ASSEMBLAGE ORGANIZATION OF STREAM FISHES: THE EFFECT OF RIVERS ON ADVENTITIOUS STREAMS

In 1985 Grossman et al. published a rebuttal to criticism of their 1982 paper on stochastic organization of an Indiana stream fish assemblage by Herbold (1984), Rahel et al. (1984), and Yant et al. (1984). Because I was particularly troubled by Grossman et al.'s (1985) assertion that the conclusions of their earlier paper had been strengthened rather than weakened, I present a different perspective of their 1982 results, questioning the validity of the study because of unrecognized methodological problems. I also present data from a comparable Indiana stream and from published studies, from which I draw conclusions about the nature of stream fish assemblages that differ from those of Grossman et al. (1982).

An apparently overlooked problem that affects Grossman et al.'s conclusions concerns their choice of a study stream. Yant et al. (1984) also criticized their choice, but my criticisms present a new perspective. The stream chosen for study, Otter Creek, is a third-order adventitious stream of the sixth- or seventh-order Wabash River. (Stream order is a hierarchical classification of streams proposed by Kuehne [1962], in which the smallest, permanently flowing stream is designated as first order, the union of two first-order streams becomes second order, the union of two second-order streams becomes third order, and so on.) Adventitious streams are small feeder tributaries of much larger streams, and stream order does not follow the usual hierarchical progression: adventitious streams (typically of first to third order) differ in stream-order rank by at least three from the receiving mainstream (which is of fourth order or greater). This definition is similar to the "tributary additions to master streams" of Vannote et al. (1980, p. 132) and Minshall et al. (1985, p. 1049). The interface between the tributary and the mainstream represents a discontinuity in the stream continuum (Vannote et al. 1980). The effects of this discontinuity on the mainstream community and ecosystem properties are hypothesized to be localized (Vannote et al. 1980), but they may be widespread if the tributaries are relatively large (Bruns et al. 1984; Minshall et al. 1985). The effect of the discontinuity on tributary streams does not appear to have been considered, however, and the effect may be particularly strong for fish assemblages in smaller adventitious streams. Since many stream fishes seasonally migrate upstream (Hynes 1970; Hall 1972; Karr and Gorman 1975; Gorman 1976; Toth et al. 1981; Schlosser 1982) and since these migrations appear to be synchronized with reproductive periods and seasonal pulses in stream metabolism (Hall 1972), the impact of mainstream fish assemblages on those in adventitious streams is probably significant.

The results of a long-term study at Black Creek, an adventitious tributary of the

Am. Nat. 1986. Vol. 128, pp. 611–616.

Maumee River in Indiana, suggest that, in comparison with their mainstream headwater counterparts, adventitious streams have smaller resident fish faunas and their assemblages undergo large seasonal dynamics because they are strongly influenced by proximal river assemblages, particularly in their lower reaches (Karr and Gorman 1975; Gorman 1976; Toth et al. 1981). Recognition of the nature of adventitious streams is apparently lacking in the major stream-fish literature, an observation indicating that fish assemblages in these streams have not been given special treatment. Mendelson (1975) provided a seasonal analysis of a fish assemblage in an adventitious stream, although he gave no special recognition to the stream's adventitious condition. The stream, Roxbury Creek, is a third-order tributary of the sixth- or seventh-order Wisconsin River, and the assemblage is dominated by four riverine minnows (*Notropis atherinoides*, *N. dorsalis*, *N. spilopterus*, and *N. stramineus*). Mendelson (1975, figs. 2 and 3) attributed the seasonally fluctuating abundances of these dominant species to migrations into and out of the Wisconsin River.

In retrospect, the choice of Otter Creek by Grossman et al. (1982) for studying the stability of fish-assemblage organization and structure was unfortunate because of its adventitious condition. The predominant species of the Otter Creek assemblage (Grossman et al. 1982, table 1) included species that have been shown to migrate seasonally from rivers into adventitious streams (i.e., *N. atherinoides*, *N. chrysocephalus*, *N. stramineus*, *N. spilopterus*, *N. umbratilus*, *Ericymba buccata*, and *Campostoma anomalum*; Karr and Gorman 1975; Mendelson 1975; Gorman 1976; Toth et al. 1981, 1982). In addition, their study site was located close to the Wabash River (5 km upstream, on the edge of a river floodplain) with a dam immediately upstream. By blocking the upstream movement of riverine fishes, the dam concentrated individuals at the study site (Yant et al. 1984). Most of these blocked migrants probably returned to the river more quickly than they would have if they had had access to upstream reaches. The study site's proximity to the river and dam probably resulted in greater dynamics in assemblage composition. Evidence of faunal dynamics accentuated by the proximity of a river and a dam to Grossman et al.'s sample site can be found in Whitaker and Wallace (1973) and Whitaker (1976). Although Grossman et al. (1985) admitted that the dam may have caused problems, they insisted that the situation is not unusual since most streams have dams.

In their rebuttal, Grossman et al. (1985) claimed that their single 120-m sampling site was of sufficient size to encompass all the habitats used in the lifetimes of many of the species studied (this would follow the guidelines for long-term studies of communities proposed in Connell and Sousa 1983). Although no direct evidence was presented for their site, numerous references containing accounts of home-range characteristics of stream fishes were cited. Grossman et al. also provided some of their unpublished data on the home-range tendencies of four fishes in an Appalachian stream. They showed that the home ranges of the four species were relatively small (less than 15 m) and well within the size of the Otter Creek site (120 m). But this site is situated in an extensively forested upland region of the southern Appalachian Mountains and is not comparable with the Otter Creek site, which is on the lowland portion of a Midwestern watershed dominated by agriculture. As discussed below these differences appear to affect the degree of movement of stream fishes. Also, Ross et al. (1985) pointed out that the ichthyological literature is full of contradictory accounts of fish movements and home-range characteristics and that generalizations about a species' vagility are suspect without verification.

Ross et al. (1985) argued that in order to study assemblage stability of stream fishes, a number of locations within a watershed must be monitored to avoid making spurious interpretations. A review of two relevant mark-recapture studies that include a number of sample sites is enlightening. In Mendelson's (1975) study of Roxbury Creek, a total of 507 individuals of the four dominant species were marked during the spring of 1966 and the spring of 1967, but only 2% were ever recaptured among six pools in the lower 1.6 km of the stream. Of the four species marked, three were also among the most abundant species in Grossman et al.'s study (*N. atherinoides*, *N. spilopterus*, *N. stramineus*). Results of a mark-recapture study in another adventitious stream in Indiana, Black Creek, were similar (Karr and Gorman 1975; Karr, Gorman, and Ratcliffe, unpubl. data). In the lower 10 km of the channelized portion of Black Creek, 1202 fish were marked at three sites during the spring of 1976. Many of the species marked were the same as those encountered by Grossman et al. (1982): *C. anomalum*, *E. bucatta*, *Lepomis cyanellus*, *N. chrysocephalus*, *N. spilopterus*, *N. stramineus*, *N. umbratilis*, *Pimephales notatus*, *P. promelas*, *Semotilus atromaculatus*. Fish were monitored by biweekly sampling at 14 100-m stations distributed over the watershed. Overall, only 5.4% of the marked fish were recaptured (4.2% were recaptured at original marking stations). Of the 1.2% not recaptured at their original marking stations, most had moved several kilometers and one individual was recaptured 9 km upstream. No recaptures were made 3 mo after marking. In contrast to the lower-drainage mark-recapture study, 34% of 1084 marked fish from a wooded unchannelized upland station were recaptured once at the original marking location, 20.7% were recaptured at least twice, and 6.2% were recaptured 12 mo after marking. Thus, fish appear to be more vagile in the lower portions of adventitious streams (e.g., Roxbury Creek, Black Creek, Otter Creek), whereas in upland areas farther from the influence of riverine populations, stream fishes appear to be more sedentary (as at the upland Appalachian stream site of Grossman et al. 1985).

Vagility also appears to be influenced by the degree of habitat heterogeneity (Karr and Gorman 1975; Gorman 1976). In areas where habitat heterogeneity is low (channelized streams, lowland streams, and rivers), fish vagility is high and assemblage composition appears to be seasonally dynamic. In streams where habitat heterogeneity is higher, vagility is lower and assemblage composition more stable. Grossman et al. (1982) did not assess fish movement, and although they described the habitat structure of their study site as diverse, they regarded this condition as being due to the presence of the dam and not representative of conditions downstream from their site, where the stream was contained in a silty-sandy channel. I suspect that fish movement in their study area was similar to that in the lower portion of Black Creek because their study station was located on the lowland floodplain of a large river.

Some stream fishes are more vagile than others and even under optimal habitat conditions would not be contained in small reaches of stream. A good example is the minnow *Hybognathus nuchalis*, which is common in larger streams and rivers throughout the Midwest but not in smaller streams (Cross 1967; Pflieger 1975; Smith 1979). In Grossman et al. (1982) this species showed considerable variability in sample size over the 12 yr of their study. The variability in the abundance of *H. nuchalis*, as well as that of other pool-dwelling species (in the sense of Herbold 1984) in Otter Creek, may be partially explained by intermittent mass movement of individuals into and out of the Wabash River. Another consideration is that during summer and winter some species are more sedentary, but during autumn and especially spring, large migrations of stream fishes may be observed (Hall 1972; Karr and Gorman 1975; Toth et al. 1981, 1982). For example, during late summer or fall, *Dorosoma cepedianum* young-of-year and *N. spilopterus* adults underwent mass migrations into Black Creek from the Maumee River (Karr and Gorman 1975; Toth et al. 1981). Mendelson (1975) provided evidence of fall migrations of *N. spilopterus* into Roxbury Creek from the Wisconsin River. The data tables of Grossman et al.'s original paper suggest that similar migrations may have occurred in Otter Creek as well. However, Grossman et al. could not detect these migrations because they had only one sampling station. In contrast, migrations were easily detected in Black Creek because of frequent sampling at numerous stations distributed over the watershed.

A final criticism of Grossman et al. (1982) concerns the lack of separate treatment of young-of-year fishes (YOY) in their analyses. This problem was briefly covered by Yant et al. (1984) and discussed in detail by Schlosser (1985), but not in the context of adventitious streams. Schlosser showed that YOY density, species richness, and species composition are all highly variable between years in comparison with the adult portion of the resident population in an upland central Illinois stream (Jordan Creek). Furthermore, Schlosser suggested that YOY are sensitive to stochastic processes, whereas adults appear to be responsive to deterministic processes that regulate assemblage structure. Although many YOY in upland reaches may be attributed to adults in the area, this is not the case in adventitious-stream locations close to the receiving river (such as Grossman et al.'s Otter Creek site). Indeed, some of Grossman et al.'s numerically dominant species (*N. chrysocephalus*, *N. spilopterus*, *N. umbratilus*, and *C. anomalum*) migrate into adventitious streams in Indiana as adults, spawn, and depart (Karr and Gorman 1975; Gorman 1976; Toth et al. 1981). Since they did not distinguish YOY from adults, it is impossible to ascertain these important patterns in their data. Obviously, inclusion of YOY into analysis of assemblage stability heightens the level of perceived dynamics but the effect is greater for adventitious sites.

Because most streams of any size (fourth order and above) in the midwestern United States are often heavily disturbed, studies of less-disturbed habitats are apt to be done in short, adventitious streams. The results of Grossman et al. (1982) are probably typical of an adventitious stream, and the presence of a dam at their sampling site and the inclusion of YOY in their analyses probably increased the perceived level of assemblage instability. In any case, their results cannot be generalized and applied to other streams. What can be generalized from recent literature is that attributes of assemblage structure in stream fishes are affected by the following factors: environmental variability (Schlosser 1982; Ross et al. 1985), habitat structure (Gorman and Karr 1978; Schlosser 1982; Moyle and Vondracek 1985), age of the individual (Schlosser 1985), ecological differences among species groups (Herbold 1984; Rahel et al. 1984), and drainage position in relation to the master stream (Schlosser 1982). Recognition of adventitious streams in future research may help to clarify attributes of stream fish assemblages and thereby contribute to the development of stream-ecosystem theory (Minshall et al. 1985).

ACKNOWLEDGMENTS

I wish to thank B. Herbold and three anonymous reviewers for their useful suggestions for improving this paper.

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Submitted November 14, 1985; Revised February 18, 1986; Accepted April 28, 1986

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