REVIEW ARTICLE

Rotifers of temporary waters

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While ubiquitous, temporary waters vary greatly in geographic distribution, origin, size, connectivity, hydroperiod, and biological composition. However, all terminate as active habitats, transitioning into either dryness or ice, only to be restored when conditions improve. Hydroperiod in some temporary habitats is cyclical and predictable, while in others it is sporadic. Although the rotifer communities of temporary waters are subjected to unique selective pressures within their habitats, species share many of the same adaptive responses. Here, we review temporary waters and their rotiferan inhabitants, examining community composition, life history, and evolutionary strategies that allow rotifers to flourish in these fluctuating environments.

1 Introduction

Temporary waters, also termed astatic, ephemeral, intermittent, vernal, seasonal, or periodic, are those in which the entire habitat alternates between the presence of liquid water and its absence. Water loss can occur via direct drainage, percolation, evaporation, or freezing, with fluctuations in hydroperiod (wet phase duration) being daily, seasonally, annually, or longer [1, 2]. Accordingly, life in temporary waters is adapted to a dual existence, flourishing when the habitat contains liquid water, but migrating or enduring its absence. For rotifers, which are incapable of active migration to another habitat, occupancy of temporary habitats is linked to tolerance mechanisms and/or passive dispersal. The two main subclasses of rotifers, bdelloids, and monogononts, use different strategies to survive in a dormant ametabolic state. Bdelloids undergo quiescence, marked by a change in metabolism progressing into the anhydrobiotic state of the xerosome [3]. Adult bdelloids as well as their eggs can survive repeated cycles of freezing and thawing [4, 5]. In contrast most monogononts undergo a true, endogenously regulated diapause [6] in the form of diapausing embryos (resting eggs). As adults, monogononts possess little capacity to withstand freezing [7] unless extraordinary methods are employed [8]. However, the subitaneous embryos of Brachionus plicatilis are capable of surviving freezing using cryopreservation techniques [9]. Regardless of the dormancy mechanism, survivors are poised to repopulate the habitat when liquid water returns. In addition, community dynamics are affected because rotifer dormant stages can undergo passive dispersal. As a result temporary waters are useful systems to test ecological theory [10–13], including metacommunity theory [14, 15], dispersal theory [16, 17], the effects of fragmentation on food web networks [18], and ecosystem processes in disturbed habitats [19, 20].

The first account of the rotifers of temporary waters appears to be Van Leeuwenhoek’s description of rotifers in rain gutters [21]. Since then there have been numerous reports of rotifers in ephemeral habitats, but most of these deal with habitats that dry, all but ignoring cryogenic systems. While some studies merely report species’ presence, others provide more detailed analyses [22, 23] or combine observational and experimental data [24–26]. Here, we review the rotifers of temporary waters by describing types of temporary habitats, examining various methods of sampling, and exploring their life history and evolutionary strategies. For additional discussion of the...
distribution of rotifers across environment types, including permanent systems, consult Pejler [22] and references cited therein. Rotifers that live in the thin film of water of the limnoterrestrial (which also may alternate between liquid and dry/frozen) are not covered in this review: these habitats include the edaphon of terrestrial [27] and bog soils [28, 29], and water films on damp mosses and lichens [30].

2 Characterizing temporary waters

The processes that produce the basins in which temporary waters arise are diverse. Like lakes, which are grouped into lake districts [31], temporary waters also have localized distributions [13, 32]. Perhaps due to this diversity, temporary waters defy a simple, consistent classification. Several features may be important to our understanding of the dynamics of temporary waters. These include the following: basin composition (edaphic conditions); water source; predictability of filling/thawing; seasonal timing and absolute duration of the hydrologic cycle; surface connectivity; and composition of biotic components. As a result several ways of categorizing temporary waters have been promoted [2, 25, 33–36]. Alternatively, Örstan [23] suggested a novel categorization based on likelihood of drying as a function of number of rotifer generations.

3 Categories of temporary waters

Accounts of rotifers in temporary waters are numerous and widely scattered in the literature, but many times these reports are only anecdotal with the main emphasis being on microcrustaceans and/or insects. Here, we review 10 general categories of temporary waters (Table 1), with the caveat that there is some overlap among these groups.

3.1 Drought lakes

Most lakes are viewed as being permanent, but in aridlands they can dry completely. For example, Lake Chilwa, a shallow lake in southeastern Malawi (Africa), undergoes periodic drought [37] and the rotifer community is reset after a drought/filling cycle. In an inland saline lake in Argentina, rotifer species diversity was low but stable over two consecutive filling cycles, and was likely constrained by high conductivity [38].

3.2 Marshes

Freshwater marshes are composed of both flowing and stagnant waters, but some are inundated seasonally [39] and in drought years may burn. Once considered marginal land, many marshes were drained; however, upon restoration they quickly become good habitat for zooplankton [40]. Some non-tidal salt marshes also are temporary, with a hydroperiod that alternates between being flooded with marine and/or freshwater inputs, and dryness [41]. In a similar fashion, coastal ponds can dry [42, 43], but may be subjected to inundations of fresh- or brackish waters. Such sites offer an opportunity to study osmoregulatory ability in rotifers from habitats with fluctuating salinities (see below) and have been the focus of several studies on adaptation and evolution of rotifers in temporary waters [44, 45].

3.3 Phytotelmata

Plant hollows that hold water are natural microcosms, and may be short-lived (e.g., leaf axils) or endure for decades (e.g., tree holes; [16]). The volume entrained within these systems varies from a few mLs in leaf axils, to a few L in tank bromeliads, to >5 L in tree holes [46].

Traps of pitcher plants (e.g., Sarracenia) possess rotifers, but most research on these systems focuses on the dynamics of the mosquito-inquiline community [47, 48]. Rotifers in these phytotelmata are limited mostly to bdelloids (Habrotrocha rosa and Philodina roseola), which are consumed by dipteran larvae [49–51]. According to the study of Petersen et al. [50] ~70% of Sarracenia purpurea traps contain H. rosa, but Bate-man [52] reported a higher rate (ca. 95%). In a comprehensive survey of S. purpurea in three states in the northeastern USA, Błędzki and Ellison [28] report five other species in addition to H. rosa: Cephalodella anebodica, Keratella mixta, Lecane lunaris, Notholca acuminata, and Polyarthra vulgaris. By excreting nitrogen and phosphorous, rotifers are important in the mineral nutrition of these communities [53]. Presumably, rotifers live as inquilines in other pitcher plants, but no systematic surveys have been done.

Rotifers also have been reported in the leaf axils of certain plants (e.g., Dipsacus, Scirpus), tank bromeliads, and other water-filled cavities of plants [54, 55]. Although they can be quite abundant in forests, tree holes have been relatively neglected as a habitat for study [56, 57]. A common tree hole inhabitant, Habrotrocha thienemanni, is capable of achieving dense populations of >56 000 inds. L⁻¹ [58].

3.4 Seasonally flooded basins and depressions

Depressions in the landscape include interdunal ponds, playas (pans, vleys), pools in forests and shrublands (including Carolina Bays), prairie potholes, gueltas in desert regions, brackish coastal ponds, tree tip ups, and limestone turloughs. Depending on the local conditions,
Table 1. Categories of temporary waters ordered by general hydroperiod characteristics

<table>
<thead>
<tr>
<th>Category</th>
<th>Examples</th>
<th>Inundation frequency</th>
<th>Hydroperiod (duration; washout)</th>
<th>Hydrology (filling; discharge)</th>
<th>Food web (grazing or detrital)</th>
<th>Likely population sourcesa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drought lakes</td>
<td>Lake Chilwa, Lake Meerimajeel</td>
<td></td>
<td>Fluctuating water levels in drought</td>
<td>Periodic droughts; washout potential low</td>
<td>Precipitation, rivers; evaporation</td>
<td>Both</td>
</tr>
<tr>
<td>Marshes</td>
<td>Wetlands that dry partly or in drought completely, gueltas</td>
<td></td>
<td>Usually predictable</td>
<td>Varies greatly (months, decades); washout potential low</td>
<td>Precipitation, flow, water table; evaporation/ percolation</td>
<td>Both</td>
</tr>
<tr>
<td>Phytotelmata</td>
<td>Pitcher plants, leaf axils, tree holes</td>
<td></td>
<td>Spring into late summer</td>
<td>Varies greatly; days to decades; washout potential high</td>
<td>Precipitation, plant fluids; evaporation/ percolation</td>
<td>Detrital</td>
</tr>
<tr>
<td>Seasonally flooded depressions</td>
<td>Interdunal ponds, playas, seasonal pools, brackish ponds, limestone turloughs</td>
<td></td>
<td>Varies: rare and unpredictable to predictable by season</td>
<td>Days, weeks, or months; washout potential low</td>
<td>Precipitation and water table; evaporation/ percolation</td>
<td>Both, varies on category</td>
</tr>
<tr>
<td>Lotic systems</td>
<td>Washes and intermittent channelized seeps</td>
<td></td>
<td>Varies: rare and unpredictable to predictable by season</td>
<td>Weeks, months or longer; washout potential high</td>
<td>Precipitation; evaporation/ percolation</td>
<td>Both</td>
</tr>
<tr>
<td>Small aridland basins</td>
<td>Rock pools (huecos, tinajas), aguelmans</td>
<td></td>
<td>Often rare and unpredictable</td>
<td>Days, weeks, months; washout potential high</td>
<td>Precipitation; evaporation</td>
<td>Both</td>
</tr>
<tr>
<td>Cryogenic systems</td>
<td>Cryoconite holes, melt water pools, ponds that freeze completely</td>
<td></td>
<td>Summer, but unpredictable</td>
<td>Days, weeks, or months; washout potential high</td>
<td>Melt water, flow or refreezing</td>
<td>Grazing</td>
</tr>
<tr>
<td>Artificial basins</td>
<td>Cattle tanks, depressions from warfare, fish ponds, quarries, rice paddies</td>
<td></td>
<td>Seasonal, but varies with use</td>
<td>Seasonal to long term; washout potential seasonal (low to high)</td>
<td>Precipitation; evaporation/percolation</td>
<td>Both</td>
</tr>
<tr>
<td>Small containers</td>
<td>Bird baths, cups, mesocosms, tires, rain barrels and gutters</td>
<td></td>
<td>Seasonal</td>
<td>Days, weeks, months; washout potential high</td>
<td>Precipitation; evaporation</td>
<td>Grazing</td>
</tr>
<tr>
<td>Habitats associated with roads</td>
<td>Drainage ditches, tire ruts and potholes, footpath prints</td>
<td></td>
<td>Depends on local conditions</td>
<td>Days to weeks; washout potential moderate to low</td>
<td>Precipitation; evaporation/percolation</td>
<td>Both</td>
</tr>
</tbody>
</table>

a) A, anemochory of dormant stages (diapausing embryos in monogononts and xerosomes in bdelloids); H, hydrochory of active or dormant animals from other populations; D, dormant stages produced by in situ population; S, active or dormant animals from surface runoff; Z, zoochory of dormant stages.
these basins fill by seasonal rain, a rise in the water table, or snowmelt, with water disappearing by evaporation and/or percolation. Depressions between dunes can function as catch basins for seasonal rains, and upon filling can develop robust communities. Several studies have been reported on the numerous ephemeral dune ponds of Doñana National Park (Spain). For example, Serrano and Fahd [59] found that species richness of both crustaceans and rotifers was significantly correlated with the length of the hydroperiod. Accumulative species richness ($A$) and mean, single collection species richness ($M$) varied as a function of hydroperiod: long ($A = 35, M = 5.98$); intermediate ($A = 41, M = 5.09$); short ($A = 24, M = 5.62$). This report indicates that sites with intermediate hydroperiods are more speciose when the survey is accomplished over a longer timeframe, a fact that is missed by single samples: see also [60–62]. Other complicating factors include differences in aquifer source, as well as the biotic and abiotic constituents [63]. Flooded areas following seasonal monsoons in a gypsum dune series in White Sands National Monument (New Mexico, USA) contain few rotifers species (e.g., bdelloids, Hexarthra fennica, H. polydonta), which is likely a function of the high sulfate concentrations of these habitats (EJW unpub. data).

Other habitats that have not received adequate attention include the Carolina Bays of the eastern USA [64], wetland potholes of North American prairies [65], and tree tip ups. Tree tip ups are temporary pools that sometimes form when strong winds uproot a tree, creating a shallow depression that may fill with water long enough for a rotifer community to develop.

3.5 Lotic systems

Temporary streams and floodplain basins fill during seasonal rains, sometimes very rapidly; others arise from seeps (intermittently flowing springs). These flow for varying distances, filling small basins along the way [66–68]. Landscape use has an effect on the sediment egg bank of these habitats. For example, Frisch et al. [69] found differences in species composition when comparing rotifers hatched from sediment taken from a temporary stream flowing through agricultural lands as compared to two reference zones.

3.6 Small aridland basins

Rock pools are common in aridlands with exposed impervious bedrock. Because these basins often occur in clusters, they represent a metacommunity with the individual basins varying in size, spatial arrangement, and potential for surface connectivity [15, 70]. Ranging in size from $<1$ to well over 1000 L, these habitats are subject to rapid filling and potential washout from seasonal, but sporadic, rains. Many small pools dry within a few days, but larger ones may persist for much longer. Depending on their location these basins are subject to both deflation and deposition of aeolian sediments and wide diel swings in water temperature. Rotifers with unique life history adaptations [26], as well as cryptic species have been recovered from rock basins: e.g., the Epiphanes senta complex [71, 72].

3.7 Cryogenic systems

Rotifers are found in ice habitats that span several scales. They are present in the interstitial film of water on the ice grains of algal patches on snowfields [73]. When a small mass of dust, rock, or organic debris on the surface of a glacier is sufficiently warmed to melt water, a cryoconite hole will form; such holes or puddles can present opportunities for colonization. Smagowicz [74] reports Keratella serrulata in temporary melt water puddles from a glacier on Mt. Turbacz (southern Poland). On a larger scale, some shallow ponds in polar regions and alpine tundra freeze solid in the winter, yet rotifers are present even if the habitat is never completely ice-free [75]. Everitt [76] reported presence of five bdelloids and five monogononts in Deep Lake Tarn, a pool that freezes solidly in the Antarctic winter.

3.8 Anthropogenic basins

Systems of human origin that temporarily may hold water are too multifarious for complete treatment here, but include cattle tanks, rice paddies, quarries, fish ponds, and depressions associated with the actions of warfare [32]. Cattle (stock) tanks commonly are constructed by enlarging an existing pool, damming a stream, or building a walled tank. Because stock tanks typically are subject to heavy organic load from fecal material, these systems are often hypertrophic and are home to rotifers that are tolerant to high nutrient concentrations (e.g., Euchlanis dilatata, E. senta). Rice paddies usually are hypertrophic as well, and contain numerous species [77–81]. For example, in their study of a rice paddy and an adjacent fish pond in Laos, Segers and Sanoamuang [78] recorded 135 species, with 41.5% present exclusively in the paddy.

3.9 Small containers

This category differs from the previous one by size and the original intent of use. Almost any type of receptacle that can hold water for more than a few days is a potential habitat for rotifers, including discarded cups and tires [82], birdbaths [83–85], cemetery vases, rain gutters [21], and small tree hole analogs [86]. While it may be assumed that
any species is capable of colonizing these habitats, bdelloids are commonly present: e.g., *Abrochtha meselsoni*, *Adineta vaga*, and *P. roseola*.

### 3.10 Habitats associated with roads

When roadside drainage ditches and tire ruts or potholes become filled with water, they become temporary habitat for rotifers. However, it appears that little research has been done on these sites beyond casual examination [87–91]. In seasonal ponds that form in permanent road ruts in St. John, US Virgin Islands, one of us (EJW) found high densities of *Asplanchna sieboldii*, *Brachionus angularis*, and *Filinia novaezealandiae*, as well as *Daphnia sp.*, *Volvox sp.*, and a variety of ciliates. These habitats warrant further research.

### 4 Sampling temporary waters

Strategies for sampling temporary waters depend on the volume of the basin, but in practice these are usually no different than those used in permanent systems (Table 2). The ultimate goal of sampling a water body of any size is to obtain a truly representative sample of the biota present. Given the naturally heterogeneous nature of many temporary waters both spatially and temporally, one must be particularly cognizant of the site, time, and frequency of sampling. Depending on the goal of the study, sampling may be qualitative or quantitative. Qualitative sampling often involves collecting plankton tows from various points in a water body, while quantitative sampling strives to determine species abundance in a given volume of water. Methods for sampling the open water are more well developed and a variety of devices (e.g., Van Dorn grab samplers, composite samplers) are available that are suitable for sampling larger temporary waters. For smaller or more fragile systems, specialized methods are often needed. For example, Yanoviak and Fincke [92] have described sampling methods for tree holes and other phytotelmata; these may be adapted for sampling other habitats with small volumes. Yet, the potential for temporal fluctuations in active/dormant communities should be considered; samples taken immediately after inundation may not reflect community dynamics toward the middle or end of the wet phase. In addition, application of traditional sampling techniques in small basins or those in the last stages of drying may result in serious alteration to community composition: i.e., the act of sampling can influence the trajectory of community development. Moreover, in deserts and other fragile systems where water is limited and/or a critical resource for animals, care should be taken so as not to damage the resource.

Another method of ascertaining the species present in a habitat, even one that is dry, is to revive dormant propagules from the sediments [93–96] or blowing dust [97]. Samples should be taken from several sites, as the distribution of propagules may not be uniform.

Sample preservation techniques depend on the ultimate fate of the material. As noted in Wallace and Snell [98], for taxonomic identification some species must be examined live, while others are best identified when preserved in buffered formalin solution. Lugol’s iodine and Rose Bengal stain can be used to enhance visibility for counting purposes. Materials to be used for DNA analyses are better preserved in 95% EtOH. Thus, it is often advantageous to prepare both alcohol- and formalin-preserved material from field samples.

### 5 Temporary waters: Contributions of rotifer research to ecological and evolutionary theory

In the following section, we present specific examples of how studies of temporary waters have informed our understanding of ecological and evolutionary concepts.

#### 5.1 Biodiversity

Traditionally, estimates of aquatic biodiversity have focused on lakes, rivers, and other permanent water sources. However, it is becoming increasingly clear that temporary waters can make significant contributions to rotifer species richness (Table 3). It is not surprising that the number of rotifer genera and species recorded varies depending on habitat. Several rotifer species were first recorded from temporary waters (Table 4). A few examples illustrating species diversity and endemism of rotifers in temporary habitats, and the effect of neglecting these sites in regional surveys of species richness, are given below.

Temporary waters in Australian floodplain basins develop substantial communities [99, 100]. In a survey of >100 ephemeral pools along the River Murray, Shiel et al. [101] reported over 250 rotifer species; however, the mean diversity of these sites was low and very variable: $S = 10.9$, with ~43% singletons. Further, such temporary waters harbor high levels of endemism. For example, Shiel and his colleagues (pers. com.) compiled a list of described endemics from Australia; 43% of these were found in ephemeral habitats or their sediments.

In a study of habitats on the island of Minorca, De Manuel [102] found that of 45 monogonont taxa, 51% were found only in permanent habitats, 18% only in temporary habitats, and 31% in both. The richness of the permanent sites was 37 species, and that of temporary waters was 23. Thus, nearly 1/5th of the rotifer diversity on this island would have been missed if only permanent habitats were
examined. In a survey of >160 Chihuahuan Desert aquatic habitats (96 permanent; 67 temporary), we (EJW and RLW, unpubl. obs.) identified over 250 rotifer species (ca. 12% of all known monogononts). Species richness varied dramatically between permanent habitats (1–48) and temporary habitats (1–33), with ~10% of species only found in temporary habitats.

### 5.2 Dispersal

Investigation of dispersal and colonization dynamics of temporary habitats has led to the development and testing of the Bass Becking Principle and the Monopolization Hypothesis. The Bass Becking principle of “Everything is everywhere, but nature selects” [103–106] has been...
attributed quite regularly to not only bacteria but also zooplankton, especially rotifers [107]. While many zooplankton species are reported to be cosmopolitan, this feature has been rejected as a characteristic of these taxa; rotifers have a biogeography [108–111].

An important model of regional patterns of species distribution and gene flow is the monopolization hypothesis (MPH). Based on the idea of persistent founder effects and rapid local adaptation [112, 113], the MPH argues that historical colonization events of aquatic systems play

Table 3. Examples of the rotifer biodiversity of temporary habitats

<table>
<thead>
<tr>
<th>Geographic locations</th>
<th>Site description</th>
<th>Diversitya)</th>
<th>Refs.b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Chilwa, Malawi</td>
<td>Periodic drought lake</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>Temperate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asperg, Germany</td>
<td>Ephemeral ditches and pools</td>
<td>10</td>
<td>32</td>
</tr>
<tr>
<td>Mikolajki, Poland</td>
<td>Small astatic ponds (n = 8)</td>
<td>19</td>
<td>78</td>
</tr>
<tr>
<td>Aridland</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chihuahuan Desert (TX, USA)</td>
<td>Ephemeral playa</td>
<td>21</td>
<td>35</td>
</tr>
<tr>
<td>Chihuahuan Desert (TX, USA)</td>
<td>Tinajas (n ~ 10) series of cascading pools</td>
<td>5</td>
<td>15</td>
</tr>
<tr>
<td>River Murray, Australia</td>
<td>Isolated billabongs (n = 13)</td>
<td>18</td>
<td>52</td>
</tr>
<tr>
<td>West Azarbaijan, Iran</td>
<td>Temporary ponds (n = 3)</td>
<td>11</td>
<td>29</td>
</tr>
<tr>
<td>Cold</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Devon Island (NWT, Canada)</td>
<td>Solitary pools (n = 8) that freeze from the bottom up</td>
<td>13</td>
<td>66</td>
</tr>
<tr>
<td>Hyrnebeen Glacier (Spitsbergen)</td>
<td>Cryoconite holes (n = 8)</td>
<td>3</td>
<td>5</td>
</tr>
</tbody>
</table>

a) Bdelloids not included.
b) References: 1, Kalk [37]; 2, Klement [175]; 3, Klimowicz [170]; 4, Walsh, unpubl. obs.; 5, Shiel, per. commun.; 6, Viayeh and Spoljar [172]; 7, Species list, De Smet, per. commun.; 8, De Smet and Beyens [174]; 9, De Smet and Van Rompu [133].

Table 4. Examples of rotifers that were first recorded from temporary waters

<table>
<thead>
<tr>
<th>Speciesa)</th>
<th>Habitat</th>
<th>Location</th>
<th>Refs. b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abrochtha carnivora</td>
<td>Seasonal wetland</td>
<td>Barbados</td>
<td>[1]</td>
</tr>
<tr>
<td>Temperate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lecane herzigi</td>
<td>Roadside pool</td>
<td>Strahan, Tasmania</td>
<td>[2]</td>
</tr>
<tr>
<td>Trichotria buchneri</td>
<td>Creek bed</td>
<td>Cue, Western Australia</td>
<td>[3]</td>
</tr>
<tr>
<td>Aridland</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachionus pinneaus</td>
<td>Rehydrated, dry sediments</td>
<td>River Murray, Victoria, Australia</td>
<td>[4]</td>
</tr>
<tr>
<td>Cephalodella sp. nov.</td>
<td>Rock pools (huecos)</td>
<td>Chihuahuan Desert, TX, USA</td>
<td>[5]</td>
</tr>
<tr>
<td>Hexarthra sp. nov.</td>
<td>Rehydrated, dry sediments</td>
<td>Bonegilla, Victoria, Australia</td>
<td>[6]</td>
</tr>
<tr>
<td>Cold</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Floscularia wallacei</td>
<td>Shallow lake, freezes to the bottom</td>
<td>Bungert Hills, East Antarctica</td>
<td>[7]</td>
</tr>
<tr>
<td>Pentatrocha gigantea</td>
<td>Shallow tundra pools (mos)</td>
<td>Barentsøya, Svalbard</td>
<td>[8]</td>
</tr>
<tr>
<td>Lecane piepelsi</td>
<td>Temporary pond</td>
<td>De Panne, Belgium</td>
<td>[9]</td>
</tr>
<tr>
<td>Lepadella deridderae deridderae</td>
<td>Tundra polygon trench</td>
<td>Point Barrow, Alaska</td>
<td>[10]</td>
</tr>
<tr>
<td>Lepadella d. alaskae</td>
<td>Puddle of submerged moss</td>
<td>Cambridge Bay, Victoria Island, NWT, Canada</td>
<td>[10]</td>
</tr>
<tr>
<td>Lepadella beyensi</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a) Species have been standardized for validity according to Segers [176], but an exhaustive examination of the literature has not been done to determine whether these species have been recorded elsewhere since their original publication.
b) Refs.: 1, Ricci et al. [131]; 2, Koste et al. [177]; 3, Koste et al. [178]; 4, Langley et al. [118]; 5, Schröder et al. [26]; 6, Segers and Shiel [171]; 7, De Smet and Gibson [179]; 8, De Smet [180]; 9, Segers et al. [181]; 10, De Smet [182].
predominant roles in determining genetic structure of present day populations, establishing prioritization effects and thus minimizing potential for new colonists to impact genetic diversity. The MPH attempts to explain the paradox that despite evidence for high dispersal capacity in zooplankton, gene flow often is restricted among populations. However, some workers argue that there is little evidence showing wide and frequent dispersal and that founder effects may confound estimates of gene flow [114, 115]. Thus, Bohonak and Jenkins [115] argue that dispersal and colonization are two separate processes. Both ideas were developed based on the assumptions that aquatic habitats are somewhat temporary over geologic time and that connectivity among sites can be high [116, 117].

Rotifers may disperse among temporary waters by water, wind, and/or animals. Supporting the idea of high dispersal capacity, communities become quickly established in experimental mesocosms whether they are supplemented with sediments containing dormant propagules [118, 119], or not (EJW, per. obs.). One of us (EJW) established six, 67 L mesocosms in the Chihuahuan Desert and followed zooplankton colonization patterns over 9 weeks. All mesocosms were colonized by algae and ciliates (week 1) and rotifers (week 2); 10 rotifer species were found by week 7. No microcrustaceans were found. These results rival those of Holland and Jenkins [120], who report 10 rotifers and two microcrustaceans over 25 weeks. Of the rotifers in the Chihuahuan Desert mesocosms, six were found in nearby natural habitats and six were hatched in a separate study of dried sediments taken from the study site.

Flooding connects habitats that had been cut off by drought, redistributing diapausing embryos among these isolated sites [121]. Thus, large, permanent water bodies can resupply smaller basins that do dry with active animals (e.g., [122–126]). Interestingly, greater rotifer biodiversity can be obtained by rehydrating dry sediments than can be collected from snapshot sampling of active communities of either ephemeral or permanent habitats [127]. More recently Frisch et al. [17] investigated colonization success of zooplankton in 48 newly constructed ponds in Doñana National Park. While these researchers reported that copepod and cladoceran success was positively correlated with relative position, connectivity, and surface area, no significant features were found for rotifer colonists.

### 5.3 Dormant communities

Depending on the system, sediments may hold a large reserve of propagules (i.e., an egg bank), which is critical in re-establishing the rotifer community after drought [121, 127, 128]. Langley et al. [118] compared the rotifer communities that developed in mesocosms to which either sterilized or un-sterilized sediment had been added. Of some 54 species observed in their mesocosms after 35 days of filling, 22% had not been recorded in active water bodies in the area and four were new to science. In another study, Walsh and her colleagues (per. obs.) found that rehydrated sediments from 11 temporary habitats in the Chihuahuan Desert yielded 32 species, seven of which had not been found in surveys of the active habitats.

The factors affecting survival of dormant rotifers in dry sediments include salinity, temperature, and UV light; however, in damp sediments, humidity, microbial activity, and predators also are important and need to be assessed in greater detail. Both bdelloid xerosomes [129] and monogonont diapausing embryos [42] deteriorate over time, although in bdelloids desiccation actually may improve individual fitness up to a point [130]. One of us (HAS) found variation in hatching rates of diapausing embryos obtained from a series of ponds that differ in hydroperiod, and different rates of production and lipid content of diapausing embryos made in the laboratory by brachionidids from these ponds (Table 5). Potentially, hydroperiod may influence the quality and thus viability of diapausing (permeabilizing) diapausing embryos as in [183], then staining with Nile Red as in [184].

<table>
<thead>
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<th>Table 5. Spearman rank partial correlation coefficients (rho) of traits with hydroperiod for Iberian ponds, controlling for salinity</th>
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| Rotifer trait | BSA | CVF | HOY | TIR | TON | TOS | SAL | Rho | p-Value*
| Diapausing embryo hatching (%) | 62 | 47 | 36 | 84 | 17 | 10 | 20 | −0.795 | 0.006
| Diapausing embryo production (total embryos) | 207 | 22 | 133 | 159 | 452 | 857 | 38 | 0.291 | 0.004
| Diapausing embryo lipids (pixel intensity) | 3.9 | 16.0 | 11.9 | 7.6 | 29.0 | 4.7 | 19.4 | −0.265 | 0.005
| Mean values are shown per pond, with standard error in parentheses. BSA, Balsa de Santed; CVF, Laguna del Camino de Villafranca; HOY, Hoya Rasa; TIR, Laguna de Tírez; TON, Poza Norte, Cabanes-Torreblanca Marsh; TOS, Poza Sur, Cabanes-Torreblanca Marsh; SAL, Salobreja. Hydroperiod categories were taken from [42]. Lipids were quantified by first decapsulating (permeabilizing) diapausing embryos as in [183], then staining with Nile Red as in [184].
| *Significant partial correlations (two-tailed). |
of diapausing embryos (e.g., by selecting for more/less maternal investment).

5.4 Species interactions

Rotifer communities of temporary waters have provided model systems in which to characterize types and strengths of species interactions. In particular, temporary wetlands, as well as cryoconitic and phytotelmatic habitats provide simple communities that can be easily sampled, manipulated, and followed.

Abrochthia carnivora rehydrated from sediments collected from a seasonal wetland in Barbados [131] presents an example of a unique type of species interaction that was first characterized in a temporary habitat – carnivory in a bdelloid rotifer. All other bdelloids feed on bacteria, algae, and detritus. Carnivory in this species may be an adaptation to ensure adequate energy acquisition before entering diapause of an unknown duration.

Cryoconitic habitats are subject to diel freeze–thaw cycles in summer and completely freeze during winter. These sites contain communities composed of ciliates, insects, nematodes, rotifers, and tardigrades that function as part of a simple food web along with green algae, diatoms, and heterotrophic bacteria and fungi [132]. Rotifer species found in cryoconite holes on a glacier in Spitsbergen include both bdelloids (Macrotrachela insoluta, Philodina acticorns) and monogononts (Dicanophorus permollis, Encentrum mucronatum, Keratella cochlearis, Keratella quadrata, Lecane closterocerca) [133]. Presence of the voracious carnivore, D. permollis, indicates a tritrophic food web in this otherwise simple ecosystem. In frozen habitats like these, rotifers likely arrive as windblown propagules [97].

In a recent study that combines field and laboratory experiments of invertebrate communities found within the pitcher plant S. purpurea, Knittel [134] shows trade-offs that may promote coexistence, but results varied between the local and regional community scale. At the local level, evidence was found for a trade-off in competitive ability versus predator tolerance; this appeared to be mediated by intrinsic factors of the species such as body size. Yet, he did not observe trade-offs expected to be associated with coexistence for the regional scale.

5.5 Population and community dynamics

A good example of how population and community dynamics change in response to filling cycle is seen in Lake Chilwa [37]. Before Chilwa dried in 1966–1968, three species of rotifer were present mainly in the wet months and only at 1–5% of zooplankton abundance (Brachionus calyciflorus, Keratella tropica, Filinia apoliensis). During drying the water became very turbid, highly alkaline, and extremely saline (>12 000 μS cm⁻¹). Active zooplankton populations declined and, of course, disappeared when the lake dried completely. When the lake refilled the zooplankton community was dominated by K. tropica, which comprised some 50–80% of zooplankton abundance. In the post-filling phase (1969), rotifer diversity increased to include four additional species: Asplanchna brightwellii, F. opoliensis, Filinia sp., and Testudinella patina. Nonetheless, population levels declined, presumably from intense predation by cyclopoid copepods. On the other hand, near the end of a dying event in Lake Meemjageel (Australia) when the water was very turbid and quite warm (~40°C), B. calyciflorus and A. sieboldii dominated the zooplankton, achieving densities >3700 inds. L⁻¹ [135]. However, upon rewetting the zooplankton community recovered slowly, but with a suite of uncommon zooplankton, including Brachionus dichotomus. Thus, both of these lakes seem to exhibit at least a limited hysteresis in the pattern of rotifer species loss and restoration.

Playas have been the subject of ecological studies that follow the population dynamics of the community [24], assess influence of contaminants [39], and discover new species: e.g., Macrotrachela sonorensis [136]. Two extensive studies on species in seasonally flooded depressions have been reported. In South Africa Hutchinson et al. [137] provide a comprehensive survey of the pans and other inland waters, but those data still await a detailed review. In their survey of more than 100 sites in Mongolia, Jersabek and Bolortsetseg [80] list more than 240 taxa in 55 genera, with potentially 16 species being new to science. It is likely that many more new species will be discovered in aridland waters. In two desert playas at Hueco Tanks State Park and Historic Site, Walsh and her colleagues found a total of 45 species, as well as several unidentified bdelloid species. The rotifer community of these sites underwent pronounced seasonal succession, albeit with small population sizes. For example, in one site, Platias quadricornis (found during the entire filled period) and Brachionus quadridentatus were dominant during the summer months, followed by several species during the late summer and early fall (e.g., Lecane quadridentata, Collotheca sp., Epiphanes chihuahuensis, E. dilatata, Euchlanis triquetra, and Squatinella rostrum). Two species were prominent in late fall and early winter (P. quadricornis and Rotoria sp.), followed by dominance of Keratella spp. during winter months (Fig. 1).

Seasonal forest pools that fill in the spring and/or fall are common and important habitat for small vertebrates and some invertebrates (e.g., fairy shrimp), but knowledge of the rotifer community often is limited to a few species such as the bdelloids, P. roseola and Rotaria citrina, and the monogonont, E. senta [11]. Large populations can develop rapidly in these systems, with different species dominating through the hydroperiod. For example, in the temporary...
ponds of an Italian shrubland, Seminara et al. [138] found that *Brachionus urceolaris* and *Filinia terminalis* were common just before the summer drought, but upon rewetting in the fall the pond was recolonized by a community dominated by *B. quadridentatus*. However, this autumnal community collapsed and a different assemblage, comprising *K. tropica*, *P. vulgaris/dolichoptera*, and *Sinantherina socialis*, developed over the winter.

5.6 Adaptations

5.6.1 Frequency of mixis

In most monogonont rotifers, diapausing embryos are the product of sexual reproduction and hence the frequency, duration, and timing of mixis are important determinates of long-term population persistence in temporary habitats. The frequency of mixis has been characterized for a small number of species in lab and field studies. Fussmann et al. [139] reported that offspring produced early or late in a female’s reproductive series had a lower probability of being mictic than those produced by mid-aged females. In this study, no females produced 100% mictic offspring. Smith and Snell [140] in a laboratory chemostat experiment showed that *B. plicatilis* populations subjected to short hydroperiods evolved a higher propensity for sex and dormancy. Interclonal variation in the propensity for mixis was reported in two monogonons (*Epiphanes ukera* and *Rhinoglena frontalis*), where the proportion of mictic daughters ranged from 14 to 50% [141]. In field studies, Schröder et al. [26] reported that the stem females of an undescribed species of *Hexarthra* from rock pools in the Chihuahuan Desert immediately produced mictic females. This feature likely provides a long-term adaptive strategy for a population that lives in ephemeral habitats that may dry up within a few days or weeks after a rain (see Bet-hedging below). In addition, in populations of *B. plicatilis* from ponds of varying hydroperiod in the Iberian Peninsula, diapausing embryo hatching frequency is negatively correlated with habitat permanence ($\rho = -0.795$, $p = 0.006$; Table 5).

5.6.2 Bet-Hedging

*Hexarthra* n. sp. has a life cycle that deviates radically from the norm in its highly ephemeral habitats. In this case, rather than hatchlings from diapausing embryos developing into amictic stem females, $\geq 85\%$ develop as mictic females [26] with males and diapausing embryos.

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appearing within 2 days of filling. Embryonic development rates and time to maturity are quicker in this taxon than in animals from more permanent habitats [26]. These traits are proposed as important bet-hedging strategies for survival of the population, facilitating the production of diapausing stages that can ensure population survival in the event of a dry spell.

5.6.3 Osmoregulation

The defining feature of temporary habitats is the pronounced change they undergo as they dissipate. The habitat may disappear quickly by freezing, or slowly by evaporation, or very slowly by percolation into the ground. In each case, there are concomitant changes in the physical and chemical factors. Addition of large amounts of water to a basin also can quickly alter water temperature, chemistry, and osmotic conditions [99, 142]. In fact, during flashfloods, the volume of an entire pool can be replaced many times over within minutes. Moreover, some spates are capable of scouring a basin [143] or filling it with rock debris (pers. obs.). We do not know much about the ability of rotifers to withstand such rapid changes, although some works have investigated ability to tolerate specific stressors such as salinity shifts.

Green [144] proposed that Asplanchna priodonta osmoregulates after observing individuals increasing or decreasing the contractions rate of their bladders as a function of salinity. Based on reports of the salinity of the habitats in which they are found, Bayly [145] suggested that B. plicatilis, H. fennica, and Hexarthra jenkiniae should be osmoconformers. Further evidence for osmoconforming in B. plicatilis came from studies with a microcryoscope [146]. However, Lowe et al. [147] reported elevated ATP consumption at high salinities and activity of Na+/K+ ATPase as evidence of osmoregulation in B. plicatilis. It is clear that the mechanisms of salinity tolerance need further study.

5.6.4 Desiccation, heat, and UV radiation tolerance

Tolerance to prolonged desiccation, high temperature, and ultraviolet radiation (UVR) as embryonic propagules (monogononts), or anhydrobiotic embryos and adults (bdelloids), is critical to persistence of rotifer populations in ephemeral habitats. This is especially true in desert regions where dormant stages in shallow, dried sediments may be exposed to full sunlight for months with temperatures reaching up to 60°C [148]. Most work on tolerance to these environmental extremes in monogononts has been limited to the B. plicatilis species complex. Smith et al. [149] review existing knowledge on the hsp stress proteins and using a variety of molecular tools show that stress proteins hsp 40, 60, and 70 are required for thermal tolerance in Brachionus manjavacas. Further, Denekamp et al. [150, 151] note that diapausing embryos express genes for low molecular weight hsp. Unlike in other species that enter anhydrobiosis, desiccation tolerance in bdelloid rotifers is not dependent on production of the stabilizing sugar trehalose [84, 152, 153], and in fact several species lack the genes encoding these sugars [84]. Late embryogenesis abundant (LEA) proteins [151, 153] and multiple copies of alpha tubulin [154] appear to be important in desiccation tolerance. In addition, ability to recover from anhydrobiosis is dependent on time and other environmental conditions.

Damaging effects of UVR and presence of protective adaptations have been demonstrated for a variety of invertebrates, including rotifers [155, 156], and are best characterized in bdelloids. In a seminal paper, Gladyshev and Meselson [157] demonstrated that bdelloids have an extraordinary tolerance to ionizing radiation that is probably mediated by DNA repair mechanisms for double stranded breaks. More recently Krisko et al. [158] show that anti-oxidants also are involved in this tolerance. In a recent study on monogononts, it was found that UVR exposure can modulate hsp gene expression in a brachionid species [159]. Yet overall, studies on the effects of UVR on dormant stages are rare [160, 161].

5.6.5 Experimental evolution and rapid adaptation

Although theoretical work has predicted associations of sex and dormancy with ephemeral habitats [162] and field studies have noted correlations of hydroperiod with species’ presence or traits, few experiments have been done to demonstrate casual evolution. However, the ability to maintain long-term semi-continuous or continuous flow-through (chemostat) cultures has been employed to follow evolutionary changes in the laboratory. These studies have revealed loss of sex in constant laboratory cultures [163], associated evolution of mixis with adaptation to heterogeneous environments [164], and suggested the potential for eco-evolutionary dynamics where investment in sex and dormancy involves a feedback with population growth [165]. Rotifers have been proposed as good models for macro- and microevolutionary research [166], and recently permanent and ephemeral laboratory cultures of B. plicatilis sensu stricto were established to experimentally test evolution in response to manipulation of hydroperiod. Over 385 days or ≤ 84 generations (six simulated growth seasons) ephemeral versus permanent cultures evolved to produce greater numbers of diapausing embryos, maintain higher
frequencies of sexual females, and more readily induce mixis [140]. Individuals’ longevity was not affected by hydropereiod, potentially due to the long hydropereiod duration (9 weeks) of ephemeral cultures relative to the short generation time (~4 days).

6 Conclusions and suggestions for further research

Here, we reviewed an assortment of temporary waters, unified by presenting an aqueous habitat for rotifer community development but at times transitioning into an inhospitable terrestrial realm of dried sediment or ice. The majority of temporary waters across the globe have received little attention despite their potential importance in contribution to local and regional biodiversity and in providing ecosystem services. For instance, the vast array of the habitats that occur in desert ecosystems have received little attention by researchers (e.g., [62, 67, 110, 167]). Several quantitative differences exist among temporary water bodies, such as hydropereiod duration and frequency of drying/freezing. Yet, whether these differences result in graded selection pressures (e.g., for dormancy) and/or thresholds exist (e.g., minimal hydropereiod duration necessary for survival) remains unclear. Likewise, qualitative distinctions occur, such as whether the wet phase is broken by desiccation or by freezing. The relative importance of qualitative versus quantitative differences in structuring rotifer communities, and the degree of abiotic and biotic similarity among different hydropereiod categories, warrants further research. What researchers may classify as ephemeral habitat may be nearly permanent in relation to the short life cycles of rotifers. Understanding the selective pressures these environments impose will require careful consideration not only of the abiotic context they present, but also the colonists’ life history. Capacity for rapid evolution clearly exists. However, it remains poorly understood whether species–hydropereiod or trait–hydropereiod correlations primarily are due to survival of just those taxa pre-adapted to these fluctuating habitats, or of local adaptation in situ. Important themes for future work will include synthetic studies to address these questions across a diverse array of temporary habitats and supplement the more commonly investigated types (e.g., seasonal ponds) with those less often investigated (e.g., cryoconite holes), as well as testing the mechanisms underlying patterns in species/trait distributions.

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