Environmental constraints in temporary fresh waters and their consequences for the insect fauna

D. DUDLEY WILLIAMS

Division of Life Sciences, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, Ontario, Canada M1C 1A4

Abstract. Temporary fresh waters are defined as bodies of fresh water that experience a recurrent dry phase of varying length that is sometimes predictable in both its time of onset and duration. The aquatic insects that live in these habitats are strongly influenced by 2 main groups of constraints, physicochemical and biological factors. Taxa particularly well-represented in temporary running waters are the Ephemeroptera, Hemiptera, Coleoptera, Trichoptera, and tipulid and chironomid Diptera. With the exception of Ephemeroptera, all these groups are common also in temporary lentic waters, but the latter also support many species of Odonata, together with culicid, ceratopogonid and ephydrid Diptera. In general, however, the diversity of aquatic insects is lower in temporary than in permanent waters. Seasonal succession of species is commonplace in temporary waters, affecting food web structure. Adaptations to drought are reviewed, and traits common to the most successful taxa include a highly flexible life cycle, temperature-linked development, possession of a diapausing or otherwise protected egg, and high powers of dispersal. A trend towards terrestrialsation of immature stages is noted amongst at least some members of even strongly aquatic taxa. Several directions for future research are discussed including study of the controlling influence of the biological environment on the fauna and the former's interaction with physicochemical influences, temporal variation in the structure of food webs, and genetic analyses of populations. A recommendation is made for greater quantification in data collection, particularly on seasonal changes in species abundance, their life histories, and trophic relationships, as this will allow greater opportunity for modelling the community dynamics of these ecologically distinct habitats. Finally, the concept that temporary waters constrain their faunas is exposed as being based more on human perception than on fact.

Key words: aquatic insects, temporary fresh waters, environmental factors, faunal adaptations, faunal composition, faunal dynamics, life history, migration, colonisation, physiological tolerance.

Although many saline/brackishwater habitats exhibit intermittency (see Williams 1987), this review will be limited to temporary fresh waters—although some of the issues discussed may be equally applicable to either habitat category. Temporary fresh waters occur in many parts of the world and may loosely be defined as bodies of fresh water that experience a recurrent dry phase of varying length that is sometimes predictable in both its time of onset and duration. This definition sets them apart from those permanent waters which may occasionally experience a drought but which contain faunas that are generally intolerant of water loss—although the degree of faunal overlap may differ geographically (Boulton and Suter 1986). In a recent attempt to tidy up a perceived inconsistency in the terminology applied to temporary waters, Comin and Williams (1994) have proposed subdividing temporary running waters into: (1) intermittent—those which cyclically contain water or are dry at times of the

year that are more or less predictable; and (2) episodic—those which contain water on a more or less unpredictable basis. Temporary lentic waters are similarly subdivided.

Although most temporary waters are of natural origin, their faunas contain many opportunistic and pioneering species that have successfully colonised a variety of artificial habitats such as cisterns, rain-filled tyres, bird baths, and rice paddies (Williams 1987). As a habitat, individual temporary waters generally vary more in their physical and chemical environment than adjacent, permanent fresh waters. Such extremes demand that the faunas of temporary waters evolve to have one or more strategies if they are to successfully exploit the rich resources and/or freedom from competition and vertebrate predation that these habitats often provide.

Temporary fresh waters are traditionally considered most abundant in drier parts of the globe. While it is true that arid and semi-arid

TABLE 1. A summary of the main types of naturally occurring temporary waters.

Ubiquitous temporary waters:

Intermittent and episodic ponds, lakes, springs, streams and rivers; the margins of permanent ponds, lakes, streams and rivers; floodplains; liquid dung.

Arid and semi-arid regions:

Sections of permanent "dryland" running waters; prairie streams; drypans; billabongs, kopjes, temporary inland saline waters; desert rain pools.

Humid tropical regions:

Pitcher plants; leaf axils; large flower bracts; tree holes; bamboo stem habitats; coconut shells; cocopod habitats; rain pools; empty snail shells.

Temperate regions:

Seasonal wetlands; peatland pools; pot-holes; kettle ponds; solution ponds; oxbow ponds; woodland pools; turloughs; vernal ponds; autumnal ponds; pitcher plants; tree holes; teasels; rain pools; ironpan pools; empty snail shells.

Maritime regions:

Tidal wetlands; supralittoral tide pools; cup fungi; saturated moss.

Arctic/Antarctic regions:

Snowmelt pools; glacial streams; aestival ponds.

regions characteristically possess the major, and perhaps more spectacular, types of temporary inland waters (see review by Comin and Williams 1994), humid tropical, temperate and even maritime climates also provide conditions suitable for the formation of temporary waters, although these may be less obvious. A summary of ubiquitous and regional temporary waters is presented in Table 1.

Rather than dwell on the obvious diversity in type, size, and geographical peculiarity of temporary waters (summarised in Williams 1987), in this paper I identify and describe those environmental factors which are common to the majority of temporary fresh waters and which most strongly influence their insect faunas. Initially, I follow the commonly held tenet that these factors *constrain* the faunas.

The constraining factors

Important environmental factors may be divided into 2 groups: physicochemical and bio-

logical. The former have received most attention, as they are perceived to strongly constrain the fauna. However, limited study may have underestimated the importance of biological processes (see Williams et al. 1990).

Major influences in the physical environment, together with pertinent interactive effects, are summarised in Fig. 1. Of fundamental importance is the pattern of disappearance of the water, whether predictable (i.e., part of a stable cycle) or unpredictable (i.e., random, or linked to vagaries of local climate) (Williams and Hynes 1976, Wiggins et al. 1980, Delucchi 1988). One might assume that adaptations to deal with predictable disappearance of the water (intermittent waters) evolve more readily than those required to deal with random disappearance (episodic waters). However, a strategy such as "bet-hedging" (Stearns 1976, Baird et al. 1987) would seem to be suited to both situations, although it might optimise rather than maximise reproductive effort in episodic waters. Linked to disappearance of the water is the length of the dry period and decrease in habitat size (area and depth) (Williams and Hogg 1996). Decreasing depth may increase insolation which, through changes in primary production and wind-induced aeration, may change dissolved oxygen concentrations in the water. Primary production also may be affected by changes in turbidity (Barclay and Knight 1984). Oxygen will be further affected by changes in water temperature which will increase as the water disappears in summer-dry water bodies (e.g., autumnal ponds; Wiggins 1973), but will decrease in winter-dry bodies (e.g., aestival ponds; Daborn and Clifford 1974). Temperature changes result in subtle changes in water density which may affect the smaller life cycle stages of insects. Ionic concentration tends to rise significantly as temporary waters dry out which may affect pH and perhaps have direct osmotic consequences for insects, too. Water chemistry is likely to have a major influence on the fauna but, apart from aspects related to dissolved oxygen and pH, has been poorly studied. However, leachates from newly inundated riparian leaf litter are likely to promote changes in water chemistry, and the release of tannins has been shown to inhibit feeding, causing high mortality, in pond-dwelling pericard crustaceans (Cameron and LaPoint 1978). The implications of the addition of beneficial leachate materials, such as proteins and

FIG. 1. Summary of major physical and chemical factors that influence insect faunas of temporary fresh waters. An arrow indicates that the "boxed" factor has been shown, or is likely, to have an effect on insects (sometimes indirectly through another boxed factor); interactions between factors are shown by the lines joining the factor boxes.

carbohydrates, from riparian litter are unknown but perhaps they parallel those known for permanent fresh waters (see review by Lush 1981). The impact of such processes will be related to local patterns of leaf fall in conjunction with the timing of inundation and, in lotic habitats, the prevailing discharge. Nutrient input from sub-

surface (hyporheic) connections with permanent, interstitial water bodies recently has been demonstrated to influence the algal growth in an intermittent stream with obvious consequences for benthic herbivores (Valett et al. 1994).

In temporary running waters, a number of

FIG. 2. Summary of biological factors that influence insect faunas of temporary fresh waters (see Fig. 1 for explanation of arrows; note that interaction lines between factors have not been added due to uncertainty stemming from the lack of research on these factors specifically in temporary waters).

discharge-related factors (e.g., temporal pattern, maxima-minima) influence insects both directly and indirectly, the latter through correlation with several of the other physicochemical factors shown in the model (Fig. 1) (Boulton and Lake 1990). In both lotic and lentic temporary water bodies, the size and type of bed substrate particles are likely to exert influences ranging from suitability as attachment sites during the wet phase to protection from desiccation during drought (Boulton 1989).

Features of the biological environment are summarised in Fig. 2. Whereas it is not difficult to identify the influence of single biological factors, assessing their relative importance and linkage is less easy owing to lack of research specifically on temporary waters. Strong biological features include the succession of species so characteristic of temporary waters (e.g., Williams 1983, Jeffries 1994), seasonal influx of aerial colonisers (Fernando 1958, Nilsson and Svensson 1994), and temporal changes in the food base—as surplus bed nutrients from the

dry phase are used up, fungal and other decomposers process allochthonous bed materials, and phyto- and zooplankton become established (Bärlocher et al. 1978, Wiggins et al. 1980, Maher and Carpenter 1984). As a result of changes in the food base, together with variation in the numbers of predators (both as aquatic species succeed each other and as terrestrial ones invade the shrinking habitat), the structure of the food web must be subject to change (see later discussion). So, too, will the extent and intensity of inter- and intraspecific competition (Morin et al. 1988, Johansson 1993), although it has been argued that, in general, biotic interactions may contribute relatively little to community structure given the demanding requirements of the physicochemical environment (Poff and Ward 1989). In addition, a number of changes affect individual insects, such as modification of growth, morphology and life history (Harrison 1980, Landin 1980, Juliano and Stoffregen 1994), that may be classed as genotype-environment interactions.

Strongly influencing community structure, indirectly and especially through trophic processes, will be many of the physicochemical factors already considered (Fig. 2). However, from this suite of factors, habitat duration (length of the aquatic phase) is emerging as being perhaps the most important. For example, in a study of the relative influences on the invertebrate community of a Sonoran Desert stream, the dry phase was deemed to be more important than spates (Boulton et al. 1992), although floods may increase in influence as intermittency becomes less prolonged (Poff and Ward 1989). Further, Schneider and Frost (1996) concluded that the processes structuring temporary pond communities in Wisconsin were hierarchically organised by habitat duration.

Consequences for the fauna

Faunal composition

The above suite of factors determines whether an aquatic insect species can survive in a water body that is subject to drying, and also how well its population fares. How does this survival translate into the composition of the fauna? Do, for example, temporary waters support as many species as permanent waters?

A low-resolution view of the major groups of aquatic insects (including Collembola) known to occur in temporary waters is presented in Fig. 3 (Orders). The horizontal axis in this figure represents a relative scale of habitat permanence. Habitats in which the water "lasts indefinitely" (definition of "permanent" in the Oxford English Dictionary 1990), such as springs, are placed at the high permanence end, while temporary streams are placed at the low permanence end. Extending this logic, episodic streams would be placed at a lower permanence level than intermittent streams. However, as there has been little distinction between these two latter habitat types in the past literature, the present analysis has necessitated combining distributional records under the more general category of "temporary" streams. In temporary lotic waters, there are no records for the Neuroptera and Lepidoptera (although pyralid larvae have been collected from a stream in southern Australia, A.J. Boulton, University of New England, personal communication), and the Plecoptera and Odonata are poorly represented.

Particularly well-suited to temporary streams are the Ephemeroptera, Hemiptera, Coleoptera, Trichoptera, and Diptera. Higher resolution (Fig. 3, Diptera) shows that the Tipulidae and Chironomidae (Nematocera) dominate the temporary stream dipteran fauna (Williams and Feltmate 1992), whereas brachycerans are comparatively rare.

With the exception of mayflies (although a few species may attain large populations in vernal pools, Wiggins et al. 1980), all those orders commonly found in temporary running waters also are common in temporary ponds (Fig. 4). In addition, the odonates are well-represented. The most common nematoceran Diptera in temporary ponds are the Tipulidae, Culicidae, Ceratopogonidae, and Chironomidae, together with the brachyceran Ephydriidae (Fig. 4). Odonates and dipterans also are well-represented in highly specialised habitats such as phytotelmata—the water-retaining structures formed by terrestrial plants (Corbet 1983, Beaver 1985).

A number of observations can be made from these data. First, they indicate that, at the level of orders and families, temporary waters do not support as diverse insect faunas as are found in permanent waters. By way of a more detailed analysis, comparison of the insect species in 3 water-filled ditches in southern Ontario shows a decrease in the numbers of both insect and other invertebrate species with increasing length of the dry period (Table 2). These ditches lie within a 5-km radius in Waterloo County, Ontario, and form part of the Grand River drainage basin. They flow over moderate to strongly calcareous soils with a pH range of 7.8 to 8.0, which are under heavy agriculture. The faunas were sampled in late April, a time of year when all the ditches contained running water and insect diversity was at a maximum. A similar relationship between species diversity and flow duration has been shown for some streams in Australia (Boulton and Suter 1986).

Secondly, some very general inferences can be made about the adaptive traits and trade-offs demonstrated by different taxa. For example, it appears that Plecoptera seem less able to deal with standing water conditions than with drought, and survive drought only in running water habitats. Conversely, several dipteran families (e.g., Ptychopteridae, Tabanidae, and Empididae) are capable of living in temporary standing waters but not apparently in tempo-

LOTIC HABITAT PERMANENCE

FIG. 3. Overview of the relative importance of different aquatic insect orders and dipteran families across a gradient of running water habitat permanence (thick line indicates "well represented", thin line indicates "moderately well represented", broken line indicates "present but not significantly so"; information taken mainly from Merritt and Cummins 1984, Williams and Feltmate 1992).

Dipteran families

LENTIC HABITAT PERMANENCE

FIG. 4. Overview of the relative importance of different aquatic insect orders and dipteran families across a gradient of standing water habitat permanence (thick line indicates "well represented", thin line indicates "moderately well represented", broken line indicates "present but not significantly so"; information taken mainly from Merritt and Cummins 1984, Williams and Feltmate 1992).

TABLE 2. Comparison of the insect and non-insect faunas of 3 Ontario water-filled ditches with different degrees of permanence, shown as the number of months in the year in which water was present. Absence of a particular taxon is shown by a dash.

Taxonomic group	Length of wet period		
	11 months	8 months	6 months
Collembola	—	<i>Isotomurus</i> sp.	<i>Isotomurus</i> sp.
Hemiptera	—	<i>Gerris buenoi</i>	—
	<i>Sigara</i> sp.	<i>Sigara</i> sp.	—
Trichoptera	<i>Ironoquia punctatissima</i>	—	—
	<i>Hydropsyche betteni</i>	—	—
	—	<i>Limnephilus rhombicus</i>	—
Coleoptera:			
Hydrophilidae	—	—	<i>Helophorus orientalis</i>
	—	—	<i>Helophorus grandis</i>
	—	—	<i>Helophorus lacustris</i>
Elmidae	<i>Stenelmis</i> sp.	—	—
	<i>Optioservus</i> sp.	—	—
Diptera:			
Chironomidae			
Tanypodinae	—	<i>Natarsia</i> sp.	—
	<i>Thienemannimyia</i> sp.	—	—
Diamesinae	<i>Diamesa</i> sp. A	—	—
	—	<i>Diamesa</i> sp. B	—
Orthoclaadiinae	<i>Cricotopus</i> / <i>Orthocladus</i> sp.	—	—
	<i>Orthocladus</i> sp.	—	—
	—	<i>Cricotopus</i> sp. A	—
	<i>Cricotopus</i> sp. B	—	—
	—	—	<i>Pseudosmittia</i> sp.
Chironominae			
Chironomini	<i>Endochironomus</i> sp.	—	—
	<i>Micropsectra</i> sp.	<i>Micropsectra</i> sp.	—
	—	<i>Polypedilum</i> sp.	—
	—	<i>Paratendipes</i> sp.	—
Tipulidae	<i>Antocha</i> sp.	—	—
Ceratopogonidae	<i>Bezzia</i> / <i>Probezzia</i> grp	<i>Bezzia</i> / <i>Probezzia</i> grp	—
Simuliidae	<i>Simulium venustum</i>	—	—
Dolichopodidae	—	—	—
Syrphidae	<i>Tubifera</i> sp.	—	—
Total insect taxa	16	11	5
Other invertebrates	15	10	8

rary running waters (although there are records of empidids from a semi-permanent spring in Germany and from two temporary streams in Australia; O. Gathmann, University of Toronto, personal communication, and Boulton and Lake 1992a, respectively). Despite their considerable powers of flight, Trichoptera and aquatic Hemiptera and Coleoptera do not colonise phytotelmata significantly. Neuropterans have not developed the capability of living in temporary

habitats even though they are found in a range of permanent waters. Whereas some of these inferences may be spurious because of inadequate study of temporary waters, they nevertheless point to some interesting avenues for future research into evolutionary trends in habitat selection amongst aquatic insects. Particularly useful would be determination of why the Plecoptera, Odonata and brachyceran Diptera are poorly represented in temporary streams, yet the Ti-

pulidae and Chironomidae are successful; why mayflies are not widespread in temporary ponds despite being occasionally abundant locally; what mechanisms, physiological or otherwise, result in decrease in species diversity with decrease in the length of the aquatic stage of the habitat; and why the Trichoptera, Hemiptera and Coleoptera are poorly represented in phytotelmata. In addition, there needs to be more extensive surveying of habitats to confirm the global nature of temporary water communities and to extend/confirm the known ranges of taxa along the permanent-temporary water habitat gradient.

Faunal dynamics

An ecological feature, identified earlier and characteristic of most temporary waters is species succession through the different phases of the habitat. For example, temporary streams in temperate regions go through 3 stages: (1) a fall-winter running water stage; (2) a spring pool phase, as flow stops and a series of disconnected pools remain; and (3) a summer terrestrial stage (Williams and Hynes 1976). There is sufficient replacement of species throughout these stages that the structure of the faunal community differs substantially over time. Similar successions of species have been recorded in semi-arid foothill streams in central California (Abell 1984), in a desert stream in central Arizona (Boulton et al. 1992), and in 2 streams in southern Australia (Boulton and Lake 1992b). Despite the obvious conclusion that such structural changes must be accompanied by functional changes in the community, very few quantitative attempts have been made to address the latter. Assignment of species in Kirkland Creek, Ontario, to major functional feeding groups illustrates these changes (Fig. 5; further details of this study site are given in Williams and Hynes 1976). Compared with the fall-winter running water stage, which is dominated by collector-gatherers, the spring pool stage shows a marked increase in macropredators—primarily due to aerial colonisation by adult beetles and hemipterans. Both adults and their off-spring prey on members of the aquatic community. In 2 intermittent streams in Australia, predator numbers also peaked before the habitat dried; scraper densities rose in the late spring/early summer coincident with increased

periphyton growth; and collector-gatherers and collector-scrappers were well-represented throughout the year (Boulton and Lake 1992b).

Faunal adaptation

The loss of water from temporary habitats imposes a potential catastrophe on aquatic fauna. Aquatic insects have countered this "terrestrialisation" of their habitat by means of physiological tolerance, migration, and life history modification. Although the adaptations shown by individual species are varied, members of the same major taxonomic groups tend to employ similar stages in their life cycles. For example, mayflies, lepidopteran, and mosquitoes largely survive drought as eggs (Lehmkuhl 1973, Ingram 1976, Wood et al. 1979), many beetles and hemipterans survive as adults (Macan 1939, Nilsson and Svensson 1994), and stoneflies survive as diapausing early instar nymphs (Harper and Hynes 1970). Chironomids may diapause as larvae or eggs (Thienemann 1954, Williams and Hynes 1977).

Physiological tolerance frequently involves some form of diapause. In its simplest form, arrested or retarded growth may result as a direct consequence of water loss from the insect's tissues. The insect thus becomes dormant when dehydrated but resumes growth when water is restored (Hinton 1960). In other cases, there is a more programmed arrest of development for which a formal set of criteria is required before growth can continue (reviewed by Danks 1987). This is the case for mosquitoes such as *Aedes vexans*; for example, where a conditioning process is necessary before diapause can be broken (Horsfall 1956). Clearly such a mechanism has a safety feature built into it to prevent premature resumption of growth.

Active seasonal migration necessitates substantial powers of flight, coupled with mechanisms for locating and evaluating new bodies of water. It has been studied most in the Hemiptera and Coleoptera, and timing is very important in the process. Typically, adults having overwintered in some permanent body of water, disperse in early spring in search of newly-formed ponds. Here, eggs are laid and the young grow quickly under conditions of plentiful food and reduced competition. Adults of this new generation mature shortly before the dry phase and fly to new overwintering habitats

FIG. 5. Comparison of the trophic structures of the invertebrate communities of Kirkland Creek, a small temporary stream in Ontario, during the fall-winter stream stage (upper) and the spring pool stage (lower). Taxa present (see Williams and Hynes 1976) were assigned to functional feeding groups based on unpublished data and the dietary information provided in Merritt and Cummins (1984). No quantities have been assigned to the various links, and the size of the circles simply reflects the number of taxa present in a particular feeding group.

in a second dispersal in summer (Fernando and Galbraith 1973). Adult *Stenophylax* caddisflies are known to fly away from drying streams to hibernate in nearby caves. When flow resumes, they return to lay their eggs (Bouvet 1977). Other limnephilid adults have been observed to return, under high relative humidity, to dry pond basins where they deposit their eggs under logs or in other protected locations. Embryonic development proceeds, in the absence of water, within a protective gelatinous matrix and the larvae emerge when the pond refills (Wiggins et al. 1980). One study has shown that all of the dominant insects (beetles, corixids, and several dipterans) living in a seasonally flooded marsh persisted through repeated colonisation from nearby permanent habitats, rather than by physiological tolerance (Batzler and Resh 1992). Boulton (1989) similarly found that most of the insects living in 2 temporary streams in southern Australia over-summered in nearby permanent streams.

Life history modification in aquatic insects is influenced by both internal factors (such as physiology, behaviour, and morphology), which tend to restrict life history traits within certain genetically pre-determined ranges, and factors in the environment (such as water loss, temperature, food, photoperiod, and other biota), some of which also can impose range limits (reviewed by Williams 1991). For the most part, the insects of temporary waters exhibit traits of *r*-selected species (sensu MacArthur and Wilson 1967), especially high powers of dispersal, rapid growth, short life-span, small size, and opportunistic/generalistic feeding, although comprehensive dietary studies are rare. On the negative side, they may suffer from poor competitive abilities (e.g., McLachlan 1993).

Much work needs to be done to test if temporary water insects do in fact conform to these traits, as some studies would suggest otherwise. For example, the position on the *r*- and *K*-selection continuum of the pitcher plant mosquito *Wyeomyia smithii* (Coquillett) is believed to shift with time, perhaps associated with the highly specialised resource available in these very small temporary waters (Istock et al. 1976). In a comparison of wing length in 10 species of *Chironomus*, McLachlan (1985) found an unexpected increase in mean length with increasing habitat duration. According to *r*-selection predictions, species from more ephemeral habitats should

have greater flight capacity by virtue of long wings. Interestingly, McLachlan (1983) has shown that adult females of the African chironomid *Chironomus imicola* Kieffer emerging from remote temporary rockpools are uniformly large compared with females emerging from pools that occur in clusters. One explanation is that females from remote pools have greater distances to fly and are more fecund. In comparison with males from the same remote pools, the females have longer and broader wings that beat more slowly and have a longer stroke; wings that beat faster with a shorter stroke in males benefit competitive aerobatic manoeuvring in mating swarms (McLachlan 1986). Broader wings, combined with possibly greater energy reserves by virtue of a larger body, may effectively increase dispersal range in the females.

Variations in aquatic insect life history traits among 3 basic types of temporary water are modelled (based on Stearns 1976) in Fig. 6. This interpretation is preliminary in light of the limited empirical data available, but it is presented both as a platform for critical re-examination of the application of *r*-*K* selection theory to the inhabitants of temporary waters and in the hope that it will stimulate further research. The loss of water in all 3 waterbody types is seen as providing sufficient selective pressure for commonality of traits such as egg diapause; however, while some *r*-selected traits (e.g., good powers of dispersal, medium to high fecundity) benefit inhabitants in all 3 types of water, there is discrepancy in the perceived selective advantage of others (e.g., longevity). Indeed, in some cases (e.g., growth rate and pattern), opposing traits seem to apply, but then Pianka (1970) has argued that no organism is entirely *r*- or *K*-selected and that, generally, a balance is struck that maximises the adaptive value of features drawn from either type of selection. Models, other than those based on *r*-*K* continuum theory, that also underline the importance of habitat in determining life history strategies may prove to be more applicable to temporary fresh waters. These models have been reviewed by Southwood (1988) and Williams (1991).

Many of the orders and families that are most successful in temporary waters (summarised in Table 3) are widely separated phylogenetically, representing both exo- and endopterygotes. Some have an ancient lineage (the Ephemeroptera and Odonata arose in the Upper Carbon-

FIG. 6. A predictive model of the desirable adaptive traits of aquatic insects in 3 basic types of temporary waters that differ in their seasonal periodicity and predictability. The dark line indicates the length of generation time (G) of a hypothetical insect species relative to cycle periodicity (P) of the environment—the latter could, in this context, be equated to the hydrographs of 3 waterbody types. The concept is based on one proposed by Stearns (1976).

TABLE 3. Summary of some of the main adaptive characteristics of the aquatic insect orders and dipteran families most commonly encountered in temporary waters (information derived from Williams and Feltmate 1992).

Traits	Ephem- erop- tera	Odo- nata	Hemip- tera	Cole- optera	Tipu- lidae	Culi- cidae	Cera- topogo- nidae	Chiro- nomi- dae	Ephyd- ridae	Tri- chop- tera
Global distribution	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Occur in lotic & lentic waters	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Highly adaptable life cycle	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Highly diverse immature forms	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Development strongly linked to environmental temperature	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Egg diapause	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Desiccation-protected eggs, or staggered egg hatching	✓	✓	?	✓	?	✓	?	✓	?	✓
Parthenogenesis known	✓	no	✓	✓	✓	✓	✓	✓	✓	✓
High powers of dispersal	no	✓	✓	✓	✓	✓	✓	✓	✓	✓
Long-lived adults	no	✓	✓	✓	✓	✓	✓	some	some	✓
Generalist feeders	✓	no	some	✓	✓	✓	✓	✓	✓	many
Terrestrial ancestors	no	no	✓	✓	?	?	?	?	?	?
Trend towards terrestrialsation known for some immature stages	✓	✓	✓	✓	✓	no	✓	✓	✓	✓
Water surface/air breathers	no	no	✓	most	most	✓	some	no	✓	no

iferous), whereas other are more recent (e.g., the earliest known chironomids are from the Lower Cretaceous). However, most of the traits listed are common to all the groups, and several of the others are possessed by at least some members of each group. Particularly pertinent traits are a highly flexible life cycle, temperature-linked development, possession of a diapausing or otherwise protected egg, and high powers of dispersal. Also noteworthy is the presence of a trend towards terrestrialsation of immature stages, seen to some degree even in the strongly aquatic mayflies, odonates, and caddisflies (Anderson 1967, Watson and Theischinger 1980, Erman 1981, Williams and Feltmate 1992, McCafferty and Lugo-Ortiz 1995, Nolte et al. 1996). Some, but not all, of these traits agree with *r*-selected species predictions. For further discussion of the evolutionary history of aquatic insects, crustaceans, and mites in temporary pools, see Wiggins et al. (1980).

The title of this paper implied that insects that live in temporary waters are strongly limited ("constrained", *sensu strictu*) by their local environment. Is this premise supported by the available data? Yes, indeed, there is evidence that temporary water communities are some-

what less diverse than those of permanent water bodies and, yes, the physicochemical environment is more harsh. However, virtually all of the aquatic insect orders contain at least some species capable of living in temporary waters. Further, a wide variety of adaptations across a broad phylogenetic background has resulted in over two-thirds of these orders being well represented in these habitats. Viewed from this perspective, perhaps the concept of temporary waters *constraining* their faunas is based more in on human perception than on fact.

Where do we go from here?

Greater research effort should be devoted to studying the controlling influences of the biological environment as these may exert selective pressures that are different, or act at a different level of intensity, from those operating in permanent waters. In addition, there are still many aspects of the physical environment in temporary waters that we do not understand. For example, because many temporary waters are small they are subject not only to wide seasonal fluctuations in their physical and chemical characteristics, but also to variation over much short-

er time spans. Recently, F. Stössel, Swiss Federal Institute for Environmental Science and Technology (personal communication) has documented substantial diel changes in oxygen, water temperature, and density. How the insects of temporary waters react physiologically and behaviourally to these changes is unknown, as is whether the evolution of life history strategies is in response to environmental extremes or environmental variance. We should also accumulate more quantitative data on the adaptive traits shown by temporary water insects to allow a thorough re-examination of the applicability of *r*-K selection theory. For example, in a recent, innovative approach that combined field-collected data with manipulative laboratory experiments, Schneider and Frost (1996) found that a life history model best explained patterns of species presence/absence in Wisconsin ponds. However, patterns of taxon abundance were better fitted to a model in which the importance of competition and predation in structuring communities increased with extension of the aquatic phase. Further, although based on experiments using anurans, competition and predation in temporary ponds were observed to interact to determine the different consequences of the date of drying to the relative success of each of 4 sympatric species (Wilbur 1987). The latter 2 studies identify a further avenue of inquiry, namely the relative influence of physicochemical and biological factors and how this might change over time and/or habitat stage.

Relatively little is known about temporal variation in the structure of freshwater food webs (Tavares-Cromar and Williams 1996), despite the highly dynamic nature of these habitats. Temporary fresh waters, in particular, provide ideal sites for such analyses not only because of their generally compact nature but also because the strong seasonal succession of species likely maximises differences in the web. A study by Kitching (1987) of trophic dynamics in water-filled tree holes exemplifies this potential. From the limited data available on larger temporary waters, the findings of Closs and Lake (1994) point to considerable complexity that increases dramatically over time. This complexity is in contrast to the "trophically simple" nature of temporary stream communities predicted by Poff and Ward (1989).

Another area that requires study concerns the genetics of insect populations and how the col-

onisation process affects genetic variability. Is, for example, heterozygosity reduced in a population derived from a limited number of colonising adults (see Schmidt et al. 1995), or as a result of inbreeding in isolated habitats (see Hughes et al. 1995)? An alternative hypothesis is that temporary waters actually contribute to the maintenance of adequate gene flow among certain insect metapopulations (Williams and Hogg 1996).

Finally, although now beginning to be recognised (Batzler and Wissinger 1996), the whole concept of temporary waters as having conservation value needs to be investigated scientifically. It is possible, for example, that some, especially remote, temporary waters allow the persistence of rare and endangered invertebrate species (Williams and Hogg 1996). Further, the importance of larger temporary waters as habitat and sources of invertebrate food to migratory birds and amphibians is becoming more widely appreciated (Finlayson and Moser 1991).

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