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HABITAT STRUCTURE AND STREAM FISH COMMUNITIES[1]

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Abstract. Stream habitat complexity is correlated with fish species diversity in selected Indiana and Panama streams. Habitat diversity was measured along 3 dimensions judged important to a wide range of fish groups and applicable to many stream conditions: stream depth, bottom type, and current. Increasing community and habitat diversity followed stream-order gradients. Natural streams supported fish communities of high species diversity which were seasonally more stable than the lower-diversity communities of modified streams. After disturbances such as channelization, seasonal peaks in species diversity attain levels typical of undisturbed streams. Because seasonal changes in stream quality are high, the stability of the fish community is lower in modified than in natural streams. The general correlation between habitat characteristics and presence and absence of fish species suggests that most fishes of small streams are habitat specialists.

Key words: *channelization; community structure; fish communities; habitat structure; Indiana; Panama; seasonality; species diversity; streams.*

INTRODUCTION

General evidence that fish have evolved to exploit specific habitats includes highly adapted body form and mouth structure (Keast and Webb 1966, Hynes 1970, Lowe-McConnell 1975). Vertical segregation of sympatric *Notropis* (shiners) in pools appears to be based on morphological and behavioral adaptations; each species seeks its habitat optimum while feeding opportunistically on available resources (Mendelson 1975). Similarly, darters subdivide riffles horizontally on the basis of current and substrate (Winn 1958). These studies and extensive anecdotal evidence (Trautman 1957, Cross 1967, Pfleiger 1971) suggest that 3 components of stream environments—substrate, depth, and current—are important in the microhabitat specialization of stream fishes.

In an aqueous environment, chemical characteristics of the medium are also of major importance to organisms (Hynes 1970, Warren 1971) as reflected by the recent emphasis on reversing trends toward deteriorating water quality. There is a developing body of knowledge showing minimum water quality characteristics (temperature, dissolved O_2, etc.) for survival of fishes but no cohesive set of theories has been developed relating habitat structure to fish community structure. The key to understanding patterns of community diversity among stream fishes may be the definition, understanding, and measurement of relevant habitat characteristics under the influence of seasonally dynamic physicochemical conditions. We have examined these relationships in several watersheds with differing physiographies and degrees of disturbance in an effort to answer the following questions:

1) Is there a predictable relationship between habitat structure and fish community structure in small stream environments?
2) Does this relationship hold for a variety of streams, both temperate and tropical?
3) How is this relationship affected by seasonal changes in stream environments?
4) How is this relationship affected by man-made modifications of stream channels and watersheds?

STUDY AREAS

Three watersheds were selected for study: 2 in Indiana represent disturbed and relatively undisturbed temperate watersheds and 1 in Panama is an undisturbed tropical watershed. All sample stations were in first-, second-, or third-order streams.

Disturbed temperate watershed

Black Creek (BLCK) is a tributary of the Maumee River ≈24 km northeast of Fort Wayne, Indiana (Allen County). The broad (0.6 × 5.6 km), flat watershed of BLCK receives ≈920 mm of annual rainfall (Table 1). The upper reaches of the watershed are situated on a gently rolling glacial till plain. The middle area flows across an old beach zone of ancient Lake Maumee while the lower half flows across old lake bottom. Most stream channels in the watershed have been ditched at least once in the last 50 yr with some extensive ditching in the past 4 yr. All sample stations on the BLCK channel were ditched in 1973–1974. The permanent flow-relief is ≈24 m of which ≈9 m are taken up by entrenchment of ditch banks. Major water sources are field tiles, artesian seepage, runoff, and effluent from septic tanks (Karr and Dudley 1976).

The BLCK basin is intensively cultivated—81% of the area (Karr and Gorman 1975)—with few wooded sections. Most of the streams are unshaded (≈80%) due to ditching, and summer water temperatures sometimes exceed 32°C, resulting in extensive fila-

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TABLE 1. Watershed characteristics for Black Creek (BLCK), Indian Creek (INCK), and Rio Frijoles

Stream	Annual rainfall (mm)	Watershed area (km^2)	Permanent flow-relief (m)	Max drainage relief (m)	Discharge (m^3/s) monthly mean			Percent		Major land uses
					Min	Max	Peak	Ditched	Shaded	
BLCK	920	55	24	41	.035	2.9	278	>90	<20	Agriculture
INCK	970	58	60	86	1.3	7.5	≈45	≈20	≈80	Agriculture, woodland, residential
Rio Frijoles	≈2500	34	≈70	200	...	...	...	≈0	≈100	Forest

mentous algal blooms which choke stream channels. During major rainstorms and during winter and spring thaws, high discharge rates and flooding conditions are common. A series of 8 main-channel and 5 tributary stations were sampled regularly for fish. One of the tributary stations was situated in a forested area (Wertz Woods—WW) containing a 500-m stretch of natural stream channel which served as a "control" for headwater ditched areas. An additional area was sampled on an adjacent watershed (Wann Creek—WNCK) which had not been disturbed for at least 7 yr.

Relatively undisturbed temperate stream

Indian Creek (INCK) is a tributary of the Wabash River ≈16 km west of Lafayette, Indiana (Tippecanoe County). The long (18 km), narrow (4 km) watershed of INCK receives ≈970 mm of rainfall each year (Table 1). The upper portion of the watershed is situated on a flat glacial till plain (permanent flow-relief ≈15 m) where the stream is sluggish and extensively pooled. At about middrainage, INCK begins to cut rapidly down to the river floodplain and forms a complex array of rocky riffles and pool areas (permanent flow relief 45 m; total for watershed 60 m). Chief water sources are springs, marshes, and sewage effluent, the last of which helps to maintain a flow even during dry periods of late summer and fall.

The watershed area is largely agricultural with extensive forested tracts along the lower course where steep slopes make cropping difficult. Only some intermittent streams on the fringes of the watershed have been ditched, leaving most of INCK with a natural channel, of which ≈80% is heavily shaded.

Water flows in the INCK watershed were more stable and persistent than in BLCK because extensive forest produced a more controlled release of water to the stream channel. Water quality parameters also differed between the 2 streams: BLCK was generally more silty (up to 7×) and had 2 to 3× the nitrogen and phosphate levels.

Two INCK study areas were chosen to contrast upstream and downstream communities; 1 was near the headwaters (first order) and another was just upstream from the Wabash River floodplain (third order). The 2 sample stations on INCK were selected to minimize local effects of pollution.

Undisturbed tropical stream

The Rio Frijoles, which discharges into Gatun Lake, is located ≈5 km northwest of Gamboa on the Pipeline Reservation in the Panama Canal Zone. The watershed is heavily forested with rugged terrain (maximum relief of ≈200 m). This area has been relatively undisturbed since the turn of the century when the United States commenced canal-building operations. Annual rainfall is ≈2500 to 2600 mm (Table 1), most of which occurs during the rainy season from April to December.

Because it was difficult to reach up- and downstream areas of the same stream, streams of various sizes within the Rio Frijoles watershed were chosen according to their accessibility from the road. Limbo Creek was representative of the smallest flowing streams (first order) during the wet-season sampling, Rio La Seda was a second-order stream, similar to midstream stations in Indiana, and Rio Frijolito was considered third order and was comparable to downstream INCK and BLCK.

In summary, a series of 15 sample stations in 5 different streams represent 3 different stream orders.

METHODS

Field studies in the BLCK watershed began in early 1974 but monthly or biweekly sampling for all stations was not initiated until April 1975 and continued through July 1976. The 2 INCK stations were sampled regularly (bimonthly) from November 1974 to July 1976. During some winter periods, samples were not obtained due to ice cover. Streams in Panama were sampled during the rainy season in July 1975.

Fish sampling

Sample stations were chosen to include riffles and pools and were paced off to 100-m lengths (50 m in Panama). In the WW, a set of 3 pools with combined length of ≈30 m was sampled. Minnow seines (1.2 × 4.5 m) with 6-mm mesh were used in most sampling in temperate zone watersheds. A shorter, smaller-mesh net was used in the Panama studies. The seine used in Panama was modified to form a bag and thus trap the more evasive tropical fish. In sampling BLCK, a seine was placed at the lower end of a sample area and at least 2 seine sweeps were made downstream through the area. This method removed at least 80% of the individuals. For more complex areas such as INCK, WW, and Panama, stations were broken into smaller segments and seined until capture rates declined to near 0. Typically, this required 5 to 12 seine hauls in the most complex streams sampled.

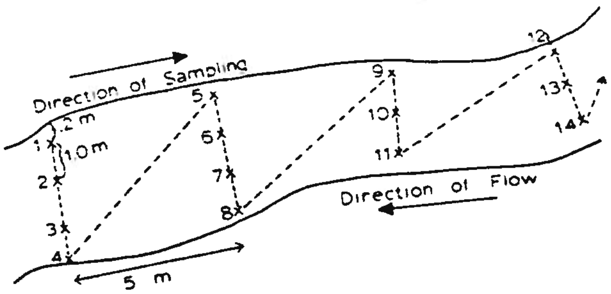

FIG. 1. Location of sample points in measurement of habitat structure. Sampling starts at the downstream border of study area. Point samples are taken starting 0.2 m from left bank (looking upstream) and at 1.0-m intervals across the stream. Further transects are taken at 5-m intervals moving upstream.

Fish samples were preserved in 20% Formalin solution and returned to the laboratory, except for most BLCK samples, which were released immediately after field tabulation. Identification of Indiana fishes (**Appendix A**) followed classification of Trautman (1957) and Nelson and Gerking (1968), while classification of Panama fishes (**Appendix B**) followed Meek and Hildebrand (1916), Hildebrand (1938), and Miller (1966). Fish species diversity (FSD) for each sample was estimated using the Shannon–Weiner equation using natural logarithms.

Percent change (PC) between samples was estimated using the reciprocal of the Percent Similarity (PS) index after Renkonen (1938) and Whittaker (1952, 1972). This index was used to estimate differences between upstream and downstream samples (spatial heterogeneity) and to estimate community change at a particular station over time (temporal heterogeneity).

Habitat structure

Stream habitat structure was measured in June and September 1975, and March 1976 for BLCK, WW, and WNCK, and in June, September, and November 1975, and April 1976 for INCK. Measurements for the Panama streams were taken during the wet season in July 1975.

Stream habitat was measured in 3 dimensions: depth, bottom type, and current. Four depths, 9 bottom substrates, and 5 current categories were recognized (Table 2). Stream depth categories were chosen as representative of habitats found in the small streams sampled; 0–5 cm corresponded to shallow edges and riffles, 5–20 cm to riffles and shallow pools, 20–50 cm to pools, and >50 cm to deep pools. Bottom types (substrates) were categorized into physical and biotic structures. Among the physical forms, categories 1–5 corresponded to alluvial material of increasing size from silt to rocks with category 6 as clay parent material (clay pan). Biotic categories (7 and 8) included vegetation (aquatic plants and filamentous algae) and litter (leaves, twigs, and branches). A miscellaneous category, 9, was reserved for unusual items such as bedrock slabs or large tree trunks. Currents were estimated by observing the movement of water about a measuring pole. In areas without current, no ripples are created around the pole; as current increases, the ripple effect increases. Currents were assigned to 5 classes (Table 2) and corresponding velocities were calibrated using a float and stopwatch. Although velocity estimates are accurate up to moderate currents, this technique underestimates fast and torrent velocities.

Point samples were taken in a regular fashion in each study area (Fig. 1). Beginning 10–20 cm from the left bank, points were taken at 1-m intervals across the stream. For very narrow streams (maximum 1 m wide) such as Limbo Creek and WW at low flow, 0.33-m intervals were used. Repeated sets of points were taken across the stream at 5-m intervals moving upstream. Sample data showed that a minimum of 90 to 160 points were required at structurally complex sites (WW, INCK, and Panama) and 60 to 80 points for simple areas (BLCK) for adequate measurement of habitat diversity. Habitat sampling was generally conducted on the same day as fish sampling with the ex-

TABLE 2. Description of categories used in measuring stream habitat

Dimension		Category number and description				
		1	2	3	4	5
Depth	Range (cm) Description	0–5 Very Shallow	5–20 Shallow	20–50 Moderate	>50 Deep	
Current	Flow velocity (m/s) Description	<.05 Very slow	.05–.2 Slow	.2–.4 Moderate	.4–1.0 Fast	>1.0 Torrent
Bottoms	*Diameter (mm) Description	<.05 Silt	.05–2 Sand	2–10 Gravel	10–30 Pebble	>30 Rock

* Additional bottom categories include clay pan (6), vegetation (7), litter (8) and miscellanous (9).

ception of September 1975 when BLCK habitat samples were taken 1 wk after fish sampling. No changes in weather conditions occurred during this interval.

Habitat diversity was calculated using the Shannon-Weiner equation. Diversities were calculated for each habitat dimension alone and then in combinations of depths and bottoms (36 categories), currents and bottoms (40 categories), and finally depths, bottoms, and currents (180 categories). Because of interdependency, only certain combinations of these dimensions existed in these streams. For instance, we found no rock-bottom torrents >50 cm deep, or silt-bottom riffles.

Combinations of habitat dimensions were tried to determine which dimension or combinations were better predictors of FSD. The effect of combining dimensions increased the number of categories geometrically and thereby increased the habitat diversity index additively because this index is an exponent.

Mean habitat indices were calculated for each dimension by averaging the number of values for each category. This allowed each stream site to be characterized as shallow, sandy, slow, etc. In the bottom-type dimension, only the alluvial categories (1–5) represent continuous variation, so calculation of mean habitat indices was restricted to those categories.

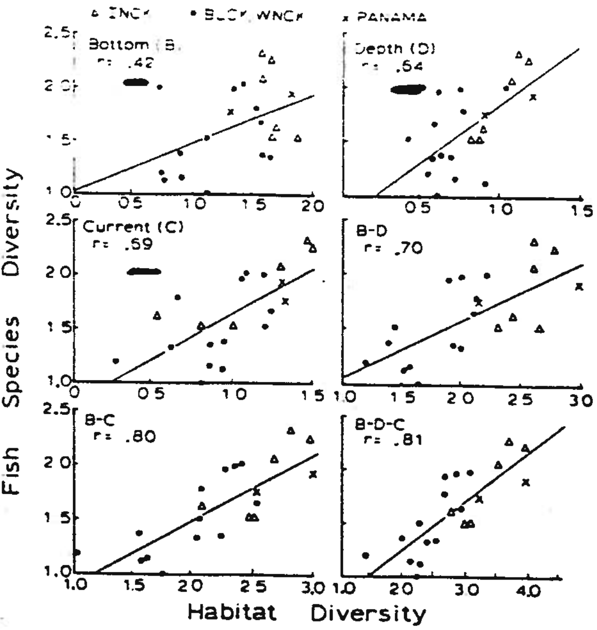

FIG. 2. Regressions (r) of fish species diversity against habitat structure diversity for streams in Indiana and Panama.

RESULTS

Habitat diversity and fish community diversity

When FSD was regressed on stream habitat diversity (HD), significant regressions ($p < .01$) resulted for both current (C) and depth (D) dimensions but not for the bottom type (B) dimension (Fig. 2). Combinations of dimensions (BD, BC, BDC) against FSD also yielded significant regressions, indicating that complexity of stream habitat structure accurately predicts FSD. Samples used in these regressions include most BLCK stations for June 1975; WNCK, June 1975; INCK, June, September and November 1975; and Panama, July 1975. Other samples were excluded from this analysis for reasons outlined in the following section.

The relative importance of the 3 dimensions varies among the stream systems. For example, the slope of the bottom type diversity fits BLCK, WNCK, and Panama data reasonably well, but is inadequate for INCK (Fig. 2). In INCK, the glacial till-derived substrate is similar in both upstream and downstream areas such that rubble normally associated with riffle areas is often found in pools. Similarly, depth diversity works well in INCK and Panama, but not in BLCK because this stream system is uniform in depth due to channelization (Fig. 2). Current diversity fails in Panama because currents are similar over the range of streams studied. Overall, each dimension alone lacks the discrimination necessary to separate habitats over a range of stream types.

Another factor to consider in these diversity measures is their applicability to various groups of fishes. For instance, bottom and current diversities might be more important predictors of riffle-guild diversity (darters, sculpins, etc.) than for some pool-guild fishes (minnows, suckers, sunfish, etc.).

Thus, a combination of the 3 habitat dimensions—bottom, depth, and current—is most appropriate to a wide range of stream physiographies and fish groups. We will refer to the composite of the 3 dimensions as habitat diversity.

Problems in measuring habitat diversity

We have found that seasonal changes (see below) in fish distributions and flow regimes in streams play a major role in determining fish community structure. As a result, it is important to control for this variation much as researchers studying avian communities have emphasized periods with increased breeding activity. The following situations modify the general relationship between habitat structure and community diversity.

1) Habitat measures must not be made in stream environments uninhabitable by fishes. Among streams sampled, some were so small that large porportions (>50%) of the habitat sampled included very shallow (<1 centimetre) water. Typically, such areas are uninhabitable by fishes and most fish concentrate in dispersed pools, indicating that habitat measures in upstream areas should be restricted to the pools themselves. Because we did not recognize this problem before we sampled habitat, the far upstream stations in Panama and the WW stations were eliminated from the regression analysis.

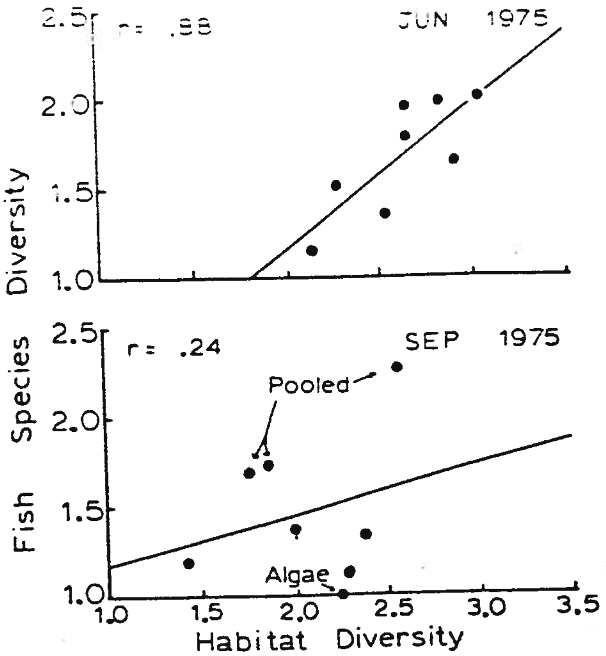

FIG. 3. Regressions (*r*) of fish species diversity on habitat diversity for June 1975 and September 1975 in Black Creek. Note that regression is significant in June but not in September when pooled areas and dense algal concentrations affect fish community structure.

2) Habitat must be sampled in flowing streams. During September 1975, much of BLCK dried up, causing large numbers of fishes to retreat to the remaining pools. When habitat measures included large proportions of these pools, HD predicted lower FSD than occurred. Because fish were not selecting their optimal stream habitat but merely being forced into pools by a shrinking stream, exclusion of such data is warranted.

3) Streams that are excessively choked with algae should not be included in regressions of FSD and HD. During September 1975, flowing areas of stream in BLCK were choked with filamentous algae, and few fish species were present. Habitat measures in these areas predicted a higher FSD than occurred. A regression of algal abundance against FSD yielded a significant and negative regression. While most species avoided algae-choked areas, a few species, such as *Ericymba buccata*, thrived in them.

The overall effect of declining habitat quality (algal blooms and/or streams drying up) can be seen when relationships between FSD and HD are examined for June and September in BLCK (Fig. 3). Thus, most September data for BLCK were excluded from the analysis of Fig. 2. However, fish in more natural streams such as INCK were not forced to move into pools because their stream environment remained more stable.

4) The stream habitat and fish community must be in relative equilibrium with fishes utilizing their habitat optima. During March 1976, many BLCK fishes were migrating upstream in search of spawning areas (Karr and Gorman 1975). Also, the stream environment was unstable due to frequent spring floods. March HD-FSD regressions were not significant. The slope for the regression was lower than the overall 1975 regression, indicating similar FSD at all stations due to the surge of migrants moving throughout the watershed.

In contrast, data from BLCK during June 1975 gave a significant regression (Fig. 3). During June, discharge rates remained relatively stable: stream substrates were clean and channels devoid of algal buildup. INCK, on the other hand, generally maintained a more seasonally stable discharge rate and habitat structure suitable for fish populations; HD and FSD were remarkably stable throughout the year.

5) Studies of fish communities should be avoided when short-term chemical changes in streams have devastated fish communities. These may result from natural events or spills of toxic material. Fish kills at 2 BLCK stations in September 1975 necessitated elimination of points from the analysis. This problem is different from that in terrestrial, e.g., bird, communities where short-term chemical contamination is less likely.

Future attempts to examine correlations between habitat structure of streams and fish diversity must use caution. Data from ecosystems not approximating evolutionary equilibrium conditions can be expected to diverge from the linear relationships outlined here. Disequilibria may occur throughout the year or seasonally due to natural events (spring floods) or the effects of human activities.

Changes in fish communities in space

Many published studies have shown increased community diversity in stream fishes from upstream to downstream areas (Shelford 1911, Thompson and Hunt 1930, Larimore et al. 1952, Larimore and Smith 1963, Sheldon 1968) with most emphasizing community expansion by species addition. Sheldon (1968) speculated that the primary factor in increased community diversity was increasing depth downstream. Our data from BLCK clarify the ecological conditions behind this conclusion, and, at the same time, show the importance of considering both species composition and relative abundances.

In June, for example, BLCK depth and alluvial particle size increased downstream to Station 1C (Fig. 4). Between 1C and 2A, all 3 dimensions changed, resulting in a shallow, gravelly stream with a moderate current. At station 3C near the river, the stream slowed down and became deeper and more sandy. Fish communities in BLCK changed with varying stream habitat characteristics (Fig. 4). Many species declined or increased in abundance between stations 1C and 2A. Moving downstream, habitat and species abundance remained relatively stable to station 3B and

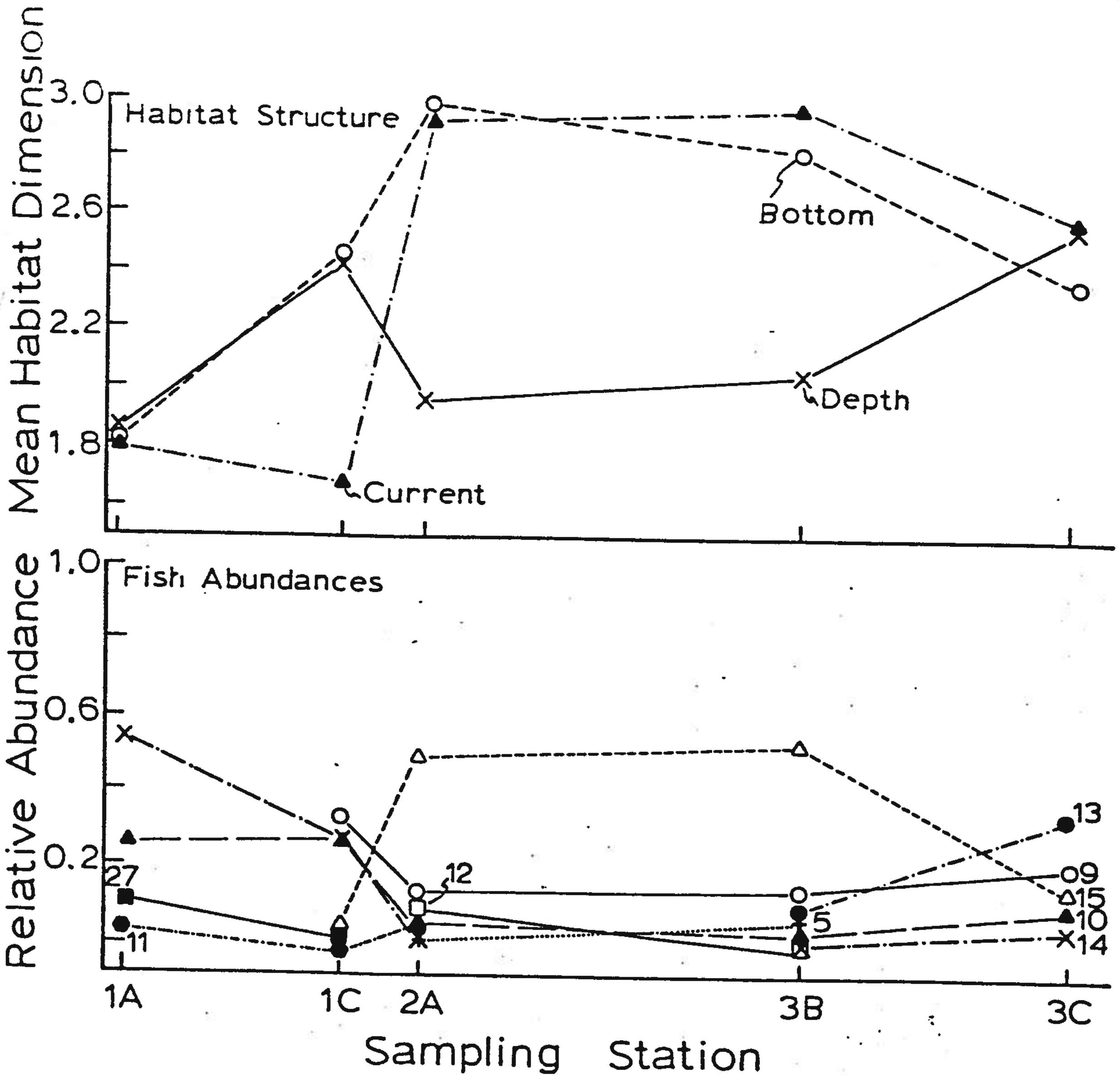

FIG. 4. Changes in habitat structure and abundances of fish species along a stream order gradient at Black Creek. Station numbers indicate stream order. Code numbers identify fish species listed in **Appendix A**.

then shifted at 3C where the influence of backwaters from the Maumee River became important. BLCK was rather unnatural in having a sequence of simple, homogeneous habitats which produced abrupt changes in community structure. As measured by percent change, BLCK fish communities varied by 83 to 93% from upstream to downstream areas.

In contrast, INCK was a more natural stream with increasingly heterogeneous habitat in downstream areas. Community change (PC) in INCK was smaller (63 to 73%) between upstream and downstream stations. Along the stream-order gradient in Panama, habitat changed only a small amount and fish communities changed by only 24%. Thus, we conclude that changes in fish communities along a stream-order gradient are due to changes in habitat characteristics and may be reflected as species addition, species replacement, or by changing relative abundances.

Fish communities in natural and modified drainages

Structurally diverse natural streams typically have a great deal of buffering capacity: meanders tend to moderate the effect of floods, pools offer excellent refuges for fishes during dry periods, and tree shade decreases heat loads and minimizes the oxygen-robbing effect of decomposing and extensive algal blooms (Karr and Schlosser 1977). Examples of streams having some degree of these buffering characters, INCK and WW, had higher HD and FSD along with in-

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TABLE 3. Number of species and temporal change in fish communities as expressed by percent change (Whittaker 1972). Numbers in parenthesis indicate stream order(s)

Stream	Fish species (*n*)	Stations (*n*)	Mean percent change
			June–September 1975
Black Creek	5(1)	5(1.2.3)	68
Wann Creek	14(2)	1(2)	70
Wertz Woods	9(1)	1(1)	40
Indian Creek	10(1)	2(1.2)	33

creased stability of community composition and habitat structure. Parallel results have been found in bird communities; with increased complexity of forest environments comes an increase in buffering of physical extremes resulting in more diverse and stable bird communities (Karr 1976).

The reliability of stream environments may be reduced by man's modifications of these systems to suit his needs. Ditching increases stream gradients by meander removal and channel shortening. Also, bottoms are dredged to create a uniform, poolless, unstable substrate. These attempts to increase drainage efficiency result in little buffering from floods and droughts and increases their severity. Since some recent and extensive ditching efforts on BLCK, flash floods have occurred as a result of localized thunderstorms.

Another stream modification procedure which enhances instability is the removal of shade-producing vegetation, and the sloping of banks. This maximizes solar heating of the water and increases problems from algal blooms. Also, massive deforestation of drainage basins enhances the impact of floods and causes silt pollution problems via increased soil erosion (see review by Karr and Schlosser 1977). The discharge of sewage effluents may also be detrimental to fish, but in areas below the septic zone, the more constant flow of water may help to stabilize the downstream fish populations during drought periods (Karr and Dudley 1976).

Varying degrees of buffering present among our study streams was evident in the structure and stability of the resident fish communities (Table 3). Community structure in BLCK was simple in each area and unstable. WNCK usually had a more diverse community but seasonal stability was low. INCK and WW, however, had both diverse and relatively stable communities. (June and September data are compared. June is the period when the fauna is closest to equilibrium, following spring floods. September is the end of the low-flow period, the effects of which are exacerbated by man's modification of the watershed.)

Even though WNCK was subject to the same unstabilizing influences as the BLCK, it showed remarkable recovery. The stream's habitat structure was more diverse, with greater pool formation and dense bulrush thickets which stabilized the stream channel and provided partial shading. This stream structure supported a more diverse community but not a more stable one. The destabilizing influences of massive stream and watershed modification tend to strip the stream ecosystem of some equilibrium capability (homeostatic mechanism). Thus, BLCK and WNCK biotic communities and habitats changed dramatically seasonally.

In contrast, INCK and WW had remarkable complexity and stability of stream and adjacent terrestrial habitats. The added factor of a stabilized habitat structure allowed the stream some degree of homeostatic equilibrium and was reflected in the stability of the fish community.

From this study of an assortment of streams it is evident that natural processes and structures enhance the reliability of a basically unstable system. Habitat complexity increases community complexity, and environmental stability appears to control community stability. In the succession of a ditched stream after disturbance, the habitat and community complexity recover first while stability requires a longer period or may never by achieved as long as overlying unstabilizing influences persist on the watershed.

Because large-scale watershed modifications in the U.S. have continued for perhaps 200 yr, it is now difficult to evaluate the extent to which stream communities have been altered. Larimore and Smith (1963) found considerable changes in the fish fauna in Champaign County, Illinois, USA, in the past 60 yr. The changes they found were associated with large-scale modification of watersheds. Recent deterioration of the Great Lakes fisheries has been tied to over-exploitation of fish populations and to massive deforestation and modification of the watersheds over the last century (Smith 1972). Destruction of suitable spawning habitats in tributaries along with increased water temperatures has added to the decline of lake salmonids and to the success of the sea lamprey.

DISCUSSION

Studies of the relationship between habitat structure and community diversity were pioneered by R. H. MacArthur (MacArthur and MacArthur 1961, MacArthur 1964). He demonstrated that bird community diversity increases with increasing complexity of vegetation. Later, this general relationship was substantiated with mammals (Rosenzweig and Winakur 1969), lizards (Pianka 1967, 1969), and with further studies of bird communities (MacArthur et al. 1966, Karr 1968, Karr and Roth 1971, and Recher 1969, among others).

More recently attempts have been made to apply the same principles in aquatic environments. The number of substrate types is a good predictor of species richness for marine decapod crustaceans (Abele 1974), benthic insects (Allan 1975), and freshwater molluscs (Harman 1972). Because these groups spend their adult life on the substrate, it is not surprising that species richness is correlated with substrate diversity. Fishes, however, are more prone to use stream environments in a 3-dimensional way. That fishes depend on a vertical habitat component was suggested by Sheldon (1968). The multidimensional character of fish habitats was recognized by Tramer and Rogers (1973). Our results support and extend their intuition and conclusions. First, fishes tend to specialize on specific habitat types (Zaret and Rand 1971, Mendelson 1975, the present study). Second, the fish community characteristic of a segment of stream is determined by the complexity of habitats present in the area, especially the horizontal heterogeneity component. Third, the importance of periodic phenomena, such as low-flow and water-quality characteristics, in determining fish community structure is clear. Fourth, within a habitat type there will be some specialization on food resources if such resources are reliably available (Zaret and Rand 1971, Mendelson 1975, this study).

These results are an early step toward the application of an expanding body of theory in community ecology to stream fish communities. In addition, it is clear that they are relevant to consideration of a number of applied problems in stream ecology. Future studies should attempt to detail the relationships of habitat structure and water quality parameters to species distributions and community structure in fishes and other aquatic organisms. The relevance of this approach to the management of aquatic ecosystems is outlined in more detail by Karr and Schlosser (1977).

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Appendix A. Faunal list of Indiana fishes with stream localities (Black Creek—BLCK, Wertz Woods—WW, Wann Creek—WNCK, Indian Creek—INCK).

CLUPEIDAE: 1. *Dorosoma cepedianum* (gizzard shad), BLCK, WNCK. CYPRINIDAE: 2. *Cyprinus carpio* (carp), BLCK, WNCK; 3. *Notemigonus crysoleucas* (golden shiner), BLCK, WW, WNCK, INCK; 4. *Semotilus atromaculatus* (creek chub), BLCK, WW, WNCK, INCK; 5. *Rhinichthys atratulus* (blacknose dace), INCK; 6. *Nocomis micropogon* (river chub), INCK; 7. *Phenacobius mirabilis* (suckermouth minnow), BLCK, WNCK, INCK; 8. *Notropis umbratilis* (redfin shiner), BLCK, WW, WNCK, INCK; 9. *Notropis cornutus* (common shiner), BLCK, WW, WNCK, INCK; 10. *Notropis biennius* (river shiner), INCK; 11. *Notropis spilopterus* (spotfin shiner), BLCK, WW, WNCK, INCK; 12. *Notropis stramineus* (sand shiner), BLCK, WNCK, INCK; 13. *Ericymba buccata* (silverjaw minnow), BLCK, WW, WNCK, INCK; 14. *Hybognathus nuchalis* (silvery minnow), INCK; 15. *Pimephales promelas* (fathead minnow), BLCK, WW, WNCK, INCK; 16. *Pimephales notatus* (bluntnose minnow), BLCK, WW, WNCK, INCK; 17. *Campostoma anomalum* (stoneroller), BLCK, WW, WNCK, INCK. CATOSTOMIDAE: 18. *Carpiodes cyprinus* (quillback carpsucker), BLCK, WNCK; 19. *Catostomus commersoni* (white sucker), BLCK, WW, WNCK, INCK; 20. *Hypentelium nigricans* (northern hogsucker), INCK; 21. *Erimyzon oblongus* (creek chubsucker), WW, WNCK, INCK. ICTALURIDAE: 22. *Ictalurus melas* (black bullhead), BLCK, WNCK, INCK; 23. *Ictalurus natalis* (yellow bullhead), BLCK, WW, WNCK, INCK. CYPRINODONTIDAE: 24. *Fundulus notatus* (blackstripe topminnow), BLCK, WW, WNCK. COTTIDAE: 25. *Cottus bairdi* (mottled sculpin), INCK. CENTRARCHIDAE: 26. *Micropterus salmoides* (largemouth bass), BLCK, WW, WNCK, INCK; 27. *Lepomis cyanellus* (green sunfish), BLCK, WW, WNCK, INCK; 28. *Lepomis gibbosus* (pumpkinseed), BLCK, WNCK; 29. *Lepomis macrochirus* (bluegill), BLCK, WW, WNCK, INCK; 30. *Pomoxis nigromaculatus* (black crappie), BLCK. PERCIDAE: 31. *Percina maculata* (blackside darter), BLCK; 32. *Etheostoma nigrum* (Johnny darter), BLCK, WW, WNCK, INCK; 33. *Etheostoma blennioides* (greenside darter), INCK; 34. *Etheostoma caeruleum* (rainbow darter), INCK; 35. *Etheostoma spectabile* (orangethroat darter) BLCK, WW, WNCK, INCK.

A single specimen of *Hybopsis amblops* (bigeye chub), not listed above, was found in reexamination of collections from Indian Creek.

Appendix B. Faunal list of fishes from Rio Frijoles drainage in the Panama Canal Zone.

CHARACINIDAE: 1. *Gephyrocharax atricaudata*, 2. *Bryconamericus emperidor*, 3. *Hyphessobrycon panamensis*, 4. *Roeboides occidentalis*, 5. *Brycon petrosus*, 6. *Piabucina panamensis*. GYMNOTIDAE: 7. *Hypopomus brevirostris*. LORICARIIDAE: 8. *Plecostomus plecostomus*, 9. *Ancistrus chagresi*, 10. *Loricaria uracantha*. PIMELODIDAE: 11. *Pimelodella chagresi*. PYGIDIIDAE: 12. *Pygidium striatum*. ANGUILLIDAE: 13. *Anguilla rostrata*. CYPRINODONTIDAE: 14. *Rivulus montium*. POECILIIDAE: 15. *Brachyrhaphis cascajalensis*, 16. *Neoheterandria tridentatus*, 17. *Poecilia sphenops*. CICHLIDAE: 18. *Aequidens coeruleopunctatus*, 19. *Geophagus crassilabris*.