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Movement Patterns of Stream Fishes in a Ouachita Highlands Stream: An Examination of the Restricted Movement Paradigm

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Abstract.—The restricted movement paradigm (RMP), which states adult fish do not move out of a pool or restricted stream reach, does not fully define the movements of stream fishes. Although stream fishes may spend the majority of their time in a home pool, they also make regular exploratory trips away from the home pool. Recapture of Ouachita Highlands stream fish marked with passive integrated transponder (PIT) tags showed that the majority of the uniquely marked fish in this study were in the pools of initial collection. The following percentages of marked fish were recaptured outside the pool of initial collection: 12% of creek chub *Semotilus atromaculatus*; 33% of blackspotted topminnow *Fundulus olivaceus*; 12% of green sunfish *Lepomis cyanellus*; and 14% of longear sunfish *Lepomis megalotis*. Standard lengths and weights did not differ significantly between nonmobile and mobile recaptured fish, and patterns of multiple recaptures indicated exploratory, round-trip movements. Such regular exploratory trips suggest that the area of use by and critical habitat for stream fishes may be greater than commonly estimated.

Populations of stream fishes have been viewed as completely homogeneous and mobile (Linfield 1985; Fausch and Young 1995) or as relatively discrete units exhibiting restricted movement (Gerking 1953; Hill and Grossman 1987; Heggenes et al. 1991). These two views of fish movement have profoundly different implications for the management and conservation of stream fishes. Therefore, a better understanding of the patterns and processes of fish movement is necessary to delineate fish populations.

Many studies of fish movement have indicated that stream fishes are sedentary, never leaving a particular pool or stream reach (e.g., Berra and Gunning 1972). Gowan et al. (1994) termed this concept the "restricted movement paradigm" (RMP). Restricted movement is defined as recapture from the area where the fishes were initially marked and released (Gerking 1959). Examination of the data from such studies shows that although a majority of fishes studied are sedentary, leading authors to conclude that movement is restricted, a proportion of fishes in every study do move, sometimes for long distances (Gerking 1953; Hill and Grossman 1987; Heggenes et al. 1991). Funk (1957) proposed that populations of fishes are composed of both mobile and sedentary fractions. Few studies have addressed whether individuals exhibit one strategy or the other exclusively or switch from mobile to sedentary behaviors. However, a study of individually marked brown trout *Salmo trutta* showed frequent-switching behavior (Harcup et al. 1984).

Populations of fishes are not likely to be completely sedentary. Studies of recolonization suggest that fishes are mobile and respond rapidly to habitat in which no fish are found (Larimore et al. 1959; Peterson and Bayley 1993). Recolonization of defaunated stretches of stream can begin immediately after a disturbance, and sedentary species such as longear sunfish *Lepomis megalotis* can recolonize within 2 weeks (Peterson and Bayley 1993). The identity of such colonists has been poorly studied, but rapid colonizers may represent the mobile component of a nearby population.

We examined the RMP by investigating patterns of movement of individually marked fishes in a Ouachita Highlands stream. By using individually

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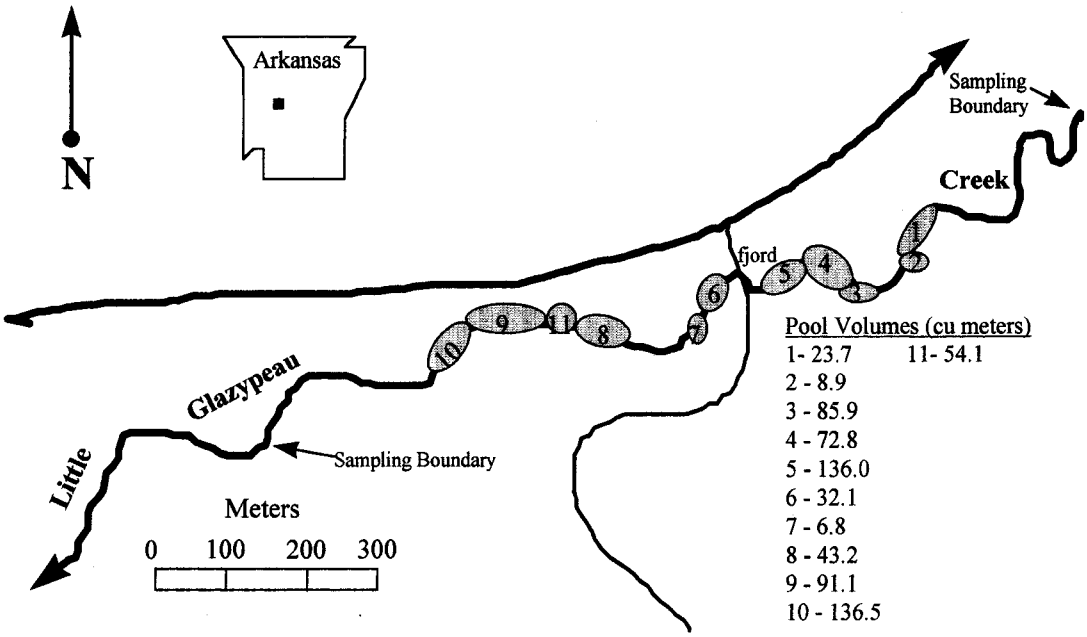

FIGURE 1.—Location of the Little Glazypeau Creek study site.

marked fishes, we were also able to determine if mobile fishes were a discrete component of the population or if individual fishes switched between mobile and sedentary behaviors.

Study Site

Little Glazypeau Creek (Ouachita River drainage) is in the Ouachita Highlands of Arkansas (Garland County; Figure 1). It is a low-order stream with riffle–pool sequences. The substrate ranges from small cobble to boulders and the water is clear. The riparian zone consists of deciduous hardwood and pine forest. During the dry season of late summer to winter, pools in Little Glazypeau Creek are connected by shallow riffles; however, the study site was isolated upstream of pool 1 and downstream of pool 10 during the fall of 1995. Water temperature ranged from 20°C to 25°C during the study.

The study site was 500 m long and had 11 study pools ranging in length from 10 m to 59 m. Because the 11th pool was added during the second sampling trip, it is numerically out of sequence with the other pools. Additional 300-m stretches were sampled upstream and downstream of the study area to detect long-range movements of marked study specimens. The total sampling area was 1.1 km long. During each sampling episode, pool length, width, and depth and water velocity were recorded for each study pool. (Table 1).

TABLE 1.—Water volumes and velocities in study pools of Little Glazypeau Creek.

	Water volume (m^3)			Water velocity (m/s)		
Pool	Mean	SD	Range	Mean	SD	Range
1	24	6	17–36	0.01	0.031	0–0.2
2	9	2	7–14	0.02	0.048	0–0.23
3	85	8	71–95	0.01	0.030	0–0.18
4	74	11	57–92	0.02	0.028	0–0.24
5	136	24	97–166	0.01	0.012	0–0.12
6	32	5	21–39	0.02	0.029	0–0.22
7	7	2	5–11	0.05	0.095	0–0.43
8	39	17	22–69	0.02	0.032	0–0.31
9	93	26	57–123	0.01	0.019	0–0.14
10	140	37	108–218	0.01	0.024	0–0.27

Methods

Creek chub *Semotilus atromaculatus,* blackspotted topminnow *Fundulus olivaceus,* longear sunfish, and green sunfish *Lepomis cyanellus* were marked in May 1995. Nine collections (one per month) were conducted during May, July, August, and October of 1995 and 1996 and May 1997 to monitor movements and mark additional individuals. Fishes were collected by electrofishing with a backpack shocker. Initial sampling indicated that two passes within a pool resulted in depletion of the focal species. We continued to use two passes in each study pool on subsequent trips to ensure

sampling effort was consistent. We conducted single sampling passes in all areas between the study pools and the 300-m stretches upstream and downstream of the study site on each trip to sample for marked fish.

Date and location of collection (pool number or intervening area) were recorded for all of the study species captured. Fish were anesthetized, weighed (g), and measured (standard length, SL, 1.0 mm). Each fish collected from the study pools was marked with a subcutaneous injection of artist's latex paint (Freeman 1995). The color and position of the mark represented a specific pool. Passive integrated transponder (PIT) tags were injected into creek chub, green sunfish and longear sunfish large enough to accommodate them (>70 mm for creek chub and >65 mm for the sunfishes). Each tag had a unique numeric code that identified individuals. Fish were released to the location of collection upon recovery from anesthesia. A prior experiment showed the tagging procedure caused no mortality (Johnston and Smithson 1999). Study species collected on subsequent trips were checked for a paint mark and scanned for presence of a PIT tag. All fish that had no paint mark were marked, and untagged fish that fit the tagging criteria were tagged by the same procedures used on the initial collection trip.

Fish recaptured in the pool of initial collection, or home pool, were classified as nonmobile. They were assigned a value of zero meters moved (Freeman 1995). Fish recaptured outside of the initial pool of capture were classified as mobile. The distance traveled by a fish recaptured outside the initial collection pool was measured as the midpoint of the initial pool to the midpoint of the recapture pool (Stott 1967; Bruylants et al. 1986).

Data for all recaptured fish were examined to determine temporal and species-specific differences in movement behavior. Fish recaptured more than once were counted each time they were captured. To test for differences in movement behavior between species, the numbers of nonmobile and mobile fish recaptures were compared by chi-square analysis of mutual independence. Comparisons were made between standard lengths and distances moved of all recaptured fish to determine if there was a correlation between these two variables. Correlation analysis was also used to determine if there was a significant relationship between the number of days between tagging and recapture of fish and the distance moved upon recapture. A G-test for mutual independence was used to test for significant differences among collecting trips in frequency of recaptured fish showing movement (Sokal and Rohlf 1981).

To determine if the nonmobile and mobile groups were discrete, we compared characteristics of the tagged fish that did not move to those that did. We used t-tests with assumed unequal variances to evaluate the effect of fish size on movement behavior. Standard lengths of the recaptured fish that moved and those that did not move were compared, as were their weights.

The movement patterns of fish recaptured at least twice were examined to determine individual plasticity of movement. Movement behavior was divided into three categories: no movement, one-way movement, and complex movement. Recaptures found only in the home pool were assigned to the no-movement category. One-way movement indicated recaptures were made in any pool other than the pool of marking. Fish recaptured in one or more nonmarking pools and subsequently in their home pools were assigned to the complex-movement category.

To determine if emigration from the study reach confounded the recapture results, we compared recapture rates at times the study site was hydrologically isolated up- and downstream with recapture rates at times of through flow by means of G-tests for independence. Recapture rates compared across collections estimated sampling efficiency and overall activity of fishes.

Results

We found no evidence that movement of fishes into or out of the study site compromised our results. Recapture rates (all study species combined) on sampling dates when the study site was hydrologically isolated did not differ significantly from recapture rates on all the other sampling dates ($G = 0.0368$; df = 5; $P > 0.999$). Overall recapture rates generally increased over time: July 1995—8.5%; August 1995—24.5%; October 1995—25.5%; May 1996—40%; July—26.5%; August 1996—37%).

The majority of all four monitored species were recaptured in the pool of initial collection. Smaller proportions of the recaptured fish were collected outside of their home pools (Table 2).

There was a significant difference in the ratio of nonmobile to mobile recaptures between the four study species ($\chi^2 = 9.458$; df = 3; $P = 0.031$). No differences were found in movement behavior between creek chub, green sunfish, and longear sunfish when the contingency table was subdivided ($\chi^2 = 0.002$; df = 1; $P = 0.966$), but the proportion

TABLE 2.—Numbers of fish marked and recaptured (including multiple recaptures) in Glazypeau Creek.

Species	Number marked	Number (%)[a] recaptured	Number (%)[b] recaptured in home pool	Number (%)[b] recaptured out of home pool
Creek chub	112	25 (22)	22 (88)	3 (12)
Blackspotted topminnow	163	30 (18)	20 (67)	10 (33)
Green sunfish	679	201 (30)	176 (88)	25 (12)
Longear sunfish	364	231 (65)	199 (86)	32 (14)

[a] Percentage of number marked.
[b] Percentage of total number recaptured.

of mobile blackspotted topminnow was significantly greater than that of the three other study species combined ($\chi^2 = 7.69$; df = 1; $P = 0.006$). Nevertheless, standard lengths and weights did not differ significantly different between nonmobile and mobile fractions for any study species (Table 3). Moreover, correlation analysis showed no relationship between standard length of recaptured fish and distanced moved from the pool of initial collection to the pool of recapture (creek chub: $N = 25$, $r = 0.205$, $P = 0.414$; blackspotted topminnow: $N = 30$, $r = 0.041$, $P = 0.836$; green sunfish: $N = 201$, $r = 0.117$, $P = 0.284$; longear sunfish: $N = 231$, $r = -0.073$, $P = 0.493$). There also was no significant correlation between the number of days from tagging to recapture and distance moved (creek chub: $N = 21$, $r = -0.252$, $P = 0.314$; green sunfish: $N = 89$, $r = -0.0564$, $P = 0.640$; longear sunfish: $N = 91$, $r = -0.116$, $P = 0.213$).

Subsequent analyses were restricted to sunfishes because recaptures of other study species were too few and only sunfishes were recaptured more than once. The ratio of nonmobile to mobile recaptures did not differ between green and longear sunfishes ($G = 13.88$; df = 7; $0.05 < P < 0.10$), so recapture data for the two species were combined.

The majority of green and longear sunfishes recaptured outside their home pools were collected in the pools adjacent to the pools of initial collection (Figures 2, 3. Of the mobile sunfishes, 70% moved less than 100 m (Figure 4); the most distant recaptures were 453 m for a green sunfish and 506 m for a longear sunfish.

Of the 19 green sunfish recaptured more than once, 18 showed no movement from their initial pool and only 1 showed complex movement (Table 4). In contrast, nearly one-third of longear sunfish recaptured at least twice showed one-way or complex movements.

TABLE 3.—Mean standard lengths (mm) and weights (g) ± half-95% confidence intervals (CI) for nonmobile and mobile recaptured Little Glazypeau Creek fish.

Species and variable	Nonmobile: mean ± CI (range)	Mobile: mean ± CI (range)	P (t-test)
Creek chub			
Length	98.45 ± 8.12 (72–132)	107.8 ± 8.54 (99–114)	0.198
Weight	19.89 ± 4.37 (8.1–40.1)	25.47 ± 3.34 (23.2–28.8)	0.074
Blackspotted topminnow			
Length	57.35 ± 3.23 (43–72)	56.10 ± 2.24 (48–60)	0.538
Weight	3.57 ± 0.63 (1.6–7.1)	3.05 ± 0.47 (2.3–3.8)	0.210
Green sunfish			
Length	69.41 ± 2.24 (34–122)	70.96 ± 3.06 (44–114)	0.703
Weight	11.23 ± 3.09 (1.3–53.6)	12.57 ± 4.07 (2.3–41.6)	0.560
Longear sunfish			
Length	68.38 ± 2.08 (40–120)	68.36 ± 10.50 (33–105)	0.997
Weight	12.19 ± 3.60 (2.1–60.1)	13.07 ± 4.12 (1.3–39.1)	0.694

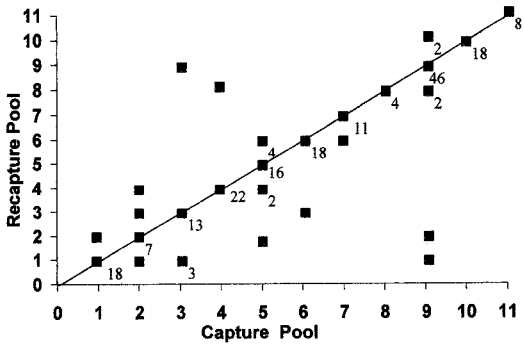

FIGURE 2.—Comparison of recapture pool with initial capture pool for green sunfish in Little Glazypeau Creek. Pool numbers are along the axes. Numbers next to data squares are numbers of fish recaptured (including multiple recaptures) in particular pools; squares with no numbers represent single recaptures.

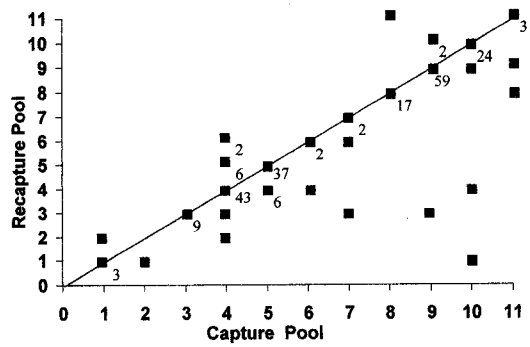

FIGURE 3.—Comparison of recapture pool with initial capture pool for longear sunfish in Little Glazypeau Creek. Conventions are those of Figure 2.

Discussion

The results of this study do not entirely support the restricted movement paradigm as defined by Gerking (1959). Although the majority of recaptured fish were in their home pools, some mobile fish also were recaptured. The mobile fish were collected predominately in pools adjacent to home pools, but some individuals traveled as many as 10 pools away. These results agree with other movement studies in showing that stream fish populations comprise a large static group and a small mobile group (Funk 1957; Stott 1967; Bruylants et al. 1986; Heggenes et al. 1991; Freeman 1995).

There was no temporal influence on the vagility of fish populations in this study. Ratios of nonmobile to mobile recaptured fish did not change significantly between the collecting trips of late May to mid-October, and movement did not increase as time between tagging and recapture increased.

We found no differences in length or weight between the nonmobile and mobile recaptures for the study species. Previous investigators designated static and mobile groups within a population, suggesting that these groups were discrete (Gowan et al. 1994). Prior reports indicated that the mobile component consisted of displaced intermediate-sized or less-fit individuals (Funk 1957; Bruylants et al. 1986; Heggenes et al. 1991; Gowan and Fausch 1996), that large fish were nonmobile (Larimore 1952), that large fish were mobile (Gerking 1953; Tyus and McAda 1984), or that the nonmobile and mobile groups did not differ (Stott 1967; Berra and Gunning 1972). Still other studies implied that nonmobile and mobile fishes were not in discrete groups, but that individual fish switched movement behavior (e.g., Harcup et al. 1984).

The multiple recapture of individuals in this study shows that fishes displayed complex, or exploratory, movement behavior. Coupled with the finding that there are no distinguishing characteristics of fishes that were mobile, this behavior suggests that movement plasticity was at the individual level. At any one time, a proportion of the population traveled outside of their home pool and that proportion was constantly turning over.

This type of behavior may not be exceptional. McVey (1955) reported complex movement behavior for three species of centrarchids that were recaptured several times in a lake. Fifty percent of bluegills *Lepomis macrochirus* recaptured twice or more displayed complex movement. Forty and 25 percent of multiple longear sunfish and green sunfish, respectively, exhibited complex movement. Large brown trout were detected shifting back and forth from daytime cover structures to nighttime cover structures in a stream (Clapp et al. 1990). Power (1984) suggested that "temporary migrant" loricariids left home pools to assess alternative habitats and then returned; she also provided evidence that fishes can remember habitats and that this capacity allows fishes to evaluate their home pool habitat in relation to other pools. Assessment of alternative home sites during regular exploratory trips provides an opportunity for recolonization (Freeman 1995). Complex movement enables species that are considered sedentary, such as longear sunfish, to recolonize defaunated areas

Although the number of our recaptured fishes was small, we assume, using the "slice in time" approach, that we obtained a representative sample of what was occurring. Because we used only one sampling method, however, larger individuals may

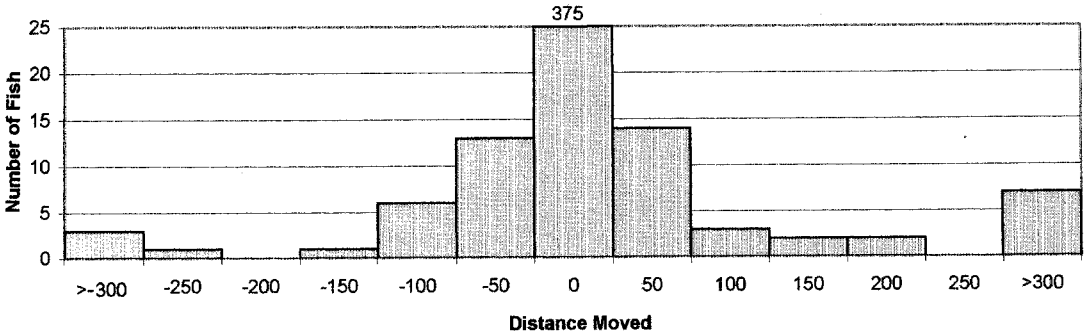

FIGURE 4.—Frequency distribution of distance moved (m) by recaptured green and longear sunfishes (combined) in Little Glazypeau Creek.

have been overrepresented in our samples. Low recapture rates, a common characteristic of mark–recapture studies of fishes, suggest marked fishes move out of the study area (Gowan et al. 1994). In our study, this hypothesis was not supported. Recapture rates did not differ between times the study site was hydrologically isolated and times it was not. Recapture rates increased as the study progressed, supporting the theory of restricted movement. A less-than-perfect recapture rate is due to sampling inefficiency, fish mortality, and the absence of those fish making exploratory or permanent trips out of the collecting area. Annual natural mortality of bluegills can be 56% (Ricker 1945). The percent of sunfish making exploratory trips away from a home pool in our study was 12–14%, so the percentage of tagged fish available for recapture may have been as low as 30% if mortality rates approached that for bluegill. The final overall recapture rate obtained in August 1996 was 37%. This suggests we obtained good results from our sampling efforts. We conclude that the samples collected provided representative data on the movement behavior of the study species.

The restricted movement paradigm does not fully define movements of stream fishes. In many home range studies, home range is defined as the area traveled routinely (e.g., Berra and Gunning 1972; Hill and Grossman 1987) and hence as the area where the majority of recaptures occur. Some studies suggest pools can be considered discrete units (Gerking 1959; Matthews 1986). Regular exploratory movements, however, extend the scale of importance of habitat beyond that of a home pool. Home range studies should encompass the range of movement by the mobile component, which may also represent common movement behavior. The purpose of exploratory movements may be to carry out some routine process that requires a different location. For example, Clapp et al. (1990) found that brown trout required a variety of habitats for a variety of purposes. In addition to defining the scale of habitat importance, routine exploratory movement of stream fishes is a mechanism for recolonization because it provides fishes an opportunity to assess alternative habitats. Sheldon and Meffe (1994) concluded that recolonization is a result of high mobility and "density-proportional equilibrium." Recolonization occurs by immigration balancing emigration with a continuing turnover.

This study demonstrated relatively restricted movement of stream fishes, suggesting that the selected species spend the majority of their time in a home pool but make visits into adjacent pools. This behavior implies that fisheries managers should consider larger areas of habitat as critical to stream fish populations. Additional information about the frequency and extent of exploratory movement is needed in order to predict the response of fish populations to disturbance, the impact of stocking fish, and the spatial requirements needed to manage a species.

TABLE 4.—Movement behaviors of Little Glazypeau Creek sunfishes recaptured two or more times.

Species	Number of fish recaptured at least twice	Movement behavior: number (%)[a]		
		No movement	One-way movement	Complex movement
Green sunfish	19	18 (95)	0	1 (5)
Longear sunfish	28	17 (61)	5 (18)	6 (21)

[a] Percentage of fish recaptured at least twice.

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