Seasonal and Longitudinal Changes in Invertebrate Functional Groups in the Dolores River, Colorado[1]

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Abstract. A 46 km section of the Dolores River, in southwest Colorado, was studied to determine the relative abundance of invertebrate functional groups over an altitudinal gradient of 500 m during three seasons. The Dolores River is a third order stream with an average width of 11 m in the upper 8 km of the study area. In the lower 38 km of the study area, it is a fourth order stream with an average width of 15 m. Benthic invertebrates were collected with a modified Hess sampler in October 1980, and March and August 1981, from 11 stations on the Dolores River. Despite little change in either stream order, width or apparent food resources in the study area, there were noticeable differences in the relative abundance of functional groups, with shredders most abundant upstream and collectors most abundant in the mid-reaches. The observed trends were highly dependent upon season with shredders abundant at most stations only in spring. This was a result of life history patterns of winter stoneflies, the primary shredders. Collector-gatherers were most abundant at the upper-middle stations in summer, but were less abundant in the other two seasons. In general, the pattern appeared to conform more to the altitudinal shifts in benthic species composition than to stream order or width. This led to shifts in the assigned functional groups without noticeable changes in food resources.

Longitudinal changes in invertebrate species composition has been documented for a number of streams in Colorado (Allan 1975; Dodds & Hisaw 1925; Ward 1981; Ward & Berner 1980). These studies have concentrated on faunal replacement and species distribution along an altitudinal gradient but have not specifically addressed the functional relationships. According to current stream theory, changes in food sources along the stream gradient should be accompanied by concomitant changes in the functional organization of invertebrate communities (Cummins 1975; Vannote et al. 1980). Using this concept, Hawkins and Sedell (1981) compared the relative abundance of functional groups of four streams of increasing stream order and found generally good agreement with stream continuum theory. A recent study along a stream gradient in Idaho also concluded that functional groups change along the continuum with the greatest change occurring near the headwaters (Bruns et al. 1982). This paper summarizes benthic invertebrate collections conducted on the Dolores River in southwest Colorado over three seasons and compares the results to generalizations proposed in stream continuum theory (Vannote et al. 1980).

MATERIALS AND METHODS

Site Description

The Dolores River lies in the upper Colorado River basin in southwest Colorado (Fig. 1). It arises in the San Juan Mountains and flows roughly south, southwest through the study area. The upper Dolores River and some of its tributaries have been adversely influenced to varying degrees in the past by metal mining activity (Bingham 1968; Anaconda Minerals Co. 1981). Mine drainage enters the Dolores River from three primary sources in the Rico area: a series of settling ponds between Stations D-2 and D-5,

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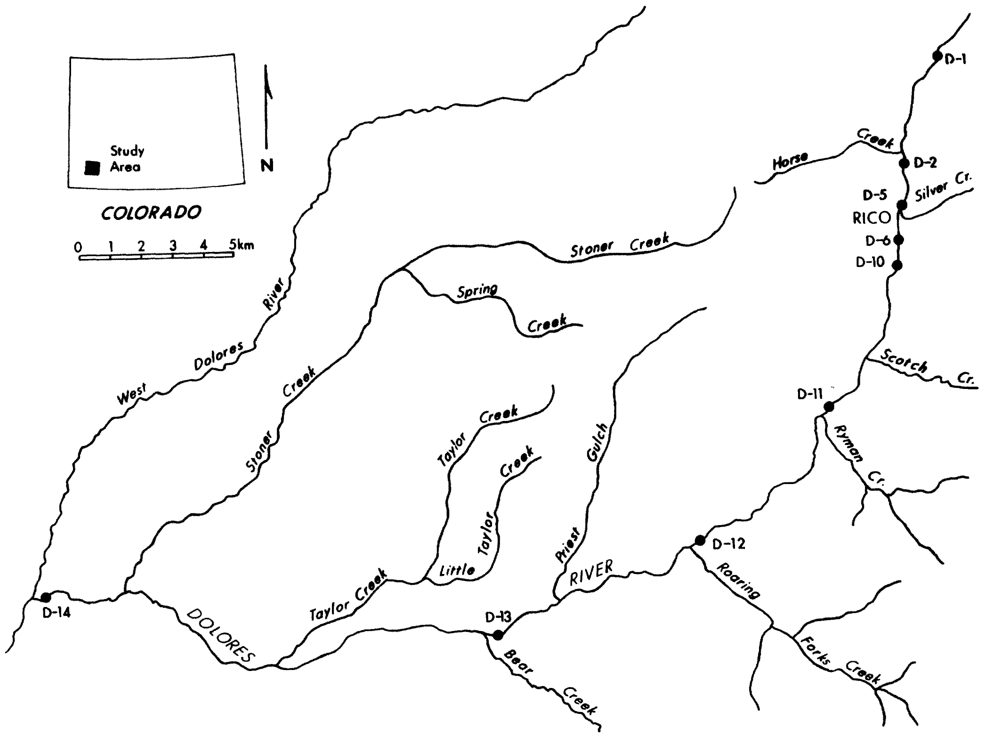

Fig. 1. Locations of sampling stations on the Dolores River, Colorado.

abandoned tailing ponds on Silver Creek, which enters the Dolores River between Stations D-5 and D-6, and abandoned mine adits between Stations D-6 and D-10. The drainage is not acidic and primarily adds suspended metals. The lower portion of the study area is generally undisturbed with some agricultural activity and residential property.

Nine stations were established in October 1980 on a 46 km section of the Dolores River over an altitudinal gradient of 500 m (Fig. 1). In the upper 8 km of the study area, the Dolores River is a third-order stream with average width of 11 m (Table 1). It is a fourth-order stream in the lower 38 km with an average width of 15 m. At the upper Station, D-1, the river meanders through a broad glaciated valley. The stream banks are lined with willows, with aspen and spruce on the valley walls. Substrate at this station is rubble-boulder. At Station D-2 the Dolores River flows through a narrower valley with less woody riparian vegetation and rubble and large boulder substrate. From Station D-5 to D-11, gradient decreases gradually and substrate remains rubble-boulder. Willows and alders line the banks in this area with large cottonwoods intermittently abundant. Substrate is rubble and large boulders at Stations D-12 and D-13. Although willows and alders grow along the stream, these stations are shaded by large cottonwoods and spruce trees. The river valley widens out at D-14 with willows and alders along the south bank and a large rubble bar on the north bank.

Since changes in food resources are important to the discussion of functional groups, some observations on possible food sources were made although these sources were not measured directly. Riparian shading of the stream was a factor only at the middle stations, D-12 and 13. Lack of shade is common in western streams where woody riparian vegetation, consisting primarily of smaller willows and alders, can offer little shade to a

TABLE 1

Physical characteristics of sampling stations on the Dolores River, Colorado (width and discharge values are for August 1981).

Station	Stream Order	Stream Width (m)	Discharge m^3/s	Gradient (%)	Elevation (m)	Distance Downstream (km)
D-1	3	7.3	1.41	0.9	2761	0.0
D-2	3	12.0	2.11	2.2	2688	4.0
D-5	3	10.4	1.86	1.3	2661	5.5
D-6	3	11.9	2.00	1.4	2652	6.2
D-10	3	11.0	2.14	1.2	2636	7.8
D-11	4	12.2	2.60	1.2	2566	13.2
D-12	4	13.4	2.68	1.0	2487	20.7
D-13	4	16.8	2.40	1.0	2405	29.1
D-14	4	16.8	2.97	0.8	2249	46.0

stream the size of the Dolores River. Input of leaf litter did not appear to differ between stations and natural leaf packs were rarely observed. Debris dams were not present at any of the stations and large particulate organic matter did not appear to accumulate to any great degree. Despite the lack of shade, periphytic algae appeared to be sparse, rarely visible as a thin film on the rock surfaces. Periphyton biomass exibited no downstream trend, averaging 1.5 mg/cm^2 ash free dry weight in both the third-order upper 8 km section and the fourth-order lower 38 km section (Anaconda Minerals Co. 1981).

Sample Collection and Analysis

Nine stations on the Dolores River were sampled in fall 1980 and spring and summer 1981. A modified Hess sampler which encloses 0.1 m^2 and has an average net mesh size of 700 μm was used to collect three benthic invertebrate samples at each station. Samples were preserved in the field with 95% ethanol containing Rose Bengal biological stain and returned to the laboratory where the organisms were hand sorted from the debris, identified and counted. Identification were made to the lowest practical taxonomic level using available keys. Taxa were assigned to one or two of five functional groups (Shredder, Scraper, Collector-gatherer, Collector-filterer and Predator) using the tables found in Merritt and Cummins (1978). Some taxa, such as heptageniid mayflies, have less defined feeding methods and were placed into two functional categories, scrapers and collector-gatherers. The list of taxa collected and the functional group they were assigned to is presented in Table 2. Estimates of densities of each functional group were determined and relative abundance calculated for each station over the three seasons. For taxa assigned to more than one group, density was divided and added to each classification for the calculations.

RESULTS AND DISCUSSION

There was little apparent change in the Dolores River in terms of stream order, stream width or food sources, parameters normally associated with changes along a stream continuum (Vannote et al. 1980). Nevertheless, certain functional groups exhibited a definite downstream pattern through the study area (Fig. 2). Notably, these downstream patterns exhibited no apparent relation to input of mine drainage. It has been shown that benthic densities were reduced at stations below the mining activity, without large reductions in number of species (Anaconda Minerals Co. 1981). The effects appeared to be non-selective, favoring no particular taxon. Thus, while total density may have decreased, there was little apparent effect of the input of mine drainage on the relative abundance of the functional groups (Fig. 2).

TABLE II

Species list and funtional group classifications of benthic invertebrates from the Dolores River, Colorado.

Taxa	Functional Group
INSECTA	
Ephemeroptera	
Baetis tricaudatus	C-G
Baetis bicaudatus	C-G
Rhithrogena hageni	C-G,S
Rhithrogena robusta	C-G,S
Cinygmula sp.	C-G,S
Epeorus longimanus	C-G,S
Epeorus deceptivus	C-G,S
Ameletus sparsatus	C-G
Ameletus velox	C-G
Paraleptophlebia heteronea	C-G
Drunella grandis grandis	C-G
Drunella doddsi	S
Drunella coloradensis	C-G
Attenella margarita	C-G
Ephemerella infrequens	C-G
Plecoptera	
Chloroperlidae	P
Pteronarcella badia	Sh,S
Pteronarcys californica	Sh
Prostoia besametsa	Sh
Taenionema nigripenne	S
Zapada haysi	Sh
Claassenia sabulosa	P
Megarcys signata	P
Isogenoides elongatus	P
Isogenoides zionensis	P
Diura knowltoni	P
Cultus aestivalis	P
Isoperla fulva	P
Capnia spp.	Sh
Trichoptera	
Hydropsyche sp.	C-F
Cheumatopsyche sp.	C-F
Arctopsyche grandis	C-F
Hydroptila sp.	Sh,S
Rhyacophila coloradensis complex	P
Rhyacophila angelita	P
Rhyacophila acropedes	P
Rhyacophila oreta	P
Glossosoma sp.	S
Brachycentrus americanus	C-F
Brachycentrus occidentalis	C-F
Lepidostoma sp.	Sh
Dicosmoecus sp.	S
Oligophlebodes sp.	S
Diptera	
Atherix pachypus	P
Simulium sp.	C-F
Hexatoma sp.	P
Antocha sp.	C-G
Hesperoconopa sp.	C-G
Dicranota sp.	P
Erioptera sp.	C-G
Protanyderus sp.	P
Bibiocephala sp.	S
Pericoma sp.	C-G
Palpomyia sp.	P
Hemerodromia sp.	P
Chelifera sp.	P
Orthocladius sp.	C-G
Psectrotanypus sp.	P
Cricotopus sp.	Sh
Thienemannimyia sp.	P
Microspectra sp.	C-G
Parametriocnemus sp.	C-G
Eukiefferiella sp. 1	C-G
Eukiefferiella sp. 2	C-G
Diamesa sp.	C-G
Coleoptera	
Optioservus castanipennis	S,C-G
Zaitzevia parvula	C-G
Heterlimnius corpulentus	C-G
Helichus striatus	S
Narpus sp.	C-G
Oreodytes crassulus	P
HYDRACARINA	P
MOLLUSCA	
Gastropoda	S
OLIGOCHAETA	C-G
TURBELLARIA	P

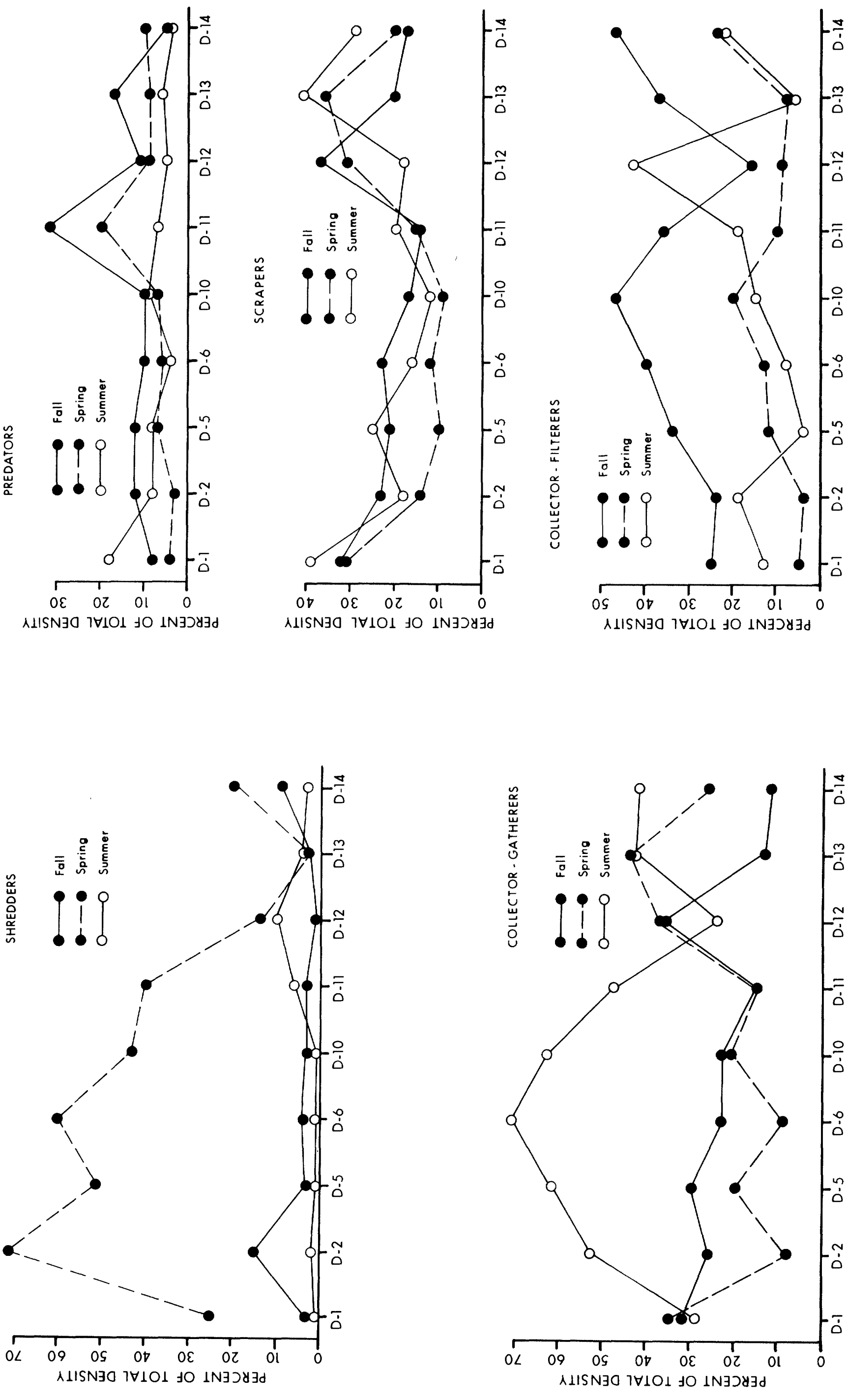

Fig. 2. Relative abundance of functional groups over three seasons at stations on the Dolores River, Colorado.

Shredders exhibited a downstream pattern of relative abundance that was highly dependent on season. They dominated the benthic invertebrates in spring, having the greatest numerical importance at the upper stations and gradually decreasing in abundance downstream. Shredders were relatively less abundant at all the stations during summer and fall. This spring abundance of shredders differs from the study by Hawkins and Sedell (1981), which reported a shredder predominance in third-order streams during all seasons, with a fall maximum in abundance. The spring abundance observed in the present study appears to be primarily due to the life history patterns of shredding stoneflies such as *Prostoia besametsa* and *Capnia* spp. These winter stoneflies were abundant in spring and are the predominant shredders in Colorado mountain streams (Short & Ward 1980a, b, 1981; Short, Canton & Ward 1980). The small rise in shredder importance at the lowest station in spring was due to the caddisfly *Lepidostoma* sp. rather than stoneflies.

Collector-gatherers did not exhibit a consistent downstream increase as would be expected (Hawkins & Sedell 1981; Vannote et al. 1980) but rather a trend more similar to the shredders (Fig. 2). Gatherers were relatively most abundant in summer and were most important at the upper-middle stations with gradually decreasing importance downstream. Mayflies were the most abundant gatherers. Gatherers exhibited no clear pattern of relative abundance during the other two seasons.

As postulated in the stream continuum (Vannote et al. 1980), predators did not exhibit significant changes in relative abundance through the study area. Only slightly increased abundance at Station D-11 was observed in fall and spring due to greater numbers of chloroperlid stoneflies.

Scrapers generally exhibited the greatest abundance at the uppermost station and lower stations during all seasons (Fig. 2). This was due primarily to abundance of scraping mayflies and caddisflies, which are typically dominant members of mountain stream communities (Allen 1975; Canton & Ward 1981; Short & Ward 1980a; Ward & Berner 1980). Scrapers and scraping collector-gatherers are abundant throughout the study area. This may be due to the more open canopy typically found in montane streams, which favors rock scrapers feeding on periphyton (Wiggins & Mackay 1978).

Collector-filterers did not present the pattern expected along this length of stream. During fall, filterers were abundant upstream due to the filter-feeding caddisflies *Brachycentrus americanus* and *Arctopsyche grandis*. However, the abundance of filterers at the lowest stations was due primarily to net-spinning caddisflies (*Hydropsyche*). Filterers did not vary significantly in relative abundance in any season.

The Dolores River does not change significantly in stream size through the study area. Yet some functional groups did exhibit marked downstream shifts in relative abundance whereas others exhibited relatively little change. Although historic mining activity has been shown to adversely effect invertebrate communities, it did not appear to directly correlate with changes in the relative abundance of Dolores River functional groups.

This study demonstrated that longitudinal changes in the relative abundance of functional groups can occur along stream gradients that do not vary greatly in stream order or width. In addition, the trends occurred despite an apparent lack of significant differences in food resources. Notably, the observed trends were not consistant over the seasons.

This study suggests that documenting stream continuum theory using relative abundance of invertebrate functional groups may be ecologically misleading. The trends noted in the Dolores River appeared to occur primarily as a result of life history phenomena and altitudinal shifts in species composition rather than any apparent changes in food resources. Thus, the changes in relative abundance of functional groups noted above become merely artifacts of seasonal variations in species composition. It is possible that shifting relative abundance of functional groups may be as site specific, as seasonal and as dependent on species' life histories as are a species' food habits.

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