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**Density of Fish and Salamanders in Relation to Riparian Canopy and Physical Habitat
in Streams of the Northwestern United States¹**

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Relationships between density of fish and salamanders, riparian canopy, and physical habitat were investigated by studying 10 pairs of streams. Among vertebrate taxa, salmonids and sculpins were more abundant in streams without riparian shading than in shaded streams. Abundance of salamanders was not affected by canopy type. Densities of both salamanders and sculpins were correlated with substrate composition, whereas salmonid abundance was not or only weakly so. Salamanders were found only at high-gradient sites with coarse substrates, and sculpins were most abundant at lower-gradient sites with finer-sized sediments. An interaction was observed between the influence of canopy and that of physical setting on density of both invertebrate prey and total vertebrates. Among shaded sites, densities decreased as percent fine sediment increased, but a similar relationship did not exist among open sites. Removal of the riparian vegetation surrounding a stream may therefore mask detrimental effects of fine sediment. These data provide one reason why it has been difficult in the past to generalize about the effects of fine sediment on stream biota.

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Dix paires de cours d'eau ont été étudiés en vue de découvrir les relations entre la densité des poissons et des salamandres, la voûte présente sur les berges et l'habitat physique. Parmi les taxa de vertébrés, les salmonidés et les chabots sont plus abondants dans les cours d'eau dont les berges sont dépourvues d'ombrage que dans les cours d'eau ombragés. L'abondance des salamandres n'est pas influencée par le type de voûte. Il y a corrélation entre la densité à la fois des salamandres et des chabots et la composition du substrat, tandis qu'avec les salmonidés, la corrélation est nulle ou faible. On trouve des salamandres seulement à des sites à fort gradient et substrat grossier, alors que les chabots sont plus abondants aux sites où le gradient est plus faible et les sédiments sont plus fins. On a observé une interaction entre l'influence d'une voûte et celle d'un arrangement physique sur la densité tant des proies invertébrés que de la totalité des vertébrés. Parmi les sites ombragés, la densité diminue à mesure qu'augmente le pourcentage de sédiments fins, alors qu'une telle relation est absente parmi les sites découverts. L'enlèvement de la végétation des berges d'un cours d'eau peut donc masquer les effets nuisibles d'un sédiment fin. On voit ici une raison de la difficulté, dans le passé, à généraliser sur les effets d'un sédiment fin sur les biocénoses fluviales.

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FISH and amphibian species are conspicuous and important components of stream communities. They are often top predators in stream systems, and many species are important resources having either recreational or economic value. Considerable research has been directed toward maintaining and improving the productivity of stream systems. Much of this research has focused on vertebrate species and factors that influence their abundance. Food and habitat are two of the most important factors often emphasized (Chapman 1962; Hall and Knight 1981).

This report describes the results of a 2-yr field study that was designed to evaluate the relative importance of food sources and certain habitat features on the abundance of vertebrate species in streams of the Pacific Northwest, USA. Previous research in this geographical region has focused on the effect of watershed perturbation on aquatic resources (Hall and Lantz 1969; Burns 1972; Moring 1975; Moring and Lantz 1975). Results of these investigations were often equivocal, and it was difficult to specify and distinguish effects of alterations of habitat, food sources, and other factors on abundance of aquatic biota (Hall et al. 1978). More recent work has emphasized the role that the surrounding riparian canopy may play in determining abundances of stream biota (Lyford and Gregory 1975; Hall et al. 1978; Gregory 1980; Murphy and Hall 1981; Bisson and Sedell 1983). These studies and others (Albrecht 1968; Hunt 1979; Newbold et al. 1980) have provided convincing evidence that streams with open canopies are more productive than heavily shaded streams. Habitat modification on the other hand is usually characterized by intrusion of fine sediments into streambeds, a phenomenon that may both reduce available habitat and create unstable conditions (see reviews by Gibbons and Salo 1973; Iwamoto et al. 1978). Very little research exists, however, that evaluates the relative importance or interactions of canopy and physical factors. We therefore developed a research program to assess how abundance of fish and salamanders in streams varied in relation to both riparian canopy and physical charac-

ter of the streambed.

We have reported initial results of this study based on an analysis of six streams (Murphy et al. 1981). Those results showed that canopy played a dominant role in determining abundance of most biota, often masking effects of substrate character. The range of fine sediments in the streambeds among these six sites, however, was relatively small (0–30% sand < 1 mm). The objectives of the study reported here were to examine streams with much greater levels of fine sediment (up to 80%) while retaining a study design that also allowed us to examine effects associated with riparian canopy. Also, by integrating our results with developing theory of stream ecosystems (Cummins 1974; Hynes 1975; Vannote et al. 1980), we hoped to contribute to a broader and more ecologically sound basis for the evaluation of watershed perturbation on stream communities (Karr and Schlosser 1977; Karr and Dudley 1981; Hall and Knight 1981; Rosenberg et al. 1981).

Methods and Materials

STUDY DESIGN

Our general study design was an extensive posttreatment type in which sites were paired (Hall et al. 1978) (Table 1). We use the term site to denote a single stream reach. The term site pair is used when considering patterns that varied across paired sites. Within site pairs, stream reaches differed mainly in the amount of shading by the surrounding riparian canopy. One site had extensive riparian vegetation that shaded most of the streambed; the other site had little riparian vegetation surrounding it and received direct solar radiation. This design allowed us to control, within pairs, other factors (e.g. aspect, discharge, nutrients, temperature) to a much greater degree than found in most other field studies. We attempted to locate the two sites within a pair on the same stream with the open site downstream from the shaded section. On three streams,

TABLE 1. Physical characteristics of the study streams. Sites are paired with shaded (S) and open (O) sections.

Site	Abbrev.	Site pair	Sampling date	Drainage area (km ²)	Gradient (%)	Mean elevation (m)	Aspect	Mean width (m)	Percent shading	Channel stability ^a	% sediment < 1 mm	
											Riffles	Pools
Mack Creek (S)	MACKS	1	14 Aug. 1978	5.4	10.0	760	N	5.9	75	45	3	0
Mack Creek (O)	MACKO	1	14 Aug. 1978	5.5	10.0	730	N	4.6	0	47	3	2
Rock Creek (S)	ROCKS	2	25 Sept. 1979	14.2	2.0	243	W	5.0	67	52	1	3
Rock Creek (O)	ROCKO	2	25 Sept. 1979	15.0	2.0	243	W	3.6	0	62	2	2
Little Lost Man Creek (S)	LLMS	3	23 Aug. 1979	8.1	8.0	439	NNW	2.9	90	75	5	4
Little Lost Man Creek (O)	LLMO	3	23 Aug. 1979	8.0	8.0	439	NNW	3.4	23	69	4	6
Harry Weir Creek (S)	HWCS	4	25 Aug. 1979	7.5	14.0	424	SW	2.2	79	79	4	13
Copper Creek (O)	CPCO	4	25 Aug. 1979	7.3	18.0	585	SW	1.8	2	110	6	12
Mill Creek (S)	MILLS	5	14 Aug. 1978	6.4	1.0	360	S	2.5	75	45	3	29
Fawn Creek (O)	FAWNO	5	14 Aug. 1978	6.8	1.0	500	E	2.8	0	105	4	19
Elkhorn Creek (S)	ELKS	6	06 Sept. 1979	9.6	0.5	152	W	3.8	94	116	33	48
Elkhorn Creek (O)	ELKO	6	06 Sept. 1979	11.1	0.5	152	W	2.9	0	117	37	76
Rainbow Creek (S)	RAINS	7	11 Sept. 1979	5.1	0.5	152	SE	2.2	75	112	36	50
Hammer Creek (O)	HAMO	7	11 Sept. 1979	8.9	0.5	152	NE	2.0	0	115	25	32
Spout Creek (S)	SPTS	8	02 Oct. 1979	16.1	0.7	229	SW	1.2	73	114	42	59
Spout Creek (O)	SPTO	8	02 Oct. 1979	23.7	0.7	229	SW	1.9	0	110	55	76
Upper Mary's River (S)	UPMS	9	11 Oct. 1979	8.1	0.4	304	SW	2.4	80	117	60	76
Upper Mary's River (O)	UPMO	9	11 Oct. 1979	8.0	0.4	304	SW	1.4	0	124	61	84
Lower Mary's River (S)	LMS	10	09 Oct. 1979	14.5	0.3	304	S	5.6	70	126	57	85
Lower Mary's River (O)	LMO	10	09 Oct. 1979	11.5	0.3	304	S	2.7	0	123	52	89

^aCalculated by method of Pfankuck (1975).

however, the open section was upstream of the shaded reach. Also, sites of three pairs were located on different streams but were on neighboring watersheds. These deviations from our preferred pairing were probably not significant. Within all pairs, sites were of similar size and, with two exceptions, aspect (Table 1).

Across pairs we chose streams that differed greatly in the amount of fine sediment (0–80%) within the surficial sediments, although other characteristics varied as well. For example, gradients (slopes) differed among sites because we could not always find streams that varied in sediment character independent of gradient. Also, mean elevation of sites varied between approximately 150 and 760 m.

The study design helped to control for effects of confounding variables, although it did not eliminate such problems completely. As discussed above, the two sites within any pair were in close proximity so they would be influenced by similar abiotic conditions. Increases in temperature (Brown and Krygier 1970) and nutrient concentrations (Likens et al. 1970; Fredriksen 1972; Vitousek et al. 1979) following alteration (e.g. clear-cutting) of watersheds have been reported, but these effects were minimal in our study. For example, maximum summer temperature in the open section of Mack Creek was only 3°C higher than in the shaded section (18.5 vs. 15.5°C), and total annual degree-days differed by less than 4% (shaded = 2036, open = 2108). Differences in nutrients between paired sites also would have been small, because concentrations usually fall to predisturbance levels within 6 yr (Fredriksen 1972; Dahm and Gregory unpublished data) of disturbance. The watershed surrounding Fawn Creek, the most recently disturbed site that we sampled, was partially clear-cut 7 yr prior to the study (Murphy et al. 1981).

Across pairs, three factors other than substrate character would most likely affect biological pattern and thus confound interpretation of data: temperature, nutrients, and habitat parameters other than amount of fine sediment. Some systematic variation in stream temperature with altitude or latitude would be expected. For the streams we studied, the amount of this variation was not great. The maximum temperature observed in the shaded section of Mack Creek, the site of highest elevation, was 15.5°C. Temperature data were not available for the low-elevation sites that we sampled, but Kerst (1970) observed a maximum stream temperature of 22°C in Oak Creek, a low-elevation shaded stream in the Oregon Coast Range. Elevation of this site was 152 m, the same elevation of our lowest sites (Table 1). The sites in Redwood Creek National Park exhibit maximum temperatures similar to those in the Oregon Coast Range (22°C, Iwatsubo et al. 1975). Thus the greatest difference in maximum temperature among sites of similar canopy was about 6°C.

Concentrations of nitrogen and phosphate among most streams in the areas sampled are similar and generally low. Most streams in mountainous watersheds of Oregon and northern California have nitrate (NO_3) concentrations of 0–0.1 mg/L (USGS 1976; Bradford and Iwatsubo 1978; Naiman and Sedell 1979; Sollins et al. 1980). Phosphorous levels are similarly low (0.01–0.07 mg/L). Streams receiving moderate agricultural runoff can have higher levels of both nitrate (0.2–1.1 mg/L) and phosphate (0.02–

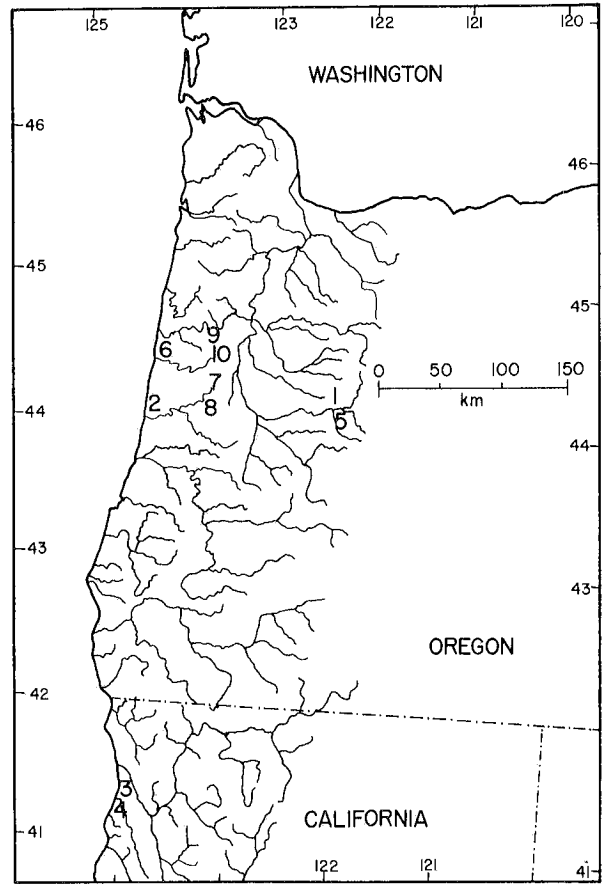


FIG. 1. Map of the study area. Numbers indicate approximate locations of the 10 site pairs. Site pairs 1 and 5 are located in the Cascade Range of Oregon. Site pairs 2, 6, 7, 8, and 9 are located in the Oregon Coast Range. Site pairs 3 and 4 are located in the Coast Range of northern California. See Table 1 for key to site abbreviations and index to sites.

0.26 mg/L; USGS 1976). Hence the four pairs of streams open to grazing (Elkhorn, Spout, Upper, and Lower Mary's River) may have had higher concentrations of these nutrients than the other sites. However, within the range of concentrations reported for this area, we would expect little effect on most biological processes (Bisson et al. 1975; Triska and Sedell 1976; Speir 1979; Gregory 1980).

Differences in gradient, channel morphology, and water velocity associated with differences in amount of fine sediment cannot be dismissed as insignificant to biological pattern. Our design could not control for the separate effects of these variables. All of these variables interact to provide the physical setting of each site (Leopold et al. 1964). Our design allows us to evaluate the relative influence of canopy and physical setting on density of biota, but not to separate effects of, for example, current vs. that of fine sediment. We use percent fine sediment as an index of differences among sites in physical habitat and consider the probable importance of each separate variable in the discussion.

SITE LOCATION

Streams were sampled in three different geologic provinces to provide extremes in fine sediment (Fig. 1). Watersheds in these areas export vastly different amounts of sediment: $13\text{--}68\text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ (Fredricksen 1970), $53\text{--}102\text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ (Beschta 1978), and $2600\text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ (Karlin 1979) for Oregon Cascade Range, Oregon Coast Range, and Northern California Coast Range streams, respectively. Two pairs of sites are located in the western Cascade Mountains $\sim 70\text{ km}$ east of Eugene, Oregon ($44^{\circ}15'N$, $122^{\circ}15'W$). These sites were part of a more intensive study conducted the year before (spring through autumn 1978) on six streams and are described by Murphy et al. (1981). Data from the summer sampling period for these streams in 1978 are included in the data set from the more extensive survey conducted during the summer of 1979. During 1979 six additional pairs of sites were sampled on streams that drain the coastal mountains of Oregon ($44^{\circ}15'N$, $124^{\circ}00'W$), and two other pairs were sampled in coastal watersheds of Redwood Creek National Park in northern California ($41^{\circ}15'N$, $124^{\circ}00'W$). All sampling was conducted between late August and early October. The most southerly streams were sampled first (Aug. 23–25) and the northern streams last (Sept. 6–Oct. 9). This schedule compensated for some of the phenological and seasonal differences associated with latitude.

SAMPLING

General sampling procedures are described in detail in Murphy et al. (1981). Density and biomass of vertebrates were estimated by the removal method (Zippin 1956). We used an electroshocker to capture animals. In conjunction with the vertebrate sampling, macroinvertebrates were sampled from both riffle and pool habitats. Three invertebrate samples (0.1 m^2) were taken from each habitat. Only those individuals retained by a 1-mm mesh were considered in this analysis. These individuals were identified and counted, and their biomass was estimated from length–weight equations (Smock 1980, and unpublished data). Taxa were assigned to functional feeding groups based on tables in Merritt and Cummins (1978). Surficial sediments were characterized from core samples taken in triplicate from both riffles and pools. A 0.25-m^2 metal core was driven into the stream bed and 10–15 L of substrate was removed. Particles were wet sieved into the following size-classes: $< 0.05\text{ mm}$, $0.05\text{--}1\text{ mm}$, $1\text{--}4\text{ mm}$, $4\text{--}16\text{ mm}$, $16\text{--}50\text{ mm}$, and $> 50\text{ mm}$. Percent composition was calculated based on volume after organic matter was removed either by hand or combustion (550°C , 24 h). Shading of the streambed was measured with an angular canopy densiometer (Brown 1969) at the time of sampling. Ten estimates were taken at each stream section. These data were used to calculate mean shading at each reach. Stream stability was estimated at each site by the method of Pfankuck (1975). Low values indicate more stable conditions than high values.

PHYSICAL CONTRASTS AMONG SITES

In Table 1 we list major physical parameters associated

with each site. Field measurements of shading and size composition of streambed sediments showed that sites conformed to our original study design. Percent shading was obviously different within pairs, and no large differences existed in shading among sites for each of the canopy types. Percent sediment $< 1\text{ mm}$ was very different among sites ($F_{1,9} = 10.93$, $P < 0.025$), and no differences in sediment composition existed within pairs ($F_{9,9} = 0$, $P > 0.63$, two-way ANOVA).

INVERTEBRATE BIOTA

Although terrestrial invertebrates accidentally entering a stream can occasionally be a significant food source (Chapman 1966a; Hunt 1975), aquatic invertebrates are an important and often dominant food for salmonids, salamanders, and sculpins (Antonelli et al. 1972). Not all invertebrates found in streams are prey for vertebrate predators. Some groups such as large, well-protected mollusks are seldom eaten (e.g. mussels and clams), whereas other taxa such as those insects without protective cases are common food items. For this reason we partitioned invertebrates into three groups: (1) total invertebrates (TI) including all insects, mollusks, and crustaceans, (2) a second group that is generally without cases, and were in large part members of the collector–gatherer (CG) functional group (Cummins 1973), and (3) total invertebrates excluding mollusks and very large crustaceans (TM). Taxa in the collector–gatherer group included many mayflies (Ephemeroptera) and Diptera (mostly Chironomidae) as well as some representatives from other taxa.

VERTEBRATE BIOTA

Thirteen taxa of vertebrates were encountered during the course of the study: three salmonids (rainbow trout, *Salmo gairdneri*; cutthroat trout, *S. clarki*; and coho salmon, *Oncorhynchus kisutch*), three sculpins (reticulate sculpin, *Cottus perplexus*; prickly sculpin, *C. asper*; and coastrange sculpin, *C. aleuticus*), redbelt shiner (*Richardsonius balteatus*), speckled dace (*Rhinichthys osculus*), western brook lamprey (*Lampetra richardsoni*), two frogs (*Ascaphus truei* and *Rana aurora*), a salamander (*Dicamptodon ensatus*), and a garter snake (*Thamnophis* sp.). In this report we only consider salmonids, sculpins, and *D. ensatus*. Other taxa were either rare or common at only one site. *Rhinichthys osculus* was found at Spout Ck (open), and *L. richardsoni* was collected at both Elkhorn sites, the open site on Upper Mary's River and the shaded section of Lower Mary's River. These taxa made up no more than 10% of the vertebrate fauna at these sites. For analysis, salmonid taxa were combined as were cottid taxa. We used the following values for the equation ($M = a \cdot X^b$) to estimate biomass, where M = biomass in grams (wet), X = length in mm, and a and b are constants. For salmonids $a = 2.11 \times 10^{-4}$ and $b = 2.37$, for sculpins $a = 3.31 \times 10^{-3}$ and $b = 1.71$, and for the salamander $a = 3.50 \times 10^{-5}$ and $b = 3.02$. Values for the constants a and b were either taken from Murphy (1979) or determined from field samples.

TABLE 2. Results of two-way ANOVA for association of site and canopy with abundances of invertebrates. Results are based on $\log_{10}(x + 1)$ transformations of mean abundances observed at each site.

		Total invertebrates		Collector—gatherers		Total minus mollusks	
Source of variation	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Riffle densities</i>							
Site	9	0.71	0.688	1.46	0.292	1.17	0.411
Canopy	1	7.55	0.023	7.25	0.025	6.45	0.032
<i>Riffle biomass</i>							
Site	9	7.45	0.003	1.42	0.304	1.47	0.289
Canopy	1	2.30	0.164	9.23	0.014	6.41	0.032
<i>Pool densities</i>							
Site	9	2.17	0.133	0.96	0.522	1.86	0.185
Canopy	1	0.26	0.622	1.30	0.284	0.57	0.469
<i>Pool biomass</i>							
Site	9	9.94	0.001	1.13	0.432	2.12	0.139
Canopy	1	0.10	0.763	1.93	0.198	0.77	0.402

ANALYSES

Differences in vertebrate and invertebrate abundances associated with canopy and the gradient in physical conditions were analyzed by two-way ANOVA and paired *t*-tests (Snedecor and Cochran 1967). Data were further examined by correlation analysis both within canopy types and for all sites combined to check for relationships between sediment character, invertebrate abundance, and vertebrate abundance. $\log_{10}(x + 1)$ transformations were used on all data to normalize data sets and stabilize variances with the exception of those data calculated as percentages (% sediment < 1 mm). For percentage data an arcsin transformation was used (Elliott 1971). Abundance data on which analyses were based are provided in the appendix.

Results

INVERTEBRATES

For riffle habitats, canopy almost always had a significant effect on abundance (Table 2). Only the difference in total invertebrate biomass between canopy types was not statistically significant. Where differences were significant, means for sites without canopies were greater than those for shaded sites (multiplicative factors of 2.5 for TI densities, 3.3 for CG densities, 2.4 for CG biomass, 2.8 for TM densities, and 1.4 for TM biomass, see Appendix). For pool samples no significant differences in means between canopy types were observed. Significant differences in means among site pairs (gradient effects) were found only for biomass of total invertebrates, a consequence of higher abundances of mollusks in lower-gradient streams with high percentages of sand.

Although ANOVA indicated that differences in mean

abundances among paired sites for most groups of invertebrates were not significant, variation in densities across sites depended on canopy. Among shaded sites, densities of invertebrates in riffle habitats decreased as percent fine sediment in the substrate increased (Fig. 2). This was true for total invertebrates ($r = -0.78$, $P < 0.01$), collector-gatherers ($r = -0.90$, $P < 0.001$), and total invertebrates excluding mollusks ($r = -0.92$, $P < 0.001$). Open sites ($r = -0.04$ to -0.17) and combined sites ($r = -0.09$ to -0.36) did not show these trends. Neither were these trends observed for pool habitats. Biomass of total invertebrates, which was dominated by mollusks, increased as fine sediment increased ($r = 0.79-0.95$) in both riffle and pool samples and for both shaded and open sites. Biomass of nonmollusks did not vary significantly with amount of sand.

VERTEBRATE ABUNDANCE

Vertebrate abundance was significantly influenced by both canopy and physical gradient (Table 3). Differences in abundances among canopy type were evident for salmonids and sculpins, but not salamanders. Differences among site pairs were highly significant for benthic feeding vertebrates (salamanders and sculpins) but were either not significant or only weakly so for salmonids (Table 3). Paired *t*-tests for significant differences in abundances between shaded and open streams gave results identical to the two-way ANOVA for combined taxa as well as individual taxa.

When all sites were combined, correlation analysis revealed that density of total vertebrates was associated with abundance of invertebrates other than mollusks (e.g. collector-gatherers and total minus mollusks) but not with amount of fine sediment (Fig. 3 and 4). Biomass also was correlated with invertebrate abundance but also showed an

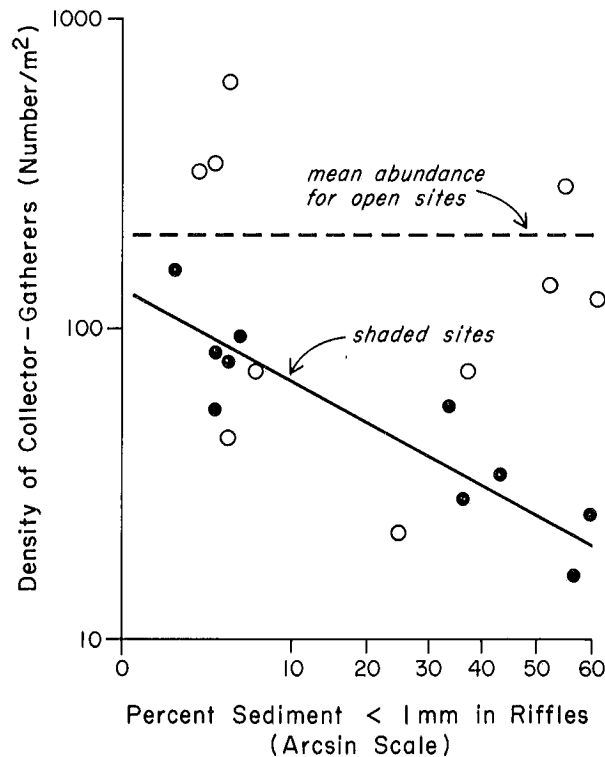


FIG. 2. Density of benthic invertebrates (collector-gatherers) in relation to percent fine sediment < 1 mm in surficial sediments. Data for riffle samples only. Dark circles are shaded sites, open circles are sites with open canopies. Correlation coefficients are $r = -0.90$, $P < 0.01$ for shaded sites; $r = -0.10$, $P = \text{ns}$ for open sites; $r = -0.34$, $P = \text{ns}$ for combined sites. The line for shaded sites was fitted by regression analysis. For these data, $\log_{10} \text{density} = 2.98 - 0.019x$, where $x = \arcsin$ percent fine sediment < 1 mm. The broken line indicates mean abundance for open sites.

inverse relationship with amount of fine sediment. When only shaded streams were considered, both vertebrate density and biomass showed significant associations with invertebrate abundance and percent fine sediment. Associations were pos-

itive with density of invertebrates, but were negative with percent fine sediment. When only open sites were considered, vertebrate biomass was correlated with density of collector-gatherer invertebrates and total invertebrate density excluding mollusks, but not percent fine sediment. Density of total vertebrates was not significantly associated with either density of invertebrates or percent fine sediment in open sites.

Salmonids, salamanders, and sculpins were not all found at all sites (Fig. 5). Salamanders were restricted to reaches with little sand (< 30%), sculpins were found in reaches often with high amounts of sand (to 80%), and the two taxa were seldom observed in the same stream. Salmonids occurred over a broader range of sites than did either salamanders or sculpins.

When we examined each taxon separately and considered only those sites at which a taxon was present, correlations between vertebrate abundance and both fine sediment and invertebrate density were similar to those observed for combined taxa (Table 4). Correlations between abundance and fine sediment were generally negative for all three taxa and stronger for shaded sites than open sites. Associations between vertebrate abundance and invertebrate density were generally positive and also stronger for shaded sites than open ones.

Our data as shown in Fig. 2 and 4 indicates that as percent fine sediment increased the relative difference in abundance between shaded and open streams increased. We calculated the relative difference in abundance between paired sites with the equation $\Delta\% = (\text{open} - \text{shade})/\text{shade}$ and calculated correlation coefficients for these values versus mean percent sediment < 1 mm $[(\text{open} + \text{shaded})/2]$. For collector-gatherer biomass, $r = 0.69$ which is significant at $P < 0.05$ for $n = 10$. The r value for the association with collector-gatherer density (0.31) was not significant. Correlation coefficients for both total vertebrate biomass ($r = 0.79$, $n = 10$) and sculpin biomass ($r = 0.79$, $n = 6$) were significant ($P < 0.01$ and $P < 0.05$, respectively). Correlations for neither salmonid density ($r = -0.33$) nor biomass ($r = -0.38$) were significant ($n = 6$) and both were negative rather than positive. The slightly negative relationship observed for salmonids also can be seen by examining Fig. 5. The relative abundance of salmonids was greater in open streams than shaded streams for sites with little fine sediment,

TABLE 3. Results of two-way ANOVA for association of site and canopy with abundances of stream vertebrates. Data were transformed as in Table 2.

Taxon	Source of variation	df	Density		Biomass	
			F	P	F	P
Total vertebrates	Site	9	2.89	0.065	6.22	0.006
	Canopy	1	29.18	<0.001	28.32	0.001
Salmonids	Site	9	2.24	0.123	3.45	0.040
	Canopy	1	4.05	0.075	7.55	0.023
Salamanders	Site	9	6.26	0.006	13.71	<0.001
	Canopy	1	0.08	0.781	0.26	0.622
Sculpins	Site	9	6.62	0.005	9.56	0.001
	Canopy	1	9.33	0.014	8.89	0.015

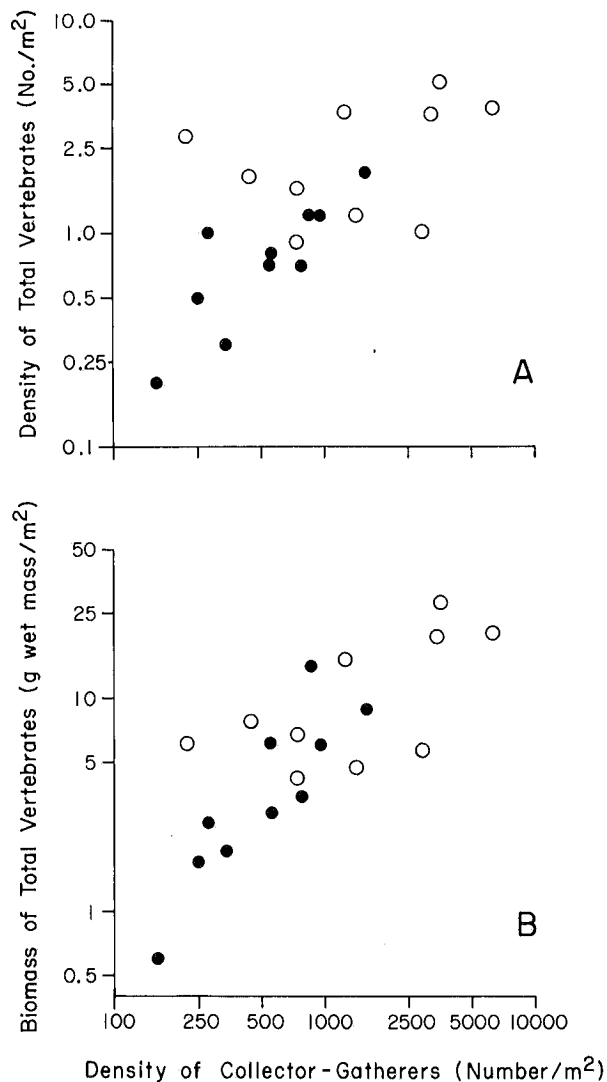


FIG. 3. Abundance of total vertebrates (density and biomass) in relation to density of collector-gatherer invertebrates found in riffle habitats. Symbols as in Fig. 2. Correlation coefficients for density of vertebrates are shaded sites, $r = 0.84$, $P < 0.01$; open sites, $r = 0.36$, $P = \text{ns}$; combined sites, $r = 0.66$, $P < 0.01$. For biomass of vertebrates: shaded sites, $r = 0.86$, $P < 0.001$; open sites, $r = 0.64$, $P < 0.05$; combined sites, $r = 0.79$, $P < 0.001$.

but there was little difference within pairs at sites with more fine sediment. This trend was true both for relative abundance as shown in Fig. 5 and absolute abundance (see Appendix).

Discussion

Our data confirmed our earlier observations that streams with little or no shading have more abundant vertebrate populations than similar, but shaded streams. Moreover, this was true over a broad range of sediment levels and was also true for most invertebrate groups. The higher autotrophic produc-

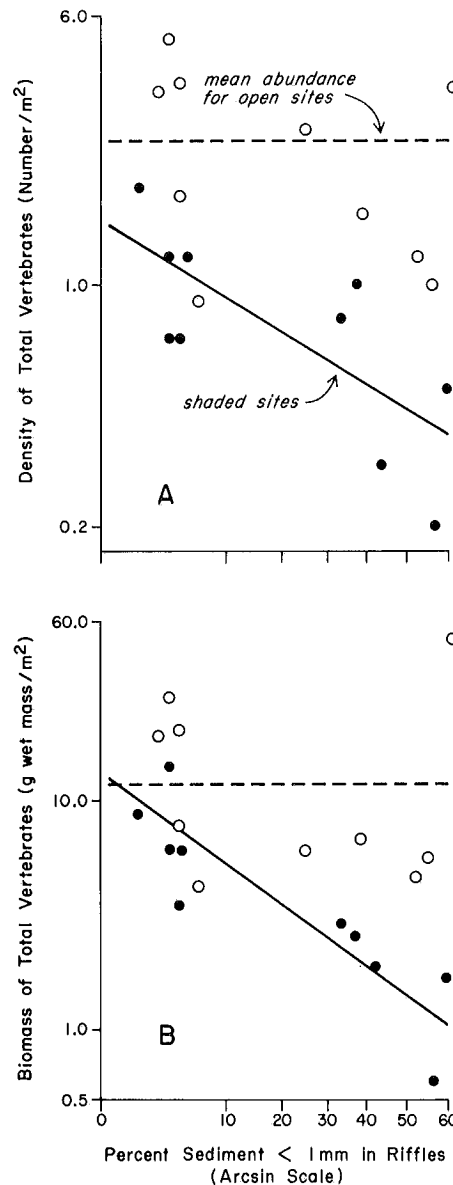


FIG. 4. Abundance of total vertebrates (density and biomass) in relation to percent fine sediment < 1 mm in riffles. Symbols as in Fig. 2 and 3. Correlation coefficients for density of total vertebrates are shaded sites, $r = -0.73$, $P < 0.01$; open sites, $r = -0.33$, $P = \text{ns}$; combined sites, $r = -0.34$, $P = \text{ns}$. For biomass of vertebrates: shaded sites, $r = -0.88$, $P < 0.001$; open sites, $r = -0.38$, $P = \text{ns}$; combined sites, $r = -0.52$, $P < 0.05$. Regression equations for shaded sites are $\log_{10} \text{ density} = 0.25 - 0.021x$, and $\log_{10} \text{ biomass} = 0.89 - 0.024x$, where $x = \arcsin \text{ percent fine sediment} < 1 \text{ mm}$.

tion that occurs after canopy removal or in naturally open stream sections (McIntire and Colby 1978; Gregory 1980; Naiman and Sedell 1980; Triska et al. 1982) seems to be the causative agent responsible for greater invertebrate abundance and thus secondarily for higher abundances of sculpins and

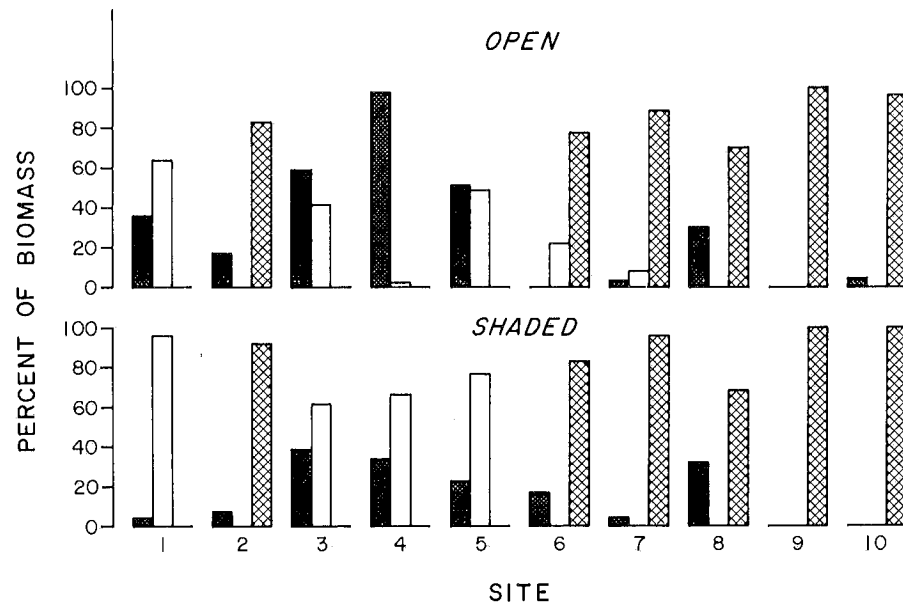


FIG. 5. Percent of total vertebrate biomass contributed by different taxa at each site. Histogram bars represent salmonids (solid), salamanders (white), and sculpins (cross-hatching).

TABLE 4. Correlation coefficients (r) for associations between stream vertebrates and two environmental variables: percent fine sediment and invertebrate density (collector-gatherers). Relationships are given for shaded, open, and combined sites.

Taxon	Sites	<i>n</i>	Densities		Biomass	
			<i>r</i>	P	<i>r</i>	P
<i>Percent fine sediment</i>						
Salmonids	Shaded	8	-0.85	**	-0.63	ns
	Open	8	-0.59	ns	-0.60	ns
	Combined	16	-0.64	**	-0.48	ns
Salamanders	Shaded	4	0.14	ns	-0.56	ns
	Open	6	-0.65	ns	-0.21	ns
	Combined	10	-0.70	*	-0.30	ns
Sculpins	Shaded	6	-0.77	ns	-0.81	*
	Open	6	-0.35	ns	-0.16	ns
	Combined	12	-0.40	ns	-0.36	ns
<i>Invertebrate density</i>						
Salmonids	Shaded	8	0.70	*	0.60	ns
	Open	8	0.46	ns	0.54	ns
	Combined	16	0.55	*	0.63	**
Salamanders	Shaded	4	0.82	ns	0.04	ns
	Open	6	0.66	ns	0.68	ns
	Combined	10	0.52	ns	0.56	ns
Sculpins	Shaded	6	0.80	ns	0.92	**
	Open	6	-0.24	ns	-0.28	ns
	Combined	12	0.56	ns	0.74	**

salmonids. It is important to note that significant associations between the abundances of vertebrate taxa and invertebrate prey were observed only for certain invertebrate taxa and only for data collected from riffle areas. Data from pool habitats produced few significant correlations. Our results support the

contention that riffle habitats are the primary food-producing areas for salmonids and probably sculpins as well (Mason and Chapman 1965; Waters 1969a). Invertebrates in riffle habitats tend to be dominated by grazing or collecting insects (Hawkins et al. 1982) that often enter the drift and thus

become more susceptible to predation (Waters 1969a). Invertebrates in pool habitats are often larger and have either protective cases or shells (e.g. many Trichoptera, snails, clams). Because of these characteristics and because most invertebrates in pools would not usually drift, they would probably be less susceptible to predation by salmonids and sculpins than are riffle invertebrates.

We should also point out that invertebrate density was often more strongly correlated with vertebrate abundance than was invertebrate biomass. On the other hand, biomass of vertebrate predators was more strongly correlated with invertebrate abundance than was vertebrate density (Fig. 3, Table 4). We cannot completely explain these trends. However, invertebrate prey of both salmonids (e.g. Antonelli et al. 1972; Elliott 1973; Fahy 1980; Allan 1981) and sculpins (Andreasson 1971; Antonelli et al. 1972) tend to be dominated by Chironomidae and Baetidae, taxa of characteristically small individuals and high turnover (P/B) ratios (Waters 1969b; Benke et al. 1979). Furthermore, canopy removal tends to increase the abundances of both of these groups (Newbold et al. 1980; Hawkins et al. 1982). Vertebrate biomass, rather than numbers, may provide better correlations with prey abundance, if vertebrate populations in streams are generally food limited as our results suggest and if feeding territories are established and dominated by larger individuals that can exclude more numerous small individuals (Chapman 1966b; Finger 1980).

The observed negative correlations between percent sand in surficial substrates and abundance of both invertebrates and vertebrates imply a detrimental effect caused by fine sediment. Similar relationships have been observed by others (Lemly 1982; see Gammon 1970 for review). Because other variables (gradient, current) were themselves correlated with percent fine sediment, we cannot distinguish unequivocally the separate effect of fine sediment. There are, however, strong reasons to suspect that fine sediment is the major variable responsible for the observed correlations. Sand can fill in interstitial spaces between stones, an important habitat for both benthic invertebrates and vertebrates. Loss of this habitat should adversely affect those taxa that depend on it. Excessive amounts of sand can also lead to loss of spawning gravels. Also, streams with a large percentage of sand in their substrates would be prone to the detrimental effects of scour (Sorensen et al. 1977; Iwamoto et al. 1978). Clearly, the action of fine sediment, or its interaction with other correlated physical variables, imposes constraints on the type of community that can develop in a system.

Regardless of the specific importance of fine sediment, one of the most important outcomes of this study is the demonstration that the physical environment of a stream system can have varied effects on stream communities, depending upon whether the stream is shaded or not. Opening the riparian canopy surrounding a stream apparently mitigated and sometimes completely masked the otherwise detrimental effect associated with decreasing habitat quality (i.e. changes associated with accumulation of fine sediment). Food availability and habitat appear to interact to influence both invertebrate and vertebrate abundance.

The reasons for the observed interaction between substrate and canopy on invertebrate abundance are not clear.

Increased food quality associated with algal production apparently compensates for a decrease in habitat quality associated with increased levels of fine sediment. This may be especially true for those taxa (e.g. many Chironomidae) that are not restricted to larger substrates. The interaction observed for vertebrates appears to be largely an indirect effect associated with availability of invertebrate prey. Vertebrate abundance showed patterns among sites similar to invertebrate prey (cf. Fig. 2 and 4) and was strongly correlated with invertebrate abundance (Fig. 3).

We believe that we have distinguished systematic patterns in the abundance of stream biota that are often obscured because of the many complex processes that occur in streams. On the other hand, other questions have arisen and many remain unanswered. The patterns that we observed between canopy types probably reflect differences in the productivity of these systems. Attributing exact causal mechanisms to differences among sites is more difficult. Because the percentage of fine sediment varied with gradient, we cannot be sure that the patterns we observed were due to differences in fine sediment, gradient, or current velocities associated with gradient.

A conclusion that we caution against is that opening the canopy surrounding a stream will always result in a more productive and thus a more desirable type of stream system. There are two caveats that must be considered. The first is that our focus and approach were purposefully restricted and we usually compared either small open sections of stream or streams in small clear-cut watersheds to their shaded counterparts. Opening of the riparian canopy on an extensive basis would almost certainly cause other parameters such as temperature to change (Brown and Krygier 1970; Karr and Schlosser 1977) that could adversely affect production of vertebrates rather than increase it. Second, the integrity of natural stream systems is not solely determined by productivity of stream biota (see Karr and Dudley 1981). Stream organisms are adapted to complex sets of parameters, and although an environmental change may increase production, it also may cause drastic shifts in community structure associated with the loss of many taxa typically found only in unmodified stream systems (Hynes 1963; Lemly 1982).

We believe future research on stream biota should stress multifactor approaches explicitly designed to distinguish the interactive effects that habitat, food sources, and other factors play in shaping stream communities. Such approaches would provide an ecologically sound basis from which to understand both differences among natural stream systems and also those systems modified by man's activities.

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Appendix

Abundance of invertebrates, salmonids, salamanders, and sculpins at the study sites. Abbreviations for invertebrate groups are collector-gatherers (CG) and total minus mollusks (TM). Densities and biomasses are per m². Invertebrate biomass reported as mg dry mass; vertebrate biomass as g wet mass.

Site	Site pair	Riffle invertebrates			Pool invertebrates			Vertebrates			
		Total	CG	TM	Total	CG	TM	Salmonids	Salamanders	Sculpins	Total
Densities											
MACKS	1	1690	840	1690	5350	2900	5350	0.3	0.9	0	1.2
MACKO	1	5590	3460	5590	2280	1530	2280	4.2	0.9	0	5.1
ROCKS	2	2490	1550	2450	1510	1180	1480	0.1	0	1.8	1.9
ROCKO	2	3710	3200	3700	3140	2440	3100	0.2	0	3.4	3.6
LLMS	3	2360	950	2340	12190	2660	11900	0.6	0.6	0	1.2
LLMO	3	1310	440	1300	5660	3180	5560	1.0	0.8	0	1.8
HWCS	4	2080	780	2060	2800	1230	2680	0.2	0.5	0	0.7
CPCO	4	1700	730	1700	2430	450	1540	0.9	0	0	0.9
MILLS	5	1350	550	1230	2000	750	1890	0.4	0.3	0	0.7
FAWNO	5	9970	6220	9970	3470	1990	3460	2.7	1.1	0	3.8
ELKS	6	1510	560	1180	9550	8250	8760	0.1	0	0.7	0.8
ELKO	6	1920	730	1160	3080	710	1940	0	0	1.6	1.6
RAINS	7	1190	280	690	2030	1280	1470	0	0	1.0	1.0
HAMO	7	1510	220	610	700	100	220	0	0	2.8	2.8
SPTS	8	1730	340	690	5290	1630	2270	0	0	0.3	0.3
SPTO	8	7840	2890	7300	6360	760	2730	0.1	0	0.9	1.0
UPMS	9	930	250	520	3250	830	1820	0	0	0.5	0.5
UPMO	9	4840	1240	3440	4570	1030	3430	0	0	3.7	3.7
LMS	10	1100	160	250	1410	700	910	0	0	0.2	0.2
LMO	10	2880	1390	1760	3470	1440	2430	0	0	1.2	1.2
Biomass											
MACKS	1	188	28	188	259	87	259	0.6	13.0	0	13.6
MACKO	1	1072	117	1072	1196	105	1196	8.3	14.9	0	23.2
ROCKS	2	532	164	321	721	373	684	0.7	0	8.1	8.8
ROCKO	2	731	346	428	649	400	505	3.2	0	15.8	19.0
LLMS	3	475	100	458	3313	305	3070	2.4	3.7	0	6.1
LLMO	3	347	66	330	1645	491	1490	4.6	3.2	0	7.8
HWCS	4	2488	85	2359	873	269	850	1.2	2.3	0	3.5
CPCO	4	1045	100	899	1537	115	1124	4.1	0.1	0	4.2
MILLS	5	571	77	227	1873	36	1468	1.4	4.8	0	6.2
FAWNO	5	802	234	802	2211	130	489	10.0	9.8	0	19.8
ELKS	6	1054	101	254	5167	1332	1463	0.5	0	2.4	2.9
ELKO	6	7319	121	638	7387	161	516	0	1.5	5.4	6.9
RAINS	7	1144	41	142	7449	304	357	0.1	0	2.5	2.6
HAMO	7	5523	34	271	5792	16	43	0.2	0.5	5.4	6.1
SPTS	8	5909	45	161	38045	439	627	0.6	0	1.3	1.9
SPTO	8	7555	318	782	9211	51	613	1.7	0	4.0	5.7
UPMS	9	57781	45	94	14311	257	547	0	0	1.7	1.7
UPMO	9	20983	134	504	13605	382	876	0	0	14.6	14.6
LMS	10	4040	33	248	7529	286	339	0	0	0.6	0.6
LMO	10	12480	220	383	15502	209	398	0.2	0	4.5	4.7