Effects of habitat isolation on the recovery of fish assemblages in experimentally defaunated stream pools in Arkansas

David George Lonzarich, Melvin L. Warren, Jr., and Mary Ruth Elger Lonzarich

Abstract: We removed fish from pools in two Arkansas streams to determine recolonization rates and the effects of isolation (i.e., riffle length, riffle depth, distance to large source pools, and location), pool area, and assemblage size on recovery. To determine pool-specific recovery rates, we repeatedly snorkeled 12 pools over a 40-day recovery period. Results indicated the effects of isolation on percent numerical recovery, but no effects of pool area or assemblage size. Numerical recovery of assemblages in pools separated from neighboring pools by short riffles occurred by day 30 whereas more isolated pools had not reached 70% numerical recovery by day 40. Recovery also was more rapid in downstream pools and in pools that were closer to large source pools. Finally, recovery patterns differed among species and size-classes, with large fish (<100 mm total length) recolonizing pools more rapidly than small fish. This is the first study to quantify species- and assemblage-level recolonization rates at the scale of individual pools and the effects of isolation on recovery. The findings of this study have potentially important implications for research aimed at understanding the ecology of stream fishes and predicting the consequences of land-use activities.

Résumé : Nous avons recueilli des poissons dans certaines des fosses de deux cours d'eau de l'Arkansas pour évaluer la vitesse de repeuplement et les effets de l'isolement (c.-à-d. longueur et profondeur des rapides, distance jusqu'aux grandes fosses d'origine et emplacement), de la superficie de la fosse et de la taille des assemblages sur le repeuplement. Pour déterminer la vitesse de repeuplement en fonction de la fosse, nous avons inspecté en plongée libre 12 fosses à plusieurs reprises durant une période de 40 jours. D'après les résultats obtenus, nous avons conclu que l'isolement influe sur le repeuplement numérique, tandis que la superficie de la fosse et la taille des assemblages n'ont pas d'effet. La reconstitution numérique des assemblages était complète au 30e jour dans les fosses séparées des autres fosses par de courts rapides; dans les fosses plus isolées, elle n'avait pas atteint 70 % au 40e jour. Nous avons aussi constaté que le repeuplement était plus rapide dans les fosses d'aval, ainsi que dans celles qui se trouvaient plus près des grandes fosses d'origine. Par ailleurs, le mode de repeuplement diffère selon l'espèce et la classe de taille, les poissons de grande taille (longeur totale <100 mm) repeuplant les fosses plus rapidement que les poissons de petite taille. C'est la première fois qu'on quantifie le repeuplement en fonction de l'espèce et de la taille des assemblages dans des fosses individuelles et qu'on évalue l'effet de l'isolement. Les résultats de nos travaux pourraient être d'une grande utilité pour l'étude de l'écologie des poissons des milieux lotiques et pour la prévision des conséquences des différentes formes d'utilisation des sols.

[Traduit par la Rédaction]

Introduction

Episodic disturbances, such as floods and droughts, contribute significantly to the organization and stability of stream communities by affecting the abundance and distribution of fishes (Meffe 1984; Erman et al. 1988; Pearsons et al. 1992; Strange et al. 1992). The rate of community recovery from these disturbances 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 year, e.g., Niemi et al. 1990). Recovery of fish assemblages in short reaches and habitat units can occur on a 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 et al. 1992).

One significant shortcoming of research on fish recolonization is the typical use of invasive postdisturbance sampling methods that permanently remove fish from surveyed habitats and thereby alter natural recovery patterns. This approach precludes use of repeated sampling of defaunated habitats that is necessary to accurately determine rates of recovery associated with different habitat conditions (e.g., habitat size, habitat complexity). Sheldon and Meffe (1995)

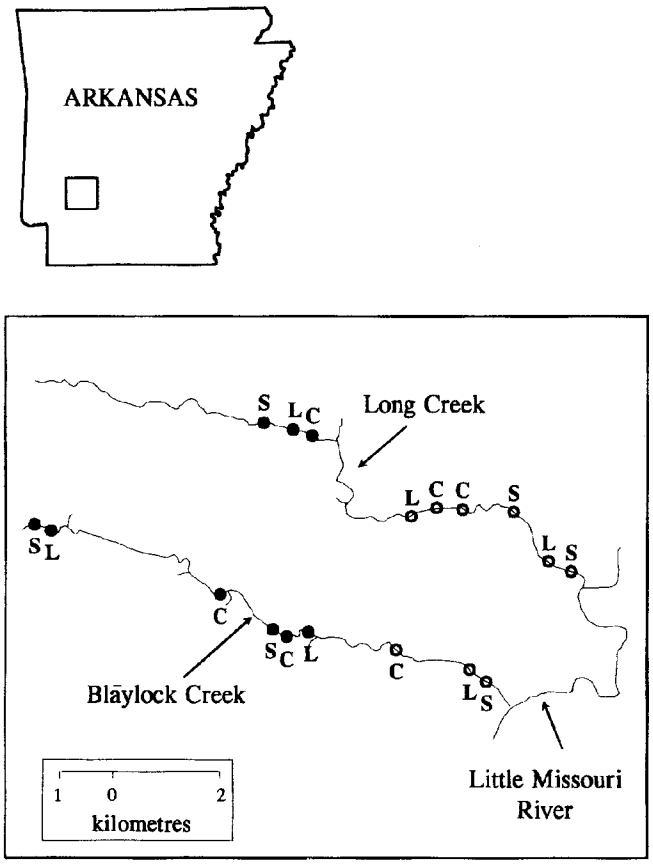
Received May 13, 1997. Accepted March 9, 1998.

D.G. Lonzarich[1] and M.R.E. Lonzarich.[2] University of Oklahoma, Biological Station, Kingston, OK 73439, U.S.A.
M.L. Warren, Jr. USDA Forest Service, Forest Hydrology Laboratory, 1000 Front St., Oxford, MS 38655, U.S.A.

[1]Author to whom all correspondence should be addressed. Present address: Department of Biology, University of Wisconsin–Eau Claire, Eau Claire, WI 54702, U.S.A. e-mail: lonzard@uwec.edu
[2]Present address: Department of Biology, University of Wisconsin–Eau Claire, Eau Claire, WI 54702, U.S.A.

© 1998 NRC Canada

Fig. 1. Location of 12 experimental and 6 control pools in Long and Blaylock creeks. Upstream pools are represented by solid circles and downstream pools by open circles.



speculated that differences in fish recolonization rates in upstream and downstream pools may have been due to distance from source populations or differences in habitat characteristics. Their study provided insights into the mechanisms that shape patterns of recolonization, but many questions about the ecology of fish recolonization and resilience of fish communities remain unanswered. For example, will fish assemblages in small habitat units recover more rapidly than assemblages in large habitats by virtue of differences in the size of assemblages? Is colonization influenced by the degree to which stream habitats are isolated from one another, as would be predicted by island biogeography theory (MacArthur and Wilson 1967)?

Identifying the effects of habitat disturbance on biotic recovery would at the very least require comparisons of recovery rates across habitats that differ in quality. However, we suspect that it also important to examine the influence on recovery of the spatial distribution of habitats in specific stream segments. The size and distribution of habitats (e.g., pools, riffles) in a stream segment may influence faunal recovery in disturbed areas by influencing rates of movement between equivalent habitat types (e.g., pools) and the composition of potential colonists. Many studies have examined the consequences of land-use activities on habitat quality and the ecology of stream fishes (e.g., Shirvell 1990; Hicks et al. 1991; Lonzarich and Quinn 1995). By contrast, little attention has been given to the ecological effects of habitat isolation (but see Gerking 1953) even though the distribution of habitats can be altered by land-use activities (Karr and Schlosser 1978). One potentially important consequence of changes in the spatial distribution of habitats may lie in the ability of fish to track resources and move among suitable habitat types (e.g., pools). In gaining access to suitable habitats, pool-dwelling fishes may need to cross habitats, such as shallow-water riffles, that can either have high energy costs or pose high predation risks (Harvey and Stewart 1991; Lonzarich and Quinn 1995). Because the ability of fish to track changes in resources will be influenced by the costs associated with movement, the distance between habitats or the depth of corridors may contribute significantly to patterns of assemblage recovery.

In this study, we examine patterns of recolonization of fishes in experimentally defaunated stream pools standardized to evaluate the effects of isolation on faunal recovery. To develop estimates of recovery rates for individual pools and habitat conditions, we conducted repeated snorkeling surveys of experimental pools over a 40-day period. Our experimental design allowed us to evaluate effects on recovery of several factors contributing to isolation of a pool habitat: the distance between pool habitats, the depth of corridors between pool habitats (i.e., riffles), the distance to large "source" pools, and location in the drainage. Our primary objectives were to (*i*) estimate pool-scale recovery rates of fishes and (*ii*) evaluate the influences on recovery rates of pool isolation and two other potentially important factors: pool area and predisturbance assemblage size.

Materials and methods

Site selection

We carried out experiments between July and August 1995 in two tributary streams of the Little Missouri River in the Ouachita National Forest, Arkansas (34°22′30″ lat., 93°52′30″ long., Fig. 1). Long and Blaylock creeks are relatively short (<20 km), low-gradient systems that flow through forested and mountainous terrain. General characteristics of the streams included bedrock, cobble, and gravel substrates, dense riparian vegetation, and well-developed pool and riffle habitats. Previous research has shown that the proportion and average size of pool and riffle habitats in the two streams were very similar (Clingenpeel 1994). Likewise, fish assemblages in the two creeks were nearly identical when measured in terms of species composition, rank dominance, and densities (D.G. Lonzarich, unpublished data, Table 1). Based primarily on differences in the length of adjacent riffles, we selected 12 experimental pools in the two streams (six in each stream) and assigned them to one of two treatment categories: (*i*) short-riffle pools and (*ii*) long-riffle pools. Short-riffle pools were separated from the adjacent upstream and downstream pools by riffles <10 m (mean = 9.1 m) (Table 2). Long-riffle pools were separated from adjacent pools by riffles that were at least 20 m long, although this distance typically exceeded 35 m (mean = 46 m). Along with riffle length, we examined the effect of pool position on recovery by assigning the 12 pools into upstream and downstream categories (Fig. 1).

In addition to the 12 experimental pools, we randomly selected six pools as unmanipulated controls (Table 2). Although we did not remove fish from these pools, we monitored their assemblages in

© 1998 NRC Canada

Table 1. Comparisons of fish densities (individuals/m^2) for target species in the two study streams.

Species	Blaylock Creek	Long Creek
Central stoneroller (*Campostoma anomalum*)	0.80	0.82
Striped shiner (*Luxilus chrysocephalus*)	0.47	0.56
Creek chub (*Semotilus atromaculatus*)	0.38	0.17
Orangebelly darter (*Etheostoma radiosum*)	0.16	0.16
Yellow bullhead (*Ameiurus natalis*)	0.06	0.04
Longear sunfish (*Lepomis megalotis*)	0.05	0.11
Northern studfish (*Fundulus catenatus*)	0.05	0.06
Bigeye shiner (*Notropis boops*)	0.03	0.03
Greenside darter (*Etheostoma blennioides*)	0.02	0.02
Smallmouth bass (*Micropterus dolomieu*)	0.02	0.03
Northern hog sucker (*Hypentelium nigricans*)	0.01	0.02
Redfin shiner (*Lythrurus umbratilis*)	0.01	0.01
Bluntnose minnow (*Pimephales notatus*)	*	
Green sunfish (*Lepomis cyanellus*)	*	
Blackspotted topminnow (*Fundulus olivaceus*)		*
Freckled madtom (*Noturus nocturnus*)		*
Logperch (*Percina caprodes*)		*
Rock bass (*Ambloplites rupestris*)		*
Slender madtom (*Noturus exilis*)		*
Total density	2.06	2.03

Note: Estimates are based on electrofishing surveys of 24 pools in each of the two streams conducted in summer 1994 (D.G. Lonzarich, unpublished data). An asterisk indicates that fewer than five individuals were collected at all sites combined.

the same way as for the experimental pools. We added controls to describe the natural dynamics of pool assemblages and to identify the presence of any temporal trends that could have influenced interpretations of biotic recovery in the experimental pools.

For each pool, we measured total length, width, area, maximum depth, substrate composition (boulder, cobble, gravel), distance to the stream mouth, and distance to the nearest large pool (>250 m^2). Biological characteristics measured included species richness, total assemblage, and individual species densities. With the exception of riffle length, the average physical dimensions, species richness, and fish densities of the riffle treatments were not different (Table 2, $P > 0.05$, two-sample t-test), although the statistical power of tests on physical habitat variables was generally low ($\beta > 0.90$). Typically, downstream pools were larger and bordered by deeper riffles than those upstream (Table 2, $P < 0.05$, two-sample t-test). On average, control pools were smaller and had higher fish densities than experimental pools.

Fish surveys

In this study, we focused on a subset of the fish species in the two streams. Because of concerns with sampling efficiency, we did not include small juvenile fishes (<25 mm) or bottom-dwelling species that often hide within the substrate and become difficult to locate using visual census techniques. Bottom-dwelling species not surveyed included northern hog sucker (*Hypentelium nigricans*), orangebelly darter (*Etheostoma radiosum*), greenside darter (*Etheostoma blennioides*), and yellow bullhead (*Ameiurus natalis*). Numerically, these species and small juveniles were a minor component of the pool assemblages in the study streams, generally accounting for <10% of all fish collected by electrofishing. Species collected in this study included central stoneroller (*Campostoma anomalum*), striped shiner (*Luxilus chrysocephalus*), redfin shiner (*Lythrurus umbratilis*), bigeye shiner (*Notropis boops*), northern studfish (*Fundulus catenatus*), creek chub (*Semotilus atromaculatus*), longear sunfish (*Lepomis megalotis*), and smallmouth bass (*Micropterus dolomieu*). Because the last three species ranged considerably in size, we distinguished two size categories: small (25–100 mm total length) and large fish (>100 mm total length).

We removed fish from experimental pools by isolating each pool with 6-mm-mesh block seines and sampling with a Smith–Root battery-powered, backpack electrofisher. Pools were then sampled between four and seven times until no fish were collected on two consecutive passes. When removed from experimental pools, individuals were either sacrificed or relocated up to 500 m downstream into pools below barriers that prevented upstream movement. We evaluated the effectiveness of the electrofishing technique in removing target species by conducting snorkeling surveys in the isolated pools immediately upon the completion of sampling. In snorkeling counts of six of the 12 experimental pools, we observed only three fish that belonged to the target group of species.

Snorkeling census

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. Control pools were snorkeled at 10-day intervals for 40 days. To minimize observer error, the same observer conducted surveys of all pools censused, and on each date, two consecutive censuses were performed at each control and experimental site. The mean of these two counts was used in statistical analyses. We evaluated the precision of this census technique by comparing snorkeling data with electrofishing data for the fish predisturbance census.

To confirm that riffles would not contribute a significant number of colonists to experimental pools, we electrofished six upstream riffles adjacent to treatment pools (three long-riffle and three short-riffle pools) on the final day of the recovery experiment. The results indicated that fish assemblages in riffles were very different from those in pools. Riffles contained only five of eight target species and lower numbers and smaller fish than pools (Table 3).

© 1998 NRC Canada

Table 2. Mean (range) physical habitat and predisturbance assemblage characteristics of treatment and control pools.

	Pool characteristics				Riffle characteristics		Biological conditions	
	Length (m)	Width (m)	Area (m^2)	Depth (cm)	Length (m)	Depth (cm)	Density (fish/m^2)	Species richness
Riffle length								
Short	30 (15–59)	6.0 (4.9–7.1)	182 (74–418)	68 (50–100)	9.1 (2–20)	13.1 (7–18)	0.92 (0.6–1.5)	6.3 (5–8)
Long	30 (14–48)	6.5 (5.0–8.5)	202 (83–406)	60 (50–80)	46.4 (20–69)	12.8 (7–18)	1.18 (0.9–1.9)	6.2 (5–8)
Pool position								
Upstream	29 (14–50)	5.5 (4.9–6.1)	155 (74–262)	63 (50–85)	27.4 (2–60)	9.9 (6–12)	0.95 (0.51–1.6)	6 (5–7)
		*	**			**		
Downstream	31 (18–59)	6.9 (5.7–8.5)	223 (104–418)	65 (50–100)	25.5 (2–69)	15.5 (13–18)	1.18 (0.7–1.7)	6.7 (6–8)
Control pools	30 (11–47)	5.0 (4.5–6.1)	159 (52–283)	67 (55–100)	21.6 (5–54)	16 (11–20)	1.52 (0.89–2.1)	5.8 (4–8)

Note: Significant within-treatment differences: $*P < 0.05$, $**P < 0.01$ (two-sample t-tests).

Table 3. Catch-per-unit-effort (CPUE) and size of target species in Long and Blaylock creeks.

	CPUE (fish/100 m^2)			Mean standard length (max. standard length) (mm)		
Species	Riffle		Pool	Riffle		Pool
Central stoneroller	1.2	*	9.0	57 (82)		60 (103)
Striped shiner	0.5	*	5.1	55 (108)	*	69 (104)
Smallmouth bass	0.1		0.4	50 (63)	*	96 (207)
Redfin shiner	<0.1	*	0.1			50 (64)
Bigeye shiner	<0.1		0.3	48 (48)		51 (52)
Creek chub	0.1	*	0.9	63 (95)	*	97 (155)
Northern studfish	<0.1	*	0.7	72 (85)		70 (95)
Longear sunfish	0.0	*	1.0			77 (116)
Total	1.90	*	17.3			

Note: Values represent means from six pools and six associated riffles in the two streams. Significant differences: $*P < 0.05$ (two-sample t-test).

From these findings, we were confident that riffles did not provide a significant source of colonists to the experimental pools.

Statistics

Results from both streams were combined in all statistical analyses unless we detected significant differences in recovery between the two streams. We estimated pool-specific recovery rates (per day) for assemblages (species richness, percent similarity, total numbers), target species (numbers), or target size-classes (numbers) by linear regression analysis. Percent similarity was calculated using the percent similarity index (Wolda 1981). Because the absolute number of fish in control and experimental pools varied widely, we determined a relative number of fish for each pool by dividing counts (individuals per pool) obtained for any post-disturbance census by counts obtained on day 0. The model that best explained the relationship between time and recovery had the following linear form:

$$\ln(\text{Recovery}) = \ln(a) + b\ln(\text{day} + 1)$$

where ln(Recovery) represented the natural log of either assemblage (species richness, percent similarity, or relative numbers), species, or size-class recovery and b, the regression coefficient, represented the recovery rate (ln(Recovery)/ln(day + 1) – ln(a)). Although assemblage and species recovery rates generally declined towards an asymptote over time, we did not use an asymptotic regression model in these analyses. For our data, asymptotic regressions did not explain changes in recovery as well as logrithmic regressions. The same conclusion was reached in a similar study by Sheldon and Meffe (1995).

We used ANOVA and regression models to evaluate patterns of recovery between treatment groups and across pools. To test whether recovery differed between pools in each of the two treatment categories (riffle length and pool position), we compared mean recovery rates (b) for treatment categories using a two-way ANOVA. We used one-way ANOVA to compare differences in mean recovery rates among species and between size-classes. We determined the effects of other independent variables (i.e., riffle depth, distance to large pool, pool area, and predisturbance assemblage size) on pool-specific recovery rates by least squares regression analysis. Finally, we generated multiple regression models to describe the relative importance of each independent variable on assemblage recovery rates. Only uncorrelated variables were in-

© 1998 NRC Canada

Table 4. Comparison of mean fish densities (individuals/m^2 ± 1 SE) estimated from electrofishing and snorkeling surveys of 12 treatment pools in Long and Blaylock creeks.

Species	Electrofishing	Snorkeling
Central stoneroller	0.61±0.23	0.62±0.22
Striped shiner	0.24±0.03	0.24±0.03
Longear sunfish	0.08±0.02	0.11±0.04
Creek chub	0.07±0.03	0.09±0.04
Northern studfish	0.03±0.01	0.06±0.03
Redfin shiner	0.03±0.01	0.03±0.01
Bigeye shiner	0.02±0.01	0.03±0.02
Smallmouth bass	0.02±0.01	0.02±0.01
Total density	1.10±0.26	1.21±0.29

cluded in this analysis. We performed log-transformations on data that deviated significantly from normality.

Results for control pools were examined by regression analysis to evaluate temporal variation in species richness, percent similarity, and assemblage and species relative numbers. Comparisons of results for control and experimental pools were made on days 0, 10, 20, 30, and 40 using two-sample *t*-tests.

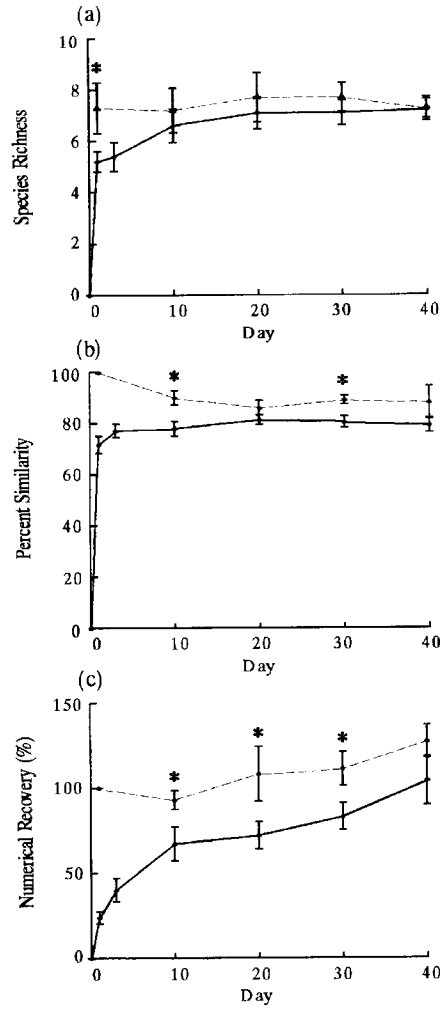
Results

Snorkeling surveys produced results that were comparable with those obtained in electrofishing surveys. Estimates of total fish per pool for the two methods were highly correlated (Pearson product-moment correlation coefficient, r = 0.95, n = 12, $P < 0.01$). Further, there was little difference between the two methods in the average densities of individual species and species rank (Table 4). Average assemblage similarity between the two techniques was 95%.

When measured in terms of species richness and percent similarity, the recovery of assemblages to predisturbance conditions occurred relatively rapidly and at similar rates in all 12 pools (Figs. 2*a* and 2*b*). Pool-specific recovery rates in species richness and overall percent similarity were not associated with any measured physical (riffle length, pool size, distance to large pool) or biological variable (initial assemblage size, $P > 0.20$). On average, the number of species per pool exceeded 50% of predisturbance values by day 10. By day 20, species richness stabilized, although at a value slightly lower than the predisturbance mean (Fig. 2*a*). With the exception of day 1, the mean number of species in experimental pools was not significantly different from means in control pools across all comparable dates ($P > 0.30$). Patterns of recovery based on percent similarity were similar to patterns described for species richness (Fig. 2*b*). Pool assemblages recovered to nearly 80% (range 49–89%) of their predisturbance composition by day 3 and fluctuated only slightly over the remainder of the recovery period. Species dominant in initial surveys (e.g., central stoneroller, striped shiner, creek chub) remained dominant during the recovery period. In control pools, percent similarity values (relative to initial assemblage structure) varied only slightly over the 40-day period (range 78–98%). Moreover, percent similarity values from control and experimental pools for comparable dates generally were very similar.

Species that returned most rapidly to experimental pools included the two most common and widespread species, central stoneroller (1.6 days) and striped shiner (1 day), but also two relatively uncommon species, bigeye shiner (2 days) and northern studfish (5.3 days). Redfin shiner was the slowest to recolonize the pools (19.2 days) and was also the least common species in the two streams.

Fig. 2. Temporal trends for three assemblage characteristics (species richness, percent similarity, percent numerical recovery) in experimental (solid lines) and control pools (broken lines). Error bars represent ± 1 SE. Significant differences between control and experimental pools on comparable dates are indicated (*$P < 0.05$, two-sample *t*-tests).



In contrast with species richness and similarity, percent numerical recovery of assemblages occurred at a relatively slow rate (Fig. 2*c*). Typically, the relative number of fish increased rapidly during the earliest phases of the recolonization period, with some pools achieving 50% of their predisturbance numbers by day 3. Towards the conclusion of the recovery period, the number of fish per pool generally stabilized or increased very slowly. The number of fish in control pools varied more dramatically than values for species richness and percent similarity and appeared to increase slightly over the course of the study period (r^2 = 0.11, P = 0.09) (Fig. 2*c*). Unlike species richness and percent similarity, the mean number of fish in experimental pools was lower than the mean number of fish in control

© 1998 NRC Canada

Table 5. Two-way ANOVA results showing effects of riffle length and pool position in the drainage on numerical recovery rates.

Source	Sum of squares	df	*F*-ratio	*P*-value
Length	0.009	1	26.7	<0.01
Position	0.004	1	12.4	<0.01
Position × Length	0.001	1	3.6	0.10
Error	0.002	8		

pools on all comparable dates except day 40 (two-sample *t*-test).

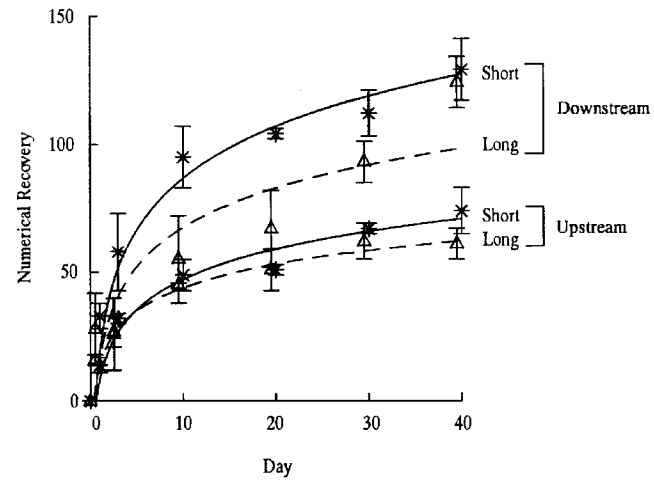
Numerical recovery was influenced strongly by factors that isolated experimental pools from potential colonists. We detected significant within-treatment differences in recovery rates for both riffle length and pool position ($P < 0.05$, two-way ANOVA) (Table 5). Recovery patterns were similar in the two streams, and significant relationships between time and recovery were found for all 12 experimental pools. For both upstream and downstream sites, numerical recovery was much more rapid in pools isolated by short riffles than by long riffles (Fig. 3). In short-riffle pools, assemblages reached full numerical recovery by day 30 whereas assemblages in long-riffle pools reached only 75% of their predisturbance densities by day 40. For the entire recovery period, the mean (± 1 SE) recovery rate (*b*) in large-riffle pools was 30% lower (0.13 ± 0.01) than the rate for short-riffle pools (0.19 ± 0.01). Consistent with the assemblage-level results, numerical recovery for individual species was more rapid in short-riffle pools (Table 6). Of the eight target species, two showed significant between-group differences in recovery over time.

Pool location in the drainage also had an effect on numerical recovery. For both long- and short-riffle pools, upstream assemblages recovered more slowly than those downstream (Fig. 3). On average, assemblages in downstream pools achieved full recovery by day 30 of the recolonization period whereas assemblages in upstream pools had not reached 70% recovery by day 40. The mean recovery rate (± 1 SE) for assemblages in upstream pools was 30% lower (0.13 ± 0.01) than downstream sites (0.18 ± 0.01). Three of seven species that occupied both upstream and downstream locations recovered to predisturbance numbers more rapidly downstream (Table 6).

The remaining factors that were associated with numerical recovery of assemblages were riffle depth and the distance to nearest large source pool. By contrast, neither predisturbance assemblage size nor pool area influenced numerical recovery rates of assemblages ($r^2 = 0.01$, $P > 0.50$). Riffle depth had a positive effect on numerical recovery rates ($r^2 = 0.37$, $P < 0.05$), although this relationship was confounded by pool position. We found no relationship between numerical recovery rate and riffle depth when we tested pools within each position category separately. Numerical recovery rates of assemblages were correlated negatively with the distance to large source pools ($r^2 = 0.44$, $P < 0.05$). This pattern held even when we tested pools within each riffle length or pool location category independently.

When we combined all independent variables in a multiple regression analysis, the resulting model included riffle length (Length), distance to large source pool (Distance), and riffle depth (Depth) as significant predictors of pool-specific numerical recovery rates ($P < 0.01$). The model $b = 0.21 - 0.01 \ln(\text{Distance}) - 0.055(\text{Length}) + 0.006(\text{Depth})$ explained nearly all of the variation in recovery rates among the 12 pools ($r^2 = 0.95$).

Fig. 3. Comparisons of percent numerical recovery for the riffle length and upstream and downstream treatment categories. Error bars represent ± 1 SE. Data points and error bars are offset to increase clarity.



Size-class and species comparisons

Broad differences were detected in the recovery rates of size-classes and different taxonomic groups (Fig. 4). Large fish recolonized experimental pools at a faster rate ($b = 0.19$) than small fish ($b = 0.13$) ($P < 0.05$, one-way ANOVA). For species included in this comparison (smallmouth bass, creek chub, and longear sunfish), large fish completely recovered to their predisturbance numbers by day 30. Small individuals had not even achieved 70% numerical recovery by the same date. Among the most common species in the two streams, three (smallmouth bass, central stoneroller, and longear sunfish) returned to predisturbance abundances by day 40 (Figs. 4*b* and 4*c*). By contrast, recovery rates for creek chub and striped shiner were much slower ($P < 0.01$, one-way ANOVA). For creek chub, numerical recovery was just slightly greater than 50% by day 40 (Fig. 4*c*).

Discussion

General trends in recovery

For general patterns of recovery across all 12 pools, we found rapid recovery (<40 days) in overall numbers, species richness, and percent similarity in experimental pools of Long and Blaylock creeks. Average values of all three measures of assemblage structure (species richness, percent similarity, and relative numbers) and relative numbers of most species and size-classes returned to predisturbance levels by the end of the 40-day sampling period. We attribute this high degree of resilience and predictable structure of assemblages to recolonization rates by species and size-classes in proportion to their abundance in neighboring habitats. However, it

© 1998 NRC Canada

Table 6. Species regression coefficients (± 1 SE) showing recovery rates (*b*) for different treatments.

	Riffle length			Location in drainage		
Species	Long		Short	Upstream		Downstream
Central stoneroller	0.13	*	0.21	0.15	*	0.19
	0.03		0.03	0.04		0.02
Striped shiner	0.10	*	0.15	0.09	*	0.14
	0.02		0.01	0.02		0.02
Smallmouth bass	0.17		0.20	0.19		0.17
	0.01		0.02	0.05		0.01
Creek chub	0.10		0.08	0.11		0.08
	0.02		0.03	0.03		0.02
Longear sunfish	0.15		0.18	0.13	*	0.20
	0.02		0.03	0.02		0.02
Redfin shiner	0.27		0.25	0.19	$P < 0.10$	0.34
	0.03		0.08	0.03		0.08
Bigeye shiner	0.28		0.35			0.32
	0.01		0.08			0.04
Northern studfish	0.14		0.15	0.09	$P < 0.10$	0.19
	0.06		0.03	0.02		0.05

Note: Coefficients were derived using the following model: ln(Percent recovery) = ln(*a*) + *b*ln(day + 1). Significant differences: $*P < 0.05$ (one-way ANOVA).

should be noted that this type of proportional colonization was not always evident for individual species (i.e., creek chub and striped shiner).

General trends in assemblage and species recovery described in this study were similar to those of two recent studies that investigated fish recolonization at the scale of habitats and short stream reaches (e.g., Peterson and Bayley 1993; Sheldon and Meffe 1995). Peterson and Bayley (1993) recorded assemblage recovery in <10 days in stream reaches ranging from 46 to 113 m and Sheldon and Meffe (1995) within 23 days in short pools (10–23 m in length). Moreover, results from all three studies indicate that species richness and percent similarity recover to predisturbance levels more rapidly than total numbers of fish.

Agreement in the findings of these studies reinforces the view of Sheldon and Meffe (1995) that stream fishes can be highly mobile and that spatially restricted episodic disturbances may produce only short-term impacts on fish assemblages. However, as Sheldon and Meffe (1995) cautioned, impacts can become severe under conditions of chronic disturbance or for populations of rare species or locally adapted genomes.

Most species recovered to their predisturbance numbers at similar rates, although two very common cyprinids (creek chub and striped shiner) colonized pools at rates about 50% lower than other species. These results indicate that recolonization rates for individual species cannot be predicted solely by knowing their proportions in neighboring habitats. Other factors, such as differences in home range size, also may influence species recovery patterns.

In addition to species-specific differences in recolonization, our results indicated that large fish (>100 mm) recolonized pools more rapidly than small fish. Little has been published on size-specific patterns of recovery (Detenbeck et al. 1992), and the literature on movement by stream fish has yielded mixed results on the mobility of different size-classes. For example, Bachman (1984) suggested that a negative correlation between home range size and fish length in brown trout (*Salmo trutta*) was caused by large fish outcompeting small fish for optimal foraging locations. Alternatively, it also has been shown that home range size increases with fish size (Allen 1951; Gerking 1953; reviewed by Minns 1995). A possible explanation for this relationship is that large fish have higher energy demands and require larger foraging areas (Gerking 1953). Of the species surveyed in this study, longear sunfish are known to exhibit size-specific movements consistent with the second view (Gerking 1953; Gunning and Shoop 1963).

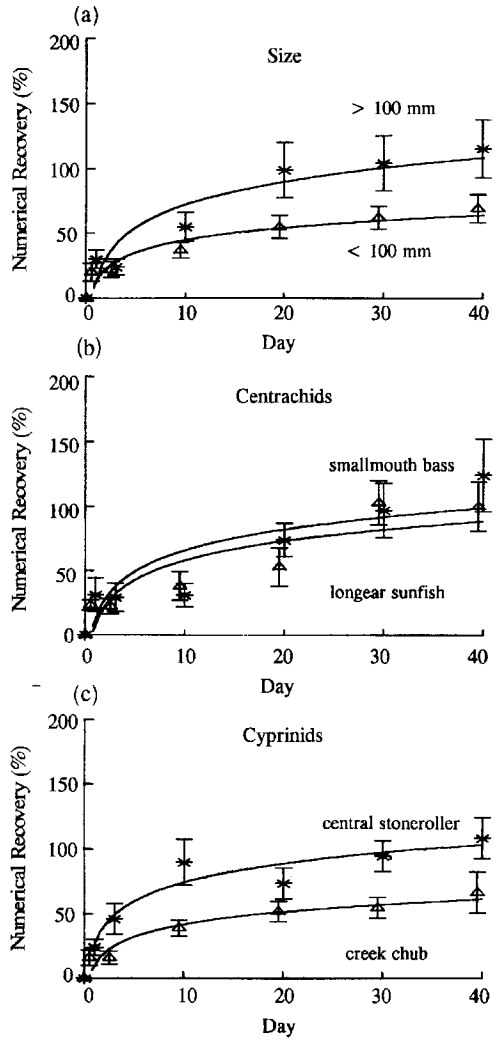
Effects of physical factors on recovery

Physical factors can influence fish recolonization (reviewed by Detenbeck et al. 1992). However, most studies that have examined these influences have been carried out at relatively large spatial scales (i.e., reaches, streams) and focused on large-scale stream attributes such as latitude, gradient, stream order, watershed size, barriers to migration, and distance to source populations. Of these factors, only those that directly affected rates of movement (i.e., barriers to migration and distance to source populations) were correlated with recovery patterns (Detenbeck et al. 1992). Our study has shown that factors affecting rates of movement are also important determinants of fish recolonization when this process is measured at the scale of habitat units. All four measures of pool isolation (riffle length, riffle depth, position in drainage, and distance to large pools) affected numerical recovery. The only measured variables not linked to movement (pool size and predisturbance assemblage size) also had no apparent influence on rates of numerical recovery.

Generally, the least isolated pools (downstream, short riffles) achieved full recovery by day 20 whereas estimates for the most isolated pools (upstream, long riffles) were typically much greater than 40 days. The length of time necessary for these pools to achieve full recovery will be influenced by various factors, including seasonal changes in stream flow, fish behavior, and abundance.

© 1998 NRC Canada

Fig. 4. Percent numerical recovery for different species and size-classes across all 12 experimental pools. Error bars represent ± 1 SE. Data points and error bars are offset to increase clarity.



The influences of isolation on numerical recovery of stream habitats have been discussed to varying degrees in previous studies. Peterson and Bayley (1993) suggested that riffle depth may have lengthened the recovery time of stream assemblages in a Missouri river. Although their conclusion was based on circumstantial evidence from one riffle, it is supported by the positive relationship between riffle depth and assemblage recovery rates detected here. The role of isolation on fish recolonization also was discussed by Sheldon and Meffe (1995) who described differences in assemblage-level recolonization rates of upstream and downstream pools. They speculated that the distance from source areas (i.e., neighboring streams) could have been responsible for this pattern. However, it was acknowledged that both upstream and downstream sites contained undisturbed habitats that could have provided significant numbers of colonists to the defaunated pools and that physical gradients may have been important. We also suspect that differences in recovery rates between upstream and downstream pools in our study were at least partly influenced by habitat differences. For example, upstream riffles were shallower than those downstream (10 versus 15 cm) and recovery was associated with riffle depth.

One other significant finding of our study was that numerical recovery rates declined as the distance of experimental pools to large source pools increased. Sedell et al. (1990) asserted 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 in these two streams were two times larger than average-sized pools, also may serve as important sources of immigrants to neighboring upstream and downstream habitats.

In the present study, experimental pools were isolated from neighboring pools by riffles ranging from <10 to slightly more than 50 m in length. Over this range, numerical recovery varied greatly. Mean recovery rates were 33% slower in the isolated pools, and time to full recovery ranged from <20 days in short-riffle pools to much greater than 40 days in long-riffle pools. While our data indicate that isolation can influence fish recolonization of habitats following disturbances, there may be other ecologically important consequences of this isolation. For example, routine movements of fish between habitats may depend to some extent on the spacing of habitat units. In fact, this was suggested by Gerking (1953) in a study of fish movement. Gerking (1953) found that only a very small percentage of tagged individuals representing several different species moved between two pools separated by a long riffle.

The importance of habitat isolation to the ecology of stream fishes may vary widely across streams and geographic regions in association with physical factors and land-use activities that determine channel characteristics. Riffle lengths in our streams were probably representative of conditions in many small eastern upland stream systems, but they were 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, sandy-bottom Gulf and Atlantic Coastal Plain streams may lack physical conditions promoting riffle development. Logging, agriculture, and other land-use activities carried out along streams also can lead to changes in the channel course or reduce the availability of in-stream elements (e.g., large woody debris) that create habitat (Karr and Schlosser 1978). Such changes reduce the abundance, and therefore the spacing, of pools in streams. Although numerous studies have described significant impacts of land-use disturbances on stream fishes, they generally have been focused at the scale of individual habitat units. We found that assemblage recovery, measured within habitats, was related to reach-scale characteristics (i.e., riffle depth, length, distance to large source pools) that affect habitat isolation. These results have potentially important implications for research aimed at understanding the ecology of stream fishes and predicting the consequences of land-use activities.

Acknowledgments

We are grateful to the Ouachita National Forest for granting access to Long and Blaylock creeks and to Dr. W. Matthews for providing advice and support in the development of the study. We acknowledge A. Clingenpeel and B.

© 1998 NRC Canada

Crump for allowing us to use their field equipment and J. Guldin for administrative support. The work was funded by the USDA Forest Service, Ouachita Mountain Ecosystem Management Project, Southern Research Station.

References

Allen, R.K. 1951. The Horokiwi stream. A study of a trout population. N.Z. Mar. Dep. Fish. Bull. **10**: 1–231.

Bachman, R.A. 1984. Foraging behavior of free ranging wild and hatchery brown trout in a stream. Trans. Am. Fish. Soc. **116**: 1–32.

Beechie, T.J., and Sibley, T.H. 1997. Relationships between channel characteristics, woody debris and fish habitat in northwestern Washington streams. Trans. Am. Fish. Soc. **126**: 217–229.

Clingenpeel, J.A. 1994. A cumulative effects analysis of silvicultural best management practices using Basin Area Stream Survey methods (BASS). USDA Forest Service, Southern Region, Ouachita National Forest, Hot Springs, Ariz.

Detenbeck, N.E., DeVore, P.W., Niemi, G.J., and Lima, A. 1992. Recovery of temperate stream fish communities from disturbance: a review of case studies and synthesis of theory. Environ. Manage. **16**: 33–53.

Erman, D.C., Andrews, E.D., and Yoder-Williams, M. 1988. Effects of winter floods on fishes in the Sierra Nevada. Can. J. Fish. Aquat. Sci. **45**: 2195–2200.

Gerking, S.D. 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology, **34**: 347–365.

Gunning, G.E., and Shoop, C.R. 1963. Occupancy of home range by longear sunfish (*L.m. megalotis*) and bluegill (*L. m. macrochirus*). Anim. Behav. **11**: 325–330.

Harvey, B.C., and Stewart, A.J. 1991. Fish size and depth relationships in headwater streams. Oecologia, **87**: 336–342.

Hicks, B.J., Hall, J.D., Bisson, P.A., and Sedell, J.R. 1991. Responses of salmonids to habitat changes. Am. Fish. Soc. Spec. Publ. **19**: 483–418.

Karr, J.R., and Schlosser, I.J. 1978. Water resources and the land–water interface. Science (Washington, D.C.), **201**: 229–234.

Lonzarich, D.G., and Quinn, T.P. 1995. Experimental evidence for the influence of depth and structure on the distribution, growth, and survival of stream fishes. Can. J. Zool. **73**: 2223–2230.

MacArthur, R.O., and Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

Meffe, G.K. 1984. Effects of abiotic disturbance on coexistence of predatory–prey species. Ecology, **65**: 1525–1534.

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

Niemi, G.J., DeVore, P., Detenbeck, N., Taylor, D., Lima, A., Pastor, J., Yount, J.D., and Naiman, R.J. 1990. Overview of case studies on recovery of aquatic systems from disturbance. Environ. Manage. **14**: 571–588.

Pearsons, T.N., Li, H.W., and Lamberti, G.A. 1992. Influences of habitat complexity on resistance to flooding and resilience of stream fish assemblages. Trans. Am. Fish. Soc. **121**: 427–436.

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

Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A., and Hawkins, C.P. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environ. Manage. **14**: 711–724.

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

Shirvell, C.S. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Oncorhynchus mykiss*) cover habitat under varying streamflows. Can. J. Fish. Aquat. Sci. **47**: 852–861.

Strange, E.M., Moyle, P.B., and Foin, T.C. 1992. Interaction between stochastic and deterministic processes in stream fish community assembly. Environ. Biol. Fishes, **36**: 1–15.

Wolda, H. 1981. Similarity indices, sample size and diversity. Oecologia, **50**: 296–302.

© 1998 NRC Canada