

12 Temporary Woodland Ponds in Michigan

Invertebrate Seasonal Patterns and Trophic Relationships

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Temporary woodland ponds are relatively small, shallow wetlands that retain water for a few weeks to several months out of the year. Most of the energy flow within these habitats stems from microbial degradation of leaf litter deposited by surrounding trees and shrubs. The composition of the invertebrate community found within any particular pond is related to its size and the duration of flooding. The invertebrates that inhabit these ponds show varying degrees of adaptation to ephemeral habitats, but nearly all are characterized by rapid larval growth. Medium- to large-sized ponds exhibit a predictable seasonal succession of species, a pattern that has evolved in response to both physical constraints and biotic interactions. The early-season inhabitants are particularly well adapted to the ephemeral habitat and cold temperatures characteristic of early spring in Michigan. These animals feed primarily on the abundant microbial community present on the leaf litter and within the water column, and avoid heavy predation pressure by beginning development before the appearance of most of the predators. Most of the ponds' inhabitants that are not specifically adapted to ephemeral habitats are predators. These are generally insects that overwinter in permanent water and recolonize temporary ponds each spring. By consuming a high-quality food source such as animal protein, these migrants are able to develop rapidly and thus ensure completion of the larval phase before the ponds dry.

TEMPORARY PONDS

Prior to Euro-American settlement, the wooded landscape of southern Michigan was dotted by innumerable ephemeral ponds formed millennia ago in vast glacial outwash plains. Although only a small percentage of these temporary woodland ponds remains today, they represent a fairly common yet remarkably understudied aquatic habitat. Woodland ponds can range in size from a few square meters to over a hectare, although most are probably less than 0.4 ha. Maximum water depth is generally less than 1.5 m, and the average depth is usually under 1 m. These small woodland ponds are generally unsuitable for waterfowl production compared to larger, more open habitats, a factor which may explain the relative inattention these wetlands have received in the scientific literature. Ponds may begin to flood in late autumn or winter, reaching maximum size in the early spring as a result of snowmelt and spring rains. A distinction has been made between vernal pools (Fig. 12.1a), which flood only in the spring, and autumnal ponds (Fig. 12.1b), which flood in the autumn and remain wet until the following summer (Wiggins et al. 1980). It should be pointed out that the flooding which occurs in autumn often only covers the deepest parts of these ponds, and much of the pond area remains dry until the following spring. While the flooded area of an autumnal pond may provide important overwintering habitat for some aquatic invertebrates that lack specific adaptations for drying and freezing (see Batzer and Sion, this volume), much of the well-adapted temporary pond fauna remains unaffected by this flood event. Thus, while the presence or absence of water during the autumn and winter will influence faunal composition somewhat (Kenk 1949, Wiggins et al. 1980, Batzer and Sion, this volume), we believe that the size and duration of a particular pond during the vernal phase has an even more pronounced influence on community composition.

The duration of flooding is directly related to area and depth. All of these water bodies are closed depressions and dry from evaporation and groundwater outflow. Most are dry by the middle of summer, and some may undergo a second, somewhat accelerated cycle of flooding and drying in the mid-to-late summer as a result of heavy precipitation and drying in the mid-to-late summer as a result of heavy precipitation from thunderstorms. Flooding during this aestival (summer) phase is generally smaller in areal extent than during the vernal phase. Small vernal pools flood only in the spring.

Temporary woodland ponds occur in forested landscapes and are thus bordered on all sides by trees (e.g., red maple, silver maple, elm, cottonwood) and shrubs (e.g., dogwoods, alder, spicebush). Trees frequently occur within the flooded portions of the ponds as well as the borders (Fig 12.1b). Because of the intense shading from trees and shrubs along the margins of these ponds, often very little emergent vegetation is present, or the emergent plants may occur only in relatively small areas that receive sufficient sunlight. In addition, submerged aquatic vegetation (including submerged macrophytes and mats of filamentous algae) generally does not occur in these ponds. After the trees

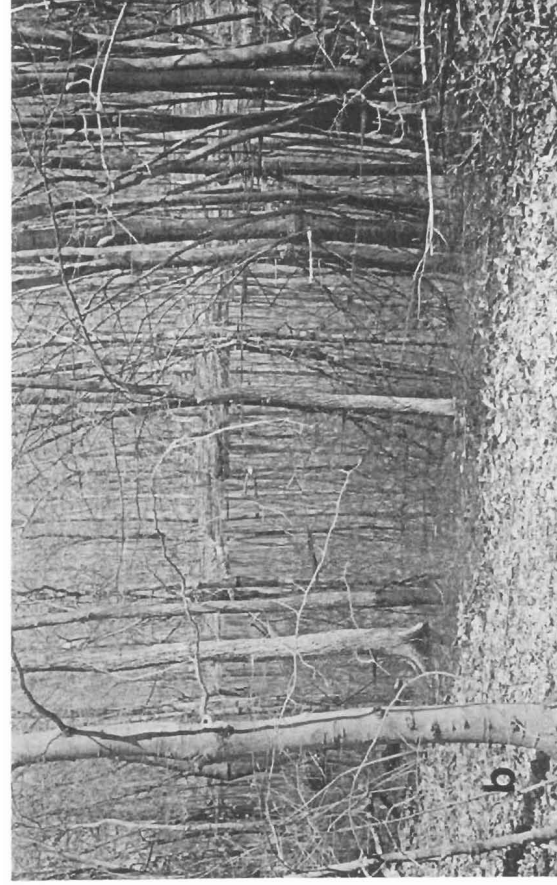


Fig. 12.1. Examples of temporary woodland ponds. (a) Small vernal pool (approximately 4 m in diameter). (b) Autumnal-vernial pond during the vernal phase. Note the abundant leaf litter in each pond.

leaf out in the spring, the ponds themselves may receive little direct sunlight, a factor which may limit algal growth compared to more open types of wetlands (e.g., Kenk 1949). The surrounding woodland vegetation is also important for the input of substantial amounts of leaf litter into the dry basins in the fall. Barlocher et al. (1978) recorded an average of 132.8 g/m² of leaf litter (ash-free dry mass) falling into Ontario pond basins in the autumn.

In southern Michigan water temperatures range from 3°C in the early spring when ice is still present, to 27°C in the summer. Because of the shallow nature of these bodies of water, daily water temperature fluctuations of 5°C are not uncommon in the spring, particularly in the small ponds (Fig. 12.2). In addition, a thin layer of ice frequently covers the surface at night during the early spring. Early in the season pH generally ranges from 7–7.5 and gradually becomes more alkaline (7.5–8) as the ponds shrink in size during the late spring and summer. Due to the large surface-to-volume ratio, ice-free ponds do not often become anoxic, but anaerobic conditions exist in the underlying sediments. Dissolved oxygen and pH also undergo diel fluctuations as a result of increase algal respiration at night (Williams 1987).

SEASONAL PATTERNS—VERNAL PHASE

In a landmark paper on temporary pond ecology, Wiggins et al. (1980) divided temporary pond breeding inhabitants into four groups (Table 12.1), based on their adaptations (or lack thereof) to the dry phase of these habitats and also on their oviposition/colonization habits. Animals that are particularly well adapted to life in these temporary environments (Groups 1–3) are basically year-round residents, spending the dry phase in some drought resistant stage (often the egg stage). Organisms which lack drought resistance (Group 4) must move to permanent water before the ponds dry and then recolonize the temporary ponds the following spring. This latter category is characterized by species with excellent colonizing abilities and rapid larval development.

The composition of the invertebrate community present in any given pond is related to its size and duration of flooding (Schneider and Frost 1996; see also Schneider, this volume). Small ponds of only a few weeks' duration contain relatively few species and are dominated by ostracods and mosquito larvae of the genus *Aedes*. In addition, gastropods, triclad turbellarians (planarians), cladocerans, and occasional predatory beetle larvae (family Dytiscidae) may be present. Amphipods (*Crangonyx*) have been surprisingly abundant in several small vernal pools we have sampled. Amphipods are not thought to be particularly well adapted to the dry and frozen conditions that characterize vernal ponds during the autumn and winter (Wiggins et al. 1980, Batzer and Sion, this volume), and their presence in these short-duration (8–10 weeks) vernal pools remains an enigma. Isopods, which are also poorly adapted to temporary ponds, were occasionally recovered from a few vernal pools. Their presence may be explained, however, by the cooccurrence of

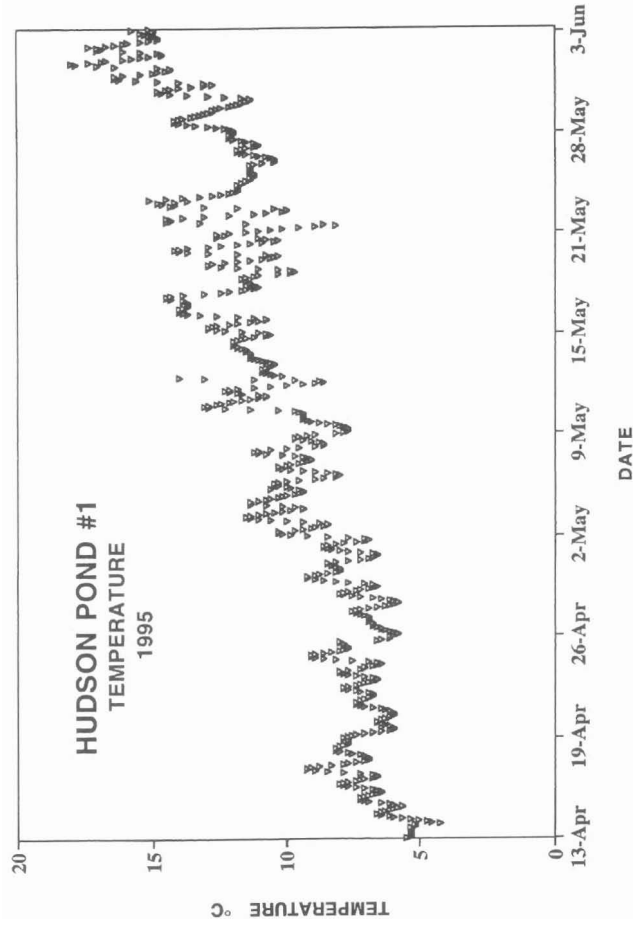


Fig. 12.2. Temperature data for a small vernal pool in southern Michigan. Each symbol represents a reading taken at approximately 1.5-hour intervals.

crayfish in these particular ponds. Crayfish burrows may provide a refuge in temporary habitats for poorly adapted organisms such as isopods (Wiggins et al. 1980).

The relatively few number of species present in these small pools suggests relatively simple trophic relationships (Schneider and Frost 1996). Medium- to large-sized ponds, persisting for four to six months in the spring and summer, generally contain a large diversity of invertebrate organisms and are characterized by a fairly predictable succession of species. While there may be some invertebrates active during the winter in autumnal ponds—generally small crustaceans such as copepods, ostracods, and cladocerans—the primary season of invertebrate activity begins when ice melts along the margins of the ponds, usually in late February or early March in southern Michigan. If the ponds are sufficiently flooded, *Aedes* mosquito eggs that were deposited in the dry basins by females the previous season begin to hatch. Analyses of soil samples from temporary ponds indicate that the vast majority of mosquito eggs are laid near the margins of maximum flooding extent (James 1966, Iversen 1971). Thus, if insufficient precipitation occurs, resulting in lower than normal water levels, little hatching will take place.

In addition to *Aedes* mosquito larvae, other early-season inhabitants of medium to large-sized temporary woodland ponds include fairy shrimp (order

Anostraca), small crustaceans (copepods, cladocerans, ostracods), midge larvae (Chironomidae), phantom midge larvae (genus *Mochlonyx*), caddisfly larvae (primarily *Limnephilus*), and gastropods (e.g., *Physella*). Except for *Mochlonyx*, which preys upon small crustaceans and perhaps some first-instar mosquito larvae, there are few predators during this early part of the season. Conditions at this time are harsh, with cold water temperatures (<10°C) and frequent ice formation on the surface, factors which do not appear to harm the organisms listed above. Mosquito larvae have been shown to survive 10 days of ice cover on a woodland pond in Ontario (Westwood et al. 1983), and Walker (1995) demonstrated that larvae continue to feed, albeit more slowly, at temperatures down to 0°C. Most of the predators in temporary woodland ponds do not appear until water temperatures exceed 10°C on a regular basis. One of the few predators that appears to have solved physiological problems associated with cold and ice is the dytiscid beetle larva, *Agabus erichsoni*, the eggs of which hatch almost simultaneously with those of mosquitoes. Cold early spring temperatures and short-term ice cover do not seem to have a negative impact on this species, whose primary prey appears to be mosquito larvae (James 1961, Higgins, unpublished data).

As temperatures warm in mid- to late April, more species—chiefly predators—make their appearance within the ponds. Dragonflies and damselflies (*Sympetrum* and *Lestes*), present as eggs laid within the basin the previous summer, hatch out as very small individuals and consume small crustaceans during their early instars. Eggs of a predatory caddisfly, *Polycentropis crassicornis* (Polycentropidae), hatch in late April, and the larvae initially feed on small crustaceans that become trapped in the caddisflies' silken retreats constructed within the leaf litter (Higgins, unpublished data). Adult water striders (Gerridae) and backswimmers (Notonectidae) that overwintered in permanent water recolonize these temporary environments and begin breeding at this time, as do several species of beetles (e.g., Dytiscidae: *Acilius*, *Colymbetes*, *Dytiscus*, *Rhantus*; Hydrophilidae: *Hydrochara*, *Hydrochus*, *Tropisternus*; Gyrimidae: *Gyrinus*). Eggs of chorus frogs (*Pseudacris triseriata*) and salamanders (*Ambystoma*) that were laid in the ponds in late March or early April hatch by mid to late April. *Ambystoma* larvae are the only important vertebrate predators in temporary woodland ponds.

Adult mosquitoes begin to emerge from the ponds in early to mid-May of most years. By this same time, fairy shrimp have completed development, deposited eggs, and died. Limnephilid caddisflies, which have been feeding continuously on leaf detritus for two months, reach their final instar by the middle of the month and begin pupating in late May. With the emergence of mosquitoes, the pupation of caddisflies, and the disappearance of fairy shrimp, the invertebrate fauna becomes dominated by predatory species in late May. In addition to the species listed above, other migrants arrive, including giant water bugs (Belostomatidae), broad-shouldered water striders (Veliidae), water boatmen (Corixidae), water scorpions (Nepidae), and some additional beetle species. In addition, migratory green darner dragonflies (*Anax junius*)

TABLE 12.1. Summary of Life History Groups for Invertebrates Inhabiting Temporary Woodland Ponds

Group ^a	General Characteristics	Examples
1. Overwintering residents	Permanent residents with drought-resistant stage Passive dispersal only Generally noninsect invertebrates	Cladocerans, copepods, ostracods, fairy shrimp, planarians, gastropods, fingernail clams
2. Overwintering spring recruits	Nearly permanent residents with drought-resistant stage (usually the egg stage) Adults oviposit in water before pond dries	Some dytiscid beetles (e.g., <i>Agabus</i>), <i>Polycentropis crassicornis</i> caddisfly, soldier flies (Stratiomyidae)
3. Overwintering summer recruits	Nearly permanent residents with drought-resistant stage (usually egg stage) Adults oviposit in dry basin	<i>Aedes</i> and <i>Psorophora</i> mosquitoes, caddisflies (<i>Limnephilus</i>), damselflies (<i>Lestes</i>), dragonflies (<i>Sympetrum</i>)
4. Nonwintering spring migrants	No drought-resistant stage, must recolonize pond each spring Excellent dispersal capabilities Overwinter in permanent water	All hemipterans (e.g., Corixidae, Gerridae, Notonectidae, Veliidae), some dytiscid beetles (e.g., <i>Acilius</i> , <i>Colymbetes</i> , <i>Dytiscus</i>), green darner dragonfly (<i>Anax junius</i>)

^aFrom G. B. Wiggins, R. J. Mackay, and I. Smith, Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie Supplement 58:97–206, 1980.

oviposit in large temporary ponds in April and May, and the voracious predatory larvae can become quite abundant in some ponds by mid-May. Phantom midge larvae (*Chaoborus*) also become abundant at this time. Many of these migrants are opportunistic and are not particularly adapted for ephemeral habitats, except that they are all characterized by rapid larval development.

There are few changes in the invertebrate faunal composition in June. With the advent of warm temperatures and less precipitation, the surface area and volume of these ponds begin to shrink, with concomitant increases in organism densities and nutrient concentrations. As the abundant predatory species increase their body sizes, shifts in their preferred prey may drastically alter relative abundances within the faunal assemblages. The general paucity of nonpredatory macroinvertebrates at this time of the year means that predators are feeding on predators, and foodwebs may become very complex.

Adult *Sympetrum* dragonflies and *Lestes* damselflies begin emerging from the ponds by July 1, and *Anax* dragonflies emerge in mid- to late July from the larger ponds. By mid-July most of the medium-sized ponds have dried and the larger ponds have shrunk to only a small fraction of their maximum size. By this time almost all insects have completed larval development and emerged as adults, and cladocerans have produced abundant epiphya, or drought-resistant eggs. The active invertebrate fauna at this time is characterized by adult insects (primarily bugs and beetles) capable of flying to permanent water, as well as other invertebrates that can burrow into the moist soil and/or form a drought-resistant stage (e.g., gastropods, planarians, and ostracods).

Even the largest of the temporary woodland ponds usually lose all surface water by early August. Undoubtedly there are some insect larvae that do not complete development by this time and perish. In drought years even insects that are well adapted to ephemeral habitats may become stranded. In most years, however, insects that perish from desiccation are either typical temporary pond migrants (i.e., Group 4 of Wiggins et al. 1980) that failed to complete development, or they represent oviposition mistakes by insects more typical of permanent water. An example of this latter category is the presence of early-instar dragonfly larvae of the genera *Libellula* and *Aeshna* in some of the larger temporary ponds during the summer. These insects are typical residents of permanent ponds, and most species require at least one year for larval development. In years of high precipitation in which some of the usually temporary ponds do not dry, these insects may survive and complete development the following year. The usual consequence of such oviposition mistakes, however, is complete larval mortality (Higgins, unpublished data).

SEASONAL PATTERNS—AESTIVAL PHASE

In most years heavy precipitation during the mid- to late summer can cause dry (or nearly dry) basins to flood again, triggering another cycle of inver-

tebrate activity. The surface area of flooding during this aestival phase is generally less than half that of the much more extensive vernal phase. A few invertebrates appear to be specifically adapted to this later period of flooding. The floodwater mosquitoes *Aedes vexans* and *Aedes trivittatus*, as well as mosquitoes in the genus *Psorophora*, are particularly well adapted to summer rain pools. Although some eggs may hatch in the spring along with other species of *Aedes*, most *A. vexans* and *A. trivittatus* eggs, and all those of *Psorophora*, hatch following reflooding in the summer (Carpenter and LaCasse 1955). Unlike spring species of *Aedes* that oviposit primarily near the margins of the vernal extent of flooding, *A. vexans* also oviposits extensively in the interior portions of pond basins (Enfield and Pritchard 1977), a strategy that ensures hatching during summer flood events. Development is extremely rapid, with first-instars appearing within a few hours of flooding and adults emerging in less than a week. Densities of *A. vexans* larvae can reach several hundred per liter in these habitats (Dixon and Brust 1972), and the large number of biting adult females that emerge make this species a serious pest of humans during the summer (Carpenter and LaCasse 1955, Wood et al. 1979). Another species of mosquito, *Psorophora ciliata*, which may have coevolved with *A. vexans*, is predatory in larval instars II–IV, feeding primarily on *A. vexans* larvae (Breeland et al. 1961).

Other inhabitants of these aestival pools are either permanent residents (e.g., small crustaceans, planarians, gastropods) or opportunistic migrants (e.g., *Anopheles* mosquitoes, several species of beetles and bugs). This latter group includes adult insects of species typical of more permanent water, some of which may oviposit and attempt to complete an additional generation in these summer rain pools. While some of these migrants appear within one or two days of flooding (e.g., *Anopheles* mosquitoes), predatory beetle larvae (e.g., *Acilius*), as well as most other predators, do not appear until several days after inundation. This lag time between inundation and the appearance of predators allows the rapidly developing mosquito larvae to feed and grow relatively unmolested. Drought-resistant eggs deposited by insects and other arthropods that are well adapted to temporary ponds do not hatch at this time because they require a cold period followed by a warm-up in order to break their diapause (Horsefall and Fowler 1961, Wiggins et al. 1980). In addition, most of these eggs are deposited near the margins of the vernal extent of flooding and are not inundated by summer flood events.

The aestival phase is usually very brief, with surface water persisting for only a month or less. Animals that are specifically adapted to aestival pools, such as the mosquito species listed above, must be capable of extremely rapid development for this life history strategy to be successful. This strategy can be viewed as an evolutionary trade-off between risks and benefits. Although there is the risk of desiccation before larval development is completed, the larvae occupy a warm, nutrient-rich, and relatively predator-free environment in which development can occur rapidly.

TROPHIC RELATIONSHIPS

Temporary woodland ponds are detritus-based, heterotrophic habitats, with energy flow stemming predominantly from the leaf litter that falls into the basins. Emergent, submergent, and floating vascular plants are not common and thus contribute little to the overall energy budget. Although primary production in the form of algal photosynthesis takes place, the intense shading by the surrounding woods in these ponds reduces its input compared with more open bodies of water, particularly later in the spring (Moore 1970). Algal production that occurs in the early spring prior to tree leaf-out, however, may provide a significant food source for filter-feeding organisms (e.g., cladocerans).

Leaf litter that falls into the dry basins in the autumn is initially colonized by terrestrial microbes (principally fungi) that begin the process of decomposition. Barlocher et al. (1978) examined protein and fungal biomass levels in experimental leaf packs placed in vernal pools in Ontario. Higher protein levels (corresponding to higher levels of fungal biomass) were observed in leaf packs that were exposed to terrestrial microbes and aerobic decomposition compared with leaf packs that were submerged in water for the same period of time. All protein levels declined rapidly, however, following submergence in the spring. The authors concluded that the protein-rich detritus of temporary ponds supports the required rapid development of animals that inhabit these ephemeral environments (Barlocher et al. 1978).

The rapid decline in leaf litter protein levels following submergence observed by these researchers suggests, however, that there is more than just high-protein detritus supporting temporary pond fauna through larval development. The relative paucity of shredding detritivores in these habitats (Fig. 12.3), compared with many lotic situations, also suggests that other trophic pathways may be more important than direct feeding on leaf litter. Indeed, the early spring fauna is characterized by a diverse filter-feeding guild comprised of cladocerans, ostracods, fairy shrimp, and—at least part-time—mosquito larvae. Larvae of *Aedes* mosquitoes, in addition to filtering microorganisms and detritus from the water column, are also known to graze biofilm from the surfaces of leaf litter (Merritt et al. 1992). These larvae can apparently grow as well filtering pond water alone as they can when provided with detritus on which to graze. In a field experiment conducted in 1996, we examined the growth of 30 first-instar mosquito larvae (*Aedes stimulans*) in each of 15 microcosms provisioned with either conditioned leaves, nonconditioned leaves, or no leaves. No difference in time to adult emergence or adult weight was observed among the three treatments (Table 12.2; see also Walker and Merritt [1988] for similar results with treehole mosquitoes). These results suggest an abundance of planktonic food sources of importance to the trophic hierarchy at least equal to that of the enriched leaf detritus. But are the two related?

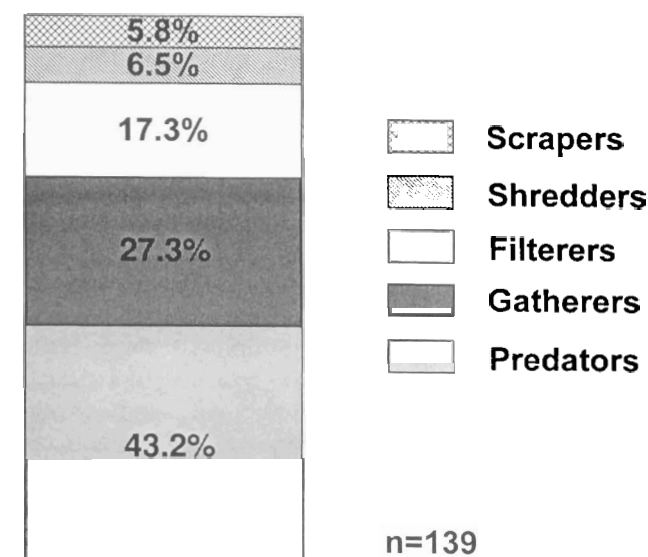


Fig. 12.3. Functional feeding group composition (by genera) of invertebrates in temporary woodland ponds.

It has been demonstrated that the degree of microbial colonization of leaf litter plays an important role in subsequent growth rates of invertebrate detritivores in both terrestrial and aquatic habitats (e.g., Barlocher et al. 1978, Suberkropp et al. 1983, Lawson et al. 1984, Merritt et al. 1984, Arsuffi and Suberkropp 1989, Walker et al. 1997). The dry phase of temporary ponds appears to be the most important period of microbial colonization of leaf litter, due to the prevalence of terrestrial fungi as the major decomposers (Barlocher et al. 1978). This microbial colonization process begins as soon as water levels begin to decline in the late spring or summer. As a pond loses surface water and shrinks in size, the leached-out and highly recalcitrant leaf detritus from the previous year becomes exposed and the moist surfaces are rapidly colonized by a host of fungi, bacteria, and protozoa. The celluloses and hemicelluloses contained in the leaves are principally exploited by terrestrial fungi, which depolymerize these complex compounds via cellulolytic enzymes into simpler carbohydrates (Ljungdahl and Eriksson 1985). Terrestrial fungi, principally white-rot fungi, are also important in breaking down lignin, which binds to the celluloses and hemicelluloses in leaves (Ljungdahl and Eriksson 1985). Although some lignin degradation occurs during the aquatic phase (Chamier 1985), the process is slow compared to that which occurs during the terrestrial phase, and many of the celluloses and hemicelluloses remain bound and unavailable for enzymatic degradation (Webster and Benfield 1986). The leaf surfaces are also colonized during this terrestrial

TABLE 12.2. Growth of First-Instar *Aedes stimulans* Mosquito Larvae in Field Microcosms Supplied with no Leaves or with 3 g (Initial Dry Mass) of Conditioned or Unconditioned Leaves, Wild Ginger Pond, Lansing, Michigan, 1996

Microcosm Treatment	n	Days to Emergence				Adult Mass (mg)			
		Males		Females		Males		Females	
		p	mean	p	mean	p	mean	p	mean
Conditioned leaves	5	47.43	0.913	.22	0.583	0.999	0.641	0.978	
Nonconditioned leaves	5	46.93		.89	0.587		0.636		
No leaves	5	47.41		.39	0.586		0.662		

phase by bacteria and their protozoan predators (Bamforth 1977), many of which secrete extracellular compounds (Nalewajko 1977). A similar colonization occurs on leaves that fall into the dry basins in the autumn. In this way the complex structure of the leaves is slowly converted into microbial biomass.

It is suggested here that when the ponds reflood in the spring to their maximum size (and when they partially reflood in the summer to form aestival ponds), the heavily enriched surfaces of the leaf detritus provide a nutrient broth in the form of dissolved and fine particulate organic matter stemming from the inundated fungal biomass, byproducts of lignin degradation (Kirk 1984), partially degraded celluloses, and the biomass and extracellular compounds of bacteria and protozoa. These dissolved substances, principally dissolved organic carbons and nitrogens (DOC and DON), are used by planktonic and attached heterotrophic bacteria, and a microbial bloom ensues. At this same time, algal growth may also be stimulated from DON and the sunlight available before trees leaf out in the spring. The resulting growth in the microbial community in turn supports the vast filter-feeding guild characteristic of the early spring fauna of temporary woodland ponds. In addition, following inundation, aquatic hyphomycetes readily colonize and degrade the dead terrestrial fungal cells (which contain little or no lignin), resulting in a substantially higher biomass of hyphomycetes and associated microorganisms than would be possible with the recalcitrant leaf detritus alone (Chamier 1985). This helps support invertebrate scrapers and gathering collectors as well as shredding detritivores.

Trophic relationships within temporary woodland ponds are closely tied to the seasonal succession and adaptational strategies (Table 12.1) of the associated fauna. Animals with drought-resistant stages may begin/resume development soon after the ponds reflood, triggered by physiochemical cues within the water (e.g., Horsefall 1956, Horsefall and Fowler 1961). The organisms that initially appear early in the spring are generally those that take advantage of the microbially enriched water and detritus, i.e., filter-feeders, gathering collectors (e.g., certain chironomid midge larvae), and detritivorous shredders (primarily limnephilid caddisflies). These species can apparently tolerate the low temperatures and frequent ice cover characteristic of this time of the year. Even though growth is slower in this cold environment (Atkinson 1994), development occurs in a relatively nutrient-rich and predator-free environment. This strategy of beginning development early in the spring may have initially evolved as an adaptation for survival in small, ephemeral habitats. A reinforcing factor may have been predator avoidance in time. By hatching early, organisms such as mosquito larvae and fairy shrimp—animals with few defensive mechanisms—feed and grow relatively unmolested by predators. The majority of predators do not appear until weeks later. By the time most of the predatory larvae of the odonates and beetles make their appearance, these potential prey species are generally too large for the small, early-instar predators to catch effectively. Insects that develop in cold tem-

peratures reach larger body size than those reared at higher temperatures (Brust 1967, Atkinson 1994), and the larvae of spring species of *Aedes* are some of the largest in this genus (Wood et al. 1979). Thus, the early spring inhabitants of temporary ponds may escape predation in time by beginning development early and achieving larger body sizes than their potential predators. As previously stated, only some dytiscid beetles in the genus *Agabus* that overwinter in the egg stage have apparently evolved to take advantage of the abundant prey available early in the spring. By beginning development early in the spring, larvae of these beetles are able to exploit even small ponds of only a few weeks' duration, habitats unavailable for other beetle species that appear later in the season.

Although there are relatively few predators early in the spring, the number of predatory species increases substantially as the water temperature rises. Predator diversity reaches its peak in mid-May, with predators often becoming the dominant functional group within the ponds at this time. Most predators in temporary woodland ponds can be classified as either opportunistic migrants (Group 4 of Wiggins et al. 1980) or cyclic colonizers (Batzer and Wissinger 1996, Wissinger 1997), i.e., they generally lack specific adaptations to survive drought and overwinter in permanent-water habitats. Figure 12.4 illustrates that over half the predatory genera found in these ponds belong to this life history category. More striking, perhaps, is the very high proportion of predators within the Group 4 category itself (Fig. 12.5). The dominance of predators in this category is not terribly surprising given that animals in this group must recolonize ponds every year, breed, and complete larval de-

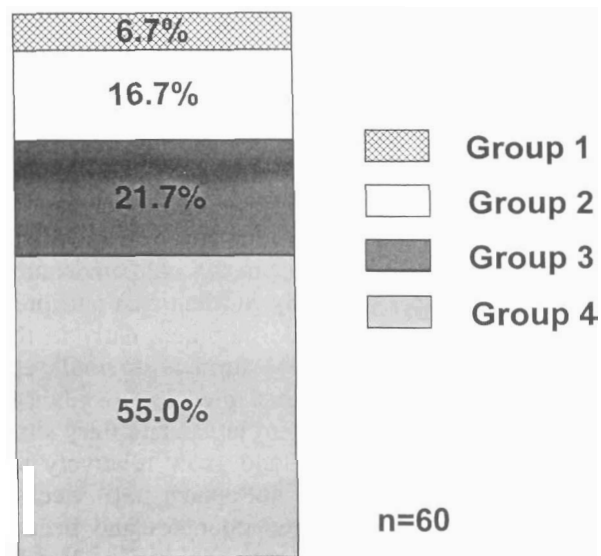


Fig. 12.4. Predator composition by life history strategy in temporary woodland ponds.

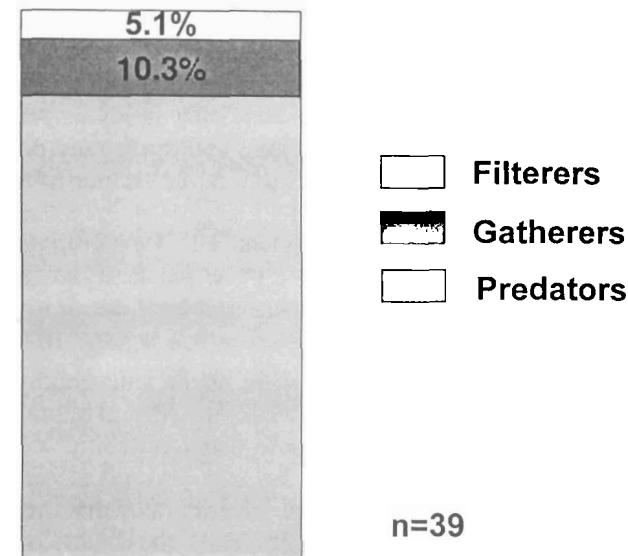


Fig. 12.5. Functional feeding group composition for Wiggins et al. (1980) Group 4 life history strategy.

velopment before the ponds dry. The consumption of animal protein allows the larvae of these relatively late arrivals to develop very quickly, the assimilation efficiency of predators being highest among trophic groups (Wotton 1994). Relatively rapid development is a characteristic of most animals breeding in ephemeral habitats, particularly those organisms that lack adaptations for coping with the dry phase.

Conversely, this probably explains the total lack of shredding detritivores exhibiting a Group 4 strategy (Fig. 12.5). Although the leaf litter of temporary ponds may be enriched by the microbial processes described above, it is still a relatively poor food source, and detritivorous animals must consume large quantities to maintain growth. One of the few shredding insects, the caddisfly *Limnephilus indivisus*, begins development early in the spring—sometimes hatching the previous fall in autumnal ponds (Wiggins 1973)—a strategy which helps to ensure that the 8–10 week development will be completed before the pond dries. For a migrant species that arrives at a pond later in the spring, a feeding strategy based on consuming leaf detritus would be risky; growth would be slow and there would often be insufficient time to complete development. Interestingly, limnephilid caddisfly larvae in temporary ponds are known to be occasionally cannibalistic (Wissinger et al. 1996) and have been reported to be infrequent predators of mosquito larvae (Downe and West 1954, Baldwin et al. 1955). Cargill et al. (1985) demonstrated the importance of lipids in the diet of final-instar shredding caddisflies. The accumulation of triglyceride reserves during the last larval instar is apparently essential for

completion of the larval stage and subsequent adult reproduction (Cargill et al. 1985). Although lipids are available in aquatic hyphomycete fungi (Cargill et al. 1985), incidences of cannibalism and predation in otherwise detritivorous insects may be a means of quickly acquiring lipids as well as protein. This diet supplementation of protein and essential lipids may provide a boost in growth rates and ensure survival through the larval period (Wissinger et al. 1996).

CONCLUSIONS

In summary, temporary woodland ponds are small, microbially driven wetlands that may be flooded from a few weeks to several months out of the year. What may initially appear a harsh and uncertain habitat actually exhibits a reasonably predictable cycle of flooding and drying, as well as a fairly predictable seasonal succession of species. Invertebrates that are well adapted to this ephemeral habitat have evolved within the constraints of the physical environment and in response to community interactions (Schneider and Frost 1996, Williams 1996). Both abiotic and biotic factors appear to have shaped the observed succession of species, with early-season, cold-adapted inhabitants simultaneously taking advantage of the microbially enriched environment and minimizing predation pressure by beginning development before most of the predators appear. Many of the insects that arrive later in the spring are migrants with no special adaptations to the dry phase of these ponds. The vast majority of these species are predatory in at least the larval stage, employing a trophic strategy that permits rapid growth in a shrinking environment.

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LITERATURE CITED

Arsuffi, T. L., and K. Suberkropp. 1989. Selective feeding by shredders on leaf-colonizing fungi: Comparison of macroinvertebrate taxa. *Oecologia* 79:30-37.

- Baldwin, W. F., H. G. James, and H. E. Welch. 1955. A study of mosquito larvae and pupae with a radio-active tracer. *Canadian Entomologist* 87:350-356.
- Bamforth, S. S. 1977. Litters and soils as freshwater ecosystems. Pages 243-256 in Cairns, Jr. (ed.), *Aquatic Microbial Communities*. Garland, New York.
- Barlocher, F., R. J. Mackay, and G. B. Wiggins. 1978. Detritus processing in a temporary vernal pool in southern Ontario. *Archiv für Hydrobiologie* 81:269-295.
- Batzer, D. P., and S. A. Wissinger. 1996. Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology* 41:75-100.
- Breeland, S. G., W. E. Snow, and E. Pickard. 1961. Mosquitoes of the Tennessee valley. *Journal of the Tennessee Academy of Science* 36:249-319.
- Brust, R. A. 1967. Weight and development time of different stadia of mosquitoes reared at various constant temperatures. *Canadian Entomologist* 99:986-993.
- Cargill, A. S., II et al. 1985. The role of lipids as feeding stimulants for shredding aquatic insects. *Freshwater Biology* 15:455-464.
- Carpenter, S. J., and W. J. LaCasse. 1955. *Mosquitoes of North America*. University of California Press, Berkeley, CA.
- Chamier, A.-C. 1985. Cell-wall-degrading enzymes of aquatic hyphomycetes: a review. *Botanical Journal of the Linnean Society* 91:67-81.
- Dixon, R. D., and R. A. Brust. 1972. Mosquitoes of Manitoba. III. Ecology of larvae in the Winnipeg area. *Canadian Entomologist* 104:961-968.
- Downe, A. E. R., and A. S. West. 1954. Progress in the use of the precipitin test in entomological studies. *Canadian Entomologist* 86:181-184.
- Enfield, M. A., and G. Pritchard. 1977. Estimates of population size and survival of immature stages of four species of *Aedes* (Diptera: Culicidae) in a temporary pond. *Canadian Entomologist* 109:1425-1434.
- Horsefall, W. R. 1956. Eggs of floodwater mosquitoes (Diptera: Culicidae). III. Conditioning and hatching of *Aedes vexans*. *Annals of the Entomological Society of America* 49:66-71.
- Horsefall, W. R., and H. W. Fowler, Jr. 1961. Eggs of floodwater mosquitoes VII. Effect of serial temperatures on conditioning of eggs of *Aedes stimulans* Walker (Diptera: Culicidae). *Annals of the Entomological Society of America* 54:664-669.
- Iversen, T. M. 1971. The ecology of a mosquito population (*Aedes communis*) in a temporary pool in a Danish beech wood. *Archiv für Hydrobiologie* 69:309-332.
- James, H. G. 1961. Some predators of *Aedes stimulans* (Walk.) and *Aedes trichurus* (Dyar) (Diptera: Culicidae) in woodland pools. *Canadian Journal of Zoology* 39:533-540.
- . 1966. Location of univoltine *Aedes* eggs in woodland pool areas and experimental exposure to predators. *Mosquito News* 26:59-63.
- Kenk, R. 1949. *The Animal Life of Temporary and Permanent Ponds in Southern Michigan*. University of Michigan, Museum of Zoology, Miscellaneous Publication 71.
- Kirk, T. K. 1984. Degradation of lignin. Pages 399-437 in D. T. Gibson (ed.), *Microbial Degradation of Organic Compounds*. Marcel Dekker, New York.

- of the detritivore *Tipula abdominalis* (Diptera: Tipulidae). *Canadian Journal of Zoology* 62:2339-2343.
- Ljungdahl, L. G., and K.-E. Eriksson. 1985. Ecology of microbial cellulose degradation. Pages 237-299 in K. C. Marshall (ed.), *Advances in Microbial Ecology*, vol. 8. Plenum, New York.
- Merritt, R. W., R. H. Dadd, and E. D. Walker. 1992. Feeding behavior, natural food, and nutritional relationships of larval mosquitoes. *Annual Review of Entomology* 37:349-376.
- Merritt, R. W., W. Wuerthele, and D. L. Lawson. 1984. The effect of leaf conditioning on the timing of litter processing on a Michigan woodland floodplain. *Canadian Journal of Zoology* 62:179-182.
- Moore, W. G. 1970. Limnological studies of temporary ponds in south-eastern Louisiana. *Southwestern Naturalist* 15:83-110.
- Nalewajko, C. 1977. Extracellular release in freshwater algae and bacteria: Extracellular products of algae as a source of carbon for heterotrophs. Pages 589-624 in J. Cairns, Jr. (ed.), *Aquatic Microbial Communities*. Garland, New York.
- Schneider, D. W., and T. M. Frost. 1996. Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society* 15:64-86.
- Suberkropp, K., T. L. Arsuuffi, and J. P. Anderson. 1983. Comparison of degradative ability, enzymatic activity, and palatability of aquatic hyphomycetes grown on leaf litter. *Applied and Environmental Microbiology* 46:237-244.
- Walker, E. D. 1995. Effect of low temperature on feeding rate of *Aedes stimulans* larvae and efficacy of *Bacillus thuringiensis* var. *israelensis* (H-14). *Journal of the American Mosquito Control Association* 11:107-110.
- Walker, E. D., M. G. Kaufman, M. P. Ayers, M. H. Riedel, and R. W. Merritt. 1997. Effects of variation in quality of leaf detritus on growth of the eastern tree-hole mosquito, *Aedes triseriatus* (Diptera: Culicidae). *Canadian Journal of Zoology* 75:706-718.
- Walker, E. D., and R. W. Merritt. 1988. The significance of leaf detritus to mosquito (Diptera: Culicidae) productivity from treeholes. *Environmental Entomology* 17:199-206.
- Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17:567-594.
- Westwood, A. R., G. A. Surgeoner, and B. V. Helson. 1983. Survival of spring *Aedes* spp. mosquito (Diptera: Culicidae) larvae in ice-covered pools. *Canadian Entomologist* 115:195-197.
- Wiggins, G. B. 1973. A contribution to the biology of caddisflies (Trichoptera) in temporary ponds. *Life Science Contributions of the Royal Ontario Museum* 88:1-28.
- Wiggins, G. B., R. J. Mackay, and I. Smith. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. *Archiv für Hydrobiologie, Supplement* 58:97-206.
- Williams, D. D. 1987. *The Ecology of Temporary Waters*. Croom Helm, Timber Press, Portland, OR.
- . 1996. Environmental constraints in temporary fresh water and their conse-
- Wissinger, S. A. 1997. Cyclic colonization in predictably ephemeral habitats: A template for biological control in annual crop systems. *Biological Control* 10:4-15.
- Wissinger, S. A., et al. 1996. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine wetlands. *Ecology* 77:2421-2430.
- Wood, D. M., P. T. Dang, and R. A. Ellis. 1979. *The Mosquitoes of Canada* (Diptera: Culicidae). *The Insects and Arachnids of Canada, Part 6*. Publication 1686, Biosystematics Research Institute, Research Branch, Agriculture Canada, Ottawa, Ontario, Canada.
- Wotton, R. S. 1994. Particulate and dissolved organic matter as food. Pages 235-288 in R. S. Wotton (ed.), *The Biology of Particles in Aquatic Systems*. Lewis, Boca Raton, FL.