Effects of riffle length on the short-term movement of fishes among stream pools

D.G. Lonzarich, M.R. Lonzarich, and M.L. Warren, Jr.

Abstract: Recent research has suggested that the within-habitat dynamics of fish populations and assemblages can be affected by the spatial distribution of habitats within streams. In this study, we determined the extent to which pool isolation (length of riffles connecting adjacent pools) influenced fish movement in two Arkansas streams. We marked individuals from 12 pools assigned to two treatment categories: pools separated by long riffles (>50 m) and those separated by short riffles (<10 m). Repeatedly snorkeling pools for 3 days in 1995 and 1997, we discovered substantial emigration (>20%) and significant effects of riffle length. Total emigration from short-riffle pools was three times higher (29%) than movement from long-riffle pools (10%). Further, marked fish in short-riffle pools moved upstream and downstream with equal frequency, whereas fish in long-riffle pools moved twice as often downstream. Collectively, these results indicate significant effects of habitat spacing on short-term movement patterns by fish. In streams, where fish are distributed within a mosaic of habitats of varying quality, such movements may allow individuals to assess spatial variability in resource conditions (e.g., food, predators). Because land-use activities can alter habitat spacing, these findings have important implications for fish conservation in degraded streams.

Résumé : Des recherches récentes semblent montrer que la dynamique des populations et des assemblages de poissons au sein des habitats peut être influencée par la répartition spatiale des habitats dans les cours d'eau. Dans la présente étude, nous avons déterminé dans quelle mesure l'isolement des fosses (longueur des radiers reliant des fosses contiguës) influait sur le déplacement des poissons dans deux cours d'eau de l'Arkansas. Nous avons marqué les individus prélevés dans 12 fosses réparties en deux catégories expérimentales : fosses séparées par des radiers longs (>50 m) et fosses séparées par des radiers courts (<10 m). Des opérations répétées d'observation en plongée avec masque et tube pendant 3 jours, en 1995 et 1997, nous ont permis de découvrir une émigration importante (>20%) et des effets significatifs liés à la longueur des radiers. L'émigration totale des fosses à radiers courts était trois fois plus grande (29%) que les déplacements des poissons des fosses à radiers longs (10%). De plus, les poissons marqués dans les fosses à radiers courts se déplaçaient vers l'amont et vers l'aval avec une fréquence égale, tandis que les poissons des fosses à radiers longs se déplaçaient deux fois plus souvent vers l'aval. Collectivement, ces résultats indiquent que l'espacement des habitats a des effets significatifs sur les patrons de déplacement à court terme des poissons. Dans les cours d'eau, où les poissons sont répartis dans une mosaïque d'habitats de qualité variable, de tels déplacements peuvent permettre aux individus d'évaluer la variabilité spatiale de l'état des ressources (p. ex. la nourriture, les prédateurs). Étant donné que les activités d'aménagement des terres peuvent modifier l'espacement des habitats, ces résultats ont des incidences importantes pour la conservation des poissons dans les cours d'eau dégradés.

[Traduit par la Rédaction]

Introduction

Biologists have long been interested in the movement of fish in streams. Studies on movement contribute towards understanding the habitat needs of different species (reviewed by Gowan et al. 1994) and in delineating the spatial boundaries of populations (e.g., Hill and Grossman 1987; Freeman 1995). Additionally, knowledge of fish movement patterns can be useful in predicting the effects of physical barriers, which in streams exist in many forms. For example, persistent barriers such as waterfalls and debris dams can block migratory movements of fish, limiting access to stream reaches (e.g., Kruse et al. 1997) or restricting gene flow between populations (e.g., Congdon 1995; Fausch and Young 1995). In intermittent streams, dry riffle habitats create temporary barriers to interhabitat movement that can affect species richness and incidence patterns within isolated pool habitats (e.g., Taylor 1997).

To a lesser, although potentially important, extent, pool isolation also can arise in perennial streams where habitats are organized into discrete patches. Under such conditions, differences in water depth and current between pools and riffles may affect the degree to which pool-dwelling fishes traverse riffles to access neighboring pools. Gerking (1953) was probably the first to discuss this possibility when he proposed that long riffles separating adjacent pool habitats could act as behavioral barriers to movement and that fishes within individual pools could be viewed as discrete populations. Matthews et al. (1994) also speculated that riffles act as size-selective barriers to movement and affect pool as-

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semblage dynamics. Recent experiments have added weight to these earlier observations by showing that long riffles slow fish recolonization to defaunated pools (Lonzarich et al. 1998) and reduce fish movement between pools in experimental streams (Schaefer 1999).

Unlike waterfalls, riffles are neither permanent nor absolute barriers to fish movement. However, riffles are a much more common type of barrier in streams, and under certain conditions, their affects on interhabitat movement may lead to important ecological consequences. Because differences between stream habitats tend to be greatest during base flows, it may be at these times (e.g., summer) that riffles, especially long riffles, become effective barriers. While not preventing movement, long riffles may significantly reduce daily excursions between habitat patches and limit the ability of fish to track variability in food resources and predator densities.

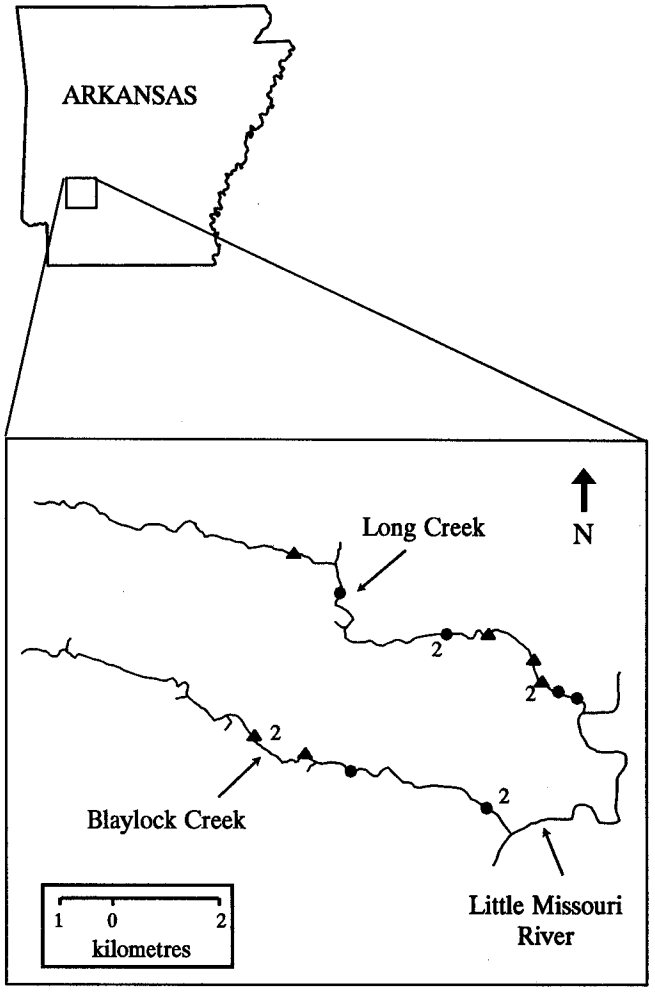
The potential impacts of habitat patchiness may be most severe in degraded streams where land-use activities modify stream channels or reduce the availability of habitat-forming woody debris (e.g., Karr and Schlosser 1978; Keller and Swanson 1979; Schlosser 1991). Such changes can reduce the frequency of pool habitats (Ralph et al. 1994), which in turn increases interpool distances (e.g., Beechie and Sibley 1997). Although many ecological impacts have been linked to land-use changes, much of the relevant research has focused on habitat-units (e.g., pools) or stream-scale responses. While recent research has begun to address the effects of land-use activities on habitat connectivity, fragmentation, and heterogeneity (e.g., Schlosser 1991, 1995; Ward 1998), the emphasis is on large spatial scales (i.e., riverine landscapes) and moderately long time scales (e.g., generations).

We strongly believe that efforts to better understand the ecology of stream fishes and, more specifically, the consequences of land-use activities will benefit from research aimed at addressing the relationship between fish movement and habitat patchiness. We undertook this study to characterize short-term, small-scale movements by a suite of pool-dwelling fishes in two Arkansas streams and to identify the extent to which these movements were affected by pool isolation (defined here by the length of riffles connecting adjacent pools). Our specific objectives were to (*i*) quantify fish movement over a 3-day period and (*ii*) describe whether pool isolation affected the degree or direction of overall and species-specific movement.

Materials and methods

We carried out this study in August of 1995 and 1997 in two tributary streams of the Little Missouri River in the Ouachita National Forest, Arkansas (Fig. 1). Long and Blaylock creeks are relatively short (<10 km), moderate-gradient systems that flow through predominantly forested and mountainous terrain. General characteristics of the streams included bedrock and gravel substrates and dense riparian vegetation. The proportion and average size of pool and riffle habitats in the two streams were similar (Clingenpeel 1994) as were the composition, rank dominance, and densities of fish species (Lonzarich et al. 1998). Physical and biological conditions during the two years of the study also were very similar. Flow conditions, as reflected by average riffle depth, did not differ between the two years (two-sample t test, $P = 0.87$). Further, the relative abundances of the five target species during the 1995 and 1997 surveys were very highly correlated (Spearman rank test, $r = 0.90$).

Fig. 1. Location of short-riffle (●) and long-riffle (▲) pools in Long and Blaylock creeks (34°22′30″N, 93°52′30″W). Sites labeled with the number "2" were included during both survey years.



Experimental design

We assigned 12 pools from the two streams equally into two different treatment categories based on riffle length. Short-riffle pools were separated from adjacent upstream and downstream pools by riffles <10 m long (mean = 8.1 m, 1 SE = ±1.5), and long-riffle pools were separated from adjacent pools by riffles ≥25 m long (mean = 50 m, 1 SE = ±12.2) (Table 1). With the exception of these differences, the average physical dimensions of pools in the two treatment groups were similar (two-sample t test, $P > 0.10$) (Table 1). Of the six pools in each treatment, two were surveyed in both 1995 and 1997. Although it was unlikely that the same individuals were collected in both years, we nonetheless combined the 1995 and 1997 data from these pools; thus, each treatment consisted of six replicated pools.

We marked a subset of the fish species that commonly occur in the two streams. We did not mark juvenile fish (<50 mm total length) or cryptic bottom-dwelling species, which are difficult to locate using visual survey techniques. We included central stoneroller (*Campostoma anomalum*), striped shiner (*Luxilus chrysocephalus*), northern studfish (*Fundulus catenatus*), longear sunfish (*Lepomis megalotis*), and smallmouth bass (*Micropterus dolomieu*).

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Table 1. Physical characteristics of short-riffle and long-riffle pools in Long and Blaylock creeks.

Treatment	Mean width (m)	Mean length (m)	Mean area (m^2)	Mean depth (cm)	Riffle length (m)
Short riffle	6.4	27	181	52	8.6
Long riffle	6.3	32	198	55	51

Note: With the exception of riffle length, average habitat conditions of pools were statistically similar for both treatments (two-sample t tests, $P > 0.10$).

At each site, we collected fish by isolating the experimental pool with 6-mm-mesh block nets and sampling with a Smith–Root battery-powered backpack electrofisher. We typically sampled each pool for 30 min to 1 h or until no target species were collected on two consecutive passes. Fish were marked with treatment-specific caudal fin clips (i.e., long-riffle pools: upper caudal; short-riffle pools: lower caudal) and held overnight in a covered 2 × 2 m holding pen. We held fish because preliminary surveys indicated potentially high rates of emigration immediately after marking as a probable result of handling stress. In reviewing the methods of several movement studies, we discovered that this practice is not common. Typically, marked individuals are released immediately after being handled (e.g., Hill and Grossman 1987; Mundahl and Ingersoll 1989; Gatz and Adams 1994). While this approach may be acceptable in many situations (see Gowan and Fausch 1996), a recent study by Nordwall (1999) showed that electrofishing significantly increased the mobility of brown trout (*Salmo trutta*), especially within 24 h of handling (F. Nordwall, Department of Aquaculture, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden, personal communication). Because we allowed fish to recover from handling for approximately 24 h before removing the block nets, we felt that the risk of stress-related emigration was reduced, especially when compared with other movement studies.

The morning after marking, we released individuals from the holding pens but did not remove the block nets for 1 h. This allowed fish to move freely within the experimental pool and to reacclimate to pool conditions. Thirty minutes after removing the block nets, we initiated snorkeling surveys for marked fish in upstream and downstream pools immediately adjacent to the experimental pool. Simultaneous surveys of the two pools were completed hourly between 11:00 and 17:00 (six censuses) on day 0 and once per day between 11:00 and 14:00 on day 1 and day 3 for a total of eight censuses of marked fish. On day 1 and day 3, we expanded our snorkeling censuses to include the experimental pool and the second upstream pool and second downstream pool in the study reach. On day 0, we limited censuses of the experimental pool to the final survey (17:00) in order to minimize the risk that snorkeling might artificially inflate emigration.

We used visual census techniques rather than electrofishing, largely because our sampling design required repeated fish counts over short periods. We have shown previously that population estimates generated from snorkeling surveys in these streams are nearly identical to those generated from more invasive and labor-intensive electrofishing surveys (Lonzarich et al. 1998). High water clarity provided excellent conditions for identifying marked fish from distances up to 3 m.

An important assumption of our study was that marked fish observed in upstream and downstream pools accurately reflected emigration from experimental pools and was not biased downwards by fish emigrating from an experimental pool to become established in intervening riffles. Although we previously found strong differences in the pool and riffle assemblages of these streams (Lonzarich et al. 1998), we tested this assumption by tracking changes in the percentage of marked fish within experimental reaches. Our decision to accept or reject this assumption was based on an evaluation of the degree to which the total number of marked fish in long-riffle and short-riffle study reaches approximated the total number marked.

Statistics

We computed the proportion of emigrants (for each survey period) and the direction of emigration (either upstream or downstream) for all experimental pools. To test for treatment differences in emigration, we used two-sample t tests based on the maximum proportion of emigrants per pool (across all surveys). In long-riffle pools, the maximum number of known emigrants was typically observed on day 3, while in short-riffle pools, the maximum number was most often observed on day 1. Where proportion data deviated from normality, we performed square root arcsine transformations prior to analysis. We determined the directionality of movement by dividing the maximum number of marked fish that emigrated downstream by the combined number of emigrants. From this approach, values above 50% indicated a downstream bias in movement and below 50% indicated an upstream bias. To determine whether movement within a treatment was statistically biased in either direction, we employed the chi square goodness-of-fit test using the total number of upstream and downstream emigrants per treatment.

Results

General patterns of movement

We marked nearly 1800 individuals of the five target fish species, or an average of 147.7 (1 SE = ±19.7) individuals in each experimental pool (Table 2). Most marked fish were central stoneroller and striped shiner, and with the exception of striped shiner, we marked comparable numbers for each species in the two treatment categories. Our rates of resighting marked fish were high. For example, we observed an average of 70% (1 SE = ±3.5%) of the marked fish on the last hourly census of day 0 and 59% (1 SE = ±3.4%) on the last census (day 3).

We documented considerable movement of marked fish over the 3-day trial period. Overall, nearly one fifth (19%) of all marked individuals were observed in pools upstream or downstream of the experimental pools by day 3. Total movement by smallmouth bass (19%), central stoneroller (22%), and striped shiner (19%) were slightly higher than estimates for northern studfish (15%) and longear sunfish (13%). Overall movement was not directionally biased (52% of marked fish moved downstream and 48% moved upstream, Table 3). The only species showing any directional bias was smallmouth bass, which moved upstream twice as often as downstream (65 versus 35%, respectively; chi-square goodness-of-fit test, $P = 0.06$).

Treatment differences

Marked fish emigrated from short-riffle pools much more frequently (up to 10-fold) than from long-riffle pools. When examining emigration patterns on day 0, we found that 10%

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Table 2. Total and average number of fish marked (per pool) from short-riffle and long-riffle pools in the two study streams.

Species	Short riffle	Long riffle	Average per pool
Central stoneroller	455	407	71.8
Striped shiner	177	363	45
Northern studfish	23	18	4.3
Longear sunfish	132	106	19.8
Smallmouth bass	42	43	7.1
Total	829	937	147.7

(1 SE = ±1.0%) of the marked fish in short-riffle pools had emigrated by the first survey. By comparison, no emigrants were observed from long-riffle pools until at least the third hour, and generally very few fish emigrated on day 0 (1.4%). This pattern held for the duration of the 3-day survey period. For all species combined, an average high of 29% (1 SE = ±1.5%) of marked fish were observed outside of experimental short-riffle pools whereas the average high for long-riffle pools was only 10% (1 SE = ±0.9%), or three times less than the percentage moving from short-riffle pools ($P < 0.01$). Because we confined snorkeling surveys to the two pools upstream and two pools downstream of the experimental pools, we consider these to be conservative estimates of movement.

In an effort to estimate the amount of movement beyond the study site boundaries, we graphed changes in the average percentage of marked fish within each study reach across the 3-day survey period (Fig. 2). These results show that the proportion of marked fish counted within long-riffle reaches did not change over time. In contrast, the percentage of marked fish declined sharply over time in short-riffle reaches from 67% for day 0 to 50% for day 3 (repeated measures ANOVA, $P = 0.02$). Assuming that all of these individuals (17%) moved beyond study reach boundaries by day 3, the actual percentage of fish emigrating from short-riffle pools appeared to be much higher than the average emigration of 29% that actually was observed.

To better describe the shape of the relationship between riffle length and emigration, we produced a multiple regression model using movement data collected for all 24 upstream and downstream riffles that were adjacent to the 12 experimental pools. Incorporating as factors both the potential emigrant pool (i.e., number tagged) and riffle length, our multiple regression model explained 60% of the variation in the emigration patterns of the target species. The model (emigrant number = 25.0 − 8.5 × ln riffle length + 0.09 × number tagged) showed that emigration was negatively affected by riffle length and to a much lesser degree positively correlated with the number of potential emigrants.

Fish from long-riffle pools not only emigrated less frequently, but they also showed a strong directional bias to movement that was not evident in short-riffle pools. Although marked fish from short-riffle pools moved upstream and downstream with equal frequency (chi-square goodness-of-fit test, $P = 0.70$, Table 3), emigrants from long-riffle pools moved downstream twice as often as they moved upstream (67 versus 33%; chi-square goodness-of-fit test, $P < 0.01$). This pattern held for three of the four species that moved from long-riffle pools. The exception was smallmouth bass, which showed a tendency to move upstream more often than downstream (chi-square goodness-of-fit test, $P = 0.07$).

Table 3. Percentage of marked fish that moved into sites downstream of experimental pools.

Species	All pools (%)	Long-riffle pools (%)	Short-riffle pools (%)
Central stoneroller	51	74**	45
Striped shiner	52	71**	46
Northern studfish	50	—	50
Longear sunfish	59	77[b]	45
Smallmouth bass	35[b]	23[b]	75[a]
Overall	52	67**	48

Note: Values were derived by dividing the number of marked fish downstream by the total number of emigrants. For each species, directional bias in movement was computed by chi-square goodness-of-fit test. *$P < 0.05$; **$P < 0.01$.

[a]Insufficient data for analysis.

[b]$P < 0.10$.

Treatment differences for individual species were highly variable, although there were strong similarities within families. Results for the two cyprinid species (central stoneroller and striped shiner) showed consistently high rates of movement from short-riffle pools (36 and 33%, respectively) and low rates from long-riffle pools (7 and 9%,) (two-sample t tests, $P < 0.01$). For northern studfish, we only observed movement from short-riffle pools (26%). By contrast, estimates of emigration for the two centrarchids revealed no general pattern. Smallmouth bass moved more often from long-riffle pools (28 versus 10%), although this difference was only weakly significant (two-sample t test, $P = 0.09$), whereas longear sunfish emigrated with equal frequency from pools in the two treatments. We note, however, that the average movement by longear sunfish from long-riffle pools was affected strongly by results from one site. When we removed the data from this site, the average for this species declined more than 50% (13 to 6%). This new estimate was slightly lower than the average movement from short-riffle pools (14%, two-sample t test, $P = 0.07$).

Discussion

General patterns of movement

Based on observations encompassing nearly 1800 marked fish, movement patterns within our two study streams could be generally described as a diffusive process, with target species spreading equally in upstream and downstream directions from experimental pools.

Even if we exclude individuals that moved beyond the study area boundaries, the levels of movement documented here are high when compared with results from similar studies. Minimally, one fifth of all marked fish emigrated from experimental pools, moving 30–100 m into neighboring habitats, over the 3-day trials. These numbers are remarkable, given that most studies report significantly less movement over much longer periods of time. For example, in an 18-month study, Hill and Grossman (1987) estimated that the home range size of three small warmwater fish species was less than 20 m. Specific home range estimates for smallmouth bass and longear sunfish are slightly higher,

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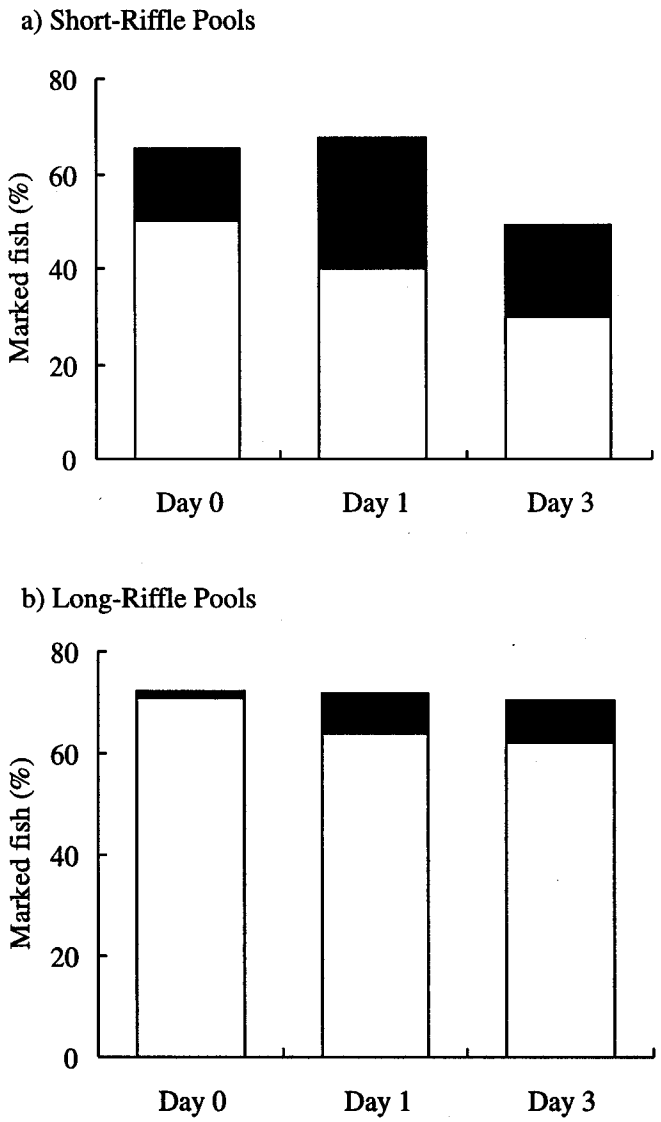
Fig. 2. Percentage of marked fish moving from (black bars) and remaining within (white bars) (*a*) short-riffle pools and (*b*) long-riffle pools on each day of the 3-day survey period. Only in the short-riffle treatment did daily percentages of fish observed in experimental pools decline significantly over time (repeated measures ANOVA, $P = 0.02$). Percent emigrants for day 0 reflect data for marked fish observed one pool upstream and one pool downstream of the experimental pool. For day 1 and day 3, these percentages were based on marked fish observed two pools upstream and two pools downstream.



ranging from 30 to 100 m (Gerking 1953; Berra and Gunning 1972). Mundahl and Ingersoll (1989) estimated that central stoneroller moved an average of only 35 m in 1 month.

Although we cannot estimate maximum movement distances for our marked fish, our results do not support the long-held view of restricted fish movement first proposed by Gerking (1953, 1959). Since his seminal work, research on fish movement has overwhelmingly supported the idea that stream fishes are restricted to relatively small areas (see review by Gowan et al. 1994). This view of spatially discrete populations has important biological implications. For example, it forms the basis for the strong species–habitat relationships often found in streams (e.g., Gorman and Karr 1978). Moreover, habitat and species management decisions are by necessity based on information concerning the home range size of target species.

Funk (1955) and Gowan et al. (1994) presented strong challenges to the restricted movement model. In his study of fishes in Missouri streams, Funk (1955) recorded extensive movement by 14 species (up to 40 km) and concluded that stream fish populations consist of both mobile and sedentary individuals. More recently, Gowan et al. (1994) measured extensive movement in stream-dwelling brook trout (*Salvelinus fontinalis*) and argued that field studies might be seriously biased against detecting movement. They were particularily critical of the cavalier dismissal of characteristically low recapture rates (<50%) in data analyses of traditional movement studies. They claimed, and we agree, that low recapture rates may in fact represent the movement of fishes beyond study area boundaries. Supporting the view of extensive fish movement are studies on fish recolonization that measure movement indirectly. These studies have universally shown very rapid (i.e., hours to months) movement into defaunated reaches and habitat-units (e.g., Matthews 1986; Sheldon and Meffe 1995; Lonzarich et al. 1998). Recently, Warren and Pardew (1998) found retention rates within 36-m segments of <30% of marked fishes, suggesting up to a 70% emigration rate over a 17-day period. Smithson and Johnston (1999) also measured movement as high as 33% for fishes in a nearby Arkansas stream.

Effects of riffle length on movement

Our results indicate a very strong relationship between the proximity of neighboring stream pools (as determined by intervening riffle lengths) and daily interhabitat movements of fishes. These findings are consistent with a previous study where we found that long riffles significantly slowed fish recolonization to defaunated pools (Lonzarich et al. 1998). Schaefer (1999) also reported an effect of riffle length on movement in an artificial stream channel; however, ours is the first study to quantify the degree to which riffles restrict short-term fish movement between patches in natural streams.

In some respects, these findings are not surprising, given that ecologists have long recognized the effects of habitat isolation, or interpatch distance, on the movement of organisms between equivalent habitat patches (e.g., Forman and Godron 1986; Forman 1995). As is true for organisms in other spatially heterogeneous environments, fish in streams are distributed within a mosaic of habitats of varying quality (e.g., food availability, predator densities, physical conditions). Under these conditions, fish may make frequent explorations of different habitats (e.g., pools) in search of food resources (Fraser and Sise 1980). However, as indicated by our results, long riffle corridors can limit these excursions by pool-dwelling species and therefore may reduce the ability of individuals to evaluate differences in resource conditions (e.g., food, predators) across pools. Matthews (1998) also speculated that shallow riffle corridors, acting as filters to the movement of small-bodied prey and large-bodied predators, could affect predator–prey relationships in stream reaches.

As suggested by Matthews (1998), water depth probably contributes significantly to the restricted movement of fish

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through riffle corridors, possibly due to the fact that shallow waters expose fish to terrestrial predators (e.g., Power 1984, 1987). We would add water currents as a factor as well, especially for long riffles, where strong currents may prove difficult to negotiate. Although direct tests of these potential factors are lacking, Warren and Pardew (1998) measured strong effects of water current on fish movement across shallow-water road crossings, and we found that fish from long-riffle pools moved significantly less frequently against the current (upstream) than with the current (downstream). We also have measured a negative effect of water depth on fish recolonization to defaunated stream pools (Lonzarich et al. 1998).

While we suspect that these factors are important determinants of fish movement through long riffles, we are careful not to extrapolate beyond the temporal scope (i.e., hours or days) and low-flow conditions that characterized our study. In fact, we question whether potential survival or energy costs associated with traversing long riffles affect patterns of fish redistribution during floods or seasonal migrations to spawning or wintering habitats. Still, the timing of this study (the summer) coincided with a critical period in the life cycle of stream fish species. Not only is this the season when fish experience their most favorable growing conditions, it is also when competition and threats of predation, especially for juveniles, can be very intense.

The potential effects of pool isolation that we envision are derived from two streams with moderately high pool to riffle ratios. We would not expect any habitat isolation in sandy bottom streams that lack the physical conditions necessary to promote riffle development. However, we would predict even more severe effects of pool isolation in small, high-gradient, and gravel-bottom mountainous streams where neighboring pools can be isolated by long stretches of shallow water and high-gradient riffles (e.g., Beechie and Sibley 1997).

In conclusion, we believe that our results add significantly to our understanding of how spatial variability in habitats affects the distribution and dynamics of fish populations and assemblages in streams. Moreover, because land-use activities can change channel characteristics and alter the spacing of stream habitats, our findings may aid in efforts to better predict the ecological consequences of such activities.

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