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Community Dynamics of the Benthic Fauna in a Woodland Springbrook

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INTRODUCTION

This study was undertaken to examine in detail the organization and operation of the benthic community in a small woodland stream, Morgan's Creek, Kentucky. For the most part, previous ecological studies on North American streams have been general surveys or applied studies, in which the benthic fauna is treated superficially. Even the more detailed faunistic studies are of limited value because they were confined to only a part of the year, the animals were not treated as individual species populations, or there was not a sufficiently detailed examination of pertinent environmental features.

The stream chosen for study originates as a spring and thus offers the advantages of relatively constant discharge, temperature, and chemical conditions at its source, as well as a gradient of environmental features, which become progressively modified downstream. Furthermore, it represents a relatively simple natural situation in relation to size, faunal composition, and maintenance of a single basic habitat type (rubble-riffle) throughout the length of the stream. The comparative simplicity of the benthic community, the location of the stream in a region where the taxonomy of several major aquatic groups is relatively well known, and the cooperation of a number of specialists permitted study at the species level of most important animals. A number of investigators, including HYNES (1960, 1961), MACAN (1961, 1963), and MAYR (1963), have emphasized the importance of basing ecological-faunistic studies at the species level: and

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the ability to do so in the present study has been an important factor in its success.

Eight collecting sites were selected, based on bottom type, flow characteristics, and degree of vegetative cover, to obtain representative sampling of the stream and to provide certain areas which would be comparable with one another. The basic habitat studied was the rubble-riffle, but a station was established at the spring source, and others included a cascade area, a pool, and a reach at the confluence with the Ohio River. Following preliminary work during 1962, a program of bi-weekly collections was initiated in February 1963 and carried out at all stations until February 1964; additional bi-weekly collecting continued through September 1964 at the five stations most typical of the stream.

Results of the Morgan's Creek study concerning trophic structure (MINSHALL, G. W., 1967) and the life histories of a mayfly (MINSHALL, J. N., 1967) and two stoneflies (MINSHALL & MINSHALL, 1966) are given elsewhere. Previous ecological studies on springs or spring streams include those by NIELSEN (1950), BERG (1951), NOEL (1954), SLOAN (1956), ODUM (1957), TEAL (1957), THORUP (1963), and MINCKLEY (1963). In addition several publications on small streams by JONES (1949, 1950), ILLIES (1952), HYNES (1961), and MACAN (1961, 1962, 1963) contain information on stony stream communities pertinent to the present theme.

DESCRIPTION OF MORGAN'S CREEK

Morgan's Creek begins as a rheocrene at the mouth of Morgan's Cave in Otter Creek Park, Kentucky, U.S.A. The drainage basin lies along the northern boundary of the Mississippian Plateau region between two major drainages, Otter Creek and Doe Run. The mean annual temperature for the Mississippian Plateau region is about 14°C (BROWN & LAMBERT, 1962), with extremes of –18°C and 38°C (U.S. Weather Bureau, 1958). The average annual precipitation at Evans Landing, Indiana, just north of Morgan's Creek, is about 44 inches, with the precipitation relatively well distributed throughout the year (U.S. Weather Bureau, 1960).

At present the valley of Morgan's Creek is wooded with a young, second-growth deciduous forest, in which oak (*Quercus* spp.) and maple (*Acer* spp.) are the chief components. Along the stream banks sycamore (*Platanus occidentalis* L.) also is common. Previously, the vegetation (see OWEN, 1857) was typical of a mature oak-hickory climax forest. During the 1800's much of the area was cleared of timber (RIDENOUR, 1929; VAN ARSDEL, 1939), but by the early twentieth century reforestation had begun. Otter Creek Park was

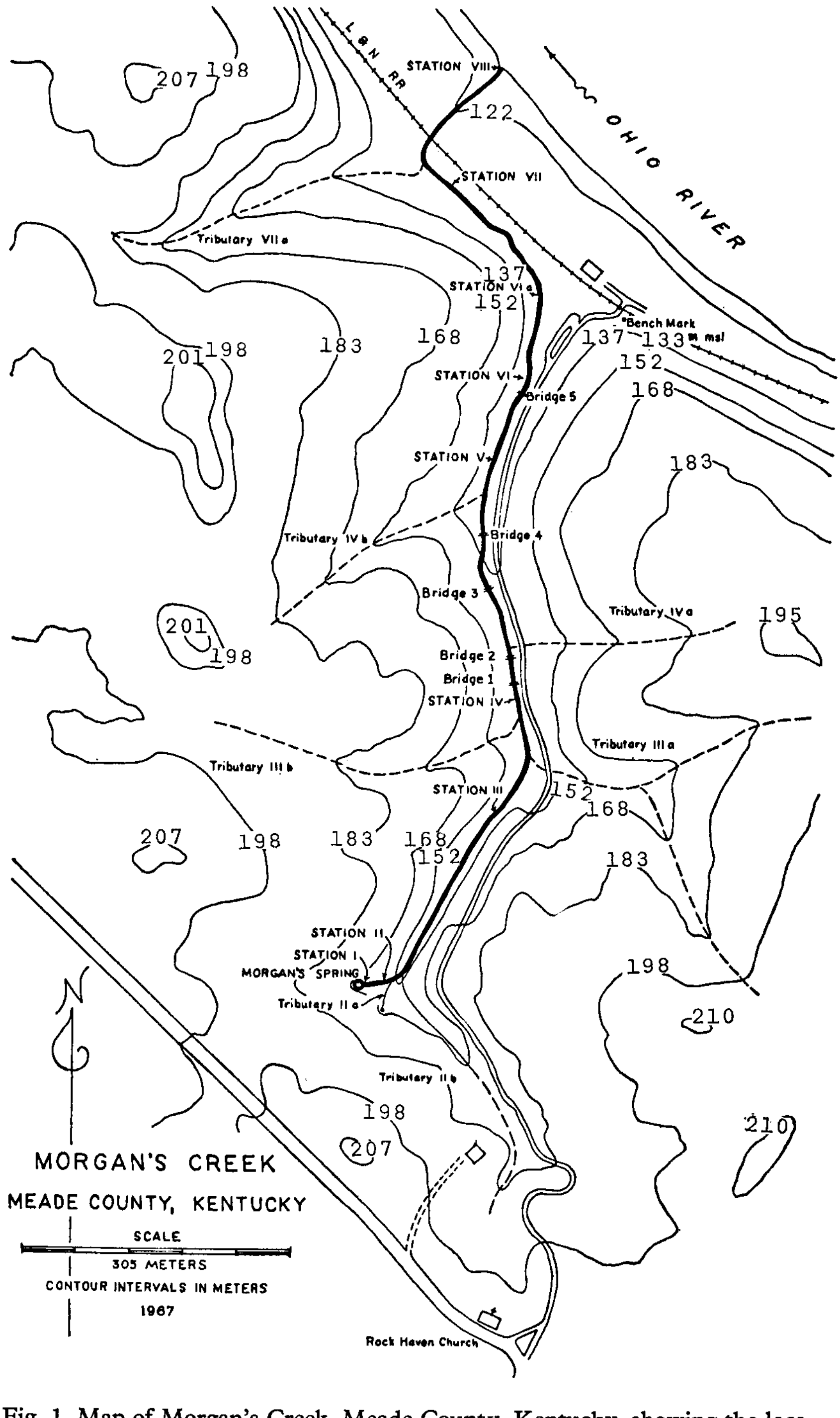


Fig. 1. Map of Morgan's Creek, Meade County, Kentucky, showing the location of the sampling stations, the spring source, and otherp rominent features. Distances originally measured in feet; scale and contours converted to nearest 1.0 meters.

established in the late 1930's and the forest has remained relatively undisturbed since then.

Station I (Fig. 1) lies just outside the mouth of Morgan's Cave and is at a much higher elevation than the other stations (Fig. 2). The

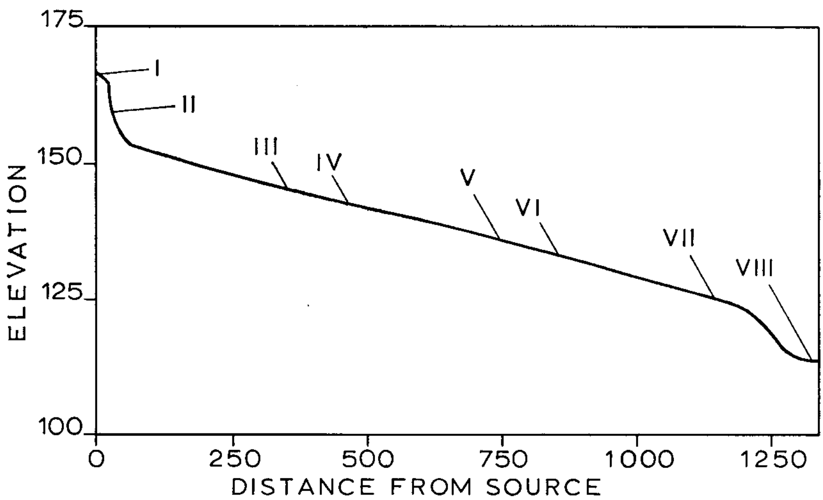


Fig. 2. Vertical profile of Morgan's Creek. Both scales are in meters.

spring is at the base of a sheer limestone bluff and the immediate area is well sheltered from the usual influences of the atmospheric weather. Station II is located on a 45° slope, about 25 m below the source. During moderate-to-high discharges the area is a cataract, but ordinarily most of the flow is subsurface. Just below Station II, the stream passes into a steep-sided ravine, through which it flows for approximately 460 m. This section, represented by Station III, is well protected by the valley slopes and by the forest, which forms a dense canopy over the stream during the growing season.

The first sampling site after the valley begins to widen is Station IV. Here the stream dissects a small clearing and for the first time becomes exposed to the full influence of the atmospheric climate. Conditions at Station IV are characteristic of the area from Tributary IIIb to the vicinity of Bridge 3. The marked reduction in riparian vegetation beginning at Station IV persists to just below Station VIa. This area encompasses Station V, the largest and deepest pool in the stream, and Station VI. Conditions represented by Station VI are common to the section extending from just above Bridge 5 to a point where the dense vegetation recurs, except that the lowermost portion is briefly flooded each spring by backwaters of the Ohio River.

A number of changes occur soon after the stream bends north-west toward Station VII. Tree cover again becomes dense and steep banks rise rapidly on either side of the creek. The situation is a reversal of the changes at Station IV. Station VII lies well within the flood plain of the Ohio River and the river deposits up to 1 m of mud and silt in this area each spring. The blanket of mud kills or drives out the normal stream inhabitants in the area. Much of the deposit that remains after the floodwaters recede is slowly eroded away during the remainder of the year. Station VIII is situated approximately 1335 m from the source, at a point where the stream is exposed to the full influence of atmospheric weather and frequently is inundated by the Ohio River.

METHODS

Chemical

The chemical analyses made in this study follow standard limnological procedures (ELLIS, WESTFALL & ELLIS, 1948; WELCH, 1948; RAINWATER & TATCHER, 1960). Percentage saturation of dissolved oxygen was determined from MORTIMER'S nomograph (MORTIMER, 1956). When the samples for chemical analysis were collected, the lowermost station accessible at the time was sampled first, and the sequence proceeded upstream. Excluding Station VIII, the entire series usually was collected within an hour after the first sample was taken. Samples were collected at approximately the same time of day throughout the study. Collections were made weekly at all stations, except II and VIII, from 1 February 1963 to 1 February 1964. All samples from a given series were analyzed by the same individual. On the basis of preliminary analysis, conditions at Station II were found to be similar to those at Station I, with the exception of the pH-carbon dioxide-carbonate complex. Station VIII was sampled according to the above schedule except during periods of inaccessibility due to high waters from the Ohio River. After 1 February 1964, the sampling frequency was reduced to bi-weekly intervals and Stations II, V, and VIII were dropped from the program.

Physical

Information on temperature was obtained from instantaneous readings, made at the various stations each time the creek was visited (usually at weekly intervals) and maximum and minimum measurements, also usually at weekly intervals, by recording thermometers buried in the stream at Stations I, IV, and VII. Temperature measurements were made at the same time water samples were collected.

On nearly all occasions, these measurements were made between 9: 30 and 11: 30 AM. The time elapsed between the measurement at Station VII and the last measurement, at Station I, rarely exceeded 1 hour and usually was nearer a half hour. Temperature measurements were taken near the water-streambed interface.

Rate of flow was determined at weekly intervals by the cork-float method over a 19-m reach-riffle section at Station IV; the values represent the mean of three measurements on each date. As estimates of mean discharge values from short-term studies are likely to be too high (MINCKLEY, 1963), modal values have been used for characterization of the prevailing discharge in Morgan's Creek.

The length of the stream, including all its windings, was determined by actual measurement. Substrate composition was determined by visual estimate. The classification of substrate particle size is that of CUMMINS (1962).

Biological

Standard samples of the benthos were collected bi-weekly from 15 February 1963 through 26 September 1964, but several collections are missing from the autumn and winter of 1963—1964. Samples from Stations III and IV on 23 November 1963 were improperly preserved and were discarded; logistical problems due to snow and ice cover on 21 December 1963 and 4 and 18 January 1964 made it impractical to collect at Stations II–VIII; II, V, VII, and VIII; and IV–VIII, respectively. Likewise, one entire series is missing for August 1964. No adjustment has been made in the values for Station VIII for times that a sample could not be obtained due to inundation of the area by the Ohio River. It is believed that most of the usual stream fauna was eliminated during such times. In February 1964, after a full year of sampling at bi-weekly intervals, the three 'atypical' stations (II, V, and VIII) were dropped from the sampling program. Recolonization of the sampled area was assumed to occur within the two-week interval (see MOON, 1940; WATERS, 1964).

Collections were taken with a triangular pond net with a mesh size of 24 threads per cm. The particular mesh size was chosen to overcome difficulties encountered by MACAN (1958, 1963) and HYNES (1960, 1961) for coarse (6—10 threads per cm) and fine (40—80 threads per cm) mesh nets. Both HYNES and MACAN noted that the coarse netting misses nearly all tiny animals and many fairly small ones, whereas the fine netting fails to retain many individuals 6—7 mm and over.

In practice, the net was held vertically against the streambed and the area immediately upstream was agitated by kicking and scraping with the feet. Sampling proceeded in an upstream direction and continued for 5 minutes. All samples were collected by the same individual. These data were supplemented by qualitative collections and observations of the fauna in the major tributaries and in the mainstream. Qualitative samples from the mainstream were collected at least bi-weekly and often more frequently. On two occasions (19 July 1963 and 17 July 1964) data were obtained which permit a rough estimate of the area covered by a 5-minute sample of each of the stations. The approximate areas (m^2) covered at Stations I (6.1, 5.5), III (7.7, 6.1), IV (5.7, 5.1), V (6.0, —), and VI (5.2, 4.8) agree reasonably well. The estimate for Station II (0.8, —) is appreciably smaller than any of the other samples, whereas the areal estimates at VII (14.9, 13.3) and VIII (13.1, —) are considerably higher than the others.

The sampling method was not very effective in the capture of crayfishes or the stone-cased Trichoptera. Individuals of both species of crayfishes were able to avoid the net, and no attempt was made to sample specific habitats these animals were known to prefer. The stone cases of *Glossosoma intermedium* and *Neophylax autumnus* increased the weights of these animals and many remained on the bottom rather than being swept into the net. The substrate at Station I is largely unaltered bedrock and offered no major interference to the collection of individuals of these species, but at the remaining stations many fell between the stones and thus escaped the sampling net.

With few exceptions immature forms of the insects were named by association with their respective adult stage. Terrestrial adults were obtained by various means, including collections from along the stream bank and rearing of larvae or mature nymphs to the adult stage, both in the stream and under near-constant temperature conditions (8—14°C) in the laboratory.

Results

Environment

Substrate

The principal inorganic substrate types in Morgan's Creek are rubble, bedrock, and sand (see Cummins, 1962 p. 495). The streambed at Station I is a limestone slab, which is free of loose rock except for a few boulders and a small amount of cobble. At Station II the substrate is chiefly unstable boulder and cobble-sized rubble; downstream the occurrence of larger stones becomes reduced. The bottom at Station III consists of a thin layer of cobbles and pebbles intermixed with some gravel and coarse sand. From Station IV through

VII the substrate is thicker and more compacted than at Station III and is predominantly loose, flat cobble- and boulder-rubble overlying a fairly stable base of coarse sand, gravel, and pebbles. At Station VIII, the substrate differs markedly from the rest of the creek, being of smaller grades of sand, silt, and clay, mixed with some plant debris.

Sedimentation ordinarily was limited to the reaches and pools, but even there the buildup seldom was extensive. An exception was the region below Station VIa, which periodically received heavy deposits of mud and silt from floodwaters of the Ohio River.

The most important source of organic substrate was allochthonous detritus, chiefly in the form of tree leaves. Higher plants were absent from the creek, and moss and filamentous algae had only a limited distribution. A number of authors have mentioned the significance of leaf packets in the distribution of benthic fauna (FRISON, 1935; BADCOCK, 1954a,b; MINCKLEY & COLE, 1963; and others), but to my knowledge only EGGLISHAW (1964) has attempted to measure this quantitatively and over an entire year. As could be expected, the amount of dead leaf material in Morgan's Creek varied seasonally. Concentrations were greatest during late autumn-winter, averaging 18—42 g dry weight per 5-minute sample, and were greatly reduced following spring rains. The lowest values occurred during the summer (average 1—6 g). The mean concentrations for Stations III and IV were appreciably higher than those for any of the other stations (about 20 g per year as compared with 8—16 g at I, II, V, VI, and VII; values for Station VIII never exceeded 1 g).

Water Movement

Current velocities at Station IV ranged from 9 to 84 cm/sec. The highest values (all 30 cm/sec or greater) prevailed throughout March of both 1963 and 1964. The best estimates of current velocity at the source and each of the riffle stations during modal flow are: 19 (I), 20 (III), 26 (IV), 27 (VI), and 35 (VII) cm/sec. Modal discharge was 0.007 m^3/sec. The greatest discharges occurred in March and major fluctuations continued through May (Fig. 3).

Major habitat types in Morgan's Creek were grouped on the basis of flow characteristics (cascade, riffle, reach, pool) and the predominant type of inorganic substrate (rubble, bedrock, sand). The predominant substrate-current combination is the rubble-riffle complex. About 83% of the stream has a rubble bottom and 79% has a riffle type of flow; 73% of the riffles have rubble bottoms.

Temperature

Temperatures at Station I were relatively constant throughout the study (range 9.8—14.0°C), (Fig. 4). At Station II, the only variations

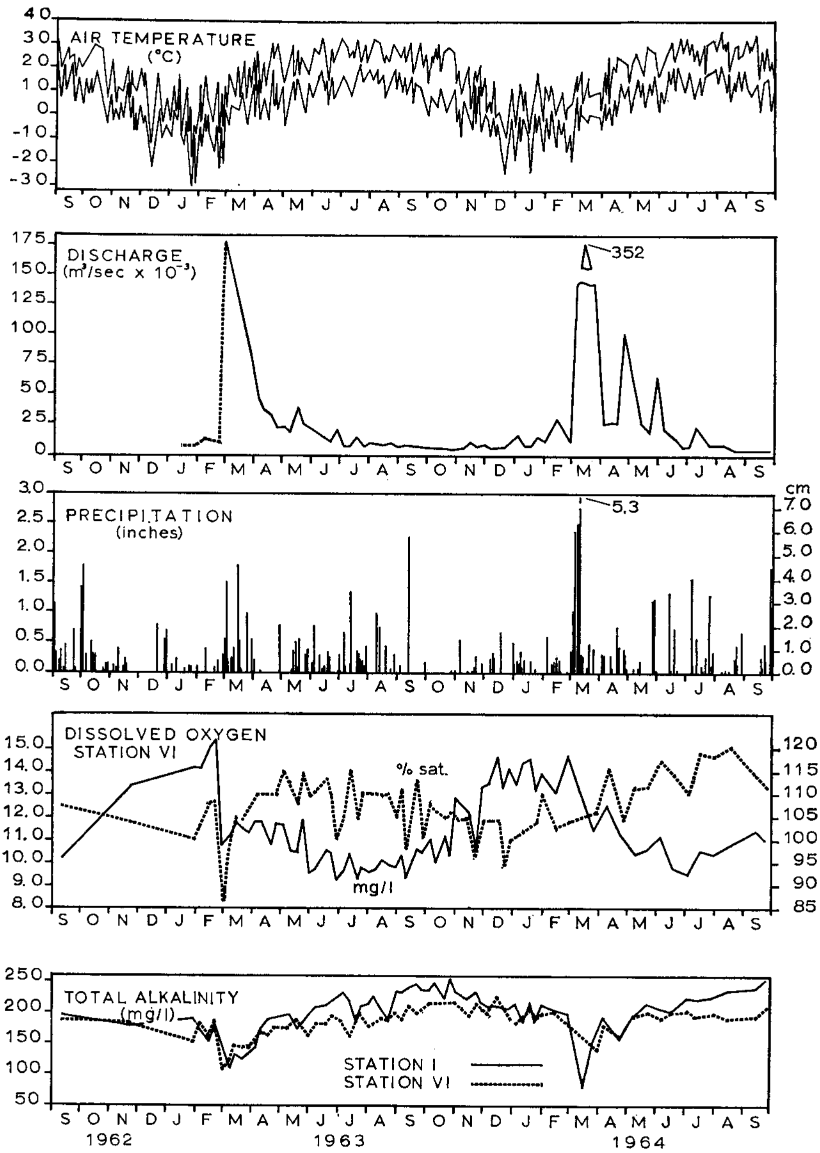


Fig. 3. Selected environmental features for Morgan's Creek: (a) air temperature maxima and minima from Evan's Landing, Indiana, 4.5 miles northeast of Morgan's Creek; (b) weekly measurements of discharge from Station IV; (c) daily precipitation values from Evan's Landing, Indiana; (d) weekly measurements of dissolved oxygen, in milligrams per liter and percent saturation, at Station VI; (e) weekly determinations of total alkalinity at Stations I and VI.

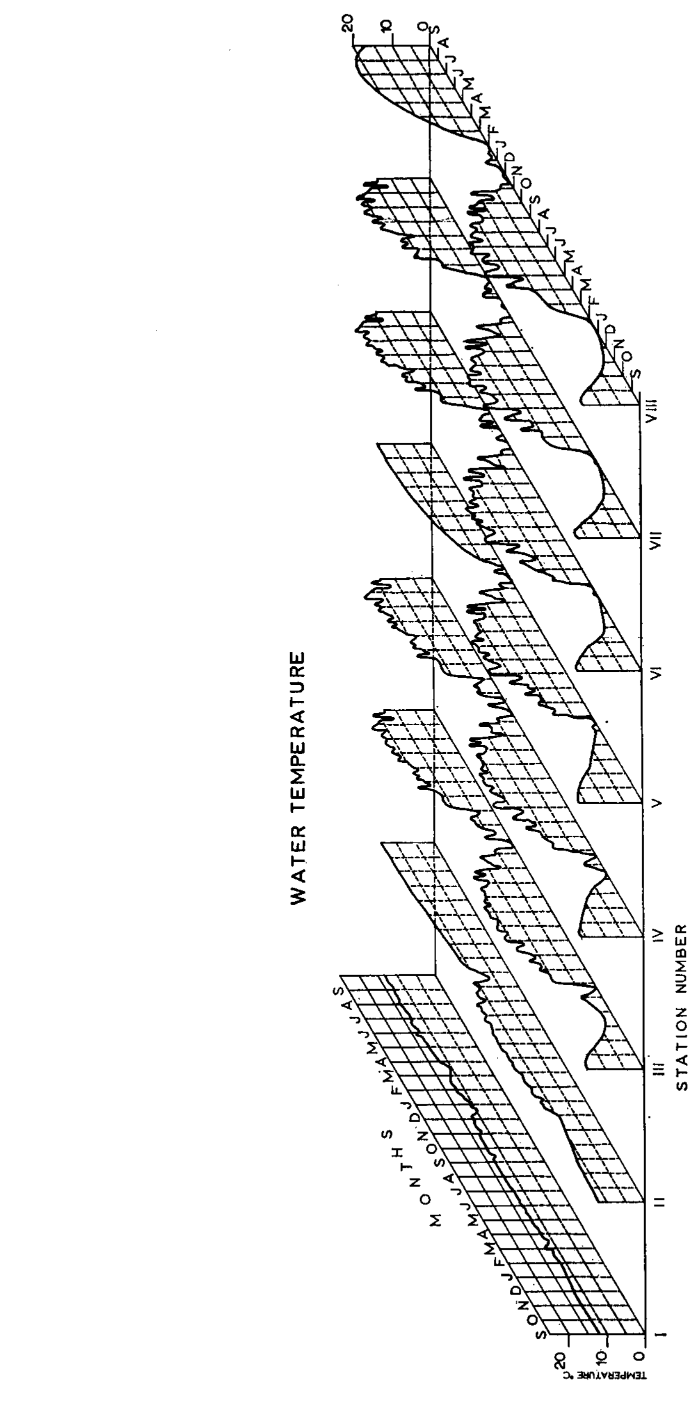


Fig. 4. Water temperature relationships in Morgan's Creek, based on instantaneous temperature readings.

were small to moderate and occurred during periods of air temperature extremes. Station III, because of its sheltered location, is insulated against rapid fluctuations during the summer. In the autumn, when the leaves are shed, the area becomes more susceptible to atmospheric variations. However, the proximity of Station III to the source and the narrowness of the valley help to maintain temperatures near 6°C during periods when temperatures at the lower stations are near 0°C. Temperature fluctuations at Stations IV—VIII followed those at Station III, except that there tended to be a depression of low-temperature fluctuations and an increase in the magnitude of summer variations. This trend reached a peak at Station VI and decreased slightly thereafter.

Freezing temperatures persisted much longer at Station VII than at Station IV. On two occasions (14—28 December 1963 and 11—18 January 1964), the temperature at Station VII remained at 0°C over the entire interval; this was never the case at Station IV. Ice seldom formed above Station IV. Near-zero temperatures rarely occurred at Station III; when they did, they were of short duration. Interestingly, the maxima for Stations IV and VII were the same in both 1963 and 1964; these were reached during the first week of August in both years. Station I was the coolest station from May through October, whereas from November through February it was the warmest.

One of the most striking features of the seasonal temperature pattern was the rather narrow limits in temperature fluctuation during any given interval. In general, maximum-minimum fluctuations at Station IV were within 5°C of each other, with the greatest variation (about 12°C) in April 1964. Thus the organisms at Station IV were subjected to rather small temperature variations within a given period and the transition from one season to another or from the annual maximum to the minimum was a gradual one. The variation at Station VII was somewhat greater, being more on the order of 7° to 10°C. The greatest range (15°C) was in August 1963.

Carbon dioxide, alkalinity, and pH

Values for free carbon dioxide in Morgan's Creek never surpassed 26 mg/l, while total alkalinity concentrations ranged from 88 to 255 mg/l (Fig. 5). Fluctuations in pH were confined to a relatively narrow range; the maximum and minimum at Station I were 8.1 and 7.2, respectively, and the variation at the remaining stations never exeeded 0.6 pH units. Low hydrogen ion concentrations occurred during the summer and persisted into October. There was no discernable decrease in pH in the autumn as might be expected if carbon dioxide production from decaying leaves were important (SLACK, 1955).

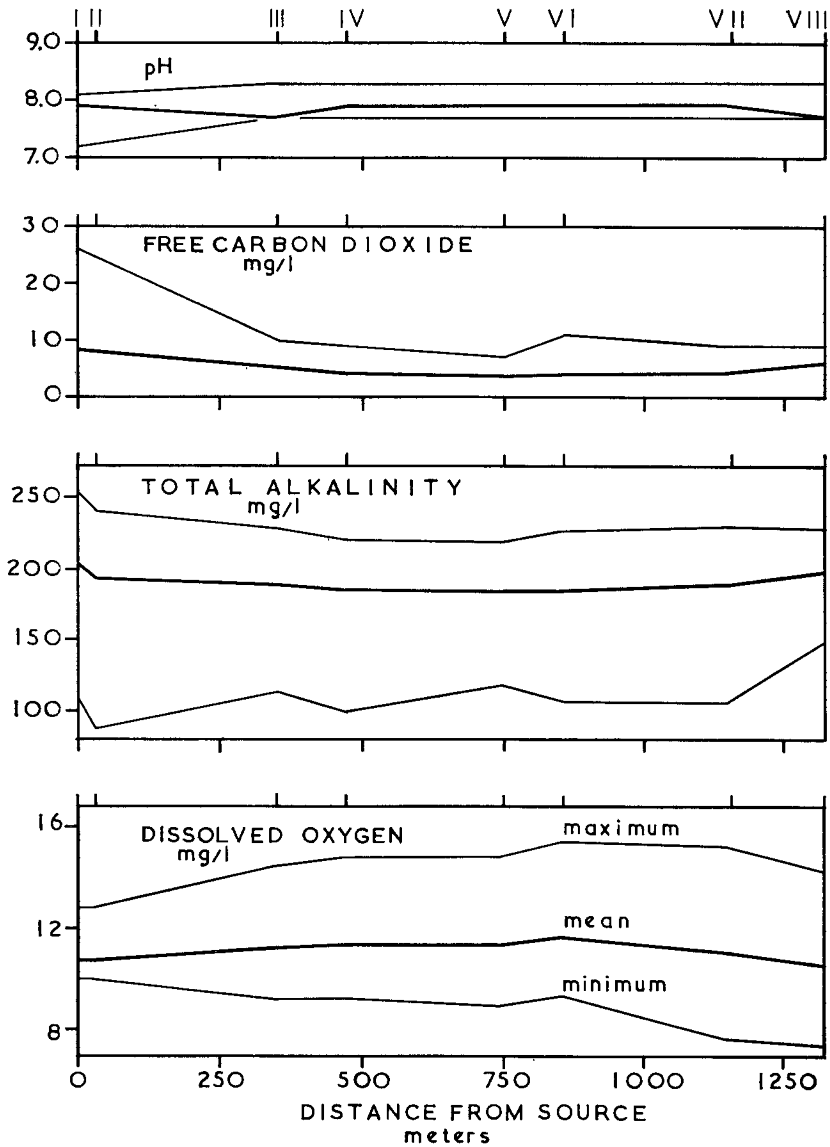


Fig. 5. Summary of longitudinal variations in pH, free carbon dioxide, total alkalinity, and dissolved oxygen for Morgan's Creek during the period 1 February 1963 through 1 February 1964.

The proximity of Station I to the underground source of Morgan's Creek explains most of the differences between that Station and the remainder of the creek as regards both free carbon dioxide and carbonates. Station I, on the average, has lower pH and higher free carbon dioxide and akalinity values than elsewhere in the stream. The loss of free carbon dioxide from the water as it passes Stations I and II accounts for the increase in pH and the decrease in alkalinity at Station III. Marl deposition at Station I and elsewhere also was related to the loss of carbon dioxide (see BACK, 1961).

Alkalinity data from Stations I and VI (Fig. 3) show the seasonal trends of this component. Similar patterns have been reported by GAUFIN (1959) for the Provo River, Utah, and NEEL (1951) for Boone Creek, Kentucky. The lowest values were obtained during periods of high discharge and undoubtedly were due to dilution by rainwater and the short period the water was in contact with the ground. Extremely high values occurred during September and October 1963. The same trend is indicated for the autumn of 1964, although complete data for that period are lacking. As with free carbon dioxide, fluctuations in alkalinity were most pronounced at Station I and leveled off at the downstream stations.

Dissolved oxygen

In Morgan's Creek, because of a large surface-to-volume ratio, relatively cool temperatures, and a predominance of turbulent flow, oxygen probably is never scarce (Fig. 5). However, factors other than oxygen concentrations per se, particularly the diffusion gradient (AMBÜHL, 1959; WHITFORD, 1960) and, indirectly, temperature and rate of flow (MACAN, 1963), may be important in determining the actual availability of oxygen. Dissolved oxygen concentrations, as measured during the regular sampling, rarely fell below 8.5 mg/l or 94% saturation. The lows for Stations VII and VIII are unusual; both were recorded on 7 June 1963. The seasonal trends of dissolved oxygen are illustrated by Station VI (Fig. 3). A similar, but more pronounced, seasonal pattern was noted by SLACK (1955) for two small streams in Indiana and by NEEL (1951) for Boone Creek.

Generally, the oxygen content of the water emerging from the cave was near saturation. This probably is due to the open nature of the cave system, which allows the water to achieve equilibrium with the air before it reaches the surface. In this respect Morgan's Creek differs from most other spring streams which have been studied. Silver Springs, Florida (35—60% saturation; data from ODUM, 1957), Root Spring, Massachusetts (25—65% saturation; TEAL, 1957), and Doe Run, Kentucky (70—85% saturation; MINCKLEY, 1963) are all unsaturated at their sources.

Fauna

Community composition

The invertebrate fauna is listed in Table I. For convenience the taxa are grouped according to abundance. Those which were taken only occasionally (Group III) are not considered further.

Three species of *Asellus* were found, two of which (*A. brevicaudus* and *A. intermedius*) were difficult to distinguish in the smaller instars. The data for these stages have all been included under *A. brevicaudus*. *A. intermedius* was never taken above Station VI; hence the data for Stations I through V refer strictly to *A. brevicaudus*. *A. brevicaudus* was the predominant form even where the ranges of the two overlapped. Of nearly 1500 *Asellus* collected in the 5-minute samples at Station VII, only 98 could be assigned to *A. intermedius*.

Gammarus minus was the predominant animal at every station except VIII. The bulk of individuals at Station I was concentrated into 9 taxa; yet more individuals were collected at Station I than from any other site in Morgan's Creek. In addition to *G. minus*, the most abundant groups were *Phagocata gracilis*, *Baetis amplus*, *Ochrotrichia unio*, and *A. brevicaudus*. On a percentage basis the number of taxa which were relatively important increased from 9 at Station I to 14 at Station II. The taxa which were abundant at Station I were also abundant at Station II, although the order of importance was somewhat different. *Epeorus pleuralis* was the most abundant of any except *Gammarus*. A notable decrease in total numbers occurred between the source and Station III, largely due to declines in the abundance of *G. minus*, *P. gracilis*, *B. amplus*, and *O. unio*; increases at Station III in practically every other taxon failed to offset the loss. Little further change in total numbers was noted between Stations III and IV. More taxa (31) were present at Station III than at any other collecting site, but the fauna at Station IV was only slightly less varied. Below Station IV, the diversity of persistent animals became progressively less and there were fewer individuals. Losses occurred in practically every taxon, but *Asellus* was a notable exception. The most pronounced decreases were registered for *P. gracilis*, many of the Ephemeroptera, and *Diplectrona modesta*. The number of taxa which contributed significantly to the total was reduced to 10 at Station VI; only 6 of the 26 taxa present at Station VII were numerically important. The impact on the totals, of the reduction in numbers of most of the stream inhabitants, was lessened at Station VII by increases in numbers of Tubificidae and Diptera (especially Tendipedidae).

The pool at Station V supported fewer individuals than any riffle station, but Station VIII had the most depauperate fauna of any collecting site. Likewise the species composition of both stations was

TABLE I

Invertebrate fauna of Morgan's Creek: total numbers[1] collected in the regular 5-minute samples, 15 February 1963 through 1 February 1964. Taxa for which no totals are given were collected at some other time during the study or were taken only in qualitative collections.

	I	II	III	IV	V	VI	VII	VIII	TOTAL
I. Abundant and rarely absent from any catch made at an appropriate time of the year.									
Gammarus minus SAY	51019	16202	28194	43333	3584	39566	1534	0	183432
Asellus brevicaudus FORBES	1511	390	1284	1977	1204	2871	518	15	9770
Phagocata gracilis (HALDEMAN)	3484	335	791	1441	107	526	22	0	6706
Tendipedidae[2]	409	135	1209	962	302	634	1897	298	5846
Baetis amplus TRAVER	3067	430	4	10	0	0	0	0	3511
Tubificidae	5	1	17	219	148	166	1478	921	2955
Ochrotrichia unio complex (ROSS)	2228	130	15	3	0	0	1	0	2377
Epeorus pleuralis (BANKS)	101	980	544	247	0	88	5	0	1965
Diplectrona modesta BANKS	7	48	1363	412	0	117	16	0	1963
Baetis herodes BURKS	2	2	732	204	196	184	166	2	1488
Simulium spp. (at least 2 species)	249	637	65	21	0	5	27	0	1004
II. Common: taken regularly though rarely or never in large numbers.									
Antocha saxicola OSTEN SACKEN	355	39	83	11	1	2	0	2	493
Centroptilum rufostrigatum McD.[3]	0	0	189	78	95	17	37	0	470
Rhyacophila parantra ROSS	72	44	180	54	0	1	0	0	351
Paraleptophlebia moerens McD.	1	4	62	52	146	53	0	0	318
Orconectes rusticus rusticus (GIRARD)	0	0	28	78	49	122	5	0	282
Neophylax autumnus VORHIES	11	5	89	62	0	8	5	0	180
Isoperla clio (NEWMAN)	0	0	76	48	25	25	3	0	177
Cambarus tenebrosus HAY	27	6	33	52	25	30	2	0	175
Pseudocloeon carolina BANKS	0	1	97	55	0	4	11	0	168
Pericoma sp.	52	27	56	0	0	0	1	0	136
Dixa sp. (prob. *modesta* JOH.)	39	74	6	1	1	1	1	0	123
Ectopria sp.	0	1	52	45	8	13	1	0	120
Nigronia fasciata WALKER	0	1	40	15	2	9	6	0	73
Glossosoma intermedium (KLAPÁLEK)	42	7	11	2	0	0	0	0	62
Asellus intermedius FORBES	0	0	0	0	0	0	61	1	62
Baetis phoebus McD.[3]	0	1	10	22	0	0	21	0	54
Nemoura delosa (BANKS)	0	0	27	11	1	9	2	0	50
Sialis joppa LATREILLE	0	0	38	4	2	0	1	0	45
Isogenus decisus WALKER	0	0	13	21	2	6	1	0	43
Leuctra sibleyi CLAASSEN	0	0	15	12	3	8	0	0	38
Allocapnia rickeri FRISON	0	0	0	0	0	7	24	0	31
Nemoura vallicularia WU	0	17	2	0	0	0	0	0	19
Subtotal (less *Gammarus*)	11662	3315	7131	6119	2317	4906	4312	1239	41055
Total	62681	19517	35325	49452	5901	44472	5846	1239	224487

III. Rare.

Phagocata morgani (STEVENS & BORING) | *Dineutus* sp. | *Euparyphus* sp.

Lumbricullidae | *Pycnopsyche* sp. | *Stratiomys* sp.

Dixa sp. (prob. *modesta* JOH.)	39	74	6	1	1	1	1	0	123
Ectopria sp.	0	1	52	45	8	13	1	0	120
Nigronia fasciata WALKER	0	1	40	15	2	9	6	0	73
Glossosoma intermedium (KLAPÁLEK)	42	7	11	2	0	0	0	0	62
Asellus intermedius FORBES	0	0	0	0	0	0	61	1	62
Baetis phoebus McD.[3]	0	1	10	22	0	0	21	0	54
Nemoura delosa (BANKS)	0	0	27	11	1	9	2	0	50
Sialis joppa LATREILLE	0	0	38	4	2	0	1	0	45
Isogenus decisus WALKER	0	0	13	21	2	6	1	0	43
Leuctra sibleyi CLAASSEN	0	0	15	12	3	8	0	0	38
Allocapnia rickeri FRISON	0	0	0	0	0	7	24	0	31
Nemoura vallicularia WU	0	17	2	0	0	0	0	0	19
Subtotal (less *Gammarus*)	11662	3315	7131	6119	2317	4906	4312	1239	41055
Total	62681	19517	35325	49452	5901	44472	5846	1239	224487

III. Rare.

Phagocata morgani (STEVENS & BORING)
Lumbricullidae
Branchiobdellidae
Attheyella carolinensis CHAPPUIS
Asellus stygius (PACKARD) (15)
Isotomurus sp.
Stenonema interpunctatum (SAY) (6)
Gerris remigis SAY
Trepobates subnitidus ESAKI
Microvelia americana (UHLER)
Gelastocoris sp.
Sigara alternata (SAY)

Dineutus sp.
Pynopsyche sp.
Tipulidae (170)
Dicranota sp.
Hexatoma sp.
Limnophila sp.
Pedicia sp.
Tipula abdominalis (SAY)
Tipula trivittata
Tipula sp.
Atrichopogon websteri
Palpomyia sp.

Euparyphus sp.
Stratiomys sp.
Tabanus sp.
Hemerodromia sp.
Roederiodes sp.
Scatella sp.

Recorded as terrestrial adults only.
Rhyacophila carpenteri MILNE
Dolophilus moestus (BANKS)
Cyrnellus marginalis (BANKS)
Hydropsyche sp. (prob. *dicantha* ROSS)
Psychoda sp.

Recorded from tributaries only.
Ameletus lineatus TRAVER (Trib. IIb; common)
Argia sp., *Calopteryx* sp., *Caborius* sp. (drainage area adjacent to Station V)

1. Twenty-two sets of samples, each set from the same date at all eight stations. Data for 23 November and 21 December 1693 and 4 and 18 January 1964 were excluded in order to put all stations on a comparable basis. Periods during which Stations VII or VIII were flooded and could not be sampled were not excluded, since the inundation generally was accompanied by a complete removal of the stream benthos.
2. Includes *Corynoneura* sp., *Diamesa* sp., *Orthocladius* spp., *Paratendipes albimanus*, *Pentaneura decolorato*, *Pentaneura* sp., *Trissocladius* sp.
3. Abundant in 1964.

much less diverse than elsewhere in the stream. At Station V only 8 of the 19 taxa present were numerous enough to be considered important, whereas at Station VIII the abundant forms were concentrated into 2 of the 6 taxa.

Of 13 species of fish collected from Morgan's Creek, *Rhinichthys atratulus* (HERMANN) and *Semotilus atromaculatus* (MITCHILL) were the most characteristic, comprising about 45 and 15% of the total, respectively. *R. atratulus* inhabited the riffles, while *S. atromaculatus* was most abundant in the reaches and pools. Both *R. atratulus* and *S. atromaculatus* maintain breeding populations in Morgan's Creek. No fishes were present above Station III; species composition remained fairly simple downstream to Station V, the limit of upstream movement of migrants from the Ohio River. Of the other vertebrates collected from the stream, only the salamanders *Eurycea bislineata* (GREEN) and *Desmognathus fuscus fuscus* (RAFINESQUE) were common.

Life histories

A detailed account of the life history of *Epeorus pleuralis* (MINSHALL, J. N., 1967) and data on the growth and development of *Isogenus decisus* and *Isoperla clio* (MINSHALL & MINSHALL, 1966) are already published. Additional information on the life histories of most of the other abundant and common invertebrates in Morgan's Creek will be published later (see also MINSHALL, 1965). In order to simplify

TABLE II
Mean number[1,2] of individuals taken with a fine mesh net.

Seasonal		February	April	July	September
A. Species most abundant in spring (February—April)					
Asellus brevicaudus	1963	110	36	36	34
(Isopoda)	1964	185	14	46	63
Rhyacophila parantra	1963	11	4	∠1 (1)	1
(Trichoptera)	1964	8	4	1	3
Diplectrona modesta	1963	68	20	2	8
(Trichoptera)	1964	12	9	9	73
Isoperla clio	1963	6	∠1 (8)	0	∠1 (4)
(Plecoptera)	1964	4	∠1 (4)	∠1 (1)	7
Isogenus decisus	1963	2	∠1 (7)	0	0
(Plecoptera)	1964	∠1 (2)	∠1 (2)	0	0
Leuctra sibleyi	1963	2	∠1 (2)	0	0
(Plecoptera)	1964	∠1 (1)	∠1 (2)	∠1 (2)	∠1 (9)
Nemoura vallicularia	1963	0	∠1 (1)	0	0
(Plecoptera)	1964	0	0	∠1 (1)	0
Epeorus pleuralis	1963	33	30	0	0
(Ephemeroptera)	1964	1	14	0	0
Neophylax autumnus	1963	8	2	∠1 (4)	0
(Trichoptera)	1964	2	2	0	∠1 (1)

	Seasonal (cont.)		February	April	July	September
Short Seasonal Cycles	*Allocapina rickeri*	1963	1	0	0	0
	(Plecoptera)	1964	4	0	0	0
	Nemoura delosa	1963	∠1 (2)	4	0	0
	(Plecoptera)	1964	0	2	0	0
	Pseudocloeon carolina	1963	∠1 (2)	12	∠1 (1)	0
	(Ephemeroptera)	1964	0	9	∠1 (2)	∠1 (1)
	Baetis amplus	1963	5	209	4	∠1 (7)
	(Ephemeroptera)	1964	∠1 (3)	138	13	1
	Paraleptophlebia moerens	1963	4	8	0	0
	(Ephemeroptera)	1964	∠1 (3)	∠1 (7)	4	0
	Ochrotrichia unio	1963	10	112	1	0
	(Trichoptera)	1964	0	29	∠1 (1)	∠1 (1)
	Simulium spp.	1963	6	20	2	∠1 (3)
	(Diptera)	1964	∠1 (1)	29	8	2
	B. Species most abundant in summer (July—September)					
Long Seasonal Cycles	*Orconectes rusticus*	1963	∠1 (2)	1	3	2
	(Decapoda)	1964	∠1 (7)	∠1 (1)	8	4
	Cambarus tenebrosus	1963	∠1 (4)	∠1 (8)	1	3
	(Decapoda)	1964	∠1 (11)	∠1 (3)	∠1 (1)	∠1 (5)
	Nigronia fasciata	1963	∠1 (3)	∠1 (3)	∠1 (9)	∠1 (5)
	(Megaloptera)	1964	∠1 (2)	∠1 (1)	2	∠1 (2)
	Sialis joppa	1963	∠1 (1)	0	∠1 (3)	1
	(Megaloptera)	1964	∠1 (7)	0	1	∠1 (9)
	Glossosoma intermedium	1963	0	0	2	∠1 (2)
	(Trichoptera)	1964	∠1 (3)	0	∠1 (3)	0
	Pericoma sp.	1963	0	2	2	0
	(Diptera)	1964	0	∠1 (1)	4	∠1 (3)
	Centroptilum rufostrigatum	1963	0	0	1	1
	(Ephemeroptera)	1964	0	0	25	18
	Baetis phoebus	1963	0	∠1 (2)	∠1 (6)	∠1 (4)
	(Ephemeroptera)	1964	0	∠1 (7)	36	13
	Non seasonal					
	Gammarus minus	1963	1214	1333	1295	945
	(Amphipoda)	1964	2450	620	1740	2420
	Phagocata gracilis	1963	55	37	32	71
	(Turbellaria)	1964	92	43	68	86
	Baetis herodes	1963	43	29	1	1
	(Ephemeroptera)	1964	11	3	71	120
	Ectopria sp.	1963	1	2	0	∠1 (3)
	(Coleoptera)	1964	2	∠1 (5)	7	5
	Antocha saxicola	1963	12	8	6	∠1 (1)
	(Diptera)	1964	4	2	4	1
	Dixa sp.	1963	∠1 (2)	∠1 (5)	∠1 (1)	∠1 (2)
	(Diptera)	1964	∠1 (13)	0	∠1 (1)	∠1 (2)
	Tubificidae	1963	∠1 (3)	2	37	5
	(Oligochaeta)	1964	26	2	6	3
	Tendipedidae	1963	90	143	20	7
	(Diptera)	1964	45	127	78	145

1. Mean number = total numbers per 5-minute sample from Stations I, III, IV, VI, and VII ÷ number of collections taken during the month. The number of collections was 5, 10, 10, and 10, respectively for 1963, and 15, 9, 15, and 10 for 1964.
2. When the mean is less than 1 (∠1), the total number collected is given in parenthesis.

treatment of the data for the present purposes, the abundant and common species (excluding *Asellus intermedius*) have been arranged according to the time of year in which they were most abundant (Table II). Mean values were used to adjust for differences in the frequency of collections during the various months.

The benthic invertebrates were divided into two major categories, depending on whether or not they show seasonal changes in abundance (see HYNES, 1961). Those which possess such seasonal cycles were further separated, on the basis of season of greatest abundance, into spring (A) and summer (B) fauna. The first nine species in Group A exhibit extended seasonal life cycles ('slow seasonal cycles' of HYNES), in which the hatching period is relatively long and growth is slow and continues over a long period. The remainder have short life cycles (HYNES' 'fast seasonal cycles'), in which growth is rapid and, in general, the hatching period relatively short. All of those in Group A, except *Asellus brevicaudus*, which spends its entire life in the stream, and *Neophylax autumnus*, which aestivates beginning in June, emerge or pupate in the spring of the year. (*Baetis amplus* also has a secondary period of emergence in the autumn). Species in Group B all have long seasonal cycles. *Orconectes rusticus* and *Cambarus tenebrosus* complete their entire life cycles in the stream; *Nigronia fasciata*, *Sialis joppa*, and *Glossosoma intermedium* pupate in early spring; the remainder pupate or emerge in summer or early autumn. Taxa classed as nonseasonal showed no seasonal change in numbers and generally exhibited no seasonal change in size distribution. *Gammarus minus* and *Phagocata gracilis* clearly belong to this category. *Baetis herodes* apparently is an opportunist, which though possessing a definite seasonal cycle, was most abundant during different seasons in the two years.

Distribution

The longitudinal distribution of various taxa in Morgan's Creek is given in Fig. 6. *Pericoma* sp., *B. amplus*, *Ochrotrichia unio*, *G. intermedium*, *Rhyacophila parantra*, and *Nemoura vallicularia* essentially were restricted to the upper portion of the creek. Most of the others, except *Allocapnia rickeri*, had more extensive distributions; but *A. brevicaudus*, *G. minus*, and *Baetis herodes* were the only species found at all stations. Many species were absent or reduced in numbers in

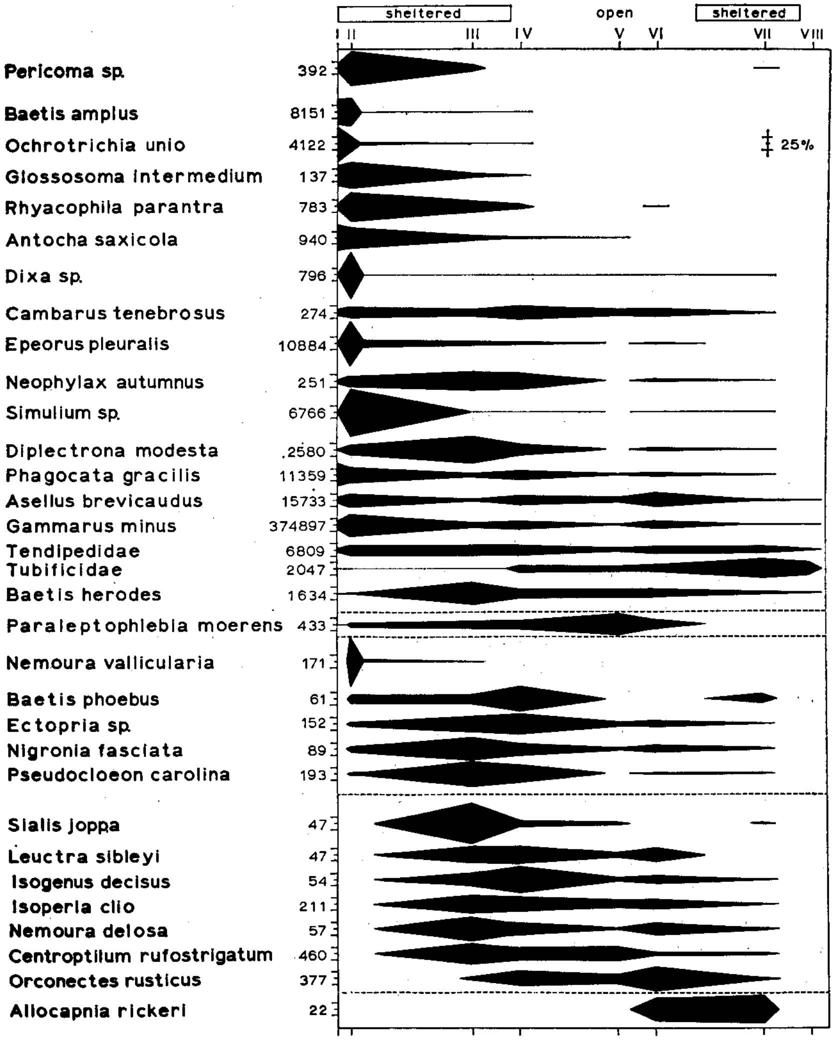


Fig. 6. Longitudinal distribution of benthic animals in Morgan's Creek. The width of the kite at each station indicates the percentage, as calculated from totals in Table I. As a further adjustment, all values were first converted to a comparable areal basis, relative to Station III. Thus, width of kite = (area covered per 5-minute sample at any station ÷ area covered at Station III) X totals from Table I. Numbers to the left of the figure are the sum of the adjusted values for all stations. Some interpretation, based on further collecting, has been made in regard to the extent and magnitude of the distribution within intervening sections.

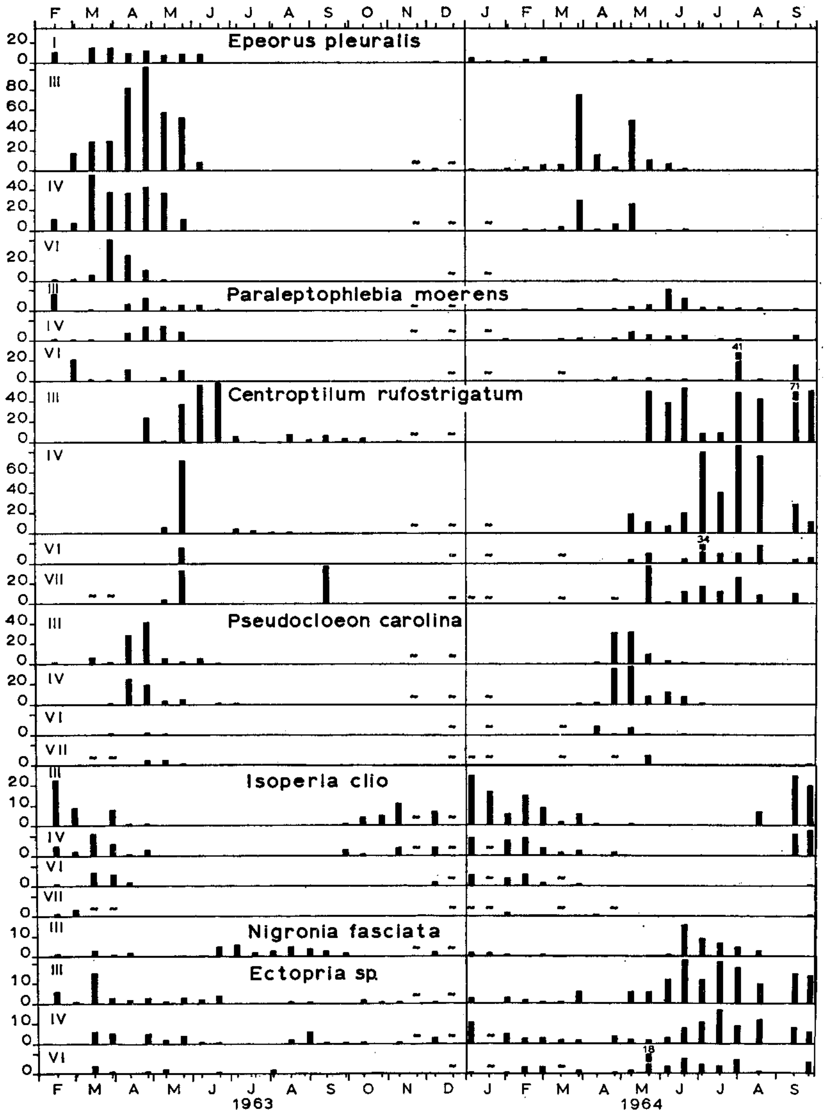
the pool habitat (Station V); only *Paraleptophlebia moerens* reached its greatest abundance at Station V. Station VIII was even less suitable; only five of the 32 taxa shown occurred there. It is noteworthy that all but one (*Allocapnia*) of the 32 taxa occurred together only at Station III, but only three taxa were absent from Station IV.

ANDREWARTHA & BIRCH (1954) emphasized the fact that distribution and abundance of animals generally are two aspects of a single phenomenon and pointed out that 'the study of abundance in different parts of the distribution is itself a study of the causes of rareness and commonness in species' (p. 665). Thus, in Fig. 6 variation in the width of each kite provides a measure of a species' reaction to conditions at the various stations. Presumably, the peak in an animal's abundance corresponds to the point at which conditions for it are most suitable, i.e., the 'optimum', relative to the range of conditions available. The position of these peaks for the various species is evident from the figure. The number of taxa with optima at the various stations are: I (3), II (9), III (9), IV (3), V (1), VI (1), VII (2), and VIII (0). *Cambarus tenebrosus*, *Asellus brevicaudus*, Tendipedidae, and *Leuctra sibleyi* were nearly equally abundant at several places along the stream.

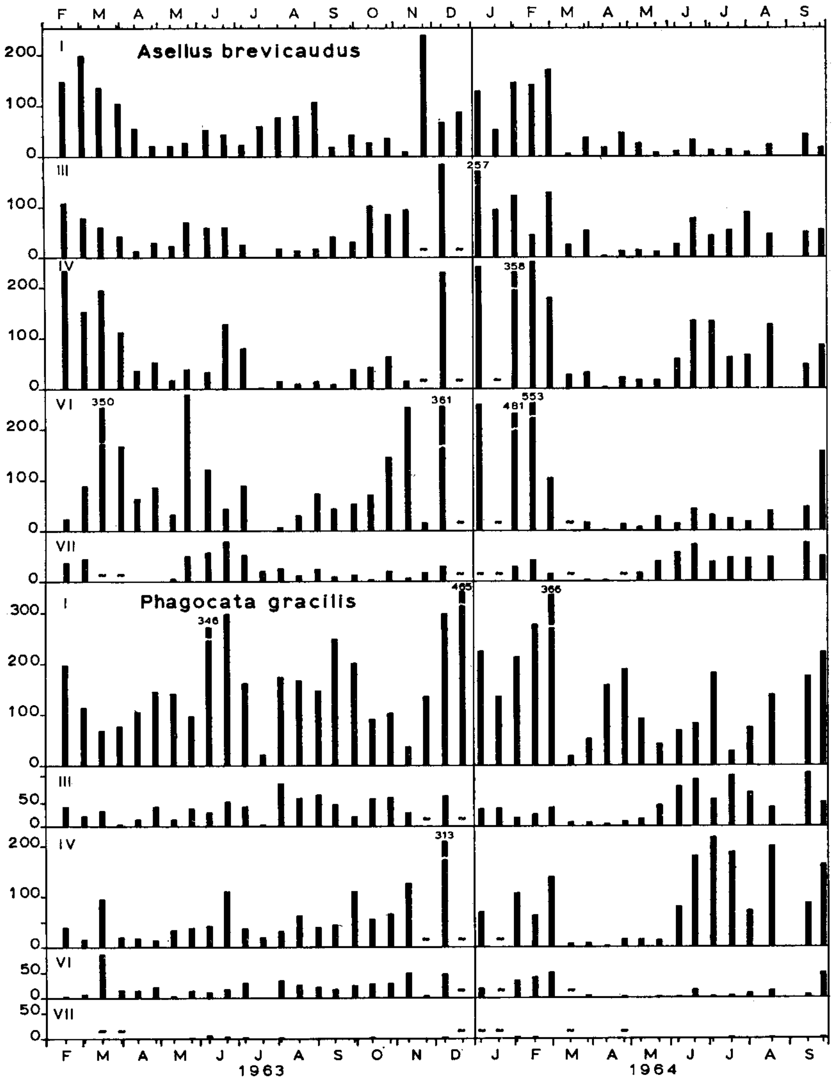
Seasonal variation in numbers for some of the more common species is shown in Fig. 7. The absence of Ephemeroptera in the summer of 1963 in contrast to the situation in 1964 is striking. Other members of the fauna present at the time showed similar but less obvious differences in the two summers. No satisfactory explanation for the summer 1963 low is apparent, but a similar situation was found when the stream was visited in the summer of 1965. Much of the fauna suffered large reductions in March of both 1963 and 1964, concurrent with abnormally high discharges (Fig. 3). During the three periods mentioned above the entire community was affected, indicating the operation of density independent factors rather than internal population controls. Many of the other changes are associated with life history phenomena, including, for the seasonal forms, initial appearance in the collections each year following hatching, population buildup due to recruitment of young, and a gradual decline in numbers as recruitment ceases and individuals die or mature and emerge from the stream.

Food

The food relationships of the fauna of Morgan's Creek are treated in greater detail elsewhere (MINSHALL, 1967). The main source of food for the herbivores is allochthonous leaf detritus; diatoms are the only other important source of plant material for the primary consumers. The Ephemeroptera, Tendipedidae, and *Asellus* are the



Epeorus pleuralis
Paraleptophlebia moerens
Centroptilum rufostrigatum
Pseudocloeon carolina
Isoperla clio
Nigronia fasciata
Ectopria sp.
F M A M J J A S O N D J F M A M J J A S
1963
1964



Asellus brevicaudus
Phagocata gracilis
F M A M J J A S O N D J F M A M J J A S
1963
1964
I
III
IV
VI
VII
200
100
0
300
50
350
361
257
358
481
553
346
465
366
313

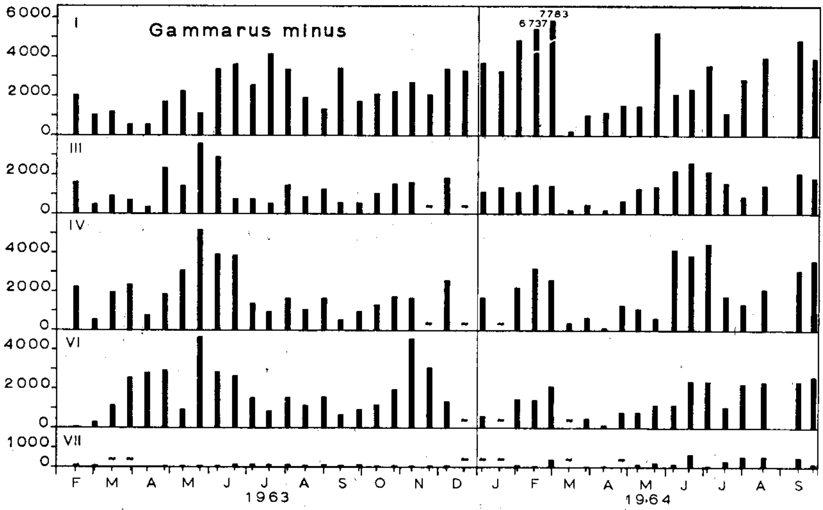


Fig. 7. Numbers per 5-minute sample for certain abundant and common benthic animals in Morgan's Creek. A ~ indicates no sample was taken.

principal herbivores; and although the omnivores *Gammarus minus*, *Cambarus tenebrosus*, *Orconectes rusticus*, *Diplectrona modesta*, and *Rhyacophila parantra* ate a variety of foods, the main part of their diet also consisted of detritus. Aside from fishes and salamanders, *Phagocata gracilis*, *Isoperla clio*, *Isogenus decisus*, *Nigronia fasciata*, *Sialis joppa*, and *Antocha saxicola* are the most important carnivores. Some differences were noted in the amount of plant material present at each of the stations, but these were not consistent with numerical differences in the fauna.

Discussion

Distribution in relation to environmental factors

With the exception of Station VIII, Morgan's Creek supports essentially a single community type, best typified by the relationship at Station III (Table I). The community at Station III is composed of numerous, relatively small populations, a situation which is indicative of a climax community (Engelmann, 1966). Also, Station III lies in one of the least disturbed portions of the valley, a wooded area much as it must have been before the coming of settlers. The significance of the latter lies in the fact that there appears to be a close relationship between the climatic factors determining the deciduous forest biome and those controlling the climax assemblages in small-stream communities (Ross, 1963).

Reduction of the vegetation along Morgan's Creek has created a number of changes, including an increase in the temperature variations and summer maxima, and the removal of much potential food in the form of fallen leaves. These changes are most noticeable below Station IV. Station IV is close enough to the uncleared section of the valley that it is not so much affected. However, below this point both species diversity and numbers of individuals begin to decline. Downstream from Station IV the community becomes one of increasing disclimax, the ultimate cause of which is the continued suppression of the riparian vegetation.

Variations within the basic community type in Morgan's Creek appear to result chiefly from an interplay of three environmental components: temperature, substrate, and flow. Similar conclusions for other streams have been reached by NEEDHAM (1930), IDE (1935), SPRULES (1947), BERG (1948), and others. Certain other factors such as pH, free carbon dioxide, alkalinity, and dissolved oxygen were present in concentrations which were both within the known limits of tolerance for freshwater macroinvertebrates in general and which did not vary importantly over the length of the creek. The influence of biotic factors is difficult to assess on the basis of present information; it is further obscured by the more pronounced effects of certain of the abiotic environmental factors.

The limitation of species at spring sources has been noted by a number of authors, including IDE (1935), SPRULES (1947), BERNER (1950), SLOAN (1956), and MINCKLEY (1963), and would seem to be related to the nearly constant environmental conditions found there. This could serve to limit all but those species whose developmental optima fall within these narrow limits of variation.

Of the environmental factors considered, only temperature and substrate limitations appear to offer a suitable explanation for the reduction in species diversity and increase in numbers of individuals at Station I. At Station II, where the substrate becomes rubble but the temperature and chemical conditions of the water remain closely comparable to those at Station I, the number of species comprising an important part of the total increases from 9 to 14 and total abundance per unit area shows a similar increase. Thus, the change from bedrock to rubble substrate appears to be the factor primarily responsible for the increase in species diversity and production between Stations I and II.

The importance of substrate as a basic factor determining the distribution of the benthic macrofauna has been emphasized by a number of investigators, including PERCIVAL & WHITEHEAD (1929),

TARZWELL (1937), LINDUSKA (1942), SMITH & MOYLE (1944), PENNAK & VAN GERPEN (1947), and SPRULES (1947). However, since the streambed in Morgan's Creek is predominantly rubble, differences due to this factor are not likely to be important over much of the stream. Specifically, Stations III, IV, and VI appear to have similar substrates and should be comparable in respect to this factor. Subtle or minor differences in faunal composition due to substrate may occur at these stations but were not detectable in the present study. In general, the effect of substrate appears to vary locally within Morgan's Creek and seems to be superimposed mainly on the temperature regime, which varies in a gradient along the stream.

The diversity of species and abundant assemblage of individuals occurring at Stations III and IV appear to be associated with changes in the temperature regime. Below Station II flow and substrate differences become less pronounced and temperature begins to play a more important role. In the upper part of the stream, temperatures favor the cool-water forms; further downstream they permit a diverse and numerically balanced fauna, and finally only the most hardy eurytherms.

A consideration of the season and location of greatest abundance for the benthic fauna in Morgan's Creek (Table III) helps to point out certain relationships in regard to temperature. The fauna appears to fall into three distinct groups: (1) cool forms — seasonal species restricted to the upper portion of the stream, (2) temperate forms – seasonal species with optima in the middle and lower portions of the stream, and (3) eurythermal forms – nonseasonal species with widespread distribution and seasonal species uniformly distributed over large sections of the stream (see also Fig. 6). The temperate forms may be further subdivided into (a) cool-temperate, those limited to a period when the temperature is relatively cool throughout the stream, and (b) warm-temperate, those active mainly during the summer. *Dixa* sp. and *Antocha saxicola* do not fit readily into the scheme but on the basis of distribution alone appear to be cool and cool-temperate forms, respectively. *Allocapnia rickeri* grows and emerges during the winter when the lower section of the stream, to which it is restricted, is at or near freezing. Consequently, it seems to be more a cold-water species.

The cool-water species might be expected to be most abundant at Station I and to decrease progressively downstream. Optima at Station II, rather than at Station I, perhaps best can be attributed to substrate differences as explained earlier. Interpretation of variations in the distribution of the temperate forms is more difficult. Theoretically these species can occur over much of the year at most of the stations; hence the influence of temperature as a limiting factor for

TABLE III

Summary of temporal and spatial distributions of invertebrates in Morgan's Creek, Kentucky, based on season and location of greatest abundance. See text for further explanation.

Distribution		Upper (I–II)	Middle (III)	Lower (IV–VI)	Uniform over large stretches
Seasonal	Spring	*Baetis amplus* *Epeorus pleuralis* *Nemoura vallicularia* *Ochrotrichia unio* *Rhyacophila parantra* *Simulium* sp.	*Diplectrona modesta* *Isoperla clio* *Neophylax autumnus* *Nemoura delosa* *Pseudocloeon carolina*	*Asellus intermedius* *Isogenus decisus* *Paraleptophlebia moerens*	*Asellus brevicaudus* *Leuctra sibleyi*
		↑ COOL FORMS ↓		↑ TEMPERATE FORMS ↓	
	Summer	*Baetis amplus* (2nd generation) *Glossosoma intermedium* *Pericoma* sp.	*Centroptilum rufostrigatum* *Nigronia fasciata* *Sialis joppa*	*Baetis phoebus* *Orconectes rusticus*	*Cambarus tenebrosus*
Non Seasonal		*Gammarus minus* *Phagocata gracilis*	*Baetis herodes*	*Ectopria* sp.	↑
				←	EURYTHERMAL FORMS

these species is less clear. However, since it is mainly the cool and cool-temperate forms which decline in abundance or disappear at the lower stations, it seems likely that the decrease in numbers and kinds of animals in the riffles between Stations IV and VIa is associated primarily with the greater temperature extremes and longer duration of high temperatures in this area.

Within the limits set by temperature, other factors may be expected to exert their influence. The absence or reduction in numbers of many species at Station V presumably is a reflection of the unsuitability of the pool habitat for normal stream species. However, certain groups, including *Cambarus tenebrosus*, *Orconectes rusticus*, *Baetis herodes*, *Paraleptophlebia moerens*, *Centroptilum rufostrigatum* and *Isoperla clio* are not so restricted by the absence of shallow, rapidly flowing water and elsewhere in the stream may be as successful in the reaches as in the riffles.

On the basis of temperature extremes alone, Station VII might be expected to maintain a community structure similar to that of Station VI or to show a slight additional decline in numbers. The marked decreases which actually occurred at Station VII are more explicable on the basis of periodic inundation and silt deposition by the Ohio River. A number of comparable situations are known (reviewed by CORDONE & KELLEY, 1961) in which the deposition of sediment in streams has resulted in the disruption of benthic animal populations. The differences in community structure at Station VIII largely are due to the sand-mud substrate and to frequent inundation by the Ohio River.

Effect of spate on the community

As shown previously some of the most pronounced decreases in total numbers of the benthic fauna occurred as a result of spates. This is particularly true of the abnormally high discharges in March 1964. Even though the discharge recorded on the day the benthos samples were collected (0.35 m^3/sec) was about 27 times that prior to the spate, the maximum discharge was actually much higher (ca. 1.7 m^3/sec) and probably occurred soon after the peak in rainfall, several days earlier (Fig. 3).

Actual population changes in response to the spate can be seen from Fig. 7. Additional information can be obtained from Table II by comparing the mean values for before (February) and after (April) the spate occurred. Of the animals listed in Group A, only *Asellus brevicaudus* was markedly reduced in abundance. Most of the species with long seasonal cycles decreased slightly or remained fairly constant, and only *Epeorus pleuralis* showed an increase after the flood. Those with short seasonal cycles managed to increase in numbers by

April in spite of the flood. As might be expected the high discharges had little effect on the fauna of Group B. Those species which were present at the time of the spate apparently were hardy enough or well enough protected to withstand the onslaught of the torrent. By virtue of their life cycles, the most vulnerable (and most abundant) stages of the animals in this group usually are not present during March.

The nonseasonal fauna were the most grieviously affected by the spate. The Tendipedidae were the sole exception, probably due to the inclusion of several species within the taxon; losses suffered by one group are masked by increases in other, later-growing forms. The most serious losses were sustained by *Gammarus minus* and *Phagocata gracilis*. The magnitude of these changes is well illustrated by Fig. 7, which also provides an insight into the recovery of the populations from the effects of the flood. The initial increase in numbers following the spate probably reflects the return of animals to the main stream areas from refuges in the pools and along the edges of the stream. Thereafter, the populations slowly and steadily began to recover. With *G. minus* the peak in numbers apparently was reached in late June-early July. Although only adults were present in collections taken during the spate, young and juvenile *G. minus* made up 18% of the population by May and 41% in early July, indicating that recovery was due mainly to recruitment of young. In contrast, *Asellus brevicaudus* showed some recovery following the spate, but its numbers remained comparatively low thereafter. Presumably these responses reflect differences in the ability of nonseasonal and seasonal species to recover from density independent catastrophes.

Unusually high discharges differ from the other environmental factors discussed above in that they are not restricted to local or longitudinal variations but affect the entire stream in a similar way over its whole length. NELSON & SCOTT (1962) considered discharge the principal physical factor limiting the biomass of the benthos at any one time. To a large extent this was true also for Morgan's Creek, especially because of the marked effect of high discharge on the *Gammarus* population (see also MINCKLEY & COLE, 1963). Heavy runoff, which typically recurs during the first part of each year and sporadically at other times, results in large and widespread changes in population density over the entire stream. However, the effect is not permanent and recovery is relatively rapid. SPRULES (1947) detected a similar reduction in animal numbers following heavy runoff but noted that the effect was minimized in areas where the bottom was relatively stable and composed of materials large enough to provide shelter.

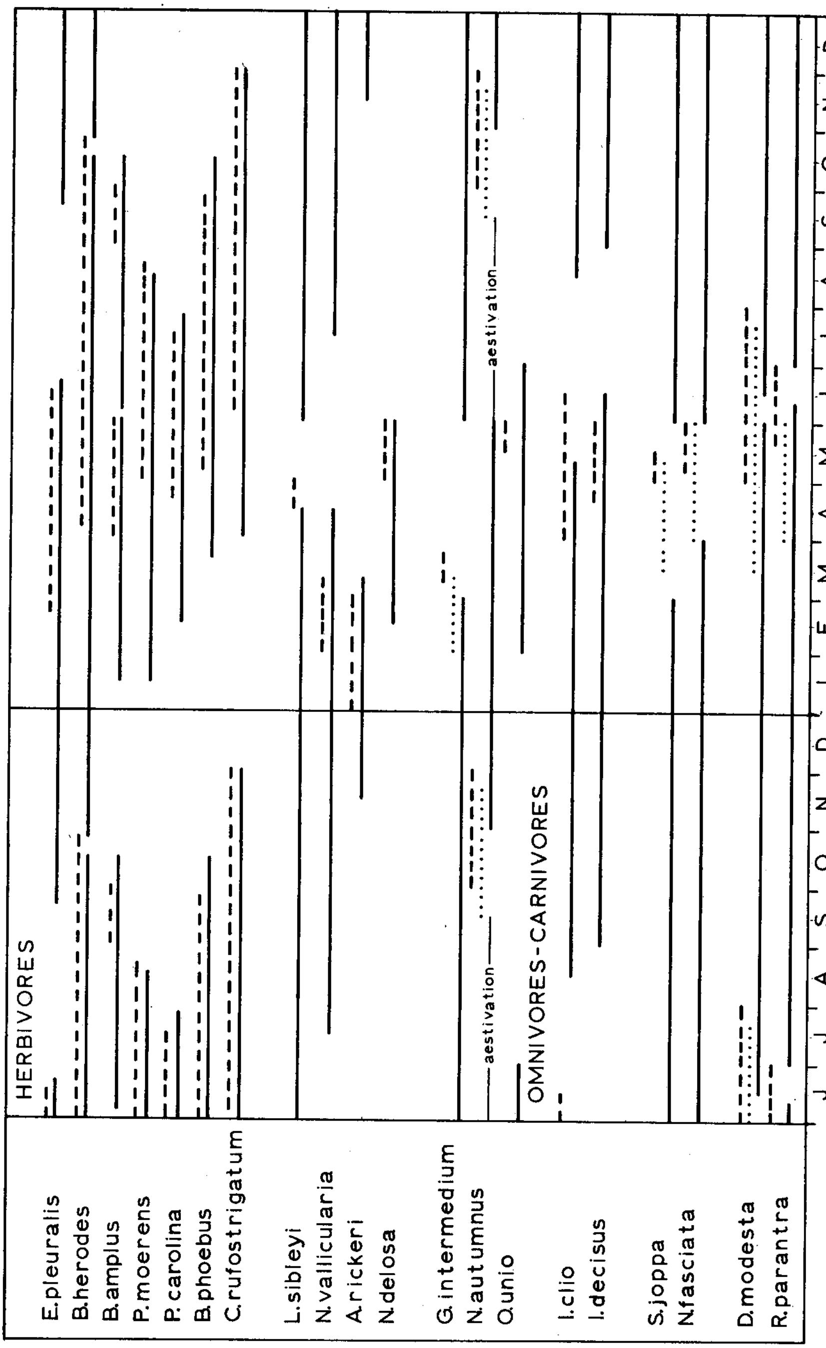


Fig. 8. Summary of life history information for selected species in Morgan's Creek. The presence of nymphs or larvae is indicated by a solid line, pupae by a dotted line, and adults by a dashed line.

Apparent coexistence of related species

In the benthic community of Morgan's Creek there are a number of potentially competitive species which apparently coexist. The Ephemeroptera, Plecoptera, and Trichoptera particularly are represented by several species each, which, in addition to being rather closely related, have similar niches. Even within these groups there is considerable isolation in time (Fig. 8), notably during the early stages of development. Thus, competition between the young of the various species largely is prevented by a staggering of their life cycles. Similar conclusions were reached for the crayfishes *Orconectes rusticus* and *Cambarus tenebrosus* (PRINS, 1965; MINSHALL, 1965). Such succession in time may be coupled with size differences and habitat preferences to yield pronounced niche specificity (HUTCHINSON, 1964) In particular, the combination of seasonal succession, food habit differences, and microhabitat preferences appears to appreciably reduce competition in these situations (see FRISON, 1935; HYNES, 1961; MAYR, 1963).

Differences in spatial distribution are a further means by which isolation can take place. While such separation is not complete (Fig. 6), the optima of the species frequently do not coincide and probably reflect the relative ability of the species to compete or coexist under the different conditions prevalent at each station.

A partial longitudinal division exists among the herbivorous Plecoptera in Morgan's Creek in which *Nemoura vallicularia* and *N. delosa* occur together at the source and coexist with *Leuctra sibleyi* at Station III. *N. delosa* and *L. sibleyi* are the only two at Stations IV and V and occur together with *Allocapnia rickeri* at Stations VI and VII. *N. delosa* occupies areas of rocky substrate, whereas *N. vallicularia, L. sibleyi*, and *A. rickeri* are found among dead leaves. Competition between the two species of *Nemoura* is reduced by differences in their spatial distribution as well as by a staggering of their life cycles. Their seasonal and longitudinal distributions, in turn, seem to be related to differences in temperature tolerance, since *N. delosa* occurs in warmer parts of the stream and times of the year than does *N. vallicularia*. Likewise, although *L. sibleyi* and *N. delosa* have similar distribution patterns, they are separated from one another in the timing of their life cycles and by differences in substrate preference. *A. rickeri*, the most abundant plecopteran in the lower stretches of Morgan's Creek, is able to grow and emerge during a period unsuitable to the two other species which overlap its range.

The two carnivores, *Isogenus decisus* and *Isoperla clio*, are similar in a number of respects in addition to their consumer role. Superficially they closely resemble one another and both occupy the same stretches of stream at the same time of the year. It is not known how competition is avoided between these two species, although on the basis of numbers *I. clio* appears to be the more successful of the two. The initiation of its life cycle one to two weeks ahead of that of *I. decisus* may give it the necessary head start to predominate throughout the year (MINSHALL & MINSHALL, 1966). Perhaps also, the two inhabit different microhabitats as illustrated by the different locations of their optima and by differences in their ability to maintain populations in non-turbulent areas such as Station V.

All of the Ephemeroptera are herbivores. While *Baetis amplus* and *Epeorus pleuralis* numerically were the only important members in the headwater region, all eight species occurred at Stations III, IV, and VI and all except *B. amplus* were collected at Station VII. *Baetis herodes* and *Centroptilum rufostrigatum* were the only mayflies abundant at Station VII. Significantly, they also were two of the three species found at Station V (along with *Paraleptophlebia moerens*) and the only mayflies found at Station VIII.

B. amplus lives in rapidly flowing water in areas of bare bedrock; *E. pleuralis* also is found in the fastwater areas, but in regions of loose, rubble substrate (MINSHALL, J. N., 1967). Thus, the microhabitats of the two are mutually exclusive. *Baetis phoebus* lives in riffle areas, while *C. rufostrigatum*, and perhaps also *B. herodes*, is known to frequent the reaches and other less turbulent areas of the stream. *Paraleptophlebia* and *Pseudocloeon* also occupy different microhabitats. The former is found chiefly in the slow, silt-covered parts of the stream; the latter, in rapidly flowing water.

The Trichoptera were numerically important only above Station IV. Not only did all five species occur in the same general area, but they also were present during the same time of the year. *Diplectrona modesta* and *Rhyacophila parantra* were present throughout the study period, but *R. parantra* was reduced in numbers during the summer. The remaining species, *Glossosoma intermedium*, *Ochrotrichia unio*, and *Neophylax autumnus*, were most active in the stream during winter and spring.

O. unio was abundant only at Station I, where it lived within the moss in swift-water areas. This microhabitat was not occupied by any other species of Trichoptera in Morgan's Creek. *G. intermedium* and *N. autumnus* both live in stone cases on the exposed surfaces of the streambed. *N. autumnus* appears to frequent the swifter portions of the stream, where diatoms are abundant, whereas *G. intermedium*, which has a bulkier case, seems to prefer the slower waters, where detritus is more abundant. *R. parantra* and *D. modesta* are free-living species which reside on the undersides of large stones. Both species are omnivores, but not enough is known about their habits to permit differentiation of their niches.

Summary

The benthic macrofauna of a woodland springbrook, Morgan's Creek, Kentucky, was studied between February 1963 and September 1964 at eight collecting sites. The basic habitat type of the stream is a rubble-riffle complex. Four stations (III, IV, VI, and VII) were located in riffle sections at different points along the stream and additional stations were established at the spring source (I), a cascade area (II), a pool (V), and a reach at the mouth of the stream (VIII).

A total of 33 taxa were studied in detail, 30 of which were at the species level. *Gammarus minus* was the most abundant benthic macroinvertebrate in the stream. It made up 82% of the 224,400 organisms collected during the first 12 months of the study. The next most abundant species were *Asellus brevicaudus*, 4.4%; *Phagocata gracilis*, 3.0%; *Baetis amplus*, 1.6%; *Ochrotrichia unio*, 1.1%; *Epeorus pleuralis*, 0.9%: *Diplectrona modesta*, 0.9% and *Baetis herodes*, 0.7%.

Although the largest number of animals per standard (5-minute) sample was collected at Station I, the greatest density (expressed as numbers per unit area covered by a sample) actually occurred at Station II (32,370 /m^2). The remaining stations ranked as follows: I (13,160/m^2), IV (11,050/m^2), VI (10,820/m^2), III (5890/m^2), V (1260/m^2), VII (490/m^2), and VIII (120/m^2), for the period 15 February 1963 through 1 February 1964.

Information on life histories, based on differences in seasonal abundance and the duration of the life cycle, is summarized for 32 species. Of these, 24 were seasonal in occurrence and had relatively long life cycles. Two-thirds of the seasonal forms were autumn-spring growers, rather than summer growing forms.

The community organization of Morgan's Creek was examined from the standpoint of species diversity and total numerical variations at each station. The situation at Stations I and II is typical of communities existing under strongly limiting conditions. The greatest diversity of invertebrates, as well as a relatively abundant number of individuals, was found at Stations III and IV, indicating a probable climax situation in this area. Both species diversity and total numbers of individuals showed marked decreases below Station IV; this was attributed to the removal of forest cover in this region. The most important effect of the removal was the alteration of temperature conditions in the stream. However, since terrestrial leaf detritus was shown to be the most important source of plant material eaten by the herbivores, removal of the riparian vegetation could, under more severe conditions, cause the depletion of primary food supplies essential to the maintenance of the woodland stream community.

The environmental factors: water movement, temperature, carbon

dioxide, alkalinity, hydrogen ion concentration, and dissolved oxygen were measured throughout the study. The abundance and distribution of the animals are examined in relation to these components and to that of substrate. It is concluded that temperature, substrate, and water movement are among the most important factors in Morgan's Creek.

High discharge following a March spate severely devastated the fauna but had little lasting effect on the community. Species with short life cycles were able to recoup their losses quite rapidly and showed an increase in numbers soon after the flood; those with long life cycles were more seriously affected and decreased in numbers or only managed to maintain themselves following resumption of more normal discharge. The nonseasonal fauna showed the greatest decreases in numbers as a result of the spate, but their recovery was faster than for species with long seasonal cycles.

A number of closely related species, with the same basic food niche, apparently coexist in Morgan's Creek. Competition between these species is avoided through the interplay of differences in microhabitat preferences and spatial and temporal distribution patterns.

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Literature cited

AMBÜHL, H. - 1959 - The importance of flow as an ecological factor. Physical, biological, and physiological investigations on the nature and effect of current in flowing waters. (In German, English summary). *Schweiz. Z. Hydrol.* 21: 133–264.

ANDREWARTHA, H. G. & BIRCH, L. C. - 1954 - The distribution and abundance of animals. Univ. Chicago Press, Chicago. 782 p.

BACK, W. - 1961 - Calcium carbonate saturation in ground water, from routine analyses. *U.S. Geol. Surv. Water-Supply Paper* 1535-D. 14 p.

BADCOCK, R. M. - 1954a - Studies of the benthic fauna in tributaries of the Kävlinge River, Southern Sweden. Inst. Freshwater Res., *Drottningholm. Rept.* 35: 21–37.

BADCOCK, R. M. - 1954b - Comparative studies in the populations of streams. *Ibid.* 35: 38–50.

BERG, K. - 1948 - Biological studies on the River Susaa. *Folia limnol. scand.* 4: 1–318.

BERG, K. - 1951 - Notes on some large Danish springs. *Hydrobiologia* 3: 72–78.

BERNER, L. - 1950 - The mayflies of Florida. *Univ. Florida Studies, Biol. Sci. Ser.* 4: 1–267.

BROWN, R. F. & LAMBERT, T. W. - 1962 - Reconnaissance of groundwater resources in the Mississippian Plateau region, Kentucky. *U.S. Geol. Surv. Water-Supply Paper* 1603. 59.p.

CORDONE, A. J. & KELLEY, D. W. - 1961 - The influence of inorganic sediment on the aquatic life of streams. *Calif. Fish Game* 47: 189–228.

CUMMINS, K. W. - 1962 - An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *Amer. Midl. Nat.* 67: 477–504.

EGGLISHAW, H. J. - 1964 - The distributional relationship between the bottom fauna and plant detritus in streams. *J. Anim. Ecol.* 33: 463–476.

ELLIS, M. M., WESTFALL, B. A. & ELLIS, M. D. - 1948 - Determination of water quality. *U.S. Fish Wildl. Serv. Res. Rept.* 9: 1–122.

ENGELMANN, M. D. - 1966 - Energetics, terrestrial field studies, and animal productivity. *Adv. Ecol. Res.* 3: 73–115.

FRISON, T. H. - 1935 - The stoneflies, or Plecoptera, of Illinois. *Bull. Ill. Nat. Hist. Surv.* 20: 281–471.

GAUFIN, A. R. - 1959 - Production of bottom fauna in the Provo River, Utah. *Iowa State Coll. J. Sci.* 33: 395–419.

HUTCHINSON, G. E. - 1964 - The lacustrine microcosm reconsidered. *Amer. Sci.* 52: 334–341.

HYNES, H. B. N. - 1960 - The biology of polluted waters. Liverpool Univ. Press, Liverpool. 202 p.

HYNES, H. B. N. - 1961 - The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.* 57: 344–388.

IDE, F. P. - 1935 - The effect of temperature on the distribution of the mayfly fauna of a stream. *Univ. of Toronto Stud., Biol. Ser.* 39: 9–76.

ILLIES, J. - 1952 - Die Mölle. Faunistisch-ökologische Untersuchungen an einem Forellenbach im Lipper Bergland. *Arch. Hydrobiol.* 46: 424–612.

JONES, J. R. E. - 1949 - An ecological study of the River Rheidol, North Cardiganshire, Wales. *J. Anim. Ecol.* 18: 67–88.

JONES, J. R. E. - 1950 - A further ecological study of the River Rheidol: the food of the common insects of the mainstream. *Ibid.* 19: 159–174.

LINDUSKA, J. P. - 1942 - Bottom types as a factor influencing the local distribution of mayfly nymphs. *Canad. Ent.* 74: 26–30.

MACAN, T. T. - 1958 - Methods of sampling the bottom fauna in stony streams. *Mitt. int. Ver. Limnol.* 8: 1—21.
MACAN, T. T. - 1961 - A review of running water studies. *Verh. int. Ver. Limnol.* 14: 587—602.
MACAN, T. T. - 1962 - Biotic factors in running water, p. 386—406. In Symposium on the influence of current on running-water organisms. *Schweiz. Z. Hydrol.* 24: 353—484.
MACAN, T. T. - 1963 - Freshwater ecology. Longmans, Green and Co., Ltd., London. 338 p.
MAYR, E. - 1963 - Animal species and evolution. Harvard Univ. Press, Cambridge. 797 p.
MINCKLEY, W. L. - 1963 - The ecology of a spring stream Doe Run, Meade County, Kentucky. *Wildl. Monogr.* 11: 1—124.
MINCKLEY, W. L. & COLE, G. A. - 1963 - Ecological and morphological studies on gammarid amphipods (*Gammarus* spp.) in spring-fed streams of northern Kentucky. *Occas. Papers Adams Ctr. Ecol. Stud.* 10: 1—35.
MINSHALL, G. W. - 1965 - Community dynamics and economics of a woodland springbrook: Morgan's Creek, Meade County, Kentucky. Unpubl. Doctoral Dissertation. Univ. Louisville, Louisville. 261 p.
MINSHALL, G. W. - 1967 - Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology* 48: 139—149.
MINSHALL, G. W. & MINSHALL, J. N. - 1966 - Notes on the life history and ecology of *Isoperla clio* (NEWMAN) and *Isogenus decisus* WALKER (Plecoptera: Perlodidae). *Amer. Midl. Nat.* 76: 340—350.
MINSHALL, J. N. - 1967 - Life history and ecology of *Epeorus pleuralis* (BANKS) (Ephemeroptera: Heptageniidae). *Amer. Midl. Nat.* 18: 369—388.
MOON, H. P. - 1940 - An investigation of the movements of freshwater invertebrate faunas. *J. Anim. Ecol.* 9: 77—83.
MORTIMER, C. H. - 1956 - The oxygen content of air-saturated fresh waters, and aids in calculating percentage saturation. *Mitt. int. Ver. Limnol.* 6: 1—20.
NEEDHAM, P. R. - 1930 - Ecology of streams. *Biol. Lab., Long Island Biol. Assoc.* 2: 3—6.
NEEL, J. K. - 1951 - Interrelations of certain physical and chemical features in a headwater limestone stream. *Ecology* 32: 368—391.
NELSON, D. J. & SCOTT, D. C. - 1962 - Role of detritus in the productivity of a rock-outcrop community in a piedmont stream. *Limnol. Oceanogr.* 7: 396—413.
NIELSEN, A. - 1950 - On the zoogeography of springs. *Hydrobiologia* 2: 313—321.
NOEL, M. S. - 1954 - Animal ecology of a New Mexico springbrook. *Hydrobiologia* 6: 120—135.
ODUM, H. T. - 1957 - Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.* 27: 55—112.
OWEN, D. D. - 1857 - Third report of the geological survey in Kentucky made during the years 1856—1857. *Ky. Geol. Surv.*, Frankfort. 589 p.
PENNAK, R. W. & VAN GERPEN, E. D. - 1947 - Bottom fauna production and physical nature of the substrate in a northern Colorado stream. *Ecology* 28: 42—48.
PERCIVAL, E. & WHITEHEAD, H. - 1929 - A quantitative study of the fauna of some types of stream-bed. *J. Ecol.* 17: 282—314.
PRINS, R. - 1965 - Comparative ecology of the crayfishes *Orconectes rusticus rusticus* and *Cambarus tenebrosus* in Doe Run, Meade County, Ken-

tucky. Unpubl. Doctoral Dissertation, Univ. Louisville, Louisville. 114 p.

RAINWATER, F. H. & THATCHER, L. L. - 1960 - Methods for collection and analysis of water samples. *U.S. Geol. Surv. Water-Supply Paper* 1454. 301 p.

RIDENOUR, G. L. - 1929 - Early times in Meade County, Kentucky. Western Recorder Co., Louisville. 108 p.

ROSS, H. H. - 1963 - Stream communities and terrestrial biomes. *Arch. Hydrobiol.* 59: 235—242.

SLACK, K. V. - 1955 - A study of the factors affecting stream productivity by the comparative method. *Invest. Ind. Lakes Streams* 4: 3—47.

SLOAN, W. C. - 1956 - The distribution of aquatic insects in two Florida springs. *Ecology* 37: 81—98.

SMITH, L. L., JR. & MOYLE, J. B. - 1944 - A biological survey and fishery management plan for the streams of the Lake Superior north shore watershed. *Minn. Dept. Conserv., Div. Game Fish, Tech. Bull.* 1: 1—228.

SPRULES, W. M. - 1947 - An ecological investigation of stream insects in Algonquin Park, Ontario. *Univ. Toronto Stud., Biol. Ser.* 56: 1—81.

TARZWELL, C. M. - 1937 - Experimental evidence on the value of trout stream improvement in Michigan. *Trans. Amer. Fish. Soc.* 66: 177—187.

TEAL, J. M. - 1957 - Community metabolism in a temperate cold spring. *Ecol. Monogr.* 27: 283—302.

THORUP, J. - 1963 - Growth and life-cycle of invertebrates from Danish springs. *Hydrobiologia* 22: 55—84.

U. S. WEATHER BUREAU. - 1958 - Climatic summary of the United States – Supplement for 1931—1952. Kentucky. *Climatography of the United States.* No. 11—13. 41 p.

U.S. WEATHER BUREAU. - 1960 - The decennial census of the United States climate – 1960. Indiana. 4 p.

VAN ARSDEL, T. C. - 1939 - Proposed administration for the recreational demonstration project at Otter Creek, Kentucky. Unpubl. Master's Thesis. Univ. Cincinnati, Cincinnati, Ohio. 101 p.

WATERS, T. F. - 1964 - Recolonization of denuded stream bottom areas by drift. *Trans. Amer. Fish. Soc.* 93: 311—315.

WELCH, P. S. - 1948 - Limnological methods. McGraw-Hill Book Co., New York. 381 p.

WHITFORD, L. A. - 1960 - The current effect and growth of fresh-water algae. *Trans. Amer. microscop. Soc.* 79: 302—309.