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Postflood Recolonization Pathways of Macroinvertebrates in a Lowland Sonoran Desert Stream

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ABSTRACT: Most macroinvertebrate taxa recolonizing after floods in Sycamore Creek did so via aerial pathways. After frequent winter flooding, most aerial colonists were aquatic adults (Coleoptera and Hemiptera), whereas ovipositing adults (Ephemeroptera and Diptera) dominated after summer flooding. Drift and upstream movements by relatively few taxa contributed most individuals after floods. Upstream movements were greater during high discharge than during low discharge periods. Few taxa and individuals were present in sediments below 10 cm.

INTRODUCTION

Stream macroinvertebrates are periodically decimated by various natural catastrophes, such as ice scour, floods and drought. An important aspect of recovery after a catastrophe is to be found in the pathways of recolonization. These pathways influence community composition and suggest common selective forces on the life histories of species present.

Williams and Hynes (1976) identified four principal recolonization pathways of stream benthos: aerial movements, downstream drift, upstream movements and vertical movements from deep substrates. Although all four may contribute colonists, previous studies indicate that one pathway usually dominates. In permanent streams, downstream drift is most important (Townsend and Hildrew, 1976; Williams and Hynes, 1976), while in intermittent streams, aerial movements and vertical movements from deeper substrates are the two main pathways. Harrison (1966) and Hynes (1975) found aerial sources dominant in two African streams. Organisms using this pathway were aquatic adults (Coleoptera and Hemiptera) and ovipositing adults (*e.g.,* Ephemeroptera and Diptera). Williams (1977) found vertical movements predominant in two Canadian streams subject to drying. Organisms were present in dormant stages until water returned.

Recolonization processes are integral to macroinvertebrate community dynamics in intermittent desert streams as a consequence of frequent disruption by floods. Floods occur during two distinct rainy seasons in the Sonoran Desert, winter (November to April) and summer (July to October). Winter precipitation results from large-scale frontal systems that affect large areas, producing floods and extended high flows lasting from days to weeks. Summer rains, caused by locally intense thunderstorms, affect variable portions of the watershed resulting in "flash" floods that typically last only a few hours (Deacon and Minckley, 1974). In both seasons, floods scour substrates and eliminate 80-100% of the benthic fauna (Gray, 1980).

Recolonization studies of benthic invertebrates were conducted at Sycamore Creek, Arizona (33°45′N, 111°30′W), a lowland Sonoran Desert stream (*see* Fisher and Minckley, 1978, for a description of the Sycamore Creek watershed). In addition to descriptive studies of each recolonization pathway during stable-flow periods, the hypothesis that aerial pathways are used by most taxa to recolonize after flooding was tested for winter and summer floods. This hypothesis was suggested by observations on species composition and life history characteristics of Sycamore Creek macroinvertebrates (Gray, 1980). Forty of the 104 taxa present have long-lived aquatic adults capable of flight (Coleoptera and Hemiptera), and most remaining species (*e.g.,* mayflies, caddisflies and small dipterans) reproduce throughout the year and lack dormant stages in substrates. Few taxa exhibit dormancy [*e.g., Mesocapnia arizonensis* (Baumann and Gaufin) and *Tabanus dorsifer* Walker]; thus vertical movements of these from the substrate were thought unlikely to contribute many individuals. Alternatively, vertical movements could predominate if many taxa were present in active stages within substrates (Coleman and Hynes, 1970; Williams and Hynes, 1974). Initial colonists would then be those organisms present prior to flooding.

METHODS

Descriptive studies.—Aerial pathways were evaluated by field observation, colonization trays *(see below)* and marking of adult beetles. Beetle adults were marked by scratching an elytron with fine forceps. This method permanently marks each beetle but does not cause injury (Ryker, 1975). Three separate marking experiments were conducted. A total of 50 individuals of *Oreodytes* sp., *Laccophilus pictus* Regimbart, *Agabus seriatus* (Crotch), *Tropisternus ellipticus* (LeConte), *Deronectes striatellus* (LeConte) and *Berosus punctatissimus* LeConte were marked in side pools in October 1979 and censused at 4-day intervals. In August 1979, 59 adult *Tropisternus ellipticus* were collected, marked and returned to three habitats along a 10-km reach: a drying pool (20 beetles), a flowing segment with stable substrates (22) and a recently scoured segment (17). In March 1979, 12 adult *Helichus immsi* Hinton were marked and released at one site. Marked individuals were actively searched for at 2-day intervals (14 days total) after release for 2 hr.

In June 1979, after 9 weeks without flooding, measures of drift and upstream movements were made at a stable-flowing segment to evaluate these pathways during nonflood periods. Collections were made over a diel cycle with nets (270 μm mesh, 40 cm wide x 40 cm long x 15 cm high). In previous benthic sampling in Sycamore Creek, nets with 270 μm mesh captured 97% of total macroinvertebrate numbers compared to nets with 100 μm mesh and did not become clogged, as readily, with algae as the finer mesh.

Vertical and lateral distributions of macroinvertebrates in sediments were examined in July 1979 at one site. Pits were dug in the main channel (flowing water), a side channel (saturated sand with no standing water) and bank (unsaturated sand with no standing water) habitats. Samples were taken with a plastic cylinder (4-cm diam) lateral to the pit walls. Boards were used to stabilize the pit walls and minimize contamination from upper sediments. Two core samples (120 cm^3 each) were taken at 10-cm depths down to 50-60 cm.

Recolonization after floods.—The relative contribution of each recolonization pathway after flooding was assessed by trays that each allowed colonization from only one pathway. Trays were constructed of plywood, 60 μm mesh and hardware screen, similar to those described by Williams and Hynes (1976). By this method, the total number of organisms in control trays (open to all pathways) after a predetermined period should equal the sum of organisms collected from other trays open to a single pathway, *i.e.,* control = sum (aerial + vertical + upstream + drift). The principal pathway for each species would be indicated by that tray which contributed the greatest percentage of individuals relative to control trays.

Nine days were allowed for colonization of three aerial (1600 cm^2 each) and three vertical (680 cm^2 each) trays based on initial trials (Table 1). Both these techniques underestimated contributions because of extremely short life cycles and predation. Most mayflies and small dipterans in Sycamore Creek can complete development from egg to adult in 6-14 days (Gray, 1980). Emerging insects trapped in vertical trays died and deteriorated before being tallied. An extreme example of predation occurred when an aerial tray was colonized by 117 adult *Deronectes nebulosus* (Sharp), and the predator eliminated all mayflies and chironomids.

After initial trials it was obvious that drift and upstream movement trays were not selective for their respective pathways. A 9-day colonization period was sufficient to allow losses from mayfly and chironomid emergence. In addition, the trays were sites of extensive oviposition by many taxa, and 9 days were adequate for eggs to hatch. As a result, contributions from these pathways were assessed with nets set for 24-hr periods (the same nets as those used in June 1974). Boards were placed on the bottom and sides of nets to prevent the entrance of organisms from the substrate and from eddy currents. Large rocks were placed inside the nets to increase stability. Flow reduction through nets used for upstream movements was ca. 50%. Net totals were multiplied by 2.5 to convert values to a 1-m^2 area. Immigration rates, rather than total numbers of organisms collected, were used to compare pathways for each species, and the principal pathway was considered to be the one with the highest rate.

Recolonization pathways were examined after a flood in March 1979 (maximum discharge = 20 m^3s^{-1}) and a series of flash floods in August 1979. The March flood was preceded by major floods in December 1978 (159 m^3s^{-1}) and January 1979 (74 m^3s^{-1}), while no floods occurred 4 months prior to August. Both studies were conducted at sites between 620 and 650 m elevation on the main stem of Sycamore Creek.

Results and Discussion

Descriptive studies.—Although all adult beetles and hemipterans were capable of flight, not all species were equal in dispersal tendencies. Among beetles, dytiscids and hydrophilids were most vagile, while *Helichus immsi* (Dryopidae) was least active. Of 50 dytiscids and hydrophilids marked from side pools, only four individuals were recaptured. These included an *Agabus seriatus* that remained for 32 days, two *Berosus punctatissimus* (8 and 24 days), and a *Deronectes striatellus* (8 days). Of the 59 *Tropisternus ellipticus* marked in August, none was recaptured. All 12 *Helichus immsi* marked in March were found within a few meters of their release point for a 2-week interval between floods. Thus, with the last exception, the data suggest that most beetles in Sycamore Creek spend little time in any single location.

Among hemipterans, field observations supported findings of Fernando and Galbraith (1973) that corixids were the most active dispersers and naucorids the least. *Graptocorixa serrulata* (Uhler) was commonly collected in aerial trays and in ephemeral habitats outside the main stem, while *Ambrysus occidentalis* LaRivers was rarely found outside of permanent, main-channel habitats. Contrary to Smith's (1975) observations, *Abedus herberti* Hidalgo was observed in flight on several occasions.

Of taxa with short-lived, terrestrial adults, only *Mesocapnia arizonensis* was capable of flight (males are brachypterous). In general, mayflies, caddisflies and small dipterans are capable of active flight over several kilometers and may travel farther in strong winds (Edmunds *et al.*, 1976; McDonald *et al.*, 1973; Pearson and Kramer, 1974).

Samples of diel drift and upstream movements in June 1979 indicated few taxa active in the water column during stable-flow periods. Although 21 of 40 total taxa present were collected in drift, five contributed 96% of total individuals (*Baetis quilleri* Dodds, 61%; *Cricotopus* sp., 11%; *Brillia* sp., 11%; *Simulium* sp., 8%, and *Dicrotendipes* sp., 5%). These plus three others (*Centroptilum* sp., *Micropsectra* sp. and *Pentaneurini* spp.) were the only taxa to exhibit behavioral drift (Waters, 1972), with peak activity near midnight (Fig. 1). The other 12 taxa (*e.g.*, oligochaetes, beetle larvae and large dipterans) rarely drifted and did so in association with disintegrating algal mats. Dance and Hynes (1979) also found few taxa actively drifting in a temporary stream; thus most macroinvertebrates in such habitats remain associated with substrates.

Only 10 taxa moved upstream and 93% of all individuals were of the taxa that drifted (*Dicrotendipes* sp., 41%; *Cricotopus* sp., 25%; *Brillia* sp., 13%; *Baetis quilleri,*

Table 1.—Experimental tests to determine in-stream time for colonization trays in Sycamore Creek, Arizona. Total numbers and taxa of macroinvertebrates are mean values from two control trays (680 cm^2 each) filled with cobble-gravel substrates

Days in stream	Total no.	Total taxa
3	1238	21
6	1607	18
9	1706	18

13%, and *Simulium* sp., 1%). Upstream movements exhibited the same diel pattern, but numbers of individuals were only 4% of those in drift (Fig. 1).

Most taxa and individuals were in the upper 10 cm of substrate (Table 2). Principal taxa below this depth were chironomids (*Cricotopus* sp.) and ceratopogonids (*Probezzia* sp. and *Dasyhelea* sp.). One *Helicopsyche mexicana* Banks was at 30 cm, the same depth reported for *H. borealis* in a Canadian stream (Williams and Hynes, 1974). One *Tabanus dorsifer* Walker was found at 40 cm. Burger (1977) reported that this species diapauses deep within substrates. No taxa were found at any depth along the bank; thus the habitat boundaries of macroinvertebrates appear defined by the areas of saturated substrate.

Recolonization after floods.—Nearly two-thirds of total taxa recolonized by aerial pathways in both seasons (Tables 3 and 4); thus the hypothesis was supported. The remaining taxa were derived primarily from drift, while upstream and vertical movements were the principal pathways of only a few taxa. Most individuals were derived from drift and upstream movements, although they belonged to relatively few taxa (*Probezzia* sp. and chironomids in winter, mayflies and *Cricotopus* sp. in summer). Thus large numbers of a few taxa were derived from drift and upstream movements and few individuals of many taxa were derived from aerial sources. Vertical movements contributed few individuals in summer but were more important after winter floods. The dominance of a few taxa in drift and upstream movements, particularly *Baetis quilleri* and certain chironomids, was consistent with nonflood samples.

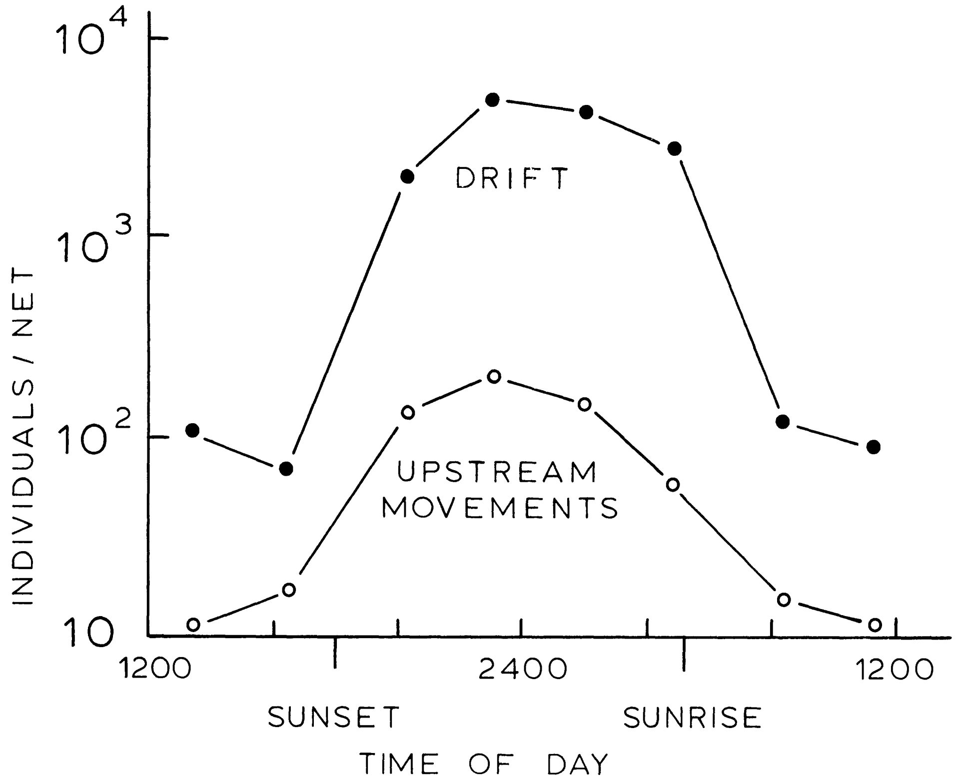

Fig. 1.—Total macroinvertebrates collected in diel drift and upstream movement samples in Sycamore Creek, Arizona, 6-7 June 1979 (62 days after flooding). Net totals X 55 = No. m^{-3} s^{-1}

TABLE 2.—Vertical distribution of macroinvertebrates in sediments of Sycamore Creek, Arizona, on 27 July 1979. Habitats are main channel (flowing water), edge sandbar (saturated sand with no standing water) and bank (unsaturated sand). Tallies = no. organisms per 240-cm^3 sample

	Main channel sediment depth (cm)						Channel edge sediment depth (cm)							Bank (all sediment depths)
Taxon	0	10	20	30	40	50	0	10	20	30	40	50	60	
Ephemeroptera														
Tricorythodes dimorphus Allen	34	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichoptera														
Helicopsyche mexicana Banks	23	9	0	0	0	0	1	0	0	1	0	0	0	0
Ochrotrichia sp.	13	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera														
Enochrus carinatus (Horn)	0	0	0	0	0	0	7	1	0	0	0	0	0	0
Diptera														
Euparyphus sp.	2	1	0	0	0	0	1	0	0	0	0	0	0	0
Tabanus dorsifer Walker	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cryptolabis sp.	0	0	0	0	0	0	5	4	3	0	0	0	0	0
Probezzia sp.	10	0	1	0	3	0	21	13	10	7	3	3	0	0
Dasyhelea sp.	0	0	0	0	0	0	33	14	8	13	1	1	0	0
Cricotopus sp.	40	0	3	1	1	0	0	0	0	0	0	0	0	0
Brillia sp.	105	0	0	0	0	0	0	0	0	0	0	0	0	0
Tribelos sp.	1	1	0	0	0	0	18	2	0	0	0	0	0	0
Micropsectra sp.	0	0	0	0	0	0	1	1	0	0	0	0	0	
Pentaneurini sp.	0	0	0	0	0	0	14	1	0	0	0	0	0	0

TABLE 2.—Continued

	Main channel sediment depth (cm)						Channel edge sediment depth (cm)							Bank (all sediment depths)
Taxon	0	10	20	30	40	50	0	10	20	30	40	50	60	
Non-Insects														
Physa virgata Gould	0	0	0	0	0	0	8	0	0	0	0	0	0	0
Acari	22	1	0	1	0	0	0	0	0	0	0	0	0	0
Total number	250	12	4	2	4	0	109	36	21	21	5	4	0	0
% of total	91	4	2	1	2	0	56	18	11	11	2	2	0	
Total taxa	9	4	2	2	2	0	10	7	3	3	3	2	0	0

Seasonal differences were evident in the predominant aerial colonists. In winter, nonreproductive beetle and hemipteran adults (as judged by the absence of eggs) were

TABLE 3.—Macroinvertebrate colonization pathways after summer flooding, Sycamore Creek, Arizona, August 1979. Principal pathway indicates pathway used by a majority of individuals of each species. Data for aerial and vertical pathways from colonization trays; drift and upstream pathway data from nets

	No. m^{-2} day^{-1}				
Taxon	Drift	Upstream	Aerial	Vertical	Principal pathway[1]/
Ephemeroptera					
Baetis quilleri Dodds	2581	469	197	5	D
Leptohyphes packeri Allen	181	6	72	0	D
Tricorythodes dimorphus Allen	112	0	19	1	D
Trichoptera					
Helicopsyche mexicana Banks	0	0	58	*	A
Cheumatopsyche arizonensis (Ling)	0	0	a	0	A
Culoptila cantha (Ross)	0	0	a	0	A
Ochrotrichia sp.	25	12	0	0	D
Coleoptera					
Laccobius sp.	0	0	1	0	A
Gyrinus sp.	0	0	*	0	A
Psephenus murvoshi Brown	0	0	*	0	A
Odonata					
Progomphus borealis McLachlan	12	0	1	*	D
Ophiogomphus bison Selys	0	0	*	0	A
Hetaerina sp.	0	0	7	0	A
Lepidoptera					
Paragyractis confusialis (Walker)	0	0	a	0	A
Diptera					
Tabanus dorsifer Walker	*	0	0	1	V
Euparyphus sp.	0	34	2	0	U
Cryptolabis sp.	0	0	12	0	A
Culiseta incidens (Thomsen)	0	0	*	0	A
Probezzia sp.	12	25	48	1	A
Dasyhelea sp.	0	0	5	*	A
Cricotopus sp.	406	170	0	29	D
Corynoneura sp.	0	0	5	0	A
Dicrotendipes sp.	0	0	1	*	A
Tribelos sp.	0	0	*	0	A
Pentaneurini sp.	0	1	6	1	A
Oligochaeta	0	0	0	32	V
Total number	3329	717	434	70	
% of number	73	16	10	1	
(26) Total taxa[2]/	6	1	17	2	
% of taxa	23	4	65	8	

* = less than 1 individual/m^2/day

a = egg masses present

[1]/ = D = drift, A = aerial, V = vertical, U = upstream

[2]/ = Principal pathway only

the principal colonists, while ovipositing adults of other groups dominated in summer. This difference can be attributed to frequent winter floods that greatly reduced, or eliminated entirely, populations with short-lived adults such as caddisflies. In contrast, aquatic adults exhibit behavioral avoidance of floods and therefore suffer few losses. Isolated summer floods have relatively little effect on all populations, despite high losses of immatures, because adults that left the stream prior to flooding are present to rapidly recolonize (Gray, 1980).

A pronounced effect of flooding, compared to nonflood periods, was a greater proportion of individuals moving upstream relative to downstream drift. Ratios of drift to upstream movement for all taxa were 25:1 in nonflood periods and 1.5-4.6:1 after floods, suggesting that behavioral tendencies for upstream movement are relatively greater following high discharge (Minckley, 1964; Williams, 1977).

Floods are an important selective pressure in lowland desert streams (Gray, 1980).

TABLE 4. — Macroinvertebrate colonization pathways after winter flooding, Sycamore Creek, Arizona, March 1979

Taxon	No. m^{-2} day^{-1} Drift	Upstream	Aerial	Vertical	Principal pathway[1]
Ephemeroptera					
Leptohyphes packeri Allen	2	0	0	0	D
Plecoptera					
Mesocapnia arizonensis (Baumann& Gaufin)	11	2	0	2	D
Coleoptera					
Deronectes nebulosus (Sharp)	1	1	5	0	A
D. aequinoctialis (Clark)	0	0	7	0	A
D. yaquii Zimmerman & Smith	0	0	2	0	A
Enochrus carinatus (Horn)	*	0	1	0	A
Hydroporus sp.	*	0	2	0	A
Bidessus sp.	*	0	1	0	A
Tropisternus ellipticus (LeConte)	0	0	*	0	A
Berosus punctatissimus LeConte	*	0	2	0	A
Helichus immsi Hinton	1	*	0	0	D
Hemiptera					
Abedus herberti Hildalgo	2	0	0	0	D
Ambrysus occidentalis LaRivers	*	0	0	0	D
Graptocorixa serrulata (Uhler)	0	0	*	0	A
Diptera					
Probezzia sp.	579	221	1	56	D
Simulium sp.	2	0	0	0	D
Cryptolabis sp.	0	0	*	0	A
Euparyphus sp.	0	0	*	0	A
Syrphidae sp.	0	0	*	0	A
Cricotopus & *Eukiefferiella* spp.	65	7	10	41	D
Pentaneurini sp.	0	0	1	0	A
Total number	663	231	32	99	
% of number	65	23	2	10	
(22) Total taxa[1]	8	0	14	0	
% of taxa	36	0	64	0	

* = less than 1 individual/m^2/day

[1] = Principal pathway only

Dormant stages in substrates are selected against as a consequence of severe substrate scour; thus benthic organisms avoid floods by leaving the stream as aerial adults. Consequently, postflood recolonization occurs primarily from aerial sources. The numerical dominance of drift as a source of individuals probably represents a secondary dispersal of propagules from limited oviposition sites, in particular, along channel edges where the substrates are more stable.

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