

## WHY STUDY ECOLOGY IN TEMPORARY POOLS?

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### ABSTRACT

Temporary pools, loosely and broadly defined in this journal issue to include all standing water bodies that intermittently dry, are collectively very common worldwide and diverse in physical and biological characteristics. We outline four fundamental reasons to study ecology in temporary pools. First, lessons learned about the effects of ephemerality on biotic processes in temporary pools are not necessarily limited to temporary pools. Ephemerality may have similar effects in other patchy, temporary habitats on biota such as mushrooms, fallen fruit, carrion, etc. Second, temporary pools provide a convenient system for testing ecological theory because they are small, abundant, have well-defined borders, and have simple food webs. Consequently, they are relatively easy to manipulate and replicate. Third, temporary pools are breeding habitats for medically important organisms including etiological agents, vectors, and reservoirs of diseases. Fourth, temporary pools, whose numbers and quality have been dramatically reduced by man over the past century, have a unique set of species in need of protection. Thus, temporary pool research should continue to play an important role in developing ecological theory and, conversely, ecological theory should be applied to solving problems associated with temporary pools.

### INTRODUCTION

Temporary pools, though probably understudied considering their ubiquity, their potential importance, and their alarming rate of elimination and degradation, are receiving increasing attention from ecologists (Williams, 1987; Wilbur, 1997; Schwartz and Jenkins, 2000). What is a temporary pool? Definitions vary and for this journal issue, we loosely and broadly define “temporary pool” to include any habitat that intermittently has standing water and that, once inundated, holds water long enough on occasion for some species to complete aquatic phases of their life cycle. Our definition purposely ignores size as a taxonomic classification and thus includes water bodies that might be classified elsewhere as temporary lakes, temporary ponds, or phytotelmata (water-filled

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depressions in or on plants). Inundation can come from rains, snow melt, underground springs, tidal inundation, ocean spray, irrigation by man, and, to consider an extreme case of both temporal and spatial scale, condensation. We consider pools to include the entire vegetation gradient from devoid to vegetation-choked. This definition thus incorporates a wide variety of water bodies such as water-filled tree holes, inter-tidal (salt marsh and rocky coast) pools, supra-tidal pools, freshwater earthen and rock pools, rice fields, dew (condensation) drops, playas, and many more. Although we defined temporary pools from a physical standpoint of intermittent standing water, we recognize that, in physiological terms, "temporary" is different for different species and does not necessarily mean that the pool must dry. For example, in a supra-tidal rock pool that does not dry entirely but reaches very high salinities through evaporation, many species cease to exist, at least in active stages, even though water still stands.

#### WHY STUDY ECOLOGY IN TEMPORARY POOLS?

Below, we outline four compelling reasons that motivate the study of ecology in temporary pools: (1) habitat ephemerality is a common problem for organisms in a variety of habitats aside from temporary pools; (2) temporary pools provide a highly tractable system for addressing basic ecological questions; (3) temporary pools are breeding habitats of many medically important species; (4) the unique communities found in temporary pool habitats are in need of conservation and protection.

##### *REASON #1: EPHEMERAL HABITATS ARE DIVERSE AND COMMON IN NATURE*

Our understanding of the importance of ephemerality in influencing life histories, population dynamics, and community organization in temporary pools is not necessarily limited to understanding ecological processes in temporary pools alone. Habitat types that are ephemeral on an ecological timescale are diverse and abound in nature. Examples include fungi (Shorrocks and Charlesworth, 1980), dung (Valiela, 1974), fruits (Atkinson, 1985), carrion (Hanski, 1987), plants (Denno et al., 1996), and many others (e.g., Finn, 2001). Although these habitats may differ from temporary pools with respect to spatial unpredictability (McLachlan and Ladle, 2001), we might still expect convergence in species' responses to ephemerality or temporal unpredictability. All of these ephemeral habitats, like temporary pools, house various insect species with complex life cycles that must complete metamorphosis before these habitats dry out. Wet soils in water-limited ecosystems with wet pulses are also ephemeral habitats for many plant species: once seeds germinate, the individual plants must mature and produce seeds before the soils dry. Like other ephemeral habitats, species using isolated temporary pools may exist over a larger spatial scale as patchy populations or metapopulations (Briers and Warren, 2000; Bohonak and Roderick, 2001) and thus encounter similar dispersal problems.

Ecologists have learned that temporary pool organisms may have various traits that allow them to succeed in an ephemeral habitat. Do "terrestrial" organisms utilizing other ephemeral habitats use strategies similar to those of temporary pool organisms? One

strategy of many temporary pool species is developmental plasticity in response to habitat drying. In a wide taxonomic range of temporary pool species that must metamorphose and exit pools before the pools dry, individuals can shorten their development period and begin metamorphosis when environmental cues indicate that the aquatic habitat will disappear (e.g., Wilbur and Collins, 1973; Juliano and Stoffregan, 1994). Do species with complex life cycles using “terrestrial” ephemeral habitats display the same developmental plasticity in response to habitat permanence? Terrestrial analogs of this plasticity exist in many plants, e.g., flowering earlier and at a smaller size when stressed by drought conditions. Terrestrial arthropods display considerable developmental plasticity to environmental conditions (review in Nylin and Gotthard, 1998), and we would expect that arthropods that oviposit into such ephemeral habitats as fallen fruit (e.g., *Drosophila*) should display such developmental plasticity to habitat desiccation.

Both temporary pool invertebrates and terrestrial annual plants increase the probability of passing progeny on to future generations by the use of drought-resistant resting stages — resting eggs in temporary pool invertebrates and seeds in the plants. Both encounter uncertainty in the length of the next wet phase. Plant ecologists have predicted and have shown empirically that plants in unpredictable, intermittently wet/moist habitats may use a bet-hedging strategy for seed germination—only a fraction of seeds in a seed bank germinates on any given wetting to increase the likelihood of persistence over time (Cohen, 1966; Philippi, 1993). Temporary pool ecologists have recently borrowed from this theory to address the same questions, in which resting eggs of many temporary pool invertebrates are also referred to as “seed banks” (De Stasio, 1989; Philippi et al., 2001). Such aquatic invertebrate resting eggs apparently show bet-hedging responses similar to those of seed banks of annual plants. Bet-hedging hatching strategies are likely to be a hot topic of research in temporary pools, not only in response to risk of habitat drying (e.g., Philippi et al., 2001), but to other risks, such as risk of predation (Blaustein, 1997; Spencer and Blaustein, 2001). Studies on hatching strategies of temporary pool invertebrates are likely to accelerate the understanding of plant germination strategies and vice versa. Detection of convergent life history strategies across taxonomic groups as different as plants and animals can provide strong evidence for the selective power of ephemerality in evolution.

#### *REASON #2: TEMPORARY POOLS ARE TRACTABLE SYSTEMS FOR STUDYING CONCEPTUAL ECOLOGY*

Temporary pools are convenient systems for addressing ecological questions for a number of reasons. First, temporary pools, relative to many other systems, have simple food webs. Thus, conducting manipulative experiments to try to understand both direct and indirect interactions in organizing communities becomes more manageable when communities are species poor. Strong (1992) predicted that systems that are both low in species richness and structurally simple are likely systems to exhibit trophic cascades. Temporary pools, relative to many other habitats, are also simple in physical structure and much of the evidence accumulated thus far supports Strong’s (1992) prediction (Blaustein et al., 1995; Blaustein et al., 1996; Arner et al., 1998; Stav et al., 2000).

Temporary pools would make a good system to test Strong's hypothesis across structural complexity and species richness gradients.

A second reason why temporary pool systems are convenient for addressing conceptual questions in ecology is that they are often small and locally numerous. Once experimental approaches became popular beginning in the 1960s as a means for trying to understand community organization, ecologists turned to ecosystems that were more feasible for manipulation. Small size facilitates manipulation: for example, it is often quite doable to remove a species from smaller pools, while generally not feasible from lakes. Moreover, "numerous" means ease of replication. Hurlbert's (1984) landmark paper on pseudoreplication stressed the importance of independent replicates in experimental design — that multiple samples within a single plot are not independent, but rather the plot serves as the sample unit. Replicating lakes for experimentation is generally not feasible. Instead, to obtain true statistical replication in lakes, enclosures are often used. Such enclosures, which are supposed to simulate full lakes, may provide legitimate replication in a *statistical* sense, but they have their own set of problems for *biological* reality (Persson et al., 1999). Even when numerous lakes are examined in the same study, manipulation is generally not possible and there is the additional problem of increased environmental and biological variation among lakes over the unavoidable larger geographic area under study. Temporary pools, on the other hand, can be numerous in a small geographic area (e.g., Spencer et al., 1999; Wilcox, 2001), thus minimizing this problem.

A third reason why temporary pool systems are convenient for addressing conceptual questions in ecology is that natural temporary pools can be mimicked quite well with semi-natural or artificial pools (Wilbur, 1989, 1997). We define semi-natural pools as pools with a natural substrate that have been dug out (earthen pools) or bored out (rock pools) by man (e.g., Walton, 2001). We define artificial pools as those with an artificial substrate such as metal horse troughs (Wilbur, 1997) or plastic containers (e.g., Blaustein et al., 1996; Marsh et al., 1999). Natural pools are, by definition, the most "natural", but "replicate" natural pools are not exactly true replicates (like snow flakes, no two natural pools are exactly alike). When the number of replicate natural pools necessary for the study is not possible, or if it is desired to further reduce variability among replicates within a treatment to a greater extent than can be achieved with semi-natural pools (Morin, 1998), artificial pools often provide an excellent tool for experimentation (Wilbur, 1997). Although such artificial pools are often referred to as microcosms or mesocosms, unlike lake micro/mesocosms, they often are of the size of the pools that they are meant to simulate. We have found small plastic pools to simulate nearby natural rock pools quite well with regard to active colonizing species assemblages. If such pools are inoculated with passively dispersing taxa, they also simulate natural rock pools well (Blaustein et al., unpublished data). An advantage of conducting manipulative experiments in artificial rather than natural pools is that in natural pools, densities of the species of interest must often be estimated, resulting in within-treatment variance across replicates, but in artificial pools, exact known numbers of individuals of such species can be added (Morin, 1998).

Semi-natural pools generally provide more natural physicochemical conditions than do artificial pools, but often at the expense of inferential power and experimental tractability. For example, Blaustein (1990) was interested in assessing the impact of a predatory flatworm on community structure in experimental rice plots. Similarly, Walton (2001) was interested in determining the importance of a predatory tadpole shrimp on community structure in dug-out experimental pools. However, among-pool variability in flatworm and tadpole shrimp egg banks already existed in the substrates and it was not feasible to remove them. Blaustein (1990) and Walton (2001) used habitat conditions that were more natural than artificial pools, but had to settle for looking at correlations or associations between “naturally occurring” densities of these predators and prey species, rather than experimentally manipulating predators and obtaining the stronger causative inference.

*REASON #3: TEMPORARY POOLS ARE BREEDING HABITATS FOR MEDICALLY IMPORTANT ORGANISMS*

Temporary lentic waters are important habitats for etiological agents and disease vectors. Examples are numerous and a few examples are as follows. Schistosomiasis, a disease caused by *Schistosoma* trematodes, can be contracted in such habitats containing the snail reservoirs (Vera et al., 1992). Cyclopoid copepods in temporary pools serve as both vectors and reservoirs for Guinea worm (e.g., Joshi et al., 1997). Many mosquito species that breed in temporary lentic environments transmit diseases such as malaria, yellow fever, elephantiasis, encephalitis, and West Nile Fever (Service, 2000). Methods for attempting to control these diseases have included spraying pesticides, physically altering the aquatic habitat, or eliminating the aquatic habitat entirely. For example, in Israel, it is believed that the reduction in the amount and quality of breeding habitats for *Anopheles Sacharovi* mosquitoes led to the cessation of malaria epidemics in Israel (Kitron and Spielman, 1989). Such pest control strategies have become less desirable now that the preservation of temporary aquatic habitats and their biota is perceived as desirable. In place of these control measures, the challenge for temporary pool ecologists will be to apply ecological theory to manipulate these habitats (physically or community-wise) in such a way that desirable aspects of these habitats (such as the unique species and biodiversity) are maintained, while disease agents, vectors, and reservoirs are minimized (Batzer and Resh, 1992).

*REASON #4: TEMPORARY POOLS HAVE A UNIQUE SET OF SPECIES WHOSE PERSISTENCE IS THREATENED BY MAN'S ACTIVITIES*

Habitat elimination and degradation of temporary lentic waters has occurred at an alarming rate in recent history (e.g., Vlamis, 2000). While these human activities may reduce the prevalence of some diseases, they have also been linked to population declines, and the local, and sometimes global elimination of nontarget species. In Israel, it is suspected that the apparent global extinction of one amphibian species and the endangered status of three additional temporary pool amphibian species are due to habitat elimination and deterioration. Much attention by ecologists has been paid to

man's effects on amphibians, where suspected agents causing deleterious effects include disease, increased ultra-violet radiation, habitat fragmentation, and habitat elimination (Alford and Richards, 1999; Blaustein et al., 2001; Kiesecker et al., 2001). Although there has been supportive evidence for all these factors and combinations of these factors as the causative agents of population declines and extinctions, ecologists still have much to learn. Ecologists also have a lot to learn about the quality and quantity of abutting terrestrial habitat used by aquatic insects and amphibians after metamorphosis (Semlitsch, 1998). The status of other taxonomic groups, such as invertebrates, inhabiting temporary pools has been investigated to a lesser degree. Many temporary pool taxa remain unidentified and undescribed (King et al., 1996). Considerable work is necessary to document biodiversity in temporary pools and to better understand the ecology of temporary pool species in order to better understand how they might be protected.

#### GENERAL PERSPECTIVE

In this paper, we outlined some reasons that should motivate ecologists to study ecology in temporary pools. For this special issue on temporary pool ecology, we purposely recruited authors with the goal of contributing to the analysis of all the problems outlined, both conceptual and applied. We suggested that lessons learned concerning effects of ephemerality on biota are not only important for understanding temporary pool systems, but also for many other ephemeral systems. Considerable work has focused on the ephemerality of temporary pool systems (Wellborn et al., 1996), but we still have much to learn. The papers of this issue contribute significantly to our understanding of autecological, population, and community responses to ephemerality (Blaustein et al., 2001; Eason and Fauth, 2001; Jeffries, 2001; Lounibos, 2001; Philippi et al., 2001; Skelly, 2001; Therriault and Kolasa, 2001). Interactions between ephemerality and multiple factors (e.g., Skelly, 2001), bet-hedging hatching strategies (e.g., Philippi et al., 2001), oviposition habitat selection (Skelly, 2001), and induced responses to desiccation will likely receive considerable attention in the coming decade.

We emphasized that temporary pools are convenient systems for testing and developing ecological theory because of their tractability. A number of papers in this issue address potential factors influencing community structure (Eason and Fauth, 2001; Skelly, 2001; Therriault and Kolasa, 2001). Temporary pools have been (Wilbur, 1997), and are likely to continue to be, an important system for developing our understanding of how biotic factors affect behavior, populations, and community structure. The importance of risk of predation in inducing various behavioral and morphological responses has been a hot topic of research over the past two decades and, if a review is conducted comparing different ecosystems, we believe that the contribution of temporary pool studies to this line of research will be shown to be disproportionately high. We suspect this to be the case for two reasons. One reason is that temporary pool predators and prey, along with their tractable habitat, provide a very convenient system for such experimentation. Second, we would expect the prevalence of induced responses to risk of predation to be higher in temporary pool species than in permanent pool species because the

presence of predators is less likely and more unpredictable in temporary pool systems. This special issue includes how perceived risk of predation by a dragonfly affects activity, growth, and color of an anuran tadpole (Trembath and Anholt, 2001), and how perceived risk of predation by a salamander larva affects hatching rates by a crustacean prey (Spencer and Blaustein, 2001). We are also likely to see temporary pool systems used increasingly for trying to understand how such induced responses to risk of predation affect population and community dynamics (e.g., Spencer et al., 2001).

The tractability of temporary pool systems, combined with applied problems of pest management and conservation, are likely to make temporary pools a well-researched system for developing and testing in the field of metapopulation theory. In this issue, Bohonak and Roderick (2001) assess methods for estimating dispersal from estimates of gene flow, while Wilcox (2001) demonstrates colonization patterns of aquatic bugs empirically.

We have emphasized that temporary pools have their own set of applied problems in need of a solution. Two papers in this issue deal with mosquito ecology and control. One is an attempt to understand how habitat permanence shapes life history strategies of mosquitoes (Lounibos, 2001). A second paper addresses how mosquito abundance may be related to the abundance of a predator (Walton, 2001). A number of papers consider conservation issues, such as the importance of rice fields in providing temporary pool habitat (Lawler, 2001), factors affecting specific anuran populations (Blaustein et al., 2001; Skelly, 2001), and factors that may affect species diversity (Eason and Fauth, 2001; Therriault and Kolasa, 2001). Unfortunately, many control methods for medically important species that utilize temporary pools (such as mosquitoes) are often incompatible with the goals of conservation. One important goal in the study of temporary pool ecology over the next decade will be applying food web and ecosystem theory towards trying to simultaneously meet both pest control and conservation goals.

We hope that this special issue on temporary pool ecology will provide increased understanding of all the problems outlined here and will serve as a stimulus for further research in this tractable, interesting, and disappearing system.

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