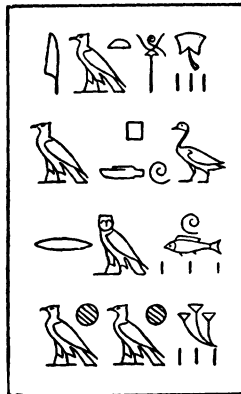


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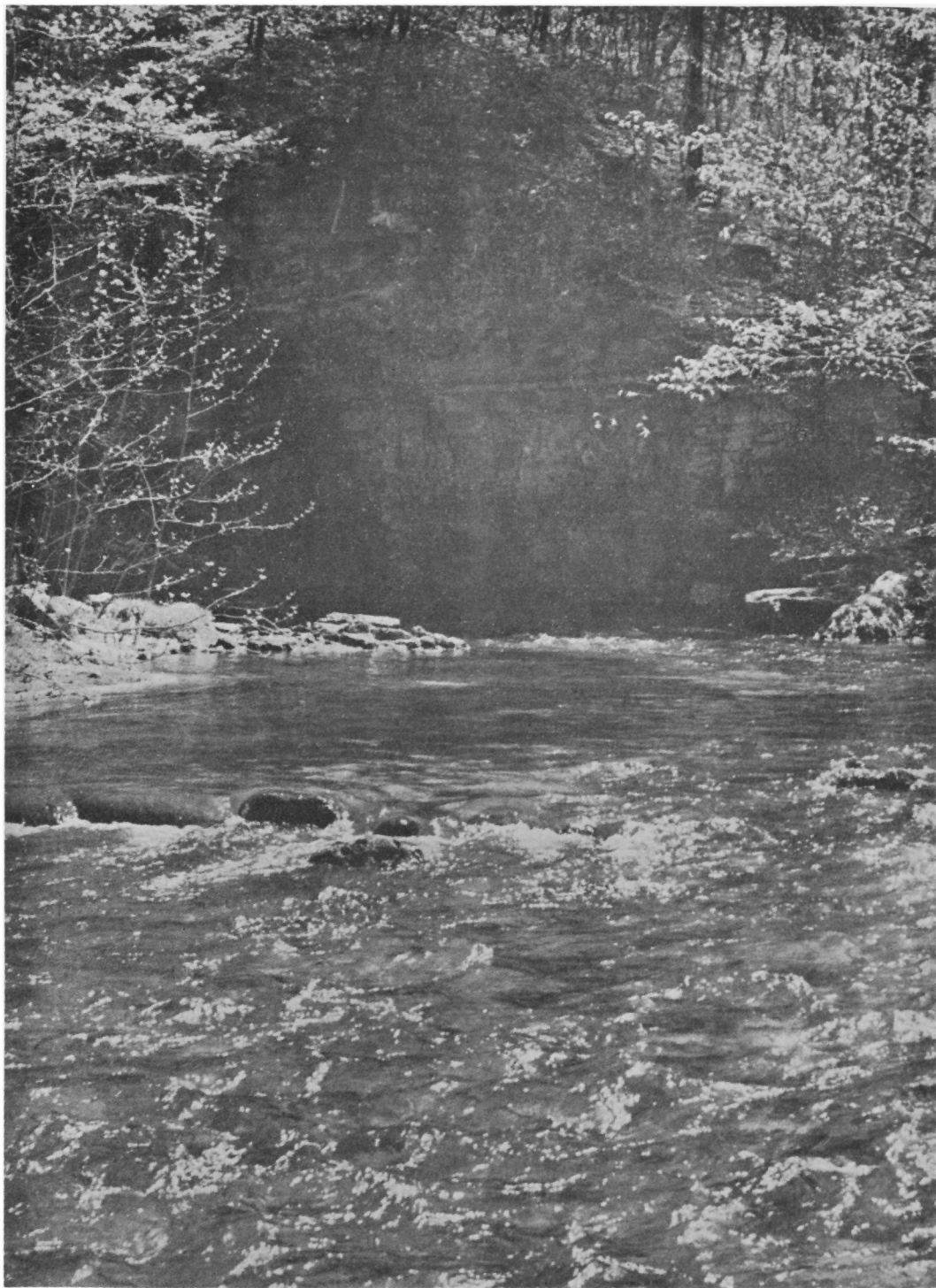
THE ECOLOGY OF A SPRING STREAM DOE RUN, MEADE COUNTY, KENTUCKY

by

W. L. MINCKLEY

SEPTEMBER 1963

No. 11



FRONTISPIECE. Spring source of Doe Run, Meade County, Ky., April 24, 1960. Photograph by Charles B. Stone.

THE ECOLOGY OF A SPRING STREAM DOE RUN, MEADE COUNTY, KENTUCKY¹

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INTRODUCTION

In recent years an increasing amount of research has been directed toward the ecology of flowing waters, mainly because of their importance in the disposal of industrial and domestic wastes. Much of the research on streams in North America has been oriented toward various aspects of pollution control, the search for indices of pollution (both biological and physico-chemical), and toward the management of streams for sport or commercial fisheries. However, many problems that now confuse findings of applied research may be solved only after accumulation of basic data.

This paper concerns an unpolluted spring stream, somewhat modified by man, and is an attempt to describe and analyze its physical, chemical, and biological characteristics. Investigations of Doe Run, Meade County, Ky., were begun in February 1959, and were intensified November 1, 1959. A year of study was completed before the downstream half of the creek was prepared for impoundment, and intensive sampling ended on July 9, 1961, when impoundment was effected.

ACKNOWLEDGMENTS

This report is based on research performed under Contract No. AT-(40-1)-2595 between the U. S. Atomic Energy Commission and the University of Louisville, with Louis A. Krumholz as principal investigator. It is a revision of parts of a dissertation submitted to the graduate faculty of the University of Louisville in partial fulfillment of requirements for the degree of Doctor of Philosophy.

Many persons assisted in the various phases of study and I am grateful to all of them. Special mention should be made of my fellow students, both graduate and undergraduate, who gave their time and energy freely in the field and in the laboratory. The landowners along Doe Run are to be given special consideration and thanks. The Kentucky Department of Fish and Wildlife Resources granted the necessary permits for collection of vertebrates

from the area. Louis A. Krumholz, University of Louisville, was available at all times for discussion of problems that arose in the course of study, and his ideas and suggestions were major factors in completion of this report. Jane S. Davis, Virginia Institute of Marine Science, prepared most of the figures.

Many persons assisted in identification of invertebrates from Doe Run: Gerald A. Cole, Arizona State University, and E. L. Bousfield, National Museum of Canada, identified malacostracans; William E. Ricker, Fisheries Research Board of Canada, Plecoptera; Herbert H. Ross, Illinois Natural History Survey, Trichoptera; Lewis Berner, University of Florida, Ephemeroptera; and Stuart E. Neff, Virginia Polytechnic Institute, Diptera. Assistance in identification of algae and higher plants was provided by Arland T. Hotchkiss and Donald R. Tindall, University of Louisville.

This paper is dedicated to my wife, Barbara, who assisted in many ways in its completion, and who deserves special recognition.

DESCRIPTION OF THE STUDY AREA

Geographic, Geologic, and Historic Information

The main spring of Doe Run (Front.) lies about 3 miles east and 0.4 mile north of Ekron, Ky., in eastern Meade County, 37° 56' N and 86° 07' W (Fig. 1). The creek flows north-northeast and is 9.7 miles long, although the distance from source to mouth by airline is only 5 miles. Doe Run enters the Ohio River about 3.5 miles east of Brandenburg, Ky.

The stream is located on a belt of Mississippian limestones that exhibit extensive karst topography and extend from central Indiana through Kentucky and into central Tennessee (Swinnerton, 1942). In Kentucky, this well-defined topographic area is called the Pennyroyal and is considered a major physiographic region of the state (Sauer, 1927).

The uplands into which Doe Run has deeply incised lie approximately 680 feet

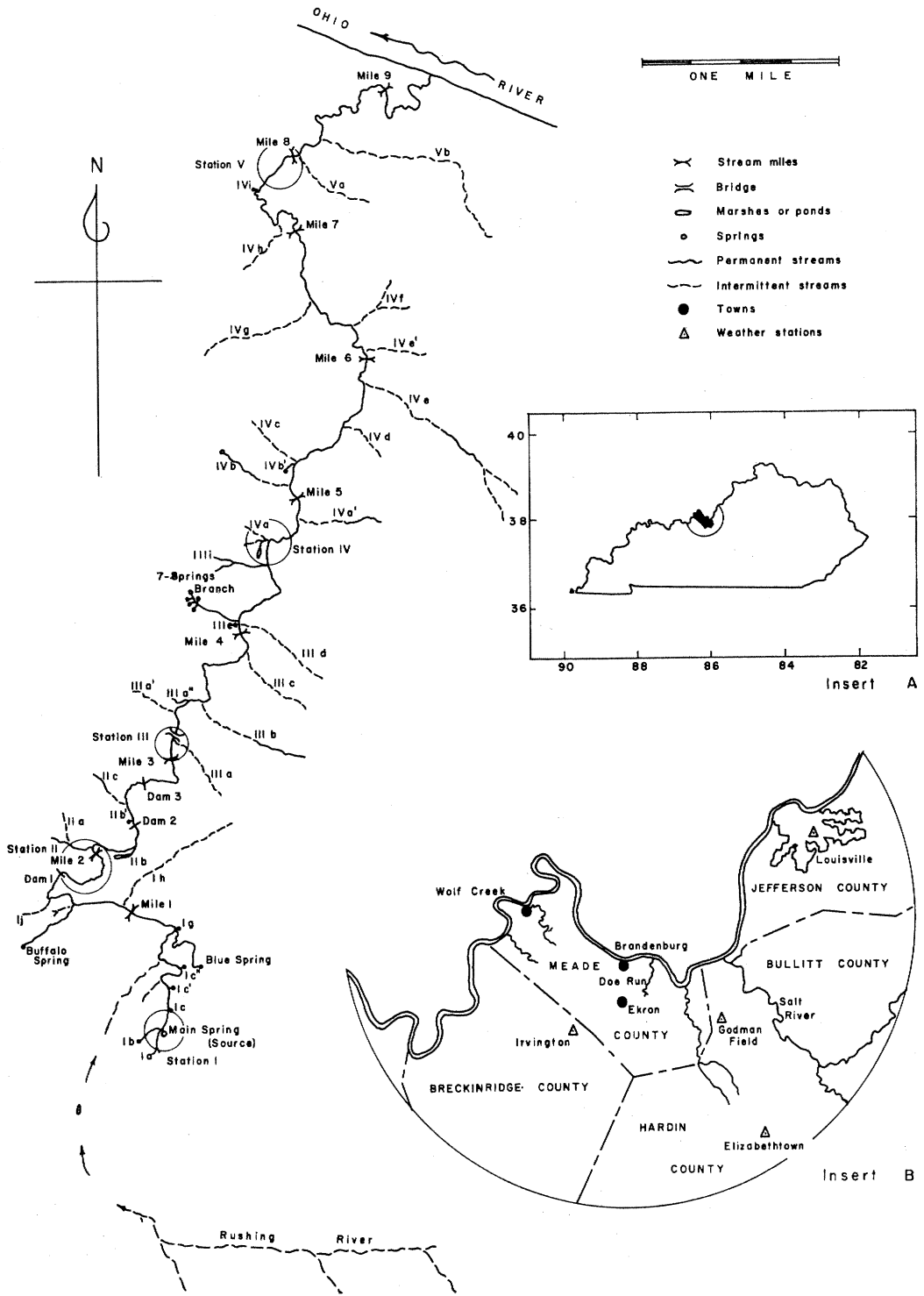


FIG. 1. Map of Doe Run, Meade County, Ky., showing tributaries, creek miles, mill dams, collecting stations, and other features. Insert maps show location of the study area in Kentucky (A), and certain geographic features of Meade and adjacent counties mentioned in the text (B).

above the mean sea level (msl) near the source; higher knobs rise to about 950 feet 1.5 miles southeast of the source. The land surface slopes gradually toward the north to about 600 feet above msl at the tops of precipitous bluffs that border the Ohio River floodplain. Compared with some parts of North America, this area shows little evidence of post-Mississippian subsidence (McFarlan, 1943). A drainage pattern of northwesterly flowing streams probably was formed in late Tertiary times, after reelevation in the early Tertiary Period had stripped off nonmarine sediments deposited on the Mississippian surfaces. The Ohio River formed in the early Pleistocene, essentially in its present configuration, by glacial damming of north-flowing streams and subsequent topping of cols toward the south and west by the ponded waters (Leverett, 1929; Netting, 1956; Walker, 1957). The glacial waters claimed preexisting stream channels, the bedrock channel of the Ohio River was cut to essentially its present level, and widening of the valley was accomplished in the Yarmouthian (Walker, *loc. cit.*). Borings made in the valley of Doe Run by the Doe Valley Corporation, Brandenburg, Ky., indicate that its rock floor lies about 320 feet above msl, thus corresponding to the general elevation of the rock floor of the Ohio River near Doe Run, 310 feet above msl (Leverett, 1929). Doe Run was a tributary to the Ohio River either at the time of rapid downcutting prior to the Illinoian, or no later than the Tazewell Glacial Substage of the Wisconsin Glacial Advance, when much of the Illinoian alluvial fill was removed from the channel of the Ohio River (Walker, 1957).

Doe Run appears to have originated from a subsurface drainage channel. The main spring issues from a foundered cave in the St. Louis Limestone. Probably the upstream 1.5 miles of stream now flows through a "valley sink," the formation of which was discussed by Sauer (1927) for the Pennyroyal area. Between Miles 1.5 and 5.0 (Fig. 1) the creek seems to follow

structural joints of the limestone, and probably developed along a solution channel. The downstream segment, where the stream flowed on the surface of Pleistocene and Recent sediments, assumed a typical meandering channel.

Prior to settlement of Meade County by white men, the area was used by Indians as a major hunting ground (Ridenour, 1929). The first settlers to explore the northern Pennyroyal found dense forests along the streams and on the knobs, and a prairie upland that they called the "barrens" because of its general lack of woody vegetation. These prairies appear to have been maintained as a fire disclimax by periodic burning by Indians, and became covered with woody plants soon after burning was discontinued (Allen, 1876; Sauer, 1927). The first settlements in Meade County were near Doe Run and Otter Creek which have high gradients and thus provided a source of power. Between 1780 and 1825, 2 water grist mills and a sawmill were established on Doe Run, and a large tannery was built (Ridenour, 1929). These industries necessitated modification of the creek by construction of dams, 3 of which are extant. After 1860, wells were drilled to obtain brine from underlying strata for the production of salt. Natural gas associated with the brines allowed limited expansion of industry in the Doe Run area (Jillson, 1922), but gas production declined rapidly after 1900 and the fields were closed. In the early 1930's, parts of Doe Run were used as recreational areas. One of the mills, built in 1820 and operative until 1930, was converted to an inn and restaurant, and the area around the inn was used for recreational purposes during 1959-1962, as were all places where roads provided access to the stream.

The major alteration of Doe Run, during and following this study, was the preparation for and impoundment of the lower creek by the Doe Valley Corporation. The effects of clearing the riparian forest and of earth moving along the banks will be discussed more fully below.

Description of the Stream

A map of Doe Run was made from an aerial photograph and by reference to topographic maps of the Guston, Rock Haven, and Laconia (Indiana) quadrangles of the U. S. Geological Survey. Creek miles were measured beginning with Mile 0.0 at the source and terminating with Mile 9.7 at the mouth. Tributaries were assigned letter designations consecutively downstream from each of the 5 permanent sampling stations (Fig. 1), so that each tributary was known by the number of the sampling station closest upstream to it, and by successive letters of the alphabet. If a tributary had a local name, that name was used in preference to the numbering system.

The major source of Doe Run is 575 feet above msl, and the stream enters the Ohio River at 374 feet; the average gradient is 20.7 feet per mile (fpm). Streams flowing on limestones often have rapidly changing gradients in different sections (Neel, 1951), and this is exemplified by Doe Run (Fig. 2).

Doe Run is about 30 feet wide throughout its length, narrowing to as little as 6 feet at some riffles in the downstream area, and widening at some large pools to more than 50 feet (Table 1). General restriction of the creek to a 30-foot channel, and the preponderance of bedrock or marl bottoms in the upstream areas permitted little pool formation, and current velocities upstream from Mile 5.3 rarely were less than 0.5 ft/sec. Exceptions to this were found in the impoundments of the 3 mill dams. In the lower part of the creek, typical pools

TABLE 1.—SOME PARAMETERS OF WIDTH, DEPTH, AND POOL-RIFFLE DEVELOPMENT IN DIFFERENT SECTIONS OF DOE RUN, MEADE COUNTY, KENTUCKY. DATA MARKED WITH AN ASTERISK (*) ARE FOR IMPOUNDMENTS, BACKWATERS, OR SECTIONS OF SMOOTH, ALMOST-LAMINAR FLOW

Mile Section	Maximum Size of Pools (feet)	Maximum Depth of Pools (feet)	Mean Depth of Riffles (inches)	Estimated Riffle-Pool Ratio
0.0 -1.1*	35 × —	3.0	12.0	1-75
1.1 -1.65*	40 × —	7.0	none	0-1
1.65-2.1	45 × 60	5.0	6.0	1- 1.5
2.1 -2.36*	50 × —	7.5	none	0- 1
2.36-2.82*	60 × —	8.0	4.0	1-100
2.82-5.3	35 × 85	7.0	6.0	1- 1.5
5.3 -9.7 ¹	30 × 350	12.0	9.0	1-100

¹ This section includes the long, slow-flowing portion of Doe Run adjacent to the Ohio River (Miles 7.7 to 9.7) which is best considered as a backwater or pool habitat.

were developed, with extensive eddies and quiet areas along the banks.

In the upstream 1.5 miles, the floodplain was relatively broad (100 to 200 yards in width), between Miles 1.5 and 5.0 it was narrow or absent and the stream flowed between precipitous bluffs of varying height, and downstream from Mile 5.0 the floodplain widened as a result of the alluvial fill, stretching 100 to 300 yards on either side of the creek.

There was a fringe of trees along most of the banks of Doe Run especially in areas of wide floodplain because of clearing and cultivation of the "bottomlands." There were few large trees in the area, and stumps and slash implied heavy logging in previous years.

Five permanent stations were established on Doe Run at the inception of the study. Station I was located at the source and extended about 0.1 mile downstream from the main spring (Front.; Fig. 1). The stream below the spring was turbulent for about 60 feet where it graded into a long section (Miles 0.03 to 1.1) characterized by generally smooth, almost laminar flow, and a bottom of sand and small gravel overlying bedrock (Fig. 3; Table 2). Between Miles 1.1 and 1.65, the stream flowed through the impoundment of the most upstream mill dam (Dam 1). Between Miles 1.65 and 2.1 the creek fell rapidly over many cataracts

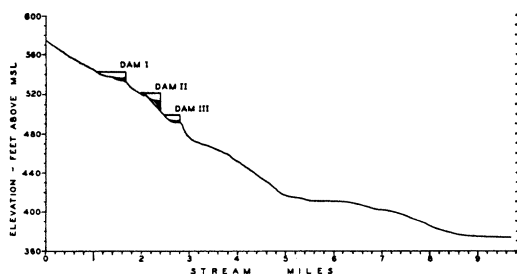


FIG. 2. Longitudinal profile of Doe Run, Meade County, Ky.



FIG. 3. Doe Run, Meade County, Ky., at Mile 0.17 looking downstream, November 11, 1960. Note bed of watercress along left bank and relatively thick riparian forest.



FIG. 4. Doe Run, Meade County, Ky., at Station II near Mile 1.75, January 28, 1962.

and swift riffles (Fig. 4). Station II was established near Mile 1.9, but collections made throughout the swift section of creek were considered from Station II except where there were pronounced differences in fauna. At Mile 2.1, the creek entered the pool held by Dam 2, the second of the mill dams. This impoundment apparently drowned a section of waterfalls and rapids. Probing at the upstream end of the pool (Mile 2.1) revealed a submerged waterfall at least 6 feet high. Water passing over Dam 2 (Mile 2.36) entered the pool formed by Dam 3 after flowing over a short section of bedrock and marl waterfalls. The bottom of the upper third of this pool was covered with marl, with some sand lateral to the current, and in the downstream two-

thirds was almost entirely a dark, malodorous muck and silt, apparently resulting from decomposition of leaves and other organic debris. Downstream from Dam 3 (Mile 2.82) the creek flowed 2.7 miles over marl, bedrock, and gravel-rubble bottoms (Table 2), with mud deposits in some large pools. Station III was in the marl section at Mile 3.1 (Fig. 1), immediately above and below a major road crossing (Fig. 5). The crossing was completed in 1958 with construction of 3 culvert tubes through which the creek passed with current velocities greater than 3 ft/sec even during periods of modal discharge. High current velocities in times of flood and shallowness of water in periods of modal discharge, apparently restricted movements of fishes and other animals upstream. With the abrupt change in gradient near Mile 5.0 (Fig. 2), the bottoms gradually changed

TABLE 2.—ESTIMATED PERCENTAGES OF BOTTOM MATERIALS IN DIFFERENT SECTIONS OF DOE RUN, MEADE COUNTY, KENTUCKY. DATA MARKED WITH AN ASTERISK (*) ARE FOR IMPOUNDMENTS, BACKWATERS, OR SECTIONS OF SMOOTH, ALMOST-LAMINAR FLOW

Mile Section	Types of Bottom Materials						
	Marl	Bedrock	Rubble	Gravel	Sand	Silt	Clay
0.0-1.1*	—	10	5	25	55	5	—
1.1-1.65*	—	2	3	10	65	20	—
1.65-2.1	—	65	10	15	8	2	—
2.1-2.36*	—	—	—	10	35	55	—
2.36-2.82*	30	—	5	10	5	50	—
2.82-5.3	65	15	10	5	3	2	—
5.3-9.7 ¹	trace	—	2	5	18	65	10

¹ See footnote, Table 1.



FIG. 5. Doe Run, Meade County, Ky., at Station III looking downstream, January 28, 1962.

from broken marl, rubble, and gravels, to silt and sand near the confluence of Doe Run with the Ohio River (Table 2). Station IV was at the downstream end of the marl section, near Mile 4.8, and Station V was in the downstream area near Mile 7.7 (Figs. 6 and 7, respectively).

Three changes have occurred in the bottom materials of Doe Run in the recent past, probably as a result of human activity. (1) Prior to modification of the stream by damming, or at some earlier date, the marl area of Doe Run extended upstream at least to Mile 1.65. Much of the material listed as rubble at Station II (Table 2), between Miles 1.65 and 2.1, was marl concretions, but there was no evidence of marl deposition in that area during this study. Cut banks near Station II revealed deposits of marl concretions as buried bars lateral to the present channel. (2) The upper 1.5 miles of Doe Run, where bedrock was thinly overlain with sand, gravel, and silt during this study, probably had smooth bedrock bottoms prior to cultivation of the floodplain and erosion of the stream banks. (3) Maintenance of navigation pools in the Ohio River impounds the lower parts of Doe Run and speeds the deposition of silt in those areas. Damming effects of the navigation pool of the Ohio River were evident in Doe Run for more than a mile upstream from the mouth.



FIG. 6. Doe Run, Meade County, Ky., at Station IV looking upstream, April 24, 1960. Photograph by Charles B. Stone.



FIG. 7. Doe Run, Meade County, Ky., at Station V looking downstream, June 13, 1961, when backwaters of the Ohio River were present.

The permanent tributaries to Doe Run had gradients that corresponded to their locations on the creek; where the gradient was relatively low in Doe Run, the tributaries were low in gradient, and between Miles 1.5 and 5.0 (Fig. 2) where Doe Run had high gradient, the tributaries had high gradient. Most of the permanent tributaries originated in springs. There were, however, 2 kinds of intermittent tributaries: (1) subsurface tributaries whose waters rose after periods of prolonged or rapid rainfall, and (2) surface streams that developed after excessively heavy rains. Of the first type, Tributaries I-c, I-c', and I-c'', thought to be inactive springs at the beginning of the study, carried large amounts of water at certain times.

An intermittent tributary called Rushing River (Fig. 1) was the only surface stream that consistently contributed any significant surface runoff to Doe Run. The stream flowed directly into Doe Run on 5 or 6 occasions during the period of study, but may have contributed much water on many occasions by passage underground into 2 large, open sinkholes about 0.5 mile from the source of Doe Run. In periods of extremely heavy rain, Rushing River flowed into sinkholes and did not rise over a low divide until its volume exceeded the capacity of the subterranean channels. When that capacity was exceeded, surface water connected with the headwaters of Tributary I-e to enter Doe Run at Mile 0.5 (Fig.

1). The fate of water that entered the open sinkholes is unknown, but presumably it entered Doe Run either through the main source or through the intermittent springs, I-c, I-c', and I-c''.

Permanent tributaries generally flowed through steep, V-shaped valleys, with the exception of those upstream from Mile 1.5 and those in the extreme lower portion and on the floodplain of the Ohio River. Permanent tributaries entering Doe Run in the upper areas (Fig. 1) had bottoms of sand and fine gravels and rose in springs generally at the same elevation as the main spring of the creek. Farther downstream, the bottoms of tributaries in the high-gradient section were bedrock, broken rubble, and marl. Most of the latter streams had gradients greater than 400 fpm and rarely were longer than a half mile.

METHODS

Physical.—Discharges were estimated regularly at Stations I, III, and V, by a modification of the cork-float method (Embody, 1927) for 14 months following October 1959, and from water levels recorded on stationary flow gauges and other objects for the remainder of the study. Measurements of high-water marks known to have been formed between sampling dates also were included, with the dates of their occurrence documented by residents of the area.

Time of flow was measured on 4 occasions using fluorescein or potassium permanganate as dyes, and one estimate of time of flow was made on the basis of drifting debris and silt, and one by the passage of rotenone-treated water in the area between Stations IV and V. Rates are based on time of average flow, by allowing about a fourth of the tracer material to pass a given point downstream from the point of application before recording the time it had been moving.

Turbidities were measured against distilled water blanks in a Bausch and Lomb Spectronic-20 Colorimeter. Samples from the strongest currents at each station were retained in jars and determinations made in the laboratory after samples were violently agitated. Data are presented as "turbidity units," roughly equivalent to mg/l, from tables obtained from the Hach Chemical Company, Ames, Iowa (Anonymous, *n.d.*). To determine the accuracy of colorimetric turbidity measurements and variation in turbidity of stream water on a short-term basis, 2 series were run. First, 10 aliquots from a single sample container showed a range from 79 to 80 units, with a mean of 79.3 and a coefficient of variability (V) of 0.71. The

second series of 20 samples collected individually from the current at Station I at intervals of about 1 minute had a range from 71 to 86 units, with a mean of 77.6, standard deviation (sd) 4.46, and V, 5.74.

Temperatures in Doe Run were measured with a Whitney resistance thermometer, maximum-minimum thermometers placed at permanent locations along the creek, and with standard, vest-pocket thermometers. All instruments were calibrated against a standard centigrade thermometer, and appropriate corrections were made. Temperatures were recorded in, or converted to degrees centigrade.

The amounts of light reaching Doe Run were measured at Stations I, III, and V, on each sampling date for 14 months following September 1959, with a PR-1, General Electric light meter, containing a photoelectric cell sensitive to the visible spectrum, and fitted with an incident light attachment. The light recorded is an index of intensities of solar radiation about 5 ft above the stream surface at each station. One to 10 measurements were made on each date, more being taken on days with little cloud cover than on overcast days. The data were converted to foot candles using tables furnished with the instrument, and all readings were corrected to 1:00 PM (EST) by factors derived from data taken in June 1960. **Chemical.**—Determinations of dissolved oxygen were made by the unmodified Winkler method (Welch, 1948) after series of comparable samples were analyzed by the Rideal-Stewart and Alsterberg modifications of that method with no discernible differences in results. Samples usually were obtained with a Kemmerer sampler from the main current, unless specific studies were being made on other parts of the stream. No corrections were applied to compensate for displacement of sample volume by reagents, but all determinations were corrected to mean barometric pressure by factors given by Mortimer (in Hutchinson, 1957). No attempt was made, however, to correct for variations caused by barometric pressures extant at the time of sampling, and this undoubtedly caused some error (Ricker, 1934b). Most samples were titrated in the laboratory unless long-term studies dictated titration in the field. Oxygen saturations were derived from Mortimer's nomograph (Hutchinson, *loc. cit.*) constructed from data of Truesdale, *et al.* (1955), or were calculated from data given by the latter authors.

Carbon dioxide in Doe Run, the free carbon dioxide plus carbonic acid (Hutchinson, 1957), was determined from data on pH and alkalinity (Ruttner, 1953). The concentration of hydrogen ions, expressed as pH, was determined electrometrically, using pocket pH meters manufactured by Analytical Measurements Corp., and by Beckman, Inc. On occasions when electrical apparatus was nonfunctional, pH values were ascertained using colorimetric techniques. Total alkalinity,

expressed as mg/l CaCO_3 , was measured using methyl purple as an indicator, and titrating with N/50 sulphuric acid.

Total iron was determined by a modification of the 2,2' bipyridine technique of the Hach Chemical Company (Anonymous, *n.d.*). Reagents for this and the following tests were obtained from the Hach Company, and were checked against known standards prior to full-scale use. Standards were prepared as recommended by the American Public Health Association (Anonymous, 1960) for each analysis, and error was 5 per cent or less in all tests used here. Duplicate series were run to indicate variations that might have resulted from the kinds of sample containers used, or from the lapse of time between collection and analysis (Table 3).

Total phosphates (ortho- plus metaphosphates) were measured spectrometrically by the ammonium molybdate-stannous chloride method, after boiling in acid (Anonymous, 1960). Samples were run within 48 hours after collection, and the possibility of error introduced by absorption of phosphate by the polyethylene containers (Odum, 1957a) or through bacterial action (Heron, 1962) was checked by running duplicate series at various times after collection. No significant differences were apparent 52 hours after collection (Table 3).

Nitrate and nitrite nitrogen were determined spectrometrically by the brucine method and by a modification of the naphthylamine hydrochlorine-sulfanilic acid techniques, respectively (Anonymous, 1960).

Biological.—Quantitative samples of benthic invertebrates were obtained with an unmodified Surber Sampler (Surber, 1937), and a 6- by 6-inch Ekman dredge. The Surber Sampler was used in riffles with marl, rubble, or gravel bottoms, but its use in beds of *Fissidens* and *Myriophyllum* was precluded by the relatively great amounts of vegetation lost. Surber samples were taken by pressing the frame tightly to the substrate and

thoroughly disturbing the enclosed quadrat by hand or with an appropriate object. Care was taken to prevent backwash at the mouth of the net, which was shown by Badcock (1949) to introduce 4 to 20 per cent sampling error. Marl riffles were sampled in the swiftest portion in which the sampler could be effectively used, and always directly on marl; the poorly consolidated surface material was broken and the surface scraped thoroughly. In riffles, each object in the quadrat was scrubbed by hand into the net. Ekman dredge samples were obtained in soft-bottomed pools, and in beds of vegetation. The jaws of the dredge were sharpened and precise samples of vegetation were obtained by plunging the device into the bed with enough force to cut through stems, roots, and substrate. On bedrock bottoms the sampler was used to cut *Fissidens* and was held firmly to the bottom as withdrawn to scrape moss, including its holdfasts, from the substrate. The relative shallowness of water in most of Doe Run allowed use of the dredge in sand or detritus bottoms, which usually clog the device or block complete closure of the jaws (Rawson, 1930). Only those samples where complete closure of the jaws was effected were used.

Surber samples were preserved *in toto* in 10 per cent formalin. Dredge samples were washed in the field in a 40-mesh sieve prior to preservation, and thus are comparable to those taken with the 40-mesh Surber netting. The preserved bottom materials, and the included organism, were sorted in the laboratory in white enamel pans or in glass dishes over a light-table, by flotation with saturated salt (Lyman, 1943) or sugar solutions (Anderson, 1959), and by hand-picking. A light-table was useful in sorting small animals from vegetation in which they were entangled, allowed easy differentiation of inhabited from uninhabited, semitransparent cases of certain caddisfly larvae, and revealed some counting error based on difficulty in distinguishing between some whole,

TABLE 3.—DUPLICATE ANALYSES OF WATER SAMPLES FROM STATION I, DOE RUN, MEADE COUNTY, KENTUCKY, SHOWING VARIATIONS DEVELOPED WITH TIME AFTER COLLECTION, WITH DIFFERING SAMPLE CONTAINERS, AND REPRODUCIBILITY OF RESULTS (DATA IN MG/L)

Sample Held in Glass, Analyzed 2 Hours after Collection					Sample Held in Glass, Analyzed 52 Hours after Collection					Sample Held in Polyethylene, Analyzed 52 Hours after Collection				
Dupli- cations	Range of Analyses	Mean	SD	V	Dupli- cations	Range of Analyses	Mean	SD	V	Dupli- cations	Range of Analyses	Mean	SD	V
TOTAL IRON														
5	0.60–0.62	0.61	0.01	1.6	5	0.61–0.62	0.61	0.01	0.8	—	—	—	—	—
PHOSPHATE PHOSPHORUS														
10	0.15–0.17	0.15	0.01	4.6	10	0.14–0.16	0.15	0.01	4.0	10	0.14–0.15	0.15	0.01	4.1
NITRATE NITROGEN														
10	1.60–1.72	1.67	0.04	2.3	10	1.57–1.67	1.62	0.03	1.9	10	1.59–1.69	1.64	0.04	2.2
NITRITE NITROGEN														
5	0.05–0.07	0.06	0.01	11.6	5	0.05–0.06	0.06	0.01	16.4	5	0.05–0.07	0.06	0.01	16.4

preserved crustaceans and their freshly cast exoskeletons. That error was discovered late in the study and amounted to 1.0 to 3.3 per cent (average 1.43) in 10 samples of isopods from Stations I and II. No factor was applied because of variability, but the error did not influence results greatly. Organisms were "rough sorted" from bottom materials and placed in 70 per cent ethanol. Then they were sorted to taxonomic categories, the preservative was removed by a modified vacuum filter using discs of conventional filter paper, and the animals were immediately weighed to the nearest milligram on a Mettler, electric, single-pan balance. Mollusks were weighed in the shells. Trichopterans except those at Station I were removed from their cases before weighing; they were small, with fibrous, self-produced cases, and the time needed to remove them was not warranted. Weights of crayfish and snails are arbitrarily excluded from calculation of relative gravimetric abundance because of difficulty in sampling the former in particular, and because of inclusion of shell in weights of snails. Alteration of weights due to shrinkage in preservative (Leonard, 1939) was not considered.

Qualitative samples were taken by various means and usually preserved in 70 per cent alcohol in the field. All major tributaries of Doe Run were sampled at least once, and samples were obtained in the mainstream from Stations I through V on various occasions. Identifications were made by standard keys such as *Ward and Whipple's Fresh-Water Biology* (Edmonson, ed., 1959), Usinger (ed., 1956), and Pennak (1953), with further reference to literature cited therein.

Food relations of invertebrates were estimated from examination of gut contents of 10 to 20 individuals of a species from each of 2 collecting periods, if that many were secured. Major collections of animals were obtained for this purpose in September 1960, in a period of modal, presumably "optimum" conditions in the stream, and others in February 1960, at the middle of "winter discharge." Some animals were not present in those periods and were analyzed from collections at other times. Field and laboratory observations were used to substantiate findings from analyses of digestive tracts when feasible, and food relations of some invertebrates are included only on the basis of such observational data.

Specimens for food analyses were preserved in weak formalin, with a small amount of copper sulfate added. That compound tends to replace certain parts of the chlorophyll in algae and other plant materials, causing them to remain green and thus aiding in identification and in determining whether the material was living or dead when ingested. The animals gulped the preservative as they died. Only the anterior parts of digestive tracts were examined in most species, although further dissection was done in some instances. A binocular microscope was used for examination

of gut contents and identifications were made by direct comparison of food items with known materials collected from Doe Run. Data were recorded by frequency of occurrence in the tracts, on a rough quantitative basis by spreading the contents of a given tract over a 0.1-mm grid and counting the numbers of squares covered by each item, and by counts of individual items. General discussion of foods of various species uses the relative terms "rare," "scarce," and "abundant," with each term implying an increasing change of one order of magnitude from a base of one item in those animals feeding on diatoms, particulate detritus, or other small-sized materials. In predatory animals, where digestive tracts rarely contained more than 10 items, the terms are subjective.

Variable numbers of the more abundant species of fishes in Doe Run were analyzed for food relations; stomachs, or the anterior parts of the digestive tracts in catostomids and some cyprinids, were excised and the contents examined at various magnifications with a binocular microscope. The volume of the contents of each stomach was estimated visually, and the relative volumes of the various food items were recorded as estimated percentages of the total material.

Fishes were collected by seines from 4 to 30 feet in length and of mesh size ranging from 0.02- to 0.5-inch bar measure, by an electric shocker delivering 110 volts A.C., by scape nets of various kinds, by 3- and 4-foot hoop nets with pot meshes of 1 inch, by experimental gill nets 125 feet long with meshes ranging from 0.75 to 1.5 inches bar measure, by pole and line, and by both powdered and emulsifiable rotenone.

PHYSICAL ENVIRONMENT

Characteristics of Flow in the Mainstream

According to Meinzer's (1923) classification, Doe Run is a spring of the second magnitude, that is, a spring with an average discharge between 10 and 100 cubic feet per second (cfs). At Station I, the average discharge between October 1959 and October 1961 was about 65 cfs, and was roughly doubled at Station III, at about 140 cfs. Data from Station V were incomplete because of the sporadic presence of backwaters from the Ohio River (Fig. 8), but the computed average was near 250 cfs.

In the light of field experience, the mean volumes of discharge seemed too great. The overall data indicated a modal volume of discharge between 20 and 40 cfs at all stations, and this range represents a realistic "normal discharge" for the stream. The

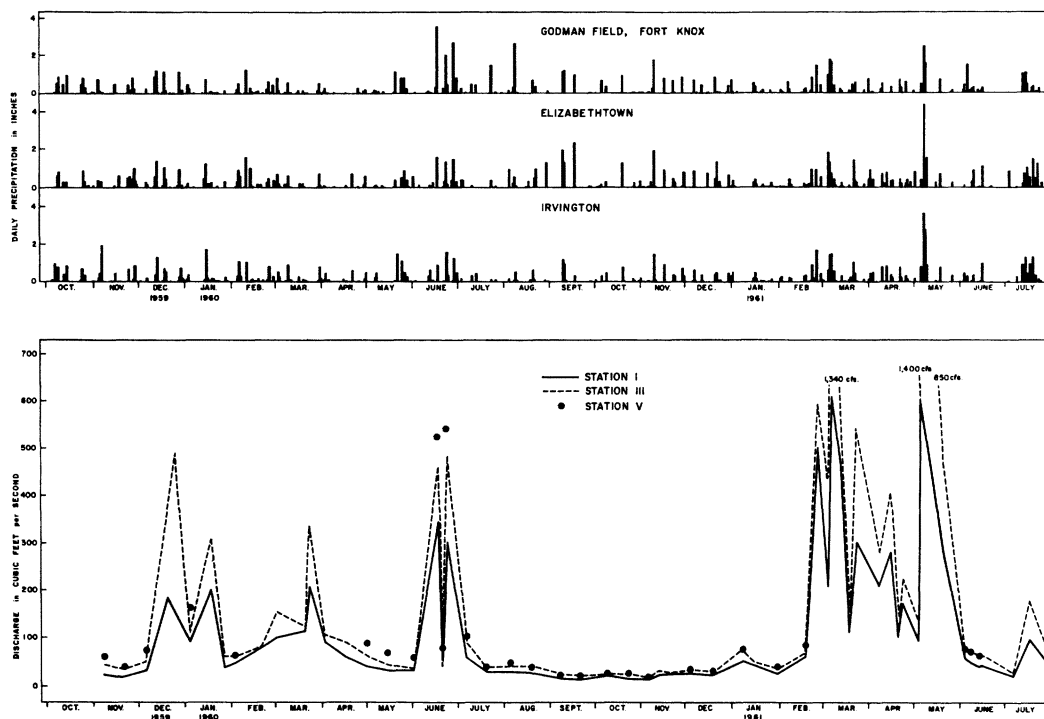


FIG. 8. Daily records of precipitation at 3 stations near Doe Run, Meade County, Ky., and records of discharge in Doe Run from November 1959 to July 1961. Dots denote records obtained at Station V when that area was not inundated by backwaters of the Ohio River.

large average discharge at each station resulted from no more than an accumulated 2 months of extremely high discharge in the 2-year period (Fig. 8). Characterization of streams on the basis of their average discharge is acceptable only if long-term records are available. In relatively short-term studies, such as this one, the modal values give a more accurate estimate of the "normal condition." Barring major changes in the stream itself, the longer that records are kept, the nearer the average of such data should approach the mode obtained in the first few years.

During 1959, 1960, and 1961, discharge of Doe Run was variable and generally high from December to June, then relatively constant from mid-June through November (Fig. 8). In 1961, the winter period was culminated between February and May by extremely high volumes of discharge.

The rapid movements of surface water into Doe Run is indicated by the close agreement between some of the dates of high discharge in the creek and those of heavy rainfall in the vicinity (Fig. 8). Rainfall in northern Kentucky varies greatly from place to place (Kendall, 1941), and such variation probably explains some high waters in Doe Run in the absence of recorded heavy rains, for example, in the period from mid-March through April 1961, and for lack of variations in discharge during other periods of relatively high, recorded rainfall (August through September 1960). Other factors contributing to the influence of rainfall on the discharge of the creek were levels of soil moisture prior to the precipitation, presence of water-holding ground cover in the form of litter or standing vegetation, presence of frozen soils in winter that permitted almost total runoff, and presumably the storage capac-

TABLE 4.—VOLUMES OF DISCHARGE IN CUBIC FEET PER SECOND AT 2 STATIONS ON DOE RUN, MEADE COUNTY, KENTUCKY, AND IN TRIBUTARIES LOCATED BETWEEN THOSE 2 STATIONS, UNDER CONTRASTING CONDITIONS

Tributary or Station	March 6, 1961 Discharge	October 15, 1960 Discharge
Station I	600	15
Trib. I-a	4	trace
Trib. I-b	5	0.5
Trib. I-c	submerged, flow ca. 50	none
Trib. I-c'	150	none
Trib. I-c''	100	none
Trib. I-d	trace	none
Trib. I-e (= Rushing River)	trace ¹	none
Blue Spring	250	4
Trib. I-g	1	none
Trib. I-h and Buffalo Spring	unknown	none
Trib. II-a	10	0.5
Tribs. II-b and II-b'	unknown	none
Tribs. II-c and II-d	trace	none
Station III	1,350	20
Total known discharge of Tribs. and Sta. I	1,170	20

¹ Trace = less than 0.25 cfs; Rushing River had carried ca. 50 cfs earlier in the day as judged from high-water marks.

ity of the underground aquifer feeding the creek, the extent and geography of which is unknown.

On occasions of high discharges, increases in water levels occurred rapidly. On June 23, 1960, during a heavy and apparently local thunderstorm, the discharge increased from about 60 cfs at 8:30 AM (EST) to near 200 cfs at 10:00 AM. The maximum discharge at Station I on that date was 300 cfs, and occurred at about 12:30 PM.

At modal discharge there was less difference between volumes of water at Stations I and V than when flood conditions prevailed, but the greater differences between stations in periods of flood reflect variation in discharge of downstream springs, rather than variations in surface runoff. On March 6, 1961, after heavy rainfall on that and the preceding day (Fig. 8), Doe Run was traversed on foot from Station I to Blue Spring, and visited at Stations II and III.

All the larger tributaries to Doe Run, the main-source spring, and 3 presumably inactive springs (Tributaries I-c-I-c''), were flowing violently, with water being forced up in boils as much as 3 feet high. Estimates of volumes of discharge for each tributary, and of Doe Run at Stations I and III, are in Table 4. The only evidence of great surface inflow during the rain was Rushing River. According to high-water marks, the flow observed was maximal for that date at both Stations I and III, and about 85 per cent of the water passing Station III was accounted for in discharge of the springs visited. The independence of Doe Run from surface water in periods of normal or subnormal discharge is illustrated by data for October 15, 1960 (Table 4).

In summer, at times of low relative humidity, high temperature, and maximal insolation, slight deficits in discharge were detected between Stations I and V, and diurnal fluctuations in discharge were noted on 3 occasions during 24-hour studies of water chemistry. These variations apparently resulted from evaporation and transpiratory activities of the riparian vegetation, and were most pronounced in the upstream area where bedrock permitted streamside vegetation no more than 2 to 6 feet of soil in which to root. The greatest such fluctuation was 2 inches recorded on August 17-18, 1961, near Station II, and the greatest diminution of volume between Stations I and V was about 1 cfs when discharge at Station I was 18 cfs.

It must be reiterated here that water sampled at Station I cannot be considered the same as that sampled at Station III a short time later in the same day, or at Station V later in the day. The concept of a column of water, long used in the study of lentic situations, is not applicable to the study of flowing systems. However, in recent years some work has been done on aspects of stream ecology by following a given mass of water from the origin of the stream to a given point downstream, and measuring certain factors as modified in

the length of the section (Schmitz, 1955; Odum, 1956, 1957a, b; and others). Studies on flood crests, sediment loads, and other features of flowing water have shown that a given mass of water tends to become dispersed and diluted, both laterally and longitudinally, as it passes down a channel (Thomas, 1958). The use of the technique, however, gives a time parameter necessary in understanding a constantly moving, integrated system such as a stream, and which is lacking in studies based on instantaneous sampling techniques.

Time of flow in Doe Run varied from section to section and in relation to discharge (Table 5). The average time of flow in the upstream 1.2 miles, where smooth bottoms allowed almost laminar streaming of currents, was about 0.6 ft/sec at a discharge of 20 cfs. This increased to more than 1 ft/sec at a discharge of 40 cfs. In the mill impoundments, the average speed of flow was about 0.2 ft/sec at 20 cfs, doubling with a doubling of discharge. In the swiftest section of the creek, between Miles 2.8 and 5.3, the average flow was about 1.0 ft/sec at modal discharge, and the velocity decreased sharply at Mile 5.3 to about 0.3 ft/sec in the low-gradient, downstream section of the creek.

These data illustrate the variability of time of flow in a given segment of stream in relation of discharge, and point out the marked variability of such data from section to section. Even more important, perhaps, in using time-of-flow techniques, is

TABLE 5.—SPEED OF PASSAGE OF WATER THROUGH DIFFERENT SECTIONS OF THE CHANNEL OF DOE RUN, MEADE COUNTY, KENTUCKY, AT DIFFERENT LEVELS OF DISCHARGE

	Discharge in cfs		
	15-25	40-50	80-100
Station I (Mile 0)	15-25	40-50	80-100
Station III (Mile 3.1)	20-30	60-70	130-150
Station V (Mile 7.7)	25-35	100-120	230-260
Stream Section	Average Speed of Flow, in ft/sec		
0.0 -1.2	0.6	1.1	1.3
1.2 -1.65	0.2	0.5	0.6
1.65-2.1	1.0	1.8	2.1
2.1 -2.82	0.2	0.5	0.6
2.82-5.3	1.0	1.6	2.0
5.3 -9.7	0.3	0.5	0.6
Time of passage, in ft/sec, from Mile 0.0 to 9.7	0.38	0.69	0.83
Time of passage, in hours, from Mile 0.0 to 9.7	37.3	20.6	17.1

the recognition of extreme variation in a single riffle before attempting to interpret upstream-downstream chemical data.

Suspended Solids and Sedimentation

Of 60 determinations of turbidity at Station I, 8 contained more than 50 turbidity units, and 3 more than 500 units (Fig. 9). Turbidities greater than 100 units were associated with periods of greatest discharge, and in periods of relatively constant discharge the slight increases in turbidity after heavy rainfall probably indicated influx of surface water into the subterranean aquifer, even though no appreciable

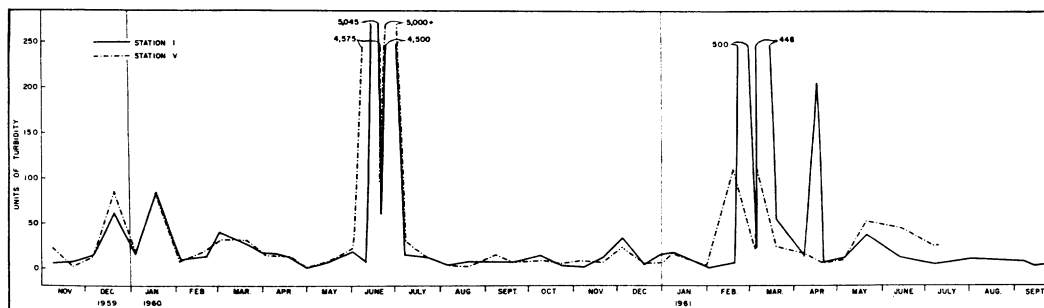


FIG. 9. Turbidities of water at 2 stations on Doe Run, Meade County, Ky. Data from Station III were omitted because of similarity to those from Station I.

changes in discharge were detected (compare Figs. 8 and 9 in the latter part of 1960). Minor fluctuations in turbidities between stations on the same date may reflect errors in sampling, or may be a function of time of flow and more long-term changes in turbidity. There appears, however, to have been some increase in the average turbidity from Station III to Station V in periods of modal flow; the means of 10 samples from each of 3 stations, taken when discharges were less than 50 cfs, are: Station I, 12.7; Station III, 12.9; and Station V, 15.3.

Generally, turbidities of less than 50 units were made up of suspended colloidal clays. Less than 10 per cent of the turbidity settled from a sample retained in a 1,000-ml graduated cylinder in a week (original determination, 33 units). At turbidities of less than 15 units, the water of the creek was somewhat "milky" in appearance, particularly in open areas that received direct sunlight, and apparently was a phenomenon of light refraction by finely divided, suspended solids. Filtration with "HA" membrane discs, pore size, 0.45 micron, resulted in total removal of turbidity that could be detected with the spectrometer. At high turbidities, specifically those in June 1960, and during high discharge in late winter and spring 1961, a much greater proportion was noncolloidal. After 24 hours, the surface water in a 1,000-ml graduated cylinder retained 30 per cent of the original determination of 5,000 units, but after a week of undisturbed settling the reading was 230 units. The largest particles found by microscopic examination of the sediment were fine sand, with a maximum diameter no greater than 0.25 mm (Twenhofel, 1939). The high turbidities in Doe Run probably originated in the drainage of Rushing River where runoff from cultivated fields moved directly into subterranean watercourses.

At times, backwaters of the Ohio River inundated Station V (Fig. 7) and allowed for considerable settling of sediments as illustrated by the average turbidities of 9

samples, collected at each of 3 stations: Station I, 142; Station III, 155; and Station V, 42 units. After clearing the downstream valley of Doe Run in preparation for impoundment, there was a pronounced increase in turbidities at Station V. Comparison of mean turbidities of 10 samples each from Stations III and V, 12.6 units and 80 units, respectively, reflects the influence of runoff from the denuded slopes and floodplain, the activities of earth-moving equipment, and transport of soil pushed into the stream during clearing operations.

Although the bottom types have been discussed, it seems appropriate to describe some specific aspects of sedimentation in Doe Run. Most sediments, excluding the marls that will be discussed later, were derived from erosion of the immediate banks, and, to a greater extent, from bed load from the subterranean channels supplying the stream. The frequency of abrupt bends in Doe Run (Fig. 1), and the degree of pool-riffle development in some sections (Table 1), allowed for many features of deposition of bed load because of great variation in competence of water passing through such an irregular channel (Braden, 1951). Also, differences in gradient allowed for deposition of deep, submerged beds of fallen leaves and other organic detritus in swift vortices downstream from obstructions in the channel, and the formation of transverse sills of gravels downstream from places where extremely swift water contacted relatively quiet waters of large pools and resulted in various kinds of hydraulic jumps (Braden, 1958). Those sills, and other deposits in the channel of Doe Run, were subject to movement in periods of high discharge.

Some major deposits in the upper 3 miles of Doe Run were associated with beds of macrophytes. Lateral bars of relatively fine sediments were formed in stands of watercress, *Nasturtium officinale* R. Br., and elongate bars were present beneath beds of *Potamogeton*, *Myriophyllum*, and *Nitella*.

One of the most puzzling deposits was the thin film of amorphous sludge formed

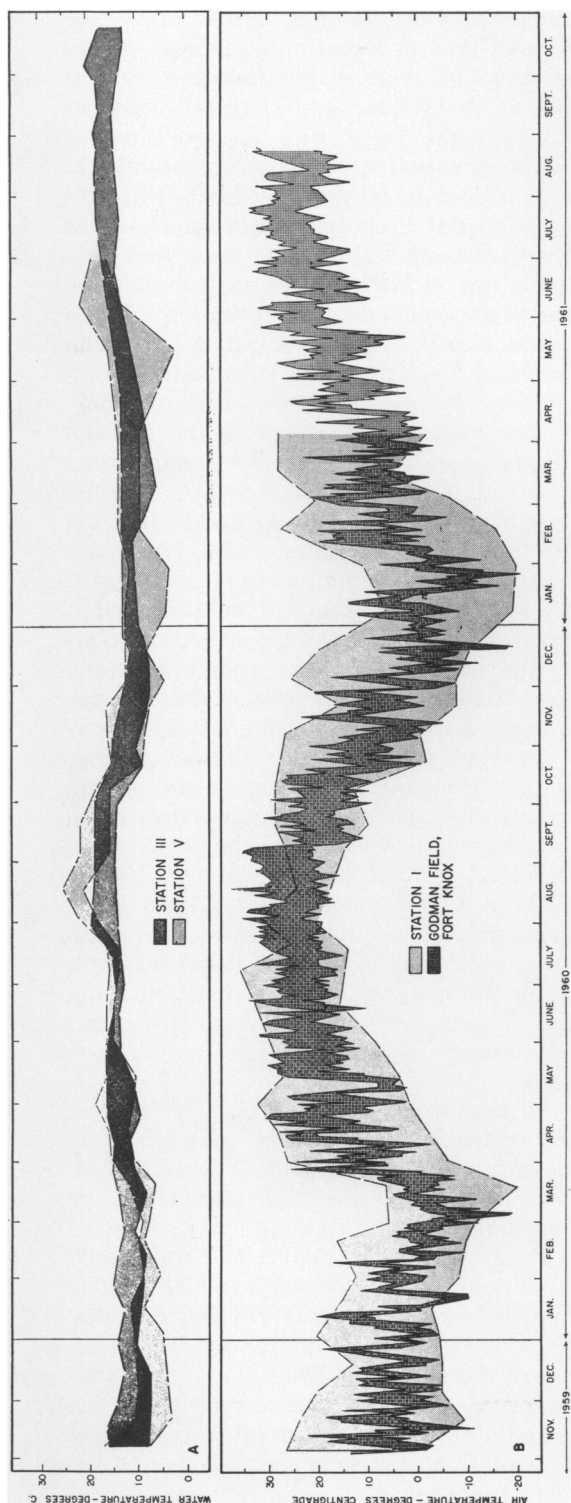


FIG. 10. Maximum and minimum water temperatures at Stations III and V, Doe Run, Meade County, Ky. (A), and maximum and minimum air temperatures at Station I compared with daily air temperatures at Godman Field Weather Station, Fort Knox, Ky. (B). In the latter, temperature changes from day to day of less than 2° C were disregarded.

in areas of moderate current after periods of high turbidity. Although the deposition of fine sediments was expected in quiet backwaters during flood, films frequently formed on stones, gravel, and vegetation in areas where velocities of flow were greater than 2 ft/sec. Violent agitation of samples of the material with distilled water resulted in suspensions frequently as stable, if not more so, than colloidal turbidities. At times, however, flocculation occurred, and the suspensoids were precipitated. Although flocculation of colloidal turbidities is known to be brought about by activity of various electrolytes, or by contact of one particle with another of opposite charge (Twenhofel, 1939; Irwin and Stevenson, 1951), it seems unlikely that adhesion to the substratum could be accomplished in the currents present, or that the negatively charged clays would be flocculated in the alkaline conditions generally persistent in Doe Run. The films appear to have been formed through biological activity and will be discussed later. Films exposed to the air dried rapidly, flaked, and fell or were blown into the water, where they sank to become incorporated into bottom sediments.

Temperature Relations

Seasonal air temperatures in the Doe Run area are moderate, the average January temperature is between 1.1 and 2.2°C, and that for July about 26°C (Kendall, 1941). Air temperature recorded at Station I by a maximum-minimum thermometer in a shaded place about 8 feet above the water compared favorably with data provided by the U. S. Army Weather Station at Godman Field, Fort Knox, Ky., 8.5 miles east and 1.8 miles south of the source of Doe Run (Fig. 10). Records of air temperature at Station I were discontinued in April 1961.

Throughout 1959 and 1960, water temperature at Station I was consistently between 13.0 and 13.5°C (usually 13.3°) in periods of modal discharge, but in spring 1961 it increased to between 13.5 and 14.5°C. The reasons for this change are not apparent, but may be related to

changes concomitant with the high volumes of discharge in 1961 (see Fig. 8). Temperatures at Station I varied somewhat in times of high discharge; the lowest temperature recorded was in January 1960, when a reading of 12.3°C was obtained, and the highest was on June 17, 1960, at 15.6°C. Variations of the same magnitude (from about 12.0 to 16.0°C) were recorded in the period of high discharge between late February and late May 1961.

Maximum-minimum thermometers at downstream stations were plagued by washout and by periodic inundation by the Ohio River at Station V. However, the records illustrate the gross features of temperature in the stream (Fig. 10). At Station III, the maximum temperature recorded was 20.0°C in August 1960, and the minimum was 6.1°C in March 1961. At Station V, the maximum and minimum recorded temperatures were 25.6 and 1.7°C, respectively. Usually, the greatest ranges of temperature occurred in late autumn and early winter at each of the downstream stations.

The major factor in warming natural waters during the day is the absorption of solar radiation, whereas cooling is controlled largely by air temperature (Ricker, 1934a). In Doe Run, the minimum water temperatures did not fall below 13.3°C at Stations III and V from late May to October, an indication that relatively high air temperatures at night were influencing water temperatures, with a resultant positive deviation from the temperature at the source. In periods of modal discharge (see Table 4), water passing from the source of Doe Run in the afternoon was heated by insolation in 1 or 2 hours, and maintained a positive deviation throughout the night so that heating began from a slightly higher point the following morning. Water that left Station I at night was delayed in the mill impoundments and received considerable insolation before reaching Station III the following day, thus maintaining the positive deviation.

Most factors influencing the rates and amounts of warming or cooling of water in

streams are interrelated. For example, the time of flow in Doe Run is decreased with increased discharge, thus the time water is subject to warming is reduced. Higher discharges in Doe Run had pronounced moderating effects on temperatures, as shown by data for summer 1960 (Fig. 10), when modal discharge began about August 1, water temperatures that had been relatively low in May, June, and July immediately rose 2 or 3 degrees at Station III, and as much as 10 degrees at Station V. At high levels of discharge, the speed and turbulence of the stream allowed little warming in backwaters, and except in the extreme discharge of 1961, when the water spread from "bluff to bluff" in places, the narrowness of the channel caused great reduction of the surface-volume ratio. Although turbulence usually increased with increased discharge, the amount of surface roughness, or "riffle," decreased as obstructions in the stream bed became more deeply covered with water. Thus, increased discharge reduced the amount of spray formed in passage over cataracts, dams, and steep inclines, and reduced the cooling effects of evaporation. In summer, careful measurements above and below Dam 2 indicated a slight decrease in temperature (0.05 to 0.1°C) downstream. The only ice that formed along Doe Run in winter, with the exception of thin layers in cut-off pools along the channel, resulted from the contact of spray with overhanging objects, and subsequent aggregation into ice concretions.

In periods of high turbidities, greater absorption of solar energy may occur in moving water (Ellis, 1936). Nevertheless, the reduction in light penetration may have a cooling effect by shading and preventing heating the bottom materials by absorbed insolation. In shallow streams such as Doe Run, in periods of low turbidity, warming of bottom materials in daytime may increase the temperature of the stream considerably. My few measurements of the temperature of sediments in upstream sections of Doe Run indicate that at maximal solar radiation the sediments are 0.1 to

0.9°C warmer than the water passing over them (16 measurements 0.1 to 1 inch below the sediment-water interface in water 0.5 to 1.5 ft deep; turbidities less than 10 units). Some heating may result from biological activity in the sediment.

The impoundments in the upper section of Doe Run allowed more warming of the water in that region than elsewhere in the stream. Preliminary investigations in the mill impoundments in June 1960 yielded surface temperatures above 25.0°C, which were much higher than any obtained at Station III. Accordingly, detailed studies were made of water movements through the pools and the concomitant modifications of temperature. Data from each of the 3 impoundments are similar, and findings in one pool are applicable to the others if minor variations in differential shading by riparian vegetation and differences in configuration of the channels are disregarded. For convenience, the pools will be referred to by the number of the dam concerned (Pools 1, 2, and 3, referring to the impoundments of Dams 1, 2, and 3, respectively).

On June 9, 1960, at an air temperature between 23.0 and 26.0°C and a discharge of about 40 cfs, a longitudinal series of temperature profiles was taken in Pool 3. The temperature of the water entering the pool was 15.3°C at the beginning of the study at 2:00 PM. The cooler water moved through the pool by a general underflow in areas of greatest depth, rose to the surface along a bar of sediments behind Dam 3, and passed over the dam into the stream below (Fig. 11A). A lens of warm water was retained in the pool and dissipated or passed over the dam at night when cooling occurred. Cross-sectional temperature profiles indicated that lenses of warmed water lay generally in the center of the pool (Fig. 11B-C), and were influenced very little by configuration of water masses beneath them. Discrepancies in isotherms resulted from movement of water during sampling, a serious drawback in the use of a single thermal element for temperature measurements in moving water.

Where cool density currents rose along the face of dams, a distinct line of demarcation was visible 1 to 3 feet upstream, presumably representing a thin boundary of mixing between the lens of warm surface water and the density current. Little warming could be detected in water going over the dam.

Wind action sometimes disrupted stratified flow in the mill pools. Such an occurrence in Pool 2 (Fig. 11D) was studied on August 3, 1960, from 8:10 until 11:30 AM. Air temperature ranged from 28.0 to 31.0°C, discharge into the pool was about 40 cfs, and the sky was cloudless. In early morning the pool was relatively homogeneous at its upstream end, but stratification and subsurface currents were beginning to form by late morning (Fig. 11D). The study was resumed at 1:30 PM, and it was found that during the 2 hours in which observations were not made there had been a rapid warming of surface water. About 12:45 PM a strong wind began blowing downstream, and by late afternoon the warmed surface water was being pushed over the dam and cool waters were being retained in the downstream part of the pool. During the afternoon, temperatures of 30.0°C were recorded at the surface in backwaters near Mile 2.3.

In winter, stratified flow in the mill pools was also present, but the configuration of the isotherms was quite different. On February 7, 1961, under a totally overcast sky and at air temperatures between 4.0 and 6.0°C, the discharge at the head of Pool 2 was 32 cfs, and water temperature was 11.2°. A longitudinal profile at points comparable with earlier studies indicated a density current in Pool 2 that must be classed as an interflow (Coker, 1954) because of the presence of differing waters both above and below the density current. This phenomenon was brought about by rapid cooling of surface water, its movement laterally and down the sides of the channel to contact colder water near the bottom and thus become concentrated in an area of maximum downstream velocity in the center of the cross section (Fig. 11F).

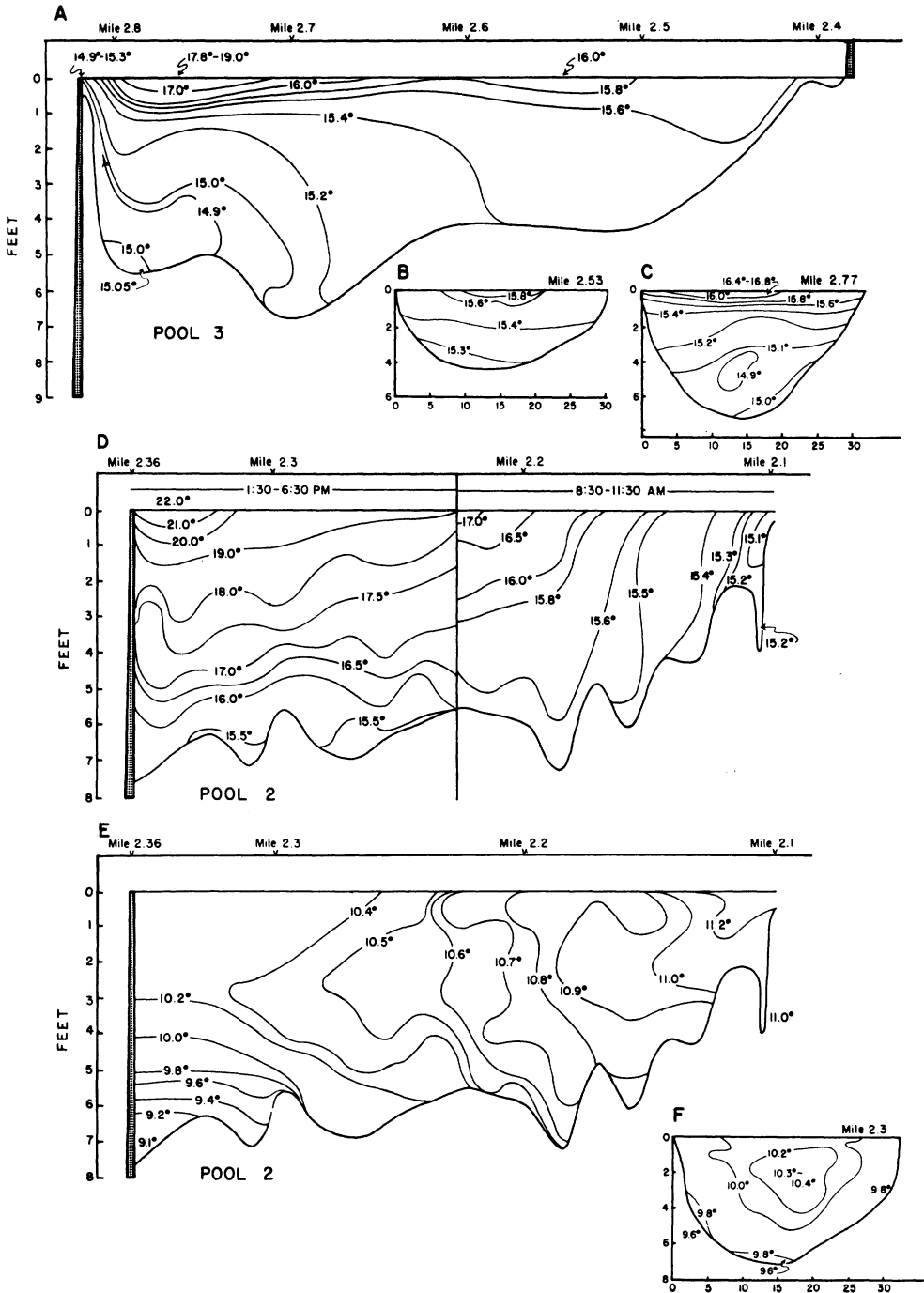


FIG. 11. Temperatures in mill impoundments of Doe Run, Meade County, Ky.: A—longitudinal profile of Pool 3, June 9, 1960; B, C—cross sections of Pool 3, June 9, 1960; D—longitudinal profile of Pool 2, August 3, 1960; E—longitudinal profile of Pool 2, February 7, 1961; and F—cross section of Pool 2, February 7, 1961.

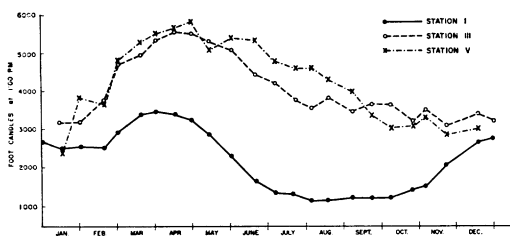


FIG. 12. Averages of incident-light measurements at 3 sampling stations on Doe Run, Meade County, Ky., 1960.

In Pool 3, a deposit of gravel, sand, and silt at the upstream face of the dam gave the cool underflow an inclined surface over which to rise over the dam in summer. In Pools 1 and 2, however, there were no such deposits, and water rose vertically about 4 and 7 feet, respectively, to clear the tops of the dams. Movements of water through Pools 1 and 2 in the manner shown in Figure 11A was occasionally seen, but less frequently than in Pool 3, probably because of the differences in vertical lift. Calculation of velocities required to lift the density current over Dam 2, using formulae of Churchill (1958), indicate a range from 0.4 to 1.0 ft/sec, varying with temperatures of the overlying water and the volume of discharge. These values are somewhat higher than those indicated in the data for time of flow (Table 4), and the discrepancies probably reflect the sporadic occurrence of the summer density currents in the pools, factors such as mixing of tracer dyes, and accumulated error in both sets of data.

Stratification, or stratified flow, occurred in some of the larger natural pools of the lower part of Doe Run, but temperature differences were less pronounced than in the impoundments. Similar stratified flows were found in pools of a small creek near Lexington, Ky., by Neel (1951), and by Slack (1955) in a creek in Indiana. In both instances the streams were smaller than Doe Run, with a greater pool-riffle ratio, and a lesser discharge.

Incident Light

There was much less light at Station I for 10 months of the year than at Stations

III and V. Light intensities at Station I were similar to those at the 2 downstream stations only in January and December (Fig. 12). Light intensities varied from date to date, and on the same day at different stations, because of changes in angle of the sun and cloud cover. There was an increase in incident light at all stations in February and March, but as the riparian foliage developed in April, levels of light ceased to rise, and then declined throughout the summer. This seasonal sequence was most pronounced at Station I, where large, overhanging trees completely shaded the water most of the day, and an understory of smaller trees and shrubs contributed to shading and scattering of incoming light. As the leaves fell in October and November, the incident light at Station I increased until it corresponded with seasonal decreases at other stations.

CHEMICAL ENVIRONMENT

Dissolved Oxygen

Concentrations of dissolved oxygen at Station I were rarely less than 70 per cent of saturation, and exceeded 85 per cent on a few occasions (Fig. 13). Prior to the period of high discharge in 1961 (see Fig. 8), the dissolved oxygen concentrations at Station I were relatively constant, but increased slightly in periods of highest discharge, and were lowest in periods of modal or submodal discharge. After the flood in March 1961, the dissolved oxygen content of the water at Station I became less predictable, and the highest and lowest values, 9.12 mg/l and 4.3 mg/l, were obtained after that flood. The reason for these changes is unknown.

Diurnal fluctuations in oxygen concentrations were erratic in samples obtained directly in the spring source. However, on July 22–23, 1961, the oxygen content 60 ft downstream increased during the daylight hours and decreased at night to the levels of samples taken at the source (Fig. 14A). These diurnal variations must be attributed to photosynthetic activities of a relatively pure stand of the moss *Fissidens julianus* (Mont.) Schimp., which cov-

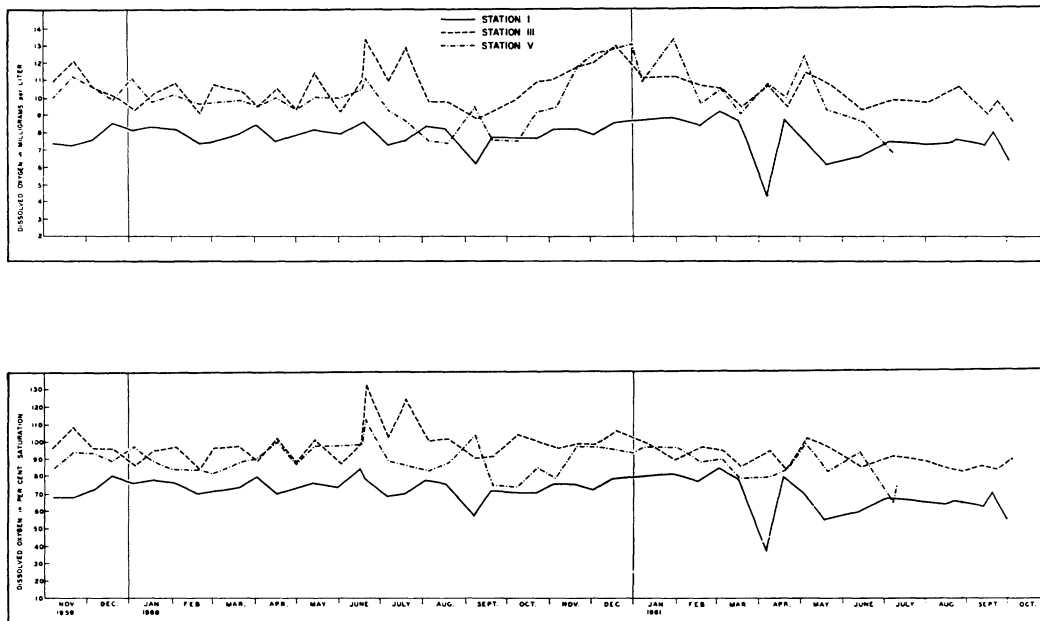


FIG. 13. Levels of saturation and amounts of dissolved oxygen at 3 sampling stations on Doe Run, Meade County, Ky.

ered about half the stream bottom in that area.

Upstream from Dam 1, prior to the high discharges of 1961, there were large beds of vegetation that quickly overcame the oxygen deficit of the spring waters in periods of high insolation, and often produced extreme supersaturations. On June 7, 1960, oxygen values ranging from 12.58 to 19.13 mg/l (saturation of 124 and 191%, respectively; water temperatures from 14.0 to 15.0°C) were obtained in Pool 1 between Miles 1.3 and 1.6; the average of 10 samples was 14.79 mg/l at an average temperature of 14.4°C. After most vegetation in the upstream areas was washed out, and at night, samples above Dam 1 retained an oxygen saturation deficit, and after a few hours of darkness the oxygen values at Dam 1 dropped nearly as low as those at Station I. This probably resulted from decomposition of leaves and other detritus in the pool, respiration of plants and animals, and replacement of water in Pool 1 (Fig. 14B).

The nearly vertical fall of water of about 7 feet over Dam 1 acted significantly in

moderating extremes in dissolved oxygen below the dam. On June 7, 1960, when saturation values were extremely high above Dam 1, dissolved oxygen content of water in riffles below the dam was 10.43 mg/l, about 103 per cent saturation. Conversely, on August 7, 1961, when saturation values of 84 to 96 per cent prevailed above Dam 1 (Fig. 14B), saturation values below the dam varied from 97 to 103 per cent (mean of 3 samples, 100%). The free fall of water over small dams is a significant factor in maintenance of oxygen levels downstream in some polluted streams; flow of water clinging to the face of a dam is less effective in aeration (Barrett, *et al.*, 1960). The latter phenomenon presumably occurred in Doe Run in periods of extremely low discharge, such as October 1961, when saturations between 85 and 90 per cent were present in riffles downstream from Dam 1, and water was flowing down the steep face of the dam rather than falling freely over it.

Samples from Mile 2.0, near the downstream end of a riffle area (Fig. 2), gen-

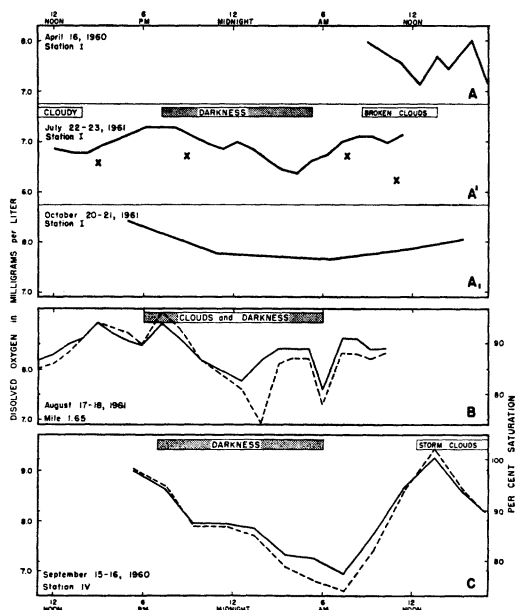


FIG. 14. Diurnal variation of dissolved oxygen at Station I (A), Mile 1.65 (B), and Station IV (C), Doe Run, Meade County, Ky., on various dates. Solid lines connect the absolute values; dotted lines, levels of saturation; and X's denote values obtained directly in the source.

erally yielded concentrations of dissolved oxygen slightly above saturation. The highest level recorded there was 13.5 mg/l in October 1960 (134% saturation), and the lowest level was 9.21 mg/l in July 1961 (93%). The average of 15 determinations was 10.31 mg/l, an average of 103 per cent saturation. The highest amounts of dissolved oxygen were present in periods of low discharge and high insolation, when thick stands of *Myriophyllum heterophyllum* Michx. and *Fissidens* were growing most rapidly, and low discharge allowed more time for water in pools and eddies to become supersaturated. The lowest values occurred in periods of high discharge and turbidity, when physical and biological aeration are least effective (Denham, 1938; Churchill, 1958).

Relations of dissolved oxygen in Pools 2 and 3 were similar to those in Pool 1, with supersaturations in daytime and slight deficits developing at night. Passage of water over the dams, however, tended to main-

tain 100 per cent saturation downstream. Supersaturations were found most often in relatively quiet water at the surface of pools in summer. Density currents, when present, exhibited some increase in dissolved oxygen in their passage through the pools, but were not as great as those in warm, quiet lenses of surface water influenced by photosynthesis of aquatic vegetation along the banks.

Dissolved oxygen content was more variable at Station III, where there were 2 seasonal highs in 1960 (Fig. 13). The first occurred in June and July and may be explained by increased photosynthesis through rapid proliferation of algae and macrophytes, and the second occurred coincidentally with cooling of water in autumn, following a long period of modal and sub-modal discharge. This latter high concentration is attributable to the cooling of the water and increasing photosynthesis resulting from reduced turbidities and relatively constant stream conditions. Depression of dissolved oxygen in September 1960, just prior to the surge in October and November, is not easily explained. It may have resulted from a combination of high water temperatures and the first heavy accumulation of fallen leaves in pools. In the high-gradient sections at Station III and between Stations III and IV, turbulence of the many riffles and cataracts would seem to preclude oxygen depletion. However, in a 24-hour study on September 15-16 at Station IV, only 1 determination with more than 100 per cent saturation was obtained, and most values were lower than 85 per cent (Fig. 14C). The high oxygen demand of leaf accumulations was demonstrated when the oxygen content rapidly decreased with shading by storm clouds. A similar "cloud effect" has been noted in other streams (Hornuff, 1957; Denham, 1938). Oxygen depletion as a result of decomposition of leaves in pools of small streams has been found in Indiana (Schneller, 1955; Slack, 1955), Illinois (Larimore, *et al.*, 1959), and elsewhere. It is probably of common occurrence in smaller streams when accompanied by reduced discharge

and high water temperatures in autumn. Covering and shading of many beds of vegetation by fallen leaves, especially in the shallow, upstream parts of Doe Run, presumably decreased oxygenation by inhibiting photosynthesis.

Downstream from Mile 5.0, the increased number and depth of pools (Table 1) allowed more accumulation of silt and organic debris than in more upstream sections. In addition, a lack of extensive vegetation, higher summer temperatures, and lentic conditions resulting from backwaters of the Ohio River, caused decreased amounts of dissolved oxygen at Station V (Fig. 13). The seasonal curves representing oxygen concentrations at Station V are more typical for streams (Butcher, *et al.*, 1930; Ricker, 1934a; Reid, 1961), in that the greatest amounts of oxygen were present in winter as a result of water temperature-oxygen saturation relationships. After impoundment of Doe Run in July 1961, seepage from the banks influenced deoxygenation of water near the mouth of the creek. The seepage water was black and malodorous, apparently as a result of decomposition of layers of leaves that had been buried previously by sedimentation from backwaters of the Ohio River.

Carbon Dioxide, pH, and Alkalinity

Subterranean waters are notoriously rich in carbon dioxide collected during passage of the water through a soil atmosphere more generously supplied with that gas than the epigeal atmosphere (Foster, 1942). Combination of carbon dioxide with water results in formation of carbonic acid, which then causes relatively insoluble carbonates to go into solution as bicarbonates. A dilute solution of bicarbonate, at equilibrium, is generally basic in pH, but in some springs, as in the Doe Run system, carbon dioxide is in excess, causing slightly more acid conditions (Shoup, 1948; Hem, 1959). This occurs when the amount of available gas is greater than the available carbonate, and in open solution channels like those presumably feeding Doe Run, this could

result from discrepancies in stone-surface-to-water-volume ratios.

At Station I alkalinities were highest in late summer, autumn, and early winter periods of modal and submodal discharge, and the related carbon dioxide and pH values were highest and lowest, respectively, at those times. The amount of free carbon dioxide was less and 40 mg/l on few occasions during periods of extreme discharge (compare Figs. 8 and 15). The diluting effect of the passage of large volumes of surface water through the aquifer feeding Doe Run was obvious in depression of alkalinities, and often in elevation of pH values above 8.0.

Alkalinity and pH at Station I fluctuated randomly with time (Fig. 16A). Downstream from the source, pH, alkalinity, and carbon dioxide levels varied with discharge, photosynthetic activity, temperature change, and deposited organic debris. Of course, turbulence caused physical loss of carbon dioxide from the water, but decomposition and accrual from tributary springs supplemented the amounts present. Physical loss due to stream turbulence was not as much as expected. On June 7, 1960, pH values exceeding 7.3 were found only in quiet backwaters in Pool 1, on the shoreward side of beds of *Nitella flexilis* (L.) Ag. In those areas, pH measurements greater than 8.0 were obtained (maximum 9.1) indicating total use of free carbon dioxide by the plants (Ruttner, 1960). Alkalinities in the backwater areas ranged from 175 to 200 mg/l, but no precipitation of carbonates, expected with the marked reduction in carbon dioxide, was found. However, Tindall (1962) found limited deposition of carbonate on *Nitella flexilis* from Doe Run. Alkalinities in the main currents of the pools were reduced from 224 mg/l at Mile 1.2, to 214 mg/l near Dam 1, but no consistent increase in pH was detected (range 7.1 to 7.3). The slight reduction of alkalinity in the main current must have resulted primarily from mixing of water from the sides, but the small amount of change emphasizes the relative

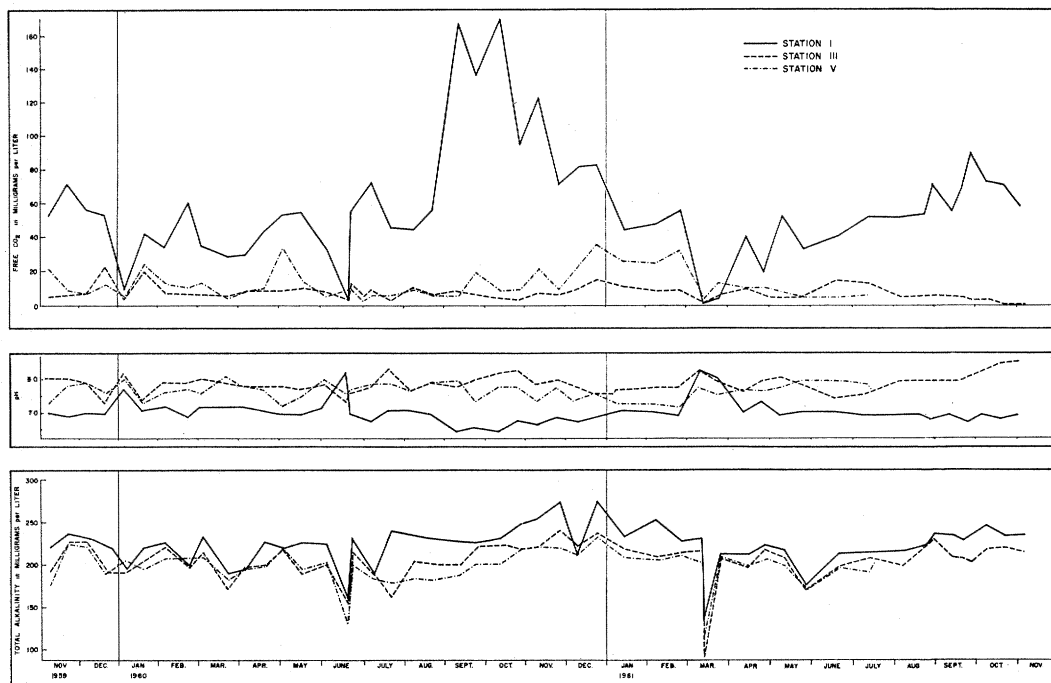


FIG. 15. Dissolved carbon dioxide, hydrogen ion concentration (as pH), and methyl purple alkalinity at 3 sampling stations on Doe Run, Meade County, Ky.

independence of lateral water masses from the main current in a stream.

Fluctuations in pH and alkalinity were not so pronounced at Mile 1.65 on August 16–17, 1961, as they presumably were before most of the vegetation was washed away. Moreover, they were erratic in time, with no obvious relation to daylight (Fig. 16B), and may represent the net physical loss of carbon dioxide in the pool, and fluctuations at the main spring. The values undoubtedly were modified by accrual of carbon dioxide from decomposition in Pool 1, but this was minimal because much of the detritus had been removed by high waters in spring 1961.

At Mile 2.0, pH values ranged from 7.0 to 8.3 in 22 samples, with high alkalinities persisting except in periods of high discharge. High pH values occurred in periods of low discharge and pronounced photosynthetic activity, and in periods of high discharge. Decomposition and respiration in Pool 2 apparently bolstered the

amounts of carbon dioxide enough to maintain equilibrium and prevent deposition of

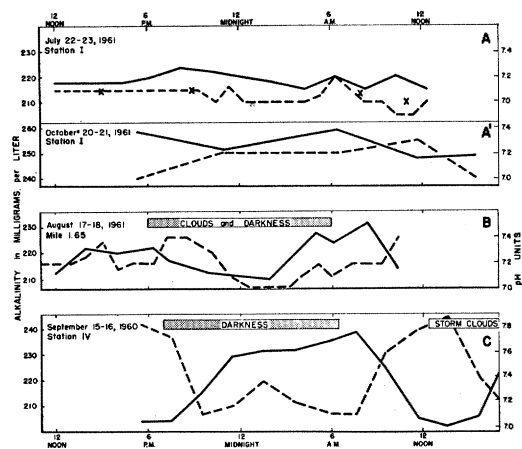


FIG. 16. Diurnal variations of pH and methyl purple alkalinity at Station I (A), Mile 1.65 (B), and Station IV (C) on Doe Run, Meade County, Ky., on various dates. Dotted lines connect pH values, solid lines connect alkalinities, and X's (in A) denote pH values obtained in the immediate source.

carbonates. As noted before, accumulation of marl was obvious on the face of Dam 2 (Mile 2.36), but not upstream from there. Because samples from Doe Run usually were obtained in daylight, the influence of photosynthesis and warming of the water caused most series to show a reduction in alkalinity between Stations I and II. Nevertheless, some samples on cloudy days, and at night, exhibited a slight increase in alkalinity in that section (on the order of 5 to 15 mg/l), suggesting solution of carbonate from the stream bed.

Downstream from Dam 2 (Figs. 1 and 2), the balance between carbon dioxide and bicarbonate was disrupted causing precipitation and accumulation of carbonate. There were marl accumulations in the upstream two-thirds of Pool 3, but the bottom in the downstream third was silt and organic muck, with little carbonate present. Again, as in Pools 1 and 2, an increase in carbon dioxide indicated by a lowering of pH, occurred from the head of Pool 3 to near the dam. On June 9-10, 1960, the pH range in the pool was from 7.8 in the upstream end to slightly less than 7.6 just above the dam.

The relationships of alkalinity, pH, and carbon dioxide in the marl area are exemplified by data from Station III (Fig. 15). There, pH values were seldom below 7.5, and often exceeding pH 8.0. Similar situations in a Virginia stream (Steidtmann, 1935), and in lakes in New York (Deevey, *et al.*, 1954) and Germany (Ohle, 1934, 1952), were interpreted as indicating presence of a stable, colloidal form of carbonate, which allowed supersaturations to exist. To test for such colloids, 6 aliquots of water from Station III were filtered through "HA" filters about an hour after collection. The original determination of 239.5 mg/l alkalinity persisted after 3 filtrations, with pH at the beginning of filtration ranging from 8.1 to 8.3. It must be concluded, therefore, that if colloidal carbonate existed in Doe Run, it was smaller than 0.45 micron in diameter. Ruttner (1948) suggested the presence of an

unrecognized form of soluble carbonate in naturally hard waters. Hastings, *et al.* (1927) and Eyster (1958) found that phosphates in solution allowed conditions of apparent supersaturation of bicarbonates to exist, and sewage effluents containing condensed phosphates and other materials inhibited deposition of carbonates in an English stream (Edwards and Heywood, 1960; Heywood and Edwards, 1962). Elucidation of processes involved in maintenance of supersaturations of bicarbonate is a study that may be of major importance in understanding the carbon dioxide relationships of limestone streams.

Reduction in alkalinity between Stations I and III was most pronounced during periods of modal discharge and high water temperature. Diurnal variations in alkalinity and pH were marked in the single 24-hour study of the marl area (Fig. 16C), indicating a significant influence of biological activity in daylight hours.

Downstream from the marl area, carbon dioxide content varied inversely with dissolved oxygen. Data for Station V indicate a slight increase in alkalinity at modal discharge when compared with data from Station III (Fig. 17), and on other occasions as in periods of high discharge and concurrent presence of backwaters of the Ohio River at Station V. This increase in alkalinity was accompanied by increase in carbon dioxide content, and decrease in pH. Some fluctuations in pH at that station and elsewhere may be attributable to organic acids entering from seepage along the banks (Wherry, 1920; Shoup, 1950).

Total Iron

The iron in Doe Run presumably originates through leaching of ferrous compounds (primarily ferrous carbonate) from soil and limestones by anaerobic and carbon dioxide-rich ground water, and from iron-rich soil particles carried as turbidity. Determinations of total iron of 0.31 and 0.36 mg/l at Stations I and III, respectively, were reduced to 0.02 and 0.03 mg/l after 3 filtrations through "HA" filter discs.

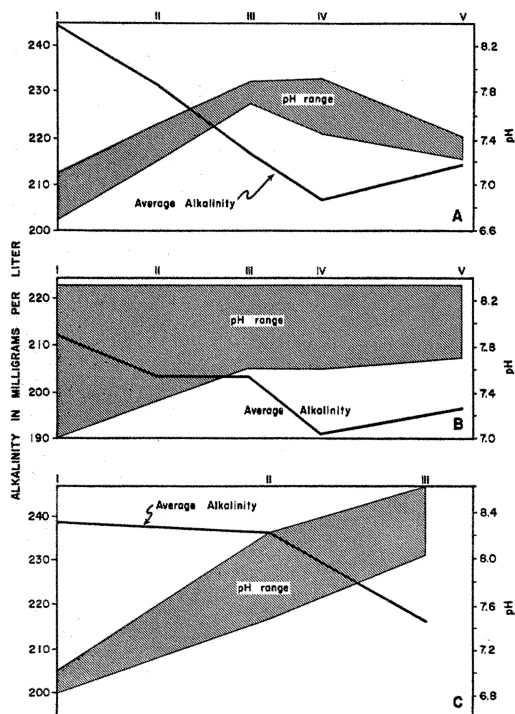


FIG. 17. Longitudinal variations in pH and methyl purple alkalinity at various levels of discharge, Doe Run, Meade County, Ky. A—4-sample series, flow 60 cfs at Station I, samples taken between 10:00 AM and 2:00 PM; B—5-sample series, flow 60–350 cfs at Station I, samples taken as in A; and, C—5-sample series, flow 40 cfs at Station I, samples taken between 11:00 AM and 2:00 PM.

These values correspond to the 0.02 mg/l solubility of ferric hydroxide given by Stumm and Lee (1960) for highly oxygenated waters.

Total iron was most abundant during periods of high discharge and turbidities, reflecting the iron in suspended sediments. Trends in iron concentrations were similar at all stations; no significant differences existed between stations in the overall amounts present (Fig. 18).

Phosphate Phosphorus

Phosphate phosphorus was highest at Station I in periods of modal discharge in 1960. This resulted from concentration or lack of dilution of the subterranean waters. In 1961, there was little increase in phos-

phates with resumption of modal discharge in June (Fig. 18). Slight, but consistent, reduction in phosphate occurred from upstream to downstream in the 1960 period of modal discharge, indicating some utilization of the material. Slack (1955) also noted a gradual downstream depletion of phosphate in 2 Indiana streams.

In times of relatively high discharge, phosphates were higher at the downstream stations than at Station I, although the increased variability at downstream stations obscures the relationship. These data agree with what might be expected because reduction of phosphate occurred when concentrations of dissolved solids were greatest and during periods of greatest growth of attached algae and macrophytes. Increases in phosphates downstream in winter may be attributed to decomposition and accrual from runoff and seepage.

Phosphate phosphorus and total iron usually were present in inverse proportions in Doe Run (Fig. 18). Small amounts of phosphate probably were bound with iron through oxidation of ferrous iron to some form of ferric phosphate as in certain lakes at turnover (Einsele, 1938). This is borne out by filtration experiments that resulted in lowering of phosphate values by only 25 to 29 per cent (from 0.32 mg/l to 0.23 mg/l) accompanied by an almost total removal of iron. These results indicate a considerable range in the presumed iron phosphate component of total phosphate phosphorus.

Some of the phosphate may come from commercial fertilizers used in the watershed, but a lack of correlation between high phosphate and high discharge seems to preclude this. Probably, the phosphate is being slowly leached from detrital material deposited in the limestones (Graf, 1960b).

Nitrate and Nitrite Nitrogen

Concentration of nitrate nitrogen generally diminished throughout the study (Fig. 18). When data for the 3 periodically sampled stations are compared, there is a decrease in amounts of nitrate from

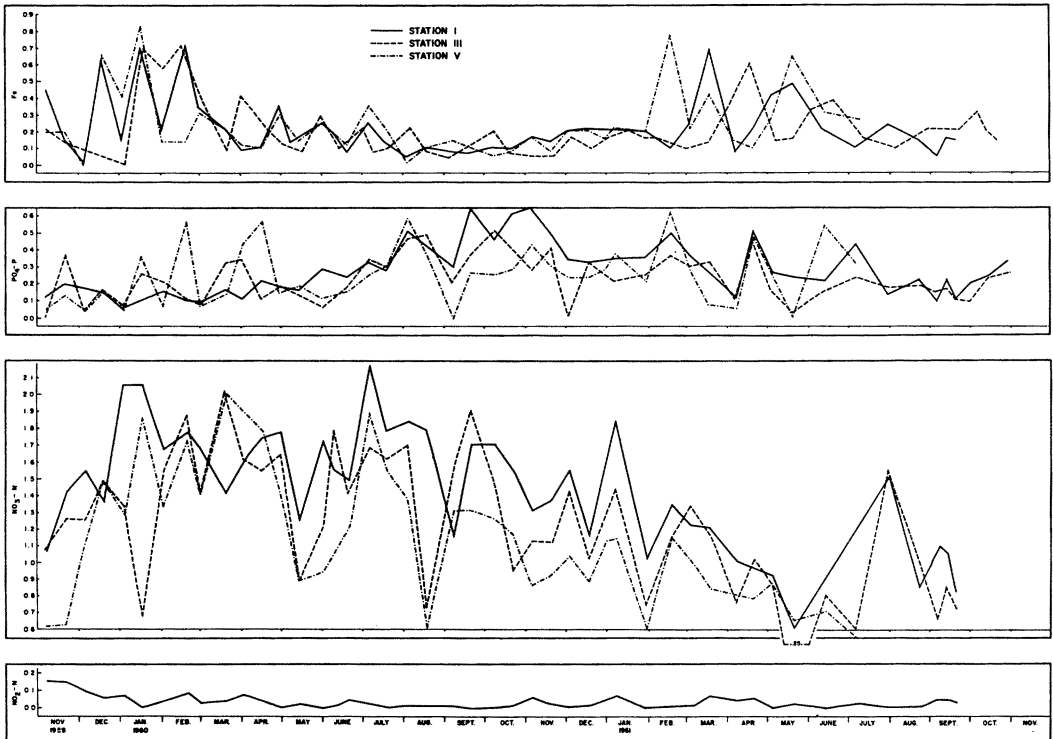


FIG. 18. Amounts of total iron, phosphate phosphorus, nitrate nitrogen at 3 sampling stations, and amounts of nitrite nitrogen at Station I on Doe Run, Meade County, Ky. All values are given as mg/l.

upstream to downstream, indicating some biological utilization over the length of the stream. Some decrease of nitrate was found in the course of an Indiana creek (Slack, 1955), and the changes were of the same order of magnitude as in Doe Run.

Nitrite nitrogen was consistently less than 0.1 mg/l, and because of its low concentration was subject to considerable error in determination. Nitrites were highest at the beginning of the study (Fig. 18), but those early data may have resulted from lack of precision in technique at that time.

Although the amounts of nitrate and nitrite nitrogen in Doe Run generally are of the magnitude found in natural, unpolluted waters, there is presumptive evidence for organic pollution of the aquifer from domestic sources. I know of one instance in Meade County where sewage was shunted directly into a flowing subterranean stream, for convenient disposal, and

sewage from rural facilities has been known to pollute many such water tables (Foster, 1942). The decrease in nitrate throughout the study, however, implies that the relatively high levels found earlier were a result of fertilizer application somewhere in the drainage area, and subsequent movement into Doe Run through surface runoff.

THE BIOTA

Algae and Higher Plants

In small, swift streams such as Doe Run, benthic algae are of primary importance since true phytoplankton rarely occurs (Eddy, 1934). Blum (1956a, 1957, 1960) provided excellent reviews on the ecology of algae in flowing waters, and his papers were used extensively in preparing this section. Identifications of algae were made using keys of Drouet (1959) for the blue-greens, and of Tiffany (1930), Tiffany and Britton (1952), Prescott (1951), and Thomp-

son (1959) for other groups; abbreviations of the names of authorities are from those works. Identifications of many diatoms were provided by Charles Brohm (pers. comm.), who made a special study of them in Doe Run.

The most usable method of classifying benthic algae from my point of view lies in the study of aspect (Symoens, 1951), or habit of growth, through consideration of structural modifications of the species concerned. Algal groupings of Doe Run fall into 4 broad categories, 2 of which were modified from Cedergrén's (1938) classification: (1) those with a firm mode of attachment and a highly flexible thallus, occurring in currents; (2) cushionlike or encrusting species that grow appressed to substrates in current; (3) matted or loosely arranged forms occurring attached or unattached in quiet pools, eddies, or in areas of almost laminar flow; and (4) subaerial species attached as encrusting mats in zones of spray, on waterfalls, on emerged stones, or on muddy banks and bars along the channel. These categories are not entirely satisfactory since some ubiquitous species occur in more than one, or there were gradational habitats where species were "out of place."

Attached Rheophilic Algae

Large, macroscopic sexual thalli of *Batrachospermum* sp. and *Lemanea* spp. were major components of the algal flora of the upstream 5 miles of Doe Run at certain times. However, *Chantransia* stages of both algae contributed most significantly to communities of encrusting forms throughout the year. *Batrachospermum* was most abundant as macroscopic thalli from October through March each winter, and occurred in sparse stands throughout the summer of 1961; it was absent as macroscopic thalli in the summers of 1959 and 1960 (Minckley and Tindall, 1963). The alga was restricted to the areas adjacent to springs in the Doe Run system, a distribution attributed to the generally constant conditions there.

Lemanea, on the other hand, inhabited

precarious substrates afforded by waterfalls, swift chutes, dams, and areas subject to continuous impact by falling water. The distribution of *Lemanea* began where *Batrachospermum* left off, and ranged from the face of Dam 1 to the swift, marl-encrusted riffles at Station IV. In the downstream portion of this range, *Lemanea* was limited to the swiftest waters and was seldom found in the marl area except on lips of cataracts where it was abundant, and where turbulent water caused physical removal of deposited carbonate. In riffles of the marl area, growth of *Lemanea* appeared limited in summer by rapid accumulation of marl after velocities were reduced and the creek assumed modal discharge. Greatest proliferation occurred in winter and spring.

Cladophora glomerata (L.) Kuetz. apparently represents, with its associates, a stream community found throughout the world in suitable habitats (Blum, 1956a). In Doe Run, *C. glomerata* was rare at Station III, but was abundant downstream from Mile 5.6 where it often covered all available substrates in swift, gravel-bottomed riffles at modal discharge, with exception of narrow channels directly in the swiftest currents. After the banks at Station IV and above were cleared of riparian vegetation, *C. glomerata* became the dominant alga in most marl riffles where it shaded the encrusting communities completely, and apparently killed them. This extension of the range presumably was in response to greater amounts of light. Blum (1957) noted that *Cladophora* in the Saline River, Michigan, disappeared with leafing of riparian trees in spring, indicating an effect of shade and a high-light requirement by the alga. The greatest abundance of *C. glomerata* in Doe Run was correlated most closely with modal discharge rather than with season (except in the indirect way that discharge was seasonal); however, when large beds were found in winter, they were invariably on unshaded riffles.

C. glomerata is markedly affected by deposition of silt in the thallus because of the

filtering action of the closely packed filaments (Blum, 1957). Siltation was followed frequently by mechanical detachment of the thalli during periods of modal discharge, causing initiation of a renewed period of local growth. This was materially augmented by accumulation of marl on some partially emerged thalli.

Cladophora fracta (Dillw.) Kuetz. grew on mill dams and in rapids adjacent to dams in the upstream 3 miles of Doe Run. It was perennial in those habitats, and often occurred, along with various encrusting forms, on shells of the snail *Goniobasis*. The alga also colonized tags used to mark various fishes at Station II. It should be emphasized here that the pattern of distribution of *C. fracta* and *C. glomerata* in Doe Run is in direct contrast with findings of Anderson and Lundh (1948). They reported that *C. fracta* substituted for *C. glomerata* when the velocity of flow decreased, and that *C. fracta* occurred downstream with *C. glomerata* most common upstream.

Characteristic associates of *Cladophora* in Doe Run were members of the diatom genera *Cocconeis*, *Diatoma*, *Synedra*, and *Cymbella*. Also, there were many species of blue-green algae and green algae, and the rhodophyte *Audouinella violacea* (Kuetz.) Ham. present. Associates of *Cladophora* in other parts of the world are discussed by Margalef (1960) as "Series 'Cladophoretalia'."

No other attached green alga was more abundant than *Cladophora* in the mainstream. Others of frequent occurrence were *Microspora stagnorum* (Kuetz.) Lagerh., *Ulothrix zonata* (Weber and Mohr) Kuetz., and *Bacillaria crassa* Hoff. and Tild., the latter from the carapaces of turtles.

Green algae with thick, gelatinous sheaths that also may be included under this general grouping, but were rare in the mainstream, were: *Stigeoclonium tenue* (Ag.) Kuetz., *Tetraspora gelatinosa* (Vauch.) Desv., and *Apicystis brauniana* Naeg.

Chaetophora elegans (Roth) Ag., *C. incrassata* (Huds.) Hazen, and *Stigeoclonium*

tenue occurred throughout late winter and spring in Tributary II-a, and also in Tributary I-j in April 1961. Generally, *C. elegans* was attached to leaves, twigs, and bedrock where flow was shallow and relatively slow. *C. incrassata*, having a more compact, gelatinous thallus, occurred in swifter waters, but was also found adjacent to colonies of *C. elegans*. *Stigeoclonium* was an uncommon component in most collections of *Chaetophora*. These algae appeared very vulnerable to washout, but rapidly recolonized open, sunlit areas, attaining maximum development in 2 to 4 weeks.

No collection of algae from Doe Run lacked diatoms, and filamentous genera such as *Melosira* and *Cymbella* occurred abundantly in swift waters throughout the creek at certain times. Diatoms also made up a major part of the epiphytes on larger algae and higher plants, with the genera already listed, plus *Diatoma* and stalked species of *Gomphonema*.

Encrusting Rheophilic Algae

Nostoc verrucosum Vauch. was one of the most widespread algae in both the mainstream and tributaries of Doe Run. It was most abundant in spring on smooth stone or concrete tops of mill dams, and also as an epiphyte on *Fissidens* near Mile 0.5, and on marl near Mile 5.6, in May 1960. A hard, compact alga, possibly *Palmella miniata* Liebl., also was epiphytic on mosses at Station I and in Tributary IV-b. It had the superficial appearance of a *Nostoc*, but was composed of small, ovoid cells separated by definite sheaths.

Many noncalcareous, encrusting algae are subaerial in some instances, but through rapid development underwater in periods of greater-than-normal discharge they retained fine silts and colloids as films on other substrates. During June 1960, I examined film accumulations for the 2-week period following high discharges. One day after the peak discharge the thin film, slightly more than 1 mm thick, was inhabited by large numbers of ciliates and

bacteria. Four days after the flood, diatoms were the dominant organisms; *Synedra*, *Achnanthes*, *Nitzschia*, and many species of *Navicula* were present. Bacteria and protozoans were not as obvious as before, and a few trichomes of an undetermined blue-green alga were on the surface of the 1-mm-thick film. After 9 days, *Phormidium autumnale* (Ag.) Gom. was abundant as a thin, irregular layer over the surface of the film; the average thickness of the overall deposit was about 1.5 mm, and many diatoms were present beneath the blue-green alga and among its loosely twisted trichomes. In 12 days, the common organism was *P. autumnale*, and a few other species, including some diatoms, were present on the surface. *Oscillatoria splendida* Grev. was present, and living diatoms were abundant inside the covering layer of *Phormidium*. Fourteen days after the flood, the mat was above water, but was being saturated by water splashing over the stone. *Phormidium autumnale* was growing rapidly in the subaerial habitat, and there were no other algae at the surface of the mat. The *Phormidium* layer was about 1 mm thick, and the overall film deposit was 3 mm, including the alga. The next time the area was visited the film had dried, flaked, and most of it had fallen into the stream.

Films of algae and amorphous "sludge," presumably developing in the same manner, were common in Doe Run after periods of high turbidities, and sometimes at modal discharge. Fritsch (1929) recorded encrusting communities of *Phormidium autumnale* and *P. retzii* (Ag.) Gom. in English streams, and suggested a succession from *Chamaesiphon* to *Phormidium* at his stations. Likewise, Nelson and Scott (1962) noted development of "microphyto-benthic ooze" in summer in the Middle Oconee River, Ga., and other such ooze deposits have been recorded in streams by many workers. Such deposits may afford a profitable line of research in understanding stream ecology, at least from the standpoint of productivity.

Films as described above, thick, gelatinous layers of diatoms, and colonies of blue-green algae, were systematically grazed by *Goniobasis* at all stations when present. Grazing by other aquatic organisms was rarely seen in Doe Run, but has been found to limit algal abundance in a number of freshwater situations (Brooks, 1954, 1955a, b; Douglas, 1958; and others).

Where substrates were submerged more than a few inches in swifter waters, and mostly in upstream areas (Stations I-III), thin mats of *Oscillatoria splendida* and *O. amoena* (Kuetz.) Gom. sometimes developed. *O. splendida* was more abundant in flowing water, however, than *O. amoena*, which usually grew in eddies and pools.

In the marl area of Doe Run, in places other than swift cataracts, chutes, or the faces of dams, a calcareous, encrusting community of algae occurred. Scraping the poorly consolidated surface layers from a "fresh" marl exposed an underlying layer of greenish-yellow algae that included *Phormidium incrustatum* (Naeg.) Gom., *P. tenue* (Meneg.) Gom., *Oscillatoria* sp., *Gongrosira lacustris* Brand, and rarely, *Chlorotylum cataractum* Kuetz. On stones recently recolonized after being exposed by low water, *Gongrosira* formed small, heavily calcified colonies that proliferated laterally to coalesce and develop a firm, crustose layer. *Phormidium* subsequently invaded these colonies and became the dominant species in "mature" marls of the stream. In swifter areas, trichomes of blue-green algae appeared unable to persist projecting from the surface of the mass, and the pseudoparenchymatous *Gongrosira* remained as the dominant organism. Fritsch (1949, 1950) also noted invasion of *Phormidium* in developing marls, but into the tufts of *Schizothrix* that made up the bulk of the calcareous communities studied by him. *Phormidium* supposedly causes calcareous crusts to become "especially stony and resistant [Blum, 1956a]."

Other algae in calcified, encrusting communities of Doe Run included many diatoms, the Chlantrisia of *Lemanea* and

Batrachospermum, various *Oscillatoriaceae*, *Cladophora*, *Vaucheria*, and sexual thalli of *Lemanea*, but all are considered incidental to marl formation. *Audouinella* was rarely taken in marls of the main channel, but was common in marl nodules on twigs and other debris near dams, and once in spray from a cataract at Station IV. *Gomotia* sp. (probably *G. holdenii* Coll.) was found on *Goniobasis* at Stations I and II, but snails from Stations III and IV usually were encrusted with *Gongrosira* and *Phormidium*.

Little information is available on the ecology of deposition of stream marls, even though they have been recorded in both recent and fossil deposits in North America and elsewhere (Graf, 1960a, b). The largest accumulations known to me occur in small, spring-fed streams of the Arbuckle Mountains, Okla., and are more than 100 feet thick and half a mile long (Emig, 1917). Other, larger deposits of this type are known in central Europe and in other parts of the world (Gessner, 1959).

Marl formation by activities of plants may occur in 3 different ways (Gessner, 1959): (1) plants may physically increase the surface area, allowing greater contact of the water with air and enhancing rapid loss of carbon dioxide and evaporation; (2) plants may extract carbon dioxide from the water and thereby cause precipitation of carbonates; or (3) they may extract carbon dioxide from bicarbonates in the water, elevate the hydroxyl-ion concentration, and promote carbonate deposition. Deposition of carbonate on a given plant necessitates, of course, that the plant grow faster than marl accumulates, except where evaporation and loss of carbon dioxide, or evaporation, are involved. Mosses were important in the deposition of marl by the first method in the Doe Run system, primarily in some tributaries and on the faces of Dams 2 and 3. Marl formed in this way was soft and tufalike, crumbling rapidly when subjected to freezing and thawing, or exfoliating in slabs and shattering on contact with the ground. Mats of larger algae, such as *Cladophora* and *Vaucheria* stranded along

the banks of the creek, often were marly to the touch, probably as a result of evaporation of water brought into the mat by capillary action (Gessner, 1959), and with invasion of blue-green algae sometimes were transformed into soft, porous "biscuits" of marl. Epiphytes on *Cladophora*, *Lemanea*, and other large algae, on higher plants (rarely), and algae living on shells and skeletons of invertebrates, apparently resulted in the encrustations found there (see Young, 1945).

Organisms contributing to marl deposition in streams include members of most divisions of algae and many higher aquatic plants (Gessner, 1959; Welch, 1935). It seems probable that many species involved in the formation of stream marls require currents because of an "inherent current demand" (Ruttner, 1953; Whitford, 1960b). Marls from Doe Run, brought into the laboratory or displaced into backwaters of the creek, were quickly overgrown by species characteristic of silted bottoms or sediment films (e.g., *Phormidium autumnale*, *Oscillatoria* spp., and diatoms). It seems logical that the need for rapid renewal of films of water near thalli or marl-encrusted algae, at least, and consequent maintenance of a high diffusion gradient of nutrients near the plant (Whitford, 1960b; Whitford and Schumacher, 1961) would be even more important for those half-buried species than for the filamentous species usually cited as demonstrating such a "demand" (*Batrachospermum*, *Lemanea*, *Cladophora*, etc.; see Whitford, 1960a, b). Also, the current assists in removal of silt deposits and the prevention of such deposition.

Formation of marl on a given substrate through algal activities occurs by secretion or precipitation of crystals of monocarbonate between algal filaments or as tubes around the filaments (Blum, 1956a; Gessner, 1959). In algae that grow in tufts, such as *Schizothrix*, crystals accumulate at the bases of the tufts, making it more compact than the terminal areas where marl is soft and relatively amorphous. In the

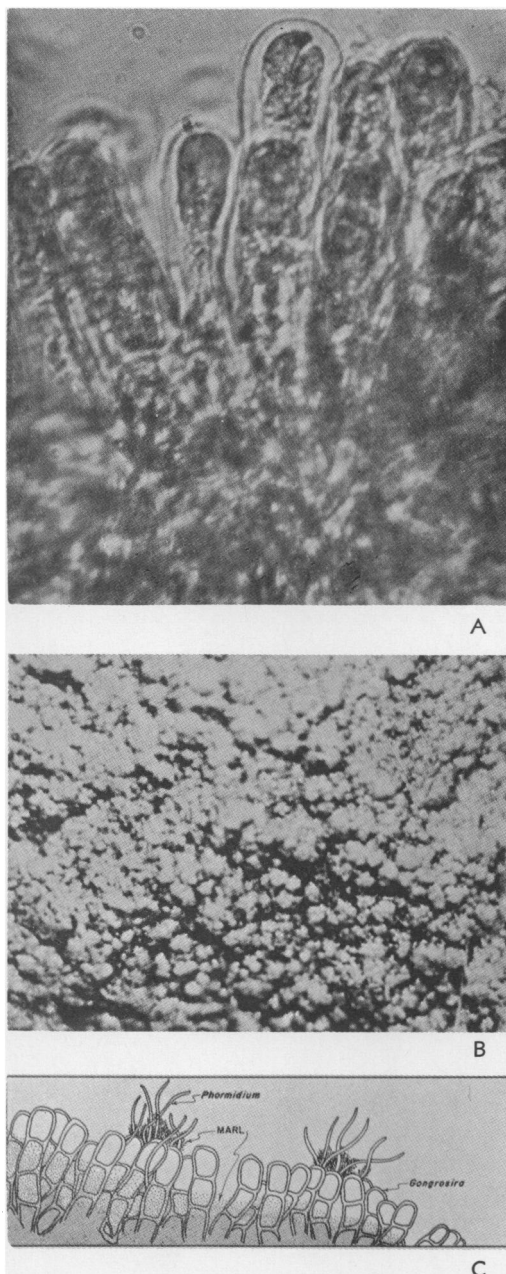


FIG. 19. Marl algae from Doe Run, Meade County, Ky.: A—photomicrograph of *Gongrosira lacustris* digested from marl with N/50 HCl; B—photograph of a "living marl" from Station IV illustrating the accumulation of carbonates in "tufts"; and C—composite sketch from photomicrographs of marl algae illustrating the projection of *Gongrosira* and *Phormidium* from the marl and some aspects of marl accumulation.

pseudoparenchymatous *Gongrosira* of Doe Run, a similar effect was obtained by accumulation of crystalline carbonates in and on the thallus of the plant, with trichomes of *Phormidium* extending out of the main mass that allowed marl accumulation similar to that formed between projecting filaments of *Schizothrix* (Fig. 19). In this way, the algal mass grew in a lamellate way, with the greatest proliferation of *Gongrosira* in spring and early summer, and a following development of more shade-tolerant blue-green algae in mid-summer and autumn. As a result, dense highly organic marl alternated with the soft, light-colored bands formed by blue-green algae (Fig. 20). This general pattern was borne out by field observations on marl deposits in Doe Run, but there were many variables, such as flaking of surface layers on exposure to weathering by low water levels. There is significant physical erosion of marl from poorly consolidated surface accumulations, indicated by denser marls being found in swifter waters, and solution of carbonates must occur when decomposing leaves cause high carbon dioxide and lowered pH in the areas of marl deposition.

The downstream end of the marl area in Doe Run has been discussed from the standpoint of water chemistry, and seems to result from reestablishment of certain carbon dioxide and pH relations, perhaps through accumulation of organic materials in large pools. However, there is the possibility that the sharp line of demarcation near Mile 5.6 was more a function of the drop in gradient and a resultant unsuitability of the area for the algal species instrumental in marl formation because of some factor related to decreased turbulence and velocity of flow. *Gongrosira* was not found downstream from Mile 5.6 and *Phormidium incrustatum* was very rare in collections from Station V. Greater amounts of light, higher water temperatures, and abundance of the larger *Cladophora* downstream could also contribute to, or indicate, the unsuitability of that area for encrusting algae.

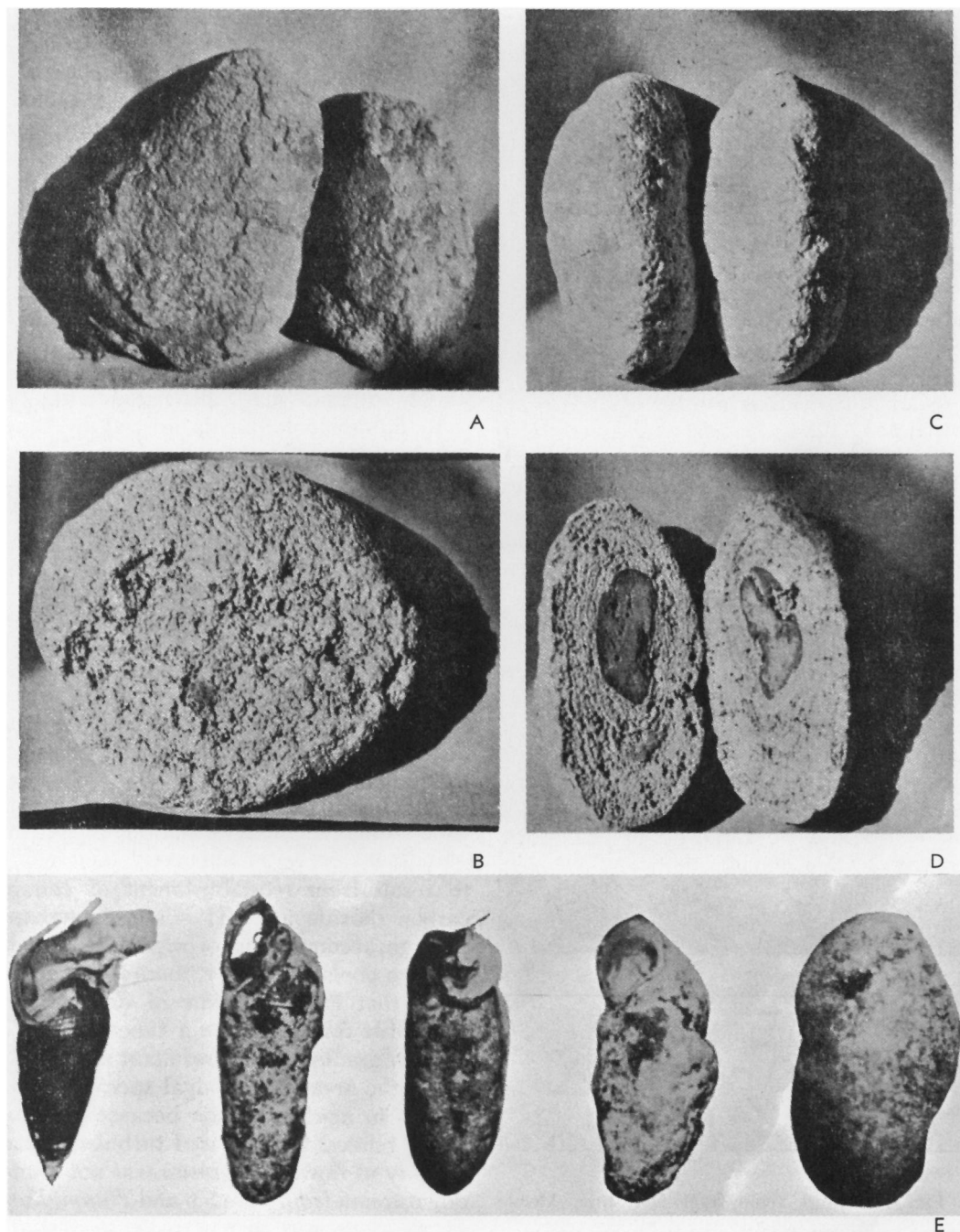


FIG. 20. Marl concretions from Doe Run, Meade County, Ky.: A—gross appearance of a dried, “living marl” nodule from Station IV; B—gross appearance of a fossil marl from Station II illustrating the number of insect “burrows” revealed after some weathering in the stream; C, D—gross appearance of a fossil marl from Station II that had been subjected to weathering on the banks, and a cross section of the same nodule illustrating lamellate deposition of carbonate around another, highly weathered, marl nodule; and E—*Goniobasis* from Station III illustrating various stages of marl encrustation.

It is noteworthy that larger macrophytes in Doe Run, including *Myriophyllum*, *Potamogeton*, and *Nitella* in the upper reaches, and various emergent forms downstream, showed little marl accumulation at any time, although all have been recorded with marl accumulations in other areas, especially lakes (Welch, 1935; Wetzel, 1960). Most of them lived in relatively swift waters in Doe Run, and Wetzel noted that water movement, such as wave action, was a major factor in prevention of surface encrustations on large, flexible aquatic plants.

Marl accumulation can be rapid in some situations (Gessner, 1959), and was considerably more rapid in Doe Run than recorded by Blum (1957) for the Saline River, Michigan (4–5 mm per year). No specific studies were made in Doe Run to ascertain the rate of deposition, but 63 consecutive rings of deposition were counted in a massive block of marl exposed around roots of a riparian sycamore tree that toppled in a windstorm of June 1960, and the rings ranged from 20 to 55 mm in width, with an average of about 25 mm. If these were annual rings of deposition the rate of accumulation was quite high. Amounts of marl found on aquatic invertebrates also indicate rapid deposition. Many of these animals cast their exoskeletons regularly, yet marl 1 mm thick was present on some stonefly naiads. In June 1960, a partially submerged can was found with marl deposits ranging from 1 to 4 inches thick on the submerged portion. The total weight of the can and wet marl was 3.5 pounds, and there was no evidence of rust or corrosion from exposure to water. Metal field equipment corroded in less than 2 months if left in the water continuously. There was evidence in the period of my study, and from the presence of abandoned, marled stream beds lateral to the stream channel, that accumulations in swift riffles caused shifting of the stream from side to side, at least within the limits of the stream bed.

Marl formations in Doe Run included

diverse organic materials. In autumn, when leaf accumulations blocked riffles of the marl area, the leaves often were cemented together forming low dams across the stream. These were removed quickly with increased discharges, but fragments of leaves and leaf impressions were common. Other detrital materials included twigs, seeds of terrestrial plants, and shells of terrestrial snails in marls from near Station IV. Twenty-five nodules, ranging from 2 to more than 18 inches in diameter, were sectioned, and *Goniobasis* shells were the center of aggregation of 7 of these. Most nodules were formed around small pebbles, previously weathered marl, or twigs, but 4 showed no apparent center of aggregation. Examination of the various layers of the nodules revealed few recognizable algal components. Apparently these are decomposed, reconstituted, or replaced by mineralization.

Marl nodules from Doe Run ranged from the size of small pebbles to more than 24 inches long and 18 inches wide. The smaller ones were spherical, or followed the outlines of the object on which they were formed, but larger ones tended to be uniformly oblong in shape and flattened vertically when lying in place. In many riffles the bottoms consisted of a totally cemented conglomerate of marl, rubble, and gravel (Minckley, 1961), and thicknesses of 2 feet were not uncommon.

Algae of Quiet Areas and Slow Currents

Blue-green algae were the most abundant benthic forms in pools, eddies, and backwaters downstream from Dam 1, and possibly in the impoundment above Dam 1 at certain times. Of these, the most frequently encountered were *Oscillatoria amoena*, *O. splendida*, and sometimes *Phormidium autumnale*. *Lyngbya birgei* G. M. Smith occurred as isolated trichomes; however, *L. patrickiana* Drouet and all others listed above were found at one time or another in relatively pure stands on silt and detritus substrates. Mats of *Oscillatoria* often were seen rising to the surface

and being carried downstream because of accumulation of gases during periods of high photosynthetic activity (Blum, 1956a, 1957, 1960). Some buoyant mats contained substantial numbers of small tendipedid larvae, snails, and once a number of oligochaetes. Thus flotation not only disperses algae downstream (Blum, *loc. cit.*) but may function in the downstream drift of aquatic invertebrates. At times of modal discharge and clear water in Doe Run, mats of *Oscillatoria* sometimes developed on the bottoms of pools in more than 7 feet of water, causing them to appear deep, blackish green in color. Samples of bottom muck from downstream parts of Pools 2 and 3 had surfaces covered by a thin, macroscopic layer of *Oscillatoria* in June 1960, but samples at the same time from Pool 1 did not have such algal growths. A thick stand of *O. limosa* (Roth) Ag. occasionally was found adjacent to a small sewage outfall near Station II. Sedimentation, or increased turbulence and velocity of flow in eddies and pools during spates, was quick to smother or displace algal growths of these and the following kinds.

Downstream from Dam 1, *Spirogyra varians* (Hass.) Kuetz., 2 or 3 undetermined species of *Spirogyra*, *Oedogonium sociale* Wittr., and a species of *Mougeotia* were found in backwaters. *Spirogyra* demonstrated little apparent habitat preference, with the exception of usually being commonest in areas of open sunlight. *Oedogonium* was rare. Downstream from Mile 5.6, *Mougeotia* grew abundantly on the shoreward side of dense *Cladophora* beds when the latter were present, and was usually heavily clogged with silt and epiphytic diatoms.

As already noted, filamentous and encrusting diatoms were abundant in more lentic areas of Doe Run. These usually were most noticeable after periods of winter discharge, and were rapidly overgrown by blue-green algae and grazed by aquatic invertebrates with onset of lower discharges. *Vaucheria geminata* (Vauch.) D. C. and *V. sessilis* (Vauch.) D.C. also were

common in backwaters, where they assumed a loose, erect branching growth form quite in contrast to the thick, felted mats in flowing waters. *Vaucheria* usually washed into quiet areas from upstream. One thriving colony of *Vaucheria* was, however, found in the old millrace at Station III growing on a mass of iron hydroxide from 4 to 8 inches thick. *Hormidium klebsii* G. M. Smith and 2 desmids, *Netrium* sp. and *Closterium* sp., were also found there, but in a place where no precipitated iron was present.

Riffles, and associated algae, were rare upstream from Dam 1, although the rate of flow other than in the impounded portion usually exceeded 1 ft/sec in the main currents. This rapid flow tended to be smooth because of the uniform bottom and the relatively deep channel, and permitted the development of a distinctive flora of algae and higher aquatic plants. The swiftest flow was dominated by *Fissidens* and *Batrachospermum* (the latter seasonally), but in long periods of modal discharge in the summer and autumn of 1960 and 1961 (Fig. 8), and the autumn of 1959, dense mats of *Vaucheria geminata* developed, sometimes choking the channel. Whitford (1956) included stands of *Vaucheria* in Florida springs with "rapids" communities of higher plants rather than with any specific algal community, and Butcher (1933) also mentioned *Vaucheria* in association with his "torrential" flora of mosses and *Lemanea*.

Maximal development of *Vaucheria* in Doe Run was from Mile 0.1 to 0.5. Growth began in backwaters, downstream from beds of watercress or behind logs and other debris, but mats sometimes grew independently in the channel, apparently from the germination of zoospores, zygotes, or from vegetative parts buried in the substrate. Germinating zygotes of *Vaucheria* that had developed weak, rhizoidal filaments in addition to caenocytic thalli often were found in collections. These rhizoidal filaments seemed to penetrate the softer substrates, and may have served to anchor

the developing thalli. Silt was rapidly deposited in beds of *Vaucheria*, even in periods of low turbidity, apparently as a result of the filtering action of the densely interwoven thalli. This may have assisted in fixing the beds to the stream bottom. The bottom inch of mats was usually compacted with silt, some of which was held by the rhizoidal filaments, but much was deposited among living filaments of the plants. With development of massive growths, however, these attachments were insufficient to hold the plants in current, and detachment often occurred, with the mats folding over one another. Slight increases in discharge also detached massive mats, rolling them as one would roll a thick rug, sometimes blocking the channel until the rolls were moved against the banks.

At times of maximum development, *Vaucheria* obviously grew over and buried other plants in the upstream section. Often the stream assumed a braided channel between masses of *Vaucheria*, and the speed of flow was markedly increased in these smaller channels. The accumulation was rapidly removed by increased discharge in winter, and large masses of algae were washed downstream or deposited on riparian objects. These masses remained alive as long as parts were in water and kept moist by capillary action. Fruiting of *Vaucheria* did not occur in submerged mats, but was commonly found in emergent mats which provided vegetative stock for subsequent periods of modal discharge. *Vaucheria* beds similar to those in Doe Run, but apparently not so extensive, have been described in alkaline streams elsewhere (Symoens, 1957; Hornung, 1959). Diatoms found in association with those beds were similar to those found with *Cladophora*, there and in Doe Run.

Dichotomosiphon tuberosus (A. Br.) Ernst was also abundant in the upstream areas of Doe Run, but was more limited in its distribution than *Vaucheria*. It formed thick, felted mats in silty areas downstream as far as Mile 0.75, and was perennial.

Growth of *Dichotomosiphon* occurred from permanent mounds of silt densely interwoven with colorless, rhizoidal filaments. The photosynthetic portions of the plant emerged from the substrate as short, interwoven, but erect, filaments on the surface of mounds that grew radially out from the center. *Dichotomosiphon* did not wash out as severely as *Vaucheria* during floods, nor was it damaged by overgrowth of *Vaucheria* when that occurred.

Even when *Vaucheria* was essentially absent from the channel of the upper area, algae other than *Dichotomosiphon* were uncommon. Encrusting communities on larger objects in the stream bed were dominated by *Chantransia* of *Batrachospermum*, and rarely by diatoms, in the area where *Vaucheria* became seasonally abundant. The few riffles were dominated by *Fissidens*. This general lack of diversity of algal species may be related to low light intensities in the area (Fig. 1), to the shifting nature of the bottoms (see Cedergren, 1938; Douglas, 1958; Margalef, 1960), perhaps to the lack of diversity in environmental conditions and an accompanying lack of diversity of available niches, or to other unknown factors.

Subaerial Algae

These algae developed most, and contributed significantly to the flora of Doe Run in periods of high discharge. *Phormidium autumnale* was the major species that formed extensive mats in zones of spray, but there were some mats of *Oscillatoria amoena*, *O. splendida*, and *O. tenuis* Ag. Some large, filamentous green algae and red algae, such as *Cladophora fracta* and *Lemanea* spp., respectively, occurred in zones of spray, usually as a result of seasonal decreases in water levels at onset of modal discharge in spring, but were unable to maintain themselves in other than saturated conditions. *Audouinella* was characteristic of spray zones in late winter and spring at mill dams, occurring as marl-encrusted colonies on twigs. *Chlorotylum*, *Gongrosira*, and *Phormidium incrustatum* also were found there, and *Cladophora*

fracta, *Spirogyra*, *Hormidium klebsii*, and *Lyngbya taylori* Drouet and Strick. were entangled on the surface of the nodules, or with filaments of other species. Diatoms, sometimes making up thick gelatinous layers on stones and twigs, became exposed after periods of high discharge, persisted in the spray as water levels fell, and disappeared within 2 weeks after the water receded.

Gleocapsa sp. (= *Anacystis* sp.; Drouet, 1959), *Cylindrospermum muscicola* Kuetz., *Oscillatoria agardhii* Gom., *O. tenuis*, *Lyngbya patrickiana*, and *Nostoc commune* Vauch., occupied mud and sand bars along the main channel and many were found on clay banks several inches above the water. Some aerial forms may have been included in samples from the creek because of high water levels, but if such were the case it was not obvious at the time of collection. *Nostoc commune* was abundant in temporary pools along the floodplain of Doe Run, as well as in the stream. *Sphaerella lacustris* (Girod.) Whitt. was found in an encysted stage on rock outcrops of Tributary II-b and in another unnamed tributary near Station IV. Likewise, *Calothrix parietina* (Naeg.) Thuret. was in subaerial habitats on bedrock on Tributary II-a.

Emergent Higher Plants

The higher emergent plants along Doe Run included several species that occurred rarely, or were restricted in distribution. These were: *Typha angustifolia* L., represented by a sparse stand near Station III; *Sagittaria latifolia* Willd., at Tributary II-d; and the sedges *Eleocharis compressa* Sull., *E. obtusa* (Lilld.), *E. acicularis* (L.) R and C, *Carex* spp., and *Scirpus validus* Vahl that occurred sparsely in downstream areas. Smartweeds, *Polygonum* spp., also were scattered over bars downstream from Mile 5.6. *Equisetum variegatum* Schleich. and *E. arvense* L. both were abundant and functioned to stabilize banks and some sand and gravel bars along the stream. The major emergent plants, however, were watercress *Nasturtium officinale* near springs, forget-me-not *Myosotis scorpioides*

L. between Stations II and III, and water willow *Justicia americana* (L.) Vahl between Miles 4.5 and 7.0.

Beds of watercress were most highly developed in the spring tributaries of Doe Run, but extensive stands developed on sand and silt deposits lateral to the main channel in the upstream portion of the mainstream, and in the midst of stream-drifted logs and branches at Station II. Downstream from Station II, beds of watercress were present in winter and spring, but became rare in summer and disappeared when stranded by lowered water levels. Reproduction by seeds was most evident in spring, when many young plants grew along the banks submerged on deposits of silt and sand. Few seedlings, however, persisted to maturity because of washout. The largest beds in the mainstream resulted from accumulation of stream-drifted plants in eddies, and proliferation from broken stems and from plants lying on the bottoms. The beds rapidly accumulated allochthonous and autochthonous debris from the current, sometimes so extensively that it formed black, malodorous muck beneath larger beds. *Nasturtium* washed out readily when subjected to strong currents, and the large hollow stems floated high in the water and were transported for some distance downstream. Washout was somewhat prevented, however, by the occurrence of *Nasturtium* beds behind larger debris and on the inside of bends and by the accumulation of bars of organic and inorganic material that tended to direct currents elsewhere. Watercress in the mill pools, or in areas downstream from Station II, usually became lax, prostrate except for the terminal parts, and flowered earlier than did plants near the springs. Freezing affected the downstream plants more severely than those near the springs. Water of the outflows caused microclimatic conditions that allowed continued growth of plants in winter. The tops of larger plants were frost-killed, causing proliferation of subterminal branches and generally thicker beds in winter and

spring than in summer and autumn.

The forget-me-not, although more terrestrial than watercress (Thompson, 1944), more or less replaced that species between Dam 1 and Station III. Forget-me-nots usually occurred in association with a mint *Mentha* sp. and various grasses, but were most abundant on the streamward side of the community, whereas mint was thickest on the shoreward side. *Myosotis* grew largest in areas of open sunlight (to 15 inches high), and flowered throughout spring, summer, and autumn. In heavy shade the plant rarely grew more than 5 inches high and was not observed to flower. It would be interesting to know what native riparian plants, if any, were replaced by *Nasturtium* and *Myosotis scorpioides*. Both were introduced to North America from Europe (Fernald, 1950), where they are part of the common streamside vegetation (Gessner, 1955).

Waterwillow was scarce in Doe Run, distributed in colonies downstream between Miles 4.5 and 6.0. The plant appeared in May, flowered, and usually was gone by September or October; it occurred on the gravelly parts of riffles, seldom in marl, and may have been limited in its distribution by the presence of marl.

Submergent Higher Plants

The charophyte, *Nitella flexilis*, usually is included with algae in studies of this kind, but is included here for convenience because of its habit of growth. *Potamogeton diversifolius* Raf. and *Callitriche* sp. occurred rarely in Doe Run. The former was represented by a single clump near the inflow of Tributary I-c', but was absent at the next visit and none was found subsequently. The species is common in sinkhole ponds of the surrounding area. *Callitriche* was found at 2 places in the mainstream, once in a pool near Station III and again in Pool 2, but was abundant in February 1961, in a small spring-fed swamp connected to Tributary IV-a.

In Doe Run, the upstream area presented a grading environment downstream, with swift, turbulent water adjacent to the

source, and a predominantly rubble bottom; a long area of shallow, particulate substrate over bedrock and relatively swift currents; a transition area where deposition of larger gravels and sands occurred; and a semilentic situation in Pool 1, with sand in the upper half grading to silt and muck near the dam. This area was inhabited, respectively, by: (1) *Fissidens julianus* that also occurred on solid substrates in more downstream areas; (2) seasonally by *Vaucheria*, an alga capable of rapid proliferation and not needing deep substrates in which to root; (3) by *Potamogeton foliosus* Raf., var. *macellus* Fern., capable of maintaining a foothold in coarse, unstable substrates by massive development of subsurface rhizomes; and (4) by *Nitella flexilis* in the sand-silt areas caused by aggradation in the mill pool. *Dichotomosphon tuberosus*, discussed above, is a form capable of maintaining its own substrate by compact matting of subsurface filaments, and was found throughout the upper 0.75 mile. *Batrachospermum* was also a major component of the community in its seasonal occurrence on solid substrates throughout the area (Minckley and Tindall, 1963), and *Nasturtium officinale* was the major emergent form.

Downstream from Dam 1, *Fissidens* again was a major part of the community, occurring with *Myriophyllum heterophyllum* in a mosaic pattern apparently dictated by the presence of bedrock riffles and extremely swift waters for the moss, and pool situations for the milfoil, usually with currents exceeding 1 ft/sec, however. *Nasturtium* was a minor component of this community, quickly colonizing exposed bars and developing stands lateral to the major currents.

Nitella flexilis was the subject of an intensive ecological study in Doe Run by Tindall (1962), and only an outline of its relations is presented here. The greatest proliferation of *Nitella* occurred in periods of modal discharge; after spates other than those of 1961, beds of *Nitella* in Doe Run resembled illustrations given by Gessner

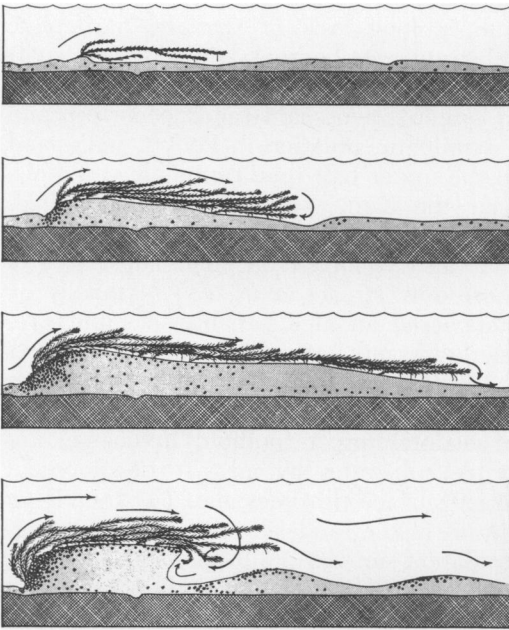


FIG. 21. Illustration of the formation of a mound of bottom materials by a higher plant in Doe Run, Meade County, Ky., and its partial wash-out (bottom).

(1955) for stands of *Paspalum repens* Berg in the Orinoco River of South America. Beds in the main channel had been removed and currents had trimmed projecting portions of plants growing on the inside of bends into an almost vertical, convex form that followed contours of the banks. The extreme flooding of 1961 nearly extirpated *N. flexilis* from Doe Run, but by February 1962 it was developing from remnants left in the sediments, the few remaining attached plants, and possibly from germination of spores. *Nitella* consistently grew on soft, silt-sand deposits and did not grow downstream from Dam 1 at any time despite substantial amounts carried there by floodwaters. This charophyte is most often found on silty bottoms of clear, sluggish streams, where streams enter lakes, and sometimes deep in lakes (Wood and Muenscher, 1956). It appears adapted to low-light environments (Daily, 1958).

Fissidens julianus usually grew in the

swiftest currents throughout Doe Run. It could, however, persist and grow in relatively slow waters and on gravel in periods of modal discharge. It proliferated rapidly early in those periods only to be covered later by *Vaucheria* or other plants. The moss often was damaged by high discharge, and removed down to its holdfasts, but the beds rapidly developed from the basal portions. In a sense, *Fissidens* was one of the most constant inhabitants of the upstream section, and probably had a much wider distribution upstream from Dam 1 prior to impoundment and consequent covering of the bedrock bottoms of that area by various sediments. *F. julianus* fruited rarely in late winter and early spring. Reproduction was primarily by vegetative proliferation from basal portions of the plant.

The largest beds of *Potamogeton foliosus* grew on elongate hummocks or mounds in the channel (Fig. 21). Most reproduction by *P. foliosus* in Doe Run resulted from spreading of rhizomes or by rooting of detached plants in downstream areas. Flowering was noted in almost all seasons, but appeared most pronounced in late summer and autumn. No seedlings were found.

Myriophyllum heterophyllum formed thick, channel-blocking beds in the swift area between Dam 1 and Mile 2.0 where it replaced *Fissidens* in areas of rubble and in "pools." The thick, adventitious roots allowed for rapid enlargement of beds, and mounds were formed similar to but not so clear cut as those in beds of *Potamogeton*. *Myriophyllum* was amazingly resistant to washout, and rarely was damaged by high discharge other than in peripheral habitats. The beds of *Myriophyllum* were almost as extensive in the rapids areas early in 1962 as they were at the beginning of the study, notwithstanding the severe flooding of 1961. Reproduction occurred by adventitious rooting, rhizomes, and by rooting of broken plants. No seedlings were found, but flowering occurred regularly in spring and summer after beds were exposed by receding water levels. When elevated from

the water, the leaf segments grew broad and serrate, quite unlike the submerged, filiform leaf segments (Muenscher, 1944).

Spatial Relations of the Flora of the Upstream Area

Stream communities of plants, or monospecific stands of higher plants or algae in streams, are governed primarily in their spatial relations by velocity of the current. This determines the nature of the substrate, which, in turn, serves to determine the kinds of plants present (Butcher, 1933; Blum, 1956a, *et seq.*). The persistence of a plant community in a stream depends on structural adaptations of the species to the situation, or if the community can modify its environment in the amount of time it has to become firmly established. It is especially those plants with linear or finely divided leaves that occur in swiftly flowing waters (Nielson, 1950a). Mosses, many of which are typical of torrential streams (Gessner, 1955), tend to flatten against the substrate and present a smooth surface to current. Algae also demonstrate many similar structural adaptations.

Most larger plants in Doe Run modified their substrates and encroached on unfavorable habitats by doing so. Plants, such as *Nasturtium* and *Nitella*, growing along the banks, persisted after high discharges in an aggrading environment where stream-carried silt and debris were deposited by sudden decreases in current. As the beds enlarged they augmented physical slowing of the water, and accumulations of silt and other materials soon formed bars lateral to and parallel with the currents. Prior to flooding of 1961, some bars apparently formed by *Nitella* in the upper end of Pool 1 extended two-thirds of the way across the channel on the inside of bends, and were more than 8 feet wide where the channel was straight.

Myriophyllum and *Potamogeton* in current soon formed elongate mounds through deposition of silt, sand, and gravel among the plants (Fig. 21). Mounds of this type were discussed by Gessner (1955, from Ruess,

unpubl.), who called them "Schwaden," and by Butcher (1933). The coarsest sediments in such mounds usually were on the upstream ends, serving to protect the structure against the current. In periods of modal discharge, long "spits" of sand and silt formed at the downstream ends of mounds, and were rapidly colonized and stabilized by adventitious rooting of plants trailing in the current, or by *Nitella* in the downstream part of the *Potamogeton* area. Also, mounds were formed by original aggradation of material near a stone or log with subsequent colonization and stabilization of the area by plants. Those formed downstream from Dam 1 by *Myriophyllum* were larger than those formed by *Potamogeton*, possibly because of protection afforded by large stones in the stream bed, or by greater width of the stream with more space for lateral encroachment by beds and for movement of water in periods of extreme discharge. In some instances, succession from *Fissidens* to *Myriophyllum* occurred with dense beds of moss on bed-rock being used for attachment of adventitious roots of trailing milfoil. Subsequent accumulations of sand and gravel around the milfoil smothered the moss and allowed expansion of mounds. *Nasturtium* also rooted on dense moss during low flow, but was removed by higher discharges.

Spatial relations of plants in the upper part of Doe Run are to be presented elsewhere, but the dispersion at the beginning of this study is illustrated in Figures 22-24. The extensive vegetation in the upper part of Doe Run in 1959 apparently had been developing for at least 10 years without influence of discharges as great as those recorded in June 1961 (Curtis Brown, pers. comm.), when the stands were severely decimated. High discharges in June 1960 damaged the stands, to be sure, but recovery was rapid in the succeeding period of modal discharge. Furthermore, the data on recolonization of the mainstream after spates in 1959 and 1960 indicate that patterns of substrate and/or current in the area usually were changed so little after a major

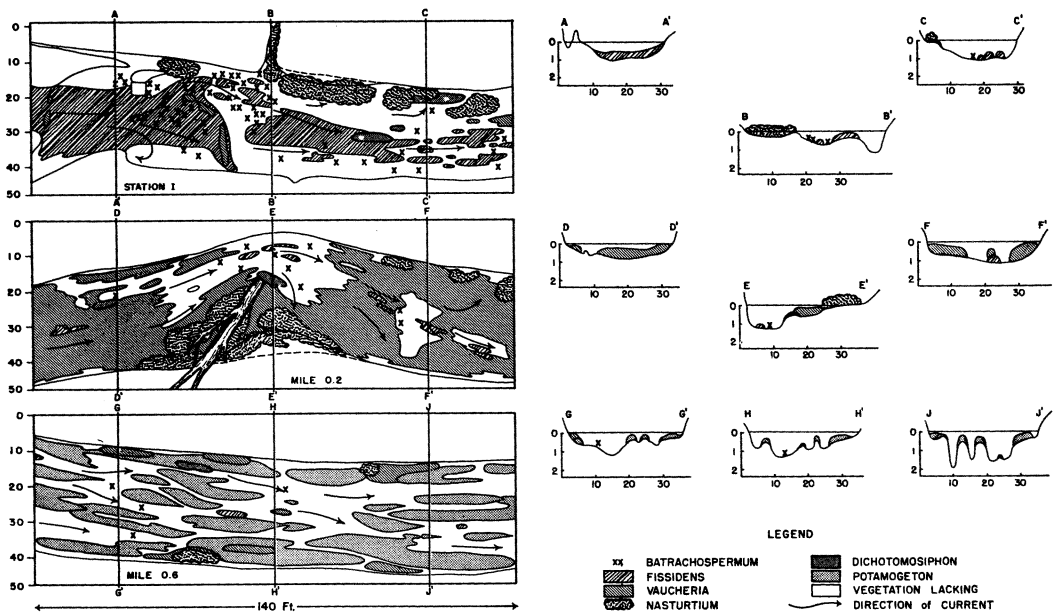


FIG. 22. Dispersion of aquatic vegetation in various areas upstream from Dam 1, Doe Run, Meade County, Ky., October 1959.

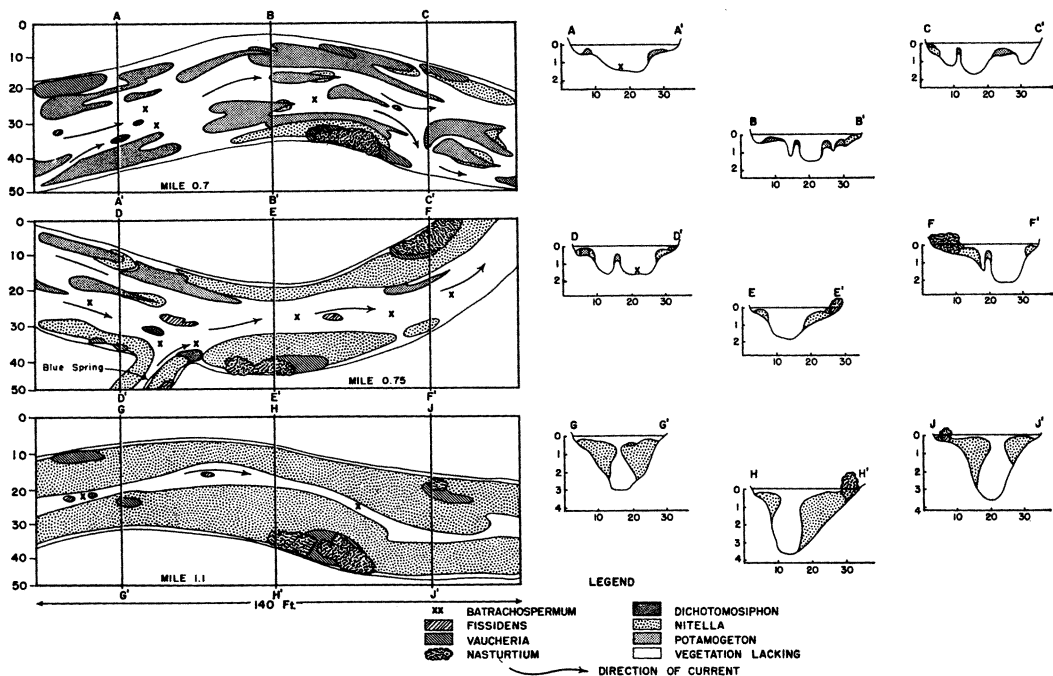


FIG. 23. Dispersion of aquatic vegetation in various areas upstream from Dam 1, Doe Run, Meade County, Ky., October 1959.

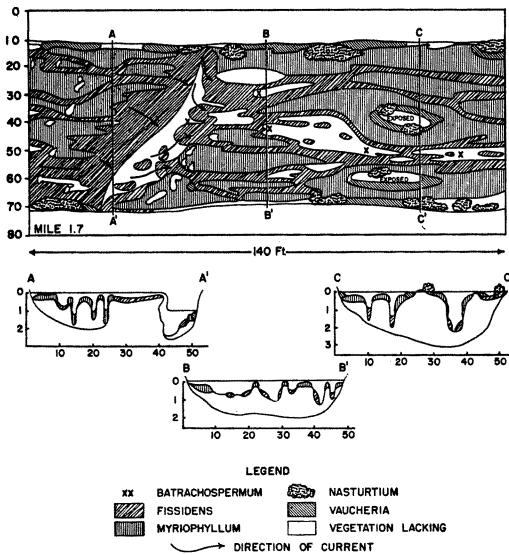


FIG. 24. Dispersion of aquatic vegetation at Station II, Doe Run, Meade County, Ky., October 1959.

washout that recovery occurred in a pattern approximating the original. Indications are that reestablishment of the plants after the scouring floods of 1961 will repeat the pattern once again, provided another catastrophic flood does not occur too soon.

The plant distribution upstream from Dam 1 differed from others described in the literature in that the few species present occurred in relatively pure stands in a linear sequence. The distribution of the sediments and currents, and thus the distributions of the plants, were perhaps artificially induced to some extent by the construction of Dam 1. Thus the area reflects the disturbance of the stream by man. Be that as it may, the gradational picture produced by this situation approximates the distribution of sediments and vegetation that might be found in the length of a much larger river if other factors were equal. It includes examples of 4 of the 5 principal higher plant communities recognized by Butcher (1933) in streams of England. In streams studied by Butcher (1927, 1933), Roll (1938, *et seq.*), Ruess (in Gessner, 1955), Gessner (*loc. cit.*), and by R. W. Edwards and his colleagues in

England (1960–1962), however, the higher plant communities usually were mosaics of small, monospecific stands, apparently developing in response to microvariations in current or substrate. The presence of a given stand of plants and the attribute of most aquatic plants for developing extensive beds from a single individual through rhizomes, adventitious rooting, and other vegetative means, would result in mosaic community structure in a mosaic environment. The mere presence of an established stand of aquatic plants is a deterrent to invasion by another species. However, the influence of that plant may encourage colonization of the area by another species, resulting in a succession of sorts.

The upper portion of Doe Run may be compared with other, larger springs where essentially monospecific stands of vegetation persisted for a long time (Odum, 1957a, b), and to lakes where the changes in substrate from stony, wave-washed shorelines grade to silt-covered bottoms of the deeper littoral zone. In springs, steady-state conditions may prevail with constant flow and ample supplies of nutrients maintaining remarkably stable subsurface meadows. In lakes, edaphic conditions are primary factors influencing the dispersion of aquatic plants if depth relations permit (Pearsall, 1920; Wilson, 1935, *et seq.*; and Roelofs, 1944). Temperature and light relations in lakes seem to have little effect unless related to depth (Pearsall, 1920), and changes in plant communities result largely from specific sedimentation coupled with certain chemical and physical conditions that develop with the maturation of the basin (Wilson, 1939). Doe Run lies somewhere between these extremes. It exhibits the more dynamic aspects of mound formation, washout and recolonization, and development of a mosaic community or “mixing” of habitats for the various species involved. The area between Dam 1 and Mile 2.1 may illustrate a more typical stream condition in the dispersion of the plants (Fig. 22), but retains a constancy usually not found in other studies

of stream communities of higher aquatic plants. It seems unfortunate that the study of hydrophyte zonation in both lakes and streams has been bypassed for more specialized forms of ecological research. The latter studies are based largely on estimates that must, through necessity, be derived from more investigation of the former (Swindale and Curtis, 1957).

Invertebrates

Major obstacles to the study of benthic animals in North American streams are the lack of knowledge of taxonomy of most groups, the great diversity of habitats, and the corresponding diversity of animals about which little specific information is available. Furthermore, the tendency for each species to reside in or to select specific areas or habitats (Dodds and Hisaw, 1925b; Percival and Whitehead, 1929; Mottley, *et al.*, 1939; Wene and Wickliff, 1940), along with the concentrations and movements of certain organisms in response to food, shelter, and other factors (Badcock, 1949, *et seq.*; Mueller, 1954; Roos, 1957; Macan, 1957; Armitage, 1961; Minckley, 1963), present serious difficulties in sampling. Stream-sampling techniques are undergoing critical scrutiny by many workers, but additional research is badly needed (see Leonard, 1939; Badcock, 1954b; Gaufin, *et al.*, 1955; Needham and Usinger, 1956; Macan, 1958; and others). The most reliable technique appears to be the consistent use of a given device by the same person (Surber, 1937, *et seq.*). Using this approach, the data will at least be comparable within themselves if local conditions at the time of sampling are taken into account. The benthos of Doe Run was sampled in this way, and was supplemented by selected sampling by myself and others.

Early in the study, a number of qualitative samples were examined for microbenthic organisms and a list of those is given by Minckley (1962). Other microbenthic animals were *Hydra littoralis* Hyman, at Station II and in vegetated areas downstream from the *Fissidens* section between Station I and Dam 1; various undetermined

nematodes, common in silty bottoms and as parasites on larger aquatic plants; the nematomorph *Gordius* sp., rare; a few Gastrotricha, *Chaetonotus* sp. and undetermined species; rotifers, *Keratella cochlearis* Ehrenberg, *Epiphanes* sp., and undetermined loricate forms; conchostrachans, *Cyzicus* sp., found in drying pools near Station V; undetermined ostracods; copepods, *Mesocyclops edax* (Forbes) and *Bryocamptus* sp.; and diverse aquatic mites (Acri). Few planktonic invertebrates were taken in limited sampling (see Pennak, 1943).

The following macrobenthic animals were collected:

PLATYHELMINTHES

TURBELLARIA

- Dugesia* sp. (near *D. dorotocephala* [Woodworth])
- D. tigrina* (Girard)
- Phagocata velata* (Stringer)
- Phagocata* sp. (near *P. subterranea* Hyman)

ANNELIDA

OLIGOCHAETA

Unidentified branchiobdellids often were found attached to the underside of the abdomen and inside the gill chambers of crayfish (*Cambarus*).

- Aelosoma* spp.
- Nais* spp.
- Lumbriculus variegatus* (Mueller)
- L. inconstans* (F. Smith)
- Chaetogaster* sp.
- Ophidonais serpentina* (Mueller)
- "*Lumbricus* spp." This designation was used for large, amphibious and terrestrial earthworms that sometimes were common beneath stones in shallow water throughout the stream system.
- Tubifex* sp.
- Limnodrilus hoffmeisteri* Clapàrede
- undetermined oligochaetes

HIRUDINEA

Placobdella sp. Leeches were attached to the carapace, plastron, and fleshy parts of large snapping turtles (*Chelydra*).

ARTHROPODA

ISOPODA

- Asellus bivittatus* Walker*¹
- A. stygius* (Packard)*
- Lirceus fontinalis* Rafinesque*
- Lygidium longicaudatum* Stoller*

AMPHIPODA

- Crangonyx forbesi* (Hubricht and Mackin)*
- Crangonyx* n. sp. (near *C. minor* Bousfield)*
- Crangonyx* n. sp. (near *C. rivularis* Bousfield)*
- Gammarus minus* (Say)*
- G. bousfieldi* Cole and Minckley
- Synurella dentata* Hubricht*

DECAPODA

- Cambarus bartoni* (Fabricius)
- Orconectes rusticus rusticus* (Girard)
- O. pellucidus pellucidus* (Tellkamp)

COLLEMBOLA

Podura aquatica L. Locally common upstream from Station IV, most often associated with stream-drifted debris along the banks but also in beds of watercress and forget-me-not, and rarely on the surface of open pools and eddies. Predation by young-of-the-year creek chubs, *Semotilus*, and water striders, *Gerris* and *Microvelia*, was heavy on populations in open water.

EPHEMEROPTERA

- Ephemera* sp.*
- E. simulans* (Say)*
- Hexagenia atrocaudata* McDunnough
- Ephemerella* sp.*
- E. subvaria* McDunnough*
- E. needhami* McDunnough
- Leptophlebia* sp.*
- Paraleptophlebia* sp. (near *P. praepe-dita* [Eaton])
- Paraleptophlebia* sp.*

¹ Crustaceans and insects identified for me by others (see ACKNOWLEDGMENTS) are marked with an asterisk. However, determined specimens were used in further identification and interpretation of the fauna, so that I am responsible for any errors.

- Isonychia* sp.*
- I. sadleri* Traver*
- Baetis* spp.*
- B. vagans* Traver*
- Pseudocloeon* sp.*
- P. carolina* Banks*
- Cloeon* sp.*
- Stenonema* sp.*
- Heptagenia* sp.*

ODONATA

- Agrion* sp. (near *A. maculatum* Beauvais)
- Argia* sp.
- Gomphus* sp.

PLECOPTERA

- Nemoura delosa* (Banks)*
- Nemoura* sp.*
- Allocapnia* sp.*
- Perlesta placida* (Hagen)*
- Paragnetina media* (Walker)*
- Isogenus subvarians* (Banks)*

HEMIPTERA

- Microvelia* sp. (near *M. pulchella* Westwood)
- Gerris* sp.
- G. remigis* Say
- Metrobates* sp.
- Gelastocoris oculatus* (Fabricius)
- Benacus* sp.
- Belostoma* sp.
- B. fluminea* Say
- Ranatra* sp.
- Notonecta undulata* Say
- undetermined Notonectidae
- Sigara* spp.
- undetermined Corixidae

MEGALOPTERA

- Sialis* sp.
- Chauliodes* sp. (near *C. penticornis* L.)

COLEOPTERA

- Peltodytes* sp.
- Laccophilus* sp.
- Agabus disintegratus* Crotch
- Gyrinus* sp.
- Psephenus herricki* DeKay
- Stenelmis* sp.
- Optioservus* sp.

TRICHOPTERA

Glossosoma nigrior Banks*
Psychomyia sp.*
Diplectrona modesta Banks*
Hydropsyche sp.*
H. betteni Ross*
Cheumatopsyche spp.*
Agraylea multiplicata Curtis
Pychnopsyche sp.
Helicopsyche borealis Hagen

DIPTERA

Tipula sp. (near *T. nobilis* Alexander)*
T. abdominalis (Say)*
Pilaria tenuipes (Say)*
Antocha sp.
Paradixa sp.*
Anopheles punctipennis (Say)
Aedes sp.
Culex pipiens L.
Chaoborus punctipennis (Say)
Simulium sp.*
Pentaneura sp.*
Procladius sp.*
Psectrocladius sp.?*
Trichocladius sp.*
Calopsectra sp. (near *C. dissimilis* Johannsen)*
Microtendipes sp. (near *M. pedellus* [Johannsen])
Tanytarsus sp.*
I. (Tanytarsus) sp.*
T. (Stictochironomus) sp.*
T. (Endochironomus) sp.*
Cryptochironomus sp.*
Tendipes (Tendipes) sp.*
T. (Limnochironomus) sp.*
T. (L.) modestus (Say)*
Glyptotendipes senilis Johannsen*
undetermined Empididae*
Culicoides sp.*
Tabanus sp.*
Atherix variegata Walker*
Scatella sp.
Limnophora sp.*

MOLLUSCA

GASTROPODA

Physa spp.
Ferrisia (Ferrisia) sp.

Pomatiopsis lapidaria Say
Goniobasis sp.

PELECYPODA

Sphaerium spp.
Pisidium spp.

Musculium sp. Represented only as "fossil" shells washed from deposits along the stream, but living in the adjacent Ohio River.

Observations on the Ecology of Abundant Invertebrates

Data on the ecology of specific animals in Doe Run varied greatly from group to group because of the vagaries of field investigations. Descriptive adjectives indicating abundance of various kinds of animals are based mostly on data in following sections, but are somewhat subjective and based on field experience, especially in species that were inadequately sampled by the quantitative methods attempted.

Turbellaria.—Flatworms were abundant above the marl area of Doe Run and in spring tributaries throughout the system. Marl deterred development of large populations, but flatworms were numerous on gravel bottoms between Mile 5.6 and Station V on occasions; no turbellarians were found at Station V or below.

Phagocata velata was most abundant in the mainstream near Stations I and II beneath the upper surfaces of beds of *Fissidens* and on undersides of flat stones or logs, twigs, and other debris, but always in relatively swift currents. At Station II, it was often associated with a larger turbellarian, *Dugesia dorotocephala*?, which also lived downstream from Station II, throughout the marl area in small numbers, and below. Similar distributions of these 2 species were found in the larger tributaries. Another species, *D. tigrina*, was present in downstream parts of smaller tributaries, throughout intermittent streams, and sometimes in the downstream portion of Doe Run.

Oligochaeta.—Few notes were obtained on oligochaetes because of the difficulties in identifying them in the field. *Aelosoma*

spp. were fairly common near Station I on sand and silt bottoms, but were not taken elsewhere. *Nais*, on the other hand, was most abundant in silt deposits at Stations III and IV. *Chaetogaster* was found in silt-detritus deposits at Station IV.

Tubifex sp. and *Limnodrilus hoffmeisteri* frequently occurred downstream from small sewage outfalls near Station II and Dam I, and abundantly in thick deposits of decomposing leaves in pools. Larimore, *et al.* (1959) found tubificids the most common animals in intermittent pools of Smith's Branch, Illinois, when heavy leaf accumulations occurred in autumn. In Doe Run, the occurrence of *Ophidonais* and "*Lumbricus*" was also associated with fallen leaves, but those animals colonized wet, packed leaves along the banks.

Isopoda. — *Asellus bivittatus*, an unusually small aquatic isopod, was the most abundant invertebrate collected in Doe Run. The largest individuals reported by Walker (1962) were less than 6 mm in total length. The species is characterized by its small size, by a general reduction of setation on the body and appendages, and by its general dark coloration marked off by unpigmented bands crossing its body near the head and on the abdomen (Walker, 1961). It appears to be adapted for life in closely packed vegetation, and the greatest numbers were found in beds of *Fissidens*. Reproduction by *A. bivittatus* occurred throughout the year but was most intense in April, May, and June, coincident with drops in winter levels of discharge and resurgence of growth by flood-thinned *Fissidens*. The number of young per female was small, rarely more than 8, but females produced more young as they became larger. Walker (1962) recorded a maximum of 18 young. A large, somewhat aberrant form of *A. bivittatus* at Station V was most common in thin beds of gravel overlying clay bottoms, and was extirpated by impoundment of the lower part of the creek. That population was incorrectly identified by Minckley (1961, 1962) and

by Walker (1961, 1962) as *Asellus brevicaudus* Forbes.

Minckley (1961) recorded *Asellus stygius*, a cavernicolous species, at 15 localities in the Doe Run system, including only 3 occurrences in caves. Since that publication, the species has been taken at 4 different places along the mainstream of Doe Run. It was never abundant in the open stream, but occurred frequently enough to be considered a consistent, but minor element of the epigeal fauna. *A. stygius* was most common in interstices of gravel beds and beneath large marl slabs in current.

Lirceus fontinalis was the largest aquatic isopod in Doe Run, but rarely occurred in the mainstream. In tributaries, however, especially those fed by seepages that dried in summer, *L. fontinalis* was the only malacostracan present. It was not taken upstream from the marl area in the mainstream, but occurred in some upstream tributaries, and reached its greatest abundance beneath dry gravel and rubble of small islands and bars, where a slight flow of water persisted in the interstices. *Asellus stygius* was also found in that habitat. In autumn, small clumps of leaves collected upstream from stones and other obstructions in the channel (termed "leaf packets" by Badcock [1954a]), and leaf dams formed on some riffles were rapidly colonized by *Lirceus*, amphipods, and aquatic insects. The isopod was often seen moving about in open pools of Doe Run and its tributaries, especially when fallen leaves littered the bottoms. Reproduction occurred throughout the year, but seemed greatest in spring (Cole, 1957).

Lygidium longicaudatum, a semiaquatic isopod, inhabited the immediate banks of the creek and its tributaries, most abundantly in moist leaves, but also in beds of mosses and liverworts. When alarmed, the animal scuttled beneath debris on the banks or into the water with little preference for either medium (Minckley, in Cole, 1959). *Lygidium* foraged on the tops of emerged beds of *Fissidens* and in clumps of watercress 2 to 3 feet from the water's edge.

Amphipoda.—*Gammarus bousfieldi* and *G. minus* were the most abundant amphipods in Doe Run. *Synurella dentata* was the only other amphipod that occurred in significant numbers in the stream system, and *Crangonyx* spp. were represented by fewer than 40 specimens in all collections made.

Gammarus minus was represented by a somewhat aberrant form in the mainstream of Doe Run, but material from the steep-gradient tributaries to the creek and from adjacent streams (Cole, 1957) appears typical. *G. minus* lived in *Fissidens* beds at Stations I and II, but was rarely seen on the surface of the beds and apparently moved about within the mass of vegetation. When disturbed from that habitat, it darted into the current and back into the vegetation (Cole and Minckley, 1961). In high-gradient tributaries, however, *G. minus* occupied almost all conceivable habitats: in mosses on steep inclines and riffles, in interstices of gravel on riffles, in moist leaves far from the flowing water, and often in pools. This species joined *Lirceus* in colonizing leaf packets in the mainstream, a habitat utilized by *G. pulex* L. in streams of Sweden (Badcock, 1954a, b), and also was present in interstices of gravel bars and small islands downstream from Station IV, its typical habitat in areas of the mainstream that lacked vegetation.

The typical habitat of *Gammarus bousfieldi* was pools, thus contrasting sharply with *G. minus* in this respect. *G. bousfieldi* is a large, setiferous, banded species, most abundant in beds of emergent vegetation along banks near Stations I and II, and in mats of leaves, roots, and detritus along the banks and in pools downstream. The general restriction of habitats of both species in the mainstream of Doe Run, their generally close relationships (both belong to the subgenus *Rivulogammarus*), and the presence of a somewhat aberrant form of *G. minus* in the mainstream with "typical" populations of that species in tributaries not inhabited by *G. bousfieldi*, brings up the possibility of character displacement and partitioning of niche by the 2 species

(Hutchinson, 1959; Cole, 1961; and others); this problem is being studied.

Although *G. bousfieldi* was not found in tributaries of Doe Run above the first major riffle, it occurred in those with generally smooth, low-gradient channels in the upstream area (Tributaries I-a, I-b, Blue Spring, Buffalo Spring, and II-a) that had thick beds of watercress and/or *Myosotis*. The species was often taken in bottom samples or by seine, from smooth, apparently undisturbed bottoms, and subsequent observation indicated that it frequently burrows into soft, silty bottoms. It is a strong swimmer, and cruises much of the time in open pools or along the banks. After periods of high discharge, *G. bousfieldi* and *G. minus* both appeared more abundant at downstream stations than before flooding, indicating a significant downstream "drift" (see Waters, 1961). After such spates, *G. bousfieldi* moves back upstream en masse (Minckley, 1963), whereas *G. minus* either maintains its upstream populations by rapid reproduction, or recolonizes upstream areas with more subtle, short-term movements in the stream channel.

Synurella dentata was abundant in Tributary III-b, and nowhere else in the system. That stream had a bedrock bottom and was intermittent in summer. Cole (1957) found the largest populations of the species in and around Louisville, Ky., in spring-brooks with dense stands of watercress. He also noted the presence of *Synurella* and *Lirceus fontinalis* in shallow, rocky headwaters of creeks, a habitat similar to Tributary III-b.

Crangonyx spp. were scattered through the Doe Run System and no distributional patterns are obvious. *C. forbesi* occurred at Stations I, IV, and V; *Crangonyx* (near *C. minor*) at Tributary III-a"; and *Crangonyx* (near *C. rivularis*), beneath a slab of marl at Station III.

Decapoda.—The 3 species of crayfishes in Doe Run occupied distinct ranges in the stream system, with some seasonal fluctuations. *Cambarus bartoni* was the largest

form, ranging up to 200 mm in length and 90 grams in weight (Minckley and Craddock, 1961), and was found only in the immediate vicinity of springs in summer, with juveniles and some adults ranging downstream to Station IV in winter, and also in caves of the area. Large *C. bartoni* foraged actively in daytime, but juveniles seldom were seen in the open. Large animals resided in beds of watercress, in *Myriophyllum* near Station II, or in detritus. In summer, however, they presumably moved into extensive burrows in the banks. Downstream, the species lived in burrows in the stream bed in summer, building crude chimneys near flat stones similar to those described by McManus (1960) in New York. Young animals lived in *Fissidens* or *Myriophyllum* and in beds of emergent vegetation along the banks; they were rare in summer. No female *Cambarus* found carried eggs, although young less than 10 mm long often were taken in the mainstream near Station I.

Orconectes rusticus was abundant downstream from Station II, at least in the mouths of all major tributaries below that area, and throughout the permanent tributaries. At Station II, *O. rusticus* was present from Tributary II-a upstream to a low waterfall at Mile 2.0, but none was taken farther upstream despite intensive collecting in that area. Likewise, in spring and summer, specimens of *O. rusticus* were rare at Station II, apparently having moved downstream into Pool 2. They returned to populate the area thickly in autumn and winter. Reproduction was obvious in April, May, and June, but occurred earlier at the downstream stations than at Station II. *O. rusticus* lived in diverse habitats, but was concentrated in vegetation when it was present.

The eyeless, unpigmented *Orconectes pellucidus* was common in caves of the area, where it occurred with *Cambarus bartoni*. A single specimen was taken in the open creek about 25 feet from the source.

Ephemeroptera.—Collections of mayfly

nymphs and imagos from the mainstream of Doe Run are thought adequate for delimiting distributions, but only 7 tributaries were collected intensively enough to merit discussion. The greatest number of species and individuals were found downstream from Dam 3 in and below the marl area (Fig. 25).

Ephemera simulans, a large, burrowing species, was found from Station IV downstream to the mouth of Doe Run. Nymphs listed as *Ephemera* sp. probably are *E. simulans*; they were small, or had indistinct color patterns on their wing pads. Nymphs lived in large pools and eddies, and always in gravel bottoms that contained considerable amounts of silt and sand. None was found on marl bottom. Ricker (1934a) and Ide (1935) both noted *E. simulans* as very abundant in bare marl gravels of Ontario streams, with populations as high as 250 per square foot in spring and early summer. Adults emerged from Doe Run in late June and throughout July, but always in small numbers.

Nymphs of *Hexagenia atrocaudata* were collected downstream from Station IV on 2 occasions, and were relatively abundant in the terminal pool of 7-Springs Branch at its confluence with Doe Run in June 1961. They had burrows in about 2 inches of fine silt overlying bedrock in a pool just lateral to a relatively swift current.

Ephemerella was one of the most abundant genera of mayflies at Station II, represented by *E. subvaria*, *E. needhami*, and a small, undetermined species. *E. subvaria* was by far the most abundant, and the largest individuals inhabited the more open riffles with gravel bottoms. Smaller nymphs were in beds of moss or milfoil, generally on the upper surfaces in association with *E. needhami* and the undetermined species, however, they did not enter the bases of the plants as did crustaceans and some other mayflies. Ide (1935) considered *E. subvaria* to have the lowest lethal temperature threshold of any of 3 closely related species of *Ephemerella*. This was postulated on the basis of early emergence dates

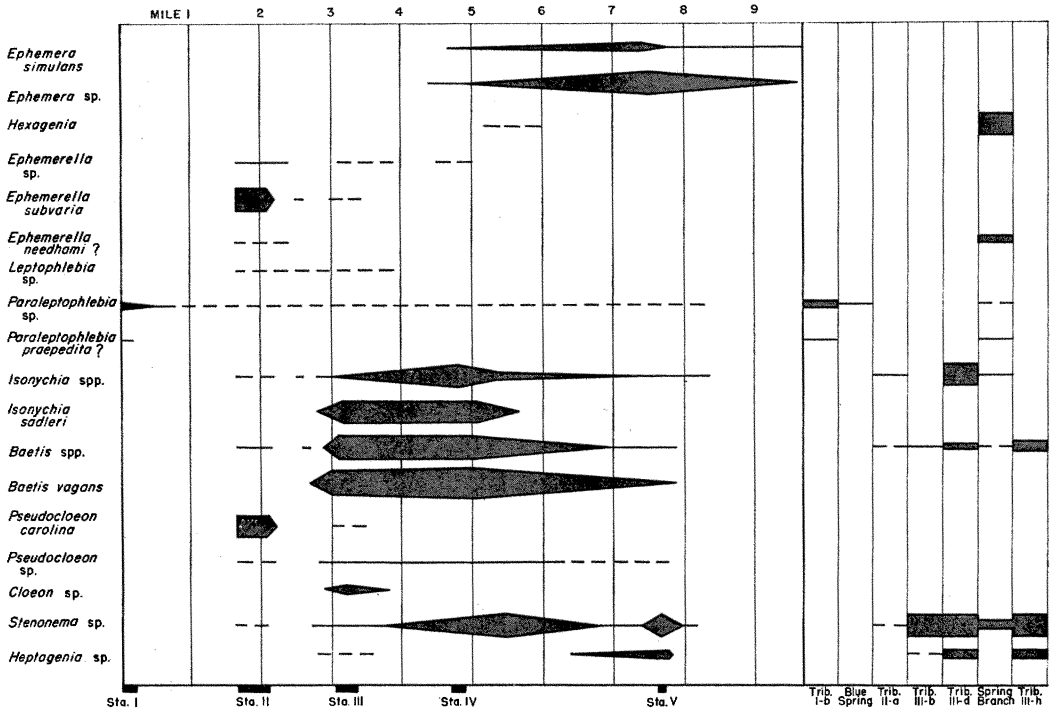


FIG. 25. Longitudinal distribution of ephemeropteran nymphs in Doe Run, Meade County, Ky., and occurrences in some of its tributaries. The width of the line indicates abundance of a species, with the widest place where the greatest numbers were present. No comparisons between species abundance are intended.

when compared with the other species. The restriction of the species to the area of Station II (Fig. 25) may be related to its need for low developmental temperatures. I found no imagos of *E. subvaria*.

The genus *Leptophlebia* was represented by a few nymphs from Station II downstream to below Station III. They occurred in eddies and soft-bottomed pools, principally in the upper parts of mill ponds, but also in dredge samples from the downstream, mud-bottomed part of Pool 3. Large numbers of nymphs also were present in the downstream pool of 7-Springs Branch.

Paraleptophlebia spp. were most common, though rare at best, at the source, in Tributary I-b, and in Blue Spring. Nymphs usually are found in gravel-bottomed, swift streams of small size (Burks, 1953), and *P. praepedita* was thought by Leonard and Leonard (1962) to be characteristic of

warmer trout streams in Michigan. In Doe Run, the nymphs swam actively when disturbed, and usually were obtained from mosses on the tops of stones.

Large, active nymphs of *Isonychia* were prevalent in riffles from Station III to Station V in late winter and early spring, and a few records were obtained at Station II (Fig. 25). Imagos of *I. sadleri* were found at Stations III and IV in June and July. On the basis of general color differences, I believe that there were at least 2 species of *Isonychia* in Doe Run, one in the main-stream (*I. sadleri*) and the other in the tributaries. *Isonychia* nymphs were almost never in quiet waters, but usually were abundant in small riffles lateral to the main currents rather than in the swiftest currents.

Tiny nymphs of the genus *Baetis* were the most abundant mayflies in Doe Run, occurring from Station II to riffles at Sta-

tion V. There were at least 3 species of *Baetis*, of which *B. vagans* was most abundant and most easily recognized in the field. It was abundant in the marl area, where it lived in the swiftest currents, in chutes of marl riffles, and directly on the upper sides of stones or gravel in riffles. At Station II, *B. vagans* often occurred with nymphs of *Ephemerella* more abundantly on beds of vegetation in swift water than on open, gravelly bottoms. The reverse was true for the *Ephemerella* spp. Percival and Whitehead (1929) found a direct contrast in English streams with other species of those genera; recently hatched nymphs of *Baetis* and *Ephemerella* occurred in beds of aquatic vegetation, and along the banks more often than larger nymphs. Harker (1953) and Macan (1957) found smaller nymphs of *B. rhodani* (Pictet) closer to the banks and farther upstream than larger individuals of the same species.

According to Ide (1935), *B. vagans* has 2 periods of emergence in Ontario streams, one in early summer and the second from mid-August to autumn. *B. vagans* emerged from Doe Run in January and February, with perhaps a smaller emergence in June. More likely, however, is an extended period of emergence from January through June, with early and late peaks (Murphy, 1922; Leonard and Leonard, 1962). On occasions, terminal-instar nymphs, seined from the stream in midwinter and warmed by sunlight for a few minutes, emerged in the net.

Pseudocloeon sp. and *P. carolina* were in swift parts of Doe Run at Station II, usually in association with aquatic plants or roots and debris along the banks. *P. carolina* inhabited open riffles in association with *Baetis* (Ide, 1935), or, when larger, along the banks in shallow, rapidly flowing water (Burks, 1953).

Flattened, sprawling nymphs of *Stenonema* occurred from Station III through the marl area to about Mile 7.0, and in rubble riffles at Station V. This distribution reflects the importance of rubble or other loose material to which the animals can cling in

current. In the upper marl area, and between Mile 7.0 and Station V, a few were found lateral to the main currents under logs, loose stones, and other debris. Fewer than 10 nymphs of *Stenonema* were obtained at Station II during the study. Nymphs representing species different from those in the mainstream were abundant in 4 or 5 downstream tributaries. An avoidance of springs is indicated by the absence of *Stenonema* from the upper parts of tributaries, and in Tributary I-b, Blue Spring, and Tributary II-a (Fig. 25). In small, downstream tributaries the animals lived side by side with *Lirceus* and various insect larvae beneath stones in mere trickles of water.

Nymphs of *Heptagenia* sp. were obtained rarely at Station III, but were more abundant in gravel bottoms overlain by silt between Miles 6.4 and 8.0.

Odonata.—Three genera of Odonata, 2 of which were damselflies, were identified from Doe Run; however, after impoundment of the downstream area a rich dragonfly fauna developed in the lake as it filled. *Gomphus* sp. was the only dragonfly collected from Doe Run and was taken only at Station V where it burrowed in silty bottoms of large pools.

Adults of *Agrion maculatum* were found at all stations but I and along most tributary streams. They were most common at Station II where naiads were associated with *Myriophyllum* in the current and also in emergent vegetation along the banks, or in beds of detritus. Males actively defended territories against other males near Station II and along the banks of Tributary II-a each spring of the study. Females oviposited on the undersides of *Myosotis* and *Nasturtium* leaves that hung in the water.

Argia sp. was rare and was found only as naiads in beds of emergent vegetation along the banks at Station III and in 7-Springs Branch.

Plecoptera.—*Allocapnia* sp. and *Nemoura* spp. were rare or difficult to secure from the mainstream of Doe Run. Nymphs oc-

curred mostly in the tributaries and also in leaf packets in the mainstream in autumn. Frison (1935) noted the occurrence of various species of *Allocapnia* in leaf deposits of Illinois streams, and Hynes (1941) noted certain *Nemoura* nymphs in English streams most often in leaf packets. Large numbers of *Nemoura delosa* were found at Stations III and IV from April to June of 1960 and 1961. Adults of *Allocapnia* and the other *Nemoura* were not obtained.

Perlesta placida, considered the most abundant and widely distributed stonefly of Illinois by Frison (1935, 1942), was common only in tributaries of Doe Run, but occurred at Stations III and IV in the mainstream. Adults were captured from May through early July.

Paragnetina media was the largest and most widespread stonefly of Doe Run, ranging from Station I as a few tiny young on 3 occasions to Station V. The species was not found in tributaries, however, except in winter in the downstream parts of Tributary II-a and 7-Springs Branch. It was most abundant in the marl area, where it was often heavily encrusted with marl and covered by small colonies of *Gongrosira* and *Phormidium*. Large nymphs lived in extremely swift water, often on tops of smooth slabs of marl in rapids, or in rubble or broken marl on riffles at Stations III and V. Its abundance decreased sharply with the beginning of greater pool-to-riffle ratios and a lack of rubble or marl bottoms near Mile 5.3 (Tables 1-2), but it was again common in rubble riffles at Station V. Adults were found on bridge abutments and streamside vegetation from early April to June.

The second largest and second most abundant stonefly, *Isogenus subvarians*, was found only in the marl area, where it lived on the undersides of stones somewhat lateral to the marl chutes in riffles with relatively uneven bottoms of rubble and gravel. It is worthy of note that this species was less often coated with marl than *Paragnetina*, perhaps because of its more

secluded habitat that allowed less chance for marl formation on the exoskeleton. However, more frequent ecdesis could have the same effect.

Other species of stoneflies in high-gradient tributaries to Doe Run were not identified.

Hemiptera.—Four species of surface-dwelling bugs were identified. *Microvelia pulchella*? was common and often mistaken for springtails when concentrated in quiet areas. It usually was associated with stream-drifted debris. *Metrobates* sp. was low in numbers, but also occurred in quiet water or in beds of vegetation. The large *Gerris* spp. were bolder, venturing across swift riffles and inhabiting other, relatively swift eddies and pools throughout the stream. Of the 2 kinds present, *G. remigis* was usually downstream whereas the undetermined species was common upstream. *Gerris* spp. apparently did not seek shelter for overwintering in Doe Run as reported by Hungerford (1920) in Kansas, probably because of favorable microclimatic conditions maintained throughout the winter by the relatively warm spring water, at least at the upstream stations.

Water scorpions, *Ranatra* sp., were taken on 4 occasions in seine hauls from *Myriophyllum* beds at Station II. All were in quiet water within 3 feet of the banks.

Other bugs recorded from Doe Run were taken only after periods of high discharge. *Belostoma* sp. was seen at Station II in April 1960, and *B. fluminea*, *Benacus* sp., and several specimens of *Sigara* sp. were taken at Station III in mid-June 1960. *Notonecta undulata*, undetermined notonectids and corixids, and additional specimens of *Sigara* were found only after the severe flooding of 1961 at Station I. All are abundant in sinkhole ponds of Meade County, and presumably were displaced into the creek during heavy rains. The insects were concentrated in quiet water near Station I.

Megaloptera.—Two adult alderflies, *Sialis* sp., were found at Station III in spring 1960. The fishfly, *Chauliodes*, however,

was abundant in suitable habitats throughout Doe Run downstream from Station II. Larvae were beneath gravel and rubble except in autumn when they lived among fallen leaves along the creek. They were often in interstices of dry gravels of small islands and bars downstream from Station IV, and in small tributaries lived beneath stones and leaves long after flow had ceased. In the last situation, larvae usually were found beneath large stones in small chambers. Pupae were not found in the stream bed, but occurred beneath stones and decomposing logs lateral to the water's edge. Pupal chambers of *Chauliodes* were seldom more than 5 feet from water and were immediately beneath a stone or log, in contrast to hellgramite larvae (*Corydalus* spp.) whose burrows for pupation are sometimes 30 feet from water and at the end of a definite tube (Chandler, 1956). Fishflies emerged the last week of May and first 2 weeks of June in both 1960 and 1961.

Coleoptera.—A number of aquatic beetles was found only after the floods of 1961, including a species of *Dytiscus*, and 2 undetermined dytiscid adults. Adult *Pelodytes* sp. were rare in beds of aquatic plants at Station II, and no larvae were obtained. Two resident dytiscids, *Laccophilus* and *Agabus*, were distributed from Station II to Station V as adults, with the latter more abundant downstream and the former upstream, but larval *Laccophilus* were taken only at Stations I and II in beds of vegetation. Whirlygig beetles, *Gyrinus*, were rare upstream from Station IV, but were locally abundant downstream. As with water striders, *Gyrinus* was active throughout the winter in Doe Run, apparently in response to the relatively warm water temperatures.

Psephenus herricki was not present in the mainstream of Doe Run, but a series was collected in the downstream part of Tributary III-i in spring 1961, a habitat later destroyed by impoundment.

Elmids were the most widespread group of beetles in Doe Run, represented by *Stenelmis* sp. and *Optioservus* sp. These

were not separated in the field and occurred both as larvae and adults. Collectively, they were found at all stations, but reached peak abundance in *Fissidens* beds and on small, gravel-rubble riffles with sparse moss cover at Station II. They were very uncommon in the marl area and were almost always coated with marl (Leonard, 1939).

Trichoptera.—*Glossosoma nigrior* was scarce at Station I, common at II, and in most of the spring tributaries of Doe Run, but was rare downstream in the marl area. Larvae of *Psychomyia* sp. were even more rare, however, occurring in small numbers at Stations I, II, and III.

Net-building hydropsychids were the most abundant trichopteran larvae in the stream, occurring most often on riffles, marl chutes, tops of mill dams, and on beds of submergent plants in swifter water. *Diplectrona modesta* was the least common of these, and was taken only downstream from Station IV. This species has been taken only from small, heavily shaded brooks in Illinois (Ross, 1953). *Hydropsyche* sp. occurred rarely at Station I (a total of 7 larvae), and with *H. betteni* was common from Station II to riffles at Station V. *Cheumatopsyche* spp., distributed in the same parts of the creek as was *Hydropsyche*, was somewhat less common than *Hydropsyche* downstream from Station IV.

A micro-caddisfly, *Agraylea multiplicata*, was the only insect other than certain dipterans that was abundant at Station I. The small, purselike cases of *Agraylea* were attached firmly to moss at Station I, and to a lesser extent at Station II, in such a position that they lay appressed to the beds and thus offered little resistance to current. Sometimes the cases were abundant enough to make the beds appear yellowish. Cases also were attached to small stones on the stream bed, to twigs or other debris, and once on open sand-silt bottom near Station I; the few occurrences at Station III were on marl riffles, and the cases were heavily encrusted with marl. Adults were obtained from March through September. After

emergence, cases remained on the moss for some time and caused difficulty in sorting of bottom samples.

Pychnopsyche sp. was obtained at all stations downstream from Dam 1, but was never abundant. It was most often in beds of stream-drifted detritus in eddies, where its case was made of small twigs, pieces of bark, and other vegetative debris. At Stations IV and V, however, the cases consisted of a large proportion of small gravel, with woody fragments attached to the posterior half.

Helicopsyche borealis was rare, being collected once at Station III, and twice at Station II. Empty cases were taken in bottom samples from *Myriophyllum* beds at Station II on 3 occasions, but subsequent to my study, *Helicopsyche* was common at Station II in August 1962.

Diptera.—Larvae of *Tipula nobilis*? and *T. abdominalis* were among the largest invertebrates other than decapods in Doe Run. *T. nobilis*? was found only at Stations I and II where it was always intimately associated with *Fissidens*. The greatest emergences of *T. nobilis*? occurred in late August, September, and October, with pupation beginning in June and lasting through September. The pupae occurred most frequently on the tops of larger stones covered by thick mats of mosses (usually species other than *Fissidens*). On September 7, 1960, I carefully removed the moss layer from a stone located near the bank in Doe Run and found 33 cast pupal skins, 15 pupae, and 51 larvae ranging from small to large in 180 square inches of moss. All stones emerged or along the banks, and with significant amounts of vegetation on them, had many pupal skins projecting from the vegetation. *Tipula abdominalis* was found from Station III downstream, and inhabited interstices of gravel bars, islands, or packets of fallen leaves that collected in autumn.

Pilaria tenuipes occurred from Station I to Station V, and usually in beds of emergent aquatic vegetation or in detritus accumulations in pools. The genus is thought

characteristic of rich organic muds at the edges of water, but usually in swamps, marshes, or lakes (Alexander, 1931). *Anotocha* sp. was common only upstream, and inhabited open, relatively soft bottoms along the banks and in pools.

Paradixa sp. was taken only at Station IV, in the shallow, lateral riffles.

Mosquitoes were quite abundant at times along Doe Run, and larval or pupal material of *Anopheles punctipennis*, *Culex pipiens*, and an unidentified *Aedes* were obtained. The former was quite abundant upstream from Dam 1, especially in thick beds of watercress or rafts of fallen leaves along the banks. *Anopheles punctipennis* characteristically breeds in clear, cool, shaded pools of streams or brooks (Matheeson, 1944). *Culex pipiens*, on the other hand, usually breeds in rain-filled cans, hoofprints, and the like, and is apparently unusual in stream situations. It was considerably more rare than *Anopheles* in Doe Run. *Aedes* sp. was recorded on the basis of 2 larvae from Station II.

Chaoborus punctipennis usually is found in lakes of Kentucky and other parts of North America, but to my knowledge it is very rarely found in smaller streams. A number of larvae were collected from a deep, quiet pool downstream from Station IV in June 1961. The species rapidly colonized Doe Valley Lake after its impoundment in July 1961, with a massive emergence approximately 3 months after the first inundation of the valley.

Simulium sp. was found from Station II to Station V on swift, open riffles, and attached to most solid substrates. Its abundance was somewhat reduced in summer in the marl area, possibly because of encrustation by carbonates on pupal cases, and it was most abundant in the high-gradient tributaries of the middle portion of Doe Run (Fig. 1).

Fifteen species of tendipedid dipterans were identified from Doe Run, but many additional forms undoubtedly occur. Because of the difficulty in identifying midges, and the problems of their taxonomy in

North America (James, 1959; and others), there are little data on their ecology. A carnivorous group (Leathers, 1922), the subfamily Pelopiinae (= Tanypodinae), included *Pentaneura* sp. and *Procladius* sp. in Doe Run. The former occurred at all stations downstream from Station II, whereas the latter was taken only at Station III. Both were found in eddies and in beds of emergent vegetation or detrital deposits. Usually they are associated with lotic conditions in streams (Curry, 1954). The remaining tendipedids identified are generally considered phytophagous or detritus feeders (Leathers, 1922). Those of the subfamily Hydrobaeninae (= Orthocladiinae), *Psectrocladius*? sp. and *Trichocladius* sp., were generally distributed in the stream, and usually were identified from samples obtained in swift waters. Specimens from Doe Run referred to *Psectrocladius*? could be the closely related *Eukiefferiella*; however, they lack a small hook on the basal portion of the mandible which should be present in the latter genus (Stuart E. Neff, pers. comm.).

The subfamily Tendipedinae (= Chironominae) was represented by 11 species in Doe Run. Of these, *Calopsectra dissimilis*?, *Tendipes* (*Tendipes*) sp., and *T. (Limnochironomus)* sp. were identified only from samples at Station II in association with submerged vegetation. A third species, *T. (Limnochironomus) modestus*, was taken in pool habitats at Station V.

Tanytarsus sp. and *T. (Tanytarsus)* sp. occurred only at Station III, but *T. (Stictochironomus)* sp. and *T. (Endochironomus)* sp. were found throughout the stream. They were in samples obtained from small riffles lateral to the channel at each station, but also occurred in samples from *Fissidens* at Stations I and II, and in emergent vegetation or detritus accumulations at other stations.

Cryptochironomus sp. occurred only at Station III, in a sample from a riffle lateral to marl. The species of this generally northern genus are flexible in their habitat requirements (Curry, 1958), and many

may be carnivorous, thus comprising a general exception to the other Tendipedinae (Curry, 1958; Wirth and Stone, 1956).

Of the 2 remaining species of tendipedids identified, *Microtendipes pedellus*? occurred throughout the creek in samples from pools, and *Glyptotendipes senilis* was taken at Station IV in a similar habitat.

Biting midges, Heleidae (= Ceratopogonidae), were represented by *Culicoides* sp. in shallow pools at Stations III, IV, and V.

Tabanus sp., the horse-fly, occurred as larvae at Stations III and IV in interstices of gravel, usually slightly above the water levels of the creek. This larva was rare when compared with *Tipula abdominalis* in the lower parts of Doe Run, but the 2 large dipterans often were taken side by side in beds of stream-drifted leaves and debris in autumn.

Atherix variegata is a large, common inhabitant of the marl area of Doe Run, and was at Stations II and V in small numbers. This species often was seen moving openly on marl riffles, and was capable of negotiating swift currents. It also inhabited small pits or "burrows" in marl surfaces.

Scatella sp. was found at Stations I and II along the banks on riparian roots, and often in emerged or slightly submerged beds of *Fissidens*. A few individuals also were taken at Station III in the small riffles lateral to the channel. The anthomyiid *Limnophora* was common downstream from Station II in small riffles and in small pits in the surface of marls, and a small, unidentified species of Empididae was collected at Station IV from a similar habitat. *Mollusca*.—Pulmonate snails were notably absent from Doe Run, but *Physa* spp. occurred in many smaller, seepage-fed tributaries, and was the only snail of this type found in the stream system (excluding semiterrestrial forms). These snails were found in the mainstream only at dams, where they inhabited spray areas and shallow pools, and downstream from Station V, in backwaters of the navigation pool of the Ohio River. *Physa* was also absent

from the larger, spring-fed tributaries, thus implying a general avoidance of cool waters.

Living *Ferrisia* were not collected from Doe Run, but appeared in laboratory tanks of vegetation stocked from Station II. Twice there was no doubt as to the provenance of the material. Empty shells of this mollusk were found in sediments from Stations I, II, and III.

Pomatiopsis lapidaria, a predominantly terrestrial species (semiaquatic), was taken in bottom samples from deep water at Station V in 1959 (Kaplan and Minckley, 1960), and was relatively abundant along the banks of the lower creek prior to impoundment.

Goniobasis was the largest and most abundant gastropod in Doe Run, occurring throughout the creek to Station V, and in 5 of the spring tributaries: Tributary I-b, Blue Spring, Buffalo Spring, Tributary II-a, and 7-Springs Branch. It was also found in those portions of some smaller spring tributaries that flowed on the floodplain of Doe Run, but did not occur above the first major incline or riffle. *Goniobasis* was extremely abundant locally in Doe Run, especially in the upstream areas, and in periods of modal flow the animals covered the bottoms near Mile 0.5 in an almost perfect random distribution. At those times populations comprised 243 to 329 individuals per square foot (10 quadrats counted), with an average density of 296, with considerably larger populations per unit area in beds of vegetation. Equally large populations of this snail were found in the Hocking River, Ohio, by Ludwig (1931). After floods, *Goniobasis* moved from pools into which they had been displaced, back onto shallow areas. The species in Doe Run was not a riffle animal, but generally inhabited vegetation or open areas where eddying currents persisted on firm bottoms. On soft, silty bottom the snail sinks deep into the substrate and its movements are obviously impaired. After floods, many *Goniobasis* were stranded on bars and small islands, where they expired,

and their shells were incorporated into the bottom sediments.

The eggs of *Goniobasis* in Doe Run were laid on undersides of stones in packets of 16 to 27 eggs in 20 packets counted. The eggs were enclosed in a jellylike substance covered by tiny sand grains and other debris, presumably through action of the current. I do not know the time required for hatching, but eggs were most common in bottom samples from July through September 1960 at Station I. Eggs also were found in October, January, and April, indicating sporadic or continuous breeding, at least by part of the population. Egg masses at Stations III and IV were covered with marl on occasions, but this did not appear to deter hatching.

Sphaeriid clams were present throughout the Doe Run system, and usually were abundant wherever there were relatively firm deposits of silt-sand, detritus beds, or relatively firm substrates beneath beds of vegetation. Reproduction was greatest in summer, judging from sizes of animals secured, but this may be an expression of better survival of young in periods of modal flow or movement of larger individuals deeper in sediments with receding water levels of summer.

Quantitative Aspects of the Invertebrate Fauna

Descriptions of Sampling Areas.—Although a general description of Doe Run and the principal collecting stations has been made, it seems appropriate to discuss in detail the areas where quantitative sampling was attempted.

Station I.—At Station I during modal discharge, most bottoms were covered by vegetation (Fig. 22), but during high discharge the amounts varied with the severity of washout. Gravel and rubble were present to about 60 ft downstream from the source. Sand and some gravel were common in backwaters, and were the principal bottom materials downstream from a small rubble obstruction at the lower end of the stony bottoms. There was some silt in the mouths of Tributaries I-a and I-b, and along the banks, and there was a thick deposit of detritus just below the inflow of I-b during modal flow. Samples were taken from the following habitats:

Fissidens Beds in the Channel. Beds of aquatic mosses tend to reduce turbulence by presenting a

smooth surface over which the water passes (Margalef, 1960). This surface results from imbrication of the tiny, flattened leaves, and produces a thin, cushionlike mat beneath which there is only nominal current and a rich supply of detrital foods filtered from the water. *Fissidens* was damaged by washout or by abrasion by waterborne materials in 2 different ways: (1) the moss with its contained invertebrates was removed en masse from recently colonized, unstable substrates and washed away, and (2) the action of the water plucked the terminal portions of the plants, thinning the beds without removing them and without extirpating the fauna. Such thinning was sustained by plants firmly attached to larger substrates and the amount of damage depended on the duration and severity of flooding. With alleviation of flood condition some silt was deposited in *Fissidens* beds in the channel, but with subsequent clear-water flow the moss was relatively free from silt within a few weeks.

Unvegetated Riffles, or the Least-Vegetated Riffles Present. There were small open channels between major moss beds throughout the year, presumably because the substrate was unsuitable. In 7 of the 15 months of sampling, however, no completely unvegetated riffles were present. Substrates consisted of small rubble and gravel overlying larger rubble and bedrock. Currents ranged from 1 to 3 ft/sec and usually were turbulent.

Nasturtium Beds, or in Such Areas After Washout. Watercress beds at Station I were subject to severe washout and samples from those areas might be considered to be from silt-sand bottoms. Seven of 17 samples included *Nasturtium*, the others were taken in areas of former beds after washout, but always immediately downstream from Tributary I-b. Accumulations of silt and detritus in the beds were sometimes black and malodorous. After washout some roots and other organic materials remained and were covered by sand and silt.

Shifting Sand Bottoms. The shifting sand bottoms at Station I were immediately downstream from the rubble obstruction and were continuously subjected to eddying currents exceeding 0.5 ft/sec. During modal flow the bottoms were somewhat stabilized, and supported sparse stands of *Batrachospermum* and diatoms.

Station II.—This station was similar to Station I in that plants covered a large part of the bottom (Fig. 24). Most quantitative sampling was done immediately below Dam 1, but some samples were obtained in comparable habitats near the mouth of Tributary II-a. Two habitats studied at Station II, *Fissidens* beds and unvegetated riffles, were similar to those at Station I. Additional areas were:

Myriophyllum Beds. Beds of milfoil are intermediate between *Fissidens* and *Nasturtium* in habitat type. The relatively large plants allow for considerable accumulation of debris and the

formation of mounds or bars as in the latter, but the finely divided leaves, flexibility, and tendency to flatten in current to form cushionlike mats, are mosslike. The bottom in beds of milfoil usually was gravel, sand, and snail shells, with silt and detritus on the downstream sides. Samples were taken from near the center of the mounds. Currents ranged as high as 2–3 ft/sec, but conditions within the beds were undoubtedly more quiet.

Open Pools with Varied Bottom Types. Larger pools at Station II usually had bottoms of sand, gravel, and shells of *Goniobasis*, mixed with silt and detritus. In autumn, leaves were a major constituent of the bottom materials, but usually were washed away by floods that sometimes cleared the materials to bedrock. As noted above, currents in pools in the upper parts of Doe Run usually exceeded 0.5 ft/sec.

Station III.—Station III was typical of the marl area, except that it was frequently disturbed by man. The station may be characterized by 2 types of pools, 1 with sharp, precipitous marl rims and rubble or marl bottoms, and the other with sand, gravel, and silt banks that sloped gently to the bottoms, and with considerable eddying of current. Such pools were adjacent to waterfalls and had swift, turbulent current. Riffles at Station III consisted of solid marl sheets or of gravelly areas maintained by human activities such as swimming and wading. Samples were taken in areas not visibly disturbed: (1) in a relatively inaccessible marl riffle upstream from the recreational area; (2) in small, rubble-bottomed riffles lateral to the marl riffle; (3) in beds of *Myosotis* growing in deep silt bottoms lateral to pools; and (4) in a large, silt-detritus-bottomed eddy. Of these, number 3 is comparable to watercress beds at Station I and will not be described further.

Marl Riffles in the Channel. The term "marl riffle" refers to riffles almost completely cemented into a solid slab by marl deposition. The depth of water at the point of sampling usually ranged from 2 to 8 inches in periods of modal flow, and currents exceeded 3 ft/sec. Currents and depths were much higher at higher discharges.

Riffles Lateral to Marl. Substrates were small marl concretions, gravel, and snail shells, with silt and detritus deposition between stones. Currents were variable, ranging to a low of 0.5 ft/sec. In low-water periods many large stones were exposed to air, especially in daytime when evaporation and transpiration of riparian vegetation caused slight reductions in water level.

Eddying Pools. Samples from the large eddy at Station III were from diverse bottom types, somewhat comparable to the open pools at Station II. The bottom ranged from small gravel and large sand after periods of flood, to deep, soft silt and detritus after summer flow. Currents in the sampling area flowed upstream at the rate of 0.25 to 0.5 ft/sec except in extreme flood. The water was about 18 inches deep at modal flow.

Station IV.—The main study area at Station IV was a large, circular pool with a series of swift marl riffles upstream and a small, marl-rubble obstruction at an old bridge abutment downstream. As with most pools in Doe Run, much of the bottom was bedrock, with silt deposits in eddies. Deep beds of detritus settled out on the bedrock bottom in periods of constant flow. Samples were obtained from 4 habitats: (1) marl riffles that differed from those at Station III only in the presence of a few large, limestone slabs; (2) from a small lateral riffle generally comparable to that sampled at Station III, but with slightly more silt and sand deposition; and from 2 additional habitats, descriptions of which follow.

Silt-Bottomed Eddy. This habitat was unique in that it remained essentially unchanged throughout the study. The silt deposit lay at the mouth of Tributary IV-a, but apparently was in an abandoned channel of Doe Run rather than an eddy. Tributary IV-a was a composite of a number of springs and a small seepage-fed marsh in a low part of the old channel (Fig. 1). The silt deposit lay about 3 feet from the main inflow of the upstream riffle, but was protected by marl deposits on roots of a streamside tree. Eddying currents flowed at 0.5 to 1.0 ft/sec, but there was little removal or deposition of silt.

Gravel-Rubble-Bottomed Eddy. This area has sufficient current to warrant consistent use of the Surber sampler, and might easily be classed with riffle habitat if it were not for its relatively great depth (12 to 18 inches) and general lack of turbulence. Some deposition of sand and silt occurred after major flooding, but was removed by subsequent flow.

Station V.—Because Station V was inundated by the Ohio River, quantitative data on the benthos are sparse. The station consisted of a single series of riffles, bordered both up- and downstream by long, relatively quiet areas. Few stones were present, even on riffles. An amazingly resistant clay comprised the bottom in most swift areas, and was overlain by silt, sand, and detritus in pools. Samples were obtained from the following areas:

Swift, Rubble-Bottomed Riffle. A short section of rubble bottom was present at the upstream end of the riffle area; however, velocity of the water was rarely less than 3 ft/sec in modal discharge and sampling was difficult at best. Also, the rubble bottom consisted of large, angular boulders, not conducive to effective sampling.

Rubble-Gravel-Bottomed Riffle, Lateral to the Channel. This habitat was similar to those at Stations III and IV lateral to the channel, except that most of the gravel at Station V was smooth, rounded erratics eroded from adjacent Pleistocene deposits. Velocities of current were variable, but the riffles were generally quite turbulent.

"Pools," in the Channel. Samples from these areas were taken more or less as a survey of the

fauna and few comparative data can be derived from them. Substrates ranged from clay to coarse sand, depths from a few inches to greater than 6 feet in periods of partial inundation by the Ohio River, and velocity of current ranged from negligible to about 1 ft/sec.

Standing Crops and Numerical Relations of the Fauna.—The fluctuant nature of invertebrate populations in a stream is well exemplified by data from Doe Run. This is true even though the stream originates in a large spring with a consequent amelioration of extremes other than discharge. Although sampling error is great, actual changes in benthic populations are subject to rapid fluctuations (Hynes, 1960), and are manifest in 3 ways: (1) by recruitment of new individuals through reproduction; (2) by death of the organisms *in situ*, from catastrophe, old age, predation, or other agents; and (3) by movement of organisms into or out of the habitat, under their own power or by physical forces in the environment. Interpretation of variations in the populations is complicated by seasonal aspects of reproduction of the different species and phenomena related to reproduction such as emergences of certain insects, by differences in response of various kinds of animals or their vulnerability to diverse changes in the environment, or by many other factors.

Riffles of the Main Channel.—*Fissidens* Beds. In beds of *Fissidens* at Station I, animal populations ranged from 18,708 individuals per square foot (ft^2) in December 1959, to 2,332/ ft^2 in July 1960. The average number of animals in 15 samples was 8,628/ ft^2 of which isopods made up 68.9 and amphipods 24.1 per cent of the total. Dipterous larvae were third in numerical abundance, followed by caddisflies, turbellarians, and oligochaetes. The greatest weight of organisms in this habitat was 28.695 g/ ft^2 in December 1959, weights of crayfish and mollusks excluded, of which 25 g/ ft^2 were amphipods. The least weight was in July 1960, 0.926 g, when the smallest numbers of animals were present. Average weight was 8.075 g, decapods and mollusks excluded, and only 8.750 when they were

included. Amphipods were by far the most abundant by weight, making up 58.8 per cent of the total, and were followed in order by isopods, 24.8 per cent, and by dipteran larvae, trichopterans, turbellarians, and oligochaetes.

Moss beds at Station II were somewhat more stable than at Station I, apparently because of more extensive bedrock bottoms, and contained a larger standing crop of animals, both in numbers and weight. Isopods and amphipods retained numerical dominance in the fauna, comprising 47.0 and 22.4 per cent, respectively, of the average 9,295 individuals/ft². It is noteworthy that isopods were both actually and relatively more numerous at Station I, but the number and relative abundance of amphipods were the same at both stations (2,082/ft², 24.1% at Station I, and 2,085/ft², 22.4% at Station II). Trichoptera larvae, turbellarians, oligochaetes, and mayflies were more abundant in moss at Station II than at Station I, but dipteran larvae were reduced in relative numerical position, falling to fourth most abundant at Station II. The greater average weight of standing crop at Station II, 10.810 g/ft², was aided substantially by the abundance of large tipulid larvae and hydropsychid caddisflies. Dipterans contributed the most weight, followed by amphipods (25.6%), trichopterans, isopods, turbellarians, and oligochaetes. A major difference between the fauna of moss riffles at Stations I and II was the greater abundance of snails at the latter, comprising an average of 12.642 g/ft² (not included in biomass data given above). When mollusks and crayfish are included in the biomass at Station II it was almost 3 times that at Station I (23.467 and 8.750 g/ft²). Numbers and weights of invertebrates in this habitat at Station II ranged from maxima of 20,004 individuals in December 1959 and 48.937 g/ft² in January 1960 (38 g of which were *Tipula*), to minima of 1,691 individuals and 1.658 g/ft² in November 1959. The last values, however, were obtained by Surber sampler and are not strictly comparable.

Major changes in animal numbers in *Fissidens*, and in other habitats of Doe Run, apparently resulted from changes in discharge or related phenomena. For example, at Station I the smallest populations were present in July–August 1960 (Table 6), following extreme discharge in June, and in June 1961 following severe flooding through spring of that year. At Station II, however, the populations were higher in *Fissidens* after the June floods than before, mostly because of great numbers of caddisflies (principally *Hydropsyche* and *Cheumatopsyche*) that colonized upper surfaces of the beds. Numbers of turbellarians in *Fissidens* beds generally increased with increases in discharge at both stations, as did oligochaetes at Station I, but at Station II, the largest numbers of oligochaetes were present during the 1960 period of modal discharge. Isopods usually were the most abundant animals, but their populations fluctuated considerably as a result of wash-out and thinning of *Fissidens*, restriction of the major breeding season to 3 months in early summer (Walker, 1962), and movement and concentration of the animals in response to unknown factors (see Allee, 1929). Some inconsistencies may relate to the chance collection of such aggregations of isopods and other forms by the sampler.

Numbers of amphipods, mostly *Gammarus minus*, were remarkably constant at both stations in *Fissidens*, and apparently were much more independent of discharge in maintaining their populations than were isopods. This may be partly explained by upstream movements after displacement by flood (Minckley, 1963).

The small trichopteran, *Agraylea*, at Station I was abundant only from March to June 1960, and its sudden decrease may be attributable to emergence in June. Dipterans also were most abundant at that station from March to June, but maintained considerable populations to the September–October period. Dipterans were generally abundant in *Fissidens* at Station II throughout the study.

Increase in the numbers of Turbellaria,

TABLE 6.—NUMBERS OF ANIMALS PER SQUARE FOOT IN RIFFLES OF THE MAIN CHANNEL OF DOE RUN, MEADE COUNTY, KENTUCKY. DATA ARE GIVEN AS AVERAGES OF 2 SAMPLES, 1 FOR EACH MONTH INDICATED EXCEPT WHERE SAMPLES ARE LACKING; THOSE CASES ARE MARKED WITH AN ASTERISK (*). DATA FOR JUNE 1961 ARE BASED ON SINGLE SAMPLES THROUGHOUT

Animal Group	November- December (1959)	January- February (1960)	March- April	May- June	July- August	September- October	November (1960)- January (1961)	June (1961)
STATION I: <i>Fissidens</i> Beds								
Turbellaria	7.5	68.0	316.0	170.0	108.0	152.0	50.0	168.0
Oligochaeta	8.0	—	28.0	148.0	24.0	134.0	66.0	—
Isopoda	9,283.5	6,596.0	6,764.0	4,230.0	2,912.0	8,690.0	4,908.0	1,096.0
Amphipoda	2,340.0	2,124.0	2,902.0	852.0	1,294.0	2,216.0	3,624.0	524.0
Plecoptera	—	—	—	2.0	—	—	—	—
Ephemeroptera	—	—	2.0	2.0	—	—	—	—
Trichoptera	0.5	—	308.0	998.0	30.0	2.0	86.0	128.0
Coleoptera	—	—	—	20.0	4.0	—	—	—
Diptera	4.5	6.0	6.0	404.0	573.0	266.0	36.0	472.0
Decapoda	3.0	—	—	—	—	—	2.0	—
Gastropoda	3.0	4.0	—	8.0	—	2.0	2.0	—
Pelecypoda	0.5	4.0	—	—	—	—	—	—
TOTALS	11,650.5	8,802.0	10,344.0	6,834.0	4,945.0	11,462.0	8,774.0	2,388.0
STATION II: <i>Fissidens</i> Beds								
Turbellaria	391.0	1,284.0	306.0	156.0	732.0	56.0	644.0	92.0
Oligochaeta	—	6.0	—	28.0	—	1,028.0	—	8.0
Isopoda	7,050.0	6,792.0	1,424.0	4,330.0	5,450.0	2,602.0	4,598.0	996.0
Amphipoda	2,550.0	2,004.0	956.0	2,152.0	2,828.0	650.0	3,984.0	1,024.0
Plecoptera	—	—	8.0	2.0	—	—	—	8.0
Ephemeroptera	353.0	104.0	54.0	206.0	120.0	236.0	332.0	72.0
Megaloptera	—	—	—	—	2.0	—	—	—
Trichoptera	348.0	3,506.0	1,321.0	536.0	2,148.0	494.0	5,140.0	208.0
Coleoptera	30.0	42.0	10.0	26.0	24.0	54.0	76.0	96.0
Diptera	119.0	450.0	268.0	910.0	914.0	1,450.0	98.0	708.0
Acridi	1.0	—	—	—	2.0	—	—	—
Decapoda	—	—	—	—	—	—	2.0	—
Gastropoda	7.0	—	2.0	44.0	20.0	1,130.0	112.0	4.0
Pelecypoda	—	—	—	4.0	—	2.0	—	—
TOTALS	10,849.0	14,188.0	4,349.0	8,394.0	12,240.0	7,702.0	14,986.0	3,216.0
STATION III: Marl Riffle								
Turbellaria	0.5	0.5	0.5	0.5	—	—	—	—
Oligochaeta	—	0.5	0.5	0.5	—	—	0.5	4.0
Isopoda	3.5	1.5	3.0	3.5	4.5	2.0	—	1.0
Amphipoda	2.0	—	3.5	3.0	2.5	—	—	1.0
Plecoptera	3.5	2.0	3.5	2.0	2.0	—	1.0	—
Ephemeroptera	30.5	16.5	116.5	84.5	187.0	57.0	10.5	6.0
Trichoptera	9.5	5.5	3.5	11.5	96.5	16.0	9.5	—
Coleoptera	2.5	—	—	0.5	1.0	—	—	2.0
Diptera	19.0	10.0	40.0	114.5	167.5	18.0	36.5	—
Acridi	—	—	—	0.5	—	1.5	—	—
Decapoda	0.5	—	1.0	1.5	—	—	—	—
Gastropoda	2.0	0.5	1.5	—	2.0	—	—	—
TOTALS	73.5	37.0	174.0	222.0	464.5	93.0	58.0	14.0
STATION IV: Marl Riffle								
Turbellaria	—	—	—	—	—	1.0*	—	—
Oligochaeta	0.5	4.0	2.5	2.5	—	1.0*	—	—
Isopoda	2.0	—	2.5	1.0	—	—	—	—

TABLE 6.—Continued

Animal Group	November– December (1959)	January– February (1960)	March– April	May– June	July– August	September– October	November (1960)– January (1961)	June (1961)
Amphipoda	2.5	—	2.0	—	0.5	—	0.5	—
Plecoptera	9.5	2.0	11.0	2.0	4.0	4.0*	1.0	—
Ephemeroptera	31.5	25.5	42.0	48.5	63.0	20.0*	32.0	88.0
Megaloptera	—	0.5	—	—	—	1.0*	0.5	—
Trichoptera	78.0	28.0	4.0	15.5	91.0	4.0*	5.0	25.0
Coleoptera	1.0	—	—	—	—	—	1.0	—
Diptera	50.0	25.5	87.0	40.0	96.0	21.0*	16.0	614.0
Acrid	2.5	—	—	—	—	—	—	—
Decapoda	—	—	0.5	0.5	1.0	—	—	—
Gastropoda	2.0	0.5	0.5	0.5	—	—	—	—
TOTALS	179.5	86.0	152.0	110.5	256.5	51.0*	56.0	727.0
STATION V: Rubble Riffle								
Oligochaeta	—	9.0	—	1.5	0.5	—	1.0*	—
Isopoda	2.5	5.0	17.0*	32.0	4.0	1.5	2.0*	—
Amphipoda	—	1.0	—	4.0	—	—	2.0*	—
Plecoptera	1.0	—	2.0*	—	—	—	—	—
Ephemeroptera	10.0	5.0	6.0*	35.0	26.5	18.5	22.0*	—
Megaloptera	—	—	—	—	—	—	1.0*	—
Trichoptera	13.5	0.5	3.0*	8.0	7.5	12.5	7.5*	—
Coleoptera	0.5	1.0	—	2.0	2.0	—	—	—
Diptera	14.0	2.0	66.0*	38.0	2.5	75.0	8.0*	—
Acrid	—	—	—	—	0.5	—	—	—
Decapoda	—	—	—	1.0	—	0.5	—	—
Gastropoda	—	2.0	—	1.0	—	1.0	—	—
TOTALS	41.5	25.5	94.0*	122.5	43.5	109.0	43.5*	—

Oligochaeta, and dipteran larvae in moss during periods of above-normal discharge may be attributable to movement into relatively stable habitats during extreme conditions. With oligochaetes and dipterans, however, these increases may have been related to deposition of sand and silt in the moss by the highly turbid waters. Removal of these sediments in periods of modal discharge was gradual, and probably was assisted by burrowing activities of the animals. Vertical movements by aquatic larvae through as much as 12 centimeters of gravel were noted by Badcock (1954a, b) as possible causes of rapid change in numbers of animals in a given habitat, and as a mechanism for avoiding severe winter discharges. Frost (1942) recorded peaks in abundance of chironomid (=tendipedid) dipterans in winter similar to those found in moss habitats of Doe Run, and attributed changes in populations to immigration from less suitable areas. Recolonization of the

entire stream from such sheltered areas in spring after recession of winter floods (Whitehead, 1935) possibly was important in Doe Run. An increase in the diversity of the fauna in winter in *Fissidens*, particularly at Station I, seems to indicate general emigration by certain forms in summer. In long periods of modal flow the fauna gradually changed to almost entirely *A. bivittatus* and *G. minus*, but substantial numbers of dipterans and oligochaetes remained in the sediments beneath and within the beds.

As a general rule, dipterans and oligochaetes increased or maintained relatively large populations throughout the creek, including the *Fissidens* habitat, during modal flow. This may have resulted from receding water levels and movement of animals from the silt and clay banks, small gravel bars, and winter-submerged islands in downstream area, into the channel of the creek to avoid desiccation. This presum-

ably would be counteracted by lateral movement on resumption of winter discharge conditions, and would result in decreased populations in the channel during those periods. Increases in numbers of some burrowing forms in pools may also result from drift and accumulation there during flood, but would be at the expense of those in the current.

Unlike the fauna at Station I, that in *Fissidens* at Station II was relatively diverse throughout the year (Table 6). Eight groups of organisms comprised at least 1 per cent of the sample at Station II, whereas at Station I there were only 5 such groups. At the specific level, the disparity between the 2 areas was even more pronounced (see Fig. 25). This situation apparently resulted from an overlapping of faunal elements indigenous to the source of the creek, and of forms more common downstream (such as caddisflies, various mayflies, etc.). There were, however, some species at Station II that were rare or absent at stations upstream and downstream.

Marl Riffles. The general absence of vegetation at Station III and the resulting paucity of plant-inhabiting crustaceans was reflected in numbers of animals per unit area. Samples from marl riffles averaged 145 organisms/ft² of which mayflies made up 44.0 per cent. Dipterans inhabiting the porous marls (tendipedids, *Limnophora*, and others) and some living on top of the marl such as *Simulium*, made up 36.6 per cent, and Trichoptera, 13.3 per cent. By weight, however, trichopterans were first with 37.1 per cent, followed in order by mayflies and dipterans. Plecoptera nymphs comprised only 1.3 per cent of the animals taken, but made up 13.4 per cent by weight because of their generally large sizes. The average standing crop on marl riffles was 0.404 g/ft² (1.607 when mollusks and decapods are included). Numbers and weights of organisms ranged from no animals in October 1960, the reasons for which are unknown, to 679/ft² in August of that year, and 1.522 g/ft² in July (1.193 of which were Hydropsychidae).

Diptera were most numerous on marl riffles at Station IV. Mayfly nymphs were second in abundance, averaging 42 individuals/ft² (24.2% of the total, and caddisflies were third with 19.2%). The average numerical standing crop was 175/ft², slightly higher than the average in comparable habitat at Station III (147/ft²); the average weight, 0.595 g/ft², was higher than the average of 0.404 g/ft² at Station III. Trichoptera made up a major part of the weight, 33.9 per cent, similar to that at Station III. Ephemeroptera and Diptera were present in almost equal weights at Station IV (21.6 and 20.8%, respectively) and were followed by stonefly nymphs (17.3%). The range of standing crops was as follows: maxima—727 individuals in June 1961 and 1.647 g in late February (= "March"); minima—8 individuals in July 1960 and 0.032 g in January 1961.

Marl riffles at Stations III and IV are comparable, not only in averages, but in numbers of individuals (Table 6). Mayfly nymphs were least abundant in January–February 1960 and in November–January 1960 and 1961, at both stations, which corresponds generally to the major emergence of the most abundant form, *Baetis vagans*. Caddisflies, principally hydropsychids, became less abundant in September–October 1960 at each station, and this may relate to their emergence, although no definite patterns were recorded. Dipteran larvae increased in summer at both stations, but were absent from marl riffles at Station III in June 1961, presumably as a result of severe scouring by spring floods. At Station IV, however, dipterans (mostly tendipedids) were more abundant after the 1961 floods than ever before, apparently because of clearing in that area. Siltation of some riffle areas, and especially the luxuriant growth of *Cladophora* on formerly marl riffles, may have produced more favorable conditions for the larvae.

Stonefly nymphs were a consistent, though minor, part of the fauna on marl riffles at both Stations III and IV, but were totally absent from those habitats in June 1961.

Rubble Riffles. As noted earlier, sampling at Station V was complicated by sporadic presence of backwaters of the Ohio River, and data are not strictly comparable to those from other stations. The swift, rubble-bottomed riffle at Station V, however, yielded average numbers of animals quite similar to those found in marl riffles (146/ft² compared with 147 at Station III and 175 at Station IV). The biomass was much smaller at Station V, averaging 0.136 g/ft² in 12 samples. Caddisflies, dipterans, and mayflies were the most abundant kinds of animals, and collectively made up 81.7 per cent of the total weight. The numbers of animals per sample ranged from 9 to 185/ft², and weights ranged from 0.003 to 0.252 g.

Invertebrates on the riffles at Station V were subjected to inundation by the Ohio River backwaters on occasions, which resulted not only in semilentic conditions but in relatively heavy siltation. The fauna consisted of organisms somewhat resistant to ponding, such as *Stenonema*, various dipteran larvae, and isopods. Organisms such as *Isonychia*, *Simulium*, and hydro-psyhids were rare, and increased in abundance in periods of modal flow, when riffle conditions persisted.

Riffles Lateral to the Channel.—Unvegetated riffles at Stations I and II. The standing crop of invertebrates on unvegetated riffles was smaller than in *Fissidens*, averaging 264 individuals/ft² in 15 samples from Station I. The greatest number of animals was present in September 1960, 1,363/ft², when the "unvegetated riffle" contained an estimated 25 per cent moss cover. Proportionately high populations were present in June 1960 at an estimated moss cover of 20 per cent (1,043/ft²). The smallest populations occurred when no moss was present, and after major washout (minimum, 26/ft² in January 1961). Isopods were most numerous, comprising 53.3 per cent of the overall total, and their numerical abundance was a reliable index of the amount of moss. Amphipods made up 25.9 per cent, followed by Trichoptera,

Diptera, Turbellaria, and Oligochaeta. Snails, beetle larvae, mayflies, and sphaeriid clams each comprised at least 0.1 per cent of the total. As in *Fissidens*, amphipods were outnumbered by isopods, but contributed a major part of the weight (43.2%). Isopods were second by weight (21.6%), and the occurrence of a number of large *Tipula* larvae caused dipterans to rank third. The average weight was 0.347 g/ft² when mollusks and decapods were excluded, but 1.090 when included.

Unvegetated riffles at Station II often contained a small amount of moss; 9 of 15 samples contained at least 10 per cent estimated moss cover. The largest number of organisms was in November 1960, 2,250/ft², when the least vegetated riffles found bore 30 per cent moss cover. Crustaceans made up 59.3 per cent of the standing crop, of which amphipods comprised 34.0 per cent and isopods 25.3 per cent. Aquatic insects made up 35.3 per cent of the fauna, thus contributing a much higher proportion than in comparable samples at Station I. The average standing crop was 505 individuals/ft². Amphipods were most abundant by weight (40.8%), followed by caddisflies, isopods, dipterans, and mayflies. The average, overall weights for 15 samples were 0.698 g/ft², 1.257 if mollusks and decapods are included, with a range in standing crop from 0.011 in July 1960, to 2.980 g/ft² in November 1960.

The abundance of animals in *Fissidens* beds at both Stations I and II was strongly reflected in the fauna of unvegetated riffles not only at times when moss was present but throughout the study period. At Station I, animals that were relatively scarce in *Fissidens* were much more important on the gravel-rubble bottoms of smaller riffles, principally because of an avoidance of the latter by crustaceans (or a preference by crustaceans for moss). In some instances, however, absolute differences indicate a preference for "unvegetated areas." For example, mayfly nymphs were found on open riffles twice as frequently as on moss, and beetles were present much of the time

TABLE 7.—NUMBERS OF ANIMALS PER SQUARE FOOT IN RIFFLES LATERAL TO THE MAIN CHANNEL IN DOE RUN, MEADE COUNTY, KENTUCKY. SEE TABLE 6 FOR FURTHER EXPLANATION

Animal Group	November- December (1959)	January- February (1960)	March- April	May- June	July- August	September- October	November (1960)- January (1961)	June (1961)
STATION I: Unvegetated Riffles								
Turbellaria	1.0	—	7.5	52.0	2.5	6.0	10.5	3.0
Oligochaeta	1.0	—	0.5	7.0	—	5.5	—	—
Isopoda	62.0	50.5	82.0	254.5	46.5	501.5	53.0	11.0
Amphipoda	19.0	27.0	88.0	55.5	32.5	186.0	95.5	18.0
Plecoptera	—	—	—	0.5	—	—	—	1.0
Ephemeroptera	0.5	1.0	3.0	—	—	—	—	1.0
Trichoptera	1.5	—	61.0	100.5	1.0	1.5	1.5	1.0
Coleoptera	—	—	—	1.0	3.0	2.0	3.0	2.0
Diptera	0.5	—	0.5	101.5	5.5	4.0	1.5	13.0
Acrid	—	—	—	—	—	—	0.5	—
Decapoda	—	—	—	0.5	—	0.5	—	—
Gastropoda	1.5	—	3.0	1.5	2.5	0.5	1.5	2.0
Pelecypoda	2.0	—	—	—	—	—	—	—
TOTALS	88.5	78.0	243.5	577.5	93.5	707.5	167.0	52.0
STATION II: Unvegetated Riffles								
Turbellaria	10.0	5.0	8.5	1.5	60.5	5.5	72.0	—
Oligochaeta	5.0	0.5	5.0	1.5	1.0	1.5	1.0	—
Isopoda	313.0	260.0	191.0	20.0	151.5	26.0	78.5	4.0
Amphipoda	114.0	96.0	100.0	17.0	324.0	27.0	608.0	9.0
Plecoptera	—	—	—	—	—	0.5	—	—
Ephemeroptera	14.0	46.0	45.5	3.5	32.5	39.0	24.0	4.0
Megaloptera	—	—	0.5	—	—	—	—	—
Trichoptera	22.0	59.0	142.0	8.5	310.5	17.5	332.0	2.0
Coleoptera	12.0	11.0	3.5	3.5	10.0	31.5	8.5	—
Diptera	8.0	4.5	8.5	8.0	66.5	44.0	18.0	5.0
Acrid	0.5	—	—	—	0.5	—	—	—
Decapoda	0.5	1.0	—	—	0.5	—	—	—
Gastropoda	2.0	0.5	2.5	0.5	0.5	—	11.5	2.0
Pelecypoda	—	—	—	—	0.5	—	—	—
TOTALS	501.0	483.5	507.0	64.0	958.5	1,925.0	1,153.5	26.0
STATION III: Gravel-Rubble Riffles, Lateral to Marl								
Turbellaria	—	—	—	—	—	—	0.5	—
Oligochaeta	7.5	2.5	—	39.5	—	—	0.5	—
Isopoda	3.0	—	3.0	29.5	1.5	2.0	6.0	—
Amphipoda	3.5	—	1.5	11.5	2.0	1.0	4.0	2.0
Plecoptera	—	—	1.0	—	—	5.0	—	—
Ephemeroptera	5.5	13.5	39.5	544.0	69.0	57.5	30.0	39.0
Trichoptera	1.0	4.5	1.5	7.0	13.5	10.0	—	1.0
Coleoptera	1.0	—	—	1.0	0.5	0.5	0.5	—
Diptera	9.5	4.0	24.0	28.5	10.5	58.5	8.0	9.0
Decapoda	0.5	—	1.0	6.0	0.5	0.5	—	—
Gastropoda	1.0	—	1.5	11.0	—	—	0.5	—
Pelecypoda	0.5	—	—	—	—	—	—	—
TOTALS	33.0	24.5	73.0	678.0	97.5	135.0	50.0	51.0
STATION IV: Gravel-Rubble Riffles, Lateral to Marl								
Oligochaeta	—	62.0	3.0	3.0	2.0*	1.0	—	—
Isopoda	1.0	—	—	—	1.0*	—	—	—
Amphipoda	0.5	0.5	—	3.0	1.0*	—	12.5	—
Plecoptera	—	—	10.0	0.5	—	—	0.5	—
Ephemeroptera	25.0	3.5	21.5	30.5	18.0*	12.0	21.0	4.0

TABLE 7.—Continued

Animal Group	November– December (1959)	January– February (1960)	March– April	May– June	July– August	September– October	November (1960)– January (1961)	June (1961)
Odonata	—	—	—	—	—	0.5	—	—
Megaloptera	—	—	—	—	1.0*	—	1.0	—
Trichoptera	6.0	—	4.5	13.0	2.0*	—	1.0	—
Coleoptera	0.5	—	—	—	—	—	—	—
Diptera	9.5	19.5	93.0	126.5	2.0*	2.0	10.0	3.0
Acri	—	—	—	1.5	—	—	—	—
Decapoda	—	—	1.0	0.5	—	1.0	0.5	—
Gastropoda	4.5	6.5	1.5	1.0	—	—	1.5	—
TOTALS	47.0	92.0	134.5	180.0	25.0*	15.5	49.5	7.0

STATION V: Gravel–Rubble Riffles

Oligochaeta	0.5	1.5	—	1.0	0.5	2.0	—
Isopoda	96.5	1.5	—	3.0	5.0	1.0	23.0*
Amphipoda	15.0	—	—	—	4.5	—	—
Plecoptera	—	—	—	2.0	—	—	—
Ephemeroptera	32.0	4.5	—	15.0	13.0	20.0	66.0*
Trichoptera	28.0	1.5	—	2.0	5.0	0.5	54.0*
Coleoptera	3.0	1.0	—	—	0.5	0.5	2.0*
Diptera	4.5	3.0	—	4.5	10.0	18.5	22.0*
Decapoda	0.5	—	—	—	—	—	—
Gastropoda	—	—	—	0.5	0.5	—	—
TOTALS	180.0	13.0	—	28.0	39.0	42.5	167.0*

on open riffles, though never so abundant as in 1 of 2 occurrences on moss (compare Tables 6 and 7). The greater diversity of the fauna at Station II and the presence of some species of aquatic insects that apparently preferred moss habitats when small then moved to open riffles as mature nymphs (such as *Ephemerella* and possibly *Baetis*) somewhat masks the numerical comparisons of the animals. In relative terms, however, the fauna of bare riffles at Station II was characterized by a greater proportion of aquatic insects, and a reduced number of crustaceans and turbellarians. Animals utilizing soft substrates, such as those seasonally present in *Fissidens* and in some habitats yet to be discussed, were also reduced in numbers in the unvegetated riffles at both Stations I and II (see oligochaetes, Tables 6 and 7).

Riffles Lateral to Marl or Rubble. The average number of animals obtained in samples from small riffles lateral to marl at Station III was almost identical to that from marl riffles, 149/ft², but their weight was only half as much (0.199 g). Mayfly

nymphs made up an even greater part of the total fauna than in marl riffles (69.7%), followed by dipterans, oligochaetes, and isopods. There was a considerably greater diversity of fauna in this habitat than in the marl riffles. Mayflies were most important in weight (46.2%) and were followed by plecopterans, dipterans, and caddisflies in decreasing order of importance. The last 3 groups made up 42.3 per cent of the average biomass. Standing crops ranged from 13 to 1,324 individuals/ft², and from 0.005 to 0.752 g.

Dipteran larvae made up 49.2 per cent of the fauna of small riffles at Station IV, with mayflies second (23.3%), and oligochaetes third (12.8%). The number of animals at Station IV was lower than at Station III, with 76 and 149 individuals/ft², respectively. By weight, however, they were more similar (IV, 0.189 g; III, 0.199 g). Oligochaetes made up a major portion of the weight (32.8%), followed by mayflies, dipterans, and amphipods. Variation in this habitat was high, ranging from 5 individuals and 0.004 g/ft² in October 1960,

to 333 individuals in May 1960, and 0.688 g in January 1961. Mollusks and decapods were represented by an overall average of 1.165 g/ft² (not included above).

Although habitats discussed here are included under the same general category, the conditions in each were somewhat different. At Station III, the small riffles were continuously supplied with water, although with considerable fluctuation in velocity and depth; however, at Station IV, the riffles were sometimes exposed by receding water levels and contained greater amounts of silt in interstices. Mayflies and caddisflies both were more abundant, relatively and absolutely, at Station III than at Station IV, and the reverse was true of the burrowing forms such as oligochaetes and dipterans. As at upstream stations, however, the abundance of many of the organisms in the swift marl riffles was reflected in the lateral riffles. For example, stoneflies were found on lateral riffles only in periods of relatively high flow, except for small individuals in late summer and autumn when leaves accumulated (mostly *Allocapnia* and *Nemoura*, Table 7). Ephemeropteran nymphs showed similar trends in abundance at both stations, increasing during and just after winter discharges and gradually declining during receding water levels and modal flow (Table 7). The increase in abundance of this group in winter is directly attributable to immigration from swifter riffles of the main channel, as indicated by Denham (1938) in tributaries of the White River, Ind. The prolonged, severe floods of 1961 markedly reduced the numbers of individuals and diversity of fauna in small riffles. The influence of high water was amplified at Station IV by siltation resulting from clearing the banks. Few animals of any kind were present on small riffles at Station IV in June 1961.

Standing crops of small riffles at Station V were almost the same as those at Station IV in average numbers of animals, but slightly less in weight. Isopods and mayflies were most common at Station V,

whereas dipterans, mayflies, and caddisflies prevailed at Station IV. Standing crops at Station V ranged from 7 to 260 individuals and from 0.009 to 0.743 g/ft².

The numbers of animals at Station V were greatest at the end of modal flow in 1959, and again in June 1961. However, the small numbers present in the interim and the lack of samples preclude discussion. It is significant that the gradual increase in numbers of animals present in the 1960 period of modal flow comprised mostly riffle species (principally *Simulium* and *Isonychia*).

Pools and Eddies with Generally Aggrading Bottoms.—*Nasturtium* Beds. Beds of *Nasturtium* present an almost-lentic environment. However, washout altered the areas by removal of plants, so that average figures are actually a composite of more than 1 type of habitat. Samples from watercress were second only to *Fissidens* at Station I in numbers and weights of animals, but greatly exceeded all other habitats if weights of mollusks are included. Numbers ranged from 24/ft² in June 1961, to a maximum of 2,652. The average for 15 samples was 893/ft², of which oligochaetes were most abundant (27.1%), followed by amphipods and dipterans in almost equal numbers, isopods, and caddisflies; other groups comprised less than 0.5 per cent each. The average biomass was 1.581 g/ft² (17.464 if mollusks were included). Amphipods were the most abundant by weight (47.8%), and were closely followed by oligochaetes (41.7%).

The large numbers of animals in this habitat were closely linked to the presence of the watercress. Vegetation was totally absent or covered less than 10 per cent of the bottom in March–April 1960, July–August 1960, and June 1961, and the smallest numbers of animals were present in those periods except for the extremely small population in September–October 1960. Crustaceans, primarily *G. bousfieldi*, were most abundant, but oligochaetes and dipterans were least abundant in the presence of plants and most abundant when

the plants were extirpated (Table 8). The small number of animals present in September–October occurred after *Nasturtium* had covered 20 to 50 per cent of the bottom, apparently effecting a decrease in numbers of burrowing forms, and no amphipods or isopods were present (Table 8). Crustaceans were generally concentrated in *Fissidens* beds at that time (Table 6).

The increase of oligochaetes and dipterans in summer in the absence of *Nasturtium* may be related to seasonal fluctuation in the populations, as may the coincident, marked increases in *Fissidens* beds and other habitats. A relation between the appearance of *Nasturtium* and decreases in annelid and fly populations, however, seems clear, and possibly may be explained by oxygen deficiencies caused by accumulation of organic debris and the marked slowing of water within the beds. Unpublished data of D. R. Tindall and myself indicate that in daytime there is as much as 40 per cent less dissolved oxygen in beds of *Nasturtium* than in the water immediately adjacent. At night, oxygen deep in the beds may reach levels that would select against animals inhabiting those strata, but would not influence those in the upper parts.

***Myriophyllum* Beds.** Beds of milfoil were about a third as productive as moss riffles at Station II on the basis of average numbers of animals (3,423/ft²), and about a fourth as much on the basis of weight (2.820 g). However, with mollusks and decapods included, there was 1.4 times as much weight in *Myriophyllum* as in *Fissidens* (32.217 g and 23.467 g, respectively). Isopods were numerically most abundant (30.4%) and amphipods made up 21.6 per cent. Unlike the *Fissidens* habitat, the accumulation of silt, sand, and sand–gravel in the mounds of *Myriophyllum* was stable enough to allow fairly large populations of burrowing oligochaetes to persist. It is notable, however, that Kreckler (1939), in studying animal populations on various aquatic plants, found oligochaetes abundant in *Myriophyllum* samples that did not include substrates.

Gastropods comprised 14.4 per cent of the numerical total in *Myriophyllum* habitat of Doe Run, and were followed by dipterans, mayflies, and caddisflies. The combined weights of amphipods and isopods were 60.3 per cent of the total. Dipterans were third, followed by oligochaetes. The weights ranged from 5.138 g/ft² in January 1961 to 1.063 in February 1960, and numbers ranged from 1,364 in January 1960 to 9,304 in August 1960.

The amazing resistance of milfoil to washout was reflected in the considerably greater stability of the standing crops of organisms than in other habitats (Table 8). As in *Fissidens* and *Nasturtium*, the numbers of dipterans and oligochaetes increased in summer in the *Myriophyllum*, and both decreased with the advent of autumn and the development of almost lentic conditions in some of the larger beds. Amphipods were consistently abundant except in September–October and November 1960–January 1961 samples; they were lowest in the former and highest in the latter period (Table 8). Isopods gradually decreased from a high of near 3,000/ft² in November–December 1950, to only 48/ft² in September–October 1960, but again increased during the 1960 modal flow to nearly 2,000. It is interesting to note changes in abundance of caddisfly larvae on milfoil compared with those on *Fissidens* at Station I. Apparently, the lack of swift currents in beds of milfoil, and possibly the relatively soft nature of the beds, caused hydro-psychid larvae to avoid the habitat, and small *Agraylea* larvae predominated. The seasonal emergence of *Agraylea* is similar at Stations I and II, but decreases in the larval population at Station II occurred somewhat earlier in the season, presumably as a response to slight warming of the water and earlier emergence.

The effects of flooding in 1961 were less evident in milfoil than in other habitats, but the fauna was nevertheless damaged, with the lowest numbers recorded during June 1961.

***Myosotis* Beds.** Forget-me-nots were ab-

TABLE 8.—NUMBERS OF ANIMALS PER SQUARE FOOT IN VEGETATED, SILTED, OR OTHERWISE AGGRADING POOL OR EDDY AREAS IN DOE RUN, MEADE COUNTY, KENTUCKY. SEE TABLE 6 FOR FURTHER EXPLANATION

Animal Group	November– December (1959)	January– February (1960)	March– April	May– June	July– August	September– October	November (1960)– January (1961)	June (1961)
STATION I: <i>Nasturtium</i> Beds, or in the Area after Washout								
Turbellaria	4.0	—	—	10.0	—	4.0	—	—
Oligochaeta	24.0	356.0	382.0	268.0	466.0	130.0	192.0	—
Isopoda	220.0	72.0	12.0	146.0	22.0	12.0	34.0	4.0
Amphipoda	734.0	150.0	46.0	100.0	18.0	152.0	444.0	4.0
Ephemeroptera	2.0	—	—	—	—	—	—	—
Trichoptera	—	—	2.0	198.0	—	—	—	—
Coleoptera	—	2.0	—	4.0	—	—	2.0	—
Diptera	62.0	40.0	328.0	764.0	236.0	116.0	64.0	8.0
Decapoda	—	2.0	—	—	—	—	4.0	—
Gastropoda	58.0	46.0	54.0	58.0	112.0	60.0	252.0	8.0
Pelecypoda	16.0	26.0	8.0	5.0	122.0	8.0	28.0	—
TOTALS	1,120.0	694.0	832.0	1,553.0	976.0	482.0	1,020.0	24.0
STATION II: <i>Myriophyllum</i> Beds								
Turbellaria	5.0	—	10.0	2.0	6.0	—	74.0	—
Oligochaeta	21.5	18.0	126.0	634.0	3,712.0	916.0*	716.0	248.0
Isopoda	2,762.0	1,094.0	498.0	237.0	744.0	48.0*	1,858.0	124.0
Amphipoda	573.5	726.0	906.0	439.0	634.0	140.0*	1,636.0	388.0
Ephemeroptera	74.0	50.0	150.0	6.0	116.0	—	10.0	64.0
Odonata	—	—	—	2.0	—	12.0*	—	—
Trichoptera	9.0	120.0	136.0	4.0	20.0	—	32.0	—
Coleoptera	0.5	2.0	10.0	—	4.0	—	8.0	8.0
Diptera	7.0	10.0	72.0	144.0	836.0	44.0*	66.0	8.0
Decapoda	1.0	2.0	—	2.0	—	—	4.0	4.0
Gastropoda	37.0	304.0	270.0	514.0	1,058.0	1,256.0*	344.0	596.0
Pelecypoda	2.0	—	4.0	48.0	26.0	8.0*	8.0	—
TOTALS	3,492.5	2,326.0	2,182.0	2,032.0	7,156.0	2,404.0*	4,836.0	1,440.0

sent at Station III only 3 of the 15 times the area was sampled, and contained a fauna similar to that in *Nasturtium* beds at Station I, and in pool habitats at other stations. The standing crop was only 1.362 g less than that in *Fissidens* habitat at Station II when the mollusks and decapods are included (22.105 g/ft²), and oligochaetes made up slightly more than half the total weight when mollusks and decapods are excluded. Diptera and amphipods comprise 41.5 per cent to include most of the remainder. Oligochaetes were likewise the most abundant numerically, averaging 429/ft² (44.9% of the total), and were followed by dipterans, gastropods, and amphipods. The smallest standing crop was in November 1960, with 208 individuals and 0.385 g/ft². Maximal populations were 2,224 individuals in April 1960

and 5.776 g in March 1960. Fluctuations in abundance of the various animals were similar to those in *Nasturtium* beds (Table 8).

Silt-Bottomed Eddy. The thick silt deposit was the most productive habitat sampled at Station IV. There were 418 organisms on the average, that weighed 0.642 g/ft² (or 5.647 g if mollusks are included). Oligochaetes were most abundant by numbers and weight, similar to the situation in beds of emergent vegetation, and dipteran larvae were second. The standing crop varied from 1,136 individuals and 1.801 g/ft² in June 1960 to 56 individuals in January 1960 and 0.022 g in February of that year.

This eddy was similar to *Fissidens* and *Myriophyllum* in that it remained essentially unchanged throughout the study. Oligo-

TABLE 8.—Continued

Animal Group	November– December (1959)	January– February (1960)	March– April	May– June	July– August	September– October	November (1960)– January (1961)	June (1961)
STATION III: <i>Myosotis</i> Beds								
Turbellaria	—	—	—	—	—	—	—	4.0
Oligochaeta	30.0	172.0	358.0	734.0	1,456.0	168.0	94.0*	92.0
Isopoda	2.0	12.0	44.0	4.0	—	4.0	—	—
Amphipoda	74.0	146.0	246.0	36.0	46.0	12.0	14.0*	160.0
Plecoptera	—	4.0	—	—	—	—	—	4.0
Ephemeroptera	6.0	6.0	86.0	10.0	24.0	6.0	—	—
Odonata	6.0	—	4.0	—	—	10.0	—	4.0
Trichoptera	—	—	2.0	—	—	—	—	—
Coleoptera	2.0	2.0	—	—	—	—	2.0*	—
Diptera	124.0	120.0	862.0	372.0	40.0	256.0	214.0*	12.0
Hemiptera	—	—	—	—	—	—	—	4.0
Decapoda	10.0	—	4.0	—	12.0	4.0	2.0*	12.0
Gastropoda	168.0	286.0	52.0	76.0	80.0	4.0	24.0*	80.0
Pelecypoda	—	2.0	2.0	98.0	94.0	10.0	26.0*	4.0
TOTALS	422.0	750.0	1,660.0	1,330.0	1,752.0	474.0	648.0*	376.0
STATION IV: Silt-bottomed Eddies								
Oligochaeta	588.0	2.0	124.0	496.0	192.0	46.0	434.0	196.0
Isopoda	—	4.0	—	—	—	—	—	—
Amphipoda	—	—	4.0	20.0	2.0	6.0	4.0	8.0
Ephemeroptera	—	60.0	2.0	4.0	2.0	2.0	—	—
Odonata	—	—	—	—	—	—	2.0	—
Trichoptera	2.0	20.0	—	—	—	—	—	—
Coleoptera	—	6.0	—	—	—	—	—	—
Diptera	18.0	62.0	168.0	250.0	74.0	28.0	6.0	80.0
Gastropoda	6.0	16.0	16.0	131.0	44.0	48.0	28.0	32.0
Pelecypoda	20.0	2.0	4.0	6.0	—	12.0	10.0	4.0
TOTALS	634.0	172.0	318.0	907.0	314.0	142.0	484.0	320.0

chaetes increased in summer as in other habitats, but also were high in the latter part of modal flow in November 1960–January 1961 (Table 8). Diptera behaved similarly, but did not show a significant increase in numbers late in 1960 as did oligochaetes. The fauna was generally consistent in its composition, perhaps more so than any other habitat sampled.

Open Pools and Eddies with Variable Bottoms.—Shifting Sand. Sand bottoms are generally considered the least productive habitat in streams because of their constant shifting and consequent unsuitability for growth and development of vegetation and the lack of cover for animals (Hynes, 1960). At Station I, the fauna of sand bottoms ranged from 16 individuals on 2 occasions to 724/ft² in June 1960; the average was 183 at a weight of 0.170 g

(3.228 g if mollusks are included). Isopods and amphipods were almost equally represented in the habitat (42.1 and 41.6%, respectively), followed by dipterans, snails, caddisflies, oligochaetes, and turbellarians. By weight, dipteran larvae were first in importance because of a few *Tipula*, followed in decreasing order by isopods, caddisflies, amphipods, and oligochaetes. Because of the generally depauperate nature of the fauna of this area, little discussion seems warranted, however, it is noteworthy that the fauna was numerically largest in periods of modal flow and smallest in periods of high discharge or following such periods (Table 9). Also, the size of the animals on such bottoms was generally small, since they were mostly young amphipods, isopods, and gastropods, with lesser numbers of other groups. These facts

TABLE 9.—NUMBERS OF ANIMALS PER SQUARE FOOT IN OPEN-POOL AND EDDY HABITATS OF DOE RUN, MEADE COUNTY, KENTUCKY (INCLUDING THOSE WITH VARIABLE BOTTOM TYPES, BUT WITH NO AQUATIC VEGETATION). SEE TABLE 6 FOR FURTHER EXPLANATION

Animal Group	November- December (1959)	January- February (1960)	March- April	May- June	July- August	September- October	November (1960)- January (1961)	June (1961)
STATION I: Shifting-sand Bottom								
Turbellaria	—	—	—	—	2.5	10.0	4.0	—
Oligochaeta	8.0	6.0	4.0	10.0	8.0	20.0	12.0	—
Isopoda	26.0	8.0	12.0	10.0	58.0	178.0	162.0	—
Amphipoda	20.0	—	12.0	10.0	8.0	62.0	56.0	4.0
Trichoptera	—	2.0	—	102.0	2.5	24.0	6.0	—
Coleoptera	—	—	2.0	—	—	—	—	—
Diptera	14.0	6.0	—	118.0	64.0	26.0	2.0	20.0
Gastropoda	8.0	2.0	22.0	12.0	30.0	20.0	76.0	4.0
TOTALS	76.0	24.0	42.0	386.0	173.0	340.0	318.0	28.0
STATION II: Pools; Bottoms Ranging from Silt to Gravel-Sand with Differing Discharges								
Turbellaria	—	—	6.0	—	—	—	8.0	—
Oligochaeta	26.0	10.0	40.0	248.0	68.0	438.0	88.0	20.0
Isopoda	20.0	4.0	132.0	2.0	12.0	2.0	16.0	—
Amphipoda	—	6.0	170.0	14.0	10.0	4.0	48.0	—
Plecoptera	—	—	—	—	—	—	2.0	—
Ephemeroptera	2.0	—	2.0	—	—	2.0	—	—
Trichoptera	—	2.0	—	10.0	—	—	—	—
Coleoptera	—	—	—	—	2.0	—	—	—
Diptera	88.0	50.0	114.0	370.0	198.0	16.0	12.0	—
Decapoda	—	—	—	—	—	2.0	—	—
Gastropoda	2.0	2.0	6.0	52.0	52.0	62.0	418.0	496.0
Pelecypoda	—	—	—	—	58.0	2.0	10.0	—
TOTALS	140.0	74.0	470.0	696.0	410.0	884.0	264.0	516.0
STATION III: Pools; Bottoms Ranging from Silt to Sand-Gravel with Differing Discharges								
Turbellaria	2.0	—	—	—	—	—	—	—
Oligochaeta	186.0	27.0	86.0	524.0	454.0	244.0	504.0	116.0
Isopoda	24.0	2.0	4.0	6.0	—	—	8.0	—
Amphipoda	68.0	2.0	166.0	70.0	2.0	—	10.0	—
Ephemeroptera	32.0	—	4.0	2.0	2.0	—	2.0	—
Trichoptera	2.0	—	—	4.0	2.0	—	2.0	—
Diptera	6.0	10.0	204.0	700.0	34.0	314.0	30.0	12.0
Hemiptera	2.0	—	—	—	—	—	—	—
Decapoda	2.0	—	—	—	—	—	—	—
Gastropoda	52.0	24.0	22.0	58.0	82.0	38.0	52.0	52.0
Pelecypoda	18.0	4.0	—	4.0	10.0	6.0	40.0	4.0
TOTALS	392.0	69.0	486.0	1,368.0	588.0	602.0	648.0	184.0

illustrate the dispersal of bottom invertebrates into peripheral habitats in periods of low discharge, and dispersal of young rather than adults from areas of optimal habitat.

Large Pools with Variable Bottoms.—Samples from pools at Station II contained numbers of animals similar to those found on unvegetated riffles at that station (531/

ft²), but differed markedly in their faunal composition. Oligochaetes, dipterous larvae, and snails made up 66.4 per cent of the total fauna, but amphipods retained some dominance (26.2%). Isopods, however, were relatively rare (4.7%). The standing crop by weight was small at 0.283 g/ft², of which oligochaetes made up 52.7 per cent. Amphipods were second in

TABLE 9.—Continued

Animal Group	November– December (1959)	January– February (1960)	March– April	May– June	July– August	September– October	November (1960)– January (1961)	June (1961)
STATION IV: Eddy; Gravel Bottom, Silted after Periods of High, Turbid Discharge								
Oligochaeta	36.0	4.5	19.0	37.5	8.0	12.5	21.5	220.0
Isopoda	1.5	—	0.5	0.5	—	—	—	—
Amphipoda	2.0	2.5	2.5	2.5	2.5	3.0	—	—
Plecoptera	0.5	0.5	—	—	—	—	—	—
Ephemeroptera	6.5	7.0	3.5	10.5	3.0	2.5	3.0	4.0
Megaloptera	—	1.0	—	—	—	—	—	—
Trichoptera	1.0	2.0	—	—	0.5	—	—	—
Coleoptera	—	0.5	—	—	—	1.0	—	—
Diptera	16.5	6.0	82.5	15.5	9.0	34.0	23.0	12.0
Hemiptera	—	—	—	0.5	—	—	—	—
Decapoda	—	0.5	—	4.0	—	0.5	—	—
Gastropoda	12.5	3.0	10.0	6.0	2.5	8.5	22.0	76.0
Pelecypoda	0.5	—	—	0.5	—	—	—	—
TOTALS	77.0	27.5	118.0	77.5	25.5	62.0	69.5	312.0
STATION V: "Pool"; Various Bottom Types in Stream Channel								
Oligochaeta	43.0	2.0	—	—	4.0	4.0	1.0	—
Isopoda	—	4.0	—	—	—	—	—	—
Ephemeroptera	3.0	—	—	—	—	—	—	—
Trichoptera	—	2.0	—	—	—	2.0	—	—
Coleoptera	2.0	2.0	—	—	—	—	—	—
Diptera	16.0	4.0	—	2.0	60.0	58.0	87.0	—
Gastropoda	2.0	—	—	2.0	—	14.0	—	—
Pelecypoda	1.0	—	—	—	—	—	—	—
TOTALS	67.0	14.0	—	4.0	64.0	78.0	88.0	—

weight followed by dipterans and isopods. The standing crop ranged from 32 to 1,412 individuals, and from 0.010 to 0.598 g/ft²; this range, however, was not as great as in unvegetated riffles.

An average of 566 individuals/ft², with a mean weight of 0.493 g if mollusks and crayfish were excluded, was obtained in samples from the large eddying pool at Station III. The fauna of this habitat was similar to that of pools at Station II in composition, both by numbers and by weight. Ranges were from 56 to 1,776 organisms in February and late April (= "May") 1960, respectively, and from 0.028 to 1.449 g/ft² in those same months.

Diptera at Stations II and III and Oligochaeta at Station II, as in pools as elsewhere, increased in summer and decreased in autumn and winter (Table 9). At Station III, however, numbers of oligochaetes increased in June 1960 after alleviation of winter discharge and they

remained relatively abundant in all subsequent samples. The greatest abundance of amphipods and isopods in pools at Station II and amphipods at Station III occurred during the winter discharge of 1960. These data indicate drift of the crustaceans downstream and accumulation in pools with sustained but moderate flooding. The rapid numerical decrease in pools with resumption of modal flow may indicate movement of isopods and *G. minus* back into riffle areas.

Bottoms in pool habitats at Station V ranged from solid clay to shifting sand. The standing crop varied in response to these conditions, and ranged from no organisms from clay bottoms on 2 occasions, to a maximum of 172 animals in November 1960 and 0.292 g in September 1960 (the latter was the weight of a single large *Pychnopsyche*). Also, the fauna was limited in taxons represented (Table 9).

Faunal Affinities of Doe Run.—Springs are

sometimes unique in possessing relict or endemic faunas (Nielsen, 1950b). Temperature moderation in a spring, with warming of water downstream in summer, but maintenance of cool conditions upstream, allows development of a recapitulation of south-to-north distributions similar to those found on mountains. Such distribution of animals in a spring stream such as Doe Run is effected by the physiological limitations of the species present. Low temperatures themselves generally are not detrimental to the well-being of an animal of temperate zones, but the maintenance of cool temperature may limit completion of the life cycle so that its distribution in the stream will be limited by the minimum temperature tolerance for growth, development, and reproduction, and by the minimum lethal high temperature (Ide, 1935).

Although some animals of Doe Run are widespread, ubiquitous, or southern in their geographic relations, many are northern in their distribution or are "spring inhabitants" in the southern parts of their ranges. The turbellarians *Phagocata velata* and *Dugesia dorotocephala*? (Pennak, 1953), the *Crangonyx* group of amphipods, and amphipods of the subgenus *Rivulogammarus* (see Bousfield, 1958) were restricted to the upstream parts of Doe Run. Of the mayflies, *Ephemera simulans* usually is a northern or northeastern form, whereas *Baetis vagans*, *Ephemerella subvaria*, and perhaps *Pseudocloeon carolina* (see Ide, 1935), may represent relict or outlying populations considerably removed to the south or the west of their normal ranges (Burks, 1953). According to Ricker (1959; pers. comm.), both *Paragnetina media* and *Isogenus subvarians* are "Appalachian and northern species" of stoneflies. *Glossosoma* is a northern trichopteran inhabiting springs in the southern parts of its range, as does *Diplectrona modesta* (Ross, 1953, 1959). Also *Hydropsyche betteni* and *Agraylea multiplicata* are northern forms, the latter being holarctic in distribution.

A relatively great geologic age for Doe Run is implied by the presence of endemic

crustaceans. It must be noted, however, that this group is the only one studied intensively from a taxonomic standpoint, yet the presence of other undescribed species is probable. Populations of *Gammarus minus* and *Asellus bivittatus* in the stream system are aberrant in some respects, and different from other local populations (Cole and Minckley, 1961).

Although not unique to Doe Run itself, the highly specialized, cavernicolous animals of the limestone region of Kentucky and adjacent states should not go unmentioned. Three of the many forms, *Asellus stygius*, *Orconectes p. pellucidus*, and a species of *Phagocata*, were collected from Doe Run, and *Amblyopsis spelaea* DeKay, a blind cavefish, has been collected from subterranean waters of Meade County (Clay, 1962; Barr and Kuehne, 1962).

Fishes and Other Vertebrates

As with many collecting techniques, those used in studies of fishes have little quantitative basis except where a body of water can be completely drained and the animals counted individually. "Minnow seines" tend to catch smaller fishes, except those small enough to go through the mesh (Paloumpis, 1958), the use of electric shockers tends to select for larger, light-colored fishes (Larimore, 1961), hoop and gill nets provide various sizes of catch depending on mesh size and the kind of "set" (Starrett and Barnickol, 1955), and rotenone is limited somewhat by the differential susceptibility of various species (Krumholz, 1948; and others). Larimore (1961) concluded that behavior of fish species, their diverse habitats, and their morphology all directly affected efficiency of electrofishing in Jordan Creek, Ill., and those factors, plus seasonal changes in behavior and distribution, changing conditions of collecting (such as variations in discharge and turbidity), and relative efficiency of the collectors, combine with other factors to make quantitative interpretation of data on diverse stream populations difficult.

Annotated List of Fishes

A total of 66 species of fishes was collected from Doe Run. Estimates of the relative abundance of each species are based mostly on frequency of occurrence in collections, and to a lesser degree on the actual numbers collected. About 250 collections or observations of fishes were made, and those species occurring in half or more of the collections are considered abundant; in more than a third of the collections, but less than half, are common; in more than a tenth, but fewer than a third, scarce; and in fewer than a tenth, uncommon to rare. Some species in restricted portions of the creek may have been common or even abundant in relation to other species in those limited areas, but cannot be so considered in the entire population. Numbers of individuals alone were not a reliable index of overall abundance because of sporadic emigration of great numbers of certain species from the Ohio River. My collections of fishes from Doe Run were culminated by eradication of the area downstream from Station IV with rotenone in July 1961 just prior to impoundment. However, data collected subsequently are included where pertinent. Comparisons of relative abundance of some fishes of the lower part of Doe Run with that in the adjacent Ohio River are made in reference to data published by Krumholz, *et al.* (1962) and to unpublished data collected in 1957, 1958, and 1959 by Krumholz and myself.

Lepisosteus osseus (Linnaeus): longnose gar. A single longnose gar was seen near Mile 8.5 after application of rotenone, but was not captured. The species is present in much of the Ohio River and often is found in creek mouths, especially as young individuals.

Alosa chrysochloris (Rafinesque): skip-jack herring. Small numbers were in the mouth of Doe Run in periods of flooding of the Ohio River, and several were seen pursuing minnows near Station V in June 1961. Two specimens were taken upstream from Station V, 1 by shocker near Mile 4.0

for the most upstream record, and the other by rotenone just downstream from Station IV in July 1961 (Fig. 26).

Dorosoma cepedianum (LeSueur): gizzard shad. This species was present at all times downstream from Station V, and probably occurred in small numbers throughout the low-gradient section (Fig. 2) below Mile 5.3 (Fig. 26). The gizzard shad was collected as far upstream as Station III in the spring of 1960 and 1961, but did not ascend swift water in culverts of the bridge at that station. Shad were watched ascending very swift waters at Station V in May 1961, however. They milled about in eddies at the foot of the riffle and ascended in a rush, directly in the center of the swiftest flow and very near the surface.

Gizzard shad appeared to be spawning in a large pool near Mile 3.75 on June 5, 1960. About 25 individuals were moving rapidly around a small, stream-drifted tree in the center of the pool, and presumed males were most often positioned on either side of a female (Langlois, 1954). Water temperatures at the upstream end of the pool were near 16.0° C, which may be somewhat low for spawning by the species (Miller, 1960), but water in the center of the pool may have been slightly warmer. No eggs were found, however, and larval shad were never obtained from Doe Run. Trautman (1957) noted movement of adult gizzard shad into clear, low-gradient waters for spawning in Ohio, but rarely into high-gradient streams.

I watched a number of *D. cepedianum* feeding along a bank in about a foot of water and over compact clay bottom at Station V. They moved in a somewhat spiral path with their bodies angled about 45 degrees to the substrate. A given individual stayed near the bottom for perhaps 3 to 5 feet, then moved upward and forward to repeat the performance. Apparently they were selecting certain items as judged by clouds of silt expelled from the opercles at short intervals. Turbidity produced by the feeding aggregation was obvious for about 25 feet downstream.

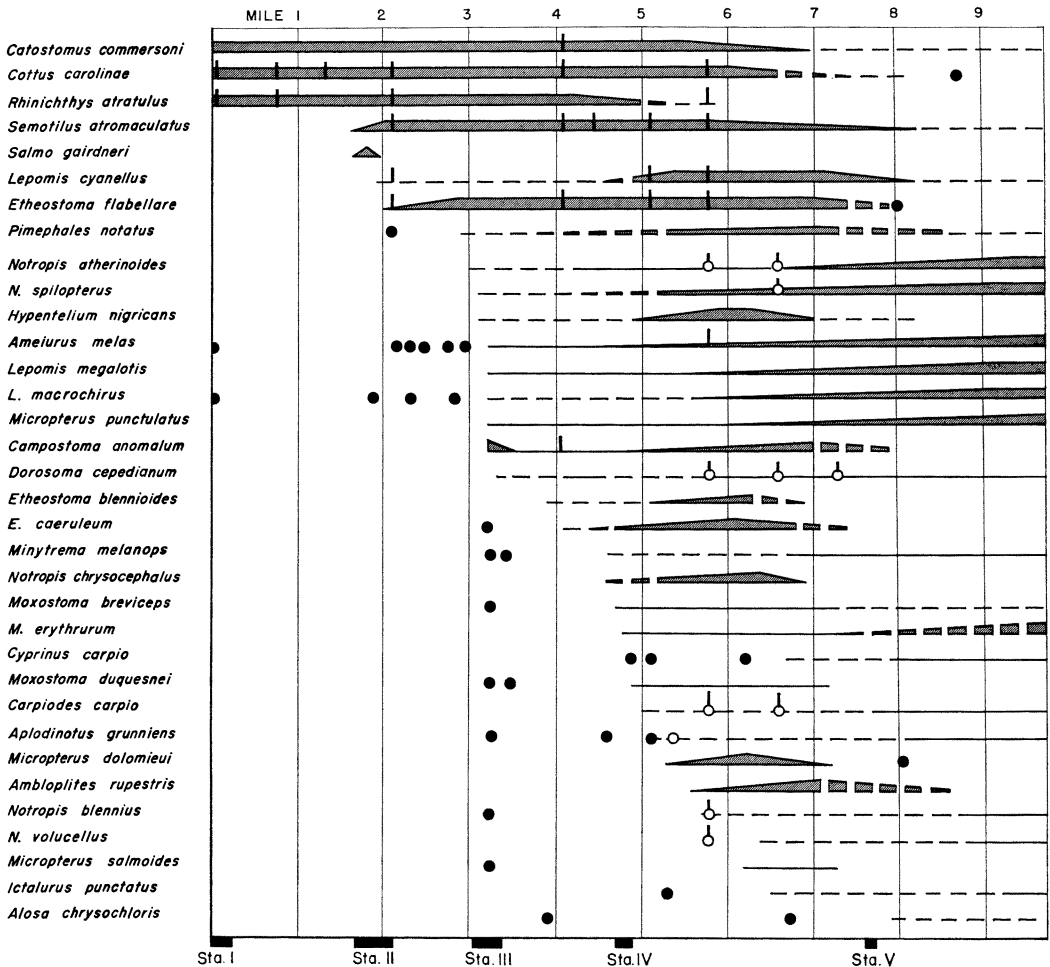


FIG. 26. Longitudinal distributions of some fishes in Doe Run, Meade County, Ky. Broken lines denote rare or occasional occurrence; width of the line, the presence (wide) or absence (narrow) of reproductive success in the area; vertical lines, occurrences in tributaries; dots, occurrences of single individual or of fewer than 5 individuals in no more than 2 collections from the area; and open circles, occurrences when backwaters from the Ohio River were present.

Eradication of fishes from the lower part of Doe Run was aimed principally at removal of this species and the carp (*Cyprinus carpio* L.), but must have failed because many young-of-the-year individuals of both species were seen in Doe Valley Lake in August 1961. This may have resulted from failure to kill all adults upstream from the new dam site, but it must be pointed out that subsequent to the rotenone treatment, flooding on July 16-17, 1961, filled the incipient lake, topped the

cofferdams, and removed much of the fill to form a short, swift rapids down the rip-rap of the downstream coffer. On July 18, a number of large carp were observed ascending these rapids, and gizzard shad may also have used this route, though none was seen.

Salmo gairdneri Richardson: rainbow trout. Trout, presumably of this species, were stocked in Doe Run in 1939 (Brown, pers. comm.), with additional stockings in May 1955 and in mid-October 1961 after

impoundment of the downstream section. A small population of trout may have persisted from the 1939 stocking through natural reproduction. In spring 1958, while collecting for the University of Kansas, I saw a large trout near Station III, and another individual, much larger than those known to be from the 1955 stock, was seen at Station IV in spring 1961.

Generally, the range of trout in Doe Run was from Dam 1 downstream to immediately below Station III (Fig. 26). A single specimen was seined at Station I in 1959. The fish were found below waterfalls to a great extent, where they lived beneath overhanging ledges, but a few were in open pools and were taken in hoop nets from the mill impoundments. Many of the 1955 stock were present near Station II in 1959, but in succeeding years the population declined more rapidly than could be explained by fishing pressure. Moreover, in spring 1959, trout were taken frequently at Station III, but they apparently moved downstream and into the Ohio River since none was taken subsequently at Station III or below. They could not have moved upstream because of mill dams. Newell (1957) found that stocked rainbow trout moved less than brook trout, *Salvelinus fontinalis* (Mitchill), but that most movement by each was downstream. One individual in Doe Run, fin-clipped in January 1960 near Mile 1.8, was taken 7 times in June and July 1961 in Pool 2, and each recapture was progressively farther downstream. In June 1961, it was caught in a hoop net from Pool 3, near Mile 2.7, and was retained.

I detected no successful reproduction by rainbow trout of the 1955 stock, but a single redd was found at Mile 1.68 in early May 1960; slight digging in the shallow gravels yielded 2 fertilized eggs. An increase in discharge in mid-May scoured the bottom and destroyed the redd.

On October 14, 1961, about 65,000 fingerling rainbow trout were introduced into the upstream part of Doe Valley Lake by the Doe Valley Corporation (near Station IV). At that time the lake had surface tempera-

tures exceeding 26° C in daytime, and there was a marked thermocline below which there were only small amounts of dissolved oxygen though temperatures were considerably lower (17–18° C). There was a small density current, however, where water of Doe Run flowed in its original channel, that may have been suitable for a few trout. Conditions were therefore such that most trout were forced to move into Doe Run proper, and considerable crowding occurred in pools and eddies. Movements noted on October 17 were mostly upstream over riffles, with the small fish rapidly returning downstream when disturbed. At least 2 screens were erected across the creek by the Doe Valley Corporation to prevent upstream movement, but they soon clogged with leaves and other debris and became relatively ineffective. Small trout were found at Station III on October 18. Subsequent increases in discharge dislodged the screens and many fish moved into the area near Station III. The presence of so many fish in such a small area apparently attracted many predatory animals, and losses the first few weeks after stocking were heavy. Numerous trout were found along the banks partially eaten, presumably as a result of mammalian activities.

Hiodon tergisus LeSueur: mooneye. A single mooneye was taken by rotenone downstream from Station V in 1959.

Esox americanus vermiculatus LeSueur: grass pickerel. Two pickerel were caught, 1 by gill net in a large, shallow pool just downstream from Station IV, and the other below Station IV by rotenone in July 1961.

Carpoides carpio carpio (Rafinesque): river carpsucker. This large, deep-bodied catostomid is generally found in deeper waters of the Ohio River (Trautman, 1957), but often occurs in creek mouths throughout the Kentucky section of that stream. River carpsuckers occurred sporadically upstream as far as Mile 5.0, that is, to the area of the beginning of high gradient, but probably were present at all times in the downstream area below Station V (Fig. 26). This and other carpsuckers apparently

moved into Doe Run in considerable numbers when backwaters of the Ohio River were present.

C. cyprinus hinei Trautman: quillback. Only young quillback were taken in Doe Run (young-of-the-year and presumed 1-year-old individuals), and most were caught below Station V.

C. velifer (Rafinesque): highfin carp-sucker. This species was collected by rotenone near the mouth of Doe Run in 1959.

Catostomus commersoni (Lacépède): white sucker. White suckers were abundant in Doe Run, especially at Station II and upstream from Dam 1. This species is to be the subject of a later, more detailed paper dealing with its life history, but a general review of its relations in Doe Run is given here.

White suckers exhibit amazing tolerance to diverse environmental conditions (Trautman, 1957; and others), but usually reach their peak abundance in headwater creeks in Indiana (Gerking, 1945), and in the area of Doe Run. Numbers in Doe Run were greatest in the deeper pools, especially in the mill ponds as judged by hoop netting, with lesser numbers occurring in swifter, shallower waters. In vegetated areas upstream from Dam 2, *C. commersoni* was often in shallow water with appreciable current, but usually in the shelter of vegetation (see Larimore, 1961). Downstream, however, where vegetation was lacking, the suckers lived in deepest pools or in smaller, shallow pools that had accumulations of debris or overhanging riparian vegetation. White suckers generally swam ahead of the electrical field of the shocker, as noted by Larimore, *et al.* (1952), but would not cross riffles and were quickly affected by the charge as they turned into the field (Minckley and Craddock, 1961). Individuals in beds of vegetation moved violently when "hit" with the electric current, became immobilized, and usually floated belly-up.

Schooling of large suckers was seldom seen, but was indicated by bunching of

certain catches in gill nets. A group of at least 17 adults was seen beneath a log at Mile 0.4 in June 1961. They rested near the bottom with their fins extended, maintaining their positions in the slight current by regular, measured strokes of the pectoral fins; no movement of the caudal fin was seen. When disturbed, aggregations in pools move quickly into debris or other cover (Fowler, 1906). It may be that "schools" of this type in streams are more a function of common use of a given area of cover and tolerance of the species for others of its kind rather than an actual schooling phenomenon indicated in studies of lake populations (see Adams and Hankinson, 1928). Young suckers in the stage that involves surface feeding (Stewart, 1926) likewise appear to congregate in response to gentle currents in eddies and backwaters.

In late 1959 and in summer 1960, 103 *C. commersoni* were marked by finclipping or by sewing small, numbered beads to the caudal peduncle with monofilament line. Of these, 19 were recovered at least once after being free from 1 day to 11 months and 4 days, a total of 28 recoveries of the 19 individuals. Only 3 individuals had moved more than 0.2 mile from the point of marking, and were the only ones that had moved over substantial riffles. The fish in Pool 2, where most hoop netting was done, were more motile than those in the pool-riffle area between Miles 1.65 and 2.1. Stream fishes generally regard riffles as barriers to movement, or as limits of their home ranges (Gerking, 1953), and the lack of obstructions in the mill pool probably allowed greater freedom of movement. Total linear movements, that is, distances on either side of the point of initial marking, were 0.26 mile (the total length of Pool 2) for a male marked at Mile 2.15, taken at Mile 2.1 a week later, and then at Dam 2 (Mile 2.36) on the succeeding day. Two fish marked in Pool 2 (Mile 2.1) were recovered at Miles 1.95 and 1.7 a week and almost a year, respectively, after the initial catch. The former had passed over a riffle and a

waterfall about 2 feet high, and the latter had moved over several riffles and 3 waterfalls that collectively amounted to about 6 vertical feet. The latter individual had the opportunity to move over obstructions in the floods of 1960 and 1961. Fish marked in the pool-riffle area at Station II usually were recovered in the same pool in which they were initially taken, but 4 had moved over small riffles to an adjacent pool (3 upstream, 1 downstream), and 2 had ascended waterfalls to the pool immediately upstream. These data substantiate the conclusion of Gerking (1953) in his statement that "the fish population of a small stream with riffle-pool development may be considered as a series of discrete, natural units rather than a single homogeneous, freely-mixing group." However, his conclusion was based on species other than the white sucker, and there is evidence that it and some species studied by him in Indiana may behave differently in certain parts of Doe Run. It is significant, however, that at Station II there was a strong tendency for white suckers to remain in restricted areas for relatively long periods.

Between Station I and the head of Pool 1 there were few areas that could be classed as pool, and suckers were not found upstream from Mile 0.4 in periods of modal flow. In periods of higher discharge and turbidity suckers were commonly taken in seines at Station I, and they spawned there, presumably at night. I have little information on movements of suckers downstream from Dam 2, but it is significant that no marked individuals from Station II were obtained by hoop nets or other means in Pool 3, or in extensive collecting by seine, shocker, or rotenone application downstream from Dam 3. I found no evidence of upstream movement of suckers for spawning or for other reasons downstream from Dam 3.

Young-of-the-year white suckers appeared at Station I in mid-April 1960 and were found there and at downstream stations (excepting Station V) from that time through early July in the surface-feeding

stage (ranging from 12 to near 20 mm in total length; Stewart, 1926). Males began to display breeding colors and tubercles in January each year of the study, and some "high" males were present through June 1960, although high water in 1961 prevented observation. Both males and females stripped easily from February to early July 1960 (fewer after mid-June), and females with fully formed ova were present throughout the year, but in reduced numbers between July and December. Some females with ripe ovaries in late summer may have matured late in the spawning season—they were usually small—or egg formation may occur more rapidly in fish of Doe Run than in others with which I have had experience. Actual spawning was not observed, but shallow depressions in a small area of coarse-sand bottom about 40 feet downstream from the source of Doe Run yielded eggs and larvae of white suckers on May 14, 1960, and again 2 weeks later. The latter was a different spawning as judged from the developmental stage of the eggs.

It is noteworthy that suckers more or less "trapped" above the mill dams of Doe Run, especially upstream from Dam 1, do not experience marked changes in water temperature. This factor is considered very important in the spawning cycle of many species (Adams and Hankinson, 1928), including white suckers, but it seems hard to believe that the magnitude of change at upper stations of Doe Run is sufficient to initiate gonadal maturation and spawning. Reproduction in response to changing light conditions is indicated for species maintaining populations in the upper parts of Doe Run (see Harrington, 1950, 1957; Hoar, 1957).

As noted before, the mill dams of Doe Run are more than 100 years old, and have acted as a barrier to upstream movements of fishes since their erection. Also, a waterfall at least 6 feet high was present near Mile 2.1 prior to flooding by Dam 2, and may have acted as a barrier to fishes for an unknown period of time prior to disturbance

by man. Suckers from the upstream section of Doe Run appear to be separable from those in the downstream sections and in the Ohio River by a number of morphological characters. Research on this problem is now under way.

Hypentelium nigricans (LeSueur): northern hog sucker. Although Trautman (1957) considered the northern hog sucker highly migratory, spending winters in deep slow-moving streams and migrating into creeks in spring to spawn, my data indicate a continuous population between Miles 3.3 and 7.0, with no extensive movements. Young hog suckers were collected in late August outside the area of greatest abundance (Fig. 26), and some adults were taken at Station III. Gerking's (1953) data from Richland and Stott's creeks, Ind., imply that hog suckers inhabit a definite home range usually consisting of a single large pool. In an earlier study (Gerking, 1950) he stressed the stability of stream populations of fishes, including hog suckers, even after major flooding. In Doe Run, no hog suckers smaller than about 25 mm total length were collected, but individuals from that size to about 100 mm were usually in shallow riffles or in eddies over clean gravel, sand, or even bedrock bottoms. Large adults showed a marked preference for deeper pools, where they were often shocked from beneath semifloating deposits of stream-drifted detritus. Large fish seldom were found in appreciable current, except in areas where 2 riffles came together around an obstruction to form a strong eddy. Several large *H. nigricans* were surprised early one morning in May 1960, on a riffle near Mile 3.75 where they may have been feeding. Since the species generally spawns in shallow, cuplike depressions in gravel (Gerking, 1950) or on open gravel riffles, and sometimes in pools (Hamilton, in Raney and Lachner, 1946), it seems unlikely that they were spawning on solid marl. Judging from the distribution of young hog suckers in summer, breeding occurred in a somewhat limited area between Station IV and Mile 7.0 or

thereabouts (Fig. 26). Spawning upstream may be restricted by the general lack of gravel bottoms. *Hypentelium* must be considered a scarce component of the fauna of Doe Run when compared to other species, but was common in the area in which it occurred.

Ictiobus bubalus (Rafinesque): small-mouth buffalo. Immature *I. bubalus* were present in the area downstream from Mile 6.7, and most common when backwaters from the Ohio River were present.

I. cyprinellus (Valenciennes): bigmouth buffalo. A large individual was affected by rotenone near Station V, but was not captured.

Minytrema melanops (Rafinesque): spotted sucker. *Minytrema* was rare, occurring in the low-gradient section downstream from Miles 5.3 to 5.6, and as 2 or 3 specimens upstream (Fig. 26). Individuals from Doe Run were generally large, but a few were less than 6 inches total length. The population may have been maintained by emigration from the Ohio River, where it is generally rare in the mainstream, or reproduction occurred in the part of Doe Run downstream from Station V and young did not move upstream until considerably larger. *Minytrema* was invariably in the largest, deepest pools as adults, but smaller individuals sometimes were in the lower parts of slow riffles or in open, shallow pools over silt-gravel bottoms. Its greatest abundance was near and below Mile 7.0 over soft bottoms. Preferences for soft, silt-detritus bottoms in streams were noted by Gerking (1945), but Trautman (1957) considered the species more characteristic of lakes or base-gradient streams with hard bottoms of sand, gravel, or clay.

Moxostoma anisurum (Rafinesque): silver redhorse. Two specimens were taken by rotenone in the extreme mouth of Doe Run, and 2 others were obtained by rotenone near Mile 7.0.

M. breviceps (Cope): shorthead redhorse. This species was uncommon in Doe Run, but occurred most frequently in collections between Miles 5.5 and 7.0 (Fig. 26) where

it inhabited areas of moderate current in shallow, open pools or at the foot of riffles, and was somewhat more abundant in the upper part of that section. It was almost always over clean gravel bottoms. The species was present in Doe Run throughout the year, and there was no evidence of a "run" of shorthead redhorse into the stream, and no reproductive activity was indicated by condition of gonads or by occurrence of young fish.

I watched a number of *M. breviceps* feeding in a shallow pool near Mile 6.0 in June 1960. They moved with their bodies held at a slight angle to the bottom in a compact group, flicking the fins rapidly and pushing between small stones and gravels with their snouts. This behavior contrasts with my observations of the related *M. aureolum pisolabrum* Trautman and Martin in the Marais des Cygnes River, Kansas, in 1958. Those fish held their bodies almost perpendicular to the bottom in a shallow riffle and actually rolled stones and gravel while feeding. *M. a. pisolabrum* has a protuberance, or "pea" on its upper lip (Trautman and Martin, 1951), which may function in this type of feeding. Hubbs and Lagler (1958) indicated that the name *aureolum* is unavailable in the genus *Moxostoma*, but failed to give reasons for their action; it is retained here pending detailed clarification (Minckley and Cross, 1960).

M. duquesnei (LeSueur): black redhorse. Black redhorse from Doe Run all exceeded 10 inches total length and usually were associated with *M. erythrurum* in the deepest pools. They were most common between Miles 5.0 and 7.0 (Fig. 26), but were a rare component of the fish fauna. This species never was found in swift waters of Doe Run. It was considered a semimobile species in Missouri streams by Funk (1957).

M. erythrurum (Rafinesque): golden redhorse. This species was the most abundant redhorse in Doe Run, but was no more than an uncommon component of the fauna. Only large individuals, from 6 to 18 inches total length, were found upstream from Station V, but young-of-the-year indi-

viduals were collected at Station V. Golden redhorse in Doe Run did not seem as easily shocked as those reported from Jordan Creek, Illinois, by Larimore (1961), possibly because of deeper pools in Doe Run and more variable conditions of collection. It is of note, however, that intensive electrofishing in a given pool apparently depleted the population of golden redhorse there; subsequent collections rarely yielded as many, and sometimes none in those pools. This may indicate relatively sedentary habits. Gerking (1953) found it resembled the hog sucker in distances moved in Richland Creek, Ind., quite different from the contention of Trautman (1957) that the species is "highly migratory." The species inhabited the same range in Doe Run as *M. breviceps* (Fig. 26), but was more often in pools and over soft, silty bottoms.

Ameiurus melas (Rafinesque): black bullhead. I chose to retain the generic name *Ameiurus* for the bullhead catfishes, at least until data are published substantiating synonymization of that genus with *Ictalurus* by Taylor (1954). The black bullhead is common in most sinkhole ponds of Meade County that I have seined, but was rarely taken in Doe Run and did not reproduce there, at least not upstream from Station IV. Specimens were taken at all stations, but the numbers upstream were especially small. Hoop nets set in Pool 2 caught 6 black bullheads, all of which were marked and released only to be caught repeatedly without addition of new individuals to the catch. Bullheads are difficult to seine because of their bottom-dwelling habits and the tendency to live in deeper pools amidst debris. Shocking is relatively ineffective because they stiffen and sink to the bottom rather than moving into sight (Larimore, 1961). The lack of specimens in collections downstream from Station IV must be attributed to these factors because substantial numbers were found in 2 large pools near Mile 5.0 during the rotenone operation of July 1961, and occasional specimens were obtained down to Mile 7.5.

The species presumably occurred throughout the downstream area but is uncommon in the Ohio River at this point. I believe that those specimens obtained from the mill ponds passed through underground waters into Doe Run, or entered through the Rushing River system. I have seen black bullheads deep in caves in Breckinridge County, Ky., and elsewhere. Populations in the downstream part of Doe Run may come from the Ohio River, or some reproduction could have occurred in the mouth with subsequent movement upstream (Fig. 26).

A. natalis (LeSueur): yellow bullhead. Two yellow bullheads were taken in hoop nets in Pool 2, 1 was preserved and the other fin-clipped. The latter was recovered again near Mile 7.0 by rotenone in July 1961. It had been free for almost a year and had moved downstream a distance of 4.9 miles between captures.

Ictalurus punctatus (Rafinesque): channel catfish. Channel catfish were very rare in Doe Run, occurring only downstream from Mile 6.5 with the exception of 1 small individual taken near Mile 5.3 (Fig. 26). According to fishermen in the downstream area, the species was never abundant in Doe Run, but was commonly caught in other stream mouths in the vicinity. It is abundant in the adjacent Ohio River.

Noturus flavus Rafinesque: stonecat. A single *N. flavus* was collected by electric shocker near Mile 6.0.

Pilodictis olivaris (Rafinesque): flathead catfish. Few flathead catfish were collected, and most were in the area downstream from Station V. The most upstream record was a juvenile obtained from a large pool at Mile 5.3.

Camptostoma anomalum anomalum (Rafinesque): stoneroller. Stonerollers were caught from Station III downstream to approximately Mile 5.5, and occasionally at Station V. Highly colored, tuberculate males were found in April and May, but young-of-the-year individuals were scarce in Doe Run, and occurred only downstream from Mile 5.0 and at Station III where gravelly bottoms were present (Fig. 26).

Marl deposition between the 2 locations may have prevented spawning. The species constructs nests at the heads of riffles on clean gravel bottoms (Langlois, 1937; Lennon and Parker, 1960), sometimes markedly altering the bottoms in the process.

Stonerollers in Doe Run inhabited shallower pools, swift eddies downstream from marl riffles, and marl- or gravel-bottomed riffles in spring. Young individuals were most often taken on riffles, usually in the most turbulent parts. Metcalf (1959) implied an association of young stonerollers with more turbulent areas in Spring Creek, Kansas, rather than with the smoother-flowing riffles.

About 85 per cent of the stonerollers collected from Doe Run were more than 3 inches total length, but none exceeded 7 inches. I consider large stonerollers more difficult to catch than small, at least by seine, but the reverse is probably true for collections made by shocker (Larimore, 1961). Nevertheless, the paucity of young fish in collections indicates a marked difference in reproductive success of the species in Doe Run when compared with other localities (Minckley and Cross, 1959; Metcalf, 1959; Lennon and Parker, 1960; and others).

Chrosomus erythrogaster (Rafinesque): southern redbelly dace. This species was represented by 2 specimens from Station II, a single individual from immediately downstream from Station III, and many specimens from Tributary IV-e. In the latter, *C. erythrogaster* inhabited the downstream portion of the small rubble-bottomed stream, which was destroyed by impoundment of Doe Run. The stream was permanent in the sense that it was spring fed and summer pool levels were maintained by subsurface percolation of water through coarse bottom materials.

Ericymba buccata Cope: silverjaw minnow. Three silverjaw minnows were obtained, 1 each from Stations II and V, and the other near Mile 7.0 by rotenone. The species is locally common in creeks near Doe Run, but rare in the Ohio River.

Hybognathus nuchalis nuchalis Agassiz: silvery minnow. This species was rare in Doe Run, and occurred downstream from Station IV. The greatest numbers were in deep pools near streamside debris such as tangled roots or drift. No specimen smaller than 4.0 inches was obtained, and many approached the maximum size of 6 inches given by Forbes and Richardson (1920) for Illinois specimens.

Hybosis amblops amblops (Rafinesque): bigeye chub. Two specimens were obtained in the rotenone operation of July 1961. They were not recognized in the field but were presumably obtained near Mile 6.5.

H. storeriana (Kirtland): silver chub. The most upstream record of this species was in Tributary IV-e during backwater conditions. Two additional specimens were caught by seine near Station V, and the species occurred in rotenone collections from the extreme mouth of the creek. Trautman (1957) stated that silver chubs often avoid silty water and sedimentation in larger bodies of water by movement into clear streams of higher gradients.

Notemigonus crysoleucas (Mitchill): golden shiner. A single golden shiner was seined downstream from the swift bridge culverts at Station III in association with other minnows.

Notropis ardens lythrurus Jordan: rosefin shiner. Five specimens of rosefin shiner were collected from Doe Run, 1 in 1958 while I was procuring fish for the University of Kansas and another in 1961 at Station III, 2 at station V in 1960, and the last by rotenone in July 1961. It is relatively abundant in Otter Creek, Meade County, Knob Creek, Jefferson and Bullitt counties, and other streams near Doe Run, but very rare in the Ohio River.

N. atherinoides atherinoides Rafinesque: emerald shiner. This species probably is the most abundant fish in the Ohio River near Doe Run, and it was classed as "abundant" in Doe Run. It occurred throughout the stream from Station III to the river (Fig. 26), but was most common in the low-gradient portion downstream from Mile

5.3. Large schools of emerald shiners usually swam ahead of an electric field, and the bottom of the stream became literally silver as the fish turned into the field. Emerald shiners were especially abundant in Doe Run when backwaters of the Ohio River were present, and large schools remained in pools of the drying creek in 1961, downstream from the impoundment.

Reproduction by *N. atherinoides* in Doe Run apparently was limited to the area downstream from Station V; individuals taken upstream at all times of year exceeded 2.5 inches total length.

N. blennius (Girard): river shiner. This species was rare in Doe Run but occurred throughout the area below Mile 5.3 and a single specimen was caught below the culverts at Station III (Fig. 26).

N. buechanani Meek: ghost shiner. Three *N. buechanani* were taken by rotenone in July 1961 near Mile 7.2.

N. chrysocephalus chrysocephalus (Rafinesque): central common shiner. This species was considered a subspecies of *N. cornutus* (Mitchill) until Gilbert (1961) presented adequate evidence for its specific identity. In Doe Run, it occurred in a restricted area as a small population of mostly large adults. There were rare occurrences of young up- and downstream from Miles 4.6 and 6.9, respectively. The limited range in Doe Run may relate more to water temperature than to gradient since its range overlaps both the high- and low-gradient sections (Fig. 2). Gilbert (1961) considered *chrysocephalus* a southern species in the process of extending its range northward (see Trautman, 1957).

N. photogenis (Cope): silver shiner. One specimen was taken at Station IV by seining at night, but repeated attempts on that and subsequent nights failed to obtain others.

N. spilopterus spilopterus (Cope): spotfin shiner. This species was common at Station III in winter, but rarely farther upstream than Station IV in summer. Spawning apparently occurred in August and September (Starrett, 1951), and young-of-the-year individuals were present at Sta-

tions IV and V in small numbers (Fig. 26). Spottfin shiners showed a definite preference for eddy habitats in Doe Run, but large adults also were typically associated with riparian debris, such as roots or overhanging bushes. Young were more often found in relatively swift water and sometimes joined schools of *N. atherinoides* in open pools.

N. stramineus stramineus (Cope): sand shiner. A number of sand shiners, apparently comprising a single school, were taken by rotenone at Station V in April 1959.

N. volucellus subsp.: mimic shiner. Specimens identifiable as *N. v. volucellus* (Cope), *N. v. wickliffi* Trautman, and probable intergrades between the two were present in the lower part of Doe Run, most of which apparently moved into the creek from the Ohio River. The form recognized as *N. v. wickliffi* was considered an "ecological subspecies" by Hubbs and Lagler (1958), and is generally more restricted to the Ohio River, while the typical form is wide-ranging in small tributaries, lakes, and some larger streams (Trautman, 1931, 1957).

Notropis volucellus ranged farthest into Doe Run in periods of backwater from the Ohio River (Fig. 26), and no young-of-the-year individuals were taken at any time. On the basis of frequency of occurrence this species must be considered rare but large schools were present in the mouth of Doe Run, in drying pools after impoundment in 1961, and the species was very abundant in some rotenone collections from the extreme downstream sections.

N. whipplei (Girard): steelcolor shiner. This species was rare in Doe Run, but was collected as single specimens throughout the creek from Station III to Station V, and below.

Phenacobius mirabilis (Girard): sucker-mouth minnow. Two specimens were seined at Station V.

Pimephales notatus (Rafinesque): bluntnose minnow. Large, open pools appear to be preferred by stream-inhabiting bluntnose minnows throughout their range (Thompson and Hunt, 1930; Starrett, 1950a;

Martin and Campbell, 1953; and others), and the species was most common in those habitats between Miles 5.3 and 7.0 in Doe Run, with lesser numbers occurring up- and downstream (Fig. 26). Large *P. notatus* were taken often in current during winter, but occurred in the deeper pools in summer; similar seasonal relations were noted by Starrett (1950a) in Iowa and by Metcalf (1959) in Kansas.

Young bluntnose minnows were found at Stations III, IV, and V, but in considerably greater numbers downstream. Spawning apparently occurred in late June, July, and early August. A single adult specimen collected in a muddy, cutoff pool at Station II (Fig. 26) may have been introduced from a fisherman's bait bucket.

P. promelas Rafinesque: fathead minnow. This species is represented by a single collection of 2 specimens from Tributary IV-e.

Rhinichthys atratulus meleagris Agassiz: blacknose dace. This species was abundant in Doe Run and occurred mostly upstream from Mile 6.0 (Fig. 26). The subspecific name is applied mostly on geographic grounds; specimens from Doe Run appear to have large mouths and other characters tending toward *R. a. obtusus* Agassiz of the Tennessee River System. Breeding males from Doe Run differ from those described by Trautman (1957) in having rust-red lateral bands rather than a suffusion of pink or red, and in the lack of color on the central pads of the pectoral fins, as opposed to a deep orange or orange-red color in Ohio specimens.

Delimiting the habitat of *R. atratulus* is complicated by its general abundance in Doe Run. Larger individuals live close to the bottoms in large, deep, eddying pools, but also on riffles in June, presumably to spawn. Some large fish were found in unusual situations. For example, in 1959 a probe of the electrofishing gear was pushed deep into the spring source of Doe Run and 6 specimens were washed out by the current. Young-of-the-year blacknose dace usually were found in quiet, shallow waters over mud bottoms until 1.0 to 1.2 inches in length, and larger individuals (to 2 inches)

inhabited progressively deeper pools and stronger eddies. Large numbers of young and yearling fish were left in overflow pools along Doe Run after floods. The species forms loosely knit aggregations, usually of roughly equal-sized fish, and apparently as a response to movement (Kuehne, 1958). Smaller blacknose dace were more pelagic than large adults, and were observed feeding at the surface on many occasions. The species was caught easily on small hooks baited with almost any animal small enough to be swallowed.

Large numbers of young *R. atratulus* were produced in 1960; however, in 1961 few young-of-the-year dace were found. The severe flooding in 1961 may have affected spawning to some extent. High discharge and siltation were major factors hindering reproductive success in the Des Moines River, Iowa, by a number of species of minnows (Starrett, 1951).

Semotilus atromaculatus (Mitchill): creek chub. *Semotilus*, although most abundant in the upstream area of Doe Run near Station III, did not occur above Dam 1, and was relatively rare in the stream below Station V (Fig. 26). Its propensity for ascending small streams (Shelford, 1911a; Starrett, 1950a) was indicated in Doe Run by its occurrence sometimes in considerable numbers in almost all tributaries sampled.

Large chubs in Doe Run sometimes approached 11 inches total length and usually were taken in hoop nets from the mill ponds and other deep pools throughout the upper sections (above IV), or by shocker in swift eddies at the foot of riffles and below waterfalls. The species provided considerable sport for fishermen in those areas. Smaller chubs often schooled with *R. atratulus* as reported by Kuehne (1958) but were somewhat more secretive and tended to occur near overhanging riparian vegetation or "cut-banks." Young-of-the-year chubs appeared in May, and often were found in association with surface-feeding stages of *Catostomus*. The resemblance of small chubs at pool surfaces near vegetation to certain top-feeding cyprinodontiform fishes was striking.

Cyprinus carpio: carp. The presence of carp in Doe Run and in Doe Valley Lake has already been discussed (see *Dorosoma*). *Cyprinus* was consistently present in Doe Run downstream from Mile 7.0, but occurrences upstream from there were unusual and limited in the largest pools.

Anguilla rostrata (LeSueur): American eel. Twelve eels were obtained from Doe Run between Station III and Mile 7.0. Although the occurrence of this species in Doe Run is not surprising, the habitats from which they were taken were remarkably consistent, and in contrast with that described by Forbes and Richardson (1920) and others. All specimens collected by electrofishing were in tangled roots of riparian trees, and in areas where strong currents entered deep, hard-bottomed pools. Those seen making initial moves after being affected by rotenone were also in this type of habitat, but rapidly swam away from rotenone-treated water, often deserting the stream and moving rapidly up the banks.

Ambloplites rupestris rupestris (Rafinesque): rock bass. Rock bass were scarce in Doe Run when compared with other fishes but were common between Miles 5.5 and 7.1. Downstream from Mile 7.1 several young-of-the-year individuals and 2 or 3 small adults (Fig. 26) were collected. The rock bass usually is considered a species of relatively swift waters in the Ohio River Basin (Forbes and Richardson, 1920), and is associated intimately with rock ledges, undercut banks, roots, and other streamside vegetation or debris (Gerking, 1945; Trautman, 1957; and others). It is interesting that in the Ozarks the species is considered an upstream fish (Funk and Campbell, 1953), as it is in Iowa (Harlan and Speaker, 1956); a species of medium-sized rivers in Illinois and Ohio (citations above); but as characteristic of downstream areas in colder streams of Ontario (Hallam, 1959); and of stream mouths and thick beds of aquatic vegetation of lakes (Adams and Hankinson, 1928).

In Doe Run, the habitats of large rock bass were similar to those utilized by

Anguilla—tangled roots along undercut banks where there was considerable current. Smaller individuals were in quieter waters, but always near drifted debris or other cover. The species is quite sedentary in streams (Scott, 1949; Gerking, 1953, 1959; Funk, 1957; and Trautman, 1957).

Chaenobryttus gulosus (Cuvier): war-mouth. This species was rare in Doe Run and ranged from 4 to 5 inches total length. Specimens were obtained singly from larger pools near Station IV and downstream to near Station V. The species reaches its greatest abundance in lakes; small numbers such as in Doe Run are more or less typical of stream populations, at least in Illinois (Larimore, 1957).

Lepomis cyanellus Rafinesque: green sunfish. Green sunfish were a rare, but consistent component of the fauna of Doe Run downstream from Dam 3, but occurrences upstream were even more infrequent, and included only large adults. Individuals taken in the upstream area may have entered Doe Run from adjacent sink-holes through subterranean watercourses, or by passage through surface streams. No young-of-the-year sunfishes of any kind were obtained upstream from Station IV, but small green sunfish were more frequently taken in the downstream area than were any of the other sunfishes.

Green sunfish ascended tributaries of Doe Run farther than any other fish except *Semotilus*. Stocks remaining in tributaries after the rotenone operation of July 1961, and probably some fish upstream from the area, reproduced successfully in Doe Valley Lake in August. This species apparently preferred shallow, quiet pools where rubble, stream-drifted debris, or overhanging vegetation provided thick cover.

L. humilis (Girard): orangespotted sunfish. One orangespotted sunfish was collected at Station V, another near Mile 7.0 by rotenone, and a third in the unlikely area of Station I. The last specimen conforms with *L. humilis* in most respects, but may be a hybrid involving *L. cyanellus*. Its origin and occurrence at Station I are enigmatic.

L. machrochirus Rafinesque: bluegill. *Lepomis macrochirus* was uncommon in the ichthyofauna of Doe Run, with the greatest part of its population occurring between Mile 5.3 and Station V. A few individuals, however, were taken at Station II, and 2 were caught at Station I, all of which were large and were presumably involuntarily displaced individuals from adjacent sink-holes where they were very abundant. The general preference of bluegills for lentic waters was expressed in their occurrence in long, shallow, slowly flowing pools in Doe Run; however, large individuals were sometimes taken in swift eddies if cover was present.

L. megalotis megalotis (Rafinesque): longear sunfish. "Longears" were only slightly more abundant than bluegills, but their numbers were more evenly distributed between the up- and downstream limits of their principal range. The largest populations, however, were in the area of distinct pool-riffle development between Miles 5.3 and 7.0 (Fig. 26).

Although green sunfish and longear sunfish are more or less associated throughout the Middle West, in the sense that both inhabit smaller streams, I have been unable to find reference to a stream population of sunfishes including substantial numbers of those species along with bluegills. In sporadic sampling of Doe Run in 1959, prior to the beginning of intensive study, I noted increased numbers of bluegills and green sunfish downstream from swift-flowing culvert tubes of the bridge at Station III. These increases occurred in April, May, and June, and were surprising because of the general dearth of sunfishes in my previous collections, but corresponding decreases of the populations occurred throughout the summer and they were again rare by the end of the year. In February 1960, after a short period of winter discharge, those species were again below the bridge, and became progressively more abundant in succeeding months. That summer they again diminished in numbers in July, occurring only rarely until

after high discharges of January. The large population accumulated in spring 1961 remained near Station III throughout the summer, fall, and winter. *Lepomis megalotis* also became more abundant in the large pool each spring, but was present all year throughout the downstream section, and at the bridge.

Of these sunfishes, *L. megalotis* occupies remarkably stable home ranges of about 100 to 200 feet of stream, usually delimited by riffles (Gerking, 1959), and is capable of returning to those areas when displaced, apparently by olfactory recognition of the "home pools" (Gunning, 1959). Of 45 specimens of *L. cyanellus* recaptured after tagging in Missouri streams (Funk, 1957), 77.8 per cent made movements of less than 1 mile (= "no movements"), and of those that had moved, 13.3 per cent had gone upstream and 8.9 per cent downstream. Green sunfish in shallow ponds of Wisconsin returned to the same area each spring, whereas displaced individuals, followed by an attachment of a floating bobber with nylon thread, returned "home" with considerable precision (Hasler and Wisby, 1958). Gerking (1950) found green sunfish living in the same pools of an Indiana creek for a considerable time, and persisting or returning there (Gunning, 1959) after severe flooding. Bluegills in Sugarloaf Lake, Michigan, returned to the half of the lake in which they were originally trapped after being displaced to the opposite side (Cooper, 1953). I know of no studies concerning movements of that species in streams.

Movements of many fishes are greatest in spring (Funk, 1957; Trautman, 1957; and others), which may be related to searching for areas suitable for nest building and other reproductive activities (Winn, 1958a; Gunning, 1959). Likewise, the possibility exists that certain individuals move to the same places each year for spawning (Hasler and Wisby, 1958). The large pool downstream from the bridge at Station III presented the most likely spawning site available upstream from Station IV. The

bedrock bottoms of pools in the marl area certainly were not suitable, and areas of particulate bottom, excluding silt or detritus, were generally in swift currents. However, in spite of the presence of "ripe" adults at Station III, no breeding sunfishes or young-of-the-year individuals were observed or collected. It must be concluded that very little, if any, reproduction by centrarchids occurred upstream from Station IV.

The most logical explanation for this situation is the low water temperature at Station III. With maturation of the gonads in spring, and the accompanying secondary sexual characteristics such as male breeding colors and presumed searching for suitable nest sites, the fish became concentrated below the barrier produced by the swift, shallow culvert, or considered the pool "suitable" (the former seems more likely). Subsequently, water temperature failed to rise sufficiently to permit reproduction, and the fish resorbed their ova (noted in *L. megalotis* and *L. macrochirus*), or moved downstream until higher temperatures were encountered. No major downstream movement of sunfishes was observed, but it seems likely that most moved slowly downstream to reoccupy various pools and eddies without spawning. Sunfishes resident between Stations III and IV presumably represent "mobile" components of the downstream populations that gradually ascended the creek and stopped in suitable habitats.

The sequence of population fluctuation in the "bridge pool" in 1961, with the fishes remaining there throughout the year, invalidates some of the above discussion. However, no reproduction took place despite the presence of adult fish. In the winter of 1960–1961 a number of large stones fell into the pool from riprap of an extensive road fill, and substantially increased the suitability of the area for a larger number of fish. It is possible that clearing the downstream portion of Doe Run, siltation, and continual disturbance by machinery and felling of trees caused movement of fish upstream and concentra-

tion below the barrier.

These interpretations are based on the assumption that certain minimal temperatures are required for reproduction by the species concerned. Such records are rarely less than 21.1°C (Witt and Marzolf, 1954; Swingle and Smith, 1950; and others), a water temperature never attained at Station III. The development of the gonads of sunfishes in Doe Run and elsewhere, however, occurs at cooler temperatures presumably in response to day length. Detailed studies of spawning cycles in warmwater fishes are badly needed to evaluate the influence of light, water temperature, and other environmental conditions.

Micropterus dolomieu dolomieu Lacépède: smallmouth bass. This species was rare in Doe Run and restricted in its distribution between Miles 5.3 and 7.2, except for an occasional small individual taken at Station V (Fig. 26). Distribution of smallmouth bass in streams has been correlated with gradient (Trautman, 1942; Burton and Odum, 1945), with the largest populations existing in streams with gradients between 4 and 25 fpm. Upstream from Mile 5.0 in Doe Run the gradient is about 35 fpm (to Mile 1.5; Fig. 2), and in the area where smallmouth bass occurred it is 4 to 6 fpm, becoming higher downstream. Smallmouth bass may have avoided the downstream area because of the generally soft bottoms and the sluicelike nature of the stream. Seldom more than a single individual was caught from a given pool in Doe Run, usually near logs, roots, or other cover, where swift currents prevailed. The species is rather sedentary in smaller streams (Gerking, 1950, 1953), and appears capable of returning to a home pool when displaced (Larimore, 1952, 1954).

Young smallmouth bass were caught only at Station V, and in very small numbers. Most specimens obtained upstream were more than 8 inches total length. The largest individual I saw weighed 2 pounds, 2 ounces after viscera and scales were removed. That fish was caught by a fisherman near Mile 5.4.

M. punctulatus punctulatus (Rafinesque):

spotted bass. Scattered individuals were caught from Station III to the mouth of Doe Run, but young were obtained only at Station V. Its typical habitat appeared to be shallower, quieter pools than that of the smallmouth bass, but it was taken also in swift eddies upstream and in the almost-lentic waters near the Ohio River. Trautman (1957) noted migration of spotted bass upstream in spring, but in Doe Run specimens were collected in spring and autumn at Station III. The presence of the species in shallow pools throughout the high- and low-gradient sections also contrasts with reports of Howland (1931) and Trautman (1942, 1957) that the species usually inhabits deep, well-shaded pools in areas with gradients less than 4 fpm. With regard to movement, Funk (1957) recaptured 24 individuals from Missouri streams, 22 of which had moved no more than a mile from the point of original tagging, and Gerking (1953) found that only 1 of 16 fish recaptured after marking had moved from the pool in which it was first caught. Habitats and behavior of this species seem to vary considerably throughout its range.

M. salmoides salmoides (Lacépède): largemouth bass. A single largemouth bass was caught on pole and line at Station III in June 1961 and no additional specimens were found until the rotenone operation of July 1961. Twelve specimens were collected then between Miles 6.2 and 7.35 from large pools with silt-covered gravel bottoms.

Pomoxis annularis Rafinesque: white crappie. This species was not obtained until 1961. Two were taken by shocker near Mile 5.5 when backwaters of the Ohio River were present, and most of the remainder were obtained in the rotenone study of July. The species was present, however, downstream from the Doe Valley Dam in small numbers, where it was seined from drying pools in association with large schools of *Notropis atherinoides* and *N. volucellus*.

P. nigromaculatus (LeSueur): black crappie. A single black crappie was taken by rotenone near Mile 6.9 in July 1961. I

found this species relatively abundant in the Ohio River near Doe Run in 1959 while fishing hoop nets.

Etheostoma blennioides Rafinesque: greenside darter. Greenside darters were rare inhabitants between Miles 4.5 and 6.2 (Fig. 26) with single occurrences at Stations III and V and a few specimens from Miles 6.2 to 6.9 in the rotenone operation of 1961.

In Ohio, greenside darters usually spawned in April when water temperatures were slightly below 18.3°C (Trautman, 1957), but spawning in Doe Run occurred in June as indicated by presence of young in collections, and condition of gonads and adults. Later reproduction in Doe Run presumably was in response to the relatively cool water temperatures earlier in the year. Winn (1958a) found spent *E. blennioides* in the Green River System of Kentucky the first week of April. No reproduction in Doe Run was detected upstream from Mile 5.3.

The habitat of *E. blennioides* in Doe Run was usually the swiftest riffles or fast eddies at the lower ends of the swiftest riffles. During winter some were obtained in pools when higher discharges produced significant current velocity there. There was no marked propensity by the fish to inhabit vegetation on riffles in Doe Run, though such a preference has been recorded elsewhere (Forbes and Richardson, 1920; Trautman, 1957). The use of vegetation for spawning (Fahy, 1954; Winn, 1958a, b; and Trautman, 1957) may have caused the apparent lack of reproduction in the marl area and its occurrence downstream where *Cladophora* was locally abundant on riffles.

E. caeruleum Storer: rainbow darter. This species was as rare as the greenside darter in Doe Run and occupied a similarly restricted distribution though ranging somewhat farther downstream (Fig. 26). It inhabited swift riffles with gravel bottoms and apparently avoided vegetation on those riffles. Young-of-the-year rainbow darters were taken as far upstream as Station IV,

and spawning apparently occurred in June and July.

E. flabellare Rafinesque: fantail darter. Two subspecies of fantail darter, *E. f. flabellare* and *E. f. lineolatum* (Agassiz), appear to intergrade in Doe Run and in other streams of the vicinity.

E. flabellare was abundant in Doe Run, occurring from Station V to Station II (Fig. 26). Its upstream distribution was abruptly terminated near Mile 2.05 immediately upstream from Tributary II-a at a low waterfall, the reasons for which are obscure. It may be that temperatures in Doe Run at Station II were seldom, if ever, high enough for breeding of this species, with most young-of-the-year and "high" males being taken in the downstream part of Tributary II-a or immediately downstream from its mouth. That tributary was spring-fed, but small and relatively unshaded, and water temperatures averaged 2°C higher in its mouth than in Doe Run on bright, warm summer days.

Young-of-the-year fantail darters first appeared in May and June, and moved immediately to quiet, warm, shallow waters, living there until nearly an inch long. Those areas have soft, semiflocculent bottoms that support a rich fauna and flora of microscopic organisms, thus providing foods for small fish; secondly, small darters are relatively alone in that habitat, which is inhabited only by very young *Cottus* on the bottoms and postlarval *Catostomus* and *Semotilus* near the surface. Water temperatures in those areas sometimes reached 30°C in summer, but the small darters remained there anyway.

Larger *E. flabellare* inhabited eddy pools, swift rubble riffles, smaller riffles in Doe Run, and often were taken in mere trickles of water between and beneath small stones at Station IV. Downstream from Station IV, where *Cladophora* developed lateral to the main currents of the riffles, there was a segregation of sizes. The smallest individuals were in less than 0.25 inch of water along the banks, slightly larger ones were in *Mougeotia* of the quiet

areas lateral to *Cladophora* beds, and progressively larger fish were found farther from the shore. Collections from the main channel, over clean gravels, yielded only a few large fantail darters, with *E. caeruleum* and occasionally *E. blennioides*.

At Station II, *E. flabellare* was commonest in beds of *Myriophyllum* in relatively quiet currents near the upstream end of Pool 2.

Hadropterus maculatus Girard: blackside darter. On the basis of characters given by Hubbs and Lagler (1958), and others (see Winn, 1958b), I consider *Hadropterus* as distinct from the genus *Percina*, with which it was synonymized by Bailey (in Bailey and Gosline, 1955). Two specimens were obtained by rotenone in July 1961. Both were large adults and were captured in large pools near Mile 7.0.

Percina caprodes caprodes (Rafinesque): logperch. This species was rare in Doe Run, occurring between Station IV and Mile 7.4, usually as single individuals. The smallest one obtained was about 4.8 inches total length and the largest near 7.0 inches. The species is rare in the mainstream of the Ohio River, but relatively consistent in its occurrence near Doe Run.

Stizostedion canadense (Smith): sauger. A single sauger was captured by rotenone within 50 yards of the mouth of Doe Run in 1959.

Aplodinotus grunniens Rafinesque: freshwater drum. This large species occurred consistently in shocking and rotenone collections downstream from the high-gradient section of Doe Run, and a few individuals were taken upstream as far as the large pool below the bridge at Station III (Fig. 26). The largest specimen seen was at Mile 3.5; its weight was estimated at 5 pounds or more. It was shocked in a long, shallow pool, but was not captured. On the basis of frequency of occurrence the drum was an uncommon component of the fish fauna of Doe Run.

Cottus c. caroliniae (Gill): banded sculpin. *Cottus caroliniae* was the most widespread and abundant fish in Doe Run, ranging from Station I to below Station V

in gradually diminishing numbers. Many preliminary aspects of its life history in Doe Run, including habitats, food habits, growth, and certain aspects of the accumulation of radioactive materials through its food web, were presented by Minckley, *et al.* (1963), and further studies on its biology are being made by James E. Craddock.

Sculpins comprised more than 75 per cent of all fish collected at Station I, and occurred at downstream stations in somewhat smaller numbers. Young individuals inhabited quiet, warm backwaters over silt-detritus bottoms (see *E. flabellare*), then gradually invaded swifter waters as they became larger to inhabit the fastest currents as adults. Extremely large adults, however, preferred pool habitats where strong currents persisted as eddies or tailwaters of upstream riffles.

Young-of-the-year *Cottus* first became abundant in Doe Run in April, with reproduction extending at least through May.

Summary of the Distributions of Fishes

As with the vegetation and invertebrates in Doe Run, the fishes were found in longitudinally restricted ranges in relation to physical features of the stream and specific differences in the behavior of the diverse animals present. Shelford's (1911a) work on the distribution of stream fishes near Chicago, Ill., formed much of the basis for physiographic interpretation of longitudinal succession in streams. In a later paper (Shelford, 1911b) he demonstrated a successional series of pond fishes, and found a primary dichotomy between lakes and streams in the great influence of biotic factors in the successional series of the former as opposed to geologic factors with the latter (Allee, *et al.*, 1955). Studies in Europe have prompted recognition of "trout" (Forelle), "grayling" (Asche), "barbel" (Barbe), and "bream" (Blei) regions occurring successively from up- to downstream (Leger, 1945; Ruttner, 1953). According to Huet (1959), these zonations result mostly from stream gradient, currents, temperature relations, physical nature of the substrate through which the stream

is cutting, composition and abundance of the flora, and size and abundance of stocks of food organisms. Thompson and Hunt (1930) found that stream width where marked differences in gradient did not occur between streams or stream sections was also an important factor in fish distribution. Gerking (1949) obtained data indicating that volume of the stream was important in the weight of fish present, a stream with frequent deep pools being more productive than one of the same size but having little deep water. The marked importance of gradient in the distribution of stream fishes was further emphasized by Trautman (1942) and Burton and Odum (1945).

In Doe Run, the 3 major factors controlling the distribution of fishes are gradient, temperature, and the presence of marl in the midsection of the stream. The effects of gradient are most pronounced when the "river fish" components of the fauna are examined (Fig. 27). Thirteen of the 31 species that I considered more or less typical of the Ohio River fauna near Doe Run maintained definite ranges in the creek, and all but 1 of which merged into the Ohio River populations (Fig. 26). The single exception, *Micropterus salmoides*, occurred in very small numbers in Doe Run, and its inclusion in Figure 26 would not have been justified had it not been for the sharply circumscribed area it inhabited. The designation of *Micropterus punctulatus* as a "river fish" is questionable, but it was consistently more abundant in the Ohio River near the mouth of Doe Run than in other nearby streams I sampled. However, the reverse is true in other regions, at least in spring and early summer (Trautman, 1957), when both types of stream were sampled by me. *Minytrema* seems characteristic of stream mouths along the Ohio River (Krumholz, *et al.*, 1962), and is therefore included with river fishes since most stream mouths along the Ohio River are flooded by navigation installations and are effectively parts of the backwaters. *Moxostoma breviceps* was the only river

fish, except the largemouth bass, that inhabited a fixed range in Doe Run and was more abundant upstream than near the mouth. Still, there was no evidence of spawning and the populations may have occurred because of a preference for the open, clean bottoms of the creek as opposed to those of the Ohio River. It is noteworthy that many of the most upstream catches of river fishes were at the barrier imposed by culvert tubes below Station III, and that most were single specimens.

A second group of fishes in Doe Run appeared most concentrated in the pool-riffle area immediately downstream from Miles 5.3 to 5.6, with scattered occurrences up- and downstream. These included *Lepomis* spp., *Pimephales notatus*, *Hypentelium*, *Ameiurus melas*, *Campostoma*, *Etheostoma blennioides*, *E. caeruleum*, *Notropis chrysocephalus*, *Moxostoma erythrum*, *M. duquesnei*, and *Ambloplites*. Some of them, principally the suckers (excluding *Hypentelium*), *N. chrysocephalus*, and the larger centrarchids, *M. dolomieu* and *Ambloplites*, may have been restricted to the area downstream from Mile 5.3 by the presence of shallow, open pools upstream, and their innate habitat preference for deep pools or more shelter (Larimore, *et al.*, 1952; many others). Their downstream distributions were presumably restricted by the lack of pool-riffle development in the lower areas, and its sluicelike configuration. The absence of gravel for spawning areas also may have limited habitation of the marl area by the latter species, and probably is a factor limiting populations of *Hypentelium*, *Campostoma*, and *E. caeruleum* there. *Campostoma*, however, reproduced successfully at the limited gravel area of Station III. Moreover, the cemented marl riffles and bedrock-bottomed pools between Station III and Mile 5.3 may have been unsuitable habitat for these bottom-dwelling, secretive forms.

Two species also included in the above category, *Etheostoma flabellare* and *Semotilus*, were more successful in maintaining populations throughout the high-gradient,

marl section (Fig. 26), and to some distance below Mile 5.3. The penetration of Doe Run by these species to Station II, with the darter not occurring upstream from Mile 2.05, but the chub present to immediately downstream from Dam 1, invites examination in light of the possible differentiation of *Catostomus commersoni* in the upstream area. The first mill dam built in Doe Run was at Mile 1.65 (Dam 1), upstream from the now-drowned waterfall at Mile 2.1. It effectively blocked upstream movement of fishes from below that waterfall even though they could cross it after the construction of Dam 2. Both *E. flabellare* and *Semotilus* occur in other springs of Kentucky and other parts of their ranges (Forbes and Richardson, 1920; Gunning and Lewis, 1956), but it is not known whether they reproduce there or merely maintain populations by upstream movements of young hatched downstream in warmer waters. It is conceivable that both species invaded the area of Doe Run above Mile 2.1 after Dam 2 was built, and have maintained small populations but are unable to pass over Dam 1. Exclusion of other species could have occurred easily because the constant, low temperatures precluded or lowered reproductive success. According to Curtis Brown (pers. comm.), *Micropterus dolomieu* was stocked upstream from Dam 2, but none was taken by me or in recent years by fishermen. That species usually spawns at temperatures greater than 17.8°C (Adams and Hankinson, 1928), or with little success at lower temperatures (Henderson and Foster, 1957). A certain segment of populations stocked in Jordan Creek, Ill., by Larimore (1954) remained there, although a significant number moved downstream and disappeared from the population. Also, all *Lepomis* spp. and *Ameiurus* spp. taken in the upstream area of Doe Run were relatively large. Possibly these are maintained by very rare reproduction that was not detected there during this study, but I am inclined to believe they entered from adjacent sinkhole ponds, and persisted there temporarily without reproducing.

Because of lack of reproduction of many fishes in and above the marl area, even after maturation of ova by females and attainment of breeding coloration by males, it is evident that low water temperature and the presence of marl restricted spawning and distribution of many species. Included here are the "creek fishes" (Fig. 27) not known to reproduce above Mile 5.3, but which reproduce downstream and presumably maintain populations by movement upstream. A few creek inhabitants, *Percina caprodes*, *Moxostoma breviceps*, *M. duquesnei*, and a few others, did not successfully reproduce in Doe Run insofar as I could determine; their populations must have depended on influx of individuals from the Ohio River.

Only 3 of the 66 kinds of fishes collected, *Catostomus*, *Rhinichthys*, and *Cottus*, maintained populations through reproduction at Station I. These fishes ranged throughout most of Doe Run in significant numbers, but *Rhinichthys* was the most restricted in its downstream distribution. *Salmo gairdneri* was introduced and did not reproduce successfully. It was most abundant at Station II, and it presumably was limited to the upstream area in response to the cooler waters.

It is of note that some species appearing closely associated in Doe Run, such as *Micropterus dolomieu* and *Hypentelium*, have also been found closely associated in other streams (Thompson and Hunt, 1930; Larimore, *et al.*, 1952; and many others). Trautman (1942) indicated that *M. dolomieu* rarely was found in Ohio streams having a gradient less than 4 fpm, but in the area of Doe Run inhabited by that species the gradient was only slightly greater (Fig. 2). The restriction of upstream range may also have been a function of gradient, because few smallmouth bass occur in streams with gradient greater than 25 fpm, and the marl area of Doe Run averaged more than 30 fpm throughout.

The rare species of Doe Run, those occurring only as single specimens or in fewer than 10 collections, comprise almost half of the 66 species obtained.

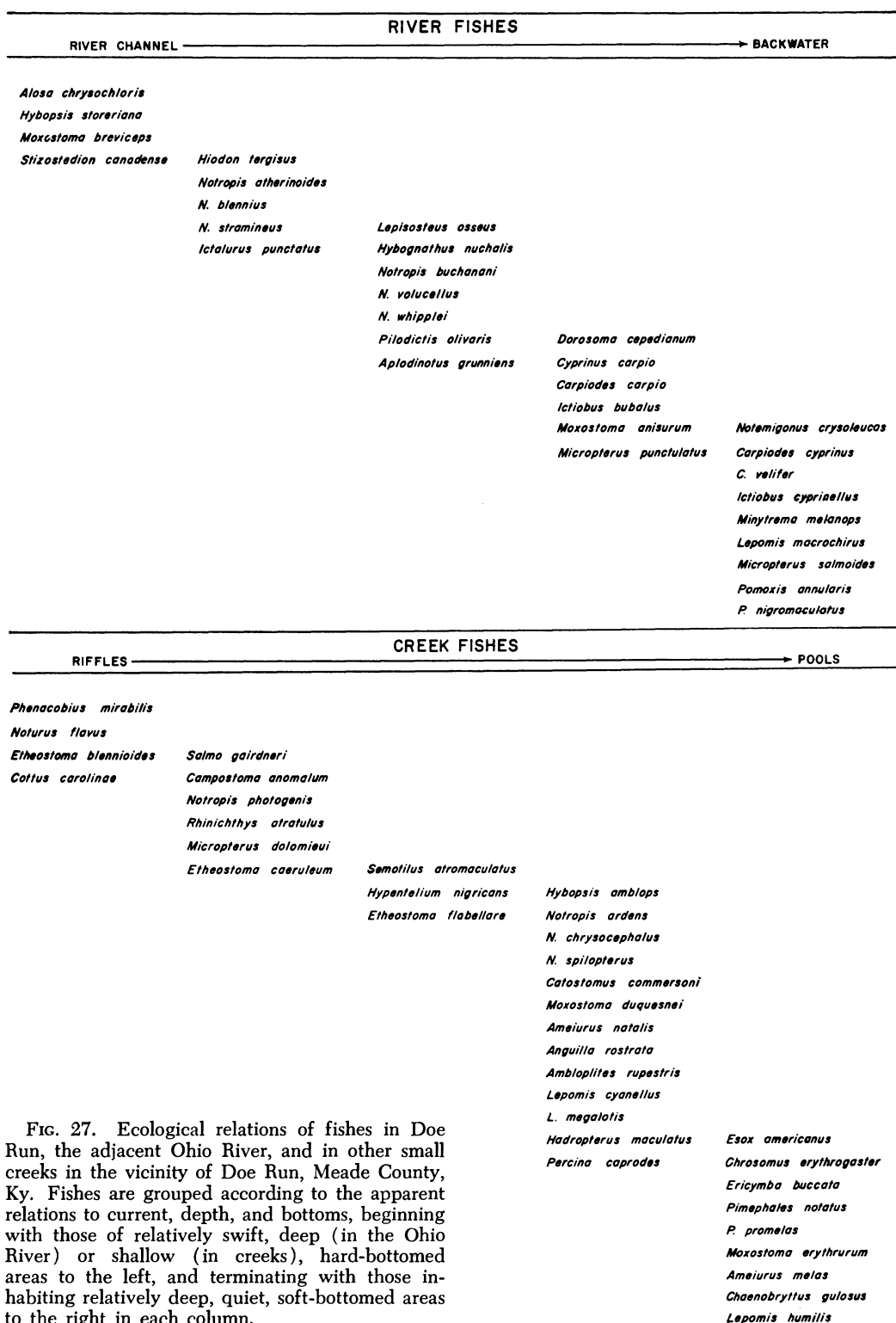


FIG. 27. Ecological relations of fishes in Doe Run, the adjacent Ohio River, and in other small creeks in the vicinity of Doe Run, Meade County, Ky. Fishes are grouped according to the apparent relations to current, depth, and bottoms, beginning with those of relatively swift, deep (in the Ohio River) or shallow (in creeks), hard-bottomed areas to the left, and terminating with those inhabiting relatively deep, quiet, soft-bottomed areas to the right in each column.

Eighteen of the 32 species classed as rare are "river fishes" (Fig. 27), and must have been strays. The remaining 14 species are more or less typical "creek species" in other streams near Doe Run, and their presence in such small numbers must indicate that the spring stream is not suitable for them. The discussions of Grinnell (1922 a, b) of the possible roles of rare and accidental birds in California were applied to the occurrence of stray or rare fishes in Iowa streams by Starrett (1950a). Rare species are available to fill niches or habitats that might become vacant by failure of year classes of resident species, for example, or possibly more importantly, to fill voids produced by changed environmental conditions in or near a given aquatic habitat. Such changes are easily demonstrated by changes of fish populations following introduction of pollutants into streams (Thompson and Hunt, 1930; many others), or the changing from lotic to lentic situations by impounding streams. Such a change usually is followed by rapid increase in species of backwaters and coincident decrease of riffle-inhabiting species (Trautman, 1939; Finnell, *et al.*, 1956; and others). Moreover, the sudden or progressive occurrence of a "rare" or "accidental" species in a given area, such as the eastward movements of *Phenacobius mirabilis* and *Lepomis humilis* (Trautman, 1957), or other changes in the dispersion and dispersal of populations (Black, 1949; Minckley and Cross, 1959; and others), may indicate climatic or land-use changes of importance not only to fishes, but as an index of the effects of man's activities. Such data are valuable in predicting and evaluating conditions of the natural environment, on which man depends for his livelihood.

Vertebrates Other Than Fishes

Information on vertebrates other than fishes was obtained incidental to other field work. However, observations and collections of amphibians and reptiles were made in some detail, and have been presented elsewhere (Craddock and Minckley, 1963). Only those animals whose life

histories involved specific interactions with Doe Run or its biota are included here.

Rana catesbiana Shaw, *R. clamitans melanota* (Rafinesque), and *R. pipiens sphenoccephala* Cope were abundant along the tributaries of Doe Run, but were rarely seen along the mainstream. *R. palustris* Le Conte was represented in our collections by a single specimen. The most abundant frog along the banks of Doe Run was the cricket frog, *Acris crepitans blanchardi* Harper. Larval anurans, including *Bufo* spp., *Pseudacris triseriata* (Wied), and *Hyla* spp., were abundant in nearby sink-hole ponds and in overflow pools along the creek, but none was collected in Doe Run.

Specimens of hellbender, *Cryptobranchus alleganiensis alleganiensis* (Daudin), mud-puppy, *Necturus maculosus maculosus* (Rafinesque), *Eurycea bislineata bislineata* (Green), *Pseudotriton ruber ruber* (Latreille), and *Desmognathus fuscus fuscus* (Rafinesque), were obtained from Doe Run or its tributaries in small numbers. Adult *Desmognathus* were the most abundant. A single newt *Diemictylus viridescens viridescens* (Rafinesque), typical of sink-hole ponds in the area, was caught near Mile 1.4.

Snapping turtles were collected at Station III, and in Pools 2 and 3. The stomach of a large specimen from Station III contained at least 143 individual *Orconectes rusticus*. Only the chelae were counted, thus considerably more than is indicated may have been eaten. Other turtles recorded from the creek were *Graptemys pseudographica* (Gray), and a "sight record" of *Trionyx* sp.

Natrix sipedon Linnaeus was the only abundant snake along Doe Run. It fed principally on *Acris* along the banks, but 1 individual contained a small unidentified minnow, and another was seen attempting to ingest a trout near Station IV. *Thamnophis sirtalis sirtalis* Linnaeus, *Heterodon platyrhinos* Latreille, and *Coluber constrictor* Linnaeus, were also taken along the stream, and undoubtedly ate such stream-side animals as frogs.

Birds of many kinds were numerous

along Doe Run. Kingfishers, *Megaceryle alcyon* (L.), were abundant throughout the length of the creek, and preyed on fishes and larger invertebrates such as crayfish. Great blue herons, *Ardea herodias* L., were frequent in the downstream sections, especially after the area was cleared prior to impoundment, and just after the eradication of fishes by rotenone. There were 6 or 8 great blue herons along Doe Run the day after the rotenone operation, presumably feeding on the fishes missed by pickup crews; none had been seen in the area for several weeks preceding that study. Green herons, *Butorides virescens* (L.), were relatively common in the downstream section of the stream throughout the study, and apparently nested there as indicated by the numerous juvenile birds in late summer.

Several species of ducks were observed, both in the downstream section at times of flooding by the Ohio River, and in the heavily vegetated area upstream from Dam 1. The species most commonly seen near the Ohio River were mallard, *Anas platyrhynchos* L., and black ducks, *A. rubripes* Brewster, but a few lesser scaup, *Nyroca affinis* (Eyton), rested on open waters of the downstream section when it was inundated. Those ducks frequenting the upstream area included the black duck, wood duck, *Aix sponsa* Linnaeus, and bluewing teal, *Querquedula discors* L. The black duck and teal usually were present only at times of migration, but a single brood of bluewing teal was produced near Blue Spring in 1960, and the wood duck was a consistent breeding bird along the creek in all years of the study.

Bronze grackle, *Quiscalus quiscula* (L.), and other "blackbirds" frequented the banks of Doe Run, especially in spring. In April 1960 I saw a number of grackles foraging among mats of aquatic vegetation stranded on riparian roots by receding water levels. Barn swallows, *Hirundo erythrogaster* Boddaert, were also frequently seen along the stream, and on 2 occasions were watched feeding on emerging mayflies near Station III. They nested

inside the culverts at that station. Riggs (1947) saw purple martins, *Progne subis* (L.), feeding on emerging mayflies on Shafer Lake, Indiana, and Burks (1953) noted that birds sometimes fed heavily on mayflies at times of peak emergences. I also saw robins, *Turdus migratorius* (L.), feeding on adult caddisflies and stoneflies along the banks of Doe Run in 1960.

Muskrat, *Ondatra zibethicus* (L.), inhabited bank dens throughout Doe Run except in the area sporadically flooded by the Ohio River. Near Dam 2 I found old stumps and cuttings undoubtedly produced by beaver, *Castor canadensis* Kuhl, but no recent signs were observed. The species must have been present on Doe Run within the last 25 years or so, judging from the condition of the cuttings.

The presence of raccoon, *Procyon lotor* (L.), and mink, *Mustella vison* Schreber, has already been noted. Tracks of raccoon were especially abundant along Doe Run, and numerous crushed exoskeletons of *Cambarus* and *Orconectes* on the tops of stones from Station II to Station IV attested to its predation on aquatic animals.

Bats were seen often in daytime flying slowly along Doe Run a few feet above the water. A single specimen, *Lasius borealis* (Mueller), was shot near Station III and its stomach contained remains of various dipterans, a few mayflies, and a single adult of *Paragnetina*.

Food Relations of the Fauna

It is apparent from the abundance of aquatic animals in Doe Run, the thick and persistent stands of macrophytic vegetation, and the overall abundance of algae, that the stream presents a highly productive system. Actual estimates of productivity were beyond the scope of this study, but some discussion of the food relations of animals may give insight into the trophic structure. Odum (1959), Darnell (1961), Ivlev (1961), and others have pointed out that animals in nature rarely comply with the conceptual "trophic levels" prevalent in some current ecological thinking, but that behavior and relative abundance of

animals resembles more the "food web" concepts of workers prior to publication of the trophic concepts by Lindeman (1942). It is increasingly evident that local variations in habitats determine the position of a given species in a trophic system. Such variations are reflected in differential availabilities of food, seasonal changes in foods in a given habitat, and changes in food habits of an animal with changes in age, size, or physiological condition (Brown, 1961a; Darnell, 1961), and a myriad of other factors. In addition, there are pronounced specific differences between kinds of animals in a given habitat. It must be pointed out that I use the term trophic in the nutritional sense which, although it is an energy transfer, it appears to involve many levels of utilization and transfer, some of which are little understood.

Invertebrates

Passive feeders.—Mueller (1955) separated stream animals into passive feeders and active feeders, the former depending on the amounts of food extant in the drifting state, and the latter predominating in small streams usually devoid of such "net plankton." Filter- and detritus-feeding organisms are generally abundant in turbid streams on solid substrates.

Hydropsyche betteni fed mostly on the diatom *Melosira* which was abundant in guts of those larvae from Station III in summer and winter. Ten animals taken in winter also contained *Cocconeis*, *Gomphonema*, several species of *Navicula*, and a few trichomes of *Phormidium* or *Oscillatoria*, all of which were rare or occurred singly. Particulate detritus was a scarce component in larvae from both periods, and sand was scarce in winter animals but absent to rare in summer. Five larvae from Station II, collected in June 1960, contained essentially the same things as those from Station III in September. The only exception was the presence of a scarce component of *Fissidens* from Station II, and that was considered detrital.

Analyses of 17 larvae of *Cheumatopsyche* sp. from Station III in winter and 4 ob-

tained in September indicated that foods were similar to those in *Hydropsyche*. However, particulate detritus was relatively more abundant than *Melosira* both in summer and winter. Sand was classed as abundant in winter, but was absent in September.

Digestive tracts of 13 *Simulium* sp. from Station III in June 1960 contained finely divided detrital materials, but 1 individual also contained a small *Navicula*.

Nymphs of the mayfly genus *Isonychia* feed passively much of the time by using their setiferous front legs as a funnel for capture of stream-drifted diatoms and detritus (Clemens, 1917). Nymphs of *Isonychia sadleri*? from Doe Run had food habits similar to *Hydropsyche*. Fourteen *Isonychia* contained *Melosira*, detritus, and sand, in order of decreasing abundance; 2 contained fragments of insects, possibly exuviae of *Baetis*? and an unidentified mayfly (see Leonard and Leonard, 1962), and 3 contained blue-green algae and some *Gongrosira*. In the latter group there was a considerable inclusion of marly sediment (estimated 50%). The nymphs were collected in September 1960.

Active feeders.—Oligochaetes feed largely on organic components of the substrate into which they burrow, passing large quantities of material through their digestive tracts. A number of *Nais* sp. and *Ophidonais serpentina* from Station IV contained no identifiable materials other than sand and particulate detritus in their guts. Intestines of *Nais* taken from *Myriophyllum* plants rather than from the substrate were filled with diatoms of many genera and a large proportion of epidermal tissue of the milfoil. The guts of *Limnodrilus hoffmeisteri* from beds of decomposing leaves near Station IV in October 1960 were filled with leaf particles, sand, and a few frustules of diatoms.

Walker (1962) reported the gut contents of 30 *Asellus bivittatus*. Her data indicated that the species feeds primarily on epiphytic diatoms associated with *Fissidens*, but she also found a few fragments of blue-green algae and some partially digested

TABLE 10.—PERCENTAGE FREQUENCY OF ITEMS FOUND IN DIGESTIVE TRACTS OF 57 *GAMMARUS MINUS* AND 66 *G. BOUSFIELDI* FROM STATION I, DOE RUN, MEADE COUNTY, KENTUCKY, SEPTEMBER 1960

Item(s)	<i>G. minus</i>	<i>G. bousfieldi</i>
Blue-green algae	3.5	28.8
Diatoms	45.6	10.6
<i>Nasturtium officinale</i>		
Epidermis	1.8(?)	63.6
Root hairs	—	43.9
<i>Fissidens julianus</i>	22.8	4.5
Particulate detritus	42.1	75.8
Animal remains	1.8	10.6
Amorphous material	89.5	28.8
Sand	47.4	80.3

remains of *Fissidens*. Verification of the last-mentioned material indicates that about 10 per cent of the food consists of epidermis of *Fissidens*. Although some unidentifiable detrital material was present, the amount was not significant.

Twenty individuals of *Asellus bivittatus* from Station V in September 1960 fed almost entirely on small leaf fragments and particulate detritus. One individual contained fragments of isopod exuviae, presumably of its own species. Specimens in laboratory aquaria fed readily on exuviae of their fellows, on commercial fish foods, on debris at the bottom, and on *Vaucheria*, but made no attempts to feed on scraps of meat or on dead invertebrates placed in the tanks.

Digestive tracts of 31 *Lirceus fontinalis* analyzed on various occasions indicated that this species is omnivorous. Detrital materials such as small leaf particles, pieces of grass, and undetermined particles were abundant in all animals examined. In addition, there were large numbers of diatoms in 18 individuals from the mainstream. Filamentous green algae (*Oedogonium*?) were found in 3 specimens from 7-Springs Branch, and blue-green algae were in 2 of 5 individuals from Station IV in September 1960. Fragments of undetermined arthropods, a small portion of an oligochaete, and head capsules of two tendipedids were in a large *Lirceus* from another spring-fed tributary to Doe Run. In the laboratory,

the isopod fed indiscriminately on most organic materials placed in the tank.

Somewhat more detailed studies were made of the foods of the amphipods (*Gammarus* spp.) in Doe Run in connection with other research on those animals (Table 10). Usually, *G. bousfieldi* was somewhat more omnivorous than *G. minus*, and the foods of the former are those most often in the pools where the amphipod lived (Cole and Minckley, 1961). The most frequent items, sand and particulate detritus, indicate considerable grazing on the open bottoms of pools, which was substantiated by field and laboratory observations. Watercress also was utilized heavily, and quantitatively was the most abundant item.

Gammarus minus fed on an amazingly small amount of *Fissidens* and diatoms considering its habitat in dense mosses of the channel. It apparently fed mostly on the undifferentiated, semiflocculent materials collected beneath the moss beds through its own decomposition, and through deposition of feces by the extremely abundant *Asellus bivittatus*. The great numbers of separated diatom frustules in the digestive tracts of *G. minus*, with no evidence of chlorophyll, may have resulted from previous passage of the diatoms through the digestive tract of *Asellus* and secondary ingestion by the amphipod. Brown (1961a) noted a similar situation in certain habitats of England, where defecation by great numbers of *Asellus aquaticus* L. supplied a rich source of detrital material for a mayfly (*Chloeon dipterum*).

Of the crayfishes of Doe Run, *Cambarus bartoni* was seen feeding on various kinds of vegetation near Station I, on smaller crayfish, on isopods (in laboratory aquaria), on detritus, and on fishes (Minckley and Craddock, 1961; Minckley, *et al.*, 1963). *Orconectes rusticus* was apparently more saprophagous, feeding on dead animals of various kinds, but also on algae and other plant materials. Of special interest was the picking up and rapid rotating of snails (*Goniobasis*) by *O. rusticus*, and to a lesser extent by *C. bartoni*, with apparent grazing of the algae on its shell.

Tipula nobilis? from Stations I and II fed almost entirely on *Fissidens*. That was the only food in 11 individuals collected at Station I in June 1960, but 3 specimens from that station in February 1960 and 2 from Station II in September 1960 contained appreciable amounts of detritus and sand (estimated 10% by volume) in addition to the moss.

Among the mayflies, 10 *Ephemerella subvaria* utilized basically the same foods as *Baetis vagans*. Both fed mostly on epilithic algae and diatoms, with some detritus. *E. subvaria* sometimes contained a few fragments of *Fissidens* or *Myriophyllum* at Station II where those plants were abundant. Summer samples of 17 *Baetis* from Station III contained a much larger proportion of detrital material than those collected in February 1960. Perhaps the higher discharges in winter remove small detrital films from stones or riffles and forces greater utilization of algae (see Jones, 1951). Brown (1961a), studying *Baetis rhodani* in streams of Great Britain, found an excellent correlation between foods available and gut contents at a given season. That species fed largely on detritus, supplemented by algae when available. At Stations III and IV in Doe Run, the gut contents of *B. vagans* were marly, and included *Gongrosira*, *Phormidium*, various diatoms, and some Chantrelle stages of a red alga (probably *Lemanea*). *Stenonema* sp., at Station IV in September 1960, fed almost entirely on diatoms and amorphous detrital materials, with sand being the most abundant item. A few trichomes of a blue-green alga were found in an individual from Station III.

Four damselfly naids, *Agrion maculatum*?, from Station II contained parts of *Asellus bivittatus*, *Gammarus* sp., an unidentified mayfly, 2 elmids larvae, and numerous tendipedids.

The large, active stonefly, *Paragnetina media*, was totally predaceous, any vegetation present having been ingested previously by prey species. No apparent differences exist in the foods of individuals collected in different seasons, with the

exception that the guts of 3 collected in February were empty, whereas all others had their entire guts filled. *Baetis* was the most important single food item, followed by tendipedids, smaller stoneflies, and *Simulium*. Of course, a large proportion of the animal material in a given gut could not be positively identified, but appeared to be arthropod material. Analyses of the guts of 12 *Isogenus subvarians* taken in September and 4 in February indicated that the foods were similar to those of *Paragnetina*. Dipterans, however, were much more numerous than *Baetis* as the identified component of the food of *Isogenus*, probably reflecting its occupancy of a habitat more lateral than the midchannel habitat of *Paragnetina*. There was a large amount of particulate detritus in some *I. subvarians* from September, which may have been ingested intentionally; leaf particles were larger than those usually found.

Surface-feeding gerrids were seen preying on springtails (*Podura*), a *Gerris* was seen attacking and eating a *Microvelia*, but for the most part they fed on terrestrial forms that fell into the water and were transported along by the current (Pennak, 1953). Most Hemiptera in Doe Run are predaceous. On one occasion *Gerris* sp. was observed trying to capture free-swimming amphipods near Station III, but none was successful. Amphipods trapped in the surface film after fish-seining operations, however, were quickly captured by water striders.

Two of the "active feeding" caddisflies of Doe Run, *Agraylea multiplicata* and *Pychnopsyche* sp., were examined for food relations. *Agraylea* contained large numbers of diatoms of various genera, dominated by the common epiphyte *Cocconeis*. The 16 *Agraylea* were obtained in September 1960 at Station II, and were very small. *Pychnopsyche* was relatively rare in the stream, but 8 individuals were dissected and the guts contained marly, particulate detritus, along with a few diatoms and some trichomes of blue-green algae.

Snails of the genus *Goniobasis* grazed on epilithic algae, diatom slimes, and on thin

mats of blue-green algae. Grazing was particularly heavy on *Chantransia* of *Batrachospermum* near Station I. In the laboratory, *Goniobasis* grazed on higher aquatic plants only when placed in a newly filled aquarium where algal development was minimal; in tanks with significant algal growth the higher plants were rarely eaten. Snails collected at Stations III and IV defecated large numbers of small, oblong, predominately marl pellets when placed in jars.

Foods of Selected Fishes

Seventeen of the more abundant species of fishes were selected for analysis of general food relations because of their consistent occurrence, at least in the lower part of Doe Run.

Stomachs of 10 *Dorosoma cepedianum*, from near Station IV, contained mostly calcareous bottom materials, diatoms, blue-green algae, some *Spirogyra*, and much detrital material. Six shad from Station V contained bottom muds and included tendipedid larvae, oligochaetes, and sparse detritus.

Foods of 23 adult white suckers, 10 from Station II and 13 from near Station III, were mostly crustaceans and insects. Fish from Station II contained about 25 per cent estimated volume of *Myriophyllum*, *Fissidens*, diatoms, and detritus, and those from Station III contained 25 per cent silt, marl, diatoms, and fine detrital material. Crustaceans comprised 28 per cent of the estimated volume, and included mostly *Gammarus bousfieldi* from Station III, but from Station II about one-third was *G. minus* along with a few *Asellus bivitatus*. The remainder of the foods was large dipterans as the most abundant insects, followed by mayfly nymphs and hydropsychid larvae. Other animals were *Goniobasis*, Sphaeriidae, and oligochaetes. Five hog suckers from Station IV contained mostly silt, aquatic insect larvae, and detritus, with the insects being characteristic of the riffle habitat of Doe Run (*Baetis*, *Simulium*, *Paragnetina*, and tendipedids). Stomachs of 5 *Moxostoma breviceps* from near Station IV contained

undifferentiated mud, detritus, tendipedids, *Cladophora*, a few oligochaetes, and some *Stenonema*. Animals made up 50 per cent by volume and plants 25 per cent. Five *Moxostoma erythrurum* from the same area as *M. breviceps* contained mud, detritus, tendipedids, oligochaetes, about 60 sphaeriids, some mayflies and amphipods, and a single *Tipula*.

The stoneroller is the classic example of a feeder on the bottom "ooze" of streams (Kraatz, 1923; Starrett, 1950b), and in Doe Run their foods consisted of diatoms, blue-green algae, and calcareous bottom materials in the 7 fish examined. A few tiny tendipedids were in each of 2 stomachs, and leaf fragments were in 3.

Ten *N. atherinoides* from Station V contained 65 per cent terrestrial insects in summer samples; the remaining foods were tendipedid larvae and mayfly nymphs. Five specimens from Station V in December 1960 contained amphipods, mayflies, and adult caddisflies. Similar foods were noted in specimens from northern Illinois by Forbes and Richardson (1920).

Foods of 17 *N. spilopterus* from Stations III and IV were similar to those reported by Starrett (1950b) in the Des Moines River, Iowa. Five collected at Station IV in June contained substantial amounts of seeds (*Platanus*), terrestrial insects, and a smaller number of aquatic nymphs and larvae (mostly tendipedids). Four from Station III contained 75 per cent trichopterans and 25 per cent mayflies in January 1960, during a period of high discharge. Tendipedids, mayflies, and terrestrial insects were the principal items in the remaining 8 specimens, 4 of which were taken in autumn, and the others in spring.

The foods of 7 bluntnose minnows from Doe Run were similar to those of *Camposotoma*, mostly calcareous bottom material, diatoms, and a few filamentous algal forms such as *Spirogyra* and *Mougeotia*. Foods of 37 *Rhinichthys atratulus*, collected at various times at the 3 upstream stations, consisted of amphipods and isopods (39%), mayfly nymphs (21%), and tendipedids, trichopterans, and oligochaetes combined

TABLE 11.—PERCENTAGE FREQUENCY OF ITEMS FOUND IN STOMACHS OF 22 *LEPOMIS MEGALOTIS* (5 EMPTY), 30 *L. CYANELLUS* (4 EMPTY), AND 20 *L. MACROCHIRUS* (3 EMPTY) FROM STATIONS III AND IV AND BETWEEN THOSE STATIONS, DOE RUN, MEADE COUNTY, KENTUCKY, JUNE 1960-1961

Item	<i>L. megalotis</i>	<i>L. cyanellus</i>	<i>L. macrochirus</i>
Oligochaeta	—	3.3	10.0
Isopoda	9.1	6.6	5.0
Amphipoda	13.6	26.4	5.0
Decapoda	18.2	36.3	—
Ephemeroptera	59.1	19.8	20.0
Odonata	4.5	3.3	—
Plecoptera	4.5	3.3	—
Coleoptera	4.5	3.3	—
Trichoptera	—	3.3	—
Diptera	31.8	6.6	55.0
Gastropoda	4.5	3.3	—
Terrestrial arthropods ¹	22.7	52.8	65.0
Fishes	—	16.5	—
Algae and higher vegetation	—	—	35.0
Unidentified materials	13.6	6.6	15.0

¹ Includes Hymenoptera (ants), Hemiptera (reduviids), Arachnida (spiders), Homoptera (leaf-hoppers), Coleoptera (scarabaeids and carabids), Orthoptera (locustids), and winged dipterans that have larval stages in water (tendipedids, simuliids, and tipulids).

(30%). A number of *Goniobasis* were found in larger fish, along with *Gammarus bousfieldi* as the most common amphipod. Smaller blacknose dace contained a larger proportion of tendipedids and oligochaetes than the larger fish, reflecting somewhat their habitat over soft, silty bottoms. Five creek chubs, ranging from 1.0 to 1.3 inches total length, had guts filled with aphids, collembolans, and mosquito larvae. Larger fish fed on more diverse foods, such as crayfish, trichopterans, tendipedids, *Tipula*, crustaceans, terrestrial arthropods, and a considerable proportion of vegetation. One individual about 8 inches long contained 27 fish eggs and a smaller individual of its own species. Diverse food habits of *S. atomaculatus* have been found elsewhere (Forbes and Richardson, 1920), and are indicated by the extreme plasticity of the species in its tolerance of different environmental conditions.

Stomachs of 9 rock bass contained 95 per cent crayfish by volume. Other animals found were 2 *Notropis atherinoides*? and

a larval *Chauliodes*. A single small rock bass contained 2 grasshoppers (Locustidae) and a *Stenonema*.

Foods of green sunfish, *Lepomis cyanellus*, in Doe Run were compared with those of longear sunfish and bluegill (Table 11). The fish were selected to conform generally in size, locality of collection, and date of collection, and thus should be comparable. The foods of *L. cyanellus* were more diversified than those of the other species, and especially more so than those of the bluegill. Although smaller aquatic organisms made up a consistent part of the diet, crayfish were found in almost 40 per cent of the stomachs, and probably comprised more than the estimated 80 per cent of the volume. The occurrence of fishes in the food is also of note since that food item was not found in the other 2 species. The most frequent items were terrestrial arthropods, which made up 8 per cent of the estimated volume. Bluegills fed heavily on terrestrial invertebrates, which made up more than 60 per cent of the volume, followed by algae and higher vegetation at 25 per cent. Diptera and mayflies made up most of the remaining volume of food in that species, with the former occurring in more than half the stomachs examined. Longear sunfish reflected their habit of frequenting eddying currents by the preponderance of mayflies in their stomachs (55% by volume, mostly *Baetis*), but also fed heavily on terrestrial insects, dipterans, and amphipods (Table 11).

Thirty-six *Etheostoma flabellare* from Station IV were analyzed, and 2 items, *Baetis* and chironomid larvae, made up 99.4 per cent of the total estimated volume (the former was more common at 84.9%). Two of the fish had eaten small stonefly nymphs.

The smallest *Cottus carolinae* in Doe Run subsist mostly on tendipedids. At Station I, food items change gradually to consist mostly of amphipods and isopods in intermediate-sized fish and then to crayfish and fishes in larger adults. At Station IV, food habits followed the availability of

food by utilizing mayfly nymphs in the intermediate size ranges, and then crayfish and fishes as adults. These generalizations are based on data obtained from about 300 sculpins and reported by Minckley, *et al.* (1963).

Variations in stomach contents of *Cottus* in Doe Run, with size of the fish, time of day, locality of capture, and other factors emphasize the survey nature of this study of the other animals of the stream, and should be kept in mind when interpreting data given here. A review of the determination of food habits of fishes was reported by Hynes (1950), and points out factors of error.

Trophic Structure

When estimated percentages of volumes of food in digestive tracts of the animals studied are arranged in "trophic spectra" (Darnell, 1961), there are distinct differences between nutritional relations of invertebrates and fishes (Fig. 28). The invertebrates comprise 2 fairly distinct groups, the primary consumers that depend

on algae, higher plants, and detritus, and a well-defined group that preys on the "primary consumers" and uses very little vegetable material. Among the fishes, only 3 of 17 species whose foods were studied can be considered primary consumers, *Camptostoma anomalum*, *Pimephales notatus*, and *Dorosoma cepedianum*, and each utilized a large amount of detritus in addition to the algae and other vegetation.

The assemblage of animals abundant at Station I is shown in Figure 29. The trophic structure there was relatively simple and self-contained: *Fissidens* and its associated epiphytes were the major producers; *Asellus bivitatus* fed on the epiphytes and *Tipula nobilis*? directly on the *Fissidens*; *Gammarus minus* fed on feces of *A. bivitatus* and on detritus from decomposition of *Fissidens* and associated plants; and *Cottus caroliniae* was the "top carnivore," or secondary consumer. *Gammarus bousfieldi*, on the other hand, was more omnivorous, and somewhat bridged the hiatus between the "detritus feeder" (*G. minus*) and the primary consumers (*Asellus* and *Tipula*).

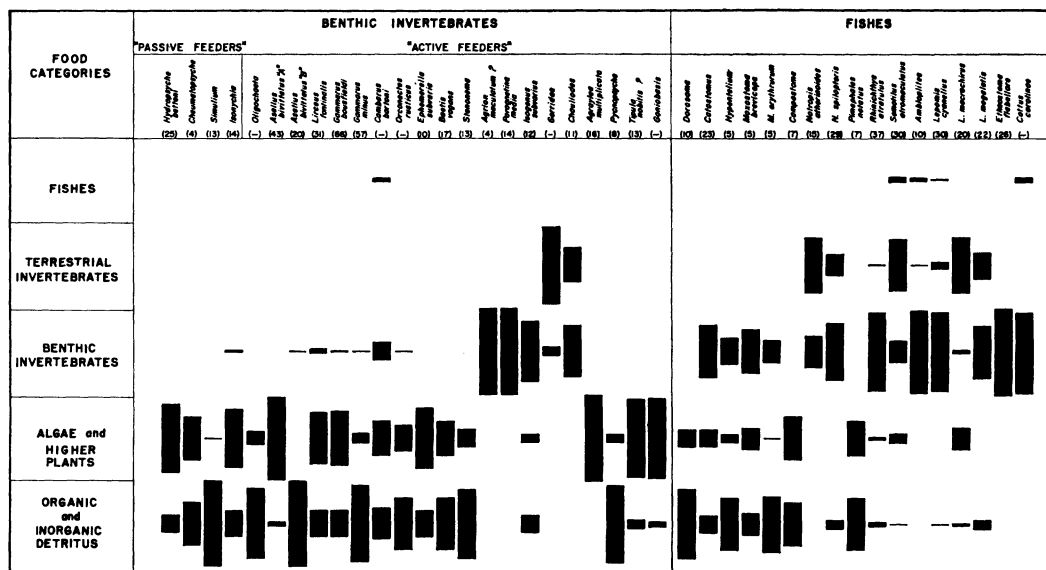


FIG. 28. Trophic spectra of some consumer species from Doe Run, Meade County, Ky. Horizontal bars represent the percentage of a given food category in the digestive tracts of a species. Those species for which the number of specimens used in food analyses is not given are included on the basis of observational data or on data of Walker (1962) and Minckley, *et al.* (1963). *Asellus bivitatus* was separated as "A" from Stations I and II, and "B" from Station V, because of obvious differences in food habits.

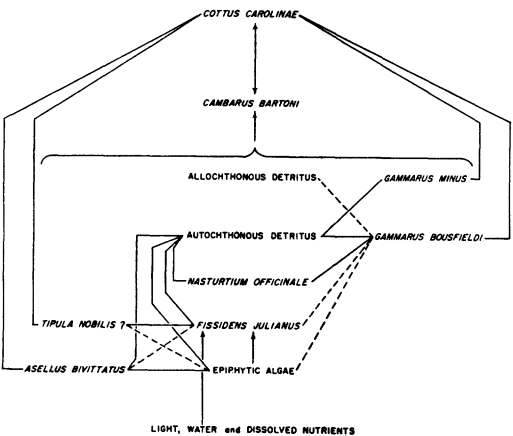


FIG. 29. Food relations of the most abundant species of animals at Station I, Doe Run, Meade County, Ky. (modified from Minckley, *et al.*, 1963).

The large, vagile, aggressive *Cambarus bartoni* encompassed all nutritional levels in its range of food selection.

When the species just discussed are excluded from Figure 28, the trophic structure of more downstream parts of Doe Run is illustrated. Detritus was more important as a food downstream than at Station I and was utilized by almost all consumers not markedly predaceous. The "top carnivores" are well separated from the primary levels when fishes are excluded; however, 10 of

the 17 fishes ate substantial amounts of detrital material, and 2 of the 7 predatory species ate significant amounts of algae in addition to their animal diets.

Examination of the primary foods of predators in Doe Run (Table 12) reveals relatively few prey species, and the most abundant ones bear the brunt of most feeding activity. When the foods of the principal prey species are examined (Fig. 28), it is apparent that detritus is at least as important as primary production in the food chains or webs (see also Muttkowski and Smith, 1929; Jones, 1950, 1951). Animals of "higher" trophic levels in Doe Run generally show no restriction to feeding on primary producers and depend heavily on detrital materials, both autochthonous and allochthonous. When secondary consumers are considered as a whole (including both predatory fishes and invertebrates), there is no distinct point of separation between the primary and secondary levels of nutritional organization. This is especially apparent if terrestrial invertebrates, listed as a separate category in Figure 28, are included as "detritus." Such action probably is justified because their provenance is the same as fallen leaves.

This analysis suffers from lack of specific information on caloric values of detritus,

TABLE 12.—PRIMARY AND SECONDARY COMPONENTS OF THE MAJOR FOOD GROUPS USED BY CONSUMERS IN DOE RUN, MEADE COUNTY, KENTUCKY, BASED ON ANALYSES OF DIGESTIVE TRACTS

Major Food Groups	Primary Components	Secondary Components
Fishes	<i>Notropis</i> spp., <i>Etheostoma flabellare</i>	<i>Rhinichthys atratulus</i> , <i>Semotilus atromaculatus</i> , <i>Cottus caroliniae</i> , fish ova
Terrestrial invertebrates	Ants (Hymenoptera), leaf-hoppers (Homoptera), spiders (Arachnida)	Hemiptera, Coleoptera, Orthoptera, Diptera, "Lumbricus," others
Benthic invertebrates	Tendipedidae, <i>Gammarus minus</i> , <i>G. bousfieldi</i> , <i>Asellus bivittatus</i> , <i>Baetis vagans</i> , <i>Cambarus bartoni</i> (as young), <i>Orconectes rusticus</i>	Oligochaeta, Turbellaria, <i>A. stygius</i> , <i>Lirceus fontinalis</i> , <i>Crangonyx</i> , <i>Stenonema</i> , <i>Ephemerella</i> , <i>Ephemerella</i> , <i>Baetis</i> , <i>Agriion</i> , <i>Paragnetina media</i> , <i>Isogenus subvaria</i> , <i>Hydropsyche</i> , <i>Cheumatopsyche</i> , Elmidae, <i>Laccophilus</i> , <i>Tipula nobilis?</i> , <i>Atherix</i> , <i>Simulium</i> , <i>Antocha</i> , <i>Goniobasis</i> , Sphaeriidae, others
Algae and higher plants	<i>Diatoms</i> , <i>Vaucheria</i> , <i>Fissidens julianus</i> , <i>Nasturtium</i> (?)	<i>Cladophora</i> , <i>Gongrosira</i> , Cyanophyta, <i>Ulothrix</i> , other algae, <i>Myriophyllum</i> , <i>Nasturtium</i> (?)
Detritus	Autochthonous: Feces of invertebrates Allochthonous: fallen leaves of riparian trees	Drifted <i>Fissidens</i> (downstream), drifted <i>Myriophyllum</i> , drifted <i>Nasturtium</i> , algal materials(?) Humus, "mud," inorganic materials

the small numbers of animals examined, and information on specific food relations of tendipedids. On the basis of published reports and cursory examination of the relative abundance of certain groups of these animals it appears that detritus-feeding species make up major parts of their numbers in Doe Run. This is borne out by the preponderance of species of the tendipedid subfamilies Tendipedinae and Hydrobaeninae that are predominantly detritus feeders and phytophagous (Leathers, 1922).

The detrital component of food of stream animals is a heterogeneous mixture of allochthonous and autochthonous debris, primarily of vegetable origin. Generally, detritus is an amorphous complex formed by the decomposition of plants that accumulates in interstices of the stream bed such as in gravels or in beds of aquatic vegetation (Jones, 1950). In streams such as Doe Run that flow through wooded areas of temperate zones, fallen leaves contribute the greatest mass of detrital material (Jones, 1951; Hynes, 1961). As floating leaves become saturated they settle in eddies and pools along the stream course, or form "leaf packets" (Badcock, 1954) against obstructions in riffles. The distinction between thoroughly digested plant foods and true detrital materials is not an easy one, but the use of copper sulfate to fix chlorophyll materially aids in the final decision. Also, collections of food materials from the stream may be used as points of reference. The presence of finely divided "grit" also seems to be an indicator of a true, amorphous detritus in the diet of an animal (Jones, 1950).

Brown (1961a) recently reviewed the importance of detritus to aquatic invertebrates (principally mayflies), and noted that for much of the year detritus may be composed of crude fibers and inorganic particles that may be indigestible by most species (see also Birch and Clark, 1953). Jones (1950) noted the high proportion of cellulose and "valueless" mineral matter in detritus, and remarked ". . . it would not seem to form a nourishing diet . . ." and "Insects feeding upon it [detritus] have

very capacious alimentary canals, feed continually and yet may display slow growth." Teal (1957) found that larval *Anatopynia* (Diptera) feeding on vegetable detritus lost considerable weight, indicating low conversion of the material to a usable form. Brown (1960) showed that algal foods were more thoroughly digested than vegetable detritus by the mayfly *Chloeon dipterum*, and indicated that more caloric value was derived from the former. However, in a later paper, Brown (1961b) indicated that algae required chewing and the expending of energy by the insect, whereas small-particle or amorphous detritus was merely brushed up by the mouthparts and passed directly into the gut.

Darnell (1961) pointed out that much detrital material ingested by fishes or other animals includes a large proportion of protoplasm in the form of bacteria (see also ZoBell and Feltham, 1938, 1942; Gneri and Angelescu, 1951). Probably much of the food value of detritus is in the form of bacterial protoplasm and large numbers of other microorganisms such as ciliate protozoans. This was noted by Minckley, *et al.* (1963) in their designation of "detrital materials (allochthonous, autochthonous, and contained food chains)" in the food webs of *Cottus carolinae* in Doe Run. Hynes (1961), furthermore, found the abundance of animals in a small stream in Wales related to the abundance of detritus (fallen leaves), with algae-feeding species occurring in summer and detritus-feeding species developing rapidly in winter (see also Jones, 1951). Unfortunately, my data are not precise enough to permit such an analysis for Doe Run.

It is apparent that accumulation of organic detrital materials in streams increases downstream from the source (Odum, 1956, 1957a, b), both through the development of animals and plants in the stream itself, and through continual accumulation of leaves, twigs, and other terrestrial materials. Often, accumulations of leaves in Doe Run were sufficient to block riffles in the downstream areas, and to cause oxygen deficits in large pools at night or on cloudy days in spite of

the relatively swift nature of the stream. Leaf accumulations often have been found to cause "black waters" in streams (Schneller, 1955; Slack, 1955; Larimore, *et al.*, 1959), and although such situations are extreme in that they may destroy the fauna through deoxygenation or other means, they serve to point out the magnitude of accumulations that may occur. It is logical that the rich source of organic material so provided would be utilized by animals, as it apparently is, and that downstream populations in streams would tend to be much more dependent on that source of food than animals of headwater or spring situations. It follows, therefore, that the lower reaches of creeks and rivers are essentially in a state of trophic unbalance, unless the total allochthonous import (Nelson and Scott, 1962) is considered in the stream's economy, and as a part of the ecosystem. This condition develops with physiographic and biotic succession in streams toward a base level, both of which cause the flowing waters to tend more and more toward a lentic situation. It is not appropriate to consider all detrital materials sedimented in the lower parts of streams as being placed in a condition "below the active metabolic level" (Odum, 1956) of the system. In Doe Run at least, these deposits are actively moved into and through the biota on the macroinvertebrate and vertebrate levels, in addition to the microorganismal utilizations. Heterotrophic bacteria and associated protozoans probably form an intermediate level of utilization between primary producers (both auto- and allochthonous) and the nutrition of the macrobiota (Darnell, 1961; Nielsen, 1962).

Gradients in trophic structure in Doe Run, from a more or less autotrophic type to a more heterotrophic type, also appear when analyses are made of animals living on riffles and in the adjacent pool, on animals living on the sides of pools and those living in the center where sedimentation of debris is more pronounced, and from the swift "oligotrophic" center of a riffle to its quieter, more "eutrophic" sides. These

systems offer a great variety of orders of magnitude in the amount and intensity of "trophic unbalance"—differences seem greatest when comparing riffle and pool, and least when comparing side and center of pool. Therefore, they illustrate some of the complex interrelations of stream ecology, and merit further research and interpretation.

SYNTHESIS

Concepts derived from stream studies contrast with those formed from study of successional, community, or other level of integration phenomena that occur elsewhere because of the prevalence of geological influence in flowing water as opposed to pronounced biotic effects in lakes (Forbes, 1925) and in most terrestrial situations (Allee, *et al.*, 1955). Streams are unique, open-ended systems (Thieneman, 1953). They pass from youth, through maturity, to old age or base level at a given point in their length, if sufficient time is allowed (Adams, 1901). They grow by upstream erosion, and ultimately produce a peneplain totally drained by a stream near base level (Nelson and Scott, 1962). A concept of a continuum of "youthful" stream conditions is tenable, however, notwithstanding ultimate peneplanation of a given area, because of the sporadic elevation of land masses that would cause a persistence of the habitat type if spring waters or runoff were present. Thus the idea that the downstream parts of rivers are the only places where stream climaxes can occur (Shelford, 1911a, 1913; Shelford, in Gersbacher, 1937; Odum, 1956, 1957a; Nelson and Scott, 1962) may be seriously questioned, especially since there are large numbers of plants and animals that display adaptations for a riffle habitat (Gessner, 1955, 1959; Butcher, 1933; Hora, 1930; Nielsen, 1950a; many others). A riffle is in essence a short section of "youthful" stream even in a watercourse that is mostly at base level.

Climaxes in the Vegetation of Streams

The concept of climax in terrestrial situations apparently has been interpreted in

different ways by different investigators (Whittaker, 1956; Selleck, 1960), and in aquatic habitats the presence of climax vegetation has been debated (Eddy, 1925, 1934; Shelford and Eddy, 1939; Blum, 1956b, *et seq.*; and others). If one accepts the monoclimate approach, with reservations as outlined by Oosting (1953), that is, with a preclimax and a postclimax, one on each side of a given climatic area, the vegetation of a lake could be considered as one or the other of these, as a hydrosere, or perhaps most logically, as a subclimax. Streams are influenced by the climax vegetation of the regions through which they pass (Margalef, 1960), and have innate chemical and biological differences not only along their individual courses, but from stream to stream, even though their basic physical characteristics may be similar (Leopold, 1962).

Whether the relatively permanent assemblages of benthic algae and higher plants in streams can be considered "climax" is debatable if one adheres to some implications of the term as it applies to terrestrial vegetation (Blum, 1956b, 1960). It may seem more realistic to consider these assemblages in the same perspective as a perpetuated disclimax, that is, as representing a set of communities adapted in such a manner that they can quickly recover from chronic and severe depletion as soon as favorable conditions recur, whereas the true climax vegetation is suppressed by some decimating factor. The use of the term disclimax, however, necessitates recognition of a climax vegetation, and such a single, specific ecological stage may not exist in flowing waters. Also, the definition of the term climax implies a successional sequence of vegetation or events that many times do not occur in streams. The first colonist of a given substrate in a stream often maintains its dominance until a major change occurs (Blum, 1956b). Hence, the problem lies in whether or not a "climate" occurs in flowing waters, and in the definition of climax that implies arriving at a terminus through succession. This problem

was not solved by the formal, latinized designations of associations or communities of aquatic plants proposed by Margalef (1958, 1960) and others, even though the communities appear extraregional in nature.

I feel that much disagreement among investigators lies in the fact that streams are biological and chemical individuals. There is an absence of specific knowledge of physics and chemistry of streams in which plant communities occur, and a general failure to recognize that the "weather" in a creek or river, that is, the variations of chemical and physical conditions from day to day, certainly averages out to a climate in a manner similar to meteorological data from terrestrial stations. Thus, streams have a climate governed by the origin of their water, the area through which they flow, biological activities occurring in them, and the meteorological climate of the region through which they pass. These factors may be compared, respectively, with the influence of mountain ranges on provenance of air masses to a terrestrial region, the influences of local topography on temperatures and rainfall, the influence of biological activity in modifying the chemical composition of the air, and the influences of the meteorological climates that surround the region. Current is a major climatic factor in streams, acting in a manner similar to rainfall on land in influencing edaphic characteristics.

An aquatic climate is not proposed without precedent (Shelford and Eddy, 1929; Clements and Shelford, 1939; Burton and Odum, 1945; and others) and appears to differ from that of terrestrial situations only in the medium involved and the methods used in measuring its different components. This is not to say that terrestrial climates do not influence aquatic ones, and vice versa, but the tendency for water to resist rapid change in temperature, for example, makes it considerably different from air, and the presence of nutrients in the medium surrounding an aquatic organism, makes water an even more different kind of place in which to live. A major influence of the terrestrial climate on that of streams is the

occurrence of abrupt, torrential rainfall, which allows full expression of the climactic nature of stream climate in the occurrence of floods.

Succession in streams is, however, more difficult to demonstrate than climate, mostly because of seasonal periodicities of various species (Transeau, 1913) and because of catastrophic events in the stream. However, many successional series may be detected if communities are examined in detail (Eddy, 1925). The realization of succession in streams often is a community that lasts not more than a season (Blum, 1956b), but which recurs time after time indicating attainment of some kind of climax condition in response to the physical properties of the habitat. Communities that are relatively permanent in time often are found in large springs. Examples of this condition are the established or seasonally prominent *Cladophora*, higher plants, and calcareous algae in Doe Run.

Because stream climates tend to be individualistic, they should be approached from stream type rather than from regional aspect (Whitford, 1960a). Equivalent habitats in streams support ecologically equivalent communities of algae and higher plants, and in this respect are comparable to terrestrial situations. Regional relations are observed in that plant communities in widely separated localities consist of the same species, or at least genera or families, and there is a tendency for rapid appearance of "characteristic" forms where suitable climatic or microclimatic conditions prevail (Whitford, 1960a). Springs similar to Doe Run should, and apparently do, have similar communities of plants, and these may represent certain subclimaxes or climaxes in the extant environments. Therefore, when one accepts the concept of climate in flowing waters he may seek the climax vegetational condition of a stream and investigate succession in that habitat. Linear "succession" in streams illustrates the above arguments very well, since it results mostly from the response of different plants or animals to the linearity of

change in the averages of various chemical and physical factors.

A physiographic approach to the study of stream organisms was first used by Shelford (1911a), and in his early work (Shelford, 1913) considered riffle communities as "quasi-climaxes," generally equivalent to lichen community colonizing a granite boulder as a climax. However, later on, Shelford (in Gersbacher, 1937) dismissed the riffle as a possible climax community, and considered only larger, base-level streams or relatively stable pools of smaller streams in that category. If I adhere to this concept, my arguments about the presence of smaller climaxes on riffles and the reassessment of Shelford's physiographic approaches to stream ecology are to no avail. However, since streams are an integral portion of the land masses of the earth, and continual or periodic rejuvenation of those land masses cause a continuum of erosion cycles, it seems illogical to assume that riffles have ever become nonexistent. The concept of climax ecological groupings, specifically those organisms morphologically suited for existence in swift water, should immediately follow recognition of the continual presence of streams per se.

The categorical dismissal of the importance of physiographic histories in interpretation of stream succession and climaxes by Gersbacher (1937) must have resulted from a lack of recognition of the primary dichotomy between lakes and streams, and was an attempt to equate the two. I feel also that the outline of stream succession, as given by Margalef (1960) and suggested by Clements and Shelford (1939), is unacceptable in the sense that it includes a final transition to a terrestrial community. Conversion of a given stream to dry land occurs, to be sure, but is usually abrupt in a geological sense, and most often is a function of major climatic change or modification by man, rather than one of vegetational succession in the stream itself. However, this statement does not apply wholly to headwater streams fed by surface runoff that may show fluctuant or sporadic cycles of flow and intermittency. Allorge

(1921) gave the only example of vegetational succession from streams to dry land that I have found in the literature.

Assemblages of Aquatic Invertebrates

Armitage (1961) pointed out the fluctuation in populations of riffle organisms and the extreme variation of riffle habitats in streams, and concluded that rather than there being discrete communities, “. . . it seems more likely that stream habitat consists of a variety of ecological factors interacting in numerous and complex ways to produce many environmental gradients along which species are distributed.” His conclusion may be true regarding the fauna of riffles of the swift, turbulent Firehole River in which he worked, but I do not see where its acceptance necessitates disregard of natural assemblages of organisms that exist in streams where pool-riffle development predominates. The 3 strata of habitation in a riffle (Shelford, 1913; Pearse, 1926)—the surface of the stones in current, between the stones in open interstices, and the sediment-filled interstices below the influence of current—may, however, be considered the basic habitats from which communities of riffle invertebrates may be described.

Fluctuations or sporadic changes in invertebrate populations resulting from local variations in environment (Moffett, 1936; Mottley, *et al.*, 1939; Muttkowski, 1929; Badcock, 1954b; Armitage, 1958, 1961) in response to diverse life cycles (Hynes, 1961; Tebo and Hassler, 1961; and others) demonstrate the dynamic nature of the fauna and the habitat rather than a total lack of community structure. I can see no basic differences between changes in the numbers or kinds of animals on a given riffle, in response to receding water levels or to life cycles of the constituent species, and changes in a decomposing log with onset of summer desiccation, and realization of life cycles of the animals present. Likewise, the changes in composition of fauna from the sides to the center of a riffle (Needham and Usinger, 1956) are no greater than those found while passing

around a hill and observing changes in vegetation or fauna resulting from differences in exposure and variation in amounts of insolation or rainfall.

My criteria for designating an assemblage of stream organisms as given above were more or less physical because I attempted to discern a sharp break in a given system, then to examine it to find whether biological groupings in one area did not occur in the other, or vice versa. Although this approach may seem subjective in first analysis (Andrewartha and Birch, 1954), there are rather definite boundaries to habitats in streams that are related to actual differences in fluid masses such as hydraulic jumps at the foot of riffles, obvious areas of shear between current and eddy, and the obvious “spillage line” at the point where water of a pool drops suddenly to the riffle downstream.

I consider 3 basic assemblages of benthic invertebrates in Doe Run, 2 of which have long been recognized as a “pool fauna” and a “riffle fauna,” and the third as the “spring fauna” defined below:

(1) The animals of swift, unvegetated riffles downstream from Station II, including the marl riffles at Stations III and IV and the rubble riffles at Station V, constitute a relatively cohesive unit (Tables 6–7). The assemblage was characterized by a preponderance of aquatic stages of mayflies, caddisflies, dipterans, and stoneflies. Many animals living in this habitat are passive feeders (Mueller, 1955) in the sense that they depend on current to bring their provisions. This grouping corresponds generally to the “*Cladophora-Hydropsyche-Etheostominae*” community of Shelford, which he considered as essentially the only “. . . type of rapid water bottom community at low attitude in middle North America” (Shelford and Eddy, 1929).

(2) The second assemblage included the animals of vegetated or unvegetated, sand- or silt-sand-bottomed pools. Gersbacher (1937) concluded that there was a single major pool community characterized by chironomid dipterans in small streams, and

by certain mollusks, the mayfly genus *Hexagenia*, and oligochaetes (*Limnodrilus*) in large creeks and small rivers. In Doe Run, pool communities were similarly dominated by dipterans, oligochaetes, and gastropods, except in *Nasturtium* beds at Station I (Table 8).

(3) The third assemblage was that of the spring, comprising a fauna dominated by crustaceans in *Fissidens* (Table 6). This major assemblage caused modification of lateral and intermingled patches of incipient communities more similar to those downstream to the extent that they were sometimes obscured, even at Station II. Such situations may be typical of cool limestone springs, with a fauna limited in numbers of species but characterized by a large number of individuals (Odum, 1957a, b). Insect larvae are generally rare at the sources of springs (Berner, 1950; Sloan, 1956), and the absence of that group alone is significant.

I do not mean to imply a lack of transitional habitat between pool and riffle, nor that all animals inhabiting riffles are present on the surface of the substrate and under influence of currents. On a given riffle there are flattened or otherwise modified animals that inhabit the tops of stones, the interstices of the bottom where a flow of water persists, and beneath stones or in sediment-filled interstices (Shelford, 1913). These last-mentioned organisms may include forms common in softer bottoms of pools. Also included on riffles are animals living in special habitats such as the leaf packets colonized by *Lirceus* and other invertebrates in Doe Run, or in temporary deposits downstream from obstructions which may be colonized by a multitude of animals from pools and riffles alike. These special or transitory habitats technically are not part of the riffle assemblage, but represent peripheral environments that occur because of the linear nature of flow in streams. Areas lateral to riffles or to the main center of velocity may be considered as transition zones between riffle and pool, but are under relative control of the riffle because of fluctuations in water level and

current, and usually are inhabited by a fauna similar in most of its constituents to that of the main riffle.

Such transitory habitats occurred in the small riffles lateral to marl and rubble riffles at Stations III, IV, and V. Here, there was a general increase in the relative abundance of animals typical of pool situations, and a shift in the proportion of active-feeding riffle animals such as mayfly nymphs, when compared with the passive-feeding trichopteran larvae. In spite of these changes, the areas lateral to the main riffle channels are obviously "riffle" when their faunal composition is compared with other habitats.

Pools comprise 2 distinct habitats for benthic invertebrates, the surface of the substrate and the area beneath that surface. Pool animals show fewer adaptations in their morphology, habits, and overall responses to their environment than animals characteristic of riffles. This is indicated by the greater numbers and diversity of species that reach their greatest abundance in pools but can also inhabit certain parts of riffles. The morphology (Dodds and Hisaw, 1924a *et seq.*; Hora, 1930; Nielsen, 1950a) and an actual physiological need of many riffle animals for current (Wu, 1931; Ruttner, 1953; and others) restricts them to that habitat. In many forms the passive-feeding adaptations, such as those found in net-building caddisflies, dictates their distribution to areas where current will supply food (Mueller, 1955). Apparently, few pool animals suffer from these restrictions. Moreover, there is evidence that basal metabolic rates of riffle-inhabiting mayflies (*Baetis*) are several times greater than that of mayflies living in ponds or pools (Fox and Simmonds, 1933), and that the food intake of the former is proportionately greater.

Pool situations at Station II and downstream were remarkably consistent in the overall composition of their fauna, in spite of the specific bottom type or the presence or absence of vegetation. Vegetation in pools, however, provides more surface area for habitation by animals (Krecker, 1939;

Rosine, 1955), protection from predation, and food for many invertebrates, either directly (Frohne, 1956) or indirectly by the development of periphyton (Young, 1945; Rosine, 1955). Vegetation in pools augments a lentic tendency already present by physically slowing the water, and contributes to eutrophication of the habitat by accumulation of autochthonous and allochthonous debris. Vegetation in streams and lakes rarely tends to alter the composition of the fauna (except, possibly, in *Nasturtium* beds of Doe Run), but almost invariably results in increased biomass (Hynes, 1960). *Nasturtium* beds at Station I and open pools at Station II were very similar in faunal composition, but differed from pool habitats downstream mostly in abundance of *Gammarus bousfieldi*. I consider these variations from the basic pool assemblages to be produced by influence of the special fauna of the spring.

All the swift-water areas at Station II and upstream were dominated by the closely matted *Fissidens*, and this, in effect, produced a pool environment in the midst of riffles. Evidence of this was obtained by introducing small amounts of fluorescein into the moss beds with a pipette and observing the time required for the dye to disappear. Dye was visible issuing from smooth moss beds upstream from Dam 1 for from 3 to 30 minutes when velocities over the beds ranged from 2 to 4 ft/sec. After the dye had apparently dissipated, pressure applied to the area forced some residual dye from the deeper parts of the beds.

The animals prevalent in the *Fissidens* community, *Asellus bivittatus* and *Gammarus minus*, were not adapted to a riffle environment, but rather to the close-spaced, quiet habitat inside the protective upper layer of moss. Conditions for large populations were enhanced by the great surface area of the moss, the protection offered, and by the abundant epiphytes and detritus.

Unvegetated riffles at Stations I and II obviously were part of the *Fissidens* or spring assemblage of Doe Run on the basis

of their faunal dominants. Because of the very large numbers of animals in the *Fissidens*, these large populations must have influenced adjacent, smaller habitats, especially when maximal amounts of vegetation were present. Animals characteristic of downstream riffles, however, formed a more significant part of the fauna of unvegetated riffles than of vegetated riffles at Stations I and II. If the crustaceans were extirpated, the faunal composition on riffles upstream would approximate that of the downstream areas (with the exception of mayflies at Station I). *Myriophyllum* beds at Station II, whose intermediate character has been stressed, somewhat bridge the gap between assemblages with faunal constituents of both riffle and pool and the crustaceans of upstream habitats.

The continuity of these communities in time and space is maintained by rate of flow, which depends on discharge. Silt deposits on riffles ultimately are removed by moving waters and deposited in pools. Maintenance of longitudinal patterns of distribution of animals in Doe Run was effected by the presence of suitable habitat, *Fissidens*, for those species characteristic of the spring. Also, because of the linearity in the system, those species were found in reduced numbers downstream primarily as a function of drift during increased discharge. Depletion of invertebrate populations in upstream areas by flood or by innate drifting is rectified by movement upstream, as in *Gammarus bousfieldi* (Minckley, 1963) and *Goniobasis*, from the mill ponds and other pools (Beauchamp, 1932; Dendy, 1944), and by upstream flight of egg-laden females of aquatic insects in response to down-valley winds or other factors (Roos, 1957). Larvae and nymphs in upstream areas must become somewhat crowded for space, and drift of these animals is presumably a mode of preventing or reducing competition, and a means of allowing the animals to disperse downstream into all areas suitable for their development (Mueller, 1954). This was substantiated by Waters (1961) who reported that the drift of animals with 2 or

more generations per year in certain Minnesota streams was correlated directly with their standing crops, and he proposed the measurement of stream drift as a new approach to estimating the productivity of streams (Waters, 1962).

Development of longitudinal distributional patterns of animals of the downstream parts of Doe Run did not correlate with substrates. The upstream limits of some species may have been a function of the relative lack of drifting foods presumably required by passive feeders (simuliids, hydropsychid larvae, and some Ephemeroptera). Temperature, however, was a major factor in Doe Run and elsewhere (Dodds and Hisaw, 1925b; Ide, 1935; and Sprules, 1947), either by its constancy at the spring that may have allowed a species to persist but not to complete its life cycle (Ide, 1935), by being so low that it was unsuitable for life of many animals of warmer, more fluctuant stream climate. Species in the spring assemblage were adapted to those conditions, occurred as stragglers, or represented more northern forms as relicts or outliers of their major centers of abundance.

The Role of Fishes

Fishes resident in Doe Run, specifically those characteristic of the stream (i.e., *Cottus*, *Rhinichthys*, *Catostomus*), and the "creek species" (Fig. 27) that maintained populations through reproduction (Fig. 26) occupied distinctly different habitats in different stages of their life cycles. For example, *Cottus carolinae*, generally considered an inhabitant of riffles, moved directly into quiet, shallow, hot, shoreline areas immediately after hatching, then as they grew they progressively invaded swifter waters only to return to pool situations in deeper currents as large adults (Minckley, *et al.*, 1963). Larvae of *Catostomus commersoni* likewise moved to quiet areas, but in gently eddying currents, where the early stages fed on neuston and terrestrial materials floating on the surface (Stewart, 1926) for a time. Then the suckers progressively moved into deeper

waters to inhabit the deepest pools as adults, although riffles were utilized for spawning and possibly for some feeding.

Because of their greater mobility, size, and greater plasticity of ontogenetic and instantaneous response to the stream environments, fishes do not fit into the assemblage systems discussed above. Rather, they are superimposed on those systems and utilize a greater proportion of the overall ecological resources of the creek than do other organisms. This is indicated by the broad spectrum of foods utilized by fishes (Fig. 28). The apparent lack of such plasticity in other animals, however, may be artificial. I will not be surprised if more detailed research on the ecology of aquatic invertebrates indicates somewhat comparable ontogenetic changes in habit or foods by some, at least in the larger species. Such changes are indicated by limited data on crayfish, and on some mayflies (Harker, 1953; Macan, 1957; Brown, 1961a) and stoneflies (Hynes, 1941).

CONCLUDING REMARKS

I hope to clarify my concept of biotic dispersion in streams by stressing ecologically equivalent communities rather than communities based on taxonomic entities. Therefore, I approached Doe Run from the standpoint of ecological equivalence of animals and plants in physically similar habitats. The composition of the flora and fauna changed in passing downstream from the source, in response to temperature, gradient, marl formation, or other factors dependent on physiological responses and plasticity of the species concerned. However, the general morphology of animals occurring in riffle habitats, for example, was similar at all stations in that they displayed equivalent adaptations to the rapid movement of the dense medium in which they lived. This is not to say that precise adaptations, such as marked flattening of the body, were displayed by each, but that the organisms occurring on a given riffle collectively displayed adaptation of some kind, be it the presence of strong hooks for attachment, flattening of the body or ap-

pendages, elaborate nets and tube construction, or a proclivity for living in burrows maintained in marl or constructed in silt-filled interstices.

The interrelations of physical, chemical, and biological phenomena in streams have been stressed repeatedly and are illustrated diagrammatically in Figure 30. Arrows pointing from causative factors to their results are deleted primarily because of reciprocity in most instances (see Major, 1961). This is not true in some instances, such as the effect of rainfall on discharge of a stream in which there could be little reciprocity, but most show some degree of reversibility. For example, the gradient of a stream affects its turbulence, depending on discharge. Conversely, the turbulence of a stream influences its competence for carrying sediments, which in turn may greatly affect the speed of downcutting and thus the speed of change in gradient, assuming no rejuvenation of the land mass. The chemistry of the water in Doe Run un-

doubtedly is affected by the bottom materials, but the deposition of marl in the midsection of the stream may be a reciprocal effect where the chemistry of the water, modified by physical and biological phenomena, is a causative factor in the type of bottom material present (Fig. 30).

There may be some ambiguity in conclusions and concepts formulated from the study of Doe Run since they are based primarily on a single stream fed by a large spring. However, after the spring water leaves its subterranean channel, it is immediately influenced by the epigeal environment through which it flows and by organisms and physicochemical phenomena within it. It is a stream that should be comparable to other streams in its ecology notwithstanding certain features of constancy or uniqueness superimposed by its origin. It is hoped that the nature of this study and any ambiguous conclusions drawn from the data will serve to illustrate and stimulate further research in descrip-

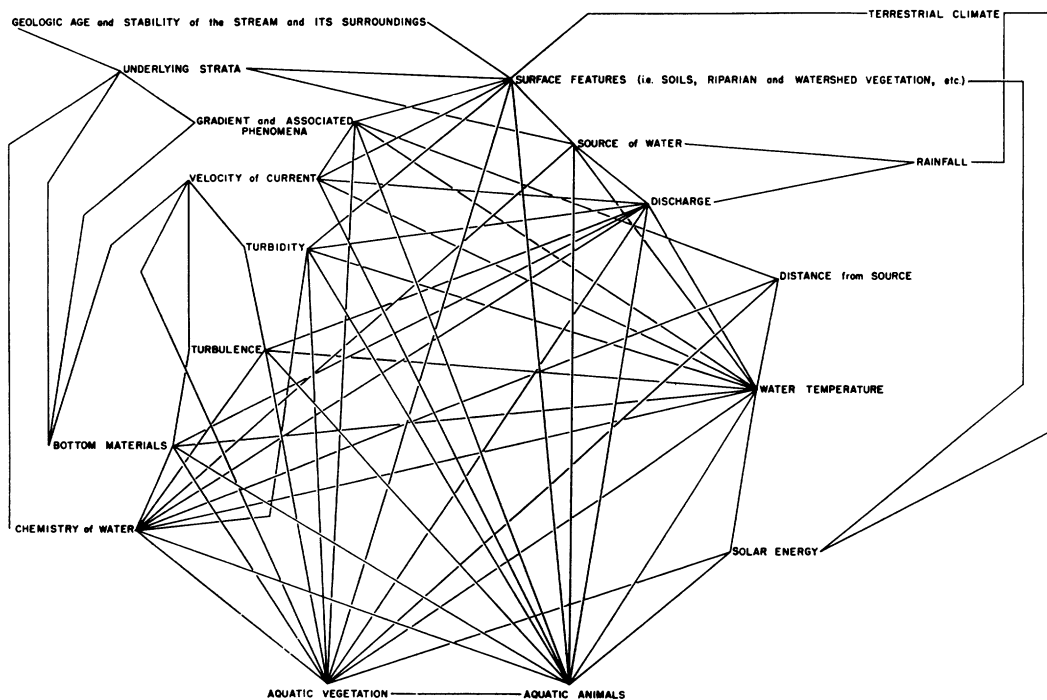


FIG. 30. Causes and effects of various factors of stream environment with special reference to Doe Run, Meade County, Ky.

tive phases of the ecology of flowing waters.

SUMMARY

1. Chemical, physical, and biological features of Doe Run, Meade County, Ky., were studied from February 1959 to May 1962, with the most intensive investigations from November 1959 through July 1961. The stream originates as a large spring, flows for 9.7 miles, and empties directly into the Ohio River. The surrounding land has a rolling, karsted topography, underlain with limestones of Mississippian age.

2. Doe Run was mapped from topographic quadrangles and an aerial photograph. "Creek miles" were designated beginning with Mile 0.0 at the source. Five stations were established as follows: Station I, Miles 0.0-0.3; Station II, Miles 1.65-2.1; Station III, Miles 3.0-3.2; Station IV, Miles 4.7-4.9; and Station V, Miles 7.7-8.0.

3. Bottoms downstream from the source graded from rubble adjacent to the spring, through gravel and sand, to soft silt in an impoundment by an old mill dam at Mile 1.65. Bottoms at Station II were generally bedrock and rubble. The areas between Miles 2.1 and 2.36 and Miles 2.36 and 2.82 also were influenced by impoundments above dams at Miles 2.36 and 2.82. A short section of marl bottom existed between Miles 2.36 and 2.5. Marl deposition dominated the bottom deposits from Dam 3 downstream to near Mile 5.3, and the gradient throughout that area was about 35 fpm. From Mile 5.3 to the Ohio River the average gradient was about 9 fpm and the bottoms ranged from broken marl and gravel in the upper part to deep silts near the river. Pool-riffle development was most pronounced between Miles 5.3 and 7.0, below which the stream resembled a deep, slowly moving sluice.

4. Discharge in Doe Run was "normal" at 20 to 40 cfs at all stations based on modal conditions. Discharge was generally greatest in December-March and lowest in August-October. Severe fluctuations occurred in June 1960 and in March-

May 1961, with discharges as great as 600 cfs at Station I (ca. 2,000 cfs at Station V) in the latter period.

Turbidities rarely exceeded more than 50 "turbidity units" (approximately 50 mg/l) except in periods of unusual discharge. After the riparian vegetation was cleared at the downstream section in preparation for impoundment, turbidities showed a marked increase at Station V.

Aspects of transport of the bed load are discussed in relation to fluctuations of discharge. Major deposits were associated with beds of macrophytic vegetation in the upstream areas. After periods of relatively high turbidities, deposits of sludgelike materials occurred on boulders in the channel, and were apparently formed through successional development of a unique assemblage of organisms.

Water temperatures at Station I were consistently between 13.0° and 13.5°C in periods of modal flow, but increased to between 13.5° and 14.5° after the extreme discharges of spring 1961. Ranges from 12.0° to 16.0° were recorded in periods of unusual discharge conditions. The maximum water temperatures recorded at Stations III and V were 20.0° and 25.6°C, respectively, and the minima were 6.1° and 1.7°. The greatest temperature ranges occurred in late fall and early winter at each of the downstream stations.

Surface water in the mill impoundments often approached 30°C in summer, but waters downstream never exceeded 20.0° at Station III. This was explained by the presence of density currents in the pools, which flowed along the bottom in summer and near the surface in winter.

5. Dissolved oxygen at Station I ranged between 70 and 85 per cent of saturation. Supersaturations of oxygen were found in the larger pools in periods of strong insolation and large stands of vegetation; passage of water over dams tended to reduce saturation levels to about 100 per cent. Samples from riffle areas usually ranged near 100 per cent saturation except in autumn when large deposits of fallen leaves apparently increased oxygen demand in pools and

caused deficits in downstream areas. The photosynthetic activity of algae and higher plants masked other factors influencing dissolved oxygen levels except after floods when vegetation was relatively sparse. In those periods oxygen tended to follow temperature relations and respond to oxygen demand in pools by remaining somewhat below saturation.

Carbon dioxide, pH , and alkalinity relations were complex and generally consisted of high carbon dioxide, circumneutral pH , and high alkalinity (200 to 280 mg/l) at the spring, a gradual loss of carbon dioxide and increase in pH between Stations I and II, then rapid elevation of pH , almost total loss of carbon dioxide, and precipitation of calcium carbonate from Mile 2.82 to Mile 5.3. Downstream from Mile 5.3, large pools and their accumulated organic materials apparently caused reestablishment of pH -carbon dioxide-alkalinity relations in such a way that marl deposition was inhibited in spite of a general, persistent supersaturation of bicarbonate in the water. Diurnal variation in these factors at stations in the marl area indicated considerable activity of the vegetation in the deposition of marl, presumably through assimilation of half-bound carbon dioxide.

Determinations of total iron, phosphate phosphorus, nitrate and nitrite nitrogen are presented and discussed.

6. Algal communities of Doe Run were placed in 4 broad categories: (1) those algae with a firm mode of attachment and a highly flexible thallus, occurring in current; (2) cushionlike or encrusting species that grow appressed to the substrate in current; (3) matted or loosely arranged algae occurring attached or unattached in quiet pools, eddies, or in areas of almost laminar flow that approximate pools and eddies because of lack of turbulence; and (4) subaerial species attached as encrusting mats and occurring in zones of spray, on waterfalls, on tops of emersed stones, or on muddy banks and bars along the channel. Algal species are discussed in relation to their spatial distributions in the creek and to certain physical and chemical

factors. Special attention is given those species associated with marl deposition. Factors influencing marl deposition in the creek, and the influence of the marl on aquatic invertebrates, are discussed in detail.

Higher plants occurred mostly upstream from the first mill dam, and formed certain depositional features and spatial associations among themselves. Emergent vegetation was relatively sparse because of the stony banks, but *Nasturtium officinale* was a major component of the upstream communities. Four major submergent plants were *Myriophyllum heterophyllum*, *Potamogeton foliosus*, *Nitella flexilis*, and *Fissidens julianus*.

The grading environment of the upstream section (above Mile 2.0) was occupied by monospecific stands of vegetation in a linear sequence that apparently resulted from the distribution of bottom sediments. It is concluded that the upstream section represents an environment for the plants intermediate between large, constant springs on one hand and "typical," fluctuant streams on the other. Thus the stream portrays both the dynamic aspects of catastrophic washout of the vegetation and recolonization, and a constancy of plant dispersion typical of larger, less fluctuating spring systems.

7. A list of invertebrates is presented. Specific ecological relations of certain abundant invertebrates are given in detail, including distribution in the stream and its tributaries, reproduction, times of emergence of aquatic insects, and behavior in relation to the various habitats in the creek. Faunal affinities include a ubiquitous group of animals and some species characteristic of or related to other species occurring in areas to the north and east.

Quantitative sampling of the benthos was done monthly from February 1959 to November 1960, with additional series in January and June 1961. Samples were obtained from preselected habitats in the creek, such as beds of *Fissidens* at Stations I and II, open pools at Stations II, III, IV, and V, and beds of emergent vegetation at

Stations I and III. Four such habitats were sampled on each date at each station; data from Station V were fragmentary because of sporadic occurrences of backwaters of the Ohio River.

The greatest number of taxonomic groups of animals occurred at Stations II, III, and IV, with decreases in both the numbers of groups and the numbers of individuals at Station V, but the greatest numbers of animals per square foot at Stations I and II. Beds of *Fissidens* were the most productive, as determined from standing crops, with maxima of 18,708 and 20,004 individuals/ft² at Stations I and II, respectively. The maximum weights recorded there were 28.695 and 48.937 g/ft², respectively, with weights of gastropods and decapods included. Average values from Station I were about 8,600 individuals and 8 g/ft², and for Station II, about 9,200 individuals and 11 g (crayfish and gastropods excluded from the weights). Standing crops of invertebrates graded from largest in *Fissidens*, through *Myriophyllum* beds, to beds of emergent vegetation, thence to stable silty bottoms, riffles in the channel, riffles lateral to the main channel, to unstable bottoms in pools, and the least was found on shifting-sand bottoms at Station I. In the upstream areas, all habitats were greatly influenced by the tremendous populations of animals in moss riffles, and showed increased standing crops in periods of modal discharge presumably because of movement of animals from moss to more peripheral habitats. The most important groups were Crustacea at Stations I and II, and insect larvae and nymphs in more downstream areas. Oligochaeta and Mollusca occurred throughout the stream system in significant numbers. Most changes in invertebrate populations seemed related to changes in discharge, either directly or indirectly, through wash-out or movements into or out of a given area. Some changes in populations could be attributed to seasonal emergence of aquatic insects.

8. Sixty-six species of fishes were collected from Doe Run, and data on the distributions, abundance, reproduction, and

movements are annotated. The 3 major factors controlling the distribution of fishes were gradient, temperature, and the presence of marl in the midsection of the stream. Thirteen of 31 species considered more typical of the Ohio River than of smaller creeks maintained definite ranges in the creek, most of which merged into populations of the Ohio River. Many of the most upstream records of those "river fishes" were at a barrier imposed by a bridge and culverts at Station III, and most were single specimens. A second group of fishes seemed somewhat restricted to the section between Miles 5.3 and 7.0 in the area of pronounced pool-riffle development, apparently avoiding the open, shallow, bedrock pools and swift currents of the upper area, and also the muddy, sluicelike lower portion of the stream. There was little reproduction by most species of fishes upstream from Mile 5.3. Marl deposition may have deterred reproduction of those species usually building nests in gravels or other loose bottom materials, and the relatively low temperatures of the upstream area appeared to inhibit reproduction of many, particularly sunfishes. Only 3 species, *Catostomus commersoni*, *Rhinichthys atratulus*, and *Cottus carolinae*, maintained populations at Station I, and those introduced into the upper area of Doe Run by fishermen or by displacement from adjacent ponds failed to reproduce.

Amphibians, reptiles, birds, and mammals that appeared to influence, or be influenced by, the stream are listed with annotations.

9. Examination of the trophic structure of Doe Run revealed a major dependence of primary consumers on allochthonous and autochthonous detrital material. The role of detritus in nutrition of aquatic animals is reviewed. Analyses of digestive tracts of invertebrate and vertebrate consumers tentatively indicate that the most "trophically balanced" section of Doe Run is nearest the spring, where allochthonous debris is minimal. Downstream from the source the amount of "trophic unbalance," in the sense of the fauna depending more on detrital

materials produced in areas other than those which they inhabit for their nutrition, increases with the accumulation of more and more detritus.

10. Arguments are presented for the existence of climates in flowing waters analogous to those found in terrestrial situations. Climate in flowing waters is defined as an average or mode of the physical and chemical characteristics of a given area in a period of time (an average "weather"). The major differences between stream and terrestrial climates are pointed out as those of magnitude of size and change, with many climates being present throughout the length of a stream and locally due to variations in gradient and water chemistry even in periods of modal discharge. Also, swift and radical variations may decimate the communities and necessitate a total resumption of succession, perhaps several times in a single season. The communities or assemblages of plants found in streams should be grouped ecologically, according to their habitats and structural adaptations, and climax conditions may be designated as based on climates present.

The physiographic approach of earlier workers is reapplied to the study of Doe Run, and put forth as a more realistic approach than those involving classification

of streams, or segments of streams, on the basis of taxonomic groupings of organisms.

Similar arguments and illustrative data are derived from analyses of invertebrate assemblages in Doe Run. Two well-defined assemblages, based on the concept of ecologically equivalent adaptation, occur in the area downstream from Station II: that of the riffles, and that of pool situations without considering bottom types or presence of vegetation. Station II is considered an area of transitions from conditions characteristic of the spring and those downstream, but is predominantly a spring or *Fissidens*-dominated assemblage on which certain elements of the downstream fauna are superimposed. The spring community is characterized by animals adapted to live in the close-spaced beds of *Fissidens* and in the cool, constant-temperature conditions. Even at Station I, however, the downstream pool assemblages are represented in *Nasturtium* beds. *Myriophyllum* beds apparently are a truly intermediate habitat, whose fauna includes elements of all other communities in the stream.

Fishes, because of their plasticity of ontogenetic instantaneous response to their environment in streams, apparently are superimposed on the other systems and are not an integral part of any given assemblages of plants or invertebrates.

LITERATURE CITED

- ADAMS, C. C. 1901. Base leveling and its faunal significance. *Am. Nat.*, 35:839-852.
- , AND T. L. HANKINSON. 1928. The ecology and economics of Oneida Lake fishes. IV. Annotated list of Oneida Lake fishes. *Bull. N. Y. State Coll. For., Roosevelt Wild Life Ann.*, 1:283-521.
- ALEXANDER, C. P. 1931. The crane-flies (Tipulidae, Diptera). *Deutsche Limnologische Sunda-Expedition. Arch. Hydrobiol., Suppl.*, 9:135-191.
- ALLEE, W. C. 1929. Studies in animal aggregations of the isopod, *Asellus communis*. *Ecol.ogy*, 10:14-36.
- , A. E. EMERSON, O. PARK, T. PARK, AND K. P. SCHMIDT. 1949. Principles of animal ecology. W. B. Saunders Co., Philadelphia. xii + 837pp.
- ALLEN, J. A. 1876. The American bisons, living and extinct. *Mem. Geol. Surv. Ky.*, 1:i-ix, 1-246.
- ALLORGE, P. 1921. Les associations vegetales du Vexin français. *Rev. Gen. Bot.*, 33:481-583 (cited in Blum, 1956a).
- ANDERSON, A., AND A. LUNDH. 1948. Algstudier i Vegean. *Bot. Notiser*, (1948):284-304.
- ANDERSON, R. C. 1959. A modified flotation technique for sorting bottom fauna samples. *Limnol. Oceanogr.*, 4:223-225.
- ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. Univ. Chicago Press. xv + 782pp.
- ANONYMOUS. n.d. Water and sewage analysis methods manual. Hach Chemical Co., Ames, Iowa. 52pp.
- . 1960. Standard methods for the examination of water and wastewater. 11th ed. Am. Publ. Health Assn., New York. xxi + 626pp.
- ARMITAGE, K. B. 1958. Ecology of the riffle insects of the Firehole River, Wyoming. *Ecol.ogy*, 39:571-580.

- . 1961. Distribution of riffle insects of the Firehole River, Wyoming. *Hydrobiol.*, 17: 152-174.
- BADCOCK, R. M. 1949. Studies on stream life in tributaries of the Welsh Dee. *J. An. Ecol.*, 18:193-208.
- . 1954a. Studies of the benthic fauna in tributaries of the Kävlinge River, southern Sweden. *Inst. Freshwater Res., Drottningholm*, Rept. 35(1953):21-37.
- . 1954b. Comparative studies in the populations of streams. *Ibid.*:38-50.
- BAILEY, R. M., AND W. A. GOSLINE. 1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. *Misc. Publ. Mus. Zool., Univ. Michigan*, 93:1-44.
- BARR, T. C., JR., AND R. A. KUEHNE. 1962. The cavefish, *Amblyopsis spelaea*, in northern Kentucky. *Copeia*, (1962):662.
- BARRETT, M. J., A. L. H. GAMESON, AND C. G. OGDEN. 1960. Aeration studies at four wier systems. *Water and Water Eng.*, Sept., (1960): 1-7.
- BEAUCHAMP, R. S. 1932. Some ecological factors and their influence on competition between stream and lake-living triclads. *J. An. Ecol.*, 1:175-190.
- BERNER, L. 1950. The mayflies of Florida. *Univ. Fla. Biol. Sci.*, 4:1-267.
- BIRCH, L. C., AND D. P. CLARK. 1953. Forest soil as an ecological community, with special reference to the faunas. *Quart. Rev. Biol.*, 28:13-26.
- BLACK, J. D. 1949. Changing fish populations as an index of pollution and soil erosion. *Ill. Acad. Sci. Trans.*, 42:145-148.
- BLUM, J. L. 1956a. The ecology of river algae. *Bot. Rev.*, 22:291-341.
- . 1956b. The application of the climax concept to algal communities of streams. *Ecology*, 37:603-604.
- . 1957. An ecological study of the algae of the Saline River, Michigan. *Hydrobiol.*, 9:361-408.
- . 1960. Algal populations in flowing waters. In *The ecology of algae*. Spec. Publ. 2, Pymatuning Lab. Field Biol. Pp. 11-21.
- BOUSFIELD, E. L. 1958. Fresh-water amphipod crustaceans of glaciated North America. *Can. Field-Nat.*, 72:55-113.
- BRADEN, G. E. 1951. Turbulence, diffusion, and sedimentation in stream channel expansions and contractions. *Proc. Okla. Acad. Sci.*, 31: 72-77.
- . 1958. The hydraulic jump in natural streams. *Ibid.*, 38:78-79.
- BROOKS, A. J. 1954. The bottom-living algae of slow sand filter beds of waterworks. *Hydrobiol.*, 6:333-351.
- . 1955a. The attached algal flora of slow sand filter beds of waterworks. *Ibid.*, 7: 103-107.
- . 1955b. The aquatic fauna as an ecological factor in studies of the occurrence of fresh-water algae. *Rev. Algol. (n.s.)*, 1:142-145.
- BROWN, D. S. 1960. The ingestion and digestion of algae by *Chloeon dipterum* L. *Hydrobiol.*, 16:81-96.
- . 1961a. The food of the larvae of *Chloeon dipterum* L. and *Baetis rhodani* (Pictet) (Insecta, Ephemeroptera). *J. An. Ecol.*, 30:55-75.
- . 1961b. The morphology and functioning of the mouthparts of *Chloeon dipterum* and *Baetis rhodani*. *Proc. Zool. Soc. Lond.*, 136:147-176.
- BURKS, B. D. 1953. The mayflies, or Ephemeroptera, of Illinois. *Bull. Ill. Nat. Hist. Surv.* 26:1-216.
- BURTON, G. W., AND E. P. ODUM. 1945. The distribution of stream fish in the vicinity of Mountain Lake, Virginia. *Ecology*, 26:182-194.
- BUTCHER, R. W. 1927. A preliminary account of the vegetation of the River Itchen. *J. Ecol.*, 15:55-65.
- . 1933. Studies on the ecology of rivers. I. On the distribution of macrophytic vegetation in the rivers of Britain. *Ibid.*, 21: 58-89.
- , F. T. K. PENTLOW, AND J. W. A. WOODLEY. 1930. Variations in the composition of river waters. *Int. Rev. ges. Hydrobiol.*, 24:47-80.
- CEDERGREN, G. R. 1938. Reofila eller det rinnande vattnets algsamhallen. *Svensk. Bot. Tidskr.*, 22:362-373.
- CHANDLER, H. P. 1956. Megaloptera. In *Aquatic insects of California, with keys to North American genera and California species*. Univ. California Press, Berkeley and Los Angeles. Pp. 229-233.
- CHURCHILL, M. A. 1958. Effects of impoundments on oxygen resources. In *Oxygen relationships in streams*. Robt. A. Taft San. Eng. Cent., Tech. Rept. W58-2:107-129.
- CLAY, W. M. 1962. A field manual of Kentucky fishes. *Ky. Dept. Fish Wildl. Res.*, Frankfort. vii + 147pp.
- CLEMENS, W. A. 1917. An ecological study of the mayfly *Chironetes*. *Univ. Toronto Stud., Biol. Ser.*, 17:5-43.
- CLEMENTS, F. E., AND V. E. SHELFORD. 1939. Bio-ecology. John Wiley & Sons, Inc., New York. vii + 425pp.
- COKER, R. E. 1954. Streams lakes ponds. Univ. North Carolina Press, Chapel Hill. xviii + 327pp.

- COLE, G. A. 1957. Some epigeal isopods and amphipods from Kentucky. *Trans. Ky. Acad. Sci.*, 18:29-39.
- . 1959. A summary of our knowledge of Kentucky crustaceans. *Ibid.*, 20:66-81.
- . 1961. Some calanoid copepods from Arizona, with notes on congeneric occurrences of *Diaptomus* species. *Limnol. Oceanogr.*, 6:432-442.
- , AND W. L. MINCKLEY. 1961. A new species of amphipod crustacean (genus *Gammarus*) from Kentucky. *Trans. Am. Microscop. Soc.*, 80:391-398.
- COOPER, G. P. 1953. Population estimates of fishes in Sugarloaf Lake, Washtenaw County, Michigan, and their exploitation by anglers. *Pap. Mich. Acad. Sci., Arts, and Lett.*, 38:163-186.
- CRADDOCK, J. E., AND W. L. MINCKLEY. 1963. Reptiles and amphibians from Meade County, Kentucky. *Am. Midl. Nat. In press.*
- CURRY, L. L. 1954. Notes on the ecology of the midge fauna (Diptera: Tendipedidae) of Hunt Creek, Montmorency County, Michigan. *Ecology*, 35:451-550.
- . 1958. Larvae and pupae of the species of *Cryptochironomus* (Diptera) in Michigan. *Limnol. Oceanogr.*, 3:427-442.
- DAILY, F. K. 1958. Some observations on the occurrence and distribution of the Characeae of Indiana. *Proc. Ind. Acad. Sci.*, 68:95-107.
- DARNELL, R. M. 1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology*, 42:553-568.
- DEEVEY, E. S., JR., M. S. GROSS, G. E. HUTCHINSON, AND J. L. KRAYBILL. 1954. The natural C_{14} contents of materials from hard-water lakes. *Proc. Nat. Acad. Sci.*, 40:285-288.
- DENDY, J. S. 1944. The fate of animals in stream drift when carried into lakes. *Ecol. Monogr.*, 14:333-357.
- DENHAM, S. C. 1938. A limnological investigation of the West Fork and Common Branch of White River. *Invest. Ind. Lakes Streams*, 1(5):17-71.
- DODDS, G. S., AND F. L. HISAW. 1924a. Ecological studies of aquatic insects. I. Adaptations of mayfly nymphs to swift streams. *Ecology*, 5:137-148.
- , AND ———. 1924b. Ecological studies of aquatic insects. II. Size of respiratory organs in relation to environmental conditions. *Ibid.*:262-271.
- , AND ———. 1925a. Ecological studies on aquatic insects. III. Adaptations of caddisfly larvae to swift streams. *Ibid.*, 6:123-137.
- , AND ———. 1925b. Ecological studies on aquatic insects. IV. Altitudinal range and zonation of mayflies, stoneflies, and caddisflies in the Colorado Rockies. *Ibid.*:380-390.
- DOUGLAS, B. 1958. The ecology of the attached diatoms and other algae in a small stony stream. *J. Ecol.*, 46:295-322.
- DROUET, F. 1959. Myxophyceae. In *Fresh-water biology*. John Wiley & Sons, Inc., New York. Pp. 95-114.
- EDDY, S. 1925. Fresh-water algal succession. *Trans. Am. Microscop. Soc.*, 44:138-147.
- . 1934. A study of fresh-water plankton communities. III. *Biol. Monogr.*, 12:1-93.
- EDMONDSON, W. T. (Ed.) 1959. Ward and Whipple's fresh-water biology. John Wiley & Sons, Inc., New York. xx + 1,248pp.
- EDWARDS, R. W., AND M. W. BROWN. 1960. An aerial photographic method for studying the distribution of aquatic macrophytes in shallow waters. *J. Ecol.*, 48:161-163.
- , AND J. HEYWOOD. 1960. The effects of a sewage effluent discharge on the deposition of calcium carbonate on shells of the snail *Potamopyrgus jenkinsi* (Smith). *Nature (London)*, 186:492-493.
- , AND M. OWENS. 1960. The effects of plants on river conditions. I. Summer crops and estimates of net productivity of macrophytes in a chalk stream. *J. Ecol.*, 48:151-160.
- , AND ———. 1962. The effects of plants on river conditions. IV. The oxygen balance of a chalk stream. *J. Ecol.*, 50:297-320.
- EINSELE, W. 1938. Über chemische und kolloid-chemische Vorgänge in Eisenphosphat-systemen unter limnochemischen und limnogeologischen Gesichtspunkten. *Arch. Hydrobiol.*, 33:361-387.
- ELLIS, M. M. 1936. Erosion silt as a factor in aquatic environments. *Ecology*, 17:29-42.
- EMBODY, G. G. 1927. An outline of stream study and the development of a stocking policy. *Contr. Agri. Lab., Cornell Univ.*, 27pp.
- EMIG, W. H. 1917. Travertine deposits of Oklahoma. *Okla. Geol. Surv., Bull.*, 29:1-76.
- EYSTER, C. 1958. Bioassay of water from a concretion-forming marl lake. *Limnol. Oceanogr.*, 2:455-458.
- FAHY, W. E. 1954. The life history of the northern greenside darter, *Etheostoma blennioides blennioides* Rafinesque. *J. Elisha Mitchell Sci. Soc.*, 70:139-205.
- FERNALD, M. O. 1950. Gray's manual of botany. 8th ed. American Book Co., New York. lxi + 1,632pp.
- FINNELL, J. C., R. M. JENKINS, AND G. E. HALL. 1956. The fishery resources of the Little River System, McCurtain County, Oklahoma. *Rept. Okla. Fish Res. Lab.*, 55:i-ii, 1-82.

- FORBES, S. A. 1925. The lake as a microcosm. Ill. Nat. Hist. Surv. Bull., 15:537-550. (Emended reprint of Forbes, S. A. 1887. The lake as a microcosm. Bull. Sci., Arts, Peoria Coll., 1887:77-87.)
- , AND R. E. RICHARDSON. 1920. The fishes of Illinois. (2nd ed.) Ill. Nat. Hist. Surv., Urbana. cxxxvi + 357pp., many pls.
- FOSTER, M. D. 1942. The chemistry of ground water. In Hydrology, physics of the earth. IX. McGraw-Hill Book Co., New York. Pp. 646-655.
- FOWLER, H. W. 1906. The fishes of New Jersey. Ann. Rept. N. J. Mus., 1905:35-447.
- FOX, H. M., AND C. A. SIMMONDS. 1933. Metabolic rates of arthropods from different habitats. J. Exp. Biol., 10:67-74.
- FRISON, T. H. 1935. The stoneflies, or Plecoptera, of Illinois. Bull. Ill. Nat. Hist. Surv., 20:i-vi, 281-471.
- . 1942. Studies of North American Plecoptera, with special reference to the fauna of Illinois. *Ibid.*, 22:233-355.
- FRITSCH, F. E. 1929. The encrusting algal community of certain fast-flowing streams. New Phytol., 28:165-196.
- . 1949. The lime-encrusting *Phormidium* community of British streams. Verh. int. ver. theoret. angew. Limnol., 10:141-144.
- . 1950. *Phormidium incrustatum* (Naeg.) Gom., an important member of the lime-encrusted communities of flowing water. Biol. Jaarboek, 17:27-39.
- FROHNE, W. C. 1956. The provendering role of the larger aquatic plants. Ecology, 37: 387-388.
- FROST, W. E. 1942. River Liffey Survey. IV. The fauna of the submerged "mosses" in an acid and an alkaline water. Proc. R. Irish Acad., B, 47:293-369.
- FUNK, J. L. 1957. Movement of stream fishes in Missouri. Trans. Am. Fish. Soc., 85:39-57.
- , AND R. S. CAMPBELL. 1953. The population of larger fishes in Black River, Missouri. In The Black River studies. Univ. Mo. Stud., 26:1-136. Pp. 69-82.
- GAUFIN, A. R., E. K. HARRIS, AND H. J. WALKER. 1955. A statistical evaluation of stream bottom sampling data obtained from three standard samplers. Ecology, 37:643-648.
- GERKING, S. D. 1945. Distribution of the fishes of Indiana. Invest. Ind. Lakes Streams, 3: 1-137.
- . 1949. Characteristics of stream fish populations. *Ibid.*, 3:283-309.
- . 1950. Stability of a stream fish population. J. Wildl. Mgmt., 14:193-202.
- . 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology, 34:347-365.
- . 1959. The restricted movements of fish populations. Biol. Rev., 34:221-242.
- GERSBACHER, W. M. 1937. Development of stream bottom communities in Illinois. Ecology, 18:359-390.
- GESSNER, F. 1955. Hydrobotanik. I. Energiehaushalt. Veb Deutsch. Ver. der Wiss., Berlin. xii + 517pp.
- . 1959. Hydrobotanik. II. Stoffhaushalt. *Ibid.* xiv + 701pp.
- GILBERT, C. R. 1961. Hybridization versus intergradation (*sic*): an inquiry into the relationships of two cyprinid fishes. Copeia, (1961): 181-192.
- GNERI, F. S., AND V. ANGELESCU. 1951. La nutrición de los peces iliofagos en relación con el metabolismo general del ambiente acuático. Rev. Inst. Nac. Invest. Cien. Nat., Mus. Argentina. Cien. Nat., 2:1-44.
- GRAF, D. L. 1960a. Geochemistry of carbonate sediments and sedimentary carbonate rocks. I. Carbonate mineralogy, carbonate sediments. Ill. Geo. Surv., Circ., 297:1-39.
- . 1960b. Geochemistry of carbonate sediments and sedimentary carbonate rocks. II. Sedimentary carbonate rocks. *Ibid.*, 298:1-43.
- GRINNELL, J. 1922a. The role of the "accidental." Auk, 39:373-380.
- . 1922b. The trend of avian populations in California. Science, 56:671-676.
- GUNNING, G. E. 1959. The sensory basis for homing in the longear sunfish, *Lepomis megalotis megalotis* (Rafinesque). Invest. Ind. Lakes Streams, 5:103-130.
- , AND W. M. LEWIS. 1956. Age and growth of two important bait species in a cold-water stream in southern Illinois. Am. Midl. Nat., 55:118-120.
- HALLAM, J. C. 1959. Habitat and associated fauna of four species of fish in Ontario streams. J. Fish. Res. Bd. Can., 16:147-173.
- HARKER, J. E. 1953. An investigation of the mayfly fauna of the Lancashire stream. J. An. Ecol., 22:1-13.
- HARRINGTON, R. W., JR. 1950. Preseasonal breeding by the brindled shiner, *Notropis bifrenatus*, induced under light-temperature control. Copeia, (1950):304-311.
- . 1957. Sexual photoperiodicity of the cyprinid fish, *Notropis bifrenatus* (Cope), in relation to the phases of its annual reproduction cycle. J. Exp. Zool., 135:529-555.
- HARLAN, J. R., AND E. B. SPEAKER. 1956. Iowa fish and fishing. Iowa Cons. Comm., Des Moines. x + 377pp., many pls.
- HASLER, A. D., AND W. J. WISBY. 1958. The return of displaced largemouth bass and green sunfish to a "home" area. Ecology, 39:289-293.
- HASTINGS, A. B., C. D. MURRAY, AND J. SENDRAY. 1927. Studies of the solubility of calcium salts. I. The solubility of calcium carbonate in salt solutions and biological fluids. J. Biol. Chem., 71:723-781.

- HEM, J. C. 1959. Study and interpretation of the chemical characteristics of natural water. U. S. Geol. Surv., Water-supply Pap., 1473: i-ix, 1-269.
- HENDERSON, C., AND R. F. FOSTER. 1957. Studies of smallmouth black bass (*Micropterus dolomieu*) in the Columbia River near Richland, Washington. Trans. Am. Fish. Soc., 86:112-127.
- HERON, J. 1962. Determination of phosphate in water after storage in polyethylene. Limnol. Oceanogr., 7:316-321.
- HEYWOOD, J., AND R. W. EDWARDS. 1962. Some aspects of the ecology of *Potamopyrgus jenkinsi* Smith. J. An. Ecol., 31:239-250.
- HOAR, W. S. 1957. The gonads and reproduction. Chapt. VII. In *The physiology of fishes*. Academic Press Inc., New York. Pp. 287-321.
- HORA, S. L. 1930. Ecology, bionomics, and evolution of the torrential fauna, with special reference to the organs of attachment. Phil. Trans. R. Soc. Lond., 218:171-282.
- HORNUFF, L. 1957. A survey of four Oklahoma streams with reference to production. Okla. Fish. Res. Lab., Rept., 63:1-22.
- HORNUNG, H. 1959. Floristisch-ökologische Untersuchungen an der Echaz unter besonderer Berücksichtigung der Verunreinigung durch abwässer. Arch. Hydrobiol., 55:52-126.
- HOWLAND, J. H. 1931. Studies on the Kentucky black bass (*Micropterus pseudaplites* Hubbs). Trans. Am. Fish. Soc., 61:89-94.
- HUBBS, C. L., AND K. F. LAGLER. 1958. Fishes of the Great Lake Region (revised ed.). Cranbrook Inst. Sci., Bull., 26:1-213, 44 pls.
- HUET, M. 1959. Profiles and biology of western European streams as related to fish management. Trans. Am. Fish. Soc., 88:155-163.
- HUNGERFORD, H. B. 1920. The biology and ecology of aquatic and semi-aquatic Hemiptera. Univ. Kans. Sci. Bull., 11:1-341.
- HUTCHINSON, G. E. 1957. A treatise on limnology. I. Geography, physics, and chemistry. John Wiley & Sons, Inc., New York. xiv + 1,015pp.
- . 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? Am. Nat., 93:145-159.
- HYNES, H. B. N. 1941. The taxonomy and ecology of the nymphs of the British Plecoptera, with notes on the adults and eggs. Trans. R. Ent. Soc. Lond., 91:459-557.
- . 1950. Food habits of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in study of fishes. J. An. Ecol., 19:36-58.
- . 1960. The biology of polluted waters. Liverpool Univ. Press, Liverpool. xiv + 202pp.
- . 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. Toronto Stud., Biol. Ser., 39: 9-76, 10 pls.
- IRWIN, W. H., AND J. H. STEVENSON. 1951. Physicochemical nature of clay turbidity with special reference to clarification and productivity of impounded waters. Bull. Okla. A. & M. Coll., 48:1-54.
- IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven. viii + 302pp. (translated by Douglas Scott).
- JAMES, M. T. 1959. Diptera. In *Fresh-water biology*. John Wiley & Sons, Inc., New York. Pp. 1,057-1,079.
- JILLSON, W. R. 1922. The conservation of natural gas in Kentucky. J. P. Morton Co., Louisville. 152pp.
- JONES, J. R. E. 1950. A further ecological study of the River Rheidol. The food of the common insects of the mainstream. J. An. Ecol., 19:159-174.
- . 1951. An ecological study of the river Towy. *Ibid.*, 20:68-86.
- KAPLAN, M. F., AND W. L. MINCKLEY. 1960. Land snails from the Doe Run Creek area, Meade County, Kentucky. Nautilus, 74:62-65.
- KENDALL, J. L. 1941. Climate of Kentucky. In *Climate and man*. U. S. Dept. Agri., House Doc. 27, 77th Congress, 1st Session. Pp. 884-893.
- KRAATZ, W. C. 1923. A study of the food of the minnow *Campostoma anomalum*. Ohio J. Sci., 23:265-283.
- KRECKER, F. H. 1939. A comparative study of the animal population of certain submerged aquatic plants. Ecology, 20:553-562.
- KRUMHOLZ, L. A. 1948. The use of rotenone in fisheries research. J. Wildl. Mgmt., 12: 305-317.
- , J. R. CHARLES, AND W. L. MINCKLEY. 1962. The fish population of the Ohio River. In *Aquatic-life resources of the Ohio River*. Ohio River Valley Water Sanitation Commission, Cincinnati. Pp. 49-89, 143-152, 166-180, 200-210.
- KUEHNE, R. A. 1958. Studies on the schooling behavior of the minnows, *Semotilus* and *Rhinichthys*. Diss. Abstr., 19:606.
- LANGLOIS, T. H. 1937. Bait culturists guide. Ohio Dept. Agric., Div. Cons., Bull., 137:1-23.
- . 1954. The western end of Lake Erie and its ecology. J. W. Edwards, Inc., Ann Arbor. xx + 479pp.
- LARIMORE, R. W. 1952. Home pools and homing behavior of smallmouth black bass in Jordan Creek. Ill. Nat. Hist. Surv., Biol. Notes, 28:1-12.

- . 1954. Dispersal, growth, and influence of smallmouth bass stocked in a warm-water stream. *J. Wildl. Mgmt.*, 18:207–216.
- . 1957. Ecological life history of the warmouth (*Centrarchidae*). *Bull. Ill. Nat. Hist. Surv.*, 27:1–83.
- . 1961. Fish population and electrofishing success in a warm-water stream. *J. Wildl. Mgmt.*, 25:1–12.
- , Q. H. PICKERING, AND L. DURHAM. 1952. An inventory of the fishes of Jordan Creek, Vermillion County, Illinois. *Ill. Nat. Hist. Surv., Biol. Notes*, 29:1–26.
- , W. F. CHILDERS, AND C. HECKROTTE. 1959. Destruction and reestablishment of stream fish and invertebrates affected by drought. *Trans. Am. Fish. Soc.*, 88:261–285.
- LEATHERS, A. L. 1922. Ecological study of aquatic midges and some related insects, with special referenc to feeding habits. *Bull. U. S. Bur. Fish.*, 38:1–61.
- LEGER, L. 1945. Economic biologique et productive de nos riverés a Cyprinides. *Bull. Franc. Piscicult.*, 139:49–69.
- LENNON, R. E., AND P. S. PARKER. 1960. The stoneroller, *Camptostoma anomalum* (Rafinesque), in Great Smoky Mountains National Park. *Trans. Am. Fish. Soc.*, 89:263–270.
- LEONARD, J. W. 1939. Comments on the adequacy of accepted stream bottom sampling technique. *Trans. 4th N. Am. Wildl. Conf.*: 288–295.
- , AND F. A. LEONARD. 1962. Mayflies of Michigan trout streams. *Cranbrook Inst. Sci., Bull.*, 43:i–x, 1–139.
- LEOPOLD, L. B. 1962. *Rivers*. *Am. Sci.*, 50:511–537.
- LEVERETT, F. 1929. The Pleistocene of northern Kentucky. *Ky. Geol. Surv., Ser. IV*, 31:i–xiv, 1–80.
- LINDEMAN, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23:339–418.
- LUDWIG, W. B. 1931. A limnological survey of the Hocking River. B. The bottom invertebrates of the Hocking. *Ohio J. Sci.*, 31:267–268 (Abstr.).
- LYMAN, F. E. 1943. A pre-impoundment bottom fauna study of Watts Bar Reservoir area (Tennessee). *Trans. Am. Fish. Soc.*, 72:52–62.
- MACAN, T. T. 1957. The life histories and migrations of the Ephemeroptera in a stony stream. *Trans. Soc. Brit. Ent.*, 12:120–156.
- . 1958. Methods of sampling the bottom in stony streams. *Mitt. int. ver. Limnol.*, 8: 1–21.
- MAJOR, J. 1961. Use in plant ecology of causation, physiology, and a definition of vegetation. *Ecology*, 42:167–169.
- MARGALEF, R. 1958. "Trophic" typology versus biotic typology, as exemplified in the regional limnology of northern Spain. *Verh. int. ver. Limnol.*, 13:339–349.
- . 1960. Ideas for a synthetic approach to the ecology of running waters. *Int. Rev. ges. Hydrobiol.*, 45:133–153.
- MARTIN, R. G., AND R. S. CAMPBELL. 1953. The small fishes of Black River and Clearwater Lake, Missouri. *In The Black River studies*. *Univ. Mo. Stud.*, 26:1–136. Pp. 45–66.
- MATHESON, R. 1944. *Handbook of the mosquitoes of North America*. (2nd ed.) Comstock Publ. Co., Inc., Ithaca. viii + 314pp.
- MCMANUS, L. R. 1960. An occurrence of "chimney" construction by the crayfish *Cambarus b. bartoni*. *Ecology*, 41:383–384.
- McFARLAN, A. C. 1943. *Geology of Kentucky*. Univ. Ky. Press, Lexington. xviii + 531pp., 117 pls.
- MEINZER, O. E. 1923. Outline of ground-water hydrology. *U. S. Geol. Surv., Water-supply Pap.*, 494:1–52.
- METCALF, A. L. 1959. *Fishes of Chautauqua, Cowley, and Elk counties, Kansas*. Univ. Kans. Publ., Mus. Nat. Hist., 11:345–400, 2 pls.
- MILLER, R. R. 1960. Systematics and biology of the gizzard shad (*Dorosoma cepedianum*) and related species. *U. S. Fish Wildl. Serv., Fish. Bull.*, 173:i–iv, 371–392.
- MINCKLEY, W. L. 1961. Occurrence of subterranean isopods in the epigeal environment. *Am. Midl. Nat.*, 63:452–455.
- . 1962. Studies of the ecology of a spring stream: Doe Run, Meade County, Kentucky. Unpubl. Ph.D. dissertation, University of Louisville. 374pp.
- . 1963. Upstream movements of *Gammarus* (Amphipoda) in Doe Run, Meade County, Kentucky. *Ecology*. *In press*.
- , AND J. E. CRADDOCK. 1961. Active predation of crayfish on fishes. *Prog. Fish-Cult.*, 23:120–123.
- , J. E. CRADDOCK, AND L. A. KRUMHOLZ. 1963. Natural radioactivity in the food web of the banded sculpin, *Cottus carolinæ* (Gill). *In Radioecology*. Reinhold Publ. Co., New York. Pp. 229–236.
- , AND F. B. CROSS. 1959. Distribution, habitat, and abundance of the Topeka shiner, *Notropis topeka* (Gilbert), in Kansas. *Am. Midl. Nat.*, 61:210–217.
- , AND ———. 1960. Taxonomic status of the shorthead redhorse, *Moxostoma aureolum* (LeSueur), from the Kansas River basin, Kansas. *Trans. Kans. Acad. Sci.*, 63:35–39.
- , AND D. R. TINDALL. 1963. Observations on the ecology of *Batrachospermum* sp. (Rhodophyceae) in Doe Run, Meade County, Kentucky. *Bull. Torrey Bot. Club*. *In press*.
- MOFFETT, J. W. 1936. A quantitative study of the bottom fauna in some Utah streams variously affected by erosion. *Bull. Univ. Utah Biol. Ser.*, 3:1–33.

- MOTTLEY, C. McC., H. J. RAYNER, AND J. H. RAINWATER. 1939. The determination of the food grade of streams. *Trans. Am. Fish. Soc.*, 68:336-343.
- MUELLER, K. 1954. Investigations on the organic drift in north Swedish streams. *Inst. Freshwater Res., Drottningholm, Rept.*, 35 (1953):133-148.
- . 1955. Produktionsbiologische Untersuchungen in Nordschwedischen Fließgewässern. *Ibid.*, 36(1954):148-162.
- MUENSCHER, W. C. 1944. Aquatic plants of the United States. Comstock Publ. Co., Ithaca. x + 374pp.
- MURPHY, H. E. 1922. Notes on the biology of our North American species of mayflies. *Lloyd Library (Cincinnati, O.) Ent. Ser.*, 2:1-46.
- MUTTKOWSKI, R. A. 1929. The ecology of trout streams in Yellowstone National Park. *Bull. New York State Coll. For., Roosevelt Wild Life Ann.*, 2:155-240.
- , AND G. M. SMITH. 1929. The food of trout stream insects in Yellowstone National Park. *Ibid.*:241-263.
- NEEDHAM, P. R., AND R. L. USINGER. 1956. Variability in the macrofauna of a single riffle in Prosser Creek, California, as indicated by the Surber sampler. *Hilgardia*, 24:383-409.
- NEEL, J. K. 1951. Interrelations of certain physical and chemical features in a head-water limestone stream. *Ecology*, 32:368-391.
- NELSON, D. J., AND D. C. SCOTT. 1962. Role of detritus in the productivity of a rock-outcrop community in a piedmont stream. *Limnol. Oceanogr.*, 7:396-413.
- NETTING, M. G. 1956. Geography of the upper Ohio Valley. In *Man and the waters of the Upper Ohio basin. Spec. Publ. 1, Pymatuning Lab. Field Biol.* Pp. 2-13.
- NEWELL, A. E. 1957. Two-year study of movements of stocked brook trout and rainbow trout in a mountain stream. *Prog. Fish-Cult.*, 19:76-80.
- NIELSEN, A. 1950a. The torrential invertebrate fauna. *Oikos*, 2:176-196.
- . 1950b. On the zoogeography of springs. *Hydrobiol.*, 2:313-321.
- NIELSEN, C. O. 1962. Carbohydrases in soil and litter invertebrates. *Oikos*, 13:200-215.
- ODUM, E. P. 1959. Fundamentals of ecology. W. B. Saunders Co., Philadelphia. xvii + 546pp.
- ODUM, H. T. 1956. Primary production in flowing waters. *Limnol. Oceanogr.*, 1:102-117.
- . 1957a. Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.*, 27:55-112.
- . 1957b. Primary production measurements in eleven Florida springs and a marine turtle grass community. *Limnol. Oceanogr.*, 2:85-97.
- OHLE, W. 1934. Chemische und physikalische Untersuchungen nordeutscher seen. *Arch. Hydrobiol.*, 26:386-464.
- . 1952. Die hypolimnische Kohlendi-oxyde-Akkumulation als produktionsbiologischer Indikator. *Ibid.*, 46:153-285.
- OOSTING, H. J. 1953. The study of plant communities. W. H. Freeman & Co., San Francisco. 389pp.
- OWENS, M., AND R. W. EDWARDS. 1961. The effects of plants on river conditions II. Further crop studies and estimates of net productivity in a chalk stream. *J. Ecol.*, 49:119-126.
- PALOUMPIS, A. A. 1958. Measurement of some factors affecting the catch in a minnow seine. *Proc. Iowa Acad. Sci.*, 65:580-586.
- PEARSALL, W. H. 1920. The aquatic vegetation of the English lakes. *J. Ecol.*, 8:163-199.
- PEARSE, A. S. 1926. Animal ecology. McGraw-Hill Book Co., Inc., New York. ix + 417pp.
- PENNAK, R. W. 1943. Limnological variables in a Colorado mountain stream. *Am. Midl. Nat.*, 29:189-199.
- . 1953. Fresh-water invertebrates of the United States. Ronald Press, New York. ix + 769pp.
- PERCIVAL, E., AND H. WHITEHEAD. 1929. A quantitative study of the fauna of some types of stream bed. *J. Ecol.*, 17:382-414.
- PRESCOTT, G. W. 1951. Algae of the western Great Lakes region. *Cranbrook Inst. Sci., Bull.*, 31:1-924.
- RANEY, E. C., AND E. A. LACHNER. 1946. Age, growth and habits of the hog sucker, *Hypentelium nigricans* (LeSueur), in New York. *Am. Midl. Nat.*, 36:76-86.
- RAWSON, D. S. 1930. The bottom fauna of Lake Simcoe and its role in the ecology of the lake. *Univ. Toronto Stud., Biol. Ser.*, 40:1-183.
- REID, G. K. 1961. Ecology of inland waters and estuaries. Reinhold Publ. Co., New York. xvi + 375pp.
- RICKER, W. E. 1934a. An ecological classification of certain Ontario streams. *Univ. of Toronto Stud., Biol. Ser.*, 37:1-114.
- . 1934b. A critical discussion of various measures of oxygen saturation in lakes. *Ecology*, 15:348-363.
- . 1959. Plecoptera. In *Fresh-water biology*. John Wiley & Sons, Inc., New York. Pp. 941-957.
- RIDENOUR, G. L. 1929. Early times in Meade County, Kentucky. Western Recorder Co., Louisville. 108pp.
- RIGGS, C. D. 1947. Purple martins feeding on emerging may-flies. *Wilson Bull.*, 59:113-114.

- ROELOFS, E. W. 1944. Water soils in relation to lake productivity. Mich. St. Coll., Agri. Exp. Sta. Tech. Bull., 190:1-31.
- ROLL, H. 1938. Die Pflanzengesellschaften östholsteinischer Fließgewässer. Arch. Hydrobiol., vol. 34 (cited in Blum, 1956a).
- . 1939a. Die Entwicklung der Potamobotanik. Int. Rev. ges. Hydrobiol., vol. 39 (cited in Blum, 1956a).
- . 1939b. Einige Waldequellen Holsteins und ihre Pflanzengesellschaften. Bot. Jahrbucher, vol. 70 (cited in Blum, 1956a).
- ROOS, R. 1957. Studies on the upstream migration in adult stream-dwelling insects. I. Inst. Freshwater Res., Drottningholm, Rept., 38 (1956):166-193.
- ROSINE, W. N. 1955. The distribution of invertebrates on submerged aquatic surfaces in Muskee Lake, Colorado. Ecology, 36:308-314.
- ROSS, H. H. 1953. The caddisflies, or Trichoptera, of Illinois. Bull. Ill. Nat. Hist. Surv., 23:1-326.
- . 1959. Trichoptera. In Fresh-water biology. John Wiley & Sons, Inc., New York. Pp. 1,024-1,049.
- RUTTNER, F. 1948. Die Veränderungen des Äquivalentleitvermögens als Mass der Karbonatassimilation der Wasserpflanzen. Schweiz. Z. Hydrol., 11:72-89 (cited from Hutchinson, 1957).
- . 1953. Fundamentals of Limnology. Univ. Toronto Press, Toronto. xvi + 242pp. (translated by D. G. Frey and F. E. J. Fry).
- . 1960. Über die Kohlenstoffaufnahme bei Algen aus der Rhodophyceen-Gattung *Batrachospermum*. Schweizer. Z. Hydrol., 22:280-291.
- SAUER, C. O. 1927. Geography of the Pennyroyal. Ky. Geol. Surv., Ser. VI, 5:i-xii, 1-249.
- SCHMITZ, W. 1955. Physiographische Aspekte de limnologischen fließgewässertypen. Arch. Hydrobiol., Suppl., 22:310-523.
- SCHNELLER, M. V. 1955. Oxygen depletion in Salt Creek, Indiana. Invest. Ind. Lakes Streams, 4:163-176.
- SCOTT, D. C. 1949. A study of a stream population of rock bass. *Ibid.*, 3:169-234.
- SELLECK, G. W. 1960. The climax concept. Bot. Rev., 26:534-545.
- SHELFORD, V. E. 1911a. Ecological succession. I. Stream fishes and the method of physiographic analysis. Biol. Bull., 21:9-34.
- . 1911b. Ecological succession. II. Pond fishes. *Ibid.*, 22:1-38.
- . 1912. Ecological succession. IV. Vegetation and the control of land animal communities. *Ibid.*, 23:59-99.
- . 1913. Animal communities in temperate America. Univ. Chicago Press, Chicago. xiii + 362pp.
- , AND S. EDDY. 1929. Methods for the study of stream communities. Ecology, 10:382-391.
- SHOUF, C. S. 1948. Limnological observations on some streams of the New River watershed in the vicinity of Mountain Lake, Virginia. J. Elisha Mitchell Sci. Soc., 64:1-12.
- . 1950. Field chemical examination of the waters in Tennessee streams. J. Tenn. Acad. Sci., 25:4-55.
- 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.
- SPRULES, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ontario. Univ. Toronto Stud., Biol. Ser., 56:1-81.
- STARRETT, W. C. 1950a. Distribution of the fishes of Boone County, Iowa, with special reference to the minnows and darters. Am. Midl. Nat., 43:112-127.
- . 1950b. Food relationships of the minnows of the Des Moines River, Iowa. Ecology, 31:216-233.
- . 1951. Some factors affecting the abundance of minnows in the Des Moines River, Iowa. *Ibid.*, 32:13-27.
- , AND P. G. BARNICKOL. 1955. Efficiency and selectivity of commercial fishing devices used on the Mississippi River. Bull. Ill. Nat. Hist. Surv., 26:325-366.
- STEIDTMANN, E. 1935. Travertine-depositing waters near Lexington, Virginia. Science, 82:333-334.
- STEWART, N. H. 1926. Development, growth, and food habits of the white sucker, *Catostomus commersonii* LeSueur. Bull. U. S. Bur. Fish., 42:147-183.
- STUMM, W., AND G. F. LEE. 1960. The chemistry of aqueous iron. Rev. Suisse d'Hydrol., 22:295-319.
- SURBER, E. W. 1937. Rainbow trout and bottom fauna production in one mile of stream. Trans. Am. Fish. Soc., 66:193-202.
- . 1939. A comparison of four eastern smallmouth bass streams. *Ibid.*, 68:322-335.
- . 1951. Bottom fauna and temperature conditions in relation to trout management in St. Mary River, Augusta County, Virginia. Va. J. Sci., 2(n.s.):190-202.
- SWINDALE, D. N., AND J. T. CURTIS. 1957. Phytosociology of the larger aquatic plants in Wisconsin lakes. Ecology, 38:397-407.
- SWINGLE, H. S., AND E. V. SMITH. 1950. Factors affecting the reproduction of bluegill bream and largemouth black bass in ponds. Agri. Exp. Sta., Ala. Poly. Inst., Circ., 87:1-8.

- SWINNERTON, A. C. 1942. Hydrology of limestone terranes. In Hydrology, physics of the earth. IX. McGraw-Hill Book Co., New York. Pp. 656-677.
- SYMOENS, J. J. 1951. Equisse d'un systema des associations algales d'eau douce. Verh. int. ver. theoret. angew. Limn., 11:395-408.
- . 1957. Les eaux douces de l'Ardenne et des rigions voisines: Les milieus et leur vegetation algale. Bull. R. Soc. Belg., 89:111-314.
- TAYLOR, W. R. 1954. Records of fishes in the John N. Lowe collection from the Upper Peninsula of Michigan. Misc. Publ. Mus. Zool., Univ. Mich., 87:1-50.
- TEAL, J. M. 1957. Community metabolism in a temperate cold spring. Ecol. Monogr., 27: 283-302.
- TEBO, L. B., AND W. W. HASSLER. 1961. Seasonal abundance of aquatic insects in western North Carolina trout streams. J. Elisha Mitchell Sci. Soc., 77:249-259.
- THIENEMANN, A. 1953. Fluss und See, ein limnologischer Vergleich. Gewässer und Abwasser, 1:13-30.
- THOMAS, H. A., JR. 1958. Mixing and diffusion of wastes in streams. In Oxygen relationships in streams. Robt. A. Taft San. Eng. Cent., Tech. Rept. W58-2:97-103.
- THOMPSON, D. H., AND F. D. HUNT. 1930. The fishes of Champaign County, a study of the distribution and abundance of fishes in small streams. Bull. Ill. Nat. Hist. Surv., 19:1-101.
- THOMPSON, J. W. 1944. A survey of the larger aquatic plants and bank flora of the Brule River. Wis. Acad. Sci., Arts, and Lett., 36:57-76.
- THOMPSON, R. H. 1959. Algae. In Fresh-water biology. John Wiley & Sons, Inc., New York. Pp. 115-170.
- TIFFANY, L. H. 1930. The Oedogoniaceae: a monograph. Publ. by the author, Spahr and Glenn Co., Columbus. 326pp.
- , AND M. E. BRITTON. 1952. The algae of Illinois. Univ. Chicago Press, Chicago. xiv + 407pp.
- TINDALL, D. R. 1962. Life history and ecology of *Nitella flexilis* (Characeae). Unpubl. Master's Thesis. University of Louisville. 77pp.
- TRANSEAU, E. N. 1913. The periodicity of algae in Illinois. Trans. Am. Microscop. Soc., 32: 31-40.
- TRAUTMAN, M. B. 1931. *Notropis volucellus wickliffi*, a new subspecies of cyprinid fish from the Ohio and Upper Mississippi rivers. Ohio J. Sci., 13:468-474.
- . 1939. The effects of man-made modifications on the fish fauna in Lord and Gordon Creeks, Ohio, between 1887-1938. *Ibid.*, 39:275-288.
- . 1942. Fish distribution and abundance correlated with stream gradients as a consideration in stocking programs. Trans. 7th N. Am. Wildl. Conf., 211-233.
- . 1957. The fishes of Ohio. Ohio State Univ. Press, Columbus. xvii + 683pp., 7 pls.
- , AND R. G. MARTIN. 1951. *Moxostoma aureolum pisolabrum*, a new subspecies of sucker from the Ozarkian streams of the Mississippi River system. Occ. Pap. Mus. Zool., Univ. Mich., 534:1-10, 1 pl.
- TRUESDALE, G. A., A. L. DOWNING, AND G. F. LOWDEN. 1955. The solubility of oxygen in pure water and sea-water. J. Appl. Chem. Lond., 5:53-63.
- TWENHOFEL, W. H. 1939. Principles of sedimentation. McGraw-Hill Book Co., New York. x + 610pp.
- USINGER, R. L. (ED.) 1956. Aquatic insects of California with keys to North American genera and California species. Univ. Calif. Press, Berkeley and Los Angeles. ix + 508pp.
- WALKER, B. A. 1961. Studies on Doe Run, Meade County, Kentucky. IV. A new species of isopod crustacean (genus *Asellus*) from Kentucky. Trans. Am. Microscop. Soc., 80: 385-390.
- . 1962. The ecology of the epigeal isopod *Asellus bivittatus* in Doe Run, Meade County, Kentucky. Unpubl. Master's Thesis, University of Louisville. 32pp.
- WALKER, E. H. 1957. The deep channel and alluvial deposits of the Ohio Valley in Kentucky. U. S. Geol. Surv., Water-supply Pap., 1411:i-iii, 1-25, 6 pls.
- WATERS, T. F. 1961. Standing crop and drift of stream bottom organisms. Ecology, 42: 532-537.
- . 1962. A method to estimate the production rate of a stream bottom invertebrate. Trans. Am. Fish. Soc., 91:243-250.
- WELCH, P. S. 1935. Limnology. McGraw-Hill Book Co., New York. xiv + 471pp.
- . 1948. Limnological methods. Blakiston Co., Philadelphia. xviii + 381pp.
- WENE, G., AND E. L. WICKLIFF. 1940. Modification of a stream bottom and its effect on the insect fauna. Can. Ent., 72:131-135.
- WETZEL, R. G. 1960. Marl encrustations on hydrophytes in several Michigan lakes. Oikos, 11:223-236.
- WHERRY, E. T. 1920. Soil acidity and a field method for its measurement. Ecology, 1: 160-173.
- WHITEHEAD, H. 1935. An ecological study of the invertebrate fauna of the chalk stream near Great Driffield, Yorkshire. J. An. Ecol., 4:58-78.
- WHITFORD, L. A. 1956. The communities of algae in the springs and spring streams of Florida. Ecology, 37:433-442.

- . 1960a. Ecological distribution of fresh-water algae. In *The ecology of algae*. Spec. Publ. 2, Pymatuning Lab. Field Biol. Pp. 2-10.
- . 1960b. The current effect and growth of fresh-water algae. *Trans. Am. Microscop. Soc.*, 79:302-309.
- , AND G. J. SCHUMACHER. 1961. Effect of current on mineral uptake and respiration by a fresh-water algae. *Limnol. Oceanogr.*, 6:423-425.
- WHITTAKER, R. H. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecol. Monogr.*, 23:41-78.
- WILSON, L. R. 1935. Lake development and plant succession in southern Vilas County, Wisconsin. *Ecol. Monogr.*, 5:207-247.
- . 1937. A quantitative and ecological study of the larger aquatic plants of Sweeny Lake, Oneida County, Wisconsin. *Bull. Torrey Bot. Club*, 64:199-208.
- . 1939. Rooted aquatic plants and their relation to the limnology of freshwater lakes. In *Am. Assn. Adv. Sci., Publ.*, 10:101-122.
- . 1941. The larger aquatic vegetation of Trout Lake, Vilas County, Wisconsin. *Wis. Acad. Sci., Arts, and Lett.*, 33:135-146.
- WINN, H. E. 1958a. Comparative reproductive behavior and ecology of fourteen species of darters (Pisces-Percidae). *Ecol. Monogr.*, 28:155-191.
- . 1958b. Observations on the reproductive habits of darters (Pisces-Percidae). *Am. Midl. Nat.*, 59:190-223.
- WIRTH, W. W., AND A. STONE. 1956. Aquatic Diptera. In *Aquatic insects of California, with keys to North American genera and California species*. Univ. Calif. Press, Berkeley and Los Angeles. Pp. 372-482.
- WITT, A., JR., AND R. C. MARZOLF. 1954. Spawning and behavior of the longear sunfish, *Lepomis megalotis megalotis*. *Copeia*, 1954:188-190.
- WOOD, R. D., AND W. C. MUENSCHER. 1956. The Characeae of New York. Cornell Univ., Agri. Exp. Sta. Mem., 338:1-77.
- WU, Y. F. 1931. A contribution to the biology of *Simulium* (Diptera). *Pap. Mich. Acad. Sci., Arts, and Lett.*, 13:543-599.
- YOUNG, O. W. 1945. A limnological investigation of periphyton in Douglas Lake, Michigan. *Trans. Am. Microscop. Soc.*, 64:1-20.
- ZOBELL, C. E., AND C. B. FELTHAM. 1938. Bacteria as food for certain marine animals. *J. Mar. Res.*, 4:312-327.
- , AND ———. 1942. The bacteria of flora of a marine mud flat as an ecological factor. *Ecology*, 23:69-78.