

AN ABSTRACT OF THE THESIS OF

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Title: PREDATOR ASSEMBLAGES IN OLD-GROWTH AND
LOGGED SECTIONS OF SMALL CASCADE STREAMS

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Assemblages of stream predators were studied in relation to habitat and trophic characteristics of 33 sections of small streams flowing through old-growth (>450 yrs), recent clearcut (5-15 yrs), and second-growth (12-35 yrs) forests of the western Cascades of Oregon. Abundance of 10 vertebrate and 29 insect taxa ranging in size from 3 mg to 20 g dry wt was quantified. Correlations were developed between taxonomic composition, diversity, and biomass of predators, and characteristics of streams including drainage area, width, elevation, gradient, canopy density, and streambed sediment composition. Community dynamics inferred from these correlations were applied to explain impacts of clearcut logging on predators.

Dominant vertebrates were the salamander Dicamptodon ensatus and the trout Salmo clarki. Common insects studied were the stoneflies Calineuria californica and Alloperla spp. and caddisflies Rhyacophila spp. Occurrence of predatory insects depended on

stream size and elevation; microdistributions depended on current regime. Occurrence of vertebrates depended on channel gradient. All fishes except S. clarki were restricted to sites less than 6% slope, whereas two salamander and one frog species were the only aquatic vertebrates present above 13% slope. Biomass of predators depended on streambed sediment concentration and exposure to sunlight. Most taxa had reduced abundance on fine substrate (sand and gravel) and in the most densely shaded sites.

Clearcutting affected both physical habitat and trophic characteristics of the streams. Accumulation of periphyton on artificial substrates placed in the streams was greater in clearcut than in adjacent old-growth sites. Volume of large organic debris and proportion of pool area were reduced in the logged sections. Effects on sediment concentrations depended on stream slope. In high gradient (> 10%) streams, concentrations of sand and gravel were lower in clearcut than in adjacent old-growth sites; in low gradient (< 4%) streams the opposite situation obtained.

Most taxa were usually more abundant in clearcut than in old-growth sites. Effects of clearcutting, however, depended on stream slope. In the high gradient clearcut sections, both greater primary production and lower sediment concentration seemed to act together to enhance abundance and diversity of predators. In the larger, lower gradient streams accumulated sediment seemed to cancel effects of

canopy removal. Effects of increased primary production seemed to decline after logging. Biomass and species richness in second-growth sites, where a dense canopy shaded the stream, tended to be lower than in clearcut sites and equalled or were lower than the amounts in old-growth sites.

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Logged Sections of Small
Cascade Streams

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PREDATOR ASSEMBLAGES IN OLD-GROWTH AND LOGGED SECTIONS OF SMALL CASCADE STREAMS

INTRODUCTION

A basic task of stream ecologists is to define relationships between the stream community and its environmental systems. The magnitude of human impacts requires that we understand the linkages between stream biota and processes of the watershed and stream. By characterizing these relationships one can gain the knowledge of community dynamics required to understand and predict management impacts. The objectives of this study were 1) to characterize critical relationships between the predator functional group of the stream ecosystem (Cummins 1974) and the physical and trophic characteristics of small streams in the western Cascades, and 2) to assess and explain logging impacts on the predator functional group. Because predators derive energy from all lower trophic levels, the predator functional group may integrate total trophic response of the system. By studying predators, I could identify environmental factors that affect ecosystem productivity and assess logging impacts on the general productivity of stream ecosystems.

As a subsystem of the stream ecosystem, the predator functional group depends on stream and watershed processes for both physical habitat and food resources. Erosional and fluvial processes

determine stream morphology and streambed sediment composition (Leopold et al. 1964). Large organic debris derived from terrestrial vegetation alters stream morphology, retains sediment and organic detritus, and acts as a reserve of nutrients and organic matter (Swanson et al. 1976). Vegetation and landforms can limit aquatic primary production (Lyford and Gregory 1975) and regulate stream temperature (Brown 1969) by shading the stream, while at the same time determining the forms and rates of inputs of allochthonous organic matter (Sedell et al. 1975). Nutrient inputs depend on lithology and soils, geomorphology, vegetation, and precipitation chemistry (Likens et al. 1977). Watershed deforestation affects both physical habitat in the stream and inputs of biotic energy and nutrients to the stream ecosystem. These effects will likely depend on the particular biological, geological, and climatic characteristics of the watershed and stream involved. A logging operation that alters stream canopy, temperature, streamflow regime, sediment load, structural organic debris, or energy and nutrient resources will likely have multiple effects on stream communities.

Longitudinal changes in community structure reflect dependence on changing environmental conditions, and community dynamics can be inferred from analysis of longitudinal succession along such environmental gradients (Major 1951). A useful explanation of longitudinal community succession would provide information about roles

of specific environmental factors and mechanisms through which they affect community structure. For this study I attempted to relate taxonomic composition, diversity, and biomass of the predator functional group to physical and trophic characteristics of small streams over a broad range of undisturbed natural situations. I also compared old-growth and logged sections of streams to assess impacts of clearcut logging. This approach provides a perspective from which to view impacts of human activities in the context of natural processes regulating stream ecosystems.

METHODS

Study Area

The study area was centered in the H. J. Andrews Experimental Forest in the western Cascade Mountains in Oregon. The steep terrain ranges 400-1600 m in elevation and is heavily forested with Douglas-fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophila). Volcanic parent material of tuffs, breccias, and basalt underlies soils ranging from shallow and stony to deep clay loam (Rothacher et al. 1967). Extensive deep-seated mass movements occur where lava flows and welded ash flow beds of the Sardine Formation cap volcanoclastic rock of the Little Butte Formation (Swanson and James 1975). A maritime climate with about 240 cm precipitation prevails. Above 1000 m elevation, snow usually accumulates during winter, whereas lower elevations receive mostly rain. Streams are generally high gradient and dominated by boulders and large organic debris. Streamflow responds quickly to storms and may be 5,000 times greater during winter storms than during summer base flow (Harr 1976).

Study Design and Sampling

Thirty-three sections of 16 streams (Appendix A) were selected for study on the basis of drainage area, gradient, and history of

disturbance (Fig. 1). I studied streams in old-growth forests to characterize natural variation and establish baseline data for comparison with logged areas. Old-growth (> 450 yrs) sites were undisturbed by logging, but in some cases clearcuts were located about 1-2 km upstream. Logged areas had been cut and burned without leaving buffer strips of vegetation along the streams.

I divided the logged sites into two groups according to their vegetation: recent clearcuts (5-15 yrs) where streams were still unshaded by vegetation, and second-growth sites (12-35 yrs) that were shaded by dense second-growth riparian vegetation. I compared old-growth and recent clearcut sites to detect initial effects of logging. Recent clearcut sites were usually studied in combination with an adjacent (50-200 m upstream) old-growth site. Since logging impacts may depend on stream size or slope, I compared adjacent clearcut and old-growth sites on streams of different size (first- to third-order) and gradient. I also examined temporal succession following logging by comparing recent clearcut and second-growth sites.

Study sections were usually about 30 m long. For each site, I subjectively classified stream habitat as pool or riffle according to whether current was wanting or turbulent, respectively. I estimated proportions of these habitats, and width and depth of stream by lateral transects at 2-m intervals. Channel gradient (%) equalled the rise in

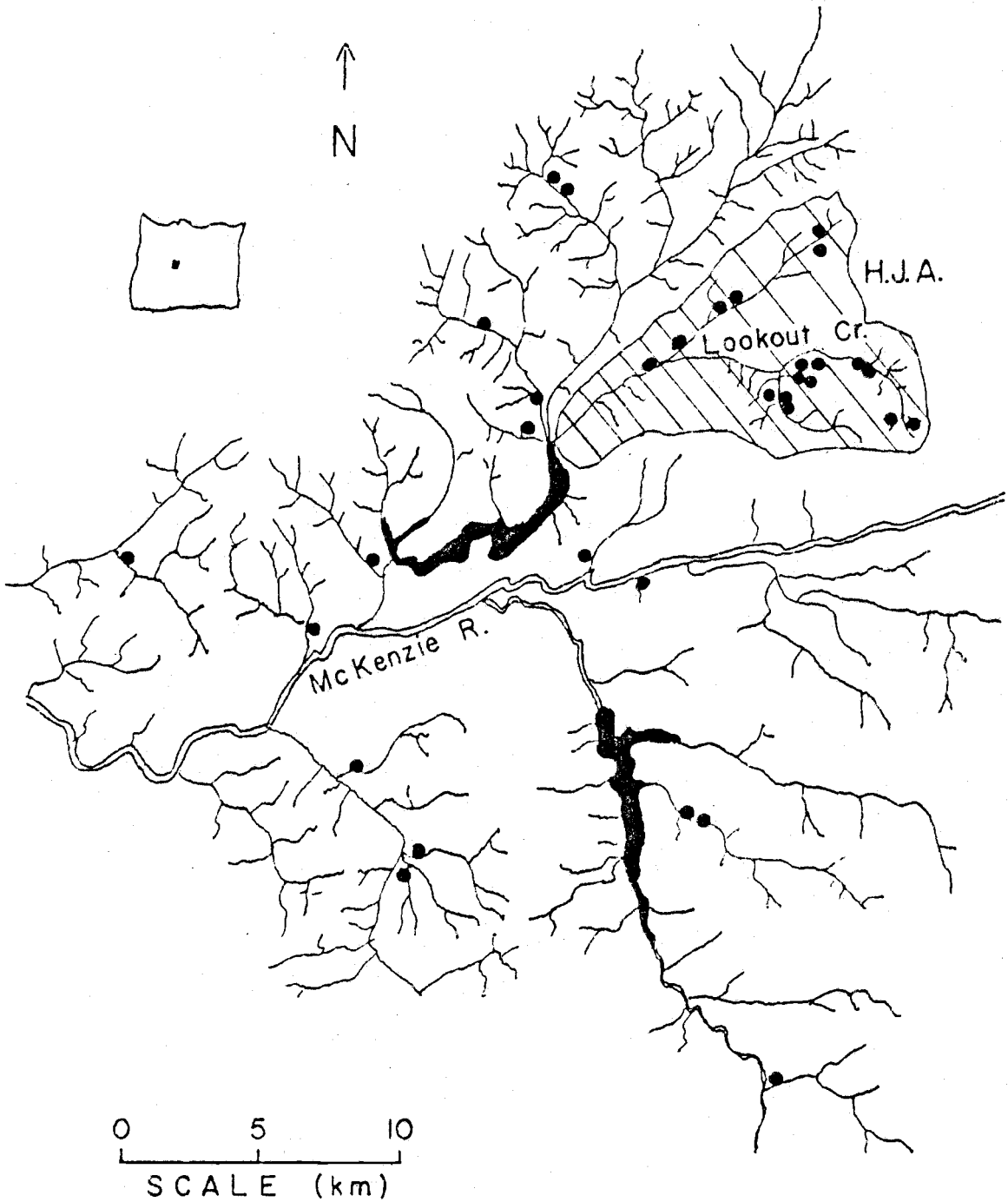


Fig. 1. Map of study area showing locations of the 33 study sites. The H. J. Andrews Experimental Forest (HJA) is cross-hatched.

elevation of the site divided by the length ($\text{m}/\text{m} \cdot 100$). I visually estimated percentage canopy closure. Stream drainage area, elevation, and stream order (Strahler 1957) were estimated from USGS topographic maps (scale 1:62,500).

I quantified size composition of sediment and the density of large crevices in the streambed surface by visually estimating the proportion of sand-gravel (< 30 cm diam) and counting large crevices ($> 25 \text{ cm}^3$) within 0.25 m^2 quadrats. Twenty quadrat samples at each site were stratified (five each) into the middle and edge of pools and riffles. The mean of the 20 samples provided ratings for sediment concentration and crevice density for each site. Pool and riffle samples were also averaged separately to provide ratings for substrate in each habitat.

I estimated the volume of large wood debris (> 10 cm diam) within a 30 m length of each site. The volume of each piece of large debris was calculated from the formula

$$\text{Volume} = (D_1^2 + D_2^2) \cdot \text{length} \cdot \pi / 8$$

where D is the diameter of either end. Debris load of each site equalled total volume of large debris per unit area (m^3/m^2).

I measured rates of accumulation of algae in old-growth and clearcut sites by placing two clay tiles (60 cm^2 upper surface) in riffle areas in each of 16 paired clearcut and old-growth sites.

After 1 month (September) I removed the tiles and measured the amount of chlorophyll that had accumulated by methods of Wetzel and Westlake (1969).

Prior to sampling, I selected a group of predator taxa whose abundance I would quantify. The selected group included all aquatic vertebrates except the tailed-frog (Ascaphus trueii), all Setipalpia (Plecoptera), most Rhyacophila (Trichoptera), and all Odonata, Megaloptera, and larval Coleoptera. Although not all inclusive, this group of taxa should be an adequate sample of the predator functional group and should exhibit behavior representative of the functional group in general.

Population size of vertebrates was estimated for all predator species in each of 31 sites, usually by mark-recapture, and in four cases by removal methods (Robson and Regier 1971). Vertebrates were collected with an electroshocker, anesthetized, measured, marked with a toe clip or fin clip, and redistributed within the site. I usually attempted recapture 1 week after marking. A series of salamanders and sculpins from several sites were frozen and later weighed (nearest mg) to generate length-weight regressions (Appendix B). A similar regression for trout was obtained from Aho's (1976) study of cutthroat trout (Salmo clarki) in the same vicinity. Trout and sculpin were readily separated into two size classes, juvenile (Age 0⁺) and adults. Biomass (g wet wt/m²) was estimated separately

by size class and summed to obtain the total for the population. As a measure of vertebrate species diversity I used the Shannon-Weiner diversity index (H')

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

where p_i is the proportion of total community biomass contributed by the i^{th} species summed for S species.

To sample predatory insects I held a square-framed net (33 cm on a side, mesh 0.33 mm) perpendicular to stream flow while disturbing 0.16 m² of streambed in front of the net. In pool habitat I disturbed substrate while directing current through the net by hand. Insects were picked from samples in the field, preserved in alcohol, and later identified, counted, and measured under a microscope. I calculated length-weight regressions for converting length data to dry weight (Appendix B). Insects from several sites were frozen rather than being preserved in alcohol. These were later identified and measured, then dried (50 C, 48 h) and weighed (nearest 0.01 mg). Weights for rare species were calculated from the regression equation of the most similar common taxon.

Biomass (mg dry wt/m²) and density (no./m²) in pool and riffle habitats were estimated by the mean of three samples from each habitat type. The mean of all six benthic samples gave an

estimate of biomass and density within sites. As a measure of species diversity I used species richness, the total number of taxa collected. Twenty-eight sites were sampled once for predatory insects during either late summer (August-September 1976) or late autumn (December 1976) after an extended period of unusually low stream flow. I combined the data from these periods for analysis.

The data consisted of two sets, community and environmental. Correlation matrices, principal component and canonical correlation analyses (Cooley and Lohnes 1971) on standardized variables were used to examine patterns within the environmental variables and relations between the community and environmental variables. I used non-parametric statistical tests (Siegel 1956) to compare adjacent clearcut and old-growth sites. Although vertebrates and insects were studied together in 26 of the 33 study sites, data were analyzed separately for these groups because vertebrate biomass was usually much greater than biomass of predatory insects, and tended to mask variation in the latter.

RESULTS AND INTERPRETATION

Stream Characteristics

Old-growth Sites

Environmental data from old-growth sites (Appendix C) were analyzed separately to characterize natural variation in the undisturbed environmental system. Because significant intercorrelation existed among the environmental variables (Appendix D), I examined the principal components. The first two principal components accounted for 71% of the original variance. Interpretation of these components was based on the factor structure (Table 1), consisting of back-correlations of the principal components with the original variables.

The first component expressed trends in stream characteristics related to stream size. Properties of streams that increased with stream size correlated positively with the first component, whereas those that decreased correlated negatively. The larger streams were less shaded, lower in gradient, had less organic debris, and more riffle area than the smaller streams. Debris volume decreased an order of magnitude from first- to third-order channels (Fig. 2). Debris was randomly distributed in first-order streams, but tended to be aggregated into debris accumulations at intervals of 20-50 m in

Table 1. Correlation coefficients between the first two principal components and the 12 original variables measured in 15 old-growth sections of first- to third-order streams. Highest coefficient for each variable is underlined.

Variable	Loading for PC1	Loading for PC2
Drainage area	<u>.86</u>	-.42
Mean width	<u>.89</u>	-.29
Mean depth	<u>.60</u>	-.25
Canopy shade	<u>-.84</u>	.02
Debris volume	<u>-.80</u>	.20
Channel gradient	<u>-.66</u>	.59
Crevice density	.54	<u>.80</u>
Sand-gravel	-.62	<u>-.64</u>
Cobble	.62	<u>.68</u>
Elevation	.00	<u>.73</u>
Pool area	<u>-.58</u>	-.06
Riffle area	<u>.85</u>	.06
Variance (%)	48	23

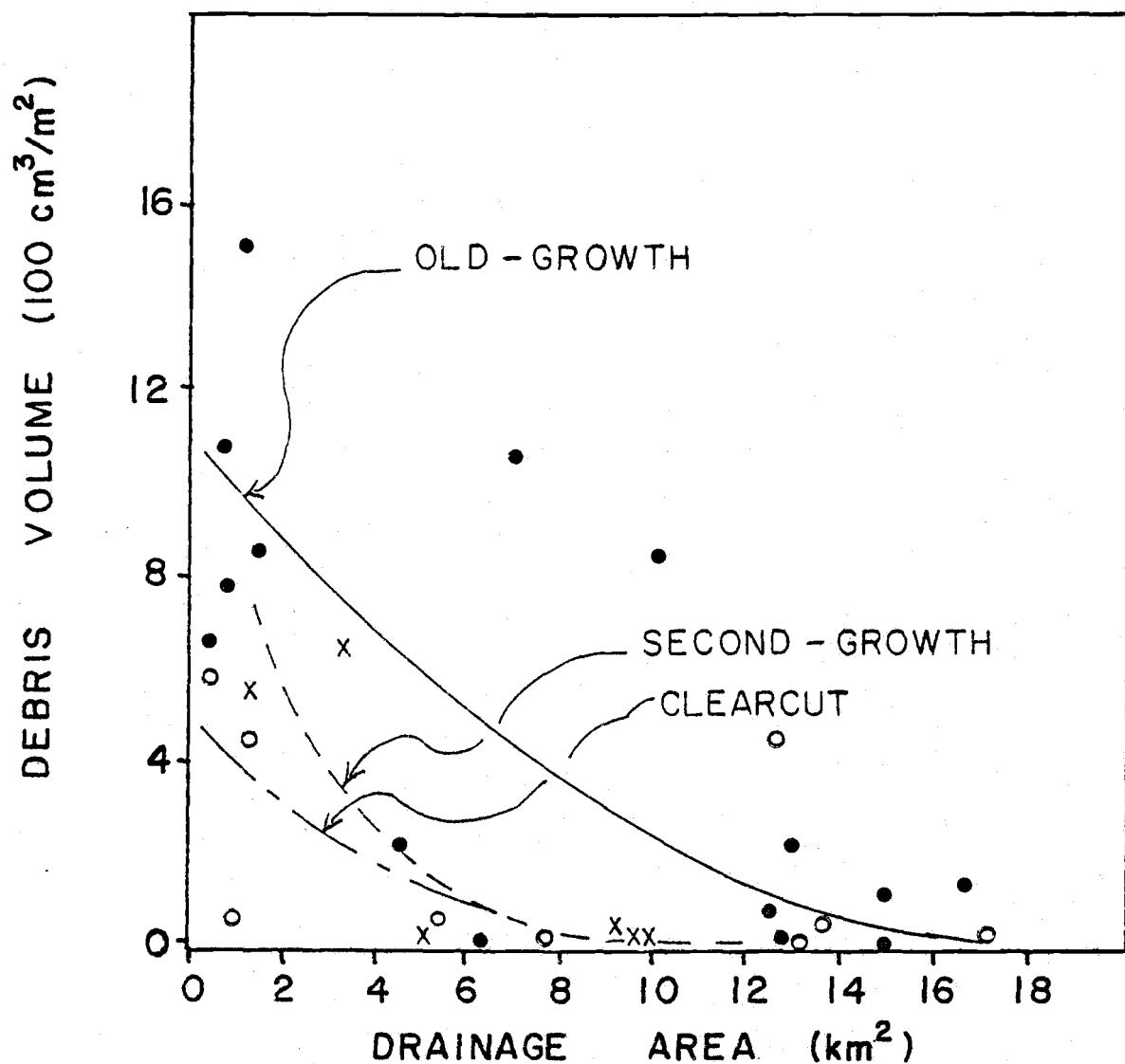


Fig. 2. Volume of large organic debris (> 10 cm diam) in stream channels in relation to drainage area for old-growth (●), clearcut (○), and second-growth (x) sites. Curves were drawn by inspection.

the larger streams. Variance was highest for data from the mid-sized streams (5-12 km² drainage area) because the length of stream studied (30 m) was insufficient to account for the larger scale heterogeneity. Reduced quantities of large organic debris in the larger streams probably resulted from an increase in total stream power (Swanson et al. 1976). Reduced debris volume also accounts for the relatively high proportions of riffle area in the larger streams because less area of stream was impounded where debris load was small.

Accumulation of chlorophyll on tiles placed in the streams was directly related to stream width and inversely related to canopy closure ($r_s = .83, -.67, n = 8, p < .01, < .05$, respectively, Appendix E). Thus for old-growth forests, as the stream became wider and canopy more open, the potential for primary production increased.

The second component of old-growth stream characteristics seemed to express a relationship between streambed sediment characteristics and geologic parent material. High correlations for site elevation and all substrate composition parameters indicated a trend toward dominance of coarser sediment in streams at higher elevations. This trend corresponds to a shift in bedrock geology from relatively young and resistant flow rock at the higher elevations to weaker and older pyroclastic rocks at the lower elevations (Swanson and James 1975).

Logged Sites

Old-growth, recent clearcut, and second-growth stream sections ranged similarly in drainage area, channel width, depth, and gradient (Table 2, Appendix C). The second-growth sites, however, were lower in elevation than the other sites because of the historical pattern of logging in the area. The recent clearcut sites were mostly exposed to direct sunlight, whereas in the second-growth sites even-aged riparian vegetation produced a denser canopy than in old-growth areas, where canopy was usually opened by fallen trees.

Table 2. Range of physical characteristics of the 15 old-growth, 10 clearcut, and 6 second-growth study sites.

Variable	Old-growth	Clearcut	Second-growth
Drainage area (ha)	30-1680	50-1690	100-980
Mean width (m)	1-6	1-6	1-4
Mean depth (cm)	4-26	4-21	5-14
Channel gradient (%)	2-18	2-13	1-13
Elevation (m)	400-1200	400-1200	300-500
Canopy shade (%)	40-95	5-40	80-100

Accumulation of chlorophyll on clay tiles placed in the streams was consistently greater in the clearcut sites than in adjacent old-growth areas ($p < .05$, $n = 8$ pairs of sites, Wilcoxon test), but the difference tended to decrease with stream size (Appendix E). In seven of eight pairs of sites, the clearcut exceeded the old-growth

in accumulated chlorophyll, but the pair of sites on the widest stream showed the opposite result. Thus clearcutting seemed to enhance aquatic primary production by removing the forest canopy, but in the larger streams that were naturally less shaded, canopy removal had a smaller effect on primary production.

Streams in logged areas contained less large organic debris than in old-growth sites of similar drainage area (Fig. 2). Large debris was lacking in every logged site larger than 4 km² drainage area, except one site that contained a log jam. Smaller streams had residual natural and logging debris equal to about half of that in old-growth sites. Debris was thus either removed intentionally during logging or was afterwards flushed from the logged sites during floods.

Large organic debris played a key role in shaping channel morphology and retaining sediment, particularly in the smaller, higher gradient streams. Because of their reduced volume of debris, logged sites had proportionately less pool area than old-growth sites. Old-growth sites averaged 47.3% pool area, whereas logged sites averaged 35.2% pool area ($p < .05$, Mann-Whitney U test). Debris removal thus reduced depositional area of the streams by about 20%.

Accumulated sediment was thus made available for transport according to the stream's energy, a function of stream slope. Surficial concentrations of sand-gravel and crevices in logged sites were strongly correlated with channel gradient, whereas storage of

sediment by organic debris in the higher gradient old-growth sites reduced these correlations (Fig. 3). The net effect was that high gradient ($> 10\%$) logged sites contained coarser sediment than old-growth sites of similar slope. Comparison of paired clearcut and old-growth sites, however, indicated that the difference in sediment concentrations reversed in streams lower than about 4% gradient. Thus the less competent, low gradient streams apparently deposited sand and gravel that was introduced by logging, but the competent, high gradient streams exported both introduced sediment and sediment that was previously stored in their channels.

The Study Taxa

Ten vertebrate and 27 insect taxa of predators were collected from the study sites (Table 3). In terms of biomass and frequency of occurrence, the dominant vertebrate was the salamander Dicamptodon ensatus, occurring in dense populations of neotenes. The cutthroat trout, Salmo clarki, was also common, although usually absent from first-order streams. Several species of sculpin (Cottus spp.) were abundant in the lower gradient ($< 6\%$) sites. I also collected a small number of Olympic salamanders, Rhyacotriton olympicus, and dace, Rhinichthys osculus and R. cataractae, in some of the first- and third-order streams, respectively. The dominant predatory insects included the stoneflies Calineuria californica

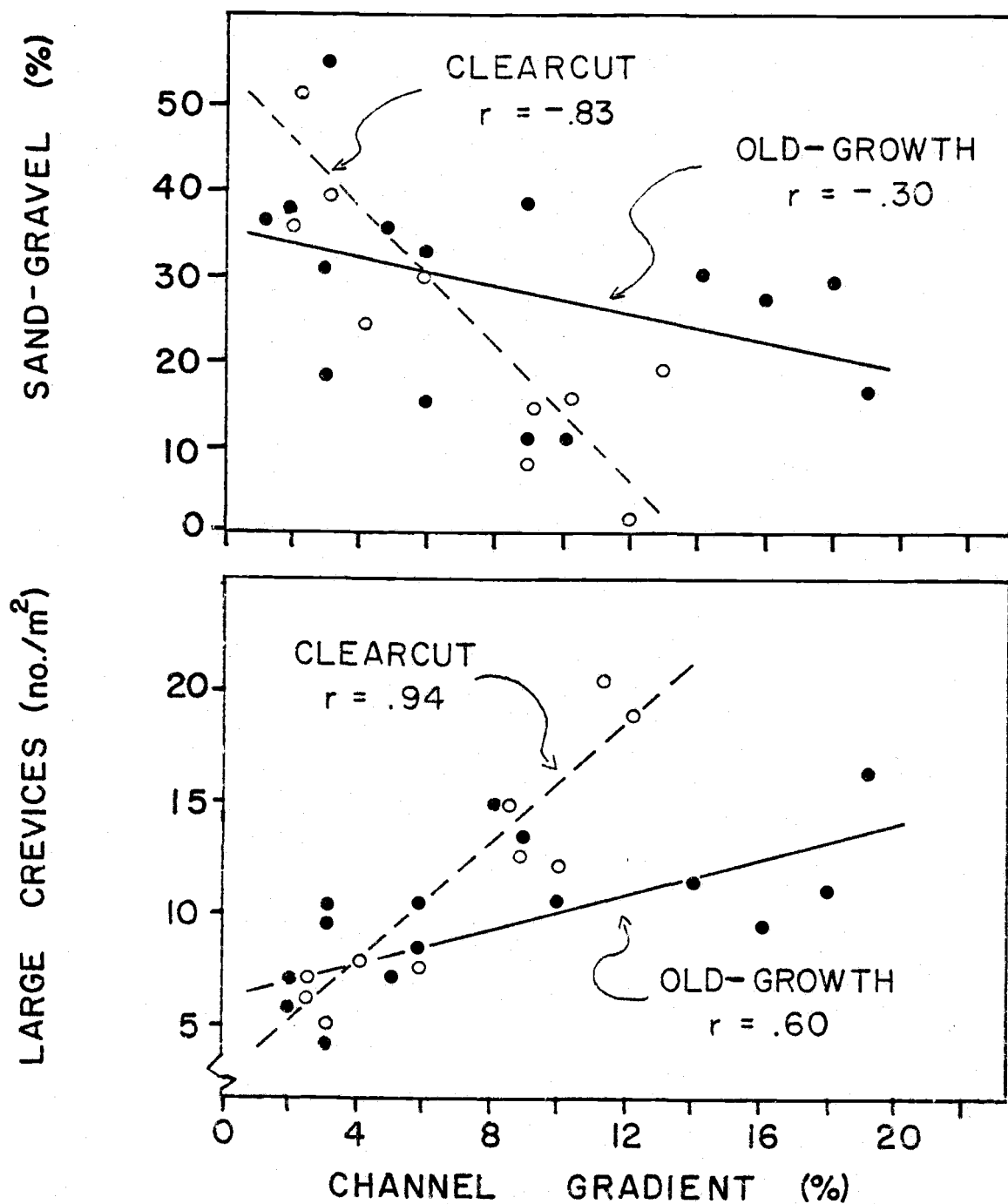


Fig. 3. Percentage sand-gravel and density of large crevices in surface substrate in old-growth (●) and clearcut (○) sites in relation to channel gradient.

Table 3. Frequency of occurrence of the selected predator taxa.^a

Taxon	No. of sites	Taxon	No. of sites
Vertebrates		Insects: Trichoptera ^b	
<u>Dicamptodon ensatus</u>	31	<u>Rhyacophila willametta</u>	27
<u>Rhyacotriton olympicus</u>	5	<u>R. acropedes</u>	22
<u>Salmo clarki</u>	24	<u>R. hyalinata</u>	18
<u>S. gairdneri</u>	1	<u>R. narvae</u>	11
<u>Cottus beldingi</u>	8	<u>R. angelita</u>	9
<u>C. confusus</u>	1	<u>R. bifila</u>	8
<u>C. perplexus</u>	1	<u>R. amaudi</u>	6
<u>C. rhotheus</u>	1	<u>R. grandis</u>	5
<u>Rhinichthys osculus</u>	1	<u>R. blarina</u>	4
<u>R. cataractae</u>	1	<u>R. vaefes</u>	1
		<u>R. kincaidi</u>	1
		<u>R. sp. A</u>	1
Insects: Plecoptera		Insects: Megaloptera	
<u>Calineuria californica</u>	28	<u>Orohermes crepusculus</u>	15
<u>Alloperla spp.</u>	28	<u>Sialis cornuta</u>	7
<u>Perlinoidea aurea</u>	18		
<u>Paraperla spp.</u>	10	Insects: Odonata	
<u>Hesperoperla pacifica</u>	9	<u>Octogomphus specularis</u>	7
<u>Doloneuria theodora</u>	8		
<u>Isogenus sp. A</u>	9	Insects: Coleoptera	
<u>I. sp. B</u>	7	Dytiscidae	4
<u>I. sp. C</u>	6		
<u>Isoperla sp. A</u>	6		
<u>I. sp. B</u>	6		

^a Keys used to identify insects were Baumann et al. (1977), Evans (1972), and Wold (1973).

^b Rhyacophila taxa listed may represent more than one species that are indistinguishable as larvae.

and Alloperla spp. Both were abundant in most sites, with Calineuria occurring primarily in riffles and Alloperla mainly in pools. The largest insects were the Megalopteran Orohermes crepusculus and the dragonfly Octogomphus specularis. Both were common and sometimes dominated biomass, but Orohermes was absent from first-order streams and Octogomphus was restricted to the lower elevations (< 900 m). Most predator taxa were uncommon. Of the 37 taxa, 27 occurred in less than a third of the study sites, whereas only three were collected in every site.

Body weight of the common taxa varied continuously from about 3 mg dry wt for the stonefly Alloperla to 10^2 - 10^4 mg for the salamander Dicamptodon (Fig. 4). A discontinuity in the size continuum occurred between Dicamptodon and Callineuria in first-order streams, but disappeared with the addition of Salmo, Cottus, and Orohermes to the community in the larger streams. This continuous array of consumer size in the predator functional group presumably results from partitioning of food resources according to particle size, and produces as an emergent property, more efficient and complete utilization of the available food resource (Wallace et al. 1975).

Predatory Insects

Patterns within Sites

To explore relationships between predators and microhabitat

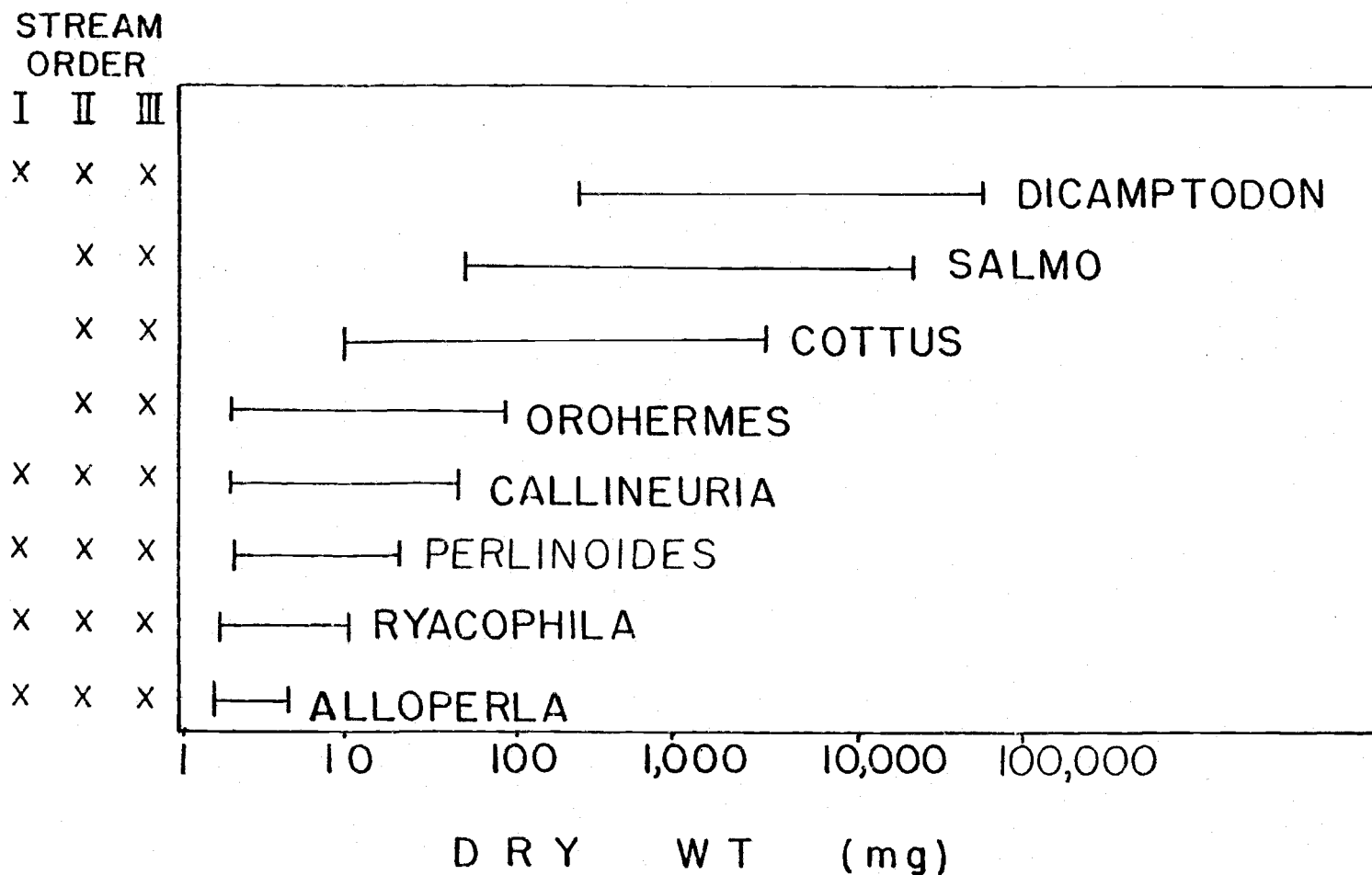


Fig. 4. Range of body weight of common predator genera. Stream order of occupied sites is indicated for each taxon. The conversion factor used to convert wet weight of vertebrates to dry weight was 0.25.

characteristics, I used canonical correlation analysis to relate density of the 13 most commonly occurring taxa (> 10 benthic samples) to eight environmental variables associated with each sample. Environmental variables included a dummy variable distinguishing pool and riffle habitats (coded 0 = pool and 1 = riffle), proportions of surface substrate in cobble or sand-gravel, and approximate volumes of organic detritus and filamentous algae retained in the sampling net. Total redundancy of the community data given the environmental data was only 13%, perhaps because of variance among streams as opposed to within streams, the large number of zero values in the data, or non-linear relationships among the variables. Only the first canonical relationship was examined in detail. It accounted for 15% of the total variance in the community data, with a redundancy of 8%.

The first factor of the environmental data had a high negative correlation with the dummy variable distinguishing pool and riffle habitats, and intermediate correlations with volume of CPOM (coarse particulate organic matter) and algae (Table 4). Thus it ordinales assemblages from slow currents with accumulations of organic matter to fast water with concentrations of algae. Taxa with negative correlations with the community factor, such as Calineuria californica and Hesperoperla pacifica, were most abundant in riffles. Taxa loading positively, such as Alloperla spp. and Octogomphus specularis, were concentrated in pools.

Table 4. Correlation coefficients between the canonical and original variables for the first canonical factors relating density of common taxa of predatory insects to microhabitat characteristics associated with each benthic sample.

Community Factor Structure		Environmental Factor Structure	
Taxon	Factor I $R_c = .71$	Variable	Factor I $R_c = .71$
<u>Calineuria californica</u>	-.56	Habitat type ^a	-.86
<u>Hesperoperla pacifica</u>	-.54	Sand-gravel	.31
<u>Perlinoidea aurea</u>	-.39	Cobble	-.10
<u>Isogenus</u> sp. A	.24	Algae	-.45
<u>Alloperla</u> spp.	.50	FPOM ^b	.31
<u>Paraperla</u> spp.	.06	CPOM ^c	.54
<u>Rhyacophila willametta</u>	-.20	Twigs, wood	.25
<u>Rhyacophila hyalinata</u>	-.44	Total detritus	.44
<u>Rhyacophila acropedes</u>	-.53		
<u>Rhyacophila angelita</u>	-.48		
<u>Rhyacophila narvae</u>	.27		
<u>Orohermes crepusculus</u>	-.10		
<u>Octogomphus specularis</u>	.32		

^a Habitat is a dummy variable scaled: 0 = Pool, 1 = Riffle.

^b Fine particulate organic matter (<1 mm diam).

^c Coarse particulate organic matter (1-16 mm diam).

Effects of clearcutting on the different predator taxa should depend on the taxon's habitat requirements. Canopy removal should enhance abundance in riffle areas more than in pools because of the direct dependence of aquatic primary production on stream velocity (McIntire 1966), and because riffles usually contain coarser sediment than pools. As a measure of habitat preference, I calculated for the eight most commonly occurring taxa (> 10 sites) the relative difference in mean biomass between pool and riffle habitats across sites. As a measure of logging impact, I used the relative difference in mean biomass between clearcut and old-growth sites. These measures were significantly related (Fig. 5). The taxa that were concentrated in riffles showed relatively greater positive differences between clearcut and old-growth sites than taxa that were concentrated in pools. Thus the apparent effect of clearcutting was to increase abundance of riffle insects more than pool insects.

Species richness of pool and riffle assemblages (Appendix E) in old-growth sites depended on different environmental factors (Fig. 6). For pools species richness was inversely related to percentage sand-gravel, but was unrelated to percentage exposure to sunlight. On the other hand, species richness in riffle habitat was unrelated to percentage sand-gravel, but directly related to percentage exposure. Thus for pools species richness depended on substrate size, but for riffles it depended on condition of the forest canopy.

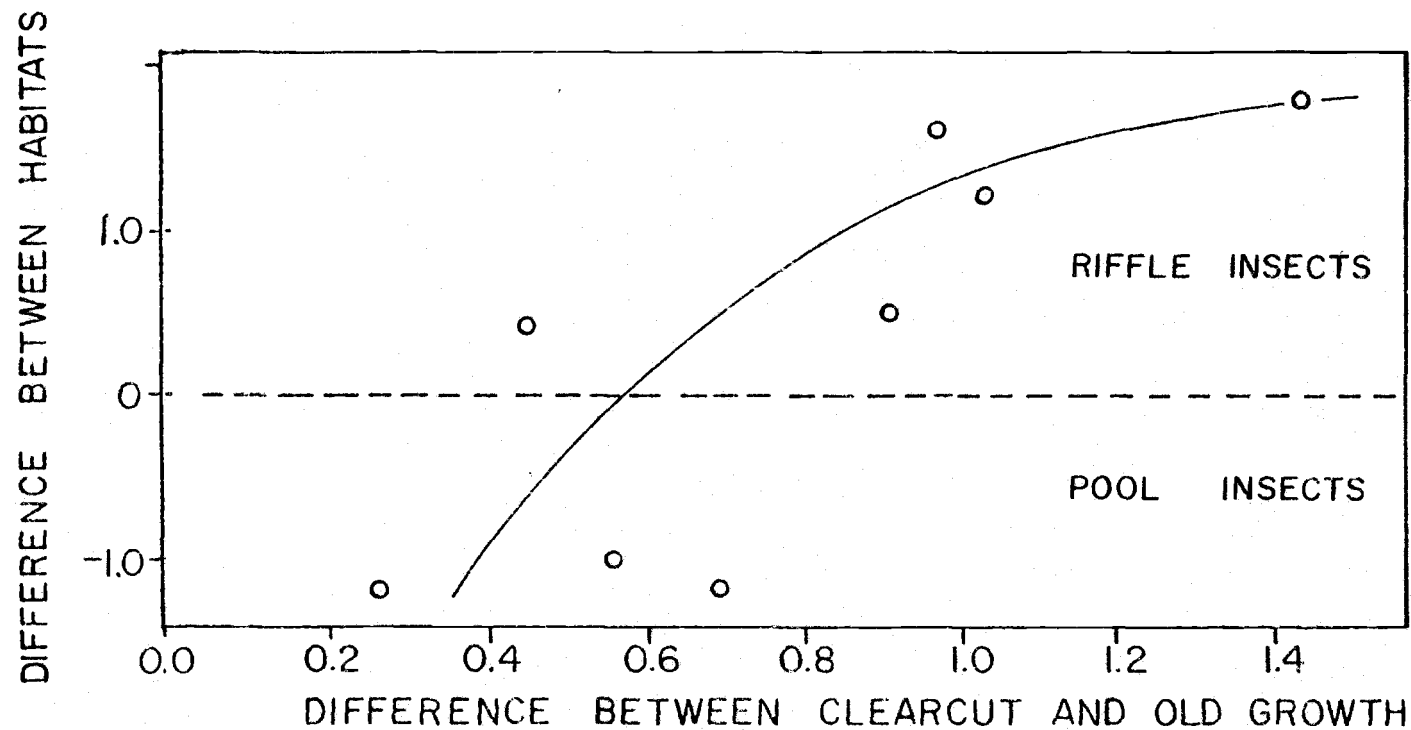


Fig. 5. Difference in biomass of insect predators between clearcut and old-growth sites in relation to habitat preference for the eight most common taxa (occurred in ≥ 10 sites). Data were normalized by transforming to the relative difference: Ordinate = mean pool biomass minus mean riffle biomass divided by the grand mean; Abscissa = mean clearcut biomass minus mean old-growth biomass divided by the grand mean. The curve was fitted by inspection ($r_s = .88$, $n = 8$ taxa, $p < .01$).

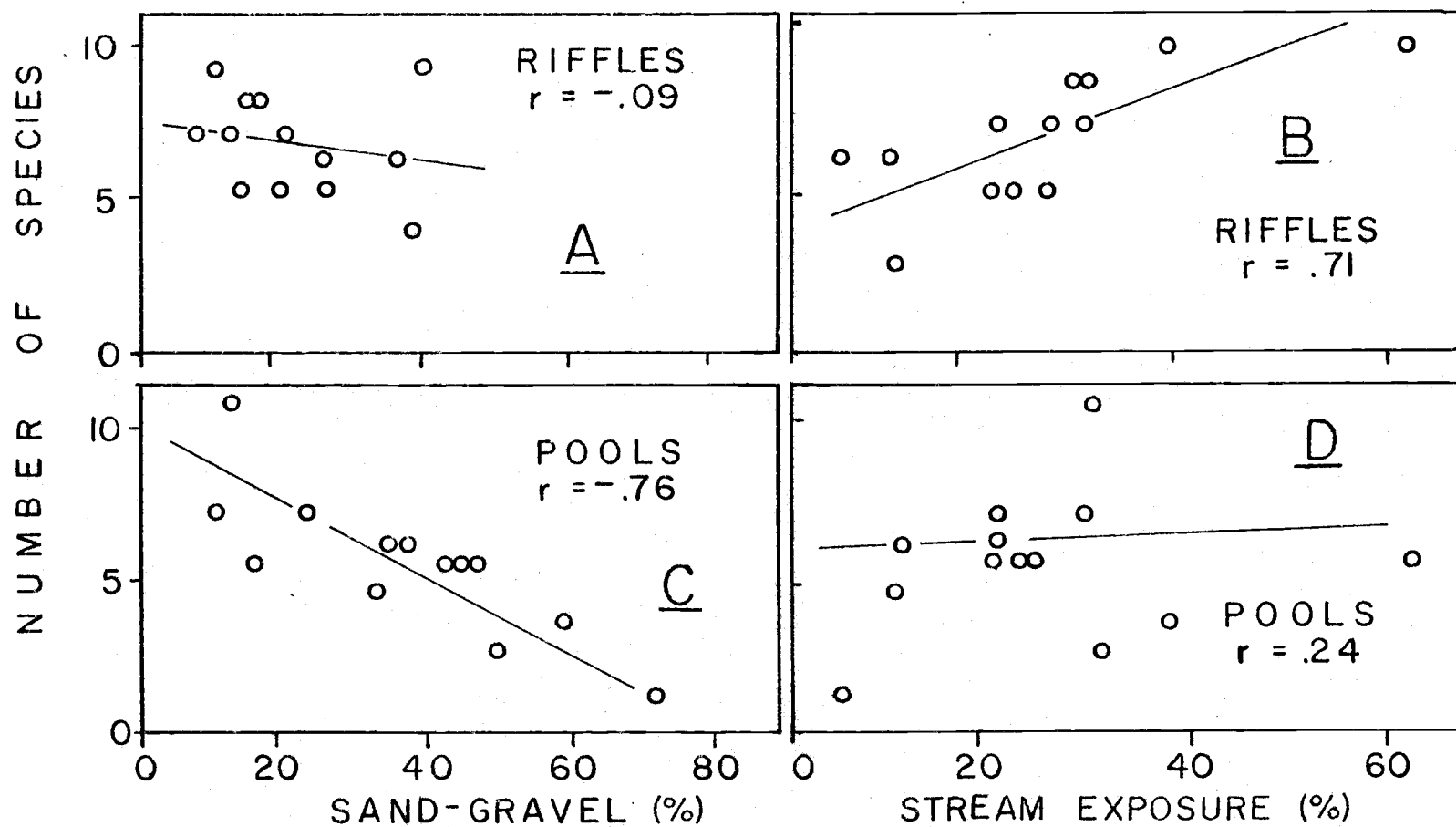


Fig. 6. Species richness of predatory insects in pool and riffle habitats in relation to percentage sand-gravel of surface substrate and exposure to sunlight in 13 old-growth sections of streams.

From the above correlations one would predict that clearcutting would affect riffle assemblages primarily via canopy removal and affect pool assemblages mainly by altering the streambed. The percentage difference in species richness and mean total density of predatory insects in riffles between paired clearcut and old-growth sites averaged 33% and 73% greater, respectively, in clearcuts (Table 5). The average percentage differences for pools, however, were only 23% and 10%. In addition, differences between pool assemblages in paired sites were significantly correlated with stream slope ($r_s = .68$ and $.78$, $n = 8$, $p < .05$, for species richness and density, respectively). No significant correlation with stream slope was found for these differences for riffle assemblages. Thus effects of clearcutting on pool assemblages depended on changes in both insolation and substrate, whereas riffle assemblages seemed to be affected primarily by changes in insolation.

Patterns among Sites

Abundance of most taxa was positively correlated with stream drainage area, mean width, and percentage cobble, and negatively correlated with percentage shade and sand-gravel (Table 6). Drainage area and channel width accounted for the highest correlation for nine of the 17 most frequently occurring taxa. To relate taxonomic composition to the environmental variables, I used canonical

Table 5. Species richness and mean total density of predators in pools and riffles in paired clearcut (CC) and old-growth (OG) sites, arranged in order of increasing stream slope.

Site pair ^a	Slope (%)	Pools			Riffles		
		CC	OG	Percentage difference ^b	CC	OG	Percentage difference
Species Richness							
CO	3	3	5	-40	8	5	60
LO	4	8	11	-27	8	8	0
MR	4	9	5	80	10	5	100
LS	9	5	6	-17	3	3	0
MA	10	7	7	0	8	5	60
WA	11	9	5	80	9	7	29
MC	13	5	4	25	5	6	-17
AR	14	11	6	83	9	7	29
Density							
CO	3	30	54	-44	124	106	17
LO	4	456	476	-4	214	132	62
MR	4	68	128	-47	116	114	2
LS	9	134	188	-29	66	114	-42
MA	11	160	176	-9	110	42	162
WA	13	274	126	117	312	158	97
MC	13	178	184	-3	156	40	290
AR	14	250	124	102	154	168	-8

^a For identification of site pairs see Appendix A.

^b $100 (CC-OG)/OG$.

Table 6. Correlations of mean biomass^a of 17 taxa of predatory insects with environmental variables. N = 28 sites, sampled August and December.

Taxon	Drainage area	Channel width	Shade	Channel gradient	Sand- gravel	Cobble	Elevation	Multiple R ²
<u>Calineuria californica</u>	.15	.26	-.21	-.09	-.27	.46*	-.06	.35
<u>Hesperoperla pacifica</u>	.56**	.31	-.21	-.35	.11	-.27	-.36	.52
<u>Perlinoides aurea</u>	.44*	.41*	-.45*	.01	-.47*	.44*	.14	.55
<u>Isoperla</u> sp. A	.65**	.57**	-.35	-.33	-.45*	-.06	-.16	.57
<u>Isogenus</u> sp. A	.10	.31	-.14	.10	-.21	.23	.21	.33
<u>Isogenus</u> sp. B	.15	.47*	-.24	.08	-.30	.36	.12	.53
<u>Isogenus</u> sp. C	-.02	-.04	-.05	.31	-.32	.33	.13	.46
<u>Alloperla</u> spp.	.12	.01	-.32	.27	-.38*	.40*	.54**	.51
<u>Rhyacophila willametta</u>	.10	.29	-.24	-.09	-.09	.13	.10	.36
<u>Rhyacophila acropedes</u>	-.33	-.45*	-.10	.48**	-.21	.20	.46*	.36
<u>Rhyacophila hyalinata</u>	.16	.28	-.24	-.14	-.19	.30	-.14	.31
<u>Rhyacophila grandis</u>	-.47*	-.71**	-.17	.56**	-.27	.16	.59**	.67
<u>Rhyacophila angelita</u>	.47*	.54**	-.50**	-.17	-.58**	.35	.11	.62
<u>Rhyacophila arnaudi</u>	.75**	.55**	-.31	-.36	-.20	-.12	-.12	.67
<u>Rhyacophila bifila</u>	-.34	-.50	-.08	.44*	-.18	.22	.36	.32
<u>Rhyacophila narvae</u>	.07	.31	-.45*	.10	-.11	.40*	.13	.60
<u>Orohermes crepusculus</u>	.28	.59**	-.15	-.31	-.10	.06	-.28	.51

*p < .05, ** p < .01, two-tailed tests.

^a Mean of six benthic samples for each site.

correlation of mean site density of the 12 most frequently occurring taxa (> 8 sites) with six environmental variables. Because of low redundancy of canonical relationships 3-6, I examined only the first two.

The first canonical factors indicated a general tendency for most taxa to have greater abundance in the larger streams (Table 7). Drainage area, mean width, and exposure to sunlight were positively correlated with the first environmental factor, and most taxa were positively correlated with the first community factor. Thus the trend in succession of predator taxa from first- to third-order streams was that of species addition rather than species replacement.

The second factors contrasted assemblages in sediment-poor high elevation sites with those in lower elevation sites, where fine sediments were more common (Table 7). Correlations of the taxa with the second factor showed it to be bipolar; some taxa had negative and others had positive correlations. Some species, like Calineuria californica, occurred at all elevations in similar abundance, whereas Alloperla spp. reached peak abundance at the higher elevations. A few species (Hesperoperla pacifica and Octogomphus specularis) were restricted to sites below about 750 m elevation. For the latter taxa, effects of factors other than sediment composition (such as temperature regime) probably restricted them to the lower elevations. Thus this canonical relationship indicates a change in taxonomic composition

Table 7. Correlation coefficients between the canonical and original variables for the first two canonical factors relating mean density of common predatory taxa to the physical characteristics of the study sites. Largest coefficient for each variable is underlined.

Taxon	Community Factor Structure		Variable	Environmental Factor Structure	
	CI	CII		CI	CII
<u>Perlinoides aurea</u>	.35	-.01	Drainage area	.65	-.33
<u>Isogenus</u> sp. A	.50	-.63	Mean width	.81	.19
<u>Rhyacophila willametta</u>	.43	.18	Exposure	.64	-.26
<u>Rhyacophila hyalinata</u>	.49	.20	Slope	-.36	-.40
<u>Rhyacophila acropedes</u>	.76	.15	Sand-gravel	-.42	.58
<u>Rhyacophila narvae</u>	.47	-.48	Elevation	.12	-.55
<u>Orohermes crepusculus</u>	.47	.31			
<u>Calineuria californica</u>	.16	.54			
<u>Alloperla</u> spp.	.17	-.62			
<u>Paraperla</u> spp.	-.17	.35			
<u>Hesperoperla pacifica</u>	.17	.12			
<u>Rhyacophila angelita</u>	.22	.30			
Variance explained (%)	16	14			
Redundancy ^a	14	10			
R ^b	.91	.84			
R ^c					

^a Redundancy (%) of the community data given the environmental data.

^c Correlation coefficient between community and environmental factors.

on an elevational gradient confounded with a parallel trend in sediment composition.

Clearcutting mimics natural downstream changes in exposure and debris loading by removing canopy and large organic debris. If the same determinants operate in both natural and disturbed situations, changes in taxonomic composition resulting from logging disturbances should also mimic natural longitudinal succession. Differences in biomass of individual species between old-growth and clearcut sites tended to parallel natural trends in biomass from first- to third-order streams. The same taxa that increased naturally from first- to third-order old-growth sites were also more abundant in clearcut than in old-growth sites (Table 8). Of the 21 most common taxa (> 5 sites), 13 averaged both greater in clearcut than in old-growth sites (stream orders combined), and also greater in third-order old-growth sites than in first- and second-order old-growth sites. Only six averaged greater in old-growth than in clearcut sites, and four of these also averaged greater in first- than in third-order old-growth sites. Thus at least until the canopy recovers to shade the stream and large organic debris is replaced, logging disturbances on these small streams may produce a shift in taxonomic composition of predator assemblages of about two stream orders downstream.

When the canopy over the stream recovers after clearcutting, effects of increased exposure to sunlight should decline. The

Table 8. The 21 most common taxa of predatory insects classified according to whether or not their mean biomass was greater in third- than in first- or second-order old-growth sites, and whether or not it was greater in clearcut than in old-growth sites (stream orders combined).

	<u>Greater Mean Biomass In:</u>		Total
	I and II order old-growth	III order old-growth	
<u>Greater Mean Biomass In:</u>			
Clearcut	2	13	15
Old-growth	4	2	6
Total	6	15	21

$p < .05$, Fisher Exact test.

old-growth, clearcut, and second-growth sites form a chronological series ranging from before logging to about 35 yrs after logging. The densely shaded, second-growth sites contained fewer of the predatory insect taxa than either old-growth or recent clearcut sites (Mann-Whitney U test, $p < .05$, Fig. 7). Biomass in the second-growth sites was also lower than in the clearcut sites, but similar to levels in old-growth sites. Because second-growth sites were at lower elevations than most other sites, they had different species complements. Large Odonate nymphs often dominated biomass in the second-growth sites, but were usually absent from other sites. This may explain why second-growth and old-growth sites had similar levels of biomass but different species richness. Temporal succession after logging at a given site, therefore, might be characterized by an initial positive response in abundance and diversity of predatory insects followed by a decline to low levels as riparian vegetation recovers and aquatic primary production diminishes.

Predatory Vertebrates

Longitudinal Succession

Longitudinal succession of vertebrates from first- to third-order streams was generally characterized by addition of fish species and reduction of amphibian abundance and diversity. Diversity and taxonomic composition of assemblages were closely related to channel

gradient and stream size (Fig. 8). All fish species except cutthroat trout were restricted to sites less than 6% gradient, whereas two salamander species and non-predatory larvae of a frog (Ascaphus trueii) were the only aquatic vertebrates present above 13% gradient. The most widespread species were Dicamptodon ensatus and Salmo clarki. Dicamptodon occurred in every site and cutthroat trout occurred in all but the higher gradient, first-order sites. Rhyacotriton olympicus was rare and was restricted to small streams ($< 1 \text{ km}^2$ drainage area). Cottus beldingi was the most common sculpin, occurring in streams lower than 6% gradient. The other species of fish each occurred in only one site. (See Appendices G-J for mark-recapture data for vertebrates).

Curvilinear regression of diversity (H') on channel gradient was significant ($R^2 = .61$), but showed a single outlier (Fig. 9), representing a site on Lookout Creek (LOCC) with lower diversity than expected from the gradient of its channel. This site was in an area of localized reduced gradient on the stream's longitudinal profile (Fig. 10). Regression of H' on channel gradient with this point removed provided a significantly better fit ($R^2 = .74$). To map distributions of vertebrates relative to this irregularity in the stream's profile, I made collections of vertebrates at eight additional locations along Lookout Creek. Cottus beldingi and Salmo gairdneri were absent from site LOCC (and upstream sites), but present in downstream reaches of similar

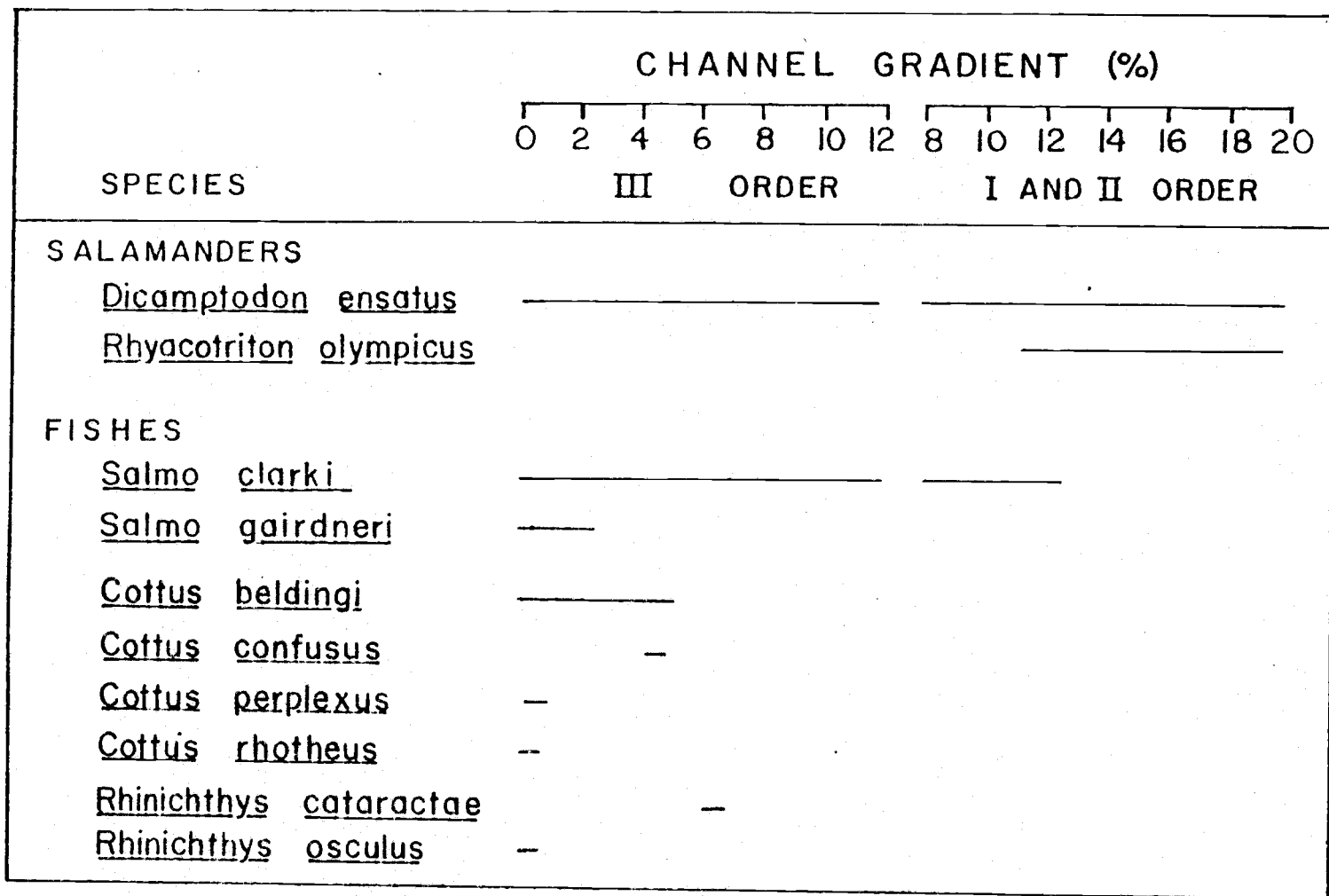


Fig. 8. Occurrence of predatory vertebrates in relation to channel gradient and stream order. Solid bar indicates range of occurrence.

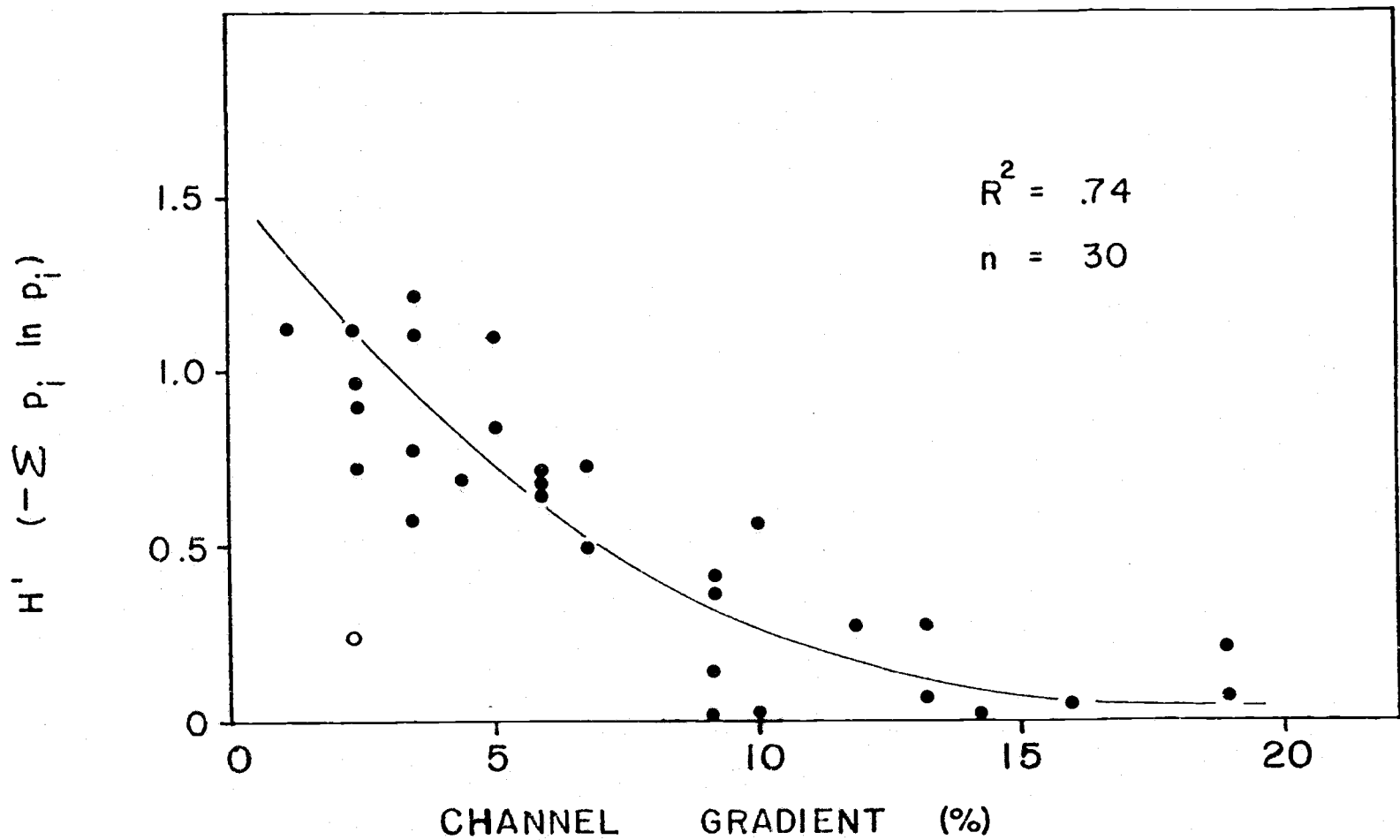


Fig. 9. Species diversity (H') of predatory vertebrates in relation to channel gradient. The outlier (open circle) was omitted for curve fitting. ($H' = 1.150 - 0.107 \text{ gradient} + 0.002 \text{ gradient}^2$).

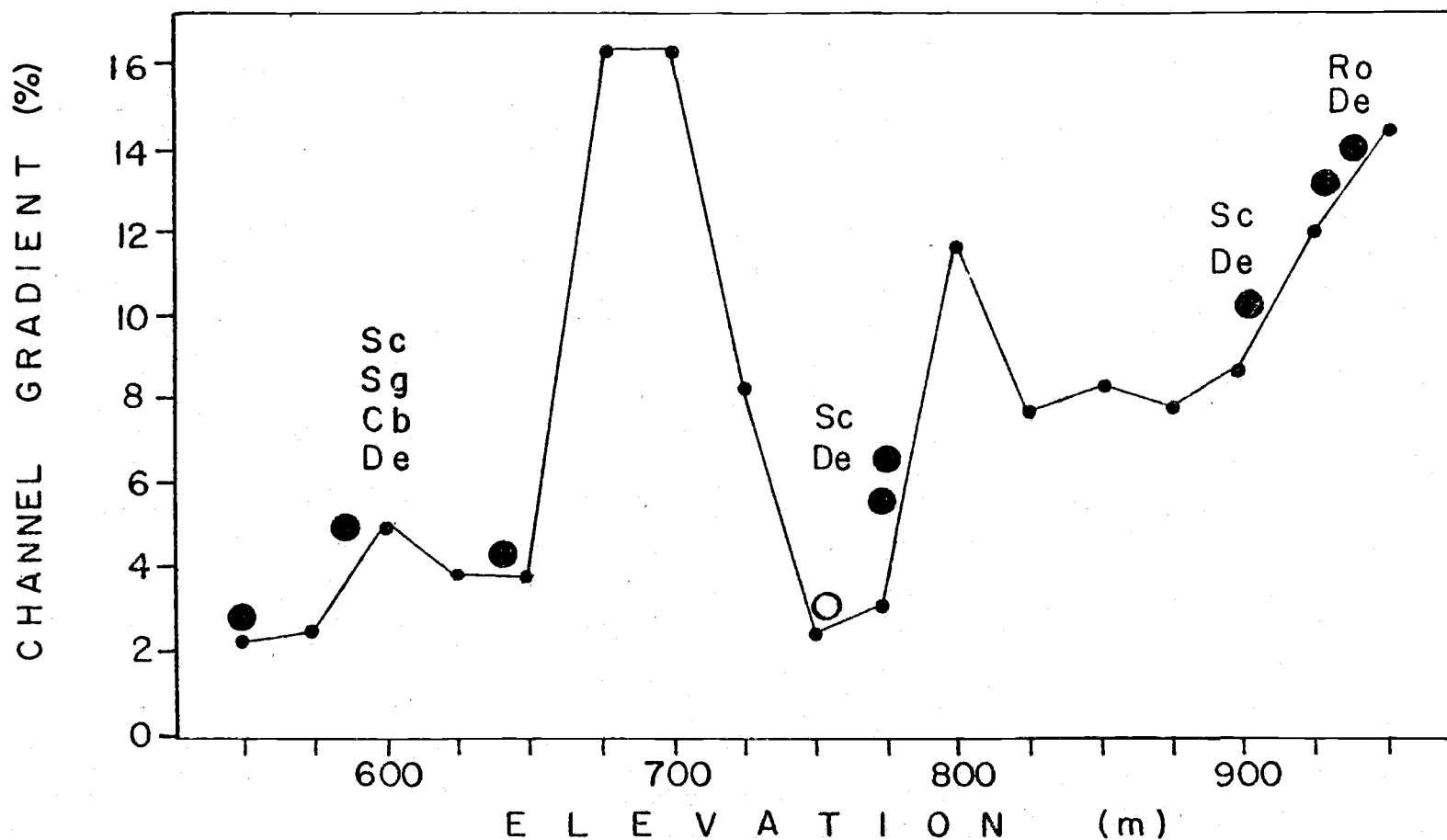


Fig. 10. Gradient of stream for each 25 m elevational increment for Lookout Creek, showing occurrence of vertebrates (Sc = Salmo clarki, Sg = S. gairdneri, Cb = Cottus beldingi, De = Dicamptodon ensatus, Ro = Rhyacotriton olympicus). Sample locations are denoted by closed circles; the site with lower than expected diversity is denoted by an open circle.

gradient. The low gradient reach of stream was probably suitable habitat that was isolated from downstream populations by the intervening high gradient reach of stream.

Relationships between total biomass of vertebrates and environmental variables may be biased somewhat because of the low diversity of vertebrates occurring in the study sites. Total biomass was more a reflection of the autecology of a few dominant species than an integrative phenomenon involving many species. Hence I examined separately relationships between the environmental variables and biomass of the dominant vertebrates, Dicamptodon and Salmo.

Salamander and Trout Biomass

The salamander Dicamptodon ensatus was the dominant predator, often making up as much as 99% of total predator biomass. The best predictor of salamander abundance was the density of large surficial crevices in the streambed (Fig. 11). Biomass ranged from 50 g/m² in streams with many large crevices to near zero in streams with mostly embedded substrate. Logging impacts on salamander biomass depended on stream slope (Fig. 12). In the high gradient (> 10%) pairs of clearcut and old-growth sites, salamander biomass was greater in the clearcut than in the upstream old-growth site, whereas the relation reversed for streams lower than 6% gradient. The difference in biomass closely tracked the

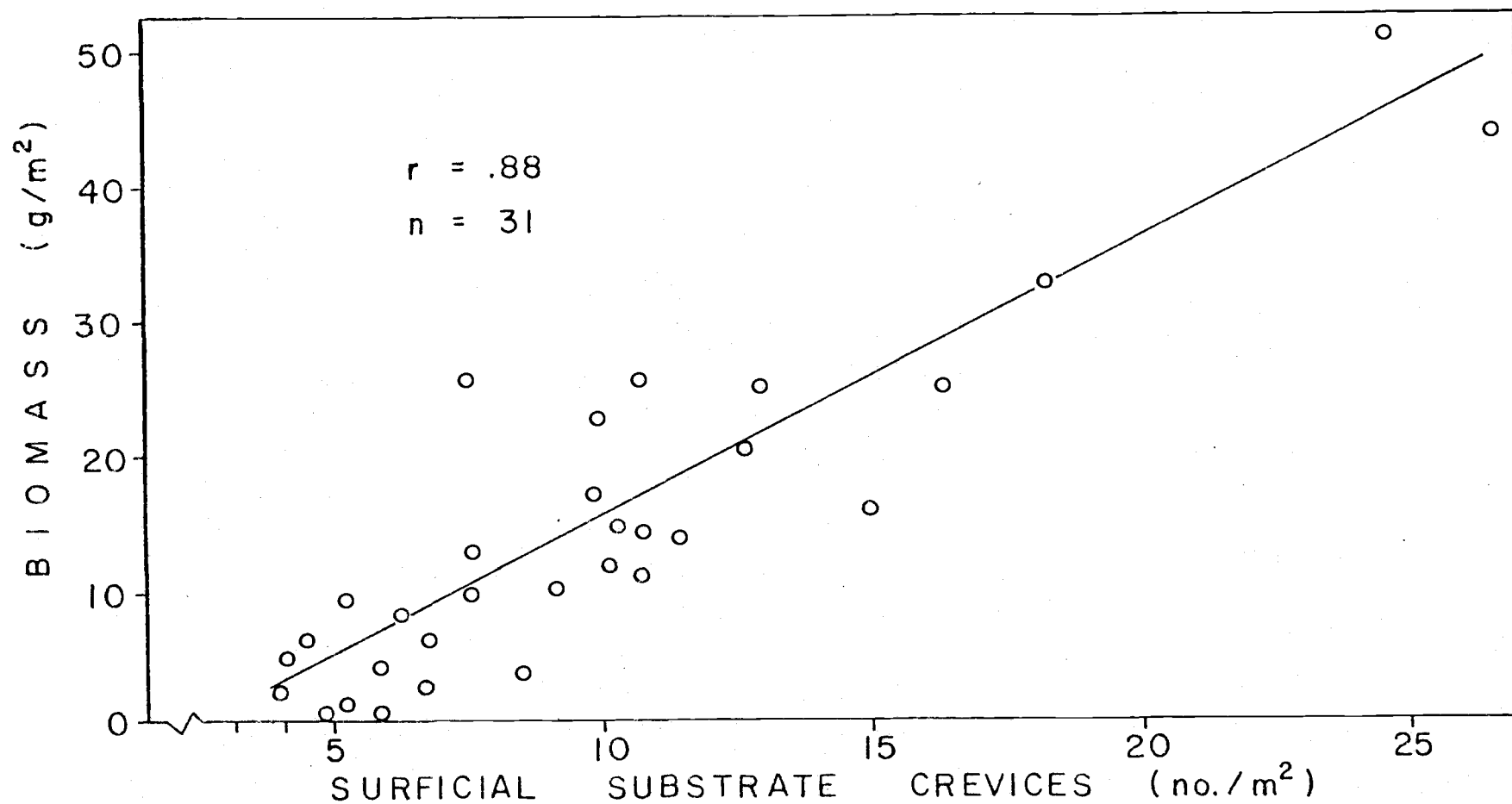


Fig. 11. Salamander biomass in relation to density of large ($> 25 \text{ cm}^3$) surficial crevices in the streambed.

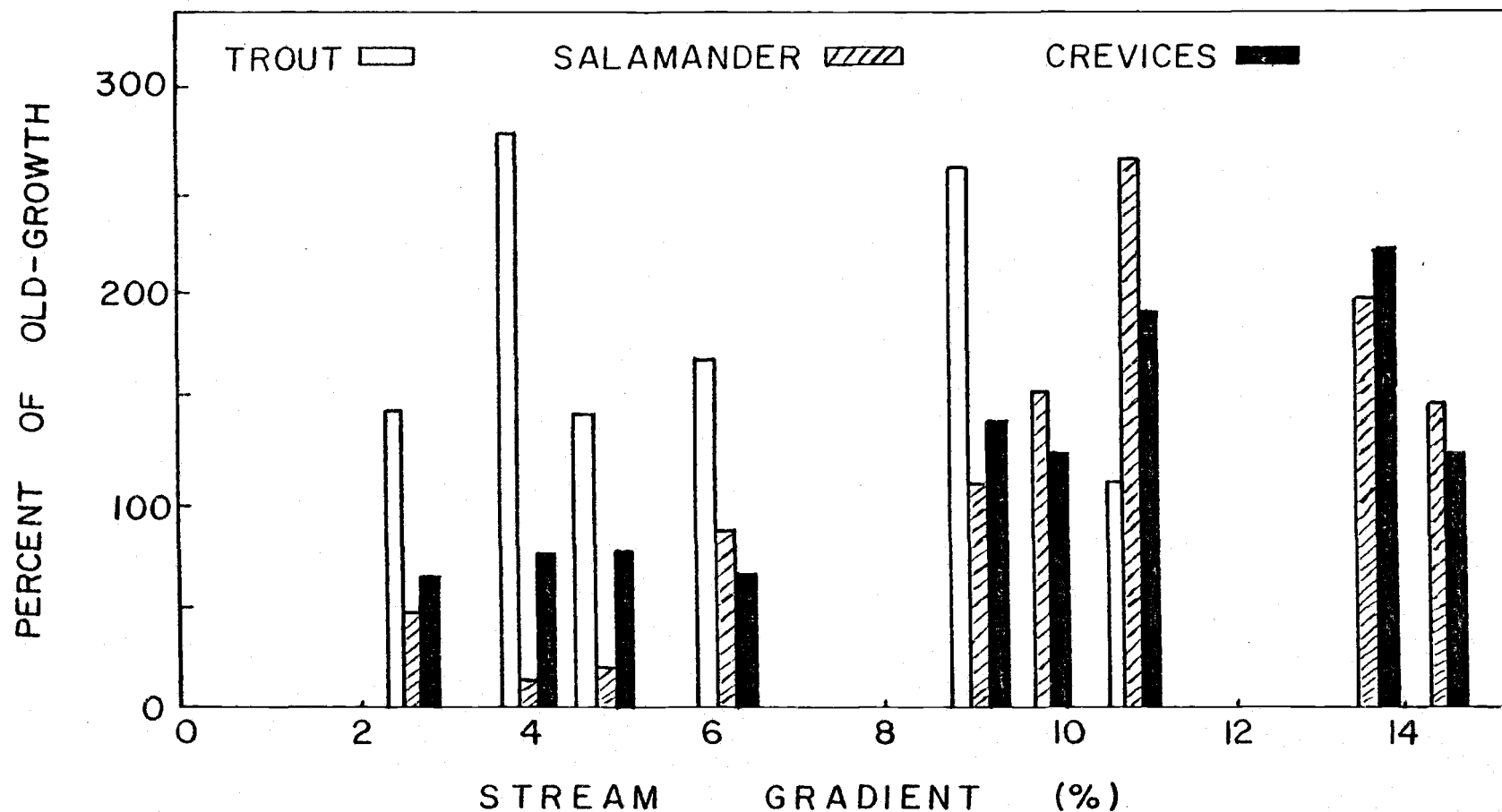


Fig. 12. Difference in biomass of trout and salamanders and density of large surficial crevices between paired clearcut and old-growth sites (CC/OG · 100) in relation to stream gradient. Trout did not occur in three of the higher gradient pairs of sites.

difference in density of substrate crevices. Salamander biomass did not differ consistently among old-growth, clearcut, and second-growth sites because sediment composition of the streambed depended more on channel slope than on recent stand history.

Biomass of trout varied independently of stream size except in the range of 1-2 km² drainage area, where abundance declined precipitously to zero in most first-order streams. Trout biomass in the larger streams (5-18 km²) depended on condition of the forest canopy, tending to be lowest in the most densely shaded sites (Fig. 13). Differences in exposure alone seemed to account for logging impacts. Clearcut sites tended to have the greatest biomass, old-growth sites had intermediate levels, and second-growth sites had the least biomass ($p < .05$, Mann-Whitney U test). In all six pairs of clearcut and old-growth sites where trout occurred, biomass was greater in the clearcut than in the old-growth complement, and differences in biomass were unrelated to sediment concentrations (Fig. 12). In contrast with salamander populations, which varied depending on condition of the streambed, trout populations depended primarily on condition of the forest canopy.

Relationships between Predatory Vertebrates and Insects

I compared biomass of vertebrates and predatory insects to examine relationships between these taxonomic segments of the

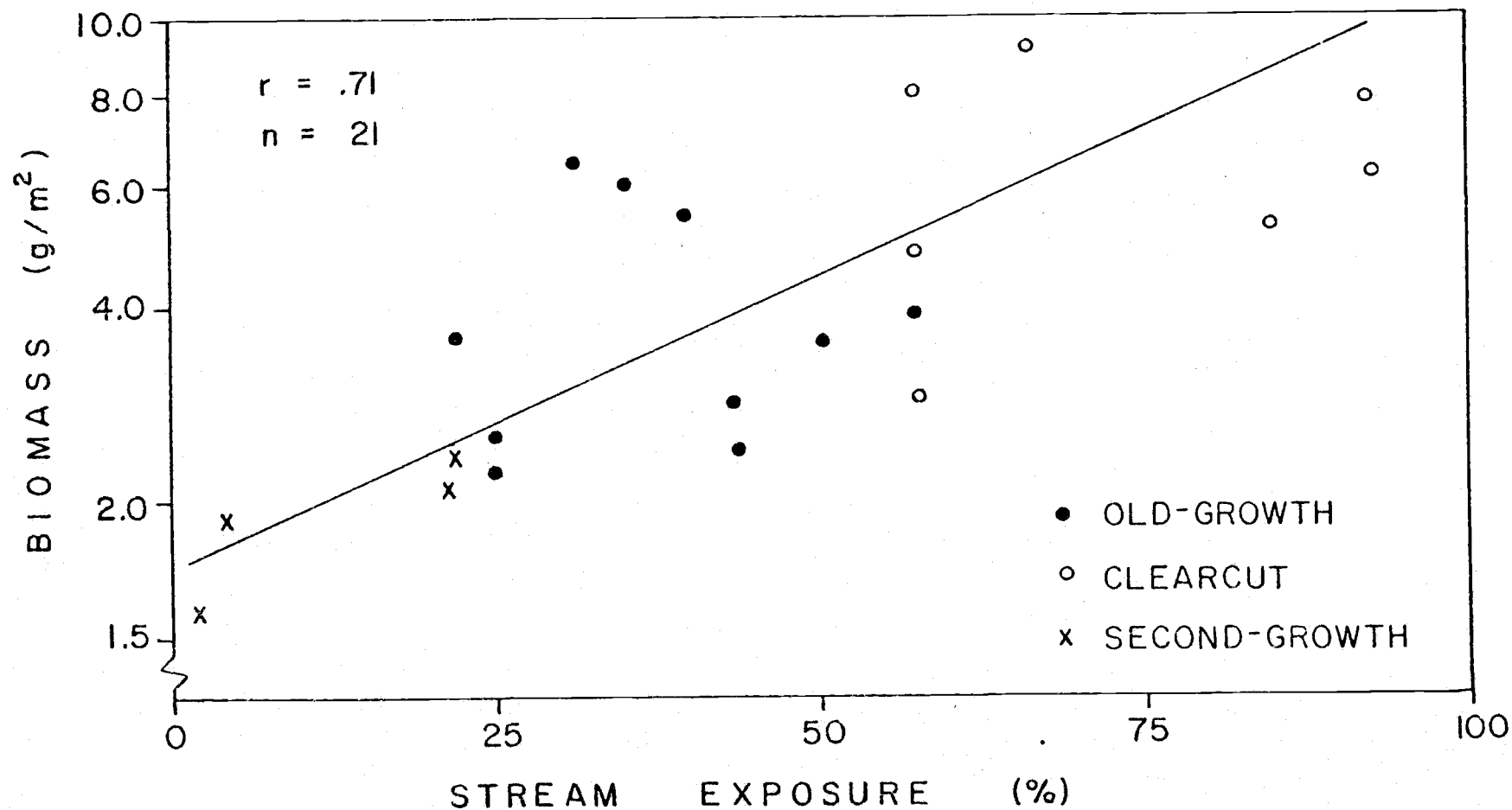


Fig. 13. Trout biomass in relation to the exposure of the stream to sunlight for third-order streams (5-18 km² drainage area). Forest stand history is indicated as old-growth (●), clearcut (○), or second-growth (x).

predator functional group. For the 26 sites where biomass of both was quantified, I found no significant ($p < .05$, two-tailed) correlation between mean biomass of predatory insects and either total vertebrate biomass or salamander biomass. Biomass of cutthroat trout, however, was positively correlated with mean total biomass of predatory insects in riffles ($r_s = .83$, $p < .01$, $n = 18$ sites $5-18 \text{ km}^2$ drainage area). Trout and riffle predators both probably depend on a third factor--their common food source. The drifting larvae and pupae that comprise much of the diet of cutthroat trout probably originate in large part as export from riffles.

Clearcutting seemed to affect both predatory vertebrates and insects similarly. Differences between paired clearcut and old-growth sites in total biomass of vertebrates and insects were positively correlated (Fig. 14). Predatory vertebrates and insects thus seemed to respond similarly to changes in streambed composition and exposure resulting from clearcutting.

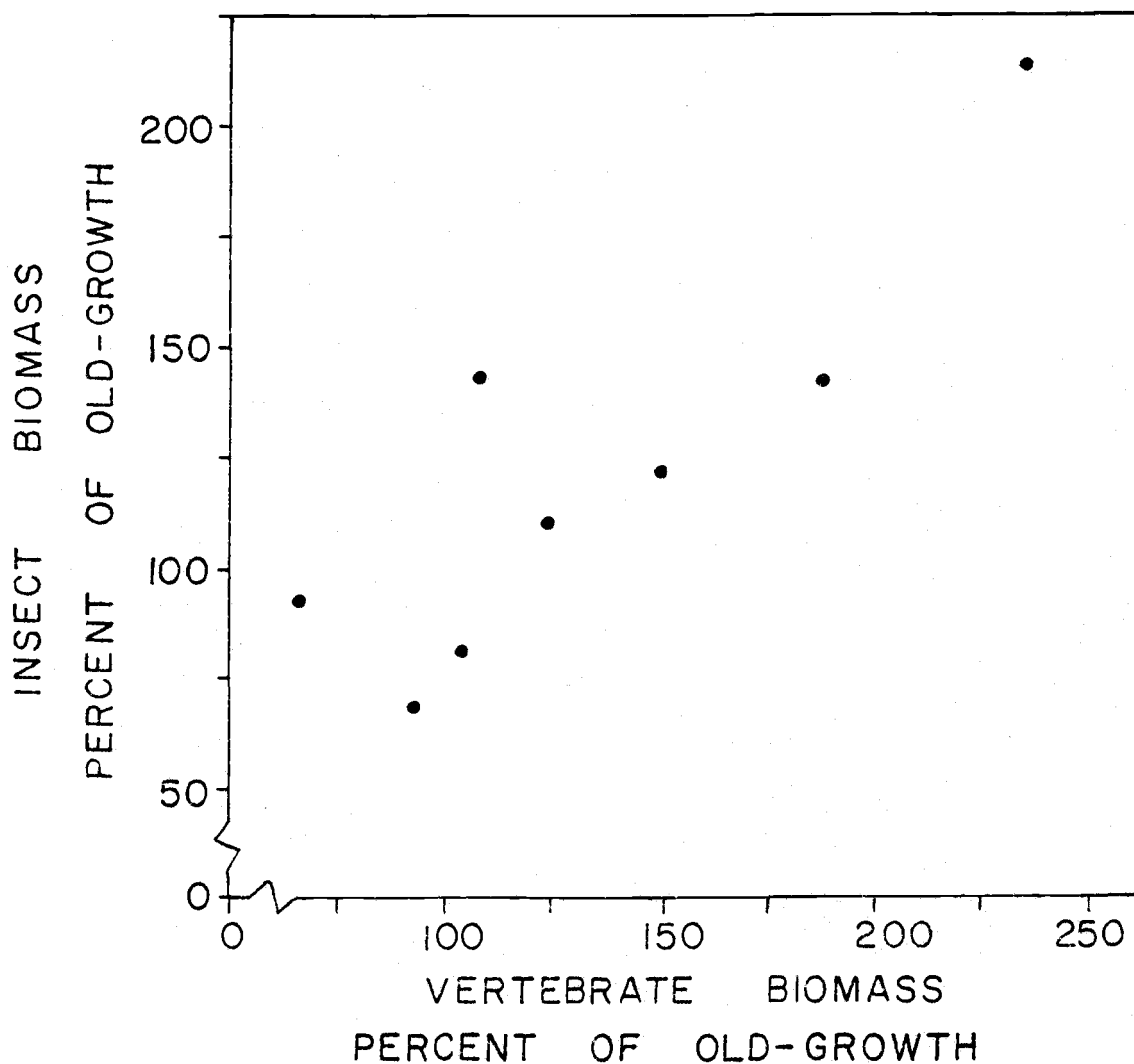


Fig. 14. Difference ($CC/OG \cdot 100$) between paired clearcut and old-growth sites in mean total biomass of predatory insects in relation to the difference in biomass of predatory vertebrates ($r_s = .83$, $p < .02$).

DISCUSSION

Patterns of community structure within and among streams reflect the community's response to different physical and trophic environments, both natural and human-caused. Pools and riffles within a stream contain different taxa, and logging disturbances have different effects in each habitat. On the spatial scale of a watershed, communities change longitudinally corresponding to longitudinal variation in geomorphic, hydrologic, and other factors. Effects of logging disturbances also vary depending on location on a stream's longitudinal profile. Logging impacts will also vary among watersheds in different geologic and climatic provinces. Results from my study should be directly applicable to other first- to third-order streams in areas with moist climate, steep, heavily forested topography, and volcanic parent material.

Patterns within Streams

The environmental factors most closely associated with differences in assemblages of predatory insects were condition of the forest canopy and of the streambed. Condition of the canopy is probably a trophic factor because it controls inputs of energy to the community. Substrate is a physical factor and acts as a template on which the trophic structure develops. These factors may vary independently, but both dense shade and concentrations of sand and gravel seemed to

produce low biomass and diversity of predators.

The interaction between sediment and shade may also be significant. Effects of sediment on stream communities may depend on the trophic status of the stream ecosystem because of differences in the relationships of heterotrophic and autotrophic processes to the substrate. Brusven and Prather (1974) recognized three patterns of microdistribution of stream insects: insects that inhabit substrate surfaces, interstices, and both. Predatory insects in heterotrophic habitat probably forage in interstices of sediment or litter where prey are shredding or collecting organic detritus. Predators in autotrophic systems probably forage both in interstices and on substrate surfaces, where prey are grazing on periphyton or filtering export from riffles. Primary production, primarily a surficial process, probably suffers less damage when coarse substrates are embedded than detrital decomposition, which is more an interstitial process. Thus fine sediment may have a smaller detrimental effect on communities in autotrophic systems than in heterotrophic systems.

A stream is heterogeneous in both trophic and physical characteristics. Fine sediment and organic detritus tend to be concentrated in zones of reduced stream velocity, and primary production varies directly with stream velocity (McIntire 1966). Different determinants for species richness of predators in pools and riffles may be explained by differences in trophic status and substrate porosity. Species

richness of predators in riffles depended on condition of the canopy, perhaps because a more open canopy stimulated production in the faster currents, leading to a greater abundance of most predator taxa there. Species richness of pool assemblages depended on substrate coarseness, perhaps because pools often contained more sand and gravel than riffles (more extreme physical conditions) and because pools were relatively heterotrophic (less response to changes in light).

Logging impacts should differ according to stream habitat. Increases in aquatic primary production after clearcutting should be greater in riffles than in pools, whereas sedimentation may be more extreme in pools than in riffles. Probably for these reasons, riffle assemblages and predator taxa preferring riffle habitat showed much greater increases in species diversity and biomass than did pool assemblages and insects. With the canopy removed, predators foraging in riffles probably received more energy from increased primary production and suffered less from sedimentation than predators foraging in pools.

The dichotomy between salamanders and trout in their response to clearcutting likewise seems to reflect differences in their foraging behavior relative to the streambed. Whereas Dicamptodon forages mainly in substrate interstices (Antonelli et al. 1972), the cutthroat trout usually forages in the water column on drifting organisms and neglects benthic prey (Brocksen et al. 1968). This may explain why

the trout was less dependent on substrate characteristics and more dependent on condition of the canopy than was the salamander.

Patterns among Streams

Both physical and trophic factors change longitudinally along streams and community structure should reflect these changes. The general increase in abundance of most predatory insect taxa from first- to third-order old-growth streams indicates increased secondary productivity as the forest canopy opens and primary production increases (Lyford and Gregory 1975). Because clearcutting removes canopy and large organic debris from small streams, it produces shifts in structure of the predator functional group of about two stream orders downstream.

Measurements of production rather than biomass, however, are required to show trends in productivity, because the contribution of a group to the food chain depends on its biomass and its rate of turnover. Both primary and secondary production have been intensively studied in Mack Creek in the H. J. Andrews Experimental Forest. Compared to an adjacent forested section, an exposed, clearcut section had about twice the total annual primary production (Gregory pers. comm.), four times the total insect emergence (Grafius 1976), and twice the production of cutthroat trout (Aho 1976). The trout diet consisted of more herbivorous insect prey in the clearcut than in the forested

section. Increased autochthonous inputs appear to supply added energy to higher trophic levels. Thus secondary production should be relatively high where shade is either naturally reduced or purposely removed.

Longitudinal distributions of fishes indicate relationships between fish populations and watershed characteristics. Studies of longitudinal succession of fishes from about first- to fourth-order streams generally have shown declines in species diversity toward the headwaters and addition of species downstream (e.g. Sheldon 1968). Species replacement seems to become more important around fourth- to fifth-order (Burton and Odum 1945).

Generally factors related to stream slope, depth, or temperature seem to produce longitudinal succession. Effects of stream slope are usually most evident in mountainous areas (e.g. Gard and Flittner 1974). Intolerance of high stream velocity and turbulence may explain the absence of most fishes from very steep streams. Upstream limits may vary. In Idaho for example, Platts (1974) found rainbow trout in streams as steep as 14% and cottids in streams as steep as 11% slope. These limits are consistently higher than I observed for these taxa in my study area. Perhaps differences in the frequency and magnitude of peak flows (Idaho receives much less precipitation than the western Cascades) allow fishes to occupy steeper streams in the Idaho Batholith than in the western Cascades.

Effects of stream size per se are probably most important in areas with low relief. In central New York, Sheldon (1968) attributed progressive additions of fish species downstream to increases in stream depth. Sheldon's steepest site had only a 3.6% slope. Factors related to both stream size or slope may be important in the same drainage system depending on the species. In my study area, slope seemed to be the overriding factor. The cutthroat trout was the only species that seemed to be restricted by stream size rather than slope.

Hydrologic variables are typically highly intercorrelated, however, making it difficult to identify critical factors when only a small number of sites are studied. I tried to obviate this by studying both high and low gradient reaches of both first- and third-order streams. Streams are patchy environments and even high gradient streams usually include areas of reduced current velocity or increased depth that appear to be suitable habitat for fish. Loss of intolerant species probably occurs during peak flows when stream energy profiles become more regular (Leopold et al. 1964), or during drought when flow is minimum. Time of sampling relative to peak or minimum flow may have a great influence on inferences drawn.

Whereas longitudinal succession of fishes has been thoroughly studied, stream salamanders have been mostly ignored. A unique feature of my study was that I quantified abundance and longitudinal

succession of both fish and salamanders. Only a few other estimates of biomass of stream salamanders exist, and these vary widely from $\approx 0.1 \text{ g/m}^2$ for three species of stream salamanders in New Hampshire (Burton and Likens 1975) to 34.3 g/m^2 for Rhyacotriton olympicus in a first-order western Cascade stream (Nussbaum and Tait 1977). This maximum value is similar to what I found for Dicamptodon, and is 2-3 times greater than that attained by the most abundant fish in my study.

Logging Impacts

The experimental design I used to assess logging impacts was unusual in that I compared adjacent logged and forested reaches at two levels of stream size and slope. Since no data were available on pre-logging conditions, I have assumed that on the average there were no differences between paired sites before logging. The main advantages of my approach were the short time required to obtain the data and the ability to infer how impacts depend on geomorphic factors. This approach should allow prediction of logging impacts in similar watersheds given information about stream size and slope.

Other effects of logging in the study area probably had less influence on the stream communities than changes in aquatic primary production and streambed sediment concentration. In Mack Creek, Aho (1976) found weekly mean temperature ranged only $0.1\text{--}1.0^\circ\text{C}$

higher in the clearcut than in the adjacent forested section. This slight increase in the usually low ambient temperature probably had little detrimental effect on the stream communities. Mack Creek clearcut, however, is a small clearcut (10 ha) and one would expect that increases in temperature will be greater where longer reaches of stream are exposed. Likewise, differences in channel morphology do not account for the observed differences in predator assemblages, for if the high biomass of trout and predatory insects in clearcut sites resulted from more extensive riffle area, then biomass should have been high also in second-growth sites. Logging impacts, then, resulted mainly from combined effects on aquatic primary production and sediment concentration.

Effects of clearcutting on primary production and sediment concentration depended on stream size and slope. Primary production in first- to third-order streams in the study area is limited by low light levels (Gregory, pers. comm.). As streams get wider, canopy opens and primary production increases (Lyford and Gregory 1975). For large, naturally open streams, canopy removal will have a relatively small effect. Debris removal exposes sediment accumulations to transport during the next peak flow (Froehlich 1975). Small, high gradient streams in clearcuts thus have reduced storage capacity for fine sediment, and introduced fine sediment will pass quickly through these areas into downstream reaches. The location of sediment

deposition depends on the competence and capacity (Leopold et al. 1964) of the stream along its longitudinal profile.

Management of large organic debris has changed during the last 20 yrs. Before about 1960 logging tended to introduce large quantities of wood debris to streams (Merrel 1951), usually in unstable configurations (Rothacher 1959). Recent management, however, tends to reduce loads of large debris by about 50% after yarding (Lammel 1972). Merchantable material is often removed from the original load that was in the channel, and cleanup tends to further reduce the stream's load of debris (Froehlich 1975). In addition, debris avalanches have occurred within the previous 10 yrs in all my larger second-growth sites (pers. comm., Dave Burwell, Rosboro Lumber Co., Springfield, Oregon, 1976; Fred Behms, private timber manager, Blue River, Oregon, 1977), and in Mack Creek clearcut (pers. comm., Fred Swanson, Dept. of Forestry, Oregon State Univ., Corvallis, Oregon, 1976). Similar events probably occurred in the other logged sites. Residual debris was probably destabilized by the logging disturbance and transported out of the channel during floods.

Recovery of the stream ecosystem after clearcutting depends on changes in forest canopy and the streambed. Elevated rates of aquatic primary production in clearcuts may be short-lived because riparian vegetation usually recovers in 10-20 yrs. Changes in the volume of large debris, channel configuration, and sediment loads

may be more important in the long term. Short harvest rotations (< 100 yrs) preclude recovery of pre-logging levels of large organic debris in streams (Swanson and Lienkaemper 1978). As a consequence, depositional zones in high gradient streams may be reduced for as long as present harvest practices and rotation periods are applied. In low gradient streams, fine sediment may increase after logging, but detrimental effects may be masked at first by increased autotrophic production. As the canopy recovers and the community shifts to a heterotrophic food base, any degradation resulting from sedimentation should become more evident.

Differences in stream gradient may explain apparent inconsistent impacts of clearcutting on stream communities. Logging impacts on trout, for example, are different in the western Cascades than in the Coast Range in Oregon, perhaps because of differences in the competence of streams and in the storage and routing of sediment through channel networks in the two geologic provinces. Parts of the Coast Range are underlain by sedimentary rock and streams in these areas are generally lower in gradient and richer in sediment than those in the western Cascades. Clearcutting in coastal watersheds without leaving a strip of vegetation along the stream increased sediment concentrations and reduced cutthroat trout populations by 40-70% (Hall and Lantz 1969, Moring and Lantz 1974, 1975). The high competence of small streams in the western Cascades, however,

reduced local sedimentation from logging; sediment was transported to stream reaches lower in the drainage network. This shift in sediment favors community development in high gradient, headwater reaches, but may depress it downstream where stream slope is lower.

Ideally one should view entire drainage networks or landscapes as ecological systems, because disturbances in headwater regions often have dramatic effects downstream. Redwood Creek drainage of northern California provides a graphic example (Janda 1977). A wave of bedload sediment derived from logging in tributary watersheds is moving through Redwood Creek, raising the level of stream bottom and local water table, and killing intolerant vegetation. Logging in the western Cascades appears to be accelerating sediment transport from small headwater streams to downstream reaches by reducing storage of sediment in high gradient stream channels and by accelerating erosion of hillslopes (Swanston and Swanson 1976). The danger is that sediment derived from a large number of first-order tributaries might overload downstream reaches. The degree of erosion and the routing of sediment through channel networks will determine long-term cumulative effects of logging on middle-order streams. Control of erosion and maintenance of natural loads of debris in small stream channels are the keys to maintaining productivity of streams throughout the drainage network.

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APPENDICES

Appendix A. Identification and location of study sites. Number and alpha code names refer to figures, tables, and appendices where sites are listed.

Site	Identification and Location
Old-growth	
1. MCOG	Tributary of McRae Cr. , 30 m upstream of CC Unit L381 ^a (R. 5 1/2 E., T. 15S., S7) ^b
2. AROG	Tributary of Mack Cr. , 30 m upstream of CC Unit L111 (R. 5 E., T. 15 S., S36)
3. WS2	Watershed 2, a tributary of Lookout Cr. (R. 5E., T. 15S., S32)
4. LSOG	Tributary of Lookout Cr. , parallel CC Unit L704C (R. 5 1/2 E., T. 15S., S32)
5. SADD	Saddle Cr. , a tributary of Mack Cr. (R. 5E., T. 15S., S36)
6. MAOG	Mack Cr. 200 m upstream of CC Unit L110 (R. 5E., T. 15S., S36)
7. MILL	Mill Cr. 50 m from McKenzie R. confluence (R. 5E., T. 16S., S18)
8. LLOG	Lookout Cr. 50 m upstream of CC Unit L703 (R. 5 1/2 E., T. 15S., S29)
9. COOG	Cook Cr. , 200 m upstream of CC Unit B421 (R. 5E., T. 15S., S7)
10. MROG	McRae Cr. 75 m upstream of CC Unit L404 (R. 5E., T. 15S., S22)
11. MTHA	Tributary of S. Fork Gate Cr. (R. 3E., T. 16S., S15)
12. WAOG	Walker Cr. 150 m upstream of CC Unit W102 (R. 5E., T. 17S., S23)
13. REBE	Rebel Cr. 100 m upstream of CC Unit R101 (R. 5E., T. 18S., S12)
14. MCRA	McRae Cr. 50 m upstream of CC Unit L504 (R. 5E., T. 15S., S27)
15. LOOG	Lookout Cr. 75 m upstream from CC Unit L701 (R. 5E., T. 15S., S25)
Clearcut	
16. MCCC	Tributary of McRae Cr. in CC Unit L381 (R. 5 1/2 E., T. 15S., S7)
17. ANCC	Tributary of Mack Cr. in CC Unit L111 (R. 5E., T. 15S., S36)
18. LSCC	Tributary of Lookout Cr. in CC Unit L704C (R. 5 1/2 E., T. 15S., S32)
19. MACC	Mack Cr. in CC Unit L110 (R. 5E., T. 15S., S32)
20. LLCC	Lookout Cr. in CC Unit L703 (R. 5 1/2 E., T. 15S., S29)
21. COCC	Cook Cr. in CC Unit B421 (R. 5E., T. 15S., S7)
22. TIDB	Tidbits Cr. in CC Unit B203 (R. 4E., T. 15S., S26)
23. MRCC	McRae Cr. in CC Unit L404 (R. 5E., T. 15S., S22)
24. WACC	Walker Cr. in CC Unit W102 (R. 5E., T. 17S., S23)
25. LOCC	Lookout Cr. in CC Unit L701 (R. 5E., T. 15S., S25)
Second-growth	
26. THER	Thermos Cr. in CC Unit B201 (R. 4E., T. 15S., S36)
27. MONA	Mona Cr. in CC Unit B222 (R. 4E., T. 16S., S1)
28. SUGA	Sugar Cr. 75 m upstream of Quartz Cr. confluence (R. 4E., T. 17S., S8)
29. CANE	Cane Cr. 50 m upstream of Quartz Cr. confluence (R. 4E., T. 17S., S8)
30. SIMM	Simmonds Cr. 100 m upstream of confluence Blue R. (R. 4E., T. 16S., S21)
31. WYCO	Wycoff Cr. 50 m upstream of Quartz Cr. confluence (R. 4E., T. 17S., S32)
Insects sampled only	
32. LOBR	Lookout Cr. 25 m upstream of Concrete Bridge (R. 5E., T. 15 S., S28)
33. SWAM	Swamp Cr. 25 m upstream of McKenzie R. confluence (R. 5E., T. 16S., S20)
Paired clearcut and old-growth sites	
AR =	AROG ANCC
MC =	MCOG MCCC
LS =	LSOG LSCC
LL =	LLOG LLCC
LO =	LOOG LOCC
MA =	MAOG MACC
MR =	MROG MRCC
WA =	WAOG WACC
CO =	COOG COCC

^a Identification code used by Willamette National Forest; ^b Range, Township, and Section.

Appendix B. Regression equations ($Y = ax^b$) relating body weight (Y) to body length (x) of individual predators from small streams in the western Cascades.

Taxon	Body length (mm)	Number	Regression Coef (b)	Y Intercept (a)	R ²
Insects: Dry Weight (mg)					
Perlidae (3 species)	4-25	80	2.69	9.07×10^{-3}	.98
<u>Alloperla</u> spp.	4-11	116	2.36	1.06×10^{-2}	.98
<u>Rhyacophila</u> (6 taxa)	4-24	108	2.13	1.48×10^{-2}	.95
<u>Orohermes crepusculus</u>	11-44	11	3.31	5.50×10^{-4}	.95
<u>Octogomphus specularis</u>	13-22	7	3.07	5.30×10^{-3}	.95
Vertebrates ^a : Wet Weight (g)					
<u>Dicamptodon ensatus</u>	25-137	35	3.02	3.50×10^{-5}	.99
<u>Cottus</u> spp. (3 species) ^b	44-122	44	3.15	6.02×10^{-6}	.91
<u>Salmo clarki</u> ^c			2.90	1.78×10^{-5}	

^a Lengths of vertebrates were measured as snout-to-vent length for salamanders, total length for sculpins, and fork length for trout.

^b Cottus beldingi, C. perplexus, and C. confusus.

^c Regression equation from Aho (1976).

Appendix C. Environmental data measured for the study sites.

Appendix C. Environmental data measured for the study sites.

Site	Stream order	Drainage area (km ²)	Mean width (m)	Mean depth (cm)	Channel gradient (%)	Surficial crevices (no./m ²)	Sand-gravel (%)	Cobble (%)	Riffle (%)	Elevation (100 m)	Shade (%)	Large organic debris (100 cm ³ /m ²)	
<u>Old Growth</u>													
1.	MCOG	I	0.3	1.0	12	14	10.9	30	16	47	12.0	90	6.5
2.	AROG	I	0.8	0.8	6	18	10.6	28	29	54	7.6	80	10.7
3.	WS2	II	0.8	1.1	9	16	8.9	28	22	65	3.6	90	7.8
4.	LSOG	I	1.0	0.8	4	9	13.3	37	23	22	10.5	90	15.2
5.	SADD	II	1.3	1.9	9	18	18.0	15	39	64	7.6	70	8.3
6.	MAOG	III	4.4	3.5	14	10	10.4	12	26	54	7.6	75	2.1
7.	MILL	III	6.2	3.5	11	3	4.0	56	6	43	3.6	60	0.1
8.	LLOG	III	7.8	3.3	20	6	10.9	33	26	50	9.3	70	10.1
9.	COOG	III	11.4	3.2	17	3	9.9	31	37	35	6.6	65	8.2
10.	MROG	III	12.4	3.6	22	5	6.6	35	18	43	6.0	80	0.9
11.	MTHA	III	12.8	4.0	12	2	6.0	36	16	79	4.0	50	0.1
12.	WAOG	III	15.0	4.4	16	3	14.7	19	30	70	6.9	70	0.0
13.	REBE	III	15.0	4.4	16	3	10.9	19	30	70	6.9	70	0.0
14.	MCRA	III	15.0	4.7	17	2	5.4	36	22	63	5.4	40	1.3
15.	LOOG	III	16.8	6.0	23	6	8.1	15	26	59	7.2	60	1.5
<u>Clearcut</u>													
16.	MCCC	I	0.5	1.5	7	13	24.3	19	44	98	12.0	5	5.9
17.	ANCC	I	0.8	0.7	7	10	11.8	16	26	74	7.6	40	0.7
18.	ISCC	II	1.3	0.9	4	9	16.3	15	37	62	10.5	30	4.2
19.	MACC	III	5.4	3.8	11	9	12.4	9	40	79	7.6	10	0.8
20.	LLCC	III	7.8	4.5	20	6	7.3	31	22	47	9.3	35	0.1
21.	COCC	III	12.4	4.0	17	2	6.6	51	19	48	6.6	10	0.2
22.	TIDB	III	12.4	3.5	20	4	7.3	24	21	41	5.7	20	4.6
23.	MRCC	III	12.9	4.0	20	3	4.9	36	22	62	6.0	40	0.0
24.	WACC	III	13.2	3.6	21	12	29.7	1	47	46	8.1	40	0.5
25.	LOCC	III	17.3	5.9	18	2	6.0	35	21	68	7.2	40	0.2
<u>Second Growth</u>													
26.	THER	II	1.0	0.5	5	13	9.9	24	28	53	4.5	100	5.6
27.	MONA	II	3.6	1.8	9	7	7.3	28	27	74	3.9	90	6.1
28.	SUGA	III	5.0	2.4	8	5	4.4	45	12	68	4.5	100	0.1
29.	CANE	III	9.6	3.6	13	2	5.4	42	22	68	3.3	80	0.1
30.	SIMM	III	9.6	4.0	13	1	6.6	28	20	77	3.3	100	0.1
31.	WYCO	III	9.8	3.3	14	7	4.0	46	24	72	4.2	80	0.1

Appendix D

ections of first- to third-order streams.

Variable

Gradient

Elevation

Percent
sand-
gravel

Crevice
density

Drainage a

-. 83**

-. 18

-. 28

. 12

Mean width

1.00

. 77**

-. 80**

. 02**

-. 69**

-. 11

-. 47

. 19

Mean depth

1.00

-. 61*

. 02

-. 36

-. 01

-. 10

-. 14

Debris volume

1.00

-. 60*

. 67**

. 22

. 36

-. 35

Percent riffle

1.00

-. 53*

-. 06

-. 48

. 52*

Channel gradient

1.00

. 26

-. 13

. 05

Elevation

1.00

-. 36

. 60*

Percent sand-gravel

1.00

-. 76**

Surficial crevice
density

1.00

*p < . 05.

**p < . 01.

Appendix E. Amount (mg/m^2) of chlorophyll a accumulated on artificial substrates after 1 month in adjacent clearcut (CC) and old-growth (OG) sites, listed in order of increasing stream size. Amounts are means of two substrates.

Site pair	Mean width (m)	CC	OG	Relative difference ^a
1	0.7	1.2	0.0	2.00
2	0.8	29.9	2.8	1.66
3	1.2	2.8	0.0	2.00
4	3.6	11.7	4.5	0.89
5	3.6	36.6	20.1	0.58
6	3.8	14.8	5.2	0.96
7	3.8	16.3	6.7	0.84
8	6.0	7.0	11.3	-0.47

^a(CC-OG)/mean.

Appendix F. Species richness, mean total biomass, and mean total density of predatory insects by habitat type and by site.

Site	Species Richness ^a		Site	Mean Total Biomass ^b		Mean Total Density ^b	
	Pools	Riffles		Pools	Riffles	Pools	Riffles
MCOG	4	6	6	104	46	184	40
AROG	6	7	8	160	274	124	168
LSOG	6	3	6	156	206	188	114
MAOG	7	5	8	342	168	176	42
MILL	4	9	10	80	90	52	94
COOG	5	5	7	86	222	54	106
MROG	5	5	7	246	186	128	114
MTHA	2	8	8	24	108	18	110
WAOG	5	7	9	70	142	126	158
REBE	7	7	9	100	564	48	104
MCRA	5	9	10	96	198	36	142
LOOG	11	8	14	700	410	476	132
LOBR	5	11	12	230	508	188	230
SWAM	1	6	6	3	91	38	66
MCCC	5	5	8	298	250	178	156
ARCC	11	9	13	214	350	250	154
LSCC	5	3	6	156	82	134	66
MACC	7	8	11	568	524	160	110
COCC	3	8	9	444	268	30	124
TIDB	5	8	10	292	290	16	100
MRCC	9	10	13	296	646	68	116
WACC	9	9	13	412	630	274	312
LOCC	8	8	11	616	832	456	214
MONA	2	5	5	236	250	34	104
SUGA	3	6	7	210	222	26	64
CANE	4	7	7	700	94	58	80
SIMM	5	5	6	462	316	72	162
WYCO	3	4	5	82	250	46	158

^aTotal number of taxa.

^bMean of three samples for habitats; Biomass = mg/m² and density = no./m².

Appendix G. Data for mark-recapture estimates of population size (\hat{N}) for salamanders (Dicamptodon ensatus) in 31 sites. $\hat{N} = M(C+1)/(R+1)$, where M = number initially marked, C = number examined for marks, and R = number recaptured.

Site	M	M	C	R	\hat{N}	Mean wet weight (g)	Biomass (g/m ²)
1.	MCOG	24	12	4	60	9.57	26.1
2.	AROG	26	22	10	54	4.85	10.5
3.	WS2	7	14	7	14	15.77	10.0
4.	LSOG	31	29	6	133	8.87	24.3
5.	SADD	26	27	5	121	10.33	32.9
6.	MAOG	53	41	6	318	8.54	14.4
7.	MILL	11	6	3	19	25.49	4.6
8.	LLOG	34	15	3	136	14.18	14.3
9.	COOG	33	23	4	158	13.84	16.8
10.	MROG	2	3	0	8	35.54	1.8
11.	MTHA	29	33	7	124	4.26	4.2
12.	WAOG	34	37	9	129	13.98	16.6
13.	REBE	14	13	3	49	19.48	10.3
14.	MCRA	12	5	1	36	39.33	9.9
15.	LOOG	5	4	0	25	20.80	3.5
16.	MCCC	24	33	5	138	11.18	51.4
17.	ANCC	25	14	8	42	11.42	13.7
18.	LSCC	29	15	3	116	7.78	24.6
19.	MACC	64	41	7	336	13.41	20.1
20.	LLCC	17	32	5	94	23.12	12.5
21.	COCC	30	35	13	77	15.28	8.5
22.	TIDB	11	12	4	29	22.99	9.5
23.	MRCC	5	1	0	10	3.16	0.2
24.	WACC	46	48	6	322	18.92	43.8
25.	LOCC	2	0	0	2	27.80	0.4
26.	THER	34	23	11	67	3.22	13.7
27.	MONA	15	11	2	60	12.84	24.8
28.	SUGA	3	3	0	12	33.66	6.6
29.	CANE	1	4	1	4	13.08	0.6
30.	SIMM	10	5	3	15	27.13	4.9
31.	WYCO	1	1	0	2	91.00	1.8

Appendix H. Data for mark-recapture estimates of population size (\hat{N}) for juvenile (0+) trout. Salmo clarki was the only trout species in 30 sites; Salmo gairdneri occurred alone in one site (SIMM). $\hat{N} = M(C+1)/(R+1)$, where M = number initially marked, C = number examined for marks, and R = number recaptured.

Site		M	C	R	\hat{N}	Mean wet weight (g)	Biomass (g/m ²)
1.	MCOG	0	0				
2.	AROG	0	0				
3.	WS2	0	0				
4.	LSOG	0	0				
5.	SADD	0	0				
6.	MAOG ^a	37	25		112	1.40	0.28
7.	MILL	37	15	4	118	1.28	1.44
8.	LLOG	9	8	1	40	1.02	0.30
9.	COOG	15	30	4	93	0.84	0.75
10.	MROG	14	24	5	58	1.61	0.56
11.	MTHA	22	20	11	38	2.02	0.60
12.	WAOG	3	0	0	3	1.60	0.07
13.	REBE	14	12	2	61	0.94	0.62
14.	MCRA	3	5	1	9	1.30	0.08
15.	LOOG ^b	16	4		21	1.36	0.24
16.	MCCC	0	0				
17.	ANCC	0	0				
18.	LSCC	10	9	4	20	1.05	0.04
19.	MACC ^a	67	43		185	1.50	0.46
20.	LLCC	17	19	7	42	1.65	0.55
21.	COCC	11	29	6	50	1.34	0.53
22.	TIDB	11	10	4	24	1.18	0.02
23.	MRCC	4	8	2	12	1.99	0.22
24.	WACC	2	0	0	2	0.82	0.02
25.	LOCC ^b	23	18		106	1.52	1.09
26.	THER	3	0	0	3	0.70	0.14
27.	MONA	7	4	2	18	1.58	0.77
28.	SUGA	16	7	4	26	1.53	0.65
29.	CANE	19	13	0	60	1.63	1.14
30.	SIMM	25	15	4	80	1.09	0.87
31.	WYCO	14	8	0	33	1.85	0.61

^a Population estimate for a 200 m section, October 1975.

^b Estimate by removal method.

Appendix 1. Data for mark-recapture estimates of population size (\hat{N}) for adult trout (I^+). Salmo clarki was the only trout species in 30 sites; Salmo gairdneri occurred alone in one site (SIMM). $\hat{N} = M(C+1)/(R+1)$, where M = number initially marked, C = number examined for marks, and R = number recaptured.

Site	M	C	R	\hat{N}	Mean wet weight (g)	Biomass (g/m ²)
1. MCOG	0	0				
2. AROG	0	0				
3. WS2	0	0				
4. LSO G	0	0				
5. SADD	0	0				
6. MAOG ^a	70	14		87	14.20	2.15
7. MILL	3	2	1	5	17.35	0.85
8. LLOG	22	15	8	39	18.74	5.40
9. COOG	27	20	16	36	18.30	4.86
10. MROG	11	14	4	33	14.57	2.76
11. MTHA	12	10	6	19	18.00	2.69
12. WAOG	3	12	2	13	14.00	2.50
13. REBE	13	14	5	33	16.25	5.77
14. MCRA	15	15	7	30	16.43	3.45
15. LOOG ^b	19	5		26	18.40	2.58
16. MCCC	0	0				
17. ANCC	0	0				
18. LSCC	3	2	2	3	14.92	0.40
19. MACC ^a	157	48		225	14.90	5.83
20. LLCC	28	27	14	52	17.49	7.22
21. COCC	23	32	13	54	17.40	7.19
22. TIDB	9	9	5	15	23.79	5.10
23. MRCC	20	25	11	43	17.10	4.30
24. WACC	1	6	0	12	32.50	2.78
25. LOCC ^b	31	13		53	18.50	6.63
26. THER	1	0	0	1	10.93	1.09
27. MONA	9	7	6	10	16.51	5.40
28. SUGA	8	3	3	8	11.60	1.52
29. CANE	2	5	1	8	16.49	1.53
30. SIMM	3	2	0	9	10.35	0.75
31. WYCO	6	10	5	11	18.92	2.08

^a Population estimate for a 200 m section, October 1975, by removal method.

^b Estimate by removal method.

Appendix J. Data for mark-recapture estimates of population size (\hat{N}) for Rhyacotriton olympicus and Cottus spp. $\hat{N} = M(C+1)/(R+1)$, where M = number initially marked, C = number examined for marks, and R = number recaptured.

Taxon	Site		M	C	R	\hat{N}	Mean wet weight (g)	Biomass (g/m ²)
<u>R. olympicus</u>	AROG		3	0	0	3	4.70	0.56
	WS2		1	0	0	1	1.12	0.15
	SADD		3	0	0	3	2.62	0.32
	MCCC		4	1	1	4	2.62	0.35
	THER		2	0	0	2	2.01	0.40
<u>C. beldingi</u> and <u>C. perplexus</u> ^a	MILL	J	11	2	0	33	1.29	0.72
		A	14	6	3	24	5.42	1.38
<u>C. beldingi</u>	MROG	J	4	6	0	30	1.93	0.33
"		A	9	8	3	22	5.09	0.64
"	MRCC	J	7	8	1	32	1.62	0.30
"		A	15	14	3	56	5.14	1.68
"	MCRA	J	37	16	4	126	1.10	0.97
"		A	19	6	3	33	3.73	1.41
"	MTHA	J	32	17	4	115	1.26	1.11
"		A	26	13	3	91	3.62	2.59
"	SUGA	J	13	3	2	17	1.79	0.50
"		A	7	2	2	7	4.39	0.50
"	CANE	J	6	3	0	24	1.42	0.40
"		A	16	8	4	29	4.30	1.35
<u>C. rhotheus</u>	SIMM	J	13	7	2	35	1.30	0.56
and <u>C. beldingi</u> ^b		A	6	5	0	36	3.74	1.13
<u>C. confusus</u>	REBE	J	6	4	1	15	1.75	0.26
"		A	21	17	6	54	12.68	7.36

J = juveniles (\leq 60 mm length).

A = adults ($>$ 60 mm length).

^a Ratio of beldingi:perplexus = 1.0

^b Ratio of rhotheus:beldingi = 10.0

Appendix K. Total biomass (g/m^2) of predatory vertebrates in paired clearcut and old-growth sections of first- to third-order streams.

Site Pair ^a	Clearcut	Old-growth	Difference
AR	14	11	3
MC	52	26	26
LS	25	24	1
LL	22	20	2
LO	8	6	2
MA	32	19	13
MR	7	6	1
WA	45	19	26
CO	16	22	-6

^aFor identification of site pairs see Appendix A.