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Evolutionary and ecological strategies of animals in annual temporary pools

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With 12 figures and 3 tables in the text

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Abstract

Animals in temporary pools can be divided into four groups according to their strategy for tolerating or avoiding drought and their period of recruitment to the community. Group 1 are year-round residents incapable of active dispersal, which avoid desiccation either as resistant stages or by burrowing into pool sediments. Group 2 are spring recruits which must oviposit on water but subsequently aestivate and overwinter in the dry basin in various life history stages. Group 3 are summer recruits ovipositing in the dry basin and overwintering as eggs or larvae. Group 4 are non-wintering migrants leaving the pool before the dry phase which is spent in permanent water; they return in spring to breed. This Group concept permits distinction in the variety of ecological strategies found in temporary pool communities, providing a sound base for community analysis and prediction. Different types

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of temporary pools are distinguished by length of wet and dry phases, marginal vegetation, and basin vegetation. The past history of a pool may be deduced from an interpretation of organisms present according to the adaptive strategies of their respective Groups. Many species in the community are ecological generalists, widely distributed in a variety of aquatic habitats yet also featuring the necessary specializations for life in temporary habitats. Early colonizers are mostly detritivorous, feeding on rich detrital food resources; they also have characteristics typical of r-selected animals. Detritivores support later, predacious colonizers. Specific communities are controlled by resource levels and durational stability of pools, and by climatic conditions. The small number of taxa represented in temporary pools appear to have evolved mainly from lineages in permanent waters, very few arising directly from terrestrial ancestors.

1. Introduction

Much of the biological literature on animals in temporary pools is concerned either with pools in relatively local areas, or with species in particular taxonomic groups. Studies of both types may be rich in information, but do not provide a comprehensive viewpoint. Few studies have attempted any synthesis. Our objective in this paper is, through synthesis of existing knowledge, to elucidate the adaptive features that have enabled aquatic animals to live in temporary pools, and to consider the unique characteristics of these habitats. This synthesis has lead us to a concept of community structure for temporary pools in which four components are distinguished, according to methods of surviving the dry period and seasonal patterns of recruitment. Subdivision of aquatic habitats and hence of their faunas is more commonly undertaken in limnology on the basis of physical and chemical attributes of the water — as for example the eucrenon-potamon system for lotic water (HYNES 1970), and the categories of lake typology for lentic waters (BRINKHURST 1974). We believe, however, that a predictive classification of temporary-pool communities depends on understanding adaptations to the dry phase rather than to the wet phase because the animals occupy pool basins for very different periods of time and their survival during the dry phase is governed by different factors. Our synthesis includes a consideration of temporary-pool animals from ecological and evolutionary viewpoints.

Frequent sampling from temporary pools in southern Ontario has convinced us that the taxa comprise a relatively small, consistent, and predictable assemblage that excludes most of the species of permanent waters. Reference to literature on these temporary-pool forms disclosed in almost every case unusual features of their biology that differed from the permanent-water species, although workers in particular taxa rarely seemed to appreciate the full significance of these features with respect to the ecology of the species. Where comparative data are available for related species, it is clear that adaptations to drought are several, that they usually originate in species confined to permanent waters, and are coincident only in species able to live in temporary waters. In most major taxa, the adaptive features are confined to certain families, genera, sub-genera, or other taxonomically restricted and presumably monophyletic sets. Thus, the evolutionary route to temporary pools is often a well-marked series of derivative specializations, although species of primitive lineages in a few taxa appear to have arisen initially in temporary pools. Reference to the literature (general papers such as BARCLAY 1966; BEVERCOMBE et al. 1973; BISHOP 1974; KENK 1949; KREUZER 1940; MARPLES 1960; MORIYA 1959; MOZLEY 1932; RUTTNER-KOLISKO 1966; RZOSKA 1961; STOUT 1964; and others cited under particular taxa) indicates that although our concepts were developed from studies in southern Ontario, they apply generally through temperate latitudes of northern and southern hemispheres with appropriate addition or substitution of taxa.

Species in freshwater invertebrate groups are frequently characterized in the literature as living in temporary or vernal pools or semipermanent waters, but the degree of precision attached to these terms is rarely indicated. In its typical form, a temporary pool is an accumulation of surface water in an isolated basin that at no time during the year has either an inlet or an outlet; water is entirely absent from the surface for part of the year. Such a pool could not receive by way of surface water connection any animal inhabitants from an adjacent stream or pond. All of the pools sampled in this study were of this type.

However, isolated pools are often encountered which could have had some connection with a permanent stream, lake, or pond as a result of high waters of spring run-off. Sites of this type may have a fauna that resembles that of temporary pools but may also include species introduced by surface connection from permanent waters. Marshes adjacent to lakes, flood plain pools beside rivers, and isolated pools of intermittent streams are examples of these qualified temporary pools.

Typical temporary pools are of two types in temperate latitudes (Fig. 1). In southern Ontario, for example, basins fill in April from melting snow and rain. Water levels decline as summer approaches and pools are without surface water by late June or early July, remaining dry until the following spring; they have an annual cycle of 3 to 4 months wet phase and 8 to 9 months dry phase. Pools of this type are designated temporary vernal pools (WIGGINS 1973), since surface water terminating the dry period is replenished in spring. In less permeable soils or in years of heavy rainfall some pool basins retain surface water in autumn, and thus have a wet phase of approximately 9 months and a dry phase of 3 months. Pools of this type are designated temporary autumnal pools (WIGGINS 1973) because the drought is terminated in autumn. It is important to note that the term autumnal is applied to such a pool throughout one wet phase, i.e. including the spring period too. Whether the aquatic fauna of a pool is without surface water for approximately 8 months or 3 months is an important biological factor that should not be disregarded. For example, animals in vernal pools overwinter in a basin that is largely dry, but those in the central basin of autumnal pools overwinter under water (see also under Limnology). In almost all of the biological literature pertaining to temporary pools or their faunas in temperate latitudes, explicit distinction is not made between these two types of pools, and a reader is left to discern the type involved from whatever data are given on water levels.

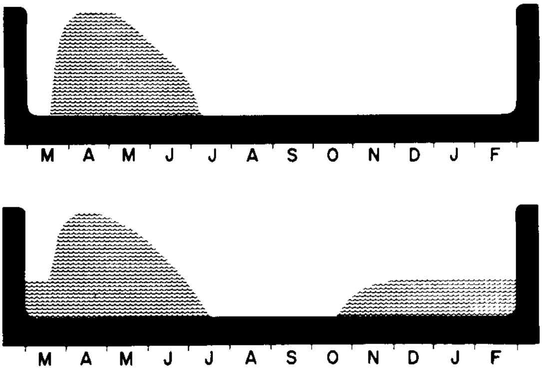

Fig. 1. Distinction between temporary vernal pool (upper figure) and temporary autumnal pool (lower figure); letters designate months, vertical scale indicates depth of water.

In two successive years with marked differences in rainfall, it is not unusual for the same basin to be a vernal pool one year and an autumnal pool the other; and in a year of particularly heavy rainfall, a permanent pool may succeed a temporary pool. Designation of a pool as temporary should not be based on the assumption that duration of surface water was the same for the preceding year as for a current year; precision in pool designations is possible only with data on the length of the dry period through the preceding summer and autumn. All pool designations in this study are based on that information. However, having established the composition of invertebrate communities in pools known to be temporary for specific periods, we find that analysis of community structure can reveal the duration of surface water in a pool basin for the preceding year (see under Limnology).

The base-line for a synthesis such as this is a list of species reproducing in pools known to be temporary. Because there are rather few records meeting these requirements in the biological literature, we have devoted much of this study to developing such a list from collections in the field. Interpretation of these field data has required recourse to detailed observations on particular taxa by many other workers. Thus, this paper is necessarily an amalgam of original data and literature review.

A distinction important in theory but difficult to apply in practice is that between animals which reproduce successfully in temporary pools and those present in them at any given time. Although presence of young stages of a species in a temporary pool demonstrates that the species breeds there, the young may not in fact reach adulthood because of high water temperatures or disappearance of surface water. Evidence of at least partially unsuccessful reproduction is presented in this paper for some groups (e.g. Nepidae and Belostomatidae, Group 4 Hemiptera); but in general we assume that a species present either as adult or larva is adapted to the conditions of at least some temporary pools.

2. Methods

2.1 Field collections

Collections and observations from many temporary pools in southern Ontario made from 1960 to 1977 have been analyzed. The main data base for this study is derived from intensive sampling of temporary pool communities in the Kendal area (see below) between 1972 and 1977; data from other pools are introduced where relevant. Small invertebrates such as rotifers and hydroids were not collected.

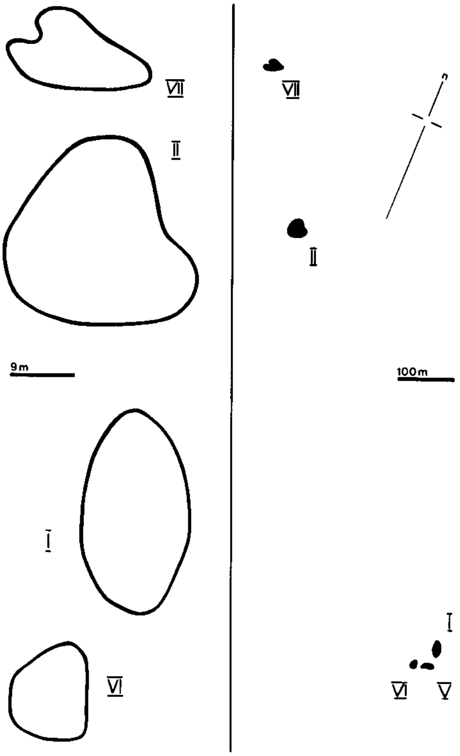

Fig. 2. Size and position of Kendal pools.

Tab. 1. Summary of surface water conditions and collections in Kendal pools, 1972—77 (dry denotes no surface water; wet, surface water present; √ denotes collection of animals made from pool; * denotes sample of soil and surface litter from dry basin; perm. = permanent pool; temp. vern. = temporary vernal pool; temp. aut. = temporary autumnal pool).

Kendal Pools	I	II	VI	VII
	perm. 1972—73 temp. aut. 1973—74	temp. vern.	perm. 1972—73 temp. aut. 1973—74	perm.
1972				
May 21	√			
May 28		√		
June 9	√	√	wet	
June 19	√	√	wet	
July 2	√	√	wet	
July 31	√	dry	wet	
Sept. 1	√	dry	√	
Oct. 8	wet	dry	wet	
Nov. 19	wet, ice cover	dry	wet, ice cover	
1973				
April 18	√	√	√	√
May 15	√	√	√	√
June 12	√	√	√	√
July 4	√	√	√	
July 17	√	dry	√	
July 29	wet	dry	√	
Aug. 21	wet	dry	√	
Sept. 9	dry	dry	dry	
Nov. 8	wet	dry	wet	
Nov. 13	√	dry	√	
Dec. 16	wet, ice cover	dry	wet, ice cover	
1974				
Jan. 8	√	dry	√	
Feb. 8		dry*		
Feb. 21		dry*		
April 5		√		
April 13	√	√		
April 15		√		
April 20	√	√	√	√
April 24		√		
May 1	√	√	√	√
May 11	√	√		
May 23		√		
June 4	√	√	√	√
July 2	√	√	√	√
Oct. 27		dry*		
Dec. 18		dry*		
1975				
Feb. 20		dry*		
1977				
Oct. 28		dry*		
Nov. 2	√	dry*	√	

Kendal pools

These pools (Fig. 2) are approximately 100 km east of Toronto in rolling country of the Oak Ridges glacial moraine, 10 km north-east of Kendal (N 44° 05′ × W 78° 31′, Durham Co.). Table 1 summarizes collections made in the Kendal pools and observations on presence and absence of surface water.

Fig. 3. Kendal pool II, wet phase.

Fig. 4. Kendal pool II, dry phase.

Kendal pool II (K II) (Figs. 3, 4) was consistently a temporary vernal pool (Table 1). At its maximum size in April K II was approximately 30 m in diameter with a maximum depth of 60 cm. Emergent semiaquatic vegetation was sparse, but as the pool began to recede herbaceous plants such as *Agrostis stolonifera*, *Alopecurus aequalis*, *Penthorum sedoides*,

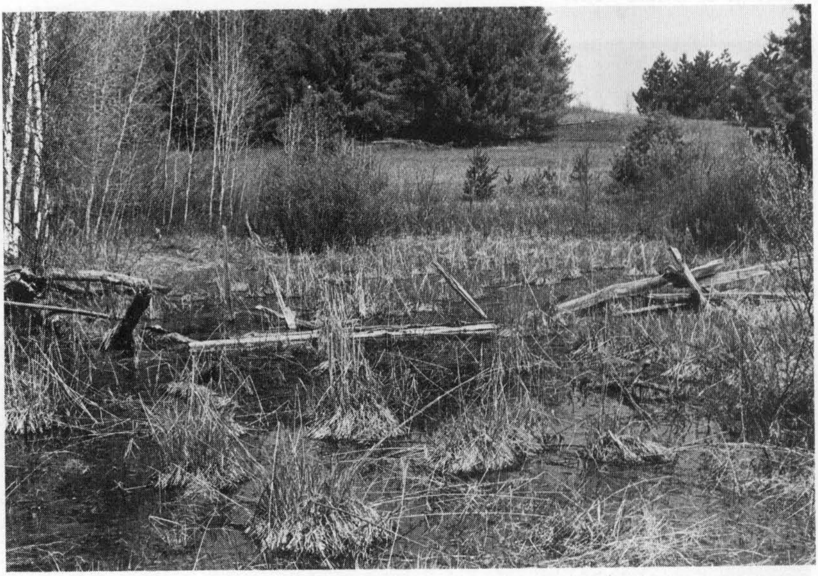

Fig. 5. Kendal pool I, wet phase.

Fig. 6. Kendal pool VI, wet phase.

Onoclea sensibilis and *Thelypteris palustris* appeared and extended during the summer to cover the entire basin with a heavy growth. Situated at the edge of a woodlot, the pool was shaded by large trees and received a heavy fall of leaves in autumn; dead branches and bark, mainly *Ulmus americana,* also littered the basin. Pasturing cattle had access to the pool. Data for K II on Trichoptera (WIGGINS 1973) and on detrital processing (BÄRLOCHER, MACKAY & WIGGINS 1978) have been published previously.

Kendal pools I and VI (K I, K VI) are 30 m apart, the two approximately 760 m distant from K II over mainly open pasture (Fig. 2). Both pools are relatively unshaded but lie partially within a stand of sapling birch *(Betula papyrifera)* and aspen *(Populus tremuloides).* K I (Fig. 5) is an ovoid pool of maximum dimensions approximately 30 × 16 m, and 75 cm in depth; K VI (Fig. 6) is a circular pool of maximum diameter 13 m and depth 150 cm. K I supports a heavy growth of *Scirpus* sp. in dense tussocks together with *Sium suave,* K VI has little vegetation; both have large amounts of dead branches and bark of *Ulmus americana.* Although K I and VI had been temporary vernal pools in some years before the study period, both held surface water from the spring of 1972 through August of 1973 (Table 1). Both pools were dry from early September until early November 1973, when surface water was again present (Table 1). Thus until July 1973 the pools were permanent whereas in 1974 they were temporary autumnal. Kendal V is a temporary pool between K I and VI, but is not treated in this paper.

Kendal pond VII is consistently permanent. The pond lies 280 m north-west of K II (Fig. 2) and is heavily shaded by trees; it is irregular in shape with maximum dimensions 12 × 22 m, and a maximum depth of 150 cm.

The four bodies of water at Kendal (Fig. 2) provide conditions of a natural experiment in temporary-pool colonization and community structure. K II is consistently temporary vernal, K I and VI fluctuated between permanent and temporary autumnal during the study period, and K VII is permanent.

Sampling was done with a D-frame net, mesh size approximately 1 mm in 1972 and 1973, 0.5 mm in 1974. Sampling methods were entirely qualitative with the objective to obtain specimens of every stage of all species present at one time. Net samples were washed and examined in white enamel pans (50 × 30 × 5 cm). Walking traverses with the net were made through vegetation; submerged and floating logs and bark were inspected. On each visit (Table 1) we sampled the pools in this way for 1 to 2 hours.

Four sets of 20 samples of soil and surface litter were taken from different areas of the dry basin of Kendal pool II on 27 October 1974, 18 December 1974, 20 February 1975, and 28 October 1977 (Table 1). Each sample, consisting of a volume of turf approximately 15 × 15 × 3 cm, was placed in a white plastic basin (32 × 27 × 10 cm), flooded with dechlorinated tap water and held at 10°C in the laboratory under a daily light regime of LD 10:14 hrs. A composite sample of living and dead plant material was taken from a variety of sites in the pool basin on 2 November 1977, flooded with distilled water in 6 plastic basins and held at 13°C and LD 15:9 hrs. Samples taken in 1974—75 were inspected at weekly intervals for the first month, thereafter at monthly intervals, and the 1977 samples were inspected weekly. Specimens were removed and preserved when first found, or noted and allowed to develop until a later date.

Other pools

Many pools were sampled (by I.M.S. & G.B.W.) during this study and records of species from specific locations are introduced into the presentation of data where useful. Temporary vernal pools include Milton I (N 43° 31′ × W 79° 53′, Halton Co.); Britannia I and IV (N 43° 38′ × W 79° 41′, Peel Co.); Port Credit II (N 43° 33′ × W 79° 35′, Peel Co.); and

Vandorf I (N 44° 00′ × W 79° 24′, York Co.). Temporary autumnal pools include Aberfoyle IX (N 43° 28′ × W 80° 09′, Wellington Co.), Aurora VII (N 43° 58′ × W 79° 35′, York Co.) and Chaffeys Locks I (N 44° 35′ × W 76° 19′, Leeds Co.).

2.2 Presentation of information

We have summarized the results of our field work to provide data on the species collected including the date or season when particular life history stages were observed; larval instars are designated as LI, LII, etc. For each major taxon, our own data from intensive study of vernal pool Kendal II are followed by relevant information from the literature, including data on species that did not appear in our collections but which were recorded elsewhere from temporary pools. These extensive references to the literature bring together many previously scattered details on the biology of temporary pool animals and thus provide maximum raw material for our ecological and evolutionary interpretations.

Tab. 2. Life-history strategies of animals in annual temporary pools. (Provisional list of genera represented in temporary pools in north-eastern North America; * denotes occurrence in vernal pool Kendal II; numbers refer to section heading in text.)

3.1 Group 1. Overwintering residents. Capable of passive dispersal only, these animals aestivate and overwinter in the dry basin of the pool either as drought-resistant cysts and eggs or as juveniles and adults.

- 3.1.1 Turbellaria
    - Planariidae: _Hymanella, Phagocata_* (Tricladida)
    - Dalyelliidae: _Dalyellia_* (Rhabdocoela)
- 3.1.2 Oligochaeta
    - Lumbricidae: _Eiseniella_*
    - Lumbriculidae: _Lumbriculus_*
    - Aeolosomatidae: _Aeolosoma_
    - Naididae: _Dero, Nais, Slavinia_
    - Enchytraeidae*
- 3.1.3 Hirudinoidea
    - Glossiphoniidae: _Batracobdella_*, _Helobdella_*
- 3.1.4 Bryozoa
    - Plumatellidae: _Fredericella_
- 3.1.5 Anostraca*
- 3.1.6 Conchostraca
- 3.1.7 Cladocera
    - Daphniidae: _Ceriodaphnia, Daphnia_*, _Scapholeberis_*, _Simocephalus_*
    - Chydoridae: _Alona, Chydorus_
    - Moinidae: _Moina_
- 3.1.8 Copepoda
    - Cyclopidae: _Cyclops_* (Cyclopoida)
    - Canthocamptidae: _Attheyella, Bryocamptus_*, _Canthocamptus_*, (Harpacticoida)
    - Diaptomidae: _Diaptomus_ (Calanoida)

- 3.1.9 Ostracoda
  - Candonidae: _Candona_*
  - Cyclocyprididae: _Cyclocypris_*
  - Cyprididae: _Cypricercus_*, _Cypridopsis_*, _Cypris_*, _Eucypris_
  - Notodromadidae: _Cyprois_*
- 3.1.10 Decapoda
  - Astacidae: _Cambarus_
- 3.1.11 Amphipoda
  - Gammaridae: _Crangonyx_
  - Talitridae: _Hyalella_*
- 3.1.12 Isopoda
  - Asellidae: _Asellus_
- 3.1.13 Mollusca
  - Gastropoda
    - Lymnaeidae: _Lymnaea_*
    - Physidae: _Aplexa_*, _Physa_
    - Planorbidae: _Gyraulus_*, _Helisoma_, _Planorbula_, _Promenetus_
  - Pelecypoda
    - Sphaeriidae: _Musculium_, _Sphaerium_*

3.2 Group 2. Overwintering spring recruits. Because oviposition is dependent on water, these animals must reproduce in the pool in spring before surface water disappears; they aestivate and overwinter in the dry pool basin mainly as eggs or larvae, as adults in only a few species of beetles.

- 3.2.1 Ephemeroptera
  - Siphlonuridae: _Siphlonurus_
  - Leptophlebiidae: _Leptophlebia_, _Paraleptophlebia_*
- 3.2.2 Coleoptera
  - Dytiscidae: _Agabus_*, _Hydroporus_*, _Rhantus_*
  - Haliplidae: _Haliplus_*, _Peltodytes_*
  - Hydrophilidae: _Anacaena_*, _Helophorus_*, _Hydrobius_*
  - Helodidae: _Cyphon_*
- 3.2.3 Trichoptera
  - Polycentropodidae: _Polycentropus_*
- 3.2.4 Diptera
  - Chironomidae
    - Chironominae: _Endochironomus_*, _Chironomus_*, _Glyptotendipes_*, _Parachironomus_*, _Paratanytarsus_*, _Polypedilum_*, _Tanytarsus_*
    - Orthocladiinae: _Acricotopus_*, _Cricotopus_*, _Eukiefferiella_*, _Hydrobaenus_*, _Psectrocladius_*
    - Diamesinae: _Prodiamesa_*
    - Tanypodinae: _Guttipelopia_*
  - Ceratopogonidae: _Alluaudomyia_*, _Bezzia_*, _Palpomyia_*, _Atrichopogon_*
  - Tabanidae: _Tabanus_*
  - Stratiomyidae: _Odontomyia_*
- 3.2.5 Acari
  - Hydryphantidae: _Hydryphantes_* (parasites of Diptera (Ephydridae), deutonymph and adult resistant); _Euthyas_, _Thyas_*, _Thyasides_, _Thyopsis_, _Zschokkea_ (parasites of Diptera (Nematocera), adult resistant)
  - Arrenuridae: _A. (Arrenurus)_* (parasites of Odonata, nymphochrysalis resistant); _Arrenurus (Truncaturus)_ (parasites of Culicidae, deutonymph and adult resistant)

Pionidae: _Piona_*, _Tiphys_*, (parasites of Chironomidae, deutonymph resistant)

3.3 Group 3. Overwintering summer recruits. With oviposition independent of water, these animals can enter the pool basin after surface water disappears; they overwinter mainly in the egg stage or as larvae in the egg matrix.

3.3.1 Odonata
Lestidae: _Lestes_* (Zygoptera)
Libellulidae: _Sympetrum_* (Anisoptera)

3.3.2 Trichoptera
Limnephilidae: _Anabolia_*, _Limnephilus_* (Limnephilinae); _Ironoquia_* (Dicosmoecinae)
Phryganeidae: _Ptilostomis_*

3.3.3 Diptera
Chironomidae: _Limnophyes_*, _Paraphaenocladius_*, _Smittia_*
Culicidae: _Aedes_*, _Culiseta, Psorophora_
Chaoboridae: _Chaoborus, Mochlonyx_*
Sciomyzidae*: _Antichaeta, Atrichomelina, Dictya, Hedria, Pherbellia, Renocera, Sepedon_*, _Tetanocera_*

3.4 Group 4. Non-wintering spring migrants. With oviposition dependent on water, these animals enter temporary pools in spring; adults of the subsequent generation(s) leave the pool before its dry phase, overwintering mainly in permanent water.

3.4.1 Ephemeroptera
Baetidae: _Callibaetis_*

3.4.2 Odonata
Aeshnidae: _Anax_ (?), _Pantala_ (?), _Tramea_ (?)

3.4.3 Hemiptera
Corixidae: _Callicorixa_*, _Hesperocorixa_*, _Sigara_*
Notonectidae: _Notonecta_*
Belostomatidae: _Belostoma_*, _Lethocerus_*
Pleidae: _Plea_
Nepidae: _Ranatra_*
Gerridae: _Gerris_*
Hydrometridae: _Hydrometra_
Mesoveliidae: _Mesovelia_
Saldidae: _Saldula_
Veliidae: _Microvelia_

3.4.4 Coleoptera
Dytiscidae: _Acilius_*, _Colymbetes, Dytiscus_*, _Graphoderus_*, _Hydaticus_*, _Laccophilus_*, _Rhantus_*
Gyrinidae: _Dineutus_*, _Gyrinus_*
Hydrophilidae: _Cymbiodyta_*, _Enochrus_*, _Hydrochara_*, _Tropisternus_*

3.4.5 Diptera
Chironomidae (Tanypodinae): _Ablabesmyia_*, _Procladius_*, _Psectrotanypus_*
Chaoboridae: _Chaoborus_*

3.4.6 Acari
Eylaidae: _Eylais_*
Hydrachnidae: _Hydrachna_*
} parasites of Group 4 Hemiptera and Coleoptera

3.4.7 Amphibia
Ranidae: _Hyla, Pseudacris, Rana_*
Ambystomidae: _Ambystoma_*

3. Data and interpretation

Successful inhabitants of temporary pools must synchronize their life histories with the annual cycle of the pool. We recognize four ways in which this synchrony is achieved and accordingly we differentiate four major Groups of species on the basis of adaptations to the dry phase, periods of occurrence in the pool basin, and periods of recruitment to the population. Genera represented by one or more species in temporary pools in north-eastern North America are listed in Table 2, with an asterisk denoting genera we collected from vernal pool Kendal II. Although major taxa are represented in more than one group, single species and most individual genera appear to be confined to one group.

In this section of the paper we define each group and summarize characteristics of component species under the headings of major taxa within the group. Most of the data concern species of temperate latitudes in the northern hemisphere but occasional references to tropical or southern hemisphere species are also included. Following analysis of the four groups we discuss general limnological, ecological and evolutionary aspects of temporary pools and their communities.

3.1 Group 1. Overwintering residents

These animals are permanent residents, aestivating and overwintering in the dry basin of the pool. There are two general types of resistance to drought (Fig. 7). In flatworms, bryozoans, and most crustaceans resistant eggs or cysts are formed and lie more or less exposed on the dry pool basin. Among taxa that do not have resistant eggs, juveniles or adults find protection in bottom sediments: oligochaetes and leeches secrete a protective coat of mucus; at least some of the snails form a mucoid epiphragm over the shell aperture; and others simply burrow into the substrate although crayfish burrows extend to the underlying water table, thereby providing refugia for some other invertebrates that otherwise would be unable to survive an extended dry phase. Both types of drought-resistance may occur among ostracods, copepods, and oligochaetes.

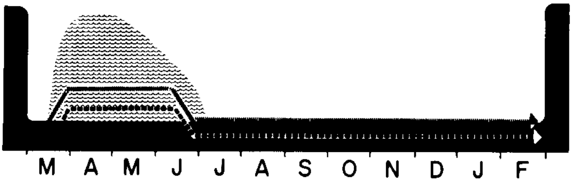

Fig. 7. Group 1 cycle; hatched line represents exposed resistant stages, dashed line represents burrowers.

Although these animals are capable of passive dispersal only, their introduction into isolated basins of temporary pools is evidently less of a problem than would be suspected because most of them are widespread in these sites. Resistant eggs or cysts are well suited for dispersal to pool basins by wind, and in the digestive tracts of birds (PROCTOR et al. 1967). Animals lacking these disseminules are more likely to be introduced by birds during the wet phase of the pool.

3.1.1 Turbellaria

Among Tricladida, the planarian *Phagocata velata* STRINGER occurred in April collections from vernal pool Kendal II, and became active 5—10 days after October, December, and February soil samples from the dry basin were flooded in the laboratory.

In April and May individuals of *Phagocata* spp. fragment into several pieces, each piece secreting a layer of slime which hardens to become a spherical cyst resistant to desiccation (KENK 1949; BALL & GOURBAULT 1975). Fragmentation is induced by high temperatures (CASTLE 1928), and is brought about by warming of the receding pool in spring. A young worm develops inside each cyst, hatches soon after water returns, and grows rapidly (KENK 1949). Evidently these cysts can overwinter in the dry basin of a vernal pool. *P. velata* is common in vernal pools of eastern North America (KENK 1944, 1949), and *P. fawcetti* was described from intermittent streams in California (BALL & GOURBAULT 1975). Whole animals of the European *P. vitta* (DUGÈS) are reported to enclose themselves in slime capsules when subjected to unfavourable conditions and there is no fragmentation (KENK 1949).

The only other eastern North American planarian characteristic of temporary waters is *Hymanella retenuova* CASTLE (BALL & GOURBAULT 1975) which is unique among planarians in having a thick-shelled resting egg cocoon that is exposed only after rupture of the body of the parent (BALL et al. in press). The cocoon lies dormant until flooded when young worms emerge. Attempts by CASTLE (1941) to induce hatching by flooding in the laboratory were unsuccessful; perhaps this is an example of diapause regulated to coincide with the seasonal cycle of the habitat. KENK's (1949) record of *Phagocata vernalis* KENK from autumnal pools in Michigan really pertains to *H. retenuova* (BALL et al. in press).

Multiple fission and encystment are rare phenomena among freshwater triclads (BALL et al. in press). That the unusual processes of reproduction by encystment and resting egg cocoon are correlated with existence in temporary pools is a clear demonstration of how evolutionary modification in two closely related advanced planarian genera has opened a transitory habitat to a rather unlikely group of colonizing animals.

A rhabdocoele turbellarian (*Dalyellia viridis* (SHAW)?, see KENK 1949), bright green because of symbiotic green algae, was common in Kendal II collections in early spring; but in the October, December, and February soil samples this species did not appear until 25—40 days after flooding, indicating that factors in addition to flooding control hatching. According to KENK (1949) rhabdocoeles of temporary pools pass the dry period as resistant eggs, and he found *Dalyellia* sp. (nr. *viridis*) only in the spring in autumnal pools in Michigan. In temporary waters in Britain Cox & Young (1974) noted that the interval between termination of drought and hatching in *D. viridis* varied from year to year, also suggesting that flooding is not the only factor inducing hatching. An obligate diapause was found in eggs of the British species *Phaenocora typhlops* (Vejdovsky) (Young 1974).

3.1.2 Oligochaeta

Three families of oligochaete annelids were represented in collections from vernal pool Kendal II: Lumbricidae, *Eiseniella tetraedra* (Savigny) (9 June 1972); Lumbriculidae, *Lumbriculus variegatus* (Müller) (4 June 1974); and Enchytraeidae (sp. undetermined, Oct., Feb. and Dec. soil samples).

Most lumbricids are exclusively terrestrial but *Eiseniella tetraedra* is a species of aquatic and sub-aquatic habitats, remaining active all year under constantly wet conditions (Reynolds 1977). Aestivation, presumably induced by drying of the soil in sites such as temporary-pool basins, occurs in a small mucus-lined cavity where the worm is tightly coiled and immobile; hibernation habits are not known (Reynolds 1977). *E. tetraedra* is a Palaearctic species now widely distributed around the world, and having obligate parthenogenesis (Reynolds 1977). These features are consistent with its role as a colonizer of isolated pools and attest to its wide ecological tolerance.

In the strictly aquatic family Lumbriculidae, *Lumbriculus variegatus* is a cosmopolitan eurytopic species of permanent and transient waters (Brinkhurst & Jamieson 1971), recorded from temporary pools in Michigan (Kenk 1949), Britain (Bevercombe et al. 1973), and elsewhere in Europe (Mrázek 1913). *L. variegatus* is reported to reproduce by fragmentation after encystment by Stephenson (1922) who found up to 16 fragments within a single cyst on the shores of lakes in Scotland, although the possibility exists that these observations really pertain to another lumbriculid *Lamprodrilus mrázeki* Hrabě (see Cook 1971), and that *Lumbriculus variegatus* is capable only of drought resistance as an adult within a cyst (Cook 1969). Sexual activity has been observed only rarely in this species (Cook 1969; Kenk 1949). *Lamprodrilus mrázeki* is known in temporary pools in Europe where fragmentation occurs within drought-resistant cysts (Cook 1971; Hrabě 1929, 1937). Although most sexually-reproducing lumbriculids have a 2-year life cycle (D. G. Cook pers. comm.), fragmentation would enable a species to reproduce annually, an asset in colonization of isolated transient waters.

In the strictly aquatic family Aeolosomatidae, two species of *Aeolosoma* were recovered from soil samples taken in autumn from dry basins of temporary pools in Michigan (Kenk 1949). Worms of this genus survive unfavourable conditions of low temperatures, and presumably drought, tightly coiled within a hardened coat of mucus (Pennak 1953).

Species in several genera *(Nais, Dero, Slavinia)* of Naididae, also a strictly aquatic family, were recovered by KENK (1949) in flooded soil samples from dry basins of temporary pools in Michigan. Naididae were seldom collected in winter but mostly in spring, suggesting that they may remain dormant in autumnal pools, subject to some stimulus other than flooding.

Enchytraeids collected in the soil samples but not in net samples from vernal pool Kendal II indicate that these worms remain permanently in the soil. Some species are amphibious, others mainly terrestrial (PENNAK 1953).

Tubificidae were encountered only rarely in the Michigan temporary pools studied by KENK (1949). Species of this family appear to be largely confined to lakes and other permanent habitats (D. G. COOK pers. comm.), and little is known about drought resistant mechanisms if in fact they exist.

3.1.3 Hirudinoidea

Leeches collected in temporary vernal Kendal II were: *Batracobdella picta* (VERRILL) (18 April 1973), and *Helobdella stagnalis* (L.) (15 May, 12 June 1973). These are assigned tentatively to the vernal pool fauna because overwintering in the dry basin of a temporary pool at this latitude has not been demonstrated unequivocally (R.W. DAVIES in litt.). Since some leeches are able to withstand dry conditions for several months by burrowing into the moist substrate and secreting a protective mucous layer (KENK 1949; PENNAK 1953), resident populations would be sustained at least in temporary autumnal pools; leeches in the 1974 collections from autumnal pools K I (*B. picta, H. stagnalis,* and *Erpobdella punctata* (LEIDY)), and K VI *(H. stagnalis)* are therefore not unexpected. It is not known whether, by this means, *B. picta* and *H. stagnalis* in vernal K II could pass an 8-month period without surface water. Collections from K II in 1973 included adults with young for each species; but in 1974 no leeches were collected from K II, even though more than twice as many collections were made, and no leeches emerged from flooded K II soil samples in 1974—75 and 1977. These restricted occurrences raise the possibility that from time to time these leeches are introduced into vernal pools in the spring. Transport by aquatic birds seems possible as the Kendal pools are close together and ducks are seen frequently on them. On the other hand, MOZLEY's (1932) reference to *Helobdella triserialis* BLANCHARD (as *Glossiphonia fusca)* as common in a vernal pool in Manitoba suggests that unless introductions were much more frequent there, this species may indeed be tolerant of overwintering in a dry pool basin.

From all other vernal pools sampled, leeches were recorded only from Britannia IV (*Erpobdella punctata,* 17 April 1972). This pool is, however, the only one in our series supporting burrowing crayfish *(Cambarus fodiens)* whose burrows are known to be sanctuaries for other aquatic invertebrates in temporary pools

(Creaser 1931). Kenk (1949) recorded "a rather rich and diversified leech fauna" from an autumnal pool in Michigan.

Feeding habits of these leeches (Mann 1962) show that they are well suited to the prey available in temporary pools. Both *Helobdella* and *Batracobdella* are fluid-feeding genera; molluscs, insects, crustaceans and worms are the principal prey of the former, amphibians and molluscs of the latter. Species of *Erpobdella* are predacious on a wide range of aquatic invertebrates.

3.1.4 Bryozoa

No bryozoans were found in vernal pool K II, but *Fredericella* sp. was common in K I and VI when these were autumnal pools. Mozley (1932) recorded *Fredericella sultana* (Blumenbach) from a vernal pool in Manitoba.

Bryozoa can reproduce asexually by statoblasts — chitin-covered disc-shaped capsules containing germinal tissue which are highly resistant to drying, cold, and other adverse environmental conditions (Pennak 1953; Rogick 1959). Germination occurs after a dormant period, when conditions again are favourable. Bryozoa would therefore seem to be well equipped to colonize transient habitats, yet they have rarely been recorded from temporary pools. The degree of desiccation which can be tolerated must be somewhat limited, and indeed, experimental evidence (Rogick 1940) shows that the viability of statoblasts stored dry at room temperature varies greatly from genus to genus; *Fredericella* is one of the genera most resistant to drying, surpassed only by *Lophopodella,* a genus of stagnant water with low oxygen concentrations (Pennak 1953). Barclay (1966) recorded *Plumatella* sp. from a temporary pool in New Zealand but during the 6-month dry period, dense vegetation ensured that the soil was always damp. Absence of other records for temporary pools in North America indicates that only *Fredericella* can withstand extreme conditions and also grow quickly enough in the short wet phase to form statoblasts before the next dry period.

3.1.5 Anostraca

Anostraca or fairy shrimp are one of the few major groups of animals that is entirely confined to transient waters. All three Kendal pools support populations of *Chirocephalopsis bundyi* Forbes which showed similar development even though KI and VI were permanent pools in 1973. Partially grown fairy shrimp were already active when the first collections were made in mid-April, and none were collected after mid-May. The resting eggs of Anostraca are well known to be resistant to drought and to remain viable for many years (Hartland-Rowe 1972); but since fairy shrimp rarely appear when pools are flooded in autumn, embryonic development must be timed for hatching in spring.

Work by Broch (1965) on *C. bundyi* in an autumnal pool in New York reveals that a complex set of environmental factors synchronizes development of eggs with the entire cycle of seasonal events characterizing temporary pools. The summer phase of embryonic development requires high temperatures, some soil moisture and aerobic conditions (i.e. exposure to high oxygen levels in air or in shallow receding water), and is inhibited by desiccation and low oxygen levels. Only when the summer phase is complete can the autumn phase of development proceed, depending on low temperatures, humidity in basin litter, and aerobic conditions. Completion of the autumn phase (by January) leads to the fully-formed metanauplius within the blastoderm cuticle alone. During the winter phase from January to spring thaw the unhatched metanauplius is in a dormant state. Hatching, which in the spring phase quickly follows the first appearance of free water, is a response to lowered oxygen tension surrounding the egg; reduction in oxygen level at the soil-water interface results from flooding decaying organic matter. Reviewing literature on development of other anostracan species, BROCH (1965) believes that the controlling factors are similar to those operating in *C. bundyi.*

BROCH'S (1965) findings show how completely dependent the development of fairy shrimp eggs is on fluctuating water levels of temporary pools. Development of the eggs depends not on desiccation or freezing, but on exposure to the high oxygen levels of ambient air. Thus embryogenesis of eggs remaining submerged in the deepest part of the basin of a pool was inhibited because of anaerobic conditions during summer; however, as the water level recedes, the oxygen level in very shallow parts may be sufficient for summer development. The autumn phase of development was inhibited in eggs lying in flooded parts of the basin, and the oxygen deficiency was exacerbated when ice formed over the flooded section. Therefore, if they are to complete the development required for hatching in spring, eggs must lie above the highest level of the pool during late November and December; but the following year's population will be derived only from the portion of that area inundated by the spring level of the pool. Thus, on a unit area basis we infer that vernal pools would be more productive of fairy shrimp than autumnal pools where anaerobic conditions resulting from early flooding would inhibit embryogenesis. The possibility may also exist that although all eggs in the basin of a vernal pool develop during the dry phase and must hatch in the spring or perish if spring levels do not reach the level of the previous year, eggs inundated in the central basin of an autumnal pool in which initial development is inhibited may form a reserve for a year of low precipitation.

Hatching shortly after the pool forms in spring requires that the metanauplius be ready to hatch after completion of the aerobic autumn phase of development, requiring only a rise in the level of the pool (BROCH 1965). This was confirmed when soil samples from Kendal II were flooded in the laboratory. October samples yielded no metanauplii, but many arose from December and February samples. At the intermediate latitudes of eastern North America, this strategy leaves open the peril of hatching in December recorded by DEXTER & KUEHNLE (1951) in Ohio, Kenk (1949) in Michigan, and Shelford (1913) in Illinois; these December individuals did not reach maturity.

As filter feeders on fine organic particles (Hartland-Rowe 1972), fairy shrimp find abundant food in temporary pools, and benefit from the absence of fish predators to which they would be excessively vulnerable. To further reduce predation, fairy shrimp appear early in the pool, completing their entire development in a short period before predacious insects, mainly migrant Coleoptera and Hemiptera of Group 4, reach their maximum density; therefore their effective predators are largely restricted to the overwintering Dytiscidae of Group 2 with which they evidently contend successfully for most *E. bundyi* are reported to live their normal life span and to suffer little from predation (Hartland-Rowe 1972). From a temporary vernal pool in Manitoba, Mozley (1932) reported however, that Anostraca were preyed upon by beetle larvae, although no estimate of net impact was given.

Environmental controls of the type elucidated by Broch (1965) are appropriate for temporary pools with the rich allochthonous organic resources of eastern North America. Hartland-Rowe (1972) points out, however, that controls are probably different in pools of more arid areas where soil moisture is very low, there is little organic material to retain surface humidity, and dissolved mineral content is often high. He cites mechanisms regulating development in *Branchinecta* in Mohave Desert pools that are controlled by changes in salinity and oxygen tension (Brown & Carpelan 1971) as an example.

Anostraca now extant are entirely resident in inland waters that either dry up or freeze solid at some time during the year (Hutchinson 1967); a number of species occur in highly mineralized waters of temporarily filled but closed basins of semi-arid regions. Tiegs & Manton (1958) uphold the view that the Branchiopoda (Anostraca, Conchostraca, and Notostraca) embody more of the hypothetical ancestral characters of the Crustacea than does any other group.

3.1.6 Conchostraca

Although no conchostracans were collected in the Kendal pools, *Lynceus brachyurus* Müller was taken in temporary vernal Vandorf I (3 June, 14 July 1960).

Conchostracan eggs are highly drought-resistant (Bishop 1967) and can remain viable for at least 5 years while dry (Mattox & Velardo 1950). Bishop (1967) found that an egg diapause in the Australian *Limnadia stanleyana* King prevented hatching during the period when widely fluctuating water levels would make successful reproduction unlikely. The eggs were dispersed in the dry bottom mud, and when pools filled with water some eggs hatched, but not all, presumably because only those near the mud surface received the appropriate stimuli; deeper-lying eggs in which embryogenesis was inhibited by darkness and low oxygen levels acted as a reserve in case there was not time for the first batch to mature and breed before another drought. While such controlling factors ensure that hatching usually occurs only under conditions favourable for development, Conchostraca also attain sexual maturity rapidly. Rzoska (1961) found that *Leptestheria aegyptiaca*, a common species in Sudanese rain-pools, was sexually mature 5 days after pool formation; thus reproduction by at least part of the population can be assured even in short-lived pools.

Lynceus brachyurus was also recorded from April to June in autumnal pools in Michigan by Kenk (1949) where maximum abundance was reached in May after the Anostraca had disappeared. Mozley (1932) recorded *Limnetis* species from a vernal pool in Manitoba, with maximum numbers in June. The relatively late occurrence of Conchostraca suggests that they are not as vulnerable as Anostraca to the burgeoning predator population in late spring. Further evidence of resistance to predation is seen in certain species that inhabit lakes where fish are present (Hartland-Rowe 1972). Occurrence in lakes raises the further question whether fluctuating water levels are as important in regulating development among all Conchostraca as they appear to be for the Anostraca (q.v.).

According to Hutchinson (1967) the Conchostraca have a long geological history dating back to the Devonian; living species are confined to fresh waters, mainly of a temporary nature.

3.1.7 Cladocera

Four species were taken in vernal pool Kendal II through 1972, 73, and 74, all members of the single family Daphniidae: *Daphnia pulex* Leydig, *Simocephalus exspinosus* (Koch) (?), *Simocephalus vetulus* (Müller) (?), and *Scapholeberis kingi* (Koch). Although identity of *Simocephalus* spp. is uncertain, two taxa are represented in K II collections, and the consensus of their characters is closest to these two names as used by Brooks (1959) and Flössner (1972) (I. Sutherland in litt.). *D. pulex* and *S. vetulus* (?) were both common in K I and VI when these were permanent pools (through 1973 to August) and also when they were temporary autumnal (after autumn 1973, through 1974). *S. exspinosus* (?) was never collected from K I or VI, and greatly outnumbered *S. vetulus* (?) in K II collections, suggesting that *S. exspinosus* may be especially adapted to vernal pools.

These four species are common and widespread. Although Brooks (1959) does not mention temporary pools as the habitat for any of them, all have been recorded previously in these habitats over a wide geographical area, e.g. Brandlova et al. (1972) in Ontario; Mozley (1932) in Manitoba; Donald (1973) in Alberta; Kenk (1949) in Michigan; Bevercombe et al. (1973) in Britain; and Barclay (1966) in New Zealand. Other species recorded from temporary pools in these studies were *Daphnia magna* Straus, *Ceriodaphnia reticulata* (Jurine); and *Chydorus sphaericus* (Müller) and *Alona guttata* Sars (Chydoridae). Only a few additional Cladocera have been recorded from temporary pools, the best known being species of *Moina* (Moinidae) which Brooks (1959) describes as common in muddy pools, such as those in brickyards. Thus at least three families of Cladocera are recorded from temporary pools — Daphniidae, Chydoridae, and Moinidae.

Cladocera are unusual in having two methods of reproduction. For most of the year, females produce unfertilized diploid eggs which develop rapidly in the brood pouch into more parthenogenetic females; but at certain times of the year some eggs develop into males which fertilize haploid eggs. The wall of the brood chamber surrounding fertilized eggs becomes hard and thick forming a dark, flattened capsule, the ephippium, which is shed when the female moults. Ephippial eggs in diapause are well known to survive drying and freezing, the embryo remaining dormant until conditions are suitable for development (Brooks 1959; Hebert 1978; Pennak 1953).

Daphnia pulex, one of the species present in K II, has three strains with different seasonal cycles (Stross 1969): in the monocyclic strain males and ephippia are produced once during the year, usually in autumn; in the dicyclic strain males and ephippia are produced in autumn and in late spring; and in the acyclic strain there are no males although ephippia may be produced parthenogenetically. That three methods of accommodating different habitat conditions can occur within a single taxonomic species indicates how labile ephippial production and diapause can be and explains how *D. pulex* can successfully inhabit a wide range of habitats. Assuming that the life cycles in these three strains of *D. pulex* represent the options available to Cladocera, only forms with late spring ephippia and summer diapausing eggs would be suited as permanent residents of temporary pools. Most Cladocera in permanent waters are monocyclic, producing ephippia in autumn in response to short-day photoperiod coupled to some density-dependent stimulus (Stross 1969, 1971a & b; Stross & Hill 1965). Dicyclic forms have a similar autumnal diapause, but also undergo summer diapause as ephippial eggs (Stross 1969). Because the late spring ephippia of dicyclic forms are produced during long-day photoperiods, Stross has proposed that the photoperiodic response is facultative — induced by short days at cool autumn temperatures but not operative at the higher temperatures of late spring; the stimulus inducing summer diapause appears to be density-dependent (Stross 1969). In late spring when water temperatures in a temporary pool are relatively high, any crowding effect is aggravated by receding water levels, and changing concentrations of food and metabolites could be acting in a density-dependent manner. There is also the possibility that some earlier phase such as an embryonic stage of the mother during development was sensitive to a particular photoperiod and thus a secondary environmental stimulus (Stross 1969). In vernal pools, only summer diapause occurs and ephippial eggs must be able to tolerate summer drought and winter cold. Study of ephippial structure might determine whether specially sculptured or thickened ephippia are present in vernal-pool species, and whether these refinements are more resistant to desiccation than unmodified ephippia.

Reactivation of diapausing eggs depends on photoperiod, with temperature and CO_2 tension also involved (STROSS 1971a). Even species in autumnal pools may remain in diapause through autumn and winter. October soil and ground cover samples from the dry basin of K II flooded in the laboratory at 10°C did not produce any Cladocera although other invertebrates appeared at various intervals between October and March. When December and February soil samples were flooded 50% of each produced Cladocera, mostly within 2 weeks of flooding. However, eggs of other Cladocera in temporary pools do hatch if the pool basin floods in autumn. Although not collected from K II, *Daphnia* sp. (cf. *cavicervix* EKMAN) was numerous in K VI after the 1973 dry period was terminated; immatures were collected on 16 December 1973, and males and sexually reproducing females with ephippia on 1 May 1974.

According to HUTCHINSON (1967), Cladocera are almost entirely freshwater animals, the few marine species to be regarded as secondarily adapted. Whether, as in other Branchiopoda, early evolution of Cladocera was influenced by conditions of temporary waters appears uncertain, but wide occurrence of diapausing ephippial eggs suggests that mechanisms for tolerating drought and freezing are among the primitive features of Cladocera. It is surprising that more of the extant species do not occur in temporary pools. Perhaps they do, but these habitats have not yet been adequately explored for Cladocera.

3.1.8 Copepoda

Collected from Kendal II in 1973 and 74 were three cyclopoid species — *Cyclops vernalis* FISCHER, *C. navus* HERRICK, and *C. bicuspidatus* (cf. *thomasi*); and two harpacticoid species — *Canthocamptus staphylinoides* PEARSE, and *Bryocamptus* sp. (*minutus* complex).

From temporary pools in Michigan, KENK (1949) recorded *Cyclops vernalis, navus, bicuspidatus thomasi* FORBES, *latipes* LOWNDES (as *gigas latipes*), and *varicans rubellus* LILLJEBORG; *Attheyella americana* HERRICK (as *A. northumbrica americana*); and *Canthocamptus staphylinoides*. From a vernal pool in Manitoba, MOZLEY (1932) recorded the cyclopoids *Cyclops vernalis* (as *viridis* JURINE), *C. ater* HERRICK; the harpacticoid *Bryocamptus minutus* CLAUS (as *Canthocamptus*); and the calanoids *Diaptomus leptopus* FORBES, and *D. oregonensis* LILLJEBORG. In Poland, WIERZBICKA (1966) recorded several cyclopoids from vernal pools: *Cyclops strenuus* FISCHER, *C. furcifer* CLAUS, *C. gigas* (CLAUS), and *C. bicuspidatus* (CLAUS). Thus, only a small fraction of the freshwater species appears adapted to conditions of temporary pools. Most of these species are common and widespread, many occurring in permanent ponds and lakes.

Cyclopoid copepods do not have thick-walled resistant eggs (PENNAK 1953), but some species such as *Cyclops bicuspidatus thomasi* undergo diapause at the fourth copepodite instar, ceasing normal planktonic existence to encyst in the bottom sediments (COLE 1953). They are able to survive the dry period of temporary pools only in this stage (CHAMPEAU 1963). Soil samples taken by WIERZBICKA (1966) from the dry basin of a vernal pool revealed that cyclopoids in diapause did not penetrate more than 4 cm into bottom sediments; although not encysted, these fourth or fifth copepodite stages evidently passed the dry period of up to 9 months in dry mud, perhaps protected by the slime material secreted by some cyclopoids (ROY 1932). Copepodites of *Cyclops vernalis,* one of the K II species, have been reactivated from dried silt samples 3 years old (RYLOV 1963). Induction of diapause is not well understood. Studying *Cyclops navus,* which is reported to remain free-swimming in the water column during diapause, WATSON & SMALLMAN (1971) concluded that the diapause was induced by photoperiod, with temperature governing the critical day-length for each species, but that only the first copepodite instar was sensitive to the stimulus. Reactivation after the dry phase appears to be a facultative response to flooding after the requirements of diapause development had been met, because KENK (1949) found that *Cyclops vernalis* and *C. bicuspidatus thomasi* were reactivated from October soil samples flooded in the laboratory, and in transient rainwater pools within 36 hours after heavy rain in October. Soil samples taken in October, December and February from Kendal II produced active copepods within 1 week of flooding in the laboratory.

Some harpacticoid copepods produce thick-walled resting eggs resistant to adverse conditions (PENNAK 1953), and we would expect that these eggs would be produced by most harpacticoids in vernal pools. Although *Canthocamptus staphylinoides* encysts at a fully grown but sexually immature stage, when it can be found in anaerobic bottom sediments of lakes (COLE 1953), PENNAK (1953) states that these cysts do not constitute a drought-resistant aestivation mechanism. KENK (1949) took *C. staphylinoides* and *Attheyella americana* throughout the winter from an autumnal pool in Michigan, and early in the spring from a vernal pool; he suggested that, rather than an elaborate cyst, the animals secreted a protective layer of slime as demonstrated for some cyclopoids (ROY 1932).

Among calanoid copepods, resting eggs with delayed hatching are produced by species in permanent waters, but these eggs have little resistance to drying (HUTCHINSON 1967). Resistant resting eggs in the Diaptomidae are a means of colonizing temporary waters, and the Centropagidae of the southern hemisphere are similarly adapted (HUTCHINSON 1967). Resting eggs of *Diaptomus stagnalis* FORBES studied by BREWER (1964) from an autumnal pool in Illinois had resistant properties. Eggs hatching in March produced adults in about 30 days, and egg sacs carried by the females were deposited on the bottom where they remained from May through March. Undergoing obligatory diapause development requiring high temperatures for 5 to 6 months, the eggs showed little morphogenesis and were resistant both to drying and to high but not low temperatures. At autumn temperatures embryogenesis was completed in about 2 weeks, after which eggs were resistant to cold temperature but not to drying or high temperature. A facultative hatching response after completion of morphogenesis allowed eggs to hatch when flooded if autumn temperatures were suitable, as they would be at lower latitudes, but otherwise the eggs entered another diapause which must be completed at low temperature and which effectively postponed hatching until spring. By this evidence *Diaptomus stagnalis* overwinters in autumnal pools either as diapausing embryos in eggs on the bottom, or as actively feeding individuals. But if the overwintering *D. stagnalis* embryo within the egg is not resistant to drying (BREWER 1964), it is questionable whether this species could persist in a vernal pool such as that in which MOZLEY (1932) found *Diaptomus leptopus* and *D. oregonensis.* Soil moisture alone might be sufficient for the overwintering period in a vernal pool, or these species might have overwintering resistance to desiccation superior to that of *D. stagnalis.* For example, *D. leptopus* has a morphologically distinct overwintering egg in addition to normal summer or subitaneous eggs (WINNER 1970); furthermore, some of these resistant eggs may remain in bottom sediments to hatch the following year (SAWCHYN & HAMMER 1968). The hatching stimulus for eggs of *D. stagnalis* was shown by BREWER (1964) to be reduction of O_2 level, brought about by bacterial action in the organic material of the bottom mud — a mechanism similar to that for hatching in Anostraca and Culicidae of temporary pools.

Variability in encystment between populations of *Cyclops bicuspidatus thomasi* and *Canthocamptus staphylinoides* was reported by COLE (1953); the population of *C. b. thomasi* in Crystal Lake, Minnesota, remained encysted throughout the summer while another population in a nearby pond excysted in midsummer and produced a second generation. This, along with other evidence on encystment, led Cole to conclude that complex environmental factors play a part in inducing and terminating encystment. This evidence also suggests that monocyclic and dicyclic strains within a taxonomic species may be involved in diapausing copepods as in cladocerans.

Unlike Cladocera, copepods have a rich marine fauna, and the freshwater representatives are of marine origin (HUTCHINSON 1967). Thus we infer that copepods of temporary pools were probably derived from groups established in permanent fresh waters.

3.1.9 Ostracoda

Ostracods are a large and principally benthic component of the temporary-pool fauna. Collections from temporary vernal Kendal II in 1973 and 74 (combined), and October, December and February soil samples flooded in the laboratory contained: (Candonidae) *Candona decora* FURTOS (13 April, Oct.-Feb. soil samples), *Candona albicans* BRADY (15 April); (Cyprididae) *Cypris pubera* MÜLLER (24 April — 2 July, Dec.—Feb. soil samples), *Cypridopsis vidua* (MÜLLER) (12 June), *Cypricercus reticulatus* (ZADDACH) (15 May, Oct.—Feb. soil samples), *Cypricercus tincta* FURTOS (no wet phase collections, Oct.—Feb. soil samples); (Cyclocyprididae) *Cyclocypris laevis* (MÜLLER) (5—13 April, Oct.—Feb. soil samples); (Notodromadidae) *Cyprois marginata* (STRAUSS) (no wet phase collections, Feb. soil samples). Combined collections from K I and VI included, in addition to most of the K II species, *Cypricercus horridus* SARS and *Cypria ophthalmica* (JURINE) in 1974 when these were autumnal pools; and *Notodromas monacha* (MÜLLER) in 1973 when they had been permanent pools for the preceding 12 months.

Much synonymy in names applied to species in earlier literature makes comparison with recent identifications difficult; in papers we cite, names have been adjusted to comply with the usage of DELORME (1970a, b, c, d; 1971). From temporary autumnal pools in Michigan KENK (1949) recorded: *Candona decora* and *C. truncata; Cypris subglobosa, Eucypris crassa* (MÜLLER), *E. fuscata* (JURINE), *Cypricercus tincta, Cypridopsis vidua; Cypria ophthalmica;* and *Cyprois marginata.* HOFF (1942) found that several species in Illinois were characteristic of temporary pools: *Candona decora, C. distincta* FURTOS, *C. inopinata* FURTOS, *C. suburbana* HOFF; *Cypria ophthalmica,* and *Cypricercus reticulatus.* HOFF also found that temporary streams in Illinois share more species in common with permanent streams than with temporary pools. Judging by the literature, most of the species above occur in permanent habitats as well, but since several occur chiefly in temporary pools (HOFF 1942, 1943), adaptations for this mode of existence should be identifiable.

Eggs of freshwater ostracods are highly resistant to desiccation, those of *Cypridopsis vidua,* for example, are enclosed in a double-walled shell of chitin impregnated with calcium carbonate (KESLING 1951). A number of species have developed from mud that has been dried for many months, and even one interval as long as 20 years is reported (PENNAK 1953). Eggs of some species, chiefly of permanent waters, develop and hatch at once; but eggs of other species, including those living in temporary pools, do not hatch for several months (HOFF 1942). Generation time is usually short, just over a month for some species, but longer for others; there may be several generations in a year although usually only one in temporary pools (HOFF 1942, 1943). For example, MCLAY (1978) found that adults of *Cypricercus reticulatus* and some other species with a single generation disappeared from a temporary pool in British Columbia before onset of the dry phase, their resting eggs lying unhatched in bottom sediments. Failure of these eggs to hatch in the late stages of the pool in spring suggests that they undergo some form of diapause development. These eggs hatched when the pool flooded in October (MCLAY 1978), and we suspect that a similarly immediate hatching response to flooding of either autumnal or vernal pools would be widespread among ostracods because their detritus-based food has little seasonal dependence.

In contrast to the single generation of most temporary-pool ostracods, *Cypridopsis vidua* completes 2 to 3 generations in a year (Pennak 1953). Occurring in all types of permanent and temporary waters (Hoff 1942), *C. vidua* is widespread and abundant (Delorme 1970b). In permanent waters this species reproduces without interruption, but passes the dry phase of temporary pools as a resistant egg (L. D. Delorme in litt.). Thus *Cypridopsis vidua* fully exploits both types of habitats with the flexibility of an ecological generalist.

In addition to the drought-resistant egg of some species, partly grown individuals of others remain in a torpid condition in the moist soil of dry pool basins; Delorme & Donald (1969) report that seventh instars of *Candona rawsoni* Tressler, a species of temporary and permanent waters on the Canadian prairies, remain alive in dry pool basins, and overwinter in frozen substrate until the pool fills again in spring. *Candona decora* survived the dry summer phase of an autumnal pool in British Columbia in torpor in bottom sediments (McLay 1978). In vernal pools in New Zealand *Candonocypris candonoides* King also resists some drying in this manner (Barclay 1966). Resistance under torpidity explains the appearance of nearly mature ostracods shortly after rain pools form in a pool basin or after soil samples are flooded (Kenk 1949).

Creaser (1931) found *Cypria ophthalmica* (syn. *C. exculpta* in part) in water at the bottom of crayfish burrows *(Cambarus diogenes)* in a dry pool basin in Missouri. This ostracod completes more than one generation in a year (Hoff 1942) and occurs in both permanent and temporary water. In Michigan it was abundant in transient rain pools in an autumnal pool basin in October 36 hours after the rain (Kenk 1949), indicating that partly developed individuals can resist some drying in torpor in damp soil; moreover, the species remained active in the autumnal pool through winter and spring.

The Ostracoda are clearly of marine origin, the freshwater groups representing at least five and probably more independent invasions (Hutchinson 1967). Furthermore, the fact that a number of genera in several different families occur in temporary pools suggests that the ultimate adaptations for transient waters are specializations derived from permanent freshwater forms.

3.1.10 Decapoda

Since burrowing crayfish may inhabit wet pastures where water never appears at the surface for any extended period, it is not surprising that they do occur in some temporary pools. One species, *Cambarus fodiens* (Cottle), occurred in only one of the pools we studied, Britannia IV, a temporary vernal pool. Since crayfish do not have resistant eggs, they can persist in temporary pools only if their burrows maintain contact with the ground water level during the dry phase.

The nature of the soil seems also to be important (CROCKER & BARR 1968), for a high clay content gives greater permanence to a long burrow; burrows as deep as 153 cm have been recorded (FAXON 1884). KENK (1949) reported that *C. fodiens* was active in (autumnal) pools only in spring, spending the remainder of the year in burrows.

Burrowing crayfish feed mainly on plants (CROCKER & BARR 1968); but their major impact on the animal community of temporary pools lies in the use of their burrows by other species to maintain contact with ground water. CREASER (1931) found large numbers of small crustaceans (copepods, ostracods, and amphipods) at the bottom of *C. diogenes* burrows in a dry pool basin in Missouri. We have circumstantial evidence that amphipods and isopods, which have no intrinsic means of drought resistance, were sustained over an 8-month dry period in crayfish burrows of a temporary vernal pool, Britannia IV. Thus crayfish may secondarily influence the community structure of temporary pools.

3.1.11 Amphipoda

Amphipods were taken from Kendal II only in 1972 (9 June, 2 July), and all were *Hyalella azteca* (SAUSSURE). The same species was taken in K I and VI in 1973 when these pools were permanent, and in 1974 when they were autumnal.

Amphipods are not normally a part of the vernal pool community because, unlike some other crustaceans, they cannot overwinter without water (E. L. BOUSFIELD in litt.). *Hyalella azteca* is one of the most common and widely distributed amphipods in North America, and living *H. azteca* have been reported in the feathers of ducks (ROSINE 1956). Sporadic occurrence of *H. azteca* in K II only in 1972 can be reasonably attributed to ducks, which are often seen on all Kendal pools.

Crangonyx rivularis BOUSFIELD was taken from another vernal pool Milton I (21 April 1972). Where ground water levels are high and substrates porous, some *Crangonyx* species have hypogean populations (E. L. BOUSFIELD in litt.), and in this way some amphipods might overwinter in vernal pool basins having these conditions. *C. rivularis* was unusually abundant in collections from Britannia IV which, although temporary vernal, was the only pool studied where burrowing crayfish *(Cambarus fodiens)* were established. We did not sample water in the bottoms of the crayfish burrows but the correlation between amphipod abundance and crayfish suggests that the burrows provide a refuge for amphipods through the 8 months of summer and winter. *Crangonyx gracilis* (prob. *pseudogracilis* BOUSFIELD) were found in burrows of *Cambarus diogenes* in a dry temporary pool basin in Missouri by CREASER (1931).

Species of *Hyalella* and *Crangonyx* can burrow into bottom materials and vegetation when surface water is absent for shorter periods during summer and autumn (KENK 1949); therefore their occurrence in autumnal pools is not surprising.

We collected *Crangonyx rivularis* from Aberfoyle IX, a rich autumnal pool (6, 11, 29 April 1970). *Crangonyx gracilis* SMITH was abundant in autumnal pools in Michigan (KENK 1949); and we suspect that many references to this and other species in temporary pools, e.g. HUBRICHT & MACKIN (1940), relate to autumnal pools.

3.1.12 Isopoda

No aquatic isopods were taken in the Kendal pools, but *Asellus forbesi* WILLIAMS was collected in another temporary vernal pool, Britannia IV (16 April 1972). This is the only pool studied in which the burrowing crayfish *Cambarus fodiens* was well established, and it seems likely that the burrows provided refuge for aquatic isopods during the dry period of approximately 8 months. Freshwater isopods are not known to overwinter in dry pool basins at any stage (E. L. BOUSFIELD in litt.), although the possibility of a hypogean refuge in porous substrates where the ground water level is high cannot be excluded.

Protection of aquatic isopods for short periods seems possible in autumnal pools that are well provided with bottom litter or vegetation; we collected *A. forbesi* in such a pool, Aberfoyle IX (6, 11, 29 April 1970). *Asellus intermedius* FORBES (syn. *militaris* HAY) appeared in autumnal pools in Michigan shortly after they began to retain surface water in December; KENK (1949) states that there can be no doubt that this species aestivates in the ground, the animals probably following the retreating water table when the pools dry, and developing to maturity. We presume they could have been aided by burrows made by crayfish active in the same pools.

3.1.13 Mollusca

Four species of molluscs were taken in vernal pool K II through the period 1972 to 74: *Lymnaea elodes* (SAY) (Lymnaeidae); *Aplexa hypnorum* (L.) (Physidae); *Gyraulus parvus* (SAY) (Planorbidae); and *Sphaerium occidentale* PRIME (Sphaeriidae). Of these four species, *L. elodes* and *A. hypnorum* were not collected in K I or VI, although *G. parvus* and *S. occidentale* were taken from both.

The three gastropods are pulmonates, as are most of the snails recorded from temporary pools. In contrast to the gill-breathing Prosobranchia, the vascularized lung or pulmonary cavity of the Pulmonata enables them to breathe atmospheric air, an essential advantage for snails living in temporary pools because the dry period is passed by juvenile or adult individuals in a dormant state. Since pulmonates are monoecious and capable of self-fertilization they are better suited as colonizers of isolated habitats than the dioecious prosobranchs. Analogous to the operculum of prosobranchs, an epiphragm of dried mucoid material is secreted by pulmonates to cover the aperture during dormancy, reducing although not eliminating moisture loss (MACHIN 1968).

Two of the K II species, *S. occidentale* and *A. hypnorum*, live in temporary waters exclusively or nearly so; the other two, *G. parvus* and *L. elodes*, are recorded from a very wide range of freshwater habitats (CLARKE 1973). Thus, molluscs of temporary pools reflect strategies of both ecological specialist and generalist. *Sphaerium occidentale*, which can live for 2 to 3 years, is extremely abundant in temporary pools (HERRINGTON 1948); surviving drought periods of 8 to 9 months in damp leaves, it is probably the most amphibious North American pelecypod (CLARKE 1973). *Aplexa hypnorum* evidently passes the dry period as a juvenile, although snails are scarce at that time and evidence is inconclusive as to whether this period is spent above ground or in the soil (ROMACH 1971). Studying *Gyraulus parvus* in a temporary autumnal pool in Illinois, STRANDINE (1941) found the percentage surviving the dry period to be highest in deepest parts of the basin where there was more soil moisture. *Lymnaea elodes* studied by JOKINEN (1978, see also ROMACH 1971) survived the dry period mainly as juveniles which moved out of the receding water, seeking and fastening to dry surfaces such as tree trunks by means of the epiphragm. These aestivating snails moved periodically, eventually coming to lie on the dry pool bed beneath leaf litter. The life span was about 15 months; adult snails usually followed the receding water and died, not from desiccation but from predation, mainly by sciomyzid larvae. Protection from sciomyzids is achieved not by the epiphragm, which the larvae can penetrate, but by movement up dry tree trunks where the snails become inaccessible (C. O. BERG pers. comm.). High morphological and physiological variability among populations of *L. elodes* was interpreted by HUNTER (1975) as evidence for the ecological generalist strategy of this species.

Emphasizing the extreme conditions of drought and low temperature (−40°C) tolerated by molluscs of vernal pools in the boreal forest-grassland ecotone of western Canada, MOZLEY (1928, 1932, 1935) cited dormancy without surface water for 9 to 11 months of the year in *Lymnaea elodes, L. caperata* SAY (Lymnaeidae); *Promenetus umbilicatellus* (COCKERELL), *P. exacuous* (SAY), *Planorbula armigera* (SAY), *P. campestris* (DAWSON) (Planorbidae); and *Aplexa hypnorum* (Physidae).

A few species of four families of aquatic Mollusca are therefore adapted to conditions of temporary vernal pools in North America. Factors distinguishing them from the majority of species in each family could be rapid growth during a short period of activity under water and in a wide range of temperatures (MACKIE 1978), and the physiological capacity for a sustained resting period in the absence of surface water. Epiphragms are generally conceded to reduce moisture loss in dormant snails (MACHIN 1968; BOSS 1974), although there are differing views concerning the ability of pulmonates to form an epiphragm. COOKE (1895) attributed an epiphragm to very few aquatic snails, but according to BOSS (1974) all pulmonate snails, both terrestrial and aquatic, are reputed to be capable of forming an epiphragm. We found that *Helisoma trivolvis* in temporary autumnal

K I did not form an epiphragm when surface water disappeared; Romach (1971) reported similar absence of epiphragm formation in this species. McNeil (1963) found that *Physa propinqua* Tryon overwintering in drying irrigation canals in Washington did not form an epiphragm although *Lymnaea elodes* (syn. *Stagnicola palustris*) did. Cheatum (1934) reported that an epiphragm was formed by some individuals in several species of *Lymnaea, Helisoma,* and *Physa,* including *H. trivolvis* and *P. sayi.* Even if epiphragms are formed by aquatic snails under certain conditions, there appears to have been no critical camparison between snails of permanent water and temporary water for effectiveness of epiphragms in moisture retention. Moreover, individuals of *Lymnaea elodes* secrete multiple epiphragms (Romach 1971), suggesting that behaviour underlying formation of the epiphragm in temporary-pool species may be distinctive. Epiphragm formation occurs in both major orders of the Pulmonata, Basommatophora (mainly aquatic species) and Stylommatophora (terrestrial species). If it is common to all pulmonates as suggested by Boss (1974), then epiphragm formation could be seen as a primitive feature subject to modification in certain taxa; but if, as other observations suggest, it is not common to all aquatic Pulmonata, epiphragm formation could be an apomorph feature derived independently in species exposed to selective forces such as drought. Whether the epiphragm or some other attribute of temporary-pool species is the key, the adaptive characters are evidently highly sensitive to selection pressure; in species of South American pulmonates, snails from permanent bodies of water were less tolerant of drying than those from populations of the same species in temporary pools (Olivier 1956).

Since aquatic molluscs have no specialized egg or cyst for dry periods, the difference between autumnal and vernal pools could be critical for some species. We would expect that the molluscan community of a consistently autumnal pool would include certain other species in addition to the more highly drought-resistant vernal pool fauna. Observations on European species in intermittent waters (Klimowicz 1959) support this view. From temporary autumnal pools in Michigan, Kenk (1949) recorded *Lymnaea elodes, L. modicella* (Say) (Lymnaeidae); *Planorbula armigera* (Planorbidae); *Physa gyrina* (Say), *Aplexa hypnorum* (Physidae); *Sphaerium occidentale, S. partumeium* (Say) (Sphaeriidae). *Musculium securis* was recorded from autumnal pools in Ontario (Mackie et al. 1976). Romach (1971) found *Helisoma trivolvis* in an autumnal pool. Our Kendal pool I also retained in autumn 1973 an abundant population of *H. trivolvis* after a dry period in late summer. We attribute this survival to the vigorous growth of an amphibious tussock-forming *Scirpus* species in K I which provided moisture-retaining microhabitats during the dry period. In K VI, 30 m distant from K I and with a similar fluctuation of wet and dry phases, there are no protective plants of this sort and no *H. trivolvis.*

For terrestrial and freshwater gastropods, Boss (1974) postulated that tolerance of pulmonates to greater environmental extremes has enabled this group to populate more northerly latitudes than prosobranchs, an advantage attributed mainly to the ability of pulmonates to survive for long periods in hibernation and aestivation. Considering aquatic gastropods alone, specializations enabling species to inhabit temporary vernal pools may then be seen as a culmination of the widening ecological scope of snails as they evolved through prosobranch and pulmonate levels.

3.2 Group 2. Overwintering spring recruits

These animals aestivate and overwinter in the dry pool basin but are capable of dispersal as adult insects, or as mite parasites on winged adult insects. Dispersal and recruitment are limited to spring, and because oviposition is dependent on water, it must occur before the pool dries (Fig. 8). Various stages survive the dry period. Ephemeroptera and Trichoptera pass the 8-month period as eggs; Coleoptera as adults, eggs or larvae; Chironomidae and Ceratopogonidae as larvae. Acari of Group 2 are parasitic on various insects of temporary pools: Pionidae parasitize Chironomidae, aestivating and overwintering as deutonymphs; Hydryphantidae and most Arrenuridae parasitize Culicidae and some other Nematoceran Diptera, aestivating and overwintering as adults or deutonymphs; *Arrenurus planus* parasitizes Odonata, aestivating and overwintering as a nymphochrysalis.

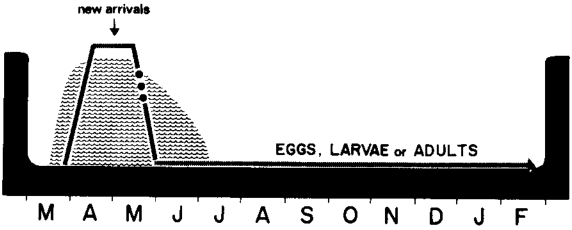

Fig. 8. Group 2 cycle; dots indicate oviposition.

3.2.1 Ephemeroptera

Larvae of *Paraleptophlebia praepedita* (Eaton) were abundant in the temporary vernal pool K II in 1972, 73 and 74 with size-classes 2, 3, and 4 (after Clifford 1970) collected in mid to late May and early June, and adults on 9 and 19 June. Samples of frozen soil from the dry basin of K II (18 December 1974) yielded *P. praepedita* larvae of size-class 1 in March 1975 approximately 3 months after flooding in the laboratory. Since the flooded soil samples were carefully inspected on a regular basis, the resistant stage was more likely a diapausing egg than a dormant larva.

We conclude, therefore, that *P. praepedita* overwinters in vernal pools as eggs on the dry basin, hatching when the basin is flooded the following spring. Eggs are probably laid on water since this is the normal oviposition behaviour for species of *Paraleptophlebia* (EDMUNDS et al. 1976), with development delayed until the eggs are exposed to a period of desiccation and/or low temperature. We find no previous reference to occurrence of *Paraleptophlebia* in temporary pools, and in fact the genus is generally regarded as confined to running waters (EDMUNDS et al. 1976). Thus, *P. praepedita* is capable of living in a much wider range of habitats than generally supposed, consistent with BURKS' observation (1953) that it was the commonest species of the genus in Illinois, as would be expected of an ecological generalist.

Siphlonurus larvae of size-classes 2 and 3 were collected from a temporary pool (Aberfoyle XI, 16 June 1972) known to have been without surface water on 29 October 1971, but the length of the period without surface water is not known. In Illinois, eggs of *Siphlonurus* spp. deposited in the spring do not hatch until the following spring, the larval habitats completely dry during summer and autumn (BURKS 1953). On the basis of these observations, *Siphlonurus* spp. would belong in Group 2.

Leptophlebia larvae of size-class 3 collected from an autumnal pool (Aberfoyle IX, 11 April 1970) indicate that eggs or larvae must have been in the pool during the previous winter, and that species of this genus can sustain summer drought. BURKS (1953) refers to two species of *Leptophlebia, L. nebulosa* (WALK.) and *L. cupida* (SAY), which occur in the spring in temporary pools in central Illinois. Further evidence to support our assignment of *Leptophlebia* and *Siphlonurus* spp. to Group 2 is provided from an autumnal pool in Oregon where *L. pacifica* (McD.) and *S. occidentalis* EATON larvae were found after a drought lasting from June through November (LEHMKUHL 1973). In the classification of mayfly life histories proposed by LANDA (1968), these are Type A2 species — univoltine, eggs in diapause until spring or summer, larval growth short and rapid (see also EDMUNDS et al. 1976).

Evidence for evolution of Ephemeroptera conforms to the general pattern in other aquatic orders that cool running waters were the primitive habitat of mayflies (G. F. EDMUNDS in litt.), and that species in temporary pools would have been derived from them. Even so, *Siphlonurus* belongs to the most primitive living family, Siphlonuridae, although the Leptophlebiidae are a higher family.

3.2.2 Coleoptera

Four families of the beetles reproducing in temporary pools are represented in Group 2, species overwintering in the dry pool basin as adults or eggs. Unless stated otherwise, collection records are composites of 1972 through 1975.

Dytiscidae

Appearance of adults of *Hydroporus despectus* SHP. (20 Feb.) and *H. fuscipennis* SCHAUM (5 April — 4 June, Feb. soil samples) in flooded soil samples from

K II demonstrates that these species overwinter in the dry basins of vernal pools. These two plus three other species of *Hydroporus* were collected from K II during the wet phase, although it does not necessarily follow that all are members of Group 2: *H. griseostriatus* (DeG.) (13 April — 15 May), *H. notabilis* LeC. (18 April — 2 July), *H. undulatus* Say (15 May — 2 July); and *Hydroporus* larvae were collected in the pool (L II—III, 9 June — 2 July). James (1961) found *Hydroporus* adults (chiefly *H. tenebrosus* LeC.) in a vernal pool in southern Ontario where they were the earliest beetles recorded, active even before mosquito eggs had hatched.

Flooded soil samples from K II produced first instar larvae of *Agabus* sp. (27 Oct. 1974, 18 Dec. 1974), confirming that these beetles can overwinter in vernal pools as eggs; the October samples had been exposed to outdoor temperatures below 0°C but not for an extended period. Three species of *Agabus* were collected as adults in K II from 1972—74: *A. anthracinus* Mannh. (4 June), *A. confinis* (Gyll.) (9—19 June), and *A. erichsoni* G. & H. (19 June — 2 July). *Agabus* larvae were collected from 13 April to 2 July, but presence of all 3 instars on 18 April is evidence of early and rapid larval development. James (1969) found eggs of *A. erichsoni* in soil samples from the dry basin of a vernal pool in southern Ontario in October, evidently deposited in May and June; the eggs were in diapause and required exposure to low temperature before hatching. Thus, as in the European *A. chalconotus* (Panz) (Jackson 1958), eggs remain in the soil for approximately 10 months. Oviposition by *A. chalconotus* with a boring action of the ovipositor in the peat pool bottom differs from the usual oviposition of *Agabus* spp. on submerged plants (Jackson 1958); and the eggs of this species are distinctive in having a more opaque and rigid chorion, and in being larger in relation to the size of the beetle than in other *Agabus* spp. All of these features could contribute to the drought resistance characteristic of *A. chalconotus* eggs. Variable rates of embryogenesis for this species enabled some to hatch quickly in the event of early flooding; but fully formed larvae remained within the egg for 2 to 3 months when flooding was delayed (Jackson 1958). James (1969) believed that *A. erichsoni* overwintered as adults as well as eggs, although in permanent pools (i.e. Group 4) because no adults were found in soil samples from the temporary-pool basin; adults appeared in the temporary pool in March and April. We collected one *Agabus* sp. adult from K II under a log in the dry pool basin (31 July).

First instar larvae identifiable only as *Rhantus* or *Colymbetes* were taken from K II soil samples (21 Feb. 1974, 20 Feb. 1975) several days after flooding in the laboratory, demonstrating overwintering in the dry pool basin, presumably as eggs. We assume that the genus is *Rhantus* since later instars of *Rhantus* sp. were common in K II collections (L II, III, 18 April — 4 July) but no specimens of *Colymbetes* were collected in K II. The only adult *Rhantus* we collected (*R. consimilis* Motsch., 18 April — 9 June) were taken so early in spring that they probably overwintered as adults, whether in the dry basin of K II (i.e. Group 2) or elsewhere in permanent water (i.e. Group 4). Either *R. consimilis* has two means of overwintering or we did not collect adults of the *Rhantus* sp. that overwinters as an egg in K II.

GALEWSKI (1971) found that shallow, ephemeral pools were one of several distinctive types of habitats utilized by European Dytiscidae, and discussed the adaptive features of species typical of these sites — chiefly members of *Agabus, Hydroporus,* and *Rhantus.*

Haliplidae

Adults of two species of *Haliplus* were collected in K II: *H. immaculicollis* HARR. (24 April — 19 June) and *H. longulus* LEC. (18 April — 2 July); no larvae were collected but a teneral adult collected (18 April). Adults of *H. immaculicollis* and *strigatus* ROBTS. were found in aestivation by WALLIS (1933) beneath pieces of wood in an inch of soil in dried basins of prairie ponds. From observations on an autumnal pool in Indiana, YOUNG (1960) suggested that *Haliplus ohioensis* WALLIS must be resistant to the dry summer phase as eggs, larvae, or pupae. *Peltodytes tortulosus* RBTS. was taken in K II (adult 28 May); a larva belonging to this genus was also collected (L I, 2 July). LEECH & CHANDLER (1956) state that at least some haliplids overwinter as larvae, commonly in damp soil above the water line; and that probably all species pass the winter as adults, some in hibernation, others active.

Since haliplids are principally algal feeders and the slow-moving adults rather vulnerable to fish predators, temporary pools would be advantageous habitats.

Hydrophilidae

Adults in three genera were found overwintering in the dry basin of vernal K II. Although larvae of *Anacaena* were not collected from K II, adults of *A. limbata* (F.) became active from soil samples (27 Oct. 1974, 18 Dec. 1974, 20 Feb. 1975) flooded in the laboratory, and were collected in the pool (5 April — 9 June). *Hydrobius fuscipes* (L.) adults also emerged from soil samples (5 April, 18 Dec. 1974), and larvae belonging to this genus were taken in June.

Adults of *Helophorus* spp. were taken in K II: *H. aquaticus* (L.) (2 July), *H. lacustris* LEC. (19 June), and *H. lineatus* SAY (9 June). FERNANDO (1958) found that certain species were among the most active colonizers of temporary pools in Britain, and that adults could overwinter in the moist soil of temporary pool basins; larvae of *Helophorus* spp. normally live in moist soil. An abundant species in southern Ontario, *H. orientalis* MOTS., is parthenogenetic and can complete several generations in a season because larval development is rapid (ANGUS 1970). Since adults and larvae of *Helophorus* spp. feed on algae and detritus, temporary pools provide an abundant food resource.

From capture records of adults in ponds and artificial tanks in southern

Ontario, FERNANDO & GALBRAITH (1973) interpret *Anacaena limbata* and *Helophorus orientalis* as species overwintering in permanent ponds and dispersing to breeding sites in spring (i.e. as members of our Group 4). However this conflict with our data may be resolved, their results reveal that both species fly actively from May through September.

Helodidae

Larvae of *Cyphon* sp. were taken in K II (19 June). Although helodid adults are terrestrial, and would seem to be the appropriate overwintering stage for temporary pool species, LEECH & CHANDLER (1956) state that these beetles overwinter as larvae.

3.2.3 Trichoptera

Larvae of *Polycentropus crassicornis* WALK. (Polycentropodidae) collected from Kendal II are assigned to Group 2 rather than Group 3 because available information indicates that water is essential for oviposition.

Polycentropus larvae were numerous in K II collections in a consistent sequence of L I (April, May) through LV (May, June); final instars when reared proved to be *P. crassicornis* WALK., the first record of net-spinning Trichoptera (Hydropsychoidea) in temporary pools (WIGGINS 1973). At that time no evidence was available to explain how the species was adapted to this habitat. Subsequently, first instar *Polycentropus* larvae were found in December soil samples from the dry basin of K II 20 days after flooding in the laboratory at 10°C; we assume that these are *P. crassicornis*. Females of *P. crassicornis* collected beside K II (19 June 1972) were sexually mature with eggs extruding from preserved specimens, and collections records reveal no evidence of adults of this species after July. These factors point clearly to oviposition in spring shortly after emergence from the pool and, although no direct observations of oviposition or eggs have been made, we assume that eggs of *P. crassicornis* remain in the dry pool basin after the water disappears for an 8-month period including winter until the pool is flooded in spring. Absence of larvae in October soil samples from K II suggests that the eggs remain in diapause until late autumn, by which time low temperatures would inhibit hatching until spring even if the pool were flooded. A similar developmental sequence of *Polycentropus* larvae was collected from K I (1 May, L II, III; 15 May, L IV, V), indicating that autumnal flooding does not lead to hatching which is substantiated by absence of *Polycentropus* larvae in K I collections made in November. Since *Polycentropus* larvae are highly predacious, we would expect obligatory spring hatching.

Almost all of the Hydropsychoidea, including most Polycentropodidae live in running waters, and phylogenetic evidence indicates that species of *Polycentropus* in temporary pools are derived from lotic forms.

3.2.4 Diptera

Four families are represented in Group 2.

Chironomidae

Chironomids occur over a wider range of habitats than any other family of aquatic invertebrates; they are successful in several extreme environments, and it is not surprising that they are among the most taxonomically diverse groups represented in temporary pools. Nonetheless, Chironomidae of temporary pools have been little studied, although larvae of some species are resistant to extremes of drought and temperature (DANKS 1971a, b).

Collections from temporary vernal Kendal II include a number of larvae that were reactivated from flooded soil samples taken from the dry basin in October, December, and February; additional larvae were also taken from a sample of frozen soil (5 April) in an area of the basin not then flooded. Larvae of most of these same taxa also occurred in April and May collections during the wet phase of the pool, and given that oviposition is dependent on water (JOHANNSEN 1905), we interpret them as representative of the Group 2 component of vernal pools. Combined data for 1972, 73, and 74 from Kendal II collections are: (Chironominae) *Chironomus* spp. incl. *C. tuxis* CURRAN and *C. stigmaterus* SAY (?) (larvae 15 April — 2 July, some reared; Dec.—Feb. in soil samples); *Endochironomus nigricans* (JOHANN.) (larvae 9 June, reared); *Paratanytarsus* spp. incl. *P.* n. sp. (larvae 15 April — 4 June, some reared; Dec.—April in soil samples); *Phaenopsectra* sp. (larvae Oct.—Feb. in soil samples); *Polypedilum* spp. incl. *P.* (s. s.) sp. *fallax* group (larvae 18 April— 2 July; Feb.—Apr. in soil samples); (Orthocladiinae) *Cricotopus* spp. incl. *C. sylvestris* (FABR.) (larvae 9 June, some reared; Feb. soil sample); *Hydrobaenus* spp. incl. *H. pilipes* (MALL.) (larvae 5—23 April, some reared; Oct.—Feb. in soil samples); (Diamesinae, Prodiamesinae *sensu* SAETHER 1976) *Prodiamesa* sp. (larvae 15 May—2 July; frozen soil sample 5 April); (Tanypodinae) *Guttipelopia* sp. (larvae 5 April in frozen soil sample). To these we add the following which, although not represented in dry soil samples, were taken as larvae mainly in early collections from Kendal II pool: (Chironominae) *Parachironomus* sp. (L II—III 13 April — 1 May); *Glyptotendipes* sp. (L IV 1 May); (Orthocladiinae) *Acricotopus nitidellus* (MALL.) (L IV(?) 9 June, reared); *Psectrocladius* spp. (L III—IV 23 May — 2 July).

Most of these same taxa were also found in temporary or semi-permanent pools in the Canadian prairies (DRIVER 1977). In Michigan, KENK (1949) found orthocladiine larvae in soil taken from dry pools in autumn, but did not identify them further or comment on their biology in temporary pools. BEVERCOMBE et al. (1973) also recorded Orthocladiinae but did not suggest how they survived drought. BARCLAY (1966) noted that the red larvae of *Chironomus zealandicus* HUDSON were always present in the bottom mud of a temporary pool in New Zealand during the wet phase.

The fine organic particles and algae on which most larvae in the Orthocladiinae, Chironominae, and Diamesinae feed are abundant in temporary pools, and larvae overwintering in bottom sediments can begin feeding as soon as the pool is flooded and temperatures appropriate. Chironomids apparently differ from the Trichoptera (Polycentropodidae) and Ephemeroptera (Leptophlebiidae) of Group 2 in not having an egg diapause; thus chironomid larvae could hatch and begin development before the pool dries in early summer. Larvae of these groups are tube-builders, clearly a respiratory asset in their sediment-burrowing existence; and their winter cocoons are also important in moisture conservation and protection from physical damage during periods of drought and freezing (DANKS 1971b). In fact, what little is known about drought resistance in chironomid larvae indicates that a cocoon is critical to that ability (DANKS & JONES 1978). Larvae of the African *Polypedilum vanderplanki* HINTON (Chironominae) persist within cocoons in dried mud of rock pools for several years (HINTON 1960). In Australia, *Paraborniella tonnoiri* FREEMAN and *Allotrissocladius amphibius* FREEMAN (Orthocladiinae) resist desiccation in dry mud within cocoons (BISHOP 1974; EDWARD 1968); and in California adults of two species of *Phaenopsectra* (Chironominae) were reared from larvae aestivating in cocoons for approximately 3 months in the dry soil of a rainpool (GRODHAUS 1976).

Chironomids tolerant of extremes of drought and temperature are viewed by EDWARD (1968) as opportunistic species with wide physiological tolerances, and by DANKS (1971b) as largely pre-adapted to seasonally frigid habitats. Just what features of chironomid biology are adaptive for temporary pools is not clear, but there seems little reason to believe that they coincide in a particularly large proportion of the species in the family. For Group 2 Chironomidae, cocoons would clearly be an important adaptation to vernal pools; cocoons are also characteristic of species in permanent waters but are not constructed until after the onset of low temperatures (DANKS 1971b; DANKS & JONES 1978). To be effective for resistance to drying in temporary pools, cocoons would probably have to be constructed as the pool dried; thus a behavioural feature established for resistance to freezing in permanent waters could also become effective in resistance to drying by a change in timing. This extension of adaptations established in permanent water into drought-resistant mechanisms in temporary waters is a pattern seen repeatedly among temporary-pool animals. If, as DANKS (1971b) suggests for chironomids of permanent waters, cocoon-building or resumption of feeding by larvae in temporary pools is not closely regulated and is a facultative response to factors such as temperature and perhaps water supply, Group 2 chironomids would be among the most flexible and efficient consumers of temporary-pool resources. Autumnal flooding would be an asset in their development; and diapause induced by photoperiod at the end of the last larval instar (DANKS 1971b) would then be important to delay emergence of adults until the return of favourable spring weather conditions. The cryptobiosis of *Polypedilum vanderplanki* (Hinton 1968) represents an adaptive extreme among Group 2 Chironomidae; but other species of this family are successful in vernal pools of temperate latitudes, apparently with less tolerance to extreme drought, suggesting a graded series of features adaptive for transient waters.

Although most Tanypodinae in Kendal II are apparently migrants (see Group 4), *Guttipelopia* sp. larvae were collected in frozen soil early in the spring (L II or III 5 April), after apparently overwintering in the dry basin. *Guttipelopia* larvae are, like all Tanypodinae, predacious (Coffman 1978), and thus dependent on an energy base very different from that of the other overwintering chironomids which feed on fine organic particles. Since larvae of Tanypodinae are evidently further distinctive among Chironomidae in constructing neither larval tubes nor overwintering cocoons, and in having limited resistance to freezing (Danks 1971b), our evidence of aestivation and overwintering for 8 months in the dry basin of a temporary pool is noteworthy. Larvae of *Guttipelopia* were also collected in K VI in 1973 (L II or III 21 August) suggesting that as K VI had been a permanent pool for the year preceding the 1973 collections, and did not dry until late summer of 1973, two generations were possible. A European species *Guttipelopia guttipennis* (v. d. Wulp) inhabits temporary pools, swamps and the littoral zone of lakes (Fittkau 1962); eggs are laid immediately after copulation, the adults living for only a few days.

Brundin's (1966) concept of phylogeny for the Chironomidae, in which warm-water lentic species of Chironominae and Orthocladiinae are derived from ancestral groups in cold lotic waters, indicates that adaptations for temporary pools are derivative features.

Ceratopogonidae

Larvae collected in 1973 and 74 from vernal Kendal II were: *Alluaudomyia* sp. (4 June, L IV); *Atrichopogon* cf. *geminus* Boesel (13 April, L II or III); *Bezzia (Pseudobezzia)* sp. (13—20 April, L III); *Palpomyia* sp. (*lineata* group) (18 April—1 May, L IV).

Larvae of *Bezzia, Palpomyia,* and *Alluaudomyia* are aquatic, and most species overwinter as larvae (W. I. Knausenberger in litt.); aquatic Ceratopogonidae oviposit in water (Thienemann 1954). Presence of instars III and IV of *Bezzia* sp. and *Palpomyia* sp. in Kendal II in April suggests that species in these taxa are members of Group 2. *Alluaudomyia* sp. larvae, with fourth instars collected in June, might also be of Group 2, although Group 4 remains a possibility. Larvae of strictly aquatic species are found throughout the winter under the ice (Thomsen 1937), and those of *Bezzia, Palpomyia,* and *Alluaudomyia* can overwinter in soft mud (W. I. Knausenberger in litt.). As in the Chironomidae, adaptation to damp substrates may enable larvae in a number of ceratopogonid genera to persist through extended periods of drought and cold. Hinton (1953) records an extreme example of drought resistance in an African ceratopogonid whose tolerance of dehydration resembles that of the chironomid *Polypedilum vanderplanki.*

Larvae of *Atrichopogon* frequently occur on damp substrates above the water line, feeding on algae (W. I. KNAUSENBERGER in litt.). *Atrichopogon geminus* larvae live among grass roots in damp soil subject to flooding (WIRTH & STONE 1956); as this species oviposits on soil covered with algae in shaded situations (BOESEL & SNYDER 1944), it may have Group 3 adaptations. BISHOP (1974) found larvae of *Dasyhelia* sp. to be common in temporary pools in Australia.

Ceratopogonids occur widely in temporary pools and other marginal aquatic habitats (see THIENEMANN 1954), and their adaptations may not be entirely circumscribed by the groups proposed here.

Tabanidae

Larvae of *Tabanus similis* MACQ. were collected from Kendal II (13 April, 9 June). The April record, at least, indicates that this species overwinters as a larva in the dry pool basin. Among Tabanidae in general, TESKEY (1969) found that larvae in *Tabanus* and related genera tend to occur in swamps and marshes, while *Chrysops* is more prominent along the margins of running waters. TESKEY also reported that *T. similis* was one of a few species characteristic of wetland habitats with a summer dry period, conditions parallel if not identical to temporary pools; and he further noted that the few species found in these sites were among the most abundant as adults, confirming that their broad ecological range was correlated with numerical abundance. *Tabanus* larvae respire atmospheric oxygen at the water surface and are predacious on other invertebrates.

Stratiomyidae

Larvae of *Odontomyia* were abundant in Kendal II (5 April — 2 July); an adult of *O. virgo* WIED. emerged from a puparium collected 9 June, although several species are probably represented in the larval collections (H. J. TESKEY in litt.). According to MCFADDEN (1967) eggs are usually deposited by females emerging in spring, larvae grow during the summer and overwinter in the final instar. Assuming this to be so for these *Odontomyia* spp., final instar larvae would be capable of resistance to drying and cold in the dry pool basin for 8 months. Tolerance of dry habitats is not unusual since most Stratiomyidae have terrestrial larvae, but *Odontomyia* is a member of the Stratiomyinae, one of the few Nearctic aquatic subfamilies (HINTON 1953; MCFADDEN 1967). Aquatic stratiomyids respire atmospheric oxygen and feed on algae and detritus (MERRITT & SCHLINGER 1978).

3.2.5 Acari

Species in three families are assigned to Group 2 — Hydryphantidae, Arrenuridae, and Pionidae; members of all of these families are found in permanent waters and their occurrence in temporary pools represents independent invasions. Apart from one subgenus of Arrenuridae, larvae of all of them parasitize adults of aquatic Diptera, mainly Nematocera, and it is noteworthy that in three disparate families life cycles have been independently adapted to permit exploitation of these hosts in temporary pools. Parasites of Diptera require some development after engorgement for the mite to reach its aestivating and overwintering stage; therefore mite populations can be sustained only if pools retain water for a period after the dipteran hosts emerge. Parasites of Odonata, species of the subgenus *A. (Arrenurus)*, require no further development for aestivation after their return to the basin, in keeping with later emergence of their hosts.

Hydryphantidae

Adults and deutonymphs of *Hydryphantes ruber* (DE GEER) were collected in K II from 15 April — 4 June in 1973 and 74; adults of *Thyas barbigera* (VIETS) in K II from 13 April—4 June 1974. The latter species was also collected from K I and VI, and *H. ruber* in K I but never in K VI, only 30 m from K I, even though many collections of mites were made there. *H. ruber* was recorded from autumnal pools in Michigan (KENK 1949) and Britain (BEVERCOMBE et al. 1973); and we found *T. barbigera* to be the most common and abundant species of Thyadinae in the temporary pools sampled in southern Ontario. Other species of Thyadinae — *Thyas stolli* KOENIKE, *Zschokkea bruzelii* LUNDBLAD, *Thyasides sphagnorum* HABEEB, *Euthyas truncata* (NEUMAN), and *Thyopsis cancellata* (PROTZ) — have been reported from temporary pools in Michigan (COOK 1955, 1959, 1974). We collected members of each of these species in temporary pools in southern Ontario, but the immediate histories of these habitats are not completely documented and it is probable that some of them were autumnal.

Adults of Hydryphantidae were collected throughout the spring wet phase of the temporary pools, and were most abundant in April immediately after the pools refilled with water. Mites of this family survive the dry phase of temporary pools as deutonymphs or adults in microhabitats with persistent moisture where they evidently are inactive. We have observed specimens of both *Hydryphantes* and *Thyas*, occasionally in substantial aggregations, in moist crevices on logs and beneath stones and other debris in dry portions of the basin of K II, Chaffeys Locks I, and other pools; and we have recovered small numbers of adults and deutonymphs by flooding samples of substrate from pools (Kendal I, Aurora VII, Britannia IV, Aberfoyle I, etc.) that had been dry from July through September. KENK (1949) reported that members of these genera can tolerate drought for considerable periods in muddy substrates of temporary pools. Our observations indicate that when water returns to a pool in early spring, deutonymphal and adult Hydryphantidae become active and females begin to oviposit shortly thereafter. After hatching, larvae seek out mature pupae of appropriate dipteran hosts, Ephydridae in the case of *Hydryphantes*, and Tipulidae, Culicidae, or Chironomidae in the case of Thyadinae (MULLEN 1974; SMITH & OLIVER 1976). As the insects emerge at the water surface, the larval mites attach to the imagoes, leaving the pool with their hosts. The mites complete engorgement on the host and drop back into the water, anchoring themselves by embedding their chelicerae in substrate material before entering the quiescent nymphochrysalis stage. Metamorphosis to the active deutonymph apparently proceeds rapidly, for both deutonymphs and adults are active during May and June as the pool is drying.

The life histories of hydryphantid mites are as yet poorly known. We have found both deutonymphs and adults in populations in early spring and throughout the year which might indicate that a 2-year life cycle is involved; if so, deutonymphs emerging from nymphochrysalises in spring must endure a second summer and winter before producing imagochrysalises and maturing as adults the following spring when water returns to the pool basin. Although as yet not documented, early spring adults may also emerge from imagochrysalises in late March or early April.

Hydryphantid mites are adapted to various marginal aquatic habitats, such as moss zones of streams and seepage areas as well as temporary pools. These mites exhibit numerous primitive attributes in both morphology and behaviour, particularly in the essentially terrestrial larval instar, and apparently represent a persistent early derivative lineage of water mites (MITCHELL 1957; COOK 1974; SMITH & OLIVER 1976). The simple life history strategy of hydryphantids restricted to temporary pools depends mainly upon the ability of deutonymphs and adults to withstand prolonged drought by becoming inactive, thereby enabling these feeding and growth instars to respond facultatively to a return of surface water in the basin. This endurance ability probably should be regarded as a primitive condition in hydryphantids, reflecting the condition of their primarily terrestrial ancestors. In temporary-pool species such as *Hydryphantes ruber* and *Thyas barbigera*, this mechanism has been integrated with a rapid rate of development of the essentially terrestrial, parasitic larvae, coinciding with an abundant supply of nematocerous Dipteran hosts during the wet phase of the pools.

Arrenuridae

Two subgenera of *Arrenurus* represented in the temporary-pool fauna have markedly different adaptations. *Arrenurus (A.) planus* MARSHALL, the only Nearctic species of the subgenus *A. (Arrenurus)* in temporary pools, is widely distributed in temperate North America (COOK 1954; MÜNCHBERG 1952). Although we found adults of *A. planus* abundantly in several temporary pool habitats in southern Ontario, only a single female specimen was collected (12 June 1973) from Kendal II during the intensive study period.

The ability of *A. planus,* and its Palaearctic sister species *A. papillator* (MÜLLER), to live in vernal pools stems from a modification that is unique among water mites — a structurally drought-resistant nymphochrysalis instar (MÜNCHBERG 1937, 1952). Under laboratory conditions MÜNCHBERG (1952) found that fully engorged larvae of *A. planus* removed from hosts from various localities in eastern North America developed a thick, parchment-like integument which he termed "nymphoderma", and then entered an extended phase of arrested development in the nymphochrysalis, even when kept in water. Further, he found that resting specimens exposed to desiccation for several weeks after leaving the host would quickly resume development and transform to deutonymphs when placed in water. On the other hand, nymphochrysalises kept in water from the time they were removed from the host developed at irregular rates, some dying from fungal infection and others transforming to deutonymphs only after 6—8 months. He concluded that desiccation was necessary to promote successful development of the deutonymphal instar. Our field observations on populations of *A. planus* in southern Ontario confirm this endurance mechanism in vernal pools. As reported by MÜNCHBERG (1952), larvae of *A. planus* are parasites of adult Odonata of the genera *Lestes* and *Sympetrum* (see Group 3), apparently attaching to the hosts as they emerge from the rapidly drying pool. The hosts are active in the vicinity of pool basins while maturing; the larval mites become engorged, develop their thick "nymphodermal" integument, and drop off into a pool basin during this 1—2 week period, usually in late June. The mites then enter the quiescent nymphochrysalis stage lasting throughout the summer, autumn, and winter exposed on the pool basin and subject to freezing. Apparently a diapause mechanism is involved, for as observed by MÜNCHBERG and confirmed by us, deutonymphal metamorphosis is not stimulated by submerging newly formed nymphochrysalises in water; the mites would not therefore be active in autumnal pools. When pools fill with water in early spring, the mites resume rapid development, emerging as free-swimming, predacious deutonymphs by mid-April. These nymphs feed voraciously, apparently mainly on ostracods, and develop quickly to enter the transitory imagochrysalis stage during which they metamorphose to adults. Maturation of the predacious adults, mating, and oviposition are completed by late May. Larvae hatching from the resulting eggs during early June seek out mature larvae of *Lestes* and *Sympetrum* prior to their final ecdysis to the adult stage. *A. planus* occurs in temporary pools that retain water for a period sufficient to permit larval *Lestes* and *Sympetrum* to complete their development. Substantial populations of *A. planus* also exploit temporary-pool conditions around the edges of basins which have fluctuating levels of water throughout the summer, autumn, and winter.

The remarkable drought-resistant nymphochrysalis instar found in *A. planus* and *A. papillator* is a derivative life history feature which is clearly an adaptation for life in temporary pools. Members of all other species of the large subgenus

A. (Arrenurus) inhabit permanent water and have ephemeral nymphochrysalises with thin integuments.

Species of a second subgenus, *A. (Truncaturus)*, although not represented in K II collections, also occur in temporary pools; we collected adults of *A. (T.) kenki* Marshall and *A. (T.) lacrimatus* Cook from autumnal pools in southern Ontario. These mites do not swim in open water, but restrict their movements to short sorties among the foliage of mosses and grasses near the water's edge; consequently they can be collected most efficiently by visual searching. Adults appeared in early spring collections, were most abundant during early May, and disappeared by the end of May with no active instars in evidence until the following spring even in the autumnal stage of the pools. Larvae of *A. (Truncaturus)* are parasites of adult Culicidae (Mullen 1974, 1975). The life history of these mites thus appears to be similar to that of Hydryphantidae inhabiting temporary pools in that adults and possibly deutonymphs are capable of enduring summer drought and the rigours of overwintering in dry pool basins.

Pionidae

Adults collected from temporary vernal K II were *Piona napio* Crowell and *Tiphys brevipes* Habeeb. Adults from K I and VI in 1974 (temporary autumnal pools) were *P. constricta*?, *P. napio* (K VI only), *P. clavicornis* (Müller) (K I), *T. americanus* Marshall (K I), and *T. brevipes*. All of these species are common and widespread in eastern North America (Cook 1956, 1960; Crowell 1960; Smith 1976); *Tiphys vernalis* (Habeeb) and *Piona mitchelli* Cook, although less common, were also found in other temporary pools in southern Ontario (Smith 1976). On the basis of our observations, these mites are restricted to temporary pools or permanent pools which undergo marked fluctuation in water level through the summer.

The life history of pionids is similar to that of hydryphantids inhabiting temporary pools, but with the distinction that only the deutonymphal instar is capable of enduring drought and overwintering. Our observations reveal that deutonymphal Pionidae become active in early spring, mature rapidly, and fix their mouthparts to submerged vegetation before entering the imagochrysalis stage. At this time, early to mid-April in southern Ontario, large aggregations of pale red pionid imagochrysalises often including members of several species can be found on submerged mosses, with each mite attached at a leaf axil. In warm weather this stage may last for only 1 or 2 days; adults emerge and mate immediately. Males die shortly afterwards, and therefore can be collected only during a very short period early in the season. Pionid males in temporary pools, especially those of *Tiphys* spp., are rather poor swimmers and usually remain among aquatic mosses where they can be collected best by visual searching; consequently they usually are absent or under-represented in dip net samples. Fertilized females are voracious predators and mature in about 2 weeks, ovipositing in early May.

Larvae hatch shortly thereafter, and seek out pupae of Chironomidae (Orthocladiinae or Chironominae) which are developing in their tubes on the substrate (SMITH 1976; SMITH & OLIVER 1976). Locating a host, the larva holds on to its integument until the pupa has risen to the surface of the water, and then attaches as an external parasite to the imago as it emerges. Engorgement is completed within 1 or 2 days and the mites drop from the host while over water. Upon returning to water the fully fed larvae anchor themselves to rooted vegetation, usually moss, enter the brief nymphochrysalis stage, to emerge as active deutonymphs while the pool is drying rapidly. As water disappears from the pool basin, pionid deutonymphs locate suitable protected sites in the substrate and remain there through the summer, autumn, and winter.

The ability of the deutonymphal instar to endure drought over the summer, autumn, and winter appears to have developed independently more than once in both *Piona* and *Tiphys* from ancestral species living in permanent water and having an unusually long deutonymphal stage (SMITH 1976). This primitive life history pattern is exemplified by *Piona carnea* (KOCH) and *P. neumani* (KOENIKE), two species of common occurrence in shallow permanent ponds and temporary autumnal pools throughout temperate North America (COOK 1960; KENK 1949; SMITH 1976), and present in K VI in 1973. Life history studies of these species and of *P. constricta* (WOLCOTT) whose members occur in a wide variety of temporary, semi-permanent, and permanent habitats, would provide valuable new insight into the process of adaptation to temporary pools by Pionidae.

Pionid and arrenurid mites represent widely divergent phyletic lineages derived from ancestral stocks in which all instars were fully adapted aquatic organisms. Larvae of these mites also parasitize relatively short-lived adult insects, nematocerous Diptera or Odonata; and it is significant that certain species in these families exploit temporary pool habitats through life history strategies resembling those of hydryphantids, depending upon a drought-endurance mechanism in the post-larval instars. The drought-endurance mechanisms which evolved independently in adults of *Arrenurus (Truncaturus)* and deutonymphs of various species of *Tiphys* and *Piona* do not involve striking morphological modifications and apparently stem from behavioural and physiological adaptations. It is interesting that these mites are structurally adapted to survive in the absence of surface water though derived from widely separated ancestral stocks restricted to permanent water. The structurally drought-resistant nymphochrysalis of *A. (Arrenurus) planus* and its sister species represents a unique evolutionary development.

Although no specific diapause mechanism has been demonstrated for mites in Group 2, none of these species is active during the summer or autumn even when water is present in pools where they are abundant during the preceding and succeeding spring. Attempts to recover aestivating specimens by flooding samples of substrate from dry pool basins during the summer and autumn have yielded very few specimens, suggesting that deutonymphs and adults of Group 2 mites undergo obligatory diapause development before resuming activity. Since larvae of these mites are obligate parasites on spring-emergent hosts and their other stages are predacious, resumption of activity in autumn would have little advantage.

3.3 Group 3. Overwintering summer recruits

These species enter the pool basin after surface water disappears because oviposition is independent of water. Oviposition may be preceded by a larval or ovarian diapause away from water, thus recruitment occurs at various times during the summer (Fig. 9). Group 3 animals tend to be colonizers. Most species overwinter as eggs, but some Trichoptera overwinter as larvae in the gelatinous egg matrix. Oviposition independent of water is a derivative behavioural feature which has evolved in parallel with moisture-retaining characteristics of the egg in most species except, perhaps, the Sciomyzidae.

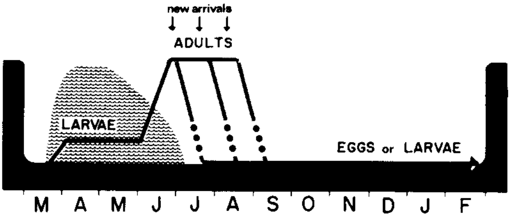

Fig. 9. Group 3 cycle; dots indicate oviposition.

3.3.1 Odonata

Larvae of only two genera, *Lestes* (Lestidae) and *Sympetrum* (Libellulidae), were taken in temporary vernal K II in 1972, 73, and 74. In 1973, species of the same two genera occurred in K I and VI after these pools had been permanent for the preceding 12 months, together with larvae of: *Enallagma boreale* SELYS, *E. hageni* (WALSH) and/or *ebrium* (HAGEN), *Coenagrion resolutum* (HAGEN) (?), *Nehalennia irene* (HAGEN), *Ischnura posita* (HAGEN) (Coenagrionidae); *Libellula quadrimaculata* L. (Libellulidae); and *Aeschna umbrosa* WALKER (Aeschnidae). Early instars of the next year's generation of *Enallagma* or *Coenagrion* sp. were also collected in July 1973; but, after both K I and VI became dry in late summer of 1973, filling again in the autumn of that year (i.e. became temporary autumnal), the odonate community in the 1974 collections was the same as in K II. These observations demonstrate that some species of *Lestes* and *Sympetrum* are able to withstand drought periods for as long as 8 months of the year; but that sympatric species in other genera cannot do so, even though in other respects the pools are suitable for their oviposition. Restriction of the odonate fauna to *Lestes* and *Sympetrum* is corroborated by collections from several other temporary pools in this same study. A major distinction of both genera is that most of their species differ from other Odonata in not requiring water for oviposition. But, as discussed below, other interdependent adaptations are also involved, with the result that in fact only certain species in both *Lestes* and *Sympetrum* are able to reproduce successfully in temporary pools. Some *Lestes* species are also the sole damselflies of temporary pools in Europe, although *Coenagrion hastulatum* CHARP. was able to tolerate a dry period of about one month in an autumnal pool (FISCHER 1961).

Two species of *Lestes* were identified in K II, *L. dryas* KIRBY and *L. unguiculatus* HAGEN, based on late instar larvae and teneral adults. A consistent pattern of development was evident through collections of all 3 years: the smallest instars were only present in the earliest collections (April, May); one collection of soil and melted snow under a layer of ice (21 February 1974) yielded three small *Lestes* larvae with no wing pads. Subsequent collections comprised successively larger instars, with teneral adults found from 12 June through early July.

Larval development of *Lestes dryas* and *unguiculatus* in K I and VI followed the same pattern as in K II, even though I and VI held water for the entire year preceding the 1973 collections, and from late autumn through the 1974 collections. Larvae of *Lestes congener* were also collected from both K I and VI in 1973.

Adaptations in *L. dryas* and *unguiculatus* leading to their successful colonization of temporary pools can be viewed as the net result of a series of specializations (Fig. 10). In general, species of *Lestes* oviposit endophytically from mid to late summer, either in plants on or beneath the water surface as in the European *L. sponsa* HANS. (CORBET 1962), or above the water surface in emergent aquatic plants (e.g. *Typha, Scirpus,* and *Sparganium*) or in riparian species (e.g. *Eupatorium* and *Salix*) overhanging the pool (BICK & BICK 1970; WALKER 1953). Eggs of some species such as *L. eurinus* SAY undergo direct development to hatch within 19 to 45 days, overwintering as larvae (LUTZ & PITTMAN 1968). In other species egg development is delayed by diapause: *L. dryas, L. unguiculatus, L. congener* HAGEN, and *L. disjunctus* SELYS (SAWCHYN and CHURCH 1973); *L. rectangularis* SAY (GOWER and KORMONDY 1963); *L. sponsa* (CORBET 1956b, 1962). After a period of normal development an obligatory diapause follows for which the optimum rate of development occurs at approximately 10°C. Eggs with only this first phase of diapause, such as those of the European *L. sponsa,* could still hatch in autumn after completion of diapause development, but by this time the ambient water temperature is usually below the lower threshold for hatching, which is then delayed until spring (CORBET 1962). A second phase of diapause controlled by decreasing daily photoperiod has been established (SAWCHYN & CHURCH 1973) for *L. disjunctus* and *L. unguiculatus,* and predicted for *L. dryas* which maintains the diapause period into winter when low temperatures always inhibit hatching. Because of this photoperiod-controlled diapause, larvae of the K II species *L. unguiculatus* and *L. dryas* cannot hatch to begin growth in autumn in either temporary

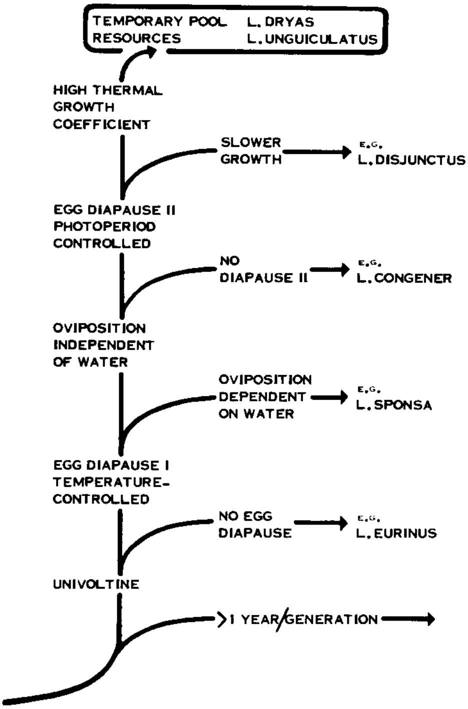

Fig. 10. Adaptive features leading to occurrence of a few *Lestes* species in temporary pools.

autumnal or permanent pools. This explains why all *Lestes* larvae in the earliest spring collections from pools I and VI were uniformly small and without wing pads even though these pools were permanent for 12 months preceding the 1973 collections and temporary autumnal preceding the 1974 collections. Post-diapause development and hatching are stimulated by a combination of rising temperature, increasing photoperiod and, in vernal pools, sufficient wetting (Corbet 1962); a high thermal coefficient for growth ensures that the larval growth rate accelerates with increasing temperature (Corbet 1962), another requisite for temporary-pool Odonata (Hodgkin & Watson 1958).

Although not found in K II, *Lestes congener* larvae were taken in 1973 collections from K I and VI after they had been permanent pools for the year preceding these collections. Because *L. congener* has a long temperature-controlled diapause, it always overwinters in the egg stage (Sawchyn & Church 1973), but along with *L. disjunctus* has not been recorded from temporary pools in Canada, possibly because the two are the latest summer species of *Lestes* (Walker 1953) and cannot complete larval development before the pools dry up.

Two species of *Sympetrum*, *S. obtrusum* (Hagen) and *S. rubicundulum* (Say), were identified in vernal K II from late instar larvae, the former dominant in numbers; teneral adults of *S. obtrusum* were also collected at the edge of the pool. A consistent pattern of development was evident in all K II collections — small instars in the collections of April and May, final instars and teneral adults in June and July. As outlined above for *Lestes*, an identical pattern of development was revealed in collections from K I and VI, indicating that in nature the egg diapause is independent of submergence by surface water during the preceding autumn. October soil samples from K II produced small early instar *Sympetrum* larvae only after an interval of approximately 2 months from time of flooding in the laboratory. December and February soil samples yielded many more larvae of *Sympetrum* (and *Lestes*), beginning in the December samples 20 days (35 days for *Lestes*) after flooding; and in the February soil samples beginning 5 days after flooding for both genera. From a study in Indiana, TAI (1967) reported that *S. obtrusum* and *rubicundulum* were temporary-pool species whose eggs hatched synchronously at high temperatures (21°C) only after completing a period of diapause development at a low temperature (10°C); and that egg development was the same in two species characteristic of permanent water, *S. vicinum* (HAGEN) and *semicinctum* (SAY). Diapause of this sort resembles that described above for *Lestes sponsa* (CORBET 1962), suggesting that only the temperature-controlled first phase of diapause is operating in *S. obtrusum*. From a study of *S. internum* MONTGOMERY and *S. rubicundulum* in an autumnal pool in southern Ontario, PETERSON (1975) concluded that eggs of those species did not hatch until spring because water temperatures were below the hatching threshold by the time the temperature-controlled phase of diapause was completed in autumn. Although they did not study egg diapause in *Sympetrum*, SAWCHYN & CHURCH (1973) interpreted some of the anomalous results of hatching times in other accounts for the European *S. sanguineum* MULL. to suggest that a photoperiod-controlled diapause influenced hatching in that species. None of these results shows clearly whether or not both temperature and photoperiod phases of diapause are operating to retard hatching of *Sympetrum* eggs, as outlined above for *Lestes*. Furthermore, information on hatching times for eggs of various species of *Sympetrum* is not consistent. Response to submergence may be the principal factor controlling hatching in some species, for eggs of the European *S. flaveolum* L. are reported to hatch in autumn shortly after oviposition in water, although not to hatch until spring if not submerged until that time (ROBERT 1958). Eggs of the European *S. striolatum* CHARP. hatched within 3 to 4 weeks of oviposition, the larvae overwintering in the fourth or fifth instar (CORBET 1956a). Collections from K I and VI pools on 2 November 1977 failed to yield *Sympetrum* or any other odonate larvae; thus whatever the mechanism, it seems clear that eggs of *S. obtrusum* and *S. rubicundulum* do not hatch until spring. As seen in *Lestes*, not only does this strategy overcome a dry period of up to 8 months of the year, but also it synchronizes hatching and growth of the predaceous larvae for spring and early summer when prey density is highest.

In contrast to *Lestes*, oviposition in *Sympetrum* is exophytic, as it is in all of the Libellulidae; females of *Sympetrum* deposit eggs by dipping the end of the abdomen into water or by dropping eggs on dry land, and there are observations of the latter behaviour for several European and North American species (NEEDHAM 1901; WESENBERG-LUND 1913). TAI (1967) reported that the elongate eggs of *S. vicinum* and *semicinctum*, species of permanent waters, were deposited in gelatinous masses; but that the more spherical eggs of the temporary-pool species *S. rubicundulum* and *S. obtrusum* were released in a bead-like string with only a thin gelatinous covering and could roll to a low resting position in the dry pool basin. He also found that eggs of the temporary-pool species had remarkable winter-hardiness and resistance to drying; and that they became dark brown on exposure to air, whereas eggs of *S. vicinum* and *semicinctum* remained yellowish white. Although he did not elaborate on the significance of these differences, it is reasonable to suppose that the darkening results from some component enhancing structural rigidity and drought resistance of eggs that remain on dry soil for an 8-month period. WALKER & CORBET (1975) observed that *S. obtrusum* is probably the commonest anisopteran in settled parts of eastern Canada in late summer; widespread abundance is consistent with the ability to range widely to colonize isolated larval habitats.

The evolutionary strategy for exploiting temporary pools is therefore similar for species in both *Lestes* and *Sympetrum*, yet remarkably uncommon when all Odonata are considered. Several adaptive features, variously represented in other species, are coincident only in those species that exploit temporary pools successfully: one-year life cycle; oviposition independent of water; temperature-controlled egg diapause; photoperiod-controlled egg diapause *(Lestes);* high thermal coefficient for growth; and modification of egg shape and chorion structure for terrestrial oviposition *(Sympetrum).* Even within *Lestes* (Fig. 10) and *Sympetrum* these features are not coincident in all species. However, of the three sections of Nearctic *Sympetrum* defined by WALKER & CORBET (1975), species characteristic of temporary pools have been assigned to section 3, although entirely on morphological evidence. Detailed analysis of larval morphology by TROTTIER (1969) also supports the close relationship of temporary-pool species of *Sympetrum.* Since Odonata first became aquatic in cool, running waters (CORBET 1962), the species in temporary pools can be considered later derivatives. Lestidae and Libellulidae are placed as moderately to highly advanced families in the Zygoptera and Anisoptera, respectively (RESH & SOLEM 1978, after FRASER 1957).

3.3.2 Trichoptera

Species in two families among Kendal II collections for 1972, 73, and 74 are members of Group 3. In the Limnephilidae two subfamilies are involved: *Limnephilus indivisus* WALK., *L. submonilifer* WALK., *Anabolia bimaculata* (WALK.) (Limnephilinae); *Ironoquia punctatissima* (WALK.) (Dicosmoecinae). Of the Phryganeidae, only *Ptilostomis ocellifera* (WALK.) is represented.

Collections of the limnephilid species show general progression in development from early to late instars from April through June. Early instar larvae of *L. indivisus* and *L. submonilifer,* also became active in the soil samples after flooding. Eggs of the limnephilids are deposited in early autumn within a gelatinous matrix under logs or in other protected sites in the dry basin of a temporary pool (WIGGINS 1973). Development proceeds immediately and the larvae hatch from the eggs in a few weeks but remain within the matrix until flooded with water. If flooded in autumn, the larvae quickly leave the matrix, build cases and begin to feed on detrital materials; if a pool does not form until spring, the larvae remain within the matrix and may pass the winter there (WIGGINS 1973). When larvae in the Limnephilinae (*Limnephilus* and *Anabolia* spp. in K II) reach the final instar in late spring they undergo metamorphosis in the pool to emerge as sexually immature adults; diapause regulated by short-day photoperiods brings them to the reproductive condition in late summer (NOVAK & SEHNAL 1963, 1965) and oviposition takes place in September in damp locations of the waterless pool basin (WIGGINS 1973). Although eggs of *Anabolia bimaculata* have not yet been found, other aspects of the life cycle indicate similarity of that species to *L. indivisus.*

A different strategy is seen in *Ironoquia punctatissima,* a member of the Dicosmoecinae. Final instar larvae crawl out of the pool to conceal themselves in plant litter around the edge where they aestivate in diapause until late summer when metamorphosis takes place (FLINT 1958; WIGGINS 1973; WILLIAMS & WILLIAMS 1975). No *I. punctatissima* larvae were collected from K II after May and many had reached the fifth instar by mid-April. The larval diapause is probably regulated by short-day photoperiod as it is in the Limnephilinae. Also like the Limnephilinae, *Ironoquia* adults oviposit in autumn in moist microhabitats, but the gelatinous egg-matrix can be distinguished from that of *Limnephilus* species by a characteristic toughened surface sculptured in a pattern of swirling lines.

Ptilostomis ocellifera larvae were rare in K II collections but occurrence of third and fifth instars in early spring (15 April 1974, L III; 20 April 1974, LV) demonstrates their adaptation to vernal pools. The group to which this species should be assigned is not immediately clear, but as we have collected gelatinous egg matrices of *Ptilostomis* in September from a dry pool basin, we assign *P. ocellifera* to Group 3. We infer that females oviposit on the dry pool basin in late summer, their reproductive maturity delayed by photoperiod-controlled diapause over summer in the same manner as the European phryganeid *Trichostegia minor* (CURTIS) (NOVAK & SEHNAL 1963, 1965) which also inhabits vernal pools (IVERSEN 1971). Eggs develop without delay, and therefore *P. ocellifera* larvae will occur in temporary pools in autumn. However, larvae in vernal K II must have remained in the dry pool basin through autumn and winter for a period of at least 6 months. *Ptilostomis ocellifera* is predacious in later instars at least (WINTERBOURN 1971), although related genera, particularly in early instars, feed on decaying plant materials (WIGGINS 1977); in light of the reduced prey density in autumnal pools, we would expect this to be so in *P. ocellifera*.

All of the K II species occurred in K I and VI in 1973 and 74, together with *Nemotaulius hostilis* (HAGEN) (18 April 1973, L V), *Limnephilus sericeus* (SAY) (18 April 1973, April—May 1974, L III—V) (Limnephilidae); *Banksiola crotchi* BANKS (18 April, 12 June 1973, L V) (Phryganeidae); *Triaenodes aba* MILNE (April—July 1973, April—June 1974, L II—V), *Oecetis* sp. (June—July 1973, L III & V) (Leptoceridae). Not all these species can sustain a dry phase because *N. hostilis, B. crotchi,* and *Oecetis* sp., known only from permanent water in North America, occurred only in 1973 when these pools had been permanent for the preceding 12 months; they did not appear in 1974 collections after the pools became dry in late summer of 1973 (i.e. when K I and VI were autumnal pools), indicating that these species find the flooded pools suitable for oviposition but cannot sustain a dry phase. *Limnephilus sericeus,* occurring in both 1973 and 74, probably has most of the attributes of its congeners in K II and its appearance in autumnal pools is not surprising; nonetheless, it has never been collected in vernal K II. Occurrence of early instars of *Triaenodes aba* in 1974 after K I and VI had become autumnal in 1973 demonstrates that a Nearctic leptocerid has some capacity to sustain periods of drought; since second and third instars appeared in April 1974, we suspect that the eggs are the resistant stage. Adaptation of *Triaenodes* to transient waters is not surprising because a European species is a pest of rice fields (MORETTI 1942).

The effect of diapause in all of the Trichoptera of Group 3 is to defer oviposition for some 3 to 4 months until the dry soil of the pool basin has been moistened through autumn rains and reduced insolation; for all of its properties of moisture retention, the gelatinous matrix surrounding the eggs would be unlikely to resist the intense desiccation which pool basins undergo in summer (WIGGINS 1973). Larvae within the matrix are quiescent in the absence of water and have a facultative response to early flooding which enables them to utilize autumnal pools, should these appear, to gain initial advantage for development in the short-lived pools of spring; for detritivorous feeders this is an appropriate strategy. Even without an autumnal pool, the larvae can use very small amounts of water to begin their free-living existence. On 8 February 1974 from a small depression in the deepest part of the K II basin we took third and fourth instars of *I. punctatissima* and second instars of *L. indivisus* in 5 cm of water at about 0°C beneath 8 cm of ice; the basin of Kendal II was entirely without surface water through autumn to the time the ground froze in December, and we believe the water resulted from a mild period in January. Gelatinous matrices located on logs where unseasonal melting has no effect can, however, retain living larvae until March, a period of 6 months without surface water through autumn and winter (WIGGINS 1973).

None of these species is confined to temporary pools, although the *Limnephilus* and *Ironoquia* species appear to achieve maximum abundance in transitory aquatic habitats. Adults of *L. submonilifer* are wanderers, sometimes occurring in late summer in houses well removed from normal oviposition sites. *Ptilostomis ocellifera* occurs over much of North America, mostly in lakes and permanent streams. Oviposition independent of water is clearly derived from the normal behaviour of oviposition in water characteristic of other Trichoptera but is not confined to temporary-pool species (Wiggins 1973). Limnephilinae species of permanent lakes and cool streams lay eggs above water within a thickened gelatinous matrix which thins and drops to the water below after larvae hatch, whereas the egg matrix of temporary-pool species remains firm (Wiggins 1973). Diapause occurs in other genera that are characteristic of permanent waters (Wiggins 1973). Therefore in the Trichoptera adaptation to temporary pools can be seen as a series of specialized features shared with various groups in permanent waters but coinciding only in species successful in temporary waters. Phylogenetic evidence reveals that lentic Trichoptera were derived from cool lotic ancestors (Ross 1956), and therefore the temporary-pool forms may be considered late derivatives in the exploitation of standing water habitats (Wiggins 1973).

3.3.3 Diptera

Four families are represented in Group 3.

Chironomidae

Among the chironomid larvae collected in both wet and dry phases of vernal pool Kendal II through 1972, 73 and 74 were unidentified species in 3 genera of the Metriocnemini (Orthocladiinae): *Limnophyes* (larvae 5—13 April; Oct.—Feb. in soil samples); *Paraphaenocladius* (larvae 13 April; Oct. soil sample); *Smittia* (larvae 13 April; Oct.—Apr. in soil samples).

Since the Metriocnemini comprise mainly terrestrial or semi-aquatic species (D. R. Oliver in litt.) which oviposit on damp soil independent of surface water (Strenzke 1950), we are assigning this component of the K II chironomids to Group 3. Although none of the K II larvae collected during the wet phase were reared, we assume that these larvae are capable of completing the final stages of development under water to emerge some time during or shortly after the existence of the pool. This being so, the temporary-pool species are among the semi-aquatic or amphibious Metriocnemini rather than the purely terrestrial.

Larvae of the Metriocnemini are detritivorous (Coffman 1978). Diapause, if it takes place at all, would probably occur at the end of larval development (Danks 1971b). We infer, therefore, that larvae of Group 3 Chironomidae could hatch and commence feeding on the abundant detrital resources shortly after oviposition in the damp basin. Thus Group 3 Chironomidae appear to have an advantage over those of Group 2 in exploiting temporary-pool resources because they can feed during the dry phase. Should feeding activity be retarded during the wet phase, semi-aquatic Metriocnemini would appear less suited to autumnal than to vernal pools; but if their feeding is not inhibited by flooding, these species would have gained remarkable flexibility.

Aquatic genera of the Orthocladiinae are assigned to Group 2, but in accordance with BRUNDIN's (1966) interpretation of phylogeny for the family, the terrestrial genera of Group 3 are clearly derived from aquatic ancestors, and ultimately from ones in cool, running waters. Thus temporary pools may have been involved in the selection processes leading to derivation of terrestrial chironomids from aquatic ancestors, with Group 2 species the probable biological antecedents of those in Group 3. Respiration for apneustic chironomids that have returned to the land-dwelling existence of their dipteran ancestors would be cutaneous, and probably dependent on some soil moisture.

Culicidae

Only the genus *Aedes* was represented in collections from temporary vernal K II, with larvae of five species during April and May of 1973 and 74: *Ae. fitchii* (F. & Y.), *Ae. provocans* (WLK.), *Ae. excrucians* (WLK.), *Ae. stimulans* (WLK.), and *Ae. euedes* H. D. & K. Over the same period these same species of *Aedes* were collected in K I, although only *Ae. fitchii* and *Ae. stimulans* in K VI. In addition, *Culex territans* WLK. larvae were taken in pools K I and VI, and *Anopheles earlei* VARGAS, *An. walkeri* THEO., and *An. punctipennis* (SAY) ? in K I.

Interpreted in relation to literature on mosquito biology, these observations reveal much about the strategies of mosquitoes for temporary pools. In northeastern North America only *Aedes*, *Psorophora*, and *Culiseta morsitans* (THEO.), are recorded from temporary pools; larvae of some species of *Psorophora* are predatory on the others which are mainly filter-feeders. *Aedes* and *Psorophora* are unique among Nearctic genera because their eggs are deposited on soil in depressions in which surface water later accumulates; thus, because their oviposition is independent of surface water, species in both *Aedes* and *Psorophora* are assigned to Group 3, although only *Aedes* was represented in our collections. The critical adaptation in *Aedes* and *Psorophora* for transient waters is a thickened egg chorion which reduces water loss but retains permeability to oxygen (CRAIG & HORSFALL 1958). Unlike other mosquitoes, the larger part of the life cycle of univoltine species of *Aedes* and *Psorophora* is spent in the egg stage (CRAIG & HORSFALL 1958) and these eggs can remain dormant for several years (HORSFALL 1955).

The five species of *Aedes* we collected as larvae are members of the subgenus *Ochlerotatus*, as are most of the *Aedes* species occurring in vernal pools; but larvae of a sixth species, *Ae. vexans* (MG.) (subgenus *Aedimorphus*) became active in December soil samples from K II 3 weeks after flooding in the laboratory at 10°C.

This species is multivoltine, and able to produce up to three successive generations in a year (Horsfall et al. 1973) without the obligatory diapause of the univoltine *Aedes (Ochlerotatus)* species. Eggs of *Ae. vexans* resist desiccation and the number of generations or broods produced at a given site depends upon the frequency at which eggs are flooded. Time of occurrence of *Ae. vexans* larvae in K II is not known, but in contrast to the other species of *Aedes* in the dry basin K II, *Ae. vexans* eggs would be capable of hatching if surface water accumulated during summer. In a situation of this kind in southern Ontario (James 1960), larvae of *Ae. vexans* hatching in July perished when surface water quickly dried up. Although water in autumnal pools could stimulate hatching, larvae of *Ae. vexans* do not normally appear unless the water temperature is above 15°C (Horsfall et al. 1973), conditions that would rarely occur in a temporary autumnal pool in southern Ontario. Hatching and development of *Ae. vexans* from K II soil samples flooded at 10°C is therefore unexpected; the lower temperature may account for the fact that only 2 larvae were observed from a total of 20 soil samples. Both of these general types of life cycles are complicated by the fact that eggs of a single female may not all hatch at the same time, thus giving rise to different broods; for example, eggs of *Ae. canadensis,* a typical vernal pool species, can also hatch when flooded in autumn, i.e. in a temporary autumnal pool, because some eggs undergo diapause while others do not (Horsfall 1955).

Most species of *Anopheles* overwinter as adults, depositing eggs on the water surface in spring; eggs of most *Anopheles* are not resistant to desiccation or to low temperature (Horsfall 1955). Larvae of three species of this genus were taken in K I in 1973 (July), but only of *An. walkeri* (?) in 1974, reflecting the change of this pool from permanent preceding the 1973 collections to temporary autumnal for the 1974 collections; *An. walkeri,* the one Nearctic species of *Anopheles* known to overwinter in the egg stage (Horsfall 1955), could therefore inhabit temporary autumnal pools provided that development was completed before the pool dried up in spring. In both years, surface water remained in K I until mid-July, a longer period than in vernal K II where no *Anopheles* larvae were collected. Other *Anopheles* spp. could theoretically populate vernal pools as Group 4 animals, but this probably would not normally occur in Ontario because of low temperatures and short duration of surface water (Horsfall 1955).

Species of *Culex* usually overwinter as adults, and the eggs, which normally are not resistant to drying or freezing, are deposited in spring on the water surface. Larvae of *C. territans* were taken in K I and VI in 1973 (July and August) at the completion of an annual cycle as permanent pools, and in 1974 (July) when both pools had become temporary autumnal; no larvae of this species were taken in the vernal K II. Again, some species of *Culex* might enter temporary pools through eggs deposited in spring (Group 4), but could complete development only under an unusually long period of surface water. There is no diapause in *C. territans,* and the number of generations in a year appears to be a function of temperature (HORSFALL 1955).

Although none were collected in the Kendal pools, larvae of some species of *Culiseta* (syn. *Theobaldia*) are recorded from temporary pools (HORSFALL 1955; BEVERCOMBE et al. 1973). Species overwinter as adults which oviposit in spring on the water surface, or as larvae in permanent water; and eggs of some show resistance to drying (HORSFALL 1955). Thus, larvae of *Culiseta* in autumnal pools are dependent on early flooding but those in vernal pools can only be explained through either Group 3 or 4 strategy.

The hatching stimulus for aedine eggs in a temporary pool is a decreasing level of dissolved oxygen rather than simply a low level around the eggs (HORSFALL 1955; JUDSON 1960). Considering aedine mosquitoes over-all, three types of hatching response are exhibited when eggs are flooded (HORSFALL et al. 1973), depending on ambient levels of dissolved oxygen. Type I eggs, which hatch with no appreciable depression in oxygen, are characteristic of multivoltine species ovipositing in water where the level of dissolved oxygen remains fairly stable; *Culex* and *Anopheles* eggs are also of this type. Type II eggs will hatch whenever oxygen levels are depressed, the pattern to which *Ae. vexans* normally adheres. But Type III eggs will hatch in response to a decreasing level of oxygen only after they have been exposed to specific environmental conditions required for diapause development. A period of desiccation followed by low temperature is involved in some species of *Aedes* (KHELEVIN 1958), and photoperiod may also exert some influence (KAPPUS and VENARD 1967); December and February soil samples from K II produced many *Aedes* larvae a few days after flooding in the laboratory but few were obtained from the October soil sample. Type III species are univoltine and for the most part comprise *Ae. (Ochlerotatus)*, the group to which the snow-melt or temporary vernal pool mosquitoes belong. Most Nearctic *Aedes* are members of this subgenus; and the success of the temporary pool forms among mosquitoes generally can be gauged from the fact that approximately one-half of the 150 species of Nearctic mosquitoes belong to *Aedes* (ROSS 1964). This marked ecological success of temporary-pool aedine mosquitoes may be viewed as one of the later developments in mosquito evolution for *Aedes* and *Psorophora* are placed among the most advanced genera in the phylogeny of the Culicidae (ROSS 1951).

KALPAGE & BRUST (1973) have shown that females of *Ae. (Finlaya) atropalpus* (COQ.) oviposit preferentially in water in which pupae and fourth instar larvae have developed, indicating the presence of a chemical attractant resulting from successful larval development. The attractant is stable, and solutions evaporated to dryness can be restored to their original effectiveness by adding water. An attractant of this sort would be of enormous value to univoltine species of *Ae. (Ochlerotatus)* if effective in damp soil.

Chaoboridae

Larvae of *Mochlonyx* occur in temporary pools where they are predacious on copepods, ostracods, cladocerans, and mosquitoes (JAMES 1957); algae and fungi are also consumed (O'CONNOR 1959). *Mochlonyx* was collected only once in Kendal II, during its final stages (2 July 1974, L IV); occurrence of larvae at this late date is unusual although hatching is not synchronous (O'CONNOR 1959). Studies of *M. velutinus* (RUTHE) in Ontario (JAMES 1957) and of *M. cinctipes* (COQ.) in Ohio (O'CONNOR 1959) show that both species are univoltine; eggs deposited under leaves on damp soil of the pool basin in May and June undergo partial development during summer to overwinter in diapause, hatching in March shortly after the pool is flooded. Both studies were based on populations in vernal pools and do not test the possibility of hatching in an autumnal pool. Larvae were found in one December soil sample from K II 25 days after flooding in the laboratory, suggesting that eggs are ready to hatch by late autumn if flooded at an appropriate temperature. Since *Mochlonyx* larvae are predators, particularly on *Aedes* mosquitoes (CHODOROWSKI 1968), hatching confined to spring would be expected. *Mochlonyx* larvae grow rapidly and adults begin to emerge from pools in early May in Ontario (JAMES 1957).

Most *Chaoborus* species in temporary pools belong to Group 4, but BORKENT (1979) has shown in Alberta that *Chaoborus cooki* SAETHER overwinters in temporary pool basins as eggs. Since neither oviposition nor eggs were observed in the field, independence from water for oviposition is unconfirmed; but unlike *Chaoborus* species of permanent waters, eggs of *C. cooki* have a dark thickened chorion (BORKENT 1979), suggestive of the resistant eggs of related aedine mosquitoes which are deposited on damp soil. Therefore we place this species provisionally in Group 3. Although we did not collect *C. cooki* in any of the temporary pools studied in Ontario, BORKENT (1979) provides data illuminating characteristics of a temporary-pool species. Eggs of *C. cooki* with thickened chorions are deposited in a spherical mass, have delayed hatching, and the first instar larvae have a relatively large egg burster; eggs of the closely related *C. trivittatus*, a species overwintering as larvae in permanent waters (see Group 4), do not have a thickened chorion, are deposited in a spiral disc which forms a floating egg raft, hatch within 3 days, and first instars have a smaller egg burster. In an interpretation of phylogeny of *Chaoborus* based on morphological evidence from all stages, the temporary-pool species *C. cooki* is shown to be evolutionarily advanced in relation to species inhabiting permanent waters.

Sciomyzidae

Larvae in this family feed entirely on molluscs, some specializing on terrestrial and others on freshwater species (BERG & KNUTSON 1978). Thus sciomyzids occurring in temporary pools are wholly dependent upon the few species of

Mollusca (Group 1) that have become adapted to these rigorous aquatic habitats. Most aquatic Sciomyzidae feed on snails, but larvae in one Nearctic genus feed on sphaeriid clams (BERG & KNUTSON 1978; FOOTE 1976).

From vernal pool K II, two species of Sciomyzidae were collected as larvae: *Tetanocera loewi* STEYSKAL (18 April 1973); and *Sepedon fuscipennis* LOEW (2 July 1974). From autumnal pools, these species were collected: Kendal I — *T. loewi* (11 May 1974, larvae), *Atrichomelina pubera* (LOEW) and *Pherbellia* sp. (4 June 1974, puparia); Aberfoyle IX — *T. loewi* (19 April 1970, larvae); Britannia IV — *Tetanocera vicina* MACQUART (4 April 1970, larvae), *T. loewi* (28 April 1970, larvae), and *Dictya* sp. (31 May 1970, larvae).

Aquatic Sciomyzidae deposit eggs on emergent or shore-line vegetation; since they are not dependent upon surface water for oviposition, entry into the temporary-pool community is accessible to them during dry periods as for Odonata, Trichoptera, and other members of Group 3. In contrast to most other members of Group 3, Sciomyzidae of temporary pools include multivoltine as well as univoltine species; most Sciomyzidae have life cycles in which extended oviposition periods result in indistinguishable overlapping generations (BERG & KNUTSON 1978).

The snail-feeding sciomyzids, *Tetanocera vicina* and *T. loewi*, are both univoltine species living in temporary pools, adults emerging from puparia in early summer but not becoming sexually mature until late summer when they oviposit (BERG & KNUTSON 1978). Delay in sexual maturation suggests a reproductive diapause controlled by short-day photoperiod similar to that in *Limnephilus* caddisflies of temporary pools. According to BERG & KNUTSON (1978), eggs of *T. vicina* hatch as soon as embrvonic development is complete, and can thus begin early feeding in autumnal pools; if this is a facultative response to flooding similar to that of *Limnephilus* spp., *T. vicina* larvae in a vernal pool basin would remain within the egg until the spring thaw. Should the response not be facultative, *T. vicina* would be totally dependent on autumnal pools and unable to exploit pools that were solely vernal, a distinction to which future field observations might be directed. By contrast, eggs of *T. loewi* deposited in autumn appear to remain in diapause throughout the winter, hatching under the influence of long-day photoperiods and higher temperatures of spring (BERG & KNUTSON 1978); thus larval feeding and growth of *T. loewi* would be confined to spring, and this species specialized for vernal pools alone. If so, *T. loewi* appears also to be unusual among temporary pool animals in having two consecutive periods of diapause development within the life cycle, both photoperiod dependent: a reproductive diapause in the adult circumventing summer drought of the larval habitat, and a second embryonic diapause apparently synchronizing hatching with the return of surface water in vernal pools. Since temporary-pool snails upon which sciomyzid larvae feed would become available whenever the pool is flooded, *Tetanocera* species may be partitioning food resources through temporal restriction in larval feeding. Further illustrating the specificity of life cycle adaptations in the genus *Tetanocera* is the collection of *T. ferruginea* FALLEN from K VI (21 Aug. 1973, larvae); this species is multivoltine (C. O. BERG, in litt.), and K VI had been permanent for the preceding 12 months.

Although not represented in any of our collections, *Hedria mixta* STEYSKAL is another univoltine sciomyzid of temporary pools, unusual among Sciomyzidae in being confined to these habitats, and in preying on snails that are well below the water surface (FOOTE 1971). Eggs are deposited on *Typha* leaves in summer; embryogeny proceeds immediately to completion but hatching is delayed until spring by diapause which appears to require an extended period of low temperature for completion (FOOTE 1971). *Antichaeta melanosoma,* another sciomyzid not represented in our collections, oviposits in spring on egg capsules of snails, mainly *Aplexa hypnorum,* and the larvae feed on developing embryos (KNUTSON & ABERCROMBIE 1977); with increasing size, the fly larvae feed on mature *A. hypnorum,* and as the pool disappears form puparia in which they overwinter in diapause. Specialized in this way for vernal pools, both of these species would appear unable to exploit molluscs in autumnal pools.

Pherbellia sp. was collected as a puparium (4 June 1974) in K I, at that time a temporary autumnal pool. *Pherbellia* includes both univoltine and multivoltine species; larvae are actually terrestrial and drown in water (BERG & KNUTSON 1978), but certain species feed on aquatic snails that become exposed as temporary pools dry out. Completing larval development rapidly on stranded snails, these species resist summer drought and winter cold as diapausing pupae in basins of temporary pools, but the puparia float with spiracular plates exposed to air and are thus able to withstand any flooding that may occur in autumn or spring (BRATT et al. 1969).

Among temporary-pool Sciomyzidae classed as multivoltine is *Sepedon fuscipennis,* collected in K II. Summer drought is passed away from the temporary pool, the species breeding continuously in permanent lentic habitats and producing several overlapping generations; adults enter reproductive diapause in late summer, influenced by declining temperature and short-day photoperiod (BARNES 1976), and live through autumn and winter to mate and oviposit in spring (BERG & KNUTSON 1978; NEFF & BERG 1966). Therefore *S. fuscipennis* larvae appear unable to enter temporary pools until spring. With oviposition in spring, this species might be considered an overwintering spring recruit of Group 4; but since oviposition is independent of water, and adults are not dependent on permanent water for overwintering, we consider *Sepedon fuscipennis* as an exceptional case in Group 3.

Species of *Dictya* reproduce continuously throughout the year with no evidence of diapause at any stage (VALLEY & BERG 1977), and normally overwinter as pupae (C. O. BERG pers. comm.). Therefore we assume that larvae of this genus collected from a temporary pool in spring (Britannia IV, 31 May 1970) came from springtime oviposition. In an autumnal pool *Dictya* sp. might be capable of completing an autumn and a spring generation. *Atrichomelina pubera* has habits and life cycle similar to *Dictya* spp., except that this species feeds also on dead snails (FOOTE et al. 1960), thus exploiting snails exposed in the basin of receding pools.

Clams in the family Sphaeriidae are also eaten by sciomyzids, and are the exclusive larval food of the Nearctic genus *Renocera* and the European *Knutsonia lineata* (BERG & KNUTSON 1978). Of three species of *Renocera,* one completes at least two generations per year and inhabits permanent waters; the other two are univoltine and live in pools and marshes of a temporary nature (FOOTE 1976). *Sphaerium occidentale,* a common and widespread sphaeriid largely restricted to temporary pools, is among the prey species of *Renocera* spp. (FOOTE 1976). The flies emerge and oviposit in spring; larvae feed on clams, enter the pupal stage during the final phase of the pool, remaining in diapause until spring (FOOTE 1976).

In summary, since most sciomyzid larvae are dependent on atmospheric air for respiration and many are terrestrial in habits (BERG & KNUTSON 1978), it is not surprising that the shallow transient waters of temporary pools are favourable habitats for those species that have turned to exploiting their molluscan inhabitants. This is reflected in adaptations to temporary pools that are more specialized for Sciomyzidae than for other insect families of these habitats. There is marked specificity in prey: larvae of *Tetanocera* prey on snails near the water surface; *Hedria* prey on submerged snails; *Atrichomelina* and *Pherbellia* prey on aquatic snails stranded by receding water; *Antichaeta* prey on eggs of certain snail species; larvae of *Renocera* prey on Sphaeriidae. Some sciomyzid species are confined to vernal pools, and others are able to utilize both vernal and autumnal pools. Most predators in temporary pools are so synchronized that they do not commence feeding until well into the spring period when populations of crustaceans and insects reach maximum abundance; because the molluscan prey of Sciomyzidae are available at any time after flooding, larvae of some species begin feeding in autumnal pools. The autumn molluscs are, however, all that remain of the breeding populations after the rigorous summer drought; all temporary-pool molluscs reproduce in spring, the young undergoing rapid development, and thus the vernal pool period provides much higher prey density even for predators on molluscs. The Sciomyzidae illustrate a wide assortment of the specializations enabling an animal group to exploit temporary-pool resources.

3.4 Group 4. Non-wintering spring migrants

Because oviposition is dependent on water, these animals enter temporary pools in spring; however, adults of the subsequent generation(s) leave the pool before onset of the dry phase which they spend chiefly in permanent waters (Fig. 11). Thus, by the entirely different strategy of avoidance rather than tolerance of desiccation, Group 4 animals are still able to exploit the rich resources of temporary pools. Most of Group 4 are predators, and their rather late spring recruitment to the temporary pool community coincides with larger prey size and density than if they overwintered in the pool basin. It is through enhancement of dispersal and colonizing tendencies that Group 4 animals have evolved to exploit temporary pools.

Adults of Group 4 Ephemeroptera *(Callibaetis)* and Diptera (*Chaoborus*, Tanypodinae) emerging from the receding pool must ultimately deposit in permanent waters the eggs from which overwintering larvae will hatch. Group 4 Coleoptera and Hemiptera emerging from a temporary pool often complete another generation in permanent water; but ultimately it is the adult that overwinters in permanent waters. Group 4 Acari are parasitic on Coleoptera and Hemiptera of this same group. If a second generation is completed by the host in permanent waters, its mite parasites would also have to be adapted to a permanent water community; but if the same host individual overwinters to colonize a temporary pool the next spring, its parasitic mites must remain on their host for 9—10 months — a remarkable ability among water mites.

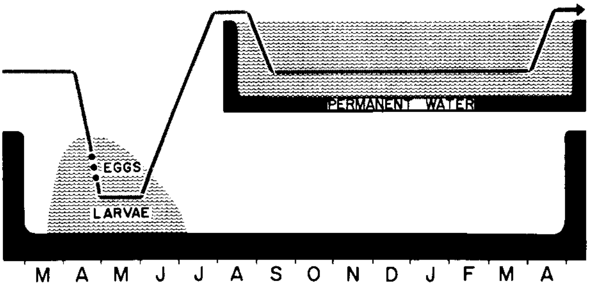

Fig. 11. Group 4 cycle; dots indicate oviposition.

3.4.1 Ephemeroptera

Larvae of *Callibaetis ferrugineus* (WALSH) were abundant every year in vernal pool K II, but never appeared earlier than June, with size-classes 1 and 2 (after CLIFFORD 1970) followed by 3 and 4 in July. In K VII (permanent) and K I and VI (both permanent from spring 1972 to summer 1973), *C. ferrugineus* overwintered as larvae; size-classes 2 and 3 were collected in April 1973, class 4 in May 1973, and adults on 12 June 1973. However, surface water disappeared from K I and VI in late summer of 1973, and was not replenished until about November of that year; and under these conditions of an autumnal pool, *Callibaetis* larvae did not appear in the 1974 collections from K I and VI until July. On the basis of these data, we assign *C. ferrugineus* to Group 4 because it overwinters in permanent pools, completing at least one additional generation, and with adults dispersing to temporary pools each spring.

Callibaetis appears to have several unusual life history features when compared with other mayflies. Females have been observed to live for 1—3 weeks (BURKS 1953) instead of the much shorter periods typical of the order. Females are known to be ovoviviparous (EDMUNDS 1945), or nearly so in that the eggs hatch within a few minutes of being laid. *Callibaetis* species also have one of the shortest larval developments known in mayflies — from egg to adult in 5—6 weeks. All these adaptations are superbly oriented towards exploiting temporary vernal pools. The longer adult life extends the time available for dispersal to new habitats; ovovivipary shortens the whole developmental period, and the rapid larval growth means that even if immigrating adults do not reach a pool until May or June, there is still time for one or perhaps two generations to develop before the pool dries. *Callibaetis* species also disperse more widely than most other mayflies and tend to oviposit in unusual sites such as garden pools (G. F. EDMUNDS pers. comm. and 1945); larvae occur in the water in leaf axils of bromeliads in Mexico (EDMUNDS et al. 1976). In LANDA's (1968) arrangement of mayfly life histories, *C. ferrugineus* belongs to Type B1 or B3 — two or more generations per year, larvae hatching in autumn emerge in spring to produce the spring-summer generations (see also EDMUNDS et al. 1976).

3.4.2 Odonata

Collection of larvae of *Anax junius* DRURY in Vandorf I, one of the other vernal pools studied, is of particular interest because sexually mature adults move into Ontario from areas south of the Great Lakes early in the spring to oviposit (WALKER 1958); the earliest Ontario record for an adult is 4 April (BUTLER et al. 1975). Larval populations of *A. junius* in southern Ontario were thought to be sustained entirely from early-season migrant adults, those of the next generation moving southward again in the autumn in a sexually immature condition (WALKER 1958); several observations are on record of large aggregations of *A. junius* in the vicinity of Point Pelee, Ontario, on the north shore of Lake Erie (NISBET 1960; WALKER 1958). However, a study by TROTTIER (1971) revealed that two populations were present in Ontario, one with larvae arising from resident adults, the other from migrants. In the Toronto area, residents overwintered as half-grown larvae, larval development extending through 11 months, from July to June of the following year. Migrants by ovipositing earlier, were able to complete larval development by September, a period of 3 months. Although larvae of the resident population of *Anax junius* could not complete development in pools undergoing an annual vernal cycle, larvae of the migrant population might, assuming oviposition in May as observed by BUTLER et al. (1975), complete their 3 months' development before the pool dried up. TROTTIER (1966) suggested that a migrant population he studied near Montreal completed development in 2 to 3 months from eggs deposited in April or May; although in strict terms not temporary, the pond habitat of this population showed a substantial seasonal drop in level. Since the length of mature larvae of this species is approximately 45 mm (TROTTIER 1971), the specimens from temporary vernal Vandorf I (2 larvae, length 30 and 33 mm, 14 July) must have been the progeny of migrant females; it is probable that the pool disappeared before these larvae could have completed development, but this observation suggests that the migrant population is probing temporary vernal pools where selective pressure for a high thermal coefficient of growth is great. If *Anax junius* were found to be occasionally successful in completing larval development in a vernal pool in southern Ontario or perhaps more consistently in such pools south of the Great Lakes, it would be assigned to our Group 4. Thus the strategy for vernal pools in *Anax junius* would be similar to that in Coleoptera and Hemiptera, which overwinter in other habitats and return to vernal pools in spring for reproduction. According to WALKER (in BAGG 1958) the individuals moving southward in autumn do not return in spring, for the wings of dragonflies become battered and torn after they have been flying for a month or more, and the wings of the spring animals in Ontario are uninjured. Similar movements of *A. junius* in autumn have been observed in Maine, Massachusetts, Connecticut and Pennsylvania (BAGG 1958). Where the migrants pass their overwintering generation is not known, although the Ontario population could arise from central Pennsylvania where adults emerge in Late March, and where there also are two periods of emergence in populations of *A. junius* (WHITE & RAFF 1970). An early season influx of migrants was also recorded in northern Illinois (YOUNG 1967).

Species of the libellulid genera *Pantala* and *Tramea*, well known as migrant colonizers of small pools at lower latitudes (CORBET 1962), also illustrate Group 4 strategy for temporary pools. In the spring, migrant females establish larval populations of *P. flavescens* (FAB.) (in southern Quebec, TROTTIER 1967) and *T. lacerata* HAGEN (in extreme southern Ontario, WALKER & CORBET 1975); teneral adults occur in late summer. Although not yet found in known temporary pools in Canada, species in both genera are often recorded from these habitats farther south (WALKER & CORBET 1975), where, for example, larval development of *P. hymenea* was completed in 5 weeks in Oklahoma (BICK 1951). Factors influencing colonization of temporary pools by migrant dragonflies are further discussed by CORBET (1962).

In the tropics, adults of the libellulid *Erythrodiplax funerea (*HAGEN), which reproduce in temporary pools, are reported by MORTON (1977) to remain in aestivation in forested areas during the dry season from November through May. With the return of heavy rains, their dull brown body colour becomes black, distinctive black wing patches appear, and they move to small pools in open areas. Thus, with the problems of winter removed, some dragonflies remain localized during an adult life of approximately 6 months to gain access to temporary pools.

3.4.3 Hemiptera

All species encountered in temporary vernal Kendal II are assigned to Group 4. Like most aquatic Hemiptera, temporary-pool species overwinter as adults in permanent waters, colonizing pools through springtime dispersal flights at the approach of sexual maturity (HUNGERFORD 1919). Since species differ markedly in their tendency to disperse (BROWN 1951), those developing in temporary pools clearly are among the most highly adapted colonizers. Therefore, among species of temporary-pool Hemiptera there will be strong selection pressure for early dispersal to small pools in spring, rapid development of the next generation, and dispersal again to permanent waters. Dispersal by flight is an important aspect of the biology of many families of Hemiptera (SOUTHWOOD 1960); normal flight ranges for Corixidae, for example, may be as much as 80 km (POPHAM 1964). Depending on latitude, species in families such as Corixidae (HUNGERFORD 1919), Gerridae (VEPSÄLÄINEN 1974b), and Notonectidae (STREAMS & NEWFIELD 1972) may complete more than one generation in a season. VEPSÄLÄINEN (1974a) has shown that diapause in gerrids delays sexual maturity in adults until spring if their larval development takes place during periods of reducing day length. Because Hemiptera of temporary pools generally overwinter as sexually immature adults, we assume that a similar diapause operates in all of them.

In the following discussions, collection records for 1972, 73, and 74 are combined. Since larval identification to species has not been possible, we assume that larvae taken in a pool subsequent to collection of adults are conspecific with them, or with some among them. In addition to the families discussed here, certain others were recorded from a temporary pool in New York by HUNGERFORD (1919): Hydrometridae *(Hydrometra)*, Mesoveliidae *(Mesovelia)*, Veliidae *(Microvelia)*, and Saldidae.

The interpretation of phylogeny for aquatic Hemiptera by CHINA (1955), and USINGER (1956) (see RESH & SOLEM 1978) suggests that shore-dwelling bugs such as Gelastocoridae are the primitive groups, and more aquatic families such as Corixidae are later derivatives, with species in the Naucoridae that are completely independent of atmospheric air at the water surface the most advanced. POPHAM (1964) proposed that temporary pools were the primitive habitat for aquatic Hemiptera.

Corixidae

Species represented in K II were: *Callicorixa audeni* (HUNGERFORD); *C. alaskensis* (HUNGERFORD); *Hesperocorixa atopodonta* (HUNGERFORD), *H. michiganensis* (HUNGERFORD), *H. vulgaris* (HUNGERFORD); *Sigara alternata* (SAY), *S. decoratella* (HUNGERFORD), *S. grossolineata* (HUNGERFORD), *S. knighti* (HUNGERFORD), *S. modesta* (ABBOTT), and *S. solensis* (HUNGERFORD). No corixids were taken in the April 5 collection in K II, adults alone from 13 April to 15 May, and by 4 June when larvae first appeared in collections L III were already present; L IV—V dominated the July collections in the declining stages of the pool. We do not know which species reproduced in K II, but we assume that larvae completing development are the progeny of those collected as early season adults.

Since pools I and VI were permanent from spring 1972 through summer 1973, and autumnal from autumn 1973 through 1974, they might have served as overwintering sites; in fact, not even all of the K II species were collected from them, suggesting that cues in selecting pools for hibernation and for reproduction are different. However, the permanency of K I and VI was reflected in the occurrence of *Palmacorixa nana* WALLEY (K VI, 17 July 1973), a species characteristic of permanent water because it overwinters as L IV (HUNGERFORD 1948) and adults rarely fly (R. AIKEN pers. comm.). *Sigara mathesoni* HUNGERFORD (K VI, 15 May 1973) and *Hesperocorixa kennicotti* (UHLER) (K VI, 1 May 1974) were other species collected in K I and VI but not in vernal K II.

Restriction of the Corixidae in K II to three genera — *Sigara, Callicorixa,* and *Hesperocorixa* — is a substantial reduction from the six genera of this family in southern Ontario, and emphasizes that temporary-pool adaptations are far from the norm. In Britain, species of the same three genera, along with *Corixa,* were the most active in spring and summer flight activity (BROWN 1951, 1954; MACAN 1939), and were also the major colonizers of temporary pools and other small aquatic habitats (FERNANDO 1959; POPHAM 1964).

Temporary-pool corixids congregate in autumn in larger, permanent water bodies where they overwinter, dispersing again in spring with some tendency to select small water bodies (PAJUNEN & JANSSON 1969). Evidence suggests that adults in flight differentiate pools on the basis of size by means of reflected light (BROWN 1954; FERNANDO 1959) and colour (POPHAM 1943); and succession of corixid species has been correlated with increasing organic matter in the soil (MACAN 1938). In addition to spring and autumn peaks in movement, there must also be some flight activity in summer by species completing development in drying vernal pools such as K II, and this has been detected for temporary rock pool species in Finland (PAJUNEN & JANSSON 1969). Where polymorphism for flight musculature has been studied, corixids in less stable habitats such as temporary pools always have normal power of flight (YOUNG 1961).

Since corixids feed upon small crustaceans, insect larvae, and oligochaetes (JANSSON & SCUDDER 1972), and also are phytophagous (HUNGERFORD 1919), they are the best suited of all aquatic Hemiptera to the food resources of temporary pools, particularly in early spring.

Notonectidae

Only *Notonecta undulata* SAY was represented in K II collections. Adults were taken from 18 April, and the first collection of larvae on 12 June comprised instars II and III; collection of L II—V on 4 July 1973 and 2 July 1974 suggests that only part of the population would have been able to complete development before the pool disappeared. This same species was collected in K I and VI — with no others in K I, but two additional species, *N. insulata* Kirby (18 April — 29 July) and *N. borealis* Bueno & Hussey (29 July), in K VI collections.

Extensive observations by Hungerford (1919) confirm that *N. undulata* is the common species of temporary pools in North America, and also the most widely distributed Nearctic species; it is tolerant of a wide range of conditions in temporary and permanent waters (Toth & Chew 1972) and euthermal in activity and reproduction (Ellis & Borden 1969). Among six eastern species of *Notonecta*, *N. undulata* occurred most frequently in small to medium ponds where there was little or no emergent vegetation, and was the first to complete a generation (Streams & Newfield 1972).

In K VI, *N. insulata* occurred most frequently in collections. *N. borealis*, unusual among *Notonecta* because it overwinters as an egg (Rice 1954), was collected in K VI only in 1973 when that pool was permanent.

Notonectids feed upon a variety of arthropods, and *N. undulata* showed preference for mosquitoes (Ellis & Borden 1970; Toth & Chew 1972), an abundant prey group in early season temporary pools.

Belostomatidae

The two species found in K II were first collected on June 9: *Belostoma flumineum* Say (♂ bearing eggs) and *Lethocerus (americanus* Leidy?) (L II). Although the entire development of *L. americanus* may be completed in 33 days under natural conditions (Rankin 1935), probably some of the developing populations of both species in temporary vernal K II were unable to complete metamorphosis to the winged stage because collections in the final stages of the pool (2 July 1973, 1974) yielded *Belostoma* L I to III and *Lethocerus* L IV. The same taxa were collected in K I and VI; *Belostoma* evidently had completed development by 29 July 1973 (K VI) with adults still present on 21 August, and *Lethocerus* had reached L V by 17 July 1973 (K I).

Nepidae

Adult *Ranatra fusca* Pal. de Beauv. were taken in K II in May, but since collections shortly before the pool dried up (2 July 1972 and 1974) yielded only L I and II, it is doubtful that few if any of this species are able to complete development in vernal K II. Even in the longer-lived K I and VI, L IV and V were not found until late July by which time K II was dry. Undeveloped flight muscles reduce the colonizing ability of a European species *R. linearis* (L.) (Brown 1951), but apparently this aspect of North American *Ranatra* species has received little attention.

Gerridae

Several species of *Gerris* were represented in K II collections: *G. marginatus* SAY, *G. buenoi* KIRKALDY, *G. comatus* DRAKE & HOTTES, and *G. dissortis* DRAKE & HARRIS. Since gerrids overwinter as adults in vegetation adjacent to permanent water (CHENG & FERNANDO 1970), and are therefore distinctive among the temporary-pool Hemiptera considered here, overwintering strategy for species inhabiting temporary vernal pools poses no unusual physiological demand. A problem of dispersal exists, however, for wing polymorphism is common, with adults of many *Gerris* species predominantly micropterous and incapable of flight. All adult gerrids collected in K II were macropterous. Univoltine species of *Gerris* in temporary pools are, in fact, always macropterous, in contrast to species of running water and lakes which are frequently micropterous or apterous (BRINKHURST 1959, VEPSÄLÄINEN 1974b). However, according to CALABRESE (1979), all of the species collected in K II are bivoltine, *G. marginatus* and *G. dissortis* being strictly macropterous, *G. buenoi* polymorphic and *G. comatus* dimorphic. The overwintering generation in *G. buenoi* and *comatus* is largely macropterous (CALABRESE 1979), as would be expected in species that colonize isolated habitats in spring, but up to 50 per cent of the summer generation in these two species was composed of adults incapable of flight (CALABRESE 1979). Based on populations from a wide range of habitats, these figures reflect an average population structure; but such a high proportion of flightless progeny seems unlikely from individuals colonizing temporary pools. We infer that either there is genetically linked polymorphism combining strong colonizing dispersal with a high proportion of macropters in all generations, or the proportion of macropters is increased by some environmental stimulus intrinsic to temporary pools.

The four *Gerris* species of K II represent two subgenera: *G. (Gerris) marginatus, buenoi,* and *comatus;* and *G. (Limnoporus) dissortis* (CALABRESE 1977). *G. (Gerris)* species occur mainly in lentic habitats; and although *G. (Limnoporus)* species occur in both lentic and lotic sites, *G. (L.) dissortis* is distinctive among them in being entirely macropterous.

3.4.4 Coleoptera

The majority of beetles reproducing in K II were not detected in soil samples, and in the absence of evidence that they overwinter in the pool basin, we assign them to Group 4 as spring migrants; most Coleoptera breeding in temporary pools evidently are in this category (FERNANDO 1958; JAMES 1969; SOUTHWOOD 1962). Like the Hemiptera, Group 4 Coleoptera are strong fliers with peaks of flight activity in spring and autumn (FERNANDO 1958; SOUTHWOOD 1962). Most appear to locate new habitats by sight because FERNANDO (1958) caught many in traps in which a sheet of glass simulated reflections from a water surface. Striking similarity in the beetle fauna of temporary pools in widely scattered parts of eastern

North America was noted by YOUNG (1960), which we interpret to mean that only particular species of aquatic Coleoptera are adapted to exploit these habitats. Dytiscids and gyrinids are predaceous as both larvae and adults; hydrophilids are mostly phytophagous as adults but predaceous as larvae. Collection records are composites from 1972 through 1974.

Dytiscidae

Larvae representing five genera were collected in K II: *Acilius* (L I—III, 1 May — 4 July), *Dytiscus* (L I—III, 15 May — 2 July; L III, 1 May), *Graphoderus* (L III, 4 June), *Hydaticus* (L I, 12 June), and *Laccophilus* (L I—III, 9 June — 4 July); adults collected in the same genera were *Acilius semisulcatus* AUBÉ (11 May — 2 July) and *Laccophilus maculosus* (GERM.) (18 April — 2 July). Presence of final instar larvae of *Dytiscus* on 1 May seems anomalous with spring arrival, and no adults were collected over 3 years; but observations by JAMES (1969) on *Dytiscus fasciventris* SAY and *Acilius semisulcatus* AUBÉ from temporary pools in southern Ontario justify assignment to Group 4, and also indicate that *Agabus erichsoni* (see under Group 2) can be included in this group.

Observations for *Rhantus* in K II are inconclusive (see Coleoptera, Group 2). *R. consimilis* adults collected from 18 April to 9 June indicate that this species overwinters as an adult, which could be elsewhere in permanent water (i.e. Group 4) or in the dry K II basin (i.e. Group 2). JAMES (1969) found *R. binotatus* (FAB.) ovipositing in vernal pools in southern Ontario, but *R. tostus* LEC. only in permanent ponds in the same area; and he also found adults of *Colymbetes sculptilis* HARR. in late March, and ovipositing in April, suggesting that this species is either an early spring migrant (Group 4) or that it overwinters as an adult in the dry pool basin (Group 2). Indications above that *Agabus erichsoni* and perhaps *Rhantus consimilis* might overwinter both as adults and as eggs are subject to confirmation. Over the 3-year period, the dytiscid genera *Hygrotus, Ilybius, Liodessus,* and *Desmopachria* were recorded in K II only as adults, but in the absence of any larvae in our collections these genera are not discussed further as members of the temporary pool community.

Gyrinidae

Larvae of *Gyrinus* sp. were collected in K II (28 May — 4 July); adults of *G. affinis* AUBÉ (12 June), and *G. lecontei* FALL (19 June — 4 July) included a teneral specimen of the latter species (4 July), indicating that some gyrinids can complete development in temporary vernal pools. JAMES (1961) recorded the same two species in April from vernal pools in Ontario. *Dineutus* sp. was recorded once in K II (L II, 4 July).

Hydrophilidae

Adults of *Tropisternus mixtus* LEC. (1 May — 2 July), *Enochrus hamiltoni* HORN and *E. ochraceus* (MELSH.) (4 June — 2 July) were taken in K II; larvae belonging to these genera were also collected (9 June — 2 July). These are considered to be spring migrants, as are *Cymbiodyta* sp. (9 June) and *Hydrochara* sp. (28 May — 19 June), collected only as larvae. Observations by RYKER (1975) in Oregon indicate that *Tropisternus ellipticus* LEC. adults fly in spring from overwintering sites in permanent ponds to temporary (autumnal?) pools where they reproduce; adults of this spring generation disperse to produce a summer generation in rock pools formed along river margins by receding water levels, and summer-generation adults subsequently return to permanent ponds where they overwinter.

3.4.5 Diptera

Species in two families are assigned to Group 4; both families are also represented in other groups.

Chironomidae

Almost all larvae of the subfamily Tanypodinae appeared in collections from Kendal II only in the latter half of June and in early July; only *Guttipelopia* of this subfamily was taken in a soil sample. From K II, Tanypodinae collected in 1972, 73 and 74 were: *Ablabesmyia* spp. incl. *A. monilis* (L.) (L IV, pupae 9 June — 2 July); *Guttipelopia* sp. (L II or III 5 April, in frozen soil); *Psectrotanypus* spp. incl. *P. dyari* (COQ.) (L III, IV 4 June — 2 July, pupae 12 June — 2 July); *Procladius* sp. (pupa 2 July). In contrast to the relatively late collections from K II, those from K I and VI included third instars of *Ablabesmyia*, *Psectrotanypus*, and *Procladius* on 18 April 1973 when these pools were permanent, indicating that larvae of these species overwinter in permanent pools.

The seasonal occurrences of most Tanypodinae differ from other chironomids of K II, principally Orthocladiinae and Chironominae whose larvae occur both in early spring and in dry soil samples (see Group 2). Since there is no evidence for overwintering of most of the Tanypodinae larvae in the dry basin, the adults probably emerged from permanent waters early in the spring and dispersed to oviposit in isolated pools such as K II; and we assume that like other members of Group 4, adults of the next generation again disperse to oviposit in permanent ponds or perhaps autumnal pools. These species are necessarily multivoltine, and probably wide-ranging in flight. Since Tanypodinae are mainly predators on microcrustacea and insects (COFFMAN 1978), timing of their larval feeding mid-way through the temporary-pool cycle is appropriate. They do not construct tubes and do not burrow in bottom sediments as most other chironomids do (DANKS 1971b). The single exception in Kendal II collections to our hypothesis that Tanypodinae exploit temporary pools as migrants is *Guttipelopia* sp., discussed under Group 2.

Although Tanypodinae on the Canadian prairies were reported to be more characteristic of semi-permanent and permanent than of temporary waters (Driver 1977), species of *Psectrotanypus* and *Procladius* did occur in temporary pools, and *Ablabesmyia* spp. were taken in semi-permanent ponds.

Chaoboridae

Larvae of *Chaoborus*, predators on small invertebrates, are usually considered to be members of the zooplankton in lakes and permanent ponds, but some species are also encountered in small pools, including vernal pools and even water-filled ruts in muddy roads (Cook 1956; Peus 1934; Reisen 1973). Larvae of three species were represented in collections from vernal pool K II: *C. americanus* (Johannsen), *C. flavicans* (Meigen), and *C. trivittatus* (Loew); the same three were collected in K I, but only *C. americanus* and *C. flavicans* in K VI.

In 1973 collections from K II, no *Chaoborus* larvae were taken in the collection of 18 April, but on 15 May *C. trivittatus* (L III, IV) were collected, and *C. americanus* (L IV) and *C. flavicans* (L IV) on 12 June, indicating that larvae of these species do not overwinter in vernal pools, but that the pools are colonized by ovipositing females in the early spring stages of the wet phase. This is consistent with the observation that *C. trivittatus* and *C. americanus* (Fedorenko & Swift 1972), and *C. flavicans* (Parma 1971) overwinter only as instar IV larvae. No *Chaoborus* larvae came from the flooded soil samples from K II (27 October, 18 December 1974; 20 February 1975; 28 October 1977) — additional evidence that these species do not overwinter either as diapausing, drought-resistant eggs or as dormant larvae. However, in the 18 April 1973 collection from K I and VI, during their permanent period through 1972 to the summer of 1973, *C. americanus* (L IV, pupae) and *C. flavicans* (L IV) were taken, providing further evidence that larvae overwinter in permanent waters. Larvae overwintering in the nearby and consistently permanent K VII could also be a reservoir for *Chaoborus* females dispersing to the temporary pools in spring.

In contrast, Peus (1934) suggested that *C. flavicans* overwintered in dry pool basins as diapausing eggs in the same way as *Aedes* mosquitoes. Parma (1971) raised the possibility that larvae survive a dry period buried in the bottom mud, although it is not clear whether he meant to explain the ability of *C. flavicans* to overwinter in vernal pools or to withstand the shorter drought period of autumnal pools. Overwintering of eggs in temporary pool basins is now known, however, for *C. cooki* (Borkent 1979, see Group 3).

Eggs of most *Chaoborus* are deposited on the water surface (Saether 1972), but in the absence of diapause to retard their development, larvae could hatch to overwinter in an autumnal pool at latitudes where surface water collected early enough and ovipositing females were active sufficiently late in the autumn. These factors would explain occurrence of *Chaoborus* larvae in an autumnal pool in

November in British Columbia (Spencer 1929). However, in 1974 when Kendal pools I and VI were temporary autumnal, our collections revealed no evidence of overwintering larvae, and *C. americanus* (L III, IV) first occurred in June — evidently a result of the same early spring colonization as in the temporary vernal K II.

In these *Chaoborus* species at least one additional generation is completed in permanent water before dispersal of the females for oviposition in temporary pools the following spring. Although multivoltinism is common in species inhabiting smaller bodies of water, univoltine life cycles are characteristic of *Chaoborus* species in lakes; both types have been found in some species, e.g. *C. flavicans* (Parma 1971). Bradshaw (1973) has shown that *C. americanus,* the dominant species in our collections, overwinters in permanent waters as final (L IV) instars in diapause; and that two physiological morphs exist together, one responding more quickly than the other to spring conditions of long-day photoperiod and abundance of food. Metamorphosis of the early morph is successful under conditions of continuously increasing temperature; short-term return of freezing temperatures results in low survival. The late morph, completing development more slowly, ensures that at least a part of the population will emerge under favourable conditions. Bradshaw (1973) suggests that the two extremes in this polymorphic population most effectively exploit the opposite and unpredictable extremes characteristic of a temperate spring climate.

Colonization of temporary pools and other transient water bodies, clearly an aspect of the biology of such species as *C. flavicans* and *C. americanus,* appears not to have been considered in Bradshaw's study. The early-emergent morph could also be interpreted as a colonizing component of the population which reaches the adult stage as early as possible to ensure maximum development time in ephemeral waters for the next generation. Since adults of the next generation emerging from temporary pools evidently disperse again to permanent waters to establish their overwintering generation, gene frequencies in the residual population could be influenced by selection for the early morph in transient waters. Selection for the early morph in temporary pools could result from the rich food resources (small crustaceans and insect larvae) together with total absence of fish predators. A higher proportion of females in the early morph than in the later one (Bradshaw 1973) is also consistent with this interpretation since success of the early morph depends heavily upon the effectiveness of gravid females in dispersal and oviposition. Furthermore, the early morph would have a greater tendency for dispersal than the late morph because selection would act against the late morph in transient waters where eggs were deposited too late for larvae to complete development. Successful colonization of temporary pools by these species may therefore be strongly influenced by spring weather conditions, a warm spring selecting for the early morph but against the late one.

3.4.6 Acari

Water mites of the genera *Eylais* (Eylaidae) and *Hydrachna* (Hydrachnidae) belong to Group 4.

Eylaidae

Combining data from 1973 and 74, deutonymphs and adults of *Eylais* were collected in Kendal II 4 June — 2 July, and in K VI 1 May — 29 July; adults also occurred in most of the other temporary pools sampled in southern Ontario, but since species discrimination in *Eylais* depends largely upon larval characters (LANCIANI 1969), we are unable to apply specific names to our material. KENK (1949) found *Eylais* sp. to be common in autumnal pools in Michigan from April to June. Members of this genus are common inhabitants of temporary pools in eastern North America (LANCIANI 1969, 1970 a, b) and of shallow ponds throughout the world (COOK 1974).

Larvae of *Eylais* parasitize adult Hemiptera of the families Belostomatidae and Corixidae (LANCIANI 1969) and Coleoptera of the families Haliplidae, Dytiscidae, and Hydrophilidae (LANCIANI 1970 a, b), fastening in sub-elytral air spaces because the mite larvae are air-breathing. Several species of the genus restricted to permanent water have a larval stage of short duration and overwinter as eggs. LANCIANI (1970 a, b) found that in species restricted to temporary pools in New York (*Eylais mitchelli* LANCIANI, *E. glandulosa* LANC., *E. major* LANC., *E. vernalis* LANC., and *E. harmani* LANC.), larvae attach to the host during June or July shortly before it leaves the drying pool basin to migrate to a permanent body of water. Larvae remain attached to the host throughout its stay in permanent water during summer, autumn, and winter — in some cases up to 10 months. Larval maturation is completed early the following spring after the host returns to a temporary pool, the mites only then transforming to nymphochrysalises which remain attached to the host by larval mouthparts. Metamorphosis to the deutonymphal instar is rapid, and the mites leave the host to become active predators. After feeding on ostracods for several days, mature deutonymphs anchor to plant tissue and form imagochrysalises from which adults subsequently emerge. Mating occurs immediately, and females oviposit several days later. Larvae are ready to attach to emerging adults of the next host generation just before the insects migrate from the rapidly drying pool basin. Extension of the larval stage to 9 or 10 months in these mites is a striking evolutionary development providing adaptation both to behaviour of the hosts and to conditions in temporary pools.

Still other species of *Eylais* (*E. discreta* KOENIKE, *E. falcata* LANC., and *E. ovaliparous* LANC.) complete a second generation; engorged larvae leave the host after it reaches permanent water, complete deutonymph and adult stages, and the larvae of the next generation parasitize hosts again before winter (LANCIANI 1969, 1970 a, b).

Thus, three groups of *Eylais* species differ functionally in the timing of the resting stage: those restricted to permanent waters have overwintering eggs; univoltine species of temporary pools overwinter as larvae on their hosts; and bivoltine species with a generation in each habitat overwinter as larvae on the host, but unlike univoltine species, do not enter the resting stage in summer. Diapause acting at different times in the life cycle and regulated by different thresholds seems the likely mechanism for all three groups. LANCIANI (1970a) has shown that several possible areas of attachment are used by parasitizing *Eylais* larvae on coleopteran hosts. Most temporary-pool species do not attach to the membranous wings, presumably because the direct effect of moving wings or the indirect effect of damage to the wings by the mite (and hence impaired host dispersal) would reduce the mite's chances of survival. A single exception, *Eylais harmani,* does attach to membranous wings of beetles in the dytiscid genus *Hydroporus* (LANCIANI 1970a), and our observations (see under Coleoptera, Group 2) reveal that two of the same species parasitized by this mite, *Hydroporus fuscipennis* and *H. despectus,* overwinter as adults in the dry basin of vernal pools. This intriguing correlation suggests that mite larvae do attach to the membranous wings of a non-migrant host when completion of their own cycle is not affected. Evidence here is mainly indirect, but should parasitizing mite larvae be found on beetles overwintering in the dry basins of vernal pools, the mites would be assigned to Group 2.

Eylaidae appear to be an early derivative group of water mites, and temporary pools probably were an important habitat for the genus *Eylais* throughout the evolutionary history of the family. As in Hydryphantidae (Group 2), eylaid mites retain an essentially terrestrial existence as larvae (LANCIANI 1969, 1970a, b; SMITH & OLIVER 1976); however, in all other instars members of *Eylais* are fully adapted aquatic organisms unable to withstand drought.

Hydrachnidae

Adults of two species of *Hydrachna* were collected in Kendal II: *H. baculoscutata* CROWELL in 1973 and *H.* sp. nr. *comosa* (KOENIKE) in 1972. These and other species were collected in most of the temporary pools sampled in southern Ontario, with adults common from late May to early July. KENK (1949) recorded several species of *Hydrachna,* presumably adults, from autumnal pools in Michigan in the spring. Mites of this genus occur in shallow water habitats throughout the world (COOK 1974).

The completely aquatic larvae of *Hydrachna* are also parasitic on aquatic Coleoptera and Hemiptera, but attack a wider range of hosts including Nepidae and Notonectidae than do the essentially terrestrial *Eylais* larvae. Although detailed life history studies have not been published for species of *Hydrachna* inhabiting temporary pools, the adaptive mechanism permitting exploitation of this habitat is probably similar to that found in univoltine species of *Eylais.* The possibility of bivoltine *Hydrachna* species with one generation in temporary pools and another in permanent water as in *Eylais* cannot yet be dismissed.

Eylaid and hydrachnid mites represent early derivative lineages associated with temporary pool habitats and long-lived hosts, Hemiptera and Coleoptera. Mites of these families clearly reflect widely separate phyletic origins both in morphology and larval behaviour; larval eylaids are primarily terrestrial air-breathers restricted as parasites to subelytral sites within the hosts' air supplies, and larval hydrachnids are primarily aquatic. In both groups post-larval instars are fully aquatic organisms unable to withstand drought; thus exploitation of temporary pools by mites of these families necessitates a life history strategy ensuring avoidance of the drought phase of the pools. Adaptive strategies focusing upon modified larval behaviour exploiting host longevity have apparently developed in parallel in eylaids and hydrachnids inhabiting temporary pools. Adaptive mechanisms are well illustrated in *Eylais* where the bivoltine life history and the extended larval stage stem from the pre-adaptive association of parasitic larvae with their relatively long-lived migratory hosts. Members of bivoltine species exhibit rapid developmental rates at each life history stage, and regular utilization of vernal pool habitats depends upon both successful completion of the intervening generation in permanent water, and location by summer larvae of appropriate hosts that migrate to temporary pools in spring. In univoltine species whose deutonymphs and adults are active only in vernal pools, the mites undergo obligatory arrested development as parasitic larvae confined to their hosts throughout the dry phase of the habitat. Annual recolonization of temporary pools in spring depends mainly on the successful return of the year-old hosts to these habitats.

3.4.7 Amphibia

Although they are the only non-invertebrates included in this study, amphibians are a conspicuous and vocal element of many temporary vernal pools, and the strategy of frogs and salamanders for transient waters is clearly that of Group 4 invertebrates. Larvae of the salamander *Ambystoma* sp. and of the wood frog, *Rana sylvatica* LeConte were collected in temporary vernal Kendal II. These same two, along with the green frog *Rana clamitans* Rafinesque were collected in K I and VI.

In a vernal pool, the timing of metamorphosis must be a compromise between the risk of transforming at a small size and the risk of remaining in a shrinking habitat. A most interesting theory on the ecology of amphibian metamorphosis presented by Wilbur & Collins (1973) suggests that metamorphosis is initiated by endocrine mechanisms responding to a certain size threshold coupled to the physiological effect of the recent rate of growth. If body size is small but growth rate is fast, then metamorphosis is delayed in order to capitalize on growth opportunities in the pool. If growth rate is slow, then once a minimum size is reached, metamorphosis proceeds because the risks of survival on land, even at a small size, are less than the dangers involved in the uncertainty of the larval habitat. WILBUR & COLLINS relate the probability of metamorphosis occurring at a certain time to the degree of stability of the habitat. In stable habitats, individuals remain in the pool until they reach the optimum size for metamorphosis, variable growth rates resulting in variable larval periods but a small range in size at transformation. In temporary pools, selection favours the facultative timing of metamorphosis over a wide range of body sizes and larval periods. Thus species such as the bull frog *Rana catesbeiana* SHAW with a fixed size for metamorphosis (WILBUR & COLLINS 1973) and a long larval period is restricted to permanent waters. *Rana clamitans* also has a fixed transformation size (WILBUR & COLLINS 1973) and we find it only in pools such as K I and VI which dry late in the summer, presumably because the vernal pool has too short a wet period for the optimum size to be reached. *Ambystoma,* on the other hand, appears to be able to metamorphose over a wide range of sizes. WILBUR & COLLINS (1973) found that metamorphosing individuals of *A. tigrinum* GREEN in an early-drying pool were ½ the weight of individuals in the late-drying pool, and ⅙ the weight of individuals in a permanent pond, with corresponding differences in length. SHOOP (1974) found that *A. maculatum* SHAW could metamorphose at a small size early in summer and thus avoid drought, or continue to grow and transform at a larger size in permanent pools. The exact mechanism triggering the initiation of metamorphosis is not yet known; WILBUR & COLLINS suggest that as the rate of growth appears to be involved, a growth hormone such as thyroxine may be an agent. We speculate that this in turn might be affected by other endocrine activity responding to stresses such as rapidly rising temperature, decreasing oxygen, and crowding in the receding pool.

Another interesting aspect of amphibian adaptation to vernal pools is their ability to locate in spring those that would likely retain surface water long enough for the larvae to complete development. In our observations, for example, the characteristic calls of tree frogs (Hylidae), *Rana clamitans,* and toads *(Bufo)* were never heard at K II, but were very common at K I and VI where surface water was present for a longer period. Work by OLDHAM (1967) indicated that *R. clamitans* adults located breeding pools in spring from olfactory cues. If so, each species probably has specific cues — a possible explanation for the clearly different response of species to the three Kendal pools. Similar cues were only recently discovered for mosquitoes (KALPAGE & BRUST 1973), and thus the possibility remains that olfactory signals guide other animal inhabitants to temporary pools.

3.5 Taxa not placed to group

Larvae in several families of Diptera collected in vernal pool Kendal II are not assigned to one of the four groups because we do not have sufficient biological information about them, either directly or from the literature.

Tipulidae

Because many tipulids are terrestrial, occurrence of larvae of this family in a temporary-pool basin is difficult to interpret. From vernal pool Kendal II we collected (5 April — 9 June) larvae of *Tipula (Pterelachisus)* sp. and *T. (Yamatotipula)* sp.; and from soil samples from the dry pool basin (Oct., Dec.) flooded in the laboratory, larvae of *T. (Pterelachisus)* spp. and *Nephrotoma* sp. became active. These data seem to indicate that at least some tipulids live in temporary pool basins, although they may do so as terrestrial larvae tolerant of flooding. Basins of temporary pools with high levels of soil moisture and plant materials during the dry phase would be favourable sites for the detritivorous tipulid larvae.

Dixidae

Larvae of *Dixella* sp. were collected from temporary vernal pool Kendal II (15 May). Dixid larvae are aquatic (NOWELL 1963), and some species oviposit directly into water (NOWELL 1951); but eggs of *Paradixa californica* (JOHANNSEN) are deposited at or above the water line (HUBERT 1953), and in both cases the eggs are embedded in a gelatinous matrix. Observations by these authors indicate that embryonic development proceeds without delay; but there is evidence for some tolerance of drying by eggs and developing embryos of *P. californica* on the banks of pools where the water receded (HUBERT 1953). Available information suggests, then, that a degree of drought-resistance in eggs and a tendency toward oviposition independent of water have been evolved in some dixids; if this were to account for occurrence of *Dixella* larvae in temporary vernal pool Kendal II, embryos or larvae would have to overwinter without surface water as Group 3 Culicidae and Trichoptera do — for which there appears to be no evidence at present. There is also the possibility that Group 4 strategy could be involved, with larvae overwintering in permanent water to emerge as adults in early spring, dispersing to colonize temporary pools. The means by which dixids live in vernal pools is unknown.

Dolichopodidae

Larvae of this family were collected in temporary vernal pool Kendal II (20 April), and late instars were activated from October and December soil samples flooded in the laboratory. Dolichopodid larvae are therefore able to overwinter in the dry pool basin, but these might be more terrestrial than aquatic in habitat since many species are semi-aquatic (SMITH 1952). The specimens have not been further identified, and no assignment to group can be made.

Ephydridae

A single larva of *Hydrellia* sp. was collected from vernal pool Kendal II (9 June 1972). Larvae of this genus are leaf miners of aquatic and semi-aquatic plants (DEONIER 1971). The record bears mentioning because larvae in the water mite genus *Hydryphantes,* which were collected in K II, are parasitic on ephydrid adults.

4. General considerations

4.1 Limnology

Astatic pools

Lentic waters of a temporary or astatic nature may be seasonally astatic, and therefore temporary on an annual basis, or perennially astatic with dry periods occurring at longer and irregular intervals (Decksbach 1929). As Hartland-Rowe (1972) has pointed out, seasonally astatic waters can therefore range from pools lasting only 2—3 weeks to those that are dry for equally short periods. For pools at temperate latitudes, we think it useful to subdivide this wide range into vernal and autumnal pools (see Fig. 1 and Introduction) separated by the cold winter dry period which is an important biological distinction between them. We have not dealt with temporary pools of tropical latitudes, but it seems likely that in the absence of low temperatures, wet and dry seasons would impose similar selective pressures on the organisms (Fernando 1958).

Although *temporary pond* is frequently applied to transitory lentic waters, we consider *temporary pool* to be a term more appropriate for the small, shallow, and highly ephemeral waters that must logically be included under this category of habitat. We prefer to restrict *pond* to small lentic waters of sufficient permanence to support submerged aquatic plants, and normally fish as well. In the literature, *temporary pool (pond)* is frequently applied to basins that lose much of their surface water but do not dry completely (e.g. Cole & Fisher 1978; Jokinen 1978; O'Brien et al. 1973, etc.). Marked seasonal fluctuation in level is the denominator common to these pools and those that are strictly temporary, with the latter a special case of the former. Many lentic invertebrates are tolerant of the general condition of pools with fluctuating water levels; but few can live in pools that are strictly temporary, although species adapted to temporary pools are common in pools with fluctuating levels. Because of variation in underlying strata and annual precipitation, fluctuating pools cannot be assumed to be strictly temporary unless an observer has previous knowledge. However, pools that were never completely dry during the preceding year can be detected from an interpretation of the organisms present in relation to latitude and sympatric species. For example, at the latitude of southern Ontario, occurrence in early spring of larval Zygoptera other than certain species of *Lestes* would indicate that a pool was not dry the preceding summer. The same history would be revealed by Anisoptera other than certain *Sympetrum* spp. (see Odonata, Group 3), or by the presence of *Nemotaulius* or *Banksiola* larvae (see Trichoptera, Group 3). Similar clues can be derived from an intimate knowledge of other taxa.

At temperate latitudes, temporary autumnal pools which form in basins retaining surface water in autumn are distinguished (Fig. 1) from temporary vernal pools which do not form until spring (WIGGINS 1973). The shorter dry phase of 3—4 months in autumnal pools, combined with a longer wet phase of 8—9 months, has important biological implications. Firstly, composition of the animal community can be altered because species with tolerance to relatively short periods of drought through summer and autumn, but with no intrinsic means of overwintering without water, would survive in temporary pools only on the condition of an autumnal wet phase. Among these are amphipods and isopods (see Crustacea, Group 1); some leeches (see Hirudinoidea, Group 1); some molluscs (see Mollusca, Group 1); some caddisflies (*Triaenodes aba* (Leptoceridae), see Trichoptera, Group 3); some mosquitoes (*Anopheles walkeri, Culiseta* spp., see Culicidae, Group 3). Secondly, surface water in autumn enables overwintering species with a facultative response to flooding to begin post-embryonic growth. Many organisms gain several weeks in development against the uncertain duration of the spring wet phase, e.g. Turbellaria *(Phagocata)*, Cladocera *(Daphnia)*, Ostracoda *(Candona, Cypridopsis)*, Copepoda *(Cyclops, Canthocamptus, Diaptomus)*, Chironomidae, Tabanidae, Sciomyzidae, and Trichoptera (Limnephilidae, Phryganeidae); some crustaceans complete additional generations. Thirdly, overwintering mortality in species lacking a specialized resistant stage, e.g. Group 1 annelids and molluscs, Group 2 chironomids, would be less in autumnal than in vernal pools because winter stress would be reduced when organisms are submerged and under more constant conditions. Conversely, species well adapted to vernal pools and with a resting stage resistant to 8—9 months of summer and winter extremes without water may be less successful when basins flood in autumn; for example, in Anostraca (see Group 1), the autumn phase of embryonic development is inhibited in eggs lying in flooded parts of the basin of autumnal pools (BROCH 1965). In addition to differences in composition of the animal community brought about by the longer wet phase in autumnal pools, the plant community is likely also to include species that are more dependent on water; plants in recurrent vernal pools are more likely to be amphibious species in such genera as *Alisma, Scirpus,* and *Sium.* Furthermore, detrital processing is less rapid and efficient under water than in dry basins of vernal pools (BÄRLOCHER, MACKAY & WIGGINS 1978).

Aestival ponds were so named (WELCH 1952) because biological activity is restricted to the summer months, owing to the fact that the entire water column and much or all of the bottom sediments freeze during winter. Even though the basins of aestival ponds retain water throughout the year, DABORN & CLIFFORD (1974) suggest that these are effectively winter-dry habitats, differing from other seasonally astatic waters in having the dry phase a function of temperature rather than water supply. Animals in an aestival pond can tolerate an interruption of their development by freezing in ice as larval or sub-adult stages until released in spring

(Daborn 1974). Our interpretation is that adaptation to the winter-dry phase of an aestival pond is freezing tolerance by animals that are never subjected to severe desiccation, and is not the same as adaptation to the summer-winter dry phase of a vernal pool in which animals are subjected to both moisture loss and freezing. Overwintering of coenagrionid larvae (*Coenagrion* and *Enallagma* spp.) in the ice of an aestival pond (Daborn 1974) would not have occurred in a strictly temporary pool, demonstrating that aestival ponds lie within the realm of permanent ponds and not astatic or temporary pools.

The fact that some turbellarians, annelids, insects, crustaceans, and molluscs can tolerate freezing in ice for several months (Daborn 1974, Holmquist 1973) indicates that freezing of an autumnal pool would not be fatal to active aquatic stages in these and probably other taxa. Thus we suspect that the diapause mechanism operating in many vernal pool species serves less as protection against freezing and more as a timing adjustment to avoid the vicissitudes of transient waters and to align the development of predators with maximum prey density. Furthermore, snow cover probably protects animals in a pool basin from low temperature extremes. Before snow falls in November or December, the dry basin of Kendal II is frozen at least for several centimetres; but on 12 March 1972 at an air temperature of −4.5°C, the dry basin under 90 cm of snow was not frozen and registered +1°C at a soil depth of 3 cm.

We consider intermittent or temporary streams to be quite different from temporary pools, both physically and biologically. The hyporheic habitat of streams is utilized by many groups of benthic organisms (Williams & Hynes 1974), and clearly functions as a refuge during periods when water recedes below the surface of the stream bed (Williams & Hynes 1977). Sub-surface water of stream channels is likely to be sustained from groundwater sources, thereby supporting dormant stages of benthic animals with no particular tolerance to drought. Most of these animals are rheophilic species physiologically unsuited to temporary pools.

Nutrients and detritus

Temporary pools in certain areas such as the grassland biome of North America, frequently have high concentrations of inorganic ions far exceeding levels in sea water (Hartland-Rowe 1966). Few species live in these saline pools apart from certain Crustacea, chiefly Anostraca and Notostraca. Most temporary pools maintain ionic concentrations compatible with the majority of freshwater organisms, even though their isolated low-lying basins have been filled annually by watershed run-off for hundreds if not thousands of years. Under these conditions, it seems surprising that nutrients do not accumulate at least to levels in which blooms of planktonic algae would frequently occur, but rarely is this so; some temporary pools in the Canadian prairies have total dissolved ion concentrations lower than permanent and semi-permanent ponds in the same area (Driver & Peden 1977).

We infer from this that only limited amounts of nutrients are available to planktonic algae in the water column because the nutrients may be trapped in bottom sediments as in permanent ponds studied by TERRELL (1975). Furthermore, dissolved nutrients in temporary pools coming out of solution every summer may be chemically combined or adsorbed on organic particles in ways that prevent return to the original dissolved form during the succeeding wet phase. Nutrients accumulating in the bottom sediments of temporary pools would, however, be available to the roots of vascular plants, and may be an important factor in the rich growth on many temporary-pool basins during the dry phase. Thus, terrestrial plants could serve to re-cycle sediment-held nutrients in temporary-pool basins, incorporating them in plant tissues available to aquatic detritivores in the next wet phase. Temporary pools of this type, based largely on autochthonous resources, would be confined to sites open to the sun. Pools heavily shaded by trees would depend more on the allochthonous resources of leaf fall, where re-cycling of nutrients from sediments would seem theoretically less effective in the total nutrient budget than in basins supporting heavy growth of rooted vascular plants. Thus at the beginning of the wet phase, nutrients available to the animal community in pools based largely on allochthonous resources would comprise a relatively smaller component re-cycled from basin sediments than in pools based more on autochthonous resources. We would expect that, owing to the effect of shade on their small basins, temporary pools would span a wide range of limnological conditions. In fact, in a study of temporary pools in Louisiana MOORE (1970) found that heavily shaded pools were heterotrophic, supporting little phytoplankton; but exposed pools were autotrophic and rich in phytoplankton.

Although beyond the scope of the present study, the terrestrial plants that grow in the basins of temporary pools during the dry phase may be seen as the obverse of the aquatic animal community. These plants must be tolerant of flooding for several months in the spring, capable of initial growth during the declining stages of the pool and rapid growth thereafter to complete reproduction. Plants adapted to highly variable conditions would be best suited to these basins, as are their aquatic animal counterparts. The ecological return on the evolutionary investment by the plants would be consistently high ground moisture and nutrient levels in friable organic sediments. The more terrestrial plant species of the basin community would probably be inhibited by conditions of autumnal pools, and we would expect a greater tendency toward amphibious and aquatic plants in these basins.

In quality of food resources, temporary pools reveal some distinct characteristics. Observations on detrital processing in vernal pool Kendal II (BÄRLOCHER, MACKAY & WIGGINS 1978) suggest that detritus decomposes faster when exposed to air during autumn and winter, and has a higher protein content upon flooding in spring than when submerged continuously in permanent pools. Detritivorous trichopteran larvae showed a preference for feeding on leaves with higher protein levels. Thus, rapid development in spring, critically important to temporary-pool animals, may in fact be augmented by the protein-rich detritus combined with high temperatures. A rise in aquatic production following a dry phase underlies, in fact, the waterfowl management practice of alternately draining and flooding marsh lands (COOK & POWERS 1958). By the 17th century periodic dry-fallowing was practiced on carp ponds by German fish-culturists, and became widely established as part of European pond culture technique (NEESS 1946). Carp-growing ponds are wintered dry, and at regular intervals are dried down for a full year; these practices lead to increased fish production. Decomposition of organic materials in dry pool basins is relatively rapid and complete because terrestrial hyphomycetes are able to grow where oxygen is not limiting (BÄRLOCHER, MACKAY & WIGGINS 1978); but decomposition of organic materials when continuously submerged is slower and often incomplete because aero-aquatic fungi and bacteria replace the terrestrial hyphomycetes and oxygen is frequently limiting. Where bottom sediments are not well aerated, accumulation of partially oxidized compounds may increase soil acidity and inhibit bacterial fixation of atmospheric nitrogen (NEESS 1946). Thus after several centuries of observation and experimentation to increase productivity in small ponds, man has succeeded in duplicating the natural cycle of temporary pools. Other possibilities for exploiting the high fertility of temporary pools were raised by MOZLEY (1944).

Conclusions

From the foregoing discussion, we see that within the rather broad term of temporary pool there is a wide range of particular habitats each shaped by a distinctive combination of several factors: length of wet and dry phases, marginal vegetation and its shading effect, basin plants and their role in autotrophy and production of detritus, dissolved ion levels from the surrounding watershed, and temperature. In North America, for example, pools in the eastern deciduous forest biome may be shaded or exposed; pools in the grassland biome are usually not heavily shaded by marginal trees; in arid sections of the grassland biome the water often holds high concentrations of dissolved ions from the surrounding watershed; and pools at high latitudes or elevations may be relatively long-lived but prevailing low temperatures do not allow completion of larval development before winter. Since these factors combine in differing intensities to determine the characteristics of particular temporary pools, they also determine what organisms will be present (Table 3). Thus the concepts of evolutionary and ecological strategies proposed here probably apply to communities in all types of temporary pools (Fig. 12). At a more detailed level, however, little is yet known about the influence of these factors on individual species.

Tab. 3. Comparison of animal communities in permanent ponds and different types of temporary pools.

Pool characteristics	Symbol in Fig. 12	Groups present	Groups eliminated
permanent pond		normal pond fauna incl. Groups 1 and 4, most Group 4 overwintering	Anostraca; some Group 2, most Group 3
water fluctuates widely but never disappears	○	Groups 1, 2, 3, 4; some spp. of normal pond fauna	most of Group 4 not overwintering
open temporary autumnal pool with short dry phase <1 month; rich basin vegetation provides moist microhabitats during dry phase	△	Groups 1, 2, 3, 4; a few invertebrates normally intolerant of drought; some Group 4 could overwinter	fish
temporary autumnal pool with dry phase extended into low temperatures of late autumn, too long for moist microhabitats to sustain species intolerant of desiccation	▲	Groups 1, 2, 3, 4; non-diapausing species active in autumn	species unable to resist or avoid drought; Group 4 overwinter elsewhere
temporary vernal pool (e.g. Kendal II)	●	Groups 1, 2, 3, 4; active in spring and early summer	
temporary vernal pool, highly ephemeral	■	Group 1, some Group 2 Diptera	Groups 3, 4
temporary vernal pool, ephemeral, saline	□	Group 1 Crustacea	most of Groups 2, 3, 4

4.2 Ecology

Our general thesis is that temporary pools constitute a discrete type of freshwater lentic habitat, and that the period of drought imposes conditions for animal occupants so demanding that only a small minority of species in each major freshwater group have become adapted to these habitats. The benefits of breeding in the short-lived vernal pool have apparently provided a powerful selective force favouring species having some means of bridging the dry phase. Successful species must be able not only to tolerate or avoid drought but also to detect a wet phase of sufficient duration for the development of their progeny or to predict that a pool of appropriate duration will subsequently form in a particular basin. Therefore a number of structural, behavioural and physiological adaptations are necessary before species can gain access to the resources of temporary pools.

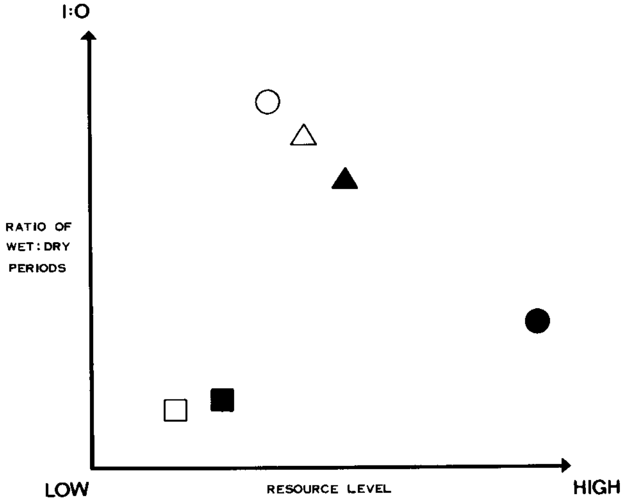

Fig. 12. Ecological strategies and the habitat templet (modified from SOUTHWOOD 1977) in astatic aquatic environments. Ordinate = durational stability assessing harshness of habitat against time; abscissa = resource level in terms of vegetation, which governs insolation influencing autotrophy/heterotrophy and moisture-retentive microhabitats. Symbols as defined in Tab. 3.

Structural adaptations to resist drying are prominent among animals in Group 1, and include, for example, special cysts in Turbellaria *(Phagocata)* and Lumbriculidae, statoblasts in Bryozoa, egg cocoons in Turbellaria *(Hymanella)*, ephippia in Cladocera, and other types of resistant eggs in Turbellaria *(Dalyellia)* and most microcrustaceans. Resistant eggs also occur in Group 2 Ephemeroptera, Trichoptera, and Coleoptera *(Agabus)* and in Group 3 Odonata, Chaoboridae, Culicidae, and some Sciomyzidae. Additional resistant forms include the nymphochrysalis of *Arrenurus* mites in Group 2 and the puparium of some Sciomyzidae in Group 3. Serving the same purpose as these toughened waterproof coverings are various secretions such as mucus lining retreats of oligochaetes, epiphragms of snails, silken cocoons of chironomids, and gelatinous egg matrices of limnephilid Trichoptera. All provide some protection against desiccation.

However, few of the above modifications are confined to inhabitants of temporary pools. Many of the resistant coverings appear to have evolved in permanent waters where they protect the organism during unfavourable periods or serve as disseminules. For example, ephippia and statoblasts are produced before periods of high or low temperatures and in response to low concentrations of dissolved oxygen (HEBERT 1978; PENNAK 1953); chironomid cocoons are made at low temperatures (DANKS 1971b; DANKS & JONES 1978); many pulmonate snails secrete epiphragms (BOSS 1974); and thickened egg matrices are made by many limnephilid Trichoptera of lakes and streams (WIGGINS 1973).

Behavioural adaptations include burrowing to avoid drought, migration either to avoid drought or to colonize newly formed pools, and responses to cues that stimulate oviposition. Again, few of these adaptations appear to have evolved in temporary-pool species alone. Vertical displacement into deeper sediments by lake-dwelling chironomids and other Diptera is a common response to extremes of temperature (DANKS 1971b), and migratory Odonata, Hemiptera and Coleoptera are found in a wide range of permanent aquatic habitats. However, egg-laying behaviour probably is specialized to some extent for temporary pools even though oviposition apart from water (such as that characteristic of many limnephilid Trichoptera, WIGGINS 1973) and endophytic oviposition (such as that characteristic of many odonates) are seen in permanent-water species also. How is a suitable habitat detected by new arrivals? Responses to size and colour of water body and to organic matter have been suggested (see Hemiptera, Group 4). Group 3 species which oviposit in dry basins in anticipation of water to come probably respond to humidity levels. Research on mosquitoes has revealed chemical attractants coupled with specific sensory receptors (see Culicidae, Group 3), and similar attracting substances could influence oviposition by migrants in general.

Various sensory adaptations are necessary for recognition of suitable habitats and oviposition sites, including recognition of suitable hosts by parasites. Physiological adaptations are involved in tolerating rising temperatures and ionic concentrations of receding pools, and in appropriate responses to drought and to flooding. One example of such a response is seen in animals as different as Anostraca and aedine mosquitoes where hatching is stimulated by decreasing levels of dissolved oxygen brought about by rapid microbial decomposition of newly-submerged organic matter. Perhaps, rather than responding to flooding alone, as has often been supposed, many other species with resistant eggs are activated by the effects of decomposition. Such a mechanism would have selective value for organisms which depend on microbially enriched organic particles for food as do so many of the first inhabitants of newly-formed pools.

Tolerance of fluctuating water levels and accompanying extremes of physical and chemical conditions might be presumed to have terrestrial origins; but in fact most inhabitants of temporary pools appear to have evolved from permanent aquatic habitats. In Group 1, many species have a facultative response to flooding, particularly those whose resistant stages are juvenile or adult such as oligochaetes, molluscs, some copepods, and some ostracods. Although effectively protected, these animals are not highly specialized for annual cycles of drought and flood. Some species bridging the dry phase as eggs may also have a facultative response to flooding but some eggs may not respond to the hatching stimulus, either because they are beyond its effect (e.g. deeper in the substrate) or because of natural variance in the response threshhold. Examples of such egg reserves are seen in certain Anostraca and Conchostraca. Many Group 1 species, especially the micro-crustaceans, have the potential for more than one generation per year which together with small size and rapid rates of development make them efficient colonizers when dispersed by wind or animals; they are found in a wide range of aquatic habitats. The exceptions to this generalization are species having a seasonally controlled diapause, including some of the few specialists in temporary pools — the Anostraca. Species in Group 4 are also good colonizers because of their migration. Although by definition not confined to temporary pools, they appear to show a marked preference for such pools when breeding. Thus they appear to be specialized in being able to differentiate between temporary and permanent water, and perhaps in some way to sense how long the wet phase will last to ensure that progeny have time to complete development; whether the cues are entirely visual or chemical is still not known. A measure of the high specificity of pool selection by Coleoptera is shown by their mite parasites. Several mite species reproduce only in temporary pools (see Acari, Group 4) indicating that when selecting its host, the mite anticipates the appropriate final destination where both will breed. Thus in Coleoptera and also in Hemiptera, spring migratory flights may not be as random as suggested by FERNANDO (1958). Similar recognition of temporary pools is shown by insects in Groups 2 and 3, although migration far away from the parent pool is less evident. In both these Groups, oviposition is probably controlled in part by seasonal cues because most species are univoltine. Seasonal cues could include certain temperatures or oxygen concentrations in the late-spring pool for Group 2, combinations of temperature and relative humidity characteristic of summer or autumn, particular stages in the succession of terrestrial vegetation, and the direction of changing photoperiod.

Among aquatic organisms, temporary-pool species represent the extreme in seasonal regulation of life cycles, contrasting with aseasonality in underground waters, some springs, and ocean depths. In general, the synchrony between pool and animal cycles is closer in Groups 2 and 3 than in Groups 1 and 4 because of different responses to flooding. Resistant stages in Groups 2 and 3 are usually under a seasonally controlled diapause, and hence can respond only at certain times of year. In Group 2 there is little proof of diapause, but evidence from seasonal occurrences, including our laboratory observations of flooded soil, indicates that with the exception of larval Chironomidae and adult Coleoptera, most species do not become active when flooding occurs in autumn, and we infer that diapause does occur.

Diapause in Group 3 is better understood. An egg diapause is present in Odonata, Culicidae, *Chaoborus* and some Sciomyzidae (e.g. *Hedria*). Little is known about the life histories of Group 3 chironomids; we recovered larvae from flooded autumn and winter soil samples, and larvae are typically the diapausing stage in the family. Other sciomyzids (e.g. *Renocera*) have a pupal diapause, and still others have an ovarian diapause (e.g. *Tetanocera*). Diapause in Group 3 Trichoptera is either larval *(Ironoquia)* or ovarian (e.g. *Limnephilus*) during summer drought, and oviposition is delayed until autumn. Trichoptera are unusual in that properties of the gelatinous egg matrix allow eggs to hatch out of water in autumn but larvae to remain quiescent within the matrix until flooded.

Groups 1 and 4 contrast with the above in that life cycles are frequently multivoltine and less tied to seasonal controls. Diapause in Group 1 has been documented in only a few cases, e.g., certain species of Rhabdocoela, Anostraca, Cladocera, and Copepoda; many resting stages may simply be quiescent during the absence of water. Members of Group 4 cope with the drying habitat by an alternative strategy — they disperse to permanent pools. The active migrants appear not to be under the influence of diapause although they may be in a non-reproductive state when migrating to permanent water in autumn. The only Group 4 life cycles that clearly include diapause tying them to a particular series of events are those of univoltine parasitic mites whose larvae enter diapause after attaching to their migrating hosts.

Whatever the life cycle pattern, there is one prime requisite for all animals in temporary pools: a rapid rate of development during the wet phase. Development may be completed in a few weeks (or days in the tropics), frequently accelerated by changing physical and chemical factors in receding pools. As the water volume diminishes, temperatures respond rapidly to increasing air temperatures of late spring, raising the probability that high thermal coefficients for development are an important adaptation for temporary-pool animals (CORBET 1962; HODGKIN & WATSON 1958). When we have observed immature and non-resistant stages in drying pools, they have usually been members of Group 4 and we presume they were either the offspring of late-arriving migrants or an unsuccessful second generation in the pool. This lack of synchrony is not unexpected in Group 4 species which seem to be less regulated by seasonal cues than species whose drought-resistant stages are controlled by diapause. However, when dispersal from permanent water, and hence immigration to vernal pools, is delayed by spring maturation of overwintering larvae, the new generation must develop extremely rapidly; *Callibaetis ferrugineus* has achieved this through ovovivipary.

The timing of recruitment is frequently correlated with feeding behaviour and therefore may be interpreted in terms of available food resources. The earliest species in spring and the ones most likely to hatch on flooding, especially in autumnal pools, are usually detritivorous. They are well represented in Group 1, particularly by species feeding on fine organic particles, and their response to flooding is consistent with the use of a food resource that is readily available. Detritivores in Group 3, such as aedine mosquitoes and Trichoptera, also appear early in vernal pools; and the Trichoptera will leave the egg matrix in autumn if flooded.

Predators rarely hatch on autumnal flooding and tend to be bound by diapause to a spring hatching date (e.g. *Polycentropus, Lestes, Sympetrum, Mochlonyx*). The fact that almost all members of Group 4 are predacious, and are the last to appear in a vernal pool, strongly suggests that predator recruitment is timed to coincide with abundant prey resources whereas facultative hatching would expose predators to uncertain food supplies even in an autumnal pool. A notable exception in autumnal pools are certain sciomyzids, but in this case their exclusively molluscan prey overwinter as juveniles or adults, and become active when flooded. Additional support for our interpretation of the timing of recruitment is provided by the Corixidae which are more detritivorous than other aquatic Hemiptera and are usually the earliest immigrants of Group 4. Another aspect of this sequence is that vulnerable prey such as Anostraca gain some relief from predator pressure by being active early in the wet phase.

Only a small minority of species in a few invertebrate families of the total freshwater fauna occur in temporary pools. This depauperate fauna has been attributed to the inability of its members to compete in permanent waters (ÄRDO 1948), and to the fact that it comprises extreme specialists (DAHM 1966). Certain species and pools could be invoked in support of these views. We believe that temporary pools such as Kendal II are populated mostly by ecological generalists which, although certainly having many specializations enabling them to live in these rigorous habitats, are often common and widespread species of permanent ponds and marshes, too (although often with fluctuating levels; see Data and Interpretation for numerous examples). This considerable proportion of the temporary-pool fauna operates under the seeming paradox that (organismic) specialization leads to (ecological) generalization. It is because temporary pools are populated to a large extent by ecological generalists that the faunas of pools from widely separated areas have a marked similarity at generic or specific levels.

Ecological generalists owe their success to many of the adaptations we have described in temporary-pool animals. Species having the ability to tolerate a broad range of environmental conditions, rapid development, marked seasonality in their life cycles, and effective dispersal mechanisms have a high probability of success in temporary pools. The rather small number of taxa that have penetrated temporary pools are those in which these and other attributes coincide. As noted earlier, a number of these adaptations appear to have originated in permanent water. The evolutionary route from cool streams (where many aquatic insect groups originated) to lentic habitats was accompanied by increasing tolerance to extremes of temperature and other factors. Similar adaptive changes in permanent lentic forms could allow entry to temporary pools. For example, genetic material resulting from the origin of Crustacea in the ocean might explain the dominance of Group 1 Crustacea in ephemeral saline pools. Similarly, we have noted that amphipods of temporary pools in northeastern North America are closely related to the few permanent water species that are recorded as having both hypogean and epigean varieties (KENK 1949; PENNAK 1953); relatively small changes in the latter genotypes could give rise to facultative burrowers capable of moving from the epigean pool to a hypogean retreat during drought, provided a suitable moist subterranean habitat is available. Another parallel can be seen in the Trichoptera where two of the few families represented in saline waters, Limnephilidae and Phryganeidae, are also the families most commonly represented in temporary pools.

Dispersal of temporary-pool animals may be active or passive. Group 1 species depend on passive transport. Small resistant eggs and cysts not only survive drought in situ but also are highly efficient disseminules capable of being carried by wind or in the digestive tracts of animals (MAGUIRE 1963; PROCTOR et al. 1967). Clams and ostracods have been observed clinging with tightly closed valves to migrating Hemiptera and Coleoptera (FRYER 1974), and amphipods can be carried in the feathers of waterfowl (ROSINE 1956). Asexual reproduction increases the effectiveness of dispersal because a single disseminule or propagule may be adequate to begin a new population. Some of the more widespread members of Group 1 are those with asexually produced cysts or statoblasts and those capable of parthenogenesis such as many Ostracoda and all Cladocera. The rapid population growth achieved by parthenogenesis is clearly an asset in an ephemeral environment. However, sexual reproduction has the advantage of providing an array of genotypes from which each local environment can be exploited to the best advantage (HEBERT 1978). Cladocera of temporary pools have cyclical parthenogenesis; populations in fluctuating environments are reestablished from ephippial eggs produced by sexual reproduction, and then well-adapted genotypes are multiplied by parthenogenesis. HEBERT's (1978) interesting comparison of lacustrine populations of *Daphnia* with those of temporary pools notes that sexuality and the randomness of genotypic frequencies are least in permanent habitats. Interpreting these observations in light of the possible origin of Cladocera in ephemeral pools, we suggest that parthenogenesis provided a means of effective dispersal from the ancestral habitat, but that retention of sexual reproduction ensures production of individuals best fitted to meet changing environmental conditions.

Active migrants are less likely to be solitary colonizers, and parthenogenesis is accordingly less of an advantage in Groups 2, 3 and 4, where it rarely occurs. However the one genus known to have parthenogenetic species, *Helophorus* in Group 2, is not as active as most Coleoptera because some species overwinter as adults in the dry pool basin. The abundance of *Helophorus* species in southern Ontario may well be explained by the effective dispersal achieved by single propagules (gravid females).

Migratory behaviour appears to have evolved in species whose habitats are sometimes unsuitable for breeding (JOHNSON 1969), species with the most ephemeral breeding habitats having higher powers of dispersal than species in permanent habitats (SOUTHWOOD 1962). Where differences exist in structures such as wing length, stable but isolated habitats favour short-winged forms and no dispersal, whereas temporal uncertainty in moderately scattered habitats favours long-winged forms (VEPSÄLÄINEN 1974b). Some migrants are polymorphic in their adaptive characteristics such as the timing of maturation in *Chaoborus* (BRADSHAW 1973) and wing length in *Gerris* (CALABRESE 1979; JÄRVINEN & VEPSÄLÄINEN

1976) depending on local environmental conditions. Such flexibility is additional evidence of the adaptive success of generalists in temporary pools.

What are the advantages of breeding in temporary pools, and in vernal pools in particular, rather than in permanent water? An earlier paper (BÄRLOCHER, MACKAY & WIGGINS 1978) on Kendal pool II showed that protein levels in decaying plant material were higher in this vernal pool than in permanent pools. Dense vegetation invading the dry basin in summer increases the amount and diversity of plant detritus whose decay by fungi is enhanced by aerobic conditions during autumn. When flooding occurs in spring, rich food resources are therefore available for detritivores who in turn form abundant prey for predators. The rich ecosystem can be explained in part by "pulse stability" (ODUM 1969). The annual perturbation imposed by drought followed by rapid aerobic decomposition releases a pulse of plant nutrients on flooding, and a bloom of new vegetation. This regular cycle maintains the ecosystem in an early successional stage in which efficient colonizers will have an advantage. The optimal strategy for colonization is to produce many progeny as quickly as possible. Initial entry is achieved by efficient dispersal, and fecundity by rapid development and early maturation, i.e. a short generation time. Success in temporary pools will therefore be favoured by r-selection which maximizes the intrinsic rate of natural increase, r (PIANKA 1970). Typical r-selected animals are small (as are most inhabitants of temporary pools, especially those in Group 1); they are not often under seasonal control and are capable of more than one generation per year (Groups 1 and 4); and they can disperse widely (all Groups, but especially some members of 1 and 4). SOUTHWOOD (1977) has argued that since migrant insects have lower fecundity than non-migrants (because energy allocated to flight means less energy going to egg development), the migrants are actually sacrificing maximum values of r in favour of breeding elsewhere. This implies that the breeding habitat is more favourable than the habitat already occupied (SOUTHWOOD 1977) and provides an explanation for movement in Group 4 away from permanent water to temporary pools.

Parallels can be seen between pools and islands where the colonizers are also favoured by r-selection. However we must point out that although principals of migration and extinction developed for island biogeography (MACARTHUR & WILSON 1967) have been applied to small water bodies (e.g. HUBBARD 1973; MAGUIRE 1971), they do not apply to temporary pools because the pools are available only for the period of colonization and productivity. In stable habitats, this period is followed by entrenchment as the environment becomes more crowded and the carrying capacity, K, is approached. The optimal strategy at this stage is to produce a few extremely fit offspring which will be favoured by K-selection to have slower development, larger body size, greater competitive abilities, and more efficient use of resources (PIANKA 1970). In short-lived pools the carrying capacity may never be reached; but as soon as the first, mainly detritivorous colonizers multiply and predators begin to arrive, some K-selected characteristics will be favoured. As PIANKA (1970) emphasized, no organism is completely r-selected or K-selected. The position of species along the r-K continuum will depend on the risk involved in any one situation. Some organisms will maximize their powers of dispersal (r-selected) in order to hedge the risk in many pools; but most Group 4 migrants, being predators, also have K-selected traits and are late colonizers. Other organisms maximize egg production and rates of development (r-selected) to hedge the risk through numbers. Still others maximize individual survival through resistant mechanisms or finely timed life cycles (K-selected) as, for example, in Group 3.

Competition for food is probably unimportant in a pool like Kendal II with much organic detritus although it might be more acute in pools of arid regions. There are no large predators such as fish or those invertebrates that require more than one year to complete development. Thus predation pressure here is lower than in permanent ponds, especially during the early part of the wet phase. The absence of predatory fish, which tend to feed selectively on large zooplankton, may explain the relatively larger sizes of temporary-pool calanoid copepods (COLE 1966) and Cladocera (HEBERT 1978) compared with their lacustrine relatives. Large zooplankton have an advantage over small relatives in that they are less likely to fall prey to invertebrate predators, and will leave more offspring since egg number is positively correlated with body size. Reduced stress from biotic factors coupled with rich food resources are the rewards for breeding in temporary pools.

In the animal community of temporary pools there is not just one optimal ecological strategy for gaining the rewards, but several. One of the merits of our concept of Groups is that it emphasizes this mixture of strategies and provides a framework for community analysis and prediction. Some Groups will be more successful than others depending on environmental conditions in particular pools. The Group concept is based on ecological rather than taxonomic characteristics, and reveals, for example, that all Chironomidae in a temporary pool are not equal, nor are all Culicidae, Chaoboridae, Ephemeroptera, Odonata, Trichoptera, Coleoptera, or Acari; within each of these major taxa very different strategies are operating. Thus when a high annual rate of extinction is demonstrated for species of Chironomidae in temporary pools in the Canadian prairies (DRIVER 1977), it is important to appreciate that extinction of most Tanypodinae (for which we postulate a Group 4 strategy) may be from factors extrinsic to the pools that would prevent immigration from overwintering sites in permanent water; while extinction of Chironominae and most Orthocladiinae (Group 2) would more likely be caused by factors intrinsic to the pools since these species probably overwintered in the basins.

By following the habitat templet of SOUTHWOOD (1977) and reducing the many habitat variables to two main factors, resource levels (x-axis) and durational stability (y-axis), we have arranged different pool types along a gradient of environmental harshness (Fig. 12). Corresponding changes in the animal community are shown in Table 3. If a third (z) axis is introduced to span climatic conditions from pole (origin of graph) to equator, we suggest that all types of temporary pools can be defined within this matrix. The faunas of these pools follow the general principle of an inverse relationship between community diversity and habitat adversity.

4.3 Evolution

In the physical development of Earth, freshwater temporary pools probably came into existence at least as early as permanent bodies of water, at the time when rain began to fall and collect on the surface. Thus temporary pools would have preceded the origin of life. For reasons developed earlier (see Limnology), temporary pools provide a favourable trophic environment for certain types of aquatic animals. These pools probably have undergone few changes in this respect since Silurian and Devonian times when vascular plants were established on land, particularly in damp sites (DOBZHANSKY et al. 1977), thus affording a basic food resource for detritivorous macro-invertebrates. Algae would have been present even before that time. Granting this ancient origin, we may consider how temporary pools have figured in the evolutionary history of aquatic animals; the evidence suggests that they have done so in several very different ways.

The earliest inhabitants of temporary pools probably included Anostraca, Conchostraca, and Cladocera of Group 1, and to them would be added the Notostraca; these taxa make up the extant Branchiopoda (sensu HUTCHINSON 1967), regarded as the most archaic living Crustacea by TIEGS & MANTON (1958). Conchostraca are known from the Devonian (HUTCHINSON 1967), Notostraca from the Permian (LONGHURST 1955), and Anostraca of uncertain affinities from the Devonian and perhaps earlier (HUTCHINSON 1967). With the exception of the Cladocera, all of them are now almost entirely confined to temporary waters because these sites are free from fish predation (HUTCHINSON 1967). We think it likely that the marine ancestor(s) of the Branchiopoda first became adapted to fresh waters of a permanent nature. Jawed fishes appearing in Devonian fresh waters would have introduced major new predatory pressures (DOBZHANSKY et al. 1977) on the vulnerable larger branchiopods, favouring expansion into transient waters free of fish, and subsequently extinction of their permanent-water forebears. Evolution of temporary-pool lineages from predecessors in permanent water is analogous with our hypothesis for insects (see below). Cladocera are entirely freshwater, save for a few that are secondarily marine (HUTCHINSON 1967), but apparently with relatively few extant species in temporary pools; widespread occurrence of ephippia through this group suggests that resistance to drought may have had some general influence in their early evolution. Daphniidae and Chydoridae date at least from the Permian (SMIRNOV 1971), and ephippia of *Daphnia* and *Moina* from the Tertiary (FREY 1971). Ostracoda and Copepoda are clearly of marine derivation, and since several separate freshwater invasions can be recognized in each taxon (Hutchinson 1967), the temporary-pool species probably arose by way of permanent fresh waters. Turbellaria of temporary pools are believed to have been derived from species in permanent water (Ball et al. in press).

Groups 2, 3, and 4 consist almost entirely of insects and mites, animals that have invaded fresh waters from terrestrial ancestors; respiration is a major physiological problem, particularly for apneustic larvae respiring dissolved oxygen. Among the insects of temporary pools in this category are species in the Ephemeroptera, Odonata, Trichoptera, Chironomidae, Chaoboridae, and Ceratopogonidae. These insects, and also Plecoptera which have been recorded from autumnal pools in Oregon (Lehmkuhl 1971), experience least respirational stress in cool running waters; and the most primitive of them according to independent phylogenetic evidence (see Data and Interpretation) occur in such habitats. Therefore, because aquatic insects with larvae respiring dissolved oxygen were initially cool-lotic-adapted, invasion of temporary pools was not possible until they became lentic-adapted. Even after respirational problems were overcome, the paucity of species in temporary pools compared with numbers in permanent lentic sites indicates that recurrent drought and related problems have been more severe physiological barriers than respiration. Aquatic insects whose larvae are dependent on atmospheric oxygen are lentic adapted, and in temporary pools comprise Hemiptera, Culicidae, Sciomyzidae, Stratiomyidae, and Coleoptera. Temporary-pool lineages in the Stratiomyidae and Sciomyzidae probably did enter these habitats directly from terrestrial ancestors (see Groups 2 and 3). This may also be true for Hemiptera if Popham (1964) is correct in his suggestion that members of this order first became aquatic under conditions of temporary pools. Culicidae (principally *Aedes* and relatives) were derived from permanent-water ancestors (Ross 1951). The original habitat of aquatic Coleoptera was probably permanent lentic waters, from which species adapted to temporary pools would have arisen (R. E. Roughley in prep.).

Like aquatic insects, water mites were derived from terrestrial ancestors, and although phylogenetic relationships of the mites are not clear, some general trends may be identified. Five families, Hydryphantidae, Arrenuridae, Pionidae, Eylaidae, and Hydrachnidae are represented in temporary pools. Concordant evidence from a variety of sources indicates that Hydryphantidae, which have terrestrial larvae, may be the earliest derivative living family of water mites. If so, temporary pools could have been the ancestral habitat in which mites first diverged into an aquatic existence. Along with terrestrial mites of the superfamilies Trombidioidea, Calyptostomatoidea, and Erythraeoidea, water mites belong to the Parasitengona, a group characterized by a derivative life history pattern featuring a parasitic larval instar and reduction of protonymphal and tritonymphal instars to calyptostases. Parasitengona are thought to represent the sister group of the superfamily

Anystoidea, and to have originated from terrestrial stock having a free-living, active, larval instar and three active nymphal instars between egg and adult (KRANTZ 1978). Certain features of the life history in hydryphantid water mites suggest that their strategy for exploiting temporary pools (see Group 2) represents a preliminary grade in the adaptation of water mites to aquatic habitats, and could have originated during the formative evolution of Parasitengona.

Assuming that protoparasitengone-anystoid mites became adapted to feed on the abundant aquatic and subaquatic invertebrates concentrated at the margins of temporary pools, a plausible sequence leading to differentiation of an ancestral parasitengone can be proposed. Transition of a predator-prey relationship into one of parasite-host would seem easily made by the mite larvae feeding for longer periods on larger hosts such as teneral insect imagoes. The relatively small mite larvae could have been transported on insects from their original habitat to similar ones with the opportunity to found new populations. Once established, this relationship would have resulted in fully-fed larvae being regularly introduced into temporary pool margins where prey populations were high, but where water levels were receding. Consequently there would be selective pressure on the mites to concentrate their subsequent feeding and maturation into the short period before disappearance of surface water, when prey populations would diminish rapidly. Accordingly, temporal and functional reduction of the protonymphal and tritonymphal instars could have occurred, leaving the deutonymph as the only active nymphal instar. This would have conferred the distinct advantage that nearly all of the time available while prey were abundant could be devoted to feeding by the deutonymph, thereby ensuring the growth of robust individuals best suited to endure prolonged drought and greatly reduced food supply. Integration of these adaptations into the life history would lead to differentiation of an ancestral parasitengone stock adapted to exploit intermittent aquatic habitats. Further modification could have lead to appearance of an ancestral water mite stock similar to extant hydryphantids; because aquatic invertebrates would become extremely concentrated in the receding waters of temporary-pool basins it would have been of further advantage for deutonymphal and adult mites to become adapted for life beneath the surface film to exploit the abundant prey resources, yet retaining the ability to endure drought by becoming inactive. According to this provisional hypothesis, a hydryphantid-like stock could have arisen in temporary pools, and persisted relatively unmodified for an extended period of time, giving rise to a succession of derivative parasitengone groups exploiting different insects as hosts. Therefore, unlike most groups of aquatic insects, mites may have begun their aquatic existence in temporary pools. But, apart from the Hydryphantidae which evidently represent a persistent early derivative group retaining many of the characteristics attributed to this ancestral stock, the disparate phylogenetic relationships of other taxa represented in temporary pools indicate several subsequent, independent, and secondary invasions of this habitat. For water mites, temporary pools pose the dual problems of survival during drought, as well as synchrony between parasitic larval stages and dispersing adult stages of the hosts, and also between predacious deutonymphs and adults and their prey during the wet phase of the pool.

Thus we see that invertebrates in temporary pools have different origins. The majority are derived from lineages that are highly diverse in permanent waters, and most of the insects in fact have their ultimate origins in cool, lotic habitats. At least some of the separate lineages of Crustacea which are of independent marine origin probably first became adapted to permanent fresh waters before invading temporary pools; it is an open question whether the Branchiopoda inhabited permanent waters before temporary pools. A very few of the temporary-pool species appear to have been derived directly from terrestrial ancestors. As we have emphasized throughout Data and Interpretation, adaptations equipping animals to live successfully in temporary pools are very much broader than drought resistance alone. Many adjustments to their physiology, behaviour, and structure are involved. We can recognize only some of these modifications, and in certain taxa a sequence of adaptive features of diminishing generality is apparent, as for example in the odonate genus *Lestes* (Fig. 10).

In addition to an important role in the adaptive radiation of aquatic invertebrates, temporary pools may also have had a major impact in the evolution of vertebrates. Environmental change is recognized as a stimilus to evolutionary advance (DOBZHANSKY et al. 1977), and seasonal drought in freshwater habitats has been invoked to account for the invasion of land by vertebrates. For early amphibians, ROMER (1967) has postulated that seasonal drying of rivers would have encouraged the fish ancestors of tetrapods to move along drying channels to larger pools, thus placing a selective advantage on development of limbs and lungs. However, assuming analogy with living amphibians, we infer that during the wet season, ancestral amphibians could also have been under selection pressure to deposit eggs in isolated marshes and temporary pools where the vulnerable larvae would not be exposed to predatory fish. Thus, evolution of legs and lungs could be as much a result of selection for leaving permanent waters for better oviposition sites as for seeking permanent waters as refuges during dry seasons. Recognizing that the red beds of the late Palaeozoic, which are rich in early tetrapod fossils, give evidence of widespread seasonal drought, ROMER (1967) extended the idea of the influence of seasonally drying aquatic habitats to account for another major advance in development of land vertebrates — evolution of the terrestrial reptilian egg. He suggested that if amphibian eggs are laid in a pond, drought leads to death of larvae. Given the rapid embryonic and larval development seen in some extant amphibians (WILBUR & COLLINS 1973), we suspect that drying of a pool would not necessarily lead to larval death.

Contrasted with all other types of aquatic habitats, annual temporary pools (and streams) are the paradoxical combination of widely fluctuating yet constant conditions. Differences between wet and dry phases are unparalleled for single sites, with every sort of intermediate; and yet this cycle can be constant year after year with only minor deviations. Changing environments seem more likely to influence evolutionary events when they occur in consistent regular cycles as annually transient waters do. For similar reasons, HINTON (1968) suggested that temporary pools were likely sites for the origin of life. Finding that a number of organisms could sustain extraordinary exposure to heat, drying, and certain chemicals, and yet resume normal activity when returned to water (see Chironomidae, Group 2), HINTON (1960, 1968) attributed this ability to cryptobiosis, a state when the metabolic activity of the organism comes reversibly to a standstill. He argued that cryptobiosis is a primitive characteristic of protoplasm, thereby requiring that the chemical processes first engendering life occurred not in the sea but on land, although agreeing that much of the early elaboration of life took place in the constant environment of the sea. HINTON believed that conditions of small pools subject to alternate wet and dry periods were the most likely sites which could accumulate the requisite highly concentrated solutions of chemical compounds subject to wide variation in composition under different conditions of acidity and alkalinity. "The formation of increasingly complex organic compounds is entirely compatible with alternate hydration and dehydration of the reacting systems. During periods of dehydration, the organic compounds would be blown about and accumulated in different proportions ... thus a far greater variety of reacting systems could be obtained than would ever be possible in a continuously wet environment" (HINTON 1968: 55). If indeed life did originate under such conditions, only a tiny proportion of total animal diversity found the way back to temporary pools.

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6. Summary

Animal species in temporary pools have many structural, behavioural and physiological adaptations for surviving or avoiding drought. Some of these adaptations also occur in species of permanent waters but are coincident only in the few species of the freshwater fauna inhabiting temporary pools. Thus species in temporary pools form a small, consistent, and predictable assemblage. Field data from temporary pools in southern Ontario together with relevant information from the literature are used to derive a concept of animal community structure in these pools.

Temporary-pool communities comprise four different components according to methods of surviving the dry period and seasonal patterns of recruitment. Group 1 animals are permanent residents capable of only passive dispersal; they aestivate and overwinter in the dry pool basin, either as stages resistant to desiccation (certain Turbellaria, Bryozoa, Anostraca, Cladocera, Copepoda and Ostracoda) or while protected in the pool's bottom sediments (Oligochaeta, Hirudinoidea, Decapoda, and Mollusca). Group 2, capable of some dispersal, includes certain Ephemeroptera, Coleoptera, Trichoptera, and Diptera, together with parasitic mites; these animals oviposit on water in spring, and then aestivate and overwinter in the dry basin in various stages of the life cycle. Group 3, consisting of certain Odonata, Trichoptera and Diptera, are summer recruits which can enter the pool basin after surface water has disappeared because oviposition is independent of water; eggs or larvae overwinter. Group 4 includes species of Ephemeroptera, Odonata, Hemiptera, Coleoptera, Diptera, mite parasites of Hemiptera and Coleoptera, and also Amphibia. Group 4 species have well-developed powers of dispersal; they leave the disappearing pool, usually pass the dry phase in permanent water, returning to oviposit in the temporary pool the following spring. This Group concept allows distinction to be made among the varied ecological strategies for exploiting resources of temporary pools, and provides a framework for community analysis and prediction.

Precision in defining temporary pools from water levels during the preceding year is emphasized. The past history of a pool may be deduced from an interpretation of organisms present according to the adaptive strategies of the Groups to which the animals belong. Distinction is made between two types of temporary pools in temperate regions — vernal pools and autumnal pools. Aestival ponds are shown to be functionally distinct from temporary pools. Temporary pools encompass a wide range of particular habitats, each shaped by a distinctive combination of several factors: length of wet and dry phases, marginal vegetation with its shading effect, and basin plants with their role in autotrophy and production of detritus.

The first animals to appear in spring are mostly detritivorous, feeding on rich food resources provided by plant detritus. The richness can be explained partly by pulse stability and partly by the rapid decay of dead vegetation exposed to air in autumn and winter which results in a high protein content when the detritus is flooded in spring. Detritivores in turn support later predacious colonizers, especially those of Group 4. Most animals in temporary pools are ecological generalists, often common and widespread species of permanent ponds and marshes. Yet these same generalists also have the necessary specializations for life in temporary habitats, such as efficient dispersal mechanisms, rapid development, early maturation, and some means of ensuring survival during unfavourable periods. Success is therefore favoured by r-selection, and early colonizers of temporary pools are typical of r-selected animals. Some K-selected characteristics may be seen in later colonizers, but in short-lived pools the carrying capacity may never be reached because these pools are available only for a period of colonization and productivity, and not for the period of entrenchment that favours K-selection. On a global scale, temporary pools and their respective communities can be arranged within a matrix defined by resource levels, durational stability, and climatic conditions.

In the physical development of Earth, freshwater temporary pools probably came into existence at least as early as permanent bodies of water, thus preceding the origin of life. The small number of species that exploit temporary pools appear to have evolved mainly from lineages in permanent waters, very few arising directly from terrestrial ancestors. Freedom from predatory fish and access to under-exploited resources appear to have been major selective advantages for animals evolving to exploit temporary pools. Because they undergo consistent annual cycles encompassing an exceedingly wide range of ecological conditions in single sites temporary pools stimulate evolutionary change.

Zusammenfassung

Tierarten in temporären Tümpeln besitzen manche Anpassungen in bezug auf Struktur, Physiologie und Verhalten, um Trockenperioden zu überleben oder zu vermeiden. Einige dieser Anpassungen findet man auch bei Bewohnern permanenter Gewässer; ihr gemeinsames Vorkommen beschränkt sich jedoch auf die paar Arten der Süßwasserfauna, welche temporäre Tümpel besiedeln. Feldbeobachtungen an temporären Tümpeln im südlichen

Ontario und Informationen aus der Literatur werden benützt, um ein Konzept der Struktur von Tiergemeinschaften in solchen Tümpeln zu erstellen.

Gemeinschaften temporärer Tümpel bestehen aus vier Gruppen, die sich in ihrer jahreszeitlichen Rekrutierung und in ihren Strategien zum Überleben der Trockenperiode unterscheiden. Tiere der Gruppe 1 sind ortsgebunden und werden nur passiv von Tümpel zu Tümpel verbreitet; sie überdauern die Trockenperiode im Tümpelbecken entweder als austrocknungsresistente Stadien (gewisse Turbellaria, Bryozoa, Anostraca, Cladocera, Copepoda und Ostracoda) oder geschützt in den Bodensedimenten (Oligochaeta, Hirudinoidea, Decapoda und Mollusca). Gruppe 2, bei der eine gewisse aktive Verbreitung möglich ist, umfaßt einige Ephemeroptera, Coleoptera, Trichoptera und Diptera sowie parasitische Milben. Diese Tiere legen ihre Eier im Frühling auf dem Wasser ab und verbringen die Trockenperiode im Becken in verschiedenen Stadien ihres Lebenszyklus. Gruppe 3, bestehend aus gewissen Odonata, Trichoptera und Diptera, kann das Tümpelbecken auch besiedeln, nachdem das Oberflächenwasser verschwunden ist, da bei ihr Eiablage unabhängig von der Gegenwart des Wassers möglich ist; hier überwintern Eier oder Larven. Gruppe 4 enthält Arten der Ephemeroptera, Odonata, Hemiptera, Coleoptera, Diptera, Milben, die Hemiptera und Coleoptera parasitieren, sowie Amphibien. Arten der Gruppe 4 besitzen gut entwickelte Fähigkeiten zur Verbreitung; sie verlassen den austrocknenden Tümpel und verbringen die Zwischenzeit im allgemeinen in permanenten Gewässern, um im folgenden Frühling zur Eiablage in temporäre Tümpel zurückzukehren. Dieses Gruppenkonzept erlaubt eine Unterscheidung zwischen den verschiedenen ökologischen Strategien, welche die Ausbeutung des Nahrungsangebotes temporärer Tümpel erlauben, und schafft einen Rahmen zur Analyse und Interpretation der Gemeinschaft.

Die Bedeutung einer genauen Definition temporärer Tümpel aufgrund des Wasserstandes des vorhergehenden Jahres wird betont. Die Vorgeschichte eines Tümpels kann aus den adaptiven Strategien der vorhandenen Tierarten abgeleitet werden. In gemäßigten Regionen können zwei Typen unterschieden werden: Frühlingstümpel und Herbsttümpel. Sommertümpel sind funktionell verschieden von temporären Tümpeln. Länge der Trocken- und der Naßphase, Ufervegetation und ihr Beschattungseffekt, die Pflanzen im Becken des Tümpels und ihre Rolle in Autotrophie und Detritusproduktion beeinflussen alle den Charakter dieser Gewässer.

Die ersten Tiere, die im Frühling auftreten, sind zum größten Teil Detritusfresser, welche sich von einem reichen Angebot an zerfallenden Pflanzenresten ernähren. Der Nahrungsreichtum beruht zum Teil auf Pulsstabilität und zum Teil auf dem raschen Abbau toter Vegetation, die im Herbst und Winter der Luft ausgesetzt ist, was in proteinreichem Detritus im darauffolgenden Frühling resultiert. Detritusfresser dienen ihrerseits späteren, räuberischen Einwanderern, die häufig zur Gruppe 4 gehören, als Nahrung. Die meisten Tiere in temporären Tümpeln sind ökologisch wenig spezialisiert und kommen häufig auch in permanenten Tümpeln, Weihern und Sumpfgebieten vor. Sie besitzen jedoch die notwendigen Adaptationen, die für den Erfolg in temporären Habitaten notwendig sind, wie wirksame Verbreitungsmechanismen, rasche Entwicklung und Anpassung, um ungünstige Perioden zu überleben. Erfolg wird deshalb begünstigt durch r-Selektion, und frühe Besiedler temporärer Tümpel sind typische r-Strategen. Einige K-selektionierte Eigenschaften können in späteren Besiedlern beobachtet werden. Vermutlich wird jedoch in kurzlebigen Tümpeln die Populationskapazität selten erreicht. Sie stehen den Tieren nur für eine kurze Periode der Kolonisation und Produktion zur Verfügung und nicht für die relativ lange Zeitspanne, die für das Wirksamwerden der K-Selektion erforderlich ist. Auf einem globalen Maßstab können temporäre Tümpel in einer Matrize eingeordnet werden, die bestimmt wird durch Art und Menge des Nahrungsangebotes, zeitliche Stabilität und klimatische Bedingungen.

In der physikalischen Entwicklung der Erde sind temporäre Tümpel vermutlich mindestens so früh aufgetreten wie permanente Gewässer und sind somit älter als das Leben. Die wenigen Arten, die heute temporäre Tümpel besiedeln, scheinen zum überwiegenden Teil von Vorfahren in permanenten Gewässern abzustammen, während direkte Abstammung von terrestrischen Vorfahren sehr selten ist. Vermeiden räuberischer Fische und Zugang zu einem wenig ausgebeuteten Nahrungsangebot scheinen die wichtigsten selektiven Vorteile für Tiere gewesen zu sein, die sich an eine Existenz in temporären Tümpeln anpaßten. Da in diesem Habitat jedes Jahr die ökologischen Bedingungen an einem einzelnen Ort große Schwankungen durchlaufen, fördern temporäre Tümpel evolutionäre Veränderungen.

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