Spatial and temporal patterns in the fish assemblages of individual pools in a midwestern stream (U.S.A.)

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Synopsis

The composition and consistency of fish assemblages in 14 adjacent pools (6–120 m long) of a clear-water, limestone and gravel creek in midwestern U.S.A. were quantified in eight snorkeling surveys over 19 months, to establish a baseline of natural variation in the system at this scale. The fauna of the stream was dominated numerically by minnows (Cyprinidae), sunfish and black bass (Centrarchidae), and topminnows (Funduli-dae). The pool fish fauna of the total 1 km reach (including all 14 pools) was highly consistent throughout the study, despite two major floods. Assemblages in individual pools generally were consistent, but there was more variation within pools than at the scale of the entire reach. Throughout the study, most individual pools remained within discrete subsets of the total occupied multivariate space in a principal components analysis based on fish species abundances. Sunfishes (*Lepomis* spp.) and bass (*Micropterus* spp.) were more consistent in their distribution among pools than were minnows (Cyprinidae) or a topminnow (*Fundulus*). There were 25 significant correlations in occurrence of species pairs among stream pools, out of 91 possible comparisons of the 14 most abundant taxa in the reach. Many pools contained assemblages either dominated by large centrarchids or by abundant cyprinids and juvenile centrarchids, but intermediate assemblages also were observed. The dynamics of distribution of fish species and fish assemblages among individual stream pools are likely influenced by a combination of species-specific behaviors and habitat selection, predator constraints on use of individual pools by small fishes, riffles as size-selective barriers to fish movements between pools, dispersal of young-of-the-year fishes, and abiotic phenomena like floods. Individual stream pools appear to be discrete habitat units for fishes, and do represent an appropriate scale for biologically meaningful studies of fish assemblages or their effects on streams.

Introduction

Many fish ecologists have focused on structure or stability of stream fish assemblages (Gorman & Karr 1978, Harrell 1978, Matthews & Hill 1980, Grossman et al. 1982, 1990, Moyle & Vondracek 1985, Ross et al. 1985, Matthews 1986, 1990, Matthews et al. 1988, Matthews & Meador 1992). In these and other fish communities (e.g., reef fishes, Ogden & Ebersole 1981) patterns in community structure or in the perceived degree of assemblage stability are influenced by the spatial scale of obser-

vations. Stability of fish community structure has been analyzed at the scale of entire streams (Ross et al. 1985, Matthews 1986, Matthews et al. 1988). Grossman et al. (1982), Schlosser (1987), Ross et al. (1985) and Matthews (1986) also evaluated structure or stability of fish assemblages in 100–300 meter reaches of stream (usually encompassing several riffles and pools). The smallest scales at which ecologists have evaluated consistency of lotic fish assemblages are within adjacent 10 meter sections (Finger 1982), 4–15 m long 'mesohabitats' (Meffe & Sheldon 1988, 1990), or individual pools and riffles (Bart 1989, Schlosser & Ebel 1989).

We suggest that in selecting spatial scales for stream fish research investigators should consider the spacing of biologically meaningful units, in contrast to deciding a priori about linear distances for study. Individual pools, particularly if separated by partial barriers like shallow riffles, may be important natural units with regard to biotic interactions like predator-prey relationships (Fraser & Sise 1980, Petranka 1983, Power & Matthews 1983, Cooper 1984, Hemphill & Cooper 1984, Power et al. 1985, Fraser et al. 1987, Harvey 1991). For typical pool-dwelling fishes, shallow riffles represent a semi-permeable impediment to movement, not a total barrier. Riffles decrease but do not preclude movement among pools by predators and prey, or by potential competitors. Some species of fish traverse riffles more readily than others, particularly when a riffle is only 5–10 cm deep. Under those conditions, we have observed small fishes like cyprinids to cross riffles readily (Power et al. 1985, Matthews personal observation), whereas larger fish such as adult largemouth bass, *Micropterus salmoides*, cross shallow riffles infrequently and with considerable difficulty. Within any stream the depth of riffles and the degree to which they limit movement of fish varies as stage level changes. Nevertheless, we propose that in typical small riffle-pool streams, an appropriate unit of scale for asking biological questions about fish assemblage structure or interspecific interactions is that of individual pools.

To test the hypothesis that pools are biologically discrete units, we evaluated quantitative consistency and structure of fish assemblages in a 1 km reach of one midwestern (USA) stream at the spatial scale of individual pools. We quantified across time (1) assemblage consistency in individual pools, (2) consistency of the collective pool assemblage of the entire 1 km reach, (3) consistency in distribution of individual species across pools, (4) numbers of prey vs. numbers of predators within pools, and (5) effects of floods on consistency of fish assemblages in individual pools and on distribution of individual species across pools.

Methods

Brier Creek is a low-gradient, prairie-margin stream with a total mainstream length of 24 km in Marshall County, Oklahoma. The fish fauna (30 known species) of Brier Creek was described in detail (Smith & Powell 1971), and stability of fish assemblages of the watershed and at five large sites (each 200–400 m of stream reach) was documented by Ross et al. (1985) and Matthews et al. (1988). The headwaters of the stream drain pasturelands. Flow ceases in headwaters for much of the year, producing oxygen and temperature fluctuations and absolute values that are harsh for fishes (Matthews 1987). Farther downstream, the creek is bordered by a gallery forest of large deciduous trees, and subsurface springs maintain flow (base flow discharge of 0.1–0.2 m^3 sec^{-1} in all but extreme drought). In 16 years we have studied this stream, flow in the midreach ceased only in summer 1980. During most of the year the midreach of Brier Creek is characterized by medium to large pools separated by shallow riffles, with clear water and physicochemical conditions not harmful to resident fishes (Matthews 1987).

In a 1 km reach of Brier Creek there was a series of 14 such pools ranging 6 to 120 m in length, and 45–160 cm in depth, separated by shallow riffles 1–20 m long and < 10 cm deep at base flow. General conditions in these pools have been described (Power et al. 1985, Matthews et al. 1987), Power & Stewart 1987, Harvey et al. 1988, Harvey 1991, Gelwick & Matthews 1992); they were mapped in detail by Power & Matthews (1983). Individual pools were 2–10 m wide, with substrates including silt and sand, with much sandstone bedrock and fractured lime-

stone substrate. Canopy cover varied (in season) from nearly complete to approximately 75% open. The water was consistently clear except immediately after floods, and profuse, but highly seasonal, growths of algae such as *Rhizoclonium* and *Spirogyra* provided shelter or cover for small fishes. We have documented elsewhere that grazing by herbivorous central stoneroller minnows, *Campostoma anomalum*, plays a major role in regulating distribution and standing crops of algae in these stream pools (Power & Matthews 1983, Power et al. 1985) and influences a variety of ecosystem phenomena (Gelwick & Matthews 1992).

In these 14 pools of Brier Creek (Fig. 1 of Power & Matthews 1983) we enumerated all fish by species in eight snorkeling surveys on: 8 and 19 November 1982; 14 March, 5 May, 10 and 24 June, 5 September 1983; and 30 May 1984. There were major floods in April and June 1983. The flood of 14 June, detailed in Power and Stewart (1987), was physically devas-

tating, cresting 3.45 m above base flow, with a very rapid stage rise, and scouring or moving most of the bed. Snorkeling is well-established as an effective, nondestructive method to enumerate fishes in clear streams (Goldstein 1978, Power et al. 1985, Moyle & Vondracek 1985). Methods were as in Power & Matthews (1983). In each pool one observer (WJM or BCH) slowly swam in an upstream direction (typically 15–20 minutes per pool), zig-zagging as needed in wider pools, recording the numbers and species of fishes on underwater slates or waterproof paper. We estimated the total length of all large species during snorkeling surveys. The centrarchids were separated into two size classes for analysis of snorkeling data (Polis 1984). Snorkeling surveys were conducted only when water was sufficiently clear to provide bank-to-bank vision underwater, and never when visibility limited our ability to identify or enumerate small fishes. Pool 12 (Power & Matthews 1983) was omitted on three dates because

Table 1. Fishes identified in eight snorkeling censuses of Brier Creek, Oklahoma, with total numbers of each observed.

Common name	Scientific name	Size (mm total length)	Total number observed
Black basses (BASS)*	*Micropterus* spp.	≥ 100 mm TL	273
Black basses (BASS)*	*Micropterus* spp.	< 100 mm TL	84
Longear sunfish (LS)	*Lepomis megalotis*	≥ 75 mm TL	1583
Longear sunfish (LS)	*L. megalotis*	< 75 mm TL	172
Green sunfish (GS)	*L. cyanellus*	≥ 75 mm TL	2128
Green sunfish (GS)	*L. cyanellus*	< 75 mm TL	2346
Bluegill (BG)	*L. macrochirus*	≥ 75 mm TL	119
Bluegill (BG)	*L. macrochirus*	< 75 mm TL	4
Redear sunfish (RSF)	*L. microlophus*	≥ 75 mm TL	8
Orangespotted sunfish (OS)	*L. humilis*	all	10
Bigeye shiner (BS)	*Notropis boops*	all	2812
Blacktail shiner (BTS)	*Cyprinella venusta*	all	76
Red shiner (RS)	*Cyprinella lutrensis*	all	1114
Bullhead minnow (BHM)	*Pimephales vigilax*	all	71
Central stoneroller (CS)	*Campostoma anomalum*	all	6560
Blackstriped topminnow (BST)	*Fundulus notatus*	all	1600
Common carp (CC)	*Cyprinus carpio*	all	6
River carpsucker (RCS)	*Carpiodes carpio*	all	18
Spotted sucker (SS)	*Minytrema melanops*	all	41
Bullhead catfish (BHC)**	*Amieurus* sp.	all	236
Gizzard shad (GZS)	*Dorosoma cepedianum*	all	5
Freshwater drum (FD)	*Aplodinotus grunniens*	all	76
Orangethroat darter (OD)**	*Etheostoma spectabile*	all	67

* Include both largemouth bass, *M. salmoides* and spotted bass, *M. punctulatum*.
** Excluded from analyses due to cryptic habitats.

of a suspended turbid layer. The observers had several years of experience snorkeling or collecting Brier Creek fishes by seining, and could identify all taxa with confidence underwater. Bullhead catfishes, *Ameiurus* spp., and orangethroat darters, *Etheostoma spectabile*, were excluded from analyses because their use of cryptic microhabitats made accurate censuses by snorkeling problematic. Early in this study, a second observer (on high banks, located to avoid frightening fish) confirmed that few if any other fish escaped detection by the underwater observer.

Similarity of fish assemblage composition within pools over time was estimated by Morisita's index (Wolda 1981, Smith & Zaret 1982; calculating formula and discussion of interpretation in Matthews 1986). Morisita's index ranges from zero to approximately 1.0. As with any similarity index, there are no absolute cut-offs, but we regarded values 0.0–0.5 as 'low' and > 0.75 as 'high' (Matthews 1986, Matthews et al. 1988). For comparison, we also calculated Schoener's index (= percent similarity index), but results for Schoener's and Morisita's indices followed similar trends (c.f., Linton et al. 1981), and only Morisita's index results are reported. Smith & Zaret (1982) present analyses suggesting Morisita's index to exhibit very little bias and recommending its use in ecological studies. The relationship between potential predator and prey per pool was ex-

amined by comparing the numbers per pool of *Micropterus* bass > 100 mm TL plus all *Lepomis* > 75 mm as 'predators' with the sum of the numbers of the following 'prey' categories: bass < 100 mm, all *Lepomis* species < 75 mm, and all minnows and topminnows except the bigeye shiner, *Notropis boops*. Behaviorally, bigeye shiners mostly occurred at the extreme head of pools in shallows not patrolled by bass, so they were not included in our overall predator-prey comparisons (although a separate analysis, including bigeye shiners and not shown, gave similar results, and we did include this species in comparisons of predator-prey numbers across flood events). Because this study was directed at whole pools as biological units, we followed Gelwick & Matthews (1992) in emphasizing numbers of fish per pool, instead of densities per unit area.

Pairwise relationships between fish taxa were evaluated by product moment correlation of abundances of the 14 most abundant taxa (= taxa observed more than 50 times), across all pools and dates (= 109 samples). We selected a critical level of 0.01 to exert table-wise alpha control yet avoid the unduely harsh effect a full Bonferroni alpha adjustment of $0.05/210$ (= 0.00024) would exert on these tests (Huang & Sih 1990 Williams & Ruckelshaus 1993). Because here we seek only trends and not a rigorous test of any given taxon-pair, lowering alpha to 0.01 should protect against undue Type I error with-

Table 2. Loadings (= correlation with) of individual original variables (fish taxa) on principal components axes I, II, and III.

Taxon	Axis I	Axis II	Axis III
Bass > 75 mm	0.674	– 0.376	– 0.224
Bass < 75 mm	0.024	0.154	0.174
Longear sunfish ≥ 75 mm	0.384	– 0.669	0.169
Longear sunfish < 75 mm	– 0.300	– 0.417	0.313
Green sunfish ≥ 75 mm	– 0.355	– 0.600	0.353
Green sunfish < 75 mm	– 0.669	– 0.017	– 0.302
Bluegill ≥ 75 mm	0.515	– 0.235	– 0.057
Bigeye shiner	– 0.106	– 0.032	– 0.791
Red shiner	– 0.678	– 0.239	– 0.170
Central stoneroller	– 0.562	0.237	– 0.221
Blackstriped topminnow	0.220	– 0.417	– 0.333
Blacktail shiner	– 0.526	– 0.273	– 0.194
Bullhead minnow	– 0.518	– 0.595	0.012
Freshwater drum	0.443	– 0.260	– 0.490
Percent of variance accounted for	22.2	14.2	10.8

out incurring excessive Type II error. Choosing p = 0.01 allows that by chance approximately one out of all 91 comparisons could be considered significant due to Type I error. An unweighted pair group (UPGMA) clustering of taxa, based on the correlation coefficients, provided a summary of occurrences of taxa in common.

Relationships among those 14 taxa were further deduced from a principal components analysis (PCA) based on the correlation matrix of date- and pool-specific abundance data. The PCA was carried out so that samples (= a pool on one date) were the items classified, and species were 'characters' sensu Sneath & Sokal (1973). Species abundances were standardized so that mean of each species was zero, and its standard deviation was 1.0, and the PCA carried out on the resulting z-scores (Sneath & Sokal 1973). Principal components analysis reduces a larger suite of characters (here, species) to a lesser number of orthogonal axes. Loadings of (= correlations with) each individual character on each PCA axis indicates the degree to which that character relates to the axis, and suites of characters (species) with high absolute loadings on a given axis, therefore tend to vary together (Gauch 1982). The PCA also provides an objective evaluation of similarities and differences among all samples, as depicted by scatterplots of axis scores.
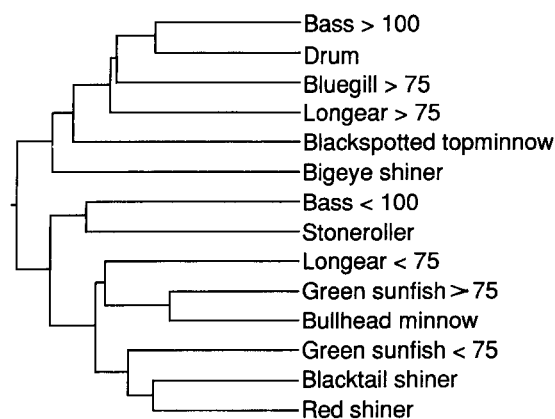
Fig. 1. Phenogram from UPGMA clustering of pairwise correlation coefficients for the most abundant taxa in Brier Creek pools.

Results

We made a total of 19437 fish observations divided into 23 species of 'ecotaxa' (including size classes) in 8 snorkeling censuses (Table 1). Central stoneroller, *Campostoma anomalum* (33.8%), bigeye shiner, *Notropis boops* (14.5%), green sunfish, *Lepomis cyanellus* < 75 mm TL (12.1%), green sunfish > 75 mm TL (10.9%), blackspotted topminnows, *Fundulus notatus* (8.2%), and longear sunfish, *Lepomis megalotis* > 75 mm TL (8.1%), numerically dominated the fish fauna.

The first three axes of the PCA accounted for 22.2, 14.2, and 10.8%, respectively, or 47.2% collectively of the total variance (Table 2). On axis I, large

Table 3. Significant correlations (p < 0.01) in abundance of common fishes from 8 censuses of 14 pools in Brier Creek Oklahoma (n = 109; one pool was too turbid to census on 3 dates). R-values for significant associations are also provided; significant positive/negative associations are shown by ± superscripts; species acronyms are from Table 1.

	Bass < 100	LS ≥ 75	LS < 75	GS ≥ 75	GS < 75	BG ≥ 75	BTS	BHM	RS
Longear sunfish ≥ 75	0.33+								
Longear < 75 sunfish									
Green sunfish ≥ 75		0.32+	0.25+						
Green sunfish < 75	0.36-	0.26-							
Bluegill ≥ 75	0.39+	0.26+			0.26-				
Blackstriped topminnow		0.35+							
Blacktail shiner					0.33+				
Bullhead minnow			0.28+	0.50+			0.29+		
Red shiner	0.25-				0.38+		0.47+	0.45+	
Central stoneroller	0.40-	0.32-			0.32+	0.26-			0.29+
Freshwater drum	0.23+					0.28+			

600 ┐

500 ┤

Prey (indiv. per pool)
400 ┤

300 ┤

200 ┤

100 ┤

0 ─┬─────┬─────┬─────┬─────┬─────┬─────┬
0   25   50   75   100   125   150
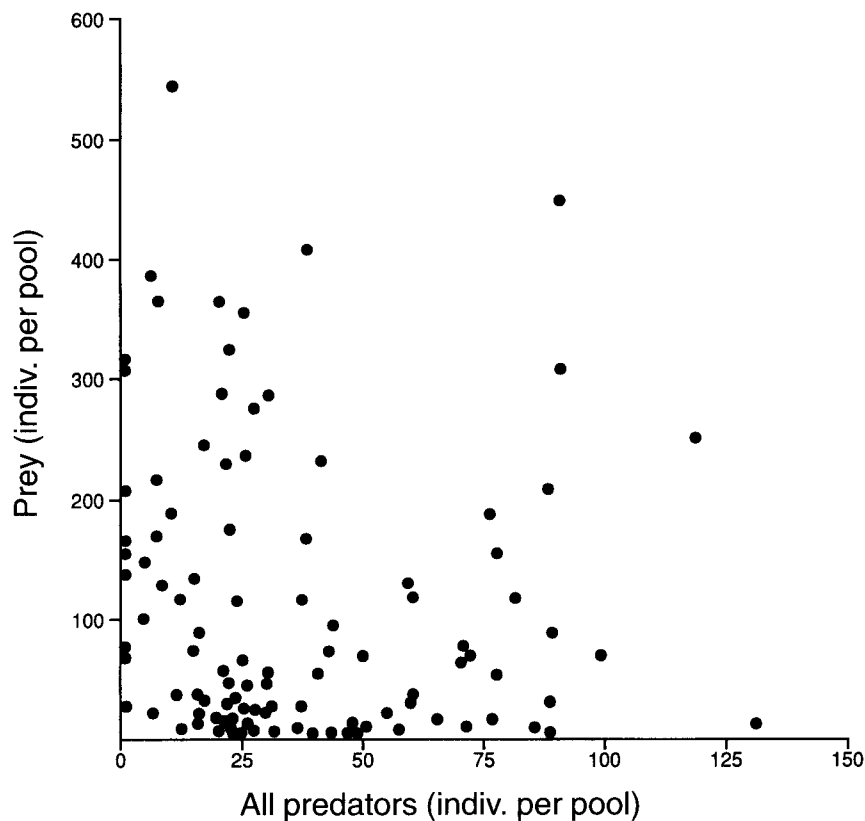
All predators (indiv. per pool)

Fig. 2. Numbers of potential prey taxa (small *Lepomis* and *Micropterus*, and all minnows and topminnows except bigeye shiner, see 'methods') vs. numbers of all potential predators (large *Lepomis* and *Micropterus*), per pool, in all surveys in Brier Creek.

Micropterus bass and bluegills had highest positive loadings, and small green sunfish and minnows (including blacktail shiners, red shiners, bullhead minnows and central stonerollers) had largest negative loadings. Large longear and green sunfish and bullhead minnows all showed high negative loadings on axis II. Only bigeye shiners loaded strongly on axis III (Table 2), further suggesting that this species varies independently of other taxa at the whole-pool scale.

Twenty-five (18 positive, 7 negative) of 91 possible correlations of abundance among the 14 most abundant taxa were significant at the $p < 0.01$ level (Table 3). A phenogram from UPGMA cluster analysis of pairwise correlation coefficients for the 14 species (Fig. 1) showed two primary clusters, with separation of species in a pattern congruent with their common loadings on the PCA axis I. In the phenogram, large bass and bluegills were in the upper cluster, whereas small green sunfish, stoneroll-

ers, bullhead minnows, blacktail shiners and red shiners were in the lower cluster. In Figure 1 three of the four taxa that we categorized as 'predators', i.e., large bass, large bluegills and large longear sunfish were in one cluster, and seven of the eight members of the lower cluster were taxa we considered 'prey'. The patterns from the PCA loadings and the cluster analysis of taxa suggested that there could be segregation of predator and prey taxa among pools of Brier Creek.

Consistent segregation of predators and prey among pools could suggest that Brier Creek fish assemblage dynamics are predator-controlled. However, this did not appear overall to be true. A plot of numbers of potential prey vs. all potential predators (including bass > 100 mm and sunfish > 75 mm) per pool (Fig. 2) showed a continuum from pools with many predators and few prey to pools with few predators and many prey, but numerous pools were intermediate. At least some taxa of predators (e.g.,
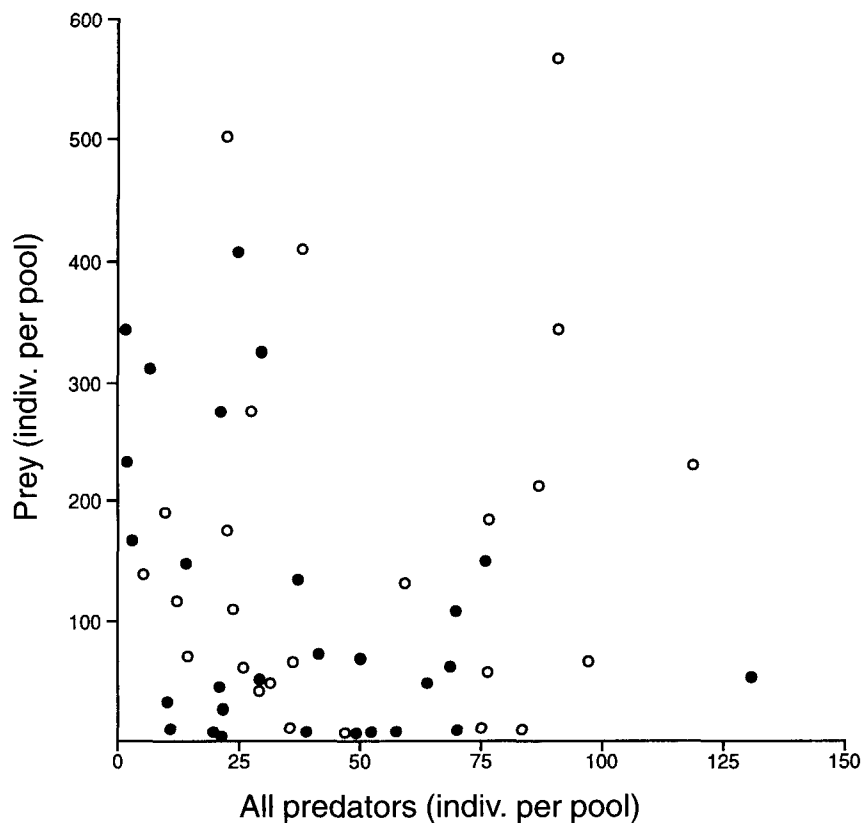
Fig. 3. Numbers of potential prey (including bigeye shiner) vs. potential predators (as in Figure 2), per pool, in two surveys before major floods (solid circles) and in two surveys after those floods (open circles).

large bass) can regulate the distribution of some prey taxa (e.g., stonerollers) in Brier Creek (Power et al. 1985), but other prey seemed not to be so predator-constrained. For example, blackstriped topminnows, which typically swim near the surface of the open water of pools, often occurred in pools with large bass and sunfish. These topminnows were positively associated with large longear sunfish (Table 3) and were in the same phenogram cluster as large bass, large bluegill, and large longear sunfish (Fig. 1). Apparently, the behaviors and/or microhabitat selection of some potential prey species facilitate their occupancy of predator-dense pools, whereas other potential prey species, e.g., other minnow species, are scarce in such pools.

An additional possibility existed that typical predator-prey relationships among pools might be disrupted by floods. To test this possibility, we graphed (Fig. 3) numbers of prey (including bigeye shiner) vs. numbers of total predators, by pool, in

two surveys before major floods (14 March and 10 June 1982) and, separately, in the two surveys following those floods (5 May and 24 June 1982). Although not tested statistically due to lack of independence of points, it is obvious that in the samples before the floods there were few prey in pools with large numbers of predators, whereas in the surveys immediately after the floods there were large numbers of prey in some pools with large numbers of predators.

In contrast to results when all large centrarchids were included as predators, graphical examination of numbers of *Micropterus* bass > 100 mm and potential prey taxa in Brier Creek (Fig. 4) suggested that large bass were effective predators that constrained the numbers of prey. The numbers of prey varied widely in the absence of bass, but in pools with high numbers of large bass, there were low total numbers of prey. One collection in Figure 4 appears as a partial exception in which 57 prey oc-
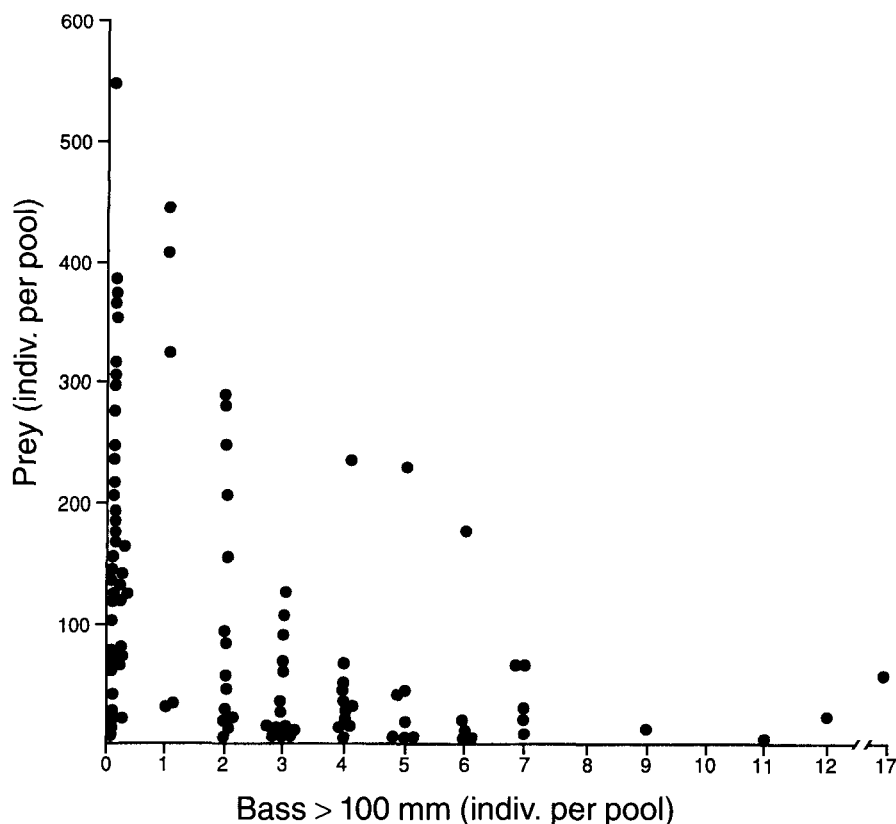
Fig. 4. Numbers of potential prey (as in Figure 2) vs. numbers of *Micropterus* > 100 mm TL, per pool, in all surveys in Brier Creek.

curred in a pool with 17 bass > 100 mm. However, all of these prey were blackstriped topminnows, whose ability to occupy pools with bass was noted above. Comparison of Figures 2 and 4 suggest that a few large *Micropterus* bass may be more effective than

even a large number of adult sunfish as predators controlling prey per pool.

Taxa differed in consistency of distribution among pools. Typically, bass and sunfish showed high consistency in occurrence among pools in successive surveys, and changed little in distribution

Table 4. Similarity in distribution of individual taxa across time (eight censuses), among 13 pools of Brier Creek, based on Morisita's index, comparing within each taxon its pool-to-pool abundance in successive sampling intervals. The intervals from 14 March–5 May and 10–24 June each included a major flood event.

Taxon	Morisita's Index		
	Mean across seven intervals	14 March to 5 May	10 June to 24 June
Bass < 100 mm	0.892	0.974	0.911
Longear sunfish ≥ 75 mm	0.876	1.000	0.949
Green sunfish ≥ 75 mm	0.778	0.926	0.836
Green sunfish < 75 mm	0.709	0.493	0.821
Bigeye shiner	0.579	0.503	0.729
Red shiner	0.678	0.468	0.715
Central stoneroller	0.608	0.808	0.267
Blackstriped topminnow	0.652	0.578	0.426

among pools after flood events (Table 4). Smaller fishes (cyprinids and blackstriped topminnows) generally varied more among pools across time intervals, including floods in April and June 1983 (Table 4). A very large flood in June resulted in more distributional change in stonerollers and topminnows than in other taxa.

The composition of the pool fish assemblage for the entire 14 pool reach (i.e., summed across all pools on each date) changed little during any of the intervals between surveys (Morisita's indices for each of the seven intervals ranged from 0.83 to 0.98). Thus, at the scale of the whole reach, the assemblage of pool fishes showed high consistency despite the floods in April and June.

Similarity of fish assemblages within individual pools was more variable than was the pooled assemblage for the whole reach. Morisita's index of similarity for successive surveys of individual pools ranged from 0.07 to 1.00 (Table 5). However, Morisita's index exceeded 0.80 in 47.4% of all possible cases, with a median value of 0.78 (Fig. 5), suggesting typically rather consistent assemblages of fish in individual Brier Creek pools. Composition of the fish assemblages within individual pools changed no more on average during time intervals of severe floods than during all other time intervals (one-way
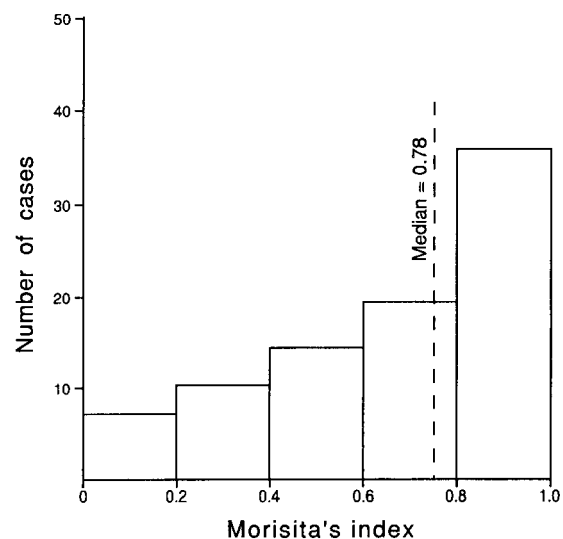

Fig. 5. Frequency distribution of values for Morisita's index, for 95 comparisons of fish assemblages in individual pools from one survey to the next.

ANOVA of time periods with values of Morisita's index for individual pools as replicates, p = 0.24).

There was no significant difference among individual pools in mean similarity (Table 5) of fish assemblages across all intervals (one-way ANOVA, p = 0.27), even though the pools were physically quite different. The pool with the highest mean sim-

Table 5. Morisita's index of similarity of fish assemblages within Brier Creek pools, across time intervals indicated.

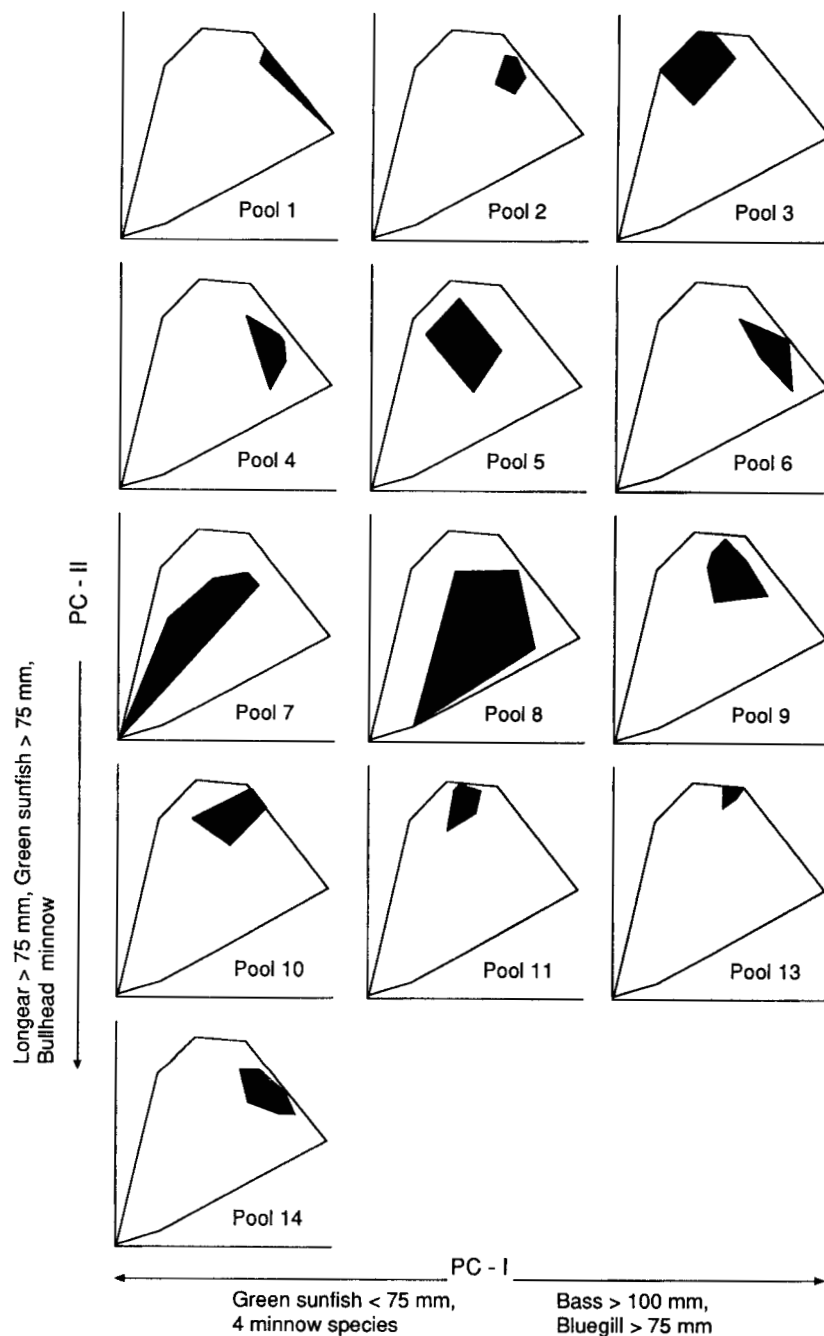| Pool	8 Nov 82 to 19 Nov 82	19 Nov 82 to 14 Mar 83	14 Mar 83 to 5 May 83 (Flood)	5 May 1983 to 10 Jun 83	10 Jun 83 to 24 Jun 83 (Flood)	24 Jun 83 to 5 Sep 83	5 Sep 83 to 30 May 84	Mean	Std. dev.
1	1.00	0.33	0.29	0.29	0.99	0.52	0.99	0.63	0.35
2	0.47	0.85	0.84	1.00	0.53	0.84	0.91	0.78	0.20
3	0.99	1.00	0.94	0.22	0.73	0.47	0.61	0.71	0.30
4	0.98	0.73	0.82	0.79	0.81	0.77	0.56	0.78	0.12
5	0.93	0.74	0.92	0.73	0.66	0.88	0.07	0.70	0.30
6	0.87	0.64	0.41	0.87	0.87	0.47	0.13	0.61	0.29
7	0.99	0.55	0.67	0.69	0.73	0.47	0.70	0.69	0.16
8	0.94	0.34	0.89	0.31	0.23	0.16	0.08	0.42	0.35
9	0.90	0.46	0.84	0.49	0.20	0.92	0.84	0.66	0.28
10	1.00	0.93	0.84	0.82	0.70	0.96	0.99	0.89	0.11
11	0.94	0.95	0.51	0.39	0.91	0.78	0.74	0.75	0.22
12	omit	omit	omit	0.75	0.48	0.38	0.97	omit	omit
13	1.00	0.85	0.97	0.92	0.80	0.80	0.10	0.78	0.31
14	0.11	0.37	0.96	0.98	0.99	0.96	0.51	0.70	0.36
Mean	0.86	0.67	0.76	0.66	0.69	0.67	0.59		
Std. dev.	0.26	0.24	0.22	0.27	0.25	0.25	0.36		

Fig. 6. Scatterplots of principal components axes I and II for all 109 visual samples of pools across time in Brier Creek, with the total multivariate space occupied by all samples enclosed by the large polygon (which is identical in each case), and the total multivariate space occupied by each pool across all survey dates depicted by the solid polygon.

ilarity between sampling periods (Pool 10, average Morisita's index = 0.89) was relatively small and shallow, and never contained large bass. The pool with the lowest mean similarity between samples

(Pool 8, average Morisita's index = 0.42) was relatively large and heterogenous, and contained from 0 to 6 large bass at different times.

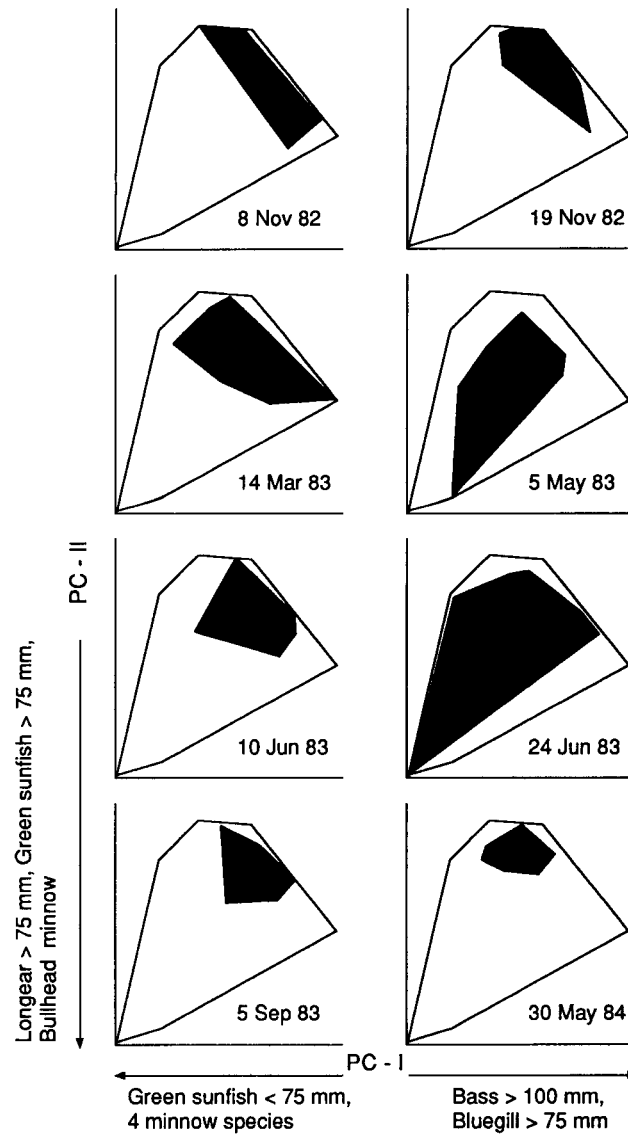To further depict baseline variation in Brier

Fig. 7. Scatterplots of PC axes I and II as in Figure 6, but with solid polygons bounding the total multivariate space occupied by all pools on a single survey date.

Creek pool fish assemblages across time, a scatterplot of sample similarities from the PCA is useful. Figure 6 shows the distribution of all 109 pool samples across all times on PCA axes I and II, with directional trends in species abundances associated with each axis. Identical copies of this scatterplot are shown for each pool with a polygon bounding the total space occupied by that pool throughout the eight surveys. The space occupied on the scatterplot for 11 of 13 pools (pool 12 omitted due to 3 missing dates) was small relative to the total space

occupied by all pools, suggesting that most individual pools remained in a relatively discrete subset of multivariate space throughout the study. Two exceptions, pools 7 and 8, each had one sample strongly displaced in multivariate space (toward the lower left in Figure 6) after a flood. We also asked how multivariate space occupied by all pools at any one time related to the multivariate space occupied by pools across all times. Figure 7 is the same PCA scatterplot, but with polygons bounding the points representing all pools in a single survey. Most indi-
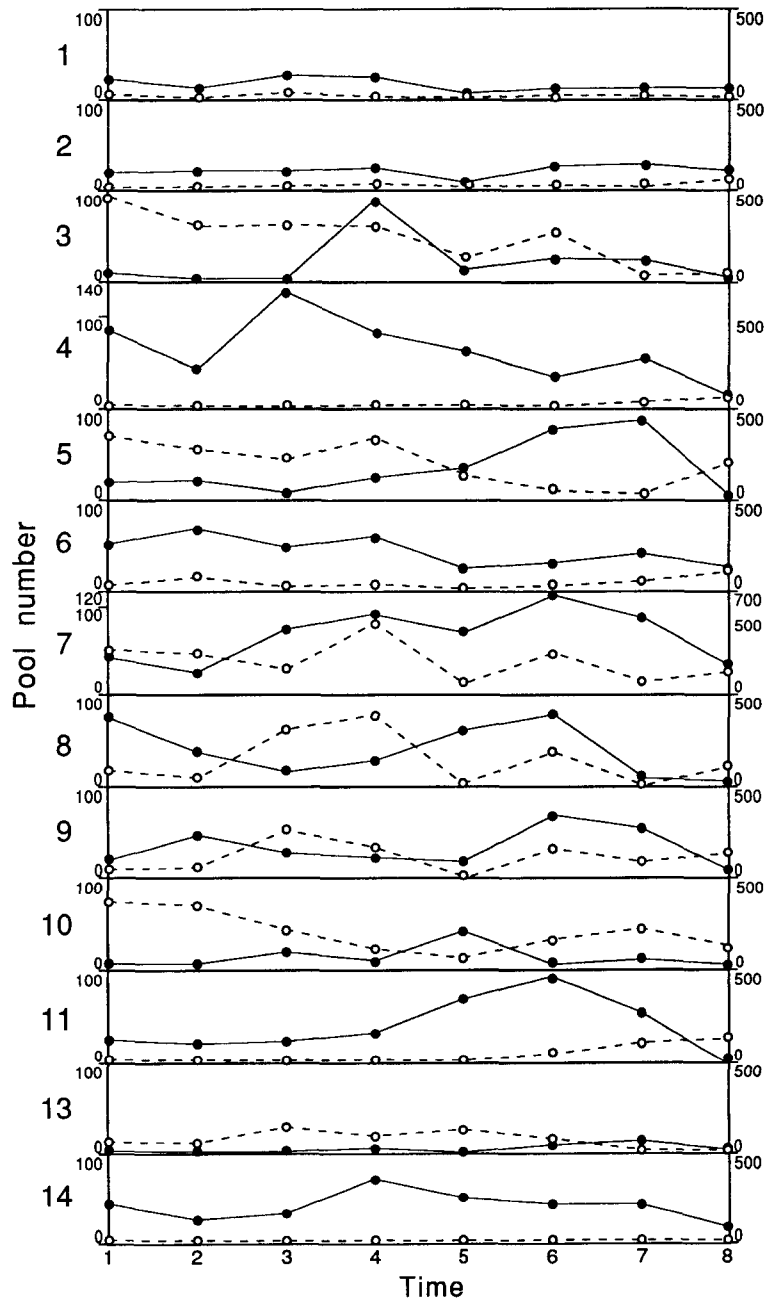
Fig. 8. Numbers of large centrarchids ('predators' as in Figure 2) (= solid circles; scale of abundance on left side of figure) and numbers of all 'prey' as in Figure 2 (= open circles; scale of abundance on right side of figure), in individual pools of Brier Creek across eight survey times.

vidual pools were more discrete in multivariate space across time (Fig. 6) than was the suite of different pools at any one time (Fig. 7). The one exception was the last survey (May 1994) when all pools

were more similar to each other than they were in previous surveys.

Finally, we documented in each pool, separately, the magnitude of temporal variation in two ecologically important groups of fish: (1) the large centrar-

chids ('predators', above) and (2) all minnows and small centrarchids, with the exception of bigeye shiners ('prey', above) (Fig. 8). Note that the prey and predators are on different vertical axis scales, because of an approximate 5:1 overall ratio in their maximum abundance. In most pools the abundances of each group of fish appeared rather similar across time, or changed only gradually between surveys. Exceptions were pools 3, 4, and 11, in which there were abrupt changes in abundance of predators in some intervals, and pools 7 and 8, in which there are marked changes in numbers of prey during some intervals. There also was a general decline in numbers of predators across the entire reach in the last interval (from September 1983 to May 1984). In spite of these exceptions, the general picture in Figure 8 was of only modest changes in numbers of these two groups of fish across most time intervals in most pools.

Discussion

Loadings of taxa on PCA axes 1 and 2, correlation of species abundances, and clusters of associated species in a correlation-based phenogram indicated that many Brier Creek pools contained either (1) high numbers of large *Micropterus* and large *Lepomis* or (2) many minnows and small sunfishes. However, this distinction was not absolute, as numerous pools contained substantial numbers both of large (predators) and small (prey) fishes. The pattern of fish distribution among pools in Brier Creek was consistent in part with Schlosser's (1987) predictions for fish assemblages in pools dominated by large centrarchids, but some pools were obvious exceptions. The pattern also was consistent with results from experimental manipulations of largemouth bass, which displaced small fishes in Brier Creek pools (Power et al. 1985, Harvey 1991). Avoidance of adult centrarchids by some fishes can explain part of the pattern in Brier Creek, but some small taxa e.g., bigeye shiner and blackstriped topminnows occupy pools with potential predators. Perhaps by so doing they benefit from a reduced number of other small fishes within a pool.

Positive relationships between large bass and

large longear sunfish and bluegills could relate to the 'bigger-deeper' hypothesis that suggests larger fish have innate preferences for deeper water, where they are less vulnerable to terrestrial and avian predators (Power 1984a). Alternatively, Werner et al. (1983) showed that bluegills too large to be eaten by bass grew faster in the presence of large bass, presumably because of reduced competition with juvenile sunfishes. The distribution of large green sunfish, which are more likely (on the basis of body and head morphology) to compete for food resources with large bass than are longear sunfish or bluegills (Werner 1977), was not positively related in Brier Creek to the distribution of large bass. Another hypothesis for association of some large sunfish with large bass in this stream is suggested by Harvey (1991), who showed that survival of fish larvae was greater in the presence of large bass, because of the negative effect of bass on small fishes which are predators of larvae. Bass and sunfish frequently nest in the same pools in Brier Creek (Matthews personal observation). The effect of bass on potential egg/embryo/larvae predators could provide a reproductive advantage (at least re. survival of larvae) for adult sunfish in pools with large bass, although subsequent dispersal of juveniles might lessen this advantage.

Our results showed larger taxa (centrarchids) more consistent over time than smaller species (e.g., cyprinids) in their distribution among pools. Differences in the potential for movement across riffles by large, deep-bodied centrarchids versus small-bodied fishes may account in part for this pattern. Large centrarchids have difficulty in crossing the shallow riffles in Brier Creek at base flow (although we have seen frightened bass cross shallow riffles, literally swimming on their sides). A large flood event in June 1983 appeared to result in more change in distribution of small than of large fish taxa. Topminnows (*Fundulus* spp.) are poorly adapted morphologically for swift water. Matthews (1986) found a similar displacement of the congeneric *Fundulus olivaceus* in a flood of an upland stream. More consistency in distribution of centrarchids than of small fishes also agrees with the known affinity of centrarchids for home pools (Gerking 1959, Berra & Gunning 1972).

Graphical examination of total predator and prey numbers in Brier Creek pools suggested that although large bass appear to constrain some prey species (Power et al. 1985, Harvey 1991), potential predators do not as a group preclude use of pools by prey taxa. The numbers of prey varied widely in the presence of both low and high numbers of total potential predators, and numerous pools contained large numbers both of prey and of 'predators' (mostly sunfish > 75 mm). Apparently, although sunfish > 75 mm can eat smaller fishes, they are not sufficiently effective predators to preclude pool use by these potential prey. Additionally, patterns of total predators vs. prey in Brier Creek pools could have been influenced by relative differences between taxa in effects of floods, as above. Greater movement by small than large taxa during flood periods (above) could interrupt ephemerally any patterns of predator-prey segregation among pools (as we found previously for bass and stonerollers; Power et al. 1985). Clearly, a detailed assessment of prey species occurrence with predators should include species-specific characteristics such as schooling behavior, morphology, feeding requirements, or use of microhabitat, all of which might influence their susceptibility to predation. For example, the topminnows' use of near-surface habitat, countershading, and relatively restricted activity patterns may reduce the probability of its detection or capture by bass.

For the entire 1 km reach of Brier Creek (with abundances summed across all pools) there was high quantitative consistency of the fish fauna. This result corroborates earlier findings by Smith & Powell (1971), Ross et al. (1985) and Matthews et al. (1988) that in this stream many 'whole reach' fish assemblages are rather stable across time. This part of the creek flows continuously in most years, and offers an overall high heterogeneity of riffle and pool habitat with a variety of structure. Deep, physically stable pools within the study reach may be important to the maintenance of stable fish assemblages at the 200–400 m scale (Schlosser 1987). Stream reaches without deep refugia from drought or winter cold may have fish assemblages that are destroyed by such events, and then depend on the vagaries (or patterns) of colonization processes in the reestablishment of a fish assemblage (Matthews 1987). This fits the overall pattern in Brier Creek (Matthews et al. 1988), where headwater assemblages are less stable than those downstream.

Why are assemblages in individual pools more variable than the entire reach? Part of the answer is obvious: the total composition of pool fauna at the scale of an entire reach will not change with movements of fish unless they migrate out of or into the 1 km stream segment. More limited movements of fish among pools would be undetected in analysis of total reach stability. Perhaps a better question is what causes low consistency of fish assemblages in some individual pools (without comparing this stability to that calculated for the entire reach).

Many mechanisms could cause changes (or the appearance of changes) in the composition of assemblages in individual pools. Sampling error (although we presume it to be small) might affect a given pool substantially, but be averaged out when 14 pools are combined at the whole reach scale. Juveniles of some species may have a 'wandering state' (Gerking 1959) which could account for some instability of assemblages in a given pool. Power et al. (1985) and Harvey (1991) also observed rapid emigrations of minnows (i.e., stonerollers and bigeye shiner) from pools when predatory largemouth bass were introduced. Fishes may occupy individual pools in patterns that reduce inter and/or intraspecific competition. For example, Power (1984b) found that herbivorous loricariid catfishes occupied pools in Panama in proportion to the periphyton production within each pool, in agreement with the ideal free distribution model (Fretwell 1972). Both predation risk and food availability are likely to influence habitat selection by fishes; Gilliam & Fraser (1987) showed that stream minnows are capable of selecting habitats which minimize the ratio of predation risk to food intake. Finally, several of the mechanistic phenomena above require fish to occasionally 'sample' habitat quality across pools, and the snapshot of fish distribution that we obtain on any given day may capture some individuals in sojourn in non-optimal habitat, i.e., where they might not remain for long.

Seasonal dynamics of reproduction and recruitment may also change distributions of fishes among

stream pools. Our observations indicate that young-of-the-year of some species become widely distributed among pools, including those in which spawning does not take place, in summer and early autumn. For example, in summer 1988 adult stone-rollers were restricted to and apparently repro-duced in only a few of the Brier Creek pools, but thousands of their young-of-the-year appeared in all 14 pools in the reach (Matthews personal obser-vation). Subsequent differential survival of these YOY among pools could influence pool-to-pool distribution of juveniles and adults.

In contrast to a prediction of Schlosser (1987), consistency of fish assemblages was not detectably higher in larger pools. We regressed the mean simi-larity (mean Morisita's index value) for each pool across the entire study on two measures of pool size: maximum depth and pool volume. Mean stability of pools was not significantly related to depth of pool (p = 0.34) or to pool volume (p = 0.08).

We examined quantitative structure and consis-tency of stream fish assemblages in 14 natural stream pools to estimate their integrety as fish hab-itat units. In a substantial proportion of the cases in Brier Creek, fish assemblages in individual pools changed little in the weeks or months between sur-veys. Overall, Brier Creek pools in the PCA scat-terplots did not vary randomly in multivariate hab-itat space, and, in contrast, most remained in an identifiable subset of the total space occupied by the suite of pools. There was also evidence from the similarity indices that the fish assemblage in many pools remained rather constant across sampling in-tervals, as the median value for Morisita's index of 0.78 is relatively high.

Studies at the scale of individual stream pools are attractive in that pools have fish assemblages that are readily quantified, that are defined by natural semi-permeable barriers (riffles), and in which the degree of natural temporal variability can be deter-mined in a straightforward manner. The baseline of natural variability of fish assemblages in stream pools that we have documented encompasses two substantial flood events, and provides a frame of reference against which results of experimental ma-nipulations or anthropogenic disturbances could be judged. Individual stream pools, separated by shal-low riffles, represent potentially important, biolog-ically meaningful units for fish assemblages, and should comprise a useful spatial scale for experi-mental research or biological monitoring programs.

References cited

Bart, H.L., Jr. 1989. Fish habitat association in an Ozark stream. Env. Biol. Fish. 24: 173–186.

Berra, T.M. & G.E. Gunning. 1972. Seasonal movement and home range of the longear sunfish, Lepomis megalotis (Rafi-nesque) in Louisiana. Amer. Midl. Nat. 88: 368–375.

Cooper, S.D. 1984. The effects of trout on water striders in stream pools. Oecologia 61: 376–379.

Finger, T.R. 1982. Fish community-habitat relations in a central New York stream. Journal of Freshwater Ecology 1: 345–352.

Fraser, D.F. & T.E. Sise. 1980. Observations of stream minnows in a patchy environment: a test of a theory of habitat distribu-tion. Ecology 61: 790–797.

Fraser, D.F., D.A. DiMattia & J.D. Duncan. 1987. Living among predators: the response of a stream minnow to the hazard of predation. pp. 121–127. In: W.J. Matthews & D.C. Heins (eds) Community and Evolutionary Ecology of North American Stream Fishes, University of Oklahoma Press, Norman.

Fretwell, S.D. 1972. Populations in a seasonal enviroment. Prin-ceton University Press, Princeton. 217 pp.

Gauch, H.G., Jr. 1982. Multivariate analysis in community ecol-ogy. Cambridge University Press, Cambridge. 298 pp.

Gelwick, F.P. & W.J. Matthews. 1992. Effects of an algivorous minnow on temperate stream ecosystem properties. Ecology 73: 1630–1645.

Gerking, S.D. 1959. The restricted movements of fish popula-tions. Biol. Rev. 34: 221–242.

Gilliam, J.F. & D.F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68: 1856–1862.

Goldstein, R.M. 1978. Quantitative comparison of seining and underwater observation for stream fishery surveys. Prog. Fish Cult. 40: 108–111.

Gorman, O.T. & J.R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59: 507–515.

Grossman, G.D., J.F. Dowd & M. Crawford. 1990. Assemblage stability in stream fishes: a review. Environ. Manag. 14: 661–671.

Grossman, G.D., P.B. Moyle & J.O. Whitaker, Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. Amer. Nat. 120: 423–454.

Harrell, H.L. 1978. Response of the Devil's River fish community to flooding. Copeia 1978: 60–68.

Harvey, B.C. 1991. Interactions among stream fishes: predator-induced habitat shifts and larval survival. Oecologia 87: 29–36.

Harvey, B.C., R.C. Cashner & W.J. Matthews. 1988. Differential effects of largemouth and smallmouth bass on habitat use by stoneroller minnows in stream pools. J. Fish Biol. 33: 481–487.

Hemphill, N. & S.D. Cooper. 1984. Differences in the community structure of stream pools containing or lacking trout. Verh. intern. Ver. theor. ang. Limnol. 22: 1858–1861.

Huang, C. & A. Sih. 1990. Experimental studies on behaviorally mediated, indirect interactions through a shared predator. Ecology 71: 1515–1522.

Linton, L.R., R.W. Davies & F.J. Wrona. 1981. Resource utilization indices: an assessment. J. Anim. Ecol. 50: 283–292.

Matthews, W.J. 1986. Fish faunal structure in an Ozark stream: stability, persistance, and a catastrophic flood. Copeia 1986: 388–397.

Matthews, W.J. 1987. Physicochemical tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. pp. 111–120. In: W.J. Matthews & D.C. Heins (eds) Community and Evolutionary Ecology of North American Stream Fishes, University of Oklahoma Press, Norman.

Matthews, W.J. 1990. Fish community structure and stability in warmwater midwestern streams. pp. 16–17. In: M.D. Bain (ed.) Ecology and Assessment of Warmwater Streams: Workshop Synopsis, U.S. Fish and Wildlife Service, Biological Report 90.

Matthews, W.J., R.C. Cashner & F.P. Gelwick. 1988. Stability and persistence of fish faunas and assemblages in three midwestern streams. Copeia 1988: 945–955.

Matthews, W.J. & L.G. Hill. 1980. Habitat partitioning in the fish community of a southwestern river. Southwest. Nat. 25: 51–66.

Matthews, W.J., A.J. Stewart & M.E. Power. 1987. Grazing fishes as components of North American stream ecosystems: effects of Campostoma anomalum. pp. 128–135. In: W.J. Matthews & D.C. Heins (eds) Community and Evolutionary Ecology of North American Stream Fishes, University of Oklahoma Press, Norman.

Matthews, W.J., R.C. Cashner & F.P. Gelwick. 1988. Stability and persistence of fish faunas and assemblages in three midwestern streams. Copeia 1988: 947–957.

Meador, M.R. & W.J. Matthews. 1992. Spatial and temporal patterns in fish assemblage structure of an intermittent Texas stream. Amer. Midl. Nat. 127: 106–114.

Meffe, G.K. & A.L. Sheldon. 1988. The influence of habitat structure on fish assemblage composition in southeastern blackwater streams. Amer. Midl. Nat. 120: 225–240.

Meffe, G.K. & A.L. Sheldon. 1990. Post-defaunation recovery of fish assemblages in southeastern blackwater streams. Ecology 71: 657–667.

Moyle, P.B. & B. Vondracek. 1985. Persistence and structure of the fish assemblage in a small California stream. Ecology 66: 1–13.

Ogden, J.C. & J.P. Ebersole. 1981. Scale and community structure of coral reef fishes: a long-term study of a large artificial reef. Mar. Ecol. Progress Series 4: 97–103.

Petranka, J.W. 1983. Fish predation: a factor affecting the spatial distribution of a stream-breeding salamander. Copeia 1983: 624–628.

Polis, G.A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? Amer. Nat. 123: 541–564.

Power, M.E. 1984a. Depth distributions of armored catfish: predator-induced resource avoidance? Ecology 65: 523–528.

Power, M.E. 1984b. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. J. Anim. Ecol. 53: 357–374.

Power, M.E. & A.J. Stewart. 1987. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. Amer. Midl. Natur. 117: 333–345.

Power, M.E. & W.J. Matthews. 1983. Algae-grazing minnows (Campostoma anomalum), piscivorous bass (Micropterus spp.) and the distribution of attached algae in a small prairie-margin stream. Oecologia 60: 328–332.

Power, M.E., W.J. Matthews & A.J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. Ecology 66: 1448–1456.

Ross, S.T., W.J. Matthews & A.A. Echelle. 1985. Persistence of stream fish assemblages: effects of environmental change. Amer. Nat. 126: 24–40.

Schlosser, I.J. 1987. A conceptual framework for fish communities in small warmwater streams. pp. 17–24. In: W.J. Matthews & D.C. Heins (eds) Community and Evolutionary Ecology of North American Stream Fishes, University of Oklahoma Press, Norman.

Schlosser, I.J. & K.K. Ebel. 1989. Effects of flow regime and cyprinid predation on a headwater stream. Ecol. Monogr. 59: 41–57.

Smith, C.L. & C.R. Powell. 1971. The summer fish communities of Brier Creek, Marshall County, Oklahoma. Amer. Mus. Nov. 2458.

Smith, C.L. & T.M. Zaret. 1982. Bias in estimating niche overlap. Ecology 63: 1248–1253.

Sneath, P.H.A. & R.R. Sokal. 1973. Numerical taxonomy – the principles and practice of numerical classification. W.H. Freeman, San Francisco. 573 pp.

Werner, E.E. 1977. Species packing and niche complementarity in three sunfishes. Amer. Nat. 111: 553–578.

Werner, E.E., G.G. Mittlebach, D.J. Hall & G.F. Gilliam. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540–1548.

Williams, S.L. & M.H. Ruckelshaus. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. Ecology 74: 904–918.

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

Fish imagery in art 61: Troll's *Dance of the Fish Charmers*

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This is the second work by contemporary artist Ray Troll in this series. Troll is an Alaskan artist, with an advanced degree in Fine Art from Washington State University. Like *Sockeye Sunset* (EBF, 1993), this work reflects Troll's ability to draw fish with considerable accuracy, his focus on Alaskan themes, and his fertile imagination. *Dance of the Fish Charmers* shows masked Northwest Coast Indians and three of the fish their culture depended upon: sockeye salmon, *Oncorhynchus nerka,* cabezon, *Scorpaenichthys marmoratus,* and redbanded rockfish, *Sebastes babcocki.* In this drawing, Troll shows these fish in both Western and Northwest Coast Indian art styles. The presence of the artist among the dancers is a comment on how much his own livelihood has come to depend upon fish!

Dance of the Fish Charmers (1985, 46× 56cm, colored pencil on paper) is used courtesy of the artist (The Troll Line, P.O. Box 8874, Ketchikan, Alaska 99901).