American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2458 MARCH 19, 1971

The Summer Fish Communities of Brier Creek, Marshall County, Oklahoma

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INTRODUCTION

In the areas of intensive agricultural land use in the central United States, natural water courses have undergone extensive changes during the past several decades. Forests have been cleared, altering temperature and runoff cycles and increasing turbidity and silting rates; prairie vegetation has given way to row crops and pasture; and exotic fish species have been introduced adding to the stresses caused by human sport and commercial predation. The recent increase in the use of agricultural chemicals has loomed as a serious threat, and pesticides and fertilizers are now important factors in the aquatic environments. Undoubtedly all of these human activities have had, and will continue to have, profound effects on the aquatic environment.

In spite of these disturbances, however, stream fish assemblages are able to maintain a high degree of stability. Barring drastic environmental changes, one can return to a particular locality, at the same time of year, one, two, or five years later and collect essentially the same species approximately in the same relative numbers (Hubbs and Hettler, 1959, p. 13).

A biologist familiar with the fishes of a particular region can predict quite accurately what species will be present at a given spot even before

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he begins to collect there. If all the fishes in a section of stream are eliminated by a natural or man-made catastrophe, the new populations that become established subsequently will be reasonably similar to the original fauna that was eliminated. All of these observations indicate that the interspecies relationships among fishes are predictable and that assemblages of fish species are biocoenoses of ecologically interacting forms, i.e., they are true communities and not merely fortuitous associations.

Modern ecology is much concerned with the origin and maintenance of diversity in organism communities, but such studies can only be meaningful insofar as they are based on clearly distinguished, stable associations of interacting forms.

The purposes of the present study have been to explore methods of recognizing and describing assemblages of fish species of a small stream and to arrive at a meaningful definition of the term "community" as it applies to these fishes.

THE STUDY AREA

Brier Creek is a direct tributary of the Red River arm of Lake Texoma (fig. 1). It drains approximately 23 square miles in Marshall County, southwest of the town of Madill in southern Oklahoma. With the filling of Lake Texoma in 1944, the lower one and three-quarter miles of Brier Creek Valley was flooded and became a broad bay of the lake. An abrupt constriction of the valley forms the present mouth of the creek.

Four different physical habitats are present in Brier Creek: 1) the lowest 1.5 miles is a meandering base-level stream with occasional patches of sand and gravel in an otherwise muddy bottom; 2) the next 7.5 miles is a series of permanent pools and riffles with a predominantly sand and gravel bottom and some silty mud in the pools; 3) north of state highway 32, i.e., approximately 9 miles from the present creek mouth, the bottom changes to massive limestone bedrock with large cobbles interspersed with sand, gravel, and finer sediments. This section is about 3 miles long. During the summer, flow ceases and the riffles dry, leaving a series of disjunct pools. 4) The upper 2 to 3 miles of the mainstream and its larger tributaries are ephemeral and almost completely dry during the summer although there are a few spring-fed pools that probably contain water the year round, and serve as refugia for some fish species. Here the bottom is mostly sandy with patches of gravel, bedrock, and large cobbles.

Ephemeral tributaries and the uppermost parts of the mainstream flow through open pasture and fields of row crops including cotton,

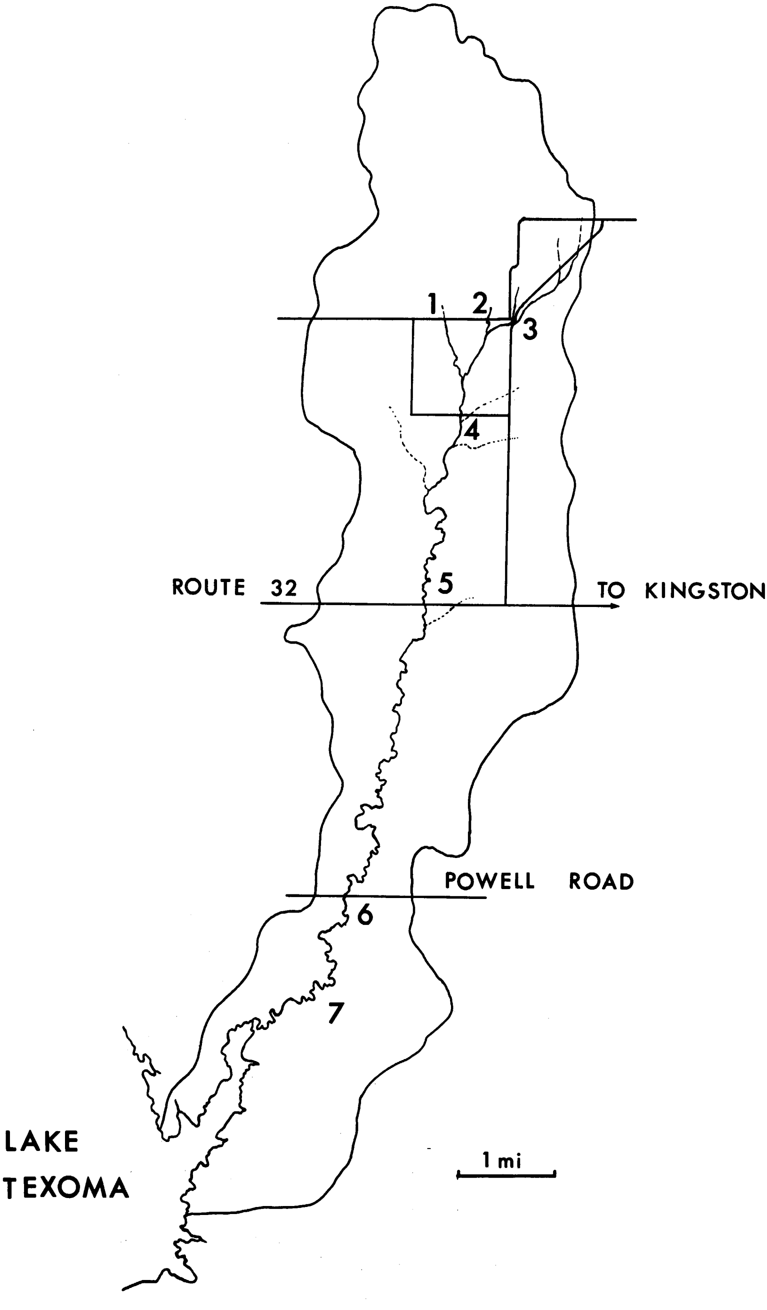

Fig. 1. Map of Brier Creek drainage basin showing collecting stations.

sorghum, corn, and peanuts. The banks of the lower two-thirds of the stream are wooded. Much of the drainage basin is used for cattle pasture and more than 100 small farm ponds are indicated on the U. S. Geological Survey topographical maps.

METHODS

Seven stations were established for sampling on a regular basis. These sites were selected because of their accessibility by road or boat, and because they were representative of the major physical habitats of Brier Creek. All collecting was done with small nets; a 15-foot bag seine (¼ inch mesh in the wings and ⅛ inch mesh in the bag, with extra weights on the foot rope) was used in the pools and a 4-foot long ⅛-inch mesh minnow seine was used in the riffles.

Standardization of the sampling effort is difficult in streams in which obstructions frequently interfere with the operation of the net, and so we tried to continue our efforts until the preserving jar contained approximately the same volume of specimens as the previous sample from the same station. The success of this approach is perhaps indicated by the fact that the total weights of fish collected at stations 4, 5, 6, and 7 are 4180, 5023, 5062, and 4397 grams respectively. At the headwater stations 1 and 3, the combined weights were 288 grams and 354 grams respectively. Station 2 was sampled only four times and cannot be compared in this way.

All specimens caught were preserved immediately in 10 per cent formalin. In the laboratory the fish were sorted, measured, blotted dry, and weighed before being transferred to isopropyl alcohol for permanent storage. The data from each sample (species names, numbers of individuals, and total weight for each species) were punched on paper tape. Programs written in BASIC language for use with a CEIR Multiaccess computer terminal were used for tabulating the data, arranging the species in order of abundance, computing diversity indices, combining individual collections, and tabulating the frequency of occurrence of the individual species.

Multivariate factor analyses were performed by Miss Jennifer Yeh using FORTRAN IV programs designed and written by D. M. Vincent Manson of the American Museum of Natural History.

The following localities were sampled on a regular basis:

Station 1: is a small pool approximately 10 × 20 feet situated under a bridge on the road between sections 7 and 18, T. 6S., R. 5E.

This is on the west branch of Brier Creek, approximately 12.7 miles from the mouth. It is the uppermost permanent water in this branch;

north of this point the stream course runs through cultivated fields, apparently carrying only runoff water. Downstream the stream channel has been straightened where it courses between open fields. The altitude at this station is approximately 795 feet above sea level and the gradient between stations 1 and 4 averages 31.8 feet per mile. The pool itself appeared to be spring fed for there was no surface water coming into it, but there was a slight trickle of water at the outlet on June 17. One week later this had ceased and the adjacent stream bed remained dry during the rest of the study period. Samples were collected June 17, 23, 30, and July 8, 14, 22, and 31.

Station 2: is also a small pool under a bridge on the road between sections 7 and 18, T. 6S., R. 5E. This is on a tributary to the east branch of Brier Creek. There was a slight trickle on June 17, but by the following week the stream had stopped flowing and by July 14 the pool had disappeared completely. There is a house and some willow trees upstream from the bridge; downstream the creek runs through open pasture. This station is approximately 805 feet above sea level and the gradient between here and station 4 is approximately 37.5 feet per mile. Samples were collected June 17, 23, 30, and July 8.

Station 3: is situated at the junction of sections 7, 8, 17, and 18, T. 6S., R. 5E., where the east branch of Brier Creek receives a tributary from the north. On June 17 there was a large pool at least 15 × 75 feet at the confluence of the mainstream and the tributary. One week later this pool had shrunk to one-fifth its size and the rest of the main creek was dry. During the next week, the mainstream dried completely, and the final samples were taken from a small pool in the tributary under the bridge on the section road between sections 8 and 17. The elevation here is 800 feet and the gradient between stations 3 and 4 is approximately 37 feet per mile. The bottom was predominantly sand and gravel with some mud in the pools sampled and some bedrock and cobbles in the adjacent parts of the stream. Small pools in the tributary were shaded by tall Johnson Grass. Overhanging banks and a large block of concrete from a washed-out section of bridge or road provided shelter for the fishes. Samples were taken on June 17, 23, 30, and July 8 and 14.

Station 4: is a section of the main Brier Creek centered approximately 100 yards downstream from a "low-water bridge" on the road separating sections 18 and 19 in T. 6S., R. 5E. There is considerable exposed bedrock here, with large limestone slabs and boulders 2 or 3 feet in diameter. There is also some gravel and cobbles in the riffles and sand and finer sediments in the pools. The riffles became quite dry in early June, but some of the deeper pools still had depths of up to 5 feet at the end of

July. Collection dates were June 19, 26, and July 3, 10, 17, 25, and 31. The samples were taken from several large pools in this part of the stream, in order to minimize the effect of sampling error.

Station 5: is a stretch of permanent riffles and pools in the vicinity of the State highway 32 in sections 30 and 31, T. 6S., R. 5E. The bottom was mostly coarse sand and gravel with some exposed bedrock in both pools and riffles. The gradient between stations 5 and 6 averaged 9.3 feet per mile. There was continuous flow throughout the study period although a few hundred yards upstream the flow disappeared in a rocky riffle area. Collecting dates were June 1, 16, 23, 30, and July 8, 14, 22, and 31.

Station 6: is in the permanently flowing part of the stream in sections 12 and 13, T. 7S., R. 4E., above and below the bridge on Powell Road. The stream course meanders through thickly wooded floodplain land used for pasture. The bottom is generally sand with gravel in the riffles and some mud in the pools. There is very little or no exposed rock but in many places the banks are undercut and logs, roots, and tree limbs provide good cover. Underground springs can be detected by cool water. Toward the end of the sampling period there was still a substantial flow of water in the riffles, and the presence of water-borne debris high in the trees testified to the occasional flooding that occurs. This station is approximately 640 feet above sea level and the gradient is 13.3 feet per mile. Collections were made on June 6, 23, 26, and July 3, 8, 14, 22, and 31.

Station 7: is downstream in the base level part of the stream profile, in section 14, T. 7S., R. 4E. Accessible only by boat, it was about 1 mile upstream from the mouth of Brier Creek. The bottom was largely mud with about 25 per cent sand and gravel. Some of the pools are at least 9 feet deep. Seining was difficult because of the many logs and branches in the streambed. During the period of our sampling, the lake level was about 620 feet above sea level. Collections were made at this station on June 19, 27, and July 4, 10 (two samples), 24, and 31.

THE FISHES OF BRIER CREEK

Thirty-three species and hybrid combinations were collected in 53 samples from the seven stations. Tables 1 and 2 summarize the occurrence of these species. Because the upper sections of the stream are subject to drying and the lower reaches are periodically flooded, it is apparent that the fishes must frequently redistribute themselves after periods when the environment becomes unsatisfactory. Eight species occur throughout the basin; the rest fall into three categories.

Some are clearly lake-dwelling species that make their way into the lower, base-level section of the stream. The following species are in this category:

1. *Dorosoma petenense*
2. *Dorosoma cepedianum*
3. *Carpiodes carpio*
4. *Notropis venustus*
5. *Hybopsis storeriana*
6. *Notemigonus crysoleucas*
7. *Cyprinus carpio*
8. *Gambusia affinis*
9. *Menidia audens*
10. *Pomoxis annularis*
11. *Morone chrysops*
12. *Aplodinotus grunniens*
13. *Percina caprodes*
14. *Lepomis microlophus*

A second category includes those species that are truly stream residents although some also occur in the lake. They are:

1. *Notropis boops*
2. *Notropis lutrensis*
3. *Campostoma anomalum*
4. *Pimephales vigilax*
5. *Labidesthes sicculus*
6. *Fundulus notatus*
7. *Ictalurus natalis*
8. *Micropterus salmoides*
9. *Micropterus punctulatus*
10. *Lepomis macrochirus*
11. *Lepomis megalotis*
12. *Lepomis cyanellus*
13. *Lepomis humilis*
14. *Etheostoma spectabile*

The third category consists of species that are prominently represented in the upstream samples but are absent or uncommon at the midstream and lower stations. *Notemigonus crysoleucas, Pimephales promelas,* and *Ictalurus melas* seem to belong to this group and *Lepomis cyanellus* and *Lepomis macrochirus* probably do too. *Notemigonus* in particular was taken only at stations 1, 2, 3, and 7 but not in between. Although we cannot be certain, we believe that some or all of these fishes represent introductions as a result of their having escaped from farm ponds.

Assignment of a species to one of these categories involves more than simply its pattern of occurrence. For example, *Labidesthes sicculus* and *Cyprinus carpio* both occurred at stations 4 and 5 but *C. carpio* is a lake species that does not seem to reproduce in the stream, whereas *L. sicculus* is typically a stream species. From the fact that our specimens of *L. sicculus* were young of the year we conclude that there is a small reproducing population in the stream. Additional considerations are included in the following annotated list:

Annotated List of the Fishes of Brier Creek

1. *Dorosoma cepedianum:* The gizzard shad and its congener *D. petenense* were collected only at station 7. An abundant plankton-feeding species in the open waters of the lake, both adults and juveniles were taken in the stream. The adults were collected early in June, later some juveniles

were taken although they were less numerous and somewhat larger than the threadfin young of the year.

2. *Dorosoma petenense:* Threadfin shad young of the year were numerically abundant at station 7, but no adults were collected in Brier Creek, possibly because they were able to avoid the seine better than adult gizzard shads. From July 4 to August 1 the modal size shifted from 22.8 to 28.6 mm. (fork length), indicating a mean growth rate during this period of approximately 1.4 mm. per week. The threadfin was extremely abundant in the upper layers of Lake Texoma; on July 23 more than 5000 juveniles (17 to 32 mm.) were collected in less than two hours of trawling at the surface of the lake.

3. *Carpiodes carpio:* The river carpsucker was taken only once at station 4 during the period when the pools were separated by dry riffles. Thomas White also collected several juveniles a few hundred yards downstream from station 4. These collections suggest that there is a small resident population in the large permanent pools in the stream although the preferred habitat is in the back waters and tributaries of the Red River and Lake Texoma.

4. *Notropis boops:* At stations 4 and 5, the bigeye shiner is the most abundant cyprinid present in pools although it is seldom taken in the riffles. Marking and recapture studies by White indicated little migration between pools during the low-water seasons of the year and this is substantiated by field observations. June collections contained tuberculate males. *Notropis boops* was collected only twice at station 2 and not at all at stations 1 and 3. It was present in small numbers at stations 6 and 7. The large eye indicates that it is primarily a sight feeder and this may account for its reduced dominance in the turbid waters at station 7.

5. *Notropis lutrensis:* The red shiner occurs throughout the stream drainage and was collected at every station, but it was the dominant form only in the upper reaches of the stream at stations 1, 2, and 3.

6. *Notropis venustus:* The blacktail shiner was taken at stations 6 and 7 in moderate numbers. A large stream and lake species, it is not abundant in small or swiftly flowing streams such as Brier Creek.

7. *Cyprinus carpio:* Carp were taken only at stations 4 and 5. All individuals were half-grown or young adults 5.45 inches to 8.63 inches long. Neither young nor large adults were collected although large individuals undoubtedly occur in the lower reaches of the stream. This species appears to be a wanderer that occasionally becomes trapped in the pools during low water, but it appears not to spawn successfully above the base level section of the stream.

8. *Pimephales promelas:* The fathead minnow, occurred at all stations

except 6. It was abundant only in the upper reaches; lower and farther downstream it was largely replaced by the bullhead minnow, *Pimephales vigilax*. This is a common bait and farm pond species, and we suspect that it owes its presence in the upper reaches of Brier Creek to escapes from one or more of the numerous farm ponds in the drainage. At stations 2 and 3 it was a dominant species and occurred in every collection from these stations. The presence of numerous young of the year at station 3 indicates that the species spawns in the creek.

9. *Pimephales vigilax:* The bullhead minnow was collected at stations 4, 5, 6, and 7, but not at the headwater stations 1, 2, and 3. Riggs and Bonn (1959) found that the relative abundance of this species in Lake Texoma increased between 1948 and 1958.

10. *Campostoma anomalum:* The stoneroller minnow prefers running water and is prevalent only where there is noticeable current. At station 6 it was common in the riffles and infrequent in the pools. It did not occur at station 7, but it was prominent in the headwater pools before they disappeared.

11. *Notemigonus crysoleucas:* The golden shiner occurs in the headwater areas and also in the base level part of the stream represented by station 7. This species is widespread in lakes and ponds and, like the fathead minnow, is commonly stocked for forage or bait. It seems likely that it is found in the upper reaches of the stream as a result of having escaped from farm ponds. Riggs and Bonn (1959) reported that it was not known from the main body of the lake although a few specimens were taken in Buncombe Creek.

12. *Hybopsis storeriana:* This species is a lake and large river form. A few half-grown specimens were taken at station 7.

13. *Ictalurus melas:* The black bullhead is limited to the headwater stream and is replaced by the yellow bullhead farther downstream. It may also be a farm pond escapee.

14. *Ictalurus natalis:* Replaces the black bullhead downstream. Common at station 6 where the juveniles were taken in the riffles. Both species occurred at station 4 and 5, but only *I. natalis* was taken at stations 6 and 7.

15. *Fundulus notatus:* Common throughout the stream from stations 2 and 3 to the mouth. This surface-living species is not limited to any particular bottom type and undoubtedly moves readily throughout the basin.

16. *Gambusia affinis:* Mosquitofish occurred only at stations 6 and 7. It was rare at station 6. During the daylight hours, this species remains in or near vegetation close to shore and may be missed unless the seine

is deliberately passed through such areas. Because of its restricted habitat, it is sporadically represented in the collections. Its absence from upstream collections remains enigmatic as it is taken in smaller streams elsewhere in its range.

17. *Menidia audens:* This species is extremely abundant along the lake shores and was taken sometimes in large numbers at station 7. One specimen was collected at station 6.

18. *Labidesthes sicculus:* A single individual was collected at station 4 and one series of 11 half-grown young at station 5. These were all small suggesting that there is a reproducing population in the creek, but the species is perhaps the rarest in the creek. Riggs and Bonn (1959) traced the decline of *L. sicculus* and concomitant increase of *Menidia audens* in Lake Texoma after 1952.

19. *Micropterus salmoides:* Common throughout the stream. Small specimens were collected fairly efficiently, but larger individuals of this species and the spotted bass were sometimes able to escape the seine. Thus, their contribution to the biomass may be biased downward. Juveniles were commonly taken in the upper reaches.

20. *Micropterus punctulatus:* The spotted bass is also widespread in Brier Creek, and at most stations it outnumbers the largemouth bass. Both species of black bass probably wander considerably, and the adults can be considered transients at any particular spot.

21. *Lepomis macrochirus:* The bluegill occurs in moderate numbers throughout the stream and hybridizes with the green and longear and perhaps other sunfishes, but it was not especially abundant at any of our stations. Juveniles of this species were taken only in the downstream stations 5, 6, and 7.

22. *Lepomis megalotis:* The longear sunfish is easily the most abundant species in the stream and males guarding the nests were found throughout the collecting period. These males are especially vulnerable to seining and may be present in the collection in disproportionately high numbers.

23. *Lepomis microlophus:* The redear sunfish has apparently increased since 1958. Riggs and Bonn (1959) reported it as very rare with no records between 1953 and 1958, but it is now frequently taken from the lake, and we collected it as far upstream as station 4.

24. *Lepomis humilis:* The orangespotted sunfish was the dominant species at station 1, and individuals were taken infrequently at downstream stations 4 to 7. This species is silt tolerant and considerably smaller than the other local members of the genus; males as short as 50 mm. were in full breeding colors. Trautman (1958, p. 506) has discussed the conditions favoring this species as it has expanded its range eastward in Ohio.

25. *Lepomis cyanellus:* The green sunfish occurs in fair numbers throughout the Brier Creek drainage. It hybridizes readily with other sunfishes and because of its distinctive characters was involved in most of the recognized hybrids.

26–28. Hybrid sunfishes: The most common hybrid combination was *L. cyanellus* X *L. megalotis* (26). Green sunfish and bluegill hybrids (*L. cyanellus* X *L. macrochirus* [27]) were much less common and we recognized *L. macrochirus* X *L. megalotis* (28.) only once. It appears that occasional backcross combinations occur that may not always have been recognized. Hybrids have been treated as separate species in calculating diversity indices on the ground that they represent gene pools as distinct as those of the species from which they arose.

29. *Pomoxis annularis:* The white crappie is a lacustrine species occasionally taken at station 7. Because of its large size even a single individual made a large contribution to biomass of the sample. No young of the year were found in the creek.

30. *Etheostoma spectabile:* the orangethroat darter is the only species of this genus in the creek. It is primarily a riffle species although occasionally an individual was taken near the end of the pool near the riffles. At station 4 where the riffles became dry in mid-July, orangethroats were caught over gravel bars in the pool, but they became much less common as the season progressed, perhaps because of vulnerability to predation in this secondary habitat for the species.

31. *Percina caprodes:* The logperch is a lake-dwelling species that moves into the lower parts of the stream. It was taken only at stations 6 and 7.

32. *Aplodinotus grunniens:* A single half-grown specimen was collected at station 7 on August 1, 1969. This species is extremely abundant in the lake.

33. *Morone chrysops:* This is also a lake-dwelling species but the young were regularly taken at station 7. Large schools of white bass were commonly seen feeding at the surface of the open lake.

Gars, *Lepisosteus* sp. were sometimes seen basking near the surface in the lower parts of the stream but none was taken in our samples. However, a gar skeleton was found in the bank at station 4, suggesting that the species wandered into the stream during high water. They do not form a significant element in the summer communities, however, except possibly in the base-level section of the stream.

SPECIES DIVERSITY

Ecologists are currently placing considerable emphasis on the use of information theory indices for describing the relative abundance of the members of the community. In general low index values indicate that fewer species are present and that some of these are numerically preponderant. Higher values indicate more species present in more nearly equal numbers. In an effort to better understand the usefulness of these indices as applied to our samples we computed Shannon Weaver values for each sample and for the combined data from each station using the following formula:

$$H = - \Sigma p_i \log (\text{base } 2)\, p_i$$

in the form given by Lloyd, Zar, and Karr (1968, p. 258). Both number and biomass data were used in the calculations. The rationale for the use of biomass data has been discussed by Dickman (1968).

For these calculations transparent juvenile sunfishes that could not be identified with confidence and hybrid sunfishes were treated as separate entities on the ground that they play distinct roles in the community structure. The following results are illustrated graphically in figure 2.

Station 1

Because of the small size of this pool, sampling undoubtedly affected the populations and a slight trend toward lowered diversity indices (both number and biomass) throughout the period which may have resulted from the attrition due to sampling (fig. 2A, B).

Station 2

Diversity indices for the second and third samples were higher possibly because the fishes were concentrated into two small pools so that all species were equally vulnerable to sampling. Certainly no great importance can be attached to diversity indices in this small sample.

Station 3

A great number of juvenile minnows were present in the large pool early during the study period, but as it dried up and disappeared fewer juveniles were taken in the sample. Thus, the disproportionally high numbers of a few species were reduced, resulting in a slight increase in both biomass and number diversity indices.

Station 4

Number diversity indices for the seven samples showed considerable variation but no particular trend.

Five species, *Notropis boops, N. lutrensis, Pimephales vigilax, Fundulus notatus* and *Lepomis megalotis* were present in all of the samples. *Notropis*

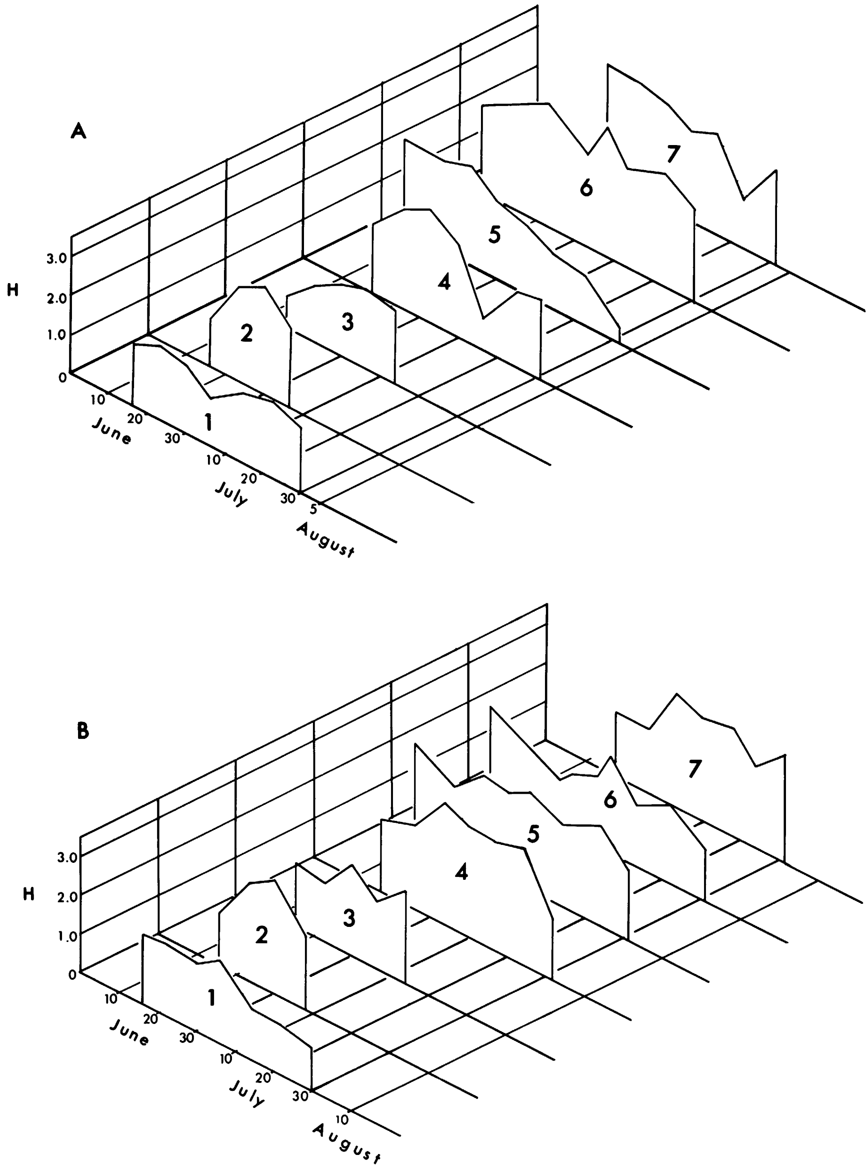

FIG. 2. Diversity indices for each of seven sample stations June–July, 1969 showing trends and fluctuations in number indices (A) and biomass indices (B). Only station 5 shows a regular decrease in number diversity as *Notropis boops* became more strongly dominant in the samples.

boops was numerically dominant in most of the samples, but the presence of large individuals of such species as *Carpiodes carpio, Cyprinus carpio,* and *Micropterus salmoides* in some samples made the distribution patterns of biomass much more erratic.

Biomass diversity showed a general increasing trend with the exception of the last collection in which a larger carp was taken which resulted in a low index value. A subjective impression is that the larger fish seemed to become emaciated as the season progressed.

Moreover, there seemed to be fewer intermediate-sized fishes so that the population came to consist of very large and very small individuals. We believe this is a reflection of the predation regime in the pools. The large fishes were unable to prey on the fry effectively, but they were able to crop off the intermediate sizes. As the vulnerable sizes were reduced, the large predators began to exhibit symptoms of starvation.

Station 5

This is the most stable of the stations sampled, six species, *Notropis boops, N. lutrensis, Fundulus notatus, Lepomis megalotis, Lepomis cyanellus,* and *Etheostoma spectabile* were taken in all of the samples. Only one hybrid sunfish was recognized from this section. Number diversity indices show a regular decrease throughout the period but the biomass indices showed no recognizable trend.

Apparently this station is near the center of the pool and riffles environment and is therefore the most "typical" in that it lacks headwater species (such as *Pimephales promelas*) which occurred at station 4, and the downstream species such as *Percina caprodes* which occurred at station 6.

The decrease in number indices seems to be due chiefly to the large number of juvenile *Notropis boops* in the latter samples. We suggest that this is because they reached a size that was retained by the net mesh. Early in the sampling period young of the year were not taken effectively either because they were in the gravel or passed through the net.

Station 6

Percina caprodes, Gambusia affinis, Notropis venustus, Menidia audens, are all indicators of the proximity to base level of this station. *Campostoma anomalum* is a riffle dwelling form, the others are widely distributed, occurring in all parts of the stream except for the headwaters. The number diversity indices showed little trend during the study period but the biomass indices generally decreased. This may be the result of rapid growth of young of the year and year-old *Lepomis megalotis.*

Station 7

Throughout the period there was an increase in the relative number of juvenile threadfins in the samples, which resulted in a decrease in the number diversity index and an increase in the biomass diversity, as the large numbers of the small fishes approached or surpassed the biomass contribution of larger species such as *Lepomis megalotis* and *macrochirus*.

Although diversity indices are useful tools for describing complex data and comparing similar samples, it appears that their usefulness is limited. Their inability to deal with individual species is a serious drawback in working with natural communities. It would, for example, be perfectly possible for two samples to have the same diversity index and yet not have a single species in common. Or they might have the same species present and the same index but have the dominance order changed or even reversed. For these reasons we believe that one should use great caution in seeking explanations for diversity as reflected in information theory indices. They can be a useful descriptive tool but one must avoid trying to extract information that they do not contain.

THE FISH COMMUNITIES OF BRIER CREEK

Shelford (1911) and Shelden (1968) have observed that the linear succession of stream fish associations is owing predominantly to the addition of species toward the stream mouth, and this is generally true in Brier Creek. The headwater stations 1, 2, and 3 had eight to 10 species, the middle reach stations 4, 5, and 6 had 19 to 21 species, and the downstream, base level station 7 had 27 species. Replacement of one species by another was observed in only a few instances. *Ictalurus melas* was replaced by *I. natalis* in the lower reaches, *Pimephales vigilax* replaced *P. promelas,* and *Notropis venustus* increased with concomitant reduction in dominance of *N. lutrensis.*

There are also significant shifts in relative abundance measured in terms of relative numbers and relative biomass, between the upstream and downstream stations (table 1). Moreover, certain species are more consistent, i.e., present in a higher percentage of the samples, at some stations than at others (table 2). Any analysis of community structure must therefore consider all of these parameters and not merely the species lists for the several stations. Although one can deal subjectively with the faunal list, consideration of the complexities of relative abundance and consistency of occurrence requires objective mathematical treatment.

Multivariate analysis provides such an objective method for picking out characteristic groups of species and for evaluating the contribution of each species to the over-all pattern. In essence we consider the environ-

TABLE 1

Numbers and Biomass of Fishes Collected at Seven Stations in Brier Creek June–August 1969

	1	2	3	4	5	6	7
Notemigonus crysoleucas	1(5)	1(5)	4(24)	—	—	—	—
Hybrid: *Lepomis macrochirus* X *Lepomis cyanellus*	—	—	3(23)	—	—	—	—
Carpiodes carpio	—	—	—	1(100)	—	—	—
Ictalurus melas	5(98)	—	7(125)	3(76)	1(31)	—	—
Cyprinus carpio	—	—	—	1(671)	2(111)	—	—
Labidesthes sicculus	—	—	—	1(1)	11(1)	—	—
Campostoma anomalum	34(31)	10(14)	2(1)	9(18)	340(42)	50(56)	—
Pimephales promelas	31(6)	16(15)	305(43)	31(14)	1(1)	—	2(1)
Notropis lutrensis	64(42)	29(18)	25(6)	583(82)	114(160)	39(53)	276(119)
Lepomis cyanellus	5(20)	43(10)	150(85)	93(321)	30(126)	24(402)	6(13)
Lepomis humilis	88(82)	7(1)	—	49(29)	1(3)	1(2)	1(2)
Lepomis macrochirus	1(4)	—	5(32)	41(377)	19(1614)	38(301)	116(855)
Lepomis megalotis	—	46(12)	3(14)	562(1056)	185(1546)	234(3501)	203(1917)
Fundulus notatus	—	20(7)	9(1)	204(71)	74(31)	160(80)	56(28)
Notropis boops	—	9(1)	—	2234(603)	2229(1037)	223(230)	68(13)
Micropterus salmoides	—	7(9)	—	10(282)	18(57)	13(52)	63(148)
Pimephales vigilax	—	—	—	107(25)	9(1)	18(33)	280(96)
Ictalurus natalis	—	—	—	3(29)	5(2)	50(19)	2(1)
Micropterus punctulatus	—	—	—	53(223)	40(37)	43(36)	79(41)
Lepomis microlophus	—	—	—	2(72)	1(19)	1(12)	1(4)

TABLE 1—*(Continued)*

	1	2	3	4	5	6	7
Hybrid: *Lepomis megalotis* X *Lepomis cyanellus*	—	—	—	2(125)	1(36)	5(102)	1(3)
Etheostoma spectabile	—	—	—	27(5)	239(68)	159(68)	5(1)
Hybrid: *Lepomis megalotis* X *Lepomis macrochirus*	—	—	—	—	—	1(10)	1(4)
Notropis venustus	—	—	—	—	—	24(81)	138(181)
Gambusia affinis	—	—	—	—	—	1(1)	18(5)
Percina caprodes	—	—	—	—	—	3(22)	14(20)
Menidia audens	—	—	—	—	—	1(1)	1186(235)
Dorosoma cepedianum	—	—	—	—	—	—	72(355)
Dorosoma petenense	—	—	—	—	—	—	1681(130)
Hybopsis storeriana	—	—	—	—	—	—	3(4)
Pomoxis annularis	—	—	—	—	—	—	3(153)
Aplodinotus grunniens	—	—	—	—	—	—	1(4)
Morone chrysops	—	—	—	—	—	—	8(23)
Notemigonus crysoleucas	—	—	—	—	—	—	10(41)
TOTALS	229(288)	188(92)	513(354)	4016(4180)	3320(5023)	1088(5062)	4294(4397)

[a]The figures in parentheses represent the total weight in grams in all the samples collected at that station.

TABLE 2
CONSISTENCY OF OCCURRENCE OF FISHES FROM SEVEN STATIONS IN BRIER CREEK
JUNE–AUGUST, 1969[a]

	1	2	3	4	5	6	7
Notemigonus crysoleucas	14	25	60	—	—	—	—
Hybrid: *Lepomis macrochirus* X *Lepomis cyanellus*	—	—	40	—	—	—	—
Carpiodes carpio	—	—	—	14	—	—	—
Ictalurus melas	57	—	40	43	13	—	—
Cyprinus carpio	—	—	—	14	25	—	—
Labidesthes sicculus	—	—	—	14	25	—	—
Campostoma anomalum	86	75	40	43	88	88	—
Pimephales promelas	57	100	100	71	13	—	25
Notropis lutrensis	100	75	40	100	100	75	88
Lepomis cyanellus	43	75	100	86	100	75	25
Lepomis humilis	100	25	—	43	13	13	13
Lepomis macrochirus	14	—	60	71	88	88	100
Lepomis megalotis	—	50	40	100	100	100	100
Fundulus notatus	—	75	40	100	100	100	88
Notropis boops	—	50	—	100	100	88	50
Micropterus salmoides	—	50	—	71	38	63	88
Pimephales vigilax	—	—	—	100	25	50	100
Ictalurus natalis	—	—	—	29	13	88	13
Micropterus punctulatus	—	—	—	100	88	88	88
Lepomis microlophus	—	—	—	29	13	13	13
Hybrid: *Lepomis megalotis* X *Lepomis cyanellus*	—	—	—	14	13	13	13
Etheostoma spectabile	—	—	—	71	100	88	50
Hybrid: *Lepomis megalotis* X *Lepomis macrochirus*	—	—	—	—	—	13	13
Notropis venustus	—	—	—	—	—	50	100
Gambusia affinis	—	—	—	—	—	13	63
Percina caprodes	—	—	—	—	—	25	63
Menidia audens	—	—	—	—	—	13	88
Dorosoma cepedianum	—	—	—	—	—	—	38
Dorosoma petenense	—	—	—	—	—	—	88
Hybopsis storeriana	—	—	—	—	—	—	38
Pomoxis annularis	—	—	—	—	—	—	38
Aplodinotus grunniens	—	—	—	—	—	—	13
Morone chrysops	—	—	—	—	—	—	50
Notemigonus crysoleucas	—	—	—	—	—	—	50

[a]Numbers in each column are percentage of the samples from that station in which the species was present. For example, *Notemigonus crysoleucas* was present in 14 per cent of the samples from station 1.

mental influence of each species to be a significant element in the environment of every other species. The program used here was originally developed for comparing the chemical content of large numbers of rock samples (for a discussion of the development of the method and the details of its mathematical basis, see Manson, 1967). In effect each species is assigned a position on the surface of an N-dimensional hypervolume where N is the number of samples being compared. In this case N = 7, because the individual samples for each station were pooled. Initially the raw data from the seven collecting stations are used as the basis for calculating interstation resemblances. Next a set of idealized dimensions is fitted by principal component analysis so as to encompass most of the observed variance between the actual stations. These idealized dimensions are roughly equivalent to abstract reference collections.

The program used here provides an index to the position of each species in terms of the idealized reference stations and also indicates how much of the observed variance associated with each station is accounted for by the idealized reference collections. This is an indication of whether the data are adequately represented by a given number of dimensions. If the data can be described adequately in terms of three idealized dimensions they can be represented graphically, but if more than three dimensions are required to account for most of the variance they cannot.

Similarities and differences among the actual collections can be measured in terms of their share of the variation present in the principal reference collection. A comparison of the results of this part of the analysis is given in table 3. Although the four measures of community, faunal list, relative numbers, relative biomass, and consistency of occurrence give different values, the patterns are the same. In each case stations 1, 2, and 3 form a group, stations 4, 5, and 6 form a second group, and station 7 stands alone.

Data for relative biomass could not be represented in three dimensions, hence could not be plotted. The relative positions of the species based on presence or absence data alone are presented in figure 3. This plot reveals no particular trends and several species have the same values, hence it is not possible to assign the species to a particular community on the basis of this plot. When relative numbers and consistency of occurrence are considered, however, there are clearly evident trends and the position of each species in relation to the three endpoints—upstream, midstream, and downstream communities—can readily be assessed (figs. 4 and 5).

These two aspects of the multivariate analysis, objective assessment of resemblance between stations, and assigning individual species with respect to the idealized end points more than justify the labor involved in coding the data and running the analysis. In a small stream like Brier Creek one can readily reach similar conclusions on the basis of subjective impressions, but in more complex and subtle environments analysis of this sort is essential to the recognition of community assemblages. Even in Brier Creek one finds it difficult to assess the relative distinctiveness of the assemblages occurring at the various stations. Our first inclination was to recognize the assemblages at stations 1 and 4 as distinct from that of 2 and 3, and distinct from station 5, thus dividing the fauna of Brier

TABLE 3
UNROTATED FACTOR COMPONENTS FROM MULTIVARIATE ANALYSIS OF SEVEN COLLECTING STATIONS USING FOUR KINDS OF RAW DATA[a]

Stations	Occurrence	Number	Biomass	Consistency
1	0.462	0.021	0.046	0.092
2	0.466	0.019	0.018	0.125
3	0.462	0.033	0.043	0.108
4	0.364	0.273	0.445	0.392
5	0.390	0.171	0.284	0.324
6	0.127	0.228	0.385	0.377
7	−0.234	0.918	0.754	0.751

[a]The figures in each column measure proportion of variance present in principal reference community associated with each actual collecting station.

Creek into five rather than three communities. In retrospect this is probably the result of overemphasis on the physical appearance of the habitats and our inability to evaluate intuitively relative abundance of large numbers of species.

THE HEADWATER COMMUNITY

(STATIONS 1, 2, AND 3)

The headwater community occurs in the high gradient, intermittently flowing part of the stream where the bottom is typically mud, or sand and gravel with occasional bedrock outcrops. It is composed of relatively few species, of which all are tolerant of high temperature and occasional dense silt. These are pioneer species that can recolonize the area quickly after summer drying has eliminated the fish population. Eight to ten species of fish occurred at each station and the total fauna for these three stations was twelve species and hybrid combinations. Diversity indices based on both numbers (1.12 to 1.98) and biomass (1.03 to 1.98) are

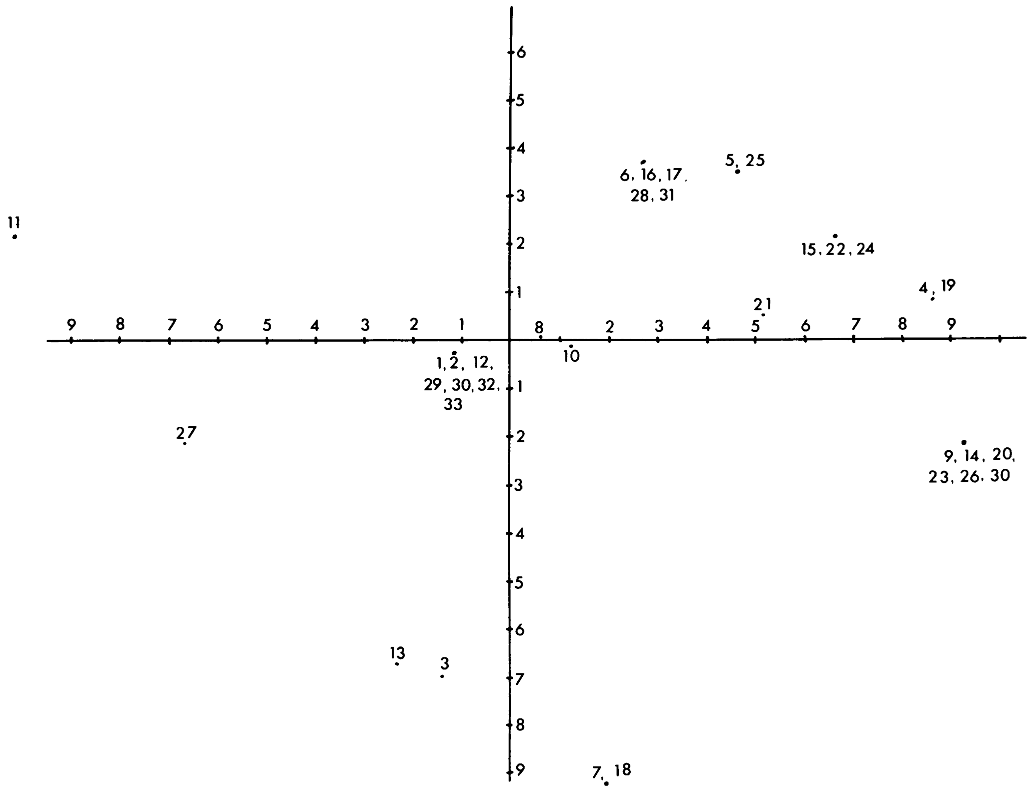

Fig. 3. Results of multivariate analysis of the fish communities of Brier Creek based on faunal lists. Dots, with numbers corresponding to the annotated list of species in the text, indicate the relative position of each species with respect to the idealized reference collections. Trends are not clearly shown by these data.

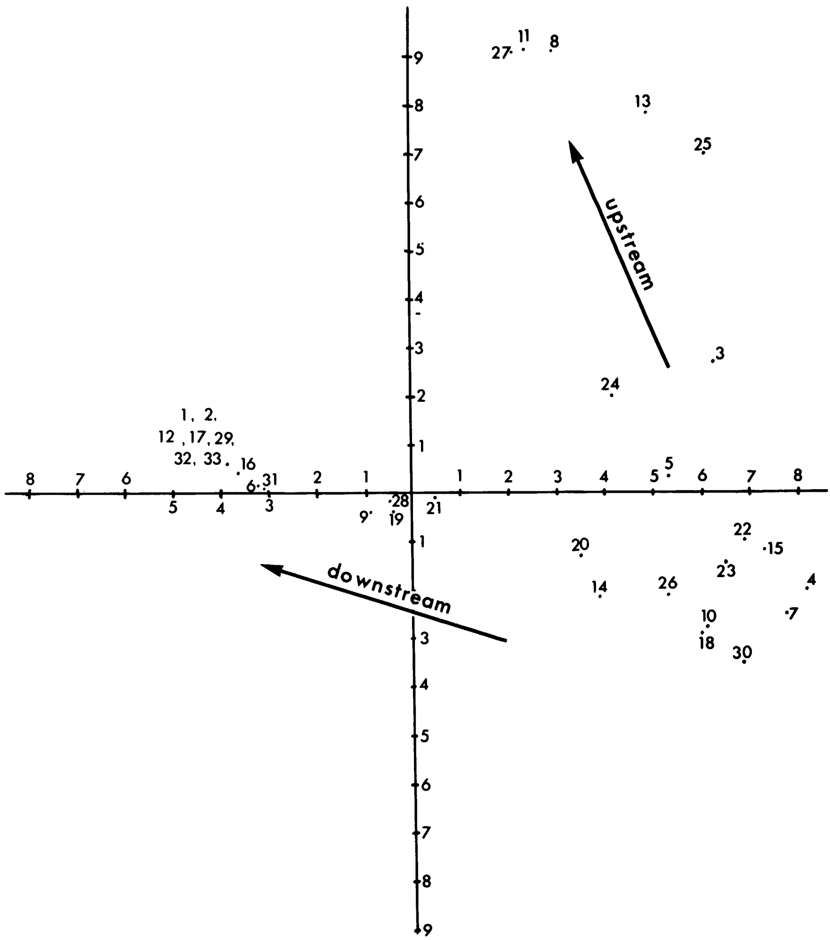

FIG. 4. Results of multivariate analysis of the fish communities of Brier Creek based on relative numbers. Dots, with numbers corresponding to the annotated list of species in the text, indicate the relative position of each species with respect to the idealized reference collections. Upstream-downstream trends are indicated.

relatively low. The most typical species, that is, those nearest to the generalized endpoint in figures 4 and 5 are: 8. *Pimephales promelas,* 11. *Notemigonus crysoleucas,* 13. *Ictalurus melas,* 27. Hybrid *Lepomis cyanellus* × *L. macrochirus*.

There are perhaps two subdivisions here. One is an ephemeral assemblage dominated by *Pimephales promelas* and *Lepomis cyanellus*. This subcommunity occurs in sections of the stream that dry completely each summer and repopulate during the wetter parts of the year. The other is

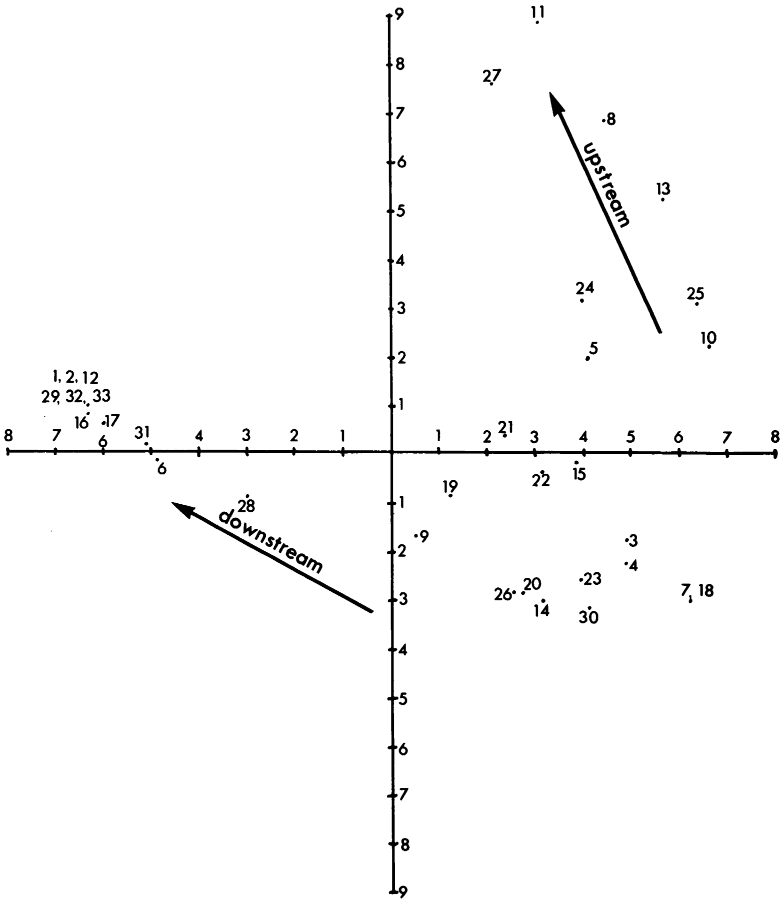

FIG. 5. Results of multivariate analysis of the fish communities of Brier Creek based on consistency of occurrence. Dots, with numbers corresponding to the annotated list in the text, indicate the relative position of each species with respect to the idealized reference collections. Upstream-downstream trends are indicated.

found in more permanent parts of the stream, represented by our station 1, and is dominated by *Notropis lutrensis, Ictalurus melas,* and *Lepomis humilis. Lepomis humilis* and *N. lutrensis* were represented by young of the year and apparently spawn there but no young of the year *melas* were taken and this species, like several others, may not reproduce in the pool but may come in when there is sufficient flowing water in the creek.

In spite of their conspicuous dominance of station 1, *Lepomis humilis* and *Notropis lutrensis* do not rate as indicators of ephemeral headwaters for they are widely distributed throughout the stream, and in fact, have wide geographic ranges in central United States.

Notropis lutrensis feeds on phytoplanktonic algae and insects. *Lepomis humilis* feeds on insects and invertebrates and *Ictalurus melas* feeds on bottom-dwelling invertebrates and detritus. Individuals of *Campostoma* feed on diatoms and small bottom invertebrates, aufwuchs, and benthos.

THE MIDSTREAM COMMUNITY

(Stations 4, 5, and 6)

The midstream community consists of species that require more stable conditions of temperature, oxygen and silt load. Because there is a greater diversity of the habitat, there is a larger number of species (19–21) and higher diversity indices (number 1.2–2.6, biomass 1.3–2.8).

The midstream community has two subdivisions: the riffle assemblage, dominated by *Campostoma anomalum* and *Etheostoma spectabile;* and the pool assemblage, dominated by *Notropis boops* and *Lepomis megalotis.*

Stations 4, 5, and 6 each contained 20 or 21 species. There is some species replacement and several pronounced changes in relative rank between the upstream and downstream stations. *Notropis lutrensis* ranks second in numerical abundance at station 4, fifth at station 5, and eighth at station 6. *Ictalurus melas* and *Ictalurus natalis* occurred in equal numbers at station 4 but at station 5 *melas* was less abundant than *natalis* and at station 6 only *natalis* was present. *Pimephales promelas* was present in small numbers at stations 4 and 5 but not at 6. *Lepomis humilis* and *Lepomis microlophus* were present in low numbers at all three stations. *Labidesthes sicculus,* present at stations 4 and 5, was replaced by *Menidia audens* at 6. *Percina caprodes* and *Gambusia affinis* occurred only at station 6. Other shifts in composition and dominance will be obvious from tables 1 and 2.

The food resource sharing patterns can be summarized as follows: In the riffles young of the year catfishes and darters are benthos feeders, whereas *Campostoma anomalum* feeds on the aufwuchs on the gravel. In the pools *Fundulus notatus* and *Gambusia affinis* feed at the surface and *Notropis boops* feeds in the upper layers and at the surface. The sunfishes *L. megalotis* and *L. macrochirus* feed at all levels and the two species of *Micropterus* are midwater predators. The carp and carpsuckers feed on benthic invertebrates as do the species of *Pimephales* and *Ictalurus*. Thus, all levels in the water column are exploited by one or more species.

Although there is a sharp ecological separation between riffle and pool species, we consider these to be parts of a single community. The distinction between pool and riffle is obvious but it is not qualitatively distinct from the differences between sand spawners and rock spawners or between midwater and surface feeders.

THE DOWNSTREAM COMMUNITY

(STATION 7)

Fishes of the base-level section of the stream are lake or large river species with a few typical stream forms. This assemblage is therefore transitional between a true lake assemblage and the midstream community. Lake Texoma, however, because it is a comparatively young impoundment and undoubtedly is still undergoing a species succession, cannot be considered a typical lake. Indeed, it may be more accurate to view Lake Texoma as an extension of the base-level section of Brier Creek than the reverse!

Twenty-eight species were taken at station 7, but the diversity indices (number 1.09 to 2.95, biomass 1.54 to 2.95) are not appreciably higher than at the midstream stations because of the numerical preponderance of *Dorosoma petenense* and *Menidia audens* and the biomass preponderance of *Lepomis megalotis* and *Lepomis macrochirus*.

The most typical species of the base level community are:

1. *Dorosoma cepedianum*
2. *D. petenense*
6. *Notropis venustus*
12. *Hybopsis storeriana*
16. *Gambusia affinis*
17. *Menidia audens*
29. *Pomoxis annularis*
32. *Aplodinotus grunniens*
33. *Morone chrysops*

Plankton feeders in this community include the two species of *Dorosoma* which are filter feeding plankton grazers and those such as *Notemigonus* that feed on individual plankton. *Gambusia, Fundulus, Menidia,* and *Notropis boops* feed at or near the surface. Midwater carnivores include *Morone chrysops, Lepomis cyanellus, Pomoxis annularis* and the two species of *Micropterus;* benthic feeders are *Pimephales vigilax, Etheostoma spectabile, Ictalurus natalis,* and *Aplodinotus grunniens.* (There are no riffles but *Etheostoma spectabile* is infrequently taken over gravel bars).

Although we have no evidence at this time, we suspect that the composition of the fish fauna in this section of the stream may undergo drastic seasonal changes and the division of the resources would be expected to undergo corresponding changes.

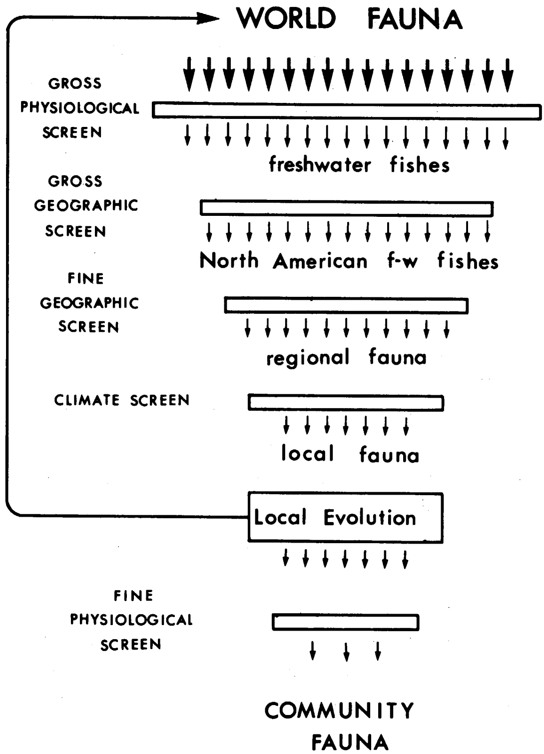

FIG. 6. The fauna of a fish community in a small stream in North America viewed as the result of passing the world fish fauna through a series of screens. The gross physiological screen rejects all marine species. The gross zoogeographic screen rejects species of other continents by denying them access to this continent. Further zoogeographic and local climate barriers restrict the fauna still more. Finally, tolerance limits for the physical, chemical, and biological factors of the immediate habitat determine the species composition of the community.

DISCUSSION

The three fish communities of the Brier Creek drainage are geographically localized but they are not entirely associated with particular habitat types. The headwater community is found in both permanent spring fed pools and ephemeral pools that dry completely during the summer months. The midstream pool and riffle community is present in the permanently flowing gravel bottom parts of the stream and also in the intermittent, rocky bottomed section.

These communities are periodically disturbed by floods and drying and reestablish themselves when conditions again become favorable. The similarities between stations 1, 2, and 3 which are on separate branches of the stream and therefore separated by considerable distances and between stations 4, 5, and 6 which occupy specifically and recognizably different habitats suggest that it is primarily the interactions between the fish species that determine community structure. Although it is common practice to speak of assemblages of species associated with particular types of habitats as "habitat communities," one must keep in mind that the same habitat can support different communities in different regions and, as in Brier Creek, a community can occupy more than one physical habitat. The habitat community therefore is meaningful only for specific areas and under specified conditions.

Communities are most easily described by the list of species of which they are composed. The faunal composition of the community is determined by general extrinsic physical and chemical factors which preclude those species that cannot tolerate the existing conditions. The presence of a particular assemblage of species in a given place can be viewed as the result of passing the fauna of the world through a series of ever finer screens. To take the example of a small stream in midcontinental North America, we can view the world fish fauna of 20,000-plus species as having passed through a gross physiochemical screen that eliminated all marine and brackish water species. Then there is a coarse zoogeographic screen that eliminated the freshwater fishes of the other continents merely by denying them access to our particular stream. The total North American fauna has then passed through finer and finer zoogeographic, climatic, and ecological screens until there is an assemblage of perhaps 75 to 100 species that have had access to the area in question and whose lethal limits coincide with the conditions present in our stream. In this sense the fauna is the product of the lethal limits for the species present and it is essentially autecological in nature. The accompanying figure (fig. 6) illustrates this successive screen principle. This is a useful model because for many species we can determine exactly which screens block their occurrence at a particular location.

The faunal composition of the community is perhaps its least important parameter, at least, a list of the species present conveys a minimum of information about the community structure, although it is frequently the only kind of information available. Certainly for extinct communities we must be content with faunal lists because we know too little about the vagaries of preservation and subsequent sampling to be able to draw valid conclusions based on relative number and biomass data.

The concept of relative abundance in the community as measured by numbers or biomass, seems to us to be more significant than a simple enumeration of the species present as we can conceive of different communities with exactly the same faunal lists. In the present case we have no doubt that constant monitoring of station 5 for a few months would yield a list of all of the species known from the drainage and it is likely that every species at times occurs throughout the stream.

Most of the species of fishes that occur in Brier Creek are able to tolerate a considerable range of physical and chemical conditions, but there are always some microhabitats that are more desirable than others and these are reflected in higher survival rate, faster growth, and better reproduction which are, in turn, reflected in greater abundance, either in terms of numbers or biomass, in the optimal environments. (It must be recognized that some species always occur in low numbers even in the most favored environments. For them their consistent presence is a better measure of "success" than either number or biomass.) Relative numbers and relative biomass are not merely different measures of the same phenomenon although both must be the result of the interactions between the component species. Numbers can be increased only through reproduction or immigration, whereas biomass can be increased through reproduction, immigration, and growth. The growth rate is variable and under extremely adverse conditions can even become negative. Moreover, because individuals belonging to different species reach different sizes their contributions to the whole biomass will be quite different and frequently the most abundant species accounts for a relatively small part of the total biomass. The importance of relative numbers lies in the fact that all interspecies interactions—predator prey, competition, reproduction—are interactions between individuals. The significance of biomass is in the share of the energy budget that is demanded by a given species. Both parameters are important and usually they are closely parallel. Nevertheless they are different and must be considered separately.

The community is the product of a long evolutionary history that has resulted in mutual co-adaptations for sharing the available resources in the general environment. The concept of resource sharing provides an explanation for the ability of groups of species to live together in the same general region with a minimum of direct interspecific competition. This is perhaps most easily observed in space and food sharing mechanisms but we anticipate that complex co-adaptations of predation, defense, and reproductive patterns will eventually be found to regulate the relative abundance of the component species of the community and lead to long-term stable equilibriums.

Exotic species such as the carp, which may have evolved similar tolerance limits in different geographical areas often cannot assume an equilibrium role in the new environment and either out-compete and exclude the local species or fail to maintain themselves. In Brier Creek it appears that the local stream fishes are better suited to the habitat and the carp exists as an occasional straggler but does not reproduce there. Although many facets of competition are poorly understood, it appears that selection favors the individuals that are specialized in such a way as to be able to take advantage of resources that are not as readily available to competing species. These specializations make it possible for the association to continue. Thus we can view the community as being united not by similarities among the component species but by their differences. In this sense, one can consider ecological unity the inverse of taxonomic unity although both are the result of, and subject to, evolutionary changes.

SUMMARY

Seven stations in a small stream in southern Oklahoma were studied weekly during June and July, 1969. Thirty-three species were collected and these fall into three assemblages. An upstream ephemeral assemblage, a midstream pool and riffle assemblage, and a downstream base-level assemblage. These communities are distinguishable on the basis of faunal lists, relative numbers, relative biomass, and consistency of occurrence as measured by percentage of the samples in which the species are present.

Multivariate analysis permits the degree of resemblance between the stations to be expressed objectively and also provides a convenient means of assessing the relative roles of the component species. Faunal lists provide the least amount of information; calculations based on relative numbers and relative biomass give more meaningful results.

Diversity indices are commonly used expressions of relative abundance. These were calculated for each sample and their trends and fluctuations during the sample period are examined for each station. These indices are useful tools but have the drawback of ignoring the identity of the component species. Resource-sharing patterns in the three communities are discussed briefly.

ACKNOWLEDGMENTS

Field work for the present study was made possible by a National Science Foundation Fellowship (No. GY 5407) granted to Charlie R. Powell. Dr. Loren G. Hill, Director of the University of Oklahoma Biological Station provided every possible support. Dr. Daniel Isaak, Dr. Clarence Harms, Mr. Thomas White, and Mr. Kevin Hopkins assisted in the field work. Mrs. Norma Rothman carefully rechecked all sorting and identifications in the laboratory. Computer programming assistance was generously provided by Dr. Vincent Manson and Miss Jennifer Yeh of the Department of Mineralogy, the American Museum of Natural History. Computer time was provided by the American Museum of Natural History.

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