Structure of Benthic Macroinvertebrate Communities in a Midwestern Plains Stream[1, 2]

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Abstract. Functional group structure of benthic macroinvertebrate communities was compared among three distinct reaches of the Redwood River, a plains stream in southwestern Minnesota. Deciduous leaf-fall comprised the allochthonous organic input to the upstream site, typical of a woodland stream; at the middle site, fine particulate organic matter, derived from soils in agricultural croplands, comprised the main allochthonous import; and at the lower site, soil-derived particulates and zooplankton from an impoundment comprised the main organic import. Mineral fine particulates, primarily silt, entered the stream during most of the year. The upstream site was most similar to other woodland streams in its functional invertebrate structure, with shredders and collectors both well represented. In the middle and downstream communities, collectors were quantitatively most important, with gatherers in depositional reaches and filterers in erosional reaches. Instability of physical habitat, influenced by heavy siltation from agricultural croplands appeared to favor a community of generalist collectors.

Numerous recent developments in stream ecological research have improved greatly our understanding of the small woodland stream ecosystem, wherein the importance of allochthonous organic detritus as an energy source has been stressed (Anderson & Sedell 1979; Cummins 1974; Cummins & Klug 1979). In the typical deciduous woodland stream, inorganic substrates are generally stable, and the main allochthonous energy source is the autumn leaf-fall (Anderson & Sedell 1979). The means by which deciduous leaves are processed by aquatic macroinvertebrates and other organisms determine community structure, in which different functional groups perform successive detritus processing, e.g., shredders, gatherers, filterers (Anderson & Sedell 1979; Cummins 1973, 1974; Cummins & Klug 1979; Wallace & Merritt 1980; Wallace, Webster, & Woodall 1977; Wiggins & Mackay 1978). Progressive changes in community structure have been extrapolated to higher order streams based on the decreasing importance of coarse detritus from riparian vegetation, increasing transport of fine organic materials from upstream, and increasing algal production (Cummins 1975; Vannote, Minshall, Cummins, Sedell, & Cushing 1980).

In contrast to the woodland stream, the plains stream of midwestern North America differs in two important respects: 1) the substrate is commonly composed of finer mineral particles such as sand and silt and may be highly unstable, varying seasonally with great fluctuations in discharge, and 2) the main allochthonous detritus consists of fine particulate organic matter derived from surrounding croplands or plains, supplied throughout the open-water (ice-free) season, rather than in a major pulse at one time. Intensive studies of the structure of the macroinvertebrate community in plains streams would now appear useful, particularly to draw the contrast with the typical woodland stream.

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Toward the objective of drawing this contrast, the benthic macroinvertebrate structure was studied in the Redwood River, a plains stream in southwestern Minnesota.

STUDY SITE

The Redwood River is a major tributary to the Minnesota River draining a watershed of 1914 km^2, mostly agricultural cropland, in southwestern Minnesota. The Redwood flows 142 km in a northeasterly direction from its headwaters on the Coteau des Prairies, an upland plain and the most prominent topographic feature of the region.

Three study sites were chosen to typify major community types and environmental regimes characteristic of plains streams in the region. The Camden (upstream) site was located on the slope off the Coteau des Prairies in a wooded valley cut deeply into glacial till. Camden was least affected by agricultural practices and shared some of the characteristics of typical woodland streams (Table 1).

The Vesta (middle) site was located on a lowland plain between the Coteau and the Minnesota River valley. Cultivated fields encroached within a few meters of the channel; large quantities of silt and fine soil detritus entered the channel with snow melt and rain showers so that the water was almost always turbid. Substrates were subject to severe alteration by scour and deposition with extremes of discharge.

The Ramsey (downstream) site was below an impoundment, Lake Redwood, on the steep slope into the Minnesota River valley where the Redwood descends through a deep canyon with steep walls of weathered precambrian granite. Here the river received particulate organic matter from three sources: leaves from riparian vegetation, fine detritus which came through the reservoir from upstream, and plankton produced in the reservoir (MacFarlane & Waters 1982).

MATERIALS AND METHODS

The benthos was sampled at approximately monthly intervals from November 1974 through October 1975. Ten samples were obtained in a random manner from each site each month using a 0.1 m^2 Surber sampler with 471 μm mesh netting. Substrates were sampled to a depth of 10 cm. Field observations of substrate characteristics were recorded for each sample including substrate composition, observable vegetation, amount and

TABLE I

Selected physical characteristics of the Redwood River study sites.

Characteristic	Camden	Vesta	Ramsey
Stream Order	2nd	3rd	3rd
Gradient[a] (m/km)	3.6	0.7	19.0
Channel Width (m)	8	10	20
Water Temperature Range (°C)	0-24	0-31	0-28
Annual Mean Discharge[b] (m^3/s)	1.3	1.9	2.9
Substrate[c]	Small pebbles	Coarse sand	Small cobbles
Median ϕ Diameter	-4.6	-0.5	-6.5
Mean % Silt	0.06	4.34	0.09
Allochthonous Detritus	CPOM	FPOM	FPOM
Predominant Source	leaves	soil	soil
Sestonic FPOM[d] (g/10,000L)	0.29	0.13	0.65
Predominant Type	detritus	detritus	plankton detritus

[a]Minnesota Conservation Department (1959)
[b]U.S.G.S. gaging stations at Marshall (35 yrs.), Seaforth (1 yr.), and Redwood Falls (41 yrs.).
[c]From ten substrate samples per site collected in June and July.
[d]Dry weight concentration from 24-h drift samples collected in June and July, size range 100-1000 μm.

kind of detritus, and degree of siltation. These observations were used to follow seasonal changes in the substrates and to evaluate the stability of substrate characteristics.

All members of the macrobenthos were sorted into taxa and weighed (wet). Standing stock data were later collated into appropriate functional groups based on the ecological tables provided by Merritt and Cummins (1978). When more than one functional group was listed for a single taxon, the first one listed was assumed predominant; no attempt was made to arbitrarily partition the standing stock of a single taxon between two or more functional groups.

RESULTS

Benthic communities in the Redwood River differed in varying degrees from the functional groups structure characteristic of a typical woodland stream (Table 2). Shredders, a predominant functional group in small woodland streams, represented an important part only at Camden, 13.7% of the standing stock, presumably because this reach was more similar to woodland streams where deciduous leaf-fall is the major source of imported particulate organic matter. Shredders comprised only a small part of the benthos in the lower communities.

A predominance of collectors in all three communities was especially notable. Collectors accounted for 72% of the standing stock at Camden and for over 90% at Vesta and Ramsey. These are proportions more typical of higher order streams (Cummins 1975; Vannote et al. 1980) and presumably reflect the overwhelming importance of allochthonous fine particulates in this plains stream. Filterers predominated in erosional reaches and gatherers in depositional reaches.

A large standing stock of filterers at Ramsey was comprised largely of hydropsychid caddisflies. These dense hydropsychid populations were apparently sustained in part by the drift of plankton from Lake Redwood, including large quantities of zooplankton during most of the year (MacFarlane & Waters 1982). Refined mechanisms for partitioning food and habitat resources probably assured the success of filtering specialists (Mackay & Wiggins 1979; Wallace et al. 1977), whereas a more generalist strategy prevailed in most functional groups (Tables 3).

Gatherers attained their highest standing stock at Ramsey sustained by large imports of fine detritus from upstream and probably with a significant supplement from benthic primary production. Coarse substrates provided the most complex physical habitat structure in this reach, minimized habitat alteration by scour, and presumably facilitated the exploitation of particulate resources.

TABLE II

Mean annual standing stocks (g/m^2 wet) and percent of mean annual standing stocks for macroinvertebrate functional groups from three communities in the Redwood River.

	Camden			Vesta			Ramsey		
Functional Group	Mean	95% C.I.	%	Mean	95% C.I.	%	Mean	95% C.I.	%
Collector-gatherers	8.7	(5.8-10.8)	32.3	11.3	(4.9-16.8)	53.9	22.4	(13.6-28.3)	35.8
Collector-filterers	10.7	(5.3-13.5)	39.7	7.7	(2.2-12.0)	37.1	34.3	(18.7-44.1)	54.9
Shredders	3.7	(1.0-5.1)	13.7	0.0	(0.0-0.1)	0.1	0.7	(0.1-1.1)	1.1
Scrapers	1.2	(0.8-1.5)	4.4	0.8	(0.4-1.2)	3.9	1.3	(1.0-1.6)	2.1
Piercers-hervbivores	0.2	(0.1-0.3)	0.9	0.5	(0.1-0.8)	2.6	0.2	(0.1-0.3)	0.4
Predators-piercers	1.1	(0.4-1.6)	4.0	0.1	(0.0-0.2)	0.3	0.1	(0.0-0.1)	0.2
Predators-engulfers	1.4	(0.8-1.8)	5.0	0.4	(0.1-0.7)	2.1	3.5	(2.0-4.5)	5.5
Totals	27.0		100.0	20.8		100.0	62.5		100.0

The minor importance of scrapers would seem incongruous for largely unshaded reaches like Vesta and Ramsey. Heavy siltation may handicap the more specialized scrapers leaving an abundant resource to generalist collectors. Significantly, the major scrapers collected were also functional generalists.

TABLE III

Summary of major macroinvertebrate taxa by functional group. Alternative functional classifications are listed for facultative representatives. Sites: C=Camden, V=Vesta, R=Ramsey.

Functional group		Sites	Alternative function
SHREDDERS			
Insecta			
Plecoptera			
Pteronarcidae	*Pteronarcys*	C	Predators, Scrapers
Taeniopterygidae	*Taeniopteryx*	C	Gatherers, Scrapers
Trichoptera			
Limnephilidae	*Pycnopsyche*	C, R	Scrapers
	Limnephilus	V	
Diptera			
Tipulidae	*Prionocera*	C, R	
SCRAPERS			
Insecta			
Ephemeroptera			
Heptageniidae	*Heptagenia*	V	Gatherers
Baetidae	*Pseudocloeon*	C	Gatherers
Coleoptera			
Dryopidae	*Helichus*	V	Gatherers
Elmidae	*Optioservus*	C	Gatherers
	Stenelmis	C, V, R	Gatherers
Gastropoda			
Physidae	*Physa*	C, V, R	Gatherers
Ancylidae	*Ferrissia*	C	
COLLECTOR—GATHERERS			
Insecta			
Ephemeroptera			
Heptageniidae	*Stenacron*	C, V, R	Scrapers
	Stenonema	C	Scrapers
Baetidae	*Baetis*	C, V, R	Scrapers
Tricorythidae	*Tricorythodes*	V, R	
Caenidae	*Caenis*	C, V, R	Scrapers
Potamanthidae	*Potamanthus*	V	
Ephemeridae	*Hexagenia*	C, V	
Polymitarcidae	*Ephoron*	C, V	
Diptera			
Chironomidae	Chironominae	C, V, R	Filterers
	Orthocladiinae	C, V, R	Scrapers
Tabanidae	*Chrysops*	C, V	
Crustacea			
Decapoda			
Astacidae	*Orconectes*	C, V, R	Shredders
Amphipoda			
Talitridae	*Hyalella*	C, V, R	Scrapers
Oligochaeta			
Haplotaxida			
Tubificidae		C, V, R	
Turbellaria			
Tricladida			
Planariidae		R	Predators

Table III continued

Functional group		Sites	Alternative function
COLLECTOR—FILTERERS			
Insecta			
Ephemeroptera			
Siphlonuridae	*Isonychia*	C	Predators
Trichoptera			
Hydropsychidae	*Cheumatopsyche*	C, V, R	
	Hydropsyche	C, V, R	
Diptera			
Simuliidae	*Simulium*	C, V, R	
Pelecypoda			
Sphaeriidae	*Sphaerium*	C, V, R	
	Pisidium	C, V	
PIERCERS—HERBIVORES			
Insecta			
Trichoptera			
Hydroptilidae		C, R	Scrapers, Gatherers
Hemiptera			
Corixidae		C, V, R	Gatherers
PREDATOR—PIERCERS			
Insecta			
Coleoptera			
Dytiscidae	*Liodessus*	R	
Diptera			
Rhagionidae	*Atherix*	C, V	
PREATORS—ENGULFERS			
Insecta			
Plecoptera			
Perlidae	*Acroneuria*	C	
	Perlesta	C	
Odonata			
Calopterygidae	*Calopteryx*	C	
Coenagrionidae	*Argia*	R	
Libellulidae	*Libellula*	V	
Trichoptera			
Polycentropidae	*Polycentropis*	R	Filterers, Shredders
Megaloptera			
Sialidae	*Sialis*	C, V, R	
Diptera			
Tipulidae	*Dicranota*	C	
	Pilaria	C, V	
Ceratopogonidae	Culicoidinae	C, V	
Empididae	*Roederiodes*	C	
Hirudinea			
Rhynchobdellida			
Glossiphoniidae	*Glossiphonia*	C	
	Helobdella	C, V, R	

Discussion

The kind and timing of particulate imports to the Redwood River appeared to have a strong influence on the structure of benthic communities. In contrast to woodland streams where deciduous leaf-fall in autumn is the major input of detritus, the major import to the Redwood River was fine particulate soil detritus from agricultural cropland throughout the open-water season. Consequently, the major role typically played by shredders in woodland streams was much reduced in this plains stream, and the functional structure was dominated by collectors, both gatherers and filterers depending on the distribution and transportation of detritus. This predominance of collectors may represent a shift in the stream continuum toward the headwaters, similar to that proposed by Vannote et al. (1980), due to perturbation by soil particlates. Mineral silts and clay were also imported to the stream from the same cropland source; their distribution and transportation in the stream appeared to affect both the physical habitat of benthos and availability of detritus as food. Instability of the physical habitat, caused by the large import, deposition, and transportation of mineral fine particulates, probably provides the generalist collectors with a competitive advantage and consequent predominance (Cummins & Klug 1979). Extreme physical fluctuation would seem characteristic for plains streams, and a high complexity in species function may act in place of high species diversity to maintain system stability (Vannote et al. 1980).

At Camden, however, detritus imports were more typical of woodland streams in kind (deciduous leaves) and timing of introduction (autumn). The greater importance of shredders in this community appeared to be the direct consequence. Siltation of benthic habitats was least severe at Camden and therefore had less effect on the functional structure, which was more similar to a woodland stream.

Physical instability was most apparent at Vesta, where, discharge, detritus import, and siltation were most directly influenced by agriculture. Substrates at Vesta typically experienced heavier siltation and severe scour during extremes of discharge. Habitat spatial structure was less complex, and the depositional habitats appeared particularly vulnerable to alteration. Removal of natural vegetation cover and cultivation of croplands increases fine particulate imports as well as the proportion of mineral to organic particulates (Bormann, Likens & Eaton 1969; Likens, Bormann, Johnson, Fisher, & Pierce 1970; Musgrave 1947). The instability of physical habitat and high import of fine particulates, both organic and mineral, apparently were the factors favoring the development of structure that was dominated by functional generalists particularly among the gatherers and scrapers; this community would seem to be the kind exhibiting the greatest opportunistic exploitation of resources.

At Ramsey, below Lake Redwood, the most notable feature of the functional structure was the predominance of filterers, sustained by sestonic drift from the impoundment. However, the relatively great importance of mineral silt also created a degree of instability to the physical substrate at this site; reduced discharge and increased silt/detritus deposition in late summer favored a displacement of specialists by generalists.

The distinction between gatherers and scrapers was probably the least meaningful. It is common for aquatic insects to be facultative participants in more than one functional group (Cummins & Klug 1979), and this apparently is particularly important for these members of the plains stream benthos. The major gatherers in the Redwood River were functional generalists, gatherers and scrapers, exploiting the benthic primary production of this shallow plains stream. The actual proportion of the standing stocks supported by scraping rather than gathering was not determined but probably would be large (Minshall 1978).

Two general contrasts may be drawn between the plains stream sites and the small woodland streams from which the functional groups system was developed. First, the greater importance of collectors, whether gatherers or filterers, appeared to be a consequence of the finer size of imported particulate ditritus and the longer season of its introduction to the stream from the agricultural terrestrial community. Whether gatherers or filterers predominated appeared to depend on the physical factors controlling the distribution of the soil-derived organic particulates within the channel, e.g., whether organic particulates are accumulated in a depositional habitat or are transported in swifter currents, respectively. Second, severe instability of the physical environment in the plains stream appears to favor generalists which predominate by opportunistic feeding, while specialists such as shredders and scrapers are notably less important.

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