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Invertebrate Resistance and Resilience to Intermittency in a Desert Stream

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ABSTRACT.—Invertebrate responses to water loss were investigated during drying, dry and rewetting phases in Sycamore Creek, an intermittent Sonoran Desert stream. Some taxa were resistant to drying because they could tolerate rapidly changing water quality and/or move upstream to avoid stranding. Community shifts occurred at one site when it became isolated from up- and downstream reaches; taxa such as beetles, hemipterans, and the snail *Physella virgata* became dominant. No community changes were detected at a second site which remained connected with upstream reaches by surface flow. Mortality after water loss was severe as few individuals survived longer than 10 days. Low resistance during the dry phase was associated with rapid moisture loss from sediments. Invertebrate persistence in intermittent reaches was due to recolonization after rewetting; however, density increases after floods which reestablished flow at dry sites were lower than reported values for perennial sites in Sycamore Creek. Slower rates of recovery may reflect the composition, reduced size and remoteness of macroinvertebrate colonist pools. Nonetheless, invertebrate persistence in desert streams where both flooding and drying are frequent is due largely to their ability to rapidly recolonize disturbed sites.

INTRODUCTION

In temporary streams, drying is a key environmental feature influencing distribution, abundance and life histories of the aquatic fauna (Boulton and Suter, 1986; Stanley and Fisher, 1992; Boulton and Lake, 1992b). Intermittent conditions have led to a variety of physiological (*e.g.*, Crowe, 1971; Tauber *et al.*, 1984; Berra *et al.*, 1989) and behavioral (Bouvet, 1977; Boulton, 1989) adaptations. Survival during periods of declining and disappearing discharge is a result of either avoidance or tolerance of changing environmental conditions. Physiological tolerance to habitat water loss is well documented in organisms of temporary ponds and pools (reviewed by Wiggins *et al.*, 1980; Williams, 1985), but also occurs among inhabitants of temporary streams (reviewed by Williams, 1987). Avoidance may be behavioral (*e.g.*, burrowing into substrates, Williams *et al.*, 1974), or may involve life history modification during drying (Taylor, 1983; Delucchi and Peckarsky, 1989), emigration (Momot, 1966), or recolonization after disturbance (*e.g.*, Williams, 1977; Sagar, 1983; Benzie, 1984).

Discharge in desert streams is characterized by flash floods and drying. Both disturbances invariably influence life histories and community dynamics of the aquatic biota. While much attention has been given to invertebrate responses to flooding (Gray, 1981; Gray and Fisher, 1981; Fisher *et al.*, 1982; Meffe and Minckley, 1987; Grimm and Fisher, 1989), far less is known about the effects of drying on macroinvertebrates in these ecosystems. Given the widespread occurrence of intermittency in desert streams and the importance and conspic-

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uousness of macroinvertebrates in these systems (Fisher and Gray, 1983), we wanted to determine how invertebrates coped with drying. This was done by addressing the following questions: (1) what general community changes occur during drying, and (2) what are the mechanisms responsible for persistence of invertebrate populations in intermittent desert streams? Persistence over time is a product of resistance to drying (the percentage of change which occurs during the period over which the system is rapidly shrinking but still wet; resistance I), resistance after water loss (changes which occur during surface water absence; resistance II) and recovery after rewetting (resilience) (Stanley and Fisher, 1992). Field surveys and experiments were used to determine resistance and resilience of aquatic macroinvertebrates in Sycamore Creek, an intermittent Sonoran Desert stream.

STUDY SITE

Sycamore Creek arises in the Mazatzal Mountains and flows south to the Verde River in Arizona's Sonoran Desert. Elevation in the mid-basin area where this study was conducted is 610 m and precipitation averages 300–400 mm annually, falling mostly during winter storms (December through March) and summer monsoons (late July–September) (Thomsen and Schumann, 1968). Stream flow is often continuous throughout much of the basin during winter; however, in summer the creek becomes intermittent and over 50% of the channel can lose surface flow during dry years (Stanley, 1993). Drying may begin as early as April and continue throughout the year until sufficient precipitation and reduced evapotranspiration reverse the trend of water loss. Within a single kilometer there may be both perennial sites and sites that flow as briefly as three months annually. The mid-basin area of Sycamore Creek is characterized by low gradient, unshaded gravel runs and pools interspersed with rocky riffles. Sediments are dominated by coarse sand and pebbles (5–50 mm) which may reach depths of 200 cm in some areas, but are typically 50–100 cm deep (Valett *et al.*, 1990). Summer water temperature varies between 20 and 30 C.

Routine invertebrate sampling was conducted at two gravel reaches during 1989 and 1990. Site I was a large (140 × 20 m) reach which maintained flow between February and June in 1989 and between late March and June in 1990. Drying was characterized by disappearance of flow at the downstream end of the reach followed by loss of upstream connection, creating an isolated pool before complete water loss. Site II (122 × 15 m) typically flowed for at least 7 months, and often dried only partially. Drying at this site was characterized by loss of flow from the downstream end of the reach in mid-summer (June–July), then a rapid upstream recession of surface water. In 1990, flow into the upper third of the reach persisted throughout the summer; however in 1989, drying of this reach was complete as the upstream recession of water progressed into the riffle above this study site.

METHODS

During drying.—Macroinvertebrate community changes during water loss were assessed by randomly collecting five core samples (core size = 80 cm² inserted to a depth of 10 cm) from wetted areas of both sites I and II in 1989 and site I in 1990. Samples were collected every two weeks before the start of drying, then weekly after flow became intermittent. Samples were elutriated, filtered through a 250 μm net, preserved in 70% ethanol in the field, then later sorted and identified in the laboratory under ×10 magnification.

To determine if invertebrates actively avoided ongoing drying, traps were constructed to collect individuals moving up- and downstream at site II. Traps consisted of funnels (20 cm tapering to 5 cm in diameter) to which 50 μm mesh bags were attached. Three pairs of traps were placed 1 m apart along a transect perpendicular to stream flow. Each pair

consisted of an upstream-facing trap and a downstream-facing trap. The lower halves of the trap openings were gently pushed into the sediments just above the sink (the point at which surface water disappeared) and left in place for 28 h on 5–6 August 1990. Mesh bags were replaced every 4 h, and their contents rinsed out and preserved in 70% ethanol. Sink location was also recorded at the time of sample collection as its position was first 3 m below, then later 4 m above the traps. Differences in abundance of individual taxa and total numbers of individuals moving up- or downstream were determined using Kruskal-Wallis tests (Zar, 1984) with Bonferroni-corrected significance levels (*i.e.*, level of significance = 0.05/number of tests).

After water loss.—Stream sediments were collected with an 80 cm² core sampler from five reaches (sites I and II plus three similar reaches located between sites I and II which had also lost surface flow during May and June). Water loss was monitored closely in order to ensure that samples were collected from an area in which time of drying was known precisely, then 2 cores were collected from each site 1, 3, 6, 10, and 15 days after drying to determine invertebrate survival after disappearance of surface water. A small subsample was also taken from each core for sediment moisture determination. Samples were returned to the laboratory in plastic bags and flooded with distilled water. After 24 h of inundation, sediments were elutriated and filtered through a 50 μ m net. Viable organisms were collected and identified under a $\times 10$ dissecting microscope.

After rewetting.—To determine if macroinvertebrates were able to rapidly recolonize previously dry stream reaches after rewetting, samples were collected from site I within two days after rewetting on three separate dates in 1990. Samples were collected on 30 March following a large winter flood which rewetted extensive areas of previously dry stream channel and after two summer floods (17 August and 5 September) which caused temporary rewetting of this site. Five sediment cores were taken randomly within the wetted stream, preserved in 70% ethanol and returned to the lab for identification and enumeration. Four to six liters of water was also collected with a small bucket and filtered through a 250 μ m net to gather larger, more mobile individuals from the water column.

Resilience (rate of recovery following disturbance; Webster *et al.*, 1974) was measured on three occasions: following the March 1990 flood at site I and at site II, and during a period of ongoing drying at site II in 1989. Resilience was measured as the slope of the line of invertebrate density over time since flooding. Density data were $\log(x + 1)$ transformed to meet assumptions of the linear regression model, then differences in resilience were assessed by a multiple comparison of slopes of the transformed data versus time, and Tukey's HSD test was used to identify significantly different lines (Zar, 1984) at a significance level of 0.05.

RESULTS

Invertebrate resistance to drying.—There were no consistent changes in invertebrate density associated with drying during 1989 or 1990 at either site (Fig. 1). Effects of drying at site II were confounded by a flood on 23 July which significantly reduced densities (Student's *t*-test, $t = 4.60$, $P < 0.001$). Postflood recovery was negligible as there was no significant difference between densities 2 days after and 6 weeks after flooding (Student's *t*-test, $t = 0.65$, $P > 0.50$), and unlike other postflood sequences (Grimm and Fisher, 1989), days since flood was not significantly correlated with invertebrate numbers (Table 3).

There were distinct taxonomic shifts during the week preceding complete water loss at site I, but not at site II. Although there were no changes in number of taxa over time, macroinvertebrate communities became dominated by winged insects (coleopterans and hemipterans) and the snail *Physella virgata* (Table 1). On the final day of drying at site I

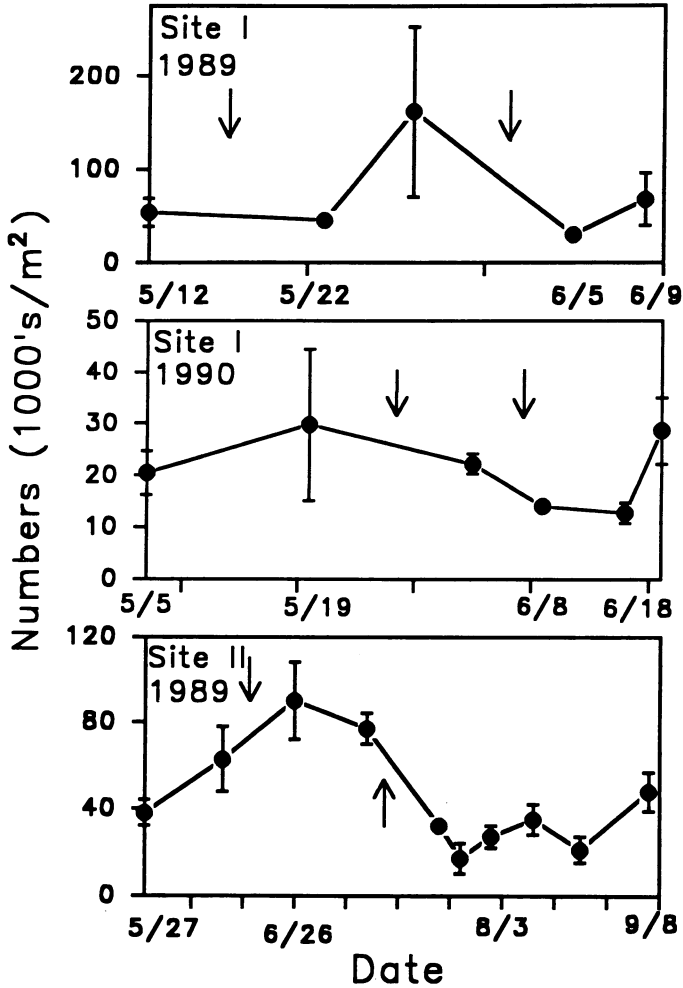


FIG. 1.—Mean invertebrate densities during drying at site I in 1989 and 1990 and at site II in 1989. The first downward-pointing arrow in each panel indicates the approximate date when flow became discontinuous; the second downward arrow signifies loss of upstream flow into the site (site I only). Upward-pointing arrow indicates the timing of a flood at site II. Error bars represent ± 1 SE

in 1989, snail densities were so high that an area of ca. 0.3 m^2 was completely filled with snails to a depth of 30 mm. Also abundant was the midge *Chironomus*, which is distinctive because of its bright red color caused by presence of hemoglobin, enabling it to tolerate low dissolved oxygen concentrations (Erikson *et al.*, 1984). Mayflies, which had been common before drying became extreme, were rare or absent this time.

A total of 2397 individuals from 27 taxa were captured moving up- or downstream during drying at site II (1727 individuals from 23 taxa moving upstream, 670 individuals from 19 taxa moving downstream) (Fig. 2). No individual taxon showed significant upstream movement, but there was significant upstream movement for total number of individuals collected

TABLE 1.—Percentage of snails (*Physella virgata*) and winged adult Coleoptera and Hemiptera present in benthic samples during drying at two sites

Date	Stream surface area (m ²)	% snails	% winged adults
Site I 1989			
12 May	858	0.5	1.6
22 May	536	1.6	1.5
27 May	309	2.6	0.9
5 June	43	11.9	10.6
9 June	1	68.2	3.4
Site I 1990			
30 March	308	0.0	0.0
2 April	263	0.0	0.0
6 April	043	0.0	0.0
14 April	724	0.0	0.0
22 April	708	0.0	0.0
5 May	706	0.0	1.1
19 May	686	0.0	2.4
2 June	495	0.5	15.9
8 June	317	3.4	15.1
15 June	64	17.9	43.4
18 June	2	51.8	21.5
Site II 1989			
27 May	764	13.0	0.0
12 June	754	21.7	1.7
26 June	518	13.5	0.4
10 July	210	2.2	2.4
24 July	684	3.9	0.0
28 July	414	0.4	1.5
3 Aug	186	0.0	0.0
11 Aug	125	0.8	0.6
22 Aug	117	0.0	2.0
8 Sept	40	0.1	0.9

($P = 0.0003$). During the monitoring period, sink location fluctuated from 3.5 m below the traps at 0800 h to 4.7 m above the traps at 1600 h, exposing them between 1230 h and 2000 h; however, individuals were still captured during this period. Greatest invertebrate movement in both directions occurred between 2400 h and 0400 h, while fewest individuals moved up- or downstream between 1600 h and 2000 h. In all but one sampling period (2000–2400 h), net movement was upstream (Fig. 2). In contrast to these results, downstream movement at a perennial site in 1979 was significantly greater than upstream movement (10,205 drifting downstream versus 594 moving upstream; $P < 0.001$, Wilcoxon paired sample test) and for all 3 h sampling period downstream drift was greater than upstream movement (Fig. 2; Gray and Fisher, 1981).

Invertebrate resistance after water loss.—Only 12 taxa were collected during field surveys of dry reaches (Table 2). Sites which dried slowly (water loss occurring over 3–4 days) had more taxa and individuals than rapidly drying sites (complete water loss within 2 h), but few individuals persisted at any site beyond 10 days and only 5 individuals were found two

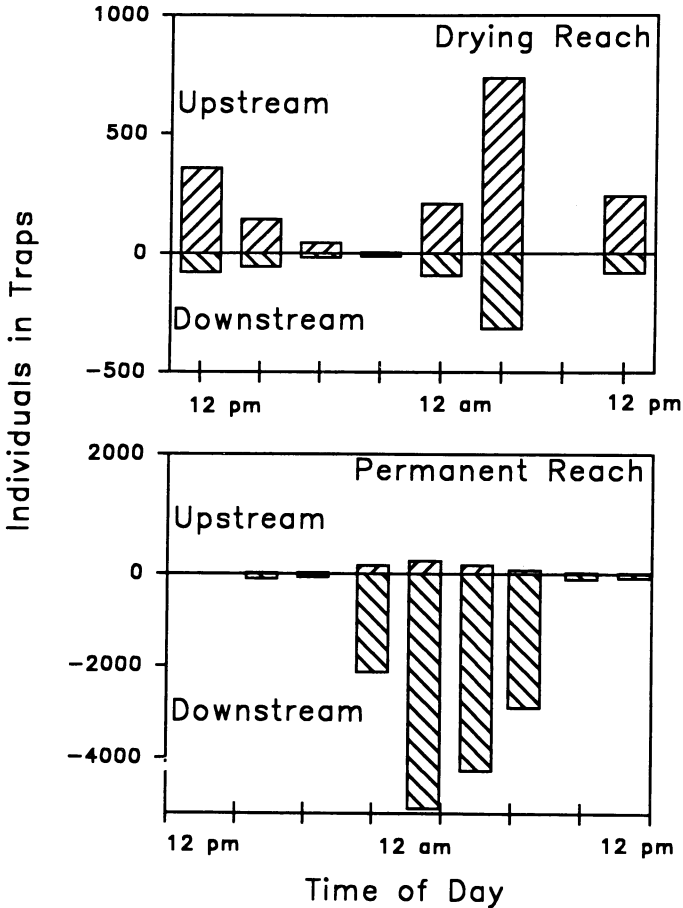


FIG. 2.—Total number of macroinvertebrates captured in traps moving upstream and downstream in drying (top) and perennial (bottom) reaches. Bottom panel is modified from Gray and Fisher (1981). Note that 0400–0800 samples from the drying site were lost

weeks postdrying (Fig. 3, Table 2). There was a significant relationship between number of individuals present and sediment moisture for all samples ($r^2 = 0.46$, $P < 0.05$). *Physella virgata* and tipulid larvae and pupae were the most abundant taxa after water loss. The tipulids appeared to be completing larval development, as samples collected from days 1 and 3 were dominated by larvae whereas pupae were most common on day 6.

Resilience after rewetting.—Number of taxa collected from benthic sediments and the water column soon (≤ 2 days) after floods which rewet site I varied from two taxa after a winter flood on 30 March to seven taxa following a summer flood on 17 August and six after a flood on 5 September. Early successional assemblages were dominated by chironomids and oligochaetes in March, but hemipterans and coleopterans were the most common taxa collected after the two summer floods. Nonflying individuals present immediately after rewetting in August and September were predominantly dipteran larvae (Chironomidae and Ceratopogonidae). Over 70 *Probezzia* (Ceratopogonidae), many of which were final

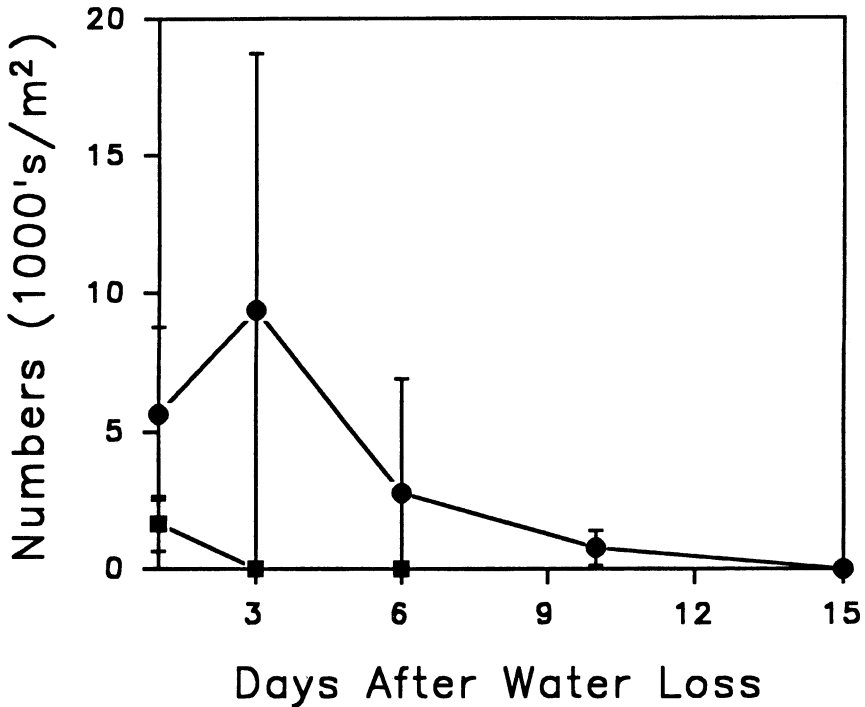


FIG. 3.—Average densities of benthic macroinvertebrates found in reinundated sediments from a site where drying progressed rapidly (squares) and a site where drying was prolonged (circles) during July, 1990. Error bars represent ± 1 SE

instar larvae, were collected from a single core sample in August just 2 days after flooding and flow resumption.

Maximum benthic invertebrate densities occurred within a month after rewetting at sites I and II in March 1990 (Fig. 4). Recovery rates following these two floods and the autumn flood at site II in 1989 were compared to assess differences in resilience. Recovery rates varied significantly among sequences ($F = 12.84$, $P < 0.0005$) as resilience was greatest at site II after rewetting in 1990, and lowest following the autumn flood at the same site in 1989 (Table 3).

DISCUSSION

Resistance I.—Invertebrate densities may increase (Extence, 1981), decrease (Boulton and Lake, 1992b) or remain unchanged (Hynes, 1975; Chessman and Robinson, 1987) in streams during drying. Decreases have been attributed to intolerance of deteriorating water quality (Boulton and Lake, 1992a, b) and intensified predation (Larimore *et al.*, 1959), whereas increases are caused by mobile organisms congregating in ever-diminishing habitats (Smith and Pearson, 1987). Like most drying streams, physicochemical conditions shifted rapidly during sampling, particularly at site I (Stanley, 1993), and undoubtedly had adverse effects on the benthos. For instance, sediments and surface water often became anoxic during drying, favoring invertebrates using atmospheric oxygen (*e.g.*, adult beetles, corixids) or hemoglobin (*Chironomus*). Taxa with high dissolved oxygen requirements (*e.g.*, mayflies)

TABLE 2.—Abundance of taxa collected in field surveys from five different sites in dry reaches. Abundance is expressed semiquantitatively (+ = present [1–2 individuals per sample], C = common [3–10], and A = abundant [>10]). Larvae are denoted by L, pupae by P

Taxa	Days since water loss				
	1	3	6	10	15
Annelida					
Oligochaeta	C	C	C	+	+
Crustacea					
Copepoda		+			
Ostracoda	C		+		
Hydracarina					
Hydracarina	+	C	+		+
Insecta					
Coleoptera					
Hydrophilidae (L)	+	+		+	+
Diptera					
Tipulidae (L)	A	A	+		
(P)		+	C		
Chironomidae	+	+		+	
Ceratopogonidae					
<i>Probezzia</i>	C	A	+	+	+
Tabanidae					
<i>Tabanus</i>	+	+	+	+	+
Gastropoda					
Physidae					
<i>Physella virgata</i>	C	C	+	+	
Planorbidae					
<i>Helisoma</i> sp.	+	+	+		
Total number of taxa	10	11	9	7	5

were notably absent during the final days of drying at site I. Density decreases due to predation are also likely given increased numbers of fish and predaceous beetles and bugs. Benthic samples from site I were littered with insect body parts and empty snail shells during the final days preceding water loss, and were likely remnants of predation. In many temporary streams, densities of predators rise sharply during drying (Stehr and Branson, 1938; Hynes, 1975; Abell, 1984). Wiggins *et al.* (1980) suggested that predator recruitment in temporary pools is timed to coincide with peak prey densities, and this may also apply in intermittent streams (Boulton and Lake, 1992b).

Observed upstream movement of invertebrates demonstrates that some individuals can keep pace with drying. Similar behavior has been observed in other temporary streams (Delucchi, 1989), but this ability was clearly limited. Although invertebrates chased receding water margins upstream, drying was often faster than invertebrate movement, leaving individuals stranded on the dry stream bed. Despite the absence of significant differences

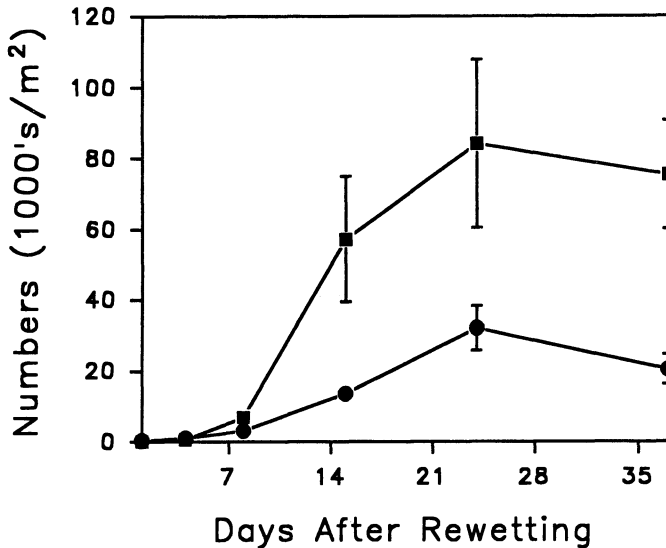


FIG. 4.—Postflood recovery of macroinvertebrate densities following rewetting of sites I (circles) and II (squares), beginning on 30 March, 1990. Error bars are ± 1 SE

in up- versus downstream movement within any taxon, some are clearly more vagile than others. Failure to detect taxon-specific differences was likely due to small numbers of individuals per taxon captured in traps. Community shifts at site I suggest that *Physella* can follow receding stream margins, as can various beetle and bug species. Rather than avoid drying pools, some beetles and hemipterans may in fact seek out such habitats as they offer abundant food. For instance, Gray (1980) observed eight belostomatid adults (*Abedus herberti*) fly into two adjacent drying pools and consume 20 fish within a matter of a few hours.

In contrast to site I, there were no marked density or taxonomic changes at site II during drying. This is likely due to the faster rate of drying and continued connection with the upstream riffle at this site. Apparently, effects of drying are detectable only when reaches become discontinuous and isolated. Delucchi (1988) was also unable to find differences

TABLE 3.—Slopes of lines expressing changes in macroinvertebrate density vs. time after a rewetting flood (sites I, II in 1990), a flood during drying (site II in 1989), and floods at perennial sites (from Grimm and Fisher, 1989). Values in parentheses are standard errors

Site	Slope (SE)	r ²
Site I 1990	0.76 (0.15)	0.698
Site II 1990	2.82 (0.69)	0.627
Site II 1989	0.39 (0.20)	0.345
Grimm and Fisher (1989)		
Winter-spring	1.33 (0.56)	
Summer	1.37 (0.98)	
Autumn	2.45 (1.04)	

between temporary and permanent stream communities at sites which never lost their upstream connections. Community changes in isolated reaches, on the other hand, are common, and their development has been well documented in a variety of studies (reviewed by Williams, 1987). Abell (1984) referred to this assemblage as the "summer clean-up crew" as it is dominated by scavengers and predators.

Resistance II.—The length of time Sycamore Creek macroinvertebrates are able to tolerate water loss is brief in comparison to those in temporary streams in Australia (Boulton, 1989) and southern Canada (Williams and Hynes, 1977). In Sycamore Creek, few macroinvertebrates have resting stages or use refuges during dry periods (Boulton *et al.*, 1992b) resulting in a virtual absence of resistance to periods of water absence. This may reflect extreme temperatures of exposed sediments (>60 C; Stanley, 1993), rapid elimination of remaining sediment moisture and sediment scour upon rewetting (Gray, 1981). In most studies reporting drought tolerance, invertebrates are able to persist in moist refuges such as algal mats (Strandine, 1941), crayfish burrows (Boulton, 1989) or deep sediments (Clifford, 1966; Williams, 1977). Moist benthic refuges simply do not exist in dry desert stream channels.

Although hyporheic sediments are generally cooler and moister than surface sediments and often remain saturated long after disappearance of surface flow (Stanley and Valett, 1992), the hyporheic zone of Sycamore Creek is not an important refuge for benthic species (Boulton *et al.*, 1992b). One possible exception is the ceratopogonid larva *Probezzia*, which is common in both benthic and hyporheic zones and was abundant immediately after one summer flood. It is unclear why the hyporheic zone does not serve as a refuge for the benthos, particularly given the existence of a diverse, obligate hyporheic fauna in some Sonoran Desert streams (Boulton *et al.*, 1992c). Although numerous surface taxa were collected from the hyporheic zone in a South Australian arid-zone stream, Cooling and Boulton (1993) felt that these individuals were probably passive colonists and unlikely to be an important source of recolonists after rewetting. The high degree of specialization needed to survive hot dry conditions may be far greater than for persistence via recolonization (Hynes, 1975), and the physical conditions (*e.g.*, reduced oxygen and food availability, small size of interstices) in the hyporheic zone may make it a poor refuge for benthic macroinvertebrates in dryland streams (Gagneur and Chaoui-Boudghane, 1991).

Resilience.—Recovery rates following flooding were significantly different in the three sequences examined in 1989 and 1990. Resilience was greatest after a flood rewet site II in 1990, and least after a summer flood which occurred during a period of drying at the same site in 1989. Recovery rates at site I in 1990 and site II in 1989 were less than mean recovery values reported for perennial reaches in Sycamore Creek (Table 3). Larimore *et al.* (1959) suggested that recovery in intermittent streams is a function of the extent of the area affected, distance from a colonist source, or season, whereas Boulton and Lake (1992a) found that historical effects (*e.g.*, timing of water loss the previous year) strongly influenced recruitment in two Australian temporary streams. Rapid postflood recovery in Sycamore Creek is due to recolonization by ovipositing adults with short generation times (Gray and Fisher, 1981).

We suggest that slower recovery rates in previously dry sites are a result of changes in the composition of the recolonization pool. Drying may affect the pool of potential recolonists in three ways. First, assemblage structure may shift away from taxa with aerial adults (mayflies, chironomids, caddisflies) to one dominated by snails (*see* Table 1 and Boulton *et al.*, 1992a). Secondly, habitat shrinkage reduces the total number of invertebrates present before flooding. Finally, drying can increase the distance between colonization sources (perennial sites) and intermittent sites. Although ovipositing adults are relatively mobile, travelling from perennial to more distant intermittent sites is likely to delay recovery,

particularly in summer when high temperatures and low humidity reduce adult longevity by as much as 50% and mortality rates are high (Jackson, 1988). Before rewetting in 1990, there was more than 2.5 km of dry channel upstream and 1.2 km downstream of site I, whereas perennial stream reaches were within 800 m of site II, and, consequently, resilience was greater at the latter site. However, more information on recovery at sites of varying flow permanence and distance from perennial sites (*i.e.*, from a source of colonists) is needed to further develop and test these hypotheses.

Invertebrates cope with intermittency in desert streams via resistance to drying and resilience after rewetting. Resistance to drying is characterized by tolerance of physico-chemical extremes in drying pools, and/or avoidance of desiccation by moving upstream or flying among sites during periods of water loss. However, as few taxa demonstrate resistance during drying, taxonomic shifts are common as non-resistant species become scarce. This has important implications for postflood recolonization trajectories for floods occurring during drought periods. There is virtually no survival after water loss; resilience, rather than resistance, has been favored among Sycamore Creek and other arid land stream benthos (Harrison, 1966; Hynes, 1975; Gagneur and Chaoui-Boudghane, 1991). Adaptations favoring recovery by recolonization allow invertebrate populations to persist through both flooding and drying in these lotic ecosystems where such hydrologic extremes are the rule rather than the exception.

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