

EFFECTS OF CANOPY, SUBSTRATE COMPOSITION, AND GRADIENT ON THE STRUCTURE OF MACROINVERTEBRATE COMMUNITIES IN CASCADE RANGE STREAMS OF OREGON¹

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Abstract. The relative importance of surrounding riparian vegetation and substrate composition on invertebrate community structure was investigated in six streams in Oregon, USA. We found that canopy type was more important than substrate character in influencing total abundance and guild structure. Streams without shading had higher abundances of invertebrates than did shaded streams. Most guilds were influenced by qualitative differences in food availability rather than quantity of food or substrate composition. Open streams had higher abundances in the collector–gatherer, filter feeder, herbivore shredder and piercer, and predator guilds. Contrary to expectations, shredders were no more abundant in shaded streams than in streams lacking a riparian canopy. Scraper density was inversely related to standing crop of aufwuchs, but biomass was positively correlated with quantity of aufwuchs. Examination of dominance–diversity curves showed that both canopy and substrate influenced ranked abundances of taxa, but neither canopy nor substrate strongly influenced number of taxa. Differences in community structure were not always revealed by analysis of community-level properties, although differences in both the absolute and relative abundances of individual taxa were observed.

Key words: *community structure; functional groups; guilds; land use practices; macroinvertebrates; Oregon; riparian canopy; streams; substrate.*

INTRODUCTION

Differences among stream ecosystems in food availability and habitat structure can strongly influence both the structure and function of stream communities (e.g., Hynes 1970, 1975, Vannote et al. 1980). Land use practices can modify both streamside vegetation, an important determinant of food availability, and the character of surficial sediments, an important aspect of habitat (e.g., Karr and Schlosser 1977, 1978). Macroinvertebrate communities in streams respond to changes in these two factors. However, because populations are concomitantly influenced by both factors it is often difficult to specify the causal mechanisms underlying observed patterns of community structure. The main goal of this study was to determine the relative significance of canopy type and substrate composition as determinants of community structure and invertebrate abundance in Oregon Cascade Range streams.

In a previous paper (Murphy et al. 1981) we described differences in vertebrate communities (fish, amphibians) among the same streams on which this report is based. In that paper, we showed that abundances of most vertebrate species were strongly associated with overall abundance of the invertebrate community and that degree of shading apparently determined both invertebrate and vertebrate abundance by affecting availability of primary food sources

(algae, high-quality detritus). We did not develop detailed analyses of either food sources or invertebrates but presented only those data necessary to explain patterns of vertebrate abundance. We now present a detailed analysis of differences in invertebrate communities among these streams and discuss the relative importance of food and habitat as determinants of abundances of different guilds and taxa.

STUDY AREA AND METHODS

During 1978–1979 we studied communities in six streams of the western Cascade Mountains of Oregon. In our previous paper (Murphy et al. 1981) we described the study area and general sampling program in detail. Here we provide summary data on streams sampled (Table 1) and describe sampling and methods directly relevant to the invertebrate community.

Study design

Six stream sections were studied (Table 1). Three sites were on relatively high-gradient sections ($\approx 10\%$) and provided stream substrates that consisted mostly of boulders and cobbles. Three other sites were on lower-gradient sections ($\approx 1\%$); substrates here consisted of cobble and gravel with significant amounts of sand. Because gradient and mean particle size are generally correlated, we could not vary substrate composition independently of gradient. Within each set of three streams, sections with an old-growth coniferous canopy, a second-growth deciduous canopy, and no canopy (clear-cut) were chosen for study. This design allowed us to contrast streams with different primary

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TABLE 1. Summary of stream environments at each study site (modified from Murphy et al. 1981).

Parameter	Name of stream					
	Mack	N. F. Wycof	Mack	Fawn	Cougar	Mill
Riparian age (yr)	10	35	450	7	35	450
Canopy type	clear-cut	deciduous	coniferous	clear-cut	deciduous	coniferous
Dominant riparian vegetation	Herbs and Shrubs	Red Alder	Douglas-fir and Hemlock	Herbs and Shrubs	Red Alder	Douglas-fir and Hemlock
Percent shaded	0	85	75	0	85	75
Percentage of watershed logged	10	32	10	36	70	65
Elevation (m)	730	500	760	500	500	360
Watershed area (km ²)	5.5	4.0	5.4	6.8	8.2	6.4
Minimum discharge (m ³ /s)	0.07	0.03	0.07	0.06	0.09	0.02
Temperature (maximum°C)	18.5	15.5	15.5	20.0	14.0	18.0
Aspect	N	SW	N	E	W	S
Approximate gradient (%)	10	10	10	1	1	1

food sources and substrate character. Replication of streams was not possible because of time constraints imposed by sampling and sample processing. Because differences in temperature among streams can affect community composition and structure, we attempted to choose sites with minimal differences in temperature. Maximum temperatures were observed during late summer (August) at all sites (Table 1). A trend existed for streams without shading to have slightly higher maximum temperatures than shaded reaches; however, temperatures during most of the year were similar among sites.

Sampling and analysis

In addition to invertebrates, we sampled a number of environmental variables that we expected to vary with canopy and substrate composition. Each stream was sampled for invertebrates with a Surber sampler as modified by Newbold et al. (1980) during June, August, and October 1978. Three riffle samples and three pool samples were taken in each sampling period. A total of 108 benthic samples was taken (3 samples per habitat $\times$ 2 habitats $\times$ 3 seasons $\times$ 6 sites). For analysis, individual samples for a habitat and site were lumped for each season. A total of 18 sample means (3 seasons $\times$ 6 sites) was used to compare invertebrate data among streams (see below). At irregular intervals over the year (June 1978–June 1979), organic matter (aufwuchs), and chlorophyll standing crops on cobble substrates were determined, and respiration rate and chlorophyll associated with interstitial organic matter were estimated. Respiration rate was measured with a Gilson respirometer, and amount of chlorophyll pigment was estimated by acetone extraction (see Murphy et al. 1981 for details). We did not measure the surface area of cobbles on all dates that the aufwuchs was sampled. For this reason aufwuchs quantity and chlorophyll standing crop are reported for six dates, whereas chlorophyll associated with the aufwuchs is reported for nine dates. During August 1978 substrate composition and organic storage were quan-

tified by taking six benthic cores (three riffles and three pools) at each site. Particulate organic matter (POM) was partitioned into a coarse fraction (>1 mm; CPOM), a fine fraction (50 μ m–1 mm; FPOM), and a very fine fraction (0.45–50 μ m; VFPOM). These data are reported in terms of ash-free dry matter (AFDM). During October and November, standing crops of deciduous leaves were estimated by picking leaf material from 0.1-m² quadrats of stream bottom. Three riffle and three pool samples were taken each of these months for a total of six samples for both riffle and pool habitats. When more than one estimate of a variable was determined over the year, these values were used as replicates in describing mean differences among streams (see below).

Analyses of chlorophyll associated with VFPOM were performed only on material from pools because sufficient quantities of VFPOM from riffles could not be collected. During the process of analysis we noticed high levels of pheophytin *a*, occasionally close to 100% of measured pigment. It was not clear whether such high levels were typical, or if degradation of pigment occurred during transport to the laboratory and before we could process samples. From an invertebrate consumer's view, chlorophyll *a* may be no better a measure of food quality than pheophytin *a* (i.e., is live algae better than dead algae?). For these reasons we report the sum of the two pigments as an index of aufwuchs and detritus quality in these streams. Chlorophyll pigment was converted to algal biomass using the ratios of Lyford and Gregory (1975). For the same study area, they estimated biomass:chlorophyll *a* ratios at 54 in shaded streams and 75 in unshaded streams of this size. We caution the reader that our chlorophyll data do not provide quantitative estimates of chlorophyll or algal standing crops. We include these data because they do serve as an index of differences in autotrophic activity among sites and allow us to examine qualitative relationships between invertebrate abundance and food quality.

Field experiments were conducted during summer

(July–August) to investigate relationships between substrate composition and invertebrate abundance with somewhat more control. Trays of rubble (≈ 5 cm in diameter) embedded 0, 25, 75, and 100% with sand (≈ 1 mm) were placed in areas of three different current velocities (0, 15, and 30 cm/s) in each of the low-gradient streams. Each site thus had 12 trays for invertebrate colonization and accumulation of organic matter. Planar surface area of each tray was 600 cm², and each was 5 cm deep. All particles and animals $>100 \mu\text{m}$ in diameter were retained when the trays were removed after 30 d. Organic material and animals were preserved in ethanol.

Only invertebrates retained by a 1-mm sieve are considered in this report. Smaller animals were difficult to identify, and although at times they were a significant portion of total numbers, subsamples showed that they never comprised $>5\%$ of total biomass. These data represented a reasonable compromise between efficiency and reliability of processing (counting, measuring, and identification) and data that were representative of true differences, or lack thereof, between streams. After sorting, the individuals of each taxon were counted, and lengths (head to tip of abdomen) measured. Biomass of all taxa was estimated by empirically derived length–mass relationships or from published length–mass relationships (Smock 1980). All taxa were assigned to guilds (see Terminology). Most taxa were put into only one group, but some were placed into two. For the latter, half of the density and biomass in the taxon was assigned to each guild. Taxa which fit into more than two groups were considered generalists and placed into a separate guild. Hawkins and Sedell (1981) list most of the taxa encountered during this study and the guilds into which they were placed.

Comparison of invertebrate community structure was based on analysis of both bottom samples and tray samples. In addition, detailed analysis of tray samples from open (clear-cut) and shaded (old-growth) streams allowed us to examine effects of both shading and substrate composition on the absolute and relative abundances of specific taxa.

Analysis of variance and correlation were used to examine data statistically. In this study we have treated seasonal samples as replicates. We recognize that if samples from one season are not independent of samples from other seasons, analysis of variance is not valid. Invertebrate samples were taken 2 mo apart. Life cycles of many of the taxa encountered are short (<6 mo), and we observed distinct changes in taxonomic composition between seasons. Furthermore, we lumped taxa into guilds for most analyses, so abundance was not dependent on life history phenomena of single taxa. For these reasons, we believe that seasonal samples were meaningful replicates and that analysis of variance indicated real difference, or lack thereof, among communities. We also used similar

analyses for environmental data. Analysis of variance was used to identify any broad differences in these variables that existed among sites and were associated with the contrasts in canopy type and substrate composition. One effect of using seasonal samples as replicates was to increase the within-site error term which reduced the chance of detecting between-site differences. Because of the relatively high error introduced by seasonal replicates and the relatively low number of samples ($N \leq 9$ after lumping), a significant F test probably indicated distinct differences between sites.

Terminology

In this report we use a number of terms the meanings of which are often either ambiguous or not clearly defined. We use *community structure* to refer to the number of taxa and their absolute and relative abundances in a community and to the manner in which taxa are apportioned among guilds. *Trophic structure* refers to the structural patterns within communities that are revealed when taxa are classified based on their feeding relationships. In this study we have assigned taxa to *guilds*. It is important at this point to distinguish the terms guild (sensu Root 1967) and *functional group* (sensu Cummins 1973). Guild and functional group classifications may often be synonymous, but the two concepts are fundamentally different (MacMahon et al. 1981). We use the term guild to describe the various but limited strategies that aquatic invertebrates have evolved to exploit food sources. A guild classification considers not only how resources are exploited but also what resources are eaten. The term functional groups stems from an ecosystem perspective and emphasizes method of feeding, a classification that bridges community structure and ecosystem function (i.e., the conversion of one kind of organic matter to another state by certain types of consumers). Our approach differs from a functional group approach in that processes are not emphasized. When addressing community-level phenomena such as structure and organization, we believe a guild classification is a natural and appropriate classification, because ideally it reflects the selective forces that have shaped strategies of resource exploitation. A strict functional group classification does not necessarily imply the effect of past selective forces, although it may. Our assignment of taxa to guilds closely parallels the functional designations given taxa by Merritt and Cummins (1978). If type of food is considered, their classification provides the basis for a guild classification as well as a functional one.

Taxa were assigned to the following guilds based both on their method or behavior of food acquisition and what they eat: *collector-gatherers* (CG), which feed on fine or very fine particulate organic matter (FPOM and VFPOM); *scrapers* (SC), which harvest organic films (aufwuchs) growing on cobbles and other substrates; *shredders* (SH), which feed on coarse par-

ticulate organics (CPOM), consisting mainly of allochthonous detritus; *filterers* (F), which trap and feed on suspended organic matter, *wood gougers* (WG), which feed on woody debris; *generalists* (G), which feed on a variety of food sources; *herbivore shredders* and *piersers* (HSH), which feed on macrophytes including macroalgae by either chewing or piercing (we will often shorten this term to herbivore shredder); and *predators* (P), which feed on other invertebrates.

Throughout this report we refer to both quantity and quality of food sources. Quantity refers to mass of organic matter per unit area expressed as ash-free dry mass (AFDM). Quality refers to differences among detrital or aufwuchs food sources in either the amount of microbial respiration occurring or the amount of chlorophyll per unit area or per unit AFDM. We assume that differences in these measures are indicative of differences in nutritional quality of organic substrates to consumers (Anderson and Cummins 1979).

RESULTS AND INTERPRETATION

Contrasts of environments among streams

Percent composition of particle sizes of mineral substrates differed significantly between high- and low-gradient streams (see Murphy et al. 1981 for data). High-gradient sites were dominated by boulders and cobble with 9–25% of total sediment as sand and gravel; low-gradient sites had higher percentages (36–58%) of sand and gravel. No differences in substrate composition were observed among streams with different canopies.

Food sources were partitioned into interstitial organic matter (i.e., particulate detritus) and aufwuchs. Both gradient and canopy affected food sources (Table 2). Low-gradient streams had larger quantities of detritus than did high-gradient streams. Among streams with different types of canopies, deciduous second-growth sites had more leaf material, whereas open (clear-cut) sections had higher quantities of aufwuchs and higher quality detritus (respiration rate and chlorophyll content). No differences existed among sites with respect to chlorophyll content of the aufwuchs.

Our estimates of chlorophyll and algal biomasses attached to cobbles were generally lower than estimates reported by Lyford and Gregory (1975) and Gregory (1980) for other streams in the area. The reason is probably due to our method of sampling. We removed attached matter from rocks, using a wire brush, and then estimated AFDM and chlorophyll. Gregory (1980) estimated chlorophyll by immersing cobbles in acetone extractant. Our method evidently failed to remove all attached algae (Karlström 1978). However, seasonal trends and differences among sites were similar to those observed by Gregory, so our estimates should be a realistic index of differences among sites.

Abundance of different guilds

Canopy affected more groups than did gradient for riffle habitats (Table 3). In almost all cases where significant differences were observed, open sites had either higher densities or higher biomasses of different guilds than did the shaded sites. This was true for collector-gatherers, filterers, herbivore shredders and piersers, predators, and total invertebrates. Only generalists, a group which mainly consisted of the snail *Juga plicifera* (Lea) (previously *Oxytrema*), showed higher abundances in shaded sites. Gradient, and presumably substrate composition, had little influence on abundance. Only generalists (i.e., *Juga*) showed a significant difference between high- and low-gradient sites; they were more abundant in the latter. A significant interaction between gradient and canopy was observed for density of predators and both density and biomass of generalists.

Few significant differences among means for guilds were observed for pool samples. Canopy had a strong effect only on wood gougers, which had higher biomass, although not density, in second-growth deciduous sites than in others. Densities of herbivore shredders and piersers were greater in the high-gradient sites, but biomasses were not significantly different among sites. Generalists were more abundant in terms of both density and biomass in pools of low-gradient sites than in pools of high-gradient reaches. Trends in total biomass were strongly influenced by generalists and paralleled the pattern observed for this group. Mean individual biomass of *Juga* (excluding shells) was usually high compared with all other groups. Although densities were not extremely high, snail biomass approached 80% of total invertebrate biomass for some sites. Total density did not parallel density of generalists, and no significant differences in total densities were observed between gradients.

Analysis of percent composition of different guilds showed that relative abundance (density or biomass) did not always parallel patterns of absolute abundance (Table 4). An increase or decrease in absolute abundance did not always result in a similar change in relative abundance. For generalists, both absolute and relative abundance showed similar patterns among sites. In general for all other guilds, relative abundance was influenced not only by their own absolute abundances but also by the abundances of all other groups. These data are interesting in that the relative abundance of scrapers was not always highest in streams without shading, and neither was the relative abundance of detritivore shredders always highest in shaded streams.

Comparison of abundances of invertebrate guilds (Table 3) with differences in food sources and substrate composition observed among sites (Table 2) and correlation analyses revealed that invertebrates from riffle habitats were more likely to be associated with

TABLE 2. Results of two-way ANOVA for effects of gradient and canopy on quantity and quality of food sources. To number of samples for the different variables are: leaves, $N = 6$ per habitat at each site; total detritus, $N = 3$ per habitat at each site; aufwuchs (AFDM), $N = 6$ per habitat at each site; aufwuchs (chlorophyll and algae), $N = 9$ per habitat each site; detritus quality, $N = 9$ per site for chlorophyll pigment and algae, $N = 6$ per site for respiration; for aufwuchs quality, $N = 6$ per site. Respiration (as O_2) = $\mu L \cdot g^{-1} \cdot h^{-1}$. HG = high gradient, LG = low gradient, OG = old-grow, CC = clear-cut, SG = second-growth. No significant interactions were observed.

Habitat	Measure	Gradient			Canopy			
		HG	LG	P†	OG	CC	SG	P†
Leaves (AFDM, g/m ²)								
Riffles		0.8	0.9	NS	0.2	0.1	2.4	**
Pools		6.2	1.9	NS	1.3	0.2	10.6	*
Total detritus (AFDM, g/m ²)								
Riffles	Total	36.8	91.4	*	61.2	64.3	66.7	NS
	VFPOM	6.2	14.5	*	10.3	6.9	13.9	NS
	FPOM	15.6	54.4	**	34.8	36.8	33.4	NS
	CPOM	14.9	22.5	NS	16.1	20.6	19.4	NS
Pools	Total	187.3	456.6	*	410.7	211.1	344.1	NS
	VFPOM	20.4	53.6	**	40.3	24.3	46.4	NS
	FPOM	51.2	206.0	**	191.4	80.4	114.0	NS
	CPOM	115.6	197.0	NS	179.0	106.3	183.7	NS
Aufwuchs								
Riffles	AFDM (g/m ²)	1.3	1.7	NS	1.3	2.0	1.3	NS
	Pigment (μg/m ²)	1600	1970	NS	1970	2080	1300	NS
	Algae (mg/m ²)	99	132	NS	106	156	83	NS
Pools	AFDM (g/m ²)	1.8	2.3	NS	1.8	3.2	1.3	*
	Pigment (μg/m ²)	1860	2470	NS	2310	2910	1280	NS
	Algae (mg/m ²)	125	157	NS	125	218	79	NS
Detritus quality								
Pools	Pigment (μg/g VFPOM)	268	146	NS	93	294	136	**
	Algae (mg/g VFPOM)	19	10	NS	5	30	9	**
	Respiration (VFPOM)	250	194	NS	117	376	172	***
	Respiration (FPOM)	185	136	NS	86	269	127	**
Aufwuchs quality								
Combined	Pigment (μg/g AFDM)	1401	1141	NS	1504	1246	1054	NS
	Algae (mg/g AFDM)	88	74	NS	81	93	68	NS

† Significance level of F value: *** = $P < .001$; ** = $P < .01$; * = $P < .05$; NS = nonsignificant.

environmental variables reflective of food quality rather than quantity of organic matter or substrate composition (Figs. 1 and 2). Abundances of collector-gatherers, filter feeders, and herbivore shredders and piercers were positively correlated with either respiration rate of detrital material or with algal biomass. Scraper density was negatively associated with both algal biomass and quantity of aufwuchs, although scraper biomass showed a weak positive relationship with both of these variables. Associated with these trends, mean biomass of individual scrapers increased as algal biomass or aufwuchs quantity increased. Predators were strongly and positively correlated with abundances of collector-gatherers and filterers. Baetidae and Chironomidae were the most abundant taxa in each of these guilds and are commonly found in the guts of invertebrate predators.

In pool habitats, abundance was correlated with quantity of detritus for some guilds but rarely with

quality parameters. Generalists were correlated with CPOM, POM, and leaf material. Wood gougers were correlated with leaf material. Correlation coefficients for these associations were: generalist density with CPOM ($r = .89$, $P < .01$) and POM ($r = .79$, $P < .05$), generalist biomass with leaf standing crop ($r = .85$, $P < .05$) wood gouger biomass with leaf standing crop ($r = .97$, $P < .01$); $N = 6$ in all cases. Correlations between other guilds and the environmental variables measured were not significant.

Data from tray samples revealed differences in guild abundance among canopy types similar to those observed for bottom collections (Table 5, cf. Table 3; see Appendix A for ANOVA Table). Furthermore, differences in the abundances of some groups that were not statistically significant based on bottom samples (i.e., scrapers, generalists, and total invertebrates) were statistically different based on tray data. Substrate composition was seldom important, affecting the

TABLE 3. Results of two-way ANOVA for effects of canopy and gradient on abundance of invertebrates. Probability of differences among means based on F values after $\log_{10}(x + 1)$ transformation. Degrees of freedom = 1, 12 (gradient); 2, 12 (canopy); and 2, 12 (interaction). Values listed are arithmetic means calculated before transformation. No interactions for pool samples were significant.

Riffles									Pools							
Guild†	Gradient‡			Canopy‡				Gradient × canopy inter- action	Guild†	Gradient‡			Canopy‡			
	HG	LG	P	OG	CC	SG	P			P	HG	LG	P	OG	CC	SG
Density (No./0.1 m ²)																
CG	238	220	NS	108	360	220	*	NS	CG	330	191	NS	159	240	383	NS
SC	51	22	NS	32	29	48	NS	NS	SC	8	2	NS	3	5	7	NS
SH	42	40	NS	34	43	46	NS	NS	SH	69	28	NS	33	53	60	NS
F	17	30	NS	24	40	6	NS	NS	F	7	6	NS	5	9	6	NS
WG	...	...	NS	...	0	...	NS	NS	WG	2	1	NS	2	...	2	NS
G	2	6	*	7	2	2	NS	*	G	3	23	**	17	7	15	NS
HSH	18	9	NS	12	26	3	*	NS	HSH	33	2	**	22	27	3	NS
P	40	60	NS	31	73	47	*	**	P	123	82	NS	88	130	90	NS
T	408	388	NS	248	574	372	NS	NS	T	575	335	NS	329	472	565	NS
Biomass (mg/0.1 m ²)																
CG	7.6	9.1	NS	5.4	13.9	5.9	**	NS	CG	15.6	14.6	NS	18.3	12.1	14.8	NS
SC	3.9	7.5	NS	3.6	11.6	2.0	NS	NS	SC	1.5	2.2	NS	0.8	3.3	1.3	NS
SH	3.4	1.9	NS	2.3	2.7	3.0	NS	NS	SH	40.9	15.4	NS	10.2	22.8	51.4	NS
F	3.7	4.2	NS	2.9	7.9	1.2	**	NS	F	0.5	0.2	NS	0.2	0.1	0.7	NS
WG	...	...	NS	...	0	0.1	NS	NS	WG	3.0	5.6	NS	1.1	0.8	11.0	*
G	0.6	9.7	**	12.6	1.6	1.3	*	**	G	1.2	216.6	***	58.2	39.8	228.7	NS
HSH	0.2	0.5	NS	0.5	0.8	0	NS	NS	HSH	0.2	...	NS	0.1	0.2	...	NS
P	21.3	17.8	NS	14.9	34.8	8.9	*	NS	P	26.0	49.9	NS	50.2	31.1	32.6	NS
T	40.9	50.7	NS	41.9	73.3	22.3	**	NS	T	88.7	304.4	**	139.1	110.2	340.5	NS

† CG = Collector-Gatherers; SC = Scrapers; SH = Shredders; F = Filterers; WG = Wood-Gougers; G = Generalists; HSH = Herbivore Shredders and Piercers; P = Predators; T = Total animals; ... = <1 individual, <0.1 mg, or <1%.

‡ HG = high gradient; LG = low gradient; OG = old-growth; CC = clear-cut; SG = second-growth.

abundances only of shredders and filter feeders. In both these cases trays with higher amounts of fine substrate had higher abundances of animals. Current was also an important factor affecting the abundances of

scrapers, shredders, filter feeders, generalists, and herbivore shredders and piercers, and a significant interaction between current and canopy was observed for some guilds. Neither canopy-substrate interac-

TABLE 4. Relative abundances of different guilds at different sites. Values are means of all three seasons and were calculated from mean abundance data given in Table 3. Symbols defined in Table 3.

		Riffles					Pools				
		Gradient		Canopy			Gradient		Canopy		
	Guild	HG	LG	OG	CC	SG	HG	LG	OG	CC	SG
Relative abundance (%)											
Density	CG	58	57	44	63	59	57	57	48	51	68
	SC	13	6	13	5	13	1	1	1	1	1
	SH	10	10	14	7	12	12	8	10	11	11
	F	4	8	10	7	2	1	2	2	2	1
	WG	...	...	...	0	...	...	...	1	...	...
	G	...	2	3	...	1	1	7	5	1	3
	HSH	4	2	5	5	1	6	1	7	6	1
	P	10	15	13	13	13	21	24	27	28	16
Biomass	CG	19	18	13	19	26	18	5	13	12	4
	SC	10	15	9	16	9	2	1	1	3	...
	SH	8	4	5	4	13	46	5	7	23	15
	F	9	8	7	11	5	1	...	...	...	...
	WG	...	...	...	0	...	3	2	1	1	3
	G	1	19	30	2	6	1	71	42	40	67
	HSH	...	1	1	1	0	...	...	...	...	...
	P	52	35	36	47	40	29	16	36	31	10

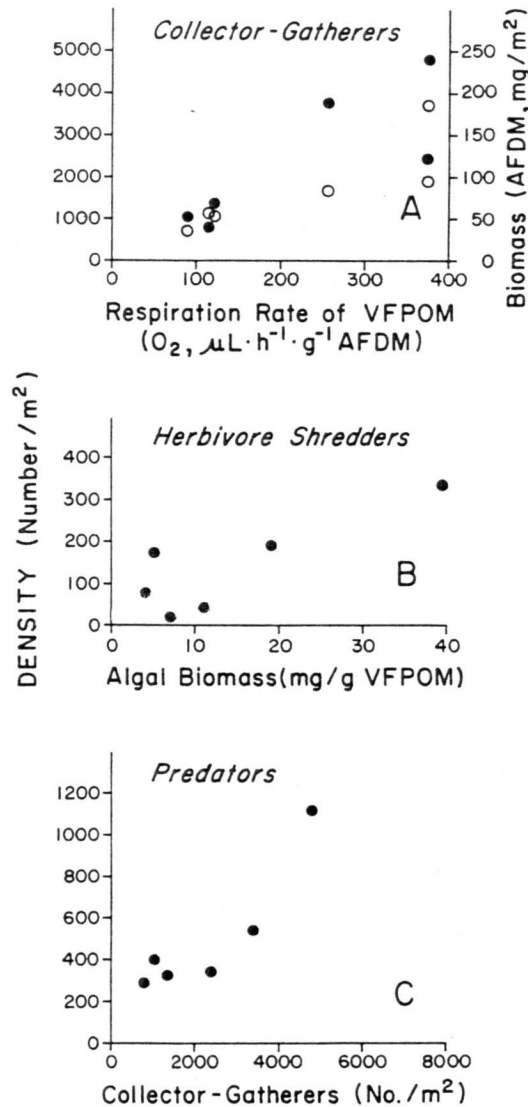


FIG. 1. Relationships between abundances of selected guilds and different food sources. Data from riffle samples only. Densities are indicated by filled circles, biomasses by open circles. Linear correlation coefficients for data without transformation are: collector-gatherers (A), $r = .83$, $P < .05$ for densities, $r = .84$, $P < .05$ for biomasses; herbivore shredders (B), $r = .84$, $P < .05$ for densities; predators (C), $r = .89$, $P < .01$ for densities. $N = 6$ in all cases.

tions nor current-substrate interactions were commonly significant. In general, most groups were most abundant in trays placed in areas with no riparian shading and in the highest current velocity.

Both canopy and current also affected the accumulation of detritus in trays (Table 5; see Appendix B for ANOVA Table). Among canopy types both CPOM and FPOM were lowest in abundance in the open site and highest in the stream with the deciduous canopy. Among currents, standing crops of both organic fractions were highest in trays placed in the slowest cur-

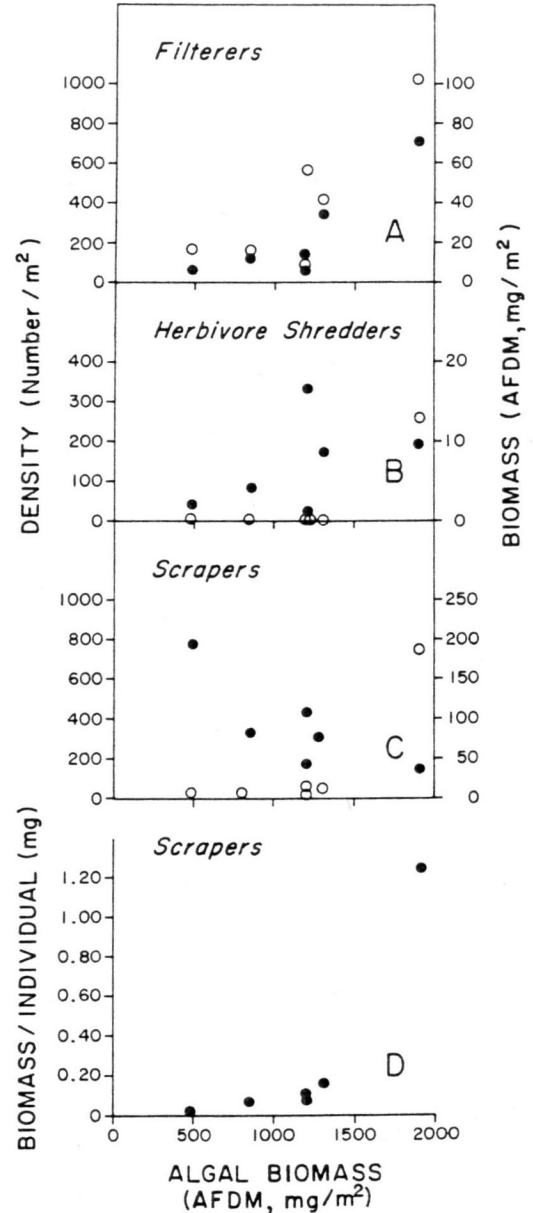


FIG. 2. Relationships between abundances of selected guilds and standing crop of algae on cobbles. Symbols as in Fig. 1. Filterers (A), $r = .83$, $P < .05$ for densities, $r = .83$, $P < .05$ for biomasses; herbivore shredders (B), $r = .81$, $P < .05$ for biomasses, $r = .48$, $P = \text{ns}$ for densities; scrapers (C), $r = -.80$, $P < .05$ for densities, $r = .81$, $P < .05$ for biomasses; scrapers (D), $r = .81$, $P < .05$ for all data points, $r = .84$, $P < .05$ for five smaller values. Note that density of herbivore shredders shows a positive relationship both with algal biomass on cobbles (Fig. 2) and with algal biomass associated with VFPOM (Fig. 1).

rent and lowest where current was greatest. Substrate composition had no effect on amount of CPOM, although a slight but not significant difference existed among trays for FPOM. Trays with no sand had lowest

TABLE 5. Mean densities of invertebrates (per 600 cm²), mean number of taxa (NTAXA), and mean quantity of CPOM and FPOM in the experimental trays. Means are given for each treatment of the three main factors. Symbols defined in Table 3.

	Canopy			Current (cm/s)			Substrate (% sand-embedded)			
	OG	CC	SG	30	15	0	0	25	75	100
TOTAL	258	641	231	423	361	345	354	334	449	368
CG	120	508	117	258	258	229	246	219	312	216
SC	14	9	18	25	10	7	12	11	17	15
SH	22	12	20	35	12	6	9	7	28	28
F	6	4	6	14	1	1	2	4	3	12
G	54	4	18	15	20	41	34	28	17	21
HSH	0	18	0	14	3	0	2	8	4	9
P	43	86	50	61	58	61	49	56	68	66
NTAXA	16	21	19	21	20	16	18	18	21	20
CPOM (g AFDM)	0.9	0.5	1.8	0.6	1.3	1.3	1.1	1.3	0.9	1.0
FPOM (g AFDM)	2.1	1.9	4.8	1.6	3.0	4.3	2.3	3.0	3.4	3.1

amounts of FPOM, and amount of FPOM tended to increase with increasing amount of sand.

These data do not allow us to distinguish unequivocally between the direct effects of canopy, current, and substrate on invertebrate abundance and the effects of accumulated detritus. Within a site both detritus and invertebrate abundance were highest in trays with the most sand. Both detritus and many invertebrate taxa accumulated in the trays by a similar mechanism (drift); thus, it is unclear whether there was active selection by invertebrates for trays with greater amounts of detritus. The most pronounced pattern existed among streams rather than within a site and was due to differences in canopy. Among streams, highest abundances of total invertebrates in trays were found

in the open stream, where the least amount of detritus occurred (Table 5).

Community structure

Based on bottom samples, a few strong differences in either total number of taxa or number of taxa within different functional groups were observed among sites (Table 6). Scrapers had more taxa in high-gradient streams than in low-gradient streams and were the only guild to exhibit significant differences between gradients. Among canopy types both collector-gatherers and herbivore shredders and piercers had more taxa in streams traversing the clear-cuts. Differences in number of taxa for these groups among sites paralleled differences in densities (cf. Tables 6 and 3).

Total number of taxa found in the tray samples during summer were similar among all three low-gradient sites (OG = 57, CC = 57, SG = 58). However three-way ANOVA indicated that all major factors (canopy, current, and substrate) and all but one of the interaction terms probably influenced the number of taxa found in a tray (see Appendix A). Number of taxa was highest in trays with no shading, faster currents, and highest amounts of sand (Table 5). Lowest number of taxa was found in shaded trays under the old-growth canopy, in the lowest current speeds, and with minimal amounts of sand.

Communities observed in the open and shaded sites exhibited different dominance-diversity curves (Fig. 3), and a Kolmogorov-Smirnov test for goodness of fit between the two curves indicated they were significantly different ($P < .01$). The two most common taxa in the clear-cut site made up a greater percentage (51%) of the total community than did the two most abundant taxa in the old-growth section (34%). Because of this, the next eight taxa were less important (i.e., their relative abundances were less) in the clear-cut than in the old-growth site. Much of the remaining portion of the curves was very similar. This analysis indicated that community structure differed between the two

TABLE 6. Two-way ANOVA for effects of gradient and canopy on cumulative number of taxa in different functional groups and mean number of taxa per sample. Data from bottom samples. Values are arithmetic means for each treatment. Analysis performed on nontransformed data. Seasons were used as replicates. Some taxa were assigned to more than one functional group so that total functional taxa (TFT) is numerically greater than total real taxa (TRT). NTAXA = mean number of taxa per 0.1-m² sample unit. Other abbreviations as in previous tables. Degrees of freedom = 1, 12 (gradient) and 2, 12 (canopy).

Group	Gradient			Canopy			
	HG	LG	P	OG	CC	SG	P
	Number of taxa						
CG	21.0	21.4	NS	20.7	24.0	19.0	*
SC	9.6	6.6	**	9.3	6.8	8.0	NS
SH	13.2	10.7	NS	12.2	11.0	12.7	NS
F	4.9	6.4	NS	5.3	6.2	5.5	NS
WG	1.2	1.1	NS	1.2	0.7	1.7	NS
G	1.2	1.9	NS	1.3	1.3	2.0	NS
HSH	2.0	2.1	NS	1.5	3.2	1.5	**
P	23.7	25.6	NS	21.8	25.8	26.2	NS
TFT	76.8	75.8	NS	73.3	79.0	76.5	NS
TRT	72.1	72.2	NS	68.3	74.2	74.0	NS
NTAXA	32.9	30.6	NS	30.7	32.7	31.8	NS

TABLE 7. Comparison of invertebrate communities in substrate trays representing different environmental conditions. Taxa comprising $\geq 1\%$ of total number of individuals in at least one treatment are ranked in order of decreasing abundance. Treatments are: shaded (S), open (O), nonembedded (N), and embedded (E).

Canopy treatment			Substrate treatment				
Rank at old-growth site	Taxon	Treatment with highest density	Old-growth shaded site		Open site		
			Rank in nonembedded treatment	Taxon	Treatment with highest density	Rank in nonembedded treatment	Taxon
1.	<i>Juga plicifera</i>	S	1.	<i>Juga plicifera</i>	N	1.	Orthocladini spp.
2.	Orthocladini spp.	O	2.	<i>Micropsectra</i> spp.	N	2.	<i>Rheotanytarsus</i> sp.
3.	<i>Micropsectra</i> spp.	O	3.	Orthocladini spp.	E	3.	<i>Paraleptophlebia</i> spp.
4.	<i>Calineuria californica</i>	S	4.	Pentaneurini sp.	N	4.	<i>Baetis parvus</i>
5.	<i>Zapada cinctipes</i>	S	5.	<i>Glossosoma</i> sp.	N	5.	<i>Centroptilum</i> sp.
6.	<i>Paraleptophlebia</i> spp.	O	6.	<i>Baetis parvus</i>	N	6.	<i>Rheotanytarsus</i> sp.
7.	<i>Baetis parvus</i>	O	7.	<i>Paraleptophlebia</i> spp.	E	7.	<i>Heptagenia</i> sp.
8.	Pentaneurini sp.	O	8.	<i>Psectrocladius</i> sp.	E	8.	Pentaneurini sp.
9.	<i>Glossosoma</i> sp.	S	9.	<i>Calineuria californica</i>	E	9.	<i>Ameletus</i> sp.
10.	<i>Thienemanniella</i> sp.	S	10.	<i>Polycentropus</i> sp.	N	10.	<i>Paraleptophlebia bicornuta</i>
11.	<i>Cinygmula</i> sp.	S	11.	<i>Ptychoptera</i> sp.	N	11.	<i>Baetis</i> spp.
12.	<i>Rheotanytarsus</i> sp.	S	12.	<i>Ameletus</i> sp.	N	12.	<i>Thienemanniella</i> sp.
13.	Pentaneurini sp.	S	13.	<i>Zapada cinctipes</i>	E	13.	<i>Calineuria californica</i>
14.	<i>Polycentropis</i> sp.	S	14.	<i>Hydropsyche</i> sp.	E	14.	<i>Oreodytes</i> spp.
15.	<i>Hydropsyche</i> sp.	S	15.	<i>Thienemanniella</i> sp.	E	15.	Pentaneurini sp.
16.	" <i>Alloperla</i> " spp.	S	16.	Pentaneurini sp.	N	16.	<i>Agraylea saltsea</i>
17.	<i>Heterlimnius</i> sp.	O	17.	<i>Cinygmula</i> sp.	E	*17.	<i>Skwala</i> sp.
18.	<i>Lepidostoma</i> spp.	S	18.	<i>Rheotanytarsus</i> sp.	E	18.	<i>Juga plicifera</i>
19.	<i>Baetis</i> spp.	O	19.	<i>Ceratopogonidae</i> spp.	N	19.	Chironomini spp.
*20.	Chironomini spp.	O	*20.	<i>Wormaldia</i> sp.	E	20.	<i>Malenka</i> sp.
21.	<i>Rheotanytarsus</i> sp.	O	21.	" <i>Alloperla</i> " spp.	E		
22.	<i>Agraylea saltsea</i>	O	22.	Pentaneurini sp.	E		
23.	<i>Heptagenia</i> sp.	O	23.	<i>Lepidostoma</i> spp.	E		
24.	Pentaneurini sp.	O	24.	<i>Heterlimnius</i> sp.	E		
25.	<i>Ameletus</i> sp.	O	25.	<i>Baetis</i> spp.	E		
26.	<i>Skwala</i> sp.	O	26.	<i>Despaxia</i> sp.	E		
27.	<i>Paraleptophlebia bicornuta</i>	O					
28.	<i>Centroptilum</i> sp.	O					
29.	<i>Oreodytes</i> spp.	O					
30.	<i>Malenka</i> sp.	O					

* Taxa prior to this are ranked in order of abundance in either the shaded or the nonembedded treatments. Subsequent taxa are those that accounted for $\geq 1\%$ of total density only in the open or the embedded treatments but may have had higher densities than some previously ranked taxa.

communities by a shift toward a greater degree of dominance (lower evenness) within the 10 most common taxa. The relative abundances of less common and rare taxa were unaffected.

These same data were compared at the individual taxon level. Taxa were ranked according to order of abundance in the old-growth site. The abundance of each taxon in the open site was then compared to its abundance in the shaded old-growth site. For the 10 taxa most common in the shaded section, densities of 5 taxa were more abundant and 5 were less abundant in the open stream compared with the shaded section (Table 7). Of the nine other taxa that comprised at least 1% of total numbers in the shaded section, all but two had lower densities in the open site. In contrast, 11 other taxa that were either not found in the shaded site or whose relative abundances were $< 1\%$ of the total comprised 1% or more of the total in the open stream. Thus although major differences were

not apparent in proportions of taxa within the two communities (Fig. 3), lack of a riparian canopy affected communities by increasing the abundance of some of the dominant taxa found in the shaded section, decreasing the abundance of less-common (but $\geq 1\%$ of the total) taxa, and increasing the abundance of taxa not typically found or usually uncommon in the shaded stream. The overall result was that of a total of 30 taxa, 12 had greater abundances in the shaded section and 18 had greater abundances in the open section.

We also compared data from trays in which stones were completely embedded with sand (treatment), with data from trays in which no sand was added (control). Dominance curves for the two sets of trays from the shaded section were different (Fig. 3; Kolmogorov-Smirnov test, $P < .01$). The main difference was that the most common taxon in the control trays was more abundant than the most common taxon in the treat-

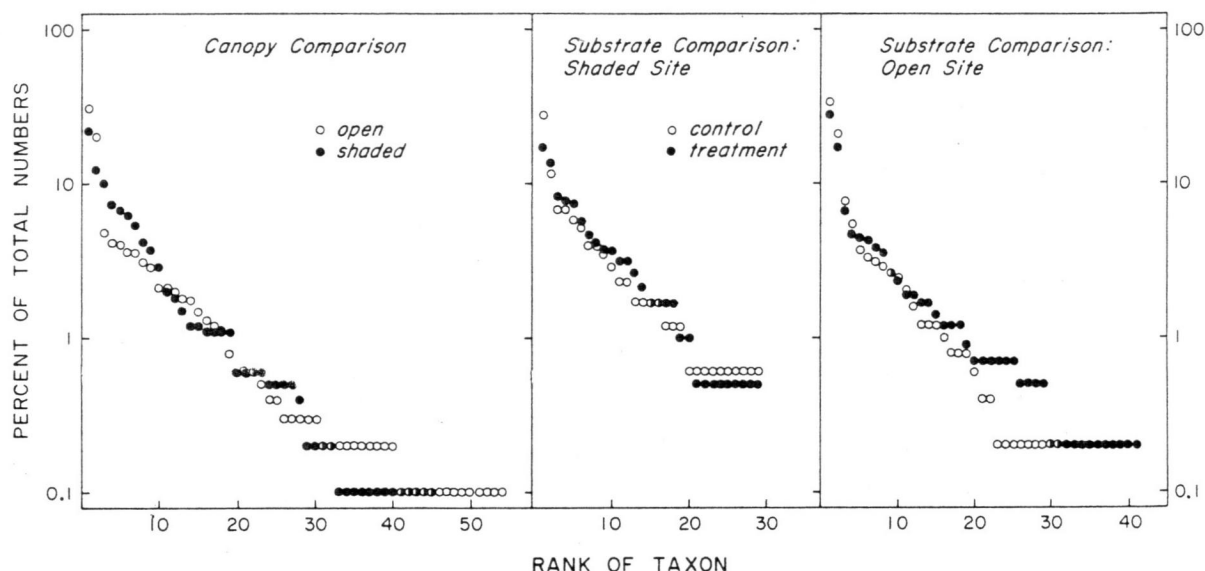


FIG. 3. Dominance-diversity curves for invertebrate communities found at sites with open and shading canopies and in trays in which either no sand was added (control) or sand completely filled all interstitial spaces (treatment). Substrate comparisons are for both the shaded site and open site.

ment trays. Curves constructed from data in the open section were also different (Fig. 3; $P < .01$); the four most abundant taxa in the control trays showed slightly higher relative abundances than their counterparts in the treatment trays. The most rare taxa from the control trays were slightly less abundant than rare taxa from the treatment trays.

Comparison of differences in abundances of specific taxa showed that embedding the trays with sand generally caused a decline in density of the dominant taxa in both shaded and open environments (Table 7). This trend was especially apparent for the most abundant five or six taxa. If the top 10 taxa are arbitrarily chosen for examination, 6 of 10 taxa showed lower densities in the embedded trays relative to control trays in the shaded stream. For the open site, 9 of 10 taxa had lower densities in embedded trays than in control trays. These results were significantly different from those expected by chance only for the open site. If we compare all taxa accounting for $\geq 1\%$ of total density for all trays, no significant difference was observed in the net number of taxa that either increased or decreased in abundance for either site. These results indicate that a moderate shift from one set of taxa to another set occurred between control and treatment trays but that the general pattern of relative abundance of taxa within trays did not change. Furthermore, the number of taxa that declined in abundance was matched by an equivalent number that increased.

DISCUSSION

Abundance of invertebrate guilds

Patterns of distribution and abundance of invertebrates in streams are in large part a function of the

specific requirements of different taxa and the particular environmental complex that exists at any section of stream. Food and substrate are two of the most important aspects of environment and have accordingly received a great deal of study (e.g., see review in Hynes 1970). In this study, we have attempted to assess the relative effects of food and substrate on invertebrate abundance. Within the range of conditions encountered, our results indicate that canopy, or lack thereof, was more important than substrate character in determining the abundance of different guilds of invertebrates. Canopy development appeared to decrease the amount of high-quality food available to consumers. Temperature effects cannot be completely ruled out but were probably minimal in this study.

A growing body of literature has demonstrated or implicated food quality as an important variable governing either growth rates or the abundances of specific taxa or groups (e.g., Cushing 1963, Bärlocher and Kendrick 1973, Iversen 1974, Mackey 1977, Ward and Cummins 1979, Hawkins and Sedell 1981; and see reviews by Anderson and Cummins 1979, Cummins and Klug 1979). Our results imply that food quality in streams is strongly linked to algal production. Algae generally have lower C/N ratios than other primary food sources in streams (Boyd 1973, see Anderson and Cummins 1979). Increased primary production can result not only in higher standing crops of *aufwuchs*, but also in increased concentrations of both live algae and high-quality detritus (i.e., that derived from algae) in both fine sediments (this study, Hawkins and Sedell 1981) and in the water column (Swanson and Bachmann 1976, Naiman and Sedell 1979). Guilds which can consume food sources linked to algal production

usually showed greatest abundances in stream sections without canopies (i.e., CG, F, HSH, G).

Scrapers, which were expected to be most strongly affected by shading and most abundant in streams without shading, did not exhibit a marked difference in density among canopy types. In fact, densities of scrapers in riffles were generally lowest in streams without canopies, although biomass was greater in open sections than in shaded reaches. During the study we did not measure either primary production or scraper production and hence cannot evaluate the relationships that existed between scraper density, biomass, and production and algal production. From data that we did gather, we can postulate relationships that may exist between scraper abundance and quantity of aufwuchs. These relationships do not depend on a knowledge of actual production dynamics. Taxa within the scraper guild appear to be highly adapted morphologically to a rather special stream environment, the tops and sides of rocks and other large substrates. Food and physical habitat are intimately linked. For those taxa that harvest thin films of aufwuchs material, large accumulations of algae may physically exclude them from necessary habitat and limit access to required food. Our results show that densities of scrapers declined with increasing quantity of aufwuchs, whereas scraper biomass remained constant or increased. The overall result was that mean individual biomass of scrapers increased as aufwuchs biomass increased. Anderson and Cummins (1979) showed a similar trend for *Glossosoma* and the photosynthesis:respiration ratio in streams. However, the difference in mean individual biomass that we observed was mostly the result of shifts in taxa within the guild among sites rather than differences in biomass of individuals within a taxon. Taxa with small- to medium-sized individuals, such as *Glossosoma*, many Heptageniidae, *Apatania*, and *Neothremma*, were found in shaded sites, whereas taxa with larger larvae, such as *Dicosmoecus* and *Neophylax*, were more common in open sites. An interesting hypothesis is that larger individuals can exploit thicker layers of aufwuchs, whereas smaller individuals cannot. An alternative hypothesis is that these relationships are not causal but rather reflect the influence of a third variable (e.g., current) on both quantity of aufwuchs and size of scraper.

Herbivore shredders-piercers, a guild that exploits macrophytes and large filamentous or mat-like forms of algae, increased in both density and biomass as algae increased in abundance. Density but not biomass also was positively related to algal biomass in VFOM. This result would have been expected if small instars function as collector-gatherers rather than obligate herbivore shredders or piercers. Our results agree with those of Towns (1981) who showed algal piercers to be more abundant in an open section of stream than in an experimentally shaded section.

Predators appeared to benefit indirectly from in-

creased light reaching the stream by increasing in abundance as availability of prey taxa, specifically collector-gatherers and filterers, increased. Invertebrate predators were often significantly correlated with abundances of potential prey (CG, SH, F, or total animals excluding predators). Similar correlations have been observed by Fahy (1975) and Hawkins and Sedell (1981). We have previously shown that vertebrate predators are more abundant in streams with open canopies and are strongly correlated with abundance of collector-gatherers (Murphy and Hall 1981, Murphy et al. 1981).

The shredder guild was a second group for which our observations did not agree with our initial expectations. We expected shredders to be most abundant in streams with deciduous canopies (second-growth alder) and least abundant in streams with no riparian canopy. It is surprising that streams in clear-cut sections had densities and biomasses similar to those in second-growth sections. Lack of differences in shredder abundances among canopy types could occur for a number of reasons. Categorization of feeding behavior of taxa within this group may not be very accurate at this time. Many taxa that we classified as shredders may be more facultative in both their feeding behavior and food requirements than we originally suspected. This is probably true for many of the Nemouridae, Capniidae, and Leuctridae, but we also found high densities and biomass of caddis shredders (*Lepidostoma* spp. and others) in open sections. Both aufwuchs and macroalgae, either alive or after sloughing and entering the coarse detritus pool, may be as suitable a "shreddable" food source as is leaf detritus. An alternative explanation is that availability of food preferred by shredders may not have differed greatly among sites. We did not measure organic inputs over the entire year. We only measured standing crops of detritus twice, and we did not partition total CPOM into different sources (deciduous tree leaves, conifer needles, herbaceous leaves, algae, etc.). Also, one open stream (Mack clear-cut) was directly below an old-growth section and may have been influenced by organic matter originating from upstream. In general, however, our data indicate that a simple open-shaded contrast among sites was not sufficient to produce distinct differences in shredder abundances.

We found wood gougers only in those sites surrounded by a well-developed riparian zone. In these streams (OG and SG) accumulations of large woody debris were common. We did not specifically sample this habitat, but a few individuals of wood-associated taxa such as the elm beetle *Lara avara* LeConte and the caddis *Heteroplectron californicum* McLachlan (Anderson et al. 1978) were collected in both riffles and pools. Because their numbers were so low in the habitats sampled, statistical differences among sites were usually not evident. However, they were nearly always more abundant and exhibited larger biomasses

in shaded streams, particularly in streams with alder canopies. Anderson et al. (1978) found higher densities of gougers in Coast Range streams than in the Cascades, and attributed this to greater quantities of alder in the former.

We cannot draw inferences concerning factors that regulate the abundance and distribution of generalists as a guild because one taxon, the snail *Juga plicifera*, comprised over 95% of all individuals assigned to this group. Nevertheless, because *Juga* was such an important component of the invertebrate assemblage at some sites, it is useful to consider factors affecting its abundance and ecology. Based on our results, the distribution of *Juga* was shown to be influenced by at least four factors: gradient, canopy, substrate character, and current. Two-way ANOVA indicated that both gradient and canopy significantly affected its pattern of abundance and that an interaction existed between the two treatments. *Juga* was absent from all high-gradient streams. The effect of gradient may be an effect of current rather than substrate composition, an interpretation consistent with Ludwig's (1932) observations that snail densities decreased with increasing current.

The difference in abundance of *Juga* among canopy types was probably not due to differences in food availability or quality, but rather to past and present differences in substrate dynamics among streams. Individuals of *Juga* were conspicuously absent from the low-gradient stream in the clear-cut watershed but were abundant in both low-gradient shaded streams. The clear-cut watershed is unstable, and massive erosion and channel rearrangement occur each winter. Scour associated with winter storms in this stream would continually reduce populations of this long-lived invertebrate (age up to 7 yr). Scour in the forested watersheds is not as intense because the upper slopes and headwaters are relatively stable. Recolonization for these snails also would be much slower than for insect taxa with winged adults. *Juga* is abundant in more stable streams in the study area that lack canopies (Hawkins and Sedell 1981), and unpublished experimental data show that they grow more rapidly on algal food sources than on leaf detritus (D. A. McCullough, *personal communication*). Thus, the apparently significant interaction of canopy and gradient was probably in this case a spurious result due to historical factors and not due to the treatments under consideration.

Although *Juga* was restricted to low-gradient reaches where mean substrate size was smaller than in high-gradient reaches, they nevertheless exhibited decreasing abundances with increasing amounts of fine sediment in experimental trays. Increased embeddedness evidently decreased the area of solid substrate available for attachment and feeding, resulting in lower densities. Although the apparent interaction seen from the ANOVA of field samples was quite likely an arti-

fact, a real interaction may very well exist between substrate and current (see Appendix, ANOVA for canopy, current, and substrate). The percent decline in abundance as embeddedness increased appeared to be greater for trays in low current velocities than in high velocities.

The tray data allowed us to examine relationships among abundance of animals, current, and substrate, but the quantity of detritus that accumulated in trays is a confounding variable. Abundances of some guilds, as well as accumulation of potential food material, were affected by current and substrate, and the data are insufficient to unequivocally distinguish the interrelationships among animal abundance, substrate, and quantity of detritus. Our results are in this respect similar to those of Rabeni and Minshall (1977), Bjornn et al. (1977), and Williams and Mundie (1978).

Among sites, food quality rather than quantity probably determined the major differences in pattern of abundance of different guilds. Abundances were seldom correlated with amount of detritus, contrary to the observations of Egglisshaw (1964, 1968) and Hawkins and Sedell (1981). Within sites, quantity of detritus was less important than other factors (e.g., current). These observations are significant in that a large amount of past research has focused on the importance of detritus in stream ecosystems (e.g., Nelson and Scott 1962, Vannote 1969, Cummins 1973, Fisher and Likens 1973, Hynes 1975, Anderson and Sedell 1979). Much of this work was oriented toward determining the sources and fates of organic carbon in streams, much of which is detrital. Toward this goal, invertebrates have been shown to be important links in processing detritus in streams (Cummins 1974, Anderson and Sedell 1979), and yet we have not adequately considered how symmetric the relationships between detrital dynamics and invertebrate abundances really are (e.g., Malmquist et al. 1978). A major portion of the organic carbon in streams can be present as detritus of poor nutritional quality, and large differences in quantity of detritus may represent very small differences in actual food availability. Recent research has begun to emphasize qualitative differences in food sources, but much of this work still focuses on detritus, especially detritus of allochthonous origin.

Minshall (1978) has questioned the general importance of allochthonous detritus in stream systems and argues that autotrophic production can contribute a significant if not major portion of the total energy (carbon) to many streams. Our results indicate that even where allochthonous detritus may be very abundant, invertebrate consumers may be mainly influenced by the amount of autotrophic production occurring in a stream. Furthermore, current was found to be more important to invertebrate abundance than quantity of detritus. Abundances of scrapers, shredders, filter feeders, and herbivore shredder-piercers all increased with increasing current velocity. McIntire (1966, 1968)

has shown that for current velocities similar to those examined here, both production and standing crop of the periphyton community was highest where current velocity was greatest. The greater availability of periphyton food sources as current velocity increases may partly explain the trends in animal abundance that we observed.

Trophic structure and guild distinctions

Trophic structure should have reflected differences in the relative availability of food sources if: (1) guild classification accurately characterized real differences in the feeding behavior and food requirements of the taxa encountered; (2) food availability was adequately categorized; and (3) consumer populations track abundance of food resources. As mentioned earlier, our sampling was not thorough enough to unequivocally distinguish differences in food availability among sites. We also gathered no data that examined the growth and production of consumer populations relative to different food sources. The contrasts in canopy type among streams do provide circumstantial evidence that present classifications of macroinvertebrate feeding guilds may not be very sensitive to broad differences in available food sources. Abundances of collector-gatherers, scrapers, and shredders often responded in rather similar ways to the differences in food that did exist among sites. There may exist more similarities than differences in the ecology of these groups. Many taxa probably do not separate into discrete guilds but rather show a great deal of overlap both in what they eat and how they exploit different resources. Differences in guild abundance among sites could therefore be rather subtle and would manifest themselves as gradual differences in abundance and distribution along continua of food availability.

Many taxa may be much more generalized in not only food eaten but also their feeding behavior than we originally thought. Groups such as Baetidae, Ephemerellidae, Nemouridae, Leuctridae, many Limnephilidae, and others have generalized mouthparts which may function equally well in consuming large particles (leaf litter, macroalgae), attached food (aufwuchs, if thick enough), or loose particles (FPOM). We do feel that guild classification is an extremely valuable and necessary approach to examining invertebrate communities, but ecologists should realize that in many cases distinctions may be by necessity somewhat arbitrary. Caution should therefore be used when basing either inference or theory on present classifications. Sufficient empirical evidence is not yet available from which we may examine the degree of ecological similarity or difference that truly exists among taxa both within and among guilds.

Some of our results are contradictory to earlier studies that examined functional organization of invertebrates in streams. In a previous study, guilds were shown to be predictably distributed along a longitudi-

dinal stream gradient (Hawkins and Sedell 1981, see also Vannote et al. 1980), and their distribution was related to either quantity or quality of food resources. In this study, modification of canopy and thus food sources among similar-sized streams did not always evoke patterns of trophic structure that we would have expected based on previously observed associations between guild abundance and food sources along river continua. These different observations are not necessarily incompatible but rather may reflect our failure to consider the multiple environmental requirements of taxa. After manipulation (i.e., canopy removal) of a shaded headwater stream, many food sources may be similar to a naturally open downstream reach, but other factors probably are not. By manipulating stream systems we may create conditions favorable to organisms with broad tolerances rather than for different sets of specialists.

Community structure: number of taxa

Our analyses revealed ambiguous results with respect to the effect of canopy and substrate on either mean number of taxa within a sampling unit or the cumulative number of taxa encountered over all samples. Results derived from the bottom samples were not similar to those from tray samples. The reasons for this discrepancy are not clear, although bottom data were from three dates, and tray data were from only one. The additional variance acquired in the analysis due to using seasons as replicates may have been sufficient to obscure real differences in number of taxa among sites. Conversely, real differences among sites simply may not exist regardless of the variance associated with the data. Examination of data from bottom samples taken on the same date in August as tray data, revealed similar patterns of mean number of taxa among canopy types as seen in the tray data. If tray data had been collected each date, it is likely that trends similar to the bottom data would have been observed.

To some extent our data support the contention of Minshall and Minshall (1977) who question the rather well-accepted generality that diversity or species richness of benthic invertebrate communities increases as either mean substrate size or heterogeneity increases (e.g., Bell 1969, Allan 1975, Friberg et al. 1977). In fact some studies, e.g., Wise and Molles (1979), have found more taxa on small substrates than on large ones, a result not inconsistent with our data that showed more taxa in trays with the largest amounts of sand. Evaluation of this sort of community data is complicated by at least two difficulties. First, as Minshall and Minshall (1977), Khalaf and Tachet (1980), and Williams (1980) have observed, not all taxa show substrate preferences over the range of conditions examined, and this may obscure trends which exist among taxa that do exhibit preferences. Secondly, it is not clear that percent composition, mean substrate size, or heterogeneity (Allan 1975, Wise and Molles 1979,

Williams 1980) are adequate measures of habitat structure as perceived by invertebrates.

When we analyzed our data by separating taxa into guilds and examined cumulative number of taxa observed over all samples for each site, we found that number of taxa varied directly with guild abundance for many groups. For example, high-gradient sites had more scraper taxa and higher scraper densities than did low-gradient sites. Canopy appeared to affect clearly both the densities and number of taxa in two guilds: herbivore shredders-piercers and collector-gatherers. These data indicate that the factors that influence overall abundance of a guild also influence number of taxa within a guild.

We would emphasize that the number of taxa in a community is a function of many factors. Our data from tray samples showed most major factors and interactions to significantly affect number of taxa. These results demonstrate why so many hypotheses have been proposed concerning the different mechanisms that determine number of taxa in communities (Ricklefs 1979) and why it is often difficult to generalize with regard to the distribution and abundance of guilds or taxa. For example, analysis of shredder densities produced evidence contradictory to river continuum arguments concerning the reasons for the abundance and distribution of taxa in this guild (Wiggins and Mackay 1978, Vannote et al. 1980, Hawkins and Sedell 1981). There were more taxa of shredders (Table 6, $P = .08$) in high-gradient reaches than in low-gradient streams, but canopy had no effect. Taxa assigned to this guild may therefore be restricted to small high-gradient sites (i.e., those typically shaded) for reasons other than, or in addition to, food.

Community structure: abundances of individual taxa

It is important to emphasize that significant differences can exist in community structure that are not distinguished by analysis of community level parameters such as total density, number of taxa, guild structure, or the relative abundances of taxa within communities (i.e., diversity or heterogeneity). We did not quantify differences in the abundances of individual taxa in the same manner as did, for example, Minshall and Minshall (1977), but our analysis of qualitative differences (greater or lesser abundances) between either canopy types or substrates showed that real differences in communities existed among treatments (Table 7). Many invertebrate taxa are known to have definite preferences for substrate character and other environmental variables (e.g., Percival and Whitehead 1929, Linduska 1942, Cummins and Lauff 1969, Tol-kamp 1980). The trends for different taxa to prefer different environmental conditions is certainly not surprising, and we should recognize that subtle to moderate shifts in the species composition of a community are manifested as differences in commonly measured

community level attributes when environmental conditions differ sufficiently.

Ecological analysis of stream communities

Our study design in part utilized large-scale perturbation (i.e., canopy modification associated with logging) as an experimental treatment. We showed that the type of canopy surrounding a stream can significantly influence the type of invertebrate community observed, whereas substrate character was less important over the range of conditions encountered. We believe that our results and those of others (e.g., Minshall and Minshall 1977, Newbold et al. 1980) indicate the urgent necessity of examining stream communities from a number of perspectives and based on a variety of analyses. These perspectives include examination of community level attributes, analysis of guild structure, and description of population or species level responses. Ideally all of these analyses would be interpreted within and integrated with even broader frameworks. Such frameworks would include recognition of how communities differ over broad gradients of factors such as food, temperature, light, current, and substrate. Community pattern observed at one scale (e.g., watersheds, reaches, or habitat patches) would ideally be interpreted in terms of processes that produce pattern at other scales.

This study attempted to address the relative importance of differences in canopy and substrate on stream communities. A second phase of this study has been designed to compare communities over a more extensive gradient of substrate size. Eventually the relative importance of many factors must be recognized. These sorts of data are necessary if we are to truly develop a holistic understanding of stream communities.

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LITERATURE CITED

- Allan, J. D. 1975. The distributional ecology of benthic insects in Cement Creek, Colorado. *Ecology* 56:1040-1053.
Anderson, N. H., and K. W. Cummins. 1979. The influence of diet on the life histories of aquatic insects. *Journal of the Fisheries Research Board of Canada* 36:335-342.

- Anderson, N. H., and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology* 24:351-377.
- Anderson, N. H., J. R. Sedell, L. M. Roberts, and F. J. Triska. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. *American Midland Naturalist* 100:64-82.
- Bärlocher, F., and B. Kendrick. 1973. Fungi and food preferences of *Gammarus pseudolimnaeus*. *Archiv für Hydrobiologie* 72:501-516.
- Bell, H. L. 1969. Effect of substrate types on aquatic insect distribution. *Journal of the Minnesota Academy of Science* 35:79-81.
- Bjornn, T. C., M. A. Bruvsen, M. P. Molnau, J. H. Milligan, R. A. Klamt, E. Chacho, and C. Schaye. 1977. Transport of granitic sediment in streams and its effects on insects and fish. *Bulletin Number 17, Forest, Wildlife, and Range Experiment Station, University of Idaho, Moscow, Idaho, USA*.
- Boyd, C. E. 1973. Amino acid composition of freshwater algae. *Archiv für Hydrobiologie* 72:1-9.
- Cummins, K. W. 1973. Trophic relations of aquatic insects. *Annual Review of Entomology* 18:183-206.
- . 1974. Structure and function of stream ecosystems. *Bioscience* 24:631-641.
- Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10:147-172.
- Cummins, K. W., and G. H. Lauff. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia* 34:145-181.
- Cushing, C. E., Jr. 1963. Filter-feeding insect distribution and planktonic food in the Montreal River. *Transactions of the American Fisheries Society* 92:216-219.
- Egglishaw, H. J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. *Journal of Animal Ecology* 33:463-476.
- . 1968. The quantitative relationships between bottom fauna and plant detritus in streams of different calcium concentration. *Journal of Applied Ecology* 5:731-740.
- Fahy, E. 1975. Quantitative aspects of the distribution of invertebrates in the benthos of a small stream system in western Ireland. *Freshwater Biology* 5:167-182.
- Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* 43:421-439.
- Friberg, F., L. M. Nilsson, C. Otto, P. Sjöström, B. W. Svensson, B. J. Svensson, and S. Ulfstrand. 1977. Diversity and environments of benthic invertebrate communities in south Swedish streams. *Archiv für Hydrobiologie* 81:129-154.
- Gregory, S. V. 1980. Effects of light, nutrients, and grazing on periphyton communities in streams. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Hawkins, C. P., and J. R. Sedell. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology* 62:387-397.
- Hynes, H. B. N. 1970. *The ecology of running waters*. University of Toronto Press, Toronto, Ontario, Canada.
- . 1975. *The stream and its valley*. Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen 19:1-15.
- Iversen, T. M. 1974. Ingestion and growth in *Sericostoma personatum* in relation to the nitrogen content of ingested leaves. *Oikos* 25:278-282.
- Karlström, U. 1978. Environmental factors, detritus and bottom fauna in the Rickleån—a north Swedish River. Institute of Limnology, University of Uppsala, Uppsala, Sweden.
- Karr, J. R., and I. J. Schlosser. 1977. Impact of nearstream vegetation and stream morphology on water quality and stream biota. EPA 600/3-77-097, Ecological Research Series, Environmental Protection Agency, Athens, Georgia, USA.
- Karr, J. R., and I. J. Schlosser. 1978. Water resources and the land-water interface. *Science* 201:229-234.
- Khalaf, G., and H. Tachet. 1980. Colonization of artificial substrata by macro-invertebrates in a stream and variations according to stone size. *Freshwater Biology* 10:475-482.
- Linduska, J. P. 1942. Bottom type as a factor influencing the local distribution of mayfly nymphs. *Canadian Entomologist* 74:26-30.
- Ludwig, W. B. 1932. The bottom invertebrates of the Hocking River, *Bulletin of the Ohio Biological Survey* 26:223-249.
- Lyford, J. H., and S. V. Gregory. 1975. The dynamics and structure of periphyton communities in three Cascade Mountain streams. Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen 19:1610-1616.
- Mackey, A. P. 1977. Growth and development of larval Chironomidae. *Oikos* 28:270-275.
- MacMahon, J. A., D. J. Schimpf, D. C. Andersen, K. G. Smith, and R. L. Bayn, Jr. 1981. An organism-centered approach to some community and ecosystem concepts. *Journal of Theoretical Biology* 88:287-307.
- Malmquist, B., L. M. Nilsson, and B. S. Svensson. 1978. Dynamics of detritus in a small stream in southern Sweden and its influence on the distribution of the bottom animal communities. *Oikos* 31:3-16.
- McIntire, C. D. 1966. Some effects of current velocity on periphyton communities in laboratory streams. *Hydrobiologia* 27:559-570.
- . 1968. Structural characteristics of benthic algal communities in laboratory streams. *Ecology* 49:520-537.
- Merritt, R. W., and K. W. Cummins, editors. 1978. *An introduction to the aquatic insects of North America*. Kendall-Hunt, Dubuque, Iowa, USA.
- Minshall, G. W. 1978. Autotrophy in stream ecosystems. *Bioscience* 28:767-771.
- Minshall, G. W., and J. N. Minshall. 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (U.S.A.) stream. *Hydrobiologia* 55:231-249.
- Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Science* 38:137-145.
- Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. *Transactions of the American Fisheries Society* 110:469-478.
- Naiman, R. J., and J. R. Sedell. 1979. Characterization of particulate organic matter transported by some Cascade Mountain streams. *Journal of the Fisheries Research Board of Canada* 36:17-31.
- Nelson, D. J., and D. C. Scott. 1962. Role of detritus in the productivity of rock-outcrop community in a Piedmont stream. *Limnology and Oceanography* 7:396-413.
- Newbold, J. D., D. C. Erman, and K. B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. *Canadian Journal of Fisheries and Aquatic Science* 37:1076-1085.
- Percival, E., and H. Whitehead. 1929. A quantitative study of the fauna of some types of stream-bed. *Journal of Ecology* 17:282-314.
- Rabeni, C. F., and G. W. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. *Oikos* 29:33-43.

- Ricklefs, R. E. 1979. Ecology, second edition. Chiron Press, New York, New York, USA.
- Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecological Monographs* 37:317-350.
- Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biology* 10:375-383.
- Swanson, C. D., and R. W. Bachmann. 1976. A model of algal exports in some Iowa streams. *Ecology* 57:1076-1080.
- Tolkamp, H. H. 1980. Organism-substrate relationships in lowland streams. Agricultural Research Report 907, Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Towns, D. R. 1981. Effects of artificial shading on periphyton and invertebrates in a New Zealand stream. *New Zealand Journal of Marine and Freshwater Research* 15:185-192.
- Vannote, R. L. 1969. Detrital consumers in natural streams. Pages 20-23 in K. W. Cummins, editor. The stream ecosystem: an American Association for the Advancement of Science Symposium. Technical Report Number 7, Institute of Water Research, Michigan State University, East Lansing, Michigan, USA.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science* 37:130-137.
- Ward, G. M., and K. W. Cummins. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). *Ecology* 60:57-64.
- Wiggins, G. B., and R. J. Mackay. 1978. Some relationships between systematics and trophic ecology in nearctic aquatic insects, with special reference to Trichoptera. *Ecology* 59:1211-1220.
- Williams, D. D. 1980. Some relationships between stream benthos and substrate heterogeneity. *Limnology and Oceanography* 25:166-172.
- Williams, D. D., and J. H. Mundie. 1978. Substrate size selection by stream invertebrates and the influence of sand. *Limnology and Oceanography* 23:1030-1033.
- Wise, D. H., and M. C. Molles, Jr. 1979. Colonization of artificial substrates by stream insects: influence of substrate size and diversity. *Hydrobiologia* 65:69-74.

APPENDIX A

Three-way ANOVA for the effects of canopy, current velocity, and substrate composition on the abundances of different invertebrate groups and the mean number of taxa. Data are for tray samples, and except for number of taxa, were transformed, $\log_{10}(x + 1)$, prior to analysis.

Source of variation	df	Total		Collector-gatherers		Scrapers	
		F	P	F	P	F	P
Canopy	2	27.8	.001	33.8	.001	6.9	.010
Current	2	0.8	.452	0.0	.980	15.0	.001
Canopy $\times$ current	4	2.2	.137	2.3	.119	14.2	.001
Substrate	3	0.4	.888	0.3	.798	0.5	.700
Canopy $\times$ substrate	6	3.1	.047	0.4	.880	1.4	.280
Current $\times$ substrate	6	0.3	.802	2.8	.063	1.6	.232
Error	12						

		Shredders		Filterers		Generalists	
		F	P	F	P	F	P
Canopy	2	1.7	.221	0.5	.595	147.1	.001
Current	2	13.8	.001	21.1	.001	19.3	.001
Canopy $\times$ current	4	2.1	.145	0.6	.674	9.0	.001
Substrate	3	5.7	.011	3.3	.058	1.2	.361
Canopy $\times$ substrate	6	1.1	.430	1.9	.166	2.6	.072
Current $\times$ substrate	6	2.8	.061	1.8	.178	1.6	.244
Error	12						

		Herbivore shredders		Predators		Number of taxa	
		F	P	F	P	F	P
Canopy	2	27.7	.001	16.5	.001	14.0	.001
Current	2	6.2	.014	0.5	.608	16.4	.001
Canopy $\times$ current	4	6.2	.006	5.4	.010	5.9	.007
Substrate	3	0.3	.788	1.1	.399	2.7	.096
Canopy $\times$ substrate	6	0.4	.895	0.9	.518	1.4	.283
Current $\times$ substrate	6	1.0	.468	3.3	.038	5.5	.006
Error	12						

APPENDIX B

Three-way ANOVA for effects of canopy, current velocity, and substrate composition on quantity of CPOM and FPOM. Data are from tray samples and were transformed, $\log_{10}(x + 1)$, prior to analysis.

Source of variation	df	CPOM		FPOM	
		F	P	F	P
Canopy	2	12.9	.001	22.1	.001
Current	2	5.4	.021	16.6	.001
Canopy $\times$ current	4	0.7	.595	2.7	.079
Substrate	3	0.3	.797	3.0	.074
Canopy $\times$ substrate	6	0.7	.640	1.2	.380
Current $\times$ substrate	6	1.4	.303	0.9	.491
Error	12				