Aquatic Ecology **34**: 3–8, 2000.

Temporary aquatic habitats: constraints and opportunities

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Accepted 15 December 1999

Key words: aestival, brumal, ephemeral, intermittent, seasonal, temporary, vernal

It is our pleasure to introduce a series of papers originally presented at a special session of the 1998 joint meeting of the American Society of Limnology and Oceanography (ASLO) and the Ecological Society of America (ESA). The goal of the session was to bring together aquatic ecologists to compare and contrast diverse temporary systems, and to learn from others studying similar questions in different systems. The increasing specialization among scientists has made the sharing of ideas difficult. This special session attempted to ford the differences and brought together 22 presentations on diverse temporary systems and questions. Some of these presentations have been developed into this set of peer-reviewed papers.

Interest in temporary habitats is growing slowly. This is the second compendium of papers on the topic in the last half of the decade. The first set derived from a symposium of the Entomological Society of America, and was published in the Journal of the North American Benthological Society (Vol. 15, 1996). Mackay (1996) said of those papers: 'temporary streams can be as useful as permanent ones in studies of conservation and water quality; they should not be avoided because they lack year-round flow.' We have expanded the scope of the previous effort by addressing both lentic and lotic habitats and without limitation to insects. Readers of both sets of papers may notice that similar questions continue to be addressed across taxonomic and hydrologic divisions. The goal of this paper is to set a context for the following papers, and to capture some of the ideas that motivated the session and were derived from it.

For a number of reasons, within lentic and lotic systems alike, most attention has been directed to permanent waters. The lack of attention may have to do with the fact that temporary waters are often (but certainly not always) too small for fishing, recreation, or holding water for agricultural or other uses. Without obvious utility to man they have been largely ignored. This lack of attention, and the subsequent lack of appreciation by scientists and the public, has left no defense for these endangered habitats. Yet we are convinced that such habitats, once so common, have a significant place in the geographic and scientific landscape.

Definition

Temporary waters are diverse in form and geography, including (among others): small depressions and large playas in arid and semiarid regions; tundra pools; prairie potholes; Carolina bays;riparian wetlands; phytotelmata; and stream beds that dry down to isolated pools. Indeed, a difficulty at the ASLO/ESA session was development of a definition common to all temporary aquatic habitats represented.

We define temporary aquatic systems as those in which the entire habitat for aquatic organisms shifts from being available to being unavailable, for a duration and/or frequency sufficient to substantially affect the entire biota. In this definition 'availability' has two aspects. First, availability specifically refers to the presence of liquid water and does not consider water quality. A lake undergoing severe oxygen depletion due to an algal die-off might be unavailable as a habitat for fish, but microbial life might persist, so by our definition it remains a permanent habitat by the presence of liquid water. Rather, our definition takes into account only systems in which the water evaporates (e.g., deserts) or freezes (e.g., polar habitats) for some undefined period. Therefore, these habitats are transient for aquatic organisms, shifting from uninhabitable to habitable, and then back to the uninhabitable.

Secondly, the character that best defines availability is its temporal component. Temporary habitats often lack liquid water at least annually and often for longer periods, during which aquatic organisms are not active. Aquatic organisms must either disperse to other habitats (forming spatial metapopulations; Ims & Yoccoz, 1997) or be dormant until conditions permit activity again (forming temporal metapopulations; Olivieri & Gouyon, 1997). The interval that liquid water is present (hydroperiod), and the variance in hydroperiod, is critical for individual aquatic organisms, and comprises intense natural selection for them to evolve a suite of adaptations that allows them to cope. In addition, hydroperiod has been shown to be important in determining community structure in temporary habitats (Wellborn et al., 1996; Spencer et al., 1999).

Ecological constraints and opportunities

Transient habitat availability delineates these habitats, sets their ecological boundaries and determines the unique evolutionary selection pressure for organisms in temporary aquatic habitats. Those species with adaptations to cross that boundary have an enhanced opportunity to succeed, especially if competitors or predators do not also adapt to conditions of temporary waters. Adaptations to the extreme conditions of temporary waters have long attracted attention, and continue to be an important part of research on evolutionary ecology in temporary waters.

The biota of temporary aquatic habitats have evolved mechanisms that reestablish populations when the habitat becomes available again. Typical inhabitants of temporary habitats (e.g., crustaceans, mollusks, rotifers, tardigrades, turbellarians, and hydrozoans) produce resistant eggs or are themselves able to enter a resistant resting stage (Wiggins et al., 1980; Williams, 1987) and a majority of their life span may be spent in these diapaused stages (Fugate, 1998). Diapause can be fine-tuned to environmental cues, and copepod populations can differ in the onset of diapause (Piercey & Maly, 2000). The field and laboratory work of Piercey and Maly indicates sophisticated local adaptations, fine-tuned to overcome the constraints of varying environments. Other inhabitants, principally many insects and all amphibians, use the habitat as a nursery and leave when the habitat starts to deteriorate (Wiggins et al., 1980; Williams, 1996). Most of these organisms have a terrestrial phase to their life cycle and recolonize temporary habitats when they are again available.

Because the presence and duration of temporary aquatic habitats can vary unpredictably, Stearns (1976) considered them exemplary of selection for a mixture between *r*- and *K*-strategies in life history. This mixed life history strategy has been called bet-hedging (Philippi & Seger, 1989; Simovich & Hathaway, 1997). Nix and Jenkins (2000) used a common-garden experiment to show that life history traits of a cladoceran from a short-hydroperiod, woodland pond were mixed relative to the same species from a long-hydroperiod, open pond. The woodland animals grew and reproduced well on a standardized, low-quality diet, indicating a broad suite of life history adaptations to succeed in woodland temporary aquatic habitats.

Evolutionary solutions to the constraints of inhabiting temporary waters differ among habitats and taxa. For example, invertebrates in temporary ponds disperse in space (as winged adults) or time (diapause) to overcome the constraint of temporary habitat loss. On the other hand, fishes in temporary streams are faced with a dramatic reduction in habitat and range size as a stream dries to isolated pools, and must contend with a condensed fish community and physical/chemical conditions that differ dramatically from those of a flowing stream. Magoulick (2000) found that fishes in temporary streams were concentrated during dry months into assemblages that varied among pools. Assemblages were not clearly related to abiotic conditions among pools, indicating that community composition was a result of the temporary constriction of habitat for the watershed's fishes. In addition, the close-packed assemblages may have been more interactive than in permanent streams, and potentially more susceptible to predation by terrestrial vertebrates while pooled.

Interspecific variation in adaptations to environmental conditions among and within temporary aquatic habitats can be revealed by detailed analyses of distributions. Bauder (2000) examined distributions of wetland plants in vernal pools of southern California, through three years of varying precipitation. Her analyses reveal sets of species that can be classified according to their tolerance to inundation, but also found substantial inter-annual variation in patterns that precludes reliable predictions for any one species. This study highlights the transient nature of temporary aquatic habitats, and flexibility that some species have for existence in such conditions. In addition, the vernal pools may be important refuges for some native wetland plants in southern California against invasion by exotic plant species (to date), lending an enhanced conservation value to these habitats in this semiarid region.

Given that some species are adapted to succeed in temporary waters, another challenge is dispersal to those habitats. Winged insects and amphibians are usually less constrained than crustaceans in this regard, especially among isolated habitats (Jenkins & Underwood, 1998). Temporary aquatic habitats in floodplains can be far more interconnected than upland waters by flooding, as shown by Havel et al. (2000). The Missouri River flooded at exceptionally high levels in 1993, as did other Midwestern rivers of the United States. Havel et al. then recorded crustacean species in temporary aquatic habitats in the Missouri River floodplain, including some newly-scoured habitats. Habitats more closely connected to the river contained more species, despite having few zooplankton in sediment egg banks. This study indicates the importance of the lotic link among floodplain zooplankton communities, and the opportunity that flooding provides for gene flow and range expansion among temporary aquatic habitats in floodplains.

Scientific constraints and opportunities

There are old divisions within aquatic sciences (limnology vs. oceanography), and some more recent partitions within limnology (e.g., the North American Benthological Society represents scientists specifically interested in moving water and the benthos). For a number of reasons, most attention in aquatic ecology has been directed to 'permanent' (i.e., hydroperiod > 1 year) lentic and lotic waters. As a result, we know more about communities and ecosystems in permanent waters than we do about those in temporary waters, and have less basis for protecting these unique, endangered habitats than for other systems. Of course, some important ecological research has used organisms that inhabit temporary aquatic habitats (e.g., Morin, 1987; Newman, 1989; Blaustein, 1997; Wilbur, 1997), but those and related works used the organisms as useful models of ecological interactions; the foci of those studies were less about understanding temporary aquatic habitats in general.

As evidence of the sparse information on temporary aquatic habitats, we conducted a literature search for the years 1940 through 1997. We used multiple sources, including works cited by Kenk (1949), Wiggins et al. (1980), and Williams (1987), and automated literature data bases (OVID Wilson General Science Abstracts; OCLC First Search; and ISI Science Citation Index Expanded). We looked for papers that used any combinations of words from (a) and (b) below and appearing in titles or keywords: (a) seasonal, aestival, intermittent, temporary, ephemeral, vernal, and (b) pond, playa, pool, and stream. We identified a total of only 158 papers with these descriptors between 1940 and 1997, with a maximum of 13 occurring in 1996. By comparison, 2278 articles were published in Limnology & Oceanography from 1987 through 1997, none of which dealt with temporary aquatic habitats by our search criteria. It is likely that we missed papers dealing with the autecology of biota in temporary waters, but the emphasis on 'permanent' waters is clear. Although more papers on temporary waters are being published currently than in the past, the increase has been very gradual. In addition, authors of several recent papers commented on the paucity of information on temporary aquatic habitats. Recent volumes (e.g., Simovich et al., 1997; Witham et al., 1998) make large contributions to our knowledge, and are valuable tools for those starting research on temporary habitats. We conclude that interest in these habitats and their biota has grown slowly, certainly more slowly than the rate at which the habitats are destroyed.

Because the study of temporary aquatic habitats is far less developed than the study of 'permanent' waters, basic descriptions of temporary waters (e.g., water chemistry, hydrology, species composition) continue to be vital. This is especially true for unusual systems, which can be excellent testing grounds for the generality of ecological concepts. The study by Kelley et al. (2000) describes a temporary lake in karst terrain. The lake can receive large quantities of groundwater from flooded caves that are themselves interconnected with other surface waters. Therefore, the lake has a hydrology, chemistry, and ecology unlike most other temporary aquatic habitats that have been described, and certainly unlike any others reported in this volume.

Species composition can vary widely among nearby temporary aquatic habitats (e.g., Simovich, 1998; Schneider & Frost, 1996; Spencer et al., 1999). Spatial autocorrelation statistics (join-counts) can test for non-random spatial patterns (a prerequisite to studies of processes causing species distributions). However, join-count statistics have not been widely applied in temporary waters research, perhaps because the statistics were developed for larger numbers of sites than typically included in studies. Temporary waters are often rare or widely spaced in modern landscapes, and logistic difficulties can limit an investigator's ability to sample large numbers of habitats repeatedly (but see Havel et al. (2000) for a large-scale study). Stevens and Jenkins (2000) used join-count statistics to evaluate spatial pattern in species presence/absence among a set of 15 closely-spaced temporary ponds. They tested the statistics for use with few sites, and devise a modified version to operate more appropriately for such studies. Studies on causal mechanisms for species distributions can (and should) test the null hypothesis that patterns are random. The approach of Stevens and Jenkins may help direct experimental tests of mechanisms that cause spatial patterns of species among temporary aquatic habitats (e.g., hydroperiod, predation, habitat quality), and may be useful for analyses of biotic surveys.

Unlike permanent water bodies, which are classified according to mixing status or productivity, there is no universal terminology for classifying temporary habitats. This impedes the study of habitats that are globally-distributed, occur at different times of the year, and occupy a wide variety of microgeographic sites. As a result, there have been few attempts to quantitatively compare the great variety of such habitats, besides compilations by Wiggins et al. (1980) and Williams (1987). The process of comparative limnology is nascent for temporary aquatic habitats. We hope this volume is a step toward developing a comparative approach among these diverse systems.

Another problem has been the lack of a consistent common language for comparing extremely diverse transient habitats among themselves or with permanent habitats. The common currency for those comparisons cannot be oft-studied variables such as organism densities or seasonal timing, but should be in universal terms such as net primary productivity, areal respiration rates, secondary productivity, nutrient cycling rates, etc. To study temporary aquatic habitats in these terms is a different emphasis than that we have observed and participated in to date, and part of the disparity between research on permanent and temporary waters. More efforts are needed to develop measurements of community- and ecosystem-scale processes among transient aquatic habitats, to promote better comparisons among systems.

The 'younger' state of research on temporary aquatic habitats is ironic, given that human history has been shaped by the use of fertile floodplains that are part of temporary aquatic habitats by definition. The state of science on temporary aquatic habitats is also cause for concern, because our exploitation and destruction of temporary aquatic habitats continues globally. Fifty percent of the historic wetlands have been lost in the United States (Dugan, 1993) with over 95% of the wetlands of California destroyed (Gilmer et al., 1982). These numbers don't include the losses of some temporary aquatic habitats not associated with typical wetlands (e.g., isolated ponds in the Great Plains or ponds in the dunes of the Oregon coast) but that are easily destroyed. Most of these habitats are small in diameter and shallow, and have little value to the public as they are too small to contain fish, serve as a reservoir, or provide recreation. To developers, these same traits mean that the habitats are quickly and easily destroyed and consequently they have been at an alarming rate. Habitat destruction is the primary threat to invertebrates in general, and in particular invertebrates with specific habitat requirements (Collins, 1991). If we are to rely on education of the public as a means to protect these habitats, we must better develop basic knowledge of these unique ecosystems, and transmit that information effectively beyond scientific circles. Debates about limits on collection of invertebrate inhabitants of non-permanent habitats (Belk, 1998; New, 1995) are moot when the entire habitat becomes a new mall or parking lot.

Ricciardi & Rasmussen (1999) drew attention to the high extinction rates for faunas in North America's freshwaters. It is their contention that the biota of freshwater habitats is as much in peril, if not more so, than the terrestrial biota. They point out that at least 123 species of freshwater organisms have gone extinct in North America since 1900 and predictions for the future are not appealing. What is striking is that their estimates are for permanent waters. The biota of temporary aquatic habitats is likely even more sensitive to human domination of the landscape. Many temporary aquatic habitats face temporal isolation (by definition) and geographic isolation. For example, the vagility of planktonic aquatic organisms is much more limited than their distribution would suggest (Boileau et al., 1992; Jenkins, 1995; Jenkins & Underwood, 1998). The extensive distribution of many pond-dwelling organisms is the result of insufficient taxonomy (Boileau, 1991; Hebert & Finston, 1993) in some cases, and colonization occurring on geologic time scales. The implication is that historical losses of temporary aquatic habitats may place some species at high extinction risk, especially if there is little opportunity for colonization and genetic exchange between habitats.

In detailing the conservation status of *Branchinecta*, Fugate (1998) concluded that management strategies for this genus must rest on the efforts of scientists studying all aspects of the biology of this temporary habitat dweller. The papers in this issue of *Aquatic Ecology* are a sample of vital research efforts being made by scientists in all manners of temporary habitats, studying flora and fauna alike. Temporary aquatic habitats have been, and continue to be, excellent natural laboratories to test concepts on adaptation (e.g., diapause, life history) and processes regulating community composition. We hope that the following papers help demonstrate the value of temporary aquatic habitats for addressing ecological and evolutionary questions, and the value of this work to conservation of these habitats.

References

Bauder ET (2000) Inundation effects on small-scale plant distributions in San Diego, California vernal pools. Aquat Ecol 34: 43–61

Belk D (1998) Global status and trends in ephemeral pool invertebrate conservation: implications for Californian fairy shrimp. In: Witham CW, Bauder ET, Belk D, Ferren WR Jr and Ornduff R (eds.), Ecology, Conservation and Management of Vernal Pool Ecosystems – Proceedings from a 1996 Conference. California Native Plant Society, Sacromento, CA, pp. 147–150

Blaustein L (1997) Non-consumptive effects of larval Salamandra on crustacean prey: can eggs detect predators? Oecologia 110: 212–217

Boileau MG (1991) A genetic determination of cryptic species (Copepoda: Calanoida) and their postglacial biogeography in North America. Zool J Linn Soc 102: 375–396

Boileau MG, Hebert PDN and Schwartz SS (1992) Non-equilibrium gene frequency divergence: persistent founder effects in natural populations. J Evol Biol 5: 25–39

Collins NM (1991) Insect conservation – priorities for the future. Antenna 15: 73–78

Dugan P (ed.) (1993) Wetlands in Danger: A World Conservation Atlas. Oxford University Press, Oxford, 192 pp

Fugate M (1998) *Branchinecta* of North America: population structure and its implications for conservation practice. In: Witham CW, Bauder E, Belk D, Ferren WR Jr and Ornduff R (eds.), Ecology, Conservation, and Management of Vernal Pool Ecosystems – Proceedings from a 1996 Conference. California Native Plant Society, Sacramento, CA, pp. 140–146

Gilmer DS, Miller MR, Bauer RD and DeLonne JR (1982) California's Central Valley wintering waterfowl: concerns and challenges. Trans North Amer Wildl Nat Res Conf 47: 441–452

Havel JE, Eisenbacher EM and Black AA (2000) Diversity of crustacean zooplankton in riparian wetlands: colonization and egg banks. Aquat Ecol 34: 63–76

Hebert PDN and Finston TL (1993) A taxonomic reevaluation of the North American *Daphnia* (Crustacea: Cladocera) I. The *D. similis* complex. Can J Zool 71: 908–925

Ims RA and Yoccoz NG (1997) Chap. 11 – Studying transfer processes in metapopulations: emigration, migration, and colonization. In: Hanski IA and Gilpin ME (eds.), Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, New York, pp. 247–266

Jenkins DG (1995) Dispersal-limited zooplankton distribution and community composition in new ponds. Hydrobiologia 313/314: 15–20

Jenkins DG and Underwood MO (1998) Zooplankton may not disperse readily in wind, rain, or waterfowl. Hydrobiologia 387/388: 15–21

Kelley R, Jack J and Fant M (2000) A survey of the physiochemical characteristics and the zooplankton communities in an ephemeral Karst lake. Aquat Ecol 34: 77–89

Kenk R (1949) The animal life of temporary and permanent ponds in southern Michigan. Misc. Publ. Museum Zoology, Univ. Mich. No. 71, pp. 2–71

Mackay R (1996) Temporary aquatic habitats. J. North Am Benthol Soc 15: 407

Magoulick DD (2000) Spatial and temporal variation assemblages of drying stream pools: The role of abiotic and biotic factors. Aquat Ecol 34: 29–41

Morin PJ (1987) Predation, breeding asynchrony, and the outcome of competition among treefrog tadpoles. Ecology 68: 675–683

New TR (1995) Introduction to Invertebrate Conservation Biology. Oxford University Press, Oxford, England, 194 pp

Newman RA (1989) Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. Ecology 70: 1775–1787

Nix MH and Jenkins DG (2000) Life history comparisons of *Daphnia obtusa* from temporary ponds, cultured with a low-quality food. Aquat Ecol 34: 19–27

Olivieri I and Gouyon P-H (1997) Evolution of migration rate and other traits: the metapopulation effect. In: Hanski IA and Gilpin ME (eds.), Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, New York, pp. 293–324

Philippi TE and Seger J (1989) Hedging one's evolutionary bets, revisited. Trends Ecol Evol 4: 41–44

Piercey DW and Maly EJ (2000) Factors influencing the induction of diapausing egg production in the calanoid copepod *Diaptomus leptopus*. Aquat Ecol 34: 9–17

Ricciardi A and Rasmussen JB (1999) Extinction rates of North American freshwater fauna. Cons Biol 13: 1220–1222

Schneider DW and Frost TM (1996) Habitat duration and community structure in temporary ponds. J North Am Benthol Soc 15: 64–86

Simovich MA and Hathaway SA (1997) Diversified bet-hedging as a productive strategy of some ephemeral pool anostracans (Branchiopoda). J Crust Biol 17: 38–44

Simovich MA, Sassaman C and Belk D (eds.) (1997) Studies on large branchiopod biology and conservation. Hydrobiologia 359

Simovich MA (1998) Crustacean biodiversity and endemism in California's ephemeral wetlands. In: Witham CW, Bauder E, Belk D, Ferren WR Jr and Ornduff R (eds), Ecology, Conservation, and Management of Vernal Pool Ecosystems – Proceedings from a 1996 Conference. California Native Plant Society, Sacramento, CA, pp. 107–118

Spencer M, Blaustein L, Schwartz SS and Cohen JE (1999) Species richness and the proportion of predatory animal species in temporary pools: relationships with habitat size and permanence. Ecol Lett 2: 157–166

Stearns SC (1976) Life-history tactics: a review of the ideas. Quart Rev Biol 51: 3–47

Stevens PH and Jenkins DG (2000) Analyzing species distributions among temporary ponds with a permutation test approach to the joint-count statistic. Aquat Ecol 34: 91–99

Wellborn GA, Skelly DK and Werner EE (1996) Mechanisms creating community structure across a freshwater habitat gradient. Annu Rev Ecol System 27: 337–363

Wiggins GB, Mackay RJ and Smith IM (1980) Evolutionary and ecological strategies of animals in annual temporary pools. Arch Hydrobiol Suppl 58: 97–206

Wilbur HM (1997) Experimental ecology of food webs: Complex systems in temporary ponds. Ecology 78: 2279–2302

Williams DD (1987) The Ecology of Temporary Waters. Croom Helm, London, 205 pp.

Williams DD (1996) Environmental constraints in temporary fresh waters and their consequences for the insect fauna. J. North Am Benthol Soc 15: 634–650

Witham CW, Bauder E, Belk D, Ferren WR Jr and Ornduff R (eds) (1998) Ecology, Conservation, and Management of Vernal Pool Ecosystems – Proceedings from a 1996 Conference, California Native Plant Society, Sacramento, CA