

AN ABSTRACT OF THE THESIS OF

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Title: Colonization and Development of Macroinvertebrate Communities in Laboratory Streams.

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William J. Liss

Laboratory stream communities in simulated old growth second order streams were sampled June 1984 and June 1985 to advance an understanding of their organization and development, and their response to an environmental perturbation, the toxicant dieldrin. An interpenetrating hierarchical view of habitats and community subsystems was taken to conceptualize community organization. Major habitats defined major community subsystems and microhabitats defined subcommunity subsystems. Community development was influenced by colonization from a species pool and habitat development.

Four colonizing strategies were observed including High Potential, Pulse, Trickle and Intermittent colonizers. Seventy-four percent of the community biomass for all stream samples was composed of High Potential taxa. Riffle habitats contained the highest biomass and taxa diversity, and the Rapid habitat contained the lowest biomass and taxa diversity.

Trophic organization changed with time, was different in the toxicant treated stream and was unique to each microhabitat. Fine-particle detritivores were the most ubiquitous trophic group. Microphyte herbivores greatly decreased in 1985 from 1984 levels. Community differences in the toxicant treated stream included lower biomass, fewer microphyte herbivores, lower taxa diversity, a greater number of fine-particle detritivores and a smaller range of habitat utilization. Percentage similarity of subcommunities at both the major and microhabitat organizational levels found the 1985 control stream to contain the most distinct subcommunities. Habitat associations and trophic feeding habits provided the basis for a life history classification of the community taxa consisting of Habitat Generalists, Backwater and Slow Current organisms and Rheophiles.

Colonization and Development  
of Macroinvertebrate Communities  
in Laboratory Streams

by

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# COLONIZATION AND DEVELOPMENT OF MACROINVERTEBRATE COMMUNITIES IN LABORATORY STREAMS

## INTRODUCTION

Stream communities are biological systems that constantly change; they develop and evolve over time. Ecologists' conceptions of communities have ranged from the metaphorical organismic view of Clements (1916) to the individualistic-population view held by Gleason (1917). Clements saw the community as an organismic system developing over time and capable of reproducing with fidelity. Gleason held that communities are aggregations of individuals or, at most, loose systems of populations found in a common habitat due to similar species requirements. Presently, many ecologists tend to align themselves with Gleason's view (Vannote et al., 1980; Strong et al., 1984) by viewing communities as continua along an environmental gradient. Communities reflect aspects of both views. They develop over time in a recognizable way and yet are individualistic in that each community will be unique due to differences in habitat and colonization (Wevers & Warren, 1986).

Stream community development is change in community structure and organization. Structure is the kind, abundance and distribution of species populations in time and space. Development is influenced by the species pool of available colonists and the development of the habitat (Warren, 1979; Wevers & Warren, 1986). Habitat



development is influenced by climatic, geomorphic, and vegetative changes in the watershed (Warren, 1979; Frissell et al., 1986).

Community organization involves the ways community subsystems interrelate and interpenetrate and so become incorporated into a unified whole (Warren et al., 1979; Wevers & Warren, 1986).

Hierarchical perspectives provide a means to conceptualize the organization of communities (Allen & Starr, 1982). The sort of hierarchy best suited for conceptualizing stream communities is an interpenetrating hierarchy in which subsystems are not isolated, discrete entities, but tend to intergrade or interpenetrate, particularly at their boundaries.

Habitat, trophic and life history relationships integrate to determine community organization. Habitat organization provides a template for determining community organization (Elton & Miller, 1954; Elton, 1966; Liss & Warren, 1980), that is, hierarchical organization of the community habitat provides the primary basis for hierarchical ordering of the biological subsystems composing the community (Liss & Warren, 1980). Stream habitat organization can be conceptualized according to an interpenetrating hierarchical classification scheme such as that of Frissell et al. (1986). In this classification, different levels of the habitat hierarchy differ in spatial extent and temporal frame of development and persistence. The division of habitat levels corresponds to time scales of persistence giving an idea of time available for colonization and community development.

Life history organization entails morphological, behavioral, and reproductive adaptation that enables species to colonize and

persist in habitat subsystems. Trophic organization of the community forms in response to energy and material relations that interconnect the parts of a community (Lindeman, 1942). The opportunistic nature and complex feeding habits of many species (Darnell, 1961; Merritt & Cummins, 1984) leads to a diverse utilization of food and to community interconnectedness. For trophic and life history reasons, species may occupy more than one community subsystem and move between subsystems during their life cycle. These species are analogous to Elton's (1966) girder species and provide subsystem interpenetration.

Colonization is an important aspect of life history organization. Species with different life histories have different colonizing potentials and strategies. These strategies have developed to maximize the chance of colonizing new habitats and community subsystems.

Persistence of the community and its subsystems through time depends upon habitat and species pool persistence and concordance. Human activities such as toxicant introduction can alter community organization and development and affect community persistence. The goal of this research was to advance understanding of the organization and development of stream communities and how they might respond to an environmental perturbation such as a toxicant. The research was conducted in laboratory streams which offer a way to simplify somewhat the complexity of natural stream systems by allowing environmental variables to be better regulated, defined and monitored, including colonization, to facilitate understanding of streams.

## Methods

This research was conducted using recirculating laboratory model streams designed to simulate old growth (OG) second order streams. The streams were located at the Oak Creek Laboratory of Biology, Oregon State University. Two streams were used; one was manipulated by use of a toxicant and the other left as a control. Each stream was contained in a structure 244cm x 366cm x 46cm (Fig. 1). A paddle wheel supplied current over the substrate. A slight streambed gradient was maintained over the stream course to facilitate modeling current velocities in different habitats.

Development of the stream communities was initiated and maintained through colonization from outdoor model streams (Wevers & Warren, 1986) via a vertically slotted standpipe positioned in the outdoor streams. The outdoor model streams formed the species pool for the laboratory streams. The outdoor streams were colonized by ovipositing adults and eggs and larvae from a spring-creek water source. The slotted standpipe collected organisms and eggs from all levels of the water column. Flow from the outdoor streams passed into a continuously rotating carousel (Fig. 1) which delivered equal amounts of flow with organisms to the laboratory stream intakes. One intake was for collecting drift to monitor species and densities of colonizing organisms. Organisms that colonized the stream were continuously recirculated and redistributed in the stream if they attempted to relocate downstream by drifting. A few organisms left the stream in the overflow drain.

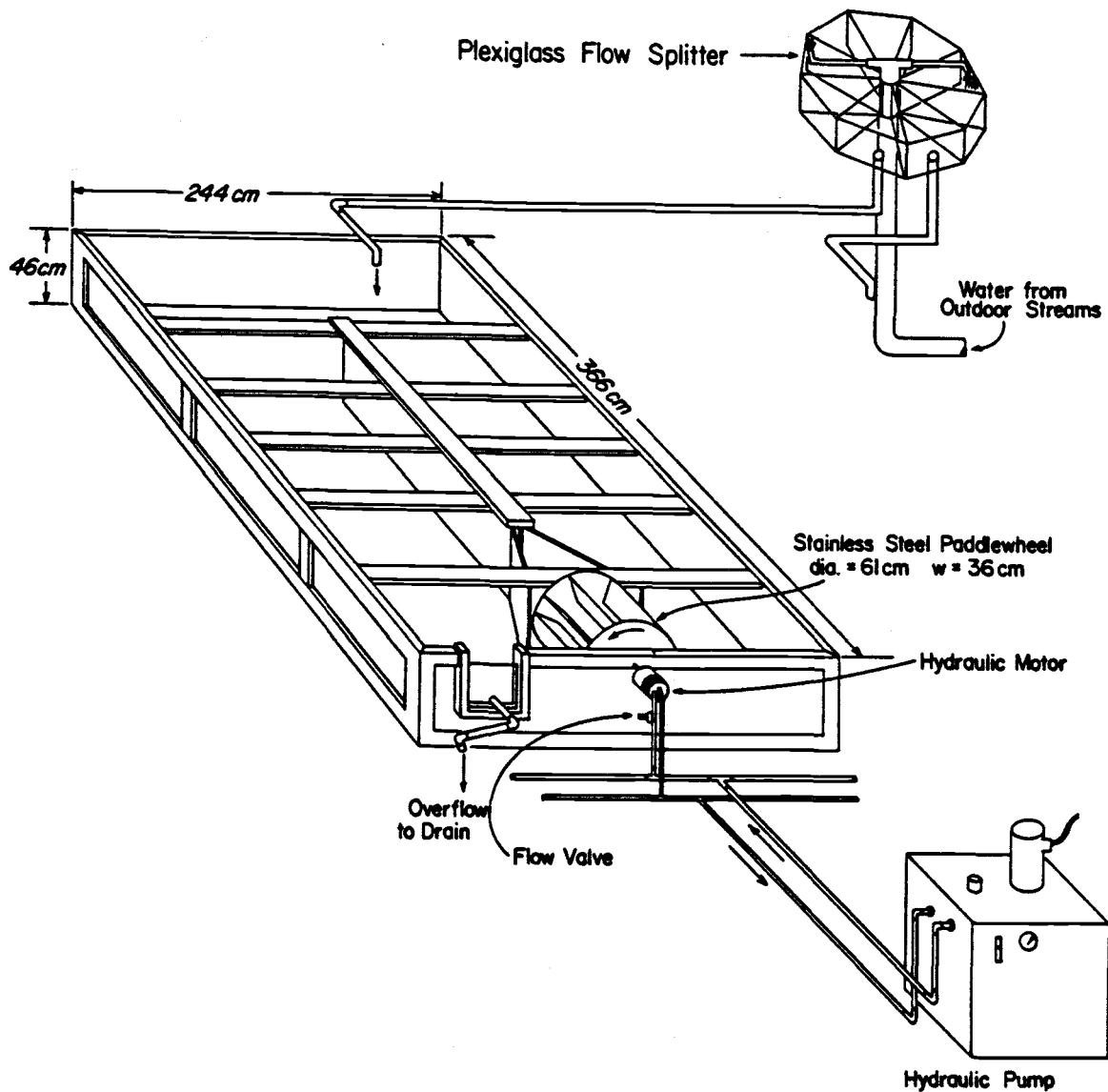


Figure 1. Schematic of the laboratory stream enclosure showing the hydraulic system which rotates the paddle wheel. Water enters the model streams from the outdoor streams via a flow splitter and exits through an overflow pipe.

Habitats of the laboratory streams (Fig. 2) were modeled after those found in second order old growth streams in the field. The habitat classification of Frissell et al. (1986) was used to identify habitats in the field and model these habitats in the laboratory. Major habitat classes included riffle, glide, rapid, cascade, pool and margin. Within these major habitats, microhabitats were identified based on associated substrates. Riffles were composed primarily of gravels and cobble. Pools held silt, sand, wood, gravels and bedrock. Cascade substrates included boulder and cobble. Cobble, wood and gravels were found in the glide, while the rapid was limited to bedrock.

Thirteen microhabitats identified for study included:

- 1) Large cobble, small boulder of cascade.
- 2) Plunge pool, bedrock bottom.
- 3) Fine gravel, bottom of pool.
- 4) Transverse cobble bar of riffle; medium gravel.
- 5) Overhanging bank, undercut margin of riffle; medium and large gravel.
- 6) Midchannel of riffle; small cobble and large gravel.
- 7) Midchannel of riffle; small, medium gravel.
- 8) Backwater pool behind log.
- 9) Bedrock bottom pool with silt and clay.
- 10) Rapid; bedrock slab at tailout of pool.
- 11) Riffle; small cobble, large, medium, and small gravels.
- 12) Backwater of glide adjacent to log; small, medium, and large gravels.
- 13) Large woody debris in glide.

Light levels, litter, riparian vegetation and stream gradient were observed and recorded in the field. Photoperiod, modeled after seasonal daylight hours recorded in the field, and daylight intensity (collected using a Li-Cor quantum radiometer) were simulated using timer controlled, metal halide lamps fitted with a shield of tarp netting that provided a filtered light effect to the streams. Litter was collected in two 0.5 m. traps at the field

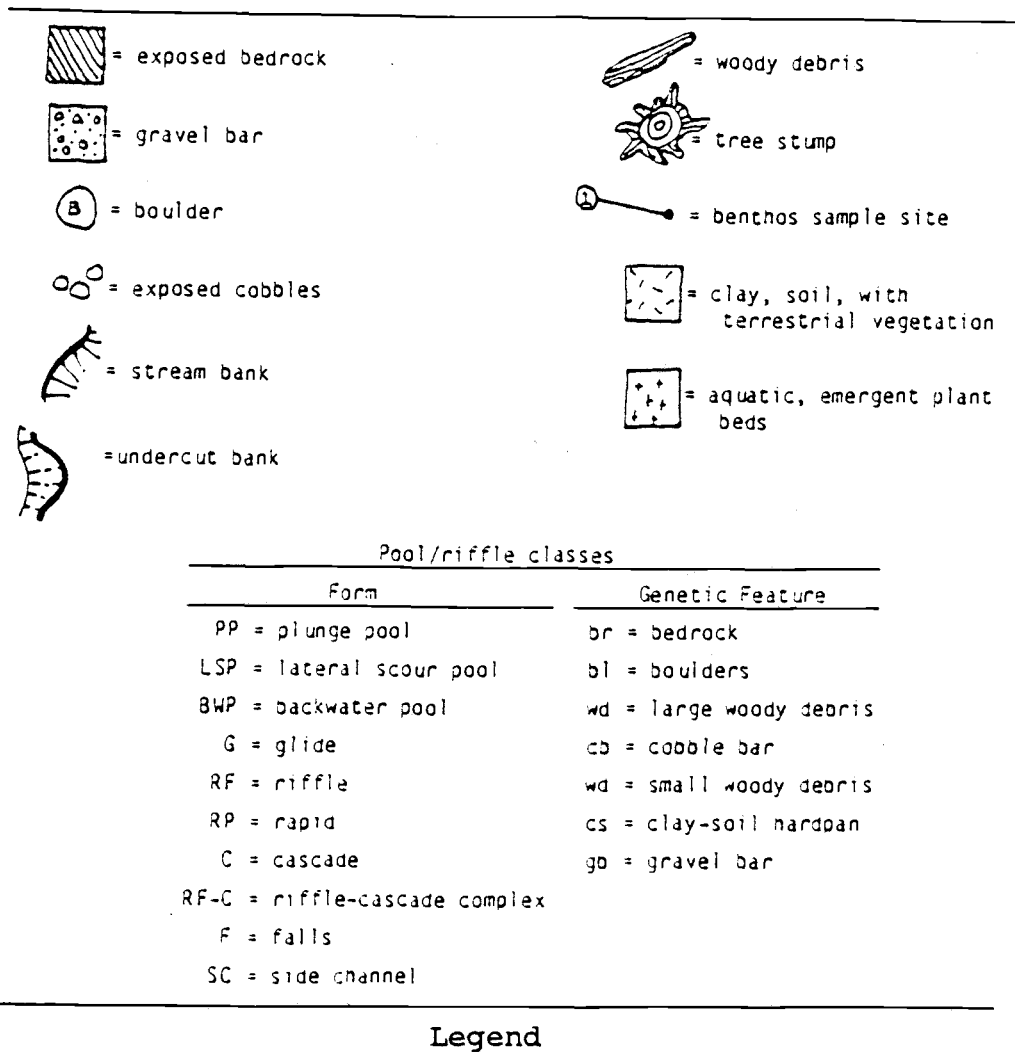
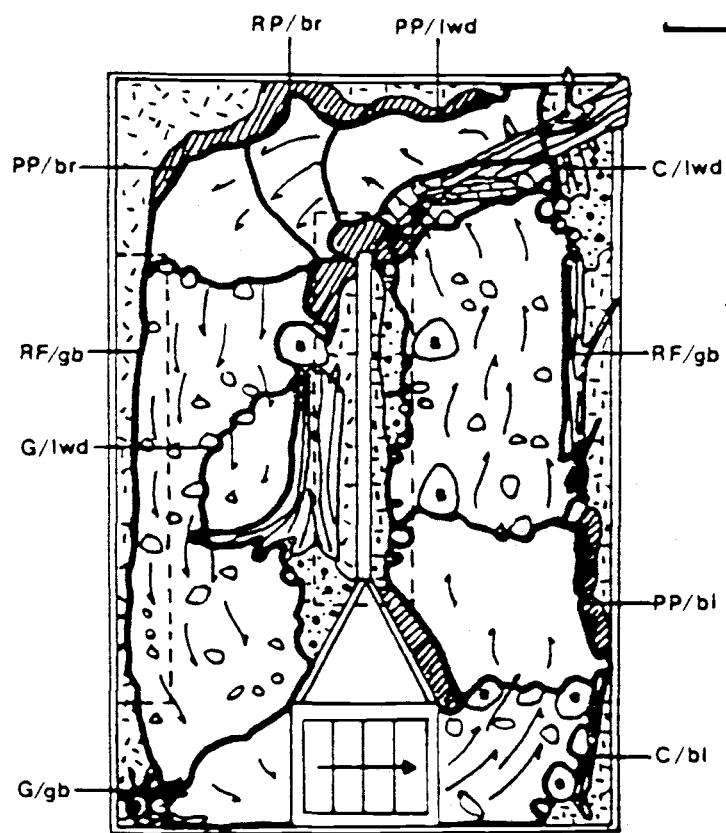


Figure 2. Habitat composition of the old growth laboratory streams.



## Old Growth

Figure 2 continued.

sites, and then dried, weighed, sorted and distributed in the lab streams. Substrate included fine and coarse gravels, small boulders and air dried woody debris (alder). Ferns and vine maples were planted in the bank along the stream edge to better simulate a natural stream setting. Water flow was maintained by a paddle wheel. The inflow/outflow exchange of water for the streams was 4 liters per minute. A stream bed gradient mimicking bed slope in the field was established in the laboratory streams channels. The wetted stream bed averaged 0.75 meters in width.

On October 17<sup>th</sup>, 1983, stream colonization and development was initiated. On September 17<sup>th</sup>, 1984, an organic insecticide, dieldrin, was continuously introduced at 0.5 ppb into one of the two OG streams. The pesticide dilution apparatus was similar to that described by Chadwick et al. (1972).

The OG streams were sampled four times per year. Only the June 1984 and 1985 samples for the control stream and the June 1985 sample for the toxicant stream were used in this research. Possible toxicant effects were assessed by comparing differences in community structure in the toxicant stream in 1985 to structure in the control stream in 1984 and 1985. On each sample date, the thirteen microhabitats were sampled in the control and toxicant stream for benthic invertebrates. The sample area within each microhabitat was isolated using a 10.2 cm. or 15.2 cm. PVC pipe core. Invertebrates were removed from large substrate by hand scrubbing with a soft brush. After scrubbing, invertebrates and sediments within the tube were removed with a wet/dry vacuum and washed into a 250 um sieve. Each sample was preserved with formalin-rosebengal solution.



Current velocity was measured at each sample site using the float meter method of drifting an object over a known distance.

Sample processing involved dividing each sample into mineral, organic and benthic invertebrate fractions. Elution separated the invertebrates and organic material from the smaller mineral fraction. Sediments and organics were separately dried in a 60°C oven. The sediments were sieved through Tyler U.S.A. Standard Testing sieves and weights of each fraction were recorded. The organic materials were weighed and sorted to qualitatively determine component proportions.

All macroinvertebrates were identified, counted and measured to the nearest 0.5 millimeter under 25x magnification. Chironomidae were identified from slide mounts of head capsules. Biomass estimates were determined for most taxa using length and frequency measurements in regression equations developed by the U.S. Environmental Protection Agency, Corvallis, Oregon (Wevers, 1983). The taxa identified in drift and microhabitat samples are listed in Table 1.

Life history and trophic relationships were established from literature (Grafius & Anderson, 1973; Edmonds et al., 1976; Merritt & Cummins, 1984). Trophic classification using functional groups followed Wevers (1983). These included macrophyte herbivores, microphyte herbivores, fine-particle detritivores, coarse-particle detritivores and carnivores. Trophic designations of taxa are given in Table 1.

Samples of macroinvertebrate drift incoming from the outdoor streams were collected once a week starting in October 1983 to

Table 1. Model stream and colonizing taxa

## Invertebrata

Cladocera (H)	Simuliidae (F)
Collembola	<u>Simulium</u> (F)
Entomobryidae (F)	Tipulidae
<u>Isotoma</u> (F)	<u>Dicranota</u> (C)
<u>Sminthurides</u> (F)	<u>Limonia</u> (F)
Eucopepoda	Ephemeroptera
Harpacticoida (F)	<u>Ameletus suffusus</u> (H)
Cyclopoida (F)	<u>Baetis</u> (H)
Gastropoda	<u>B. bicaudatus</u> (H)
<u>Physella</u> (H)	<u>B. hageni</u> (H)
<u>Gyalus parvus</u> (H)	<u>B. tricaudatus</u> (H)
Isopoda (F)	<u>Centroptilum</u> (H)
Nematoda (F)	<u>Cinygma</u> (H)
Oligochaeta (F)	<u>Epeorus (Iron)</u> (H)
Ostracoda (F)	<u>Ephemerella</u> (H)
Planariidae	<u>Ironodes</u> (H)
<u>Dugesia</u> (C)	<u>Paraleptophlebia</u> (D)

## Insecta

Coleoptera	Hemiptera
<u>Cleptelmis ornata</u> (F)	Belostomatidae (C)
<u>Optioservus quadramaculatus</u> (F)	Plecoptera
<u>Zaitzevia parvula</u> (F)	<u>Alloperla</u> (C)
Diptera	<u>Capnia</u> (D)
Ceratopogonidae (C)	<u>Calineuria californica</u> (C)
<u>Stilobezzia</u> (C)	<u>Despaxia augustus</u> (D)
Chaoboridae (F)	<u>Isoperla</u> (C)
<u>Eucorethra</u> (F)	<u>Malenka</u> (D)
Chironomidae	<u>Paraleuctra</u> (D)
<u>Alotanypus</u> (C)	<u>Pteronarcella regularis</u> (D)
<u>Brilla</u> (D)	<u>Tanionema</u> (D)
<u>Corynoneura</u> (F)	<u>Zapada cinctipes</u> (D)
<u>Eukiefferella brehmi</u> (F)	Tricoptera
<u>Micropsectra</u> (F)	<u>Hydroptila</u> (P)
<u>Orthoclaudiini</u> (F)	<u>Micrasema</u> (P)
<u>Orthocladus</u> (F)	<u>Rhyacophila</u> (C)
<u>Orthocladus-Cricotopus</u> (F)	<u>Wormaldia</u> (F)
<u>Parametricnemus</u> (F)	Limnephilidae
<u>Polypedilum</u> (D)	
<u>Prodiamesa</u> (F)	
<u>Rheocricotopus</u> (F)	
<u>Ivetenia</u> (F)	
<u>Zavrelimyia</u> (C)	
Culicidae (F)	
Dixidae (F)	
<u>Dixa</u> (F)	

## KEY: Trophic Designation

C = Carnivore  
D = Coarse-particle  
Detritivore  
F = Fine-particle  
Detritivore  
H = Microphyte Herbivore  
P = Macrophyte Herbivore

determine species and densities of potential colonizers. Comparison of taxonomic structures of pooled assemblages of organisms between habitats within streams and between streams involved the use of a resemblance measure, percentage similarity (Legendre & Legendre, 1982). The AIDN program (Overton et al., 1987) was run on an IBM AT compatible computer installed with a math coprocessor chip.

Percentage similarity is defined for sample units  $j$  and  $l$ , over all attributes  $i$ ,

$$PS_{jl} = \sum \min(p_{ij}, p_{il})$$

for

$S$  - the number of attributes

$T$  - the number of sample-units

$i$  - attribute index, range 1 . .  $S$

$j$  - sample unit index, range 1 . .  $T$

$l$  - sample unit index, range 1 . .  $T$

$n_{ij}$  - value for attribute  $i$  in sample unit  $j$

$N_j$  - summed  $n_{ij}$  for sample-unit  $j$ ,  $N_j = \sum n_{ij}$

$p_{ij}$  - proportional value of attribute  $i$  in sample-unit  $j$ ,

$$p_{ij} = n_{ij} / N_j, \text{ and } \sum p_{ij} = 1.0$$

## Results

### Colonization

Colonizers of the OG streams utilized varied strategies in attempts for successful establishment. These strategies are outcomes of particular aspects of life histories and reflect the structure and organization of the community in the large outdoor model streams, the species pool. Four strategies for colonization were identified (Table 2). Differences between the strategies involved frequency of colonization and abundance of colonists.

High Potential colonizers were characterized by high numbers of colonists and relatively continuous colonization. They were present in more than 50% of the drift samples taken from the flow splitter. High Potential colonizers averaged 1 or more individuals found in the drift sample each week for the majority of the months in which the organism was present in incoming drift. These organisms have a high likelihood for colonization due to continuous presence in incoming drift. This suggests they are highly mobile, have a high propensity to drift, are highly available in the species pool and have the potential for quick initial colonization of suitable new habitat. Five of 10 were microphyte herbivores of which three of five were mayflies known to have a high drift propensity. The cladocera are active swimmers, and Gyrulus parvus is a mobile gastropod. The two taxa of fine-particle detritivores, oligochaeta and chironomidae, were the most abundant colonizers overall. Carnivores included the mobile Planariidae Dugesia, and the net-building caddis, Polycentropus, which arrived as potentially more mobile early instars. Zapada cinctipes was the only coarse-

Table 2. Potential colonizing taxa of the laboratory streams. These taxa were collected in the flow splitter drift samples. Each value represents the average number of colonizers per week for the designated month.

Taxa Month	High Potential Colonizers										Pulse Colonizers								
	<u>Cladocera</u>	<u>Oligochaeta</u>	<u>G. parvus</u>	<u>Dugesia</u>	<u>Chironomidae</u>	<u>B. bi-tricaudatus</u>	<u>B. hageni</u>	<u>Ironodes</u>	<u>Z. cinctipes</u>	<u>Polycentropus</u>	<u>Limonia</u>	<u>Capniidae</u>	<u>Tipulidae</u>	<u>P. temporalis</u>	<u>P. debilis</u>	<u>Physella</u>	<u>Z. gregonensis</u>	<u>Malenka</u>	<u>Simulium</u>
Oct 83	3.5	1.5	0	0	4.5	25.0	1.0	0	6.5	1.0	0	2.5	0	0	0	1.0	0	0	
Nov	0.7	0.3	0.7	0.7	6.3	27.3	0.7	2.7	12.2	0.7	0	0.7	0	1.0	0.3	0.3	0.3	0	0
Dec	8.5	4.0	1.0	0.5	12.0	4.5	7.0	1.5	5.0	14.5	0	0.5	0	2.5	0	0	0	0	2.0
Jan 84	10.3	4.5	1.0	2.8	3.0	0.8	0	0.5	3.5	0.3	0	0.3	0	0	0	0.5	0	0	
Feb	3.5	0.8	0.5	1.0	9.0	1.8	0.5	0.8	3.8	0.3	0	0.5	0.3	0.8	0	0	2.0	0	0
Mar	0	0.8	0.3	1.8	12.4	0.8	0.5	1.8	7.0	0.3	0	0.5	0.3	0	0	0	0.3	0.3	
April	0.3	0.3	0	6.5	20.5	19.3	4.3	1.5	5.8	3.3	0	0.5	0	0.5	0	0	0	0.5	
May	0.5	0.8	0	9.3	23.0	0.3	2.8	0.5	1.3	1.8	0	0	0	0.3	0	0	0	0	
June	15.0	1.3	1.5	6.0	34.8	3.0	0.8	0.8	0	1.5	0	0	0.3	0	0.3	0.8	0	0	
July	3.0	6.2	4.0	2.8	116.0	12.2	0.4	0.2	2.0	0.4	1.0	0	0.8	0.2	0.2	0.7	0	0.6	0
Aug	0.5	17.5	2.5	0	69.0	37.5	0	0.5	1.5	1.5	18.0	0	17.5	0	0	2.5	0	2.5	0
Sept	3.0	1.0	0.5	3.0	12.5	25.0	3.0	0	4.0	1.5	1.5	0	0	0.5	1.5	1.0	0	0	0
Oct	0	1.0	0	2.0	47.5	70.5	2.0	0.5	8.5	0	1.5	0	3.0	0	1.5	0	0	0	0
Nov	1.0	10.5	1.0	3.0	15.5	58.0	5.5	1.0	25.0	0	4.5	1.5	0.5	0	0.5	0	0	1.0	0.5
Dec	6.5	0.5	2.5	2.5	5.0	38.5	5.5	2.0	3.5	0.5	4.5	0	0	0.5	0	0	0	0	0
Jan 85	5.3	1.0	0	6.7	2.0	12.0	0	2.0	6.5	1.3	0	0.3	0	1.0	0	0	0	0.7	0
Feb	4.0	0	0.5	6.0	3.5	6.0	3.5	6.0	1.5	1.0	9.5	1.0	0	0	0	0	0	1.0	0
Mar	1.0	0.5	0.5	18.0	3.5	5.5	0	1.5	4.5	0.5	0	0	0	0.5	0	0	0	2.5	0
April	1.5	4.0	0	0.5	7.5	1.0	0.5	0	3.5	6.5	0	0	0.5	0	0	0	0	3.0	0
May	3.5	10.5	0	5.5	13.0	4.5	0	0.5	8.5	4.0	0	0	0	0	0	0	0	2.5	0
June	2.0	17.0	0	0	11.0	10.0	1.0	0	5.0	0	0	0	0	1.0	5.0	0	0	1.0	0

Table 2. Continued

Month	Tricklers							Intermittent Colonizers																				
	Ostracoda	Collembola	Eucopepoda	Nematoda	<u>A. suffusus</u>	<u>C. integrum</u>	<u>Dixa</u>	<u>C. ornata</u>	<u>Z. parvula</u>	<u>Optioservus g.</u>	<u>Centroptilum</u>	<u>E. (Iron)</u>	<u>P. regularis</u>	Perlodidae	Isoperla	Chloroperlidae	Alloperla	<u>D. augusta</u>	<u>Hydroptila</u>	Limnephilidae	<u>Rhyacophila</u>	<u>Wormaldia</u>	Culicidae	<u>Chaoborus</u>	<u>Dicranota</u>	Ceratopogonidae	Belastomatidae	
Oct 83	1.0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nov	0.3	1.0	0.3	0	0.3	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dec	1.5	0.8	1.0	0.3	0	0	0	0.3	0	0	0	1.0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jan 84	0	0	0	0.3	1.0	0.5	0	0.3	0	0	0	0.3	0	0.3	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Feb	1.0	0.3	0.5	0	1.5	0.3	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0	0
Mar	0.5	0	0	0.8	1.8	0.3	0	0	0	0.5	0	0.3	0	0	0	0.5	0	0	0	0	0.3	0	0	0	0	0	0	0
April	0.3	0.5	0.8	0.5	0.8	1.3	0	0	0.5	0.3	0.5	0	0.3	0.3	1.5	1.3	0	0.3	0	0	0	0.5	0	0	0	0	0	0
May	0	0	0	0	0.3	1.0	0.3	0	0	0.3	0	0	0	0	0.3	0	0	0	0.3	0.3	0	0	0	0	0	0	0	0
June	0.3	0	0.8	0	0	0	0.3	0	0	0.5	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.3	0
July	1.0	0.4	3.0	0.2	0	0.2	0.3	0	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0.2	0
Aug	1.5	0.5	1.0	4.0	0.5	0	1.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	0.5	0.5	
Sept	1.0	1.0	0	0	0	1.0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0.5	0	0
Oct	0.5	1.5	1.0	0	0	0.5	1.0	0	0	0	0	0	0	0	0	0	1.0	0	0	0	0	0	0	2.0	0	0	1.0	0
Nov	1.0	4.0	0	1.0	0.5	0	1.0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	2.0	0	0.5	0	0
Dec	0	1.5	0.5	0	2.0	0.5	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0.3
Jan 85	1.0	0	0	0	1.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0.3	0	0	0	0
Feb	0.5	4.5	0	0	2.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	1.0	0	0	0	0
Mar	1.0	0	2.5	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0
April	1.0	0.5	0.5	0	0.5	1.0	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0
May	0	0	0	1.5	0.5	0.5	0.5	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	1.0	0	0	0	0	0.5	0
June	5.0	2.0	3.0	0	0	2.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

particle detritivore of the High Potential colonists. These organisms were very successful colonizers; seventy-four percent of the community biomass for all stream samples was composed of these taxa.

Pulse colonizers are characterized by infrequent appearance in the incoming drift yet relatively high numbers when present, suggesting a synchronized dispersal or seasonal variation in abundance in the species pool. Averaging for the month dampens colonization peaks. Pulse type organisms were predominately coarse and fine-particle detritivores. Physella was a summer colonizer. Winter colonizers included the Plecopteran taxa, Capniidae and Z. oregonensis. These organisms made up 14% of the biomass of the stream communities.

Tricklers arrive frequently (present in more than 40% of the drift samples) but in low numbers. They averaged more than 1.0 organisms/week for each month they appeared in the drift. For over half of the months that they were present, their average number of colonizers per week was less than 1. Five of seven taxa were fine-particle detritivores and two were mayfly microphyte herbivores. These organisms made up about 11% of the community biomass.

Low numbers of colonists (averaging 1 or fewer organisms/week each month in more than 50% of the drift samples) and infrequent appearance (present less than 35% of the months) characterized the intermittent colonizers. A major portion, 40% of the intermittent colonizers, were carnivores. These taxa comprised only 1% of the community biomass.

Some organisms colonized seasonally. Colonists with summer

peaks included oligochaetes, eucopepods, tipulids, Physella, G. parvus, ostracods and chironomids. Fall colonizers were Baetis bicaudatus, Baetis tricaudatus and Z. cinctipes. Winter colonists included Cladocera, Ameletus suffusus and Chloroperlidae. Spring colonizers were Optioservus quadramaculatus, and Polycentropus.

#### Community effects

Stream community biomass increased only slightly from 1984 to 1985 in the control stream while numbers of organisms decreased significantly from 5381 to 2308 (Fig. 3). The toxicant treated stream (85T) had a somewhat lower biomass yet similar numbers of organisms when compared to the control stream in 1984 (84C). Taxa diversity decreased from 43 in 1984 to 35 in 1985 in the control stream. In 85T, only 29 taxa were present.

Percentage similarity was used to summarize the trophic and taxa biomass information for each stream. Pooled by trophic groups, 84C and 85C were the most similar (76.1%) while 84C and 85T were the least similar (56%). Comparison by taxa biomass yielded similar results, 60.4% between 84C and 85C and 48.8% between 84C and 85T. These results indicate that community development occurred over the year in the control stream, and that 85T differed the most when comparing community structure.

#### Major habitat subsystems

There were large differences in the composition of the community subsystems in each major habitat (Fig. 4). Rapid and cascade habitats supported lower biomasses per sample than other



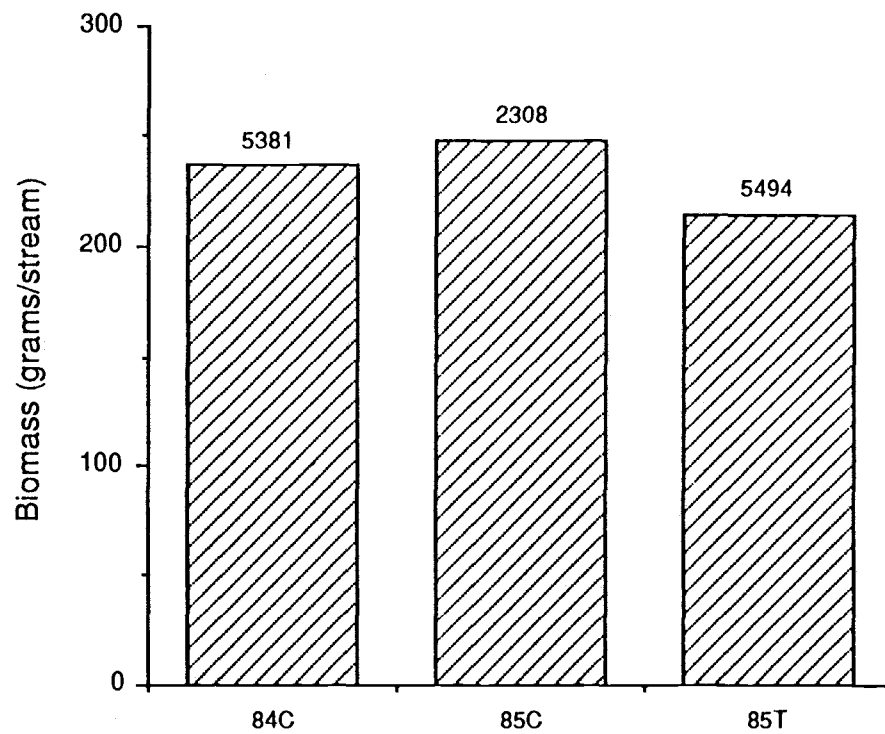


Figure 3. Community biomass at each sampling period for the old growth laboratory streams. Numbers above bars indicate the total number of organisms sampled from each stream.

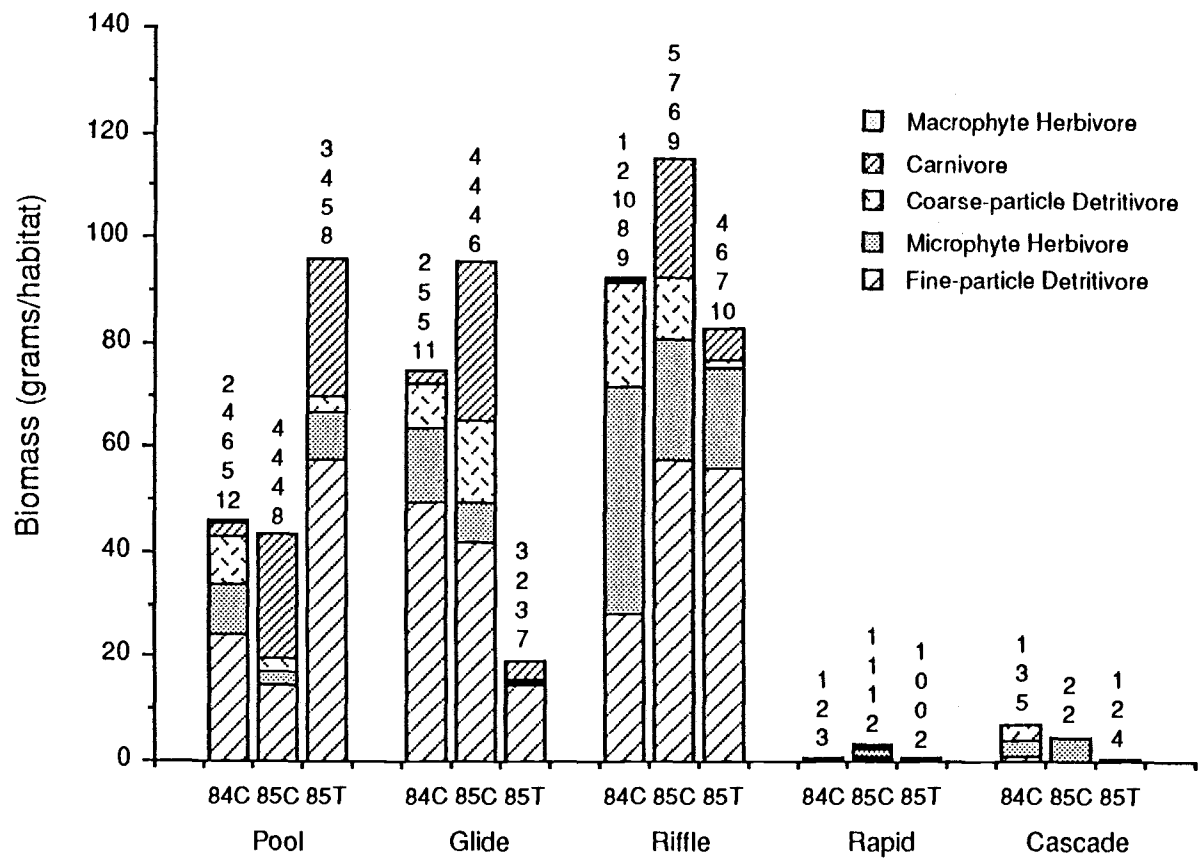


Figure 4. Major habitat subcommunities of the laboratory streams. Trophic group biomass in each habitat of each stream is represented by the bars. Numbers above each bar represent sequentially the number of taxa in each trophic group in that bar.

major habitats. Biomass was concentrated in the habitats with slower current velocity. In the pools, 85T biomass was over twice as large as 84C and 85C, while glide biomass was much lower in the toxicant stream. Fine-particle detritivores predominated in the streams each year though other taxa exhibited developmental changes. Carnivores appeared in the second year, especially in glides and riffles in 85C, and were found in the pools in 85T. Coarse-particle detritivore biomass decreased the second year. Microphyte herbivores were especially abundant in riffles. Coarse-particle detritivore and microphyte herbivore biomasses were greater than fine-particle detritivore biomass in the rapid and cascade habitats due to morphological adaptations (dorsal-ventral flattening), food preferences (large particulate organic material lodged against the substrate matrix by currents) and feeding strategies (scraping microphyte algae of sediment free substrate). An increase in taxa richness from 84C to 85C correlated with increased biomass in the riffles, pools, and glides, though overall richness decreased the second year. Except for Pool 85T, biomass was relatively low in the toxicant treated stream. Microphyte herbivores were in very low abundance in Glide 85T as were carnivores in Glide and Riffle 85T compared to the untreated streams.

Table 3 summarizes the similarities of the major habitats according to taxa biomass and trophic biomass. With decreasing mean particle size and current velocity for a depositional reach, the habitats would be ordered Cascade(C), Rapid(RA), Riffle(R), Glide(G) and Pool(P). This suggests that community subsystems of pools and glides should be more similar than the subsystems of

Table 3. Percentage similarities of composition among biological subsystems occupying the major habitats in the laboratory streams. Composition was compared by taxa and trophic group for the control streams in 1984 and 1985 (84C, 85C) and the toxicant stream in 1985 (85T). The numbers in each column represent the cumulative fraction of 10 possible habitat comparisons. Subsystem comparisons are indicated in parentheses. Comparisons are given for the interval in which their percent similarity is contained. RA= rapid, C= cascade, R= riffle, G= glide, P= pool.

Percent Similarity	84C	85C	85T
<b>a. Taxa Biomass</b>			
≥ 80%	0	0.10 (R-G)	0.10 (RA-G)
≥ 70%	0.10 (RA-C)	0.10	0.20 (R-RA)
≥ 60%	0.30 (R-P, G-P)	0.10	0.60 (P-G, P-R, P-RA)
≥ 50%	0.50 (R-G, G-RA)	0.30 (R-P, G-P)	0.60
≥ 40%	0.80 (G-C, RA-P, RA-R)	0.30	0.60
≥ 30%	1.00 (R-C, P-C)	0.30	0.60
<b>b. Trophic Biomass</b>			
≥ 80%	0.50 (C-RA, R-G, RA-G, C-R, C-G)	0.20 (C-G, RA-R)	0.30 (R-C, R-G, RA-G)
≥ 70%	0.60 (R-P)	0.30 (R-P)	0.70 (G-P, RA-C, RA-P, G-R)
≥ 60%	0.80 (G-C, RA-G)	0.40 (G-P)	0.90 (G-C, R-P)
≥ 50%	1.00 (RA-P, C-P)	0.40	1.00 (C-P)
≥ 40%		0.40	
≥ 30%		0.40	
≥ 20%		0.50 (R-RA)	
≥ 10%		0.80 (RA-P, R-C, RA-G)	

cascades and pools. In 84C, when comparing similarity in biomass of taxa (Table 3a), there are distinct differences between subsystems (only one-half of the subsystem comparisons have a similarity greater than 50%), but they are not totally discrete. Only rapids and cascades had more than a 70% similarity for 84C. In 85C, subsystems were more distinct than in 84C (Table 3a) reflecting a developmental change in community organization. Only 3 of 10 possible habitat comparisons had a percent similarity value for taxa greater than 30%. In 84C and 85C, as expected, pools and cascades were most dissimilar. Percentage similarity of subsystems in 85T more closely resembled 84C than 85C.

Comparison of similarity of biomass of trophic groups among community subsystems shows the same general pattern though the subsystems are not as distinct due to grouping of taxa into trophic categories (Table 3b). For 84C, five subsystem comparisons have  $\geq 80\%$  similarity. Cascade-Rapid and Riffle-Glide were the most similar while Rapid-Pool and Cascade-Pool comparisons were most dissimilar. In 85C, only 2 of 10 subsystem comparisons showed  $\geq 80\%$  similarity and 5 of 10 were  $\geq 20\%$  similar. Thus on a trophic group basis, subsystems also appear more distinct in 85C than in 84C. Furthermore, 85T more closely resembles 84C than 85C.

#### Microhabitat subsystems

Major habitat subsystems were composed of smaller scale microhabitats and there was some distinction between biological subsystems occupying these habitats. In the Riffle subcommunity, biomass was greatest in small and medium gravels (Fig. 5). Fine-particle detritivores were the most ubiquitous trophic group and

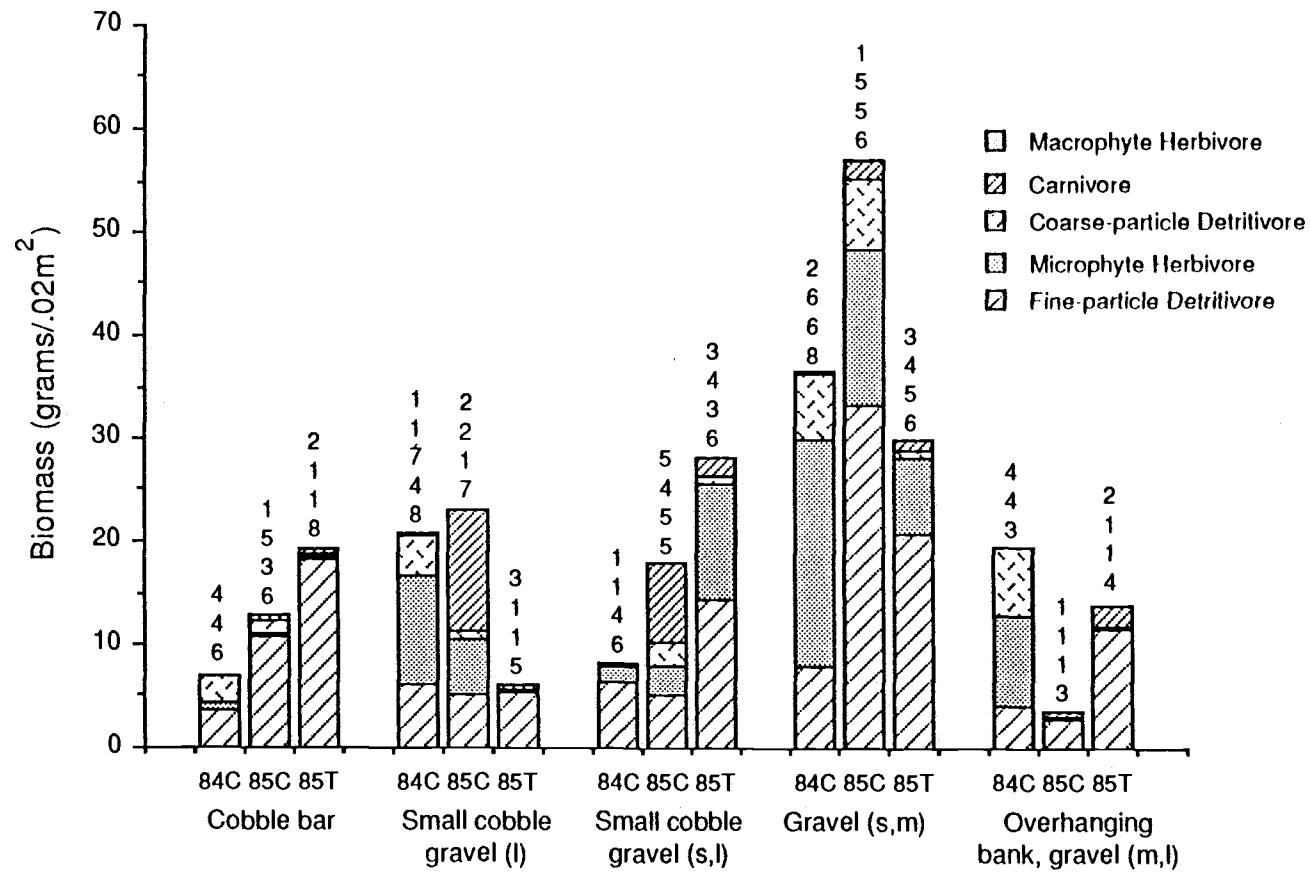


Figure 5. Trophic group biomass in the major microhabitats of the riffle subcommunity represented by the bars. Numbers above each bar represent sequentially the numbers of taxa of each trophic group. (s= small gravel, m= medium gravel, l= large gravel).

microphyte herbivores were relatively abundant in all habitats except the cobble bar. Carnivores tended to be concentrated in small cobble, large gravel during the second year in the control stream. Microphyte herbivore biomass and number of taxa decreased from 1984 to 1985. Taxa richness was largest (24) in 1984 in small cobble, large gravel, and small, medium gravel microhabitats (22). In 1985, mixed gravels had the greatest taxa richness except for the overhanging bank. 85T had larger proportions of fine-particle detritivores and fewer microphyte herbivore taxa compared to the 84C and 85C.

Pool subcommunities showed large biomass fluctuations from 1984 to 1985 with a drastic decrease from 84C to 85C for the backwater pool and a corresponding large decrease in taxa (25 to 8) (Fig. 6). In the plunge pool with fine gravel and the bedrock pool, number of taxa increased from 1984 to 1985. Fine-particle detritivores were the most abundant trophic group in all microhabitats. Carnivores provided a large portion of the biomass in the bedrock pool (85C) and the bedrock plunge pool (85T). In the toxicant stream, biomass was low in all microhabitats compared to the control stream except for the bedrock plunge pool where fine-particle detritivores and carnivores were in great abundance.

Glide subcommunity biomass was primarily located in the gravel microhabitat (Fig. 7). Similar to the pattern in other microhabitats, carnivore biomass increased from 1984 to 1985. Fine-particle detritivores were the most abundant group in the gravel microhabitat. Microphyte herbivores were relatively abundant in the wood in 84C but disappeared from the wood microhabitat in 85C. 85T

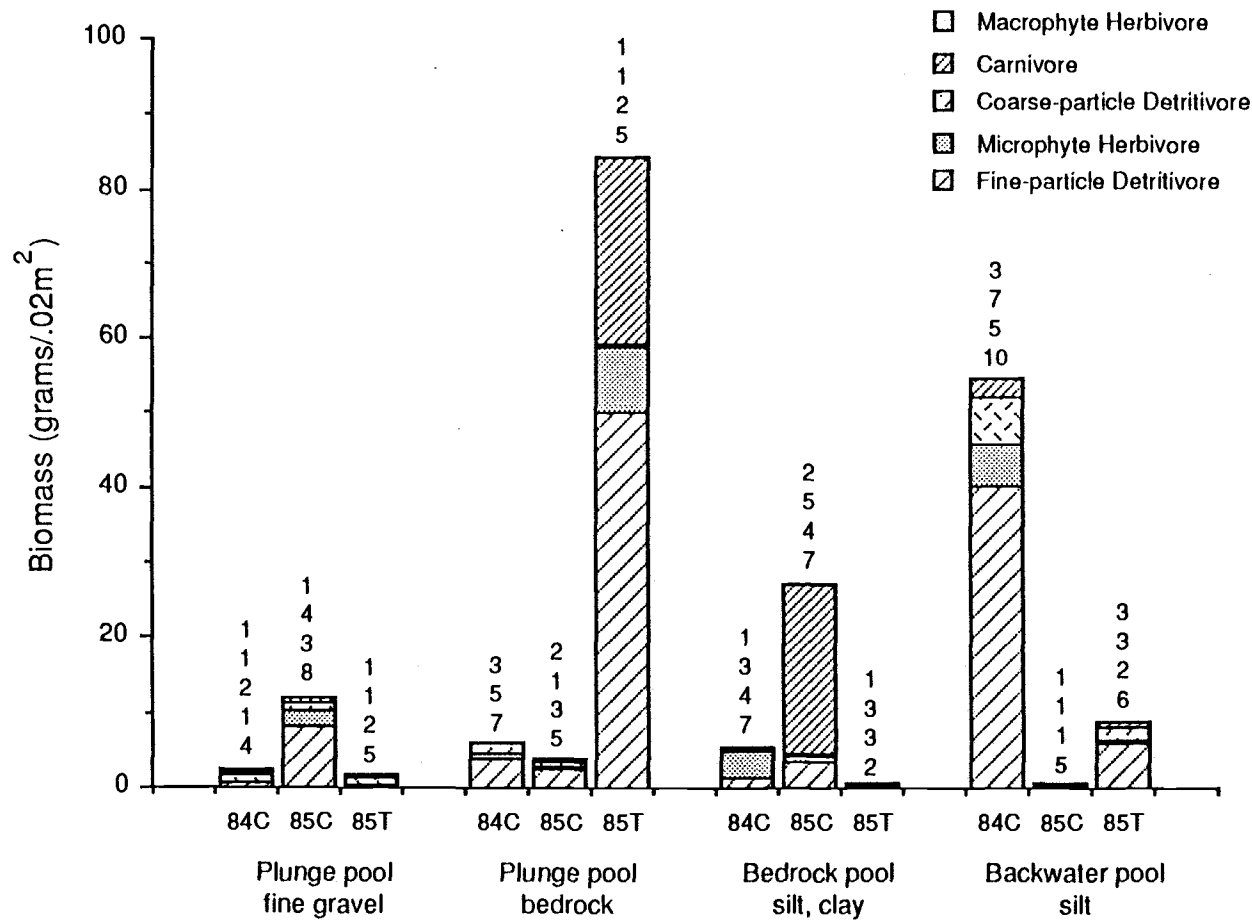


Figure 6. Trophic group biomass in the major microhabitats of the pool subcommunity. Trophic group biomass in each microhabitat of each stream in each microhabitat is represented by the bars. Numbers above each bar represent sequentially the numbers of taxa of each trophic group.



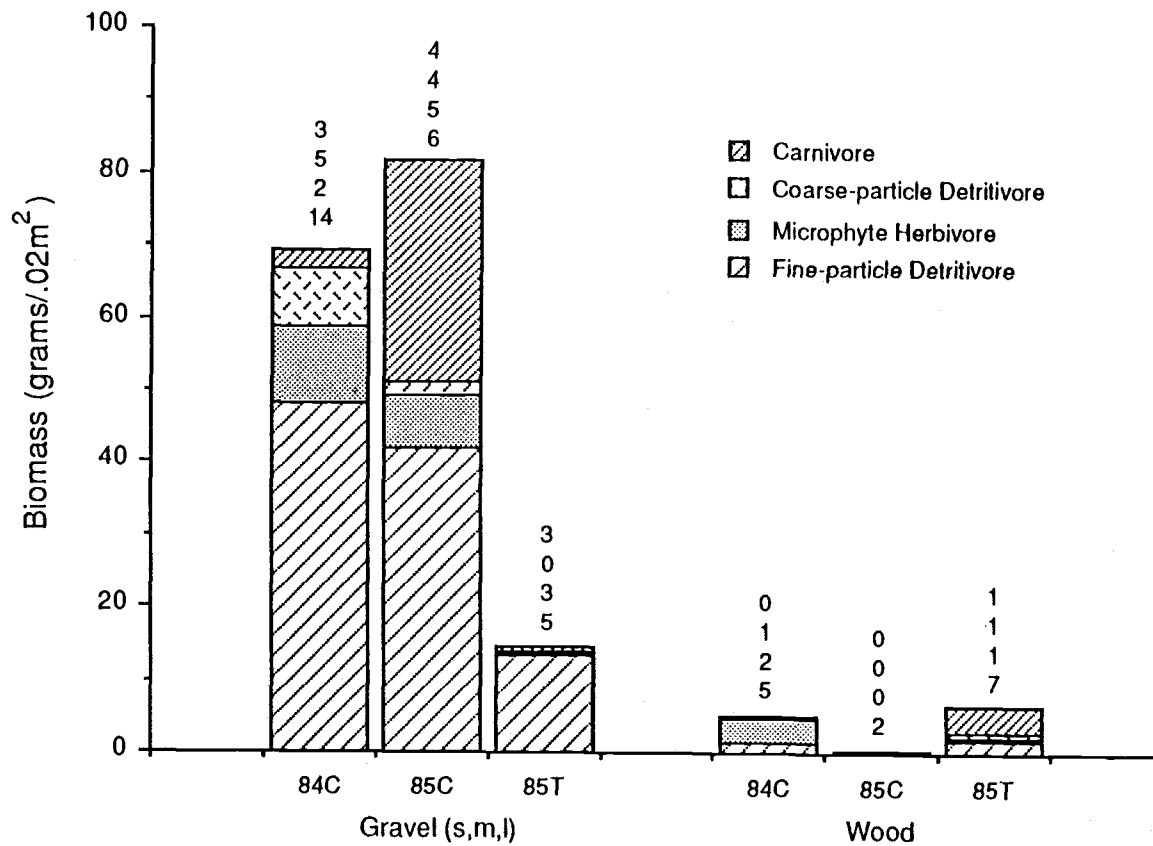


Figure 7. Trophic group biomass in the major microhabitats of the glide subcommunity. Trophic group biomass in each microhabitat of each stream is represented by the bars. Numbers above each bar represent sequentially the number of taxa of each trophic group.

had a low subcommunity biomass and few carnivores and fine-particle detritivores relative to the control stream.

Table 4 summarizes the similarities among microhabitat biological subsystems. The subsystems are relatively distinct, with 85C subsystems being less similar than 84C. In comparing similarity in biomass of trophic groups in 84C, 0.24 of the subsystem comparisons have similarities  $\geq 80\%$  and  $0.64 \geq 50\%$  (Table 4b). The greater discreteness of 85C subsystems resulted in only 0.09 of the subsystems having similarity  $\geq 80\%$  and  $0.47 \geq 50\%$ . Taxa biomass exhibited the same trends though the discreteness was more pronounced (Table 4a). Significantly, microhabitat subsystems in the toxicant stream were the most similar to each other. Using trophic biomass, 0.76 of the 85T microhabitats were 50% or more similar compared to 0.64 and 0.47 for 84C and 85C, respectively.

#### Species level effects

At the species level, differences in habitat preference among the different taxa explain larger scale differences in community structure and organization. These preferences helped create the distinct, yet interpenetrating structure of the subsystems composing the major and microhabitats. A life history classification combining trophic aspects with habitat use provides a better understanding of life history organization in the laboratory stream communities (Table 5). Life history classes include Generalist, Slow Current, Backwater, and Rheophile. Habitat Generalists are ubiquitous in the streams and are typically mobile organisms. Predators of this class are all very mobile and include Dugesia, Alloperla, and the Ceratopogonidae. Fine-particle detritivores

Table 4. Percentage similarities of composition among biological subsystems occupying the microhabitats in the laboratory streams. Composition was compared by taxa and trophic group for the control streams in 1984 and 1985 (84C, 85C) and the toxicant stream in 1985 (85T). The numbers in each column represent the cumulative fraction of habitat comparisons.

Percent Similarity	84C	85C	85T
a. Taxa Biomass			
≥ 80%	0.03	0.04	0.12
≥ 70%	0.04	0.04	0.27
≥ 60%	0.10	0.18	0.40
≥ 50%	0.22	0.31	0.54
≥ 40%	0.46	0.33	0.67
≥ 30%	0.77	0.37	0.68
≥ 20%		0.56	0.77
≥ 10%		0.74	
b. Trophic Biomass			
≥ 80%	0.24	0.09	0.26
≥ 70%	0.37	0.22	0.42
≥ 60%	0.44	0.35	0.60
≥ 50%	0.64	0.47	0.76

Table 5. Life history classification of laboratory stream taxa

## Habitat Generalists

Dugesia (C)  
Oligochaeta (F)  
Ostracoda (H)  
Harpacticoida (F)  
Z. cinctipes (D)  
Capniidae (D)  
Alloperla (C)  
Ceratopogonidae (C)  
Corynoneura (F)  
Micropsectra (F)  
Parametriocnemus (F)  
Brilla (F)  
Nematoda (F)

## Backwater

Polycentropus (C)  
Cladocera (H)  
B. hageni (D)  
P. debilis (D)  
P. gregalis (D)  
Cyclopoida (F)  
A. suffusus (H)  
Rheocricotopus (F)  
Zavreliomyia (C)  
Alotanypus (C)  
Polypedilum (D)  
Stilobezzia (C)  
Prodiamesa (F)  
Paraleuctra (D)

## Slow Current

G. parvus (H)  
Perlidae (C)  
O. quadramaculatus (F)  
Orthocladus (F)  
Orthocradiini (F)  
Tvetenia (F)  
P. temporalis (D)

## Rheophilic

B. tricaudatus (H)  
B. bicaudatus (H)  
Cinygma (H)  
Ephemerella (H)  
Pteronarcella (D)  
Taenionema (D)  
D. augusta (D)  
Leuctridae (D)  
Micrasema (P)  
Dicranota (C)  
Simulium (F)  
Orthocladus-Cricotopus (F)  
E. brehmi (F)  
Ironodes (H)

comprised the majority of the Generalist taxa (7/13). Two coarse-particle detritivores and a microphyte herbivore comprise the rest of the organisms in this group. Some organisms were present in high densities throughout the streams (oligochaeta) while others survived in low densities.

Slow Current and Backwater organisms were present in microhabitats where current was slowest, in backwater areas with little or no current, and areas of low turbulence in more exposed habitats. Life history characteristics of these organisms were generally more sedentary. Polycentropus, a net spinning tricopteran carnivore, was found in both habitats. These habitats offer some current for bringing in prey but provide protection from current strong enough to tear the net and dislodge the organism. Cladocera are free swimmers that preferred the pool and backwater habitats. The eucopepod, cyclopoida, favored the slower current habitats while the more streamlined harpacticoida resided in stronger current habitats. Five of the 14 Backwater taxa are coarse-particle detritivores including three ephemeropterans. Two microphyte herbivores, three carnivores, and three fine-particle detritivores complete the trophic breakdown of the group. Slow Current taxa were dominated by fine-particle detritivores (4/7) including three chironomids.

Taxa found predominantly in faster current were designated Rheophiles. These were more riffle oriented organisms and included the cascade and rapid habitats. These organisms are adapted to strongly cling to the substrate or are morphologically adapted to minimize drag from the surrounding water column. Microphyte

herbivores provided the largest representation (5/14). All five were ephemeroptera of which two are swimmers (B. bicaudatus, B. tricaudatus) and three are adapted morphologically to swift current (Cinygma, Ephemerella, Ironodes). The four coarse-particle detritivores were all plecoptera (Pteronarcella, Taenionema, D. augusta, Leuctridae). Dicranota, a tipulid, was the only predator in this group. Micrasema, known to be a fast water, spring creek habitat favoring organism, was only identified in two 1984 samples. With no food base, this macrophyte herbivore did not become established.

Annual development occurred in these streams. Two trophic changes were apparent. Number of carnivore taxa and biomass dramatically increased. In particular microhabitats, large numbers and biomass of carnivores were observed the second year. Dugesia concentrated in great abundance in the bedrock bottom plunge pool (85C), as did oligochaetes. Though low in abundance, Stilobezzia were dispersed throughout the toxicant stream in 1985, and were found in the backwater area of the glide (85C) after occurring only in the backwater pool in 1984. Polycentropus did not appear in any benthic samples in 1984 though stream colonization (Table 2) shows that Polycentropus was continually being introduced prior to 1984. In the control stream, in 1985, Polycentropus was a dominant taxa found in four microhabitats, though in the dieldrin treated stream, only one pupa was found.

A few taxa decreased in abundance or dramatically disappeared after the first year. A chironomid, Corynoneura, disappeared after occurring in 9 of 13 habitats in 1984. Other chironomids, Brilla,

Orthocladini and Orthocladus, were no longer present after 1984. Microphyte herbivores such as the Baetids, B. hageni and B. tricaudatus, decreased in abundance and habitat use, reducing habitat classes occupied from 12 to 7 for B. hageni and 10 to 4 habitats for B. tricaudatus. P. debilis and Z. cinctipes decreased in abundance in most of the microhabitats as well.

Differences in the development of the microhabitat subcommunities may have occurred with toxicant introduction. Taxa with greater dominance including B. hageni, B. tricaudatus, cyclopoida, capniidae, Cinygma and Z. cinctipes were found in fewer microhabitats in 85T compared to 85C. For those microhabitats occupied, biomass was generally reduced. Other taxa were reduced in biomass though they maintained about the same habitat range (harpacticoida, D. augustus, P. debilis). Ostracods, Dugesia, G. parvus and Polycentropus all had greater biomass and extended microhabitat range for 85T compared to 84C. Polycentropus was much better established in 85C (4 to 1) than in 85T. Ranges of microhabitat occurrence were greater for Dugesia and particularly G. parvus (8 to 12) in 85T compared to 85C. Dugesia developed a much higher biomass in the slower velocity microhabitats of the glide and pool major habitats.

Overall, taxa diversity was less in the toxicant stream than in the control stream. Herbivores were lower in biomass and taxa diversity. Fine-particle detritivores were greater in biomass but lower in taxa diversity. Remaining taxa generally maintained lower microhabitat ranges.

## DISCUSSION

A community's relationship to its habitat has been well established in the literature. Southwood (1977) discussed the importance of habitat to community organization. He proposed they are linked, generating feedback to each other. Others (Elton & Miller 1954, Elton 1966) have described habitat as the template for community organization. Southwood (1977) and Warren and Liss (1980) point out the importance of life history aspects including reproduction overlapping with the temporal scale of habitat persistence. These researchers discuss the need for life histories and habitat to be concordant for communities to exist.

Conceptualization of the organization of stream communities and their habitats as a hierarchy of interpenetrating subsystems simplifies interpretation and aids understanding of complex interactions. While the biological subsystems occupying major habitats and microhabitats are relatively distinct in composition of taxa and trophic groups, it must be recognized that there is a great deal of interpenetration and interrelatedness among habitats and among biological subsystems. Habitats are not sharply distinct. They tend to intergrade at their boundaries and share characteristics. Microhabitats found in two different major habitats may be very similar in nature. A riffle may have a pool like area downstream of boulders that allows pool favoring organisms to become "pocket dwellers" in the riffle. This interpenetration of microhabitats leads to an interpenetration of subcommunities with water flow helping to distribute both materials and organisms among the habitats.



In the laboratory streams, the different trophic groups were not specific to particular habitats; they were found in all major and microhabitats. Habitat Generalists, analogous to Elton's (1966) girder species, were found throughout the stream. Their life histories allowed them to exist and move about in diverse microhabitats providing subsystem interpenetration.

Rabeni and Minshall (1977) found that the relationship between substratum size and detritus was the primary influence on insect microdistribution. They suggested the matrix of substrate related to detrital collection, and specifically that small to large gravels provided the best collection matrix. The work reported here generally supported that conclusion. Biomass was large and diversity high in the riffle habitat relative to the other habitats (Fig. 2).

Successful colonization of habitats in the laboratory streams was dependent upon many factors. It is a function of drift propensity (Lemkuhl & Anderson 1972; Townsend & Hildrew, 1976), the length of time an organism is in a colonizing life history form (Bishop & Hynes, 1969), and organism movement (Table 2). Movement to different habitats depends upon habitat preferences, dispersal ability and distance from the source to the new habitat (Gore, 1982). Therefore, the structure and organization of the species pool plays a significant role in habitat colonization (Warren & Liss, 1980). Community structure also determines the success of colonists (Williams & Hynes, 1969; Diamond, 1975; Rabeni & Minshall, 1977). Gore (1982) notes that habitat development places

constraints on successful colonization. Others have argued for stochastic or nonequilibrium models of colonization (Reice, 1980) and a non-cohesiveness of stream communities (Winterbourn et al., 1981). Minshall and Petersen (1985) view initial colonization of a habitat as having random or stochastic aspects and as the community becomes more complex, interactions become more deterministic in successful colonization.

Patterns of colonization also reflect variation in abundances of organisms in the species pool (Bishop & Hynes, 1969; Lemkuhl & Anderson 1972). Patterns of abundance may be seasonal and may reflect univoltine or multivoltine life histories. Differences in year to year colonizing ability may reflect development or change in structure of the species pool.

In the OG streams, the community was not simply a replication of the incoming colonists structure and organization, but rather was codetermined both by potential colonists, which reflect the species pool, and by the development of the stream habitat. Some organisms never became well established throughout the system. Several appeared, apparently only in transit, looking for suitable habitat. These included Epeorus (Iron), Micrasema, Isopoda and Limonia. These species may have been outcompeted (Minshall & Petersen, 1985); or sufficient development of the habitat or community had not yet occurred to provide them a suitable place (Gore, 1982). The carnivores Polycentropus, Dugesia and Stilobezzia did not successfully establish in the streams until the second year, 1985, even though they were continually found in the colonization drift. Possibly, insufficient prey were present for the predators (Gore,

1982) or habitat had not sufficiently developed (Margalef, 1968). Other organisms that were abundant in incoming drift such as Ephemerella and A. suffusus were present in the community but did not develop high numbers. Some chironomids were present the first year only. E. brehmi, Corynoneura, Orthocladius, and Prodiamesa may be early colonizer types that continually exploit new habits but disappear as other species become established. Diamond (1975) called these organisms supertramps.

Reduced taxa richness the second year was evidence of stream community development. This may have occurred due to increased abundances of carnivores altering previously established community trophic organization, since fewer and larger organisms were present in 85C than in 84C.

Community subsystems in 85C were more discrete than in 84C or 85T. Development of the subcommunities from 84C to 85C provided an extra year for species to sort out life history interactions and to stabilize their subcommunities.

Fine-particle detritivores initially colonized the streams. Due to the recirculating nature of the laboratory streams, fine detritus created by other trophic groups (Cummins, 1973) continually settled in the streams since high flows were not generated to flush the particles (Wevers et al., 1988). This provided a food base that maintained fine-particle detritivores as the predominant trophic group in the streams. Microphyte herbivores were reduced the second year possibly due to a change in habitat or carnivores preying upon smaller larval instars.

In the backwater pool, subcommunity biomass in 85C was

considerably lower (Fig. 6) than in 84C. The predator, Polycentropus was the main organism still present, and very little organic material was recovered with the sample. This suggests the other organisms were stressed from both sides of the food chain.

The structure, organization and development of the community in the toxicant stream was substantially different from the control stream. Sampling at one point in time in the toxicant influenced stream (85T) for comparison with another sample taken at a single point in time in a different stream (85C) may make subtle differences between the two difficult to recognize. Based on comparison of species and trophic proportions in the toxicant and control streams, it appears as though the toxicant stream were subcommunities set back developmentally to a stage having greater similarities to the 84C subcommunities. Differences in decreased biomass, lower taxa diversity, a greater percentage of fine-particle detritivores and a low biomass of the microphyte herbivores in 85T compared to 84C made apparent the potential effects a toxicant may have on community structure. Some species tended to occur in fewer microhabitats perhaps restricting their distribution to microhabitats in which they are best adapted.

Model streams offer advantages such as simplification and ease of sampling, yet create obstacles for interpretation as well. Limitations forced upon the streams such as partially closed, circular flow systems make community integrity more difficult to maintain (Wevers et al., 1988). There is no seasonal fluctuation in flow or a true sorting of bedload (Shriner & Gregory, 1984) and the species pool is more limited than in the natural environment.

Despite these and other constraints upon laboratory work, model streams can be useful in gaining a better understanding of the nature of stream communities.

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