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The Ecology of Temporary Streams II. General Remarks on Temporary Streams

Abstract

This, the second of two papers on the ecology of temporary streams, attempts a generalization of the unique features of these habitats. The fauna is shown to consist of three main groups: permanent stream species, facultative species and specialized species. The members of certain major taxonomic groups tend to oversummer as similar stages in their life cycles and the over-summering method used reflects the type of life cycle exhibited by a particular species. These variations in life cycle lead to faunal succession. The coexistence of closely related species is shown to be common in temporary aquatic habitats and, as far as the most abundant taxa are concerned, the species composition is very stable from year to year.

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I. Introduction

This is the second of two papers dealing with the ecology of temporary streams. In the first paper (WILLIAMS and HYNES, 1976), we presented detailed accounts of the faunas of two streams in Ontario, Canada. We now propose to use these data, together with those from 14 other temporary streams in this locality, in an attempt to build a generalized picture of the temporary stream as a habitat for freshwater organisms.

II. Physical features of the habitat

Before dealing with the faunistic elements of temporary streams, consideration should be given to those physical factors which give rise to the phenomenon of intermittent stream flow. Figure 1 shows the basic components of the runoff cycle which are important in the formation of both permanent and temporary streams. Precipitation is the most important source of water and infiltrates the soil surface if it is not intercepted by vegetation or evaporated. The rate at which infiltration occurs depends on the type of soil and its aggregation. At this stage, in some exceptionally clayey soils, water may collect on the surface in small depressions and form puddles and even small trickles. The latter are often short-lived, as they can usually be

Fig. 1. The basic components of the runoff cycle.

absorbed by soil cracks and patches of more permeable soil over which they may run. These are referred to as ephemeral streams and are only apparent after periods of high storm intensity or snow melt. Infiltrated water near the soil surface is quickly subject to direct evaporation back into the atmosphere due to air currents and uptake and subsequent transpiration by surface vegetation such as grass. If the intensity of precipitation at the soil surface is greater than the infiltration capacity of the soil, and if all the puddles have been filled, then overland flow starts. When this reaches a stream channel it becomes surface runoff. Interflow, groundwater flow and direct precipitation on the channel itself also contribute, but infiltration is perhaps the single most important factor in the regulation of intermittent stream flow, for it determines how precipitation will be split up into the categories of overland, inter- and groundwater flow.

The condition of the soil is also of great importance, as for example, a bare soil surface will be directly exposed to rain which thus will tend to compact the soil and also wash small particles into open cracks and holes. This in turn will have the effect of reducing infiltration as the rain continues and may lead to overland flow. Conversely, a dense cover of vegetation will protect the soil surface so that compaction and the filling up of cracks will be less. Further, the roots of these plants may also hold the soil open and increase the normal infiltration rates.

Taking the above factors into consideration we could speculate that a large number of temporary streams would be supported by an area of land with a clay loam soil under heavy cultivation, where many of the large stands of trees and much of the bush have been cleared, where bare soil is more common than pasture and where wire fences are preferred to earth-bank hedgerows. Had this land been left uncultivated it probably would have supported a much smaller number of permanent streams. Such an area is Waterloo County, Ontario—the site of this present study.

We have seen now what factors contribute to and influence the flow of water in a temporary stream channel, but we still have to consider what happens when this flow stops and the channel becomes part of the terrestrial environment. To do this

Fig. 2. The components of subsurface water.

we must briefly look at the different types of subsurface water. Figure 2 shows the water beneath a dry streambed to consist of four zones.

Soil water is subject to large fluctuations in amount as a response to transpiration and direct evaporation, and it is this feature which separates it from the other zones of unsaturated water.

The intermediate water zone lies beneath that of the soil water and separates it from the saturated zone. The water here is sometimes referred to as suspended water since although it can move downward in response to gravity, it can also move upwards into the soil water zone should this become very dry. This zone is variable in size, being greatest in arid regions and absent in moist areas.

The lower limit of the intermediate zone is continuous with the capillary fringe. This fringe is irregular in outline and consists of water moving up through the soil (by capillary action) from the lower parts of the capillary water zone which may be as fully saturated as the groundwater. In areas of fine-grained soils, where recharge is active, the capillary fringe may extend well into the intermediate zone.

The groundwater table (G. W. T.) separates the capillary fringe from the next water zone, the groundwater, where all the material is saturated. It can move up or down in response to recharge. When a stream is flowing, the G. W. T. will be near the level of the stream surface, and as it recedes, it will lower the level of the stream unless it is offset by sudden precipitation and consequent overland flow and interflow. If it continues to recede, the stream will cease to flow and only a few pools will remain in the channel. Further recession will result in disconnection from the pools which will soon vanish due to evaporation. If the G. W. T. remains fairly close to the ground surface, the capillary fringe may extend up to the surface of the streambed and thus provide a moist environment for those stream animals that have sought refuge by burrowing. It is in situations such as this, where the G. W. T. is close to the soil surface and soil moisture is high that a relatively small input of moisture from rain, is sufficient to produce a substantial relaxation of moisture tension within the soil pores (CARSON and SUTTON 1971). The result is that the G. W. T. may rise quickly

and cause runoff in the stream channel. It is for this reason that temporary streams are quite prone to restarting for short periods after quite small amounts of rainfall.

Any further drop in the G. W. T. will result in the setting up of the other subsurface water zones mentioned and hence subjecting any animals to the large fluctuations of water content that we have already seen are characteristic of the soil water zone. Deeper burrowing of active forms to reach the saturated zone, or the coordination of a special drought resistant stage in the life cycle will now be necessary if these animals are to survive. In some cases, it is possible that a few species may obtain sufficient moisture from the condensation of dew on the ground surface to remain in the soil water zone.

III. Discussion

In general temporary streams exhibit amplitudes in both physical and chemical parameters which are much greater than those found in most permanent streams. The animals which have chosen this type of habitat have, therefore, to be extremely tolerant of these conditions if they are to survive. The period and range of flow are undoubtedly important factors, as the current may range from torrential proportions during the spring floods to zero in the summer pools. The degree and rate of descent of the groundwater table and the permeability of the bed substrate are also important in so far as they control the formation and duration of the pool stage which invariably follows the cessation of flow. These pools allow the survival of certain species which would not normally be able to live in a lotic environment and at the same time they invite colonization from many purely lentic forms. In Canada, temperature may be extremely variable ranging from near 0 °C under the winter ice to near 30 °C in the summer pools. It is the high temperatures in these pools which encourage the rapid growth of algae and enable certain species to complete a quick generation there. In those streams with a soil substrate, quite a substantial change may occur in the aggregation of the bed particles and this in turn leads to changes in porosity, permeability etc. which may control animal burrowing abilities and soil moisture content. Emergent vegetation too, is important, as we have seen that the clearing of large areas of land has been largely responsible for the increased occurrence of temporary streams in the study locality. On a smaller scale, the terrestrial vegetation in and around the stream channel may affect the moisture retention of the substrate by controlling permeability near the surface and providing a humid canopy over the bed. Frequently, as a result of all this emergent vegetation, the organic contents of the stream substrates are quite high, thus providing a plentiful food supply for aquatic detritivores. Dissolved oxygen always appears to be near the maximum, except for mid-winter, under ice conditions and possibly near the bottom of the end of summer pools. pH is quite variable, being lowest in the stream in spring and highest in the algae-choked summer pools.

An examination of the faunas found in all the temporary streams studied revealed that they belong to three main groups. The first consists of permanent stream forms which are not particularly well adapted to life in temporary streams, but because of a wide tolerance are able to survive in short-dry period streams. The second group consists of those species which are facultative, occurring in both lotic and lentic waters. And the third group consists of those species which are highly adapted and often restricted to temporary waters.

The members of certain major taxonomic groups tend to oversummer as similar stages in their life cycles, for example, as eggs—the Ephemeroptera and most Chironomidae; as larvae, or immature stages—the Ostracoda, Cyclopoida and Amphipoda and

as adults—the Gastropoda, some Odonata, the Hemiptera and Coleoptera. A pictorial summary of where these various groups oversummer in the stream channel is presented in Fig. 3. This shows eight basic means by which the fauna can cope with the summer

Fig. 3. Summary of the oversummering methods used by the fauna of a temporary stream.

drought, ranging from survival as adults on the wing to those species which burrow into the substrate or make use of the remaining pools. It should be noted, however, that not all these methods will be open to the inhabitants of each stream as, for example, in some streams the pools may dry up completely or burrowing crayfishes may not be present.

The oversummering method used reflects the type of life cycle exhibited by a particular species. Figure 4 represents the different types of life cycle noted amongst some of the more common species found in the temporary streams sampled. It is based on each species' period of activity in the stream, together with a rough estimate of its time of maximum growth (for each graph, the abscissa represents time while rate of growth is on the ordinate). There are three types of cycles evident amongst the fall-winter stream fauna:

1) in which the eggs hatch immediately on the resumption of flow and the larvae develop quickly. Maximum size is reached just before ice cover brings cooler temperatures and the larvae remain at a low level of activity throughout the winter to emerge early in the spring, for example, *Ironoquia punctatissima*, *Trissocladius* spp., *Microsectra* sp. and *Allocapnia vivipara*.

2) in which the opposite occurs, that is, slow hatching and larval development at first followed by rapid growth as the water begins to warm up in the early spring. Most are mature before the stream stops flowing, for example, *Cyclops vernalis*, *Attheyella*

Fig. 4. Diagrammatic representation of the different types of live cycle evident amongst some of the more common animals found in Ontario temporary streams.

nordenskioldii, *Tipula cunctans*, *Cypridopsis vidua*, *Hyaella azteca* and *Agabus semi-vittatus*.

3) in which there is a more even growth rate spread over the whole period of stream flow, for example, *Fonticola velata*, *Crangonyx minor*, *C. setodactylus*, *Diplocladius* n. sp., *Orthocladius* n. sp., *Sphaerium* sp., *Trissocladius* sp. and *Arctopelopia? flavifrons*. Similarly, three types of life cycles are evident amongst the spring-pool fauna:

1) in which rapid growth occurs only at the beginning of the pool stage, for example, *Paraleptophlebia ontario*, *Anacaena limbata* and *Moina macrocopa*. This arrangement lessens the chances of these species getting "caught-short" by an early dry-up.

2) in which there is an even growth rate spread over the entire pool stage, for example, *Gerris* spp., *Helophorus orientalis*, *Hydroporus wickhami*, *Anax junius*, *Buenoa* sp. and *Tubifera* sp.

3) in which multiple cycles occur in those species capable of very fast development, for example, the mosquitoes *Aedes vexans* and *Culex pipiens*. It is quite possible that in some cases, the last generations of these species get wiped out each year as the pools finally dry out. However, mosquitoes have various special adaptations, such as staggered egg hatching, which ensure the survival of at least part of the population. Growth rates for the summer-terrestrial fauna were not studied, but it is likely that they follow the pattern of the mud-loving beetle *Heterocerus* which probably had an even growth rate throughout the summer.

Two other life cycle patterns were obvious:

1) such as shown by *Pseudosmittia* sp., *Chironomus* sp., *Micropsectra* sp. and part of the *Anax junius* population, in which growth proceeds at a steady rate throughout the year with emergence probably taking place near the end of the pool stage.

2) such as shown by the crayfish *Cambarus fodiens*, in which growth spans 2 years with peaks in development during the aquatic phases.

These variations in life cycle lead to the creation of a faunal succession as we move from the stream stage through the pool stage to the terrestrial. These successions have already been considered for Moser and Kirkland creeks and a summary of the major groups involved in the other streams is presented in Fig. 5. Note that certain major taxa are characteristic of the different phases, e. g., chironomids—stream phase, beetles—pool stage and sphaerocerid dipterans—terrestrial phase.

An interesting aspect of the species occurring in temporary streams is that two or more closely related species can frequently be found coexisting. For example, in

<i>Coelenterata</i>	<i>Cladocera</i>	<i>Lumbricidae</i>
<i>Tricladida</i>	<i>Ostracoda</i> (some)	<i>Limacidae</i>
<i>Oligochaeta</i>	<i>Ephemeroptera</i>	<i>Cochlicopidae</i>
<i>Ostracoda</i> (some)	<i>Odonata</i>	<i>Heteroceridae</i>
<i>Copepoda</i>	<i>Hemiptera</i>	<i>Staphylinidae</i>
<i>Amphipoda</i>	<i>Coleoptera</i>	<i>Scarabaeidae</i>
<i>Decapoda</i>	<i>Tipulidae</i> (some)	<i>Formicidae</i>
<i>Plecoptera</i>	<i>Culicidae</i>	<i>Sepsidae</i>
<i>Trichoptera</i>	<i>Ephydriidae</i>	<i>Sphaeroceridae</i>
<i>Tipulidae</i> (some)	<i>Syrphidae</i>	<i>Ceratopogonidae</i> (some)
<i>Simuliidae</i>	<i>Psychodidae</i>	<i>Arachnida</i>
<i>Chironomidae</i>

Moser Creek, the two amphipod crustaceans, *Crangonyx minor* and *C. setodactylus* occur together, as do two species of the chironomid genus *Trissocladius* and two species of *Leptocera*. In all these cases, the food, behaviour, time of reproduction and development appear to be very similar, suggesting niche sharing. COLE (1968) suggested two explanations for this. Firstly, because of the often plentiful supply of food available in temporary waters, potential competitors may be allowed to coexist, and secondly, because there is instability in the habitat, there is a relatively short time for selective pressures to operate.

Even though the habitat may be unstable, the species composition of the inhabitants is—so far as the most abundant taxa are concerned—very stable. Reasons for this could be that the fauna is somewhat specialized due to the exacting nature of the environment, thus successful species once established remain there as a result of their specialized adaptations; or, that the harshness of the environment prevents widespread colonization by permanent stream forms. Changes in the fauna are usually only caused by a few species which either arrive as adults and stay just to feed, or which may lay eggs that are almost certainly doomed due to the species' unsuitability to this habitat. On the whole there seems to be very little wastage of species or individuals for if we compare the faunas of a temporary and a permanent stream which are connected—thus facilitating easy faunal transfer between the two—we find little overlap.

Most of the preceding discussion points to the importance of the cyclical nature of these droughts, for just as in the case of permanent streams which suffer the odd catastrophic drought, some members of a temporary stream fauna may be killed if a stream fails to go dry 1 year or if the duration or sequence of the dry period is somehow altered substantially.

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V. Summary

The physical factors that govern the formation of temporary streams in Southern Ontario, Canada are discussed, and the importance of infiltration rate and substrate condition are emphasized.

Invertebrate data compiled from 16 temporary streams in this region showed the following:

- I. The species belong to three main groups—
 - (a) permanent stream forms with a wide range of tolerance.
 - (b) facultative species.
 - (c) specialized temporary stream forms often restricted to this type of habitat.
- II. The members of certain major taxonomic groups tend to oversummer the drought as similar stages in their life cycles, e. g. eggs, larvae or adults.
- III. The over-summering method used reflects the type of life cycle exhibited by a particular species and examples are given.
- IV. The variations in life cycle lead to faunal succession from the stream stage through the pool stage to the terrestrial.
- V. The co-existence of closely related species is common in temporary aquatic habitats.

VI. References

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