

CONSEQUENCES OF POOL HABITAT ISOLATION ON STREAM FISHES

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Abstract—For fishes, stream habitat units (i.e., pools and riffles) often exist as relatively discrete patches of varying quality that are distributed in a mosaic along the stream continuum. Under these conditions, the possibility exists that the spacing of suitable patches within a stream reach may affect interhabitat movements of fishes and their pattern of distribution within habitat patches. We summarized the findings of two different, but related, studies that demonstrated how isolation of pools by long and shallow riffles affected recolonization and daily movement patterns of pool dwelling fishes in two Arkansas streams. Our results show for the first time that the spatial distribution of habitats within streams can significantly affect the abundance of species and characteristics of fish assemblages within pool habitats. Because land use activities can alter habitat spacing, our findings also have important implications for fish conservation in degraded streams.

INTRODUCTION

Characteristics of fish assemblages within stream habitats are shaped by physical and biological factors that operate at different temporal and spatial scales (e.g., Poff 1997). Stream ecologists are obligated to determine habitat variables that most influence fish and the spatial scale(s) over which they operate (Rabeni and Sowa 1996). To make predictions, stream researchers have long used information about the physical characteristics of streams and knowledge of the hierarchical nature of the stream environment (e.g., Frissell and others 1986, Naiman and others 1992). Physical features of habitat units (e.g., pools, riffles) such as area or volume (Schlosser and Angermeier 1989), depth, water current, cover, and substrate (Gorman and Karr 1978), often correlate strongly with patterns of fish diversity, richness, and biomass. At large spatial scales (e.g., reaches, watershed), important factors may include flow regime (e.g., Horwitz 1978), temperature, valley form, distance to mouth, and zoogeographic history.

Species distribution and assemblage patterns are shaped by these natural controls and changes in the physical environment that can accompany land use activities. Land use practices, especially those associated with the removal of riparian vegetation, can lead to changes in stream temperature, flow, nutrient input, and habitat quality (Hicks and others 1991, Schlosser 1991). In degraded streams, reduced availability of habitat forming woody debris can reduce the abundance of pools in a stream (e.g., Keller and Swanson 1979, Schlosser 1991). A potentially important, though poorly appreciated, consequence of such a change is that the loss of pool habitat also reduces the frequency (Ralph and others 1994) and therefore increases the spacing (e.g., Beechie and Sibley 1997) of these habitats within the stream.

Although the ecological impacts of land use disturbances have been widely studied, the historical focus was on small scale impacts occurring within stream habitats or reaches (e.g., Schlosser 1982, Hicks and others 1991). Recent

papers have addressed some of the effects of land use activities on habitat connectivity and fragmentation of streams (e.g., Schlosser 1991, Rieman and McIntyre 1995, Schlosser 1995, Ward 1998), but these efforts focused on large spatial scales (e.g., riverine landscapes) and moderately long time scales (e.g., generations). Effects of fragmentation on fish behavior (e.g., foraging, habitat selection, and response to disturbance) remain poorly understood over short time periods and at small spatial scales.

Riffles are typically the corridors connecting neighboring pools in stream systems with well-developed habitats. Characteristics of riffles (e.g., shallow depths, fast currents) may limit the ability of pool dwelling fishes to access neighboring pools. Access to neighboring pools may be particularly limited if pools are infrequent or spacing of pools is increased in association with habitat degradation. Although riffles may not preclude all fish movement, long riffles may significantly reduce excursions between habitat patches, slow immigration to new habitats, and limit the ability of fish to track variability in food resources and predator densities.

Effects of Isolation on Response to Disturbances

Episodic disturbances, such as floods and droughts, are major factors shaping the organization of stream communities (e.g., Pearsons and others 1992, Strange and others 1992). The rate at which assemblages recover from disturbance will depend strongly on how rapidly different fish species recolonize disturbed stream segments. A large body of evidence indicates that recolonization of disturbed stream segments by fishes can be fairly rapid (< 1 yr, e.g., Niemi and others 1990). Recovery of fish assemblages in short reaches and habitat units can occur on the scale of days and weeks (Peterson and Bayley 1993, Sheldon and Meffe 1995). Nevertheless, research thus far has revealed little about physical factors that contribute to recovery, especially at small spatial scales (Detenbeck and others 1992). For example, is recolonization influenced by the size of the habitats affected or by the degree to which affected habitats are isolated from source habitats as predicted by Island Biogeography Theory (MacArthur and Wilson 1967).

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Effects of Isolation on Short Term Movement

Biologists have long been interested in the movement of fish in streams though few have studied how habitats, when organized into discrete patches, may affect movement behavior. Gerking (1953) was probably the first to discuss the possible effects of patchiness 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 and others (1994) also speculated that riffles act as size selective barriers to movement and affect pool assemblage dynamics. Recent experiments added weight to earlier observations by showing that long riffles slow fish recolonization to defaunated pools (Lonzarich and others 1998) and reduce fish movement between pools in experimental streams (Schaeffer 1999).

One message that emerges from field and experimental studies is that the spatial mosaic of stream habitats may significantly influence the short term movements of fish. At least with respect to short time scales (i.e., days, weeks), the spatial arrangement of pools and riffles in streams may have significant ecological implications. For example, pool dwelling fish may need to traverse long, shallow riffles to access suitable habitats. Depending on the distance between adjacent patches (i.e., length of intervening riffles), these movements may entail high energetic costs or high predation risks (e.g., Power 1987).

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 effects of habitat patchiness on fish movement. In this paper, we summarize the major findings and discuss the general implications of two different, but closely related, studies that examined the effects of habitat isolation on recolonization and daily movement patterns of pool dwelling fishes in two Arkansas streams. Complete descriptions of the results of both experiments can be found elsewhere (Lonzarich and others 1998, Lonzarich and others, in press).

METHODS

Study Area

We carried out the experiments in the summers of 1995 and 1997 in two tributaries of the Little Missouri River in the Ouachita National Forest, west central Arkansas (34°22'30"lat and 93°52'30"long). Long and Blaylock creeks are 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 abundance, and densities of fish species (Lonzarich and others 1998).

Experimental Design

General features—We selected pools from the two streams and assigned them equally into two treatment categories based primarily on differences in the lengths of adjacent riffles. Short riffle pools were separated from adjacent up-

stream and downstream pools by riffles < 10-m long; long riffle pools were separated from adjacent pools by riffles which averaged ≥ 50 m in length. With the exception of these differences, the physical dimensions of pools in the two treatment groups were similar (Lonzarich and others 1998, Lonzarich and others, in press). The recolonization experiment included 12 treatment pools (6 pools per treatment), and the movement experiment included 16 pools (8 pools per treatment).

In both experiments, we collected fishes by isolating survey pools with 6-mm mesh block nets and sampling with a Smith Root battery powered, backpack electrofisher. For the recolonization experiment, we sacrificed collected fish or relocated them downstream of barriers to upstream movement. For the movement study, we marked collected fish with treatment specific caudal fin clips (i.e., long riffle pools, upper caudal fin; short riffle pools, lower caudal fin).

Species composition, rank dominance, and fish densities in Long and Blaylock creeks were very similar (Lonzarich and others 1998). In both experiments, we focused on a subset of fish species. Because of concerns over sampling efficiency, we did not include small, juvenile fish (< 25 mm) or bottom dwelling species that often hide within the substrate and can be difficult to locate without considerably increasing survey times. We excluded four bottom dwelling species from the survey: northern hog sucker, *Hypentelium nigricans* (Lesueur); orangebelly darter, *Etheostoma radiosum* (Hubbs and Black); greenside darter, *E. blennioides* Rafinesque; and yellow bullhead, *Ameiurus natalis* (Lesueur). Numerically, these species and small juveniles were a minor component of the pool assemblages, accounting for less than 10 percent of all fish collected by electrofishing (Lonzarich and others 1998). We included seven target species in the surveys: central stoneroller, *Camptostoma anomalum* (Rafinesque); striped shiner, *Luxilus chrysocephalus* (Rafinesque); redbfin shiner, *Lythrurus umbratilis* (Girard); bigeye shiner, *Notropis boops* Gilbert; northern studfish, *Fundulus catenatus* (Storer); creek chub, *Semotilus atromaculatus* (Mitchill); longear sunfish, *Lepomis megalotis* (Rafinesque); and smallmouth bass, *Micropterus dolomieu* Lacepede.

We quantified both recolonization and short term movement using underwater observation rather than electrofishing largely because our sampling design required repeated fish counts over short periods. We previously showed that population estimates generated from snorkeling surveys are nearly identical to those generated from more invasive and labor intensive electrofishing surveys (Lonzarich and others 1998). High water clarity in each stream provided excellent conditions for identifying marked fish from distances up to 3 m.

Recolonization protocol—We censused fish in experimental pools by snorkeling immediately prior to electrofishing (Day 0, predisturbance census), and then 1, 3, 10, 20, 30, and 40 days following the removal of target species. To minimize observer error, the same person surveyed all pools, and two consecutive censuses were performed for each survey. The mean of these two counts was used in statistical analyses.

For this summary, we limited characterization of recovery patterns for species and entire pool assemblage to changes in the relative abundance of fish within each pool. We divided counts (individuals per pool) obtained for any post disturbance census by predisturbance counts from Day 0 so that a relative abundance of 100 percent indicated complete recovery. Using relative abundance data for each survey date, we generated regression models to characterize recovery patterns and rates for each treatment group. The model that best explained the relationship between time and recovery had the following linear form:

$$\ln(\text{Recovery}) = \ln(a) + b \cdot (\ln(\text{Day} + 1)) \quad (1)$$

where recovery is either assemblage or species recovery (relative numbers), and b , the regression coefficient, represented the recovery rate. We used a two sample t test to compare differences in mean assemblage and species recovery rates (b) in the two treatment groups. We determined the effects of other independent variables (i.e., riffle depth, distance to large pool, pool area and assemblage size) on pool specific recovery rates by least squares regression. If percentage data deviated from normality, we performed square root arcsine transformations prior to analysis.

Movement protocol—We marked nearly 1,900 individuals from the 16 experimental pools. After marking, we held all fish overnight and released them into their experimental pools 30 min before we initiated snorkeling surveys. In upstream and downstream pools immediately adjacent to the experimental pool, we completed simultaneous surveys hourly between 1100 to 1700 h (6 censuses) on Day 0 and once per day on Day 1 and Day 3 between 1100 to 1400 h for a total of 8 censuses of marked fish. On Day 1 and Day 3, our snorkeling censuses included 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 (1700 h) to minimize the risk that snorkeling might artificially inflate emigration.

An important assumption of our study was that marked fish observed in upstream and downstream pools accurately reflected emigration from experimental pools and were not biased downwards by fish emigrating from an experimental pool to become established in adjacent riffles. We accepted this assumption on the basis of previous research where we found strong differences in pool and riffle assemblages of these streams (Lonzarich and others 1998).

We estimated the rate, direction, and percentage of emigrants from each pool. We determined movement rates (fish per h) by least squares linear regression models using data from Day 0 hourly surveys. Because the general shape of the relationship between time and movement was logarithmic, the model showing the best fit to the data had the following general form:

$$\text{Movement} = a + b \cdot \ln(h + 1) \quad (2)$$

where movement represented the percentage of marked fish observed outside of the experimental pool and b , the regression coefficient, represented the movement rate. We generated species specific and assemblage level linear regression models for each experimental pool. To test for

treatment differences in the rate of movement, we compared mean movement rates (b) for each treatment using a two sample t test. We determined the directionality of movement by dividing the number of marked fish that moved downstream by the combined number of emigrants. Hence, values above 50 percent indicated an upstream bias in movement and values below 50 percent, a downstream bias. We computed the percentage of emigrants from each pool by dividing the maximum number of known emigrants by the total number of fish marked in the experimental pool. We typically observed the maximum number of emigrants on Day 3 in long riffle pools and on Day 1 in short riffle pools. We tested for species and assemblage level differences in movement patterns (i.e., rate, proportion, and direction) between the two treatment groups using two sample t tests (rate and proportion) and 2×2 Chi square tests of independence (for direction). If percentage data deviated from normality, we performed square root arcsine transformations prior to analysis.

RESULTS

Effects of Isolation on Recolonization

Numerical recovery was influenced strongly by factors that isolated experimental pools from potential colonists. In short riffle pools, assemblages reached full numerical recovery by day 30, whereas assemblages in long riffle pools reached only 75 percent of their predisturbance densities by day 40 (fig. 1). Estimates of full recovery based on data extrapolation ranged from 100 to 130 d for long riffle pools. Over the entire recovery period, the mean (± 1 S.E.) recovery rate in long riffle pools was 33 percent lower (20 ± 0.6 percent per $\ln(d)$) than the rate for short riffle pools (30 ± 1.5 percent per $\ln(d)$, t test, $P < 0.05$). In addition, recovery was correlated positively with riffle depth ($r^2 = 0.37$, $P < 0.05$, fig. 2a) and negatively with distance to the nearest large source pool ($r^2 = 0.44$, $P < 0.05$, fig. 2b). These patterns held even when pools within each riffle length category were examined separately. Neither predisturbance assemblage size nor pool area had any detectable influence over numerical recovery rates of assemblages ($P > 0.50$, fig. 2c).

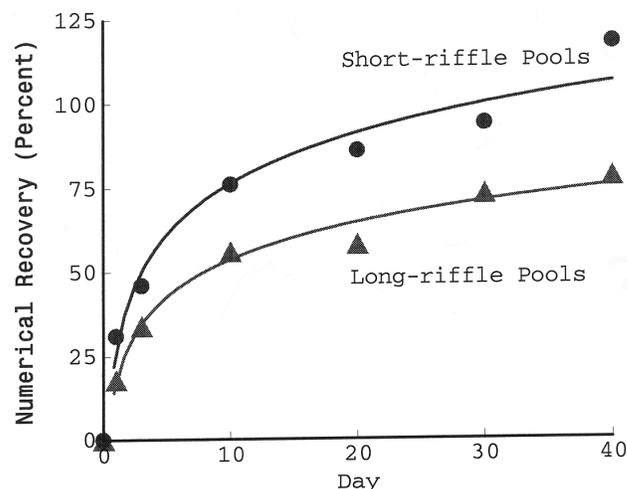


Figure 1—Comparisons of percent numerical recovery for each riffle length category. Error bars represent ± 1 S. E. Data points and error bars are offset to increase clarity.

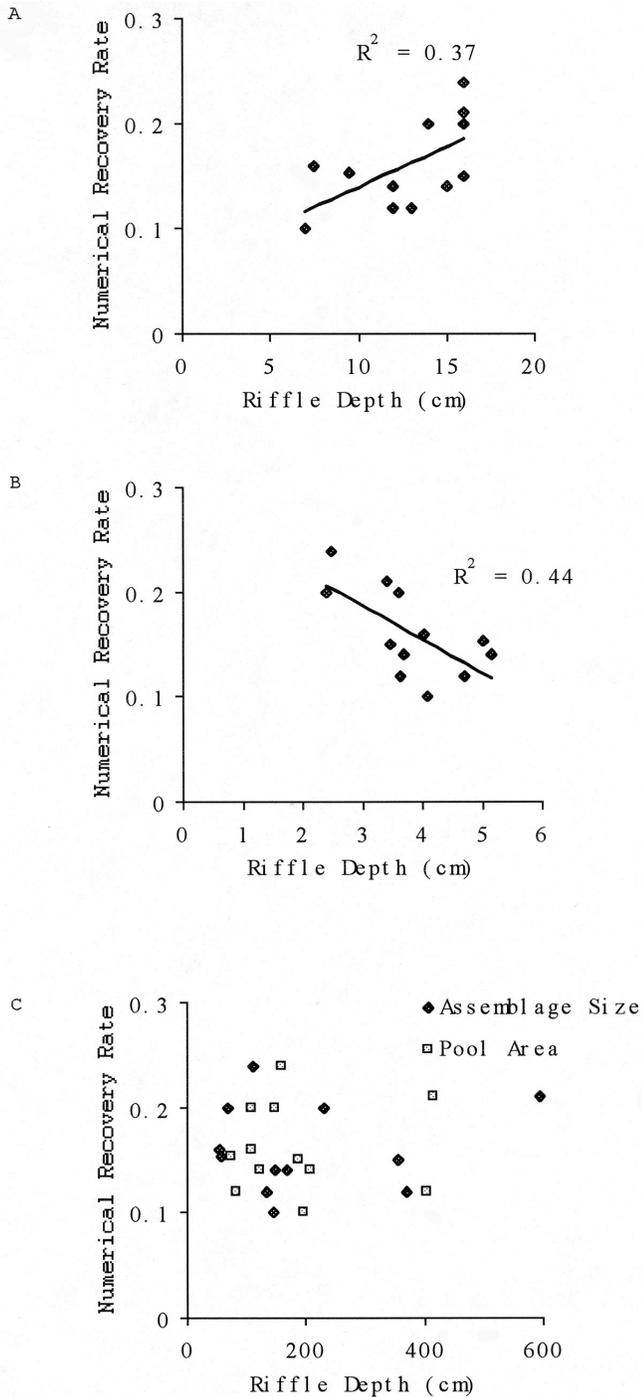


Figure 2—Relationships between estimated recovery rates (A) riffle depth, (B) Ln distance to large pool, and (C) predisturbance assemblage size and experimental pool area.

Effects of Isolation on Short Term Movement

Marked fish emigrated from short riffle pools much more frequently (up to 10 fold) than from long riffle pools. The emigration rate (± 1 S.E.) from short riffle pools on Day 0 was seven times higher ($b = 6.9 \pm 0.7$ percent per $\ln(h)$) than the estimated rate for long riffle pools ($b = 1.0 \pm 0.3$ percent per $\ln(h)$, t test, $P < 0.01$). In short riffle pools, we commonly

observed emigrants during the first count, while in long riffle sites, we did not see emigrants until at least the third hour and generally observed very few on Day 0 (< 2 percent). By Day 3, we observed an average of 30 percent ($1 \text{ SE} = \pm 3.8$ percent) of marked fish outside of experimental short riffle pools. In contrast, the average for long riffle pools was only 9 percent ($1 \text{ SE} = \pm 2.3$ percent).

When we account for all marked fish observed within each site, differences in emigration between treatments become even more trenchant. Expressed as a percentage of the total number marked, the proportion of marked fish observed within long riffle reaches did not change over time (fig. 3). In contrast, the percentage of marked fish declined sharply in short riffle reaches from 67 percent for Day 0 to 49 percent for Day 3. Assuming that all of these individuals (18 percent) moved beyond the study area boundaries by Day 3, the actual percentage of fish emigrating from short riffle pools was much higher than the observed average emigration of 30 percent.

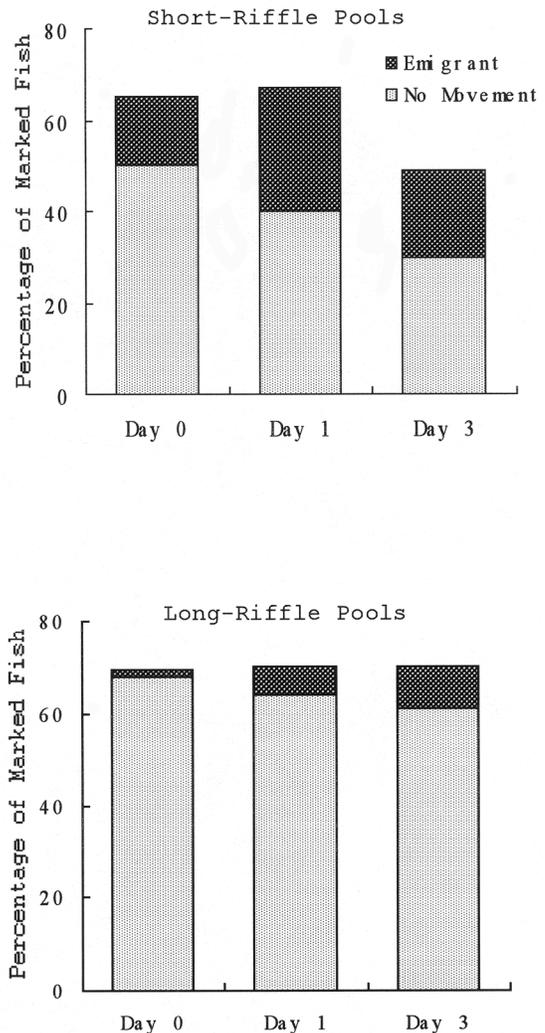


Figure 3—Marked fish (percent) emigrating from and remaining within experimental pools on each day of the three-day survey periods.

Marked fish moving from short riffle pools selected upstream and downstream directions with equal frequency (52 vs. 48 percent, respectively). In contrast, emigrants from long riffle pools moved downstream nearly twice as often as they moved upstream (63 percent vs. 37 percent, respectively, Chi square goodness of fit test, $P < 0.01$).

DISCUSSION

We summarized here the first studies to quantify how the habitat mosaic in streams can shape the response of fish to acute disturbances and limit their short term movements among habitats. Attributes of the physical environment responsible for this variability in movement behavior included riffle length, depth, and distance to large source pools.

Though poorly studied in streams, the effects of habitat isolation on the movement of organisms (e.g., Forman and Godron 1986, Forman 1995) and on the recolonization of habitat islands (e.g., Simberloff and Wilson 1969) have long been recognized by ecologists. In fact, Brown and Brussack (1990) described riffle habitats for benthic invertebrates as isolated islands that were separated by long pools of low habitat quality. Like organisms in other spatially heterogeneous environments, fish in streams are distributed within a mosaic of habitats of varying quality (e.g., resource availability, predator densities, and physical conditions). Thus, the rate at which individuals move between patches and recolonize disturbed reaches should depend on whether intervening habitats (i.e., riffles) possess properties that could impair movement. For pool dwelling species, we suspect that limited movement through long riffles may be due, at least in part, to the fact that these habitats are shallow and fast flowing. Fast flows may be difficult to negotiate, and shallow water may expose individuals to terrestrial predators (e.g., Power 1987). Although direct field evidence supporting either of these potential factors is lacking, Warren and Pardew (1998) measured a strong effect of water velocity on fish movement through road crossings, and we found that fish in long riffle pools moved significantly less frequently against the current (upstream) than with the current (downstream). We also measured a negative relationship between water depth and fish recolonization of defaunated stream pools (Lonzarich and others 1998).

We suspect that these factors contribute to variability in fish movement through long riffles but urge care in extrapolating beyond the temporal scope (i.e., days and months) and low flow conditions that characterized our experiments. We actually 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. Nevertheless, the timing of our study, the summer, coincided with a critical period in the life cycles of stream fish species. Not only is this the season when fish experience their most favorable growing conditions, it also is when competition and threats of predation, especially for juveniles, can be very intense. Further, in Arkansas, as in many other geographic regions, stream organisms are often exposed to unpredictable and potentially severe flow disturbances during the summer.

Given this context, we ask how variability in fish movement between pools affects the dynamics of populations and assemblages both at the scale of habitats and stream reaches? As reflected in our study design, we believe that there are at least two ways to approach this question. When measured over relatively long time periods (e.g., days, months), it appears that pool isolation can severely limit the rate at which fish assemblages recover from acute disturbances as predicted by Island Biogeography Theory (MacArthur and Wilson 1967). Not only is recovery affected by the distance to potential colonists, it also is affected by the proximity of large pools, which in some respects may be analogous to the mainland habitats of MacArthur and Wilson (1967). Sedell and others (1990) argued that large pools are very important to the ecology of streams because they provide stream organisms with refugia during stressful conditions (e.g., droughts, floods). Our results imply that large pools, which were two times larger than average sized pools in our study streams, also may serve as important sources of immigrants to neighboring up and downstream habitats. In view of the importance of episodic disturbances in streams, and because land use activities can alter both the stream flow regime (e.g., Rosén and others 1996) and habitat spacing, these results may help explain variability in the organization of fish assemblages in stream pools.

When viewed over much shorter time scales (e.g., hours, days), pool isolation may affect the ability of fish to track spatially variable resources (e.g., food, mates) or predator densities. Matthews (1998) described such a possibility. He speculated that differences in the ability of small bodied prey and large bodied predators to traverse shallow riffles might affect predator prey relationships in stream reaches. The assumption of open fish communities in pools appears to conflict with the restricted movement paradigm (Gerking 1953) and with the widely held view that fish within pools can be viewed as discrete populations (e.g., Gerking 1953, Matthews and others 1994). However, it is consistent with the findings of Fraser and Sise (1980) who proposed that stream fish should be sensitive to local resource availability and move between pools in search of food resources. We add that the possible benefits of moving from a pool must be weighed against the potential costs of crossing riffles. Therefore, in long riffle pools where movement can be limited, there may be a tendency towards closed community structure with local (i.e., pool scale) conditions, such as prey abundance, predator densities, and the habitat template having strong effects on assemblage organization. In short riffle pools, where the daily turnover of individuals can be very high (> 20 percent per day), the characteristics of pool assemblages and populations may show little if any relationship to local conditions. This view is similar to that of Cooper and others (1990) who found that the ability of fish predators to control the local abundance of stream insects diminished as insect exchange rates (emigration/immigration) into pools increased.

SUMMARY

The extent and nature of animal movements are key factors affecting the vulnerability of species to landscape changes (Law and Dickman 1998). Historically, stream ecologists have focused on local habitat conditions (e.g., pools, riffles)

when trying to describe and predict the factors that explain the abundance and dynamics of fish populations. The importance of habitat isolation to the ecology of stream fishes may vary widely across streams and geographic regions due to variability in the physical factors that determine channel features. Riffle lengths in our streams were probably representative of conditions in many small upland stream systems in the eastern United States but are much shorter than those found in small montane streams of the Pacific Northwest (e.g., > 80 m, Beechie and Sibley 1997). In contrast, low gradient, sand bottom streams of the Gulf and Atlantic Coastal Plains may lack physical conditions promoting riffle development. Logging, agriculture, and other land use activities along streams can lead to changes in the channel course or reduce the availability of instream elements (e.g., large woody debris) that create habitat. Such changes can reduce the abundance, and therefore the spacing, of pools in streams. For this reason, we strongly recommend that efforts to understand the ecology of stream fishes and the consequences of land use activities focus more attention on the spatial distribution and potential isolation of these habitats in streams.

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