A Limnological Study of a Tennessee Cold Springbrook

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ABSTRACT: A one-year limnological investigation was conducted on an unnamed cold springbrook in Putnam County, Tennessee. The study was undertaken to analyze the components of invertebrate biocoenoses, to record population fluxes, and to determine possible factors affecting abundance and interactions between members of the communities of a relatively uniform habitat. Fifty-nine taxa of invertebrates were recorded. Relative abundance was greatest in February and lowest in July. The surrounding deciduous forest was determined to have the greatest effect on species composition and abundance of the fauna of the springbrook.

INTRODUCTION

Small, constant-temperature springs afford as nearly perfect systems for the study of lotic communities as occur in nature. They have comparatively unchanging physico-chemical environments which reduce the variables to be considered in the field and enhance the possibilities of laboratory duplication. In spite of these advantages, there has been little well documented information concerning the dynamics of cold springbrooks throughout the year, especially in winter when the invertebrate populations are at their maxima. Dudley (1953) investigated the faunas of some springs of varying temperatures, and Noel (1954), Odum (1957), and Teal (1957) observed various aspects of cold springs in New Mexico, Florida, and Massachusetts, respectively.

This study was undertaken to analyze the components of invertebrate biocoenoses, to record population fluxes, and to determine possible factors affecting abundance and interactions between members of the communities in a relatively uniform habitat, a cold springbrook.

DESCRIPTION OF THE STUDY AREA

GEOGRAPHY, GEOLOGY, AND CLIMATE

The unnamed brook lies 2 mi WSW of Monterey, Tennessee, in eastern Putnam Co., at 36° 8′ 13″ N and 85° 17′ 30″ W (Monterey quadrangle, 1955 projection, USGS). Sixty-one meters south of the brook lies a stream with which it merges eventually. After merging, the stream flows through Tayes Hollow and empties into the Calfkiller River.

The brook, located on stony and cobbly colluvium, lies between a sandstone plateau and a limestone valley. The surrounding slopes are steep and rough with many rock outcrops, loose stones, and boulders. Soil drainage is rapid. The soil supports hardwood forests of yellow

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poplar (*Liriodendron tulipifera* L.), white oak (*Quercus alba* L.), northern red oak (*Quercus borealis* Michx.), red maple (*Acer rubrum* L.), and hickory (*Carya* spp.).

Rainfall is abundant in Putnam County; the annual maximum is 150 cm (59 inches). There is more precipitation in winter and spring than at other times. Average maximum and minimum yearly temperatures are 20.5 C (69 F) and 8 C (47 F), respectively (Jackson *et al.*, 1963).

DESCRIPTION OF THE SPRINGBROOK

This study was carried out along a 37-m portion of the brook, extending uphill from Tennessee highway 84 to a hole from which the brook emerges. The brook is a rheocrene, a spring which flows away from the source with a swift gradient (Fig. 1). It is approximately 1.8 m wide throughout its length, narrowing to as little as 0.8 m just downstream from the source and widening to as much as 2.7 m near the highway. The general restriction of the brook to its narrow channel and the preponderance of bedrock and marl substrata prevent pool formation.

Three stations were established along the brook (Fig. 1). Station I was located at the source. The spring width here is 2.3 m and the substratum consists of marl. The only aquatic vegetation present occurred at the point of emergence from the hillside and consisted of the water moss, *Fontinalis antipyretica* Hedw. Station II was 18 m from the source and is 2.1 m wide. It is on a plateau and affords

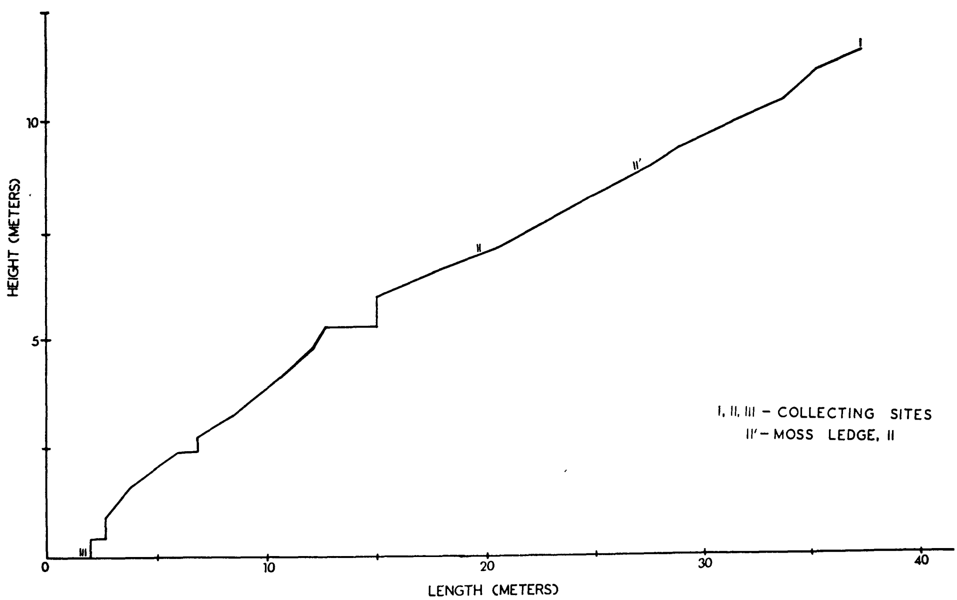

Fig. 1.—Longitudinal profile of the cold springbrook, Putnam County, Tennessee.

little surface for vegetational growth. Water moss was collected for this station from a ledge 9 m from the source. Station III was 35 m from the source. The station was covered by water moss and by filamentous green algae.

The bottom of the brook consists of bedrock covered by marl and sand. The banks are covered by a luxuriant growth of mosses. In summer the brook is heavily shaded by the surrounding deciduous forest.

Upon reaching the highway, the brook enters a culvert and flows under the road. The culvert extends out 23 cm from the far shoulder, and its bottom is 15 cm above the spring bed. Thus, organisms are allowed to drift downstream, but are precluded from upstream passage into the brook due to the sharp vertical drop of the brook beneath the downstream opening of the culvert.

METHODS

PHYSICAL METHODS

Water current velocity was measured on the days of biological and chemical analyses by means of a small Price AA mechanical current meter. Air and water temperatures were measured on the days of biological analyses with a calibrated chemical thermometer and on the days of chemical analyses with a thermistor. Specific conductance was measured in the laboratory on the days of chemical analyses with an Industrial Instruments Model RC-7P conductivity bridge equipped with a 0.1 sensor probe.

The amount of light reaching the brook was measured on two occasions (summer and winter) with a Photovolt photometer. One cell of the meter was placed in the sunlight, and another cell was placed on a stone just above the water surface in the spring bed. Both measurements were taken at 1200 hours (CST).

CHEMICAL METHODS

Chemical analyses were carried out monthly from 1 April 1965 through 1 March 1966. Water from each of the stations was transported to the laboratory in amber polyethylene bottles for immediate analysis.

Determination of dissolved oxygen was made in the field using the unmodified Winkler method (Anonymous, 1960). All determinations were corrected for altitude (Mortimer, 1956). Beginning in October 1965, replicate dissolved oxygen measurements were made in the field with a YSI Model 51 dissolved oxygen meter and with a Hach dissolved oxygen kit.

Free carbon dioxide was determined from a nomogram (Moore, 1939). Hydrogen-ion concentration was measured colorimetrically in the field (Hellige comparator) and electrometrically in the laboratory. Alkalinity, orthophosphate (stannous chloride method), and nitrate-nitrogen were measured according to Standard Methods (Anonymous, 1960). Hardness (calcium and total) and silica were determined with Hach kits (Hach Chemical Co., Ames, Iowa).

BIOLOGICAL METHODS

Preliminary qualitative sampling was carried out from January through March 1965. The benthic invertebrates were sampled quantitatively every two weeks from 1 April 1965 through 15 March 1966. Collections were taken from stones and aquatic vegetation at each of the three stations. Leaf packets were examined for animals from November 1965 through March 1966. On four occasions the plankton was qualitatively sampled.

A 0.1-m^2 frame was used for sampling the substrate. It was placed in the spring bed, stones within the area were turned, and the invertebrates collected. When possible, two samples were taken at each station to minimize error caused by the clumping of some taxa (Gaufin *et al.,* 1956). All specimens were preserved in 70% ethyl alcohol in the field for identification in the laboratory.

The 0.1-m^2 frame was also employed to sample the leaf packets. Leaves were placed in containers and returned to the laboratory, where each leaf was washed in a #60 sieve (mesh size—250μ). The organisms were hand-picked from the debris under a dissecting microscope and were preserved for identification and enumeration.

Moss and algae were collected by hand at each station. The vegetation was removed from ledges and placed in a 180-cc jar until it was tightly packed. Field measurements indicated that this amount of vegetation normally covered an area of 0.1 m^2 of the spring bed. The samples were returned to the laboratory and placed in covered finger bowls in the refrigerator (11 C) until examination. The organisms were washed from the vegetation into a #60 sieve and were preserved. Those remaining in the vegetation were hand-picked under a dissecting microscope.

The collection methods employed did not yield absolute numerical results. However, they did permit the determination of relative abundance of the more commonly occurring taxa. All organisms in the community were taken into account, and dominant taxa were easily recognized. Needham and Usinger (1956), working in Prosser Creek, California, showed that 194 samples would be required to give statistically meaningful results (.05 level) on total weight of organisms. Therefore, no attempt was made to analyze the results statistically, since it had been shown that in various lotic habitats purely quantitative routine sampling to determine weights and numerical data is impractical. Information concerning food habits was obtained primarily from field observations. Qualitative analyses of gut contents were made frequently during the study.

PHYSICAL ENVIRONMENT

Medians, maxima, and minima for physical factors are listed in Table 1.

Current.—The mean water velocity was less than the minimum of 0.5 m/sec which characterizes a springbrook as swift-flowing (Kendeigh, 1961). Although the gradient was steep (Fig. 1), the velocity was primarily dependent upon the amount of flow per unit time and upon the extent to which the flow was obstructed by irregularities of the spring bed. The flow was greatest from April through July, moderate from August through October, and least from November through February. It was sluggish in autumn and winter due to lack of rainfall and to the high quantity of dead leaves which dissected the flow. In winter the spring bed was covered by more sand than at any other time, because of the low water velocity.

Increases in water velocity occurred rapidly after rain. Prior to 5 May 1965, there were several weeks without precipitation, and the spring bed was reduced to half its normal size. On 5 May the velocity was measured before a rainstorm and approximately two hours thereafter. The results at each station were as follows:

	Before (m/sec)	After (m/sec)
Station I	0.30	1.56
Station II	0.66	0.69
Station III	0.12	0.56

Water Temperature.—Water temperature (Table 1) is dependent on altitude, aspect, and type of source (Hynes, 1961). Throughout the study temperature ranged from 11.2 to 15.8 C at Station I, 10.6 to 15.8 C at Station II, and 10.2 to 15.9 C at Station III. Maxima occurred in late May before the tree canopy developed. On 29 July 1965 the air temperature was taken in the shade adjacent to the brook and 10 m away from the brook. A difference of 8 C was found between the two locales, illustrating the cooling effect of the brook on the surrounding air.

Incident Light.—Incident light was measured on two occasions. On 8 August 1965 it measured 900 cp over the brook and 10,000 cp in unbroken sunshine. This seasonal effect was due to heavy shading of the water by the tree canopy. As leaves fell in November, the incident light increased until it coincided with that of direct sunlight.

Specific Conductance.—A linear relationship exists between specific conductance (Table 1) and total ionic concentration in fresh water (Mackereth, 1963). Egglishaw and Morgan (1965) considered streams with a concentration of greater than 400 micro-equivalents of total cations per liter to be chemically rich waters. The brook contained 1,260 micro-equivalents/l of total cations.

TABLE 1.—Medians, maxima, and minima for physical factors

Physical factor	Median	Max.-min.	Dates of max.-min.
Current (m/sec)	0.19	0.9- 0.1	1 VI 65-1 I 66
Water temperature (C)	12.6	15.8- 10.7	15 V 65-1 II 66
Specific conductance (micromhos at 25 C)	152.8	164.0-123.7	1 II 66-1 V 65

CHEMICAL ENVIRONMENT

Medians, maxima, and minima for chemical factors are given in Table 2.

Dissolved oxygen (Table 2) was lowest between May and November. It was related primarily to water temperature, and to a lesser degree to decomposing organic matter. Hynes (1961) stated that the percentage saturation rather than the amount of dissolved oxygen is the important factor in determining faunal presence or absence. The mean percentage saturation in the brook was 95%. At no time did it limit faunal presence.

Beginning in October 1965, comparative studies of dissolved oxygen were made using the unmodified Winkler method, a Hach kit, and a YSI Model 51 dissolved oxygen meter. No significant differences were found, other than temporal and economic, between the three methods.

Subterranean waters are rich in carbon dioxide collected during the passage of water through a soil atmosphere generously supplied with the gas (Minckley, 1963). The bicarbonate content of spring water when it emerges is dependent on the calcium content of the earth and on the carbon dioxide content of the water. As soon as the spring emerges, the equilibrium carbon dioxide begins to escape. If the water is rich in lime, marl is deposited (Ruttner, 1963). Marl deposition occurred at Station I in the brook.

Carbon dioxide was inversely related to *p*H, alkalinity, and hardness (Table 2). Total alkalinity and hardness were greatest during the autumn and winter due to organic decomposition. The *p*H of the brook increased due to the increase in alkalinity. Acidity of the spring water increased at flood times, and the calcium content and alkali reserves were greatly reduced. This may be attributed to dilution of the normal spring water by surface water containing less mineral matter. On 1 July 1965, chemical analyses of the brook were carried out immediately after a rainstorm. Total alkalinity was 24.9 ppm $CaCO_3$; calcium hardness, 34.0 ppm; total hardness, 51.0 ppm; *p*H, 7.0; and free carbon dioxide, 4.6 ppm.

On all sampling occasions 4.0 ppm of silica were found (Table 2).

TABLE 2.—Medians, maxima, and minima for chemical factors

Chemical factor	Median	Max.-min.	Dates of max.-min.
Dissolved oxygen (ppm)	9.3	10.6- 8.5	II 66 - IX 65
*p*H	7.3	7.4- 7.1	II 66 - IX 65
Total alkalinity (ppm $CaCO_3$)	30.6	33.7-26.7	VIII 65 - III 66
Free carbon dioxide (ppm)	3.2	4.5- 2.7	VIII 65 - II 66
Calcium hardness (ppm)	51.3	68.0-51.0	Five occasions each
Total hardness (ppm)	68.4	86.0-68.0	Four & six occasions
Nitrate nitrogen (ppm)	1.2	1.8- 0.8	IX 65 - XII 65
Silica (ppm)	4.0	4.0- 4.0	All occasions

Silica, mainly as orthosilicate, was dissolved from stones by the reaction of carbon dioxide with the silicate.

There was no detectable orthophosphate (less than 0.001 ppm) during the study, except on the rainy day of 1 July 1965. At Station III 0.002 ppm of phosphate was present, probably due to its solution from stone containing calcium diphosphate. The stone is insoluble in water, but can be eroded by a weak solution of carbonic acid, which owes its presence to the action of free carbon dioxide (Neel, 1951).

Nitrate abundance was influenced by surface runoff and by decomposition of organic debris. It decreased in autumn and winter due to more available light, which increased the photosynthetic rate (Table 2). This, in turn, increased the uptake of nitrate by plants. There was little rain during this period, and little surface runoff occurred.

THE BIOTA

ALGAE

Benthic algae are of primary importance in small, swift streams since potamoplankton rarely occurs (Eddy, 1934). The tychoplankton present is derived from the scouring of the benthos by the current, and it consists chiefly of diatoms (Butcher, 1932; Badcock, 1949). The brook was sampled on four occasions for tychoplankton. The samples of April and October 1965 yielded diatoms—*Navicula* sp., *Tabellaria flocculosa* (Roth) Kuetz., *Fragilaria virescens* Ralfs, *Anomoeoneis vitrea* (Grun.) Ross, *Caloneis ventricosa* (Ehr.) Meist., and *Synedra ulna* (Nitz.) Ehr. The samples of July 1965 and January 1966 contained no plankton. These data agreed with those of Jones (1950).

Algae of swiftly flowing waters are of two morphological types: encrusting forms and those in which the thallus projects or trails in the current (Smith, 1950). The most abundant encrusting alga was *Phormidium retzii* (Ag.) Gom. It occurred as a thin, irregular layer over the stones; the average thickness was 2 mm. Many diatoms were present beneath it and among its trichomes. *P. retzii* occurred throughout the year at Station III and during late winter and spring at Station II.

Cladophora glomerata (L.) Kuetz. was the most abundant epilithic alga. At Station II it showed a marked spring growth followed by a rapid disappearance in June and July with the leafing out of surrounding deciduous trees. Blum (1957) found that the alga disappeared with the formation of a tree canopy in spring. *C. glomerata* occurred continuously at Station III, since the habitat was unshaded. *Tabellaria flocculosa* was often associated with *C. glomerata* and gave it a reddish-brown color. Other epilithic algae present were *Microspora stagnorum* (Kuetz.) Lagerh., *Rhizoclonium hieroglyphicum* (Ag.) Kuetz., and *Oedogonium* sp. Lack of abundant algal growth in the brook may have been due to browsing, current, light intensity, instability of the spring bed, or a combination of these factors.

WATER MOSS

The only other aquatic vegetation present was the water moss, *Fontinalis antipyretica*. It can only assimilate free carbon dioxide; therefore, it is found only in habitats such as the brook where the free carbon dioxide is high (Ruttner, 1963). The moss was present at all three stations at the initiation of the study. By 15 September 1965 it had become too sparse for further collection from Station I. Its disappearance was probably due to shading by the tree canopy and a slow growth rate, coupled with collection for analysis. *F. antipyretica* was abundant on firmly fixed stones and ledges. Various diatoms, rotifers (*Dorria dalecarlica* Myers, *Keratella cochlearis* Gosse, and *Philodina* sp.), nematodes, ostracods, and copepods were associated with the moss.

INVERTEBRATES

The springbrook differed from the characteristic cold spring described by Pennak (1953) in lacking leeches and molluscs and in not having black fly larvae and planarians in abundance. The following macrobenthic animals were collected during the study: (* indicates that fewer than five organisms were collected)

PLATYHELMINTHES

Turbellaria: *Phagocata morgani* (Stevens and Boring).

ARTHROPODA

Isopoda: *Asellus militaris* Hay.

Amphipoda: *Gammarus minus* Say.

Decapoda: *Cambarus bartoni* (Fabricius).

Hydracarina: undetermined.

Collembola: *Podura aquatica* L.

Ephemeroptera: *Iron* sp.; *Ephemerella simplex* McDunnough; *Baetis vagans* McDunnough.

Plecoptera: *Nemoura* sp.; *Isogenus subvarians* (Banks); *Alloperla* sp.*; *Acroneuria abnormis* (Newman).

Megaloptera: *Chauloides pectinicornis* L.*

Trichoptera: *Rhyacophila lobifera* Betten; *Hydropsyche bifida* Banks; *Ochrotrichia unio* (Ross); *Pycnopsyche* sp.*; *Goera* sp.*; *Brachycentrus lateralis* (Say)*; *Sericostoma* sp.

Coleoptera: *Hydraena* sp.*; *Hydrochus* sp.*; *Stenelmis* sp.*; *Ectopria* sp.

Diptera: *Tipula abdominalis* (Say); *Tipula ignobolis* Loew; *Dicranota notabilis* Alexander; *Erioptera* sp.*; *Hexatoma* sp.*; *Limonia canadensis* (Westwood); *Pedicia* sp.*; *Pericoma albitarsis* (Banks); *Dixa modesta* Johannsen; *Simulium* sp.*; *Pentaneura* spp.; *Anatopynia* sp.*; *Procladius culiciformis* (L.); *Procladius* sp.; *Pelopia punctipennis* Meigen; *Prodiamesa bathyphila* (Kieffer); *Prodiamesa* sp.; *Brillia* sp.; *Metriocnemus* sp.; *Hydrobaenus* sp.; *Calospectra dissimilis* Johannsen; *Calospectra dives* (Johannsen); *Lauterborniella varipennis* (Coquillett); *Tanytarsus* (*Stictochironomus*) sp.; *Tanytarsus* (*Tanytarsus*) sp.; *Cryptochironomus* sp.; *Tendipes* (*Tendipes*) sp.; *Palpomyia* sp.; *Thaumalea* sp.; *Stratiomys* sp.*; *Eulalia* sp.*; *Dolichopus* sp.*; *Hemerodromia* sp.; *Limnophora aequifrons* Stein.

ECOLOGY OF ABUNDANT INVERTEBRATES

Turbellaria.—*Phagocata morgani* has an ecological preference for headwaters and is restricted to water between 4 and 14 C. The planarians were photo-negative and occurred on the undersides of flat stones, leaves, or debris during the day. They were most abundant on substrates in swift water. Often they occurred in dense aggregations probably related to current and/or food supply. Teal (1957) reported that *P. morgani* had no definite breeding period in a Massachusetts cold spring. This was also the case in the springbrook.

Isopoda.—*Asellus militaris* is able to take advantage of local conditions and to build a large population in the presence of abundant food (Hynes, 1963b). Reproduction is rapid; the female carries approximately 60 eggs in her brood pouch and a new brood can be produced every five to six weeks (Needham and Lloyd, 1916). Prior to November 1965, the asellid population was at a minimum (Table 3). In November leaf packets and other obstructions collected in the spring bed. The leaf packets afforded both substrate and food source for the isopods, and they were quickly colonized by mature asellids.

The first generation lasted from November through mid-January; the second, from mid-December through the remainder of the study. The newborn asellids were herbivorous and were seen first on the moss-algae substratum; as they matured, they moved onto the leaves and stones. The population decreased in size with the removal of leaf packets from the brook by decomposition and washing.

Amphipoda.—*Gammarus* is abundant where it is not likely to be swept away by swift currents (Hynes, 1963b). *Gammarus minus* aggregated among the stones, moss-algae, and leaf packets in the brook. When available, leaf packets were preferred to vegetation. *G. minus* is an omnivorous scavenger, eating algae, dead leaves, midges, mayflies, detritus, and debris (Teal, 1957; Minckley, 1963); it fed primarily on particulate detritus and diatoms in the brook.

Breeding in the brook began in early February and continued through September (Table 3). The first young appeared in March. The old generation had begun to disappear by April; most were gone by mid-July when the majority of the new generation were mature. These continued breeding through August and September. After breeding ceased at the end of September, mature amphipods entered a resting stage until spring, when they were ready to breed again. Hynes (1955) found in experimental tanks that this resting stage could be induced by lack of food.

Decapoda.—*Cambarus bartoni* was present continuously in the brook. Mature organisms and young were found throughout the year. Adults foraged actively in the daytime, but juveniles seldom were seen in the open. The young hid in leaf packets and detritus and the adults hid in burrows or under stones. *C. bartoni* was seen preying upon various Ephemeroptera, tipulid larvae, and tendipedid larvae.

Ephemeroptera.—The ecological factors in the nymphal environment most affect the distribution of mayflies. The early instars in the

TABLE 3.— The mean number of the most abundant invertebrates at biweekly intervals per 0.1 m^2 in the springbrook from 1 April 1965 through 15 March 1966

	1965																1966							
Taxon	Apr.		May		Jun.		Jul.		Aug.		Sep.		Oct.		Nov.		Dec.		Jan.		Feb.		Mar.	
Phagocata morgani	3	3	3	3	3	3	2	....	1	2	2	2	2	1	7	9	5	9	3	9	6	1	3	2
Asellus militaris	7	13	7	6	3	2	1	....	1	1	1	2	6	12	11	11	20	18	44	54	75	21	38	56
Gammarus minus	13	14	20	28	28	24	24	26	23	19	19	23	9	4	4	2	2	1	4	6	7	1	6	19
Ephemerella simplex	2	3	3	10	6	1	....	....	....	....	....	....	....	....	....	1	4	2	5	11	11	7	2	3
Baetis vagans	1	3	2	....	....	....	1	3	2	1	....	....	1	2	....	....	1	1	10	1	4	1	2	1
Nemoura sp.	3	6	3	1	1	1	....	....	....	1	....	....	....	....	1	1	2	2	11	6	15	5	9	6
Isogenus subvarians	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	2	4	3	5	3	1
Acroneuria abnormis	2	3	....	1	....	1	....	....	2	....	2	3	2	3	2	1	1	2	3	3	1	1	....	....
Rhyacophila lobifera	2	5	1	1	....	....	1	....	1	1	1	3	3	2	....	3	4	3	5	6	6	3	3	2
Hydropsyche bifida	2	1	3	2	7	2	1	2	1	1	....	....	....	1	8	6	2	2	6	7	2	2	2	3
Ochrotrichia unio	5	22	1	5	2	....	....	....	....	....	....	1	1	....	....	....	....	....	....	....	....	....	2	22
Sericostoma sp.	3	4	....	6	3	9	1	3	2	1	....	1	1	3	1	1	....	4	6	3	8	1	10	2
Tipula abdominalis	....	....	....	....	....	1	....	....	....	....	....	....	2	31	8	4	2	2	2	2	....	....	....	....
Tipula ignobilis	....	1	1	....	....	1	1	1	3	1	1	1	1	1	....	2	1	....	....	....	....	....	1	....
Dicranota notabilis	....	....	....	....	....	....	....	....	1	....	....	1	....	....	....	....	1	1	1	1	1	....	1	1
Limonia canadensis	....	....	....	1	....	....	1	....	....	1	3	3	1	1	1	5	3	1	1	....	3	2	....	1
Pericoma albitarsis	....	....	....	....	....	2	1	1	2	6	3	1	5	28	9	7	2	1	1	1	....	1	....	1
Dixa modesta	....	7	....	....	....	....	....	....	....	....	....	1	2	1	2	2	2	4	8	3	1	1	1	2
Tendipedidae	12	22	79	17	....	13	5	3	41	29	36	23	39	53	81	186	285	261	282	326	401	74	116	89
Hemerodromia sp.	....	....	....	....	....	1	2	1	1	2	2	1	2	3	1	1	....	2	2	3	1	1	3	5

brook were found in vegetation or detritus. As the nymphs grew, they moved from the vegetation to the stones to avoid entanglement in the closely knit vegetation. All larvae were herbivorous, feeding chiefly on detritus and diatoms, and occasionally on bits of filamentous algae.

Ephemerella simplex emerged from the springbrook in January and February with a lesser emergence in May. It preferred swift currents and inhabited large stones covered with vegetation. Aggregations often occurred, perhaps as a result of abundant food. Unlike *Ephemerella* spp. studied by Badcock (1949) and Macan (1957), is was not a summer species in the brook (Table 3).

Baetis vagans was highly adaptable, living in the open waters in slow to swift currents in the brook. The nymph's torpedo-shaped body is adapted for life in the swiftest of currents (Dodds and Hisaw, 1924). Some species of *Baetis* have two or three peaks of emergence per season (Ide, 1935; Minckley, 1963). In the brook, however, there was no definite emergence period. As previously noted by Leonard and Leonard (1962), there was likely an extended period of emergence which lasted from January through June.

Plecoptera.—Plecoptera nymphs are sluggish and occur in debris, masses of leaves and algae, and under stones, where there is an abundance of oxygen (Pennak, 1953). The nymphs of the suborder Filipalpia (*Nemoura*) are primarily phytophagous, whereas those belonging to the Setapalpia (*Isogenus* and *Acroneuria*) are usually zoophagous (Jewett, 1956). Egglishaw (1964) noticed that nymphs aggregated in response to food. Like the mayflies, the young stoneflies in the brook occupied moss and algae. Just before emergence, nymphs crawled onto stones or debris.

Hynes (1941) noted *Nemoura* nymphs often in leaf packets in English streams. *Nemoura* sp. occurred on moss-algae and in leaf packets in the brook. Nymphs were present throughout the sampling period (Table 3). Emergence took place in February and March. *Nemoura* fed on plant material, primarily leaf detritus.

Isogenus subvarians and *Acroneuria abnormis* were among the largest immature insects in the brook. *I. subvarians* was found from late December through March; habitats were moss-algae and leaf packet substrata. Emergence occurred in early March. *Acroneuria* nymphs lived in swift water, often on the upper surface of stones. The young were found in the vegetation in autumn. As they grew, they moved onto the stones. When this occurred, their food habits changed from herbivorous to carnivorous.

Trichoptera.—Trichoptera were present throughout the study. They pupated in winter and emerged in spring. Jones (1950) noted that predatory species prefer stony beds and swift currents; others live in the vegetation in quiet waters to escape predation. As observed by Slack (1936), most nymphs in the brook relied on moss and algae as food sources, but they devoured any plant or animal material of suitable size with which they came in contact. Encased forms in the brook ate mainly detritus.

Rhyacophila lobifera was present throughout the year. It was found primarily in the moss and algae, and secondarily in leaf packets. As noted by Badcock (1949) this naked caddis is predominantly a carnivore, eating other caddis larvae, midges, stoneflies, and mayflies. In the brook it fed also on detritus and diatoms.

Hydropsyche bifida, a net-building caddis, is confined to stones in swift water (Pennak, 1953). The young larvae in the brook were found in moss and algae; however, they moved to stones just prior to pupation. The greatest emergence occurred in June with lesser periods of emergence throughout the summer.

Ochrotrichia unio is a micro-caddis which feeds on diatoms and other algae (Percival and Whitehead, 1929). The larvae were abundant in March and April in the springbrook. They inhabited the moss and algae initially. Prior to pupation they moved onto stones.

Sericostoma sp., an uncommon trichopteran, occurs in mountain streams (Pennak, 1953). It was herbivorous, feeding on detritus, dead leaves, and algae. It occurred only on the moss-algae substratum in the brook. The young were first seen in September; emergence occurred in May. Contrary to information in Pennak (1953), early instars had cylindrical cases; later ones had conical cases.

Diptera.—Tipula abdominalis first appeared in the brook in October; as larvae increased in size, the number decreased (Table 3). Emergence occurred in March. *Tipula ignobilis* was found in moss and algae on the top of large stones throughout the year; it had an extended period of emergence. *Dicranota notabilis* was present from late summer through spring in the vegetation. *Limonia canadensis* was found on stones or algae throughout the year; it emerged from late winter through late spring.

The Psychodidae live in moss and algae growing in watersplash areas (Wirth and Stone, 1956). In the brook *Pericoma albitarsis* occurred in moss and algae from June through March; emergence began in December. *Dixa modesta* (Family Dixidae) was present primarily on stones and leaf packets from September through April.

Seventeen species of tendipedids were identified from the springbrook. Midges were most abundant in late autumn and winter (Table 3). Emergence occurred throughout the year, but was greatest in February. Few midges were present in summer. Carnivorous members of the subfamily Pelopiinae (=Tanypodinae) included *Pentaneura* spp., *Procladius* spp., *Anatopynia* sp., and *Pelopia* sp. All were found in moss, algae, or detritus. *Pentaneura* spp. were also found mainly on stones in swift water. Curry (1954) found that members of this group preferred lotic waters with marl and sand bottoms; such conditions were present in the brook. The sole diamesine present was *Prodiamesa* spp., which was abundant from November through May. Hydrobaeninae (=Orthocladiinae), *Brillia* sp., *Metriocnemus* sp., and *Hydrobaenus* sp. were generally distributed in the springbrook. The Tendipedinae (=Chironominae) was represented by five genera: *Lauterborniella, Calospectra, Tanytarsus, Tendipes,* and *Cryptochironomus.*

These were present from autumn through spring in vegetation and leaf packets.

NUMERICAL RELATIONSHIPS

Rapid fluctuations in the invertebrate populations in the springbrook are exemplified by data in Table 3. Rapid fluctuations occurred even though the brook had a constant temperature with a relatively unchanging physico-chemical environment except for discharge. Changes in benthic populations were manifested in three ways: (1) by addition of new individuals through reproduction; (2) by death of organisms 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 pressure from physical forces in the environment. Interpretation of these fluctuations was complicated by seasonal aspects of reproduction of different species and phenomena related to reproduction, such as emergence of insects.

Small cold head-water streams less than 2 m in width are generally more productive per unit area than are wider streams, due to their nearly constant environments (Needham, 1938). Standing crop can give a fairly accurate indication of the level of productivity of the benthic fauna for part of the year (Armitage, 1958). That the standing crop of insects can reflect the relative productivity of the fauna stems from the nature of their life histories. Most of the insects of lotic waters have an annual turnover. When such a species emerges, most of the population leaves the stream in a short time. Ordinarily a population of aquatic insects is not reduced to zero as the period of emergence varies from species to species, and some species have life cycles of two or three years with only a part of the population emerging in any one year (Armitage, 1958).

Carpenter (1928) stated that a plentiful supply of food may hasten larval growth and account for the early emergence of many insects from brooks. Food was most plentiful in the brook during autumn and winter when dead leaves and other detritus collected. From this time through spring the fauna continued to be depleted. The numbers were restored in autumn when the summer's layings were hatched and the larvae were grown to appreciable size.

Major changes in animal numbers in the brook apparently resulted from changes in discharge or related phenomena. Streams reduce their populations by washing animals away in the drift, such a loss being a continuous one, even in the absence of floods. Drift occurred to the greatest extent in the brook between 1 and 15 February 1966 following rains. The population dropped from 578 individuals/0.1 m^2 on 1 February to 164 individuals/0.1 m^2 on 15 February (Fig. 2). It then increased to 223 individuals/0.1 m^2 on 1 March.

Stones.—Animal populations ranged from 70 individuals/0.1 m^2 in June 1965 to 21 individuals/0.1 m^2 in July 1965, on stones in the brook (Table 4, Fig. 2). The mean number of animals in 72 samples was 39/0.1 m^2, of which insects made up 40.0% and non-insects

60.0% of the total. Of insects present, Trichoptera contributed 32.4%; Ephemeroptera, 32.4%; Diptera, 25.9%; Plecoptera, 8.1%; and Coleoptera, 1.4%. Of non-insects present, Amphipoda contributed 44.5%; Isopoda, 36.1%; and Turbellaria, 19.4% (Fig. 3).

The total number of animals on stones was small as compared with moss-algae and leaf packets. This may be attributed to the instability of the spring bed and the resulting paucity of food.

Moss-Algae.—Animal populations ranged from 768 individuals/0.1 m² in February 1966 to 43 individuals/0.1 m² in July 1965, on moss-algae in the brook (Table 4, Fig. 2). The mean number of animals in 72 samples was 267/0.1 m², of which insects composed 92.7% and non-insects 7.3% of the total. Of insects present, Diptera contributed 84.4%; Trichoptera, 9.6%; Plecoptera, 3.1%; Ephemeroptera, 2.8%; and Coleoptera, 0.1%. Of non-insects present, Amphi-

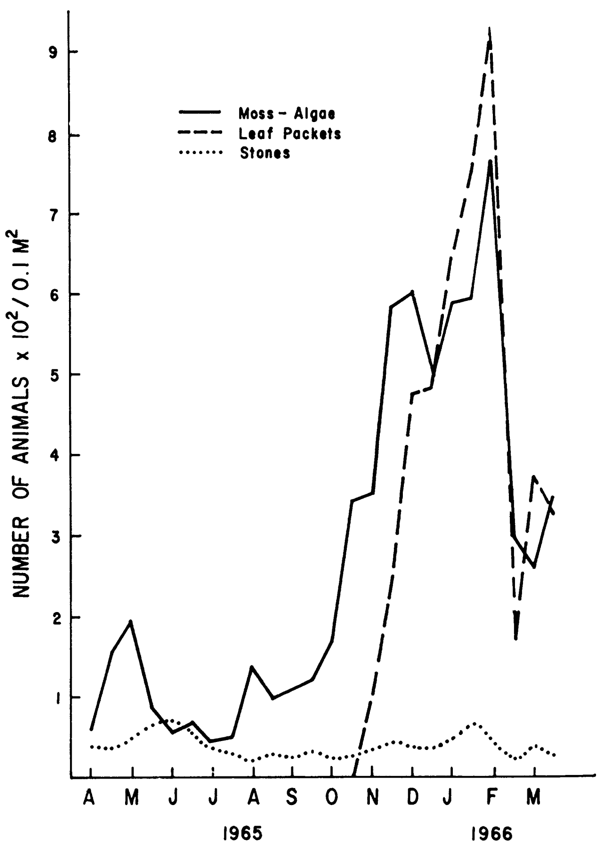

Fig. 2.—Total number of animals associated with moss-algae, leaf packet, and stone substrata from 1 April 1965 through 15 March 1966.

TABLE 4.—Number of animals per 0.1 m² of moss-algae, stone, and leaf packet substrata in the springbrook from 1 April 1965 through 15 March 1966

Taxon	1965																1966							
	Apr.		May		Jun.		Jul.		Aug.		Sep.		Oct.		Nov.		Dec.		Jan.		Feb.		Mar.	
A. Stones																								
Turbellaria	2	3	2	1	4	5	4	....	2	4	5	4	3	2	12	20	5	7	1	11	7	1	4	2
Isopoda	7	15	7	8	3	1	1	....	1	2	1	2	6	14	14	10	10	21	13	31	15	6	14	4
Amphipoda	13	9	22	24	25	24	26	19	15	18	17	16	4	3	5	2	2	1	....	3	3	1	1	2
Ephemeroptera	7	9	8	18	12	2	3	6	1	1	....	3	1	2	....	....	4	1	16	1	8	4	7	5
Plecoptera	3	2	2	3	....	1	....	....	1	....	....	....	1	2	1	....	1	....	....	4	3	1	3	2
Trichoptera	5	5	9	10	24	7	1	3	1	3	1	1	....	....	....	5	5	2	2	13	3	5	7	8
Coleoptera	1	....	....	....	1	....	....	....	....	....	....	1	....	....	....	....	....	....	....	1	....	....	1	....
Diptera	1	14	1	2	....	13	2	....	....	3	2	5	7	1	3	9	9	1	12	3	2	5	....	1
TOTALS	38	57	51	66	72	53	37	28	21	30	26	32	23	25	35	46	36	33	44	65	41	22	36	24
B. Moss-Algae																								
Turbellaria	3	2	3	4	2	1	....	....	....	....	....	....	....	....	3	....	....	1	1	2	....	2	2	....
Isopoda	6	11	6	4	3	3	1	....	2	1	1	3	5	8	7	2	2	....	3	3	16	14	18	13
Amphipoda	13	16	16	28	30	23	21	32	29	20	20	31	18	5	6	2	1	....	1	1	1	2	2	3
Hydracarina	....	....	....	....	....	....	....	....	....	....	....	....	1	2	1	....	....	....	....	1	....	....	....	....
Ephemeroptera	2	5	1	2	....	....	....	....	3	....	....	1	....	2	1	1	4	12	29	35	28	32	5	9
Plecoptera	6	16	3	....	1	3	1	....	4	1	3	7	6	4	6	4	3	6	15	20	34	26	15	7
Trichoptera	17	57	4	16	20	18	5	5	7	3	2	9	12	17	31	31	13	34	35	24	50	18	62	100
Coleoptera	....	1	....	....	....	....	....	....	....	....	....	1	1	1	1	1	....	....	1	....	1	1	....	....
Diptera	24	46	157	34	....	19	16	12	92	74	85	70	125	303	297	543	578	445	505	510	638	204	155	228
TOTALS	71	157	193	89	57	68	43	49	137	99	112	122	168	342	352	584	601	498	589	595	768	299	259	344
C. Leaf Packets																								
Turbellaria															4	3	7	15	6	11	10	....	1	2
Isopoda															11	18	41	27	114	111	193	42	86	118
Amphipoda															3	1	4	1	10	14	14	1	13	54
Hydracarina															....	....	....	....	....	2	....	....	....	....
Ephemeroptera															....	1	9	....	8	11	13	1	3	....
Plecoptera															....	3	4	6	35	24	25	17	22	17
Trichoptera															....	3	5	3	21	17	9	3	4	3
Coleoptera															....	....	....	1	2	2	....	....	1	....
Diptera															83	209	405	431	447	558	665	108	243	134
TOTALS															102	248	447	485	643	750	930	171	374	330

poda contributed 66.3%; Isopoda, 27.3%; Turbellaria, 5.4%; and Hydracarina, 1.0% (Fig. 3).

The population density of the moss-algae indicated a favorable spectrum of environmental conditions as compared with the stones. The vegetation afforded suitable shelter for such organisms as could move through it, and the fine sand which was held offered a convenient medium from which Trichoptera larvae built their cases. The vegetation also provided food material. Frost (1942) recorded peaks in abundance of tendipedids in winter similar to those found in the vegetation of the brook, and she attributed this to immigration from less suitable areas. Recolonization of the remainder of the brook from such sheltered areas occurred after recession of winter floods.

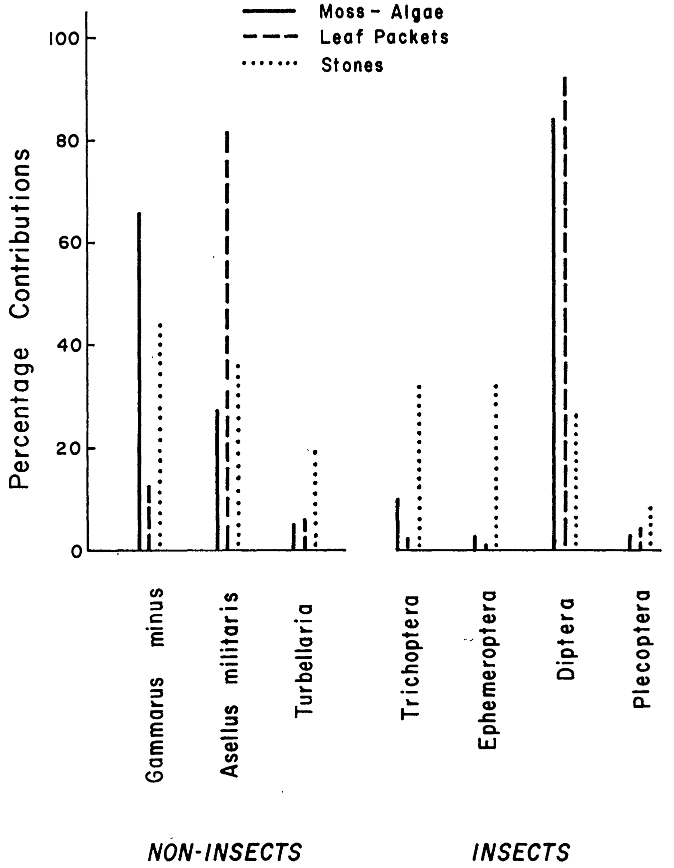

Fig. 3.—Percentage contributions of major non-insect and insect components of the moss-algae, leaf packet, and stone substrata from 1 April 1965 through 15 March 1966.

Leaf Packets.—Animal populations ranged from 930 individuals/0.1 m^2 in February 1966 to 102 individuals/0.1 m^2 in November 1965, on leaf packets in the brook (Table 4, Fig. 2). The mean number of animals in 30 samples was 451/0.1 m^2, of which insects made up 79.1% and non-insects 20.9% of the total. Of insects present, Diptera contributed 92.2%; Plecoptera, 4.4%; Trichoptera, 1.9%; Ephemeroptera, 1.3%; and Coleoptera, 0.2%. Of non-insects present, Isopoda contributed 81.2%; Amphipoda, 12.3%; Turbellaria, 6.3%; and Hydracarina, 0.2% (Fig. 3).

The population density of leaf packets was greater than that of stones or moss-algae during their presence in autumn and winter. Leaf packets, like the moss-algae, afforded both food and shelter. Animals whose motility was hindered by the vegetation could move more freely in the leaves. When the spring rains came, the organisms in the leaf packets were the first to begin to drift.

VERTEBRATES

Desmognathus fuscus fuscus (Rafinesque) was found in crevices and under stones in the brook throughout the year. Adult *Desmognathus* were the most abundant. Larvae were numerous during the winter until late February, when they transformed into adults.

Eurycea bislineata bislineata (Green) was neither as abundant as *Desmognathus* nor was it present throughout the year. Adults left the brook in autumn and hibernated under rocks near the brook. By March they had returned to the brook.

Rana palustris Le Conte was found under debris and stones on four occasions in the brook. No observations were made on its life history.

SYNTHESIS

There are two approaches to classifying lotic waters (Macan, 1961): (1) the biological approach in which collections are made at random, stations are grouped according to the species found, and factors common to all the stations inhabited by a group are sought; and (2) the physical approach in which the collector starts with an arbitrary division of the area into what appear to be distinct biotypes; he samples representative portions of each. We used the physical approach, since previous investigators have shown this to be the more feasible of the two (Percival and Whitehead, 1929; Badcock, 1949; Teal, 1957; Hynes, 1961).

The springbrook is an "open" ecosystem with a "heterotrophic" community metabolism (Odum, 1959). There were several forms of energy exchange between the brook and its surroundings: (1) dissolved and particulate organic matter in the water which entered and left the brook; (2) the organic matter that entered the water in the form of leaves; (3) the adult insects that left the system when they emerged; (4) the migration of Crustacea and aquatic insect larvae due to floods; and (5) the sunlight used by the aquatic vegetation for photosynthesis. Lotic waters have their own producers, but these are inadequate to support the large array of consumers (Odum, 1959; Hynes, 1963a). The most important source of energy consists of leaves and other plant material that falls into the water from the surrounding land (Teal, 1957; Odum, 1959; Hynes, 1961, 1963a; Ross, 1963; Egglishaw, 1965).

Ross (1963) suggested that the temperate deciduous forest superimposes ecological conditions upon the streams originating in it and running through it. The conditions include dense shade over the water in summer, a heavy autumnal fall of leaves into the water each year, and a low volume of soil erosion because of dense accumulations of litter on the adjacent forest floor. The influence of the tree canopy was seen on the springbrook. Its intense shading in summer reduced photosynthesis, and the vegetation became sparse; this, in turn, decreased the available food for the fauna and limited the numbers and kinds of species present in summer. The leaf fall in autumn provided food and shelter for the newly hatched fauna, which emerged the following spring. The cooling effect produced by the tree canopy kept the water temperature low, so that little difference existed between summer and winter temperatures.

In addition to the conditions superimposed by the physical nature of the forest, certain other conditions characteristic of the temperate deciduous forest affected the springbrook: (1) a heavy annual rainfall; (2) the uneven distribution of this precipitation throughout the year; and (3) specific temperature conditions. The rainfall was greatest from February through April 1965, and caused flooding of the brook and the subsequent migration of the fauna. The lack of rainfall in late summer and autumn resulted in a low rate of flow, producing enhanced sedimentation.

Diatoms formed an unreliable source of food at all seasons of the year in the brook, because floods swept them away. A more reliable food source was detritus. Fallen leaves contributed the greatest mass of detrital material. Minshall (1967) noted that 50 to 100% of the food ingested by herbivores and omnivores in Morgan's Creek, a woodland springbrook, was in the form of detritus. Rosine (1955) suggested that the fauna does not utilize the actual detritus, but rather eats the periphyton growing on the detritus. Egglishaw (1964, 1965) found a close correlation between the distribution of benthic animals and plant detritus; this may be due to water turbulence, which distributes animals and detritus in the same manner, or alternatively to aggregations of the fauna at sites where plant detritus is abundant.

Egglishaw and Morgan (1965) suggested that the geology of the substratum exerts a controlling effect on the fauna. The geology of the region influences the surface texture and size of component parts of the substratum of a stream, the nature of the surrounding land, and the current. The current has both favorable and unfavorable effects on the fauna: dislodgement of larvae; prevention of settlement; lack of planktonic food; interference with feeding mechanisms; suppression of gradients in physico-chemical conditions of the water; removal of sediment, settling diatoms, or debris; restriction of flood and competitive species; and deposition of silt. Ambühl (1959) and Macan (1963) found that most animals living in lotic waters show adaptations of behavior, not structure, and live between stones or in vegetation, where there is little current. Maximum population densities were found in weak currents in the brook. It is unlikely that there was a direct effect of current unless the bottom was too unstable, and some inherent ability, *e.g.*, agility, enabled the organisms to avoid the shifting substratum. The nature of the spring bed probably had both a direct and indirect influence on the fauna; directly, it determined the nature of shelter offered to animals; indirectly, it influenced the nature of the plant growth.

Several workers have suggested that water temperature is a critical factor (Dodds and Hisaw, 1925; Ide, 1935; Hynes, 1955; Macan, 1963). The temperature of the brook was nearly constant throughout the year. This probably inhibited the rate of reproduction for some individuals and allowed others to be reproductive for an extended period of time. The rate at which invertebrates feed and the efficiency with which they metabolize at different temperatures have been little investigated, although these factors may be of considerable ecological importance.

The seasonal life cycles of insects should not be overlooked. These were important in determining the variety and size of the faunal population of the brook at various seasons of the year. The entire economy of aquatic life is intimately bound up with the presence or absence of insects. It has been demonstrated repeatedly that insects, in both immature and mature stages, constitute the diet of many species of fish, or of other organisms that are eaten by fish. The lack of fish in the brook enabled us to observe the population in the absence of this major predator. The brook should be comparable to others in its ecology, notwithstanding certain unique and constant features imposed upon it by its source and surroundings.

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SUBMITTED 28 FEBRUARY 1968 ACCEPTED 9 MAY 1968