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Factors Influencing Stream Fish Recovery Following a Large-Scale Disturbance

WILLIAM E. ENSIGN[1] and KEVIN N. LEFTWICH[2]

Department of Fisheries and Wildlife Sciences, Virginia Tech
Blacksburg, Virginia 24061-0321, USA

PAUL L. ANGERMEIER

U.S. Geological Survey, Biological Resources Division
Virginia Cooperative Fish and Wildlife Research Unit,[3]
Virginia Tech, Blacksburg, Virginia 24061-0321, USA

C. ANDREW DOLLOFF

U.S. Forest Service, Southern Research Station, Virginia Tech
Blacksburg, Virginia 24061-0321, USA

Abstract.—We examined fish distribution and abundance in erosional habitat units in South Fork Roanoke River, Virginia, following a fish kill by using a reachwide sampling approach for 3 species and a representative-reach sampling approach for 10 species. Qualitative (presence–absence) and quantitative (relative abundance) estimates of distribution and abundance provided consistent measures of fish recovery for 2 of 3 species at the reachwide scale and 8 of 10 species at the representative-reach scale. Combining results across scales and estimator types showed that distributions and abundances of 5 of 11 species in the reach affected by the kill were similar to those observed in unaffected upstream and downstream reaches 8–11 months following the perturbation. Differences in distribution and abundance between the affected reach and unaffected reaches indicate that 4 of 11 species had not fully recovered during the same time period; results were equivocal for 2 other species. We attribute differences in recovery rates between these two groups to differences in parental investment in offspring. Species exhibiting rapid recovery either engage in extensive spawning site preparation or guard the spawning site following egg deposition and fertilization; species that had not recovered in the year following the kill show limited spawning site preparation and do not guard the spawning site.

Stream fish are exposed to both natural and anthropogenic disturbances that can alter population distribution and abundance. We need to understand the factors that influence population recovery following disturbances in order to effectively manage stream fish resources (Cairns et al. 1971; Hughes et al. 1990; Detenbeck et al. 1992). Factors determining recovery rates can be viewed in a hierarchical fashion (Detenbeck et al. 1992). Regional variations in climate, geomorphology, and hydrologic regime provide the large-scale habitat template determining the range of life history traits found in a stream fish assemblage (Resh et al. 1988). At a given site, local factors such as distance to source populations of potential colonists and occurrence of barriers to movement are important (Cairns et al. 1971; Gore and Milner 1990; Detenbeck et al. 1992). Finally, life history traits defining potential rates of population increase (e.g., Winemiller and Rose 1992) and vagility of individuals should determine differential recovery rates in a given assemblage.

Most studies of fish population recovery following large-scale natural or anthropogenic disturbance come from second- to fourth-order streams that have fish assemblages that are well-adapted to periodic disturbance (Niemi et al. 1990; Schlosser 1990; Detenbeck et al. 1992). Response variables are frequently limited to either qualitative (presence–absence) or semiquantitative (relative abundance) data from a limited number of "representative" sites (Niemi et al. 1990). Data on population density and spatial distribution during and after recovery from a variety of regions and stream

[1] Present address: Department of Biological and Physical Sciences, Kennesaw State University, 1000 Chastain Road, Kennesaw, Georgia 30144, USA.

[2] Present address: U.S. Forest Service, Center for Aquatic Technology Transfer, Southern Research Station, Virginia Tech, Blacksburg, Virginia 24061-0321, USA.

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sizes are needed to develop a comprehensive, predictive theory of fish population recovery following a disturbance. Furthermore, additional information on the utility and sensitivity of qualitative and quantitative response variables across spatial sampling scales (i.e., from both representative-reach and reachwide approaches; Hankin and Reeves 1988; Dolloff et al. 1993) is needed to facilitate design and implementation of effective recovery monitoring programs. Although manipulative studies can provide insight into recolonization following small-scale defaunations (Meffe and Sheldon 1990; Petersen and Bayley 1993), data for large-scale studies are usually obtained by treating anthropogenic disturbances as experiments (Sparks et al. 1990).

On 15 October 1991, a dairy farm in Riner, Virginia, accidentally released 100,000 gallons of liquid manure into Elliott Creek. In all, 22 km of stream were affected, 13 km of Elliott Creek and 9 km of South Fork Roanoke River downstream of its confluence with Elliott Creek. The Virginia Water Control Board estimated that over 190,000 fish were killed. Qualitative streamside observations over the 3 d immediately following the spill lead us to believe that the ichthyofauna was virtually eliminated from the upper 6 km of the affected reach on South Fork Roanoke. In the terminology of Bender et al. (1984) and Gore and Milner (1990), the manure spill can be classified as a level-2 pulse disturbance, which indicates that upstream and downstream sources of colonists existed following the spill and that the causal agent did not alter physical habitat available to potential recolonizers. Although the spill is regrettable, it did provide an opportunity to refine our understanding of the factors that influence fish recolonization following perturbation.

We present the results of a 2-year study that assessed fish recolonization in the affected reach. The four major objectives of the study were (1) to determine the distribution and abundance of selected riffle-dwelling fish species in the study reach during summer 1992 and 1993, (2) to assess the utility of reachwide and representative-reach approaches for determining recovery, (3) to assess the utility of qualitative (presence–absence) and quantitative (relative abundance) measures for determining recovery, and (4) to assess the role of differences in life history characteristics in determining recovery rates.

Study Area and Study Species

South Fork Roanoke (SFR) is a fifth-order stream in the Valley and Ridge Province of Virginia. Predominant land use in the watershed is agricultural, with the majority of the area in pasture or woodland. The riparian zone is largely vegetated, with willows *Salix* spp., American hackberry *Celtis occidentalis*, and sycamore *Platanus occidentalis* as the dominant woody riparian species. Total watershed area above a gauging station in the middle of the study reach (Figure 1) is 285 km^2; mean daily flow for the period of record is 3.14 m^3/s, and stream gradient is 1.7 m/km. Hydrologic records indicate that the study reach maintained continuous flow for the period of record (more than 40 years). Average stream width is 16.7 m; average pool depth is 52 cm; and maximum pool depth is usually less than 1.5 m, although some pools exceed 3 m. Although there are perennial streams entering South Fork Roanoke upstream and downstream from the affected reach, the only tributaries entering the affected reach are small and intermittent.

For the reachwide component of the study, we divided the SFR study area into three separate reaches, an upstream (US) control reach, a downstream (DS) control reach and a kill (KL) reach. The US reach included a 3-km stretch of SFR beginning near the mouth of Elliott Creek and extending upstream. The DS reach began 9 km and ended 13 km downstream of the mouth of Elliott Creek, and the KL reach included the 6 km of SFR immediately downstream of the mouth of Elliott Creek (Figure 1). Fish were collected from seven sites for the representative-reach portion of the study, two downstream, two upstream, and three within the affected reach (Figure 1).

We determined reachwide distribution and abundance of three species, Roanoke logperch *Percina rex*, Roanoke darter *P. roanoka*, and black jumprock *Scartomyzon* (=*Moxostoma*) *cervinus*. Distribution and abundance data for 10 species—white shiner *Luxilus albeolus*, crescent shiner *L. cerasinus*, bluehead chub *Nocomis leptocephalus*, central stoneroller *Campostoma anomalum*, torrent sucker *Thoburnia* (=*Moxostoma*) *rhothoeca*, black jumprock, margined madtom *Noturus insignis*, fantail darter *Etheostoma flabellare*, riverweed darter *E. podostemone*, and Roanoke darter—were obtained from the seven representative-reach sites. Juveniles and adults of all 11 species are commonly found in erosional, riffle–run habitat from the time they spawn in late spring until water temperatures drop in early winter, when they move into deep, slow-moving pools (Matthews 1990; Jenkins and Burkhead 1994; Ensign 1995). They are all either benthic or water column insectivores, with the ex-

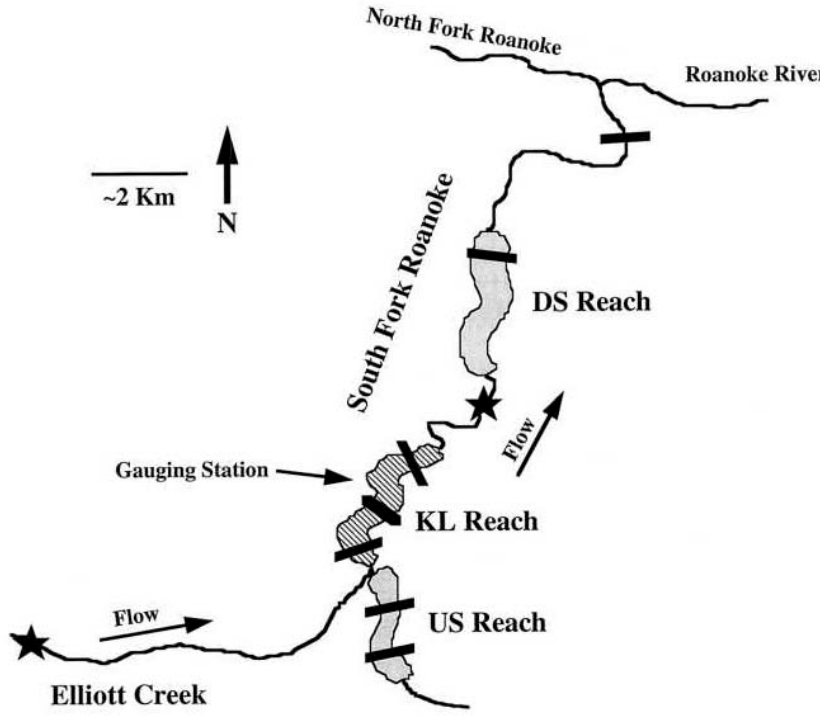

FIGURE 1.—The South Fork Roanoke River study area. Representative-reach study sites are indicated by the solid bars bisecting the river, upstream (US) and downstream (DS) reaches are indicated by solid gray, and the kill (KL) reach is indicated by cross-hatching. The upstream and downstream limits of the effect of the manure spill area indicated by stars on Elliott Creek and South Fork Roanoke River, respectively.

ception of the algivorous central stoneroller (Jenkins and Burkhead 1994). Although similar in habitat preference and trophic classification, the 11 study species differ in many life history characteristics, most notably parental investment in offspring (Jenkins and Burkhead 1994).

Methods

Data collection.—We used underwater observation to determine reachwide distribution and abundance of Roanoke logperch, Roanoke darter, and black jumprock. Sampling was conducted in erosional (riffle–run) habitat units in US, DS, and KL reaches during late May, June, and July 1992 and June and July 1993. Erosional units were visually identified as areas of shallow to moderate depth (typically less than 50 cm) with moderate to high current velocity (typically greater than 20 cm/s). Although we were unable to sample all units in each reach during both years, units that were sampled during both years were evenly distributed across the three reaches. During both years, qualitative underwater observation of fish behavior indicated that spawning activity had ceased in all reaches for all 11 study species, thereby minimizing the potential for differences among reaches related to seasonal movements for both reachwide and representative-reach sampling.

In each of the units sampled, two snorkelers entered the water at the downstream end of the unit and moved upstream in a straight line. Snorkelers attempted to maintain positions approximately one-third and two-thirds of the distance from the left ascending streambank. Observers scanned the stream bottom directly in front and to both sides of their line of travel and kept a tally of all adult Roanoke darters and all adult and juvenile Roanoke logperch and black jumprocks observed. Young-of-year were not included in the counts. Following completion of the observation pass, the length of the sampled unit was measured. Because water clarity can influence the number of fish seen, turbidity was measured at the beginning and end of each day with a Hach model 940 turbidimeter.

We estimated the density of the three species in individual habitat units using a modified line transect approach (Emlen 1971; Ensign et al. 1995).

Species-specific densities in a given unit were estimated by dividing the number of fish observed by the product of the length of the line snorkeled, the boundary width (an estimate of the maximum perpendicular distance at which a species is observed), and a correction factor accounting for the declining probability of sighting an individual fish as a function of increasing distance from the observer's line of travel. A full description of the technique, its application, and the reliability of the estimates obtained is given elsewhere (Ensign et al. 1995).

We obtained representative-reach data by conducting electrofishing surveys during August and September 1992 and 1993 at the seven sites in the study area (Figure 1). We used an AC backpack electrofishing unit and a 0.6-cm-mesh seine that was 4.5 m long and 1.5 m deep and had a 1.5-m by 1.5-m by 1.5-m bag attached. The seine was held downstream of the area to be sampled and a rectangular quadrat (4 m wide, 10 m long) immediately upstream of the seine was thoroughly electrofished. Following completion of electrofishing, the seine was lifted, and all fish retained in the net were identified and counted. The electrofished quadrat was searched, and fish observed on the stream bottom were retrieved and included in the sample.

At each site, sampling proceeded upstream along a series of transects placed perpendicular to streamflow at 15-m intervals. Quadrat locations were determined systematically. The adjoining edges of quadrats on a single transect were at least 2 m apart, with the outside edge at least 2 m from the adjacent bank. The number of quadrats on a given transect was a function of stream width and criteria previously mentioned. Spacing and location of quadrats and techniques employed during setting and lifting of the seine were designed to minimize disturbance of areas to be shocked.

Statistical analysis.—We assessed qualitative changes in fish abundance by comparing presence and absence of fish in individual sampling units within each reach between years. For the reachwide component of the study, erosional units snorkeled in both years served as the individual observations, and we used Fisher's exact test to determine differences within reaches between years. For the representative-reach portion of the study, individual quadrats served as the sampling unit and differences in reaches between years were determined with a chi-square test. If changes in the proportion of occupied sampling units in the KL reach differed significantly from that observed in the US and DS reaches, we concluded that there was evidence for kill effects in 1992. Because there were three comparisons for each species, we used a Bonferroni correction to maintain the species-specific comparisonwise error rate at $P = 0.05$. This lowered our minimum significance level to $P = 0.017$ ($0.05/3 = 0.017$).

We assessed quantitative changes in species' abundance using a Kruskal–Wallis test with each combination of year and reach as a unique group. Our response variable in the reachwide data set was fish density (number/ha), with each sampled erosional unit serving as a single observation. For the representative-reach data set we used number of individuals captured per quadrat as the response variable, with each sampled quadrat serving as an observation. Because we lacked data on fish abundance in the study area before the kill occurred, our initial null hypothesis was that there should be no significant difference among groups. Abundant evidence exists for longitudinal gradients in stream fish abundance, and given the spatial extent of our sampling, differences in abundance between the US and DS reaches could confound inferences related to recovery patterns in the KL reach. Therefore, if the Kruskal–Wallis test was significant ($P < 0.05$), we conducted a series of pairwise comparisons using Wilcoxon rank-sum tests. This process allowed us to refine our understanding of differences in abundance between the two unaffected reaches across years and to determine the importance of differences in KL reach abundance among reaches or across years. The first four tests compared abundance in unaffected reaches across years (US92 versus US93 and DS92 versus DS93; year is indicated by the last two digits) and within years (DS92 versus US92 and DS93 versus US93). The final five tests compared KL reach abundance across years (KL92 versus KL93) and KL reach abundance to US and DS reach abundance within years (KL92 versus DS92, KL92 versus US92, KL93 versus DS93 and KL93 versus US93). Because there were nine pairwise comparisons for each species, we used a Bonferroni correction to maintain our comparisonwise error rate at $P = 0.05$. This lowered our minimum significance level to $P = 0.006$ ($0.05/9 = 0.006$).

Results

Reachwide Comparisons

There were 56 erosional habitat units in the study area, and of those, we snorkeled 36 in both years, 11 in the DS reach, 15 in the KL reach, and

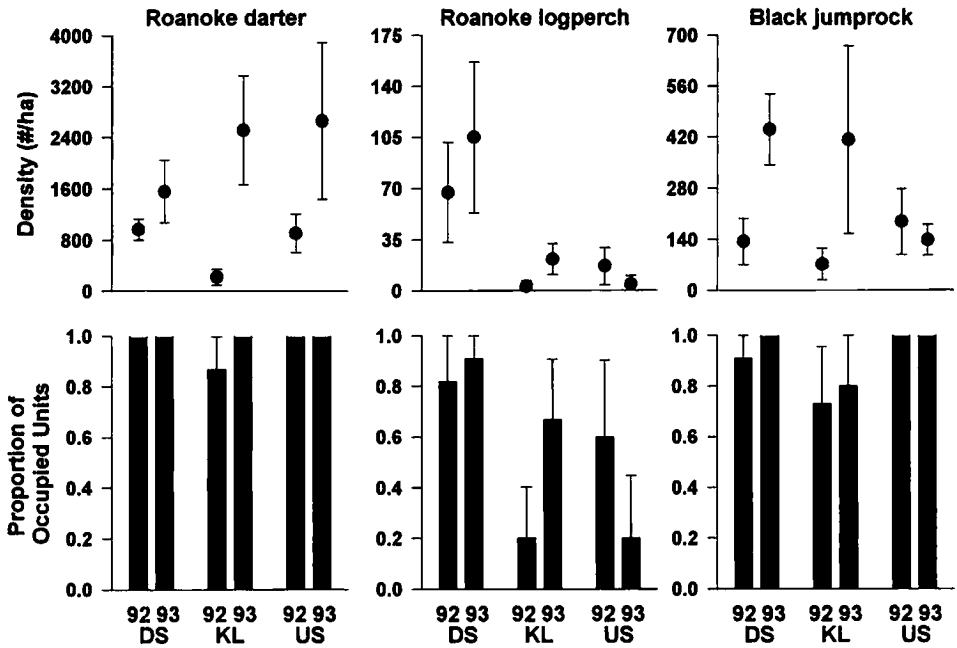

FIGURE 2.—Mean densities (upper graphs; number/ha) and proportion of habitat units occupied (lower graphs) for Roanoke darter, Roanoke logperch, and black jumprock based on the reachwide sampling data. Error bars represent 95% confidence intervals (CI) around the point estimates and the upper CI for the bar graphs.

TABLE 1.—Significance levels of pairwise Wilcoxon rank-sum tests for differences in density between reaches by year combinations and Fisher's exact test for differences in frequency of occupied units between years within reaches from the reachwide data sets for Roanoke darter, Roanoke logperch, and black jumprock. Abbreviations for reach by year comparisons are as follows: DS = downstream reach, US = upstream reach, KL = kill reach. Year is represented by its two final digits. An asterisk (*) indicates significant difference, given Bonferroni correction for multiple comparisons ($P < 0.006$ for the Wilcoxon tests; $P < 0.017$ for Fisher's exact tests).

Reach-by-year comparison	Roanoke darter	Roanoke logperch	Black jumprock
Wilcoxon pairwise comparisons			
DS92 versus US92	0.460	0.025	0.526
DS93 versus US93	0.130	<0.001*	<0.001*
DS92 versus DS93	0.042	0.293	<0.001*
KL92 versus KL93	<0.001*	0.004*	0.011
US92 versus US93	0.002*	0.088	0.850
KL92 versus DS92	<0.001*	<0.001*	0.048
KL92 versus US92	<0.001*	0.030	0.007
KL93 versus DS93	0.195	<0.001*	0.113
KL93 versus US93	0.846	0.025	0.212
Fisher's exact test			
DS92 versus DS93	1.000	0.476	1.000
KL92 versus KL93	0.483	0.003*	1.000
US92 versus US93	1.000	0.170	1.000

10 in the US reach. In 1992, Roanoke darter were observed in all units in the US and DS reaches and 13 of 15 units in the KL reach. In 1993, they were observed in all units in all reaches (Figure 2). Roanoke logperch were found in 6 units in the US reach, 3 units in the KL reach and 9 units in the DS reach in 1992; in 1993 they were found in 2, 11 and 10 units in the US, KL and DS reaches, respectively (Figure 2). Black jumprock were found in all 10 US reach units, 11 KL reach units, and 10 DS reach units in 1992 and in 10, 12, and 11 units in the US, KL and DS reaches, respectively, in 1993 (Figure 2). The number of units occupied in the KL reach differed between years only for Roanoke logperch ($P = 0.003$; Table 1).

We observed differences in density between at least one reach by year combination for all three species (Kruskal–Wallis test, all $P < 0.05$), but pairwise comparisons indicated effects attributable to the kill for only two of three species. For Roanoke darter, there were no differences between years for the DS reach or between US and DS reaches within years (all $P > 0.006$; Table 1, Figure 2). In contrast, KL reach densities were significantly lower than US and DS reach densities in 1992, and 1992 KL reach densities were significantly lower than 1993 KL reach densities (all

TABLE 2.—Significance levels of pairwise Wilcoxon rank-sum tests for differences in quadrat abundance between reaches by year combinations and chi-square test for differences in frequency of occupied quadrats between years within reaches from the respresentative-reach data sets for 10 of the species studied. Data for Roanoke logperch were not analyzed because of the low abundance of this species. Abbreviations for reach-by-year comparisons are as follows: DS = downstream reach, US = upstream reach, KL = kill reach. Year is represented by the last two digits. An asterisk (*) indicates significant difference, given Bonferroni correction for multiple comparisons ($P < 0.006$ for Wilcoxon tests; $P < 0.017$ for chi-square tests).

Reach-by-year comparison	White shiner	Crescent shiner	Bluehead chub	Central stoneroller	Torrent sucker	Black jumprock	Margined madtom
			Wilcoxon pairwise comparisons				
DS92 versus US92	0.249	<0.001*	0.003*	0.012	<0.001*	0.303	0.814
DS93 versus US93	0.005*	<0.001*	<0.001*	<0.001*	<0.001*	0.013	0.036
DS92 versus DS93	0.930	0.169	0.879	0.771	0.508	0.426	0.607
KL92 versus KL93	0.099	0.259	0.015	0.004*	0.005*	<0.001*	<0.001*
US92 versus US93	0.103	0.689	0.313	0.026	0.872	0.011	0.004*
KL92 versus DS92	0.103	0.367	0.732	0.708	0.254	0.012	0.579
KL92 versus US92	0.005*	<0.001*	0.005*	0.023	<0.001*	0.242	0.743
KL93 versus DS93	0.928	0.002*	0.013	0.007	0.005*	0.024	0.012
KL93 versus US93	0.002*	0.009	0.076	0.019	0.472	0.642	0.661
			Chi-square tests				
DS92 versus DS93	1.000	0.291	0.821	1.000	0.737	0.437	0.485
KL92 versus KL93	0.217	0.450	0.140	0.005*	0.009*	<0.001*	0.005*
US92 versus US93	0.213	1.000	0.787	0.047	0.015	0.008*	0.285

$P < 0.001$; Table 1, Figure 2). Roanoke logperch densities within the two reaches unaffected by the spill did not differ between the 2 years of the study ($P > 0.006$; Table 1, Figure 2), but KL reach densities increased significantly from 1992 to 1993 ($P < 0.001$; Table 1, Figure 2). The only change in black jumprock abundance was a significant increase in the DS reach from 1992 to 1993 ($P < 0.001$; Table 1, Figure 2).

Representative-Reach Comparisons

During 1992, we sampled 39 quadrats in the DS reach, 58 in the KL reach, and 32 in the US reach (total, 129 quadrats). In 1993, we obtained samples from 39 quadrats in the DS reach, 59 in the KL reach and 35 in the US reach (total, 133 quadrats).

There was no evidence for significant differences in the number of occupied quadrats within reaches between years for white shiner, crescent shiner, bluehead chub, fantail darter, or riverweed darter (all $P > 0.017$; Table 2, Figure 3). The number of quadrats occupied in the KL reach increased significantly from 1992 to 1993 for central stoneroller ($P = 0.005$), torrent sucker ($P = 0.009$), margined madtom ($P = 0.005$), and Roanoke darter ($P < 0.001$) (Table 2; Figure 3), although there was no change in occupied quadrats in the DS or US reach for any of these species ($P > 0.017$; Table 2). The number of quadrats containing black jumprock in both the KL and US reaches increased significantly from 1992 to 1993 ($P < 0.001$ and $P = 0.008$, respectively; Table 2, Figure 3), while there was no change in occupied quadrats in the DS reach ($P > 0.017$; Table 2).

There were significant differences in abundance between at least one reach by year combination for all 10 species (Kruskal–Wallis test; all $P < 0.05$). The patterns we observed in number of fish per quadrat between years and among reaches provides no evidence of postkill effects in 1992 for white shiner, fantail darter, and riverweed darter. For all three species, there were no significant differences in abundance between years for any of the three sampled reaches (all $P > 0.006$; Table 2, Figure 4). White shiner abundance was higher in the KL reach than in the US reach in both 1992 ($P = 0.005$) and 1993 ($P = 0.002$), but year-to-year consistency in this pattern and lack of differences between DS and KL reach abundances in both years ($P > 0.006$) (Table 2; Figure 4) suggests this may be a natural longitudinal abundance gradient. A similar pattern can be seen for both fantail darter and riverweed darter, as there are no significant differences within reaches between years ($P > 0.006$; Table 2). Differences between reaches within years are consistent with a longitudinal pattern in which highest abundance of both species is found in the US reach (Figure 4).

We found strong evidence of manure spill effects on KL reach populations of central stoneroller, torrent sucker, black jumprock, and Roanoke darter. While there were no significant differences in the number of central stoneroller, tor-

TABLE 2.—Extended.

Reach-by-year comparison	Fantail darter	Riverweed darter	Roanoke darter
Wilcoxon pairwise comparisons			
DS92 versus US92	<0.001*	<0.001*	0.951
DS93 versus US93	<0.001*	<0.001*	0.029
DS92 versus DS93	0.582	0.168	0.452
KL92 versus KL93	0.301	0.017	<0.001*
US92 versus US93	0.947	0.110	0.097
KL92 versus DS92	<0.001*	0.463	<0.001*
KL92 versus US92	0.204	<0.001*	<0.001*
KL93 versus DS93	<0.001*	0.144	0.512
KL93 versus US93	0.968	<0.001*	0.097
Chi-square tests			
DS92 versus DS93	0.818	0.332	0.496
KL92 versus KL93	1.000	0.130	<0.001*
US92 versus US93	0.400	0.780	0.331

rent sucker, black jumprock or Roanoke darter per quadrat in the US and DS reaches between years ($P > 0.006$; Table 2), KL reach abundance increased from 1992 to 1993 for all four species ($P = 0.004$ for central stoneroller, $P = 0.005$ for torrent sucker, $P < 0.001$ for black jumprock and Roanoke darter; Table 2, Figure 4). In addition to changes in KL reach abundance between years, there was also evidence for a consistent gradient in torrent sucker abundance as the number per quadrat in the US reach was higher than in the DS reach in both 1992 ($P < 0.001$) and 1993 ($P < 0.001$) (Table 2; Figure 4). In 1992, there was no significant difference in torrent sucker abundance between DS and KL reaches ($P > 0.006$; Table 2), but KL reach abundance was lower than that in the US reach ($P < 0.001$; Table 2, Figure 4). The pattern was reversed in 1993, with no significant difference between KL and US reaches ($P > 0.006$; Table 2), although DS reach abundance was lower than KL reach abundance ($P = 0.005$; Table 2, Figure 4). Roanoke darter KL reach abundance in 1992 was lower than 1992 US and DS reach abundances (both $P < 0.001$; Table 2, Figure 4), but there were no significant differences among any of the reaches in 1993 ($P > 0.006$; Table 2).

For the other three species, evidence supporting effects of the manure spill in the KL reach was equivocal. For both bluehead chub and crescent shiner, there was no significant difference in number per quadrat within reaches between years for the DS, KL or US reaches (all $P > 0.006$; Table 2), but US abundance was higher than DS abundance in both 1992 ($P < 0.001$ for crescent shiner, $P = 0.003$ for bluehead chub) and 1993 ($P < 0.001$ for both) (Table 2; Figure 4). Although KL reach abundances significantly differed from either US or DS reach abundances in at least 1 year (Table 2), a parsimonious interpretation would suggest that these differences are due to year-to-year variation in abundance in the KL reach. Margined madtom KL reach abundance increased from 1992 to 1993 ($P < 0.001$), but the number of madtom per quadrat in the US reach also increased ($P = 0.005$) (Table 2; Figure 4). Again, the simplest explanation for the observed pattern would be that the KL reach population is responding to the same factors driving increased abundance in the US reach population.

Summary of Reachwide and Representative-Reach Comparisons

At the reachwide scale, both qualitative and quantitative data sets showed that Roanoke logperch populations in the KL reach were depressed in 1992; however, both data sets failed to indicate any measurable effects on black jumprock populations in the KL reach. The two data sets provided conflicting results for Roanoke darter; the quantitative data set indicated a significant effect in the KL reach and the qualitative data set indicated no effect (Table 3).

At the representative-reach scale, both quantitative and qualitative measures of fish response indicated significant effects of the manure spill on the KL reach for central stoneroller, torrent sucker, and Roanoke darter populations (Table 3). The quantitative measure indicated a significant effect on black jumprock populations in the KL reach, but the qualitative measure indicated that populations in the KL reach may be responding in a manner similar to populations in the US reach (Table 3). The reverse is true for margined madtom; the presence–absence data indicated a kill effect in the KL reach, but the abundance data argue for some other factor as driving populations in the KL and US reaches in the same direction. Parsimonious interpretation of the observed quantitative patterns for bluehead chub and crescent shiner results in agreement with the qualitative finding of no effect, while the case for concurrent findings of no effect on white shiner, fantail darter, and riverweed darter populations in the KL reach from both the qualitative and quantitative data sets is straightforward.

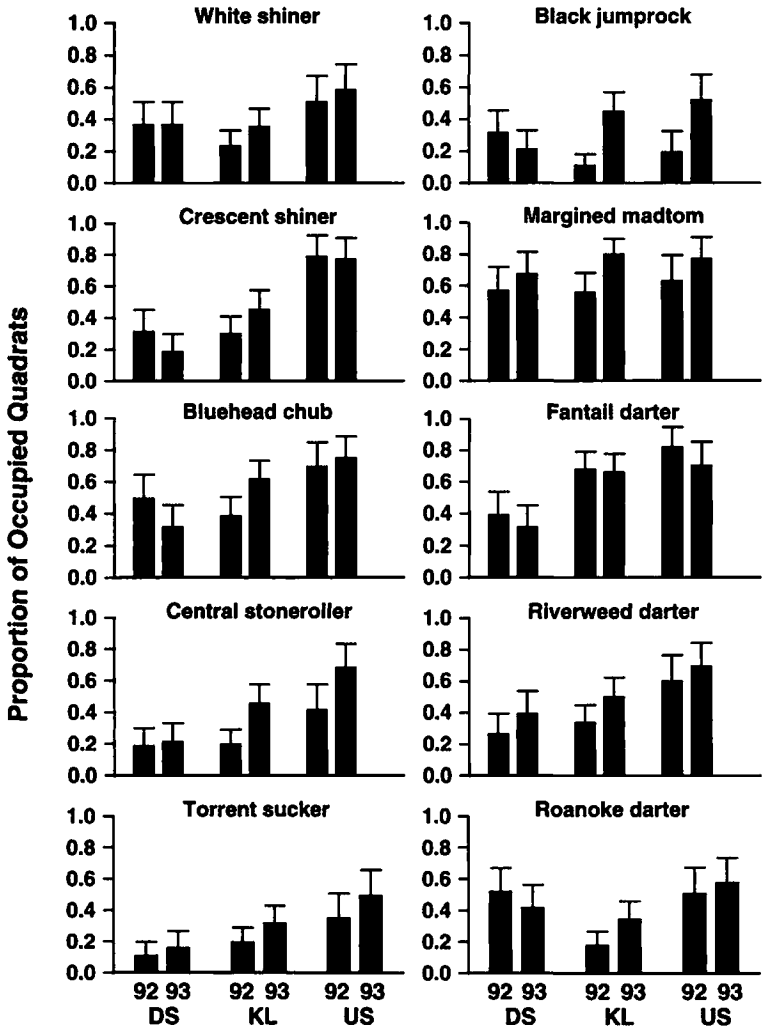

FIGURE 3.—Proportion of quadrats occupied for 10 of the 11 study species based on representative-reach sampling data. (Data for Roanoke logperch were not analyzed because of low abundance.) Error bars represent the upper 95% confidence interval for the bar graph.

Discussion

Methodological Comparisons

Our objectives were formulated to address three linked methodological questions. (1) Do qualitative and quantitative indices of fish abundance and distribution provide equivalent information at a reachwide sampling scale? (2) Do qualitative and quantitative measures of fish abundance and distribution provide equivalent information with small-spatial scale sampling within representative reaches? (3) Are there differences in the information obtained from reachwide and representative-reach samples? Comparisons among different spatial scales, data types, and study species (summarized in Table 3) can provide managers with information for the design of future recovery monitoring programs.

The results obtained from the reachwide data set showed that qualitative and quantitative measures of abundance coincide for Roanoke logperch and black jumprock but conflict for Roanoke darter (Table 3). Lack of agreement for Roanoke darter may be attributed to two factors, vagility and abundance in unaffected reaches. Although specific studies suggest that individual Roanoke darters may have high site fidelity (Lee and Ashton 1981), anecdotal evidence, particularly the rapid expan-

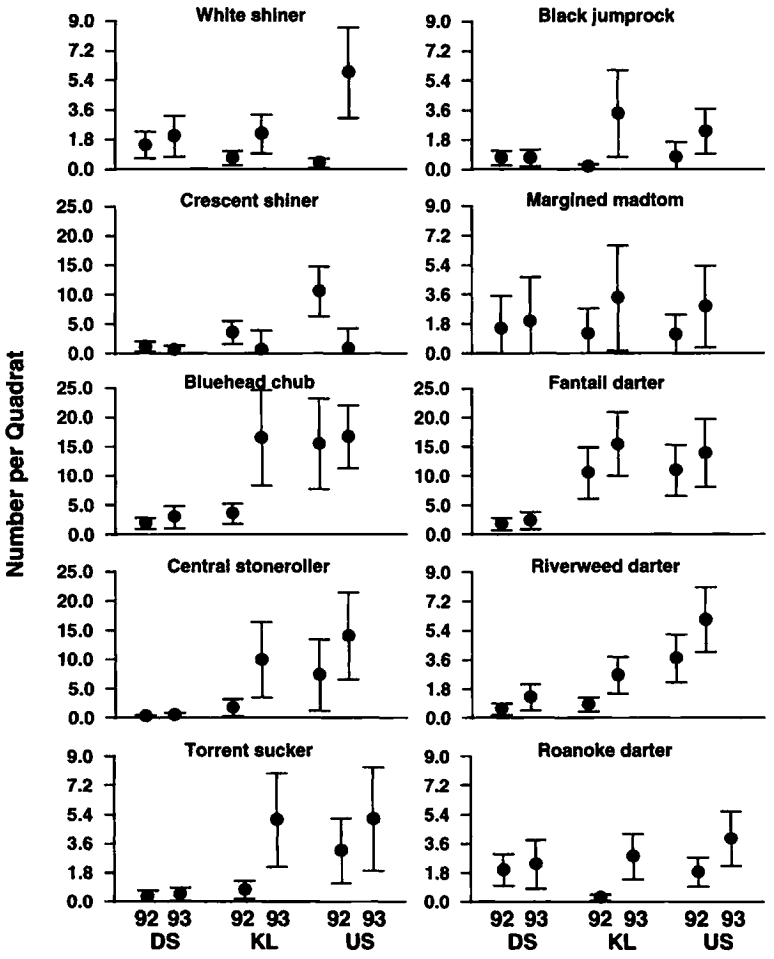

FIGURE 4.—Mean abundance (number of fish/quadrat) for 10 of the 11 study species based on the representative-reach sampling data. (Data for Roanoke logperch were not analyzed because of low abundance.) Error bars represent 95% confidence intervals around the point estimates.

sion of the species in the James River basin, indicates that at least some Roanoke darters are highly mobile (Jenkins and Burkhead 1994). Given mobile and sedentary portions of a population with moderate abundance, there is potential for a lag between occupation of habitat units by colonizers and reestablishment of original population abundance through reproductive output. Accordingly, the qualitative measure is a poor indicator of population recovery.

In contrast to Roanoke darters, black jumprocks occur in relatively low abundance and are highly mobile (as are most catostomids). Rapid random diffusion of both adults and juveniles from upstream and downstream populations is sufficient to reestablish the species in suitable habitat units and return abundance to preperturbation levels. Finally, Roanoke logperch are typically found in low abundance even under normal conditions, so it is not surprising that presence–absence and abundance measures would coincide during the early stages of recovery. Therefore, either approach would serve as a reasonable measure of recovery for species with high mobility, low abundance, or a combination of both characteristics.

At the representative-reach scale, there was good agreement between quantitative and qualitative measures for all species, except margined madtom and black jumprock (Table 3). Although we can find no reasonable explanation for the lack of agreement in the measures for the margined madtom, there is a logical reason for the differences seen for the black jumprock. The quantitative measure indicated there was no change in

TABLE 3.—Summary of evidence for species recovery following the South Fork fish kill for qualitative and quantitative sampling at representative reach and reachwide sampling scales. Evidence that populations had recovered in the year following the kill is indicated by the letter Y; evidence indicating that populations had failed to recover is indicated by the lettter N. An asterisk (*) indicates that data were not collected for the species at that sampling scale. Abundance, schooling, and parental investment characteristics are also given for each species. For abundance and parental care, H = high, M = moderate, and L = low. For schooling behavior, Y = schooling, and N = nonschooling.

	Qualitative sampling		Quantitative sampling				
Species	Representative reach	Reachwide	Representative reach	Reachwide	Abundance	Schooling	Parental care
White shiner	Y	*	Y	*	M	Y	H
Crescent shiner	Y	*	Y	*	H	Y	H
Bluehead chub	Y	*	Y	*	H	Y	H
Central stoneroller	N	*	N	*	H	Y	M
Torrent sucker	N	*	N	*	M	Y	L
Black jumprock	Y	Y	N	Y	L	Y	L
Margined madtom	N	*	Y	*	L	N	H
Fantail darter	Y	*	Y	*	H	N	H
Riverweed darter	Y	*	Y	*	M	N	H
Roanoke darter	N	Y	N	N	M	N	L
Roanoke logperch	*	N	*	N	L	N	L

black jumprock populations in the US reach between years, but the qualitative measure indicated that populations increased from 1992 to 1993. These differences can be explained if we consider both the social behavior and the natural abundance of this species. When we compare black jumprock abundance in the US and DS reaches with that of the other 10 species, only the Roanoke logperch is less abundant. Although individual black jumprocks are not rare, most occur in schools that range in size from 5 to 40 individuals. It is the only species in this study that shows both low abundance and schooling behavior (Table 3). In 1992, most fish obtained in the US reach came from large schools captured in a limited number of quadrats; however, in 1993 fish were more evenly distributed across quadrats. Although the number of individuals captured was not different, differences in spatial distribution resulted in differences in the number of quadrats occupied. Therefore, we recommend caution in the use of presence–absence data as a measure of recovery for uncommon, schooling species like the black jumprock.

If we look at comparisons across spatial scales, the results are concordant for Roanoke darter if we discount the reachwide qualitative measure for the previously stated reasons. However, if we also discount the representative-reach qualitative results for the black jumprock, then comparisons across spatial scales provide differing results for this species. The combination of low abundance and schooling behavior that resulted in differences between qualitative and quantitative measures at the representative-reach scale could also be responsible for the lack of concordance across sampling scales. At the reachwide scale, we sampled 15 erosional units in the KL, but at the representative-reach scale we sampled more than 50 quadrats from only 3 erosional units. Because of this, the probability of estimating the true abundance or distribution of the species was greatly reduced at the representative-reach scale, given the clumped distribution of the black jumprock. For species with either a random or uniform distribution, these sampling differences would not have been as important. Although we do not present the results here, we did quantify abundance and distribution of Roanoke logperch at the representative-reach scale. Given their naturally low abundance, Roanoke logperch were absent from most quadrats in US, KL, and DS reaches, which made statistical analysis of the data meaningless.

In summary, qualitative and quantitative data sets gave consistent results both within and across spatial scales, with a few notable exceptions. In designing monitoring programs to assess fish population recovery following perturbations, we recommend the use of some type of reachwide estimation technique (e.g., Hankin and Reeves 1988; Dolloff et al. 1993) and the use of either qualitative or quantitative measures of abundance and distribution for species with either low natural abundance or severely clumped spatial distributions. For species of moderate to high abundance and uniform or random distributions, quantitative sampling at a reachwide scale or qualitative or quantitative sampling at the representative-reach scale would be appropriate.

Effects of Life History

We observed differences in recovery patterns among the 11 species studied in the affected reach of South Fork Roanoke. Previous studies have shown that recovery times vary among families, size at first reproduction, maximum size or age, and reproductive guild (Detenbeck et al. 1992). Based on our results, only factors related to reproductive behavior seemed to play an important role in species recovery in the South Fork Roanoke River.

There was no clear difference in recovery rates among families; some cyprinids and some percids exhibited 1992 KL reach effects, but others did not (Table 3). Although KL reach abundance of the torrent sucker was depressed in 1992, evidence for the black jumprock is equivocal; therefore, it is difficult to make inferences about catostomids. The lack of a clear indication of recovery or lack of recovery by the margined madtom makes inferences about ictalurids problematic as well.

Depressed Roanoke logperch abundance in the KL reach during 1992 does provide some support for other studies that have shown that late-maturing species are slow to recover from perturbations (Detenbeck et al. 1992). However, there was little variability in age at first reproduction for the species we studied; therefore, it is difficult to make inferences about the effect of this factor. Although the Roanoke logperch does not initially spawn until its third year, all of the other species examined initially spawn in either their first or second year (Jenkins and Burkhead 1994).

There was little indication that maximum age or size played an important role in recovery rates. Two small, short-lived species (fantail darter and riverweed darter) showed no effects from the spill in 1992, while a third (Roanoke darter) showed strong evidence of spill effects (Table 3). At the other extreme, the large, long-lived Roanoke logperch showed 1992 effects, but the bluehead chub did not (Table 3). Although the Roanoke logperch may live slightly longer than the bluehead chub (7 versus 5 years), maximum lengths are similar for the two species (Jenkins and Burkhead 1994). Our results contrast with the findings of Detenbeck et al. (1992) that indicated large, long-lived species should be slower to recover than small, short-lived ones. However, as with age at first maturation, there was limited variability in maximum length or age for our 11 study species. Maximum lengths ranged from a low of approximately 80 mm total length (TL) for riverweed darter, fantail darter, and Roanoke darter to a high of slightly over 200 mm TL for black jumprock and bluehead chub. Maximum age ranged from 3 years for the three darters to 7 years for the Roanoke logperch (Jenkins and Burkhead 1994).

Although familial affiliation, age at first reproduction, and maximum size or maximum age fail to provide meaningful explanations for recovery rate differences, variation in reproductive behavior among the 11 study species does provide insight into mechanisms influencing recovery. All 11 species can be classified as reproductive lithophils. However, there are differences in the amount of parental investment in the selection and preparation of the spawning site, and these differences correspond with levels of population recovery observed in 1992 in the KL reach. Three of the four species showing evidence of spill impacts (Roanoke darter, Roanoke logperch, and torrent sucker) are simple lithophils. In all three cases, pairs or groups of spawners select an area containing gravel or pebble substrate in areas of higher water velocity and, during the course of the spawning act, bury eggs in the upper layers of the spawning area (Jenkins and Burkhead 1994). The fourth species exhibiting kill effects in 1992, the central stoneroller, shows slightly greater spawning site preparation. Central stonerollers also select pebble or gravel substrate in erosional areas, but males dig and defend a shallow depression or pit in the selected area. Female central stonerollers then move into the prepared area, and mating takes place (Jenkins and Burkhead 1994). There is no evidence of postspawning parental care by any of these species following egg deposition and fertilization.

The minimal parental investment in the spawning act by these four species contrasts with the more elaborate prespawning and postspawning behavior of the five species that showed no spill effects in 1992 (Table 3). Both fantail darter and riverweed darter males select and defend breeding sites. Adhesive eggs are deposited and fertilized on the underside of flat stones, and the male guards the nest aggresively during development. There is some evidence that secretory tissues in the skin of fantail darter males may release bactericides or fungicides that further facilitate egg development (Mayden 1985; Jenkins and Burkhead 1994).

Although there is little postspawning investment by the other three species, male bluehead chubs undertake extensive nest-building behaviors that are similar to those of many other species in the genus *Nocomis*. Large adult male bluehead chubs dig a pit in pebble or gravel areas and then refill

the excavated area with stones of relatively uniform size selected from the surrounding area. The effort expended by male bluehead chubs in nest construction is considerable, taking from 20 to 30 h, with completed nests ranging in size from 35 cm to over 1 m in diameter (Jenkins and Burkhead 1994). Following nest construction, females deposit eggs in shallow trenches dug by the male in the upstream edge of the pit; the eggs are fertilized by the male and subsequently covered by stones. Both the white shiner and the crescent shiner are commonly observed nest associates of the bluehead chub, and large aggregations of males and females spawn on the mounds formed by the bluehead chubs (Jenkins and Burkhead 1994; W. E. Ensign, personal observation).

The extensive nest site preparation and, in the case of the darters, nest site defense, certainly enhance survival and early development of eggs and larvae. The clear differences we observed in 1992 KL reach populations between the group of four species with limited parental investment in their progeny and the group of five species with significant investment suggests that factors that facilitated survival of early life stages in the year following the manure spill played an important role in the differences in recovery rates (Table 3). Detenbeck et al. (1992) suggested that different reproductive guilds have differential rates of recovery and that species that require generalized spawning habitat should recover more quickly than those that require specialized habitats. This may be true when the original perturbation causes degradation of specialized habitats, but when physical habitat remains relatively unaffected (as in the South Fork Roanoke kill), factors that facilitate early survival, and presumably rapid population increase, may predominate. This inference is further strengthened by differences in the type of parental investment by the species exhibiting rapid recovery. While the cyprinds expend effort in preparing the spawning site before egg deposition and development, the percids invest effort both in nest site selection and egg maintenance during development. The end result in both cases should be increased survival during the critical early life history stages.

Other Factors

The data obtained in this study can provide insights into factors other than life history tactics that affect fish population recovery. If we compare our results with other studies of the effects of a similar large-scale disturbance, the importance of local fish adaptation to regional geomorphology and hydrology becomes apparent. Studies in drought-prone streams in the midwestern United States have documented rapid recovery from stream defaunations associated with channel dewatering (Larimore et al. 1959; Bayley and Osborne 1993). For most species and sites, recovery times were much less than 1 year, despite the fact that sites were located a significant distance from a source of potential recolonizers. In these instances, the component species in the assemblage are adapted to periodic large-scale disturbance and exhibited rapid recovery. In contrast, the assemblage in the more benign South Fork Roanoke may experience periodic disturbances associated with flooding, but local refugia (i.e., backwater areas along stream margins, deep pools, velocity shelters behind large substrate, etc.) are probably abundant. Defaunations are probably limited to small, localized patches and recolonization requires only minor redistribution of the population. For example, Meffe and Sheldon (1990) found that fish communities in blackwater streams in the southeastern United States recovered to preperturbation levels 11 months after small-scale defaunations. In a similar study in Illinois, Petersen and Bayley (1993) observed recovery from a similar experimental defaunation in just a few days.

Finally, the relatively extensive immigration we observed during the first year of recovery calls into question the results of a number of studies that indicate warmwater and coolwater stream fish have limited home ranges and low vagility (Gerking 1953; McLeave 1964; Hill and Grossman 1987; Mundahl and Ingersoll 1989). Adult fish obtained or observed in the middle of the KL reach during the summer of 1992 moved a minimum of 3 km in the 8 months following the fish kill. This distance is at least two orders of magnitude greater than the home range sizes reported in the previously cited studies.

In summary, parental investment in early life stages played an important role in the ability of species to recolonize South Fork Roanoke River following the fish kill. In assessing management actions to be taken following large-scale perturbations, resource managers should realize that even though the component species of a fish assemblage are adapted to the unique combination of hydrologic and geomorphologic conditions in a basin, variability in life history tactics within an assemblage is great enough that a single endpoint for assessing recovery may not be sufficient. Furthermore, assemblages in regions where large-

scale perturbations occur infrequently may be more vulnerable to the cumulative impacts of repeated small-scale disturbances (e.g., siltation, periodic flow reductions, etc.) because the frequency of disturbance need not be as great to prevent complete population recovery.

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