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Chapter 7

TEMPORARY STREAMS: THE HYDROLOGY, GEOGRAPHY, AND ECOLOGY OF NON-PERENNIALLY FLOWING WATERS

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ABSTRACT

Temporary streams represent a significant yet understudied and particularly vulnerable portion of river networks. While the vast majority of stream and river research to date has focused on perennial flowing waters, recent work reveals that temporary streams are not only abundant and widely distributed, but also play a significant role in the hydrological and ecological integrity of lotic networks. In this chapter, we seek to summarize the current state of the science of these ubiquitous portions of river networks while simultaneously stressing the need for their future investigation. We begin by defining temporary streams and their hydrology and highlighting their abundance and extent. We then consider the ecological significance of temporary streams, including their role as faunal and floral habitat providers, biogeochemical processors, and connectivity corridors within river networks. The chapter concludes with a discussion of policy issues surrounding temporary streams and the anthropogenic disturbances they face.

INTRODUCTION

Temporary streams are channels that lack surface flow during some portion of the year. Positioned at the interface between fully aquatic and fully terrestrial ecosystems, they are among the most abundant, widely distributed, and dynamic freshwater ecosystems on Earth

[Comin and Williams 1994; Poff 1996; Williams 1996; Larned et al. 2010]. Cumulatively, they account for a significant proportion of the total number, length, and discharge volume of the world's rivers [Dodds 1997; Tooth 2000; Larned et al. 2010]. Temporary streams range in size from the smallest of episodically flowing zero-order rivulets with small drainage basins, to seasonally flowing headwaters, to higher order river reaches that are spatially disconnected at some portion of the year.

Research to date suggests that these temporary waters are not only abundant, but ecologically valuable [Meyer et al. 2003; Nadeau and Rains 2007; Larned et al. 2010], serving as animal and plant habitat, zones of nutrient and carbon processing, and connectivity corridors intimately linked to both the watersheds they drain and the river networks to which they are episodically connected. Despite periodic discontinuities in surface flow, temporary streams are intimately linked - both hydrologically and ecologically - to their watersheds and perennial waters [Cummins and Wilzbach 2005; Nadeau and Rains 2007]. Yet, temporary streams have been "historically neglected" by scientists and society at large [Larned et al. 2010]. They are understudied relative to continuously flowing perennial streams [Robson et al. 2008], poorly mapped [Meyer and Wallace 2001], and faced with numerous anthropogenic disturbances [Dodds et al. 2004; Brooks 2009]. Moreover, it is expected that streams will become increasingly more temporary due to global climate change [Lake et al. 2000; Palmer et al. 2008; Brooks 2009]. Increased awareness and knowledge of their extent and integral ecologic and hydrologic role in river networks should aid in their management and protection. Here, we review the current state of knowledge about temporary stream hydrology, geography, and ecology and demonstrate their essential role within river networks. We review the anthropogenic disturbances they face and the challenges with respect to protecting them.

HYDROLOGY

Hydrology is perhaps the most fundamental driver of physical, chemical, and biological processes in streams and is often considered a "master variable" controlling geomorphology, substrate stability, faunal and floral habitat suitability, thermal regulation, metabolism, biogeochemical cycling, and the downstream flux of energy, matter, and biota [Power et al. 1988; Resh et al. 1988; Poff and Ward 1989; Poff 1996; Poff et al. 1997; Dodds et al. 2004]. Flow magnitude, frequency, duration, timing, and rate of change together characterize a stream's *flow regime* [Poff et al. 1997]. Unlike larger streams and rivers, temporary streams have a flow regime defined by periodic drying and wetting that places them at a unique interface between fully terrestrial and fully aquatic environments. Their position at this terrestrial-aquatic ecotone sets them apart from continuously flowing portions of river networks in that they can support both land- and water- based ecosystem functions and services.

Streams may be defined according to their surface hydrologic flow duration as either perennial or temporary (also known as "non-perennial") [Hansen 2001]. Under normal circumstances, *perennial streams* flow throughout the year, whereas *temporary streams* lack surface flow for some portion of the year. Temporary streams are classified as either intermittent or ephemeral. *Intermittent streams* flow seasonally in response to snowmelt and/or elevated groundwater tables resulting from increased periods of precipitation and/or decreased evapotranspiration. The groundwater table is above the bed of an intermittent stream during some portions of the year (Figure 1c) and below it during others (Figure 1d). During periods of seasonal surface flow, the groundwater table is above the bed, and the intermittent stream receives a baseflow supply whereby it is a *gaining stream* – that is, it gains water from groundwater (Figure 1c). During dry seasons and/or dry conditions, the groundwater table is below the channel bed, and the channel lacks a source for baseflow (Figure 1d). Under these low groundwater table conditions, the intermittent channel is a *losing stream* – that is, it loses water to groundwater (Figure 1d). *Ephemeral streams* are those that only flow during and in immediate response to precipitation events. The groundwater table is situated below the streambed of an ephemeral stream throughout the entire year such that the channel never receives groundwater discharge and, in turn, lacks a baseflow source (Figure 1e,f). As a result, ephemeral streams are always losing streams.

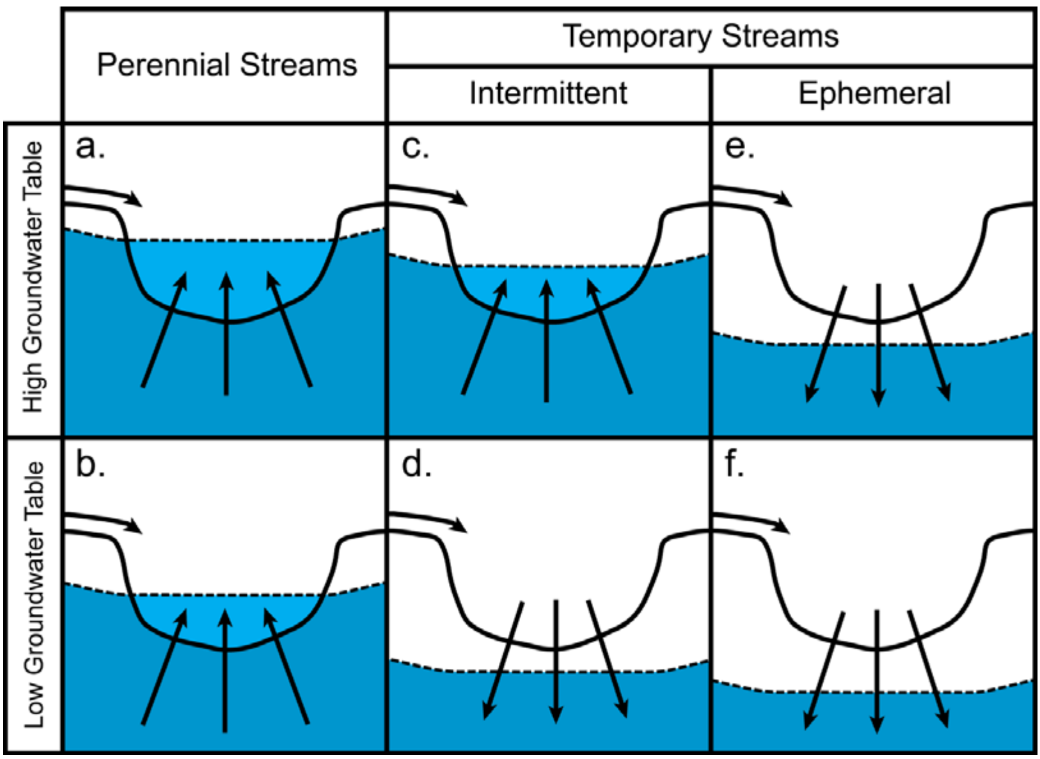

Figure 1. Channel cross-sectional schematic showing perennial, intermittent, and ephemeral streams under high and low groundwater table conditions. Dashed line indicates groundwater table elevation. Arrows indicate surface water and groundwater flowpaths. a) Perennial – High Groundwater: gaining stream. b) Perennial – Low Groundwater: gaining stream. c) Intermittent – High Groundwater: gaining stream. d) Intermittent – Low Groundwater: losing stream. e) Ephemeral – High Groundwater: losing stream. f) Ephemeral – Low Groundwater: losing stream.

Temporary streams may also be spatially discontinuous where surface water is present at some reaches of an individual tributary, but absent at others. The result is a pattern of longitudinal surface water patchiness along the tributary. Such fragmentation may result from drying and subsequent hydrologic isolation of pools along a tributary or downwelling portions of the streambed where all surface flow is subducted to subsurface flow, or *hyporheic*, pathways before re-emerging in upwelling zones at some distance downstream. Drying in a temporary stream with a pool-riffle geomorphology begins with reduced flow through the reach. As drying persists, water levels become lower, surface flow ceases in riffles altogether, and a series of separated pools results. Depending on the severity of drying as well as depth of pools, surface water may be lost entirely [Labbe and Fausch 2000] (Figure 2). Longitudinally isolated pools are especially common in arid climates and regions defined by strong seasonal wet and dry periods. Anthropogenic groundwater abstraction for municipal, agricultural, and industrial use may also lead to lowered regional groundwater tables and subsequent longitudinal isolation of pools along rivers [Dodds et al. 2004]. Even in the absence of surface flow, temporary streams may contain hyporheic flowpaths that serve as habitat refugia from drying, zones of biogeochemical processing, and hydrologic connections to downstream waters.

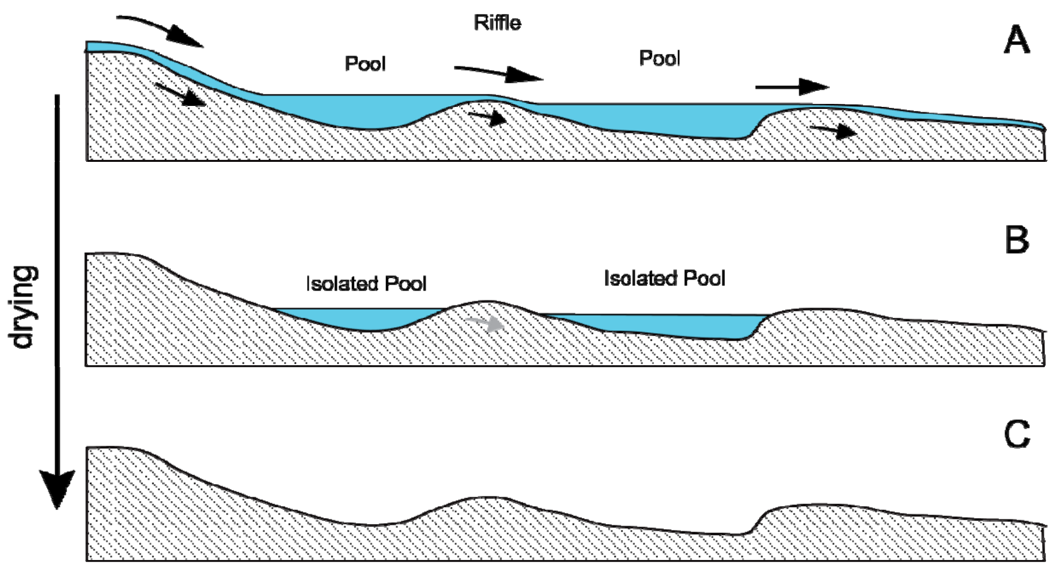

Figure 2. Contraction of a stream reach under increasingly dry conditions. Arrows indicated surface and groundwater flowpaths. A) Surface hydrologic connectivity exists throughout the reach such that pools are connected via riffles. B) As drying persists, riffles dry and pools contract until they are geographically isolated. C) If drying persists long enough, all surface water may be lost to either groundwater reserves or evapotranspiration.

GEOGRAPHY

Abundance and Extent

Temporary streams are among the most abundant, widely distributed, and dynamic freshwater ecosystems on Earth [Comin and Williams 1994; Poff 1996; Williams 1996; Larned et al. 2010]. Collectively, they account for a significant proportion of the total number, length, and discharge volume of the world's rivers [Dodds 1997; Tooth 2000; Larned et al. 2010]. While they are most abundant in arid and semi-arid regions, temporary streams are also commonly found throughout the globe between 84 deg N and 84 deg S latitude [Larned et al. 2010].

Ephemeral and intermittent streams are often positioned at the headwaters of river networks [Dodds et al. 2004] (Figure 3). Headwaters are formed by watersheds draining small parcels of land and, in turn, small volumes of water. As a result, headwaters are more susceptible to drying than downstream reaches because they have smaller drainage areas with less recharge potential for baseflow maintenance [McMahon and Finlayson 2003; Fritz et al. 2008]. Moreover, headwater catchments are often less pervious than downstream portions of watersheds, in turn resulting in minimal storage capacity to maintain baseflow [Burt 1992] and subsequent formation of temporary streams [Dodds et al. 2004; Levick et al. 2008; Brooks 2009] ranging from small ephemeral rills and gullies to larger, more well-developed intermittent channels. A study in Chattahoochee, Tennessee (USA) found, for instance, that 78% of the stream reaches within a watershed were headwaters, and that a majority of those headwaters were temporary [Hansen 2001]. In temperate regions, summer drought conditions can result in "summer-dry" headwaters. With increased precipitation and/or decreased evapotranspiration, dry headwaters rewet and account for a substantial portion of the drainage network. In fact, the temporary portion of river networks may often exceed the length of permanently flowing reaches [Dieterich and Anderson 1998].

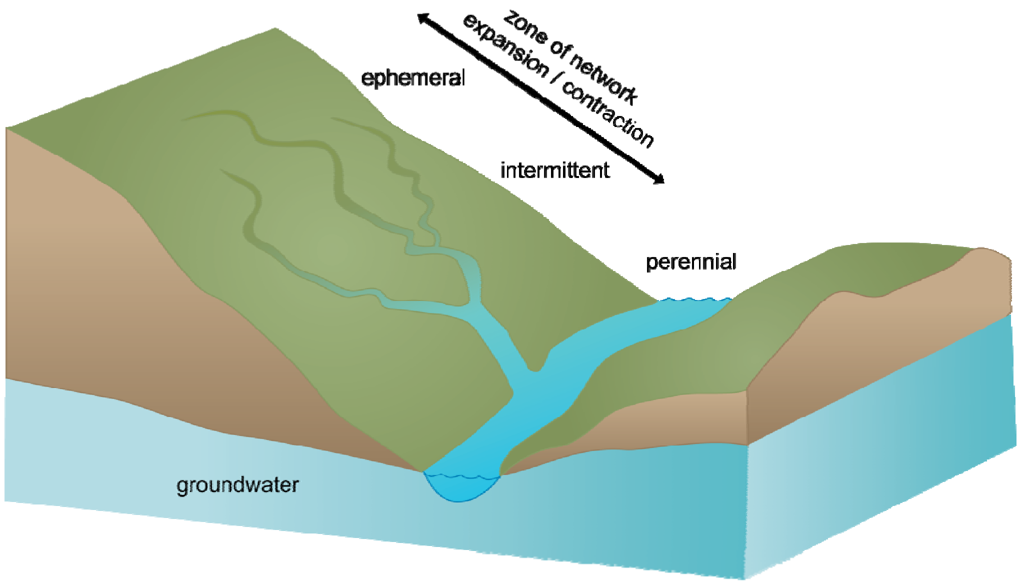

Figure 3. Typical transition from temporary to perennial streams at the headwaters of a river network. Ephemeral and intermittent reaches are a zone of network expansion under wetting conditions and contraction under drying conditions. [Modified from symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/), University of Maryland Center for Environmental Science].

Headwater rewetting results from a combination of increased soil saturation, shallow subsurface flow, a general rise of the groundwater table, and subsequent expansion of the active drainage network. Gomi et al. [2002] refer to the headwaters of river networks as "transitional channels." The transitional channels are zones of drainage network expansion and contraction under wet and dry conditions respectively (Figure 3). In mesic regions with a more continuously wet climate, transitional channels may be short, ephemeral rills that flow in immediate response to heavy rain events. The length of individual temporary channels is likely to be much longer in more xeric climates, including desert and prairie stream networks [Dodds et al. 2004].

Although a global inventory of temporary streams has not yet been compiled, several national and regional estimates exist and collectively underscore their abundance. Headwater streams cumulatively account for the greatest portion – perhaps as much as 80% - of stream length within river networks [Leopold et al. 1964; Meyer et al. 2003; Lowe and Likens 2005]. In the United States (excluding Alaska), it is estimated that ephemeral and intermittent streams, many of which are located at the headwaters, total 3,200,000 km of stream length, or nearly 60% of cumulative stream length [Nadeau and Rains 2007]. In the arid and semi-arid southwestern United States, temporary streams account for > 80% of the entire network [Levick et al. 2008]. Over 50% of the Australian mainland is drained by temporary streams [Williams 1983] (Figure 4), much of which are located in the southeast of the continent [Lake et al. 1986]. Due to the marked wet/dry seasonal precipitation pattern in the Mediterranean climate, nearly half of the river network in Greece is temporary [Tzoraki and Nikolaidis 2007]. With respect to specific watersheds, Hansen [2001] found that > 70% of the Chattooga River network (southeastern USA) is temporary, and Doering et al. [2007] estimated nearly 50% of the Tagliamento River drainage (northeastern Italy) does not flow continuously.

Figure 4. Brachina Creek, Flinders Ranges (South Australia) – one of countless temporary streams draining the Australian mainland. [Photo: A. Boulton].

In addition to headwater channels of river networks, some higher order branches – perhaps 4th and even 5th order [McBride and Strahan 1984] – exhibit temporary surface flow. Not surprisingly, temporary streams are common in more arid climates (e.g., desert and prairie streams) or regions with a pronounced dry season (e.g., streams in Mediterranean climates) [Gomez et al. 2009]. As a region enters a period of drought or a dry season, surface water is lost to both evapotranspiration and groundwater storage. The result is a retreating stream "front" characterized by longitudinally discontinuous surface flow [Larned et al. 2010]. Riffles dry and pools contract such that they become geographically separated [Fisher et al. 1982; Stanley et al. 1997] (Figure 2). Upon return of wetter conditions – a result of increased precipitation, decreased evapotranspiration, decreased groundwater abstraction, or some combination therein – an advancing stream "front" reconnects the previously fragmented tributary. In arid regions, a single large rain event can rapidly reconnect the network [Gomez et al. 2009].

Mapping

It has long been recognized that commonly used stream maps grossly underestimate actual stream length [Mueller 1979; Meyer and Wallace 2001]. The scale at which drainage networks are mapped can dramatically affect the total number and length of streams that are identified. With decreasing map resolution, fewer and only increasingly larger streams tend to be indicated [Miller et al. 1999]. Temporary streams are often individually small and therefore the most likely to be omitted as map resolution decreases [Roy et al. 2009]. Meyer and Wallace [2001], for instance, showed that the total stream length within the Coweeta Creek watershed (North Carolina, USA) on a coarse resolution 1:500,000 scale topographic map was only 3% of the length indicated on a standard United States Geological Survey (USGS), higher resolution 1:24,000 scale map. They also found that lower order streams (i.e., headwater, intermittent, and ephemeral streams) were more likely than higher order perennial channels to be unmapped at the coarser resolution.

Yet even 1:24,000 scale maps – the most common source of drainage network data in the United States - may still omit the uppermost reaches and thereby significantly underestimate total stream length within a watershed. Studies in temperate North America have shown that 1:24,000 scale maps can exclude nearly all temporary streams, resulting in >70% omission of actual stream length [Hansen 2001; Heine et al. 2004; Roy et al. 2009]. Studying the Arroyo de los Frijoles catchment in the arid southwestern United States, Leopold et al. [1964] found that contour patterns resulted in a network with nearly 260 first order channels, yet 1:24,000 scale maps identified no stream channels within the entire watershed. The researchers further identified 86 ephemeral channels in just *one* of the first order streams by physically walking its length [Leopold et al. 1964].

Ecological Significance

Because temporary streams exist at an interface between aquatic and terrestrial ecosystems they represent an "intimate ecological linkage" between the stream and its watershed [Cummins and Wilzbach 2005]. They provide valuable habitat to a wide variety of plant and animal species and function as biogeochemical hot spots that retain, process, and transform carbon, nutrients, and particulates. They are hydrologically and ecologically linked to perennial and other temporary waters with which they exchange matter, energy, and organisms.

Habitat Provision

It has long been recognized that temporary streams support a wide diversity of life [Stehr and Branson 1938]. Positioned at a terrestrial-aquatic ecotone, they provide unique habitat [Meyer et al. 2007]. Fauna and flora, both terrestrial and aquatic, have developed adaptations and life histories to cope with these hydrologically dynamic reaches where habitat can shift rapidly from high velocity, well-oxygenated riffles to stagnant, isolated pools to completely dry streambed and back. Among the many factors controlling biological communities in temporary streams, patterns of flow may be the most important [Poole et al. 2006]. Both animals and plants are faced with periodic and often rapid disappearance and reappearance of vast areas of habitat in streams that alternate between wet and dry states.

ANIMAL HABITAT

Temporary streams support a variety of fauna including macroinvertebrates, fishes, amphibians, and streamside mammals, reptiles, and birds. Whether serving as sites of oviposition, spawning, rearing, refugia from drying, or dietary hot spots, temporary streams harbor a wide diversity of animal life. While these channels undoubtedly harbor a rich diversity of micro- and meiofauna (e.g., microbes, biofilms, rotifers, crustaceans), here we focus our discussion on macrofauna habitat provision and adaptations in temporary streams.

Macroinvertebrates

While macroinvertebrate abundance and taxa richness are generally lower in ephemeral and intermittent streams relative to permanent waters [Clifford 1966; Williams and Hynes 1976b; Williams 1996; but see Flinders and Magoulick 2003], temporary streams may also support rare or unique species [Dieterich and Anderson 2000]. Lower species richness is widely attributed to the more extreme conditions and variable habitat found in temporary streams [Boulton and Suter 1986] and may also be related to reduced aquatic habitat area as the result of drying (i.e., species-area effects) [Lake 2000]. Studying stream intermittency and macroinvertebrate assemblage diversity in the Great Plains (central USA), Fritz and Dodds [2005] developed a stream harshness index based upon a suite of hydrologic flow regime variables. They found that harshness indices were high in intermittent streams, low in perennial streams, and negatively related to macroinvertebrate diversity and species richness [Fritz and Dodds 2005].

Although they lack continuous surface water, temporary streams may harbor robust and/or endemic aquatic or semi-aquatic macroinvertebrate communities [Feminella 1996; Dieterich and Anderson 2000; Stout and Wallace 2003; Robson et al. 2005; Williams 2005; Collins et al. 2007] and often share a common pool of macroinvertebrate taxa with perennial streams [Boulton and Lake 1992, Feminella 1996, del Rosario and Resh 2000, Shivago 2001, Smith et al. 2003, Collins et al. 2007, Arscott et al. 2010]. Moreover, some studies have found that temporary streams harbor a unique set of macroinvertebrate taxa not found in nearby perennial reaches [Feminella 1996; Dieterich and Anderson 2000]. Other studies, however, have found little or no difference between temporary and perennial stream macroinvertebrate communities [Beugly and Pyron 2010; Robson et al. 2008].

Why do some temporary streams boast uniquely adapted macroinvertebrate assemblages while others do not? One study attributed the lack of temporary stream-adapted macroinvertebrates to a lack of nearby permanent surface water refugia, length of drying period, and a lack of climate predictability [Arscott et al. 2010] whereby an unpredictable pattern of intermittency renders adaptation to drying unlikely. Several studies have reported general similarities between perennial and temporary streams with a limited number of taxa endemic to temporary reaches [Shivago 2001; Williams et al. 2004; Beche et al. 2006; Storey and Quinn 2008; Arscott et al. 2010]. It seems likely that rather than a duality where temporary stream communities are either unique to or largely shared with perennial streams, there exists a gradient of similarity depending on a variety of local conditions including hydrology, geomorphology, climate, competition, and predation.

Many macroinvertebrates - especially insects - in temporary stream reaches possess physiological and/or behavioral traits allowing them to persist even after surface flow has ceased [Williams and Hynes 1977; Towns 1985; Williams et al. 2004; Bonada et al. 2006; Storey and Quinn 2008]. Survival strategies used by temporary stream dwelling macroinvertebrate taxa are numerous, and Williams [1998] provides an excellent review of macroinvertebrate persistence strategies in temporary streams. Here, we discuss two strategies that are particularly important: 1) survival in refugia and subsequent colonization and 2) resistance to desiccation.

Survival in Refugia and Colonization

There are numerous permanent water refugia that macroinvertebrates use to persist when surface water disappears from stream channels. For example, some insects as well as miofaunal invertebrates have the ability to burrow down to the hyporheic zone [Stanford and Ward 1988; Palmer et al. 1992; Collins et al. 2007], though this may not be a viable survival tactic if drying occurs too rapidly and/or bed sediments are too coarse for burrowing [Boulton and Stanley 1995]. Additionally, isolated pools represent particularly valuable refugia from stream drying [Boulton 1989]. Special adaptations to survival in isolated pools may be required because these habitats often become depleted in dissolved oxygen over time. Researchers studying isolated pools along arid stream reaches have found chironomid larvae (non-biting midges) that utilize hemoglobin to tolerate low oxygen conditions [Williams and Hynes 1976; Boulton 1989; Stanley et al. 1994]. Some Ephemeroptera (mayflies) taxa are equipped with specialized gills to tolerate low oxygen levels [Boulton 1989; Miller and Golladay 1996]. Other macroinvertebrate taxa found in oxygen-depleted temporary streams can directly breathe atmospheric air. These include Coleoptera (beetles) [Boulton 1989; Stanley et al. 1994; Williams 1998], Hemiptera (true bugs) [Stanley et al. 1994; Williams 1998], and Tipulidae (craneflies) [Williams 1998].

Shorter cohort production intervals and rapid larval development enabling adults to disperse before severe channel drying allow macroinvertebrates to use nearby perennial waters as spatial refugia or terrestrial life stages as temporal refugia. The Plecopteran (stoneflies) *Riekoperla naso* accomplishes this by rapidly developing from an egg to a mature flying adult [Towns 1985]. Studying macroinvertebrate assemblages in a seasonally intermittent stream in the Great Plains (central USA), Fritz and Dodds [2004] identified the Ephemeropteran (mayflies) *Fallceon quilleri*, having an 18-day life cycle, and the chironomid (non-biting midges) *Cricotopus* sp., having a 6-day life cycle. Temporary stream dwelling Hemiptera (true bugs) larvae may mature quickly and abandon temporary reaches as flying adults [Williams and Hynes 1976]. Macroinvertebrates using such refugia can re-colonize temporary reaches quickly after surface flow resumes. Intermittent prairie stream-dwelling macroinvertebrate communities have been observed to reappear within one week of resumed surface flow [Fritz 1997].

Boulton [1989] sampled eight over-summering refuges including dried leaf litter, crayfish burrows, receding pools, a nearby permanent lake, rotting wood and bark, dry substrate from riffles and pools, and the hyporheic zone. Of the refugia surveyed, a majority of taxa were found in isolated pools, yet both pool and riffle substrata also harbored significant proportions of the total taxa. Overall, nearly 50% of taxa recorded were found in areas lacking freestanding water [Boulton 1989].

Resistance to Desiccation

Another adaptation to stream drying is the use of desiccation resistant life stages [Williams and Hynes 1976b; Williams 1996]. Evidence for survival as dormant eggs has been found for Diptera (flies) [Williams and Hynes 1976; Stubbington et al. 2009], Ephemeroptera (mayflies) [Boulton 1989], and Plecoptera (stoneflies) taxa [Dieterich and Anderson 1995]. Towns [1985] identified leptocerid caddisflies, which are known for depositing terrestrial egg masses, in an Australian temporary stream. Smith et al. [2003] found certain Trichoptera (caddisflies) taxa were able to aestivate as adults during dry periods. Boulton [1989] found that dormant water penny beetles under dry rocks became active after being submerged in water. Plecoptera (stoneflies), Trichoptera (caddisflies), and Ephemeroptera (mayflies) taxa may persist as embryos in dry streambeds, and some oligochaetes survive dry conditions as cysts [Williams and Hynes 1976]. Some chironomid (non-biting midges) taxa can survive drought in desiccation-resistant cocoons [Griswold et al. 2008].

Drought intolerant macroinvertebrates unable to locate viable refugia during dry conditions, however, may die and provide carbon and nutrient subsidies to riparian consumers, thereby linking temporary stream and terrestrial ecosystems [Williams 1987].

Fishes

Streams that lack surface water for some portion of the year may not seem like ideal habitat for fish species. However, when temporary reaches of a river network rewet, flowpaths re-emerge and allow for fish passage into once fragmented or disconnected segments. Under these conditions, fishes are able to migrate from perennial waters into newly accessible habitats, including floodplains and temporary reaches, where dietary resources may be largely untapped, competition can be low, and conditions amenable for spawning and juvenile rearing may exist [Erman and Leidy 1975; Erman and Hawthorne 1976; Hartman and Brown 1987; Junk et al. 1989; Dodds et al. 2004; Wigington et al. 2006; Colvin et al. 2009]. Murdock et al. [2010] observed large schools of fish inhabiting recently re-connected pool habitats in an intermittent portion of a prairie stream (Kings Creek, Kansas, USA) only 3 days after being reconnected via surface flow to a perennial reach. In Sycamore Creek (Arizona, USA), Stanley [1993] found that longfin dace (*Agosia chrysogaster*) built nests earlier in the breeding season and in greater numbers in recently rewetted intermittent stream reaches relative to perennial reaches, thereby suggesting a preference for the temporary reaches. Wigington et al. [2006] found that coho salmon (*Oncorhynchus kisutch*) smolts overwintered in intermittent reaches and were larger than their counterparts that overwintered in perennial reaches or river mainstems. Everest [1973] and Kralik and Sowerwine [1977] also found that intermittent streams often serve as critical refugia for juvenile salmonids during periods of high winter discharge in Pacific Northwestern (USA) streams.

In the upper Williamette River valley (Oregon, USA), agriculture and river regulation have reduced river floodplains to intermittent watercourses. Although these temporary waters are largely the result of anthropogenic modification of the watershed and stream network, 13 fish species – 90% of which were native – were found to inhabit them [Colvin et al. 2009]. Moreover, newly hatched and juvenile fishes were found in the intermittent streams, suggesting these seasonally available reaches offered conditions suitable for spawning and rearing [Colvin et al. 2009]. Yet, Colvin et al. [2009] also found that intermittent stream fish species richness decreased as distance of the intermittent stream to the closest perennial reach increased, suggesting that sites more distant from perennial waters may be less suitable fish habitat. Fish may take anywhere from hours to weeks to colonize newly re-wetted temporary stream reaches, largely depending on the distance of the temporary water to a permanent source [Larimore et al. 1959; Dodds et al. 2004]. Temporary stream reaches closer to perennial waters are likely to be wetter longer and more easily accessed upon wetting and later abandoned upon drying.

Streams in the Great Plains region of the United States represent particularly harsh environments with rapid transitions between flooding and drying [Dodds et al. 2004]. Fishes within these temporary streams are adapted to a harsh hydrologic flow regime and can migrate to permanent waters, reproduce rapidly, and persist in isolated pools with poor water quality [Pauloumpis 1958; Labbe and Fausch 2000]. Research has shown that fishes in isolated pools are able to withstand low dissolved oxygen concentrations and elevated water temperatures up to nearly 40 deg C [Erman and Leidy 1975; Mundahl 1990]. Fishes may also survive drought conditions by migrating downstream to perennial reaches [Harrel et al. 1967]. Fishes surviving in perennial stream reaches and/or pools readily re-colonize temporary reaches when surface water connectivity resumes [Reeves 1979].

Amphibians

As their name implies, amphibians (*amphíbios [Greek]: amphi = both, bio = life*) inhabit both land and water. Stream reaches alternating between wet and dry states can therefore serve as ideal habitat for animals adapted to a combination of terrestrial and aquatic life. Temporary headwaters may provide ideal habitat for salamander breeding where episodic flow results in the lack of significant fish populations and, in turn, decreased resource competition and predation pressure [Wilkins and Peterson 2000]. Supporting this, spring salamanders (*Gyrinophilus porphyriticus*) (Figure 5A) and two-lined salamanders (*Eurycea bislineata*) (Figure 5B) have been found in greater abundances in fishless headwater, albeit perennial, streams than in perennial streams with predatory fishes [Barr and Babbitt 2002; Lowe and Bolger 2002]. Wilkins and Peterson [2000] found fishless, non-channelized spring-fed seeps in the Pacific Northwestern United States supported both larval and adult Columbia torrent salamanders (*Rhyacotriton kezeri*) (Figure 5C). In a study of over 30 perennial and intermittent streams in northern California (USA), coastal giant salamanders (*Dicamptodon tenebrosus*) and black salamanders (*Aneides flavipunctatus*) were found to be significantly more abundant along intermittent stream reaches which were shaded, damp, and hydrologically disconnected from perennial sites [Welsh et al. 2005]. Collectively, these conditions result in ideal sites for egg deposition and predator avoidance.

Figure 5. Examples of salamander species that may be found in either temporary streams or fishless perennial headwaters. A) Spring salamander (*Gyrinophilus porphyriticus*) [Photo: J. Butler] B) Northern two-lined salamander (*Eurycea bislineata*) [Photo: M. Jennette] C) Columbia torrent salamander (*Rhyacotriton kezeri*) [Photo: M. Leppin].

Anurans, like salamanders, tend to inhabit temporary stream reaches for both predator avoidance and dietary resources. In an intermittent stream in west-central Kentucky (USA), pickerel frog (*Rana palustris*) and American toad (*Bufo americanus*) females were found to selectively oviposit in areas where few if any fishes were present [Holomuzki 1995]. Moreover, tadpoles of both species reduced their activity in the presence of fishes by detecting fish chemical cues and preferentially inhabited areas of the stream most inaccessible to swimming fishes (e.g., channel margins and isolated pools) [Holomuzki 1995]. Inger and Colwell [1977] compared distributions of anuran species in perennial and temporary forested streams in northeastern Thailand and noted that amphibians inhabited temporary sites in significantly greater numbers relative to permanent reaches. They also found that certain frog species (e.g., *Rana nigrovittata* and *Rana pileata*) were essentially confined to small intermittent streams [Inger and Colwell 1977]. In a study of algal quality as a dietary resource in perennial and temporary Australian streams, Peterson and Boulton [1999] found that tadpoles were better able to digest algae from newly rewetted temporary reaches, suggesting a higher quality of algal dietary resources in temporary versus permanent waters.

Streamside Mammals, Birds, and Reptiles

In addition to temporary channels themselves, riparian zones along ephemeral and intermittent streams may provide habitat and dietary resources for mammals, birds, and reptiles. When temporary streams dry, isolated pools often result. Fragmentation of stream reaches into pools effectively traps and increases the density of aquatic organisms including invertebrates, amphibians, and fishes [Boulton and Lake 1992]. As a result, pools become dietary hot spots where food may be obtained at minimal energy cost by riparian mammals, birds, and snakes [Metzger 1955; Tramer 1977; Kephart 1982; Dowd and Flake 1985].

The corridors of temporary streams may also serve as preferential edge habitat for a number of species. In the xeric southwestern United States, for instance, it is estimated that 80% of all animals use temporary stream riparian habitat and/or dietary resources at some life stage, and that greater than 50% of breeding bird species nest primarily in temporary stream riparian habitats [Krueper 1993].

Seidman and Zabel [2001] found that intermittent portions of a California (USA) stream network supported similar amounts of bat activity as perennial reaches. Similarly, Ozark big-eared bats (*Plecotus townsendii ingens*) were found to forage heavily along intermittent streams in Oklahoma (USA) [Clark et al. 1993]. Sonoran mud turtles (*Kinosternon sonoriense*) were found to be thriving alongside intermittent mountain stream corridors in New Mexico (USA) [Stone 2001]. Birds, including red-tailed hawks (*Buteo jamaicensis*) and Gila woodpeckers (*Melanerpes uropygialis*), depend on ephemeral stream riparia in arid Arizona (USA) for nesting sites found only in these terrestrial-aquatic interfaces [Johnson and Lowe 1985].

PLANT HABITAT

As well as providing valuable wildlife habitat, temporary streams and their riparia harbor substantial floral communities, particularly in arid or semi-arid regions. Streambed and streamside vegetation plays a significant role in temporary stream ecosystem structure and function. Within-channel and riparian vegetation which are both heavily influenced by flow regime [Poff et al. 1997], provide channel and bank roughness, buffer high flows, stabilize banks, mitigate wind and water erosion, and trap particulates [Levick et al. 2008]. Because temporary streams generally have a larger channel edge-to-width ratio than perennial channels, the proportion of the streambed and riparian zone that can be colonized by vegetation is often greater in temporary reaches compared to those that flow year-round [Fritz et al. 2006].

In semi-arid and arid regions, temporary streams and their riparia are often the only places in the watershed with soil moisture levels necessary to support a substantial plant community. As such, ephemeral and intermittent stream corridors may be hot spots of plant diversity and abundance relative to their watersheds [Warren and Anderson 1985]. Studying summer dry streams in northern California (USA), Waters et al. [2001] found that the mean number of plant species in the herbaceous layer along channels as narrow as 0.9 to 1.3m was significantly greater than the mean in upland sites. Temporary stream channels themselves can also be zones where terrestrial plants can establish. McBride and Strahan [1984] found that woody species including willow (*Salix* sp.), Fremont cottonwood (*Populus fremontii*), and mule fat (*Baccharis viminea*) readily established in gravel bars in a seasonally intermittent stream in northern California (USA). However, flow regime extremes of summer drought and channel-scouring winter floods led to plant mortality and loss on the gravel bars [McBride and Strahan 1984].

Temporary streams and riparia may also maintain diverse soil seed banks and support unique plant species and high plant diversity. The seed banks of temporary streams in arid regions may support wetland plant communities during portions of the year when moisture levels are sufficient for hydric species [Brock and Rogers 1998; Goodson et al. 2002; Stromberg et al. 2005; Capon 2007; Stromberg et al. 2009]. Studying the species composition of perennial and temporary stream seed banks in the Hassayampa River (Sonoran Desert, Arizona, USA), Stromberg et al. [2009] found that an ephemeral site nearly 50km from the closest downstream perennial reach harbored hydric seeds. Stromberg et al. [2009] also found that some xeric species were endemic to ephemeral but not perennial portions of the Hassayampa river network. In a study of the spatially intermittent Cienega Creek (Sonoran Desert, Arizona, USA), Stromberg et al. [2009b] found that during wetter portions of the year, ephemeral reaches boasted vegetative species richness levels equal to and sometimes greater than those in perennial reaches. But, a similar Sonoran Desert study found that as stream flows became more intermittent, diversity and cover of herbaceous species along the channel declined [Stromberg et al. 2007]. Studying moss and liverwort distributions in forested headwater stream networks throughout the United States, Fritz et al. [2009] found a general pattern of greater species bryophyte richness in temporary streams relative to those that flowed year-round.

As flow regime shifts from perennial to temporary, vegetation composition shifts toward increasingly drought-tolerant species, vegetative cover declines, trees give way to shrubs, and canopy height and cover decline [Leenhouts et al. 2006; Stromberg et al. 2007]. Working in temporary streams in the Sonoran Desert (Arizona, USA), Stromberg et al. [2005] studied the response of streamside herbaceous vegetation to changes in stream flow permanence. They found that streamside herbaceous cover and species richness declined continuously across gradients of flow permanence during the early summer dry season, and that composition shifted from hydric to mesic species at sites with more intermittent flow [Stromberg et al. 2005].

Biogeochemical Cycling

The biogeochemical functions of temporary streams include cycling of elements and compounds, particle retention, and organic matter transformation and transport [Levick et al. 2008]. Biogeochemical cycling occurs primarily through chemical transformations mediated by redox potentials. Reduction and oxidation reactions are governed by the soil profile, wind, and hydrology [Brinson et al. 1995]. As active zones of cyclical wetting and drying, temporary stream sediments are marked by alternating anoxic and oxic periods and, in turn, alternating reducing and oxidizing conditions. The pattern of temporary stream intermittency (i.e., the timing, duration, and frequency of surface flow) is likely to govern many in-stream processes, particularly biogeochemical rates.

Biogeochemical “hot spots” are areas that show disproportionately high reaction rates relative to the surrounding matrix. “Hot moments” are short periods of time that show disproportionately high reaction rates relative to longer intervening time periods [McClain et al. 2003]. Wetting-drying cycles create hot spots and hot moments [McClain et al. 2003] and have been shown to increase nitrate loss in soils [Patrick and Wyatt 1964; Reddy and Patrick 1975; Tanner et al. 1999; Eaton 2001; Venterink et al. 2002] via a coupled nitrification-denitrification process. Aerobic soils present during dry conditions promote nitrification of ammonia [Qiu and McComb 1996]. Under saturated conditions, soils become anaerobic, nitrate delivery to sediment microbial communities is increased, and the nitrate substrate is reduced via denitrification [Holmes et al. 1996]. Baldwin and Mitchell [2000] have observed this dry–wet / nitrification–denitrification coupling in river floodplains, and Pinay et al. [2007] observed high denitrification rates in a European floodplain rewetted via rainfall and flooding following a dry period. Given their cyclic dry–wet nature, temporary stream sediments are likely to function similarly to episodically inundated floodplains and prove to be biogeochemical hot spots undergoing hot moments where microbial respiration and denitrification rates are enhanced. While literature is sparse on how patterns of stream intermittency govern such rates, increased denitrification rates have been observed during high moisture conditions in temporary streams [Fisher et al. 2001; Rassam et al. 2006].

Re-wetting of dry soil can kill up to 50% of that soil’s microbial biomass via osmolysis [Kieft et al. 1987], in turn resulting in release of carbon and nutrients [Marumoto et al. 1982]. Shortly after this initial loss of soil microbial biomass, water, carbon, and nutrient availability may then stimulate rapid increases in microbial biomass [Kieft et al. 1987] and microbial processing (e.g., N mineralization, nitrification, denitrification) [Davidson et al. 1990; Fisher and Whitford 1995].

Temporary streams may also function as zones of carbon storage and processing [Towns 1985; Dieterich and Anderson 1998; Halwas and Church 2002; Acuna et al. 2004]. At the most distal branches of river networks, headwater temporary streams have a small average width and, in turn, significant canopy cover and subsequent allochthonous organic matter loading [*sensu* Vannote et al. 1980]. Shallow water, low stream power, and a generally high number of in-channel retentive structures can lead to increased sediment retention in temporary reaches [Dieterich and Anderson 1998]. Sediment retention can in turn trap organic matter via burial [Brinson et al. 1995], particularly in channels dominated by fine sediments [Herbst 1980; Metzler and Smock 1990]. Furthermore, organic matter decomposition rates within temporary streams are often slow relative to breakdown rates in perennial streams [Tate and Gurtz 1986; Fritz et al. 2006]. Slow rates of decomposition are due in part to periods of desiccation [Tate and Gurtz 1986], low microbial growth rates during dry conditions [Witkamp and van der Drift 1961], negligible or no physical breakdown of organic matter under low or no flow conditions, and reduced macroinvertebrate shredder densities [Kirby et al. 1983; but see Hill et al. 1988]. Significant allochthonous loading coupled with high retention and low decomposition rates result in the buildup of in-stream organic matter. Dry seasons or drought conditions have resulted in significant organic matter buildup in temporary streams [Larned 2000; Acuna et al. 2004].

Large standing stocks of benthic organic matter (BOM) may fuel heterotrophic activity when channels rewet [von Schiller et al. 2008]. Organic material stored in small streams can be broken down and transformed into forms more bioavailable to biota in perennial downstream waters [Richardson et al. 2005]. Although coarse particulate organic matter

(CPOM) may accumulate during dry periods, temporary streams characterized by seasonal flow may actively flush CPOM standing stocks downstream, especially if flow resumes rapidly [Gurtz et al. 1988; Hill et al. 1992; Acuna et al. 2004]. In addition to flood-induced flushing, organic matter may be exported from temporary streams via leaching or wind- or baseflow-mediated displacement [Brinson et al. 1995].

Connectivity

Despite temporal and/or spatial discontinuities in surface flow, ephemeral and intermittent streams are intimately linked hydrologically and ecologically to their watersheds and to perennial waters [Cummins and Wilzbach 2005; Alexander et al. 2007; Nadeau and Rains 2007]. Larned et al. [2010] define *hydrologic connectivity* as “the presence or absence of flowpaths between persistent patches of aquatic habitat” while Freeman et al. [2007] expand the definition, referring to it as “the water-mediated transport of matter, energy, and organisms within or between elements of the hydrologic cycle.” Although only connected episodically via surface flow to perennial waters, temporary streams, like perennial flowing waters, can move substantial amounts of water, nutrients, sediments, and animal and plant propagules throughout watersheds and waterways. Connections between temporary and permanent or other temporary waters can be longitudinal (channel ←→ channel), lateral (channel ←→ floodplain), vertical (channel ←→ groundwater), and temporal (across time) [Ward 1989; Freeman et al. 2007] (Figure 6).

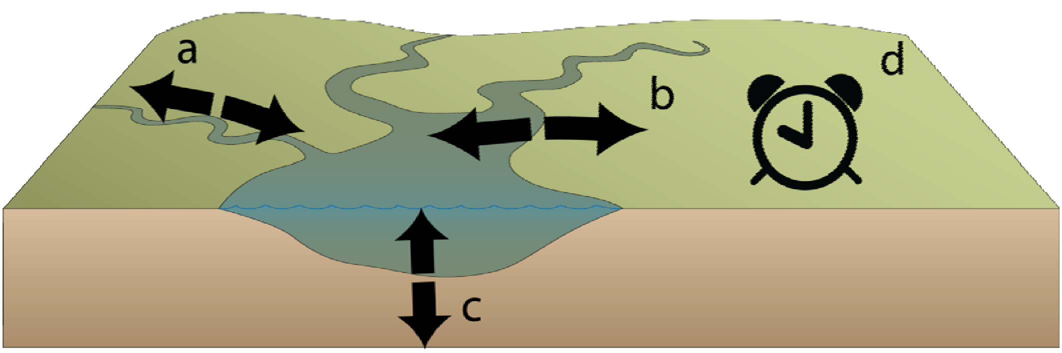

Figure 6. Four dimensions of connectivity within lotic ecosystems (after Ward 1989). a) longitudinal connectivity (channel ←→ channel). b) lateral connectivity (channel ←→ floodplain). c) vertical connectivity (channel ←→ groundwater). d) temporal connectivity (across time). [Modified from symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/), University of Maryland Center for Environmental Science].

Temporary streams act as carbon delivery pathways critical to the ecological integrity of river networks. Carbon is an important energy source for aquatic organisms, forming the base of food webs in lotic networks. Considering their abundance and periodic connectivity to permanent downstream reaches, Fritz et al. [2006] hypothesize that temporary headwaters are major downstream contributors of organic matter. Moreover, research has shown that temporary waters, including streams and floodplains, although only episodically connected to the larger river network, can be significant sources of organic carbon to rivers. Studying anabranching channels (sections of a river or stream that divert from the main channel or stem and rejoin the main stem downstream) episodically connected to the Macintyre River (southeastern Australia), Thoms [2003] and Thoms et al. [2005] found that these temporarily connected reaches not only make up as much as 87% of the river length, but that they are significant contributors of dissolved organic carbon (DOC) to the river mainstem. The amount and timing of organic carbon exported from temporary streams is a function of the pattern of hydrologic connectivity, streambed hydraulic conductivity, soil organic matter, benthic organic matter and woody debris, rate and state of organic matter decomposition, and allochthonous and autochthonous carbon inputs [Lee et al. 2004].

Ephemeral and intermittent streams may also transport nutrients throughout river networks. Alexander et al. [2007] quantified water and nitrogen transport from headwater streams to downstream waters. They found that headwaters, including ephemeral and intermittent tributaries, contributed approximately 70% of the mean annual water volume and 65% of the nitrogen flux to second order streams [Alexander et al. 2007]. Additional research on the role of temporary streams on downstream nutrient loading, however, is sparse.

Temporary streams may also serve as connectivity corridors for both animal and plant species. Surface flow in ephemeral and intermittent streams enables movement of obligate aquatic animals (e.g., fishes, invertebrates lacking a terrestrial and/or flying adult stage) and *hydrochorous* plants (those with seeds that disperse via water) into otherwise disconnected waters. Moreover, the riparian corridors along temporary streams can serve as migratory pathways for a variety of animal species. Dispersal throughout temporarily flowing portions of river networks allows for genetic exchange between subpopulations that are isolated for some portion of the year as well as opportunities for recolonization of periodically disconnected and/or uninhabitable reaches or pools [Levick et al. 2008]. Dispersal between temporarily connected waters may also allow for geneticexchange between otherwise isolated subpopulations, thereby enhancingmetapopulation genetic diversity and persistence. Some plant species exist along river networks as metapopulations [Menges 1990], with flow-mediated seed dispersal helping to maintain subpopulation connectivity. Meyer et al. [2007] warn that the loss of connectivity between small headwaters – including ephemeral and intermittent reaches – and larger downstream waters will detrimentally impact the biodiversity not only of the headwaters themselves, but of the entire river network.

Even in the absence of surface hydrologic connectivity, ephemeral and intermittent streams can contribute water, carbon, and nutrients to perennial streams. Surface water in temporary streams can be transferred to groundwater reserves or hyporheic flowpaths [Fisher and Grimm 1985; Belnap et al. 2005; Izbicki 2007]. This subsurface water may reemerge downstream in perennial waters or springs where it can be an important source of baseflow, energy, and nutrients [Fisher and Grimm 1985].

ANTHROPOGENIC DISTURBANCES

Because of their small size, large edge-to-width ratio, and intimate linkage to the catchments they drain, temporary streams are likely to be more sensitive to disturbance than larger perennial streams [Bull 1997]. Adding to their risk is the fact that temporary streams are often unmarked on standard topographic maps and have been "historically neglected" by ecologists [Larned et al. 2010]. And, perhaps not surprisingly, temporary streams often receive less regulatory protection than perennial reaches, and less mitigation may be required for their degradation [Johnson et al. 2009]. In fact, a recent Supreme Court case in the United States ruled that streams must either be "relatively permanent, standing or flowing" or significantly impact the biological, chemical, or physical integrity of perennial waters in order to be protected from dredge and fill under the US Clean Water Act [*Rapanos v. United States* 2006]. As a result of all these factors, temporary streams represent particularly vulnerable ecosystems.

Direct Disturbance

Direct anthropogenic disturbance to temporary streams may result from numerous activities including water abstraction, livestock grazing, land clearing, timber harvesting, flow diversion, agriculture, road construction, channelization and loss of riparian vegetation / floodplain connectivity, damming, urbanization, mountaintop mining, and even burial. These disturbances tend to cause alteration of the natural flow regime, loss of faunal and floral habitat, impaired water quality, and/or physical channel / floodplain modification [Dodds et al. 2004]. Many intermittent prairie streams in the Great Plains (central USA) that once meandered through native grasslands have been anthropogenically straightened to more efficiently drain extensive cropland or urban areas [Dodds et al. 2004]. The same is likely also true for once naturally braided channels in the Coastal Plain region of the eastern United States [Walter and Merritts 2008]. The result of these actions is an altered hydrology from seasonally intermittent to more ephemeral and an increase in sediment, nutrient, and contaminant export relative to native prairie streams [Dodds et al. 2004].

Furthermore, increased groundwater abstraction and flow diversion for municipal, agricultural, and industrial use can lead to excessive stream drying, loss of connectivity corridors, and elimination of pool refugia for animals [Uys and O'Keeffe 1997; Webb and Leake 2006]. Groundwater abstraction from the Ogallala High Plains aquifer in the Great Plains (central USA) has led to a lowering of the water table and resultant intermittency in streams that until recently were perennial [Dodds et al. 2004]. Impoundments including dams and farm ponds along temporary stream reaches disrupt connectivity of the lotic system and migratory and dispersal pathways for both plants and animals [Fausch and Bestgen 1997; Dodds et al. 2004].

Urbanization and mountaintop mining, in particular, may also lead to ephemeral, intermittent, and small headwater stream loss – often via direct burial. Elmore and Kaushal [2008] investigated the impact of urbanization on stream loss and found that 70% of streams with drainage basins < 260 ha (1 mi^2) within Baltimore City, Maryland (USA) were lost due to burial. Modeling stream length and hydrologic permanence in Hamilton County, Ohio (USA), Roy et al. [2009] reported 93% and 46% county-wide decreases in ephemeral and intermittent channel length, respectively, in urban versus forested catchments. Mountaintop mining may also result in temporary stream burial [Palmer et al. 2010]. In the central Appalachian ecoregion of the United States, mountaintops are commonly removed to access buried coal. Excess rock, or mine "spoil," is pushed into nearby valleys where it buries existing streams. Particularly vulnerable to these valley fills are small, temporary headwaters.

Indirect Disturbance

Climate change is perhaps the most significant indirect anthropogenic disturbance facing temporary streams. Because temporary stream hydrology is tightly linked to patterns of temperature and precipitation, these waters are particularly sensitive to climatic changes. Both the frequency and intensity of drought and, in turn, stream drying are predicted to increase under current climate change scenarios [Lake et al. 2000; Palmer et al. 2008; Brooks 2009] (Figure 7). Moreover, climate change models predict more variable temperature and precipitation patterns that will lead to increased frequency of flow extremes (e.g., flooding and drying) [Lake et al. 2000], thereby fundamentally altering natural flow regimes in temporary streams and, in turn, stream structure and function [*sensu* Poff et al. 1997]. Such changes will be exacerbated in urban areas where flow variability is already enhanced compared to forested regions [Nelson et al. 2008]. Schindler [1997, 2001] suggests that global climate change will cause increased evapotranspiration in much of North America, in turn resulting in increased temporary stream occurrence, particularly among headwaters. Refined modeling and forecasting efforts aid in the prediction of climate change impacts on temporary waters and should help guide proactive management plans. Yet, long-term monitoring will be necessary to accurately document the impacts on temporary stream hydrology and ecology [Conly and van der Kamp 2001].

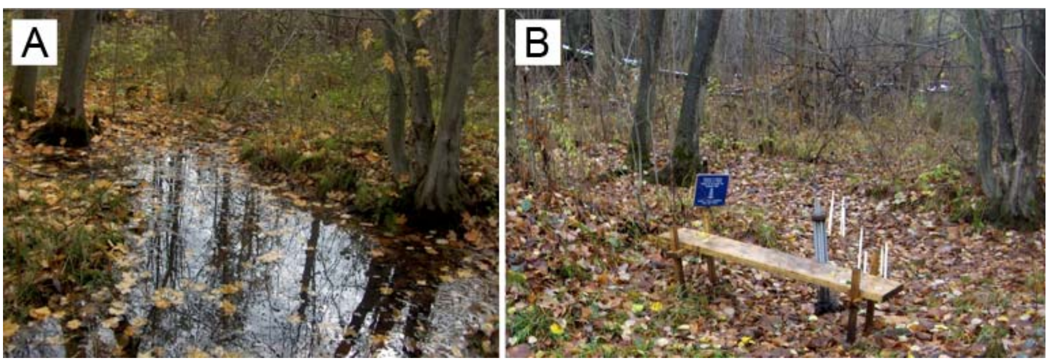

Figure 7. Headwater stream reach near the Speed River in southern Ontario, Canada. A) Stream with surface water present under average autumn climatic conditions (2008). B) Stream lacking surface water during an excessively dry autumn (2007). [Photos: C. Febria]

Human-induced intermittency, both direct and indirect, will have clear and significant impacts on the ecology of stream networks [Brooks 2009]. Increased intermittency and fragmentation of temporary waters can lead to fishery declines, loss of migratory pathways and ecosystem connectivity, disrupted downstream flow regimes, loss of biogeochemical processing capacities, and degradation of the ecological integrity of stream networks as a whole [Larned et al. 2010]. Lack of connectivity between once linked reaches or pools can lead to population bottlenecks within species unable to encounter and reproduce with conspecifics [Labbe and Fausch 2000]. Maintaining connectivity within temporary stream networks is critical for the conservation of populations and biodiversity [Labbe and Fausch 2000]. Direct anthropogenic induced intermittency resulting in rapid transitions from permanent flow regimes to temporary surface flow patterns is common and becoming more frequent [Fu et al. 2004; Bernard and Moetapele 2005; Qi and Luo 2005; Hao et al. 2008].

Indirect human-induced intermittency resulting from climate change will occur gradually and in line with broad drying patterns [Larned et al. 2010].

CONCLUSION

Temporary streams have a unique hydrologic flow regime that places them at an interface between land and water. Although often poorly mapped, recognized, and protected, they are abundant, ubiquitous, and critical to the ecological health of lotic networks. Collectively, temporary streams provide invaluable animal and plant habitat, hot spots for biogeochemical processing, and corridors of hydrologic and ecologic connectivity throughout river systems. Yet, they are faced with a multitude of direct and indirect anthropogenic disturbances to their hydrology, ecology, and even existence.

Temporary streams have been historically neglected [Larned et al. 2010] – not only with respect to scientific study – but more critically as ecosystems vital to the physical, chemical, and biological integrity of entire river networks. The functions of temporary streams must be recognized and valued in order to map, manage, and protect them properly [Levick et al. 2008]. Yet management and protection of ephemeral and intermittent streams - and arguably all small streams – is hindered by the lack of viable assessment methods and reasonable ecological expectations [Fritz et al. 2008]. There exists, therefore, a need for methods to scientifically study the structure and function of temporary streams. Considering their abundance, studies of the cumulative impacts of temporary streams and their loss on the chemical, physical, and biological integrity of lotic networks are also needed.

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