



1-31-1985

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### Recommended Citation

McArthur, J Vaun and Barnes, James R. (1985) "Patterns of macroinvertebrate colonization in an intermittent Rocky Mountain stream in Utah," *Great Basin Naturalist*. Vol. 45 : No. 1 , Article 17.

Available at: <https://scholarsarchive.byu.edu/gbn/vol45/iss1/17>

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## PATTERNS OF MACROINVERTEBRATE COLONIZATION IN AN INTERMITTENT ROCKY MOUNTAIN STREAM IN UTAH

J Vaun McArthur<sup>1</sup> and James R. Barnes<sup>2</sup>

**ABSTRACT.**— Colonization of macroinvertebrates in a headwater mountain stream was monitored using basket and Surber samplers. Taxa showed differences in colonization ability based both on dispersal ability and feeding strategy. Collector-gatherer feeding groups that could actively enter the water, i.e., *Baetis* mayflies, were the first organisms to colonize bare or new substrate. The slowest colonizers were heptageniid mayflies that colonized primarily from upstream migration. All organisms examined increased drifting behavior in response to decreases in discharge.

Intermittent streams provide a unique opportunity to study colonization by macroinvertebrates. Colonization of artificial substrate samplers begins almost immediately after they are placed into permanently flowing streams (Ulfstrand et al. 1974, Townsend and Hildrew 1976, Sheldon 1977, Roby et al. 1978). Similar patterns are seen by disturbing the substrate to remove the existing species and thereby creating open areas for colonization (Waters 1964). However, such a small area of barren substrate, completely surrounded by undisturbed habitat, is atypical of natural streams. The dry sections of intermittent streams are usually more extensive in area and should show the immigration patterns of colonizing species from permanent habitats.

The primary sources of macroinvertebrate colonization in streams are downstream drift, upstream migration, aerial sources (e.g., oviposition), and vertical migration upward from the substrate (Williams and Hynes 1976, Townsend and Hildrew 1976, Williams 1977). Williams (1977) showed that a significant fraction of colonizers in two temporary streams were from the hyporheos, and Hultin et al. (1969), Bishop and Hynes (1969), and Elliott (1971b) documented significant upstream migration of macroinvertebrates. Others (Kennedy 1955, Patrick 1959, Waters 1964) showed the importance of drift in the colonization process. Larimore et al. (1959) suggested aerial sources as being primary in the stream they studied.

We studied an intermittent section of Stewart's Creek, a mountain stream, to determine colonization patterns. We hypothesized that only migrating macroinvertebrates capable of utilizing existing stream conditions would colonize and there would be a succession of organisms. The purpose of this paper is to describe the patterns of colonization seen when water was flowing through the intermittent section of stream.

### METHODS AND MATERIALS

#### Study Site

Stewart's Creek is a small second-order (Strahler 1957) stream originating from a glacial cirque on the southeast face of Mt. Timpanogos about 33 km northeast of Provo, Utah. Glacial sediments form the substrate through which the stream channel is cut. The dominant substrate particle sizes (Cummins 1962) are cobble and large pebble. Mean annual discharge is 0.25 m<sup>3</sup>/sec; mean annual water temperature is 4–5 C. During low water years the receding groundwater level causes a 300 m section of stream to periodically dry up due to the porosity of the sediments and the slope (11%). From October 1976 to May 1978, this section of stream remained dry due to below normal winter snow pack. Following an average snowfall during the winter of 1977–1978, we anticipated that flow in the intermittent reach would resume during spring and summer of 1978. Five sampling stations were established within a 450

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m section. These included both permanent flowing upstream (UP) and downstream (LP) sites and three sites approximately 100 m apart in the temporary stream section: upper temporary (UT), a site 50 m below UP in the temporary channel, middle temporary (MT), 100 m below UT, and lower temporary (LT), which was 100 m below MT and 50 m above LP.

### Sampling

On 30 April 1978 ten 30 cm × 30 cm × 15 cm basket samplers were placed in the stream channel at each study site by digging through the snow cover. The samplers were made of steel frame covered with 4 cm<sup>2</sup> mesh hardware cloth on all sides except the top, which was open. Each sampler was filled with cobble from the stream bed. The rocks placed in the samplers were cleaned of all organisms and detritus.

Two baskets randomly chosen were removed weekly from each study site for five weeks beginning the day water entered the temporary sites. The permanent site baskets colonized for 15 d before water entered the intermittent section. Macroinvertebrates were washed from the rocks, preserved in 10% formalin, sorted in the laboratory, identified, and counted.

Since water continued to flow in the channel after all basket samplers had been removed, we continued to sample the macroinvertebrate community using Surber samplers (230 μm mesh). Two Surber samples were collected weekly from each of the temporary (UT, MT, LT) and permanent (UP, LP) sites beginning on week six for nine additional weeks. These samples were processed as described above.

A drift net (250 μm mesh) was placed weekly immediately below UP and above

LP. The nets were placed at 1700 h and removed between 1900 and 2000 h. The contents of the nets were processed as described earlier. Discharge was measured at both drift net sites and at MT with a flow meter on each sampling date.

### Analysis

Macroinvertebrate data were analyzed with categorical data analysis for cross classified data where categories were site and date. Trends across time and differences between the ratios of the cell frequencies at each site were determined using a log-linear model with orthogonal contrasts (Fienberg 1978). All analyses were performed using RUMMAGE (Scott et al. 1974), a general linear models program. Basket and Surber sample data were analyzed separately. No relationship between these two methods is intended.

### RESULTS

The resumption of flow in the intermittent stream section began 15 May 1978. After three days a cold spell stopped snowmelt and the flow was interrupted for three days, after which the stream began to flow again through the intermittent section.

### Taxa Richness

The numbers of taxa found at upper and lower permanent sites were not different (basket samplers,  $p = .521$  and Surber samplers,  $p = .227$ ) (Table 1). The upper and lower permanent sites had more taxa ( $p < .05$ ) than any of the temporary sites through both the basket and Surber sampling schedules (except the comparison of UT with LP). The UT site had more taxa ( $p < .05$ ) than did

TABLE 1. Taxa richness and density (number/m<sup>2</sup>) for starting basket samplers = SBS, ending basket samplers = EBS, starting Surber samplers = SSS, and ending Surber samplers = ESS for all sampling stations.

Site	Richness				Density			
	SBS	EBS	SSS	ESS	SBS	EBS	SSS	ESS
UP	8	15	16	26	1255	1103	3354	9742
UT	3	11	8	16	112	1589	1222	3345
MT	0	2	5	12	0	835	1089	3311
LT	0	3	6	13	0	440	1232	5534
LP	11	11	15	18	988	2778	1685	6625

MT during the basket colonization but not in the Surber sampling period. The middle temporary site never differed from LT in number of taxa, and both were lower than any other site throughout the study. Both taxa richness and density increased faster at UT than any other temporary site. The number of taxa increased linearly at all sites over time ( $p < .01$ ).

### Densities

The upper permanent site (UP) had higher densities ( $p < .01$ ) than any site except LP during the Surber sampling period (Table 1). The densities of organisms were not different ( $p > .05$ ) between middle temporary and lower temporary during the first five weeks (basket sampling) but were higher at LT ( $p < .05$ ) during the following nine weeks (Surber sampling). The permanent sites had higher ( $p < .05$ ) densities than any intermittent site throughout the study.

### Community Structure

Horn's (1966) measure of community overlap was calculated for the numbers of species at UP and LP at the start and end of each sampling method (Table 2). The value of overlap,  $R_o$ , approaches 1.0 as the amount of overlap increases. The low overlap at the beginning of the experiment ( $R_o = .43$ ) reflects the differences that had developed between the permanent sites while separated during drought conditions for approximately 1.5 to 2.0 years. Following the connection by water after the runoff event, LP and UP showed a linear increase in community overlap as LP became more like UP.

### Colonization Patterns of Selected Organisms

The general pattern across taxa was that colonization began later at MT and LT than at UT. Once colonization was initiated, densities rapidly increased until MT and LT were similar to UT. This general pattern was variable between groups of organisms.

Based on their densities throughout the study period and their feeding and dispersal strategies, the following taxa were selected for detailed analyses: *Baetis* spp. (Baetidae: Ephemeroptera), *Neothremma* sp. (Limnephilidae: Trichoptera), and four genera of

Ephemeroptera in the family Heptageniidae, *Cinygmula* spp., *Heptagenia* spp., *Epeorus* spp., and *Rhithrogena* spp. *Baetis* and *Neothremma* are both in the collector feeding functional group (Merritt and Cummins 1978), but they exhibit distinct differences in mobility. *Baetis* is an excellent swimmer, actively entering the drift (Corkum et al. 1977, Corkum 1978a,b). *Neothremma*, a sand case-building caddisfly, may be passively distributed (Minshall and Winger 1968). The heptageniids are all in the collector-gatherer feeding functional group. They are all dorsoventrally flattened and adapted for crawling and are not considered good swimmers (Corkum 1978a).

*Baetis* were the first organisms to colonize the temporary sites (Table 3). The upper permanent site baskets had more *Baetis* than all downstream site baskets ( $p < .05$ ), and UT had more than all sites below it, including LP ( $p < .05$ ). The lower permanent site had the highest density of *Baetis* during the basket sampling (1333/m<sup>2</sup>), but, over all dates, LP was lower than UP and UT ( $p < .05$ ). By the end of the Surber sampling, UP, MT, and LP had similar numbers of *Baetis* ( $p > .05$ ) and each of these sites had higher numbers of *Baetis* than either UT or LT ( $p < .05$ ).

*Neothremma* density was greater at UP than at any lower site ( $p < .05$ ) in both the basket and Surber sampling periods (Table 3), although the lower permanent site was colonized before any temporary site. The lower permanent site had more *Neothremma* than all stations above it ( $p < .05$ ) except UP ( $p > .05$ ) by the end of the basket sampling period. At the conclusion of the study a comparison of *Neothremma* density between sites showed UP > UT > MT > LT. Density was higher at LP than LT ( $p < .05$ ), but it was not different from any other site ( $p > .05$ ).

TABLE 2. Horn's (1966) measure of community overlap ( $R_o$ ) between Upper Permanent and Lower Permanent sites at the start and end of basket and Surber sampling efforts.

Sampler and period	$R_o$ °
Beginning basket sampling	.43
Ending basket sampling	.57
Beginning Surber sampling	.64
Ending Surber sampling	.74

\*1.0 = complete similarity or overlap

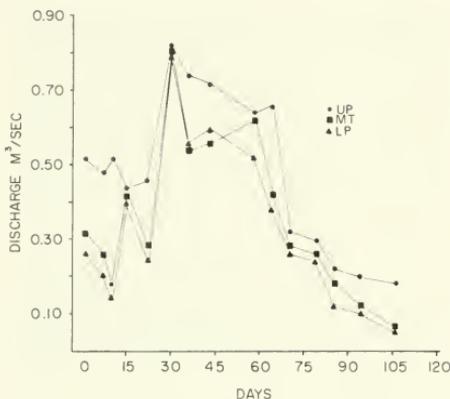


Fig. 1. Spring-summer hydrograph of Upper Permanent (UP), Middle Temporary (MT), and Lower Permanent (LP) sites on Stewart's Creek.

The upper temporary site had the fastest colonization by Heptageniidae (Table 3). During the basket sampling period there were no differences between any site except UT and LT ( $p > .05$ ), where UT was higher. The numbers of heptageniids increased over time at all the temporary sites. Middle temporary had more heptageniids than all sites ( $p < .05$ ) except LP ( $p > .05$ ), which had more than all sites during the Surber sampling.

#### Drift

Catastrophic drift, caused by high flow conditions, should be reflected in the density of organisms in the drift taken during the ascending limb of the spring hydrograph (Anderson and Lehmkuhl 1968). The patterns for total species, *Neothremma*, *Baetis*, and Heptageniidae are shown in Figure 1. At LP, drift (Fig. 1) was lowest during the ascending portion of the hydrograph (Fig. 2).

TABLE 3. Mean densities (number/m<sup>2</sup>) of *Baetis*, *Neothremma*, and Heptageniidae for starting basket samplers = SBS, ending basket samplers = EBS, starting Surber samplers = SSS, and ending Surber samplers = ESS for all sampling stations.

Taxa	UP				UT				Sampling
	SBS	EBS	SSS	ESS	SBS	EBS	SSS	ESS	
<i>Baetis</i>	256	67	217	244	11	769	89	278	
<i>Neothremma</i>	722	356	1835	4667	0	333	445	343	
Heptageniid	122	11	456	311	22	233	56	422	

The numbers of species increased in the drift over time ( $p < .05$ ) at the lower drift station (Fig. 1). Each group studied; i.e., *Baetis*, *Neothremma*, and Heptageniidae increased in numbers at the lower station between the 9th and 12th sampling weeks. It was during this same interval (9th-12th weeks) that the largest reduction in discharge occurred (Fig. 2).

At the lower site, total species, total organisms, and the density of *Baetis*, *Neothremma*, and heptageniids were positively correlated with discharge during the ascending part of the stream hydrograph (Table 4). These same groups continued to increase when discharge was decreasing ( $p < .05$ ). The upper drift net site had negative but not significant correlation coefficients ( $p > .05$ ) for both the ascending and descending comparisons.

#### DISCUSSION

The large amount of litter that accumulated in the channel during the dry period was washed out during the ascending limb of the spring hydrograph; however, leaf pack accumulations did remain in the temporary sections. We therefore expected that organisms that feed on detritus and are good dispersers would disperse throughout the intermittent area given sufficient time. *Baetis* are active drifters and good swimmers; they also feed by collecting detritus. *Baetis* were the most similar in their distribution and abundance at all study sites (Table 3) by the end of this study.

If an organism is a passive disperser, then we would expect a pattern of high densities nearer to the source of colonizers, with decreasing densities further from that source. *Neothremma* showed such a pattern. The higher densities at LP could be due to changes in flow conditions, i.e., increased

settling with reduction in flow, or upstream migration from lower adjacent permanent sections.

The increases in heptageniid density at LP and MT, larger than that of UT and LT, have two possible explanations. First, the heptageniids might have migrated upstream from below LP. Second, heptageniids may have quickly moved through the temporary sites in response to poor food or habitat conditions. A pattern similar to *Neothremma* would be expected if heptageniid drift were passive. If the organisms were moving to better feeding conditions, then they should congregate wherever a food source was found. Being poor swimmers but adapted for crawling, heptageniids may have moved up from LP through LT or down from UP through UT. Since there were no Heptageniidae found in the drift until after the sixth week, we have assumed a crawling migration for Heptageniidae into the temporary sites.

*Baetis* and Heptageniidae density at MT during July and August was greater than for the other temporary sites. Since MT is an approximate midpoint in the study sites, then the high densities may be a function of the overlap in organisms migrating up from LP and down from UP. The higher densities at middle temporary may also be due to the study terminating before equilibrium densities could be established at UT and LT. *Baetis* drift easily and were shown to be distributed with some equality throughout the study sites. Therefore, an increase in *Baetis* at any one site after sufficient time indicates a selection for a preferred habitat.

Even though there was a significant increase in discharge during the early weeks of the study, drifting organisms did not follow a similar pattern. The numbers of organisms leaving UP increased over time, but did not increase in proportion to the changes in dis-

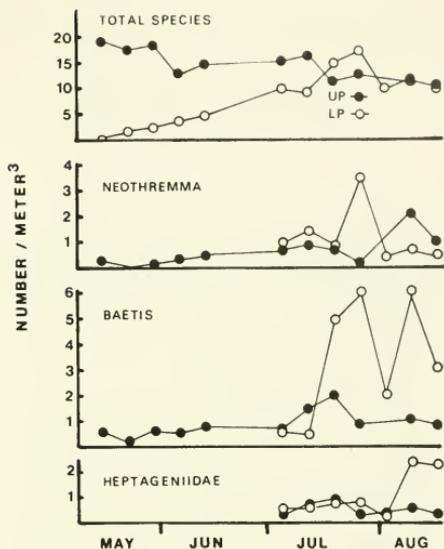


Fig. 2. Changes in the densities (number/m<sup>3</sup>) of taxa, *Neothremma*, *Baetis*, and Heptageniidae in drift below the Upper Permanent (UP) and above Lower Permanent (LP) study sites in Stewart's Creek.

charge. It was during the period of reduction in flow that drift increased most rapidly. This supports the work of Minshall and Winger (1968). This response may be a function of one or both of the following: (1) There is no net increase in drifting organisms but only a relative increase in density as the discharge decreases and (2) organisms are drifting as a behavioral response to these discharge changes. If No. 1 is correct then, after adjusting the drift densities for discharge and getting numbers/time, the ratio of any pair of data points should be unity. If the numbers of organisms/m<sup>3</sup> are actually increasing because more are actively entering the drift, then the ratios between adjusted pairs should increase

Table 3 continued.

site	MT				LT				LP			
	SBS	EBS	SSS	ESS	SBS	EBS	SSS	ESS	SBS	EBS	SSS	ESS
0	922	467	511		0	33	567	200	0	1333	622	100
0	33	144	147		0	0	44	178	256	422	78	500
0	278	367	800		0	244	456	878	11	223	267	822

TABLE 4. Correlation coefficients obtained from analysis of the relationships between either the ascending or descending limb of the hydrograph and total taxa, total numbers, *Baetis*, *Neothremma*, and Heptageniidae.

Site	Taxa richness		Densities		<i>Baetis</i>		<i>Neothremma</i>		Heptageniidae	
	Ascend	Descend	Ascend	Descend	Ascend	Descend	Ascend	Descend	Ascend	Descend
UP	-.17	-.35	-.58	-.58	-.66	-.17	-.70	-.48	-.50	-.16
LP	.84*	-.59	.91	-.77*	.95*	-.18	-.02	-.81*	.40	-.37

\* =  $p < .05$

over time and the slope of the regression of these adjusted numbers against time should not equal zero. The slope of each curve was significantly different from zero ( $t > \text{critical value}$ ,  $p < .05$ ), indicating a behavioral response of the macrobenthos.

The benthic sampling procedures used in this study were not selective for any one colonization vector, i.e., vertical (from hyporheos), aerial (ovipositing), downstream drift, and upstream migration. We felt that the influence of vertical movement and aerial colonization would be uniform throughout the study site, whereas drifting and upstream movement would show a response to distance. This response would depend on the distance from the colonization source and the dispersal ability of the organisms (Waters 1964, McLay 1970, Elliott 1971a). Some researchers have demonstrated significant upstream movement (Hultin et al. 1969, Bishop and Hynes 1969, Elliott 1971b). The distances traveled upstream were up to 600 cm/night (Elliott 1971b). At that rate an organism could hypothetically move upstream the length of the temporary section in 50 d. Although this is possible, the results of the drift measurements show that there are sufficient colonizing organisms in drift to account for the colonization patterns we described for *Baetis* and *Neothremma*.

The established stream communities, UP and LP, were the primary sources of potential colonizers. Active and passive drift organisms leaving UP would first reach UT. Once settling out, an organism may stay or leave depending on the suitability of the habitat, availability of food, space, and flow conditions.

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