To the Graduate Council:

I am submitting herewith a thesis written by James T. Norton entitled "Aquatic Insect Faunas of Intermittent Streams with an Analysis of Strategies Allowing Utilization of These Habitats." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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and recommend its acceptance:

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Accepted for the Council:

The Graduate School

AQUATIC INSECT FAUNAS OF INTERMITTENT STREAMS WITH AN ANALYSIS OF STRATEGIES ALLOWING UTILIZATION OF THESE HABITATS

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ABSTRACT

Knowledge of the survival mechanisms of aquatic insects in intermittent streams is crucial to the understanding of the ecology of these habitats. Intermittent and permanent sections of three small streams in Knox County, Tennessee were sampled for fourteen months in an attempt to determine the survival strategies of the insects present. This information, along with data from previous studies, was used to analyze the survival strategies.

It was found that Cordulegaster erronea and C. obliqua were able to survive the dry period as nymphs in the substrate, and that Ameletus lineatus and Amphinemura delosa were apparently able to use an egg diapause. Larvae of Pycnopsyche gentilis, Tipula sp. and Tabanus sp. were found in the dry substrate of an intermittent section.

The most widely used mechanisms are diapausing or drought resistant eggs, and larvae or nymphs in the substrate. Other mechanisms that have been found are nymphal diapause, imaginal diapause, prepupal diapause, pupae or adults in the substrate, adults or larvae in earthen chambers, in permanent pools and seeps, as adults encased in silt, as eggs laid above the water, by spending the dry period in permanent rivers and then migrating upstream, as a final instar that leaves the water and becomes terrestrial, and as terrestrial adults.

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I. INTRODUCTION

Three types of streams are recognized in temperate areas: permanent, ephemeral, and intermittent. Permanent streams carry some flow through the year. Ephemeral streams flow only in response to storm events. Intermittent streams are those in which at least part of the stream normally dries out during part of the year. Two primary causes of intermittency in streams can be identified. In northern or mountainous regions melting snow provides a seasonally continuous supply of water to streams that would otherwise be ephemeral (Anderson and Dicke 1960, Knight and Gaufin 1967). The other main cause of intermittency is changes in the height of the water table, due to seasonal changes in precipitation and evapotranspiration, so that the stream bed is above the water table for part of the year and below it for the rest of the year (Williams and Hynes 1977).

It is generally assumed that ephemeral streams contain no truly aquatic insects, and they have received little attention. However, Lewis and Burraychak (1979) found five species of aquatic insects in the ephemeral sections of a stream.

Intermittent streams are widespread and abundant. Clifford (1966) estimated that the total kilometers of intermittent streams exceeded the total kilometers of permanent streams in Indiana. Intermittent streams are valuable as habitats for invertebrates and small fish, spawning grounds for larger fish, and for their contributions of

energy and materials to the downstream community (Erman and Hawthorne 1976, Mitsch and Urbikas 1980).

Intermittent streams have received little attention in comparison with permanent streams and temporary ponds. Major studies looking at the survival mechanisms of aquatic insects have included those by Abell (1956, 1959) in California, Harrison (1966) in what was then Rhodesia, Clifford (1966) in Indiana, Tew (1971) in Oregon, Hynes (1975a) in Ghana, Williams and Hynes (1976a, 1977) in Ontario, and Gray (1980, 1981, Gray and Fisher 1981) in Arizona. Life history studies have included those by Oberndorfer and Stewart (1977), Snellen and Stewart (1979), and Grant and Stewart (1980). Hynes (1975b) studied the drift of invertebrates in an intermittent stream, and Dance and Hynes (1979, Dance et al. 1979, Victor et al. 1981) studied the drift in adjacent intermittent and permanent streams. Slack (1955) compared the productivity of adjacent permanent and intermittent streams in Indiana. Mitsch and Urbikas (1980) looked at the community structures of five intermittent streams in Illinois. Kirby (1982) investigated the role of shredders in detrital dynamics of three permanent and three intermittent streams in Virginia. Wright et al. (1984) compared the invertebrate faunas of permanent and intermittent sections of a stream in England.

There have been a few studies of streams that have dried up during droughts (Hynes 1958, Larimore et al. 1959, Kamler and Riedel 1960, Iverson et al. 1978, Ladle and Bass 1981, Resh 1982). Species that can survive the occasional drying up of a normally permanent stream should be able to survive the more or less annual drying up of an intermittent

stream, using the same survival mechanisms. Evidence to support this idea was found by Iverson et al. (1978).

Lentic waters are also subject to drying up. Temporary ponds have received much greater attention than intermittent streams, and these studies have recently been reviewed by Wiggins et al. (1980). The exact relationship between the two types of habitat is unclear. Wiggins et al. (1980) stated that, "We consider intermittent or temporary streams to be quite different from temporary pools, both physically and biologically." In contrast Williams and Hynes (1976a, 1977) stated that there were considerable overlaps between the two and made extensive use of the literature on temporary ponds to explain the ecology of intermittent streams. This approach seems both unwise and unnecessary.

Intermittent streams exhibit amplitudes in physical and chemical parameters that are much greater than those found in permanent streams, and the insects that have chosen this habitat have to be extremely tolerant of these conditions if they are to survive (Williams and Hynes 1977). Flows in intermittent streams may range from zero to raging torrents. The riffles, usually the most productive and diverse areas in streams (Hynes 1970), are the first areas to dry up. When the flow stops oxygen levels may drop and carbon dioxide levels rise. Temperatures are usually more variable in intermittent streams than they are in permanent streams. If insects are concentrated in pools they are subject to greater predation. Leaves decomposing in pools may lead to the condition known as "black water." This decomposition lowers the amount of oxygen and changes the water quality (Schneller 1955, Slack 1964). The effects of black water on insects have not been determined.

Species found in intermittent streams can be placed into four groups based on their success in utilizing the habitat. Successful species are those that can survive the dry stage and are able to maintain a population without inputs from permanent waters. Unsuccessful species are those that are not able to complete their life cycles in intermittent streams and are killed by the dry period. Opportunistic species are able to complete one or more generations during the wet period but are unable to survive the dry period. Migrants are those taxa that use the intermittent stream during the wet period but are able to avoid the dry period by spending it in a permanent body of water.

Survival can be in an inactive state, as diapausing or estivating eggs, larvae, nymphs, pupae, or adults. In other cases the insects can remain active, as aerial adults or by finding water in remaining wet areas or deep in the substrate.

Much of the work on intermittent streams has involved determining the survival strategies of successful species and the repopulation strategies of unsuccessful and opportunistic species. This knowledge is crucial to the understanding of the ecology of intermittent streams. It is also useful in understanding how insects are able to recover from natural and man-caused disasters (Larimore et al. 1959, Cairns et al. 1971, Lehmkuhl 1979).

II. SITE DESCRIPTION

The study streams (Fig. 1) were located at the base of House Mountain, Knox County, Tennessee. They are north of Hogskin Road, 0.9 road miles from Idumea Road and 1.2 road miles from Fulton Road (36° 06' 07.5" North, 83° 46' 08" West). Three streams were used in the study, with identifying names coined by the author: Swamp Creek was the farthest west, Main Creek was in the middle, and Side Branch was the farthest east. There have apparently been no previous studies of these streams. The flow from Swamp Creek diffused into a swampy area, and most of the water soaked into the ground. Main Creek and Side Branch were connected by a 51-m roadside ditch. Flow from these streams enters Hogskin Branch, which flows into Roseberry Creek, a tributary of the Holston River.

Swamp Creek and Main Creek cross the right-of-way of a 161-kV power line. The right-of-way is 150 feet (46 m) wide, and was recleared in the spring of 1982 (pers. comm., D. C. Quarles, Tennessee Valley Authority). These two streams were divided into upper and lower sections by the right-of-way.

The study area was covered by small to medium sized mixed hardwoods, except for the right-of-way area which was dominated by shrubs and vines.

The substrate of the lower section of Swamp Creek was mostly sand, with some gravel and rock. The flow in this section decreased slowly throughout the summer and early fall, and there was no flow in

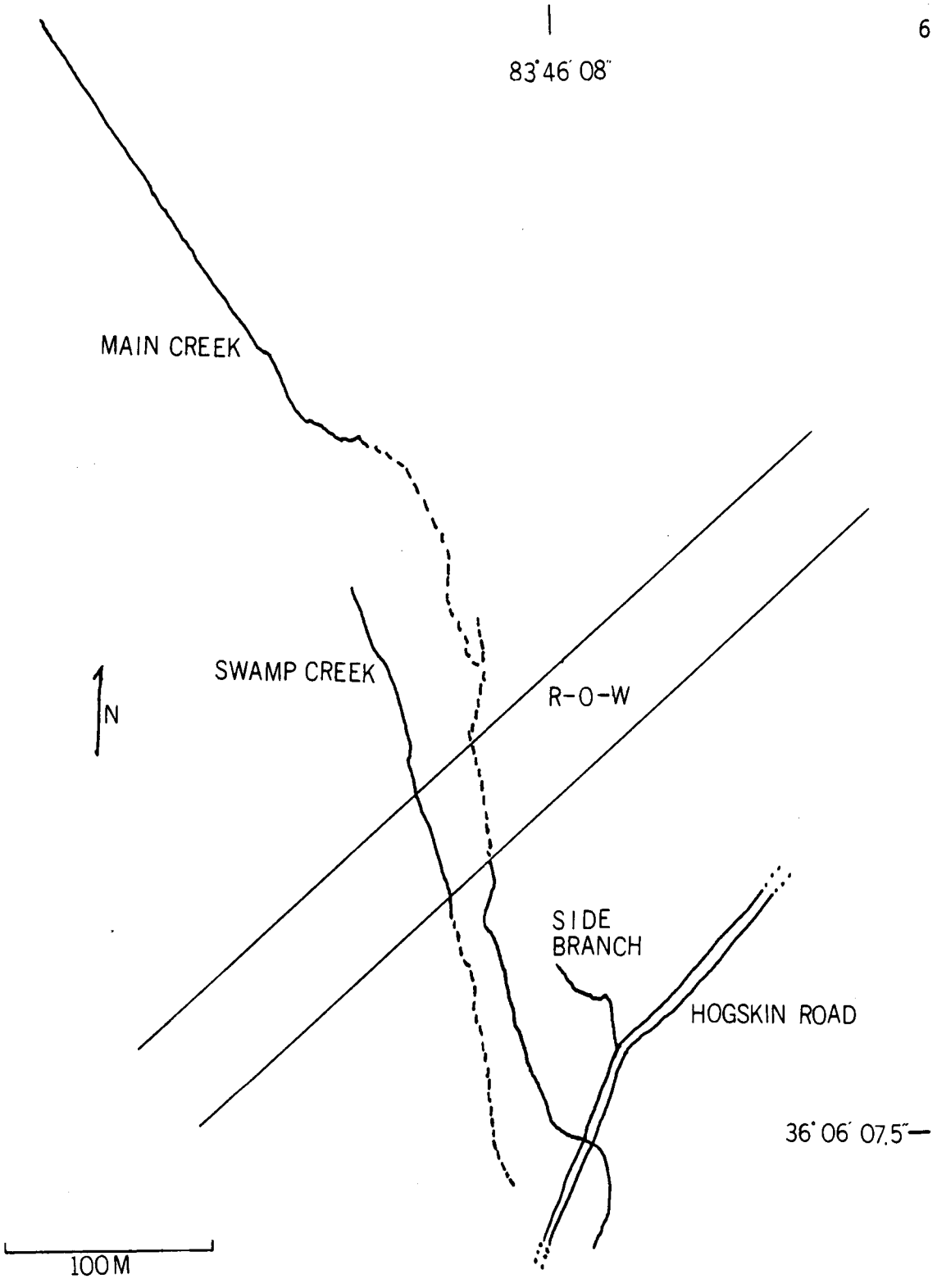


Figure 1. Map of study area on House Mountain, northeast Knox County, Tennessee. Power line right of way = R-O-W; areas of permanent flow = ———; areas of intermittent flow = - - - -.

the lower 104 m from at least 14 October 1983 to 18 November. Flow returned sometime between 18 November and 8 December when the streams were next visited. Flow was permanent in the upper 30 m of this section.

The substrate in the upper section of Swamp Creek included sand, gravel, and rock. The section was 110 m long, and flow continued throughout the study period.

The lower section of Main Creek also had sand, gravel, and rock as the substrate. This section was 146 m long. Flow was permanent in the lowest part of this section throughout the study; surface water was always present in the upper part, however flow was not always apparent.

On 6 July approximately the lower 10 m of the upper section of Main Creek was dry. The length of the dry area increased in an upstream direction until 1 September when the lower 167 m was dry. Flow returned to this area sometime between 18 November and 8 December. The substrate in this area was mostly sand and gravel. There were a number of small waterfalls with rocks, tree roots, or hard packed clay in this area. Above this area was a 71-m long area with sand, gravel, and rock that did not dry up. The upper area of this section was 200 m long, and was very steep, with the water flowing over bedrock.

Side Branch was the shortest of the study streams, and did not extend to the right-of-way. The substrate in the lowest 24 m consisted of mud, sand, and gravel and a few rocks. This area had several patches of watercress (Nasturtium officinale) in it. Flow through this area appeared to be relatively constant. Above this muddy area was a sloping rocky area which had little flow even in the spring. This rocky area was 22 m long.

III. METHODS

The literature search included a computer search of BIOSIS, and manual searches of Science Citation Index, Selected Water Resources Abstracts, Dissertation Abstracts, Masters Abstracts, and the Zoological Record. Bibliographies of these papers were used to find additional references. Recent numbers of the major journals were searched to find papers that had not yet been abstracted.

Quantitative sampling of intermittent streams presents great difficulties (Mitsch and Urbikas 1980). Low flows and narrow channels make the use of a surber sampler unreliable or impossible. As the streams dry up the insects often become concentrated in pools, with a resulting increase in the number per unit area while the actual number in the stream is unchanged or decreasing. Due to the small size of most intermittent streams it is very difficult to avoid oversampling them. In addition, the streams used in the present study are very heterogeneous, and adequate sampling of each substrate type in each stream section would have required a prohibitively large number of samples. For these reasons it was decided not to attempt quantitative sampling.

For sampling purposes Swamp Creek and Main Creek were each divided into an upper and lower section, using the right-of-way as the dividing zone. No sampling was done in the right-of-way itself. Monthly samples were taken in December 1982, January, February, and December 1983, and January through February 1984. Two samples per

month were taken from March 1983 through November 1983. It was sometimes necessary to take two days to sample all of the stream sections. Each section was sampled along its entire length.

Sampling was done by hand picking insects from rocks and leaf litter from December 1982 through March 1983, and by hand picking and using a small kick screen since then. When there was not enough current to carry the insects into the net it was necessary to kick the water into the net. Some substrate was also kicked into the screen, and it was necessary to pick the insects out of this substrate. The insects were preserved in 70% isopropyl alcohol.

On 26 August and 1 September 1983 the surface substrate of the dry part of the upper section of Main Creek was examined for the presence of insects. At the time the substrate was only slightly damp. A small garden shovel was used to dig up the substrate, which was then placed in the kick screen and examined. In addition, on 26 August samples from four locations were placed in plastic bags, taken to the laboratory, placed in a white enamel pan, and examined dry and then re-examined after water had been added.

Keys used in identification were those by Hitchcock (1974), Edmonds et al. (1976), Wiggins (1977), Bednarik and McCafferty (1979), Simpson and Bode (1980), Brigham et al. (1982), and Louton (1982). Chironomidae were identified by W. L. Pennington. Identification of the other taxa was done by myself and checked by Dr. D. A. Etnier.

IV. RESULTS AND DISCUSSION

A total of 3234 insects in 65 taxa were collected by hand picking and using the kick screen (Table 1). In the 26 August 1983 substrate samples four Tipula sp. (Tipulidae) were found. In the 1 September 1983 substrate samples one Tabanidae and one Pycnopsyche gentilis (Limnephilidae) were collected.

Animals other than insects that were present in the study streams included salamanders, isopods, decapods, gastropods, and oligochaetes. These taxa were not collected during the present study.

Indexes of similarity between the different stream sections are are given in Table 2. The formula used was:

$$\text{Index of similarity} = \frac{2c}{a+b}$$

where a = the number of species in one section, b = the number of species in the second section, and c = the number common to both sections. The highest index (greatest similarity) was between the upper section of Swamp Creek and the upper section of Main Creek. These sections were not similar in either flow regimen or substrate; the similarity may be related to the fact that these were the only sections above the right-of-way. The upper section of Swamp Creek and the lower section of Main Creek, which both had permanent flow, had a relatively high index of similarity, as did the intermittent lower section of Swamp Creek and upper section of Main Creek. The lowest similarities were those between Side Branch and the other sections. These low

Table 1. List of Taxa Found During 1982-1984 on House Mountain, Knox County, Tennessee.

Taxa	LS[a]	US	LM	UM	SB
Ephemeroptera					
Ephemeridae					
Ephemera sp.	1	0	0	0	0
Ephemerellidae					
Eurylophella funeralis	17	0	2	0	0
Leptophlebiidae					
Paraleptophlebia sp.	2	1	1	10	3
Heptageniidae					
Stenacron carolina	0	3	5	2	0
Stenonema meririvulanum	46	31	86	84	6
Siphlonuridae					
Ameletus lineatus	60	2	55	410	0
Baetidae					
Baetis brunneicolor ?	1	1	1	3	0
Odonata					
Calopterygidae					
Calopteryx maculata	4	0	1	0	1
Cordulegastridae					
Cordulegaster diastatops	0	0	0	0	1
Cordulegaster erronea	30	11	27	20	95
Cordulegaster obliqua	11	0	0	1	0
Gomhidae					
Stylogomphus albistylus	4	6	3	0	2
Petaluridae					
Tachopteryx thoreyi	0	1	0	0	0
Plecoptera					
Nemouridae					
Amphinemura delosa	33	5	22	41	3
Nemoura ? sp.	4	10	2	14	5
Leuctridae					
Leuctra sp.	25	12	13	40	1
Perlidae					
Eccoptura xanthenes	64	27	32	67	7
Perlodidae					
Isoperla clio	9	0	0	0	1
Isoperla cotta	41	1	11	36	0
Isoperla dicala	1	0	0	0	0
Isoperla holochlora	4	0	0	23	0
Chloroperlidae					
Suwallia/Sweltsa sp.	3	1	4	5	2
Hemiptera					
Corixidae	0	0	1	0	0
Gerridae					
Trepobates sp.	0	0	0	0	2

Table 1 (continued)

Taxa	LS[a]	US	LM	UM	SB
Trichoptera					
Hydropsychidae					
Diplectrona metaqui	0	0	0	12	0
Diplectrona modesta	156	115	212	282	67
Philopotamidae					
Chimarra sp.	0	0	1	0	0
Wormaldia moesta	5	5	2	3	0
Rhyacophila					
Rhycophila ledra/fenstra	0	1	1	12	1
Rhyacophila invaria group	3	8	9	7	0
Odontoceridae					
Psilotreta labida	0	0	2	0	1
Lepidostomatidae					
Lepidostoma sp.	0	2	1	1	0
Limnephilidae					
Ironoquia sp.	2	0	0	0	0
Neophylax mitchelli ?	5	1	5	12	4
Pycnopsyche spp.	66	21	25	51	9
Coleoptera					
Ptilodactylidae					
Anchytarsus bicolor	2	88	6	2	0
Eubriidae					
Ectopria sp.	0	0	2	1	0
Elmidae	0	1	0	1	0
Optioservus sp.	2	0	0	0	0
Macronychus glabratus	0	0	0	1	0
Hydrophilidae					
Helocombus bifidus	7	0	0	5	0
Dytiscidae					
Hyrdoporus sp.	4	0	1	1	1
Diptera					
Ptychoperidae					
Bittacomorpha clavipes	0	0	0	0	1
Ptychoptera sp.	0	0	10	0	13
Dixidae					
Dixa sp.	32	9	3	9	22
Tipulidae					
Dicranota sp.	0	0	0	1	0
Hexatoma sp.	1	3	2	1	2
Limnophila sp.	1	3	2	1	2
Pilaria sp.	3	1	4	1	3
Tipula sp.	48	10	29	38	11
Tabanidae					
Chrysops sp.	0	1	0	0	2
Tabanus sp.	0	1	0	0	0

Table 1 (continued)

Taxa	LS[a]	US	LM	UM	SB
Dolichopodidae	0	0	1	0	0
Simuliidae	0	0	2	3	0
Chironomidae					
Conchapelopia sp.	1	0	1	0	1
Eukiefferiella					
clarapennis group	0	0	0	0	1
discoloripes group	0	0	2	0	0
Heterotrissocladius marcidus	1	1	0	2	0
Micropsectra sp.	0	0	1	0	1
Parametriocnemus lundbecki	6	1	2	3	1
Parakiefferiella ? sp.	0	0	0	1	0
Rheotanytarsus sp.	0	0	1	0	0
Tanytarsus sp.	0	1	1	0	0
Megaloptera					
Corydalidae					
Nigronia fasciatus	3	16	27	9	11
Sialidae					
Sialis sp.	1	2	4	0	2
Total	709	400	625	1216	284
Number of taxa	39	34	44	39	33

[a]LS: Lower section of Swamp Creek. US: Upper section of Swamp Creek. LM: Lower section of Main Creek. UM: Upper section of Main Creek. SB: Side Branch.

Table 2. Indexes of Similarity Between Stream Sections During 1982-84 on House Mountain, Knox County, Tennessee.

Stream Sections	Index
Upper Swamp and Upper Main	0.767
Upper Swamp and Lower Main	0.753
Lower Swamp and Upper Main	0.744
Lower Main and Upper Main	0.732
Lower Swamp and Upper Swamp	0.712
Lower Main and Side Branch	0.710
Lower Swamp and Lower Main	0.707
Lower Swamp and Side Branch	0.667
Upper Swamp and Side Branch	0.627
Upper Main and Side Branch	0.556

numbers are probably the result of differences in substrates that are discussed below.

The substrates in different areas of the streams had a noticeable influence on the species present and their abundances. The steep uppermost area of Main Creek, where the water flowed over bedrock, contained few insects, mostly Diplectrona spp. (Hydropsychidae). Sandy areas, found mainly in the lower section of Swamp Creek and the upper section of Main Creek, contained large numbers of Ameletus lineatus Traver (Siphlonuridae). Side Branch contained relatively few insects, and had a lower index of similarity with the other streams. This was partly because of the short length of this stream, but substrate differences were also important. This stream had fewer stones and more silt than the others, and therefore had more Cordulegaster erronea Hagen (Cordulegastridae), which are normally found in silt (Huggins and Brigham 1982), and fewer individuals of the species that prefer a stony substrate, such as the Plecoptera.

Past studies of intermittent streams (Stehr and Branson 1938, Abell 1956, Clifford 1966, Tew 1971, Williams and Hynes 1976a) have found definite seasonal cycles in the inhabitants. All of them found wet season aquatic assemblages. Stehr and Branson, Abell, and Williams and Hynes also reported summer assemblages of scavengers and predators made up of terrestrial and shore species and adult aquatic beetles. Abell (1956) reported finding a rapidly appearing, temporary association just after the resumption of flow. Such associations have been found after droughts (Iverson et al. 1978, Ladle and Bass 1981), and included species that were not present before the drought. The normal

habitat of these post dry period species is not known. Williams and Hynes (1976a) found a spring pool assemblage in one of their streams, and Clifford (1966) found a dry period assemblage of adult aquatic beetles and opportunistic species. House Mountain insects can be divided into two main categories, winter-spring species that were found primarily in the intermittent sections, and year round species found primarily in the permanent sections.

Ephemeroptera

Siphlonuridae

Ameletus lineatus Traver was the second most abundant species on House Mountain. It was found mainly in the sandy areas that totally lost surface water. Clemens (1922) found a five-month egg diapause in a population of *A. ludens* from an intermittent stream in New York. Clemens noted that the number of nymphs had begun to decline by June, and that no nymphs could be found in July. By the middle of August the stream had ceased to flow. A similar pattern was found for *A. lineatus* on House Mountain, so it is possible that it also has an egg diapause. Clifford (1966) also found *A. lineatus* in an intermittent stream, and other workers (Abell 1956, Mackay 1969) have found other species of *Ameletus* in these habitats.

Heptageniidae

Stenonema meririvulanum Carle and Lewis was the third most abundant species on House Mountain. It is an uncommon species that occurs in very small spring-fed streams (Carle and Lewis 1978). They

described this species from a stream that "may partially dry up in the summer." On House Mountain the species was found primarily in the late winter and spring. The survival mechanism for S. meririvulanum on House Mountain was not determined. Harrel and Dorris (1968) and Mathis and Dorris (1968) found Stenonema sp. in intermittent streams.

Only ten Stenacron carolina (Banks) were found on House Mountain, all of them in the spring. Spurles (1947) found that S. carolina was not able to survive the dry period in an Ontario stream, and it would appear that this species is also unsuccessful on House Mountain. Spurles (1947) is the only other worker to find Stenacron in an intermittent stream.

Baetidae

Only six Baetis bruneicolor ? McDunnough were found on House Mountain, so it was apparently not a successful species there. This species was found in an intermittent stream by Spurles (1947); other Baetis species have been found by Abell (1956), Harrel and Dorris (1968), Mathis and Dorris (1968), Tew (1971), Dance and Hynes (1979), Lewis and Burraychak (1979), Mitsch and Urbikas (1980), and Gray (1981).

Ephemerellidae

Nineteen Eurylophella funeralis (McDunnough) were found. They were found in the spring, mostly in the intermittent sections. Little is known about the life history of Eurylophella, and the survival strategy on House Mountain was not determined. Eurylophella has not been reported from any other intermittent stream.

Leptophlebildae

Seventeen Paraleptophlebia sp. were found on House Mountain, mostly in the spring. Williams and Hynes (1976a) found that P. ontario is able to survive the dry period in an Ontario intermittent stream using an egg diapause. Paraleptophlebia has been found in intermittent streams by Abell (1956), Clifford (1966), Mackay (1969), Williams and Hynes (1976a), and Dance and Hynes (1979).

Ephemeridae

A single Ephemera sp. was found in the lower section of Swamp Creek.

Odonata

Few Odonata nymphs were found before April 1983 because a kick net was not used before then, and hand picking was not effective in sampling the nymphs.

Cordulegastridae

Cordulegaster sp. nymphs burrow into the substrate (Merrit and Cummins 1978). Being in the substrate would offer some protection from dessication, and this is apparently how members of this genus survived on House Mountain. Small numbers of C. erronea Hagen were found in all the stream sections, and small numbers of C. obliqua (Say) were found in the intermittent sections, mostly in the lower part of Swamp Creek. A single C. diastatops was found in Side Branch. Cordulegaster take several years to mature (Huggins and Brigham 1982), and several sizes of nymphs were found in the House Mountain samples, including those

taken in intermittent sections after the resumption of flow. There is little chance that these nymphs had drifted in from permanent sections, due to their large size and the fact that they were buried in the substrate. The nymphs would have required more than a year to grow to the sizes found, so they must have been present in the substrate during the dry period. Clifford (1966) reported finding a few C. obliqua, mostly in the fall, in an intermittent stream.

Gomphidae

Stylogomphys albistylus (Hagen) also stays buried in the substrate (Merrit and Cummins 1978) and so might also be expected to survive there. However, only four numphs were found in the intermittent sections, all in the early spring, so this species was apparently not successful in the House Mountain intermittent sections. No S. albistylus have been reported from other intermittent streams.

Petaluridae

A single Tachopteryx thoreyi (Hagen) was found in the upper section of Swamp Creek. This is a semiaquatic species that lives in damp leaves (Louton 1982).

Calopterygidae

Calopteryx maculata Beauvois was first found on House Mountain on 4 November 1983, and was never found in the sections above the right-of-way. These findings are probably the result of ovipositing by one or a few adults from other streams in the late summer or early fall. Calopteryx aequabile was found in an intermittent stream by Lewis and Burraychak (1979).

Plecoptera

Perlodidae

Four species of Isoperla were found on House Mountain. A single I. dicala ? Frison was found. Ten I. clio (Newman) were found. Harper (1973b) found that I. clio was able to survive a July-August dry period in the egg stage. Most of the eggs hatched in late August when flow returned, but a second dry period in September killed these nymphs. Harper found nymphs of I. clio the next April, and concluded that these were probably from eggs that hatched following the second dry period. It is possible that more of the insects would have survived if the dry period had been continuous. The small number of I. clio found in the present study may mean that it is not successful on House Mountain. Twenty-seven I. holochlora (Klapálek) and eighty-nine I. cotta Ricker were found during the present study. They were found mainly in the spring, and mainly in the intermittent sections. It is possible that these two species survived in the egg stage, or as small nymphs in wet substrate as reported for an undetermined species of Isoperla by Abell (1956).

Isoperla clio was found in an intermittent stream by Harper (1973b). Other Isoperla sp. have been found by Spurls (1947), Abell (1956), Clifford (1966), Knight and Gaufin (1967), Mackay (1969), Harper (1973b), and Mitsch and Urbikas (1980). Isoperla cotta, I. dicala, and I. holochlora have not been reported from any other intermittent stream.

Perlidae

Eccoptura xanthenes (Newman) has not been reported from any other intermittent stream. Related species are known to require two to three years to mature (Peckarsky 1979), however information on this species is not available. On House Mountain nymphs were found throughout the year in the permanent sections. In the intermittent sections there was a population peak in the winter and spring, but small numbers of nymphs were also found in the summer and fall.

Nemouridae

Amphinemura delosa (Ricker) has a summer egg diapause that can be used to survive a dry period (Harper 1973a). Harper found that in southern Ontario the eggs were laid in June and July and hatched in September and October. On House Mountain A. delosa was found only in the late winter and spring, and probably spent the dry period in an egg diapause. A. delosa was found in an intermittent stream by Harper (1973a).

Thirty-six Nemoura ? sp. were found on House Mountain, all of them in the spring and winter. No survival mechanism has been discovered for this genus. Other workers that have reported Nemoura from intermittent streams are Spurles (1947), Abell (1956), Knight and Gaufin (1967), Tew (1971), and Harper (1973a).

Chloroperlidae

Fifteen Suwallia/Sweltsa sp. were found on House Mountain, all of them in the spring. Chloroperlids have a one-year life cycle

(Unzicker and McCaskill 1982). Suwallia/Sweltsa have not been reported from any other intermittent streams, and no survival mechanism is known.

Leuctridae

Nymphs of Leuctra sp. were found mostly in the spring on House Mountain. Twenty nymphs were found in January and February 1984 in the area of Main Creek that had dried up, so the genus had apparently survived the dry period. No egg or nymph diapause has been reported for this genus (Harper and Hynes 1970, Harper 1973a, Unzicker and McCaskill 1982), and how it survived on House Mountain was not determined. Leuctra has been reported from intermittent streams by Spurls (1947), Mackay (1969), Harper (1973a), and Kirby (1982).

Hemiptera

Only three true bugs, two Trepobates sp. (Gerridae) and a Corixidae, were found on House Mountain. All were winged adults that had probably migrated from other streams. Trepobates has not been reported from any other intermittent streams.

Trichoptera

Hydropsychidae

Diplectrona modesta Banks was the most abundant species on House Mountain. There was a great peak in population during the spring, but a few specimens continued to be found throughout the summer. Larvae were found in both the rocky areas that did not dry up and the sandy areas that did dry up. Imhof and Harrison (1981) found that

50% of the larvae of D. modesta that they tested could survive without flowing water for thirty days in the laboratory. Few larvae of D. modesta were found in the present study during the dry period, and none were found in the substrate samples, so it seems unlikely that survival in damp substrate was the primary strategy of this species on House Mountain. Several larvae of D. metaqui Ross were found in the winter and early spring. According to Ross (1970) D. metaqui "has been found only in rocky, rapid to moderately rapid, spring-fed streams" and is "invariably associated with D. modesta." D. modesta has been found in intermittent streams by Spurls (1947) and Imhoff and Harrison (1981). Diplectrona sp. was reported by Abell (1956) and Clifford (1966).

Limnephilidae

Pycnopsyche gentilis (Mac Lachlan) was found mainly in the winter and spring in the intermittent sections. Mackay (1972) found a one-month pre-pupae diapause in this species. This would not be long enough to allow survival of the dry period, but it is possible that a period of estivation is entered after the diapause ends, as has been reported for other species (Lees 1955). A single mature larva was found in the substrate samples. The larva became active when placed in a jar of 70% isopropanol. Pycnopsyche gentilis was found in an intermittent stream by Mackay (1969). Small numbers of larvae of other species of Pycnopsyche were also found, however it was not possible to identify these to species.

Neophylax mitchelli ? Carpenter was found on House Mountain only in the spring. Many Neophylax sp. spend the summer as estivating

prepupae (Ross 1944, Clifford 1966). Sealed caddisfly cases were not collected during the present study, so it is possible that Neophylax spent the dry period as prepupae in sealed cases. Neophylax has been reported from intermittent streams by Ross (1944), Mackay (1969), and Clifford (1966).

Lepidostomatidae

Only four Lepidostoma sp. were found on House Mountain. This genus has been found in intermittent streams by Spurls (1947), Abell (1956), Clifford (1966), and Mackay (1969).

Philoptamidae

Sixteen Wormaldia moesta (Bantis) were found on House Mountain. They were found throughout the year, and how they survived on House Mountain was not determined. Clifford (1966) found Wormaldia sp. in low numbers in an intermittent stream, mostly in the spring. Abell (1956) found W. gabriella (Bantis) in intermittent Dry Creek. A single Chimarra sp. was found on House Mountain.

Rhyacophila

Rhyacophila ledra/fenstra and R. invaria group were collected during the study. The larvae were found mainly in the spring. Rhyacophila can survive in dry river beds as either pupae (Ross 1944) or larvae (Imhof and Harrison 1981) so this is possibly how they survived on House Maintain. This genus has been reported in intermittent streams by Ross (1944), Abell (1956), Mackay (1969), Tew (1971), Williams and Hynes (1976a), and Imhof and Harrison (1981).

Other

Other Trichoptera found during the study were two Ironoquia sp. (Limnephilidae) and three Psilotreta labida (Ross) (Odontoceridae).

Coleoptera

Ptilodactylidae

Little is known about the ecology of Anchytarsus bicolor (Melsheimer), a widespread but rare species (Lesage and Harper 1976, Brigham 1982). They are found in small cool brooks and springbrooks either on decaying logs or in decaying moss (Brigham 1982). The ones I found were usually in the decaying moss on the bottoms of overturned rocks, and often several larvae were found under the same rock. The larvae are known to eat decaying wood (Lesage and Harper 1976) and they probably also eat decaying moss. The larvae were found throughout the year, mostly in the permanent upper section of Swamp Creek, so they probably survive in permanent areas. Lesage and Harper (1976) found that the larvae took two or three years to mature in Quebec. A. bicolor has not been reported from any other intermittent stream. None of the adults, which are terrestrial, were found.

Other Coleoptera

No other beetles were common in the study streams. Three Ectopria sp. (Eubriidae) and two Elmidae larvae were found. Adults collected were two Opitoserves sp. and a single Macronychus glabratus Say (Elmidae), twelve Helocombus bifidus (LeConte) (Hydrophilidae) and

seven Hydroporus sp. (Dytiscidae). It is possible that some of the adults were migrants.

Diptera

Ptychoperidae

Ptychoperids are found in saturated mud at the edges of streams and marshes (Alexander 1981). A single Bittacomorpha clavipes (Fabricus) was found in Side Branch. A single Ptychoptera sp. was taken in both May and June of 1983 in this stream, and eleven were taken from December 1983 through February 1984. Ten were taken from the lower section of Main Creek in January and February 1984. The sudden appearance of Ptychoptera in this stream, and the increased numbers in Side Branch, were probably the result of ovipositing. No ptychopterids were found in the intermittent sections, nor have they been reported from any other intermittent streams.

Dixidae

According to Hynes (1970) Dixa is part of the madicolus fauna. This habitat consists of thin sheets of water flowing over rocks. On House Maintain this genus was found mostly in the spring. No good data on its life history are available, and the survival strategy on House Mountain was not determined. Dixa has been reported from intermittent streams by Abell (1956), Mackay (1969), and Dance and Hynes (1979).

Tipulidae

Little is known about the ecology of individual genera and species of the Tipulidae. On House Mountain no Tipula sp. were found

in any of the sections from 1 June 1983 to 8 December 1983. The one exception was four specimens that were found in substrate samples taken in the upper section of Main Creek on 26 August 1983. Williams and Hynes (1976a) found pupae, but no larvae, of T. cunctans in an intermittent stream during the dry season, so it is possible that some House Mountain Tipula were in the pupal stage during the dry period. Tipula has been found in intermittent streams by Abell (1956), Mackay (1969), Tew (1971), Williams and Hynes (1976a), Gray (1981), and Kirby (1982). Other Tipulidae found on House Maintain, Dicranota, Hexatoma, Limnophila, and Pilaria, were not found in sufficient numbers to determine their survival strategy there.

Other Diptera

Nine species of Chironomidae were found during the study (Table 1). Other Diptera found in the study streams were five Simuliide, one Dolichopodidae, and three Chrysops sp. and one Tabanus sp. (Tabanidae). One Tabanus sp. was found in the substrate samples.

Megaloptera

Corydalidae

Nigronia fasciatus (Walker) has not been reported from any other intermittent stream. Larvae were found in small numbers throughout the year, primarily in the permanent sections, so this is probably where they survive. N. fasciatus is confined to small cool woodland streams (Neunzig 1966).

Sialidae

Not enough Sialis sp. were found on House Mountain to determine their life history. Evans (1972) did not report finding Sialis in intermittent streams in his study of west coast Megaloptera, but other workers (Gersbacher 1937, Slack 1955, Harrel and Dorris 1968) have reported them from this habitat.

V. ANALYSIS OF SURVIVAL MECHANISMS

Introduction

The main interest of most ecologists studying intermittent streams has been in determining the survival strategies of the insects present. A fair amount of information on survival strategies is available, but it is in widely scattered references and has never been synthesized. The best summary currently available is that of Williams and Hynes (1977) based on their study of sixteen Ontario streams. However, this summary was based entirely on their own work, and did not include the findings of other workers, information on intermittent streams in other areas, or information on taxa, such as the Megaloptera, not found in their streams.

Intermittent streams represent a seasonally available, and therefore predictable, resource. Because some animals are not able to utilize intermittent streams, those that are able to survive are subject to less competition and predation. It would therefore be advantageous to be able to survive in intermittent streams, and expected that insects should have evolved a variety of techniques for utilizing these habitats.

Survival in temporary waters usually requires a complete adjustment of the life cycle of an insect (Abell 1956, Wiggins et al. 1980). For example, an insect that spends several months in diapause has to be able to complete its life cycle during the remainder of the year.

However, it appears that there is usually a single factor that contributes most to an insect's ability to survive.

There are several strategies that are not restricted to specific taxa. One of these would be for larvae to remain buried deep in the substrate during the dry period. Several studies in permanent streams have shown that insects were present deep in the substrate of streams, and that these insects migrate to and from the surface (Williams 1981). However, while some intermittent stream insect larvae have been found deep in the substrate (Ross 1944, Williams and Hynes 1976a, Gray 1980) this has not been shown to be a mechanism used by many taxa. Williams (1981) found that in one intermittent stream the number of nymphs in the substrate dropped as the stream dried up. Tew (1971) dug substrate samples from the dry bed of his study stream and then held the samples for several weeks. The only insects found were Chironomidae, and Tew noted that these could have been from ovipositing by adults that could not be kept out of the laboratory. Grant and Stewart (1980) found no nymphs of Isonychia sicca in vertical samples of intermittent Clear Creek. Gray and Fisher (1981) found that most of the insects present in substrate samples from a flowing section of intermittent Sycamore Creek and from a dry side channel were in the upper 10 cm.

No reason is known for why so few insects use this survival strategy, but some speculations can be made. The water table may fall so far below the stream bed that the insects are not able to reach it. Abell (1956) found that in most areas of intermittent Dry Creek the substrate below 3 inches (7.6 cm) was moist during the dry season. Grant and Stewart (1980) found that the water table was 33 cm below

the bed of Clear Creek. Insects have been found in the substrate below these depths, so this is probably not the reason. Another factor that may be important is that once the stream has dried up the insects have to remain deep in the substrate until flow resumes. It is possible that some insects are not able to live for that length of time buried deep in the substrate. A final factor is that a lack of surface flow may have a detrimental effect on the deep substrate. For example, flow may be necessary to bring in oxygen or food.

Another possible survival strategy would be to drift to a more permanent section of the stream before the dry phase and then return by flying, walking, or swimming once flow had resumed. This would be similar to the colonization cycle first proposed by Müller (1954) to explain how losses from drift are made up. Upstream movements by adults do occur (Williams 1981) although the numbers involved may not be enough to compensate for drift. Stehr and Branson (1938) and Harrison (1966) reported that upstream movements of nymphs were important in the repopulation of their study streams. The number of drifting organisms can increase significantly when there is a sudden drop in flow (Minshall and Winger 1968, Gore 1977), however there is no indication that more insects enter the drift as a result of the slowly decreasing flow and reduced surface area found as intermittent streams dry up. Dance and Hynes (1979) found little relationship between discharge and the number of drifting animals in an intermittent stream, and concluded that decreasing flow did not stimulate drift.

Drift is also an important factor in colonizing and recolonizing areas (Waters 1964, Townsend and Hildrew 1976). In order for drift to

be an important factor there would have to be a permanent upstream area to act as a source, a condition that would not always be met. To be useful as a survival strategy insects would have to migrate upstream before the dry period. Erman (1981) observed larvae of Desmona bethula (Limnephilidae) moving upstream, apparently as a safeguard against the drying up of the lower portions of the streams during the summer. Drift is also important in reestablishing unsuccessful species.

One mechanism for surviving an unfavorable season is to enter diapause (Lees 1955, Tauber and Tauber 1976, 1981, Masaki 1980) or estivation. Tauber and Tauber (1981) defined diapause "as a normally mediated state of low metabolic activity associated with reduced morphogenesis, increased resistance to environmental extremes, and an altered or reduced activity." In most field studies it is difficult to determine if an insect is in diapause or estivation, a mere cessation of activity. Usually, determining the difference is not critical in ecological studies. In some cases after a period of dormancy an insect will estivate until enough moisture is available to resume activity (Lees 1955, Tauber and Tauber 1976). A large number of aquatic insects are known to be able to enter diapause. However, in most cases this is a winter diapause that has evolved to allow the insect to survive that period. The environmental cues, phenology, and conditions that must be survived during the dry phase of an intermittent stream are quite different from those resulting in winter diapause. Therefore, the fact that an insect is known to have a diapause does not always mean that this diapause can be used to survive the dry period of an intermittent stream. However, a number of species have been found to be able to use

a diapause as a survival mechanism, especially in the Ephemeroptera, Plecoptera and Limnephilidae.

Nymphs found estivating in intermittent streams are typically very small first and second instars (Clifford 1966). At first this seems surprising, as young animals are usually the least tolerant of environmental stress. However, small nymphs have the advantage over larger nymphs of having less difficulty in finding interstices in the rocks in which to estivate. In addition, small nymphs, because of their higher surface to volume ratio, would have less trouble in obtaining sufficient oxygen when there was no water flowing. Finally, small nymphs may have a better chance of escaping detection by predators while estivating. Abell (1956) found that most of the insects estivating in Dry Creek were found by terrestrial predators and eaten.

When permanent pools exist in intermittent streams some insects are able to survive in them. This usually requires being able to survive a shift from a lotic to a lentic environment. For typical small pool residents, such as the mosquitos, it means having to adjust to the flowing conditions of the wet phase. All of the insects must withstand the overcrowding, increased predation, and poor water quality associated with the pools. There is little doubt that certain insects actively seek out the pools. Abell (1956) reported that he could see animals moving toward the pools as the stream dried. Riley (1920) reported on the pool-seeking behavior of adult apterous Gerris remigis (Gerridae). Stout (1982) found that when she placed larvae of the dytiscid beetle Agabinus sp. in small pools, where they would be subject to canabalism, they crawled up to two meters over dry land to return to larger pools.

Abell (1956) found that most of the insects utilizing pools also spent the wet phase in the pools, and that pools were dominated by predacious beetles that had eliminated most other forms before flow resumed. Few insects were found in the pools on House Mountain, probably because of their small size.

There are also intermittent streams that have stretches of permanently flowing water. It appears that several of the House Mountain insects use these habitats. Gray (1981) found that most of the insects in Sycamore Creek avoided drought by selectively ovipositing in permanent stretches. Abell (1956) found few animals in seepage areas of Dry Creek, however some species depended on these areas for survival.

Another survival strategy is to avoid the dry period by migrating to a permanent body of water (Southwood 1962, 1977, Johnston 1969). Southwood (1962) noted that arthropods living in temporary habitats, including temporary ponds, tend to be migratory while those living in permanent habitats tend to be non-migratory. As noted earlier intermittent streams are seasonal rather than temporary (short-lived) habitats. According to Southwood (1962) diapause is a safer method than migration in seasonal habitats. Three life cycles involving migration are possible, with reporduction in the intermittent stream, in the permanent body of water, or both. In general it is more difficult to document successful migration than it is to document other survival strategies, and few cases have been proven. It is clear that some Hemiptera and Coleoptera visit intermittent streams to feed.

It is also possible for insects to survive the dry period as adults. This can occur if there is a long active adult stage, as in

the dragonflies and beetles, or if an imaginal diapause increases the length of the adult stage, as in the Limnephilidae (Tew 1971).

Some aquatic insects lay their eggs out of the water, so that ovipositing may occur during the dry phase. To be useful as a survival strategy the eggs must remain dormant, or the hatched young protected from dessication, until flow resumes. In many temporary pond limnephilids the gelatenous matrix in which the egg masses are laid protects the eggs and larvae from dessication until water returns (Wiggins 1973). Several genera of dragonflies lay their eggs in vegatation overhanging the water. In some species of Lestes (Lestidae) there is an egg diapause that can be used to survive the dry period of temporary ponds (Wiggins et al. 1980), and it is possible that this strategy is also used in intermittent streams (Williams and Hynes 1976a).

Not all of the insects found in intermittent streams are successful. For example Hynes (1941) found that the stonefly Leuctra fusciventris was absent from streams after the dry period and apparently recolonized them every year. It is not easy to tell which species are successful in non-permanent waters (Wiggins et al. 1980). Most workers who have studied intermittent streams appear to have either greatly overestimated or underestimated the number of successful species. Stehr and Branson (1938) and Hynes (1975a) attributed most of the repopulation of their study streams to ovipositing by adults from permanent streams. Tew (1971) attributed the appearance of all of the taxa for which he could not determine a survival mechanism, 83% of the total, to ovipositing. Abell (1956) on the other hand maintained that, except for those found only rarely, all of the species were probably either

successful permanent residents or migrants. A number of studies (e.g., Fernando and Galbraith 1973, Williams and Hynes 1976b) have looked at the colonizations of water bodies by insects. Ovipositing by unsuccessful species is a waste of eggs and should be strongly selected against.

During the dry phase intermittent streams are used by terrestrial insects (Stehr and Branson 1938, Abell 1956, Williams and Hynes 1976a). These insects feed on insects that died when the stream dried up, and also on any diapausing or estivating insects that they are able to find.

Ephemeroptera

In general Ephemeroptera are able to survive in intermittent streams as diapausing or estivating eggs. This was first shown by Clemens (1922) who found a five-month diapause for eggs of *Ameletus ludens* (Siphlonuridae). It appears that *A. lineatus* is able to survive using an egg diapause on House Mountain. Williams and Hynes (1976a) found that *Siphlonuris marshalli* apparently survives as diapausing eggs, and Abell (1956) stated that this was the case for the Siphlonurinae. Tew (1971) found that *Centroptilum elsa* (Baetidae) was able to survive in the egg stage, and noted that the species was found in two other intermittent streams in the area, but not in any of the permanent ones. Grant and Stewart (1980) found that *Isonychia sicca* (Oligoneuriidae) probably survives as diapausing eggs, but were not able to demonstrate this in laboratory experiments. Abell (1956) stated that *Ephemerella* sp. (Ephemerellidae) probably survived as eggs, and Casey and Ladle (1976) determined that *Ephemerella ignita* survived as eggs

in an English intermittent stream. Williams and Hynes (1976a) found that Leptophlebia sp. (Leptophlebiidae) survived as eggs, and that Paraleptophlebia ontario apparently has drought resistant eggs.

A life cycle that is almost the reverse of the colonization cycle (Müller 1954) occurs in two mayflies, Leptophlebia cupida (Leptophlebiidae) in Canada (Neave 1930, Hayden and Clifford 1974) and Parameletus chelifer (Siphlonuridae) in Sweden (Olsson and Soderstrom 1978). Nymphs spend the dry period and the winter in permanent rivers, and then migrate up temporary streams in the spring. The usual destination is a temporary marsh, in which case the insects would not be true residents of intermittent streams, but Neave (1930) reported that some L. cupida nymphs remained in the pools of intermittent streams. The adults emerge before the marsh or stream dries up and fly back to the permanent river to oviposit.

Abell (1956) found that Baetis sp. (Baetidae) was able to survive in permanent seeps, and that Callibaetis sp. was "notably successful" and had continuous reproduction in permanent pools that received water from seepage areas.

Odonata

Temporary pond odonates tend to be migrants, while permanent stream species tend to be non-migrants (Southwood 1962). Southwood did not give any information on intermittent stream species, however a number of taxa that are normally lentic (Merrit and Cummins 1978) have been found in intermittent streams, so it is possible that these insects may be migrants. Williams and Hynes (1976a) concluded that

Anax junius (Aeshnidae) and Libellula pulchella (Libellulidae) had dual populations of residents and migrants. They did not investigate the area to which the non-residents migrated. The eggs of Lestes (Lestidae) are laid out of the water (Wiggins et al. 1980), so it is possible that they survive in the ege stage. Abell (1956) reported that the Libellulinae were "notably successful" in seepage pools. I cound that Cordulegaster erronea and C. obliqua (Cordulegastridae) can apparently survive in damp substrate.

Plecoptera

A number of Plecoptera are known or suspected of being able to survive the dry period as either diapausing nymphs or eggs. These diapauses are believed to have evolved as a mechanism for avoiding the high temperatures and possible desiccation of summer (Harper and Hynes 1970). Harper and Hynes noted that diapause in the nymphal stage is advantageous because it allows a period of growth before the diapause, and also allows the nymphs to actively seek out places in which to spend the dry period.

Snellen and Stewart (1979) found in the laboratory that Perlesta placida (Perlidae) has a differential five-to-six-month or one year and five-to-six-month egg diapause. Such a diapause is advantageous because it would allow the continued survival of a population if one year's nymphs were destroyed by an unusually severe dry period or other disaster. A differential diapause may occur in other intermittent stream inhabitants, but it has not been proved for any of them. Gray (1981) found that nymphs of Mesocapnia arizonensis (Capniidae) were

only present in Sycamore Creek in the winter, and so apparently the species has an egg diapause. Diapausing nymphs of Allocapnia vivipara have been found in intermittent streams by Coleman and Hynes (1970) and Williams and Hynes (1976a). Williams and Hynes reported finding nymphs at depths of between 5 and 25 cm. Clifford (1966) reported finding very small nymphs of A. pygmaea in wet substrate. Abell (1956) reported a similar finding for Isoperla sp. (Perlodidae). Oberndorfer and Stewart (1977) found that the perlodid Hydroperla crosbyi has a seven-month egg diapause. Harper (1973b) found that some of the eggs of Isoperla clio were able to survive a dry period. Mackay (1969) stated that Ostrocerca albidipennis (Nemouridae) may have drought resistant eggs. Harper (1973a) found that Amphinenura delosa has a summer egg diapause. Hynes and Hynes (1975) reported that the timing of the life cycle of Dinotoperla serricauda (Gripopterygidae) was different in intermittent and permanent streams in Australia, with the summer spent in an egg diapause in the intermittent streams. They stated that some of the eggs might diapause through a second summer.

Hemiptera

The true bugs, along with the beetles, are able to migrate to intermittent streams from permanent waters in order to feed. This behavior is found especially in the Gerridae and Corixidae. In addition, Hemiptera are able to survive in remaining pools (Williams and Hynes 1977). Larimore et al. (1959) found a single live adult Nepa apiculata (Nepidae) encased in silt, and Gerridae in damp chambers

under rocks. Williams and Hynes (1976a) found that Mesovelia sp. (Veliidae) could survive stream drying as adults.

Trichoptera

The Trichoptera exhibit the most varied and unusual survival strategies of any group. This is especially true of the Limnephilidae.

One mechanism shown by the Limnephilidae is leaving the drying stream and becoming terrestrial, with the older larvae and pupae living under damp leaves. Philocasca demita spends its entire life out of the water (Anderson 1967). Ironoquia parvula is aquatic in its early instars, and then becomes terrestrial in its later instars and pupae (Flint 1958), but it is not known from intermittent streams. Clifford (1966) found that I. punctatissima larvae disappeared from his study stream before it dried up, and concluded that it has a life cycle similar to that of I. parvula. A study by Williams and Williams (1975) showed that larvae of I. punctatissima do leave the water in their final instar. Clifford (1966) noted that Lepidostomata sp. (Lepidostomatidae) "disappeared at about the same time and under similar circumstances as I. punctatissima" and so might have a similar life cycle, but this has not been confirmed.

Also found in the Limnephilidae is imaginal diapause, which allows the insects to survive as adults (Tew 1971). In limnephilids with imaginal diapause newly emerged females have underdeveloped ovaries, a condition typical of taxa with imaginal diapause (Lees 1955). Tew (1971) was able to show imaginal diapause in the laboratory for Heserophylax incisus, Grammotaulius betteni, Limnephilus aretto, and

L. nogus, with specimens living for over 150 days. Tew found that the insects were totally inactive during the day, and mostly inactive at night.

Another limnephilid, Neophylax concinnus, is able to survive the dry period as a prepupa (Ross 1944, Clifford 1966). Ross found that the larvae matured by April, and then fastened their cases under stones and estivated until autumn. The adults emerged while the stream was still dry. Dicosmoecus also spends the summer as prepupae in sealed cases (Anderson 1967, Wiggins 1977) and so might be able to survive in intermittent streams, but I have found no reference of Dicosmoecus occurring in them.

Some temporary pond limnephilids lay eggs out of the water (Wiggins 1973), and it is possible that this method is also used in intermittent stream species.

Limnephilids are able to survive without surface water if they are in a protected area and remain inactive. Tew (1971) found a number of larvae of Heserophylax incisus, Limnephilus aretto, and L. nogus in an area that had been without flow for two weeks. They began to crawl about a few minutes after being placed in a pan of water. Mackay (1969) found that Pseudostenophylax uniformis was able to survive in the damp substrate of a stream. I found a single live final instar larva of Pycnopsyche gentilis in the slightly damp substrate of the upper section of stream number two.

Imhof and Harrison (1981) found two Rhyacophila vibox (Ryacophilidae), one Hydropsyche sp., two Cheumatopsyche sp., and several Diplectrona modesta (Hydropsychidae) in a stream that had had no flow

for about one week. They conducted a laboratory experiment to see if D. modesta larvae could survive without flowing water for thirty days, and found that 50% of them did survive. They attributed much of the mortality to cannibalism. Ross (1944) found several active larvae of Chimarra feria (Philopotamidae) and one healthy pupa of Rhyacophila glaberrima (Rhyacophilidae) after digging a few inches into the dry bed of an intermittent stream.

Larimore et al. (1959) determined that Ochrotrichia xena (Hydroptilidae) was able to survive a drought in either the egg or larva stage. Harrison (1966) found that Setodes sp. (Leptoceridae) larvae survived in an African stream that had been dry for nine or ten weeks. Harrison noted that it was possible to see where the larvae had started to add new sand grains to their cases after the resumption of activity. Statzner (1982) found larvae of three species of Cheumatopsyche (Hydropsychidae) immediately after flow resumed in an Ivory Coast intermittent stream and concluded that they were able to survive in the remaining stagnant pools. Abell (1956) found that Agapetus sp. (Glossosomatidae) probably survived in the egg stage. Mackay (1969) found many first instar larvae of Lipidostoma sp. (Lepidostomatidae) soon after flow resumed and concluded that the eggs may be drought resistant.

Coleoptera

Several Coleoptera are able to survive as adults or larvae in moist substrate. In addition, adult beetles are able to migrate to intermittent streams in order to feed, and then return to permanent

waters to breed. This visiting usually occurs during the summer pool stage (Williams and Hynes 1976a).

Limnebius discolor (Hydraenidae), Hypdoporus laetus (Dytiscidae) and Cymbiodyta sp. (Hydrophilidae) are able to survive as adults that actively burrow deep into the moist intersticial spaces of streams (Clifford 1966). Larimore et al. (1959) found larvae and adults of the elmids Stenelmis sexlineata, S. crenata, and Dubiraphia quadrinota in the moist sand and gravel of a drought-stricken stream, but they noted that no adults or larvae could be found in November, after the stream had been dry for several months. Their survival is apparently of limited duration and/or requires moist substrate. Williams and Hynes (1976a) reported Heterocerus sp. (Heteroceridae) living in galleries in the mud banks of an intermittent stream, however this is a subaquatic rather than an aquatic family (Merrit and Cummins 1978). Stout (1982) found Agabinus sp. (Dytiscidae) larvae in the permanent pools of an intermittent stream. In Wales, Hynes (1958) found that the larvae of Helmis sp. (Dryopidae) were able to survive a drought "in an active form." Tew (1971) found several adult Agabus sp. (Dytiscidae) in earthen chambers under rocks. Williams and Hynes (1976a) reported Rhantus sp. and Hydroporus wickhami (Dytiscidae), Helophorus orientalis (Hydrophilidae), and Peltodytes sp. (Halipilidae) as surviving as adults, but they did not give more specific information.

Diptera

More taxa of Diptera have been reported from intermittent streams than have been reported for any other order. The study of

aquatic diptera is complicated by the large number of species, difficulty in identification in some groups, pooly known life histories, and the number of opportunistic and semiaquatic species. However, data on survival strategies is available for several families.

Several of the simuliids are known to be able to survive as drought-resistant eggs. Anderson and Dicke (1960) reported this for Prosimuliium gibsoni, P. magnum, Cnephia dacotensis, C. mutata, and Eusimulium latipes. They noted that P. gibsoni and E. latipes were found only in intermittent streams during a study of 199 streams in Wisconsin, and that P. magnum was found mainly in intermittent streams. E. gouldingi was also found only in intermittent streams, and it probably also has drought-resistant eggs, but Anderson and Dicke did not report this. Casey and Ladle (1976) stated that Metacnephia sp. possibly survived as aestivating eggs in England. Williams and Hynes (1976a) stated that Simulium might spend the dry season as adults, and Abell (1956) speculated that Simulium argus and possibly other black flies spent the dry season as adults in rodent burrows, using the rodents as hosts.

Williams and Hynes (1976a) found that the tipulids Limnophila sp., Tipula cunctans, and possibly Hexatoms sp. and Helobia sp. spent the summer as pupae, and that Tropidia sp. might survive as adults. Abell (1956) stated that Antocha possibly spent the dry season as resting adults. Mackay (1969) found young larvae of Molophilus hirtipennis and Dicranota sp. in damp sand and gravel. I found four larvae of Tipula sp. in the slightly damp substrate of the upper part of Main Creek. They became active after being placed in a plastic bag with water in it.

In the Chironomidae Williams and Hynes (1976a) found that Diplocladius, Orthocladius, and Trissocladius and possibly Acriotopus, Chironomus, Diamesa, Micropsectra, Natarisa, Paraphaenocladius, and Pseudosmittia survive as eggs. They found larvae of Chironomus and Micropsectra in the dry bed of a stream, and Mackay (1969) found Brillia sera, Paraphaenocladius and Pseudorthocladius in damp substrate. Hynes (1958) reported that Diamesa sp. was able to survive a drought in Wales "in an active form." Williams et al. (1974) found small larvae of Trichocladius sp. as cohabitants with a burrowing crayfish.

The mosquitos are opportunists that are able to breed in permanent pools if they are able to avoid predation (Abell 1956, 1959, Clifford 1966, Williams and Hynes 1976a). Some tabanids are able to survive in a quiescent state (Burger 1977) and may take two or three years to develop. Williams and Hynes (1976a) stated that it was possible that Bezzia/Probezzia sp. (Ceratopogonidae) spends the dry period in the egg stage, Tropidia sp. (Syrphidae) and Hydrellia sp. (Ephydridae) as adults, and Hydropyrus subopaca as pupae.

Megaloptera

Several Corydalidae are able to survive the dry phase of intermittent streams by actively burrowing into the substrate and making estivation chambers. Maddux (1954) found Protochauliodes aridus "under rocks in cells fashioned to prevent the drying of the specimen." Maddux noted that newly hatched nymphs burrowed into the dry soil of the stream bed. Tew (1971) reported that Protochauliodes spenceri digs estivation chambers, and Evans (1972) reported this behavior for that

species and also for Neohermes californicus. Smith (1970) found larvae of N. californicus in estivation chambers, but did not observe them being dug. Larimore et al. (1959) found that Corydalus cornutus, a species found in several intermittent streams, was able to survive a drought in chambers under rocks. The behavior of digging estivation chambers by immature nymphs is probably related to the digging of pupal chambers by mature nymphs.

In general multivoltine species are not able to successfully inhabit intermittent streams. However, based on studies of nymph size and life histories in permanent streams Evans (1972) concluded that both Neohermes californicus and Protochaliodes spenceri take several years to mature in intermittent streams.

Discussion

Most of the insects in temporary waters appear to be preadapted to conditions there by behaviors that evolved in permanent waters (Clifford 1966, Wiggins et al. 1980). Most of these strategies probably evolved in order to avoid the high temperatures and possible dessication of summer (Harper and Hynes 1970). Other factors, such as avoiding predation and the lack of allocthonous food, may also have an influence.

Williams and Hynes (1977) stated that major taxa "tend to oversummer as similar stages in their life cycle." In contrast Wiggins et al. (1980) found that major taxa did not share the same strategies in temporary pools. It appears that some taxa, such as the Ephemeroptera, are largely restricted to a single strategy, while other taxa, such as

the Limnephilidae, exhibit several strategies. The biologies of different taxa limit the survival strategies that they can use. For example, adult mayflies are short-lived and the nymphs apparently unable to withstand even slight dessication, so the Ephemeroptera are dependent on egg diapauses or any remaining permanent waters. Insects are capable of only one period of diapause during their lives (Lees 1955), so semivoltine species cannot rely solely on this method. Conditions in remaining pools favor air breathing forms such as mosquitos, bugs, and adult beetles.

The conditions in a stream also limit the survival strategies that can be used, and therefore the insects that can successfully use it. Clifford (1966) stated that the length and severity of the dry period is the most important factor in determining the species present. The presence of seeps and pools and subsurface water is also important, and makes the simple comparison of different lengths of the dry period largely meaningless. In arid regions there may be two wet and two dry period each year (Hynes 1975a, Gray 1981). Another important factor is the time of year of the dry period. If the wet period comes during the normal growth period of the insects, as it would in a wet-dry season tropical area, the fauna may be very similar to that of permanent streams in the area (Harrison 1966). If the dry season is not over until late in the year, as found by Williams (1977) and in the present study, then few adult insects will remain to lay eggs. Temperature and shading of the stream are also important. Ross (1944) found immatures of three species of caddisflies in the substrate of shaded areas, but none in unshaded areas. Gaufin (1962) noted that there are more species

of stoneflies in intermittent streams in the East than the West, and attributed this to the lack of shade in the arid West, however the occurrence of flash floods in the West may also be important. High temperatures and complete dryness, as found in desert regions, kills almost all aquatic insects, even diapausing ones. However, Hinton (1960) was able to show that a temporary pool chironomid was able to enter a state of cryptobiosis and withstand extreme conditions. As noted above, liability to spates is also an important factor, with frequent floods apparently selecting against resting forms (Gray and Fisher 1981). A final factor is the substrate, which determines if insects are able to burrow down to the hyporheic zone, or are able to find interstitial spaces in which to estivate.

With these wide variations in conditions a single concept of an intermittent stream may be questioned. In fact, there is no one definition of what an intermittent stream is, and published definitions (Leopold and Miller 1956, Kerri et al. 1976, Cowardin et al. 1979, Mitsch and Urbikas 1980) are not totally compatible with each other. The definition used in this paper, those streams in which at least part of the stream normally dries up during part of the year, has biological validity as the species present have to survive the same sorts of conditions. A division into different types of intermittent streams might be worthwhile. Abell (1956) and Usinger (1956) developed classification schemes for California streams based on length of flow, fluctuations in flow, and other factors. These schemes are long and cumbersome, may not be useful in other areas, and apparently have not been used by any other workers. A more logical division would be between

those streams that dry up completely and those that do not, however such a division is not currently in use.

Williams and Hynes (1977) stated that intermittent stream inhabitants could be divided into three main groups. The first is permanent stream forms that can survive because of their wide tolerance of environmental conditions. The second is "those species which are facultative, occurring in both lotic and lentic waters." The third group is "those species which are highly adapted and often restricted to temporary waters." They did not give examples of taxa belonging to any of these groups, and the division between the first two seems artificial. There appear to be a few species that are restricted to intermittent streams, Metacnephia amorpha (Simuliidae) and Paraleptophelibia tumida (Leptophlebiidae) in England (Ladle and Bass 1981), and possibly Centroptilum elsa (Baetidae) (Tew 1971) and the black flies Prosimulium gibsoni, Esimulium latipes, and E. gouldingi (Anderson and Dicke 1960) in this country. Other taxa, such as Ironoquia (Limnephilidae), are largely restricted to temporary streams and ponds.

Other taxa have not been found in intermittent streams. Clifford (1966) stated that three groups tend to be eliminated from intermittent streams. With a few exceptions this appears to be true. The first group is semivoltine species and other taxa with growth during the dry season. This appears to be generally true, although multivoltine Megaloptera (Evans 1972), Tabanidae (Burger 1977), and Cordulegaster (Present study) are able to survive. The second group is taxa with a late summer or fall emergence. An exception to this is Neophylax concinnus which emerges while the stream is still dry (Ross 1944). The third group is those taxa with both a spring and a fall generation.

VI. SUMMARY

Ameletus lineatus and Amphinemura delosa were apparently able to use an egg diapause to survive stream drying. Nymphs of Cordulegaster erronea and C. obliqua were able to survive the dry period in the substrate. Anchytarsus bicolor, Ptychoptera sp., and Nigronia fasciatus were able to avoid the dry period by remaining mostly in the permanent sections. Based on the substrate samples Pycnopsyche gentilis, Tipula sp., and Tabanus larvae are able to survive in the substrate of an intermittent stream.

With the exception of the three species that were mainly restricted to the permanent sections there was little difference in the species present in the intermittent and permanent sections. Most of the differences in numbers were probably due to differences in substrates in the different sections.

The survival mechanisms that can be used by aquatic insects in intermittent streams are summarized in Table 3. The most widely used techniques are diapausing or drought-resistant eggs and nymphs or larvae in the substrate. These methods should require the least amount of adjustment in the life cycle, and in many cases may be "accidental" rather than specifically evolved for life in intermittent streams. More specialized mechanisms are restricted to a few taxa, and have probably evolved in order to survive in intermittent streams and temporary ponds. These mechanisms include digging estivation

Table 3. Summary of Survival Mechanisms Used in Intermittent Streams.

Taxa	Reference
EGG DIAPAUSE OR ESTIVATION	
Ameletus lineatus	Present Study
Ameletus ludens	Clemens (1922)
Siphlonuris marshalli	Williams and Hynes (1976a)
Siphlonurinae	Abell (1956)
Centroptilum elsa	Tew (1971)
Isonychia sicca	Grant and Stewart (1980)
Ephemeralla sp.	Abell (1956)
Ephemerella ignita	Casey and Ladle (1976)
Leptophlebia sp.	Williams and Hynes (1976)
Paraleptophlebia ontario	Williams and Hynes (1976)
Perlesta placida	Snellin and Stewart (1979)
Mesocapnia arizonensis	Gray (1981)
Hydroperla crosbyi	Oberndorfer and Stewart (1977)
Isoperla clio	Harper (1973b)
Ostrocerca albidipennis	Mackay (1969)
Amphinemura delosa	Narper (1973a), Present Study
Dinotoperla serricauda	Hynes and Hynes (1975)
Agapetus sp.	Abell (1956)
Lepidostoma sp.	Mackay (1969)
Prosimulium gibsoni	Anderson and Dicke (1960)
Prosimulium magnum	Anderson and Dicke (1960)
Cnephia dacotensis	Anderson and Dicke (1960)
Cnephia mutata	Anderson and Dicke (1960)
Eusimulium latipes	Anderson and Dicke (1960)
Eusimulium gouldingi[a]	Anderson and Dicke (1960)
Metacnephia sp.	Casey and Ladle (1976)
Diplocladius sp.	Williams and Hynes (1976a)
Orthocladius sp.	Williams and Hynes (1976a)
Trissocladius sp.	Williams and Hynes (1976a)
Acriotopus sp.	Williams and Hynes (1976a)
Chironomus sp.	Williams and Hynes (1976a)
Diamesa sp.	Williams and Hynes (1976a)
Micropsectra sp.	Williams and Hynes (1976a)
Natarisa sp.	Williams and Hynes (1976a)
Paraphaenocladius sp.	Williams and Hynes (1976a)
Pseudosmittia sp.	Williams and Hynes (1976a)
Bezzia-Probezzia sp.	Williams and Hynes (1976a)
NYMPH DIAPAUSE	
Allocapnia vivapara	Coleman and Hynes (1970), Williams and Hynes (1976a)
EGG OR LARVAE DIAPAUSE	
Ochrotrichia xena	Larimore et al. (1959)

Table 3 (continued)

Taxa	Reference
	ADULT DIAPAUSE
Heserophylax incisus	Tew (1971)
Grammotaulius betteni	Tew (1971)
Limnephilus aretto	Tew (1971)
Limnephilus nogus	Tew (1971)
	PREPUPA DIAPAUSE
Neophylax concinnus	Ross (1944), Clifford (1966)
	NYMPHS OR LARVAE IN SUBSTRATE
Cordulegaster erronea	Present Study
Cordulegaster obliqua	Present Study
Allocapnia pygmaea	Clifford (1966)
Isoperla sp.	Abell (1956)
Heserophylax incisus	Tew (1971)
Limnephilus aretto	Tew (1971)
Limnephilus nogus	Tew (1971)
Pseudostenophylax uniformis	Mackay (1969)
Pycnopsyche gentilis	Present Study
Rhyacophila vibox	Imhof and Harrison (1981)
Hydropsyche sp.	Imhof and Harrison (1981)
Cheumatopsyche sp.	Imhof and Harrison (1981)
Diplectrona modesta	Imhof and Harrison (1981)
Chimarra feria	Ross (1944)
Setodes sp.	Harrison (1966)
Helmis sp.	Hynes (1958)
Molophilus hirtipennis	Mackay (1969)
Dicranota sp.	Mackay (1969)
Tipula sp.	Present Study
Chironomus sp.	Williams and Hynes (1976a)
Micropsectra sp.	Williams and Hynes (1976a)
Diamesa sp.	Hynes (1958)
Brillia sera	Mackay (1969)
Paraphaenocladius sp.	Mackay (1969)
Pseudorthocladius sp.	Mackay (1969)
Tabanidae	Burger (1977), Present Study
	PUPA IN SUBSTRATE
Rhyacophila glaberrima	Ross (1944)
Tipula cunctans	Williams and Hynes (1976a)
Limnophila sp.	Williams and Hynes (1976a)
Hexatoma sp.	Williams and Hynes (1976a)
Helobia sp.	Williams and Hynes (1976a)
Hydropyrus subopaca	Williams and Hynes (1976a)
	ADULTS IN SUBSTRATE
Limnebius discolor	Clifford (1966)
Hydroporus laetus	Clifford (1966)
Cymbiodyta sp.	Clifford (1966)

Table 3 (continued)

Taxa	Reference
	ADULTS AND LARVAE IN SUBSTRATE
Stenelmis sexlineata	Larimore et al. (1959)
Stenelmis crenata	Larimore et al. (1959)
Dubriraphia quadrinota	Larimore et al. (1959)
	ADULTS IN EARTHEN CHAMBERS
Gerridae	Larimore et al. (1959)
Agabus sp.	Tew (1971)
	LARVAE IN EARTHEN CHAMBERS
Protochauliodes aridus	Maddux (1954)
Protochauliodes spenceri	Tew (1971), Evans (1972)
Neohermes californicus	Smith (1970), Evans (1972)
Corydalus cornutus	Larimore et al. (1959)
	IN POOLS
Callibaetis sp.	Abell (1956)
Libellulinae	Abell (1956)
Hemiptera	Williams and Hynes (1977)
Cheumatopsyche spp.	Statzner (1982)
Agabinus sp.	Stout (1982)
Culicidae	Abell (1956, 1959), Clifford (1966), Williams and Hynes (1976a)
	IN SEEPS
Baetis sp.	Abell (1956)
Hydropsyche sp.	Abell (1956)
	ADULTS ENCASED IN SILT
Nepa apiculata	Larimore et al. (1959)
	LARVAE IN CRAYFISH BURROWS
Trichocladius sp.	Williams et al. (1974)
	MIGRATES FROM RIVERS
Leptophlebia cubida	Neave (1930), Hayden and Clifford (1974)
Parameletus chelifer	Olsson and Soderstrom (1978)
	EGGS LAID ABOVE WATER
Lestes sp.	Williams and Hynes (1976a), Wiggins et al. (1981)
Limnephilidae	Wiggins (1973)
	ADULTS (LOCATION UNSPECIFIED)
Mesovelia sp.	Williams and Hynes (1976a)
Rhantus sp.	Williams and Hynes (1976a)
Hydroporus wickhami	Williams and Hynes (1976a)
Helophorus orientalis	Williams and Hynes (1976a)
Peltodytes sp.	Williams and Hynes (1976a)

Table 3 (continued)

Taxa	Reference
	TERRESTRIAL ADULTS
Simulium spp.	Abell (1956), Williams and Hynes (1976a)
Antocha sp.	Williams and Hynes (1976a)
Hydrellia sp.	Williams and Hynes (1976a)
	FINAL INSTAR LEAVES WATER
Lepidostoma sp.[a]	Clifford (1966)
Ironoquia punctatissima	Clifford (1966), Williams and Williams (1975)

[a]Possible

chambers (some Megaloptera), ovipositing out of the water (Lestes spp. and some Limnephilidae), imaginal diapause (some Limnephilidae), and migration of nymphs from rivers with the adults flying back (some Ephemeroptera).

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