Journal of the Minnesota Academy of Science

Volume 50 | Number 3 Article 11

1984

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ABSTRACT — Disturbance in aquatic habitats may be caused by drought, flood, changes in temperature, and unusual or unnatural introductions of particulate or dissolved substances from the surrounding land. Aquatic invertebrates survive disturbance by moving to a refuge or alternative habitat or by having resistant or specially protected stages in the life cycle. Some invertebrates are able to exploit the richer and more available food materials that may result from the disturbance. Most species in disturbed aquatic habitats are efficient colonizers; they combine one or more survival strategies with high powers of dispersal, rapid growth rates, and characteristics of ecological generalists.

Disturbed Aquatic Habitats

Aquatic invertebrates face two main types of disturbance to their habitat. One is a change in the amount of water surrounding them, as in the event of flood or drought; the other is a change in the physical or chemical quality of the water.

Drought is the most serious disturbance in any aquatic habitat. The smaller the water volume, the more likely it is that the habitat is a temporary one. Streams are less likely to dry than pools, so their invertebrate inhabitants display only a limited variety of survival strategies. Small or shallow bodies of still water support a diverse community of invertebrates with an equally diverse array of responses in the event of drought. Because this type of habitat is the breeding ground of mosquitoes, it will be the major focus of this paper.

A flood or spate is a major disturbance only in running waters, where an increase in discharge may sweep fine sands into the current and roll larger rocks downstream. Most stream-living invertebrates live on or within the stream bed and so have to be able to resist or avoid not only the mechanical disruption of their habitat but also the subsequent deposition of suspended particles.

The simplest change in water quality is that which accompanies a change in temperature. Most invertebrates are not greatly disturbed by cold unless ice forms. However, anchor ice in a stream bed can be as disruptive and as abrasive as a stream in flood, and surface ice on still water acts as a barrier between water and air. Warming temperatures are potentially more harmful especially if warming is rapid. In this case, most invertebrates are actually responding not to increasing temperature but to the corresponding decrease in concentrations of dissolved oxygen. An unusual increase in water temperature is therefore a serious physiological disturbance because of the accompanying reduction in the availability of oxygen.

A similar reduction in dissolved oxygen results when organic materials decay in water because aquatic bacteria and fungi use up oxygen as they attack and metabolize the organic matter. A natural disturbance of this kind occurs in autumn when bankside vegetation dies and falls into the water, sometimes filling small streams and pools. A more serious disturbance is the introduction of organic waste such as effluents from sewage works, food processing plants, and paper mills.

Severe chemical disturbance in aquatic habitats may also occur when a drainage basin is contaminated with excess fertilizers, road de-icing salt, or toxic metallic salts from mining or industrial processes. But where the habitat is unpolluted and permanent, the chemical composition of the water remains relatively constant. Among natural waters, only temporary pools show marked changes in water chemistry; dissolved salts become progressively more concentrated as the pools dry.

Survival Strategies

Aquatic invertebrates avoid the lethal effects of disturbance either by moving away from the affected area during the critical period or by having a resistant or protected stage that can tolerate the effect. Sometimes the potential for regeneration or recolonization is so high that the loss of individuals is counteracted by the influx of colonizers from unaffected neighboring habitats. Often two or more of these strategies are combined in any one species.

The invertebrates of temporary pools show various combinations of these survival strategies which not only provide a means of bridging the dry phase but also allow the organisms to cope with other kinds of stress or disturbance. Even if the stress is as severe as chemical poisoning, which might be used to control mosquitoes, the ecological characteristics of temporary-pool inhabitants are such that they have a good chance of survival.

The Drying Pool

In the northern United States and southern Canada, a temporary snow-melt (vernal) pool fills in March or April and is dry by July. An essential strategy for survival here is rapid

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development during the wet phase to ensure that the drought-bridging stage is reached. As water volumes diminish, water temperatures respond to the increasing air temperatures of early summer. Developmental rates are frequently accelerated by the warmer temperatures but organisms also have to cope with physiological responses to the decreasing availability of dissolved oxygen and increasing concentrations of dissolved salts as water evaporates. Many invertebrates in the pool can tolerate rather low dissolved oxygen or are air breathers. Both larvae and pupae of mosquitoes are air breathers; when they swim jerkily and rapidly upwards in a body of water, they are making for the surface film through which they draw air into a short tube on the abdomen (larva) or thorax (pupa) which leads to an internal respiratory system. This independence from dissolved oxygen assures air breathers of enough oxygen to meet the physiological (respiratory) demands of a stressful environment.

Many temporary-pool animals are species known to tolerate a broad range of environmental conditions (1). For example, the most common caddisfly (Trichoptera) larvae in vernal pools belong to two of the few families that are represented in saline waters. The presence of special osmoregulatory cells in these larvae (2) may allow them to tolerate the range of salt concentrations experienced during the life of a snow-melt pool.

As the pool dries, various drought-surviving mechanisms begin to operate. In most species, one particular stage in the life cycle is adapted for survival. Some species emigrate to a permanent pond or stream margin; some retreat into the soil of the pool basin; and some develop special structures or waterproof coverings that resist desiccation.

Emigration

Only adult insects (and amphibian vertebrates) are sufficiently mobile to move far away from a drying pool. Most of these adult insects are not themselves aquatic, but their immature stages are. They developed from eggs that hatched when the pool filled or that were laid by insects visiting the pool early in spring. Some insects that emerge from the pool remain nearby and lay their eggs in the little water that remains; these adults are not true emigrants because their eggs still have to survive the dry phase. Another group of species, including mosquitoes in the genera *Aedes* and *Psorophora*, flies farther afield and may not return to lay eggs in the pool until all water has disappeared. These adults also are not the drought-bridging stage. Yet another group of emerging adults includes several caddisflies which secrete themselves in caves, hollow trees and similar damp, dark places through the dry summer months. During this period the reproductive organs are immature, but by September the eggs are ready to be laid in damp locations, such as the undersides of logs, in the waterless basin (1). Again the adults are not the ultimate bridging stage but their interrupted maturation is a strategy ensuring that eggs are not exposed to the intense desiccation of summer.

The true emigrants include amphibious adult waterbugs (Hemiptera) and beetles (Coleoptera) which can fly from one pool to another. Some of these individuals survive in permanent bodies of water until the following spring when they return to temporary pools to breed. Other emigrants fly to permanent pools where they reproduce; overwintering larvae mature the following spring to produce adults that return to temporary pools. Not all emigrants leaving the pool depend on water in the alternative habitat. Where air temperatures are relatively mild, mosquitoes in the genera *Anopheles* and *Culex* can overwinter as terrestrial adults (1).

The survival strategy of emigration from a disturbed habitat is one for which adult insects are superbly adapted. Aquatic insects have evolved from terrestrial ancestors; even amphibious adults retain the waxy waterproof epidermis which has given insects so much success on land.

Retreat

When the quality of an aquatic habitat is no longer tolerable, some inhabitants survive by retreating into the subsurface layers of the water basin. In streams, several species avoid summer heat by burrowing deep into hyporheic layers of gravel where temperatures approach those of groundwater. Some stream-living invertebrates also may respond to the leading edge of a pulse of introduced chemicals from floods and insecticides by seeking the hyporheic refuge.

The soil of a dry pool basin is not as easily penetrated as a gravelly stream bed, and the water table may be well below the surface. However, a few pool-living invertebrates survive drought by retreating into the soil. Crayfish (Decapoda) and scuds (Amphipoda) cannot survive without water but will persist in temporary-pool basins if their burrows maintain contact with groundwater during the dry phase. In a clay soil, crayfish burrows are firm enough to contact water more than a meter below the surface (3). These burrows offer refuge to many other temporary-pool inhabitants, especially Crustacea.

Resistance

Most temporary-pool invertebrates that survive drought in the pool basin do so as resistant eggs or cysts. Examples are the eggs of microcrustacea, such as copepods, ostracods, and cladocerans, which show remarkable resio drought yet hatch within a day or two when reflooded. Sometimes eggs will hatch only if they have experienced a critical period of exposure to air (drought) or cold (winter), as is the case with fairy shrimps. This adaptation ensures that the eggs respond only to the appropriate environmental conditions of snow-melt rather than to the ephemeral water from a summer storm. The stimulus that actually triggers the hatching of fairy shrimps is a sudden decrease in dissolved oxygen caused by rapid microbial decomposition of newly submerged dead vegetation at snow-melt (4). The same stimulus promotes hatching of aedine mosquitoes. These responses show that resistant eggs are not all activated by flooding alone — an important aspect of survival if it depends on more than just the advent of water.

Aedine mosquitoes and certain damselflies (*Lestes*) and dragonflies (*Sympetrum*) are among those insects that return to the dry pool basin to lay their eggs. *Aedes* and *Sympetrum* eggs survive with a thick shell. *Lestes* eggs are inserted into the stems of semi-aquatic weeds which continue to provide a protective covering even when dry and straw-like; the eggs are released only when the straw decays after becoming submerged the following spring (1).

Eggs laid by returning caddisflies are protected by thick jelly. The eggs hatch in autumn but the tiny larvae remain quiescent in the jelly until covered by water. If a pool is filled by autumn rains, the larvae leave the jelly and begin their active life. But the jelly is sufficiently moist and cold resistant to protect larvae in the snow-covered basin of a vernal pool (5).

Eggs, then, are not the only stages capable of surviving drought while on the surface of the pool basin. Some snails survive drought as juveniles on tree trunks above the ground by closing the shell opening with a waterproof plug (6). Somewhat more protected are the larval cocoons of midges

(Chironomidae) and the mucus-lined chambers of worms (Oligochaeta) in superficial layers of soil.

Immigration and Recolonization

Why does a snow-melt pool attract colonizers when it has so many of the constraints of a disturbed habitat? Why should earlier emigrants, having safely escaped from an inhospitable habitat, return to breed there? One explanation is that the decaying vegetation in a newly-flooded pool basin is more nutritious than permanently submerged detritus (7). Vegetation invading the dry basin in summer provides a rich supply of plant detritus whose decay by fungi is enhanced by aerobic conditions in autumn. When flooding occurs in spring, various types and textures of food materials are available for detritivores, which in turn form abundant prey for predators (1). The first eggs to hatch in spring are those of microcrustacea and mosquitoes, all of which feed on fine particles of detritus. Caddisfly larvae, which emerge from their gelatinous refuge within 30 minutes of flooding, are also detritivores. Insects flying in from permanent waters appear later in the life of the snow-melt pool (having waited for their overwintering habitats to thaw) but the earliest immigrants are often water-boatmen (Corixidae), which are mostly detritivorous.

This rich new community is also relatively free from predators. Eggs of predators such as dragonflies do not hatch as soon as the pool fills, and predacious Hemiptera and Coleoptera are among the later immigrants. The delayed appearance of predators strongly suggests that predator recruitment is timed to coincide with well-established prey populations (1).

Thus, the entire animal community seems to owe its opportunities to the detrital food base, which in turn is dependent on the seasonal drought. In fact the very disturbance which might suggest that the temporary pool is an unfavorable habitat is responsible for its rich community. A cycle of disturbances occurs, with the growth of terrestrial vegetation during drought being followed by rapid aerobic decomposition; when flooded, the detritus releases a pulse of plant nutrients for a new bloom of vegetation (1, 8).

After any type of environmental disturbance, the complex community is disrupted and the ecosystem is broken down into simpler components. The rebuilding of the commmunity begins with efficient colonizers. Colonizers must have high powers of dispersal to ensure an early invasion of new habitats. They must also produce large numbers of offspring which should develop rapidly and mature early in order to take advantage of the habitat before competition from other invaders becomes severe. Active migrants are obviously able to colonize new habitats; it is interesting to note that the greatest powers of dispersal, including longer wings in insects, are characteristic of species breeding in the most ephemeral habitats (9). However, not all efficient colonizers depend on active dispersal. Small resistant eggs and cysts not only survive adverse conditions *in situ* but also are highly efficient disseminules capable of being carried by wind or in the digestive tracts of other animals (10). Asexual reproduction also increases the effectiveness of dispersal by passive migrants because a single propagule may be sufficient to begin a new population.

The best colonizers often are ecological generalists. They can tolerate a broad range of environmental conditions; they are common and widespread in various types of habitats; and they are often detritivores feeding on ubiquitous organic debris, or non-specialist predators feeding on a variety of prey. Some ecological generalists may even be somewhat flexible in their life cycles and be able to produce young at several times in the year. This characteristic is not seen in all invertebrates in snow-melt pools where the life cycle in some species must be precisly timed if the appropriate stage is to coincide with drought. But even in these pools, some generalists can rapidly take advantage of an early flood or a late drought.

Given these characteristics of efficient colonizers, it is not surprising that the earliest newcomers after disturbance in aquatic habitats are insects. Their great powers of dispersal, regeneration, and tolerance make them remarkably resilient in the face of any kind of disaster, whether natural or deliberate. It's hard to keep a bug down!

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