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The Ecology of Temporary Streams

I. The Faunas of Two Canadian Streams

Abstract

This, the first of two papers on the ecology of temporary streams, describes, in detail, the faunas of two such habitats in southeastern Canada. The adaptive mechanisms for coping with the summer drought are documented for a variety of species and faunal succession is shown to occur from the stream stage (fall-winter) through the pool stage (spring) to the terrestrial (summer).

Contents

I. Introduction	761
II. Previous literature	761
III. The study streams	762
IV. Materials and methods	763
V. The fauna of Moser Creek	764
VI. Discussion	776
VII. The fauna of Kirkland Creek	778
VIII. Discussion	784
IX. Acknowledgements	784
X. Summary	785
XI. References	785

I. Introduction

This is the first of two papers dealing with the ecology of temporary stream faunas. In it, we propose to present the detailed findings of work on two temporary streams in Ontario, Canada. This will lay the foundations for the second paper in which we will attempt to summarize what is known of these habitats and to underline how the members of what is essentially an aquatic community, deal with the terrestrial phase of their environment.

II. Previous literature

There have been few studies on temporary streams as such, but there is a copious literature dealing with temporary ponds and other small water bodies. Whereas the differences between permanent lotic and lentic habitats may be very considerable indeed, in the temporary water situation, because many of these streams flow slowly and often dry up to pools, we find considerable overlaps.

ABELL (1956) in a study of intermittency in foothill streams of central California, made extensive faunal lists and tried to explain these in terms of three groups:

1. a rapidly appearing but essentially temporary fall association which tended towards a herbivorous nature and occupied a wide range of habitats.
2. a winter and spring succession which tended to replace the fall forms and represented a step towards a more complex community.
3. a summer cleanup crew consisting mostly of predators and scavengers.

He found that these animals employed three methods of survival in the dry stages of these habitats, namely, dormancy within the habitat, transfer of activity to another environment, and retreat to a more favourable habitat to await resumption of flow. The latter was apparently the most variably and successfully used, permitting almost any sort of life history timing. Eighty percent of ABELL's temporary stream fauna were insects.

CLIFFORD (1966) in a study of a temporary stream in Indiana, divided the fauna into two groups with respect to season. The first was a late summer-fall association, characteristic of the stream when it was dry or nearly so. It consisted of adventitious species and adult aquatic beetles. The second was a later winter-spring association, characteristic of conditions of flow. Its constituents were mainly permanent residents which appeared year after year and were the basis for a stable community. Apparently, many of the latter were not specifically adapted to this kind of environment, but possessed certain pre-adaptations which favoured them over others. *Lirceus fontinalis* and *Crangonyx forbesi* were the two most abundant organisms and both survived the summer drought as small individuals buried in the substrate.

HARRISON (1966) observed that the Munwahuku stream near Salisbury, Rhodesia, became dry for 3 months during 1962-1963 and for 8 months in 1964. He primarily studied the recolonization by the fauna and found that most of the insects flew in from outside, whereas snails, oligochaetes, small crustaceans, and rhabdocoels survived as eggs or aestivating stages in the stream channel. Much of the fauna was similar to that living in nearby permanent streams.

In the Afon Hirnant, Wales, a mountain stream studied by HYNES (1958) many of the common species failed to appear following a drought. This clearly indicated that he was dealing with a non-cyclical, catastrophic drought against which the majority of the fauna was not adapted.

III. The study streams

The two streams selected for detailed study are located in Waterloo County, Ontario, Canada (43°30'N; 80°30'W) and form part of the Grand River drainage basin. In this area, the bedrock is composed primarily of brown dolomite and grey shale but with associated deposits of salt, gypsum and anhydrite (LIBERTY 1968). This calcareous composition of the bedrock is reflected in the stream sediments and fills. For most of the area, the alluvium is underlain by a complex series of kame gravels, sands and till sheets. The soils are moderately to strongly calcareous with a pH range of 7.8 to 8, and are mostly under heavy agriculture.

Moser Creek is a small temporary stream which flows for about 7 months of the year (see Fig. 1). It is about 400 m long and runs through a pasture field where it has cut a uniform channel some 50 cm deep and 80 cm wide in the clay-loam soil. Nine groundwater upwellings supply most of the flow but field drainage is also important. At its lower end it empties into a slow-flowing, meandering, silty stream fed mostly from agricultural drainage, which is a tributary of the Nith River. It consists of two sections. The upper one, because of its proximity to the upwellings, flows for longer than the lower one, where by mid-spring, all the water is absorbed into the soil. The depth of water varies from a maximum of 100 cm, with a flow rate of 50 cm/sec during the spring floods to zero when the stream dries up in early summer (see Fig. 2). Water temperature ranges from a minimum of 1.5 °C under 15 cm of ice in the winter, to 20 °C in the pools of the drying streambed in late May. The substrate consists of a tangled mass of grass roots growing in a soil of mean aggregate size equal to 3.5 mm. Marginal vegetation consists mostly of field grasses and rushes which grow profusely in the summer often forming a humidity retaining canopy over parts of the stream.

Fig. 1. Rainfall and corresponding stream water levels in Moser Creek and Kirkland Creek for 1972–73. (Negative values indicate where the groundwater table was found during the dry phases.)

Dissolved oxygen remains at the saturated level for most of the year except for the summer, when many of the pools stagnate near the bottom, and mid-winter, when thick ice effectively seals off the stream from the atmosphere. pH is normally around 8 but it may increase to as much as 9.4 in response to the increased photosynthesis during algal blooms in the summer pools.

Kirkland Creek is a tributary of the Conestoga River, joining it approximately 6 km northeast of Elmira. It has a deep sandy-gravel substrate underlain by clay with large cobbles and boulders near the surface. Water flows in the channel for about 8 months each year (see Fig. 1). During the summer months, a series of pools remain which become heavily enriched with farmyard wastes and manure from the cattle which are allowed to graze the banks (Fig. 3). The emergent vegetation, apart from field grasses, is limited to large scattered willow trees (*Salix* sp.) which have their roots in the streambed. Its source is largely agricultural field drainage. Flow rates, temperature range, pH, and dissolved oxygen were similar to those found in Moser Creek.

IV. Material and methods

Animals were collected approximately biweekly using a dipnet of 135 μ mesh in a modified kick sampling manner. This involved walking upstream while disturbing the substrate with the feet so that the dislodged animals were swept (by the current) into the net which was held vertically behind the collector. By keeping the distances walked upstream constant, the sampling method was reasonably standard. In addition, other samples were taken from in and around aquatic vegetation in order to collect the more sparsely distributed and, or, shy forms. Specialized methods were used for certain taxa, for example, flatworms – baiting with liver, and crayfishes (see method in WILLIAMS *et al.* 1974). During later sorting, only a semi-quantitative analysis of the fauna was made. This took the forms of the scale – Rare (1–10 individuals of a species/sample), Common (11–50/sample) and Abundant (51 + /sample).

Fig. 2. Moser Creek during
A. Winter ice-cover. B. Spring flood. C. Early summer. D. Late summer.

V. The fauna of Moser Creek

Figure 4 shows the temporal distribution and relative abundance of the animals of Moser Creek between the 19th March, 1972, and the 26th May, 1973, together with an approximation of conditions of water flow in the channel. Detailed information on some of the more important and, or, interestingly adapted animals follows:

Tricladida

Fonticola velata (STRINGER), a cold-water stenotherm occurred in large numbers for most of the aquatic phase of the stream. Figure 5 gives the size distribution of this population over a year. Small individuals (1–2 mm long) were seldom encountered until after the stream had been flowing for 3 or 4 weeks. Thereafter, they appeared in large numbers and grew fairly rapidly during late November, December and early January after which growth slowed down until an optimum size of 10–12 mm was

Fig. 3a Kirkland Creek during late spring.

reached. Although these individuals were of a mature size, only one of the many examined was sexually mature. They remained abundant during the drying out period, often congregating in large numbers in the pools. By the time the pools had dried up, none could be found. KENK (1944) described a similar species from temporary ponds in Michigan and recorded a fragmentation phenomenon. When stressed, individuals break off areas of tissue from their posterior ends, and these fragments then round off and become surrounded by a mucus coat which soon hardens to form a cyst which is drought resistant (CASTLE 1928). Conditions necessary for fragmentation stimulation in *F. velata* appear to be that the worms are well fed and are subjected to a gradual rise in water temperature — such as would occur in the shallow pools in the drying streambed. The resulting cysts could be commonly dug up from the top few centimetres of the substrate during the summer dry phase of the stream. In this particular habitat, it is likely that this means of asexual reproduction is solely responsible for maintaining the population and that sexual reproduction hardly occurs at all.

Fig. 3b. Kirkland Creek during late summer.

Their food in the stream is uncertain. It was thought that they were making use of the large populations of the amphipods *Crangonyx minor* and *C. setodactylus*, but sereological tests using anti-*Gammarus* serum (YOUNG *et al.*, 1964) gave no positive reactions, even though the flatworms would readily eat both species in the laboratory.

Fig. 4a

Fig. 4b

Fig. 4c

Fig. 4. The fauna of Moser Creek showing its temporal distribution and relative abundance during 1972-73, together with an approximation of conditions of water flow. Figs. 4d and 4e cf.

p. 768

- ~~~~~ = period of flow,
- ~~~~~x~~~~~ = period of flow under ice,
- = pools only,
- = dry bed.
- = abundant
- = common
- = rare

Fig. 4d

Fig. 4e

Oligochaeta

The oligochaete fauna was represented for most of the year by a mixture of Enchytraeidae, Lumbriculidae (probably *Sparganophilus* sp.) and Tubificidae — including *Tubifex tubifex* (MÜLLER). During most of the aquatic phases of the stream they were all common to abundant (with the exception of *Sparganophilus*), but their numbers declined considerably in the summer when only the Enchytraeidae and a few *T. tubifex* could be found active in the moist substrate. Some of the tubificids (probably *T. tubifex*) were observed to have secreted mucus envelopes around themselves, to which sand grains had become attached. The presence of active enchytraeids at this time is not surprising, as members of this family are not primarily aquatic, being quite common in permanently wet soil (BRINKHURST and JAMIESON 1971). A few tubificid cocoons found in late May, suggests that breeding takes place just before the stream dries up, leaving a portion of the next year's population to face the drought as developing embryos.

of their shallow nature, were considerably warmer than the mainstream and soon developed an algal flora thus providing an ideal environment in which to breed. At the onset of the dry period in July, most of the population were in the 1.3–1.5 mm (female) size range, suggesting that they prepared for the drought as near adults, probably fourth copepodite (mature females being of the order of 1.0–1.8 mm long; GURNEY 1933). During the summer, these individuals could be dug up from the region of the capillary fringe and below, and if placed in water would recover after 1 or 2 days. *C. vernalis robustus* is known to arrest its development (COKER 1933), and CHAMPEAU (1963) found that cyclopoids quite commonly do this in the fourth copepodite stage, and that as such they appear to be in some way more resistant to dehydration. WATSON and SMALLMAN (1971) in a study of the factors affecting induction and termination of arrested development in two species of cyclopoids found that daylight and temperature were the environmental cues which, in combination, caused such an arrest in two species of *Diacyclops*. One responded to short day conditions and the other to long day. Temperature was shown to affect the critical day length values associated with a transition from a long day to a short day response for each species.

An interesting feature of the Moser population was that large numbers of *C. vernalis* could be found in the water at the bottom of the burrows of the crayfish *Cambarus fodiens*. These individuals were active throughout the year, and some showed signs of having matured. They would probably have been trapped in the burrows as the G. W. T. receded, and being thereafter subjected to almost total darkness, would, if this species is physiologically similar to *Diacyclops*, fail to undergo developmental arrest.

Fig. 6. Diagram of the summer drought resistant cyst of *Attheyella nordenskioldii* (LILLJEBORG) as found in Moser Creek.

A. nordenskioldii also bred in April and May in the flood plain pools, although females carrying eggs were seen in the mainstream as early as January. Again, this species oversummers as a near adult stage (length 0.9–1.0 mm; BORUTSKII 1964), however, there appear to be two kinds of individuals which do this. One can be found near the G. W. T. and is active immediately when placed in water, while the other occurs nearer the surface and has a circular cyst secreted around itself (see Fig. 6). It requires several hours of immersion before the animal can break out and swim away. Such cysts have already been recorded for *Canthocamptus microstaphylinus* by LAUTERBORN and WOLF (1909), and for *C. staphylinus* by BERG (1938) and MOORE (1939), but some disagreement occurs as to how many layers make up these cysts. *A. nordenskioldii* has only one thin layer consisting of a transparent, homogeneous, gelatinous material to which sand grains become attached. Encysted individuals have

also been found in two other species of *Attheyella*, *A. wulmeri* and *A. northumbrica* (ROY 1932) but these differ from those observed in *A. nordenskioldii* in two respects. Firstly, they are oval in form, and secondly, the harpacticoid is not reflected but lies out straight with its apical setae protruding through the cyst wall.

DONNER (1928), experimenting on the conditions which cause cyst formation in *C. staphylinus*, showed that high water temperature rather than desiccation was the initiating stimulus. As temporary water bodies usually warm up before drying out, cyst formation as a means of surviving desiccation could well be controlled solely by temperature rise.

A. nordenskioldii nordenskioldii (LILLEJEBORG) is known to inhabit small bodies of water mainly tundra pools and brooks, in the arctic (BORUTSKII 1964).

It is generally considered that dormancy in copepods (as an egg stage in calanoids, and as near adults in cyclopoids and harpacticoids) is a mechanism for withstanding high summer temperatures with their attendant low oxygen levels (FRYER and SMYLY 1954). That the physiological methods involved in achieving this also enhance the species resistance to drought would seem to be an important factor in promoting the invasion of temporary aquatic habitats by such animals.

Amphipoda

Two closely related species of the genus *Crangonyx* occurred in Moser Creek, *C. minor* BOUSFIELD and *C. setodactylus* BOUSFIELD. It is almost impossible to tell these two amphipods apart in their early stages, as only after they have passed 5 mm in length do the diagnostic setae on the inner margins of the dactyls of the paraeopods become obvious in *C. setodactylus*. However, an attempt at separating their life histories is shown in Fig. 7.

When the amphipods first appeared after the summer 1972 drought — around the beginning of October, the population was divided into three fractions. One, a few male *C. minor* presumably left over from the previous year; two, some questionable *C. setodactylus* in the 4 mm size range; three, a large number of individuals of both species in the 2 and 3 mm size ranges. By mid-November, however, the populations of the two species could be told apart, *C. setodactylus* growing at a much faster rate than *C. minor*. By the end of December, most of the *C. setodactylus* were in the 8 mm size class and the sexes of those in the 10 mm class became readily distinguishable.

Fig. 7. Population size distribution of *Crangonyx minor* BOUSFIELD and *C. setodactylus* BOUSFIELD in Moser Creek during 1972-73.

At this time, most of *C. minor* were in or below the 5 mm class, but a few had reached 10 mm. Mid-January 1973 saw the appearance of the first ovigerous *C. setodactylus* females in the 10 mm size class, whereas none was apparent in the *C. minor* population until the beginning of April when they occupied the 7, 8 and 10 mm classes — males being of the order of 5 mm long. By late April, the first young *C. setodactylus* had been released (they were all approximately 2 mm long), but *C. minor* did not release its young until nearly 2 weeks later when they were 1 mm long. Brood sizes ranged between 20 and 35 for *C. minor* and 40 and 65 for *C. setodactylus*, and in both species the spent females died shortly after release. By May 26, 1973, when the stream was flowing intermittently, two distinct size classes were obvious, 2 mm — presumably *C. minor* and 3 mm — presumably *C. setodactylus*. These then disappeared as the stream dried up. During the summer, a large effort was made to locate these populations. Great quantities of substrate were dug up and sorted through, but only two individuals were found, both 2 mm long and both in August. A few were also found in the water of crayfish burrows, but it is unlikely that this is their normal method of overwintering. It seems that they are able to burrow down into the substrate to a level at which they find enough water to sustain them. But, experiments, under field conditions, to get them to burrow in a laboratory setup proved fruitless; large and small individuals appeared equally inept at tackling even the most porous of substrates.

The size structure of the populations which were found in the new stream in 1973 was similar to that shown in Fig. 7 for October 1972. Young ranging from 2–4 mm long indicated that only a slight increase in growth had occurred during the 3 summer months. A few adult *C. minor* also had survived.

Decapoda

Only one species of crayfish was found, *Cambarus fodiens* (COTTLE). This is a burrowing species which actively follows the receding ground water table after the stream has ceased to flow. Its life history in this habitat has been described elsewhere (WILLIAMS *et al.*, 1974).

Acari

Hydryphantes sp. and unidentified oribatids were the only two groups of mites found regularly. The genus *Hydryphantes* is characteristic of temporary ponds and is capable of surviving dry periods buried in damp soil (PENNAK, 1953) whereas, the oribatids could well have been soil water forms which happened to surface in the stream channel.

Ephemeroptera Insecta

Of the three species of mayfly present, only one, *Paraleptophlebia ontario* (McDUNNOUGH), was present in sufficient numbers to enable its growth to be followed. *Leptophlebia* sp. and *Siphonurus marshalli* TRAVER were seen as nymphs only during April and May.

Newly hatched individuals of *P. ontario* were first seen in late April, they grew rapidly during early May and emerged from the drying pools in early June. Presumably, some kind of diapausing, drought-resistant eggs were then laid which did not hatch until the following spring.

Hemiptera

Gerris remigis SAY could be found as wingless adult females and very small nymphs in early April, the females having moved up from the Nith a few weeks earlier and laid their eggs in Moser Creek. The nymphs had matured by late May and then left the drying pools. It looks as if this species only occupies Moser Creek for a short period each year when temperature is on the increase and food is plentiful. After completing a quick generation (CHENG 1966, states that egg to adult may take only 40–60 days) it returns to the permanent stream.

Trichoptera

Ironoquia punctatissima (WALKER) was extremely abundant in this habitat and survived the dry phase as a terrestrial pupa. This life cycle been described elsewhere (WILLIAMS and WILLIAMS 1975).

An undetermined species of *Limnephilus* was also found, as large larvae in small numbers during April. The development of the larva is probably similar to *Ironoquia* but the long summer period is more likely passed as an adult, as WIGGINS (1973) has recorded this for both *L. indivisus* and *L. submonilifer*.

Coleoptera

Adult *Helophorus orientalis* MOTSCH were common for most of the year, even under ice cover when most of them congregated at the surface and were obviously in a state of torpor. During late May, a few eggs were seen and the first larvae appeared just as the stream dried up to pools. Here the larvae developed until pupation took place in July when only moist soil remained. An increase in adult numbers in October suggested that this was when adult emergence occurred, although this could have been due to a fall influx of adults during their dispersal flight from nearby habitats, *H. orientalis* being an important colonizer of temporary waters (FERNANDO 1958). It is likely that this population reproduces parthogenetically (ANGUS 1970).

Anacaena limbata FABRICIUS, was the only other hydrophilid beetle taken commonly throughout the year. Its habits were very similar to those of *Helophorus*, but it seemed to breed at least a full month earlier, as mature larvae were to be found by the end of May. GALBRAITH (1971) in a study of the colonization patterns of these two species in the Waterloo County area, found them to exhibit staggered colonization and dispersal flights. He postulated that these unharmonic migrations, which were probably the result of different responses to climatic factors, could well result in reduced competition for the same habitat between the two species.

A few well grown larvae of *Tropisternus* sp. were found in the pools in June, but no adults were seen. Conversely, adult *Hydrobius* sp. were collected in October, but no larvae.

Two dytiscids were taken, both completing their life cycles in this habitat. *Hydroporus wickhami* ZAITZEV produced small larvae in late April which then grew steadily until mid-June, when they disappeared to be replaced by a few adults. Small larvae of *Rhantus* sp. also appeared in late April and were fully grown by the end of May.

Diptera: Chironomidae

Figure 8 shows the seasonal occurrence patterns of four of the most abundant genera of chironomid.

Eggs containing fully-developed larvae of *Trissocladius* spp. were commonly found

Fig. 8. Histograms showing the percentage composition, by instar, of four genera of Chironomidae collected from Moser Creek during 1972-73. (x indicates stage was present but not quantified.)

just after stream flow was re-initiated in early October 1972. By the time the next samples were taken on November 4, the majority of these chironomids were in their third instar (instars being determined by head capsule width measurements). This clearly indicates a very fast growth rate, the details of which were examined the following fall when samples were taken at shorter time intervals. As can be seen from the figure, nearly all the larvae moved through their instars at the same time, taking only about 7 days to go from first to second, and the same for second to third. By the end of December 1972, most were in their last instar and they remained thus through the winter until early April when they pupated. Pupation was well coordinated and most of the adults appeared at one time, from the second to the seventh of April. Examination of these adults showed that two species were present, *Trissocladius johannseni* (SUBL.) and *Trissocladius* n. sp. Large numbers of these adults covered the banks and mating took place almost immediately after emergence. This was followed by oviposition back into the drying stream, most of the adults having strayed little more than a few meters from where they had emerged. Eggs collected at this time, and kept in aerated stream water soon hatched, suggesting that exposure to drying is necessary shortly after oviposition in order to prevent the eggs from hatching before the stream restarted in October. *T. griseipennis* GOETGH. is known to inhabit ditches (CHERNOVSKII 1949).

Diplocladius n. sp. had a similar life cycle, but its larval growth in the fall was at a much slower pace than that of *Trissocladius*. Three instars were still evident when the first pupae appeared in early April. The summer phase is probably passed as a drought resistant egg in this species, too.

Orthocladius n. sp. had a similar growth rate to *Diplocladius*, starting from first instar larvae in early November, but the last instar larvae kept on arising well into the pool stage of the stream. Adults were rare and overwintering again seems to have been in the egg stage.

Larvae of *Micropsectra* sp. had a differential growth rate, as some larvae grew quickly and so had reached their fourth instar by the end of December, while others grew more slowly. Neither adults nor pupae were seen, but a few fully grown larvae were dug up from the dry streambed during the summer of 1972. This shows that the larvae of this species are capable of surviving without free water, and hence pupation and emergence may occur sporadically throughout the summer, even after the stream has disappeared.

Of the three tanypods also present, only one — *Natarsia* sp. was collected in any numbers. It first became apparent as half grown larvae in April and by the end of this month had pupated and emerged. No adults were collected. The other species taken were *Psectrotanypus* sp. and? *Pentaneura* sp., both in mid-April and early May.

Large larvae of *Chironomus* sp. were evident in May and could be collected along with *Micropsectra* in the dry streambed in July. It is interesting to note that both these chironomids possess haemoglobin, and are therefore, perhaps best suited to the low oxygen levels found in interstitial soil water.

Diptera: Other

Small larvae of *Tipula cunctans* SAY were seen in the stream as early as November, but not much growth took place until the following March and April. Pupae were collected from pools in late May and from amongst grass roots in the streambed in August. It is likely that the summer is passed in this stage as adults were not seen until early October. Emergence seems to be well synchronized, as on the evening of October 3, 1973, large numbers of adults were seen swarming and mating over the damp streambed. Eggs were laid shortly afterwards, as sterile substrates placed on the bed yielded small larvae a few weeks after having been immersed in water and placed in an environmental chamber. ROGERS (1942) remarked on this species as having a single generation a year with a marked autumnal flight period (September–October), the larvae being commonly found in sedge marshes.

Late instar larvae of *Aedes vexans* (MEIGEN) were abundant in pools in the streambed during June and late August, and adults were common from June onwards. There is controversy as to whether this species is capable of one or more generations per year (e.g. BARR, 1958), but since all the pools in Moser Creek dried up between these two dates, either two generations or staggered egg hatching must occur. BARR (op. cit.), in a laboratory study, showed that eggs deposited on moist surfaces would not hatch if dried out in the first day or so. However, GJULLIN and YATES (1946) demonstrated that under favourable conditions, that is, continual moisture, eggs might be viable for several years — although the hatching percentage fell off with time. Eggs laid in early October in Moser Creek would be subject to this necessary moisture until they hatched the following spring. HORSFALL (1956) showed that these same eggs subjected to adverse conditions such as drought, cold or premature submersion had to be "conditioned" before they would hatch. This conditioning could be effected by a 48 hour exposure to a wet, cold environment. Once this had taken place, the eggs would hatch

upon being subjected to the normal stimulus for the species — probably a reduction in the oxygen content of the water (e.g. in the pools formed after spring stream flow had ceased) or a temperature threshold of around 7–10 °C (e.g. as the water warmed up after winter) (GJULLIN *et al.*, 1950).

Two species from the genus *Leptocera* (Sphaeroceridae) were taken throughout the year. These larvae are not primarily aquatic as they are well-known inhabitants of animal dung, but they could well exist around the damp margin of a stream (TESKEY, personal communication)

Pisces

Only two species of fish comprising seven individuals were found in the creek during 1972 and 1973, *Semotilus atromaculatus* (MITCHELL), the common creek chub, and *Culea inconstans* KIRTLAND, the brook stickleback. Neither species bred in the creek and both populations were exterminated during the dry period. Each was, therefore, dependent on new migrations from the permanent stream each year.

Terrestrial

A variety of terrestrial animals was found to move into the creek during the summer phase, for example, Lumbricidae and their cocoons, Limacidae, Cochlicopidae — *Cochlicopa lubrica* (MÜLLER), Formicidae, Scarabaeidae, Staphylinidae and Arachnida.

VI. Discussion

The animals found in Moser Creek can be divided up, quite naturally into three successive groups based on the water conditions found throughout the year. The major components of these three groups are shown in Table 1. We should point out here, that inclusion in a particular group indicates that this is where the animal passed the most active stage of its life. Undoubtedly, there will be some overlap.

The fall-winter stream fauna consists of those animals which appear shortly after the stream has started flowing again in October or November and most have successfully reproduced before the stream stops flowing in the spring. Many of them, for example, the chironomid, *Trissocladius* and the caddisfly *Isonychia punctatissima*, grow quickly before the water cools down and then are ready, shortly after ice breakup, to mature and breed. Others, such as the chironomid *Diplocladius* and the amphipod *C. minor*, grow steadily throughout the winter and mature a little later. A few, such as *Microsectra* and *Chironomus* grow so slowly that their period of activity spans two of the groups.

The spring-pool fauna group represents those species which wait until the stream has ceased to flow and shallow pools are left. These pools, as has already been mentioned, are excellent breeding environments due to the ease with which they warm up and the abundant plant food that develops in them. There are two basic types of species which use these pools. The first, such as *Aedes vexans*, *Helophorus orientalis* and *Anacaena limbata* have been present all along since the previous fall (the mosquitoes as eggs and the beetles as adults), but they do not produce any larvae until the flow stops. Once hatched, the larvae grow quickly and mature before the pools dry up. The second consists of such animals as the beetles *Tropisternus* sp., *Hydroporus wickhami*, *Rhantus* and the water strider, *Gerris remigis*. These fly or walk in as adults just as the pools are forming, lay their eggs and often leave. The larvae quickly hatch and mature just as the last water disappears. Occasionally an unusually dry period

Table 1. Successive faunal associations in Moser Creek, together with the methods used to survive the summer dry period.

- (1) special cyst,
- (2) egg,
- (3) larva or immature stage,
- (4) pupa,
- (5) adult.

Fall-Winter Stream Fauna:

<i>Fonticola velata</i>	1	<i>Helophorus orientalis</i>	5
Nematoda	5	<i>Anacaena limbata</i>	5
Enchytraeidae	5	<i>Micropsectra</i> sp.	3+2?
<i>Spargonophilus</i> sp.?	5	<i>Chironomus</i> sp.	3+2?
<i>Tubifex tubifex</i>	1	<i>Diamesa</i> sp.	2?
Tubificidae	1?	<i>Diplocladius</i> n. sp.	2
<i>Lymnaea humilis</i>	5	<i>Trissocladius</i> sp.	2
<i>Physa gyrina</i>	5	<i>Orthocladius</i> n. sp.	2
<i>Candona stagnalis</i>	3	<i>Pseudosmittia</i> sp.	2?
<i>Cyclops vernalis</i>	3	<i>Paraphaenocladius</i> sp.	2?
<i>Attheyella nordenskiöldii</i>	1	<i>Tipula cunctans</i>	4
<i>Crangonyx minor</i>	3	<i>Helobia</i> sp.	4?
<i>C. setodactylus</i>	3	<i>Bezzia/Probezzia</i> sp.	2?
<i>Cambarus fodiens</i>	3, 5	<i>Simulium</i> sp.	5?
<i>Hydryphantes</i> sp.	5?	<i>Semotilus a. atromaculatus</i>	
<i>Isonychia punctatissima</i>	4	<i>Culaea inconstans</i>	
<i>Limnephilus</i> sp.	5?		

Spring Pool Fauna:

Nematoda	5	<i>Hydroporus wickhami</i>	5
<i>Helisoma</i> sp.	5	<i>Rhantus</i> sp.	5
<i>Gyraulus parvus</i>	5	<i>Natarsia</i> sp.	2?
<i>Hydrachna</i> sp.	5	<i>Micropsectra</i> sp.	3+2?
Oribatei	5	<i>Chironomus</i> sp.	3+2?
<i>Isotomurus</i> sp.	5	<i>Acricotopus</i> sp.	2?
<i>Paraleptophlebia ontario</i>	2	<i>Tipula cunctans</i>	4
<i>Leptophlebia</i> sp.	2	<i>Limnophila</i> sp.	4
<i>Siphonurus marshalli</i>	2	<i>Hexatoma</i> sp.	4?
<i>Gerris remigis</i>	5	<i>Helobia</i> sp.	4?
<i>Mesovelia</i> sp.	5	<i>Aedes vexans</i>	2
<i>Peltodytes</i> sp.	5	<i>Tropidia</i> sp.?	5?
<i>Helophorus orientalis</i>	5	<i>Ephydra (subopaca?)</i>	4?
<i>Anacaena limbata</i>	5	<i>Hydrellia</i> sp.	5?
<i>Tropisternus</i> sp.	4		

Summer Terrestrial Fauna:

Lumbricidae	Staphylinidae
Limacidae	Arachnida
<i>Cocklicopa lubrica</i>	
Oribatei	
<i>Micropsectra</i> sp.	
<i>Chironomus</i> sp.	
<i>Helobia</i> sp.	
<i>Leptocera</i> (Diptera) 2 spp.	
Sepsidae	
Formicidae	
Scarabaeidae	

may speed up the drying process in which case some of these species may get "caught short", however, several have pupae which are capable of resisting drought for a short while which enables the adults to emerge successfully.

The summer-terrestrial fauna consists mostly of those animals which are normally found around the banks of water bodies, and once the bed dries out, they quickly move into it. Some, such as the earthworms are probably attracted by the dampness, others like the slugs and snails come to feed on the algal mats left in the drying pools. The beetles and ants scavenge the bed for dead or dying individuals left over from the aquatic phase, and the spiders in turn follow these, their prey. A few specialized types also belong in this group, namely the flies of the families Sepsidae and Sphaeroceridae (genus *Leptocera*). These flies are generally attracted to damp decaying matter and it is, therefore, not difficult to think of them as being attracted by the decaying plant and animal material left by the pools.

Table 1 also shows the mechanics by which the species found in Moser Creek survive the summer drought. Five categories are suggested, one, as a special drought resistant cyst; two, as an egg; three, as a larva or immature stage; four, as a pupa and five, as an adult. Assignment of the categories is based mostly on observation, but in some cases (marked with a "?") it is supposition based on a closely related species. Others are instances cited in previous literature. Certain members of distinct taxonomic groups appear to have selected similar methods, for example:

Category 1, (cyst) — *Fonticola velata*, *Tubifex tubifex*, *Attheyella nordenskioldii*

Category 2, (egg) — Ephemeroptera, Chironomidae

Category 3, (larva or immature) — Amphipoda, Ostracoda, Cyclopoida

Category 4, (pupa) — *Isonychia punctatissima*, Tipulidae

Category 5, (adult) — Hemiptera, Coleoptera, Enchytraeidae, Gastropoda

VII. The fauna of Kirkland Creek

Figure 9 shows the temporal distribution and relative abundance of some of the fauna of Kirkland Creek between April 25, 1972 and July 24, 1973. The main differences between this stream and Moser Creek are that Kirkland usually flows for a month longer and a few pools remain along the length of the streambed all summer. These, as we shall see in the following synopsis permit the survival of certain additional species.

Hirudinea

Erpobdella punctata (LEIDY) and *Mollibdella grandis* (VERRIL) were the only two leeches found. During the summer drought they retreated beneath large stones or anything flat (including cow pats) which afforded protection from the sun and some moisture beneath. As the summer progressed, the leeches became smaller, presumably due to water loss, and secreted slime layers around themselves. Some even made short burrows (approximately 5 cm deep) in an attempt to find better protection. Those individuals which had reached the comparative safety of a pool remained active throughout the summer. KENK (1949) found dehydrated specimens of *E. punctata* in the top layer of soil from one of his Michigan temporary ponds and concluded generally that "the majority of these leeches are widely distributed species and none show a marked preference for temporary ponds." *M. grandis* is reported (MANN 1962) to be amphibious, leaving the water for part of the year to live in soil or under stones where it feeds on earthworms or slugs.

Fig. 9a

Fig. 9b

Fig. 9. The fauna of Kirkland Creek showing its temporal distribution and relative abundance during 1972-73, together with an approximation of conditions of water flow, Figs. 9c and 9d cf. p. 780

- ~~~~~ = period of flow,
- ~~~~~ = period of flow under ice,
- = pools only,
- = dry bed.
- = Abundant
- = Common
- = Rare

Fig. 9c

Fig. 9d

Pelecypoda

Sphaerium sulcatum (LAMARCK) occurred throughout the year. Very small individuals were found in April and May, which grew to about 1 cm by mid-August. During the summer, several were found under rocks or buried a few centimeters down in the substrate. The shells of larger specimens (up to 2 cm long) lay scattered on the surface of the bed at this time and it was assumed that they represented a large mortality from amongst the previous year's adults. It is likely, that after the drought is over, the young of the year grow and breed the following spring. This type of life

cycle has been recorded for *S. occidentale*, in a temporary pond, by KENK (1949) who stated "no individual appeared to over-winter more than once." This led to his conclusion that, for this species, maximum individual size of temporary water populations was less than that found in permanent bodies. This does not seem to be borne out by *S. sulcatum* in Kirkland Creek, but here, we have the added complication of a few adults surviving in the summer pools.

Cladocera

Moina macrocopa STRAUS occurred primarily in the summer months and then mostly in the pool sections of the stream. Occasionally it was taken over riffles, but this was probably drift from the pools. No adults were taken from December to April, but ephippia could be found. MURAKAMI (1961), in a study of this species in Japanese carp ponds, found that it had an 11 month resting phase — as an ephippial egg — and was active only during the month of May when it reproduced first parthenogenetically and then sexually. He concluded that inhibition of development of the ephippia was due to environmental factors rather than inherent ones.

Plecoptera

Allocaonia vivipara (CLAASSEN) was the only stonefly in Kirkland Creek. Adults emerged through cracks in the ice during early March and mating and oviposition took place. Nymphs were not seen until July or August when they could be dug up from the substrate as approximately 1 mm long individuals in a state of diapause (see also HARPER and HYNES 1970). The depth distribution at this time was from about 5 cm to 25 cm — the nymphs seemingly distributed at random in this range. A few nymphs which had broken their diapause were collected later in the year (mid-October) on the surfaces of the newly inundated riffles. HARPER and HYNES (*op. cit.*) state that this diapause is clearly an adaptation to survive high summer temperatures — NEBEKER and LEMKE (1968) showed these nymphs to be very heat sensitive, particularly in their later instars. This, at the same time, is a pre-adaptation which has enabled them to conquer temporary streams, so long as they can find a moist substrate in which to lie. Since, even in permanent streams the nymphs have resorted to burrowing into the substrate, access to the deeper, more moist layers of drying streambeds is not difficult for them. ROSS and RICKER (1971) suggested that *A. vivipara* is the northern offshoot of a western Appalachian ancestral group which was tending towards warmer and slower streams, and a marked tolerance of barnyard pollution. They also showed that although it thrives in many of these streams, it does so only in stretches which run through moraines and which have a gravel bottom.

Odonata

Numerous half-grown nymphs (25–30 mm long) of the cosmopolitan *Anax junius* DRURY were found in large pools in September 1972, and adults were also seen hovering over the pools at this time. TROTTIER (1971) has shown two distinct populations of this species to exist in a pond near Toronto, Canada; a larger summer (non-resident) population which developed from oviposition to emergence in approximately 3 months (June to September), and a smaller overwintering (resident) population which spent the winter as half-grown larvae and took 11 months (from mid-July to the end of June the following year) to develop. This dual population system appears to apply to this species in Kirkland Creek.

A similar life cycle might be in effect for *Libellula pulchella* DRURY, as both 24 mm long (final instar) and 12–16 mm individuals could be taken in the September 1972 pools.

Nymphs of *Lestes* sp. in various stages of growth, were also found. Members of this genus are known to occur in temporary waters, where eggs laid above the waterline may aestivate through the summer and hatch when the water returns again in fall (CORBET 1963). They are commonly univoltine.

Hemiptera

Two species of *Gerris* occurred. *G. comatus* DRAKE and HOTTES was found in both the lotic and lentic stages of the habitat, but in late summer, large numbers had congregated in the pools. As the pools shrank, many of them flew away — all the specimens examined being of the winged type. Most of the *G. buenoi* KIRKALDY examined, however, were of the wingless type and so remained in the stream channel all year round. Both species are known to frequent temporary pools (CHENG and FERNANDO 1970). HYNES (1955) suggested, in a study of the Heteroptera of pools in East Africa, that apterous specimens are probably only produced on permanent water. In the case of *G. buenoi* in Kirkland Creek then, either the few pools left each year were sufficient to act as refuge habitats, or a new population invaded each year from downstream, where the creek flows into the permanent Conestoga River.

Coleoptera

Peltodytes sp. was first seen in mid-July as very small larvae and was not seen again until adults appeared in the pools in September.

Helophorus orientalis bred about 6 weeks later in Kirkland Creek then in Moser Creek, small larvae first appearing in late July. This was probably related to the time at which pools formed in the two channels.

Fairly well developed larvae of *Tropisternus lateralis* (SAY) were found, together with adults, during late June and early July. YOUNG (1960) believes this to be one of the pioneer species in newly formed water bodies as it is seldom found in permanent situations. In Kirkland Creek, it bred in the lotic phase just as stream flow was on the decline.

Heterocerus sp. is characteristic of a family which lives in galleries in the mud banks of streams (ARNETT 1968). In a temporary stream situation, it is likely that these beetles will quickly move into the streambed once the flow has ceased.

Many more species of aquatic beetles were found in this stream than in Moser Creek. Most were collected as adults in the summer pools, and it is probable, therefore, that they were casual colonizers that just came to feed and not reproduce.

Diptera: Chironomidae

Fifteen genera of chironomid were represented in Kirkland Creek. Life cycles of those in common with the Moser Creek fauna were similar.

Diptera: Other

A species from the *Culex pipiens* (LINNAEUS) group was found abundantly in the summer pools. Throughout this period, small, medium and large larvae together with pupae occurred simultaneously suggesting a number of generations during this lotic phase of the habitat.

Pupae of *Cnephia mutata* (MALLOCH) (Simuliidae) occurred in June and large numbers of young larvae appeared soon afterwards in July. Either these survived the summer in the pools, or they died and a new hatch took place in October. Large larvae were found the following spring. The species has been recorded from temporary forest streams in Wisconsin by ANDERSON and DICKE (1960).

Tubifera sp. (Syrphidae), the rat-tailed maggot was present throughout the summer pool stage, but was most numerous when the pools became polluted with farmyard wastes in September.

Pisces

Nine species of fish representing the families Cyprinidae, Catostomidae, Gastroteiidae and Percidae were taken in Kirkland Creek. Details will be published elsewhere.

Terrestrial

Most of the groups found to invade the dry bed of Moser Creek were represented in the Kirkland Creek summer invasion.

Vertical migrations of the fauna

In order to get some idea of how the benthos is distributed in the substrate of a temporary stream before, during and after a summer drought, a series of quantitative core samples were taken from Kirkland Creek (see method in WILLIAMS and HYNES 1974). The results are shown in Table 2. In May, large numbers of animals were to be

Table 2. Quantitative distribution of benthic organisms at various depths in the substrate of Kirkland Creek before, during and after the 1972 summer drought

Date	Surface 0-5 cm	10 cm	20 cm	30 cm	40 cm	50 cm	60 cm	Total
9/ 5/72 Riffle	18.6	108	101	28	26	12	7	300.6
Pool	5.4	206	77	47	18	17	2	372.4
13/ 6/72 Riffle	55.7	146	162	67	43	19	5	497.7
Pool	28.8	111	62	47	21	17	3	289.8
14/ 7/72 Riffle	154.7	90	49	14	8	2	0	317.7
Pool	13.9	17	22	29	9	3	0	93.9
16/ 8/72 Riffle	17.8	9	3	4	1	0	0	34.8
Pool	13.8	4	1	1	3	0	0	22.8
10/10/72 Riffle	12.4	95	45	19	6	0	0	177.4
Pool	11.0	65	34	13	5	1	0	129.0
10/11/72 Riffle	20.2	137	131	32	36	8	2	366.2
Pool	16.5	112	64	22	17	12	0	243.5

found in the top 20 cm of substrate, both in the riffle and pool areas. This pattern was repeated in June, but there were more animals nearer the surface (0-5 cm) than there had been previously. In July, this upward movement became more evident and the numbers present at 10 cm and 20 cm had declined considerably. Presumably, this represented mature larvae moving towards the surface of the substrate in preparation for pupation and emergence. By mid-August, when the riffles were dry and the pools

diminishing, few animals, by comparison, were left in the substrate. However, quite a large number of assorted eggs and cocoons were present. When flow was resumed in October, the numbers of animals in the substrate started to increase once more as a result of egg hatching, etc., so that by early November, the benthos was once again distributed throughout the substrate in a pattern typical of the lotic phase of the stream.

VIII. Discussion

As with the fauna of Moser Creek, an attempt was made to divide the Kirkland Creek fauna into three groups depending on which phase of the stream they passed most of their active life. One of the main differences between this analysis and that for Moser is that here there was more overlap between the fall-winter stream group and the spring-pool group. This was undoubtedly due to the extended presence of the pools in Kirkland Creek which probably allowed species with fairly long aquatic stages to successfully complete their life cycles in this particular habitat.

Animals typical of the fall-winter stream group included, *Allocapnia vivipara*, *Cheumatopsyche* sp., *Rhyacophila lobifera*, *Cnephia mutata* and many of the chironomids. Of the latter, however, only *Orthocladus* n. sp. grew at a rate comparable to that in Moser. The others grew steadily throughout the winter and spring and no fall growth-spurt was evident. Again, this could have been a direct result of the lingering pool stage.

The spring-pool fauna was dominated by the Coleoptera, 16 genera being represented. But the majority of these (nine) were present only as adults and it is likely that they were just using the pools as summer feeding areas. Other species actively occurring in this phase of the habitat included, *Moina macrocopa*, *Candona* sp., *Cypridopsis vidua*, *Culex pipiens*, *Tubifera* sp., and *Helobia* sp. There was little chance of the animals of this group being "caught short" by drought as was the case in Moser Creek, as even in exceptionally dry years, one or two pools remained. The only problem facing late completers was that of degrading habitat, for, as already mentioned, these pools accumulated considerable quantities of organic substances and became quite eutrophic by the end of the summer.

The summer-terrestrial fauna consisted typically of species from the major taxa shown in Fig. 9 for Moser Creek. In addition, a few notable forms specializing in damp soil also became established, for example, the beetle *Heterocerus* sp. and the dipterans *Leptocera* (three spp.), *Forcipomyia* sp. and *Pseudosmittia* sp.

As before, the mechanisms used by each of the taxa found to survive the summer drought were recorded. Again, members within distinct taxa seemed to use similar methods, for example:

Category 1, (cyst) — Tubificidae

Category 2, (egg) — Chironomidae, *Caenis* sp.

Category 3, (larvae or immature) — Amphipoda, Ostracoda, Cyclopoida, Plecoptera, Other Diptera

Category 4, (pupa) — Diptera — Tipulidae

Category 5, (adult) — Hemiptera, Coleoptera, Enchytraeidae, Gastropoda, Hirudinea, Pisces

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X. Summary

The ecology of the invertebrates found in two temporary streams (Moser Creek and Kirkland Creek) in Southern Ontario, Canada during 1972–1975 is described in detail. The faunas of both streams could be divided up into three successive groups, based on the water conditions found during the course of a year, as follows:

- I. A fall-winter stream fauna consisting of those animals which appear shortly after the streams had started flowing again in the fall. Most had successfully reproduced before the cessation of flow in the spring.
- II. A spring-pool fauna representing those species which do not reproduce until the stream has ceased flowing and shallow pools are left.
- III. A summer-terrestrial fauna consisting of those animals which are normally found around the banks of the water body, but once the bed dries up, quickly move into it.

The extended pool stage in Kirkland Creek is shown to be important in allowing certain species with fairly long aquatic stages to successfully complete their life cycles in this particular habitat.

The mechanisms used by the species of both streams to survive the summer drought are examined and five categories are suggested. These are: a special drought resistant cyst, egg, larva, pupa or adult. The members of distinct taxonomic groups appear to have selected similar methods.

Vertical migrations of the fauna within the stream substrate prior to, during and after the drought are described.

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