The Ecology of Invertebrates in an Intermittent Stream[1]

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ABSTRACT

This study is concerned with the ecology and certain physiological mechanisms of macroinvertebrates in a small stream of south-central Indiana that becomes completely dry at the surface each summer. The stream fauna is dominated by two aquatic peracarid crustaceans, *Lirceus fontinalis and Crangonyx forbesi,* which occur in substantial numbers throughout the year. They survive the dry season as small animals in subsurface seepage and water-saturated air spaces of moist soil. The other aquatic animals of the stream can be divided into two groups in respect to season: a late summer-autumn association, characteristic of the stream when it is dry or nearly so, and a late winter-spring association characteristic of the stream when it is flowing or nearly so. The active summer-autumn group consists mainly of adventitious species and of adult aquatic beetles, which are permanent members of the stream. The winter-spring invertebrates are mainly permanent residents, which appear each year and constitute a uniform and stable community. With the possible exception of certain caddisflies, these species are not specifically adapted to the intermittent environment but in a sense are preadapted to it by certain favorable features of their life cycles.

L. fontinalis and *C. forbesi* have an annual cycle in the intermittent stream. Both begin to breed in March and April, months that normally exhibit the maximum amount of water in the stream. In *L. fontinalis* reproduction is terminated in summer by the early death of animals of the old generation that are still reproducing, and by an arrested growth of the new generation. Both phenomena are influenced by the onset of the dry period. In contrast, for *C. forbesi* reproduction is unvaryingly confined to the spring, with the females producing one brood and then dying prior to the drying up of the stream. Individuals of the new generations of both species grow very little during the dry summer and autumn months. Because of their small size they can survive in subsurface seepage and moist interstitial spaces. In late autumn and winter rapid growth resumes.

For *L. fontinalis* oxygen consumption declined in late spring and summer when measured at 5°C but not when measured at 13°C. If size is considered, however, the animals at 13°C also would exhibit a lower metabolic rate in summer. When exposed to water-saturated air in the laboratory, both *L. fontinalis* and *C. forbesi* from the intermittent stream lived for a longer period of time than did related organisms from a permanent stream.

Physical features of the stream bed, especially during the dry season, are pointed out as being of prime importance in determining the permanency of an aquatic fauna in small summer-dry streams. The availability of interstitial spaces is of special importance in this respect. Besides offering a suitable habitat for aquatic animals during the dry season, they are of importance when the stream is flowing by reducing the velocity of the water, which might otherwise flush out much of the aquatic fauna. The maintenance of interstitial spaces depends on local geological and geographical features. The presence of non-angular bottom materials, the absence of a heavy silt load, and protection from daily freezing and thawing during the winter are important in this respect.

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TABLE OF CONTENTS

INTRODUCTION

Many regions of the United States and elsewhere are characterized by very small streams, which usually flow for only a short period each year and regularly go completely dry in late summer and autumn. Such streams can make up a considerable part of the watershed system. These streams are numerous especially in south-central North America where large watersheds may exhibit only a few permanent or summer-interrupted streams, the remaining being the small intermittent or ephemeral type. One has only to examine a topographic map of a typical intermittent stream locality, such as parts of Kentucky, Indiana, and southern Illinois, to appreciate at least the areal importance of these small streams. The total kilometers of summer-dry streams may well exceed the total kilometers of permanent streams. Permanent streams, however, have received the major attention of aquatic biologists. This largely has been due to their greater abundance of aquatic life, especially fish, and to their role in waste disposal.

While the range of limnological research possibilities of intermittent and ephemeral streams would appear to be limited by their scanty fauna, the biological significance of such streams is much greater than would be expected on casual observation. In summer and early autumn they suggest either an environment completely devoid of aquatic life or certainly one that would present severe ecological and physiological stresses to any aquatic invertebrates living therein. After heavy rains of autumn, however, pools are formed which may at once be occupied by substantial numbers of aquatic invertebrates. In south-central Indiana the aquatic isopod *Lirceus fontinalis* Rafinesque and the aquatic amphipod *Crangonyx forbesi* (Hubricht and Mackin) especially are noteworthy in this respect. In spring when the streams are flowing, the faunae present resemble rather closely those of permanent streams of the region.

Such streams scarcely conform to our concept of a lotic environment in the same way as permanent streams. In fact over a year's time the streams could serve as common meeting grounds for terrestrial ecology, pond limnology, and stream limnology. Aquatic animals surviving in the streams must be subjected to severe and diverse environmental stresses—a flowing stream in spring, a pond situation in early summer, an apparent terrestrial situation in late summer and early autumn, and pools in late autumn and winter, which because of decomposing leaf material have a high oxygen demand and superfically resemble the hypolimnion of deep lakes.

The continuing presence of aquatic fauna despite regularly occurring dry periods prompted the investigator to question how these populations are maintained or how repopulation is accomplished. The migration of aquatic organisms into the stream via reestablished connections with permanent water bodies or via flight, as in adult insects, was a possibility and would be expected in many instances. There was also the possibility that a permanent aquatic fauna existed in such streams and that it might be typical and even restricted to such streams. How would the aquatic organisms survive the dry periods? Are there special adaptations or modifications in their life cycles that permit true aquatic animals to survive in apparently terrestrial localities? What is the nature of the dry stream bed, and is there a semblance of the aquatic environment below its surface, providing conditions amicable to life for such aquatic forms adapted to it? What, if any, contribution does the small intermittent and ephemeral stream fauna make to the productivity of associated permanent waters? These are some of the matters to be considered in determining the ecology and the biological importance of these very numerous intermittent and ephemeral streams.

This study is an initial attempt to elucidate the above problems by investigating the complex of life in a small stream that regularly goes completely dry in the summer and early autumn. The study included the seasonal community structure of the invertebrates and especially the ecology of the major invertebrates. In this respect reproductive cycles, metabolic rates, and soil and humidity factors were major points. Finally an attempt was made to develop faunistic parameters useful in classifying or at least arranging streams in a continuum with respect to duration of intermittency. Various aspects of the investigation were conducted from October 1963 to June 1965.

DESCRIPTION OF STUDY AREA

The stream chosen for study is known from topographic maps as Caldwell Hollow (Fig. 1). It is a tributary of Salt Creek, which in turn contributes to the West Branch of the White River system. The stream is located in the Norman Upland of Brown County, approximately 23 km east of Bloomington, Indiana. This is a hilly region, the entire area being dissected by small intermittent and ephemeral streams. Bedrock of the Upland is the Borden Formation characterized by sandstones, shales, and clays. Although glacial outwash material is present locally in major valleys, none is present in Caldwell Hollow. Springs are generally absent in this region. The watershed of Caldwell Hollow is completely wooded, characteristic vegetation being elm (*Ulmus americana* L.), hickory (*Carya* sp.), black cherry (*Prunus serotina* Ehrh.), and beech (*Fagus grandifolia* Ehrh.). Sycamores (*Plantanus occidentalis* L.) are common at the lower end. The materials of the stream bed are predominately sandstone particles of various sizes and shapes. Bedrock exposures of sandstone and clays are present but infrequent.

Table 1 summarizes important morphometric and meteorologic features. Caldwell Hollow was continuous with Salt Creek for only 46 days during the period October 1963 to October 1964. For most of the study period the stream was a series of widely scattered shallow pools. The most prolonged dry spell occurred from August to November 1964. During this period the stream was completely dry for 38 days, and although water was present in September, it was restricted to one pool. Although the stream is short and has a rather steep gradient, torrential floods are

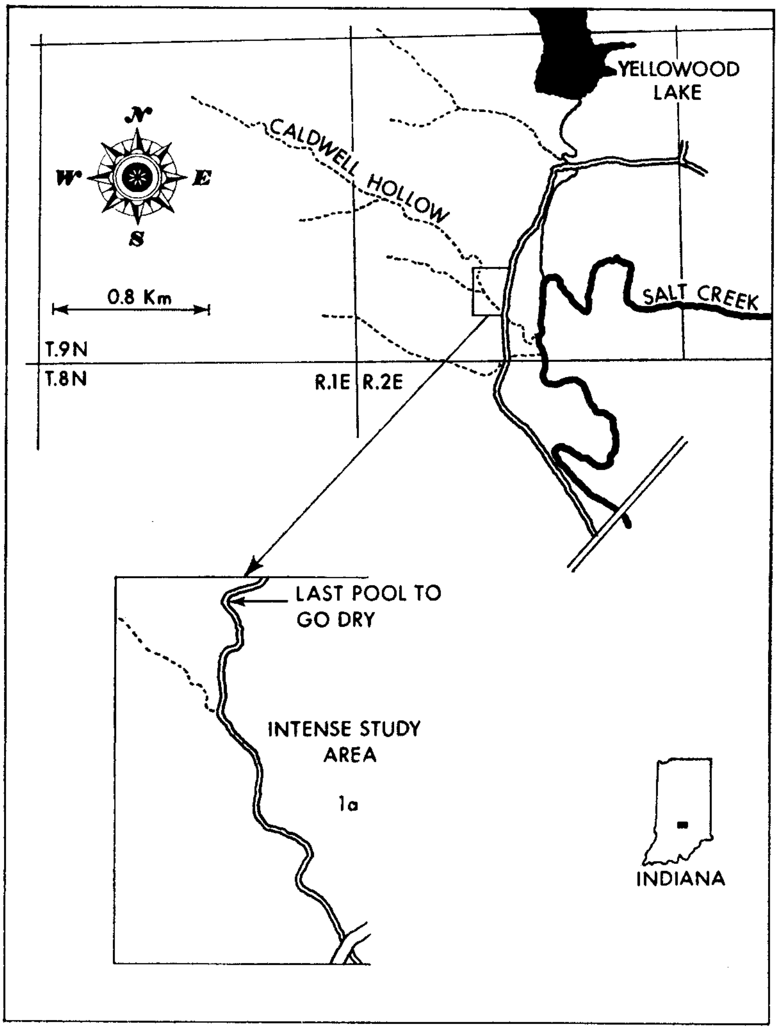

FIG. 1. Map of the study area.

rare. They probably are minimized by the large amount of lateral subsurface drainage that can take place through the loosely packed layers of gravel-size sandstone. During the study period only one flood occurred. This was 8 March 1964, when the region received over two inches of precipitation. It completely altered large areas of the stream bed, scouring out new pools and filling in old ones with sandstone particles.

Water temperatures, dissolved oxygen, and the water conditions are portrayed in Figure 2. The stream was continuous from headwaters to mouth during most of March and April of 1964. In late spring and early summer it was reduced to isolated pools. In late summer and early autumn the stream was completely dry or exhibited only transitory pools after heavy rains. Pools that did form at this time were characteristically dark brown in color due to decomposition of leaf material. Water temperatures were high, and dissolved oxygen was near depletion. Larimore *et al.* (1959), Schneller (1955), and Slack (1955) investigated various aspects of the "black water" phenomenon, but much remains to be learned, especially concerning the possibilities of released toxins.

TABLE 1. Summary of morphometric and meteorologic data, Caldwell Hollow, Indiana —October 1963-March 1965.

Origin above sea level: 228 m
Total flow length: 2.22 km
Flow length, study area: 0.32 km

Area of watershed: 3.1 km^2
Av. gradient: 31.7m/km

	No. days continuous with Salt Creek	No. days some flow in study area	No. days of isolated pools only	No. days completely dry	Monthly* precipitation (cm)	
					Total	24 hr. maximum
1963						
Oct.	0	0	19	12	0.38	
Nov.	0	0	31	0	5.38	2.67
Dec.	0	0	31	0	3.73	0.79
1964						
Jan.	0	11	20	0	5.49	1.35
Feb.	0	6	23	0	2.77	1.27
Mar.	27	4	0	0	20.70	5.69
Apr.	18	11	1	0	13.00	3.20
May	0	0	31	0	3.62	0.51
June	1	2	27	0	11.10	3.23
July	0	0	31	0	13.13	4.57
Aug.	0	0	14	17	3.28	2.21
Sept.	0	0	30	0	2.23	1.75
Oct.	0	0	22	9	0.89	0.46
Nov.	0	0	18	12	5.46	2.39
Dec.	0	6	25	0		
1965						
Jan.	12	14	5	0		
Feb.	22	6	0	0		
Mar.	31	0	0	0		

* Sources: U.S. Weather Station, Bloomington, Indiana

With the prolonged rains of autumn more permanent-type pools formed, and by January 1965 the stream was flowing again. Such initial flow usually resulted in the flushing out of accumulated leaf material and consequently in the flushing out of substantial numbers of aquatic isopods and amphipods. Although numerous sampling trips and observations were made from headwater to mouth, most of the intense work was conducted in the lower section comprising a study area of approximatedy 0.32 km (Fig. la). The last pool remaining before the stream went completely dry was located in this area.

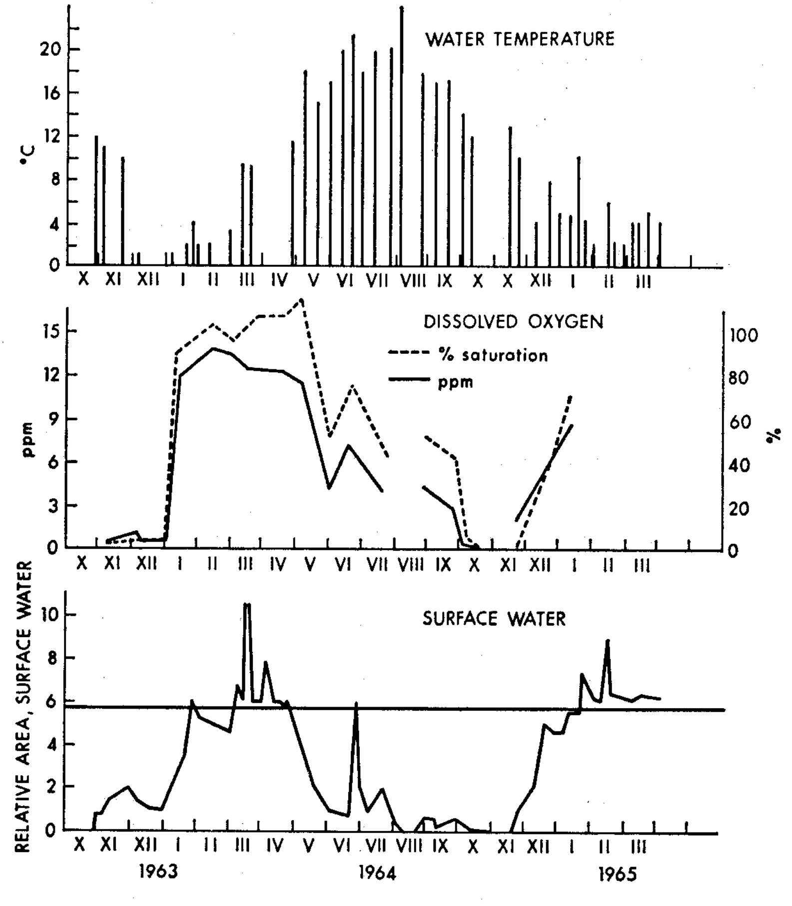

FIG. 2. Water temperature, dissolved oxygen, and visible surface water for study period, October 1963-March 1965. Surface water was determined by mapping the width and length of the stream bed on square-millimeter graph paper. Each time the stream was visited, the visible water was sketched on these maps and its total area in square millimeters calculated. When the relative area was above 5.8 (580 mm^2), the stream was flowing from headwater to mouth; below 5.8 it was a series of isolated pools or completely dry.

METHODS

Spot qualitative sampling was performed each time the stream was visited, usually at weekly intervals (Table 2). The organisms were collected from as large an area of the stream as time would allow. On some occasions the stream was sampled from headwater to mouth. Samples were collected by various hand nets, shovels, and by picking organisms off rocks and leaves with forceps. When the stream was dry, soil samples were taken from former riffle and pool areas. These were brought into the laboratory and either placed in flowing water systems for the recovery of living organisms or spread out in a white enamel pan and slowly flooded with formalin. Living organisms were observed by this method. Emergence or migration of insects were periodically monitored by insect traps.

Quantitative samples were collected usually at slightly shorter than monthly intervals (Table 2). These samples were used for the reproductive cycles of *Lirceus* and *Crangonyx* and to compare numerically the composition of the fauna on a particular sampling date. Samples were collected with a nylon hand net having 12 threads per centimeter. This size net does not sample adequately very small organisms in the one- and two-millimeter size groups. Sampling was as randomly performed as possible by working the net through selected pools and riffles (when present) over the entire study area. Samples were hand sorted in the field, the animals being transferred to 70% alcohol until they could be identified and measured to the nearest millimeter. During the times it was necessary to collect animals when the stream was dry, large quantities of moist soil were collected, flooded with formalin, and the organisms collected by a sugar flotation technique (Anderson, 1959).

For investigating the reproductive cycles of *Lirceus fontinalis* and *Crangonyx forbesi,* each specimen was sexed and then measured to the nearest millimeter from the anterior tip of the cephalothorax to the posterior end of the telson. The modification of the first two pair of pleopods for use in copulation is diagnostic of male isopods, while the short curved, outward projecting outer ramus of uropod 2 is diagnostic of *Crangonyx forbesi* males. Mature males of this species have calceoli on antenna 2. Each specimen was then tabulated in one of several categories: males, females without oostegites or having nonbristled oostegites, ovigerous females, females with young, females with empty brood pouch, and juveniles. Juveniles were animals 6 mm in length or shorter for *Lirceus* and 5 mm in length or shorter for *Crangonyx.* The number of eggs or young of each female for both species was recorded. To investigate the number of broods and incubation time of each species, several pairs of one male and one female each were observed in the laboratory at 13° C. The animals were maintained on elm leaves, the diet of *Crangonyx* being supplemented periodically with proteinaceous food, usually freshly killed specimens of the same species.

Oxygen-consumption determinations were made at approximately monthly intervals. *L. fontinalis* was collected the day before the tests and held in a 5° C room without food. Tests were run at 5° C the following morning, the animals then immediately transferred to 13° C, and the test repeated at the latter temperature the next morning. By this procedure

TABLE 2. Sampling program for study period, October 1963-April 1965. Ordinary numbers signify spot-qualitative samples, numbers in bold face denote quantitative samples, and numbers in italics soil samples.

1963			1964												1965			
Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
10	*3*	8	16	**12**	7	**2**	1	**1**	*5*	*2*	6	*4*	*12*	9	**2**	11	3	1
13	3	**20**	20	**28**	13	4	3	*11*	8	2	10	**4**	16	11	6	13	8	**12**
16	5	**22**	27		**15**	10	7	11	**17**	*9*	*13*	9	18	13	8	**14**	11	**29**
20	8	**27**			23	12	*10*	*17*	**26**	*12*	**18**	16	**27**	**16**	13		**12**	
31	10					18	10	17	*26*	*15*	**27**	25		23	**22**		**19**	
	21					**23**	**11**	**23**		*17*		30		24	**23**			
	25					25	16	25		22				25				
							16	*28*		**25**				29				
							21	**28**										
							24											
							24											
							26											

the organisms were exposed to each test temperature for approximately 16 hours prior to measurements. Grainger (1956), working with crustaceans, found the initial overshoot in oxygen consumption to last for only a matter of minutes or an hour at most before reaching a steady level when the animals are transferred to a different temperature.

A 10-cc syringe was used as the respiratory chamber. This was filled by removing its plunger and submerging the barrel in air-saturated water. Four to eight test animals were then placed in the barrel, the barrel resubmerged, the plunger inserted to the 10-cc mark and the syringe tip sealed with an air-tight rubber cap. Initial oxygen determination of air-saturated water was made according to a micro-Winkler technique described by Burke (1962). At the end of two hours at 5° C or one hour at 13° C, the respiratory chamber was removed from its water bath and vigorously shaken. A hypodermic needle attached to a 5-cc syringe was inserted through the rubber cap of the respiratory chamber and a 5-cc sample drawn off by pressing down on the plunger of the respiratory chamber. This sample was used for the final micro-Winkler titration and estimation of oxygen consumption. After the 13° C test the animals were blotted on filter paper and wet weighed.

SEASONAL DISTRIBUTION

The active fauna can be divided into two groups in respect to seasons (Fig. 3): a late summer-early autumn association characteristic of the stream when it is dry or nearly so, and a late winter-spring association typical of the stream when it is flowing or nearly so. The two dominant crustaceans, *Lirceus fontinalis* and *Crangonyx forbesi* are found in substantial numbers throughout the year, surviving the dry periods as very small animals with little growth in deep subsurface seepage and moist interstitial spaces. Certain aspects of their ecology and physiology will be detailed in a later section.

Are the other animals permanent residents of the stream or are they migratory species? If they are permanently associated with the intermittent stream how do they survive the dry periods? If they are migratory species can they complete their life cycle in this environment? To cast light on these questions a certain amount of descriptive discourse is necessary. Paucity in numbers of the various species, with two or three exceptions, made the construction of growth histograms impractical. Another factor entering here was the very short but rapid growth period, especially of the hemimetabolous spring fauna. Large quantitative samples, collected at monthly intervals and not adequately sampling very small organisms, represented in some instances only a single phase in the species' growth, since by the next sampling period the species had emerged. Therefore spot sampling, although not satisfactory for size histograms, was relied on heavily for determining the animal's history.

Starting with the summer-autumn association, the adult aquatic beetles—*Limnebius discolor* Casey, *Cymbiodyta* sp., and *Hydroporus laetus* Leech—are permanent components of the stream. They survive the dry spells by actively burrowing deep into moist interstitial spaces of the stream bed. Larvae of *H. laetus*, the only abundant beetle in the stream,

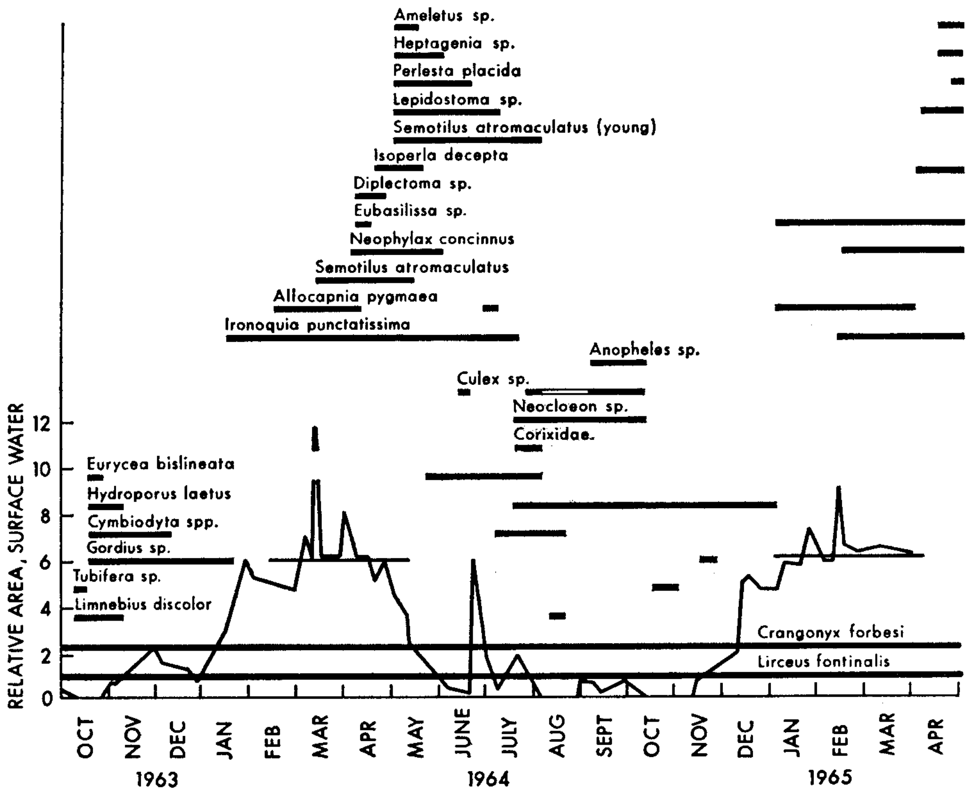

FIG. 3. Stream conditions and seasonal distribution of common invertebrates, 1963-1965. The black bars indicate the months when the various kinds of animals were found active in the stream. All aquatic insects are represented by immature stages with the exception of Coleoptera and Hemiptera, which are reported as adults.

were found mainly from December through February but never in numbers approaching those of the adults. These adult beetles could not be located hibernating during the winter months. Two other true aquatic beetles—*Agabus gasetes* Aube and *Helichus basalis* LeConte (not shown in Fig. 3)—were collected as adults on rare occasions throughout the year. Both were observed hibernating as adults in the winter months. They probably represent the only arthropods of this environment with a life cycle considerably longer than a year.

Tubifera sp., *Culex* spp., and *Anopheles* sp. are adventitious species, which complete their life cycle rapidly whenever standing water is present. A short period of flow during the last week of June 1964 (Fig. 3) temporarily wiped out the population of mosquito larvae. The seasonal distribution patterns of the salamander *Eurycea bislineata,* one of the few vertebrates of the stream, is that of the larvae, the adults being mainly terrestrial. The few remaining pools of July 1964 apparently served as temporary havens for migrating corixids, which disappeared during the dry spell of August, probably moving to more permanent type water. The migratory powers of this group, especially in relation to temporary water, has been documented by Brown (1951).

Gordius sp. were found in considerable numbers during the autumn of 1963 but were rare during the autumn of 1964. The immature stages are parasites of a number of arthropods. It is possible their host, which in this area appears to be chiefly the camel cricket *Ceuthophilus quttulosu,* was not abundant during the autumn of 1964. In October 1963 several specimens were taken from the dry stream bed in soil with little moisture. They were stiff and apparently lifeless, but once removed to water they recovered and became active. Egg masses were found in spring. Depending on the availability of the proper host, the species can complete its life cycle in the intermittent environment.

Neocloeon sp., a baetid mayfly, is a migratory species. The adults emerged from permanent waters, probably Salt Creek, in spring and oviposited in the intermittent stream. Adult females were taken in May 1963. During the first dry spell of August the nymphs, which were small, were able to penetrate deep into moist interstitial spaces and perhaps reach deep subsurface seepage. In October the nymphs were considerably larger although still quite immature as indicated by their wing pads. They were too large to penetrate deep into the stream bed, and they perished during the second dry spell. *Neocloeon* sp. can be considered a migratory species that did not complete its life cycle in Caldwell Hollow.

The winter-spring association is not unlike what might be expected in a permanent stream in the spring. There are five species of caddisfly larvae, three species of stonefly nymphs, and two species of mayfly nymphs. Considering the dry stream conditions in the summer and autumn, it might be expected these aquatic insects are the offspring of early emerging adults that had migrated in from permanent waters. In many instances, however, this is not the case.

Ironoquia (= *Caborius* Navas) *punctatissima* (Walker), a large limniphilid caddisfly, is a striking example of an aquatic invertebrate adapted to an environment that is alternatingly dry and flooded. Eggs were found in October 1963 under rocks in shaded areas of the dry stream bed. The small larvae appeared in the stream by early January 1964. In May and early June large numbers had congregated in pools that were rapidly drying up. As the pools became completely dry, the larvae and their cases disappeared. It first was thought they had been preyed upon by birds and other vertebrates and did not complete their life cycle. However, Flint (1958), working with another species *I. parvula* (Banks) found in temporary ponds in eastern United States, reported an interesting summer phenomenon. As the pond dried up the larvae actually migrated away from it, aestivated, and finally pupated in leaves near the former high-water line, a habitat which at that time was terrestrial. The pupa of *I. parvula* therefore is truly terrestrial. A terrestrial pupa could explain why Ross (1944, p. 196) never was able to raise successfully *Ironoquia* (= *Caborius*) to the adult using standard aquatic rearing methods. In Caldwell Hollow pupae of *I. punctatissima* have not been found, although larvae apparently aestivating in their cases were located in thick leaf litter to the side of a former pool. That *I. punctatissima* did complete its life cycle is evident from the small larvae that appeared during February 1965.

The larvae of *Lepidostoma* sp., a small leaf-cased caddisfly, disappeared at about the same time and under similar circumstances as *I. punctatissima*. Both species exhibited prepupal larvae during the terminal period of their aquatic life (Table 3). These larvae were shorter and much stockier than their counterparts present in May. They contained large fat deposits, especially in the abdominal segments. Such a condition could be a prelude to impending pupation or a long period of terrestrial aestivation. In respect to the latter, Hinton (1953) reports a correlation between total fat deposit of arthropods and their environment: most aquatic species display less fat than terrestrial relatives, and many species living in environments subject to drought have far more fat than those living in a stable aquatic environment. Lloyd (1921, p. 73) noted fat storage in the caddisfly larva *Neophylax concinnus* McLachlan prior to its long summer aestivation (prepupal) period. *Lepidostoma* sp. also completed its life cycle in the intermittent environment.

Neophylax concinnus is well adapted to life in an intermittent environment. The life history of *N. autumnus* Vorhies has been described

TABLE 3. Number of larvae and size distribution in *Ironoquia punctatissima* and *Lepidostoma* sp., winter and spring 1964. Numbers in heavy type are prepupal larvae = larvae with telescoped segments, sluggish, incapable of eating and probably even walking, exhibiting fat deposits (modified from Lloyd, 1921).

mm	Jan. 27	Mar. 23	Apr. 12	Apr. 23	May 11	May 24	Jun. 1	Jun. 23	Jun. 28	Jul. 5	Jul. 17
					Ironoquia punctatissima						
2	2	—	—	—	—	—	—	—	—	—	—
3	—	—	—	—	—	—	—	—	—	—	—
4	—	—	—	—	—	—	—	—	—	—	—
5	—	5	—	—	—	—	—	—	—	—	—
6	—	—	—	—	—	—	—	—	—	—	—
7	—	—	2	1	1	—	—	—	—	—	—
8	—	—	—	1	—	—	1	—	—	—	—
9	—	—	—	2	—	—	—	—	**2**	—	—
10	—	—	—	1	—	1	—	—	—	—	—
11	—	—	—	2	1	2	—	—	—	—	—
12	—	—	—	1	3	3	—	—	—	—	—
13	—	—	—	—	7	1	—	—	—	—	**1**
14	—	—	—	1	7	7	5	—	—	—	—
15	—	—	—	1	5	9	—	1	—	—	—
16	—	—	—	1	10	4	3	1	—	—	—
					Lepidostoma sp.						
3	—	—	—	—	—	—	—	—	**2**	—	—
4	—	—	—	—	—	2	—	—	**2**	—	—
5	—	—	—	—	3	4	—	—	—	**1**	—
6	—	—	—	—	1	10	2	2	—	—	—
7	—	—	—	—	2	58	17	1	—	—	—
8	—	—	—	—	—	44	34	2	—	—	—
9	—	—	—	—	—	12	3	—	—	—	—

for an intermittent stream (Ross, 1944, pp. 7 and 204) and of *N. concinnus* for permanent streams (Lloyd, 1921, p. 73). Both life histories agree closely with that of *N. concinnus* of Caldwell Hollow. The small stone-cased larvae first appeared in early spring of 1964 in riffle areas. They grew rapidly, and some entered the long prepupal (aestivating) stage in late April when isolated flow still persisted in the stream. They survived part of the dry period in the prepupal stage attached to the under side of rocks, usually in shaded areas. Pupation and emergence took place sometime in September as evidenced by discarded sclerites in abandoned cases. Adults were not found. What apparently were egg masses of this species, as described by Vorhies (1908, p. 671), were located in October and November; however they could not be cultured successfully in the laboratory. *N. concinnus* is a permanent member of the stream community, surviving the early part of the dry period in the prepupal stage, spending a short period as a pupa and adult, and the remainder in a resistant egg stage. Two other caddisflies—*Eubasilissa* sp. and *Diplectrona* sp.—were found during the spring in Caldwell Hollow. Although they were not abundant in either year they apparently are permanent members of the intermittent-stream biota.

Allocapnia pygmaea (Burmeister), a small winter stonefly, emerged from the intermittent stream during March and April 1964. Eggs were laid shortly thereafter and hatched almost immediately. Small nymphs 2 mm in length were taken in subsurface seepage in early July and exhibited little additional development during summer and autumn. In January 1965, nymphs of 2 mm again were found. They apparently resumed development shortly thereafter, as they ranged in size from 4.0 to 5.5 mm by the middle of February and from 5 to 7 mm in the first week of March. At this time emergence began and continued through early April. *A. pygmaea* therefore is a permanent component of the stream, surviving the dry periods as very small nymphs deep in subsurface seepage or moist interstitial spaces. Several stonefly genera including *Allocapnia* have been noted in other North American streams that regularly dry up in summer (Frison, 1929; Gaufin, 1962). Although there is some discussion today as to whether it is the egg or nymph that survives the drought (see discussion p. 143, Gaufin 1962), Frison (1929) demonstrated in his early paper that it was the nymph in *Allocapnia vivipara* (Claassen) and also in a species of *Taeniopteryx*.

Isoperla decepta Frison, a stonefly, and *Heptagenia* sp. (probably *maculipennis* Walsh), a mayfly, were found for very short periods each spring. Both were abundant in 1965 but only *Heptagenia* sp. in 1964 (see Fig. 4). Both emerged during May 1964. The emergence period was synchronous in *Heptagenia* sp., with oviposition occurring sometime during the ensuing 48 hours. Females were observed depositing eggs directly on the surface water of isolated pools. Emergence in *I. decepta* was staggered somewhat. By the middle of May 1965, nymphs were rare, although it was the last week in May before large numbers of females were seen ovipositing. Females did not deposit eggs directly in isolated pools but crawled beneath rocks at the side of pools or even in shallow seepage where water scarcely was visible. Small nymphs of *I. decepta* and *Heptagenia* sp. could not be found during the summer and autumn.

They apparently survive the dry months by having a long hatching period. Still, caution should be used in assigning an egg-resistant stage, especially to *Isoperla* (re. *Allocapnia pygmaea*). Interesting aspects of the life histories of the two species are the very short period when these insects are an obvious part of the stream community and their relatively advanced stage when first found. This is illustrated for *Heptagenia* sp. by Table 4.

It is suggested that both species spend a considerable part of their nymphal life in interstitial water far beneath the surface of the stream bed. This region was adequately sampled in summer and autumn, but little attention was paid to it in spring when the stream was flowing. Chappuis (1942) was one of the first to recognize interstitial water of streams as a distinct habitat, and Orghidan (1959) used the term hyporheic to distinguish it from psammal areas of lakes. Schwoerbel (1961) found stygobiontic water mites to be the most characteristic organisms in this zone, which also served as a "nursery" for various aquatic insects. The stonefly *Leuctra* spent such a large part of its nymphal life in the hyporheic zone that it exhibited a reduction in eyes. In this respect it would be interesting to know the description of the adult.

TABLE 4. Number of *Heptagenia* sp. in each size group during the spring of 1964.

	Size (mm)										
Date	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0
April 25	—	—	—	—	1	—	—	—	—	—	—
May 11	1	1	1	—	7	4	8	7	7	1	3
May 24	—	10	3	10	19	20	11	6	9	1	1
June 1	—	—	—	—	1	—	—	—	4	—	1

A few specimens of *Ameletus lineatus* Traver and *Perlesta placida* (Hagen) were found in the spring months of both years. Little data are available for these species in Caldwell Hollow, although another species of *Ameletus*, *A. ludens* Needham, is one of the few mayflies with a reported history of surviving in streams that regularly dry up (Clemens, 1922). Clemens (1922) also demonstrated in the laboratory a five-month incubation period for eggs of this species, and he believes the long egg stage allows it to exist in intermittent environments. The life history of *A. lineatus* in Caldwell Hollow would appear to be similar. *P. placida* probably has a life cycle similar to *Isoperla decepta.*

The other common animal of the spring fauna was the creek chub, *Semotilus atromaculatus*. It migrated into the stream from Salt Creek during high water of March 1964. Reproduction took place here, but the young perished during the first dry period of August, and hence it was unable to complete its life cycle in the intermittent environment. Its absence in the spring of 1965 was due to rotenone poisoning of Salt Creek during the fall of 1964.

Triclads including probably *Phagocata morgani* (Stevens and Boring) were common macro-invertebrates of the stream, but were not adequately sampled. Organisms present on few occasions included the caddisflies: *Drusinus* sp. and *Wormaldia* sp. (both in spring); mayflies: *Siphlonorus* sp. and *Paraleptophlebia* sp. (spring); dragonfly: *Cordulegaster obiquus* Say (autumn); coleopteran: *Helichus fastigiatus* (Say) (non-seasonal); dipterans: *Tabanus* sp. and Tipulidae (autumn); malacostracans: *Orconectes propinquus* (Girard) and *Asellus stygius* (Packard) (both non-seasonal); vertebrates: *Plethodon dorsalis* (winter) and *Notropis cornutus* (spring). Entomostracans and nematodes were not investigated. Molluscans were not present.

There were striking differences between the spring fauna of Caldwell Hollow and that of adjacent permanent streams in 1964. In the latter, *Drusinus* sp. *Ptilostomis* sp., hydropsychids, *Wormaldia* sp., *Leptophlebia* spp., *Stenonema* spp., *Baetis* spp., *Agrion* sp., *Psephenus* sp., and various species of Tendipedidae were common in spring and early summer. Large numbers of *Lirceus fontinalis* and a few *Crangonyx forbesi* also were found in March and April in the permanent streams. The situation was changed in the spring of 1965, due chiefly, it is believed, to the rotenoning of Salt Creek and its permanent tributaries in the autumn of 1964. Invertebrates in Salt Creek were sparse and consisted mainly of species that also were present in Caldwell Hollow. Chief among these were *L. fontinalis, Heptagenia* sp. (same species as Caldwell Hollow), *Ameletus lineatus,* and *Isoperla decepta.* In seems likely that small streams such as Caldwell Hollow, which were completely dry at the time of the poisoning, contributed substantially to the initial reestablishment of invertebrates in the poisoned stream.

The percentage composition of major invertebrates throughout the year (Fig. 4) reflects the overall dominance of the two malacostracans. With the exception of April and May when the spring fauna was well represented, *L. fontinalis* and *C. forbesi* consistently made up 80 to 90% of the total number of organisms. During June, July, and part of August, all specimens of *C. forbesi* were very small—in the 2 and 3 mm size range. They were present in deep subsurface water and moist interstitial spaces but were not quantitatively sampled.

From the above information it is possible to obtain a fairly accurate picture of similarities and differences between the fauna of this intermittent stream and that of permanent streams. Caldwell Hollow is characterized by the two crustaceans, *L. fontinalis* and *C. forbesi,* which survive the dry months as very small organisms in deep subsurface seepage and even moist interstitial spaces. All remarks must be made relative to their dominant position. Invertebrates active in the spring are mostly permanent residents of the stream. The same species appeared in both years, constituting a uniform and apparently stable community. This is in contrast to drought-stricken permanent streams or even streams that regularly are reduced to isolated pools in the summer. Here the studies of several workers (Hynes, 1958; Larimore *et al.,* 1959; and Sprules, 1947) demonstrate the immediate destruction of many invertebrates under such adverse conditions.

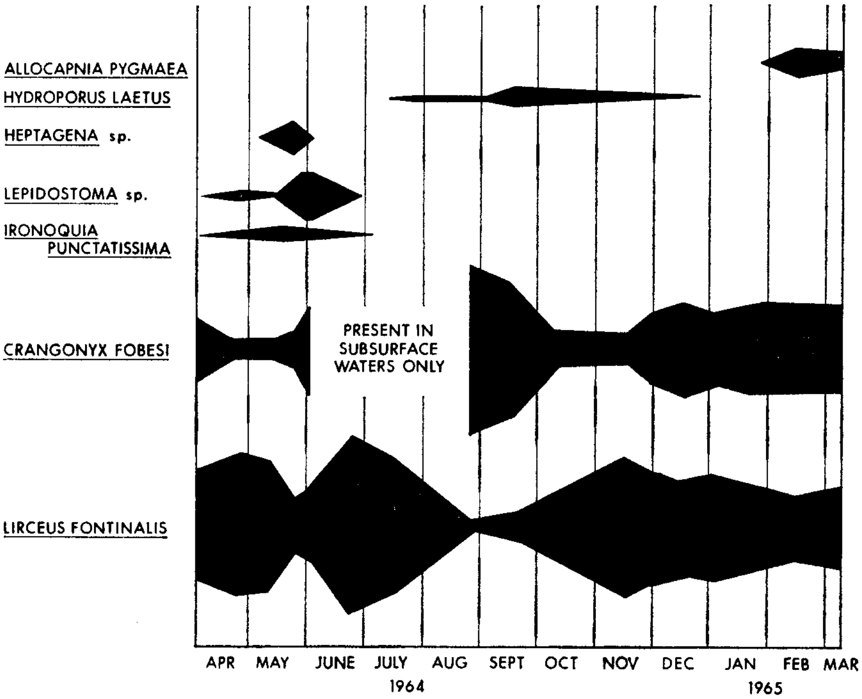

FIG. 4. The percentage composition throughout the year of invertebrates that made up at least 2% of the total monthly sample. The width of the spindle is proportional to the number of specimens taken on the sampling date.

The active spring fauna of Caldwell Hollow survive the dry periods in diverse ways, all of which are associated with favorable stages of their life cycle in relation to drought conditions. The holometabolous caddisflies appear to be the most highly adapted of the aquatic insects, surviving the dry periods as large aestivating larvae or pupae in at least a semiterrestrial habitat. Mayflies and stoneflies survive the dry spells as very small nymphs exhibiting no growth during these periods, or as eggs. All the members of the spring fauna had only one generation a year (were univoltine), exhibited little growth in the summer, and completed their life cycles in approximately one year (had annual cycles). Also, all the aquatic insects with the exception of caddisflies emerged in the spring. The regularly occurring dry periods, therefore, eliminate (1) bi- or multivoltine invertebrates, *e.g., Baetis* spp., *Stenonema* spp., and *Neocloeon* sp.; (2) animals with life cycles of two or more years, *e.g., Pteronarcys* spp., and *Acroneuria* spp.; (3) animals with a major growth period in summer and an emergence in autumn, *e.g., Hydropsyche* spp. and *Ephemerella* sp.

The above mentioned criteria characteristic of the intermittent-stream fauna are also shared by a variety of permanent-stream inhabitants. Hynes (1961) for a Welsh mountain stream reports at least eight species of mayflies and stoneflies whose life histories would seem to qualify them nicely for the intermittent environment. Other examples could be cited. Of course the intermittent-stream organisms themselves are found also in permanent waters. With the exception of the caddisflies, especially *I. punctatissima, Lepidostoma* sp., and *N. concinnus,* the species are not specifically adapted to the intermittent environment of Caldwell Hollow but are able to survive there by utilizing favorable aspects of their life cycles.

REPRODUCTIVE CYCLES OF *Lirceus fontinalis* AND *Crangonyx forbesi*

The previous discussion suggests that the life cycles of permanent univoltine species in intermittent streams can be considered in most instances "pre-adapted" rather than adapted *per se* to the adverse conditions of this habitat. Moreover, the number of the non-seasonal crustaceans, *L. fontinalis* and *C. forbesi,* far exceeds that of the seasonal fauna. The following sections are concerned with factors that may be related to the dominant position of the two malacostracans in the intermittent environment.

The specific facts of reproduction for aquatic amphipods and isopods, respectively, are reviewed by Hynes (1955) and Ellis (1961). Female peracarid crustaceans are characterized by the possession of a brood pouch, or marsupium, in which the eggs are carried and the young undergo development. In brief, the female molts releasing the oostegites to form the brood pouch. Copulation ensues, with or without a period of precopula, and shortly thereafter the eggs are released into the pouch. After a period of days the young develop and are released from the pouch. The females of most species may mate again.

Lirceus fontinalis

With reference to aquatic isopods, *L. fontinalis* in a permanent stream of Illinois reproduces throughout the year but with a peak in the spring months (Marcus, 1930). Minckley (1963) also observed reproduction in *L. fontinalis* throughout the year in a Kentucky stream. In the same stream another isopod, *Asellus bivittatus* Walker, breeds in every month, with a peak in the spring. Ellis (1961) reports gravid *A. intermedius* Forbes in a Michigan trout stream during every month, although few in winter. In an Illinois stream that is reduced to isolated pools in the summer, Allee (1912) noted breeding peaks in April and late fall for *A. communis* Say, with occasional breeding during the summer but very rarely in August and September. Of the brackish water isopods, *Idotea emarginata* (Fabricius) breeds throughout the year in Great Britain (Naylor, 1955). The trend therefore, is for temperate aquatic isopods to reproduce throughout the year, with peaks in the spring months.

In contrast, the period of reproduction of *L. fontinalis* in Caldwell Hollow is restricted to late winter and spring (Fig. 5). Laboratory experiments with three pairs of animals indicate that each female has but one brood during its reproductive phase, with an average incubation of 33 days at 13° C. Assuming this is also the situation in nature, the

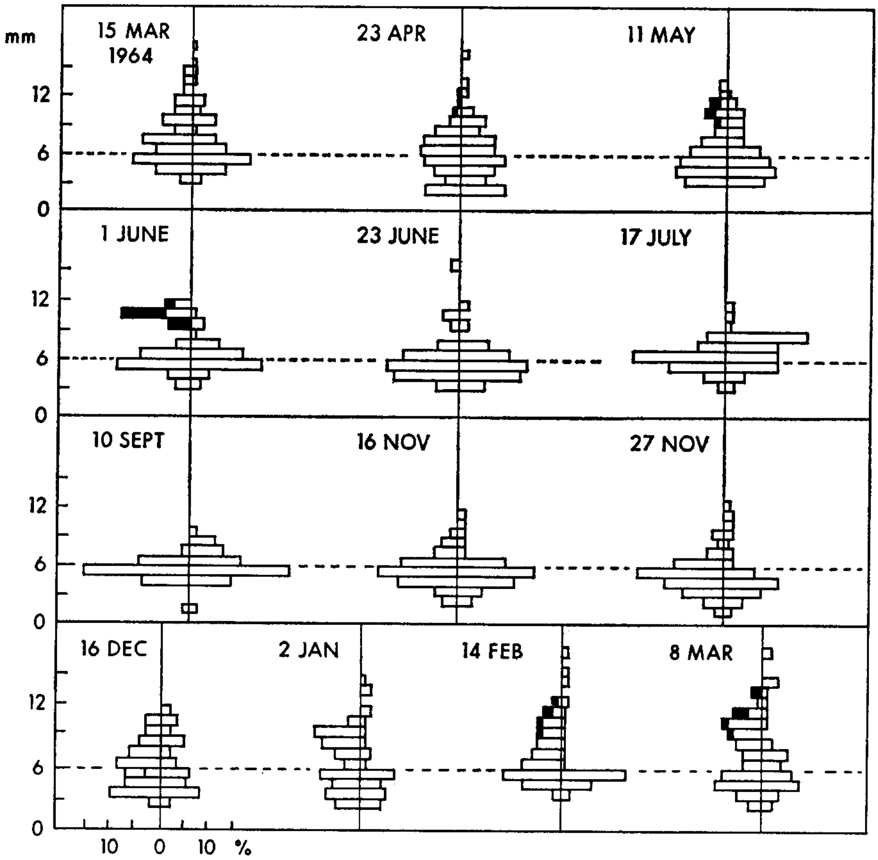

FIG. 5. Size and reproductive condition of *Lirceus fontinalis*. Juveniles are centered below the dotted line. Above this line females are on the left, males on the right of the midline. Females with brood pouches are blackened.

life cycle of *L. fontinalis* in the intermittent environment may be described as follows.

In Caldwell Hollow in 1964 and 1965 there was an annual cycle with a life span of approximately one year. The first of the large overwintering adult females became ovigerous in late March and early April 1964 (Fig. 5). With a maximum incubation time of 30 days (the water temperatures averaged 15°C at this time), the first of the new generation should have appeared in late April and early May, although the very small animals of 1 and 2 mm were not adequately sampled. This new generation grew rapidly, and some were sexually differentiated by June. Meanwhile, overwintering juveniles and smaller females had grown and became ovigerous in late May and June. Their offspring would not appear until late June. The two peaks of ovigerous females are reflected by the percentage of females with young and with empty pouches during the reproductive period and by the paucity of ovigerous specimens in the middle of the

TABLE 5. *Lirceus fontinalis.* Summary of samples collected for studying the reproductive cycle.

	1964										1965		
Sampling date	Mar. 15	Apr. 23	May 11	Jun. 1	Jun. 23	Jul. 17	Sep. 10	Nov. 16	Nov. 27	Dec. 16	Jan. 2	Feb. 14	Mar. 8
No. of specimens	190	271	351	187	152	112	83	145	115	134	125	153	153
% juveniles (less than 7 mm in length)	54	48	54	42	60	29	61	66	49	48	43	39	29
% males	19	22	23	23	21	44	28	15	19	30	25	27	32
% females* without brood pounches	27	27	18	22	19	27	11	19	32	22	32	30	30
% ovigerous females	0	3	1	5	0	0	0	0	0	0	0	4	7
% females with young	0	0	2	0	0	0	0	0	0	0	0	0	0
% females with empty brood pouches	0	0	2	8	0	0	0	0	0	0	0	0	2
Av. length of ovigerous females (mm)	—	12.0	12.5	11.0	—	—	—	—	—	—	—	12.5	12.5
Range of eggs or embryos in brood pouches		180-270	130-200	110-180	—	—	—	—	—	—	—	40-275	170-270

* with or without oostegites

period (Table 5). All overwintering animals, both males and females, had perished by the end of July. The new generations grew very little in the summer and early autumn when temperatures were high and the stream was periodically dry. It was during this time that the animals, because of their small size, were able to penetrate deep into the moist interstitial spaces of the stream bed.

In September, prior to the resumption of rapid growth, there were essentially only two size groups. One consisted chiefly of juveniles 4-6 mm long, the offspring of the early reproducing adults of the previous spring. The other group consisted of very small animals approximately 2 mm in length, resulting from the late reproducing females of 1964. Failure of reproduction to occur in late summer and fall is due to the lack of mature animals at these times. This in turn is influenced by the arrested growth of the new generation during July, August, and September and also possibly by the early mortality (due to drought) of still potentially reproductive animals of the old generation.

Growth through the winter was rapid. The first females with small oostegites appeared in the middle of December, and by 14 February the first ovigerous females of 1965 were present. These females and their larger male counterparts, therefore, probably derive from the early reproducing adults of 1964.

Factors important for the survival of *L. fontinalis* in the intermittent stream are the small size of most specimens when the stream initially goes dry and the following period of arrested growth. Since it has been determined that most aquatic isopods have a peak vernal period of reproduction, size in itself can not be considered an adaptation to the intermittent environment. Arrested growth during adverse conditions has been reported for a variety of animals. In some instances this phenomenon is reportedly due to external environmental elements and in other cases to internal or intrinsic factors.

Some obvious exogenous components to be considered in the intermittent stream during the dry period are high temperatures and decreased availability of oxygen. Both these conditions are realized in Marcus' (1930) permanent stream during the summer months where *L. fontinalis* grew and reproduced throughout the year. Hence, these factors alone are not adequate to explain the situation in Caldwell Hollow, and it is suggested that an equally important factor is photoperiodicity. The small animals survive drought periods deep beneath the stream bed, receiving little if any light until the water table again builds up in the autumn, at which time rapid growth again resumes. Stephens (1955) working with a decapod crustacean, *Cambarus virilis,* found an increased tendency for it to molt with increasing length of photoperiod. Those kept in complete darkness for 64 days failed to molt. Tempting as this hypothesis is, its verification for *L. fontinalis* would have to rest on detailed study beyond the scope of the present investigation.

Egg production was not studied in detail. The wide range in number of eggs in the brood pouch (Table 5) reflects failure of eggs to develop, capture when all eggs were not fully laid into the pouch, varying size of females (since larger females may average more eggs than smaller ones), and in some instances loss from the pouch because the eggs were not counted immediately after collection. The females with empty pouches of 8 March 1965 exhibited opaque oostegites indicating they had just molted to the mating condition, as confirmed by the dissection of eggs from the ovaries. The average number of eggs (no cleavage), embryos (somites apparent), and young (eyes apparent) was 220, 105, and 55 respectively. These data are from females throughout the reproductive period regardless of time and size. This disparity undoubtedly reflects some mechanical loss of late-stage embryos and young when stored in alcohol for long periods and also possibly early expulsion of these stages from crowded brood pouches. That it also indicates failure of some eggs to develop was demonstrated by the presence of many uncleaved eggs in the brood pouches of females when all other "offspring" were in a late embryo stage. Ellis (1961) found only 17% mortality from egg to young in *Asellus intermedius*, while Jancke, as reported by Ellis (1961), observed almost 50% mortality in *Asellus aquaticus*.

Crangonyx forbesi

In contrast to aquatic isopods, temperate aquatic amphipods usually do not reproduce throughout the entire year. Exceptions are *Gammarus minus* Say of eastern United States (Bousfield, 1958) and *Crangonyx pseudogracilis* Bousfield (= *gracilis* Smith *partim*) in Great Britain (Hynes, 1955). Although some species may have generations in the spring and autumn, such as *G. fasciatus* Say (Clemens, 1950; Hynes, 1955) and *Hyalella azteca* (Saussure) (Gaylor, 1921), most have only one generation a year. Reproduction in North American species is usually restricted to spring and early summer, with life spans of 12 to 15 months. The deep-water northern species *Pontoporeia affinis* Lindstrom is an exception, breeding during the late autumn and winter and having a life span of approximately two years (Larkin, 1948). Bousfield (1958) also indicates a winter breeding season for the northern species *Paramoera*. Little is known of reproduction in *Synurella* Wrzesniewski, *Bactrurus* W. P. Hay, and the various subterranean genera common in south-central United States.

Bousfield (1958) reports ovigerous *C. forbesi* from March to May, and this agrees with the results reported here. Ovigerous females first appeared in early April (Fig. 6), although spot collections indicated their presence in the middle of March. By the last of April ovigerous specimens had reached their peak, and in early May the new generation was present. Shortly thereafter egg production declined (Table 6). The overwintering animals started to decline in abundance during May, a time when many pools still persisted in the stream. Mature males are smaller than females in this species, and there is indication they die before the females. Sometime during June the last of the 1964 reproducing generation perished. The new generation disappeared from the few remaining pools in June and was found deep in subsurface seepage which could be located through August. An adequate sample could not be obtained from 1 June to 25 August.

As was found for *Lirceus*, growth through the summer and early autumn was slow. By November more rapid growth was taking place, and the first females were distinguishable. Females, being larger, could

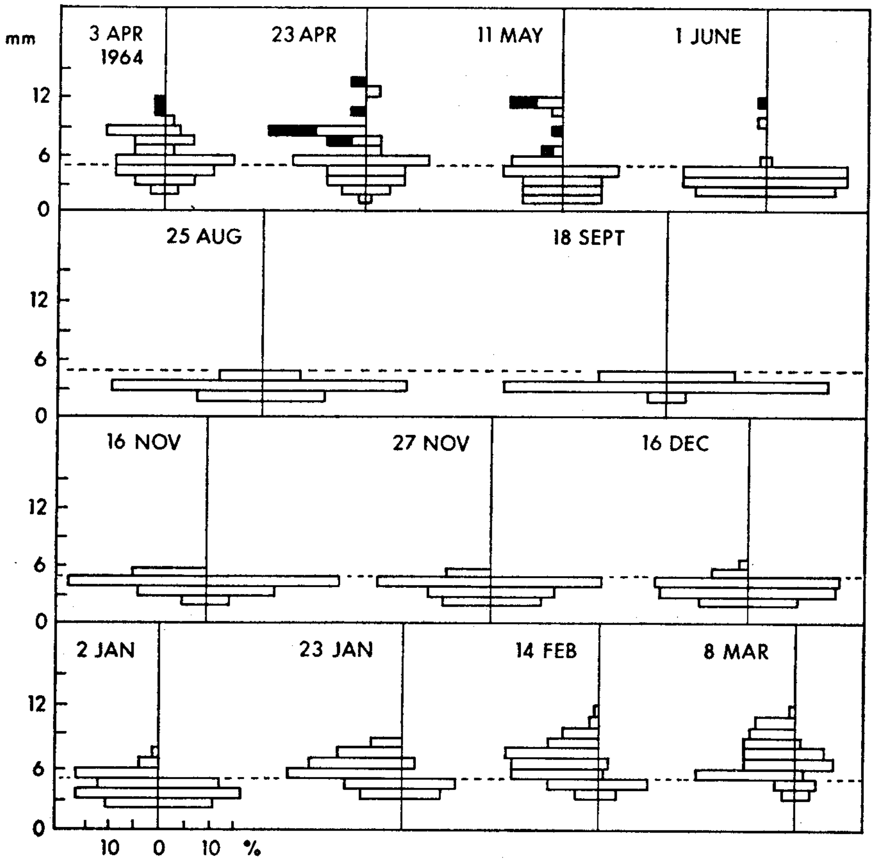

FIG. 6. Size and reproductive condition of *Crangonyx forbesi*. Juveniles are centered below the dotted line. Above this line females are on the left, males on the right of the midline. Females with brood pouches are blackened.

be recognized before males, which were not distinguished until late January. The first ovigerous female of 1965 was collected on 19 March (not indicated in Fig. 6).

Because of small although representative samples in the initial phase of the study, information on egg production is sketchy. The average number of eggs per female was 90, and although culture experiments are inconclusive, it appears that each female produces only one brood and then dies. Of six laboratory pairs, only one female became ovigerous, and it perished before carrying the brood to "term." Females that were ovigerous when brought into the laboratory produced only one brood. The decrease in size of ovigerous specimens through the reproductive period (Table 6) lends credence to the view that each female produces only one brood and then dies. Death of the adult after release of young from the brood pouch has been reported for two other species of *Crangonyx* (Bousfield, 1958, pp. 94 and 96).

TABLE 6. *Crangonyx forbesi.* Summary of samples collected for the study of reproductive cycle.

	1964									1965			
Sampling date	Apr. 3	Apr. 23	May 11	Jun. 1	Aug. 25	Sep. 18	Nov. 16	Nov. 27	Dec. 16	Jan. 2	Jan. 23	Feb. 14	Mar. 8
No. of specimens	53	40	61	88	400	300	33	68	141	88	69	217	160
% juveniles (less than 6 mm in length)	38	33	69	96	100	100	85	91	92	78	37	27	14
% males	24	17	—	1	—	—	—	—	—	—	3	3	17
% females* without brood pouches	34	30	21	2	—	—	15	9	8	22	60	70	69
% ovigerous females	4	12	2	—	—	—	—	—	—	—	—	—	—
% females with young	0	5	3	0	—	—	—	—	—	—	—	—	—
% females with empty brood pouches	0	3	5	1	—	—	—	—	—	—	—	—	—
Av. length of ovigerous females (mm)	12	9	8	—	—	—	—	—	—	—	—	—	—
Range of eggs or embryos in brood pouches	85-93	55-98	35	—	—	—	—	—	—	—	—	—	—

* with or without oostegites

It previously was pointed out that males die before the females. Since the 1965 winter sample gives no indication that males are born earlier in the season than females (the situation found in *Gammarus duebeni* Lillj. by Kinne, as reported by Hynes, 1955), it is likely they have a shorter life span than females. The more numerous females during early growth of the new generation (December, January 1965) can be explained by the larger females reaching 5 mm in length (below which all animals were considered juveniles) before males. This disparity, however, carries through the reproductive season. If April is considered the peak month of reproduction in *C. forbesi,* there is still a sex ratio of 2.2 females to 1 male. Although caution must be used in making inferences from the small April samples, it seems there may well be a preponderance of females in this species.

Generalized life cycles

From above data on *L. fontinalis* and *C. forbesi* it now is possible to describe their life histories and the significance of their reproductive cycles in relation to the intermittent environment. Late autumn and winter, when temperatures are low and the water table is building up, is a period of rapid growth for juveniles and young adults of both species. They begin to breed in March and April, months that normally exhibit the maximum amount of water in the intermittent stream. Breeding is restricted to the vernal period for both species. In *L. fontinalis* its termination appears to be facultative in part, due to the early death of still potentially reproductive animals of the old generation and the arrested growth of the new generation. Both phenomena are influenced by the onset of the dry period. In *C. forbesi,* at least in this region, reproduction unvaryingly occurs only in the spring, with adult females producing one relatively large brood and then dying prior to the drying up of the stream. All the old generation of both species perish by June and July, a time when few pools remain. The individuals of the new generations grow very little during summer and early fall when the stream is completely dry or consists only of transitory pools. The very small animals survive deep in subsurface seepage or, as will be pointed out in a later section, in moist soil *per se.* With the formation of permanent pools in late fall and influenced by falling water temperatures and possibly other factors, such as photoperiod, rapid growth resumes.

SEASONAL OXYGEN CONSUMPTION, *L. fontinalis*

It is apparent that *L. fontinalis* and *C. forbesi* exhibt little growth in summer and early autumn (Figs. 5 and 6), which are the times when the stream is dry or consists only of transitory pools. Water that is present has a low O_2 content and high temperatures (Fig. 2). Aquatic poikilotherms during this time must adjust in some way to these surroundings in order to survive. One such adaptation could be a reduced metabolic rate in summer and early autumn. Metabolic rate as used here refers to oxygen consumption per unit body weight per hour, in contrast to metabolism, which refers to total oxygen consumption of the animal per hour (after Zeuthen, 1953).

Yearly variations of metabolic rate in aquatic invertebrates have not been investigated extensively. Most data that are available have been reported only on a bi-yearly basis (*e.g.*, winter and summer). In respect to crustaceans, Edwards and Irving (1943a), working with the sand crab *Emerita talpoida* Say, found oxygen consumption four times higher in winter than in summer when measured at 30°C. The higher metabolic rate in winter was interpreted as a winter adjustment sustaining growth and activity at low temperatures. Krog (1954) obtained evidence of a lower oxygen consumption in winter than in summer for an amphipod from Alaska, *Gammarus limnaeus* (Smith), which he associated with the low oxygen content of the ice-covered lake in winter. Roberts (1957), working with the shore crab *Pachygrapsus crassipes* Randall, reported a parallelism between metabolic rate and short-term fluctuations of local temperatures in southern California but found no definite seasonal trend. Clark (1955) reported the oxygen consumption of a soil-inhabiting amphipod of the Australian rain forest, *Talitrus sylvaticus* (Haswell), to be significantly higher in winter (*e.g.*, July) than in summer (*e.g.*, January). In contrast, the amphipod *Talorchestia megalopthalma*, which inhabits the ocean beaches of eastern United States, was found to have the same metabolic rate in winter and in summer (Edwards and Irving, 1943b). However, animals of the same body size were not used throughout this study. By recalculating the data from the above study and taking into consideration body size, Rao and Bullock (1954) also projected a higher winter metabolism for *T. megalopthalma*. Frankenberg and Burbanck (1963) found no significant change during the year in the oxygen consumption of the estuarine isopod, *Cyathura polite* (Stimpson), when compared between November and March and between May and July. There are numerous reports and reviews in the literature of other compensatory mechanisms related to oxygen consumption of aquatic poikilotherms, including crustaceans. Macan (1961, pp. 170-179) reviews many of these factors in relation to ecology.

For *L. fontinalis* in Caldwell Hollow, oxygen consumption declined in late spring and summer when measured at 5° C (Fig. 7). A corresponding decrease was not evident at 13° C. However, when comparing oxygen consumption on a yearly basis, individuals in the same physiological state should be used (*e.g.*, age, sexual state, size, activity, etc.). Because of its restricted reproductive period and the early death of still mature specimens, this obviously was impossible for *L. fontinalis*. The best that could be hoped for was to use animals of uniform body size throughout the study period, but even this was impossible (Fig. 7), because only small animals were present in summer and early autumn. Although the relation of metabolic rate to body size was realized, no correction for body size was made in this study. A winter weight-specific regression coefficient of -0.29 was estimated at 13° C for *L. fontinalis*. This figure agrees closely with those of other isopods—*Asellus aquaticus* L., -0.32 at 10° C (Edwards and Learner, 1960) and *Ligia oceanica* L., -0.27 at 25° C (Ellenby, 1951). If the regression line has the same slope in all seasons, a factor not investigated, the animals at 13° C also would exhibit a lower metabolic rate in summer, when size is considered.

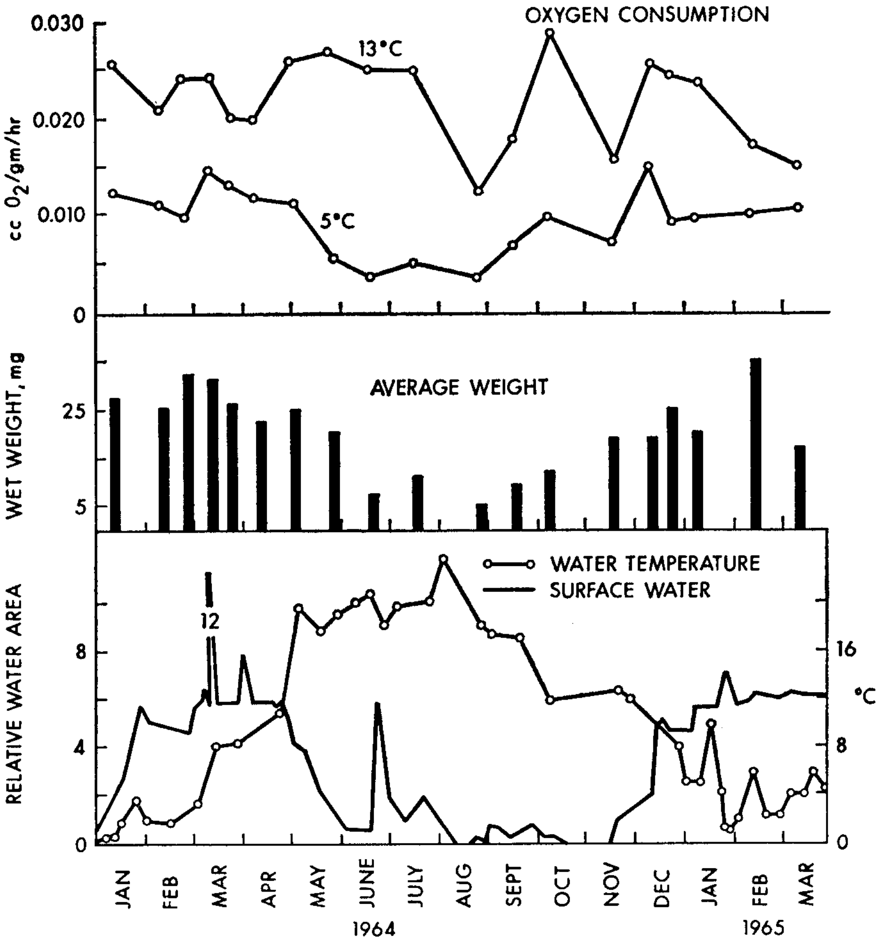

FIG. 7. Oxygen consumption of *Lirceus fontinalis*, water temperature, and visible surface water, January 1964-March 1965.

The metabolic rate at 5° C declined rapidly in May, at which time isolated pools were drying up, and water temperatures were becoming high (Fig. 7). Dissolved oxygen also was becoming depleted (Fig. 2). Temperatures started declining in August and September, and it was at this time that the oxygen consumption of *L. fontinalis* began to increase. No connection could be established between this initial autumn increase and any other changes occurring in the aquatic habitat at this time. The stream was almost completely dry, and dissolved oxygen was extremely low. Hence, the seasonal changes in metabolic rate seem related neither to regularly occurring changes in the water regime nor to changes in dissolved oxygen content. The seasonal changes follow closely but inversely that of temperature.

In this respect the lower metabolic rate of summer animals at 5° C may be due in part to a cold-depression effect, in that animals taken from their warm habitat and transferred to 5° C may have been depressed at this temperature even though they were acclimated to the test temperature. A temperature of 5° C would not depress winter animals.

An increase in oxygen consumption during the reproductive period has been reported for other invertebrates, especially molluscs (Bruce, 1926; Berg *et al.,* 1958). Knowing the life cycle of *L. fontinalis* in Caldwell Hollow it is possible to compare the oxygen consumption of reproductive and nonreproductive individuals. Animals approximately 10 mm in length, which is a sexually mature size for this species, were collected in winter and spring. No ovigerous females were used, however. The reproductive period of *L. fontinalis* extended from April to early June in 1964 (Fig. 5), but maximum oxygen consumption (5° C) appeared to be reached in March. It was declining rapidly in May, the middle of the reproductive period. If there is a connection between metabolic rate and reproduction, it was masked by other stronger compensatory factors such as temperature.

As previously mentioned, *L. fontinalis* (and *C. forbesi*) grow little during the summer. Whether or not the physiological processes are such that the animals might be considered in a state of aestivation during this period is not definitely known. Certainly, aestivation might be a process by which the animals could survive the unfavorable summer conditions, and the lower summer metabolic rate suggests such a possibility. Garten-Fischler (as reported by Eckstein and Abraham, 1959) obtained evidence of a depressed oxygen uptake in aestivating snails. In this respect it would be interesting to measure monthly oxygen consumption of *L. fontinalis* maintained at a constant temperature throughout the year to see if there is an intrinsic lowering of the metabolic rate in summer. This very phenomenon has been observed for a species of killifish (Wells, 1935).

HUMIDITY AND SOIL FACTORS

Humidity and survival of L. fontinalis

The only true terrestrial crustaceans, in the sense of living and reproducing without immersion in water, are found in the same order to which *L. fontinalis* belongs, such as the numerous species of terrestrial isopods commonly known as sow bugs or pill bugs. These organisms survive in air by occupying areas of high relative humidity. The terrestrial isopods can be arranged in a series with respect to their powers of water retention and their habitat preference. *Ligia* is least adapted to terrestrial environments, being found close to water and exhibiting low water-retention abilities. *Oniscus* is intermediate in habitat preference and water retention, while *Armadillidium* lives in drier places and has greater water-retention capacities. Recently Warburg (1965) reported a desert isopod, *Venezillo arizonicus* (Mulaik and Mulaik), with very high water-retention abilities. Lagerspetz and Lehtonen (1961) and Lagerspetz (1963) in Finland conducted a series of humidity experiments using true aquatic isopods and amphipods. Those species that lived the longest time in water-saturated air (*Asellus aquaticus* and *Gammarus duebeni*) were the same species found in temporary brackish water pools.

An experiment, using methods similar to those of Lagerspetz, was carried out with *L. fontinalis* and *C. forbesi* from the intermittent stream and with *L. fontinalis* and *Gammarus minus* from a permanent stream. Animals were blotted carefully and placed on the bottom of open, dry plastic containers. These in turn were placed in a humidity chamber containing water-saturated air at 13° C. The humidity chamber was prepared by placing water in the bottom of a desiccator. Strips of filter paper lined the walls and extended into the water. Shortly after the lid was placed on the desiccator, the air in the chamber was saturated with water vapor, a condition not unlike what might be expected in deep interstitial spaces of the otherwise dry stream bed. Animals were removed from the humidity chamber for approximately 30 seconds each day and were given tactile stimulation to determine if they still were alive. Those that did not respond were removed to water, but none recovered. After death, the animals were measured and their wet weight extrapolated from a wet weight-total length graph of non-dehydrated specimens. No correlation between body size and survival time was apparent within a species. The experiment was conducted during February and March, a time when the metabolic rate of *L. fontinalis* from Caldwell Hollow was high (Fig. 7).

Both *L. fontinalis* and *C. forbesi* from the intermittent stream lived for a longer period of time than did the organisms from the permanent stream (Fig. 8). The last specimen of *L. fontinalis* from Caldwell Hollow survived until the twenty-fourth day. By this time three of the five control animals that were in water but without food also had died. Hence, it is possible that this animal died of starvation instead of a water loss or an inadequate oxygen supply. The longer survival time of *Lirceus* from the intermittent environment when compared to the same species from the permanent stream may be ecotypic. Specimens from the permanent habitat also reached their reproductive peak at an earlier time (January and February). *G. minus,* which had the shortest survival time, never has been found in intermittent streams from this area. Ten mature nymphs of *Allocapnia pygmaea* also were tested for survival. At the end of 24 hours, eight had died and one had emerged. The remaining nymph perished prior to 48 hours.

A comparison of Lagerspetz's results with those reported here (Table 7) is complicated somewhat by different test temperatures. The work in Finland was performed at 19° C, while the above experiment with organisms from Caldwell Hollow and Leonard Spring was conducted at 13° C. It also should be pointed out that *L. fontinalis* and *C. forbesi* are larger species than *A. aquaticus* and *G. duebeni.* Even considering these differences, and of course both experiments were performed with no saturation deficit, it appears as if *L. fontinalis* is better adapted than *A. aquaticus* for longer survival periods in moist soil. The amphipod data are rather similar.

In respect to *G. duebeni,* several Scandinavian workers including Segerstrale (1946, p. 18) have observed the species moving from pool to pool via the terrestrial environment. No evidence of such migrations could be found for *L. fontinalis* or *C. forbesi* in Caldwell Hollow. However, specimens of *L. fontinalis* were observed close to the surface of the dry stream bed during May and early June when widely isolated pools still

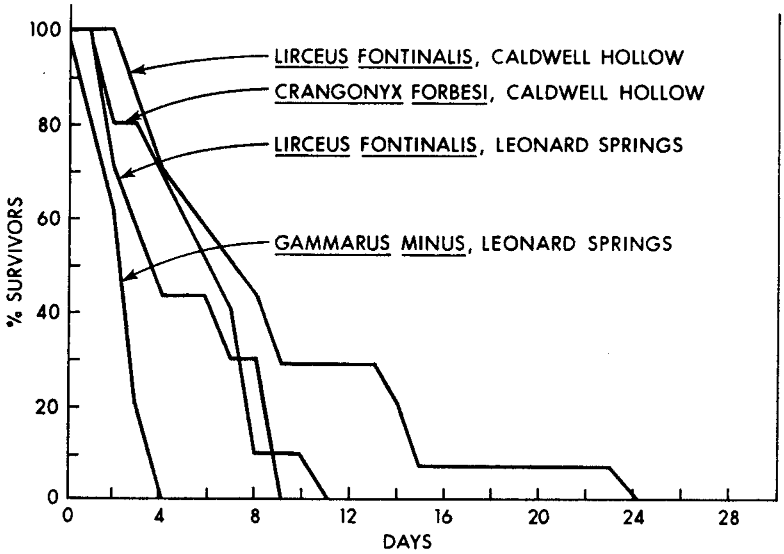

FIG. 8. Percentage survival of intermittent and permanent stream organisms in water-saturated air (100% relative humidity).

were present and subsurface seepage between these pools was rather high in the stream bed. Such near-surface occurrences, which suggest vertical migration to the suface of the stream bed, were observed only at night when atmospheric humidity was high. Hence, even though no animals were actually observed traveling up or down the dry stream bed, this would not seem an impossible task considering their survival time in water-saturated air and similar conditions that exist in the stream at certain times.

The ability to survive in moist soil would have special significance for the survival of large animals during short dry periods, *e.g.*, March

TABLE 7. Maximum and 50% survival time of intermittent-pool crustaceans from Finland and intermittent-stream crustaceans from Caldwell Hollow, Indiana, in water-saturated air at 19° C and 13° C, respectively.

	Survival time 50% of animals (*days*)	Maximum survival time (*days*)
Amphipoda		
Gammarus duebeni (Finland)*	7	9½
Crangonyx forbesi (Indiana)	6	11
Isopoda		
Asellus aquaticus (Finland)†	1¼	3
Lirceus fontinalis (Indiana)	7	24

* Lagerspetz (1963)
† Lagerspetz and Lehtonen (1961)

and April. The animals would be too large to follow the subsurface seepage downward to any appreciable depth but could survive for short periods in larger interstitial spaces containing water-saturated air.

Soil samples

In respect to the terrestrial environment it is interesting to examine more closely data collected when the stream bed was either partially or entirely dry (Table 8). Each soil sample collected contained approximately 400 cc of material. The samples were separated into the following, somewhat subjective categories.

a) *Subsurface seepage.* Sand, gravel, and mud collected from subsurface seepage in localities that were dry at the surface. These were the only samples containing any free water.

b) *Moist* and c) *dry soil.* These samples were separated arbitrarily by their dampness. Dry soil exhibited no dampness, while moist soil could be slightly damp or very damp, but it never contained visible water. It is believed that all moist soil samples contained interstitial spaces with water-saturated air, while pore spaces of dry soil samples probably were less than water saturated.

d) *Leaf litter.* Moist leaf material was collected in May and June 1964 from former pools that had had no visible surface water for at least a week.

The numbers and kinds of organisms present at any time will depend in part on the season the samples were collected in relation to the life cycles of the separate species. Another important factor is the number and size of the interstitial spaces. Approximately 200 meters before Caldwell Hollow empties into Salt Creek, a dirt road fords it (Fig. 1). During periods of rain, water in the stream above the ford is always clear, whereas drainage from the road muddies the stream below the ford and fills interstitial spaces of the stream bed. Soil samples from the lower area contained no aquatic invertebrates at all except for one adult *Helichus basalis.* This is believed due directly to the lack of interstitial spaces in this area.

Moist leaf litter apparently serves as a final, temporary "oasis" for large aquatic animals remaining in the dried-up pools (Table 8). The crustaceans here were chiefly large adults, many in both species being ovigerous. They were too large to follow the subsiding water table. Coleoptera were sparse in leaf litter, but this was due in part to their temporal distribution. The only other group present were the caddisflies *Ironoquia* and *Lepidostoma.* Both are suspected of having aestivating "terrestrial-phase" larvae and pupae. The prepupal condition was observed in both species from moist leaf litter.

Animals living in moist soil or subsurface seepage must either be small enough to inhabit the existing interstitial spaces or else have the capability to actively burrow into the soil. In the latter group belong *Orconectes, Eurycea,* and possibly some of the adult beetles. The remaining aquatic animals are small enough to survive in the pore spaces *per se.*

The size of the interstitial spaces becomes increasingly important as the stream drys up and the water table subsides. As would be expected, the large pore spaces are near the surface of the stream bed, and they decrease in size with depth. In May and early June the subsurface seepage was high in the stream bed, occupying relatively large pore spaces and maintaining water-saturated air in spaces immediately above it. Fairly large specimens of *L. fontinalis* (14 mm), *C. forbesi* (8 mm), and *I. punctatissima* (10 mm) were taken from the soil and seepage at this time. As the dry season progressed the seepage moved deeper into the stream bed, withdrawing from the larger interstitial spaces and hence making the survival of these large animals progressively more difficult. A parallel effect of this was that the water-saturated air, located above the water table, was also restricted to deeper levels containing smaller pore spaces. Short periods of rain temporarily raised the levels both of seepage and of spaces containing water-saturated air.

Organisms restricted to free water (subsurface seepage) or even those that can survive in moist soil must be of a small size during this time. During October 1963 *L. fontinalis* from moist soil averaged 3 mm in length, and in November 1963 they averaged 5 mm from subsurface seepage. Specimens of *C. forbesi* from moist soil averaged 3 mm in length during October 1963. Because of its obligate univoltine life cycle, all specimens of *C. forbesi* would be expected to be small in late summer and early autumn regardless of the stream's water characteristics. In this instance small interstitial spaces do not actively select against the large animals, of which there are none, but instead simply furnish a suitable space matrix that can be exploited by the species at a favorable time in its life cycle.

In contrast, *L. fontinalis* in permanent waters has large specimens throughout the year, which is probably its typical condition. In the dry stream, by late summer, the deep seepage and accompanying small spaces of water-saturated air are selective to small specimens of this species. As mentioned in an earlier section, the early mortality of some of the old generation, due to the above drought-related factors, accounts in part for its facultative univoltine cycle in Caldwell Hollow.

The occurrence of one large *L. fontinalis* (11 mm) in seepage during early August (Table 8) indicates that in rare instances in some locations, large interstitial spaces may extend to a considerable depth. Slack (1955), Paloumpis (1958), and Larimore *et al.* (1959), working with streams that regularly become interrupted in late summer, observed that isolated pools remaining through the dry period served as "havens" or reservoirs for aquatic animals. These pools, in many instances, were of prime importance in repopulating the streams when they again became continuous. Larimore *et al.* (1959), further pointed out that if the pools become stagnant, their inhabitants may be species unsuited for repopulation of the flowing stream.

In Caldwell Hollow the entire stream regularly becomes dry, and hence no pools can serve as repopulation foci. It is suggested that the nearest thing to a "stream haven" or faunal reservoir during the dry seasons is found in regions that contain relatively large interstitial spaces to a considerable depth. Those regions are very infrequent and almost always are located either immediately above or below former large pools, in areas where large quantities of loosely packed, coarse sandstone parti-

TABLE 8. The number and size range (mm) of species and groups of species from various types of soil samples. Samples have been grouped by month. See text for explanation of categories.

	Subsurface seepage			Moist soil			Moist leaf litter			Dry soil		
	Mo./yr.	No.	Size (*mm*)	Mo./yr.	No.	Size (*mm*)	Mo./yr.	No.	Size (*mm*)	Mo./yr.	No.	Size (*mm*)
ISOPODA												
Lirceus fontinalis	Oct/63	1	9	Oct/63	26	2-8	May/64	75	3-14			
	Nov/63	21	3-9	May/64	11	2-6	Jun/64	120	3-10			
	May/64	14	2-14	Jun/64	25	3-7						
	Jul/64	4	7-9	Aug/64	2	8						
	Aug/64	3	4-11									
Asellus stygius	Oct/63	1	4									
	Jun/64	1	3									
	Jul/64	1	3									
	Aug/64	1	4									
AMPHIPODA												
Crangonyx forbesi	Nov/63	3	3-5	Oct/63	11	3-4	May/64	122	2-14			
	May/64	12	2-8	May/64	3	2-5						
	Aug/64	4	3	Jun/64	3							
DECAPODA												
Orconectes propinquus	Nov/63	1	24									
PLECOPTERA												
Allocapnia pygmaea	Jun/64	7	2									
EPHEMEROPTERA												
Heptagenia sp.	May/64	2	4									
ODONATA												
Cordulegaster obliquus				Oct/63	1	12						
TRICHOPTERA												
Ironoquia punctatissima				Jun/64	1	10	May/64	2	15			
							Jun/64	2	9			
Lepidostoma sp.							May/64	4	5			
							Jun/64	4	3-4			

COLEOPTERA												
Hydroporus laetus	Oct/63	20	4	Oct/63	11	4						
	Nov/63	1	5*	Aug/64	26	4						
	Aug/64	1	4									
	Nov/64	11	4									
Cymbiodyta sp.	Oct/63	1	7	Aug/64	2	7						
	Nov/63	1	7									
Helichus basalis	Aug/64	2	5	Oct/63	2	5	May/64	1	5			
				Aug/64	1	5	Jun/64	3	5			
Limnebius discolor	Oct/63	18	2	Oct/63	6	2	Jun/64	1	2			
				Aug/64	9	2						
DIPTERA												
Tipulidae	Jul/64	3	4-7	Oct/63	1	3						
				Aug/64	1	3						
Tabanus sp.				Oct/63	3	3						
Tendipedidae				Oct/63	1	3				Oct/63	1	4
URODELA												
Eurycea bislineata	Oct/63	1	18	Oct/63	7	16-20				Nov/64	1	Adult
NEMATOMORPHA												
Gordius sp.										Oct/63	4	250-350
	Number of each type soil sample collected by year and month											
1963												
Oct.		2			6			3			0	
Nov.		3			0			4			0	
1964												
May		2			1			0			2	
June		0			1			1			1	
July		2			0			1			0	
Aug.		2			2			0			0	
Sept.		0			1			0			0	
Oct.		0			2			0			0	
Nov.		0			2			1			0	

* larvae

cles have accumulated. They are seldom located beneath the dry pool itself, because the pool, prior to its drying up, serves as a collecting basin for silt and small particles of detritus washed in by short periods of rain. These materials, in turn, settle into the interstitial spaces, reducing their size or eliminating them completely. Stagnation, as mentioned above by Larimore *et al.* (1959), also is characteristic of temporary pools formed during the dry periods in Caldwell Hollow. It restricts the inhabitants to adventitious species such as *Culex* and *Tubifera* and probably also affects adversely the interstitial fauna below the bed surface of the pools.

All species small enough to live in subsurface seepage do not necessarily survive in moist soil. The blind isopod *Asellus stygius* (Table 8) apparently is restricted to regions containing some subterranean water, as likewise are the small nymphs of *Allocapnia pygmaea*. In contrast, the two dominant crustaceans and adult aquatic beetles survive in spaces of water-saturated air above subsurface seepage as well as in the seepage itself.

Dry soil samples contained few organisms (Table 8). The physiological processes that maintained *Gordius* and the one tendipedid larva in dry soil are not known. Since the dry soil probably contained less than 100% relative humidity the organisms must be able to tolerate a certain fall in their moisture content. Hinton (1953) mentions that most insects can tolerate a fall in tissue moisture content of only 10 to 15 percent. He suggests those adapted to an environment that is periodically dry may take a longer time in losing this percentage. Hinton further points out, however, that a very few insects can survive much greater water losses. Among these are the larvae of the *Polypedilium vanderplankei* Hinton, found in shallow rock pools in Africa. At 65° C, in an electric oven, the larvae survived for 20 hours. In Caldwell Hollow the presence of aquatic animals, especially the dominant crustaceans, in moist soil and their absence in dry soil illustrates the narrow physical but wide ecological and physiological differences between soil pore spaces at 100% relative humidity and soil pore spaces even slightly less. This is exemplified by experiments of Edney (1951), which demonstrated that of seven species of terrestrial isopods none could gain weight and recover from desiccation at 95% relative humidity, only one species could at 98% relative humidity, while all recovered at 100% relative humidity.

DISCUSSION

With the data obtained in this study it is possible to discern certain important prerequisites for the maintenance of the permanent aquatic fauna in Caldwell Hollow. It is possible also to project and/or compare these essentials with other intermittent streams where biological studies have been carried out.

A semblance of the aquatic environment was present at all times in Caldwell Hollow. Even though the stream regularly "dried up" during the summer, water still persisted below the bed surface. This sufficed for the survival of an aquatic fauna, either in seepage itself or in water-saturated air spaces above the seepage. Survival in either locality is dependent on the availability of interstitial spaces, which in turn are determined fundamentally by stream gradient and local geology. The stream bed of Caldwell Hollow was composed mainly of non-angular sandstone fragments, which in many places extended to a considerable depth. The particles promoted the formation of numerous and relatively large interstitial spaces. Besides its shading effect, the wooded, pristine watershed accounted for a low, almost nonexistent silt load, thus maintaining the pore spaces in a relatively unclogged state. It is likely that short periods of rain during the dry seasons also aid in maintaining pore spaces by washing out accumulated detrital materials from broad reaches of the stream bed and transporting them out of the stream entirely or depositing them in the limited areas of former pools.

Besides providing a habitable environment during the dry seasons (and in other seasons) interstitial spaces also effect the velocity of the water. Jaag and Ambühl (1964) experimentally demonstrated that close to the substratum the movement of water is slowed by friction, even to the extent of creating "dead-water" zones in fissures and pore spaces between stones. These areas where flow is strongly retarded are known as Prandtl's layers after their discoverer. Jaag and Ambühl (1964) report that rheophilic animals spend most of their lives in these small, relatively quiescent water spaces.

In certain geographical regions of North America, intermittent streams have stream beds comprised chiefly of exposed bed rock or with some other type of impervious layer close to the surface. Even short periods of heavy rain will flow over the land surfaces resulting in devastating flash floods. Such events are especially common in the southwestern United States (see Leopold and Miller, 1956; John, 1964). In such streams the few "dead-water" regions, which are located near the surface of the stream bed, can not be exploited by large numbers of animals. If the organisms are not strong enough to maintain themselves against the current, heavy mortality can ensue. This is possibly one of several reasons why many small intermittent streams of the southwestern United States support a very limited macroinvertebrate population, even though the stream may have a long spring flow period. In contrast, storm water in Caldwell Hollow, and over the Norman Upland in general, infiltrates into the stream bed with much subsurface movement. It takes exceedingly heavy rains to cause high water velocities, and even when this does occur it is suspected that the aquatic fauna can find protection in relatively deeper areas of the stream bed where the numerous interstitial spaces afford protection from strong water movements.

An interesting aspect associated with water velocities is that of the stability of the stream bed and its effect on the aquatic fauna, especially during periods of high water. Since most of the stream bed of Caldwell Hollow is composed of small, non-angular fragments, the stream would be expected to be rather unstable during maximum flow. Slack (1955) observed such instability for a larger stream also located in the Norman Upland. Kamler and Riedel (1960), studying an intermittent stream in Poland, presented time-series graph of its bottom configurations that would indicate a highly unstable bed during periods of even less than normal flow, although this phenomenon itself was not discussed.

Major changes occurred in the stream bed of Caldwell Hollow during the flood of March 1964. At this time, entire riffle areas were scoured out, in some places to depths of over 60 cm. Old pools were destroyed and new ones formed. These events must have caused considerable mortality of animals inhabiting interstitial spaces. This was the only time during the study period that the stream channel was filled from bank to bank and even for a short period overflowed its banks. It was also the only time that obvious changes in the stream bed were noted. Nevertheless, minor disturbances undoubtedly occurred whenever the stream was continuous. Instability would be confined to that part of the channel with high water velocities, *i.e.*, surface flow. It would not affect appreciably the stability of regions with only subsurface seepage, which in many localities can occupy more of the stream channel than surface flow itself. In short the instability affects only a part of the habitable stream bed, and even here for only short periods.

A final aspect relating to interstitial spaces is that of the "freeze-thaw" characteristics of small streams. Newsom (as reported by Malott, 1922, p. 175) mentions that strata in the Norman Upland are soft, absorb water easily, and therefore are easily fractured by freezing. Streams entering Salt Creek from the north side, such as Caldwell Hollow, are protected from wide temperature variations, especially in the winter. In contrast streams entering from the south are exposed to wider winter temperature fluctuations, freezing at night and thawing during the day. The results are muddy, silt-laden streams flowing from the south and clear, or frozen streams entering from the north. The adverse effect of silt on interstitial spaces has been mentioned previously and would seem to be especially prevalent in intermittent streams entering Salt Creek from the south. A few spot samples taken from one of these streams in May 1964 yielded few macroinvertebrates and would tend to support such an assumption.

Turning to the permanent aquatic fauna of Caldwell Hollow, small size was a necessity for most species during the dry seasons. With the exception of the apparently highly adapted caddisflies, the permanent fauna survived in small pore spaces. Specimens of *Hydroporus laetus, L. fontinalis,* and *C. forbesi* were found as deep as 60 cm, although most were found between the surface and 25 cm. Small specimens of *C. forbesi* appeared to penetrate to the greatest depth. The consequences of the dry seasons on the species size has been discussed previously. The permanent macroinvertebrate fauna is restricted mainly to animals with a univoltine spring cycle, with a life span of not more than a year, or without a major growth period in summer or an autumn emergence.

Finally, it would be convenient to have the proper perspective of the intermittent nature of Caldwell Hollow in regards to other intermittent streams where biological studies have been carried out. No single hydrological or climatological parameter will suffice to classify intermittency, at least to the satisfaction of biologists. In the broadest sense natural aquatic channels are usually described by hydrologists as ephemeral, intermittent, or perennial (or permanent) in respect to their flow characteristics, *i.e.*, an ephemeral stream carries water only during storms, an intermittent stream is one where dry stretches alternate with flowing or standing water areas at low flow, and a perennial stream carries some flow at all times. Perennial rivers and ephemeral rills are easily separated, but the gradation from perennial streams to intermittent or especially from intermittent to ephemeral stream is often difficult to resolve objectively. For example Caldwell Hollow carries visible water for periods much longer than could result from a single storm, but at "low flow" the stream bed is completely dry.

Usinger (1956, p. 15) presents a classification of intermittent streams of California from a scheme originally formulated by Dana L. Abell (personal communication: Usinger, 1965), in which the streams are grouped by their temporal flow characteristics—*i.e.*, short flow, long flow, etc. For example, the intermittent foothill stream of California having an eight-month flow period, in which Abell (1959) studied a mosquito population, would be described as a long-flow, fluctuating, intermittent stream. Still, from a biological point of view, many local features must be considered, especially during the dry season. Of paramount importance are such components as the nature of the stream bed, water table characteristics, and the shading effect. These elements in turn depend on such a variety of geographical, geological, and climatological factors that it is beyond the scope of this report to discuss them critically in any depth.

To elaborate briefly, an intermittent stream with a long-flow period may be reduced only to isolated pools during the regularly occurring dry period. In this case, it may support a permanent and varied fauna, even a substantial fish population. In contrast, if the stream becomes completely dry during the non-flow period but retains relatively high subsurface seepage with large interstitial spaces, it may support a permanent aquatic fauna, but restricted as regards life cycles (*e.g.*, univoltine, annual, etc.)—somewhat similar to Caldwell Hollow, which, however, has a short-flow period. In still another situation the stream regularly may go completely dry during the non-flow period, with subsurface seepage drastically reduced or nonexistent. Paralleling this, the stream may exhibit an impervious stream bed having few interstitial spaces, or, as found in some arid western regions, the watershed may not be wooded, resulting in high stream-bed temperatures. In this instance, the stream's fauna may not be permanent but limited instead to adventitious and migratory species, a situation similar in many respects to that of an ephemeral rill. Although the forementioned are only idealized situations, the point is that the permanency, variety, and adaptability of aquatic fauna in so-called intermittent streams depend, among other things, on many subtle physical components. Such components are not necessarily reflected by a few criteria, descriptive of the stream's flow and non-flow state.

With the above in mind, a comparison was made between Caldwell Hollow and several other intermittent streams where pertinent biological information is available. The arrangement given below relies not so much on the described flow characteristics of the stream as on the permanency of its aquatic environment. Permanency in turn was assumed to be reflected by the type of aquatic animals (especially the life cycles of the macroinvertebrates) living in the stream. The supposition is that the dry period usually occurs in summer (at least in temperate regions), and, depending on the physical nature of the individual stream, tends to eliminate the following animals: 1) those with major growth during the dry season, including non-annual animals, *i.e.*, those with a life span of two years or more; 2) insects with a late summer or fall emergence; 3) macroinvertebrates with bi- or multivoltine reproductive characteristics, *e.g.*, those producing a generation in the fall (as well as in the spring). In short, the fauna of a stream may be a better overall reflection of the intermittent nature of the stream than are the few described parameters relating to its flowing or non-flowing period. It should be pointed out in the following arrangement that the amount of faunistic information varied widely from stream to stream, and in some instances the life cycle of a particular invertebrate could be inferred only from data of other studies. The River Susaa was used only as a reference point and because extensive faunistic information is available for it. The streams are arranged in decreasing order of permanency of their aquatic environment.

1. Permanent stream. **River Susaa, Denmark** (Berg, 1948).
   Fish: several families, including the large carnivorous species *Salmo trutta* L. and *Esox lucius* L.
   Invertebrates: includes species with possible bivoltine cycles (*e.g.*, *Caenis*); with two-or-more-year life span (*e.g.*, *Aeschna*); with fall emergence (*e.g.*, *Centroptilum*).
2. Drought-stricken (Aug.—Oct.) permanent stream. **Afont Hirnant, Wales** (Hynes, 1958).
   Fish: *Salmo trutta* and *Cottus.*
   Invertebrates: contains species with life cycles similar to those of River Susaa but temporary elimination in affected area of fall-emerging insects (*e.g.*, *Ephemerella ignita*) and of those with a bivoltine cycle or with major summer growth (*e.g.*, *Baetis tenax, Diura bicaudata, Perlodes microcephala*). After the occurrence of another egg-laying period, the above species reappeared in the former drought area, being colonized from unaffected reaches of the stream.
3. Intermittent stream. **Swinski stream, Poland** (Kamler and Riedel, 1960).
   Fish: no information available.
   Invertebrates: contains several bivoltine species and species with a major growth period in summer (*e.g.*, *Baetis* spp., *Chaetopteryx villosa, Ecdyonurus venosus*).
4. Intermittent stream. **Smiths Branch, Illinois** (Larimore *et al.*, 1959).
   Fish: several families (*e.g.*, centrachids, cyprinids, catostomids).
   Invertebrates: contains a few with bivoltine cycles or with fall emergence (*e.g.*, *Caenis, Ephoron, Cheumatopsyche*), and a few with life spans of possibly two years or more (*e.g.*, *Acroneuria, Corydalus cornutus*). The fauna was studied most intensely during a severe drought that extended over a period of years and dried up reaches that are normally wet even during the regularly occurring dry season. The drought temporarily eliminated the above species, although univoltine

species with spring emergence survived (*e.g.*, *Allocapnia*, *Rhyacophila lobifer*). Other invertebrates also surviving included adult aquatic beetles, tendipedids, and the isopod *Asellus*, probably *brevicaudus* Forbes.

5. Intermittent stream. **Brummets Creek, Indiana** (Slack, 1955).
   Fish: similar to Smiths Branch.
   Invertebrates: Although for the most part, the fauna was not broken down lower than order, summer and fall emerging *Hexagenia* were reported. Personal observation indicated bivoltine and two-year-life-span species present also.
6. Intermittent stream. **Rock Riffle, Ohio** (Stehr and Branson, 1938).
   Fish: limited to minnows (*e.g.*, *Notropis cornutus*), which are present only in fall, winter, and spring in lower reaches.
   Invertebrates: contained a few with possible major growth period in summer (*e.g.*, hydropsychids) or with a two-or-more-year life span (*e.g.*, *Corydalus cornutus*). Much of the fauna was restricted to univoltine species with spring or winter emergence (*e.g.*, Capniidae).
7. Intermittent stream. **Caldwell Hollow, Indiana.**
   Fish: limited to a temporary population of minnows (*e.g.*, *Semotilus atromaculatus*), present only during the spring months.
   Invertebrates: restricted to univoltine species without a major summer or early fall growth period. With the exception of a few Coleoptera, all species have an annual cycle. Furthermore, with the exception of some highly adapted caddisflies, all insects emerge in spring.

Several other important studies have not been arranged in the above sequence because they were directed specifically to one group of aquatic animals. These include Abell's (1959) investigation of the mosquito population of a California intermittent stream, Paloumpis' (1958) study of fish in an Iowa intermittent stream, and John's (1954) study of fish in intermittent streams of Arizona.

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