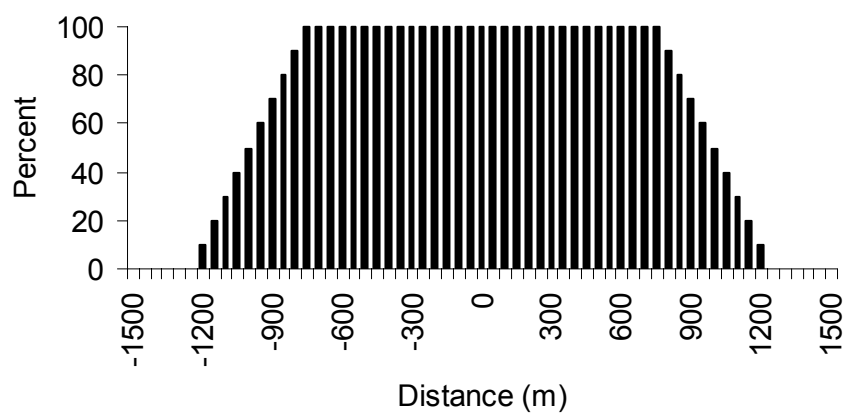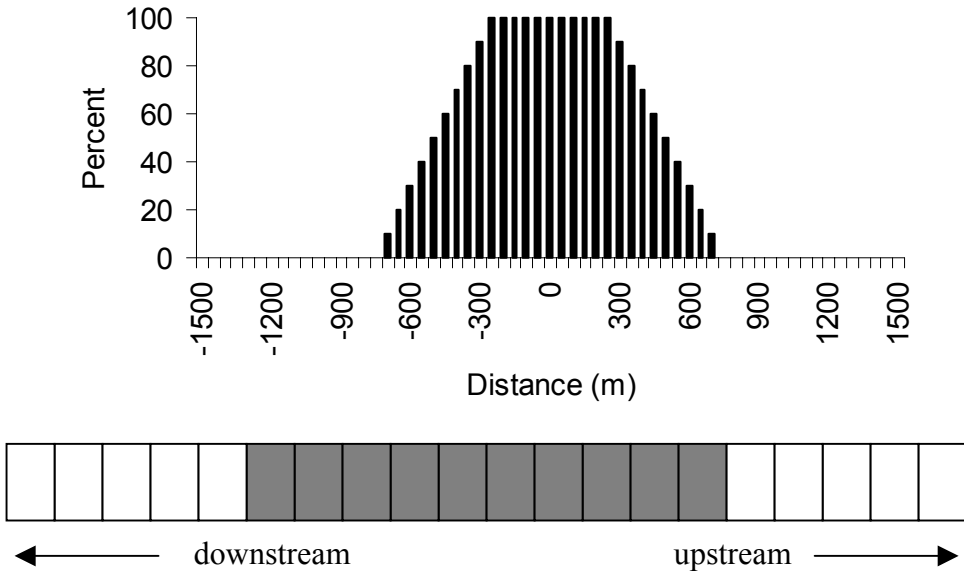
Figure 1.4 Proportion of total possible movements sampled for each distance under alternative mark-recapture study designs. Ten centrally located sites were selected for marking in both designs, but the length of stream sampled during the recapture event was twice as long in the lower graph (2000 m). All sites within each design were 50-m long.
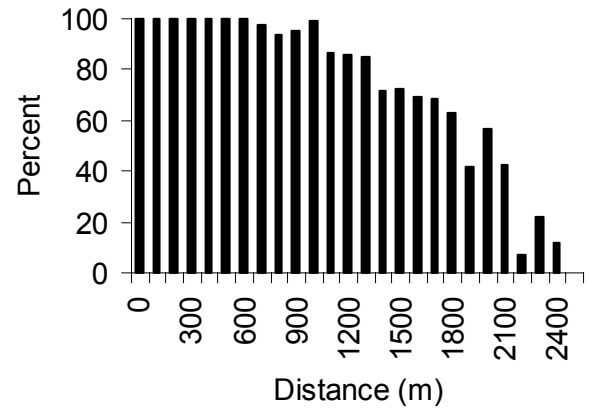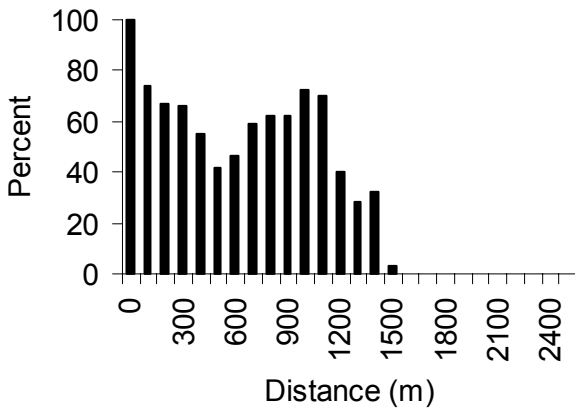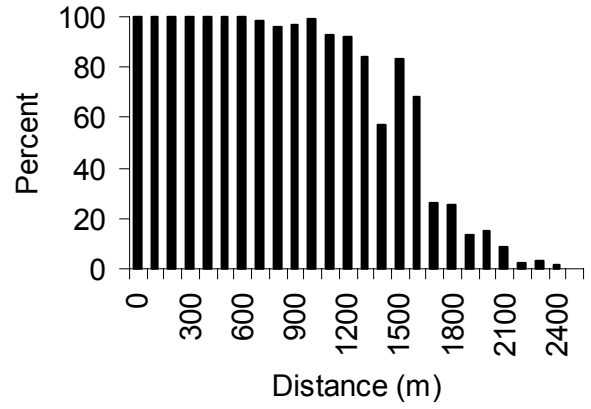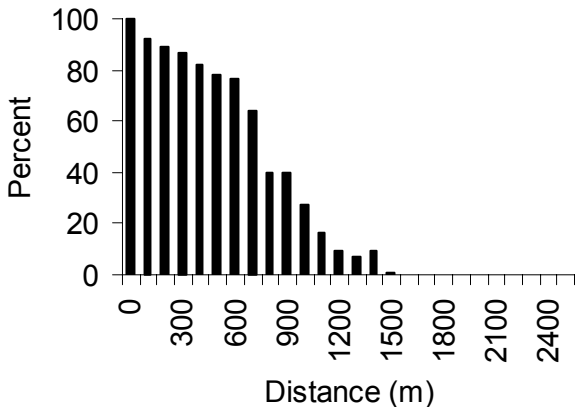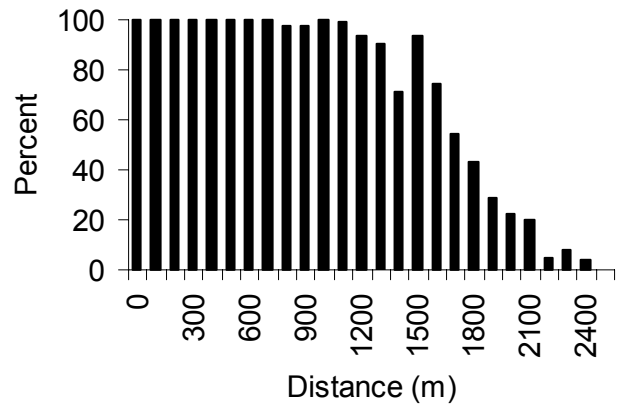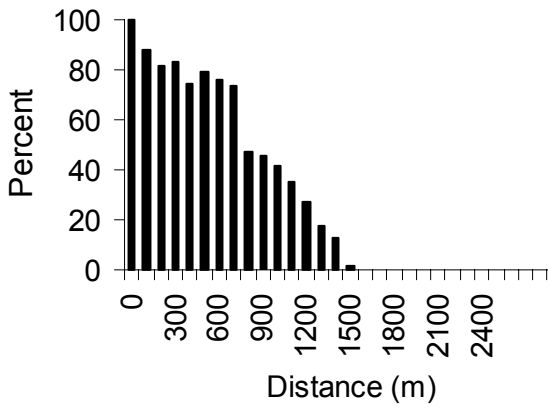
Figure 1.5 Proportion of total possible movements sampled for each distance under the reduced (1978-m recapture section; left) and full (4459-m recapture section; right) study designs. Distributions were weighted by the number of *Rhinichthys atratulus* (top), *Nocomis leptocephalus* (middle) and *Thoburnia rhothoeca* (bottom) released from each mark site during May-June 1999.
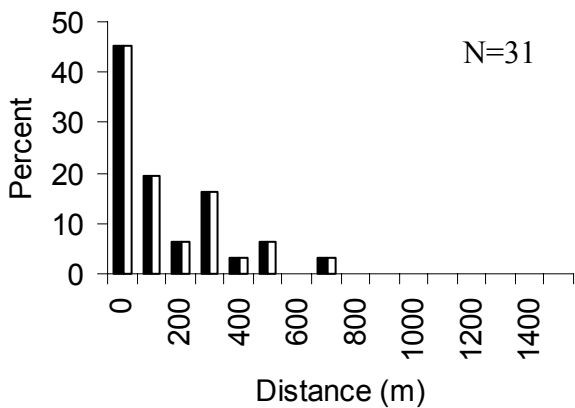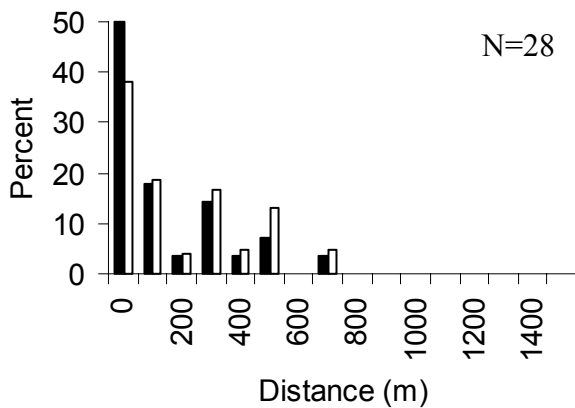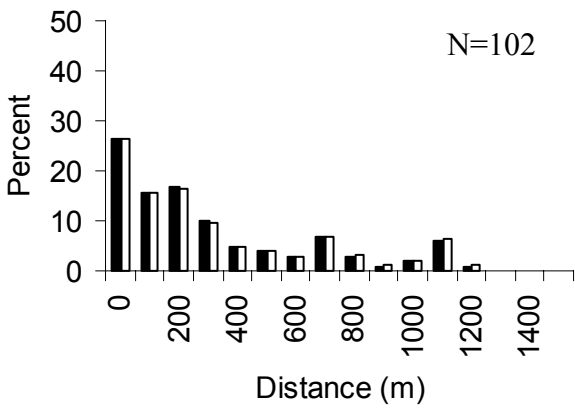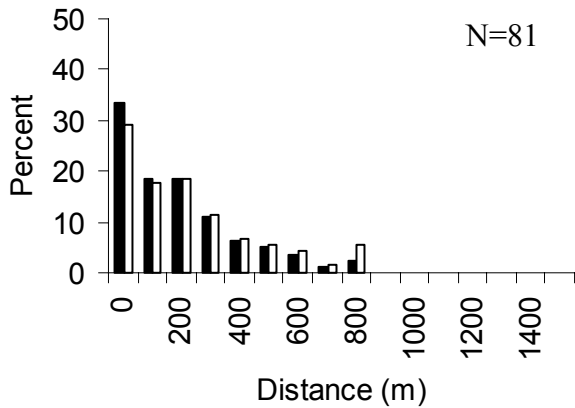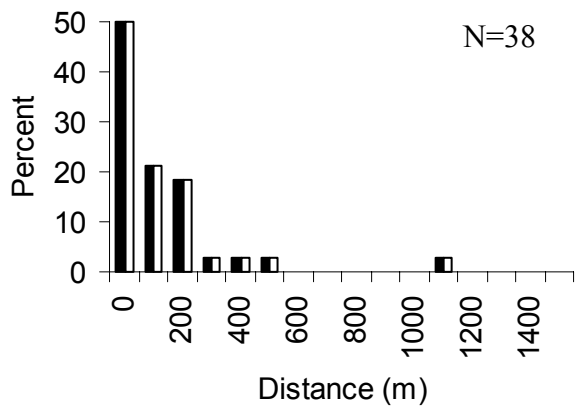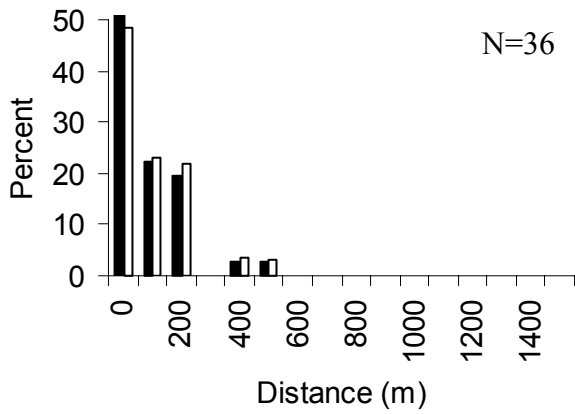
Figure 1.6. Observed (black) and adjusted (white) proportion of recaptured fish at each distance under the reduced (1978-m recapture section; left) and full (4459-m recapture section; right) study designs. *Rhinichthys atratulus* (top) *Nocomis leptocephalus* (middle) and *Thoburnia rhothoeca* (bottom) were marked during May-June 1999 and the recapture event took place during August 1999.
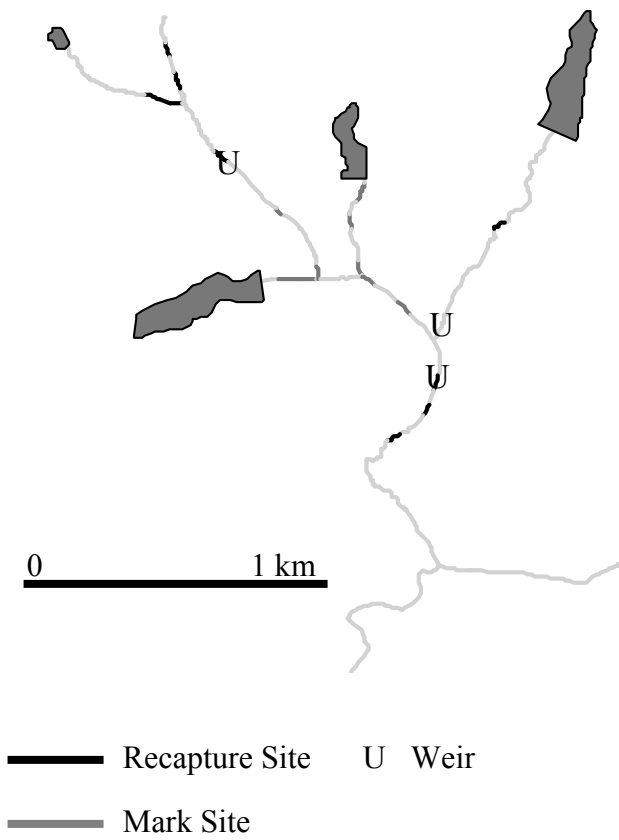
Figure 1.7 Distribution of *Nocomis leptocephalus* recaptures that emigrated from mark sites enclosed by weirs. Fish that were recaptured within the 1752-m section of stream enclosed by the weirs are not shown.
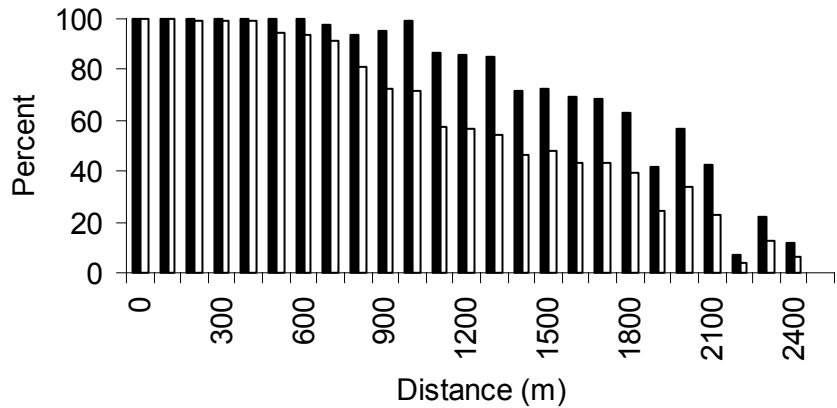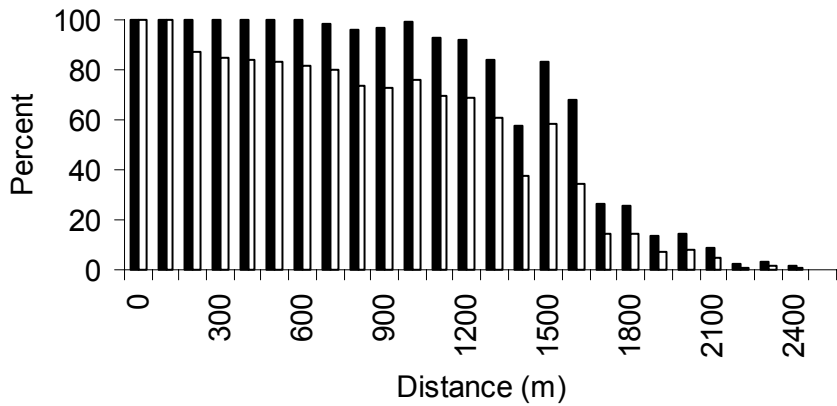
Figure 1.8 Proportion of total possible movements sampled for each distance under the closed (black) and open (white) study designs. Recapture sections were the same length (4459-m) under both designs. Distributions were weighted by the number of *Nocomis leptocephalus* (top) and *Thoburnia rhothoeca* (bottom) released from each mark site during May-June 1999.

Chapter 2. Ecological correlates of fish movement in a network of streams.

Movement is a critical demographic process that allows fishes to meet their resource needs in spatially and temporally variable stream environments (Schlosser and Angermeier 1995; Labbe and Fausch 2000). Movement also allows fishes to exploit refugia and colonize after local extinction events and is a key element of metapopulation dynamics (Meffe and Sheldon 1990; Hansson 1991; Peterson and Bayley 1993). Thus, solid conceptual and empirical knowledge of movement is necessary to improve our understanding of stream-fish ecology and also to inform conservation efforts for fishes occurring in systems that are increasingly modified by humans (Wiens 1996; Warren et al. 1997; Abell et al. 2000).

It is not enough to know the spatio-temporal scale over which fishes move-- the factors that influence movement must also be known. Fishes that readily move under certain ecological conditions may fail to do so in other situations (Gowan et al. 1994). Identifying ecological factors that drive dispersal mediated life-history events (e.g., spawning migrations) is a key step in predicting how fishes will respond to natural and anthropogenic changes in environmental conditions (Railsback et al. 1999). In addition, successful colonization may depend directly on factors influencing movement from source habitats.

What are the factors that influence movement in stream fishes? Factors measured at different spatial, temporal, and conceptual scales have been shown or hypothesized to influence different attributes of movement. Many studies have related the probability of movement to site-specific characteristics such as depth or current velocity (Heggenes 1991; Harvey et al. 1998; Aparicio and Sostoa 1999; Schaefer 2001). A few studies have also examined factors that integrate conditions over larger spatial scales. For example, Lonzarich et al. (2000) documented lower emigration rates from pools that were isolated by long riffles. Factors that vary over very short (e.g., discharge) and longer (e.g., daylength) time periods may also influence movement (Hall 1972; Dodson and Young 1977; Schlosser 1995). Most of the factors studied reflect abiotic conditions, but attributes of individual fish and biotic factors have also been examined

(Fraser et al. 1995; Minns 1995; Gowan and Fausch 1996; Hughes 2000; Schaefer 2001). For example, Gatz and Adams (1994) documented a positive relationship between distance moved and body size for *Lepomis auritus* (redbreast sunfish).

Overall, however, few studies have linked movement of stream fish to ecological factors (Gowan et al. 1994; Gilliam and Fraser 2001). Many studies that have examined ecological correlates of movement have been limited in the number of factors and movement attributes examined. There is also very little information on how ecological correlates of movement vary among species. These gaps in our knowledge do not reflect lack of interest but rather the methodological difficulties of getting even basic information about movement (Gowan et al 1994; see Chapter 1).

The primary objective of this study was to identify factors associated with the movement of fishes in a network of streams. This objective was addressed by examining three attributes of movement (probability of leaving a site between May and August, the number of fish moving upstream through traps per day, and the distance moved between May and August) and their relationships with a suite of variables related to site-specific characteristics (e.g., habitat complexity), reach-wide environmental conditions (e.g., temperature) and attributes of individuals (e.g., growth). An additional objective was to explore heterogeneity in factors influencing movement across species and streams.

MATERIALS AND METHODS

Mark-recapture study

The study area consisted of a network of streams tributary to Johns Creek (James River drainage) in Craig County, Virginia. The study area was divided into 88 sites averaging ca. 50 m in length. Focal species were marked in 15 sites during May-June 1999 and the entire network of streams was sampled for recaptures during August 1999 (Figure 2.1, mark sites not shown). All *Semotilus corporalis* (fallfish), *Nocomis leptocephalus* (bluehead chub), and *Thoburnia rhothoeca* (torrent sucker) >/= 60 mm total length (TL) and all *Rhinichthys atratulus* (blacknose dace) >/= 45 mm TL were given site-specific batch marks (photonic tags; New West Technologies, Inc.); *N. leptocephalus* and *T. rhothoeca* >/= 80 mm TL and *S. corporalis* >/= 100

mm TL were also individually marked with passive integrated transponder (PIT) tags (Biomark, Inc.).

A similar, but less extensive study was conducted over the same time period in 1998. Fishes were marked in 11 sites but lower and upper Dicks Creek, White Branch, and the section of Middle Creek upstream of the White Branch confluence were not sampled for recaptures. Mark sites were distributed in Little Oregon Creek, Middle Creek, and Mudlick Branch during both years; additional sites in lower and upper Dicks Creek were selected for marking during 1999. Some fishes were marked in additional sites near study section boundaries during both years, but these sites were excluded from analyses because of a bias toward detecting short-distance movements when long- distance movers emigrate from the study area (see Chapter 1; Porter and Dooley 1993; Appendix B).

The mark-recapture study was designed so that movement could be measured under a broad range of ecological conditions. First, the network of streams traversed many ecological gradients (e.g., temperature, stream size, depth) that potentially influence movement. Secondly, the time between mark and recapture coincided with seasonal changes in habitat characteristics (e.g., warming, drought) that may also influence movement. Finally, the focal species varied in many characteristics (e.g., body size, spatial distribution, habitat use, etc.,; see Jenkins and Burkhead 1993) and are thus likely to illustrate different relationships between ecological factors and movement.

Site-specific correlates of movement

Factors associated with the probability that an individual fish left its mark site were identified using logistic regression. Because of the large sample size required for multiple logistic regression (Agresti 1996), the primary analyses focused on the 1999 mark-recapture data set for *N. leptocephalus* (n= 104 recaptures). Data from the less intensive study in 1998 were used to test the generality of the *N. leptocephalus* model and to increase sample sizes for analyses that were conducted on *R. atratulus, S. corporalis*, and *T. rhothoeca* (torrent sucker).

Each fish recaptured during August was classified according to the response variable. Fishes captured in their original mark site or an adjacent site were categorized as non-movers and were represented by a zero in the data set. Fishes that moved beyond adjacent sites (a movement of at least 50 m) were considered movers and were represented by a one in the data

set. Thus, the logistic equation modeled the probability that an individual fish left its mark site given the vector of predictor variables for that site. When an individual fish was recaptured during both years of the study, I randomly selected one observation for removal so that independence among observations could be maintained.

Six predictor variables representing a broad range of habitat characteristics were evaluated in models. Raw data for habitat variables were collected in each mark site during transect-based surveys conducted in June 1998 and June 1999. Transects were spaced three mean-stream-widths apart and depth, current velocity, and dominant substrata were measured every 0.5m along each transect (Simonson et al. 1994). Mean depth was calculated over all sample points within the site. Current velocity was measured at 0.4 depth with a Marsh McBirney electromagnetic current meter; mean current velocity was calculated over all sample points within the site. Dominant substrata were visually classified into one of ten categories: silt, sand, gravel, pebble, cobble, boulder, bedrock, vegetation, wood, and detritus. Depth, current velocity and dominant substrata data were used to construct an index of habitat complexity (Angermeier and Schlosser 1989). This index was computed by dividing data for each variable into discrete categories (Table 2.1) and then calculating the Shannon diversity of three-dimensional category combinations for the entire site (Brower et al. 1990).

Cross-sectional area was calculated for each transect by multiplying stream width by mean depth; cross sectional area was then averaged across all transects within the site to represent stream size. Cover included all submerged and overhanging logs that measured at least 10 cm in diameter and 1m in length, along with debris dams and submerged root wads that measured at least 1m in any dimension. To adjust for differences in cover related to variation in mark site length, the number of pieces of cover per meter of stream length was used in analyses. Finally, repeated surveys during the summers of 1998 and 1999 were used to classify the intermittency of each mark site. Sites that exhibited considerable or complete reductions in stream flow were coded as ones in the data set, sites with perennial flow were categorized as zeros.

Data were also available for three biotic variables and two system-level variables. Total length (hereafter body size) was measured at recapture because TL at marking was unknown for smaller individuals that were batch-marked. However, among PIT-tagged fishes, TL at recapture was strongly correlated with TL during marking (all Spearman's rho > 0.92, all P-values <

0.0001 for *S. corporalis*, *N. leptocephalus*, and *T. rhothoeca*). Focal species density (hereafter density) was measured as the number of fish per m^2 within the site during marking. The number of *Nocomis* spawning nests per meter of site length was counted during June habitat surveys. Predators were too rare to allow for accurate estimates of predator density (e.g., *Esox niger*, chain pickerel) or were not vulnerable to our sampling methods (e.g., northern watersnake, *Nerodia sipedon*); no variable related to predation was included in analyses. The distance from each site to the nearest downstream confluence (distance to downstream confluence) and the distance between each site and Little Oregon Creek (distance to mainstem) were the two system-level variables selected for analyses; these variables represented the positions of sites within the stream network. Sites within Little Oregon Creek or lower Dicks Creek were zero m from the mainstem.

Small sample size prevented me from conducting a simultaneous analysis on all eleven predictor variables, so I carried out best-subsets regression and selected the best six-variable model for the *N. leptocephalus* data set (Sokal and Rohlf 1995). The generality of this model was then tested by using it to predict movement probabilities for *N. leptocephalus* that were recaptured during August 1998. Predicted values for this cross-validation data set were generated using data from the 1998 mark-recapture study and habitat survey. Fish with probabilities >0.50 were predicted to be movers.

Small sample sizes for *R. atratulus*, *S. corporalis*, and *T. rhothoeca* made it necessary to combine data from the 1998 and 1999 mark-recapture studies. Combined sample sizes were still relatively small (n=48, 33, and 37, respectively) compared to the *N. leptocephalus* data set and only a small number of predictor variables could be included in each model. I attempted to equalize the number of observations per predictor variable across all analyses to insure comparable power. Thus, two-variable models were fit for *S. corporalis* and *T. rhothoeca* and three-variable models were fit for *R. atratulus*.

Two alternative models were built for *R. atratulus*, *S. corporalis*, and *T. rhothoeca*. Variables that were included in the best-subset model for *N. leptocephalus* were used as predictors in simultaneous (i.e., no selection) logistic regression analyses. These models are hereafter referred to as "species-transfer models". Because all six variables could not be included, variables for species-transfer models were selected from the *N. leptocephalus* model in order of decreasing significance. Following the same approach as in *N. leptocephalus*, best-

subsets regression was also carried out on the full set of habitat, biotic, and system-level variables for these three species. However, the variable nests was removed a priori because it was specifically calculated for nest building *N. leptocephalus*. In addition, models for *R. atratulus* and *T. rhothoeca* would not converge when the intermittency variable was included in the analysis. Thus, best-subsets regression was repeated for these species without this variable, which precludes evaluating its importance in these species.

All seven logistic regression analyses were carried out in SAS version 8.0 using PROC LOGISTIC. Model fit was assessed using the generalized coefficient of determination (R^2, rescaled to have a maximum value of one), standard measures of classification accuracy, and the Hosmer-Lemeshow Goodness of Fit test (Wright 1995; Agresti 1996). If the overall model was significant at alpha = 0.05, significance of the individual regression coefficients was evaluated at the same significance level. I also tested for year effects (*R. atratulus, S. corporalis,* and *T. rhothoeca* only) before interpreting variable importance. With the exception of intermittency, all predictor variables were standardized to facilitate comparison of regression coefficients. The effect of multicollinearity on analyses was estimated by examining variance inflation factors and correlations among predictor variables.

Bi-directional fish traps

Movement rates, the number of fish moving upstream through traps per day, were measured in bi-directional fish traps (hereafter weirs). Weirs consisted of an upstream and downstream trap and four wings that led fishes into these traps (Figure 2.2). Wings were formed by attaching 6.4-mm mesh plastic cloth to 60-cm- high aluminum braces that were anchored to the stream bottom with rebar. About 35 cm of cloth was buried under stream substrata at the base of each wing to prevent fishes from swimming beneath the weir. Each trap consisted of a 60-cm x 60-cm x 60-cm aluminum-framed box that was covered with 6.4-mm-mesh plastic cloth. Fish entered traps by swimming through a 6.4-mm-mesh cone (maximum diameter 60 cm, minimum 6.4 cm) and then moving through a clear plastic cylinder (diameter 6.4 cm) attached to the small end of the cone (Figure 2.2). Cobbles were placed within each trap to provide refugia from stream currents.

Weirs were set in lower Dicks Creek, upper Dicks Creek, and Middle Creek during spring and summer 1999 (Figure 2.1). The lower Dicks Creek weir was set in the same location

during spring 2000; trap design was identical to that in 1999 except that the height of mesh wings was extended by 90 cm to permit weir operation during higher spring-time flows. Traps were checked during the morning; captured fishes were identified, checked for tags, measured, and released in their direction of travel. Traps captured fishes from 20 to 360 mm TL, but fishes < 45 mm TL were excluded from counts because most could easily pass through the weir mesh.

Twenty-four-hour escapement trials were conducted at the lower Dicks Creek weir between 25 and 27 August 1999. Test fishes were collected daily from a section of lower Dicks Creek approximately 800 m downstream of the lower Dicks Creek weir using a DC-powered backpack electrofisher. About 25 fishes were measured, fin clipped, and stocked into each trap; each fish was sized-matched so that similar numbers and size distributions of each species were stocked into both traps. Fin clips enabled me to differentiate new captures from test fish and also ensured that no fish was used in the experiment more than once. The proportion of fishes escaping from each trap was calculated separately for each species and logistic regression was used to examine relationships between species, fish length, trap direction (upstream or downstream) and the probability of escape (Gowan and Fausch 1996).

Thirty-four of 139 fishes were not recovered within traps during the 24-hour escapement trials; most escapees (26/34 = 76.5%) were from the downstream trap and this pattern held for all species tested (Table 2.2). Only three species (*S. corporalis*, *N. leptocephalus*, and *T. rhothoeca*) were considered in the logistic regression analysis because of sample size constraints. The overall model was significant (P=0.0006), but trap direction was the only variable related to the probability of escape (P = 0.0002). Given the relatively high escapement rates from the downstream trap, I restricted subsequent analyses to fishes captured in upstream traps.

Correlates of movement rates through weirs

Relationships between abiotic variables and movement rates were assessed between 26 May and 19 August 1999 in Middle Creek and lower Dicks Creek and between 29 March and 5 June 2000 in lower Dicks Creek. Data from the upper Dicks Creek weir was excluded from this analysis because low flow denied fishes access to traps during much of the sampling period.

The number of fish caught in each trap per day was regressed on stage, the occurrence of flow events (hereafter flow event), mean temperature, and daylength. Crest gauges were buried in stream substrata, bolted to bankside tree trunks, and filled with coffee grounds and cork

(Gordon et al. 1992). These gauges were checked each morning to measure water level to the nearest 0.5 cm (stage) and to determine if water levels had crested during the preceding 24 hours. Flow events were recorded when coffee grounds or cork were stuck to the inside of the gauge above the current stage, when stage increased by 1 cm or more between trap checks, and when debris accumulations on weirs were higher than water levels during trap checks. Although crest gauges can be used to record the maximum water height during a sampling interval, flow event was recorded as a categorical variable (i.e., 0= no flow event, 1=flow event) because cork and coffee grounds rarely formed discrete rings within gauges. Water temperatures were measured every 15 min in each trap using tidbit temperature loggers (Onset Computer Corporation); daily means were calculated over the same 24-hour period that traps collected fishes (ca. 0900 to 0900). Daylengths were measured to the nearest hundredth of an hour and were obtained from sunrise-sunset times published for Newcastle, Craig Co., Virginia (United States Naval Observatory Web Page).

Four alternative Poisson regression models were used to explore relationships between the number of fish caught each day (a count) and the abiotic variables. Since observations were not temporally independent, the first model (hereafter "autoregressive") estimated regression coefficients with a correlated error structure. This model uses an autoregressive parameter to adjust standard errors for regression coefficients (Littell et al. 1999; Sundar Dorai-Raj, Virginia Tech Statistics, pers. comm.). In other words, the autoregressive model corrects for temporal autocorrelation and avoids the biases encountered when ordinary statistical techniques are applied to observations that are not independent (Carroll and Pearson 2000).

None of the remaining models accounted for temporal dependencies in the data and were used only to confirm results when they provided a better fit to the data than the autoregressive model. The second model I evaluated (hereafter "regular Poisson") was identical to the first except that it ignored autocorrelation. The third and fourth models were specifically designed to fit over-dispersed data sets characterized by a large number of zeros (Lambert 1992). These zero-inflated Poisson (ZIP) models first use a Bernoulli probability model and the regressors to estimate the probability that no fishes moved (p). Non-zero observations are then modeled using Poisson regression with predicted values (λ) conditioned upon the initial estimate of p. For example, a large probability that no fish moved would result in a lower estimate of the number of fish moving on that day. ZIP and ZIP tau models make different assumptions about the

relationship between p and λ (Lambert 1992); I fit both models because my primary objective was to find the best fitting model.

Sundar Dorai-Raj (Virginia Tech Statistics Department) wrote the code for all analyses. Poisson and autoregressive models were fit using the PROC GLIMMIX macro in SAS version 8.0 (Littell et al. 1999). The basic code for ZIP models was obtained directly from Diane Lambert and analyses were carried out in S-Plus. Model fit was assessed by examining Akaike's information criterion (AIC, smaller is better), standardized residuals, and observed vs. predicted values (Burnham and Anderson 1998; Littell et al. 1999). Significance of the individual regression coefficients was evaluated at alpha = 0.05. Finally, the effect of multicollinearity on analyses was estimated by examining variance inflation factors and correlations among predictor variables.

Models were built for *Rhinichthys atratulus*, *Semotilus corporalis*, *Nocomis leptocephalus*, and *Thoburnia rhothoeca* to complement information obtained from the mark-recapture study. *Phoxinus oreas* (mountain redbelly dace) and *Luxilus cornutus* (common shiner) were also modeled because they exhibited wide variation in movement rates within Middle Creek and lower Dicks Creek, respectively. Models were built for *Noturus insignis* (margined madtom) and *Cottus caeruleomentum* (blueridge sculpin; Kinziger et al. 2000) to expand the taxonomic breadth of the analysis.

Correlates of distance moved

Relationships between distance moved and two attributes of individual fish were assessed using data from the 1999 mark-recapture study. Distance moved was calculated as the distance between mark site and recapture site midpoints, which is the minimum distance moved. Relationships between distance moved and TL were assessed for *R. atratulus*, *S. corporalis*, *N. leptocephalus*, and *T. rhothoeca*.

I also examined relationships between distance moved and relative growth in length for PIT-tagged fishes. Relative growth in length was calculated using the formula from Busacker et al. (1990)

$$\text{Relative Growth} = (Y_2 - Y_1)/Y_1$$

where Y_1 and Y_2 refer to length measurements at marking and recapture, respectively.

Distance moved, TL, and relative growth in length were not Gaussian before or after transformation, so I calculated Spearman's coefficient of rank correlation (Sokal and Rohlf 1995). Because two hypotheses were examined for each species, significance was evaluated at a Bonferroni-adjusted critical value of 0.025 (0.05/2; Rice 1989).

<center>RESULTS</center>

<center>*Intermittency*</center>

Repeated surveys during both summers indicated that sites within Mudlick Creek, upper Dicks Creek, and the section of Little Oregon Creek upstream from the confluence of Middle Creek were chronically affected by drought during the summers of 1998 and 1999. Perennial flow from springs located in the upper reaches of Middle Creek and White Branch clearly drive the hydrology of the mainstem creeks downstream of the Middle Creek confluence. Sites in the intermittent sections consisted of stagnant pools separated by long dry stretches. The upper Dicks Creek weir and stage gauge provided evidence that fishes became trapped in intermittent sections for long periods of time. After gradually dropping 25 cm between 28 May and 30 June, the upper Dicks Creek stage remained dry until a flow event on 29 July. This resumption in flow was only temporary and no water was recorded at this gauge between 8 August and the termination of the mark-recapture study on 20 August. Patterns in fish movement through the upper Dicks Creek weir closely followed this flow pattern. Only 2 fish were captured during the two long periods when the stage was dry and small numbers of fishes (2-11 per day) were captured when flow resumed between 29 July and 8 August.

Intermittency was a significant source of mortality for fishes. For example, on 9 July 1999 a member of my field crew (Doug Harpole) picked up 120 dead fishes within a 100-m section of upper Dicks Creek. Fishes obviously died when pools completely dried up but poor water quality may have also played a role. A snapshot of dissolved oxygen readings in seven isolated pools in upper Dicks Creek ranged from 0.17 to 3.75 mg/l (mean = 1.96, sd =1.14) on 15 July 1999.   Despite these harsh conditions, live fishes were collected in some of these same pools and in every intermittent mark site during the August recapture event.

<center>*Site specific correlates of movement*</center>

All seven logistic models converged and none of the Hosmer-Lemeshow tests indicated a significant lack of fit. Likelihood-ratio tests failed to reject the hypothesis that all of the regression coefficients were equal to zero for the *S. corporalis* and *T. rhothoeca* species-transfer models; all other models explained significant amounts of variation in the probability of movement. Because no significant year effects were detected for *R. atratulus*, *S. corporalis*, or *T. rhothoeca*, this variable was dropped from analyses. Correlations among predictor variables never exceeded 0.60 and variance inflation factors never exceeded 2.4.

The best-subset model for *N. leptocephalus* accurately classified 89.4% of the observations and explained 78% of the variance in probability of movement (Table 2.3). Fish marked within sites that exhibited considerable reductions in stream flow during the 1999 drought were more likely to leave spring mark sites (Table 2.3; Figure 2.3). Positive relationships were also detected for cover and body size, but only the latter appeared meaningful when plotted (Figure 2.3). None of the other predictor variables were considered significant. The model accurately classified 48 of 58 (82.8%) observations from the 1998 data set.

Overall, variables that explained a large proportion of variance in the probability of movement in *N. leptocephalus* did not transfer well to the other species. The only significant species-transfer model was for *R. atratulus* and none of the individual predictors were significant in this model (Table 2.3). Nonetheless, this model did accurately classify a large proportion of observations (87.5 %). Models for *S. corporalis* and *T. rhothoeca* accounted for very little variation in movement and exhibited the lowest measures of classification accuracy among the seven models (Table 2.3). For example, the species-transfer model for *T. rhothoeca* predicted that no individuals would emigrate from their mark sites, but 10/37 actually moved.

The best-subset models identified negative relationships between the probability of movement and distance to mainstem for *R. atratulus* and *T. rhothoeca* and between the probability of movement and habitat complexity for *S. corporalis* (Table 2.3; Figure 2.3). Distance to mainstem was not judged significant in the species-transfer model for *R. atratulus*, but this model did provide marginal evidence ($P = 0.0764$) for a relationship. No other variables were significant in the best-subset models.

Correlates of movement through weirs

Movement rates were measured on 87 consecutive days during 1999 at both weirs. However, a major flood on 17 April 2000 resulted in weir collapse and high water levels until 7 May 2000. Consequently, the 2000 data set was collected during two disjunct time periods and the number of observations (n = 50 days) was smaller than in 1999. Daylength was highly correlated with temperature (r = 0.93) and stage (r = -0.81) during spring 2000. To avoid interpretational problems resulting from multicollinearity, daylength was removed from the spring 2000 data set (Licht 1995). None of the other predictor variables were highly correlated (i.e., r > 0.70) and variance inflation factors never exceeded 1.9 during 1999 or 2000 at either of the traps. Significant relationships between the number of fish moving and the predictor variables were often driven by one or two days with unusually high movement. Below, I report only relationships that were still significant after these observations were removed.

Factors associated with movement rates through the upstream trap in Middle Creek differed among species. The number of *P. oreas* moving through the trap was positively related to flow event, temperature, and daylength (Figures 2.4 and 2.5; Table 2.4). No significant relationships were detected for *R. atratulus* (not shown). Movement rates for *N. leptocephalus* were positively related to temperature only (Figure 2.5; Table 2.4). However, it should be noted that many fish (n = 33) did move upstream during a single flow event. No significant relationships were detected for *T. rhothoeca*, but the autoregressive model would only converge after removing stage from the data set (Table 2.4). Convergence failure suggests that none of the variables measured (including stage) were related to movement rates in *T. rhothoeca* (Sundar Dorai-Raj, Virginia Tech Statistics, pers. comm.) and this interpretation was supported in scatterplots.

As documented in Middle Creek, different factors were associated with movement rates of fishes through the upstream trap in lower Dicks Creek during 1999. Movement rates in *S. corporalis* and *L. cornutus* were positively related to flow event and daylength (Figures 2.4 and 2.5; Table 2.4). *Nocomis leptocephalus* and *T. rhothoeca* movement rates were positively related to flow event only (Figure 2.4; Table 2.4). No significant relationships were detected for *N. insignis* or *C. caeruleomentum* (not shown).

Abiotic variables related to movement rates in lower Dicks Creek during 1999 were not related to movement rates through the same trap during 2000 (Table 2.4). Movement rates in *N. leptocephalus* were positively related to temperature only (Figure 2.5; Table 2.4). No other

significant relationships were found for any of the other species, but *S. corporalis*, *L. cornutus* and *C. caeruleomentum* moved more frequently during the later time period when water temperatures were higher and stage was lower; N. *insignis* only moved during the later time period (e.g., Figure 2.5). In contrast, there was no temporal trend in *T. rhothoeca*, but this species was captured on only five days.

All significant relationships detected by the autoregressive model were confirmed by the alternative analyses (not shown). Overall, no single model appeared to fit the data better than the alternatives: each of the four models provided the best fit in a similar number of analyses. However, when data sets were characterized by a large number of zeros, ZIP models were superior and improvements in fit were substantial. The autoregressive model was the most conservative; regular Poisson, ZIP, and ZIP tau models detected an additional 3, 22, and 23 significant relationships, respectively.

Correlates of distance moved

Distance moved was largely unrelated to measured variables. It was not correlated with body size in *R. atratulus* (n = 39, r = 0.04, p = 0.8025), *S. corporalis* (n = 37, r = -0.02, p = 0.9170), or *T. rhothoeca* (n = 32, r = -0.05, p = 0.7954). Distance moved was weakly correlated with body size in *N. leptocephalus* (n = 120, r = 0.19, p = 0.0336), but this relationship was not significant after Bonferroni adjustment of alpha. Distance moved was not correlated with relative growth in *S. corporalis* (n = 26, r = 0.25, p = 0.2251), *N. leptocephalus* (n = 68, r = 0.06, p = 0.6340), or *T. rhothoeca* (n = 29, r = 0.28, p = 0.1450).

DISCUSSION

Site-specific correlates of movement

The probability of leaving a site presumably depends upon relationships between fitness and site-specific characteristics; characteristics that tend to decrease fitness relative to other sites should promote emigration (Railsback et al. 1999). In this study, the probability of emigrating from a site was related to intermittency, the position of the site within the drainage network, body size, and habitat complexity. Other studies have found that emigration from sites increases when predators are present (Gilliam and Fraser 2001; Schaefer 2001), decreases (Harvey et al.

1999; Aparicio and Sostoa 1999) or increases (Gilliam and Fraser 2001) when physical structure is present, and decreases with current velocity (Schaefer 2001), depth (Aparicio and Sostoa 1999) and the length of riffle habitat adjacent to the site (Lonzarich et al. 2000; Schaefer 2001). All of these relationships occur within an ecological context. Here I attempt to connect the relationships documented in this study to the ecology of the study species and the system.

Nocomis leptocephalus was more likely to emigrate from intermittent than perennial sections. The best-subset model identified a significant relationship between intermittency and movement in 1999 and successfully predicted the probability of emigrating from sites in 1998. Intermittency was a major component of habitat change during both summers and should exert strong selection pressures on movement behavior (Poff and Ward 1989; Matthews 1998). Many studies have shown high mortality rates for fishes that become isolated in stagnant pools (Larimore et al. 1959; Chapman and Kramer 1991;Matthews 1998) and I also found many dead fishes (including *N. leptocephalus*) within intermittent reaches. Thus, the relationship between intermittency and emigration seems important for increasing survival during drought conditions.

Fishes that are adapted to emigrate from drying streams do face Matthew's dilemma of "when to stay and when to go" because dispersal corridors to perennial reaches may be ephemeral and the costs of movement (e.g., energy, predation risk) may exceed the benefits of remaining in drought resistant pools (Chapman and Kramer 1991; Matthews 1998; Aparicio and Sostoa 1999). Dispersal costs were not quantified in this study, but dispersal corridors were definitely blocked for substantial periods of time (e.g., ca. 40 days in upper Dicks Creek). The importance of immigration after drought-impacted streams are re-watered is widely accepted (e.g., Larimore et al. 1959; Bayley and Osborne 1993). In contrast, studies of the importance of emigration from these systems have produced conflicting results (Bayley and Osborne 1993; Gagen et al. 1998; Labbe and Fausch 2001).

Notably, the relationship between intermittency and movement was based only on the movement patterns of surviving marked fish that were recaptured. The importance of this relationship may be overstated if non-emigrating *N. leptocephalus* die at higher rates than emigrants, which was clearly possible given the harsh physical conditions encountered within the intermittent reaches. However, I believe that differences in survival had a weak impact on the analysis for two reasons. First, the proportion of *N. leptocephalus* recaptured was slightly higher for fish marked in intermittent than perennial sites (38.0 % vs 33.6 %). If high emigration rates

from intermittent sites only reflected higher death rates among non-emigrants, the overall proportion of fish recaptured from intermittent sites should have been relatively low. Secondly, patterns for the other species indicate that it was possible to recapture a large proportion of non-emigrating fish within the intermittent sites. For example, of twelve recaptured *R. atratulus* originally marked in an intermittent site in Mudlick Creek, ten were captured alive in that same site during August. All five of the recaptured *S. corporalis* that were originally marked in an upper Dicks Creek site were recaptured in that same site during August. I attribute persistence of fishes within these harsh reaches to the availability of deep refuge pools (Griswold et al. 1982; Chapman and Kramer 1991; Fausch and Bramblett 1991).

The probability of movement for *R. atratulus* and *T. rhothoeca* decreased with increasing distance from the mainstem creek. Both of these species exhibit their highest densities in tributary sites remote from the mainstem and these areas presumably represent high-quality habitats (Jenkins and Burkhead 1993; Angermeier and Winston 1997). These results are thus consistent with habitat use models that predict lower emigration rates from high quality habitats (Winker et al. 1995).

Higher emigration rates from the mainstem may reflect its role as a movement corridor that transfers fishes to high-density sites in tributaries (sensu Fraser et al. 1999; Gilliam and Fraser 2001). One *T. rhothoeca* that was originally marked in the mainstem during spring 1998 was recaptured in August 1999 over 1000 m away in the upper reaches of Middle Creek. Another *T. rhothoeca* made a 759-m movement from the mainstem creek into the upper reaches of Middle Creek during 1999. Similarly, one *R. atratulus* moved over 1000 m from the mainstem into Middle Creek during 1999.

Nocomis leptocephalus was also the only species that exhibited a relationship between body size and the probability of emigrating from sites. Skalski and Gilliam (2000) also found that the probability of movement increased with body size in *N. leptocephalus*, but only for slow-growing individuals. Among temperate freshwater fishes, larger species typically require larger home ranges to meet their resource needs and this may explain why small *N. leptocephalus* exhibit higher site-fidelity than larger *N. leptocephalus* (Minns 1995; Gowan and Fausch 1996).

Finally, the probability of movement decreased with increasing habitat complexity for *S. corporalis*. Gorman (1986) suggested that fishes in rivers with low habitat complexity are more mobile. At the site scale, fishes living in complex habitats should be able to meet multiple

resource needs within a small area. However, this relationship may also reflect the habitat requirements of *S. corporalis* and the relationship between habitat complexity and depth. This species prefers large deep pools and sites exhibiting high habitat complexity and high site fidelity contained some of the deepest and largest pools within the study area (Jenkins and Burkhead 1993). Selection of deep pools in complex sites may also enhance survival of *S. corporalis* within intermittent sections.

Correlates of movement through weirs

Movement rates, measured as the number of fish moving upstream through a trap per day, also reflect factors that promote emigration from sites. However, the time-scale of sampling permits analysis of factors that change more rapidly (e.g., temperature). In addition, relationships are integrated over the entire population rather than marked fishes alone. In this study, movement rates were associated with flow events, daylength, and water temperature.

Five (*P. oreas*, *S. corporalis*, *N. leptocephalus*, *L. cornutus*, and *T. rhothoeca*) of the eight species studied increased their upstream movement rates in association with flow events. Indeed, this phenomenon may be the best understood aspect of stream-fish movement (Hall 1972; Matthews 1998; Gilliam and Fraser 2001). Schlosser (1995) documented large pulses of downstream movement during periods of elevated discharge for a headwater assemblage of stream fishes in Minnesota. While upstream movement was not correlated with the natural discharge regime in his stream, Schlosser (1995) did document greater numbers of fish moving upstream through an experimental side channel with elevated discharge when compared to movement rates through a low-flow control. Flooding facilitated the downstream dispersal of a poeciliid in an intermittent tropical stream, although some of the movements may have resulted from flushing (Chapman and Kramer 1991). Other studies have documented the movement of fishes onto fringing floodplains during floods (Ross and Baker 1983; Matheny and Rabeni 1995; Matthews 1998).

Despite the documentation of flow-mediated dispersal in several studies, there is less information on why fishes move during periods of high discharge. Schlosser (1995) suggested that instream dispersal allowed fishes to move between productive beaver pond habitats and that downstream boundaries of beaver dams were more permeable to movement during high flow periods. Movements during high flow events may also permit access to spawning and foraging

habitats or may simply be a mechanism to locate refuge from the flood itself (Ross and Baker 1983; Matheny and Rabeni 1995; Matthews 1998). In this study, the occurrence of flow-mediated pulses throughout the summer suggests that their function was not restricted to synchronization of spawning movements. Fishes moving during high flow events could also access newly inundated reaches within the intermittent sections, escape from intermittent sections that became re-connected by flow, or circumvent natural barriers (e.g., waterfalls and steeply inclined bedrock slabs) to invade the upper reaches of Middle Creek (see Adams et al. 2000; Tyus et al. 2000).

Regardless of the behavioral mechanism driving these flow-mediated pulses of movement, they functioned as an important source of colonists to upstream habitats. Many fishes moved upstream during pulses and maximum movement rates were documented for *P. oreas*, *S. corporalis*, *N. leptocephalus*, and *T. rhothoeca* during flow events. To put this in perspective, 64.2 % of the *S. corporalis* captured during the 87 day trapping period moved during the 15 days associated with flow events; 30% were captured during a single flow event. Capture histories for fishes that were recaptured after moving through weirs during flow events indicate that at least some fishes colonize distant habitats. Of 10 *N. leptocephalus* that moved through weirs during flow events in 1999, six had moved an average of 290 m beyond traps by August. The remaining fish were recaptured in sites directly adjacent to weirs. One *S. corporalis* moved 676 m upstream into Middle Creek after dispersing through the lower Dicks Creek weir during a flow event. There was no evidence, however, that flow events facilitated long distance movements for *R. atratulus* or *T. rhothoeca*.

The positive relationship between daylength and movement rates reflects a seasonal effect on movement for *P. oreas, S. corporalis*, and *L. cornutus*. Movement rates for these species were relatively high during June and early July. Dodson and Young (1977) also documented a relationship between daylength and movement behaviors in laboratory-held *L. cornutus*. *Phoxinus oreas* and *L. cornutus* spawn over *N. leptocephalus* mound nests in May and June and movements by these species may allow them to access spawning habitats (Jenkins and Burkhead 1993). Weir captures by *S. corporalis* were dominated by a narrow size range of juvenile fish and likely reflected movements to rearing habitats. Low movement rates for *S. corporalis*, *L. cornutus*, *N. insignis*, and *C. caeruleomentum* during early spring 2000 could not be attributed to any of the predictor variables, but may also reflect seasonality. Many other

studies have documented seasonal movements to spawning, rearing, and over-wintering habitats (Gatz and Adams 1994; Matthews 1998; Grant and Maslin 1999; Simpkins et al. 2000). There was a strong seasonal component to movement rates for an assemblage of fishes in a North Carolina piedmont stream; the number of fishes moving was highest during the spawning season (April, May and June) and substantially lower during late summer and winter (Hall 1972).

Stream temperature affected movement rates over a narrow range of temperatures and was a significant predictor of movement for only two species. Movement rates in *N. leptocephalus* were positively associated with temperature in Middle Creek during the summer of 1999 and in lower Dicks Creek during spring 2000. The number of *P. oreas* moving upstream through the Middle Creek trap was also positively related to temperature. Examination of scatterplots suggests a threshold effect where few or no fishes move at low temperatures but the number moving at higher temperatures is highly variable. Large numbers of *P. oreas* and *N. leptocephalus* did not begin moving until temperatures surpassed 15° C in Middle Creek. No additional relationships with temperature were detected, but *S. corporalis*, *N. insignis*, and *C. caeruleomentum* were not captured in lower Dicks Creek during spring 2000 until mean temperatures exceeded 14.0 °C, 18.5 ° C, and 13.6 ° C, respectively (minimum temperature during this period was 9.25 ° C). Hall (1972) indicated that few fishes moved when water temperatures dropped below 7 ° C in a North Carolina piedmont stream.

Temperature has a strong effect on metabolism and increased movement during warming periods probably reflects increased foraging to meet higher energy demands (Gowan and Fausch 1996; Helfman et al. 1997). This relationship may also trigger movements to spawning habitats for *N. leptocephalus* and its nest associate (*P. oreas*). The threshold temperature that initiated higher movement rates in Middle Creek coincides with the second lowest temperature at which Jenkins and Burkhead (1993) observed nest building.

Correlates of distance moved

After emigrating from a site, the distance moved by an individual fish should depend upon factors that promote immigration to a new site. Longer distances presumably occur when suitable habitats are widely spaced. Suitability is determined in part by the individual habitat requirements of the species, but may also be affected by factors such as competitor density, food availability, predation, and attributes of the individual fish (Gowan and Fausch 1996; Railsback

et al. 1999). In this study, no relationships were detected between distance moved and body size or growth. Skalski and Gilliam (2000) also did not find a relationship between distance moved and body size or growth for *N. leptocephalus, Semotilus atromaculatus* (creek chub), or *Clinostomus funduloides* (rosyside dace). Similarly, Smithson and Johnston (1999) did not find a relationship between body size and distance moved among four Ouachita highland stream fishes. Although documented in some studies (e.g., Gatz and Adams 1994; Aparicio and Sostoa 1999), the relationship between body size and distance moved is clearly not pervasive.

Given the multiplicity of factors that may determine when a fish immigrates to a site (see above), it is not surprising that distance moved is not always a simple function of body size or growth. A major shortcoming of this and many other studies is the inability to characterize the habitat suitability of potential immigration sites—it is much easier to measure body size or growth than to measure attributes of all of the sites that fishes could occupy. An a posteriori examination of the data for *N. leptocephalus* suggests that such an approach would nonetheless be fruitful. Most (61/74 = 82.4%) of the fish marked in intermittent sites were later captured in perennial reaches. These fish moved significantly longer distances than fish marked in perennial sites (median = 240 vs 0 m; $P < 0.0001$; Mann-Whitney test), presumably because they had to move through longer reaches of unsuitable habitat. Gilliam and Fraser (2001) also found that distance moved depends upon attributes of reaches outside of mark sites: *Rivulus harti* (Hart's Rivulus) moved longer distances within a reach inhabited by a predator compared to a reach where the predator was absent.

Overview of N. leptocephalus movement

The three attributes of movement measured in this study reflect unique but interrelated aspects of movement. Examining these attributes provided a more complete picture of dispersal than any single attribute could; future studies should also investigate multiple attributes of movement. To illustrate the more complete picture of dispersal provided by the multiple attribute approach, I present a conceptual model of movement for *N. leptocephalus* sub-adults and adults during late spring and summer (Figure 2.6). I focus on N. leptocephalus because large sample sizes permitted more powerful analyses than were possible for the other species.

The model depicts potential movements for fish that initially occupy an intermittent stream site along with hypotheses on the adaptive value of such movements. All of the

mechanisms shown in the model were significant predictors of movement in the site-specific and movement rate analyses. No relationships were detected by the distance-moved analysis, but fishes marked in intermittent sites moved long distances to reach sites in perennial reaches. With the exception of movements from intermittent to perennial reaches, all of the mechanisms and hypotheses illustrated in the model would also apply to fish that initially occupied a perennial site. These are not shown for clarity.

The model illustrates that *N. leptocephalus* is adapted to exploit intermittent and perennial streams. Field observations and density data from electrofishing surveys support this hypothesis. For example, an intermittent site located just downstream of the Little Oregon Creek dam exhibited the highest density of *N. leptocephalus* and mound nests among mark sites in spring 1999 (Albanese, unpublished data). Subadult and adult fishes marked in this site emigrated to sites throughout the entire network of streams, but most (84%) were recaptured within perennial reaches (See Appendix B, Figure B.3C). Active nesting begins and ends later in the year in the cooler, perennial waters of Middle Creek. Nuptial male and ripe females that were marked in the mainstem creek site were later captured in the upper reaches of Middle Creek, suggesting that individual fish may spawn in the mainstem creek and then move to Middle Creek for additional spawning as temperatures become suitable. Both habitat types may also be important for early life history stages. An intermittent site had the second highest density of young of year *N. leptocephalus* among 88 sites that were sampled during August 1999, but high densities of young of year were also captured within perennial sites (Albanese, unpublished data).

Heterogeneity in movement correlates and implications for colonization

I found substantial interspecific variation in correlates of movement. For example, daylength was correlated with movement rates for only two of the six species captured in the lower Dicks Creek weir during 1999. Movement rates were correlated with a suite of factors for some species, whereas other species did not respond to any of the predictor variables (e.g., *N. insignis*). Variables that were significant predictors of the probability of movement in *N. leptocephalus* were never significant for *R. atratulus*, *S. corporalis*, or *T. rhothoeca*.

Interspecific differences in ecological correlates of movement may translate into differences in colonization ability. For example, species that move in response to flow events

should be better colonists in drought-affected systems than species that do not (e.g., *C. caeruleomentum* in this study). Admittedly, this may not lead to interspecific variation in colonization success in arid and semi-arid regions where entire faunas have been selected to persist through drought (Matthews 1998). Flow-mediated dispersers should, however, be more resilient to extirpation in humid regions subjected to increased intermittency associated with climate change and continued over-appropriation of water for human uses (Stiassny 1996; Poff et al. 2001).

Interspecific differences in the number of ecological correlates of movement suggest the multiple trigger hypothesis, which I formally introduce here. This hypothesis states that species that move in association with a large number of ecological correlates (presumed triggers) will be better colonists than species that move in association with only a limited number of correlates. In this study, movement rates for *P. oreas* in Middle Creek were positively related to flow events, temperature, and daylength. In contrast, movement rates for *T. rhothoeca* and *R. atratulus* in Middle Creek were not related to any of the factors measured. If a disturbance event extirpated populations of all three species in the upper reaches of Middle Creek, *P. oreas* would be a superior colonist because large numbers of individuals would immigrate during the next flow event or rise in temperature (see Chapter 3). Some disturbances may be accompanied by changes in ecological parameters in source areas, resulting in even faster colonization of multiple-trigger species like *P. oreas*.

There was also evidence that ecological correlates of movement varied among different parts of the stream network. For example, movement rates in *N. leptocephalus* were correlated with temperature in Middle Creek, but not in lower Dicks Creek during the summer of 1999. Movement rates for *T. rhothoeca* were correlated with flow events in lower Dicks Creek, but not in Middle Creek. The probability of movement was lower in sites distant from the mainstem for *R. atratulus* and *T. rhothoeca*.

Accordingly, differences in the ecological correlates of movement associated with stream type may lead to variation in colonization success within species. Factors that trigger colonization success in one system may be absent from another. Thus, future studies should attempt to compare movement attributes among streams with different ecological characteristics. Comparisons among systems subjected to different types of human use (e.g., urbanized vs. forested) will have direct implications for conservation.

Table 2.1 Discrete categories for current velocity, depth, and substrata that were used to create the index of habitat complexity. NA = not applicable.

Categories	Current Velocity (cm/sec)	Depth (cm)	Dominant Substrata
1	0-1	1-5	silt, sand, or gravel
2	2-15	6-30	pebble or cobble
3	> 15	> 30	boulder or bedrock
4	NA	NA	vegetation, wood, or detritus

Table 2.2 Number of fishes tested and escaping from upstream and downstream traps set in lower Dicks Creek during August 1999. Different individuals were tested on three consecutive nights but data were pooled for this comparison.

| | Upstream | | Downstream | |
Species	Tested	Escaped (%)	Tested	Escaped (%)
Semotilus corporalis	28	6 (21.4%)	25	9 (36%)
Nocomis leptocephalus	31	2 (6.5%)	30	14 (46.7%)
Erimyzon oblongus	1	0 (0.0%)	1	0 (0.0%)
Thoburnia rhothoeca	11	0 (0.0%)	10	3 (30%)
Percina notograma	1	0 (0.0%)	1	0 (0.0%)
Total	72	8 (11.1%)	67	26 (38.9%)

Table 2.3 Overall significance tests, coefficient of determination, and standardized regression coefficients for logistic models that predicted the probability that an individual fish emigrated from its spring mark site. Species transfer models were fit without variable selection; other models were fit using the best subset procedure in SAS. Species transfer models tested variables that were included in the best-subset model for *Nocomis leptocephalus.* Abbreviations are as follows: CM = the number of pieces of cover per meter of site length, HC = habitat complexity, IM =intermittency of mark site, MD = mean depth, MV = mean current velocity, SS = stream size, BS = body size, DF = density of focal species, NM = number of active *Nocomis* spawning nests per meter of site length, DD = distance to downstream confluence, and DM = distance to mainstem creek. Results of significance tests are designated as NS = not significant, A = $P < 0.05$, B = $P < 0.01$, C = $P < 0.001$, and D = $P < 0.0001$. Variables that were not tested in a model are designated NT. Variables that were tested but not included in the best fitting subset are designated NI.

| | Fit | | | | Standardized Regression Coefficients | | | | | | | |
| | | | | Habitat | | | | Biotic | | | System | |
Species/Model	R^2	CM	HC	IM	MD	MV	SS	BS	DF	NM	DD	DM
Nocomis leptocephalus												
best-subset[D]	0.78	1.01[A]	NI	4.46[B]	-0.22	NI	NI	1.00[A]	NI	1.33	NI	-1.09
Rhinichthys atratulus												
species transfer[D]	0.75	0.22	NT	NT	NT	NT	NT	0.82	NT	NT	NT	-5.05
best subset[D]	0.75	NI	NI	NT	NI	NI	NI	0.82	0.44	NT	NI	-6.16[A]
Semotilus corporalis												
species transfer[NS]	0.06	NT	NT	0.40	NT	NT	NT	0.39	NT	NT	NT	NT
best subset[B]	0.34	NI	-1.29[A]	NI	NI	NI	NI	0.48	NI	NT	NI	NI
Thoburnia rhothoeca												
species transfer[NS]	0.04	-0.32	NT	NT	NT	NT	NT	0.24	NT	NT	NT	NT
best subset[B]	0.40	-0.48	NI	NT	NI	NI	NI	NI	NI	NT	NI	-1.10[B]

Table 2.4 Model fit (AIC, smaller is better), regression coefficients, and p-values from autoregressive poisson-regression models. Models related abiotic variables to the number of fish moving through upstream traps between 26 May and 19 August 1999 in Middle Creek and lower Dicks Creek and between 29 March and 5 June 2000 in lower Dicks Creek. The autoregressive model allows estimation of regression coefficients when observations are not temporally independent. The autoregressive parameter (AR1) estimates the degree of correlation among successive errors. Predictor variables were never significant for *Rhinichthys atratulus*, *Noturus insignis*, and *Cottus caeruleomentum* and these models are not shown.

Species/Model	AIC	AR (1)	Flow	P-value	Stage	P-value	Temperature	P-value	Daylength	P-value
Phoxinus oreas										
Middle Creek 1999	350	0.23	0.94	0.0056	-0.09	0.5236	0.29	0.0033	2.46	0.0053
Semotilus corporalis										
Dicks Creek 1999	383	0.15	1.85	0.0000	0.22	0.0241*	0.22	0.0643	2.55	0.0427
Dicks Creek 2000	264	-0.03	1.26	0.1808	-0.20	0.3014	0.07	0.6872	***	***
Nocomis leptocephalus										
Middle Creek 1999	349	0.16	1.29	0.0000*	-0.42	0.0102*	0.35	0.0003	1.67	0.0042*
Dicks Creek 1999	285	0.18	1.33	0.0000	0.12	0.0676	0.08	0.3533	-0.65	0.1212
Dicks Creek 2000	205	-0.24	-0.12	0.8652	0.21	0.0000*	0.33	0.0000	***	***
Luxilus cornutus										
Dicks Creek 1999	338	0.11	0.79	0.0039	0.15	0.0153*	-0.16	0.0831	2.47	0.0242
Dicks Creek 2000	220	-0.05	-0.56	0.5813	0.17	0.0206*	0.21	0.0150*	***	***
Thoburnia rhothoeca										
Middle Creek 1999	366	0.47	0.40	0.3259	**	**	0.05	0.6948	0.41	0.7059
Dicks Creek 1999	363	0.31	0.95	0.0121	0.04	0.7423	0.00	0.9817	2.38	0.0966
Dicks Creek 2000	330	0.03	-9.50	0.9429	0.37	0.0154*	0.23	0.0953	***	***

* Relationships were not significant after removing influential observations from the data set

** The model would not converge without removing the stage variable from the data set.

*** Daylength was highly correlated with temperature and stage and was removed from these analysis.
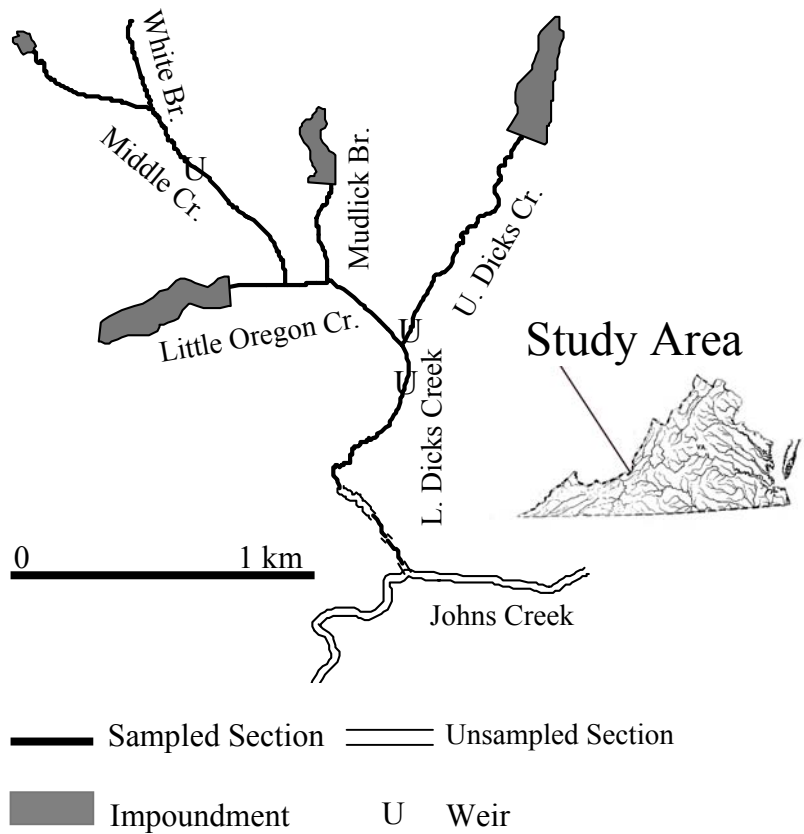
Figure 2.1 Network of streams in the James River drainage,Craig County, Virginia that was sampled during the mark-recapture study in 1999. The unsampled section of stream that was not contiguous with Johns Creek coincided with a series of beaver dams that were too deep to sample effectively. Abbreviations are U. = upper, L. = lower, Cr. = Creek, and Br. = Branch. Mark sites are not shown, but were distributed throughout the study area upstream of the beaver dams.
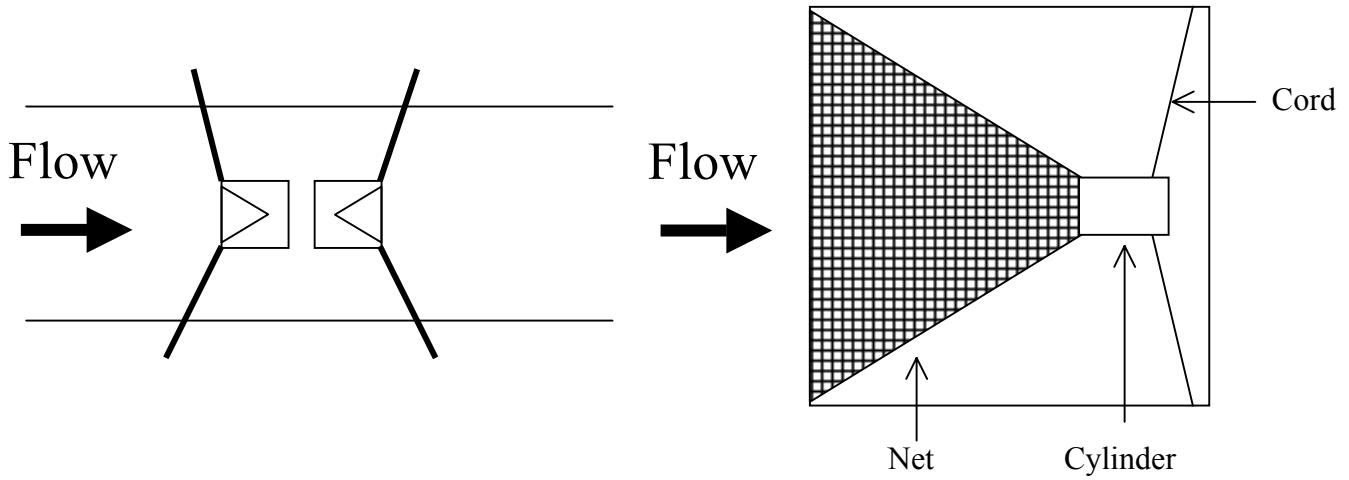
Figure 2.2 The arrangement of traps and wings for weirs with respect to stream banks and flow (left side of figure). The upstream trap is on the right; it collects fish moving upstream. Top view of the downstream trap showing mesh entrance cone, plastic cylinder attached to cone, and bungi cords which prevented the net from collapsing (right side of figure). Cobbles (not shown) were placed inside trap boxes to provide refugia from currents
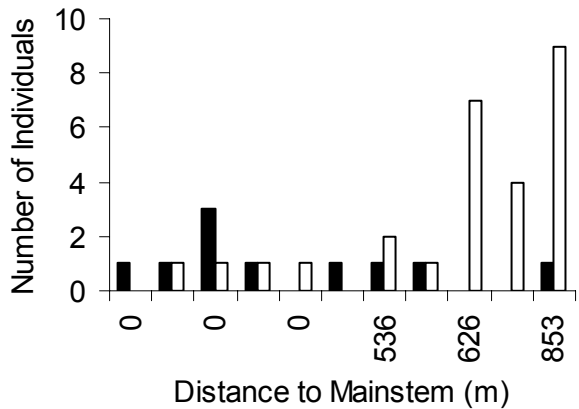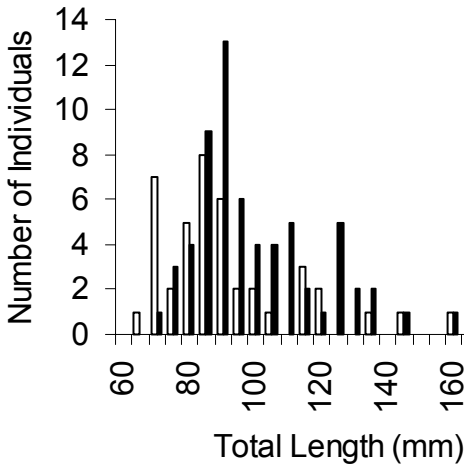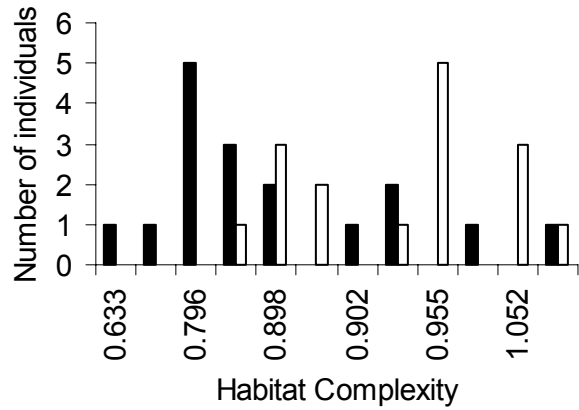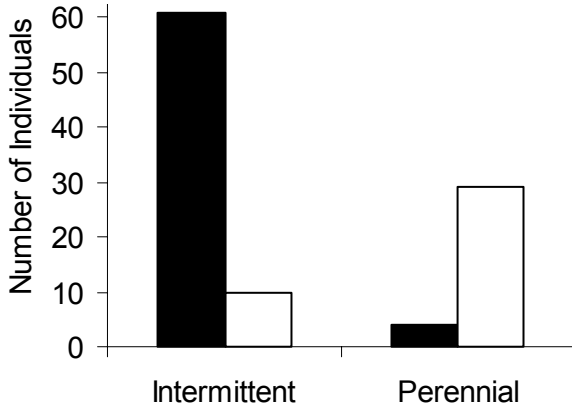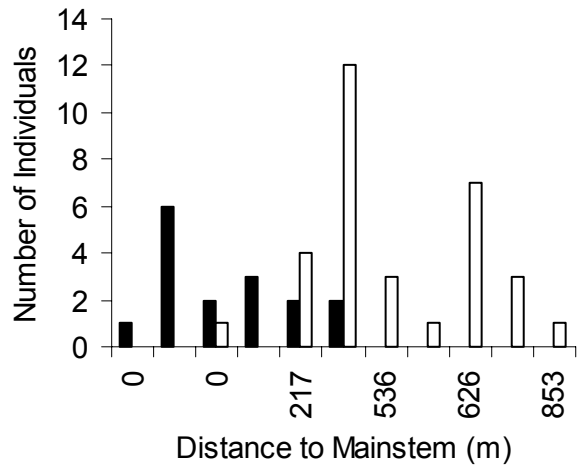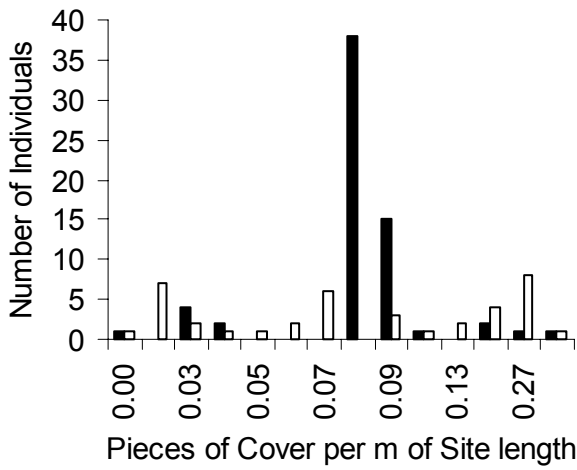
Figure 2.3 Number of *Nocomis leptocephalus* (three panels on left), *Rhinichthys atratulus* (top right), *Semotilus corporalis* (middle right), and *Thoburnia rhothoeca* (bottom right) that were captured within (stayed) and outside (moved) of original mark sites. The number of individuals that moved and stayed is plotted as a function of variables that were significant in the logistic regression analyses.
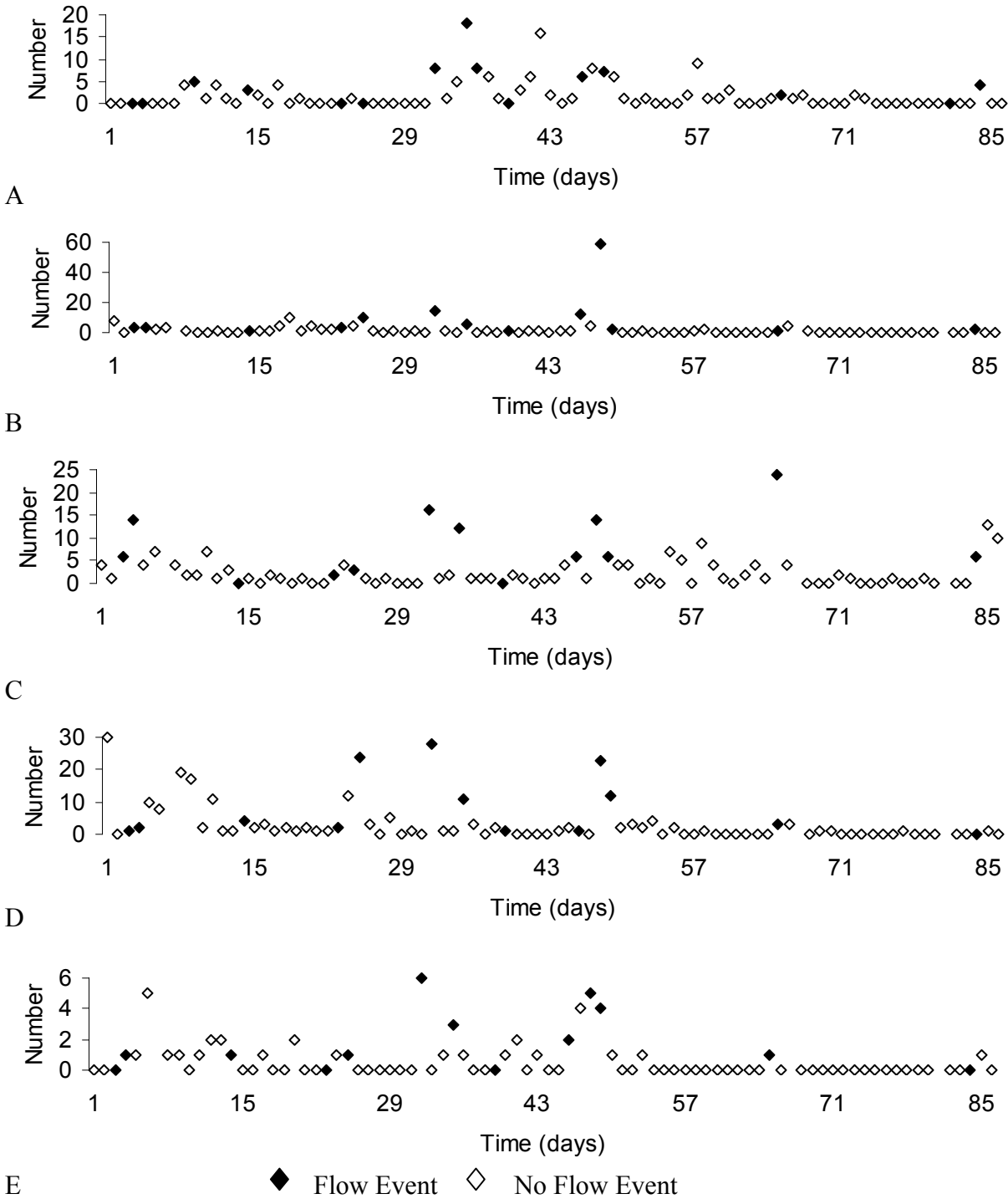
Figure 2.4 Number of *Phoxinus oreas* (A) captured in the upstream trap in Middle Creek between 26 May and 19 August 1999 and number of *Semotilus corporalis* (B), *Nocomis leptocephalus* (C), *Luxilus cornutus* (D), and *Thoburnia rhothoeca* (E) captured in the upstream trap in lower Dicks Creek between 26 May and 19 August 1999. Flow events were a significant predictor of the number of fish moving for each species.
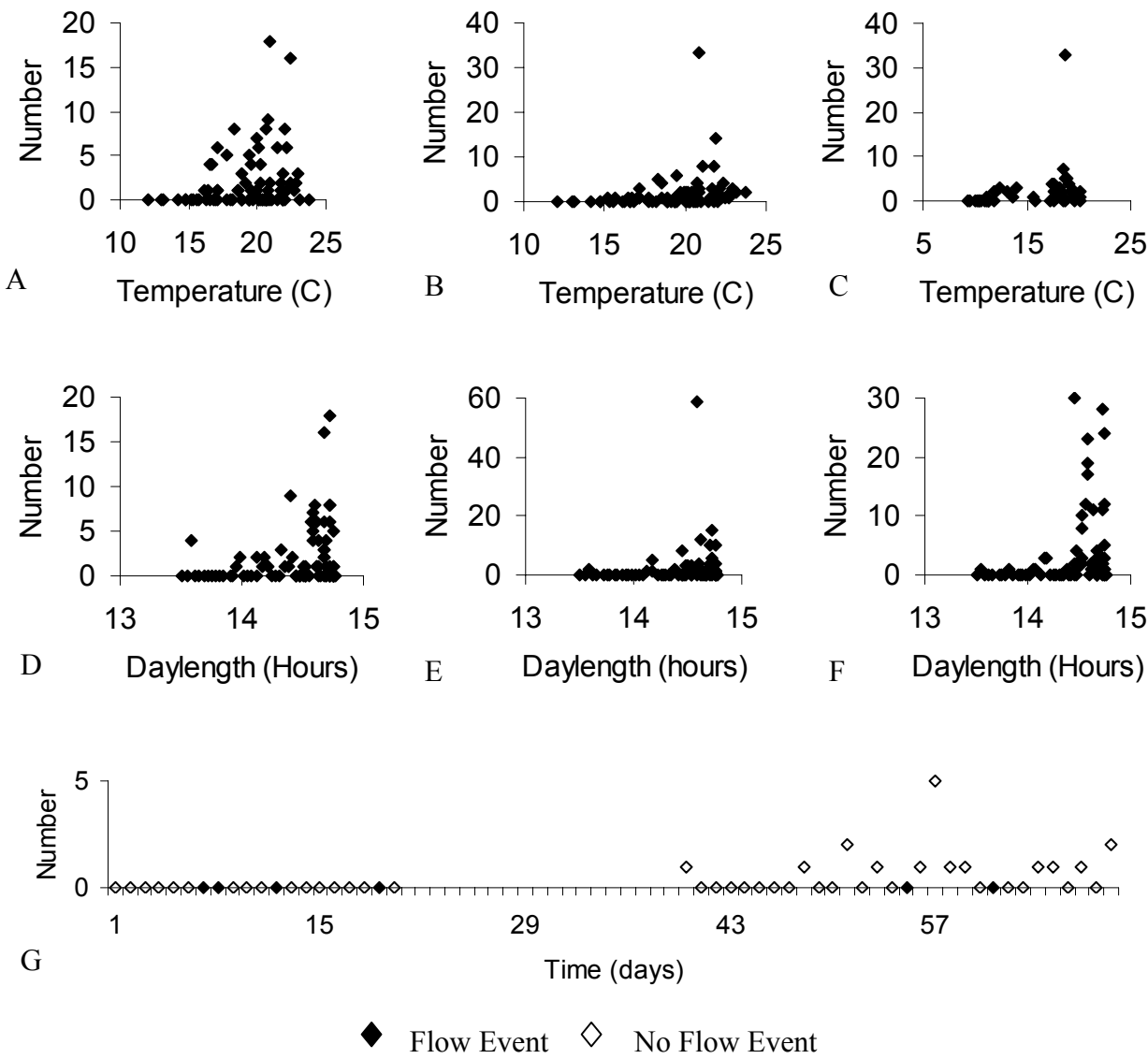
Figure 2.5 Number of *Phoxinus oreas* (A, D) and *Nocomis leptocephalus* (B) captured in the
upstream trap in Middle Creek between 26 May and 19 August 1999, number of *Semotilus
corporalis* (E) and *Luxilus cornutus* (F) captured in the upstream trap in lower Dicks Creek
between 26 May and 19 August 1999, and number of *Nocomis leptocephalus* (C) and *Noturus
insignis* (G) captured in the upstream trap in lower Dicks Creek between 29 March and 5 June
2000. With the exception of *Noturus insignis* (G), the number of fish captured are plotted
against variables that were significant in the poisson-regression analyses. No relationships
were detected for *Noturus insignis*, but movements were confined to the later time period
when temperatures were higher and stage was lower. The gap in the *Noturus insignis* data set
coincides with a high discharge period between 18 April and 6 May that prevented
measurement of movement rates.
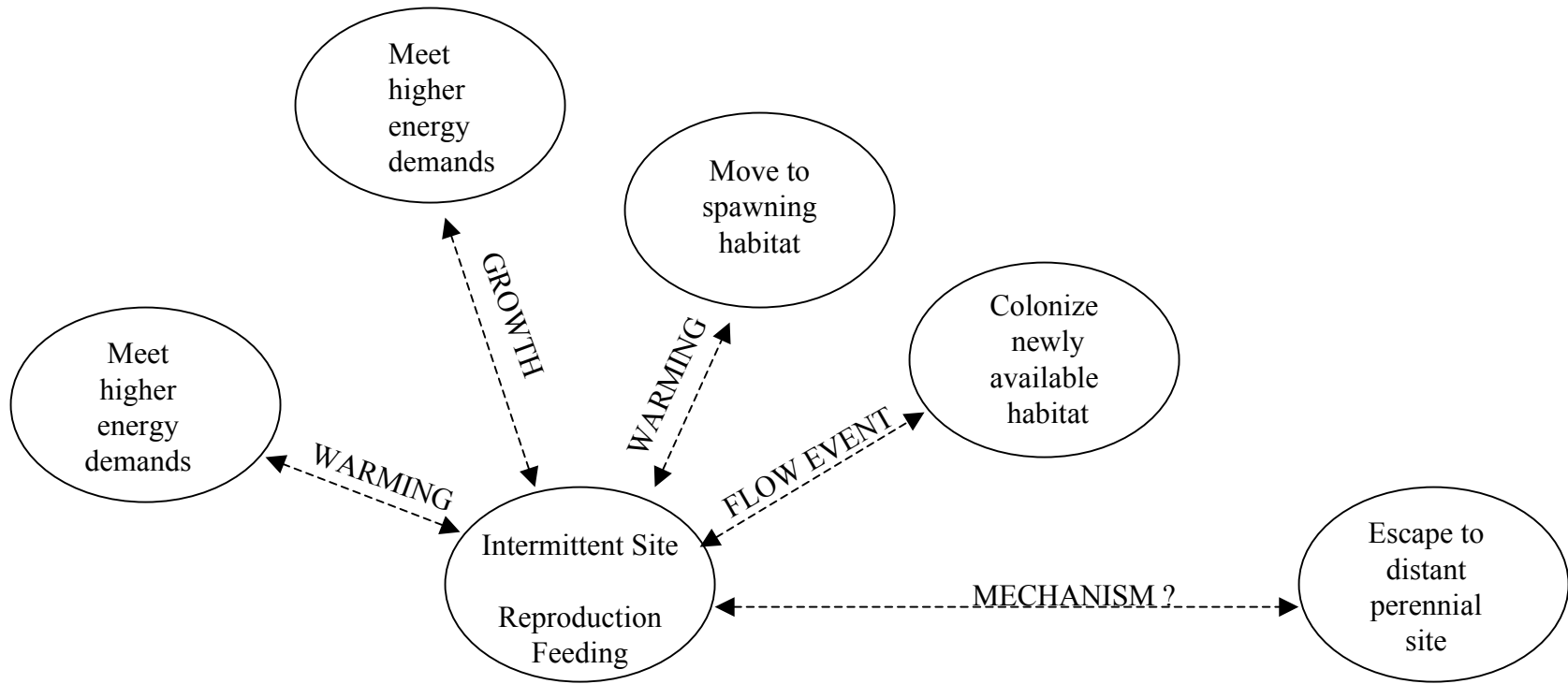
Figure 2.6 Conceptual model of dispersal for sub-adult and adult *Nocomis leptocephalus* that initially occupy an intermittent site. Arrows depict movements to new sites (ellipses) that may be in perennial or intermittent reaches; mechanisms that trigger these movements are written above arrows. The potential adaptive value of movements is given inside ellipses. Broken arrows symbolize movements that may be blocked during low flow periods. With the exception of movements from intermittent to distant perennial sites, all of the mechanisms and hypotheses illustrated in the model would also apply to fish that initially occupy a perennial site. These are not shown for clarity.

Chapter 3. Factors influencing colonization success and implications for stream-fish populations and assemblages.

INTRODUCTION

Colonization is an extremely important process that regulates the persistence of populations and impacts the structure of communities (Brown and Kodric-Brown 1977; Hanski and Gilpin 1991; Snodgrass et al. 1996; Nichols et al. 1998; Singer et al. 2001). Colonization may be a regular feature of populations that cope with environmental stochasticity (Bayley and Osborne 1993; Labbe and Fausch 2000; Taylor and Warren 2001), but may also promote the persistence of populations subjected to anthropogenic disturbance (Thomas 1994; Foppen et al. 2000). Accordingly, interspecific variation in colonization success may translate into variation in extinction risk, particularly where humans increase the frequency of local extirpations (Terborgh 1974; Angermeier 1995). Understanding factors that influence colonization success should thus be a primary goal for population ecologists and conservation biologists (Gotelli and Taylor 1999A).

Rapid colonization following defaunation (e.g., Larimore et al. 1959; Meffe and Sheldon 1990; Petersen and Bayley 1993) suggests that interspecific differences in colonization rates have no practical significance for stream fishes. It is dangerous, however, to make broad generalizations about colonization success from these studies because most were conducted at small spatial scales where only trivial movement was required to achieve colonization (e.g., Berra and Gunning 1970; Peterson and Bayley 1993; Sheldon and Meffe 1995). In addition, many studies have found evidence for interspecific variation in colonization success (Niemi et al. 1990; Detenbeck et al. 1992; Sheldon and Meffe 1995; Ensign et al. 1997). For example, Larimore et al. (1959) found high variation in colonization rates in a drought-affected stream and two species failed to repopulate the stream during four years of sampling.

What are the factors that influence colonization success in stream fishes? Detenbeck et al. (1992) reviewed 49 case studies of fish assemblage recovery and found that species with a large size at reproduction and species with complex reproductive behaviors (e.g., nest spawning) were slow to repopulate disturbed areas. Their family-level analysis indicated that centrarchids and percids colonized most rapidly, but also noted that minnows (Cyprinidae) recovered more

rapidly than larger species.   Ensign et al. (1997) evaluated a suite of factors related to colonization success in a fifth-order mountain stream in Virginia. In contrast to Detenbeck et al. (1992), they found that species with complex reproductive behaviors (e.g., egg guarding) restored population sizes more rapidly than simple spawners. At least two studies have shown a positive relationship between colonization rate and abundance (Olmsted and Cloutman 1974; Sheldon and Meffe 1995). Finally, spatial distribution will influence the location and number of potential source populations and should influence colonization rates (Niemi et al. 1990; Schlosser and Angermeier 1995). Many metapopulation models predict that the probability of colonization depends upon the fraction of sites occupied (Gotelli and Taylor 1999B).

Intuitively, movement should be a primary determinant of colonization success—fishes have to get there first. Nonetheless, it is unclear that differences in movement attributes translate into differences in colonization success. Sheldon and Meffe (1995) concluded that interspecific differences in colonization rates resulted from "proportional sampling of a mobile fauna". Their study suggests that the supply of colonists (not movement) is the primary determinant of colonization rates. Similarly, Detenbeck et al. (1992) did not find a relationship between vagility and recovery rates among nonanadromous fishes. However, the lack of accurate data on movement attributes for most fishes makes it very difficult to address relationships between movement and colonization (Gowan et al. 1994; Schlosser and Angermeier 1995; Angermeier et al. 2001).

I documented substantial interspecific variation in the number of fish moving upstream through traps per day (hereafter movement rate) in the upper James River drainage, Virginia. The primary objective of the current study is to incorporate these data into a species-level analysis of factors that influence colonization rates after experimental defaunation. I make three predictions:

1. Movement rate will be a primary determinant of colonization rates when compared to competing alternatives.

2. Species with high movement rates will recover populations before species with lower movement rates.

3. Assemblage composition will shift toward species with high movement rates.

Colonization rates may also vary with stream size. Based upon life history characteristics and observed colonization patterns, Schlosser (1990) suggested that fish assemblages in upstream sites colonized more rapidly than fishes in downstream sites. In contrast, Taylor and

Warren (2001) found a positive relationship between stream size and immigration rates, presumably because of a larger pool of immigrants in downstream areas (see also Osborne and Wiley 1992). An additional objective of this study was to compare colonization rates between a site located in the upper reaches of a tributary stream and a site located in a mainstem creek.

MATERIALS AND METHODS

Design of colonization experiment

Two sites were selected for the colonization experiment (Figure 3.1). The first site was 130 m long and was located in lower Dicks Creek. Because of higher species richness in this portion of the study area (ca. 20 native species), inclusion of this site provided an opportunity to measure colonization rates for a large number of species. The second site was 126 m long and was located in the upper reaches of Middle Creek. This site was selected to measure colonization rates for species that were abundant only in the upper reaches of this tributary (e.g., *Thoburnia rhothoeca*) and to permit the comparison between sites.

Fishes were removed from both sites between 29 June and 7 July 2000 using a Smith-Root backpack electrofisher operated at 700 volts direct current; stunned fishes were captured with 4.8-mm-mesh dipnets. Fishes were also removed from 130-160-m -long sites located directly upstream and downstream of colonization sites (Figure 3.1). Removing fish in these buffer sites prevented immediate colonization from adjacent reaches, as documented by Peterson and Bayley (1993). Prior to sampling, 6.4-mm-mesh block nets were set to prevent fishes from escaping the entire reach and to allow separation of fishes caught in buffer and colonization sites.

Nine passes were made through both colonization sites and seven or eight passes were made through each of the buffer sites. To maximize the number of fishes removed, sampling effort was increased during the last 1-2 passes by increasing voltage (up to 1000 volts) and allocating more shocking time to complex habitats (e.g., undercut banks). In addition, two shockers were operated side by side through the lower Dicks Creek removal site during the last pass. Snorkeling observations made 1-3 days before and immediately after (before block nets were pulled) defaunation samples in colonization sites, along with depletion patterns of captured fishes, were used to assess the effectiveness of removal sampling.

Captured fishes were anesthetized with MS-222, fixed in 10% formalin, and transferred to Virginia Tech when time constraints precluded processing in the field. Fishes that were processed in the field were released approximately 10 km downstream of an impassable barrier on Johns Creek. With the exception of larvae, all fishes were identified, counted, and measured to the nearest mm total length (TL).

Both colonization sites were re-sampled during 3-pass backpack electrofishing surveys conducted 1 month (early August), 3 months (late September-early October; hereafter October), and 12 months (late June) following defaunation. Because of slow recovery, the Middle Creek site was also sampled 15 months after defaunation (hereafter October 2001). Control sites located upstream and downstream of the buffer sites were sampled with 1-pass backpack electrofishing in association with defaunation and post-defaunation samples. These 100-m-long sites were sampled to assess seasonal variation in fish assemblage attributes (Figure 3.1). Fishes captured in colonization and control sites were identified, counted, measured (TL), and released back into sampling sites.

Species-level analyses

The objective of the species-level analyses was to identify factors associated with colonization rates in the lower Dicks Creek site. Except for the species noted below, these analyses included all species that were captured within the defaunation sample or in any of the post-defaunation samples (Table 3.1). *Hypentelium nigricans* was excluded from all analyses because the only fish captured during the defaunation sample was collected on the ninth pass. *Etheostoma flabellare* was excluded from all analyses because the number of fish captured did not decline with additional electrofishing passes during the defaunation sampling (i.e., a non-descending removal pattern).

Small sample sizes precluded accurate calculation of 3- pass population estimates in post-defaunation samples. However, the total number of fish captured during 3 passes was strongly correlated with population estimates in the defaunation sample (Spearman's rho = 0.99, p < 0.0001, population estimates calculated with microfish 3.0; Van Deventer and Platts 1985). Thus, the total number of fish captured during 3 passes, hereafter number of colonists, was used as the response variable in subsequent regression models. Young-of-year (YOY) fishes were excluded from this count because they could have "colonized" by surviving the defaunation (see

Effectiveness of defaunation). Since the time interval between sampling events was equal for all species, fishes adding more colonists to the site are considered to have faster colonization rates.

Four competing multiple regression models that predicted the number of colonists were built for each of the post-defaunation samples. Abundance, measured as the total number of fish captured during 3 passes in the defaunation sample, was included in each model to ensure that it did not confound relationships with the other regressors (Licht 1995; Taylor and Warren 2001). Variable importance was then determined by comparing R^2 values among models that contained abundance and one of four additional predictor variables: movement rate, spatial distribution, body size, and family. These variables were selected a priori because of their theoretical and documented importance in colonization studies (see introduction). Reproductive variables (e.g., guild, age at maturity) were not modeled because post-defaunation samples preceded recruitment of fishes that may have been spawned in the colonization site.

Movement rate was measured as the mean number of fish moving through an upstream trap in lower Dicks Creek that was checked daily between 26 May and 19 August 1999 (see chapter 2). Spatial distribution was the total number of sites (out of 60) occupied during a system-wide electrofishing survey in August 1999 (see Chapter 1). Sites measured ca. 50 m in length and 4459 m of stream was sampled. This variable was calculated to represent the diversity of source habitats for colonists. Accordingly, colonization and buffer sites were excluded from calculations. Body size was the maximum standard length (SL) reported in the species accounts of Jenkins and Burkhead (1993), which give the "typical size range of adults" rather than the largest specimen ever collected. The number of colonists, abundance, movement rate, and body size were $\log_{10}$- transformed to increase normality. Family was dummy-coded into three variables: Cyprinidae, Catostomidae, and Centrarchidae. Other families were represented by a single species and were not specifically identified in the analyses (Johnson 1998).

Simultaneous regression models were built using PROC REG in SAS version 8.0. If the overall model was significant at alpha = 0.05, significance of the individual regression coefficients was evaluated at the same significance level. Quantitative predictor variables were standardized to facilitate comparison of regression coefficients. Model fit was assessed by examining the coefficient of determination (R^2), studentized residuals, and leverage coefficients (leverage coefficients indicate the extent to which deviant values for predictor variables influence the fit of the regression line; Sokal and Rohlf 1995). Significance patterns were re-

examined after removing observations with studentized residuals > 2.0 or leverage coefficients > 3p/n (Sokal and Rohlf 1995; C. Anderson-Cook, Virginia Tech Department of Statistics, pers. comm.). The effect of multicollinearity on analyses was estimated by examining variance inflation factors and Pearson correlations among predictor variables.

There are potential shortcomings of this analysis that must be acknowledged before data are interpreted. First, models for the three separate time periods are not independent. The number of colonists captured during early time periods (i.e., August and October) could clearly influence the number of colonists captured during the later time periods (i.e., October and June). I built all three models because I wanted to identify important factors during different phases of the colonization process—identifying a single factor during multiple time periods does not equate to finding that factor important in separate experiments. Secondly, it is possible that YOY fishes surviving the defaunation could have contributed to the number of colonists captured during June 2001 (they could not be separated by size for this sample). The importance of this bias will be evaluated in the results (see *Effectiveness of defaunation*). Finally, small sample size prevented me from including all seven variables (including the three dummies) in a single model. Thus it is possible that the effects of variables in the model are overestimated because other potentially important variables were excluded (i.e., models are under-fitted ; Burnham and Anderson 1998). To address this problem, stepwise regression was used to screen the data for more complex relationships. I used a liberal alpha criterion (p= 0.15) for variable entry and removal to ensure that the largest set of "important" variables was retained. I then re-examined patterns of variable significance in an effort to confirm the results of the smaller models (C. Anderson-Cook, Virginia Tech Department of Statistics, pers. comm.). Abundance was forced into each model to statistically control for its relationship with the other regressors (Licht 1995).

Small sample size (n = 5-6 species; see Table 3.2) also prevented me from building any simultaneous regression models for the Middle Creek data set. Instead, I explored these data by examining scatterplots and building stepwise models. Values for body size and spatial distribution were the same as in the lower Dicks Creek analyses (Table 3.1). Movement rates were measured at the upstream weir in Middle Creek between 26 May and 19 August 1999 and abundance was measured within the Middle Creek colonization site (see Chapter 2; Table 3.2). Family-level variables were excluded from analyses because all but two species were cyprinids. Analyses were carried out as above except that abundance was not forced into each model. A

priori, I acknowledge that these analyses have low power. In addition, any relationships that are detected should be interpreted cautiously because of the lack of statistical control for abundance and other regressors.

Recovery analyses

The objective of the recovery analyses was to explore relationships between recovery and factors associated with colonization rates in the species-level analyses. In other words, do species with attributes that make them good colonists actually restore their population sizes faster? Fish population recovery was indexed by the degree of colonization (DC), calculated as

$$DC_i = (C/O)*100$$

For species i, C is the number of colonists in the post-defaunation sample and O is the pre-defaunation abundance within the site (Peterson and Bayley 1993). Following the species-level analysis, C and O were the total number of fish collected during three passes. Again, YOY were excluded from calculations because they may have survived the defaunation. This study thus emphasizes recovery of subadult and adult populations. Other studies suggest that rapid recovery is often accomplished by YOY fishes (Olmsted and Cloutman 1974; Matthews 1986), so the estimates of DC reported here may better reflect recovery of the full size and age range of populations. Rare species were also excluded from the recovery analysis because of the limited number of DC values that can be calculated when O values are small (Sokal and Rohlf 1995). *Ambloplites rupestris* had the smallest O value (O = 7) for species included in the analysis. I examined correlations between DC and predictor variables using Spearman's rank correlation. I chose this non-parametric measure of association because percentages are often non-normal and DC values above 100% cannot be arcsine-transformed (Sokal and Rohlf 1995).

Pre-defaunation abundance within the colonization site may not be a good baseline for recovery of seasonally variable fish populations (Olmsted and Cloutman 1974; Sheldon and Meffe 1995). I initially attempted to adjust O values according to temporal changes in fish abundance occurring within the control sites. Rarity of some fishes within control sites precluded accurate calculation of proportional changes, so it was not possible to adjust O values for each species. A BACI analysis was also inappropriate because there was only one sample collected in control and impact (i.e, defaunation) sites that represented pre-impact conditions (Stewart-Oaten et al. 1986). Thus, DC values were not adjusted for seasonality. Instead, I restricted correlation

analyses to the August and June samples because they were collected during the same time of year as the defaunation sample.

Assemblage-level analyses

The objective of the assemblage-level analyses was to characterize assemblage-level attributes throughout the recovery period in lower Dicks Creek and Middle Creek. The defaunation sample was used as a baseline for assemblage attributes, but patterns were interpreted relative to temporal changes in the control sites.

Changes in total abundance were examined by dividing the number of fishes collected during post-defaunation samples by the number of fishes collected during the defaunation sample. The Jaccard coefficient (Brower et al. 1990) was calculated using the following formula:

$$CC_j = c/S,$$

where c is the number of species common to both samples and S is the total number of species collected in both samples. This index ranges from 0 (no shared species) to 1 (identical species composition) and was calculated to compare species composition between defaunation and post-defaunation samples. The Jaccard coefficient can be strongly influenced by rare species (Matthews 1998), so species that were caught only within one sample were excluded from calculations.

Changes in species composition and relative abundance patterns were examined in two ways. First, I calculated the proportional similarity index (PSI; Brower et al. 1990) between defaunation and post-defaunation samples using the following equation

$$PSI = 1 - 0.5\Sigma \left| p_i - q_i \right|,$$

where p_i = is the proportion of total fishes for species i in the defaunation sample and q_i is the proportion of total fishes for species i in the post-defaunation sample. This index ranges from 0 (completely different) to 1.0 (identical samples), with values > 0.70 generally indicating similar communities (Peterson and Bayley 1993). Rare species have a negligible influence on PSI values and no species were excluded from calculations (Matthews 1998). Changes in composition and abundance patterns were also assessed using detrended correspondence analysis (DCA; Palmer 1993; Matthews 1998). Analyses were run on raw data using the program CANOCO (vers 4.0; C.J.F. ter Braak and P. Smilauer 1997). Rare species can have a large effect

on DCA, so species contributing less than 1% of the total catch in all samples were excluded (see Gido and Matthews 2000).

RESULTS

Site comparison

Habitat characteristics measured during June 2000 indicated substantial differences between the two sites. The lower Dicks Creek site was wider (mean = 5.5 m, s.d. = 1.6 vs. mean = 2.8, s.d = 0.7), deeper (mean = 12.2 cm, s.d. = 10.5 vs. mean = 7.4, s.d. = 5.9), and had slower current velocity (mean = 5.4 cm/sec, s.d. = 4.9 vs. mean = 7.3, s.d. = 9.6) than the Middle Creek site. The Middle Creek site was dominated by bedrock substrata whereas the lower Dicks Creek site was dominated by pebble and cobble substrata. Habitat complexity was significantly higher in the Middle Creek site (H' = 1.24 vs. 0.85, $p < 0.001$; Brower et al. 1990; see Chapter 2). Finally, daily mean water temperatures were substantially lower in Middle Creek during late May and early June of 1999 and slightly lower in Middle Creek throughout the summer of 1999 (overall mean = 19.3 °C, s.d. = 2.6 vs. mean = 20.3, s.d.= 2.1; Albanese, unpublished data).

Potential barriers to movement also differed notably in reaches adjacent to the two colonization sites. Cylindrical-metal culverts were located upstream and downstream of the Middle Creek site (See Chapter 1; Figure 1.1), but none were located within lower Dicks Creek. Stream gradient was not measured, but was substantially greater in Middle Creek--several bedrock cascades occurred upstream, downstream, and within the Middle Creek site. Vertical drops and approximate slopes for the three largest and steepest cascades were 0.7m and 30°, 0.8 m and 50°, and 0.3 m and 85°, respectively (e.g., Figure 3.2).

Effectiveness of defaunation

Defaunation was highly effective for non-YOY fishes in the lower Dicks Creek site. No individuals were captured during the last two passes for nine species and very few individuals (1-8) were captured during the last two passes for the other eight species (Appendix C). Despite the failure to deplete these species to zero, it is unlikely that many fishes survived the defaunation because of the high sampling effort allocated to the last two passes. In addition, 26 of the 29 (90%) fishes collected during the last pass were captured dead. Finally, large numbers of fishes

(11 species) were detected during snorkeling observations made before the defaunation sampling, but no non -YOY fish were detected during post-defaunation snorkeling observations.

Defaunation sampling was also highly effective for non-YOY fishes captured in the Middle Creek site. No individuals were captured during the last two passes for four of five species. However, 21 *Phoxinus oreas* (mountain redbelly dace) were captured during the last two passes. Again, it is unlikely that many *P. oreas* survived the defaunation sampling because of the high sampling effort during the last two passes. No fish were detected during post-defaunation snorkeling observations, despite the detection of large numbers of all five species during pre-defaunation observations.

In contrast to adults and subadults, defaunation sampling was not effective for YOY fishes in either colonization site. For example, 420 YOY cyprinids were collected from the lower Dicks Creek site, but 123 (29.2%) of these were collected during the ninth pass. The small size of YOY fishes makes them less vulnerable to electroshocking and difficult to see by dipnetters. In addition, many YOY were too small to be captured by our 4.8-mm-mesh dipnets. This problem was particularly important in Middle Creek where large numbers of larval fishes were captured with a 3-mm-mesh seine immediately after the defaunation sample. Snorkeling observations indicated that YOY fishes were abundant in both sites immediately after defaunation samples were completed.

The inability to deplete YOY fishes during defaunation sampling may bias the results of certain analyses. YOY were easily separated from 1+ and older fishes during the August and October post-defaunation samples and should not affect any of the analyses during these months. In contrast, surviving YOY could not be separated from true colonists during the June sample. Consequently, the number of colonists and the degree of colonization may be overestimated for June and October 2001 (Middle Creek only) samples.

Species-level analyses

Relationships among predictor variables did not bias the results of the species-level regression analyses. Log-transformed abundance was significantly correlated with log transformed movement rate ($r = 0.66$, $p = 0.0015$) and spatial distribution ($r = 0.49$, $p=0.0266$), emphasizing the importance of including abundance in each model. Spatial distribution was also correlated with log-transformed movement rate ($r = 0.48$, $p= 0.0311$). I did not consider these

relationships "too strong" in terms of multicollinearity (Licht 1995) and variance inflation factors never exceeded 2.1 in any of the analyses. Body size was not significantly correlated with any of the predictors.

Models containing movement rate and abundance explained the highest proportions of variance in colonization rates for all three time periods (Tables 3.3, 3.4, and 3.5). Movement rate was significantly and positively related to the number of colonists captured during each time period and always explained more variance than abundance (Tables 3.3, 3.4, and 3.5; e.g., Figure 3.3). *Clinostomus funduloides* had a large influence (i.e., high leverage values) on each model because of its low abundance and high movement rate and there was only moderate evidence (P= 0.0545) for a relationship between movement rate and the number of colonists after removing this species from the August data set. Removing observations with large residuals or leverage coefficients had no effect on any of the other significant relationships reported for the species-level analyses.

Abundance was never significant in the movement rate models, but was always significant in competing models (Tables 3.3, 3.4, and 3.5; e.g., Figure 3.3). In part, these results emphasize the importance of statistical control (i.e., partialling) when predictor variables are correlated. Despite its lack of significance in the movement rate model, abundance explained a considerable amount of variation in the movement rate (14-24%) and competing (23-44%) models. Thus, the relationship between abundance and the number of colonists is not spurious.

None of the other variables were significant predictors of the number of colonists (Figure 3.3). Spatial distribution did explain a sizeable portion of variance in August but not in other months (Tables 3.3, 3.4, and 3.5). Body size never explained more than 8% of the variance in colonization rates. Despite the larger size of the family models, they did not explain substantially more variation than any of the other models (Tables 3.3, 3.4, 3.5) and the August family model was unique in its lack of significance. However, it is worth noting that four or five of the species with the largest number of colonists in each month were all cyprinids (e.g., Figure 3.4). Catostomids, in contrast, never supplied many colonists to the site. The small number of species represented by the Centrarchidae and other families precluded any additional generalizations.

Stepwise models did not identify more complex relationships within the data sets. After forcing abundance into models, movement rate was the only variable that was selected during

August, October, and June. Thus, it is unlikely that the simultaneous models overestimated the effect of movement rate by failing to include other relevant variables. The exclusion of the competing variables in stepwise models suggests that these variables do not make an important contribution after controlling for the effects of movement rate and abundance.

Despite small sample sizes, step-wise models detected significant relationships during each time period for the Middle Creek data set. The number of colonists was positively related to abundance in August and October; the relationship in August was exceptionally strong and explained almost all of the variation in colonization rates (Table 3.6; Figure 3.5). The number of colonists was positively related to movement rate in June. No other variables were selected by the stepwise models.

Recovery analyses

Because of the importance of movement rate and abundance in the species-level analyses, I tested for relationships between these two variables and recovery. For the lower Dicks Creek site, movement rate was significantly correlated with DC in June (r = 0.79, P = 0.0195; Figure 3.6). In Middle Creek, abundance was correlated with DC in August (r = 1.0, P <0.0001) and June (r = 0.90, p = 0.0374). Movement rate was also correlated (r = 0.90, P = 0.0374) with DC in June. None of the other relationships were significant.

Recovery rates were highly variable over the course of the post-defaunation sampling in Dicks Creek (Table 3.7). *Phoxinus oreas* restored over half of its pre-defaunation abundance in August, but the remaining species exhibited relatively low DC values in that month. *Phoxinus oreas*, *Nocomis leptocephalus* (bluehead chub), and *Noturus insignis* (margined madtom) had relatively high DC values in October. Most species showed large increases in DC values between October and June and values were >/= 100% for five of eight species. Nevertheless, there was still a broad range (17-123 %) of DC values in June and two species (*R. atratulus and A. rupestris*) clearly did not recover.

Recovery rates also varied greatly among species and across time periods in Middle Creek. Again, *P. oreas* exhibited a relatively high DC value compared to all other species in August. *Rhinichthys atratulus and P. oreas* had the highest DC values in October. *Phoxinus oreas* and *N. leptocephalus* had the highest DC values in June, but *C. funduloides* and *R. atratulus* also exhibited large increases in DC values between October and June. *Nocomis*

leptocephalus had the highest DC value in October 2001 and was the only species to exhibit a large increase in DC values between June and October 2001. Recovery of *Thoburnia rhothoeca* (torrent sucker) has been extremely limited over the course of the post-defaunation sampling; DC values never exceeded 8% for this species and no non-YOY were captured during October 2001.

Recovery occurred more slowly in Middle Creek than in Dicks Creek. Average recovery rates were higher in Dicks Creek during August (18% vs 7%), October (48% vs 17%), and June (86% vs. 45%). Recovery rates were always higher in Dicks Creek for *P. oreas* and *N. leptocephalus*, but the opposite pattern occurred for *R. atratulus*. Low abundance and movement rates for *R. atratulus* may explain why this species recovered so slowly in lower Dicks Creek.

Assemblage-level analyses

Defaunation had a measurable effect on abundance in both sites relative to controls, but this effect was more pronounced and persistent in Middle Creek than in lower Dicks Creek (Figure 3.7). Data for October 2001 sampling in Middle Creek are not shown, but the percent of pre-defaunation abundance in the colonization site was still substantially lower than measured in the downstream control site (66 % vs. 159%).

Jaccard coefficients indicated that defaunation and post-defaunation samples in colonization sites were as similar or more similar in species composition than control sites in both streams. However, it should be noted that the proportion of shared species was relatively low in Dicks Creek during the August and October samples relative to the downstream control site and relative to all samples in June. *Esox niger*, *Rhinichthys atratulus*, *Scartomyzon cervinus*, *Exoglossum maxillingua*, *Erimyzon oblongus*, and *Ambloplites rupestris* were not present in the August 2000 sample and the latter three species had not colonized by October. None of the species present in the defaunation sample were absent from the June sample in Dicks Creek or Middle Creek. However, despite its occurrence in August, October, and June post-defaunation samples, *Thoburnia rhothoeca* was absent from the Middle Creek colonization site in October 2001.

Defaunation and post-defaunation samples in colonization sites exhibited high similarity in species composition and abundance patterns (i.e., PSI > 0.70), but similarity was clearly depressed relative to control sites during August 2000 (Figure 3.7). Both colonization sites also exhibited an increasing trend in PSI values between August and October that was not paralleled

in control sites. Samples collected during June and October 2001 (Middle Creek only, PSI = 0.86, not plotted) indicated high similarity in defaunation and post-defaunation assemblage structure.

The DCA analyses did not resolve strong axes of species turnover within streams. Eigenvalues for the first and second axes were very small for the Dicks Creek (0.13 and 0.02, respectively) and Middle Creek analyses (0.06 and 0.01, respectively). Nonetheless, there are two noteworthy patterns evident in the Dicks Creek ordination (Figure 3.8). First, the strongest gradient is associated with longitudinal position within the stream and upstream, central (i.e., the colonization sites), and downstream sites are ordered predictably along this gradient. Secondly, the colonization site exhibited a large relative shift along the second axis immediately after defaunation. This shift was concurrent with increases in the relative abundance of *P. oreas* and *C. funduloides* (rosyside dace) and decreases in the relative abundance of *Nocomis leptocephalus* and *Luxilus cornutus* (common shiner). This site shifted back towards its previous position between August and October.

DISCUSSION

Factors influencing colonization rates

When compared to competing hypotheses, movement rate models explained the largest amount of interspecific variation in colonization rates during each phase of the recovery process in lower Dicks Creek. Movement rate also explained a large proportion of variance in colonization rates in Middle Creek during June. Previous evidence for the importance of movement to colonization has been inconsistent. Indirect evidence that movement can limit colonization success comes from Olmsted and Cloutman's (1974) study of fish repopulation after a pesticide spill. Two species (*Luxilus pilsbryi* and *Notropis nubilus*) were common in the stream before the spill but failed to restore their population sizes within 1 year despite the presence of large populations in nearby reaches. Other studies have found that movement did not contribute to interspecific variation in colonization rates (e.g., Detenbeck et al. 1992; Sheldon and Meffe 1995), but these studies did not incorporate quantitative data on movement into their analyses.

The results of this study indicate that colonization did not result from "simple proportional sampling of a mobile fauna", as documented by Sheldon and Meffe (1995) in a

South Carolina stream. These authors did predict that variation in mobility might become more important when fishes are removed from longer sections of stream (Meffe and Sheldon 1990; Sheldon and Meffe 1995). This study confirms their prediction and provides a reference point to the spatial scale over which movement becomes important--fishes were removed from 416-426-m-long sites in this study. The larger spatial scale in this study is more relevant to processes that affect fish populations.

I used upstream movement rate in this study because it was the only attribute of movement that was known for each species in the analysis. Variation in movement rate could easily result from interspecific differences in abundance and these two variables were significantly correlated. However, two arguments suggest that upstream movement rate measured unique aspects of movement. First, as already noted, the effect of movement rate was significant after statistically controlling for abundance. Secondly, a spatially intensive mark-recapture study within the same study area indicated that species with high movement rates through weirs also exhibited other attributes that characterize mobile species. For example, among four species studied, *N. leptocephalus* exhibited the highest movement rate, longest median distance moved, and the highest proportion of complex movements between tributary and mainstem creek sites (Chapter 1 and Appendix B).

Abundance was also associated with colonization and explained a substantial proportion of variance in colonization rates in both streams. Other studies have found that abundant species restored populations more rapidly than rare species following experimental defaunation (Olmsted and Cloutman 1974; Sheldon and Meffe 1995). Recent studies have measured colonization using a time series of presence-absence data (i.e., a presence following an absence = a colonization event) and have also found a positive relationship between abundance and colonization rates (Gotelli and Taylor 1999A; Taylor and Warren 2001).

Sheldon and Meffe (1995) stated that recolonization has two components: "matching of colonists to the habitat template and supply of colonists", which suggests mechanisms for the relationship between abundance and colonization. Retrospectively, my experiment teased these components apart—abundance in colonization sites reflects the match of each species to habitat characteristics and movement rate is a direct measure of colonist supply. Accordingly, I interpret the relationship between abundance and colonization rates in this study to primarily reflect habitat selection. High similarity in relative abundance patterns between pre-and post-

defaunation samples (see *assemblage-level implications*) is consistent with the idea that habitat selection had a strong influence on colonization patterns.

Spatial distribution, body size, and family-level variables were never significant and rarely explained much variation in colonization rates. Stepwise models also suggested that these variables did not contribute to variation in colonization rates after movement rate and abundance were incorporated into models. Colonization rates were not associated with body size or the fraction of sites occupied among fishes in the Cimmaron River, Oklahoma (Gotelli and Taylor 1999A and B). Similarly, Taylor and Warren (2001) found no relationship between body size and colonization rates. Nonetheless, body size and family have been shown to be important in other studies and should be evaluated in future colonization experiments (Niemi et al. 1990; Detenbeck et al. 1992). Spatial distribution was measured using presence/absence data in this study. Future studies should attempt to evaluate more complex constructs related to spatial distribution. For example, distance between the colonization site and the nearest source population might also affect colonization rates (Niemi et al. 1990; Angermeier et al. 2001).

Although the primary objective of the study was to identify species-level factors associated with colonization rates, the strong differences in recovery rates between sites is noteworthy. However, lack of replication makes it impossible to sort out mechanisms for the differences. Theory and recent empirical data suggest that culverts (Warren and Pardew 1998), steep bedrock cascades (Adams et al. 2000), cooler water temperatures (see Chapter 2), higher habitat complexity (Gorman 1986; see Chapter 2), longitudinal position within the system (Osborne and Wiley 1992; Sheldon and Meffe 1995) and stream size (Taylor and Warren 2001) may have reduced movement rates into the Middle Creek colonization site. Niemi et al. (1990) could not relate recovery rates to stream gradient in their analysis of pulse disturbances, but noted that the presence of movement barriers delayed recovery times. I have recorded movements from the mainstem creek into and upstream of the colonization site in Middle Creek for *R. atratulus*, *N. leptocephalus*, and *T. rhothoeca* (Appendix B), but the proportion of fishes that do not ascend the steep bedrock cascades in this stream, if any, is unknown.

Population-level implications

Interspecific variation in colonization rates had important population level implications in this study. Although recovery could be accurately measured for only a subset of species, there

were clear interspecific differences in recovery rates that were positively associated with movement rate and abundance. Movement rate was important in both streams, but only for samples collected 12 months after defaunation. This pattern reflects progressively larger differences in population size between species with high and low movement rates. Abundance was only important in Middle Creek, but was important during both of the time periods considered.

Recovery occurred slowly in this study and population-level impacts persisted for more than a year in some species. Only one of ten species restored more than half of its pre-defaunation abundance after one month and only three species exceed this threshold after three months. In contrast, Sheldon and Meffe (1995) documented complete recovery of a large assemblage of stream fishes in South Carolina within 1 to 2 months. In Middle and Dicks Creek, recovery was still not complete for all species 12-15 months after defaunation. Two (*R. atratulus* and *A. rupestris*) of eight species in Dicks Creek had clearly not recovered by June. No species clearly recovered in Middle Creek after 12 months and only one species (*N. leptocephalus*) had restored more than 68% of its pre-defaunation abundance after 15 months. Ensign et al. (1997) found that 4 of 11 species had not fully recovered 8-11 months after a manure spill eliminated fishes from at least 6 km of a fifth-order mountain stream. In contrast, other studies have documented complete recovery of density or biomass within a year (Berra and Gunning 1970; Meffe and Sheldon 1990; Detenbeck et al. 1992).

Despite slow recovery, increasing trends in DC values suggest that most species will fully recover their populations within the next year. However, it is unclear when *T. rhothoeca* will restore its population in Middle Creek and this species best illustrates the importance of interspecific variation in colonization success. While *T. rhothoeca* was rare relative to some taxa in the defaunation sample (relative abundance = 7.4%), the upper reaches of Middle Creek (including the colonization site) contained the largest numbers of this species in the entire study area. Of 88 sites that were sampled during August 1999, sites with the second to fifth highest densities of *T. rhothoeca* were located within colonization or buffer sites. The site with the highest density was located immediately upstream of the buffer site. Surveys during May and August 1998 and spring 1999 also indicated relatively high densities of *T. rhothoeca* in the upper reaches of Middle Creek relative to other sites in the study area (Albanese, unpublished data).

Thus, the effect of defaunation sampling on this species was not trivial and may have important population or sub-population level consequences.

The failure for this species to recover may reflect partial obliteration of its source population along with attributes of its movement. *Thoburnia rhothoeca* movement rates ranked fourth out of the five Middle Creek species included in the recovery analysis. Furthermore, the probability of emigrating from mark sites was negatively related to distance from the mainstem creek for this species in the 1999 mark-recapture study (see Chapter 2). This relationship was driven by low emigration rates from high-quality habitats in the upper reaches of Middle Creek (Hansson 1991;Winker et al. 1995; Chapter 2). Thus, colonization from remaining populations in Middle Creek is expected to occur slowly.

Fortunately, movement from more distant populations should also supply colonists to the site. Despite larger population sizes in Middle Creek, *T. rhothoeca* exhibits higher movement rates in lower Dicks Creek and this stream may function as a corridor between distant populations (Chapter 2; see Fraser et al. 1999). Partial support for this hypothesis comes from observations of two *T. rhothoeca* that moved 759-1044 m from a site in the mainstem creek into the upper reaches of Middle Creek during the mark-recapture study. I have collected large numbers of torrent suckers at a site located just above the confluence of lower Dicks Creek and Johns Creek, approximately 2100 m downstream of the colonization site (sampling effort was not comparable, so this site was excluded from the discussion of density patterns presented above). Although I have never detected direct movements from this site into Middle Creek, this site may eventually supply fish to the colonization site.

Assemblage-level implications

The total number of fishes was clearly reduced in both sites one month after defaunation and this effect persisted in Middle Creek for at least 15 months. Sheldon and Meffe (1995) observed complete recovery of total numbers 31-63 days after fishes were removed. Extrapolating Peterson and Bayley's colonization rate model predicts that 90% of fish abundance would be restored to a 426-m section of stream (length of colonization and buffer sites in Middle Creek) within 30-80 days. The disparity between my study and published studies may reflect site (see *factors influencing colonization rates*) and regional variation in recovery rates, as well as differences in study design (see *implications for study design*). The implications of lower

abundance are that colonists may enjoy higher per-capita resources during the early phases of the recovery process.

The effect of defaunation on species composition was less pronounced, but potentially important. Several species were missing from the lower Dicks Creek site during August and October, but all species that were originally present in the defaunation sample had colonized by June. Jaccard coefficients indicated similar species composition (all $CC_j >/= 0.80$) between pre and post-defaunation samples in Middle Creek. However, these values are somewhat misleading. Jaccard coefficients in October and June ($CC_j = 0.83$) reflected the addition of one rare species (*L. macrochirus*), but the October 2001 coefficient ($CCj = 0.80$) reflected the loss of *T. rhothoeca*—a species that was formerly temporally persistent within the site. Species interactions are poorly documented for this fauna, but the loss of even a single species could have important ecosystem-level implications (Gelwick and Matthews 1992; Shute et al. 1997). This may be particularly important in spring-fed systems (e.g., Middle Creek) where biotic interactions are expected to be stronger or when species with specialized feeding behaviors (e.g., *T. rhothoeca*) are lost from the system (Jenkins and Burkhead 1993; Power 1988)

When abundance patterns and species composition are considered, the defaunation sampling had only a short term (i.e. < 3 months) effect on assemblage structure. These results are concordant with other colonization studies that found high similarity in assemblage structure (Meffe and Sheldon 1990; Peterson and Bayley 1993; Sheldon and Meffe 1995). High similarity seems counterintuitive—the high variation in recovery rates suggests that relative abundance patterns would have changed. These results illustrate the importance of the positive relationship between abundance and colonization rates. Species that were abundant in defaunation samples were generally abundant in post-defaunation samples. Since abundant species have a large effect on PSI values (Matthews 1998), it is not surprising that changes in the relative abundance of rare species did not affect overall assemblage similarity. DCA is more sensitive to changes in rare species, but the DCA analysis in this study did not detect any strong patterns.

Implications for study design

Lower recovery rates in this study may reflect real differences in colonization rates associated with differences in study area (Ensign et al. 1997). This study occurred in a mountainous region in Virginia and most of the streams in the area were impounded. Peterson

and Bayley's sites were in agriculturally impacted streams, many of which were channelized (Peterson and Bayley 1993). Movement rates may be higher in these systems because of low habitat complexity and because the long-history of anthropogenic disturbance may have filtered out less-mobile species (Gorman 1986; Angermeier et al. 2001). Other studies documenting rapid recovery were conducted in coastal plain systems where dispersal corridors may be more permeable to movement than in high-gradient mountain streams (Gunning and Berra 1969; Meffe and Sheldon 1990; Sheldon and Meffe 1995; Puth and Wilson 2001). Future studies should attempt to compare colonization rates in disparate environments.

Lower recovery rates may also reflect differences in study design. Fishes were removed from shorter sections of stream in many other studies that have documented rapid recovery (e.g., Berra and Gunning 1970, 20-76 m long sites; Meffe and Sheldon (1990, 4-15 m long sites; Peterson and Bayley 1993, 46-113m long sites; Sheldon and Meffe 1995; 10-23 m long sites vs. 416-426 m-long sites in this study). Clearly, the length of stream disturbed affects recovery rates and the results of small-scale studies may overestimate the resilience of stream-fish populations. This study also differed in that fishes were removed from adjacent buffer sites. Peterson and Bayley (1993) suggested that colonization was greatly influenced by short-term exploratory movements. Removing fishes from buffer sites greatly diminished opportunities for such movements and may explain the relatively slow recovery rates in this study. Thus, the buffer reach approach shifts the emphasis from short to long distance movements and may allow inferences that are more applicable to larger-scale extinction events (e.g., Olmsted and Cloutman 1974; Ensign et al. 1997).

Implications for conservation

This study documented substantial variation in colonization rates that was associated with movement rate and abundance. Recovery of population size was also associated with these factors. Conservation implications are obvious for pulse disturbances (e.g., chemical spill) that only have a short-term effect on habitat characteristics (Niemi et al. 1990). Species that are rare and less-mobile will recover their populations slowly and will be more vulnerable to extirpation in systems impacted by frequent pulse disturbances. In contrast, mobile species will be more likely to persist in the face of repeated pulse disturbances because they can exploit refugia (i.e.,

avoid extinction in the first place), rapidly colonize, and may also benefit from increased per-capita resources (e.g., spawning sites, drift, etc.) during the early phases of recovery.

Conservation implications for rare and non-mobile species are not trivial given the strong effects of a relatively small disturbance (426-m defaunation site) on *T. rhothoeca* and the fact that larger pulse disturbances still occur regularly despite efforts to prevent them (e.g., Ensign et al. 1997; Jones et al. 2001, R.J. Neves, pers. comm.). Thus, identifying relatively non-mobile fishes is an important step for proactive conservation (Angermeier 1995). Given the strong site effect in this study, such efforts must measure movement under a broad range of ecological conditions (see also Chapter 2). In addition to watershed-level efforts to protect entire fish assemblages, proactive conservation measures for non-mobile species would include establishment of aquatic reserves, population monitoring, and restoration of altered habitats that may further restrict movement (Angermeier 1995; Angermeier and Winston 1997; Frissell, 1997).

Notwithstanding the above arguments, pulse disturbances are not regarded as a major cause of fish endangerment-- channelization, changes in flow regime, urbanization, impoundments, introduced species and general degradation of aquatic habitats top the list (Robison and Buchanan 1988; Hackney et al. 1992; Etnier 1997). Thus, in many cases, suitable habitats for colonization may not be present following an extinction event (Niemi et al. 1990; Harrison 1991; Thomas 1994). In these situations, implications for sedentary taxa are more grave because colonization rates will be delayed by habitat recovery AND movement. In addition, the frequency of extirpation may be higher because declining populations are unlikely to be "rescued" by colonists (Brown and Kodric-Brown 1977). Accordingly, managers must take steps to promote colonization (e.g., dam removal, habitat restoration) and future studies should examine factors that may constrain movement (e.g., culverts, introduced predators; Warren and Pardew 1998; Labbe and Fausch 2000; Gilliam and Fraser 2001). Despite efforts to promote colonization, however, extinction rates may still exceed colonization rates for sedentary taxa and conservation efforts must also focus on reducing extinction rates (e.g., habitat protection; Thomas 1994).

Despite these important conservation implications, the significance of interspecific variation in colonization rates has been under-appreciated because of the widely documented resiliency of stream-fish assemblages. However, resiliency at the assemblage-level does not

necessarily equate to resiliency of component species. The metrics used in the study accurately depicted the strong effect of habitat selection on the recovery process but failed to reflect declines in rare species. These rare species are most important from a conservation standpoint and future colonization studies must consider assemblage level properties along with trends of individual species.

Interspecific differences in colonization rates may contribute to the widespread imperilment of stream fishes (Stiassney 1996; Abell et al. 2000; Warren et al. 2000). Extinction-colonization dynamics occurring at the level of populations and metapopulations are rarely observed (Schlosser and Angermeier 1995; Dunham and Rieman 1999), but the loss of fish populations isolated by dispersal barriers suggests that colonization is extremely important to persistence (Winston et al. 1991; Shute et al. 1997). The results of this study emphasize that fish populations may also be colonization- limited when they are not fragmented by physical barriers-- intrinsic attributes of species also affect colonization rates. If we are to abate the continued loss of stream fishes, interactions between these attributes, anthropogenic disturbance, and persistence must receive more attention from researchers and conservation practitioners.

Table 3.1 Species captured during defaunation (29 June-7 July 2000) or in any of the post-defaunation samples (August 2000, October 2000, or June 2001) in lower Dicks Creek, along with values for predictor variables used in the species-level colonization analyses. PA = pre-defaunation abundance in colonization site (total number of fish caught during 3 passes), MR = movement rate (mean number of fish moving through an upstream trap in lower Dicks Creek that was checked daily between 26 May and 19 August 1999), SD= spatial distribution (fraction of sites occupied during August 1999), BS = body size (total length in mm), FA = family, ESO = Esocidae, CYP = Cyprinidae, CAT = Catostomidae, ICT = Ictaluridae, COT = Cottidae, and CEN = Centrarchidae. See text for details.

Scientific Name	Common Name	PA	MR	SD	BS	FA
Esox niger	chain pickerel	3	0.02	18	500	ESO
Phoxinus oreas	mountain redbelly dace	9	0.30	45	55	CYP
Clinostomus funduloides	rosyside dace	0	1.58	38	80	CYP
Rhinichthys atratulus	blacknose dace	12	0.12	46	70	CYP
Campostoma anomalum	central stoneroller	1	0.81	21	150	CYP
Semotilus corporalis	fallfish	64	2.19	28	300	CYP
Exoglossum maxillingua	cutlips minnow	3	0.09	10	130	CYP
Nocomis leptocephalus	bluehead chub	192	2.91	53	160	CYP
Luxilus cornutus	common shiner	70	3.24	32	100	CYP
Lythrurus ardens	rosefin shiner	0	0.21	3	65	CYP
Erimyzon oblongus	creek chubsucker	1	0.01	17	250	CAT
Thoburnia rhothoeca	torrent sucker	4	0.63	36	150	CAT
Scartomyzon cervinus	black jumprock	3	0.30	6	155	CAT
Catostomus commersoni	white sucker	3	0.10	22	400	CAT
Noturus insignis	margined madtom	10	1.20	6	120	ICT
Cottus caeruleomentum	Blue Ridge sculpin	25	0.53	18	80	COT
Ambloplites rupestris	rock bass	7	0.02	11	200	CEN
Micropterus salmoides	largemouth bass	0	0.00	15	650	CEN
Lepomis auritus	redbreast sunfish	3	0.03	14	185	CEN
Lepomis macrochirus	bluegill sunfish	2	0.09	17	220	CEN

Table 3.2 Species captured during defaunation (29 June-7 July 2000) or in any of the post-defaunation samples (August 2000, October 2000, June 2001, October 2001) in Middle Creek, along with values for predictor variables not given in Table 3.1. PA = pre-defaunation abundance in colonization site (total number of fish caught during 3 electroshocking passes), MR = movement rate (mean number of fish moving through an upstream trap in Middle Creek that was checked daily between 26 May and 19 August 1999).

Scientific Name	PA	MR
Phoxinus oreas	204	1.84
Clinostomus funduloides	63	0.95
Rhinichthys atratulus	70	0.32
Nocomis leptocephalus	112	1.75
Thoburnia rhothoeca	38	0.51
Lepomis macrochirus	0	0.02

Table 3.3 Summary of regression models for the lower Dicks Creek colonization experiment. Fishes were removed during July 2000. The number of fish captured during August 2000 was the response variable in each analysis and there was one observation for each species captured during July or August (n=18). Abbreviations as follows: B′ = standardized partial regression coefficient and R^2 = adjusted coefficient of determination.

Model/Parameter	B′	P-value	R^2
Overall Model	NA	0.0003	0.61
Abundance	0.24	0.2623	0.14
Movement Rate	0.63	0.0049	0.47
Overall Model	NA	0.0043	0.45
Abundance	0.51	0.0242	0.29
Spatial Distribution	0.36	0.0946	0.16
Overall Model	NA	0.0097	0.39
Abundance	0.63	0.0060	0.34
Body Size	-0.23	0.2690	0.05
Overall Model	NA	0.0604	0.32
Abundance	0.55	0.0317	0.23
Cyprinidae	0.30	0.5964	NA
Catostomidae	-0.34	0.6065	NA
Centrarchidae	-0.18	0.8026	NA

Table 3.4 Summary of regression models for the lower Dicks Creek colonization experiment. Fishes were removed during July 2000. The number of fish captured during October 2000 was the response variable in each analysis and there was one observation for each species captured during July or October (n=19). Abbreviations as follows: B′ = standardized partial regression coefficient and R^2 = adjusted coefficient of determination.

Model/Parameter	B′	P-value	R^2
Overall Model	NA	0.0002	0.61
Abundance	0.37	0.0677	0.24
Movement Rate	0.52	0.0158	0.37
Overall Model	NA	0.0025	0.47
Abundance	0.61	0.0065	0.39
Spatial Distribution	0.19	0.3418	0.08
Overall Model	NA	0.0020	0.48
Abundance	0.70	0.0008	0.44
Body Size	-0.20	0.2471	0.04
Overall Model	NA	0.0037	0.55
Abundance	0.58	0.0037	0.35
Cyprinidae	0.34	0.4557	NA
Catostomidae	-0.55	0.3119	NA
Centrarchidae	-0.48	0.4084	NA

Table 3.5 Summary of regression models for the lower Dicks Creek colonization experiment. Fishes were removed during July 2000. The number of fish captured during June 2001 was the response variable in each analysis and there was one observation for each species captured during July 2000 or June 2001 (n=20). Abbreviations as follows: B′ = standardized partial regression coefficient and R^2 = adjusted coefficient of determination.

Model/Parameter	B′	P-value	R^2
Overall Model	NA	<0.0001	0.75
Abundance	0.27	0.0963	0.19
Movement Rate	0.68	0.0004	0.56
Overall Model	NA	0.0019	0.46
Abundance	0.68	0.0026	0.43
Spatial Distribution	0.08	0.7006	0.03
Overall Model	NA	0.0008	0.52
Abundance	0.68	0.0006	0.44
Body Size	-0.24	0.1601	0.08
Overall Model	NA	0.0035	0.53
Abundance	0.64	0.0017	0.39
Cyprinidae	0.72	0.1037	NA
Catostomidae	0.34	0.5298	NA
Centrarchidae	-0.01	0.9760	NA

Table 3.6. Summary of step-wise regression models for the Middle Creek colonization experiment. Fishes were removed during June 2000. The number of fish captured during August 2000, October 2000, and June 2001 were the response variables in each analysis and there was one observation for each species captured. Abbreviations as follows: B′ = standardized partial regression coefficient and R^2 = adjusted coefficient of determination.

Model	B′	Variable Selected	P-Value	R^2
August	2.97	Abundance	0.0009	0.98
October	0.84	Abundance	0.0358	0.63
June	0.74	Movement Rate	0.0341	0.64

Table 3.7 Estimates of recovery for fishes removed from the Middle Creek and lower Dicks Creek colonization sites between 29 June and 7 July 2000. The degree of colonization (DC) was measured as the proportion of pre-defaunation abundance restored at the specified time period (sensu Peterson and Bayley 1993); young of year were excluded from this calculation. The lower Dicks Creek site was not re-sampled during October 2001.

| | | 2000 | | 2001 | |
| | | August | Oct. | June | Oct. |
Species	Site	DC	DC	DC	DC
Phoxinus oreas	Middle	17%	21%	63%	68%
Phoxinus oreas	Dicks	68%	133%	100%	NA
Clinostomus funduloides	Middle	5%	16%	49%	43%
Rhinichthys atratulus	Middle	6%	26%	44%	56%
Rhinichthys atratulus	Dicks	0%	17%	17%	NA
Semotilus corporalis	Dicks	11%	25%	81%	NA
Nocomis leptocephalus	Middle	7%	15%	61%	103%
Nocomis leptocephalus	Dicks	11%	67%	119%	NA
Luxilus cornutus	Dicks	7%	46%	123%	NA
Thoburnia rhothoeca	Middle	3%	5%	8%	0%
Noturus insignis	Dicks	30%	60%	100%	NA
Cottus caeruleomentum	Dicks	20%	36%	108%	NA
Ambloplites rupestris	Dicks	0%	0%	43%	NA
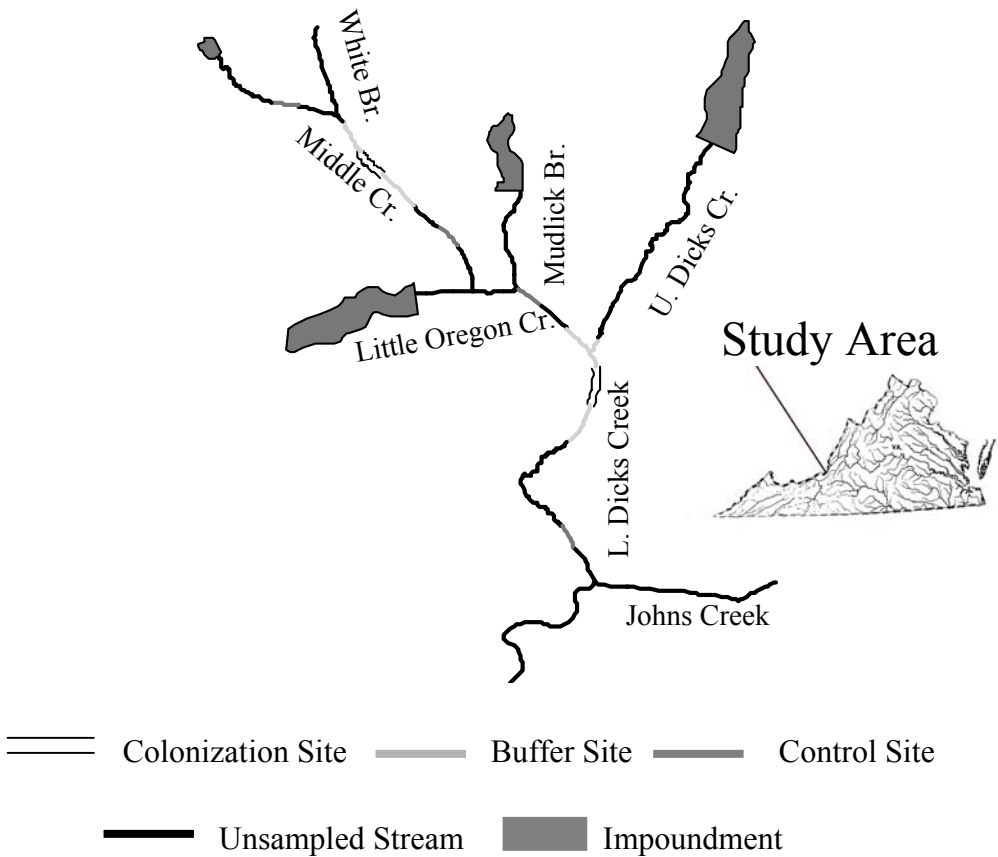
Figure 3.1 Network of streams in the James River drainage, Craig County, Virginia where the colonization experiment was conducted. Fishes were removed from colonization and buffer sites between 29 June and 7 July 2000. Colonization sites were re-sampled during August 2000, October 2000, June 2001, and October 2001 (Middle Creek site only). Control sites were sampled in association with defaunation and post-defaunation samples. Abbreviations are U. = upper, L. = lower, Cr. = Creek, and Br. = Branch.

Figure 3.2 Bedrock cascade in Middle Creek.
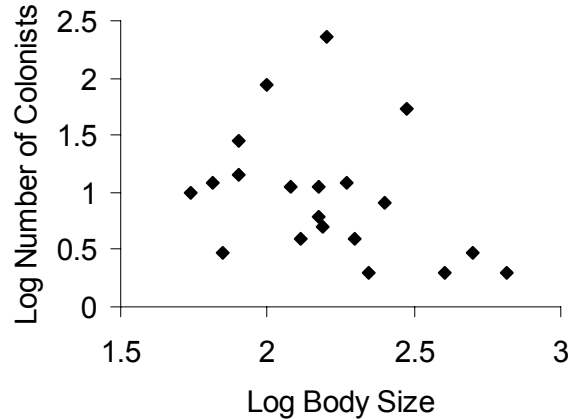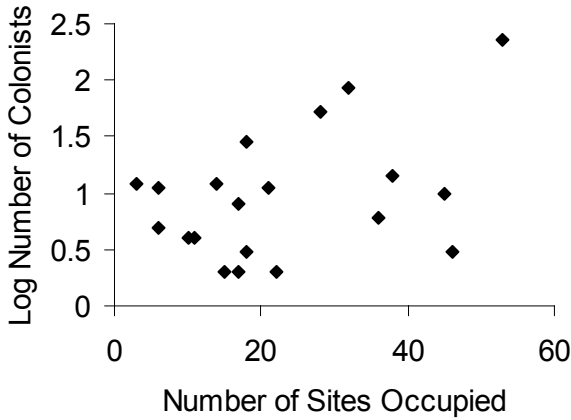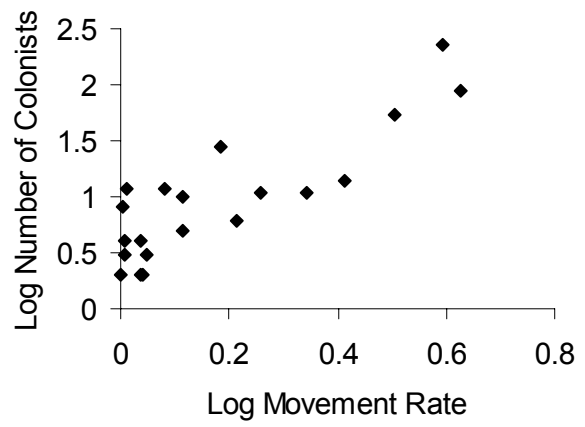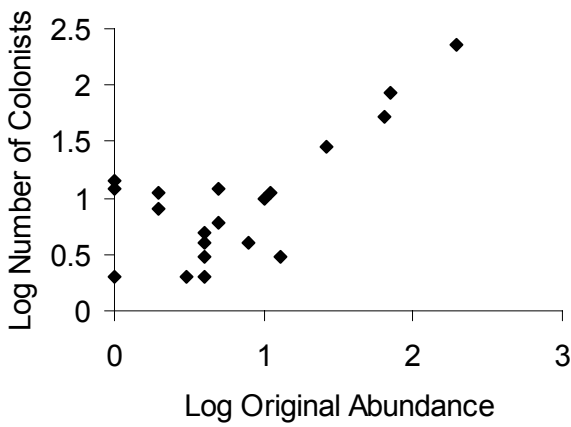
Figure 3.3 Bivariate relationships between the number of colonists in the lower Dicks Creek site during June 2001 and the quantitative predictor variables. Each point corresponds to a different species, which are listed in Table 3.1. Movement rate was the mean number of fish moving through an upstream trap that was checked daily between 26 May and 19 August 1999. Abundance was the total number of fish captured during 3 passes in the defaunation sample. The number of sites occupied was measured during a system-wide electrofishing survey in August 1999. Body size was the maximum standard length reported in the species accounts of Jenkins and Burkhead (1993). Abundance was correlated with movement rate and the number of sites occupied, emphasizing the importance of including abundance in each of the regression models. Other months are not shown, but patterns were similar.
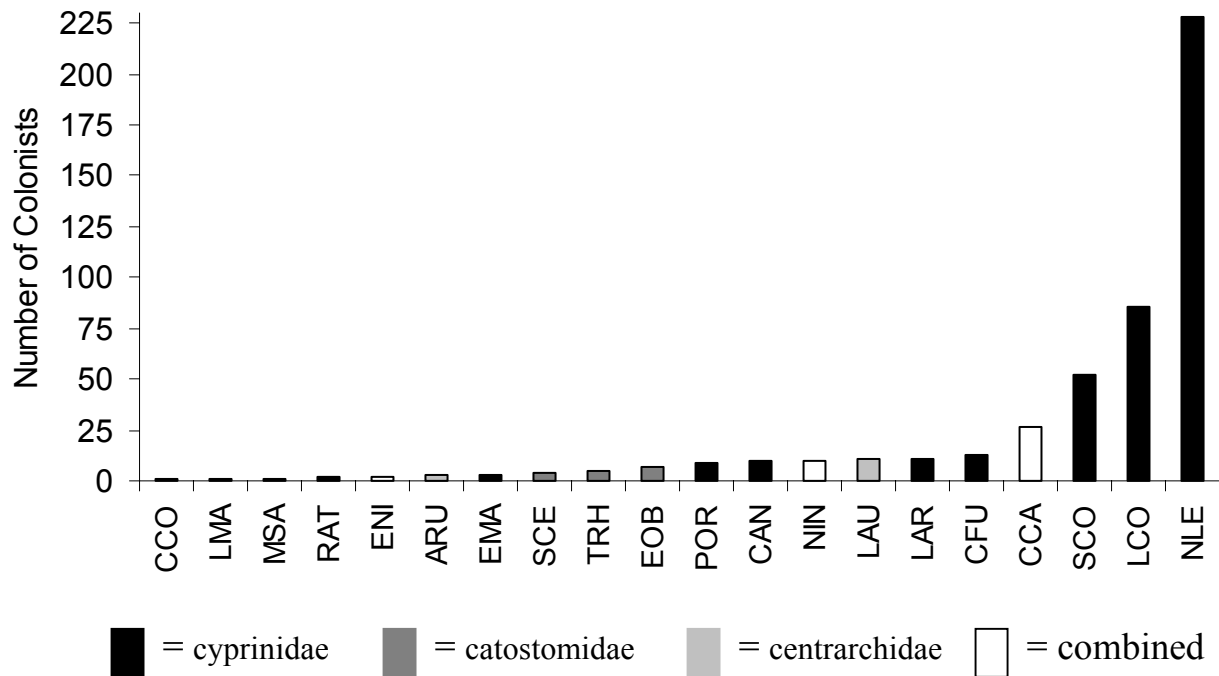
Figure 3.4 Number of fish colonizing the lower Dicks Creek site during June 2001, plotted by species and families. Patterns were similar in other months, but are not shown. Species are represented by the first letter of their genus and the first two letters of their species. The families Esocidae, Ictaluridae, and Cottidae were combined in the multiple regression analyses and are symbolized accordingly. See table 3.1 for full names of species.
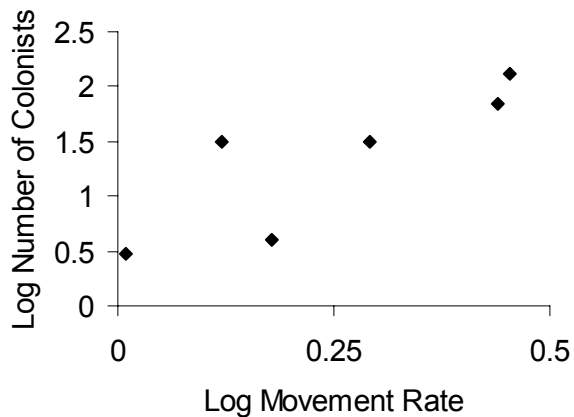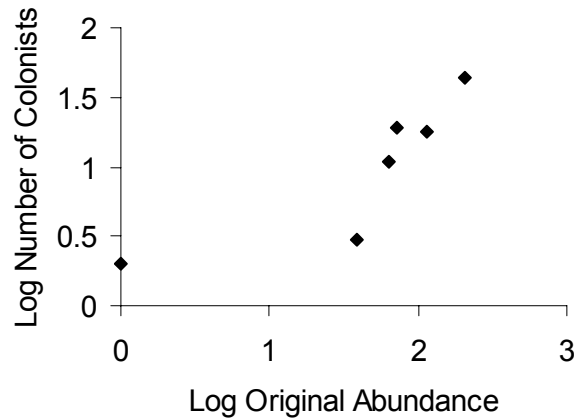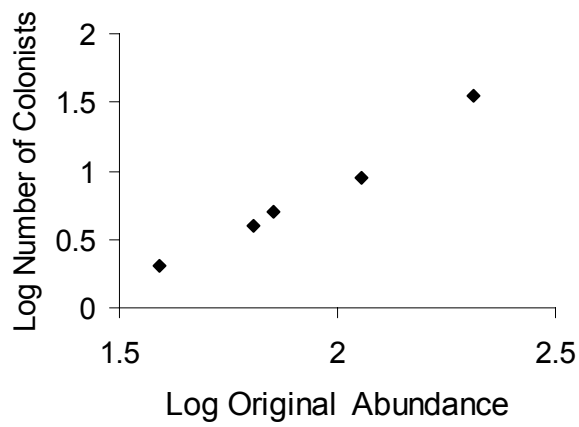
Figure 3.5 Significant relationships between the number of colonists captured in the Middle Creek site during August 2000 (top), October 2000 (middle), and June 2001 (bottom) and the quantitative predictor variables. Each point corresponds to a different species, which are listed in Table 3.2. Movement rate was the mean number of fish moving through an upstream trap that was checked daily between 26 May and 19 August 1999. Abundance was the total number of fish captured during 3 passes in the defaunation sample. No other predictors were selected by step-wise models in any month.
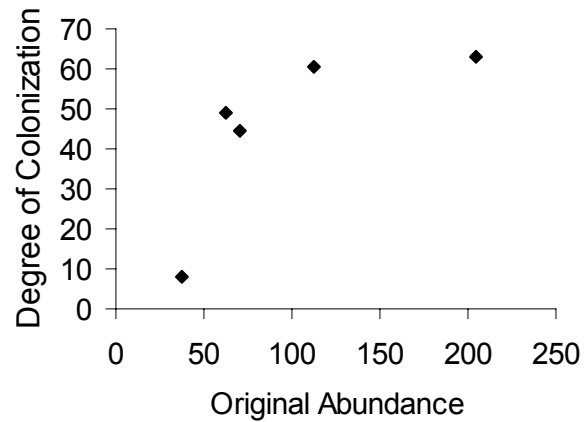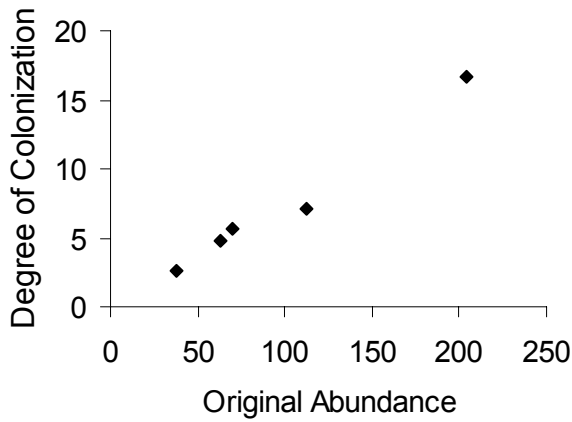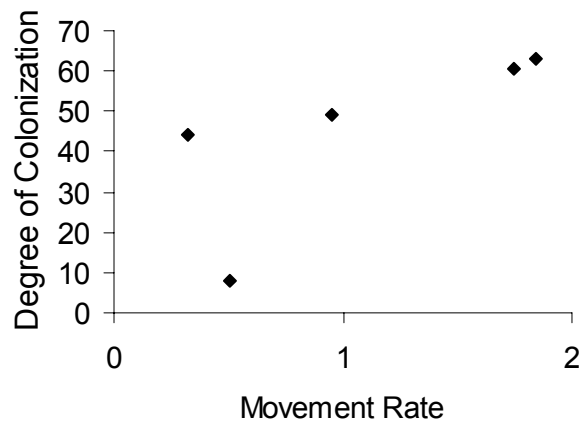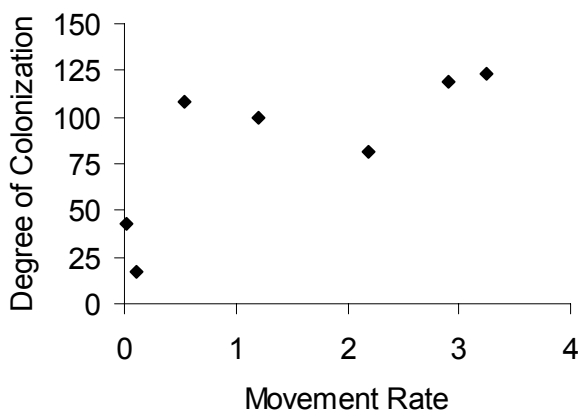
Figure 3.6 Significant relationships between the degree of colonization and movement rate for lower Dicks Creek fishes (top left) and Middle Creek fishes (top right) in June 2001 and between the degree of colonization and abundance of Middle Creek fishes during August 2000 (bottom left) and June 2001(bottom right). Each point corresponds to a different species, which are listed in Table 3.7. The degree of colonization was measured as the proportion of pre-defaunation abundance restored at the specified time period (sensu Peterson and Bayley 1993); young of year were excluded from this calculation. Movement rate was the mean number of fish moving through an upstream trap that was checked daily between 26 May and 19 August 1999. Abundance was the total number of fish captured during 3 passes in the defaunation sample. No other significant correlations were detected.
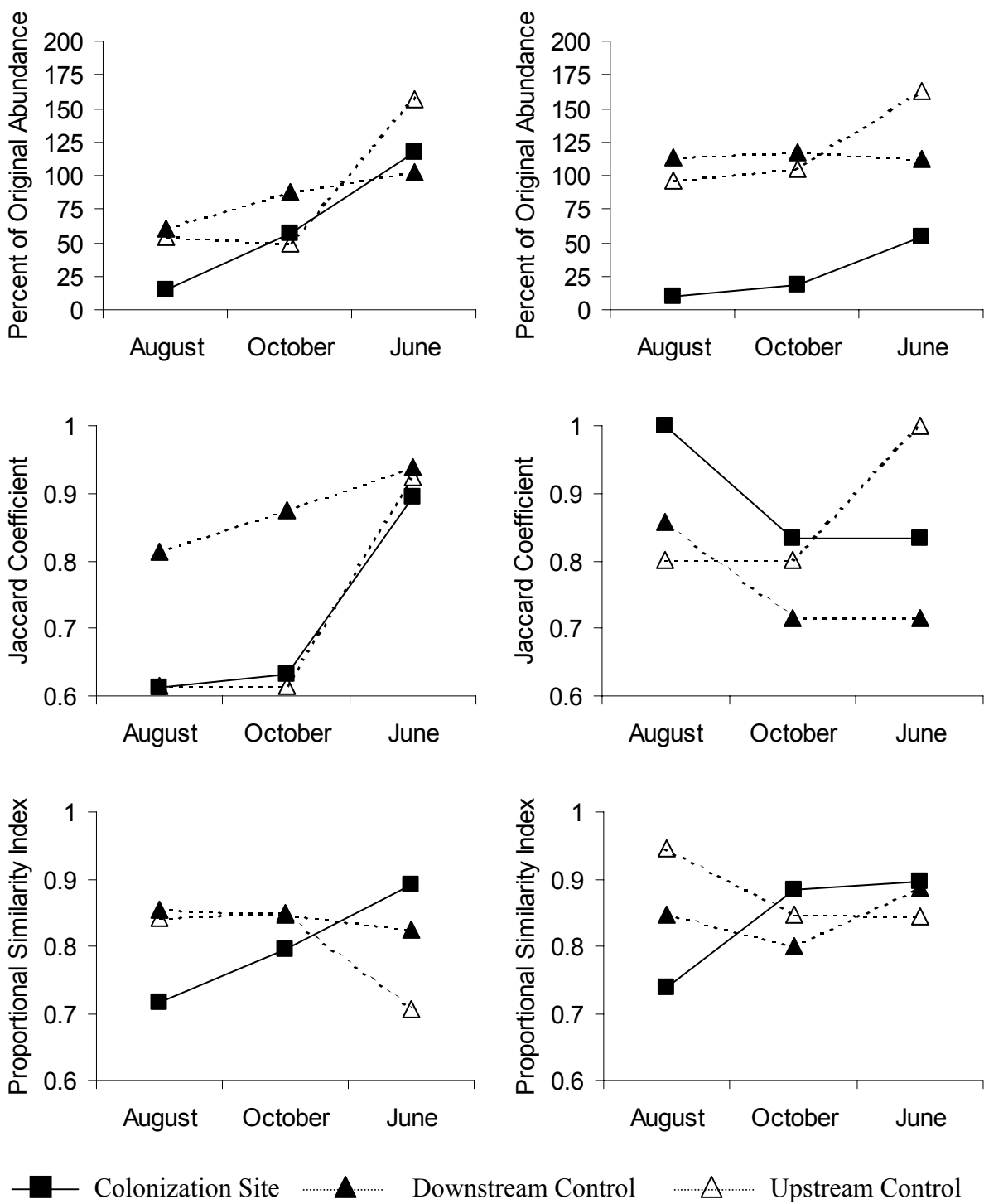
Figure 3.7 Percent of pre-defaunation abundance (top),Jaccard Coefficient (middle), and Proportional Similarity Index (bottom) values calculated to compare samples collected during defaunation (29 June-7 July 2000) and post-defaunation (dates indicated) sampling periods. Colonization and control sites are shown for Dicks Creek (left) and Middle Creek (right).
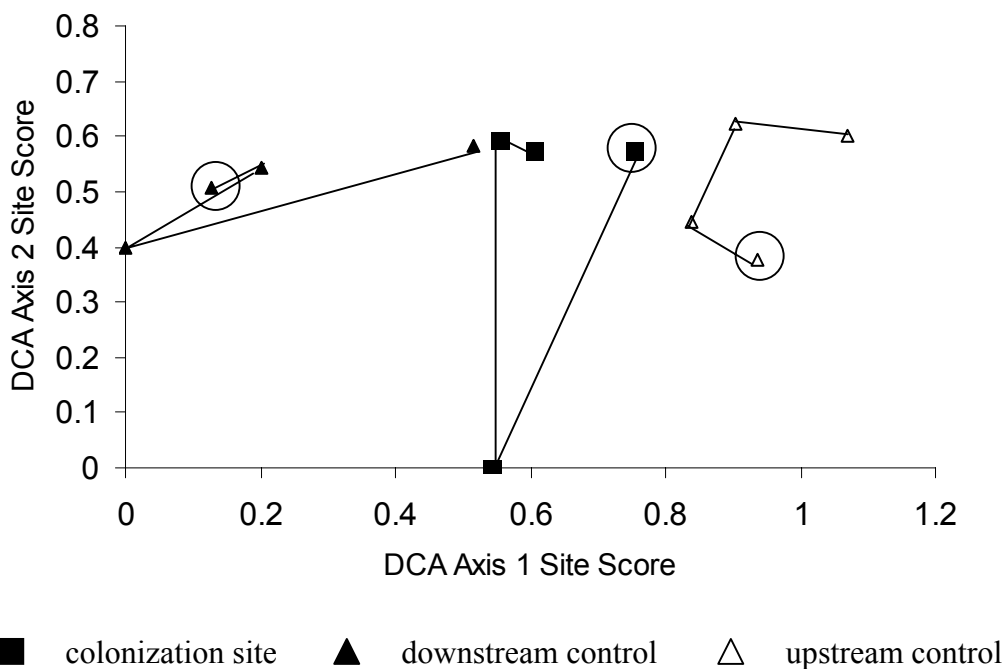
Figure 3.8 Detrended correspondence analysis (DCA) scores for control and colonization sites in lower Dicks Creek. Circles indicate the sample collected during the defaunation sampling period (July 2000) and lines connect subsequent samples collected in August 2000, October 2000 and June 2001.

Summary and Conclusions

CHAPTER 1

Mark-recapture studies sample unevenly over distance and generate biased or "distance-weighted" movement data, where short distances are sampled more frequently than long distances. The bias occurs because animals moving long distances can escape study areas, but few studies on unbounded stream-fish populations have acknowledged or attempted to mitigate for distance weighting. The objective of the first chapter was to evaluate how attributes of study design affect the degree of distance-weighted sampling and observed movement distributions of stream fish. This objective was addressed in two ways. First, I performed a simple modeling exercise to evaluate the degree to which alternative study designs sampled unevenly over distance. I then sub-sampled data from my own mark-recapture study to illustrate how attributes of study design affect observed movement distributions.

The modeling study indicated that the degree of distance-weighted sampling varies considerably with study design parameters that are typical of most mark-recapture studies on stream fish. Distance weighting increased as contiguous mark sites were added sequentially from the center of the recapture section toward recapture section boundaries. Extreme distance weighting occurred when all sites were selected for marking: the greatest effort was allocated to sampling movements of 0m and sampling effort declined with increasing distance. For a given number of mark sites, distance weighting was consistently lower when a longer section of stream was sampled during recapture. Finally, there was a zone of uniform sampling effort present in all but one of the designs. The length of this zone increased with recapture section length and decreased as additional mark sites were added.

Study design affected observed distributions for all three species in the mark-recapture study. Substantially longer maximum movements were detected for two species and median distances moved were longer for all three species when a longer section of stream was sampled during recapture. Correction factors could not accurately adjust for the distance weighting imposed by the shorter recapture section because adjustments could be made only to distances where movements were detected. Closing the recapture section to emigration indicated that a

substantial proportion of marked fish may escape study areas and go on to move relatively long distances.

This study suggests some general strategies that will reduce bias, increase recapture rates and enable detection of longer distances in future mark-recapture studies on stream fish. The ideal study would include: a limited number of centrally located mark sites, a long recapture section, and weirs that would estimate the number of fish moving distances outside of the primary recapture section. I also developed a procedure to estimate distance-weighting that can be used to evaluate bias and improve design before data are collected in future studies. While it is impossible to design a completely unbiased mark-recapture study in an open stream system, this procedure can be used to identify the zone of uniform sampling effort where distances can be estimated with minimal or no bias.

CHAPTER 2

Identifying ecological factors that drive dispersal-mediated processes (e.g., spawning, colonization) is a key step in predicting how fishes will respond to natural and anthropogenic changes in environmental conditions, but few studies have linked movement to ecological factors. The objective of the second chapter was to identify factors that were associated with the movement of fishes in a network of streams. I examined three attributes of movement for this objective: the probability of emigrating from a site between May and August, movement rates (measured as the number of fish moving upstream through a trap per day), and movement distances between May mark sites and August recapture sites. I assessed relationships between these attributes and suite of predictor variables related to site-specific characteristics, stream-wide environmental conditions, and characteristics of individual fish.

The probability of emigrating from a site was positively related to intermittency (1 of 4 species) and body size (1 of 4 species) and negatively related to distance from the mainstem creek (2 of 4 species) and habitat complexity (1 of 4 species). Movement rates were positively related to increases in flow (5 of 8 species), daylength (3 of 8 species), and water temperature (2 of 8 species). Distance moved was not related to individual-level attributes (size or growth), but was greater for fish that were initially marked in intermittent reaches.

The three attributes of movement measured in this study provided a more complete picture of dispersal than any single attribute could; future studies should also investigate multiple

attributes of movement. Examining all three attributes suggested that *N. leptocephalus* was adapted to exploit intermittent and perennial streams. This species exhibited high densities within intermittent sites during May and then emigrated to perennial reaches during late spring and summer. Fish reproduced in intermittent and perennial reaches and temperature may have triggered movement to spawning habitats. This species also moved in association with flow events, which may allow them to escape sections of intermittent streams that are isolated during low flow periods or invade habitats that are only accessible during high flows.

This study revealed that movement by stream fishes is complex, which has important implications for conservation. Interspecific variation in the number of correlates of movement suggests that species that move in association with multiple correlates will be better colonists than species that do not. Variation in ecological correlates among stream types may result in differences in colonization ability for a given species. To better understand impacts on fish populations, future studies should compare movement attributes among streams subjected to different anthropogenic disturbances.

<center>CHAPTER 3</center>

Colonization is an extremely important process that regulates the persistence of populations. Accordingly, interspecific variation in colonization rates may translate into variation in extinction risk, particularly where humans increase the frequency of local extirpations. The objective of the third chapter was to identify species-level attributes that were associated with colonization rates after experimental defaunation. I predicted that movement rate, measured as average the number of fish moving upstream through a trap per day, would be a primary determinant of colonization rates when compared to competing alternatives (abundance, spatial distribution, body size, and family). I also predicted that species with higher movement rates would recover populations before species with lower movement rates and that post-defaunation assemblages would be dominated by species with high movement rates.

Fishes were removed from a 426-m-long site in Middle Creek (tributary) and a 416-m-long site in lower Dicks Creek (mainstem) between 29 June and 7 July 2000 using multiple pass electrofishing. Both sites were re-sampled during electrofishing surveys conducted 1 month, 3 months, and 12 months after defaunation. Because of slow recovery, the Middle Creek site was

also sampled after 15 months. The number of fish colonizing each site was determined for each species and used as the response variable in regression models that tested for relationships with each of the competing predictor variables. Abundance was included in each model to ensure that it did not confound relationships with the other regressors.   The number of colonists was then compared to the number of fish in the site before defaunation to assess species-level recovery patterns. Finally, the effect of defaunation on assemblage structure was determined by comparing abundance, species composition, and relative abundance patterns between original and post-defaunation samples. To control for seasonal variation in fish assemblage attributes, patterns were interpreted relative to temporal changes in control sites.

Movement rate explained the largest amount of interspecific variation in colonization rates during each phase of the recovery process in lower Dicks Creek. Movement rate also explained a large proportion of variance in colonization rates in Middle Creek 12 months after defaunation. Abundance was also positively associated with colonization and explained a substantial proportion of variance in colonization rates in both streams. Spatial distribution, body size, and family-level variables were never significant and rarely explained much variation in colonization rates.

Movement rate and abundance were also positively associated with recovery. Recovery occurred more slowly in Middle Creek, but there was substantial interspecific variation in recovery rates in both streams. In contrast to studies that have documented rapid recovery of fish populations, several species had not restored more than half of their pre-defaunation abundance within a year. The recovery pattern for one species best illustrates the population-level implications of variation in recovery rates: *T. rhothoeca* had not restored more than 8% of its pre-defaunation abundance within 15 months.

Defaunation affected some attributes of fish assemblages in both sites. The total number of fishes was clearly reduced in both sites one month after defaunation and this effect persisted in Middle Creek for at least 15 months. Several species were missing from the lower Dicks Creek site one to three months after defaunation, but all species that were originally present in the site had colonized within 12 months. Jaccard coefficients indicated similar species composition between pre and all post-defaunation samples in Middle Creek, but *T. rhothoeca* was absent from the sample collected 15 months after defaunation. Defaunation had only a slight and short-term

(i.e., < 3 months) effect on relative abundance patterns in both sites, indicating that assemblages did not become dominated by species with high movement rates.

This study documented substantial variation in colonization rates that was associated with movement rate and abundance. Recovery of population size was also associated with these factors. Accordingly, species that are rare and less-mobile will recover their populations slowly and be vulnerable to extirpation in systems impacted by frequent pulse disturbances. Conservation implications for rare and non-mobile species are not trivial given the strong effects of a relatively small disturbance (426-m defaunation site) on *T. rhothoeca* and the fact that larger pulse disturbances still occur regularly despite efforts to prevent them. The significance of interspecific variation in colonization rates has been under-appreciated because of the widely documented resiliency of stream-fish assemblages. This study indicated that resiliency at the assemblage-level does not always correspond to resiliency of component species and future studies must consider assemblage level properties along with trends of individual species.

Literature Cited

Abell, R.A., and 10 others. 2000. Freshwater ecoregions of North America: a conservation assessment. Island Press, Washington, D.C.

Adams, S.B., C.A. Frissel, and B.E. Reiman. 2000. Movements of nonnative brook trout in relation to stream channel slope. Trans. Am. Fish. Soc. 129: 623-638.

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley & Sons, Inc., New York.

Angermeier, P.L. 1995. Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. Conserv. Biol. 9: 143-158.

Angermeier, P.L., K.L. Krueger, and C.A. Dolloff. 2001. Discontinuity of stream-fish distributions: implications for assessing and predicting species occurrence, p. 519-529 *In:* Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California.

Angermeier, P.L., and I.J. Schlosser. 1989. Species-area relationships for stream fishes. Ecology 70: 1450-1462.

Angermeier, P.L., and M.R. Winston. 1997. Assessing conservation value of stream communities: a comparison of approaches based on centres of density and species richness. Freshwater Biol. 37: 699-710.

Aparicio, E., and A. de Sostoa. 1999. Pattern of movements of adult *Barbus haasi* in a small Mediterranean stream. J. Fish. Biol. 55: 1086-1095.

Baker, M., N. Nur, and G.R. Geupel. 1995. Correcting biased estimates of dispersal and survival due to limited study area: theory and application using wrentits. Condor 97: 663-674.

Barrowclough, G.F. 1978. Sampling bias in dispersal studies based on finite area. Bird-Banding 49: 333-341.

Bayley, P.B., and L.L. Osborne. 1993. Natural rehabilitation of stream fish populations in an Illinois catchment. Freshwater. Biol. 29: 295-300.

Berra, T.M., and G.E. Gunning. 1970. Repopulation of experimentally decimated sections of streams by longear sunfish, *Lepomis megalotis*. Trans. Am. Fish. Soc. 99: 776-781.

Brower, J.E., J.H. Zar, and C. N. vonEnde. 1990. Field and laboratory methods for general ecology. 3rd ed. Wm. C. Brown Publishers, Dubuque, Indiana.

Brown, J.H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449.

Burnham, K.P., and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Busacker, G.P., I.R. Adelman, and E.M. Goolish. 1990. Growth, p. 363-387 *In*: Methods for fish biology. C.B. Shreck and P.B. Moyle (eds.). American Fisheries Society, Bethesda, MD.

Carroll, S.S., and D.L. Pearson. 2000. Detecting and modeling spatial and temporal dependence in conservation biology. Conserv. Biol. 14: 1893-1897.

Chapman, L.J., and D.L. Kramer. 1991. The consequences of flooding for the dispersal and fate of a poeciliid fish in an intermittent tropical stream. Oecologia 87: 299-306.

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

Dodson, J.J., and J. C. Young. 1977. Temperature and photoperiod regulation of rheotropic behavior in prespawning common shiners, *Notropis cornutus*. J. Fish. Res. Board. Can. 34: 341-346.

Dunham, J.B., and B.E. Reiman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecol. Applic 9: 642-655.

Ensign, W.E., K.N. Leftwich, P.L. Angermeier, and C.A. Dolloff. 1997. Factors influencing stream-fish recovery following a large-scale disturbance. Trans. Am. Fish. Soc. 126: 895-907.

Etnier, D.A. 1997. Jeopardized southeastern freshwater fishes: a search for causes, p.87-92. *In*: Aquatic fauna in peril: the southeastern perspective. G.W. Benz and D.E. Collins (eds.). Lenz Design and Communications, Decatur, Georgia.

Fausch, K.D., and R.G. Bramblett. 1991. Disturbance and fish communities in intermittent tributaries of a western Great Plains river. Copeia 1991: 659-674.

Fausch, K.D., and M.K. Young. 1995. Evolutionary significant units and movement of resident stream fishes: a cautionary tale, p. 360-370. *In*: Evolution and the aquatic ecosystem: defining unique units in population conservation. J. L. Nielsen (ed). American Fisheries Society Symposium 17, Bethesda, Maryland.

Foppen, R.P.B., J.P. Chardon, and W. Liefveld. 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. Cons. Biol. 14: 1881-1892.

Fraser, D.F., J.F. Gilliam, M.P. MacGowan, C. M. Arcaro, and P.H. Guillozet. 1999. Habitat quality in a hostile river corridor. Ecology 80: 597-607.

Fraser, D.F., J.F. Gilliam, and T. Yip-Hoi. 1995. Predation as an agent of population fragmentation in a tropical watershed. Ecology 76: 1461-1472.

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

Frissell, C.A. 1997. Ecological principles, p. 96-115. *In*: Watershed restoration: principles and practices. J.E. Williams, C.A. Wood, and M.P. Dombeck (eds.). American Fisheries Society, Bethesda, Maryland.

Funk, J.L. 1957. Movement of stream fishes in Missouri. Trans. Am. Fish. Soc. 85: 39-57.

Fuselier, L., and D. Edds. 1994. Seasonal variation in habitat use by the Neosho madtom. Southwestern Nat. 39: 217-223.

Gagen, C.J., R.W. Standage, and J.N. Stoeckel. 1998. Ouachita madtom (*Noturus lachneri*) metapopulation dynamics in intermittent Ouachita mountain streams. Copeia 1998: 874-882.

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

Gelwick, F.P., and W.J. Matthews. 1992. Effects of an algivorous minnow on temperate stream ecosystem properties. Ecology 73: 1630-1645.

Gerking, S.D. 1959. The restricted movement of fish populations. Biol. Rev.34: 221-242.

Gido, K.B., and W.J. Matthews. 2000. Dynamics of the offshore fish assemblage in a
southwestern reservoir (Lake Texoma, Oklahoma-Texas). Copeia 2000: 917-930.

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

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

Gordon, N.D., T.A. McMahon, and B.L. Finlayson. 1992. Stream hydrology: an introduction
for ecologists. John Wiley & Sons, Chichester, England.

Gorman, O.T. 1986. Assemblage organization of stream fishes: the effect of rivers on
adventitious streams. Am. Nat. 128: 611-616.

Gotelli, N.J., and C.M. Taylor. 1999A. Testing macroecology models with stream-fish
assemblages. Evol. Ecol. Res. 847-858.

Gotelli, N.J., and C.M. Taylor. 1999B. Testing metapopulation models with stream-fish
assemblages. Evol. Ecol. Res. 835-845.

Gowan, C., and K.D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado streams:
re-evaluating the concept of restricted movement. Can. J. Fish. Aquat. Sci.53: 1370-
1381.

Gowan, C., M.K. Young, K.D. Fausch, and S.C. Riley. 1994. Restricted movement in resident
stream salmonids: a paradigm lost ? Can. J. Fish. Aquat. Sci. 51: 2626-2637.

Grant, G.C., and P.E. Maslin. 1999. Movements and reproduction of hardhead and Sacramento
squawfish in a small California stream. Southwest. Nat. 44: 296-310.

Griswold, B.L., C.J. Edwards, and L.C. Woods. III. 1982. Recolonization of macroinvertebrates and fish in a channelized stream after drought. Ohio J. Sci. 82: 96-102.

Gunning, G.E., and T.M. Berra. 1969. Fish repopulation of experimentally decimated segments in the headwaters of two streams. Tran. Am. Fish. Soc. 98: 305-308.

Haas, C.A. 1995. Dispersal and use of corridors in wooded patches on an agricultural landscape. Conservation Biology 9: 845-854.

Hackney, C.T., S.Marshall, and W.H. Martin. 1992. Biodiversity of the southeastern United States: aquatic communities. John Wiley and Sons, Inc., New York.

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

Hanski, I., and M. Gilpin 1991. Metapopulation dynamics: brief history and conceptual domain. Biol. J. Linn. Soc. 42: 3-16.

Hansson, L. 1991. Disperal and connectivity in metapopulations. Biol. J. Linn. Soc. 42: 89-103.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biol. J. Linn. Soc. 42: 73-88.

Harvey, B.C. 1998. Influence of large woody debris on retention, immigration, and growth of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in stream pools. Can. J. Fish. Aquat. Sci. 55: 1902-1908.

Harvey, B.C., R.J. Nakamoto, and J.L. White. 1999. Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (*Oncorhynchus clarki clarki*) during fall and winter. Can. J. Fish. Aquat. Sci. 56: 2161-2166.

Heggenes, J., T.G. Northcote, and A. Peter. 1991. Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Can. J. Fish. Aquat. Sci. 48: 757-762.

Helfman, G.S., B.B. Collette, and D.E. Facey. 1997. The diversity of fishes. Blackwell Science, Malden, Massachusetts.

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

Hughes, N.F. 1998. Use of whole-stream patterns of age segregation to infer the interannual movements of stream salmonids: a demonstration with artic grayling in an interior Alaskan stream. Trans. Am. Fish. Soc. 127: 1067-1071.

Hughes, N.F. 2000. Testing the ability of habitat selection theory to predict interannual movement patterns of a drift-feeding salmonid. Ecol. Fresh. Fish 9: 4-8.

Jenkins, R.E., and N.M. Burkhead. 1993. Freshwater Fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Johnson, D.E. 1998. Applied multivariate methods for data analysis. Duxbury Press, Pacific Grove, California.

Johnston, C.E., and E.B. Smithson. 1999. Retention of passive integrated transponder (PIT) tags for individual identification of warmwater fishes. Proceedings of the Southeastern Fishes Council 38: 1-4.

Jones, J.W., R.J. Neves, M.A. Patterson, C.R. Good, and A. DiVittorio. 2001. A status survey of freshwater mussel populations in the upper Clinch River, Tazwell County, Virginia. Banisteria 17: 20-30.

Kinziger, A.P., R.L. Raesly, and D. A. Neely. 2000. New species of *Cottus* from the middle
Atlantic eastern United States. Copeia 2000: 1007-1018.

Koenig, W.D., D. Van Vuren, and P.N. Hooge. 1996. Detectability, philopatry, and the
distribution of dispersal distances in vertebrates. TREE 11: 514-517.

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

Lambert, D.L. 1992. Zero-inflated Poisson regression, with an application to defects in
manufacturing. Technometrics 34: 1-14.

Larimore, R.W., W.F. Childers, and C. Heckrotte. 1959. Destruction and re-establishment of
stream fish and invertebrates affected by drought. Trans. Am. Fish. Soc. 88: 261-285.

Lewis, M.A. 1997. Variability, patchiness, and jump dispersal in the spread of an invading
population, p 46-69 *In*: The role of space in population dynamics and interspecific
interactions. D. Tilman and P. Kareiva (eds.). Princeton University Press, Princeton,
New Jersey.

Licht, M.H. 1995. Multiple regression and correlation, p. 19-64. *In*: Reading and understanding
multivariate statistics. L.G. Grimm and P.R. Yarnold (eds.). American Psychological
Association, Washington, D.C.

Linfield, R.S.J. 1985. An alternative concept to home range theory with respect to populations
of cyprinids in major river systems. J. Fish. Biol. 27: 187-196.

Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1999. SAS system for mixed
models. SAS Institute Inc., Cary, North Carolina.

Lonzarich, D.G., M.R. Lonzarich, and M.L. Warren, Jr. 2000. Effects of riffle length on the short-term movement of fishes among stream pools. Can. J. Fish. Aquat. Sci. 57: 1508-1514.

Matheny, M.P., IV, and C.F. Rabeni. 1995. Patterns of movement and habitat use by northern hogsuckers in an Ozark stream. Trans. Am. Fish. Soc. 124: 886-897.

Matthews, W.J. 1986. Fish faunal structure in an Ozark stream: stability, persistence, and a catastrophic flood. Copeia 1986: 388-397.

Matthews, W.J. 1998. Patterns in freshwater fish ecology. Kluwer Academic Publishers, Norwell, Massachusetts.

Matthysen, E., F. Adriaensen, and A.A. Dhondt. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. Oikos 72: 375-381.

Means, M. L., and J. E. Johnson. 1995. Movement of threatened Ozark cavefish in Logan Cave National Wildlife Refuge, Arkansas. Southwest. Nat. 40: 308-313.

Meffe, G.K., and A. L. Sheldon. 1990. Post-defaunation recovery of fish assemblages in southeastern blackwater streams. Ecology 71: 657-667.

Minns, C.K. 1995. Allometry of home range size in lake and river fishes. Can. J. Fish. Aquat. Sci. 52:1499-1508.

Mundahl, N.D., and C.G. Ingersoll. 1989. Home range, movements, and density of the central stoneroller, *Campostoma anomalum*, in a small Ohio stream. Environ. Biol. Fish 24: 307-311.

Nichols, J.D., T. Boulinier, J. E. Hines, K.H. Pollock, and J. R. Sauer. 1998. Estimating rates of local species extinction, colonization, and turnover in animal communities. Ecol. Applic. 8: 1213-1225.

Niemi, G.J., P. Devore, N. Detenbeck, D. Taylor, A. Lima, J. Pastor, J.D. Yount, and R. J. Naiman. 1990. Overview of case studies on recovery of aquatic systems from disturbance. Envir. Mgmt 14: 571-587.

Olmsted, L.L., and D.G. Cloutman. 1974. Repopulation after a fish kill in Mud Creek, Washington County, Arkansas, following pesticide pollution. Trans. Am. Fish. Soc. 1: 79-87.

Osborne, L.L., and M.J. Wiley.   1992. Influence of tributary spatial position on the structure of warmwater fish communities. Can. J. Fish. Aquat. Sci. 49: 671-681.

Palmer, M.W. 1993. Putting things in better order: the advantages of canonical correspondence analysis. Ecology 74: 2215-2230.

Peterson, J.T., and P.B. Bayley. 1993. Colonization rates of fishes in experimentally defaunated warmwater streams. Trans. Am. Fish. Soc. 122: 199-207.

Poff, N.L., and J.V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Can. J. Fish. Aquat. Sci. 46: 1805-1818.

Poff, N.L., P.L. Angermeier, S.D. Cooper, P.S. Lake, K.D. Fausch, K.O. Winemiller, L.A.K. Mertes, M.W. Oswood, J. Reynolds, and F.J. Rahel. 2001. Fish diversity in streams and rivers, p. 315-349 *In:* Global biodiversity in a changing environment: scenarios for the 21st century. F.S. Chapin III, O.E. Sala, and E. Huber-Sannwald (eds.). Springer-Verlag, New York.

Porter, J.H. 1988. Mice in motion: dispersal in two species of *Peromyscus*. Dissertation. University of Virginia, Charlottesville, Virginia, USA.

Porter, J.H., and J.L. Dooley, Jr. 1993. Animal dispersal patterns: a reassessment of simple mathematical models. Ecology 74: 2436-2443.

Power, M.E. 1988. Effects of fish in river food webs. Science 250: 811-814.

Puth, L.M., and K. A. Wilson. 2001. Boundaries and corridors as a continuum of ecological flow control: lessons from rivers and streams. Cons. Biol. 15: 21-30.

Railsback, S.F., R.H. Lamberson, B.C. Harvey, and W.E. Duffy. 1999. Movement rules for individual-based models of stream fish. Ecol. Model 123: 73-89.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.

Robison, H.W., and T.M. Buchanan. 1988. Fishes of Arkansas. The University of Arkansas Press, Fayetteville.

Ross, S.T., and J.A. Baker. 1983. The response of fishes to periodic spring floods in a southeastern stream. Am. Mid. Nat. 109: 1-14.

Schaefer, J. 2001. Riffles as barriers to interpool movement by three cyprinids (*Notropis boops, Campostoma anomalum* and *Cyprinella venusta*). Freshwater Biol. 46: 379-388.

Schlosser, I.J. 1990. Environmental variation, life history attributes, and community structure in stream fishes: implications for environmental management and assessment. Environ. Mgmt. 14: 621-628.

Schlosser, I.J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. Ecology 76: 908-925.

Schlosser, I.J., and P.L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation, p. 392-401. *In*: Evolution and the aquatic ecosystem: defining unique units in population conservation. J. L. Nielsen (ed). American Fisheries Society Symposium 17, Bethesda, Maryland.

Scott, M.C. and G.S. Helfman. 1997. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26 (11): 6-15.

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

Shute, P.W., R.G. Biggins, and R.S. Butler. 1997. Management and conservation of rare aquatic resources: a historical perspective and recommendations for incorporating ecosystem management, p. 445-466 *In*: Aquatic fauna in peril: the southeastern perspective. G.W. Benz and D.E. Collins (eds.). Lenz Design and Communications, Decatur, Georgia.

Simonson, T.D., J. Lyons, and P.D. Kanehl. 1994. Quantifying fish habitat in streams: transect spacing, sample size, and a proposed framework. N. Am. J. Fish. Manage. 14: 607-615.

Simpkins, D.G., Hubert, W.A., and Wesche, T.A. 2000. Effects of fall-to-winter changes in habitat and frazil ice on the movements and habitat use of juvenile rainbow trout in a Wyoming tailwater. Trans. Am. Fish. Soc. 129:101-118

Singer, F.J., L.C. Zeigenfuss, and L. Spicer. 2001. Role of patch size, disease, and movement in rapid extinction of bighorn sheep. Cons. Biol. 15: 1347-1354.

Skalski, G.T., and J.F. Gilliam 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. Ecology 81: 1685-1700.

Smithson, E.B., and C.E. Johnston 1999. Movement patterns of stream fishes in a Ouachita
Highlands stream: an examination of the restricted movement paradigm. Trans. Am. Fish.
Soc. 128: 847-853.

Snodgrass, J.W., A.L. Bryan Jr., R.F. Lide, and G.M. Smith. 1996. Factors affecting the
occurrence and structure of fish assemblages in isolated wetlands of the upper coastal
plain, U.S.A. Can. J. Fish. Aquat. Sci. 53: 443-454.

Sokal, R.R., and F.J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological
research. 3rd ed. W.H. Freeman and Company, New York.

Stenseth, N.C., and W.Z. Lidicker. 1992. Where do we stand methodologically about
experimental design and methods of analysis in the study of dispersal?, p. 295-318 *In:*
Animal dispersal: small mammals as a model. N. C. Stenseth and W. Z. Lidicker (eds.).
Chapman and Hall, London.

Stewart-Oaten, A., W.M. Murdoch, and K.R. Parker. 1986. Environmental impact assessment:
"pseudoreplication in time? Ecology 67: 929-940.

Stiassny, M.L. 1996.   An overview of freshwater biodiversity: with some lessons from African
fishes. Fisheries 21 (9): 7-13.

Taylor, C.M., and M.L. Warren. 2001. Dynamics in species composition of stream-fish
assemblages: environmental variability and nested subsets. Ecology 82: 2320-2330.

Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species.
BioScience 24: 715-722.

Thomas, C.D. 1994. Extinction, colonization, and metapopulations: environmental tracking by
rare species. Conservation Biology 8: 373-378.

Tyus, H.M., C.W. Brown, and J.F. Saunders, III. 2000. Movements of young Colorado
pikeminnow and razorback sucker in response to water flow and light level. J. Freshwater
Ecol. 15: 525-535.

United States Naval Observatory. 2000. Available online at http://www.usno.navy.mil/.

Van Deventer, J.S., and W.S. Platts. 1985. A computer software program for entering,
managing, and analyzing fish capture data from streams. USDA Forest Service Research
Note INT –352. Intermountain Research Station, Ogden, Utah. 12pp.

Warren, M.L., Jr., P.L. Angermeier, B.M. Burr, and W.R. Haag. 1997. Declines of a diverse fish
fauna: patterns of imperilment and protection in the southeastern United States, p 105-
164 *In*: Aquatic fauna in peril: the southeastern perspective. G.W. Benz and D.E. Collins
(eds.). Lenz Design and Communications, Decatur, Georgia.

Warren, M.L., and M.G. Pardew. 1998. Road crossings as barriers to small-stream fish
movement. Trans. Am. Fish. Soc. 127: 637-644.

Warren, M.L., and 11 others. 2000. Diversity, distribution, and conservation status of the native
freshwater fishes of the southern United States. Fisheries 25(10): 7-31.

Wiens, J.A. 1996. Wildlife in patchy environments: metapopulations, mosaics, and
management, p. 53-84 *In*: Metapopulations and wildlife conservation. D.R. McCullough
(ed.). Island Press, Washington, D.C.

Winker, K., J.H. Rappole, and M.A. Ramos. 1995. The use of movement data as an assay of
habitat quality. Oecologia 101: 211-216.

Winston, M.R., C.M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species
due to damming of a prairie stream. Trans. Am. Fish. Soc. 120: 98-105.

Wright, R.E. 1995. Logistic regression, p. 217-244 *In*: Reading and understanding multivariate statistics. L.G. Grimm and P.R. Yarnold (eds.). American Psychological Association, Washington, D.C.

Zeng, Z, and J.H. Brown. 1987. A method for distinguishing dispersal from death in mark-recapture studies. J. Mamm. 68: 656-665.

Appendix A. Evaluation of marking techniques for small stream fishes.

Adequate marking techniques are critical for movement studies on stream fish. The purpose of this appendix is to evaluate the alternative marking techniques that were applied to the focal species in this study. This information may be very useful to other investigators because these techniques have seldom been applied to small stream fishes.

Materials and Methods

I conducted several experiments and examined data from the mark-recapture study (Chapter 1 and Chapter 2) to evaluate the different marking techniques used throughout the study. Laboratory experiments were conducted within 568-L artificial streams (Frigid Units, Inc.) housed at Virginia Tech. All laboratory held fishes were fed a variety of foods, including flakes, tablets, frozen brine shrimp and frozen bloodworms.

Passive Integrated Transponder (PIT) tag laboratory experiment.— The first experiment evaluated the effect of PIT (Biomark, Inc.) tagging on the survival and growth of *Nocomis leptocephalus* (bluehead chub). Fish were collected by seine from the South Fork Roanoke River on 23 December 1997 and stocked into an artificial stream. To create conditions more suitable for growth, water temperature was gradually raised from 4C to 16 C before the experiment began on 5 March 1998 and was held at 18 C after that. Photoperiod was held at 11L:13D until 24 March, gradually raised to 12.5L:11.5D by 23 April, and maintained at 12.5L:11.5D until the experiment ended on 1 May 1998.

A randomization procedure was used to ensure that a similar number of similar sized fish were assigned to treatment (PIT) and control (No PIT) groups. Fish were first sorted into three size groups (ca. 75-90mm total length (TL), 91-115 mm TL, and > 115mm TL) and placed into separate buckets. The first fish netted from the "small" bucket was randomly assigned to one of the treatments; the next fish netted from this same bucket was assigned to the opposite treatment.

Treatments alternated among successively captured fish within each bucket until all fish from each of the size groups were selected for the experiment.

Twenty-one (TL = 78-179 mm, mean = 111.2) and 20 (TL = 79-196 mm, mean = 110.5) fish were assigned to the treatment and control groups, respectively. All fish were anesthetized with tricaine methanesulfonate (MS222), blotted on a paper towel to remove excess water, weighed to the nearest 0.01 g with an Ohaus top-loading balance, and measured to the nearest mm TL. To prevent PIT tag weights from influencing subsequent growth measurements, treatment fish were injected with PIT tags before they were weighed. Twelve-mm PIT tags were injected into the abdominal cavities of treatment fish using a 10-cc syringe fitted with a 12-gauge needle. All fish were given elastomer tags (Northwest Marine Technology, Inc., see below) to identify individuals in the control group and facilitate recognition of any treatment fish that lost PIT tags. All fish were returned to the same artificial stream and were weighed and measured 14 and 57 days after marking. Artificial streams were inspected daily for the presence of dead fish.

Relative growth in length and weight were calculated for each fish using the formula from Busacker et al. (1990)

$$\text{Relative Growth} = Y_2 - Y_1 / Y_1$$

where Y_1 and Y_2 refer to length or weight measurements at the beginning and end of a time interval, respectively. Relative growth was estimated over a short time period just after tagging (0-14 days) and a longer time period (15-57 days). To account for the repeated measures, relative growth was compared between treatment and control fish using separate t-tests for the two time periods (Dr. Jeffrey Birch, Virginia Tech Statistics, pers. comm.). Since two tests were conducted on each growth parameter (4 total tests), significance was evaluated with a Bonferroni adjusted critical value of 0.0125 (0.05/4; Rice, 1989).

PIT field trials.— I examined data from the 1999 mark-recapture study (see chapter 2) to assess retention of PIT tags for fishes subjected to natural stream conditions. *Semotilus corporalis* (fallfish) ≥ 100 mm TL and *N. leptocephalus* and *T. rhothoeca* (torrent sucker) ≥ 80 mm TL were marked with photonic tags (see below) and PIT tags and released into the study area during May 1999. Fishes were recaptured during a spatially extensive sampling event during August 1999. The proportion of photonic-tagged fishes retaining PIT tags was calculated for each species. However, because smaller fish were also marked with photonic tags but not PIT tags, I only

considered recaptures above a species-specific cut-off size for these analyses. This cut-off size was determined by adding the 95th percentile of growth measurements to the largest size that a species was marked with photonic but not PIT tags (e.g., 79 mm for *T. rhothoeca* and *N. leptocephalus*). For example, 95% of bluehead chubs between 80 and 90 mm TL at tagging grew less than 12.7 mm between May and August. Thus, only recaptures larger than 92 mm were included in the analysis for *N. leptocephalus.*

Elastomer field trials.—Unlike PIT tags that are only suitable for tagging larger individuals (>80 mm TL) of the species examined in this study, the visible implant fluorescent elastomer tagging system (hereafter elastomer) was specifically designed for marking small fishes (Northwest Marine Technology, Inc.). After mixing the colored elastomer with a curing agent, these tags are injected into translucent body locations (e.g., between fin rays); different combinations of colors and locations allow creation of a large number of unique marks. *Semotilus corporalis*, *N. leptocephalus*, and *T. rhothoeca* recaptured during the 1998 mark-recapture study were used to estimate retention of elastomer tags injected into different body locations.

 Semotilus corporalis ≥ 100 mm TL and *N. leptocephalus* and *T. rhothoeca* ≥ 80 mm TL were tagged with elastomer and PIT tags during May 1998. Using a 1-cc syringe equipped with a 24-gauge needle, each fish was injected with a single color of elastomer (orange, blue, green, or yellow) into one of four different body locations. These body locations were selected during laboratory practice trials and were located in translucent parts of the body (Figure A.1). Fishes were recaptured during spatially extensive sampling events occurring approximately one (June) and three (August) months following marking. Retention of elastomer marks was determined by scanning body locations with the blue filter lens flashlight and glasses provided by Northwest Marine Technology, Inc. The proportion of PIT-tagged recaptures retaining elastomer marks was calculated separately for each body location and color. However, small sample size made it necessary to combine left caudal peduncle (LCP) and right caudal peduncle (RCP) recaptures for analysis.

Photonic tag laboratory experiment.—Photonic tags (New West Technologies, Inc.) are similar to elastomer in several respects; they are externally visible, fluorescent, and are suitable for marking small fishes subcutaneously. However, unlike elastomer, the photonic tagging

formulation never expires and does not require pre-mixing with a curing agent. Thus, given the mark retention problems I experienced during the 1998 mark-recapture study (see results), an opportunity existed to replace elastomer with a potentially more effective and convenient tagging system. Before making the switch, I evaluated retention of photonic tags (New West Technologies, Inc.) for laboratory-held *S. corporalis*, *N. leptocephalus*, and *Thoburnia rhothoeca*.

Nocomis leptocephalus and *T. rhothoeca* were collected with a DC-powered backpack electrofisher from a South Fork Roanoke River tributary (Goose Creek) on 12 February 1998. *Semotilus corporalis* were also collected by electrofishing, but were taken from a section of lower Dicks Creek on 26 February 1999. Fishes were stocked into two separate living streams (*N. leptocephalus* + *T. rhothoeca* and *S.corporalis* alone) and held for four days before tagging. Fishes were gradually acclimated from 9C to 17 C +/- 2 C and maintained at a 12.5L:11.5D photoperiod throughout the experiment.

Fishes were randomly assigned to treatments using a protocol similar to that used for the PIT-tagging experiment, but a smaller number of unmarked fishes were held as controls because of limited space in artificial streams. Because controls fish could not be distinguished from fishes that lost all of their tags, they were isolated from marked fishes by a screen partition that restricted them to ca. 1/3 of the artificial stream's volume.

Twenty (TL = 66-94 mm, mean = 79.9) and 18 (TL = 53-92 mm, mean = 74.6) *S. corporalis* were allocated to the mark and control groups, respectively. Sixteen (TL = 56-144, mean 88.8) and 5 (TL = 84-102 mm, mean = 92.4) *N. leptocephalus* were allocated to mark and control groups, respectively. Sixteen (TL = 64-145 mm, mean = 106.3) and 5 (TL= 92-141, mean = 112.8) *T. rhothoeca* were allocated to mark and control groups, respectively. All fish were anesthetized with MS222 and measured to the nearest mm TL before they were tagged or allocated to the control group. Pink photonic tags were injected into four to six different body locations on each treatment fish using the Pen-Ject[TM] (New West Technologies, Inc.) manual tag injector. The Pen-Ject delivers a user-specified dose of photonic tagging formulation through a 30-gauge disposable needle and was specifically designed for making discrete marks on small fishes. Tagging locations were weakly pigmented to non pigmented areas; I selected them based upon ease of application during pre-experimental trials (Figure A.1). After marking, fishes were periodically removed from artificial streams, anesthetized, and examined for marks using an

ultraviolet lamp that was purchased directly from New West Technologies, Inc. Artificial streams were inspected daily for mortalities and dead fish were visually examined for evidence of tag incompatibility (e.g., lesions around mark locations).

Photonic tag field trials.— Fishes recaptured during the 1999 mark-recapture study were used to estimate retention of photonic tags under field conditions. *Semotilus corporalis* ≥ 100 mm TL and *N. leptocephalus* and *T. rhothoeca* ≥ 80 mm TL were tagged with photonic tags and PIT tags during May 1999. Three to four locations that exhibited high retention rates during the laboratory experiment were selected for each species and each individual fish was injected into two of these different locations with pink, yellow, orange, blue, or purple photonic tags (or any combination of 2 colors). Tag application followed the procedure outlined in the photonic-tagging laboratory experiments. Fishes were recaptured during a spatially extensive sampling event occurring approximately three months (August) following marking. Retention of photonic tags was determined by scanning body locations with an ultraviolet light purchased directly from New West Technologies, Inc. However, in contrast to the 1998 mark-recapture study, the ultraviolet light was housed in dark box to increase the probability of tag detection (the TR6000=Till Rosenberer 6000 model). The proportion of PIT-tagged recaptures retaining photonic tags was calculated separately for each location and color.

RESULTS

PIT-tagging experiment.— Two treatment and one control fish never recovered from anesthesia on the first day of the experiment. An 87-mm-TL control fish died during the first re-sampling event (day 14), but no other fish died during the experiment. Two of the remaining 19 treatment fish lost PIT tags within 14 days of tagging; these fish lived throughout the duration of the experiment but their growth measurements were omitted from analyses.

Relative growth (in weight and length) of PIT-tagged *N. leptocephalus* measured 14 and 57 days post-marking was not significantly different from the control group (Table A.1). However, relative growth in weight was lower for PIT-tagged chubs after 14 days and this difference approached significance before Bonferroni correction of alpha (Rice 1989).

PIT field trials.—Fifty-three of the 58 (91.4%) *N. leptocephalus* recaptures that were ≥ 92mm TL retained PIT tags. Twenty seven of the 29 (93.1%) *S. corporalis* recaptures that were ≥ 114 mm TL retained PIT tags. All of the 26 *T. rhothoeca* recaptures that were ≥ 86 mm TL retained PIT tags.

Elastomer field trials.—Elastomer retention ranged widely across the mark locations tested during the 1998 mark-recapture study. Left caudal peduncle (LCP) and RCP marks were never lost by *S. corporalis* or *N. leptocephalus*, but three of five recaptured *T. rhothoeca* lost this mark by August (Table A.2). In contrast, *T. rhothoeca* was the only species that exhibited high retention of the chin (CHI) mark. A low proportion of *N. leptocephalus* recaptured during June and August and *T. rhothoeca* recaptured during August retained head (HED) marks, but only one *S. corporalis* lost this mark during the study. There were no clearcut differences in retention rates related to elastomer color. A higher proportion of green marks was not detected in June samples, but retention rates were similar for all four colors during August (Table A.3).

Photonic tag laboratory experiment.— *Semotilus corporalis*, *N. leptocephalus*, and *T. rhothoeca* exhibited very high photonic tag retention rates for at least some of the mark locations tested and I found no evidence for tag incompatibility during mark censuses or examinations of dead fishes. No left caudal peduncle (LCP), left mid anal (LMA), or pre dorsal-fin (PDF) marks were lost by any of the *S. corporalis* during a one year period (Table A.4). However, one to three of the PDF marks were not detected on the second, third, and fourth census events. Since no fish died between the fourth and fifth censuses, the resumption of 100% mark retention was due to the detection of previously missed tags rather than the exclusive death of fish losing the PDF marks. A large number of CHI marks were lost between 9 and 30 days and none of these marks were retained for the entire year. *Semotilus corporalis* began rapidly dying off after about 6 months, but overall mortality rates were similar in mark (65%) and control groups (66%) at the end of the experiment.

All right caudal peduncle (RCP) and center pelvic base (CPB) marks were retained *by N. leptocephalus* for more than a year (Table A.5). All LCP marks were retained on 7 of 8 census events; one of these marks was either lost or not detected during the 4th census event. Unlike the scenario for the PDF tag in *S. corporalis*, the resumption of 100% tag retention on the fifth

census could have resulted through mortality of the fish that lost its LCP tag on the 4th census. Fish started losing LMA and PDF tags after 58 days, but the proportion of LMA marks retained remained relatively high throughout the experiment. Retention of the left sub-nares (LSN) mark declined after 28 days and remained relatively low until the end of the experiment. Marked *N. leptocephalus* started dying off after 83 days while survival of control fish remained constant during this same time period.

All central caudal peduncle marks (CCP) were retained by *T. rhothoeca* on each census, but high mortality of marked fish precluded a meaningful assessment of retention rates after 83 days (Table A.6). Retention rates for upper caudal lobe (UCL), CPB, and CHI were fairly high (all > 84%) during the first 83 days of the experiment when sample sizes were large enough to permit accurate comparisons. A high proportion of lower caudal lobe (LCL) and left opercle (LOP) marks were retained up to day 58, but a relatively high proportion of these marks were lost by day 83. Similar to the pattern observed for *N. leptocephalus*, mortality of marked *T. rhothoeca* was not paralleled by losses in the control group.

Photonic tag field trials. — Overall, photonic tag locations exhibiting high retention rates in the laboratory experiments also exhibited high retention during the 1999 mark-recapture study (Table A.7). However, the PDF mark location for *S. corporalis* and the CHI mark location for *T. rhothoeca* exhibited substantially lower retention than in the laboratory experiments. Blue and purple marks exhibited the lowest retention rates (Table A.8).

<div align="center">DISCUSSION</div>

PIT-tagging.—My results suggest that PIT-tagged *N. leptocephalus* may suffer declines in growth immediately after tagging, but grow at the same rate as non-tagged *N. leptocephalus* later on. The most plausible explanation is that fish divert energy to repair damaged tissues after tagging, but this energy loss is not substantial enough to affect long-term growth rates. Thus, future studies using PIT tags should interpret data collected over short time periods (i.e., less than 1 month) with caution, particularly when conclusions are extended to an untagged population.

There was no evidence that PIT-tagging affected the survival of *N. leptocephalus*; an equal number (2) of tagged and control fish died during the experiment. All of these deaths occurred during handling and may have been associated with anesthetic overdose. Regardless of the cause, mortality of these fish would not affect the reliability of field studies because they would be removed from the study before release. Johnston and Smithson (1999) found that PIT-tagging did not decrease the survival of laboratory-held *Lepomis megalotis* (longear sunfish) and *Noturus phaeus* (brown madtom), but slightly decreased the survival of *Semotilus atromaculatus* (creek chub).

A large proportion (89.5%) of *N. leptocephalus* retained their PIT tags throughout the 58-day experiment. High retention rates were also documented for *N. leptocephalus*, *S. corporalis*, and *T. rhothoeca* during the three-month mark-recapture study. Nonetheless, since retention rates were not 100% for all species, these results emphasize the importance of tagging animals with additional marks. Smithson and Johnston (1999) attributed low PIT-tag retention rates in *Cyprinella camura* (bluntface shiner) to tag loss through injection wounds. My results are consistent with this hypothesis; the only fish that lost tags did so within two weeks of tagging, possibly before wounds had healed. Modifications to the tagging procedure that result in smaller tagging wounds may increase retention rates for PIT tags in future studies. For example, pre-puncturing injection sites with pointed scalpel blades can prevent large tagging wounds that result from forcing dull needles through thick fish skin.

In summary, PIT tags did not affect the survival of *N. leptocephalus*, had a small but temporary effect on growth rates of *N. leptocephalus*, and exhibited high retention in *N. leptocephalus*, *S. corporalis*, and *T. rhothoeca* subjected to natural stream conditions. These tags may also be effective for marking other small species of stream fish, but this should be confirmed through additional laboratory and field studies.

Elastomer and photonic tagging.—Laboratory experiments and field trials identified several tagging locations that exhibited high retention of elastomer and/or photonic tags for time periods ranging from 3 months to a year. These tagging locations can be used in future ecological investigations of *N. leptocephalus*, *S. corporalis* and *T. rhothoeca*. It is tempting to utilize these tagging locations on other species without conducting further retention experiments, but I would caution against it because of the considerable interspecific variation in retention that I

129

documented. For example, LCP and RCP locations marked with elastomer exhibited very high retention for *N. leptocephalus* and *S. corporalis (100%)*, but low retention for *T. rhothoeca* (40%).

An additional word of caution is that laboratory experiments may overestimate retention of marks subjected to natural stream environments. My laboratory experiments substantially overestimated retention for two of the 11 photonic tagging locations tested during the 1999 mark recapture study. Thus, future mark-recapture studies should attempt to validate mark retention under field conditions. When such validation is infeasible, redundant marking schemes should be adopted so that the loss of a single mark will not prevent individual or batch identification of recaptured fishes.

One interpretational problem with the field trials is that mark locations were confounded with tag color. In other words, its not clear whether marks were lost because of location or color. For both elastomer and photonic tags, substantially greater variation in retention rates across mark locations compared to mark colors suggests that mark location is the primary determinant of retention. For example, all PDF marks were lost regardless of mark color and CHI marks exhibited poor retention across all of the colors tested. In contrast, purple, the color exhibiting the lowest mark retention, actually exhibited high retention for LMA (100%, n=6), CPB (75%, n=8), and LCP (100%, n=6) marks. Nonetheless, there may still be important differences in mark retention related to color or color x location interactions that were not examined in this study.

Table A.1 Results of t-tests comparing relative growth in weight (RGW) and relative growth in length (RGL) between PIT-tagged and non-PIT-tagged bluehead chubs *(Nocoms leptocephalus)*. Relative growth was measured 14 and 57 days post-marking following Busacker et al. (1990). Significance was evaluated with a Bonferroni-adjusted critical value of 0.0125 (0.05/4).

Comparison	N PIT	N Control	Mean (SD) PIT	Mean (SD) Control	P-value
RGW14	17	19	-0.035 (0.038)	-0.014 (0.032)	0.07
RGW57	17	18	0.056 (0.090)	0.061 (0.089)	0.89
RGL14	17	19	-0.008 (0.015)	-0.003 (0.010)	0.27
RGL57	17	18	0.015 (0.021)	0.020 (0.023)	0.52

Table A.2 Proportion of recaptured fishes that retained elastomer (Northwest Marine Technology, Inc.) marks approximately 1 month (June) and 3 months (August) after tagging. N is the total number of recaptures.   Fishes were tagged with elastomer and passive integrated transponder (PIT) tags during May 1998 and released throughout a network of streams in the James River drainage, Virginia. Elastomer was injected into left caudal peduncle (LCP), right caudal peduncle (RCP), chin (CHI), and head (HED) body locations.

Species	Mark Location	June		August	
		N	% Retained	N	% Retained
S. corporalis	LCP and RCP	2	100.0	3	100.0
S. corporalis	CHI	1	0.0	0	NA
S. corporalis	HED	7	85.7	4	100.0
N. leptocephalus	LCP and RCP	19	100.0	13	100.0
N. leptocephalus	CHI	38	73.7	25	60.0
N. leptocephalus	HED	19	52.6	11	27.3
T. rhothoeca	LCP and RCP	6	83.3	5	40.0
T. rhothoeca	CHI	6	100.0	3	100.0
T. rhothoeca	HED	3	100.0	3	33.3

Table A.3 Proportion of recaptured fishes (*S. corporalis*, *N. leptocephalus*, and *T. rhothoeca* combined) that retained different colored elastomer (Northwest Marine Technology, Inc.) marks approximately 1 month (June) and 3 months (August) after tagging. N is the total number of recaptures.   Fishes were tagged with elastomer and PIT-tags during May 1998 and released throughout a network of streams in the James River drainage, Virginia. Elastomer was injected into one of three different body locations, but data were pooled across body positions for this comparison.

Mark Color	June		August	
	N	% Retained	N	% Retained
Orange	53	75.5	37	64.9
Blue	14	85.7	7	71.4
Green	15	66.7	10	70.0
Yellow	20	90.0	13	61.5

Table A.4 Proportion of *Semotilus corporalis* (fallfish) that retained photonic tags (New West Technologies, Inc.) during a 365-day experiment. Twenty fish were marked at left caudal peduncle (LCP), left mid anal (LMA), pre dorsal-fin (PDF), and chin (CHI) body locations and stocked into an artificial stream along with 18 unmarked control fish on day 1 of the experiment. The number of marked and control fish alive on each mark census is also reported.

Day	Marked	Control	LCP	LMA	PDF	CHI
9	20	18	100.0	100.0	100.0	100.0
30	20	18	100.0	100.0	85.0	10.0
65	20	18	100.0	100.0	95.0	10.0
97	20	17	100.0	100.0	95.0	5.0
135	20	17	100.0	100.0	100.0	10.0
178	18	11	100.0	100.0	100.0	11.1
275	8	7	100.0	100.0	100.0	12.5
365	7	6	100.0	100.0	100.0	0.0

Table A.5 Proportion of *Nocomis leptocephalus* (bluehead chub) that retained photonic tags (New West Technologies, Inc.) during a 379-day experiment. Sixteen fish were marked at left caudal peduncle (LCP), right caudal peduncle (RCP), left mid anal (LMA), center pelvic base (CPB), left sub-nares (LSN), and pre dorsal-fin (PDF) body locations and stocked into an artificial stream along with 5 unmarked control fish on day 1 of the experiment. The number of marked and control fish alive on each mark census is also reported.

Day	Marked	Control	LCP	RCP	LMA	CPB	LSN	PDF
14	16	5	100.0	100.0	100.0	100.0	100.0	100.0
28	16	4	100.0	100.0	100.0	100.0	100.0	100.0
58	16	4	100.0	100.0	100.0	100.0	87.5	100.0
83	16	4	93.8	100.0	93.8	100.0	56.3	75.0
122	9	4	100.0	100.0	88.9	100.0	33.3	66.7
192	9	4	100.0	100.0	88.9	100.0	44.4	88.9
289	7	4	100.0	100.0	71.4	100.0	71.4	42.9
379	7	4	100.0	100.0	85.7	100.0	57.1	0.0

Table A.6 Proportion of *Thoburnia rhothoeca* (torrent sucker) that retained photonic tags (New West Technologies, Inc.) during a 192-day experiment. Sixteen fish were marked at upper caudal lobe, (UCL), lower caudal lobe (LCL), center caudal peduncle (CCP), center pelvic base (CPB), left opercle (LOP), and chin (CHI) body locations and stocked into an artificial stream along with 5 unmarked control fish on day 1 of the experiment. The number of marked and control fish alive on each mark census is also reported.

Day	Marked	Control	UCL	LCL	CCP	CPB	LOP	CHI
14	16	5	100.0	100.0	100.0	100.0	100.0	100.0
28	16	5	100.0	100.0	100.0	100.0	93.8	100.0
58	16	5	100.0	93.8	100.0	100.0	87.5	100.0
83	13	5	84.6	69.2	100.0	84.6	15.4	92.3
122	2	4	50.0	50.0	100.0	100.0	50.0	50.0
192	1	4	0.0	0.0	100.0	100.0	0.0	0.0

Table A.7   Proportion of recaptured fishes that retained photonic tags (New West Technologies, Inc.) approximately 3 months after tagging. The total number of recaptured fishes is given in parentheses. Fishes were tagged with photonic tags and PIT-tags during May 1999 and released throughout a network of streams in the James River drainage, Virginia. Photonic tags were injected into right caudal peduncle (RCP), left caudal peduncle (LCP), center caudal peduncle (CCP), right mid anal (RMA), left mid anal (LMA), center pelvic base (CPB), chin (CHI), and pre dorsal-fin body locations.

Species	RCP	LCP	CCP	RMA	LMA	CPB	CHI	PDF
N. leptocephalus	96.0 (25)	NA	NA	95.7 (23)	97.6 (41)	98.2 (56)	NA	NA
S. corporalis	NA	100.0 (25)	NA	100.0 (3)	100.0 (19)	NA	NA	0.0 (11)
T. rhothoeca	NA	NA	89.7 (29)	NA	NA	83.3 (24)	29.4 (17)	NA

Table A.8 Proportion of recaptured fishes (*S. corporalis, N. leptocephalus, and T. rhothoeca* combined) that retained different colored photonic tags (New West Technologies, Inc.) approximately 3 months after tagging. The total number of recaptured fish is given in parentheses. Fishes were tagged with photonic tags and PIT-tags during May 1999 and released throughout a network of streams in the James drainage, Craig County, Virginia. Photonic tags were injected into eight different body locations, but data were pooled across body positions for this comparison.

Pink	Yellow	Orange	Blue	Purple
94.3 (53)	84.9 (73)	100 (72)	77.8 (45)	66.7 (30)
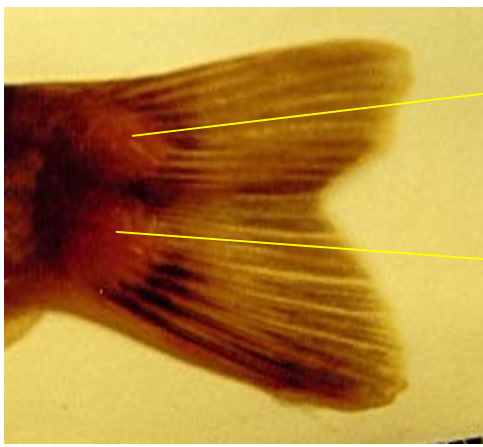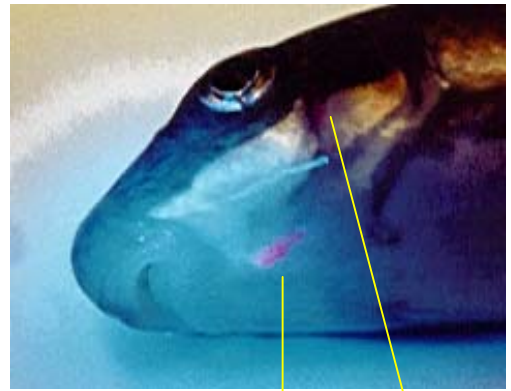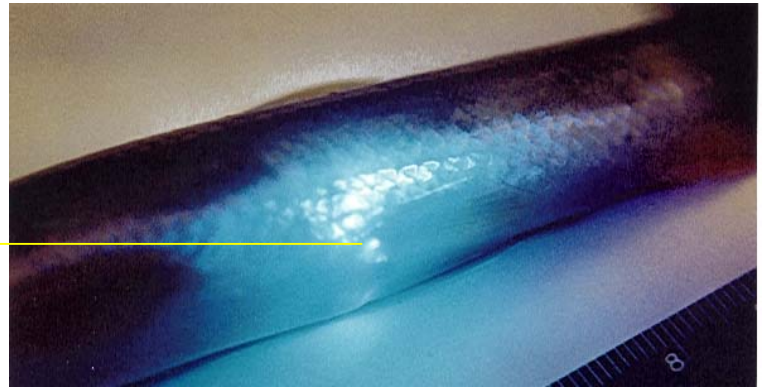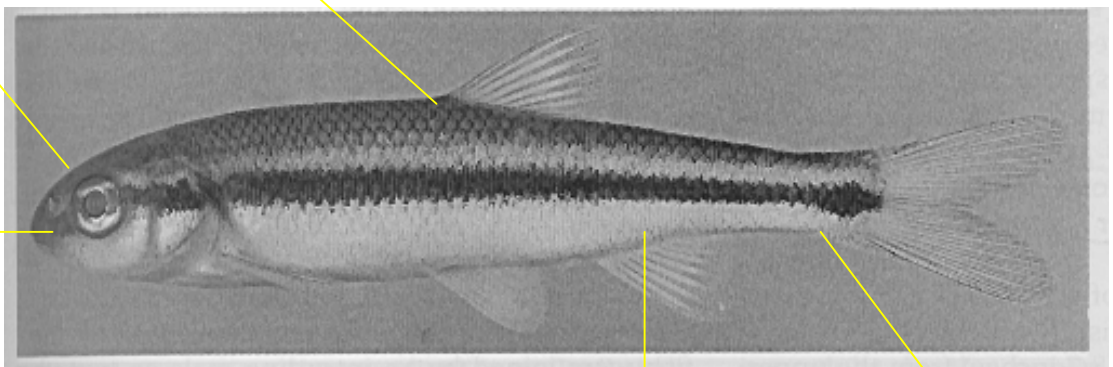
Figure A.1 Body locations for elastomer and photonic tags used to mark fishes throughout study. Two additional marks (RMA, RCP not shown) occur on the right side of the fish, opposite left mid anal (LMA) and left caudal peduncle (LCP) marks. The center caudal peduncle mark (CCP, not shown) occurs on the ventral surface of the caudal peduncle between LCP and RCP marks. Additional abbreviations are: upper caudal lobe (UCL), lower caudal lobe (LCL), chin (CHI), left opercle (LOP), center pelvic base (CPB), pre dorsal-fin (PDF), left sub-nares (LSN) and head (HED). Color photographs courtesy of Joe Grist.

Appendix B. Archive of data from the 1998 and 1999 mark-recapture studies.

The purpose of Appendix B is to archive data from the 1998 and 1999 mark-recapture studies. This data comes from the studies described in Chapters 1 and 2. However, as illustrated in Figures B.1 and B.2, fishes were marked in additional sites that are not included in Chapters 1 and 2. These sites were eliminated from Chapter 1 because of the need to include the same mark sites in the two study designs evaluated. Sites near study section boundaries were excluded from Chapter 2 to minimize a bias toward classifying fish as "stayers" when "movers" leave the study area undetected. The summary statistics reported in Tables B.2 , B.3, and B.4 are based on recaptures from all of the mark sites shown in Figures B.1 and B.2 with one exception: fishes marked in the site at the downstream boundary of the study area (ca. 20 m upstream of Johns Creek) were excluded from the 1999 data set because fish marked in the site could easily escape the study area.

Data from the 1998 study should be viewed with caution because of extreme distance weighting (CV of PS_d ranged from 52-70% in 1998 when all sites are included vs. 10-24% in 1999 when all but the downstream boundary site was included). Distance data for species with low sample sizes in both years (e.g., *Esox niger*) should also be interpreted cautiously.

Table B.1 Size of fishes marked with elastomer (1998), photonic (1999), and PIT (1998 and 1999) tags during the mark-recapture studies. Body locations for elastomer and photonic tags are breast (BRT), center caudal peduncle (CCP), chin (CHI), center pelvic base (CPB), head (HED), left anterior anal (LAA), left caudal peduncle (LCP), left mid anal (LMA), right anterior anal (RAA), right caudal peduncle (RCP), right mid anal (RMA), pre dorsal-fin (PDF), and snout (SNT). Mark techniques and positions that were not applied to a particular species are designated not applicable (NA). MP = Mark position.

Species	Elastomer Size	Photonic Size	PIT Size	Elastomer Mark Positions				Photonic Mark Positions			
				MP1	MP2	MP3	MP4	MP1	MP2	MP3	MP4
E. niger	150	100	150	RCP	HED	NA	NA	CPB	LAA	RAA	NA
R. atratulus	45	45	NA	CPB	SNT	LCP	NA	CCP	CPB	PDF	NA
S. corporalis	60	60	100	CHI	HED	LCP	RCP	LCP	LMA	PDF	RMA
N. leptocephalus	60	60	80	CHI	HED	LCP	RCP	CPB	LMA	RCP	RMA
N. raneyi	60	NA	80	CHI	HED	RCP	NA	NA	NA	NA	NA
E. oblongus	80	70	80	HED	NA	NA	NA	CPB	LMA	RMA	NA
T. rhothoeca	80	70	80	CHI	HED	LCP	RCP	CCP	CHI	CPB	NA
P. notogramma	50	50	NA	LCP	RCP	NA	NA	BRT	LAA	LMA	RMA
E. flabellare	NA	45	NA	NA	NA	NA	NA	BRT	LAA	LMA	RMA

Table B.2 Summary statistics for movement distances estimated during the 1998 mark recapture study. Fishes were marked in 15 sites during May 1998 and recapture events occurred during June and August 1998. Movement distances were calculated as differences between mark site and recapture site midpoints and were measured in meters. The number of fish marked and the proportion of marked fishes recaptured (% recap.) are also reported.

Species	No. Marked	June				August			
		% Recap.	Mean (SD)	Median	Max	% Recap.	Mean (SD)	Median	Max
E. niger	3	33.3	0.0 (0)	NA	0	0.0	NA	NA	NA
R. atratulus	138	13.0	62.9 (117.0)	0.0	452	12.3	133.3 (192.9)	0.0	559
S. corporalis	41	24.4	107.6 (119.1)	79.8	287	24.4	179.4 (175.9)	168.8	475
N. leptocephalus	328	29.0	65.3 (91.5)	36.5	452	20.4	101.7 (133.2)	51.3	508
N. raneyi	5	0.0	NA	NA	NA	0.0	NA	NA	NA
E. oblongus	3	0.0	NA	NA	NA	0.0	NA	NA	NA
T. rhothoeca	29	51.7	29.2 (43.1)	0.0	149	41.4	83.4 (111.0)	49.8	353
P. notogramma	6	50.0	0.0 (0)	0.0	0	16.7	NA	NA	0

Table B.3 Summary statistics for movement distances estimated during the 1999 mark-recapture study. Fishes were marked in 21 sites (including 3 weirs) during May-June 1999 and a recapture event occurred during August 1999. Movement distances were calculated as differences between mark site and recapture site midpoints and were measured in meters. The number of fish marked, the proportion of marked fish that were recaptured (% Recap.), and the proportion of fish marked upstream of the lower Dicks Creek weir that moved downstream through this weir and were never recaptured (% Escaped) are also reported.

Species	No. Marked	% Recap.	%Escaped	Mean (SD)	Median	Max
E. niger	9	77.8	0.0	148.2 (236.8)	59.0	638
R. atratulus	139	28.1	1.4	87.5 (186.9)	38.5	1029
S. corporalis	130	28.5	1.6	105.3 (154.1)	54.5	676
N. leptocephalus	327	36.1	1.2	246.1 (313.0)	107.5	1144
E. oblongus	11	36.4	0.0	237.8 (230.2)	258.0	435
T. rhothoeca	53	60.4	0.0	117.2 (168.7)	41.5	669
P. notogramma	5	20.0	0.0	NA	NA	0
E. flabellare	100	4.0	0.0	62.3 (36.6)	53.5	114

Table B.4 Proportion of fish marked in May 1999 that were recaptured in a different stream during August 1999.

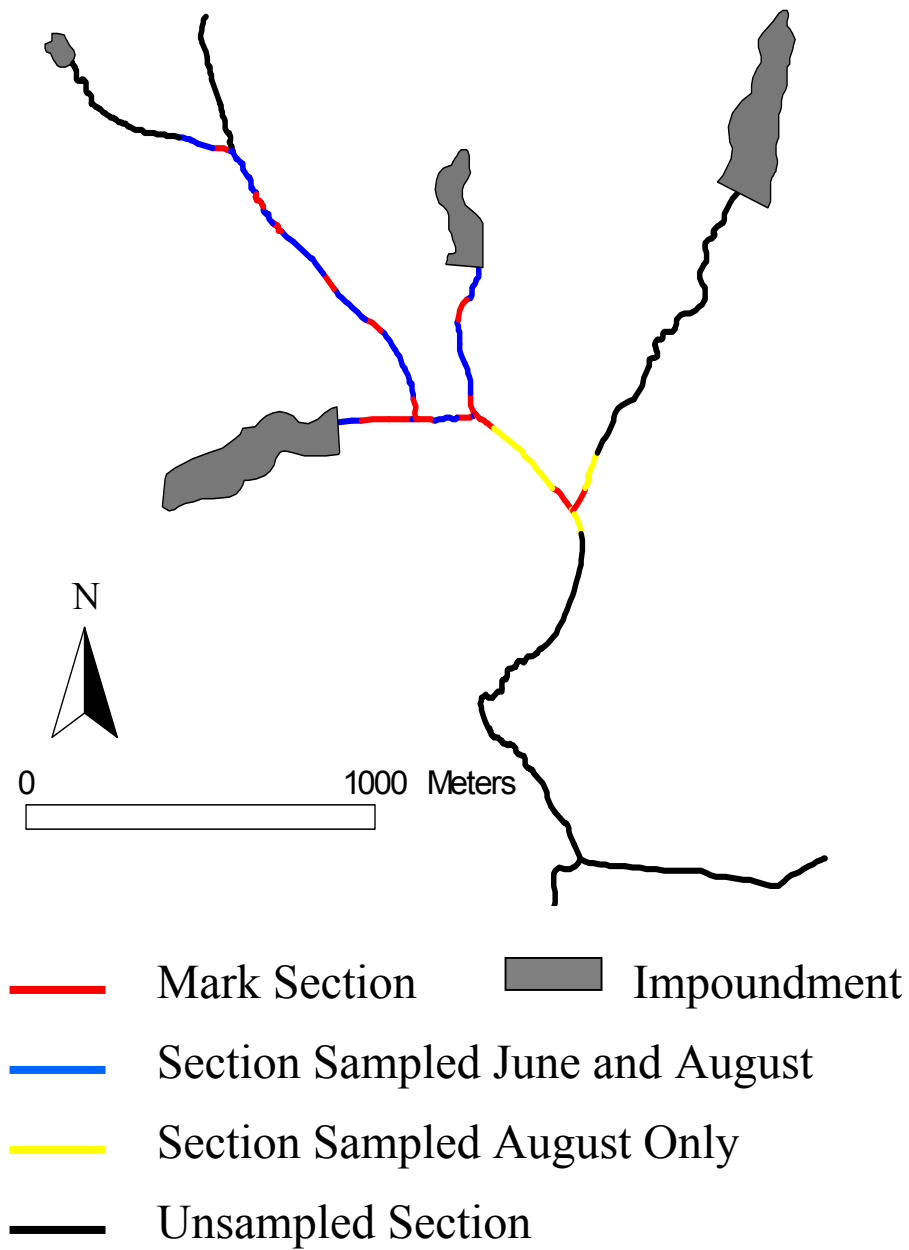| Species	% Between Stream Movements
Rhinichthys atratulus	12.8
Semotilus corporalis	16.2
Nocomis leptocephalus	24.2
Thoburnia rhothoeca	15.6

Figure B.1 Distribution of mark and recapture sites during the 1998 mark-recapture studies.
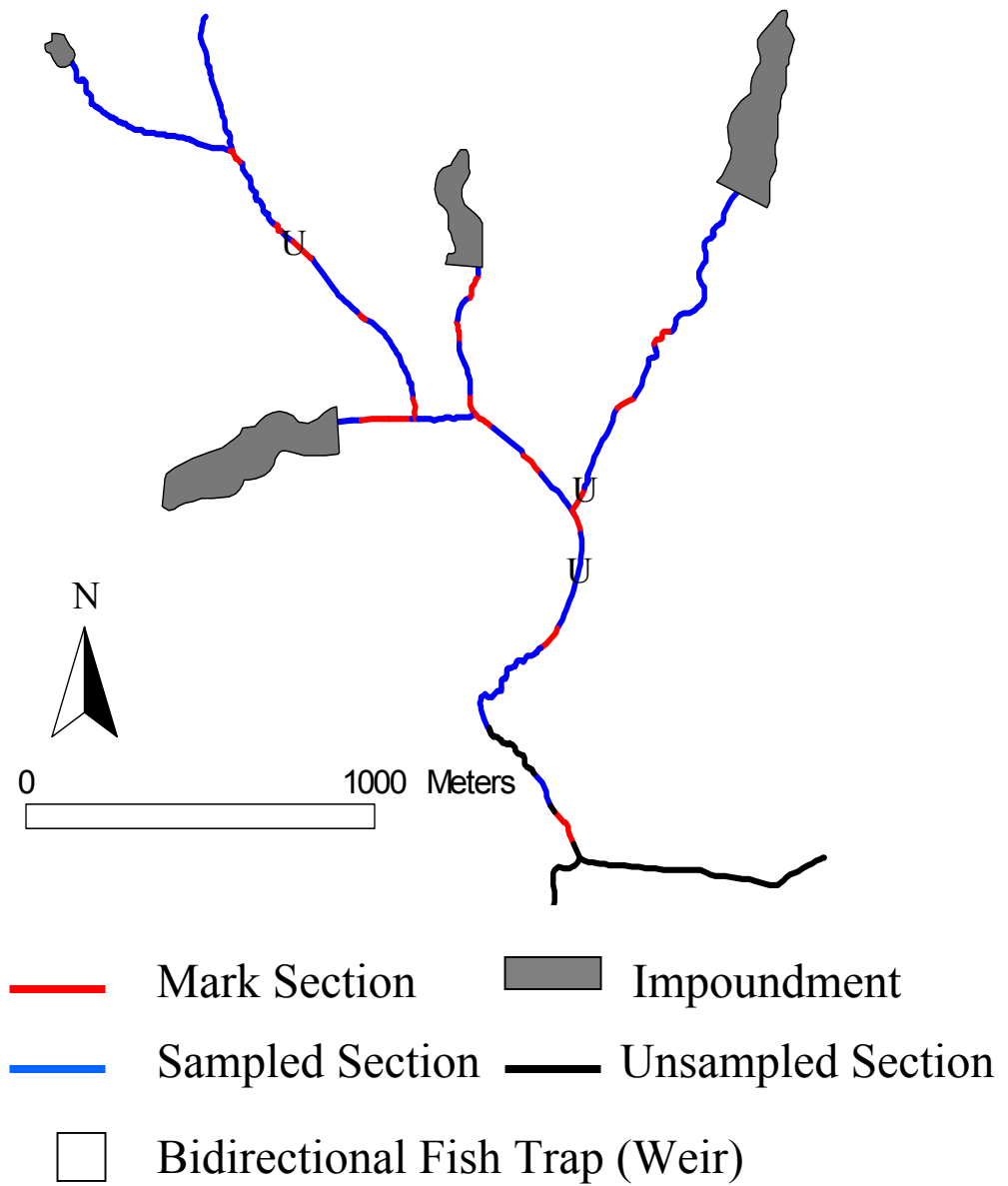
Figure B.2 Distribution of mark sites, recapture sites, and bi-directional fish traps during the 1999 mark-recapture study
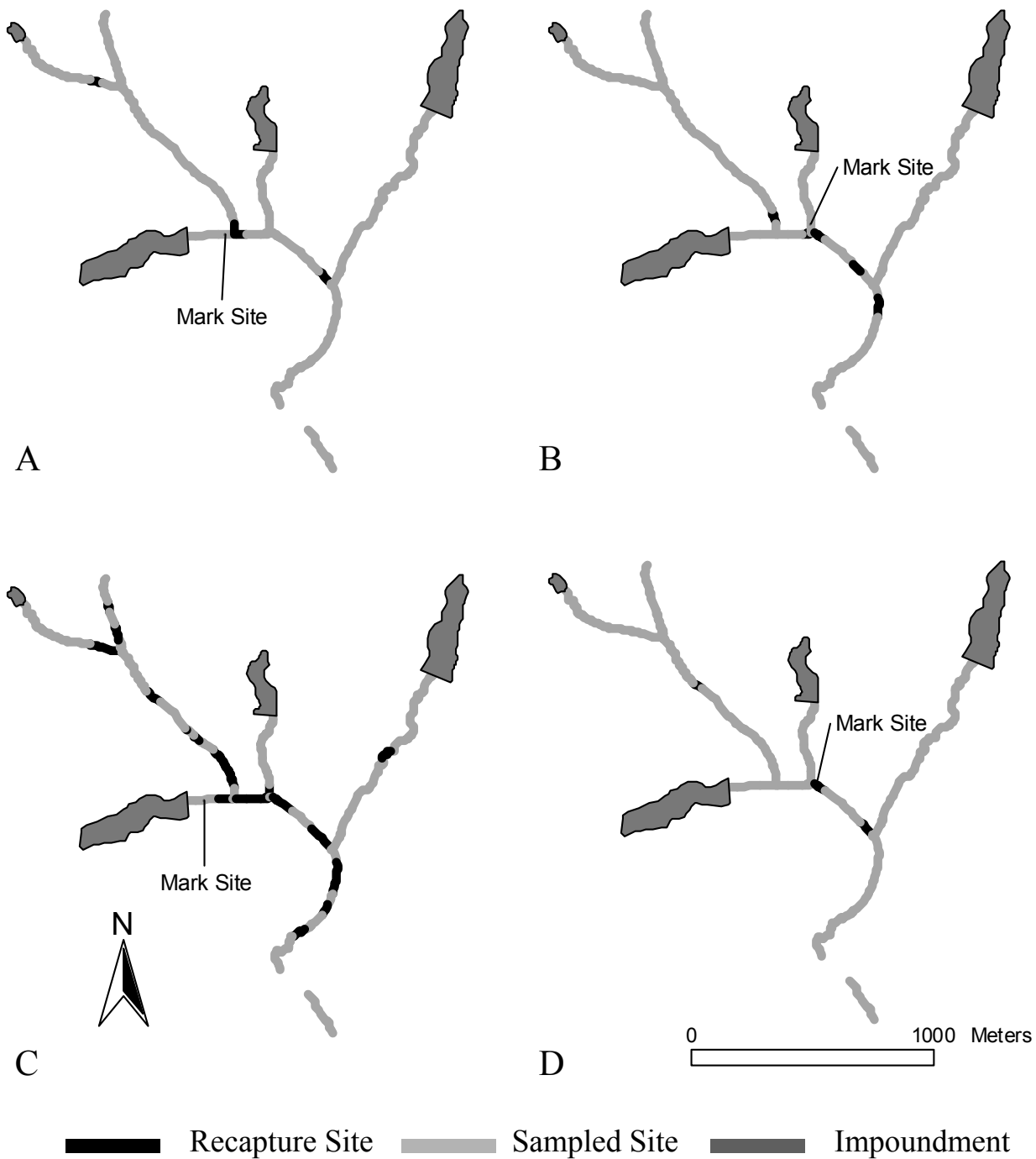
Figure B.3 Most extensive movement patterns that were detected for *Rhinichthys atratulus* (A), *Semotilus corporalis* (B), *Nocomis leptocephalus* (C), and *Thoburnia rhothoeca* (D) during the 1999 mark-recapture study. Recapture sites (black) show all of the sites that fishes moved into from a single mark site (labeled). The gap in the downstream portion of each map represents a series of deep beaver dam pools that were not sampled.

Appendix C. Catchability of fishes in the Dicks Creek and Middle Creek colonization sites during defaunation sampling.

The purpose of this appendix is to archive catchability estimates from the colonization sampling. This data is useful when evaluating the efficiency of the defaunation and recapture sampling, but may also be of more general interest.

Table C.1 Catchability (Q) of fishes in the Dicks Creek and Middle Creek colonization sites during defaunation sampling. Estimates were calculated using microfish 3.0 (Van Deventer and Platts 1985) and were based on the number of fish (including young of year) caught during the first three shocking passes. Estimates were not available (NA) for species that were only captured during one of the first three passes, exhibited a non-descending removal pattern during the first three passes, or were not present within the colonization site. SE = standard error.

| | Dicks Creek | Middle Creek |
Species	Q (SE)	Q (SE)
Esox niger	0.71 (0.16)	NA
Phoxinus oreas	0.64 (0.19)	0.34 (0.06)
Clinostomus funduloides	NA	0.66 (0.07)
Rhinichthys atratulus	0.35 (0.24)	0.51 (0.08)
Semotilus corporalis	0.43 (0.10)	NA
Nocomis leptocephalus	0.37 (0.06)	0.48 (0.07)
Luxilus cornutus	0.54 (0.08)	NA
Thoburnia rhothoeca	0.67 (0.27)	0.48 (0.12)
Catostomus commersoni	0.30 (0.18)	NA
Noturus insignis	0.31 (0.27)	NA
Cottus caeruleomentum	0.65 (0.10)	NA
Ambloplites rupestris	0.58 (0.24)	NA
Micropterus salmoides	0.63 (0.26)	NA
Lepomis auritus	0.67 (0.27)	NA

Vita

Brett Albanese was born in Rochester, New York on 16 December 1970. He spent the first 15 years of his life in Fairport, New York where he developed a strong interest in fishes. Important influences were his grandfathers' aquarium full of *Pterophyllum scalare*, "collecting trips" in Irondequoit Creek, trips to aquarium shops with his father, his mother's tolerance for aquaria in his bedroom, and weekends fishing in Canandaigua Lake. His mother, Karen Albanese, promised him a 55 gallon tank if he would move to North Carolina in 1986. He could not refuse.

Brett's interest in aquarium fishes burgeoned while attending Sanderson High School in Raleigh, North Carolina. He kept and bred a variety of east African cichlids (e.g, *Tropheus*) in his home aquaria. In part, he supported his hobby by selling the offspring of these fishes to other aquarists. More importantly, Brett worked at the Pet Company aquarium shop throughout high school where he received a healthy discount for his labors. Brett also developed skills in tropical fish identification and husbandry while working at the Pet Company. His boss, Rick Schwartz, was very supportive of Brett's interest in fishes and sent him to American Cichlid Association conferences in St. Louis and Orlando.

Brett enrolled in the Fisheries and Wildlife program at North Carolina State University in 1989. He maintained his interest in tropical fishes, but it was at NCSU that he "discovered" the fascinating native fishes in his own backyard. Important developments during this time period included "fish week" on the Flat River during fish and wildlife summer camp, a summer job collecting fishes and invertebrates in NC mountain streams, and an independent study of fish movement in a stream near NCSU. Jim Gilliam supervised this study and later supported a trip to Trinidad where Brett was temporarily re-acquainted with tropical fishes.

Brett met the love of his life, Victoria Bankov, during his last year at NCSU. Vicki was not an ichthyophile, but willingly participated in weekend seining trips in North Carolina. Brett and Vicki moved to Hattiesburg, Mississippi at the end of 1995 to attend graduate school at the University of Southern Mississippi. Brett's thesis was entitled "Life history and reproductive ecology of the flagfin shiner, *Pteronotropis signipinnis*" which he completed under the direction of Stephen T. Ross. Other highlights during this period were formal taxonomy and curatorial

training at the USM Museum of Ichthyology, fish surveys with Todd Slack, Martin O'Connell, and Steve Ross throughout the state of Mississippi, and marriage to Vicki.

Brett completed his MS in Biology in 1997 and moved to Radford, Virginia to attend Virginia Tech. He became involved in many projects while working on his PhD with Paul Angermeier. Of note was the development of a rather large collection of fishes in his basement (The "Albanese Museum of Ichthyology"), a monitoring project for *Percina rex* (his assistantship), and efforts to educate people about the fishes of Bottom Creek (A Nature Conservancy Preserve). Recently, with much help from Vicki, Brett described a new species of fish (*Lactomyzon racheli*—Appalachian milksucker) that he collected in the birthing center at Montgomery Regional Hospital. Brett, Vicki, and their daughter Rachel are moving to Trinidad to learn more about fish movement after Brett completes his PhD.