

# Communities of aquatic insects of old-growth and clearcut coastal headwater streams of varying flow persistence<sup>1</sup>

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**Abstract:** Headwater streams, varying in flow persistence from ephemeral to intermittent to perennial, provide the tightest coupling between water and land, yet they often receive the least protection during forest management. We described communities of aquatic insects in perennial, intermittent, and ephemeral channels surrounded by old-growth forest and 4- to 8-year-old clearcuts in Clayoquot Sound, British Columbia, to determine whether temporary streams have unique aquatic communities and to examine the short-term impacts of harvesting. We measured flow persistence, stream size, canopy cover, organic detritus, and algal biomass in 19 streams. We sampled aquatic invertebrates with a combination of emergence cages and kicknet samples. Temporary and old-growth streams had more organic detritus and a higher abundance of shredders. Perennial and clearcut streams had a higher abundance of some algal grazers, but not higher algal biomass. Insect richness was similar in intermittent and perennial streams of each seral stage but lower in ephemeral streams. Intermittent streams contained four taxa not found in the other stream classes; perennial and ephemeral streams had none. Communities of aquatic insects differed between streams surrounded by clearcuts and old growth, and varied with continuity of flow.

**Résumé :** Les ruisseaux de tête de bassins hydrographiques, avec une persistance de débit qui varie d'éphémère à intermittent, puis à pérenne, constituent l'interface le plus direct entre l'eau et la terre, mais ils sont les moins bien protégés dans le cadre de l'aménagement forestier. Nous avons décrit les communautés d'insectes aquatiques dans des ruisseaux pérennes, intermittents et éphémères bordés par des forêts anciennes et des coupes à blanc de 4 à 8 ans à Clayoquot Sound, en Colombie-Britannique, pour déterminer si les ruisseaux temporaires ont des communautés aquatiques uniques et pour examiner les impacts à court terme de la coupe forestière. Nous avons mesuré la persistance du débit, la taille du ruisseau, le recouvrement de la canopée et la biomasse de débris organiques et d'algues dans 19 ruisseaux. Nous avons échantillonné les invertébrés aquatiques en combinant des échantillons provenant de cages à émergence et de filets faucheurs. Les ruisseaux temporaires en forêt ancienne contenaient plus de débris organiques et avaient une plus grande abondance de déchiqueteurs. Les ruisseaux pérennes dans des coupes à blanc avaient une plus grande abondance de certains brouteurs d'algues, mais pas une plus grande biomasse d'algues. La richesse en insectes était semblable dans les ruisseaux intermittents et pérennes de chaque stade successoral, mais plus faible dans les ruisseaux éphémères. Les ruisseaux intermittents contenaient quatre taxons exclusifs qui n'ont pas été trouvés dans les autres classes de ruisseaux; les ruisseaux pérennes et éphémères en avaient aucun. Les communautés d'insectes aquatiques diffèrent selon que les ruisseaux sont bordés par des coupes à blanc ou des forêts anciennes et elles varient selon la persistance du débit.

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## Introduction

In coastal forests, the stream network and riparian areas provide travel corridors and a diversity of habitats, in addi-

tion to supporting the flow of nutrients and water in the ecosystem (Hynes 1975; Triska et al. 1984; Gregory et al. 1991). Riparian vegetation shades streams, supplies the aquatic system with nutrients, stabilizes stream banks, and

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adds structure as trees fall (e.g., Vannote et al. 1980; Triska et al. 1982; Gregory et al. 1987; Naiman et al. 2000). Headwater streams make up nearly 85% of channel length in a catchment and provide the tightest coupling between water and land (Sidle et al. 2000; Meyer and Wallace 2001; Gomi et al. 2002).

Retention of riparian forest during harvesting is widely used to protect fish-bearing streams (Young 2000). Debate continues, however, about the value of protecting small headwater channels, and standards of protection vary among and within states and provinces (Blinn and Kilgore 2001). Protection of small streams lacking fish may be justified because of the contribution these headwater channels make to downstream environments (e.g., Wipfli and Gregovich 2002). Any changes in water, nutrients, organic matter supply, and sediment flow could accumulate downstream, impacting fish-bearing reaches (Triska et al. 1982; Culp and Davies 1983; Grant 1988). Increased knowledge about the role of small headwater streams in the landscape may promote better management decisions (Meyer and Wallace 2001).

The ubiquity of headwater streams in coastal British Columbia and uncertainty about the need to protect them creates opposing perspectives about the value of riparian reserves. From an economic perspective, a high proportion of operable timber grows adjacent to headwater streams, making large buffers costly. From an environmental protection perspective, logging of headwater riparian areas may alter unique aquatic and riparian habitat (Campbell and Doeg 1989).

Management of headwater streams is complicated by variation in flow persistence. Streams can be ephemeral (carrying storm runoff), intermittent (dry for periods, often late summer and early autumn, but with continuous flow for several months), or perennial (flowing year-round). Ephemeral and intermittent streams are sometimes called temporary or nonperennial streams (Uys and O'Keefe 1997).

The degree to which headwater channels provide a unique habitat or support a distinct subset of the aquatic fauna has not been broadly considered in the Pacific Northwest, in particular for temporary streams (except see Dieterich and Anderson 1995, 2000; Muchow and Richardson 2000; Progar and Moldenke 2002). Temporary stream invertebrates have been studied elsewhere (e.g., MacArthur and Barnes 1985; Bottorff and Knight 1988; Boulton and Lake 1988, 1992; Delucchi 1988; Delucchi and Peckarsky 1989), but not with respect to management effects. Comparisons of ephemeral and intermittent streams are rare (Jacobi and Cary 1996).

This study characterizes the community of aquatic insects in perennial, intermittent, and ephemeral headwater channels (which we refer to as flow-persistence classes), surrounded by old-growth forest or 4- to 8-year-old clearcuts (different seral stages). We examined whether streams of differing flow persistence have different stream communities and compared the short-term impacts of harvesting on streams of differing persistence. We chose aquatic insects because they constitute a large component of stream biodiversity, feed fish, and have often been used as indicators of ecosystem integrity and function (e.g., Rosenberg and Resh 1993; Resh et al. 1995). Some invertebrates have adapted to intermittent

channels (MacArthur and Barnes 1985; Delucchi and Peckarsky 1989; Dieterich and Anderson 1995).

We tested a set of predictions about the benthic community, primarily examining the relative abundance of shredder (consumers of coarse organic particles, >1 mm diameter) and grazer (consumers of algae) functional feeding groups (Cummins and Merritt 1996). We based these predictions on expected shifts from allochthonous inputs to autochthonous production associated with forest harvesting (Vannote et al. 1980; Cummins et al. 1989). We predicted that within a flow-persistence class, the effect of forest harvesting would be to cause a shift to fewer shredders and more grazers. We further predicted that nonperennial streams would have more detrital storage, narrower wetted area with greater canopy closure, and receive less light to support algal growth, thereby resulting in more shredders and fewer grazers than perennial channels. We expected nonperennial channels to have lower species richness because fewer invertebrates are capable of living in temporary channels. Finally, we predicted an interaction between flow persistence and seral stage, such that there would be disproportionate effects of flow regime and harvesting on shredders and grazers. This last prediction comes from the observation that the more ephemeral a channel is in terms of its flow, the narrower it is and the greater the influence of overhanging riparian vegetation, even in recent clearcut sites. We tested these predictions using a set of small streams on the Pacific coast of Vancouver Island, Canada.

## Methods

### Study sites

The study took place on the west coast of Vancouver Island, British Columbia, Canada (49°N, 125°30'W), around Clayoquot and Barkley sounds. Clayoquot Sound is part of a UNESCO Biosphere Reserve. The region has a wet hypermaritime climate, with about 3100 mm of precipitation annually at the coast, mostly as rain, and up to 6000 mm against the coastal mountains. Stream levels vary considerably because daily rainfalls are often over 10 mm, with extreme events reaching 100 mm/day. Summers are mild (Tofino Airport 1985–1994, July: daily temperature  $14.6 \pm 0.8^\circ\text{C}$  (mean  $\pm$  SD), rainfall  $46.9 \pm 36.3$  mm; August: daily temperature  $15.1 \pm 0.6^\circ\text{C}$ , rainfall  $81.9 \pm 103.2$  mm), and some small streams stop flowing in mid to late summer. The terrain is extremely rugged. Forests are coniferous, dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), Sitka spruce (*Picea sitchensis* (Bong.) Carrière), and amabilis fir (*Abies amabilis* (Dougl. ex Loud.)). On the outer coast of Vancouver Island, fire-return intervals of 3000+ years (Gavin et al. 1997) lead to landscapes dominated by forests over 300 years old; forest structure and microclimate are determined by small-scale gap dynamics (Lertzman et al. 1996).

In 1996, we surveyed 85 headwater streams from five watersheds in Clayoquot and Barkley sounds, looking for streams of different flow-persistence class within different seral stage categories. We classified all potential study streams by seral stage (old growth or clearcut) and flow-persistence class (perennial, intermittent, or ephemeral). To

be included, the study section of a stream had to show evidence of water flow, be undisturbed by roads or forest harvesting further upstream, and not bear fish (i.e., above natural barriers to fish movement).

Three watersheds, Marion Creek, Tofino Creek, and Toquaht River, each had at least a complete set of six accessible streams, and from the potential pool of streams in each watershed, we randomly selected one perennial, one intermittent, and one ephemeral study channel in each seral stage (i.e., six streams per watershed). Old-growth stands were all unmanaged and over 300 years old; young stands had been clearcut harvested to the stream bank 4–8 years prior to the study. It was very difficult to find intermittent streams in clearcuts, as channels appeared either mostly dry or perennially flowing. We noted that very small streams in old growth supported flowing water, whereas the same-sized channel in clearcuts would often have no perceptible flow.

### Physical and biological characteristics of streams

From digital maps we calculated catchment area (to indicate stream size), elevation, and change in elevation over the catchment (to indicate drainage speed) for each stream. During site visits through the summer (biweekly in 1996 and weekly in 1997), we noted whether or not streams were flowing to confirm our classification of streams. We calculated persistence as the proportion of visits with flow and used the mean proportion from 1996 and 1997 for analysis.

We measured a number of physical and biological characteristics of the streams along a randomly chosen 60-m length of each (Table 1). To calculate mean cross-sectional area, we measured bank-full width and stream depth at six transects along the sampling reach. We used a clinometer to measure the slope of the stream channel at each transect and calculated mean slope for the reach. As an index of maximum flow, we measured the intermediate axis of the five estimated largest moveable (by high streamflow) substrate stones within 1 m of each transect and calculated mean size for the reach. We estimated relative maximum flow velocity from reach slope and substrate size.

To estimate both relative solar energy to streams and vegetation available for organic input into streams, we measured canopy cover at six randomly selected riffles along the 60-m sampling reach. From the centre of each riffle, we measured canopy cover in three directions, based on the sun's position at midmorning, midday, and midafternoon (i.e., facing 115° at an angle of 45° above a horizontal plane, facing 180° at an angle of 60°, facing 245° at an angle of 45°; calculated from data at Web site <http://www.susdesign.com/sunangle>). We used a post with a tiltable arm attached at 1.5 m, peering at a mounted grid through a tube, and counting the number of grid squares covered.

We measured the amounts of organic matter from sediment samples collected from six riffles and six pools, randomly chosen within each study section. At each site, one person held a "D-net" (0.3 × 0.3 × 0.6 m; 363-µm mesh) just downstream of a second person, who stirred an area 0.3 × 0.3 m to a depth of 0.2 m with a three-pronged trowel and by hand. In riffles, we disturbed the sediment until the water ran clear; in pools we stirred for 4 min and had to sweep particles into the net. Organic matter was scrubbed off any rocks swept into the net. Each sample was placed in a la-

belled ziplock bag and taken for processing. Several ephemeral streams were not flowing during sampling. In these streams, we removed by hand all organic matter from a 0.3 × 0.3 m area to a depth of 0.2 m from the dry stream bed. We rinsed the samples through the D-nets in the laboratory to standardize with the wet-collected samples by eliminating particles small enough to pass through the net. Each sample was washed through a set of sieves in the laboratory, and the material retained on the 1-cm, 4.75-mm, 1-mm, or 63-µm sieves was dried for 24 h, then weighed, reduced to ash (550°C for at least 2 h), and reweighed to give ash-free dry mass.

We measured the relative amounts of periphytic organic matter by taking samples of periphyton from one rock collected from each of six randomly chosen riffles, for streams that had surface water (none from ephemeral streams). We randomly selected a rock that met particular criteria: hand-sized, submerged, flat-topped rocks on the top of the substrate, exposed to the sun. We scrubbed the exposed surface of the rock with a toothbrush and vacuum filtered the sample on to glass-fibre filter paper. We kept each sample dark and cool until it could be frozen before processing. We processed the filter papers to determine chlorophyll-*a* content following the method of Strickland and Parsons (1972). We measured the surface area of the rock exposed to light by covering the rock with wax paper and tracing the shape of the scrubbed area. In the laboratory, we transferred these tracings on to aluminium foil and weighed each piece. We compared this mass with the mass of a standard unit of foil and used the ratio to convert mass into surface area.

### Aquatic insect sampling

In 1996, we tested and refined two sampling techniques: emergence traps for collecting emerging adults and kicknet (D-net described above) sampling for collecting larvae. We collected invertebrates for this study from July to September 1997 using both techniques. We secured emergence traps over two randomly selected riffles within the study section of each stream and trapped emerging adults weekly for a total of 10–18 samples per stream (some samples were lost because of storm flows or bears). Emergence traps consisted of a 0.5 × 0.5 m floating Styrofoam base with a pyramid of fine mesh "no-see-um" netting on top. A Plexiglas container and plastic trap bottle containing propylene glycol were mounted at the top of the pyramid (trap design modified from Merritt et al. 1996). Emergence traps allowed collection of insects even during periods of no surface flow.

We used kicknets to sample benthic invertebrates from gravel- and cobble-dominated riffles in flowing streams every 2 weeks over 4–8 weeks (we could not sample dry streams, particularly the ephemeral streams, using kicknet sampling). We collected samples from eight separate riffles, moving upstream at least 5 m to each new riffle. One person disturbed the bottom of the stream by stirring up rocks and sediment for 2 min, while a second person held a D-net downstream to collect invertebrates and sediment. If fewer than 100 invertebrates were collected based on a rapid visual estimate, an additional sample was collected from a different area of the same riffle, and the two samples were combined (Plafkin et al. 1989). We recorded the length and width of

**Table 1.** Biophysical parameters for perennial, intermittent, and ephemeral streams surrounded by old-growth forest (OG) or by 4- to 8-year-old clearcuts (CC).

Measurement	Seral stage	Stream persistence class			Seral stage, $F_{[1,13]}$	Stream persistence, $F_{[2,13]}$	Interaction, $F_{[2,13]}$
		Perennial	Intermittent	Ephemeral			
Persistence (% visits with flow)	CC	1±0	0.90±0.06	0.13±0.05	3.5ns	120***	4.1*
	OG	1±0	0.64±0.08	0.15±0.06			
Catchment area (ha)	CC	160±44	35±14	30±26	1.7ns	10.6**	0.3ns
	OG	275±155	10±3	5±3			
Elevation (m)	CC	320±167	260±110	333±168	0.02ns	0.1ns	0.2ns
	OG	210±72	360±170	307±159			
Change in elevation (m)	CC	1020±80	553±74	520±232	3.6ns	15.8***	0.4ns
	OG	950±87	347±112	240±69			
Cross-sectional area (m <sup>2</sup> )	CC	4.3±1.4	1.6±0.6	0.5±0.3	3.2ns	7.5**	0.1ns
	OG	3.8±2.4	0.5±0.3	0.3±0.2			
Substrate size (m)	CC	0.09±0.004	0.08±0.01	0.02±0.01	1.7ns	32.0***	3.1ns
	OG	0.08±0.01	0.05±0.01	0.03±0.01			
Reach slope (%)	CC	8.0±1.2	15.0±1.5	16.7±5.9	1.2ns	1.8ns	0.1ns
	OG	13.5±6.5	17.0±2.6	21.3±3.0			
Pool organic matter (g AFDM)	CC	87±58	88±44	216±98	4.4*	1.3ns	0.4ns
	OG	216±54	287±189	258±55			
Riffle organic matter (g AFDM)	CC	98±21	241±101	168±59	0.4ns	0.2ns	1.6ns
	OG	246±105 <sup>a</sup>	168±28	201±67			
Cover (%)	CC	5±1	1±1	11±6	148***	0.9ns	1.8ns
	OG	67±11	83±4	81±4			
Algae (µg chl <i>a</i> /m <sup>2</sup> of rock)	CC	0.029±0.004	0.073±0.046	0.41 <sup>b</sup>	0.04ns	0.7ns	1.5ns
	OG	0.213±0.063	0.17±0.078	0.12±0.007 <sup>c</sup>			

**Note:** Means and standard errors are calculated from raw data; analyses are based on appropriate transformations;  $n = 3$  for each comparison, except  $n = 4$  for old-growth perennial streams. ns, not significant ( $P > 0.05$ ); \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ . AFDM, ash-free dry mass.

<sup>a</sup> $n = 3$ .

<sup>b</sup> $n = 1$ .

<sup>c</sup> $n = 2$ .

substrate disturbed to calculate density of invertebrates per riffle.

We sorted samples under a microscope in the laboratory, identified all insects to family or genus where possible, and counted the number of individuals per taxon in each sample. Our density estimates were based on six randomly chosen samples out of the eight collected from each stream on each of two dates (13–16 August and 28 August – 5 September). Samples from other dates were not used because they did not include all 18 streams.

### Data analysis

We transformed data prior to analysis to improve normality, using either log or arcsine square root transformations as appropriate.

To examine stream characteristics, we used two-way analyses of variance for each variable, with seral stage (old growth and clearcut) and persistence class (ephemeral, intermittent, and perennial) as factors, blocked by watershed (we removed watershed from the model in most cases). We also used one-way analyses of variance and regression analyses to elucidate interesting patterns. We combined correlated physical characteristics using principal components analysis (separate analyses for each insect collection method because kicknet samples do not include the ephemeral streams).

For kicknet samples, we redesignated the original old-growth perennial stream in Tofino Creek as intermittent, because water flow, though present, was very low in August 1996. In 1997, we selected a new, larger old-growth perennial stream more comparable to the clearcut perennial stream in the same watershed. This modification means that we sampled invertebrates from a total of 19 streams, and that the two sampling techniques used a slightly different set of streams: for emergence trap sampling 18 streams as originally designated; for kicknet sampling 12 streams (no ephemerals) with a different old-growth perennial stream in the Tofino Creek watershed.

We combined data from both techniques over all sampling periods to compile a list of families and genera and to examine patterns in taxonomic richness within seral stage and flow-persistence classes. We used two-way analyses of variance to examine patterns of richness by order among stream classes, and performed post-hoc Bonferroni-corrected pairwise comparisons or orthogonal contrasts to separate the three stream persistence classes. We looked at the presence or absence of each genus or family in each stream by seral stage as an indicator of changes attributable to harvesting. We noted taxa that were found in at least two more streams of one seral stage than in the other (out of nine streams per seral stage) and totalled the number found in at least two more old-growth or two more clearcut streams. Similarly, we

looked at the presence or absence of each taxon in each stream by persistence class as an indicator of tolerance for different persistence. We noted taxa that were found in at least two more streams of a particular persistence class than in either of the other classes (out of six streams per class) and totalled the number found in at least two more of each persistence class. We used a log likelihood ratio test to compare the results with a numerically maximized multinomial likelihood calculation based on underlying binomial processes for each stream.

For analyses of absolute and relative abundance, we used a shorter sampling period. We used only data where we were able to collect invertebrates from all the streams within the same week ( $n = 2$  weeks for kicknet sampling described above, and 5 weeks for emergence trap sampling), and because the different techniques captured different sets and abundances of invertebrates, we analysed data from the two sampling techniques separately. We focussed analysis on Ephemeroptera, Plecoptera, and Trichoptera, because they are widely considered to be sensitive as indicators and are relatively larger and easier to identify than Diptera. Because this study had a strong community involvement component, and because keys beyond genus are rare for most aquatic invertebrates, identification to lower taxonomic levels was not attempted. We assigned each genus and family to a functional feeding group after Merritt and Cummins (1996).

We tested for patterns in relative and absolute abundance of functional feeding groups with respect to seral stage, stream persistence, and other stream characteristics. Again, we used two-way analyses of variance, with seral stage and stream persistence as independent variables, initially, and then probed for patterns with other characteristics.

To examine patterns in individual family abundance, we ran six different  $F$  tests on each insect family, using seral stage and persistence class, combined sequentially with continuous variables of stream size (principal component factor including physical stream characteristics), organic matter (particles up to 4.75 mm), canopy cover (above 1.5 m), and chlorophyll  $a$ . Sample sizes prevented analysis of a complete statistical model, so we used models with a single independent variable to look for patterns within individual families and compared the numbers of positive tests (based on a priori predictions) against the expected number to assess significance. Of the six variables, only persistence and size were significantly correlated with each other ( $P = 0.08$ ). We compared the number of tests matching a priori predictions with the number expected by chance (e.g., 15% at  $P = 0.15$ ) using a log likelihood ratio test.

Finally, to look for associations between the insect assemblages (abundant families:  $\geq 1\%$  of the total and present in at least 10% of the streams) and the biophysical measures taken at each site, we used a direct gradient analysis, canonical correspondence analysis (CANOCO version 4.01).

## Results

### Physical and biological characteristics of streams

Physical characteristics varied among stream persistence classes and between seral stages (Table 1). Except for canopy cover and amount of pool organic matter, both a consequence of clear-cutting, most physical characteristics were

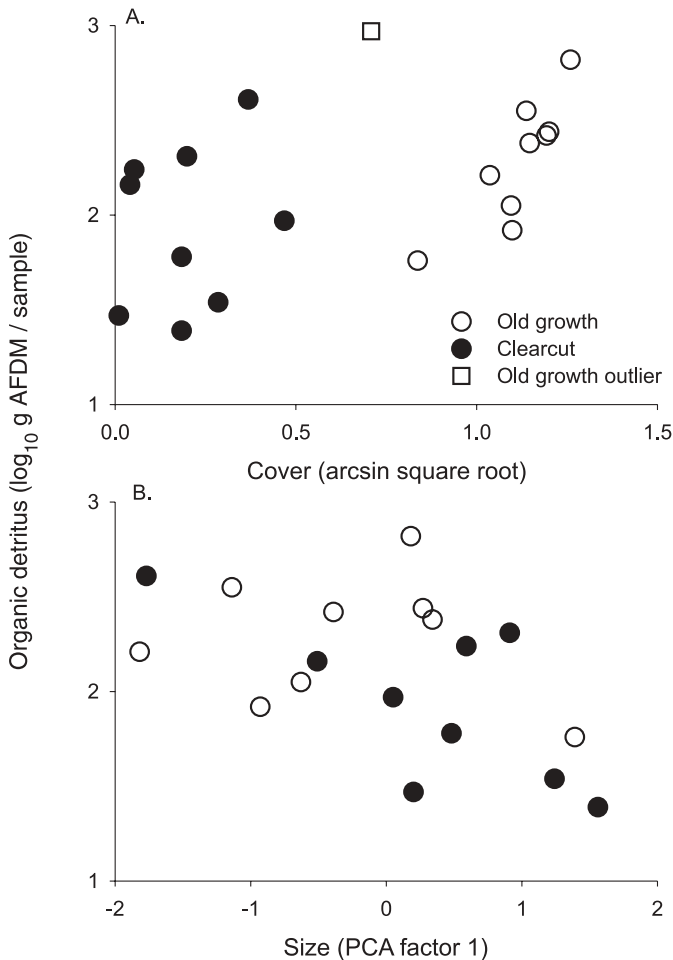
similar between streams of old growth and clearcut (Table 1). Although intermittent streams in old growth persisted for an intermediate period between ephemeral and perennial streams, intermittent streams in clearcuts were larger and flowed almost all summer (note significant interaction term), because truly intermittent streams in clearcuts were harder to find. Catchment area, change in elevation over the catchment, stream cross-sectional area, and largest moveable substrate size were all related to stream persistence class, in the order perennial > intermittent > ephemeral. Less persistent streams tended to be steeper, but not significantly. Stream persistence class did not vary by elevation.

In the principal components analysis (PCA), catchment area, change in elevation, bank-full cross-sectional area, and substrate size all loaded strongly and positively, and reach slope loaded strongly and negatively, on the first factor (capturing 57 or 65% of the variation for kicknet or emergence samples, respectively). Together, these parameters represent stream size and flow volume. The second factor represented elevation and captured a further 18 or 22% of the variation. The composite measure of stream size (first factor) correlated strongly with stream persistence class ( $r = 0.8$ ,  $P < 0.01$ ), but did not show differences between clearcut and old-growth intermittent streams. Hence, in analyses of biological factors relating to stream type or size, we used both the PCA size factor and our a priori stream classes as independent variables.

Streams in old growth had significantly greater canopy cover than streams in 4- to 8-year-old clearcuts (Table 1). We did not detect any influence of stream persistence class within either seral stage, although the two widest old-growth perennial streams (8.3 and 17.8 m) had less cover (42–55%) than the other, narrower (0.5–5.0 m) old-growth streams (74–91%). For small headwater streams in old growth, differences in width (at least from 0.5–5 m) seem insufficient to influence shading by riparian vegetation.

All three small fractions of organic detritus (0.063–4.75 mm) showed similar results; thus we combined them for analysis. Streams surrounded by old growth had greater detrital biomass settled in pools than did streams in clearcuts ( $F_{[1,15]} = 3.8$ ,  $P = 0.07$ ; Table 1). The amount of small organic particles in pools tended to increase with increasing cover, particularly in old growth, except for one outlying stream (the large, relatively flat old-growth perennial stream included in kicknet, but not emergence, samples; Fig. 1). Although we detected no influence of stream persistence class, larger streams, particularly in clearcut stands, tended to have less organic matter accumulated in pools ( $F_{[1,15]} = 3.5$ ,  $P = 0.08$ ; Fig. 1). The relationship between organic matter in riffles and stream type showed no obvious trends with either seral stage or stream persistence class. There was indication of an interaction between seral stage and size, with organic matter increasing with stream size in old growth and decreasing with stream size in clearcuts (interaction,  $F_{[1,15]} = 3.7$ ,  $P = 0.07$ ). In both pools and riffles, more organic matter had settled in steeper streams (pools: log organic matter =  $1.7 + 0.03(\text{reach slope})$ ,  $F_{[1,17]} = 6.4$ ,  $P = 0.02$ ; riffles: log organic matter =  $1.8 + 0.03(\text{slope})$ ,  $F_{[1,16]} = 15.1$ ,  $P = 0.001$ ). The steeper streams had step-pool profiles defined by debris dams, so that the local gradient was often gentler, with a bigger impact on detrital retention.

**Fig. 1.** Organic detritus in pool sediment of streams surrounded by old growth and 4- to 8-year-old clearcuts (A) with varying levels of canopy cover and (B) of varying size. The open square in Fig. 1A represents the outlying old-growth stream included in kicknet but not in emergence data. AFDM, ash-free dry mass.



Contrary to our predictions, we detected no clear trends in algal biomass relative to either seral stage or stream persistence class (Table 1). Indeed, excluding ephemeral streams, there was significantly more algae in old-growth streams ( $F_{[1,9]} = 6.2$ ,  $P = 0.03$ ), and in clearcuts, algal biomass tended to be higher in streams with lower flow persistence ( $F_{[2,4]} = 4.5$ ,  $P = 0.09$ ). Biomass of algae varied among watersheds.

### Invertebrate richness

From 19 headwater streams, we collected 39 families of aquatic insects, representing six orders (Table 2). Old-growth and clearcut streams contained similar mean numbers of families within each order, except Megaloptera (Table 3). The Corydalidae (Megaloptera) were collected more often in old-growth than clearcut streams, and more often in intermittent streams. Ephemeral streams contained fewer families of Ephemeroptera, Plecoptera, Trichoptera, and Coleoptera than intermittent or perennial streams. In contrast, ephemeral and intermittent streams tended to be richer in Diptera (some Diptera taxa collected were primarily ter-

restrial, see Table 2). We found five families or genera in at least two more old-growth than clearcut streams, and eight taxa in at least two more clearcut than old-growth streams (Table 2;  $P > 0.5$ , log likelihood ratio test). One Dipteran family, Dixidae, was found only in old-growth streams; Perlidae and *Hydropsyche* were found only in clearcut streams.

Four taxa were present in at least two more perennial than intermittent or ephemeral streams, nine taxa were present in at least two more intermittent than ephemeral or perennial streams, and no taxa were present in more ephemeral streams (Table 2;  $G = 14.0$ ,  $P < 0.001$ , log likelihood ratio test). Of the remaining taxa, 16 were present most often in both perennial and intermittent streams, and four Diptera (three primarily terrestrial) were present most often in intermittent and ephemeral streams. Of the nine taxa present in more intermittent streams, four were found only in intermittent streams in our study (Perlidae, *Hydropsyche*, *Wormaldia*, Elmidae) and might be considered specialists, and another three were found in only one stream other than intermittent channels. Conversely, of the four taxa present in more perennial streams, none were only found in perennial streams, and one was found in only one other stream.

### Patterns in functional feeding groups

As stream persistence decreased, aquatic insect communities became increasingly dominated by shredders in both clearcuts and old growth (Figs. 2 and 3). This dominance arose from two factors. First, the abundance of other functional feeding groups declined with decreasing stream persistence (scrapers, collector-filterers, and predators decreased, all  $F_{[2,12]} > 4.7$ ,  $P < 0.03$ ), with some groups (e.g., scrapers and piercers) becoming extremely rare in ephemeral streams (significant patterns in emergence data only; Table 4). Relative predator abundance changed differently with stream persistence between treatments (interaction  $F_{[2,12]} = 5.4$ ,  $P = 0.02$ ). Second, in old-growth emergence samples and in clearcut and old-growth benthic samples, the absolute abundance of shredders increased with decreasing stream persistence (Table 4). In samples of adults from clearcuts, the absolute number of shredders decreased with decreasing stream persistence, but they still dominated the community.

Shredders were more abundant in old-growth than in clearcut emergence samples (Table 4). Larval sampling revealed a similar trend ( $F_{[1,6]} = 3.5$ ,  $P = 0.1$ ). The trend for increasing proportions of shredders with decreasing stream persistence differed between old-growth and clearcut streams; the proportion of shredders increased more from perennial to intermittent streams in old growth than in clearcuts (interaction  $F_{[2,6]} = 3.8$ ,  $P = 0.08$ , Figs. 2 and 3). Recall that in old growth, intermittent streams were intermediate in persistence, while in clearcuts, they more closely resembled perennial streams.

The relationship between relative shredder abundance and biophysical stream characteristics varied between seral stages. In old growth, shredder abundance increased with increased cover (emergence:  $F_{[1,7]} = 11.9$ ,  $P = 0.03$ ; kicknet:  $F_{[1,4]} = 2.6$ ,  $P = 0.15$ ), but was not related to organic detritus (emergence:  $F_{[1,7]} = 0.8$ ,  $P = 0.4$ ; kicknet:  $F_{[1,4]} = 0$ ,  $P = 1$ ). In clearcuts, shredder abundance increased with increased

**Table 2.** Aquatic insect taxa collected from perennial, intermittent, and ephemeral headwater streams in old-growth and clearcut stands.

Taxa <sup>a</sup>	Functional feeding group <sup>b</sup>	Stream class and seral stage <sup>c</sup>					
		CC/P	CC/I	CC/E	OG/P	OG/I	OG/E
<b>Ephemeroptera</b>							
Ameletidae	Sc, Cg	+++	+++		+++	+++	
<i>Ameletus</i>	Sc, Cg	+++	+++	—	+++	+++	
Baetidae	Cg, Sc	+++	+++		+++	+++	—
Ephemerellidae, P	Cg, Sc	+++	+		+++		
Heptageniidae	Sc, Cg	+++	+++		+++	+++	
<i>Cinygma</i>	Sc, Cg	+++	+++	—	+++	+++	—
<i>Cinygmula</i>	Sc, Cg	+++	+++	—	+++	++	—
<i>Epeorus</i> , YP	Cg, Sc	+++	+++	—	+++	+	—
<i>Ironodes</i> , Y	Sc, Cg	+++	+++	—	++	++	—
<i>Rhithrogena</i> , YP	Cg, Sc	+++	+++	—	+++		—
Leptophlebiidae	Cg	+++	+++	+	+++	+++	++
<b>Plecoptera</b>							
Capniidae	Sh	++	++		++	++	
Chloroperlidae	Pr, Cg, Sc	+++	+++	+	+++	+++	++
Leuctridae	Sh	+++	+++	+++	+++	+++	+++
<i>Despaxia</i>	Sh	+++	+++	—	+++	+++	—
<i>Moselia</i> , I	Sh		+++	—	+	++	—
Nemouridae	Sh	+++	+++	++	+++	+++	+++
<i>Malenka</i>	Sh	+++	+	—	+	+++	—
<i>Soyedina</i> , OI	Sh	+	+	—	+	+++	—
<i>Visoka</i>	Sh	+++	+++	—	+++	+++	—
<i>Zapada</i>	Sh	+++	+++	—	+++	+++	—
Perlidae, YI	Pr		++				
Perlodidae	Pr	+++	+++		+++	+++	
<b>Trichoptera</b>							
Brachycentridae, I	Cg, Cf, Sh		++		+	++	
Glossosomatidae, O	Sc		+		+++	+	
Hydropsychidae	Cf	+++	+++		+++	++	
Hydropsyche, YI	Cf		++	—			—
Parapsyche	Cf	+++	+++	—	+++	++	—
Hydroptilidae	Pi, Sc	+++	+++	+	+++	++	+
<i>Agraylea</i> , YP	Pi, Cg	+++	+++	—	++		—
Lepidostomatidae	Sh	+++	+++	+	+++	+++	++
<i>Lepidostoma</i>	Sh	+++	+++	—	+++	+++	—
Limnephilidae	Sh, Cg, Sc	+++	+++	+	+++	+++	++
Philopotamidae	Cf	+++	+++	++	+++	+++	+++
<i>Dolophilodes</i>	Cf	+++	+++	—	+++	+++	—
<i>Wormaldia</i> , I	Cf		+++	—		++	—
Polycentropodidae	Pr, Cf	+++	+++	—	+++	+++	++
<i>Polycentropus</i> , YI	Pr, Cf	++	+++	—	+	++	—
Rhyacophilidae	Pr	+++	+++	+	+++	+++	++
<i>Rhyacophila</i>	Pr	+++	+++	—	+++	+++	—
<b>Diptera</b>							
Ceratopogonidae	Pr, Cg	+++	+++	+++	+++	+++	+++
Chironomidae	Pr, Cg	+++	+++	+++	+++	+++	+++
Culicidae	Cg	+	+	+		+	+
Dixidae, O	Cg				+		++
Dolichopodidae	Pr	+++	+++	+++	++	+++	+++
Empididae	Pr, D	+++	+++	+++	++	+++	+++
Muscidae (T) <sup>d</sup>	Pr	++	+++	+++	++	+++	+++
Mycetophilidae (T)	D	+++	+++	+++	++	+++	+++
Phoridae, Y	D	+++	+++	+++	+	+++	+++
Psychodidae	Cg	+++	+++	++	++	++	+++

**Table 2** (concluded).

Taxa <sup>a</sup>	Functional feeding group <sup>b</sup>	Stream class and seral stage <sup>c</sup>					
		CC/P	CC/I	CC/E	OG/P	OG/I	OG/E
Sciaridae (T)	D	+	+++	+++	+	++	+++
Simuliidae	Cf	+++	+++	+++	+++	+++	+++
Syrphidae (T)	Pr	+	+++	+++	+	+++	+++
Tipulidae	Sh, D	+++	+++	+++	+++	+++	+++
<b>Coleoptera</b>							
Chrysomelidae, O	He		+	+	++	++	+
Dytiscidae	Pr	++	++		++	+	
Elmidae, I	Cg		++			++	
Staphylinidae	Sc	+++	++	++	+	+++	++
<b>Megaloptera</b>							
Corydalidae, OI	Pr		+		+	+++	

**Note:** +, presence in one watershed; ++, presence in two watersheds; +++, presence in three watersheds; —, no data available.

<sup>a</sup>Letters indicate the type of stream where taxa were collected more frequently: O, old growth; Y, clearcut; P, perennial; I, intermittent.

<sup>b</sup>Cf, collector-filterer; Cg, collector-gatherer; D, detritivore; He, herbivore; Pr, predator; Pi, piercer; Sc, scraper; Sh, shredder (modified from Merritt and Cummins 1996).

<sup>c</sup>CC/P, clearcut perennial; CC/I, clearcut intermittent; CC/E, clearcut ephemeral; OG/P, old growth perennial; OG/I, old growth intermittent; OG/E, old growth ephemeral.

<sup>d</sup>T, primarily terrestrial.

**Table 3.** Mean taxonomic richness of aquatic insect orders ( $\pm 1$  SE) collected from perennial, intermittent, and ephemeral headwater streams in old-growth (OG,  $n = 3$ ) and clearcut (CC,  $n = 3$ ) stands.

Order	Seral stage	Stream persistence class			Seral stage, $F_{[1,12]}$	Stream persistence, $F_{[2,12]}$	Interaction, $F_{[2,12]}$	Test <sup>a</sup>
		Perennial	Intermittent	Ephemeral				
Ephemeroptera	CC	5 $\pm$ 0	4.3 $\pm$ 0.3	0.3 $\pm$ 0.3	0ns	206***	1ns	C > S > E
	OG	5 $\pm$ 0	4 $\pm$ 0	0.7 $\pm$ 0.3				
Plecoptera	CC	4.7 $\pm$ 0.3	5.3 $\pm$ 0.3	2 $\pm$ 0.6	0ns	28.5***	1.5ns	C = S > E
	OG	4.7 $\pm$ 0.3	4.7 $\pm$ 0.3	2.7 $\pm$ 0.3				
Trichoptera	CC	7 $\pm$ 0	8 $\pm$ 0.6	2.3 $\pm$ 1.9	0.9ns	13.5***	0.8ns	C = S > E
	OG	8.3 $\pm$ 0.3	7.3 $\pm$ 0.9	4 $\pm$ 1.2				
Diptera	CC	10.7 $\pm$ 0.3	12 $\pm$ 0.3	12 $\pm$ 0.6	0ns	13.4***	1.9ns	C < S = E
	OG	10 $\pm$ 0.6	12 $\pm$ 0.6	13 $\pm$ 0				
Coleoptera	CC	1.7 $\pm$ 0.3	2.3 $\pm$ 0.7	1 $\pm$ 0.6	0.1ns	3.8*	0.1ns	C = S > E
	OG	1.7 $\pm$ 0.9	2.7 $\pm$ 0.3	1 $\pm$ 0				
Megaloptera	CC	0 $\pm$ 0	0.3 $\pm$ 0.3	0 $\pm$ 0	4.5ns	6.5**	1.5ns	C < S > E
	OG	0.3 $\pm$ 0.3	1 $\pm$ 0	0 $\pm$ 0				
All orders	CC	29 $\pm$ 0.6	32.7 $\pm$ 0.3	17.7 $\pm$ 2.7	1.1ns	41.9***	1.3ns	C = S > E
	OG	30 $\pm$ 1.5	31.7 $\pm$ 0.9	21.3 $\pm$ 1.5				

**Note:** Calculations include both sampling techniques and all sampling periods. ns, not significant ( $P > 0.05$ ); \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

<sup>a</sup>Bonferroni-corrected pairwise comparisons or orthogonal contrasts comparing among the three stream persistence classes.

organic detritus (emergence:  $F_{[1,7]} = 4.9$ ,  $P = 0.06$ ; kicknet:  $F_{[1,4]} = 8.8$ ,  $P = 0.04$ ) and tended to increase with cover only in emergence samples (emergence:  $F_{[1,7]} = 4.8$ ,  $P = 0.07$ ; kicknet:  $F_{[1,4]} = 0.1$ ,  $P = 0.7$ ). Shredder abundance was not related to algal biomass.

Algal piercers (Hydroptilidae, almost all *Agraylea*) accounted for up to 9% of clearcut stream insects, but were very scarce in old-growth streams (emergence samples:  $F_{[1,12]} = 3.8$ ,  $P = 0.08$ ; kicknet samples:  $F_{[1,6]} = 10$ ,  $P = 0.01$ ; Figs. 2 and 3). Interestingly, this group, while absent from ephemeral streams, did not differ in abundance between perennial and intermittent clearcut streams (Table 5). Other

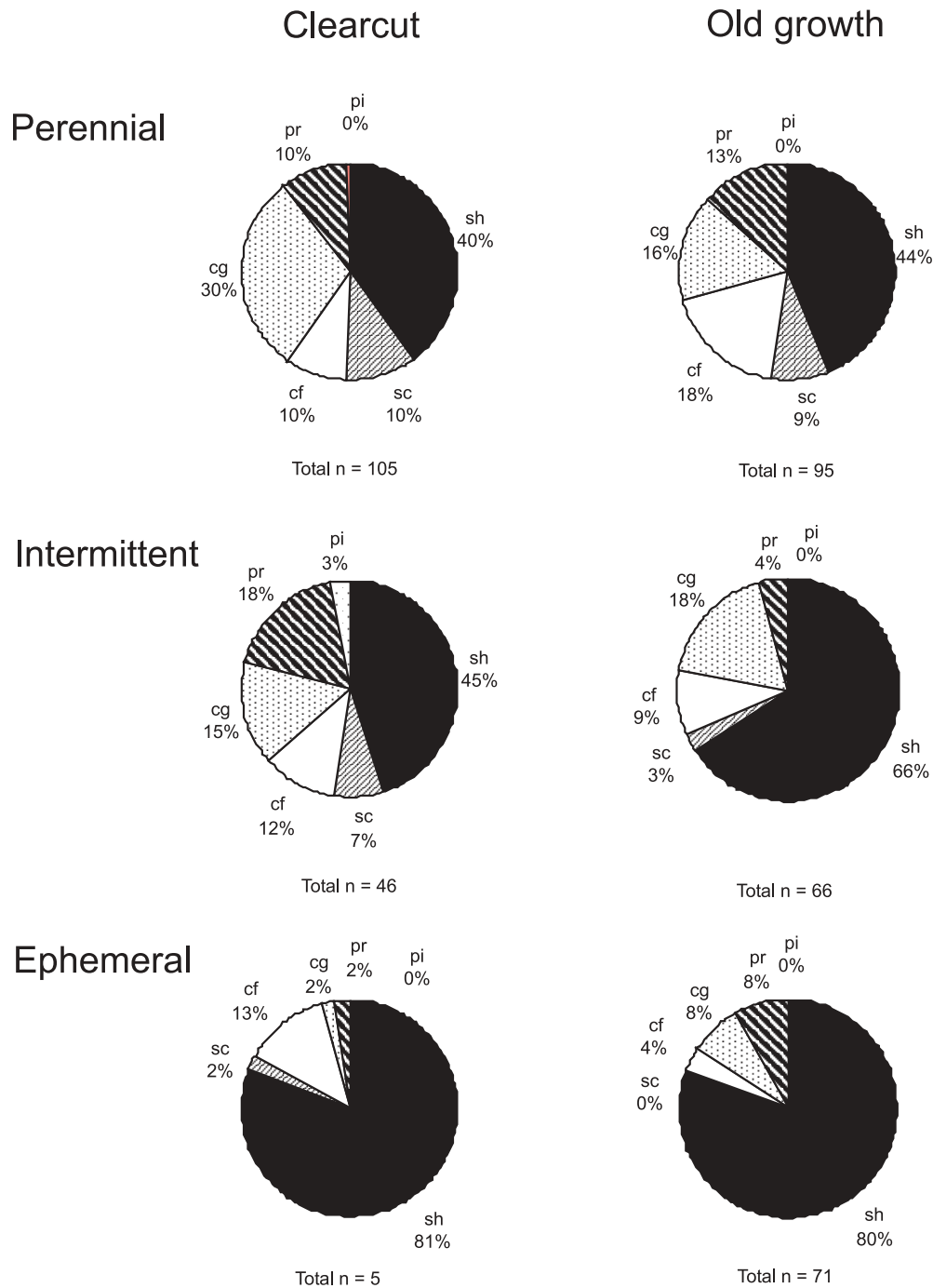
functional feeding groups showed no clear patterns in abundance with seral stage.

### Patterns in individual families

Relative abundances of each insect family were tested (ANOVA) against a priori predictions (Table 5), and of these 153 tests, 52 (34%) exhibited a trend, with 44 of these (85%) in the predicted direction, representing significantly more positive trends than expected by chance ( $G = 18.7$ ,  $df = 1$ ,  $P < 0.001$ , log likelihood ratio test). Stream persistence, size, and cover were the best predictors, with over 30% of tests giving a trend matching the predictions (persis-



**Fig. 2.** Aquatic insect community collected by emergence trap sampling (Ephemeroptera, Plecoptera, Trichoptera), represented by functional feeding group. Pie charts to left show streams surrounded by clearcuts; charts to right show streams surrounded by old growth. Stream persistence decreases down the page (perennial, intermittent, and ephemeral streams). Functional feeding groups are as follows: sh, shredders; sc, scrapers; cf, collector-filterers; cg, collector-gatherers; pr, predators; pi, piercers.

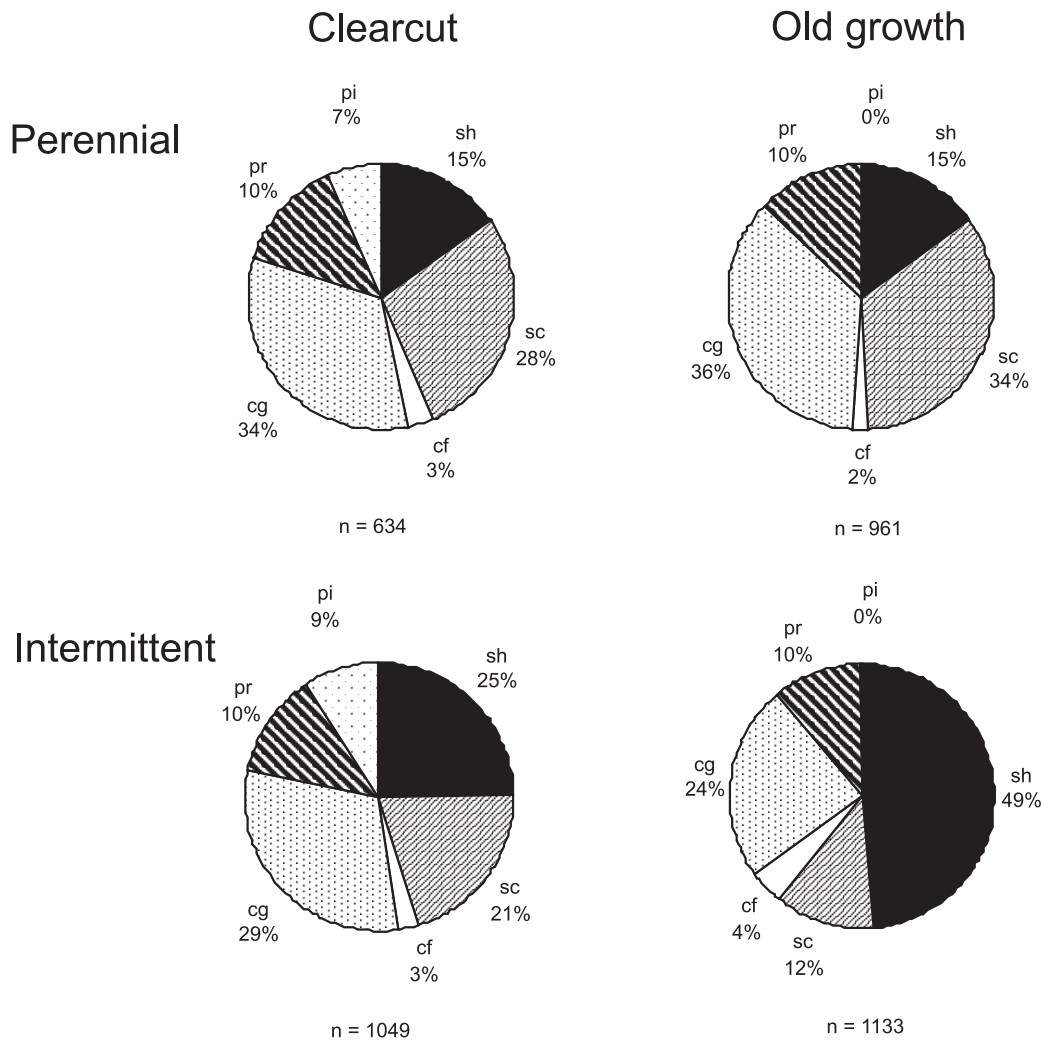


tence:  $G = 7.7, P < 0.01$ ; size:  $G = 12.1, P < 0.01$ ; cover:  $G = 3.6, P = 0.06$ ). Seral stage, organic detritus, and algae did not predict family trends, with 14–22% giving matching trends ( $P > 0.4$  for each).

We predicted that we would find more shredders in old-growth than clearcut streams, in small than large streams, and in streams with more riparian cover and more organic detritus. Of four shredder families, only Nemouridae exhibited the predicted pattern with seral stage (Table 5). Both

Leuctridae (mostly *Despaxia* and *Moselia*) and Nemouridae were more common in smaller intermittent streams as predicted and, at least in old growth, in streams with more cover. In clearcut streams, Leuctridae were more common in streams with more organic debris. We caught no adult Capniidae, and larval Capniidae (found in very low numbers) showed no patterns. Lepidostomatidae (mostly *Lepidostoma cascadense*) from emergence traps did not match any predictions and were more common in bigger,

**Fig. 3.** Aquatic insect community collected by kicknet sampling (Ephemeroptera, Plecoptera, Trichoptera), represented by functional feeding group. Pie charts to left show streams surrounded by clearcuts; charts to right show streams surrounded by old growth. Stream persistence decreases down the page (perennial and intermittent streams). Functional feeding groups are as follows: sh, shredders; sc, scrapers; cf, collector-filterers; cg, collector-gatherers; pr, predators; pi, piercers.



more persistent streams with less organic detritus. Larval Lepidostomatidae, conversely, followed the predicted pattern.

We predicted that scrapers and algal piercers would be more abundant in clearcut, larger, more persistent streams with less riparian vegetation and more algae. Ameletidae (out of four scraper families) and Hydroptilidae (the only piercer family) were more common in clearcuts. All four scraper families followed the predicted patterns with size and persistence. Larval algal piercers, however, were less common in larger than smaller streams in old growth (though found in extremely low numbers in old-growth streams). Ameletidae and Ephemerellidae increased with decreasing riparian cover in old-growth streams. Ephemerellidae increased with increasing riparian cover in clearcuts, but cover values in clearcuts were likely too low to impact their food source. Heptageniidae, Ameletidae, and Baetidae declined with increased organic matter, perhaps as an indirect effect of stream size and flow, or perhaps because rocks were covered with detritus and unavailable for algal growth

or unavailable for scraping. Heptageniidae, Baetidae, and Hydroptilidae were more abundant with increased algae in one seral stage using one sampling technique.

We predicted that collectors would increase with stream size and persistence, partly because of increased habitat diversity and partly because flowing water brings food. Philopotamidae matched predictions for size and persistence in adult samples, but showed the reverse pattern in larval samples. Hydropsychidae adults (not *Hydropsyche*) in old-growth streams exhibited the predicted pattern. No other Hydropsychidae tests had obvious trends.

We had no a priori predictions for predator abundance. Adult Chloroperlidae were more abundant in large perennial streams, and adult Rhyacophilidae were more abundant in persistent old-growth streams. Conversely, Polycentropodiidae were most abundant in intermittent streams.

#### Community structure and the physical environment

For the benthic samples, the first two ordination axes accounted for over 77% of the relationship between commu-

**Table 4.** Abundance (per square metre for kicknet samples (KN); per trap for emergence trap data (ET)) of invertebrate functional feeding groups in perennial, intermittent, and ephemeral streams surrounded by old-growth forest (OG) or by 4- to 8-year-old clearcuts (CC).

Group	Method	Seral stage	Stream persistence class			Seral stage, $F_{[1,12]}$	Stream persistence, $F_{[2,12]}$	Interaction, $F_{[2,12]}$
			Perennial	Intermittent	Ephemeral			
Shredders	ET	CC	44±31	21±10	3±2	6.7*	2.5ns	2.3ns
		OG	35±9	43±12	63±37			
	KN	CC	85±23	268±120	na <sup>a</sup>	2.2ns	9.7**	0.3ns
		OG	168±101	523±102	na			
Scrapers	ET	CC	9±4.6	3±3	0.2±0.2	0.6ns	5.7*	0.3ns
		OG	9±4	2±1	0.2±0.1			
	KN	CC	182±52	201±49	na	0.04ns	1.2ns	2.2ns
		OG	311±44	152±65	na			
Collector-filterers	ET	CC	12±9	4±1	0.7±0.4	1.0ns	5.1*	0.07ns
		OG	20±11	6±3	2±2			
	KN	CC	16±4	26±8	na	0.02ns	1.2ns	0.2ns
		OG	23±16	62±47	na			
Collector-gatherers	ET	CC	31±20	7±4	0.2±0.2	0.3ns	5.7*	0.4ns
		OG	16±5	18±7	8±4			
	KN	CC	216±64	304±71	na	0.5ns	0.1ns	1.7ns
		OG	328±47	254±46	na			
Predators	ET	CC	9±5	8±2	0.3±0.3	0.01ns	7.1**	2.3ns
		OG	13±4	3±1	2±1			
	KN	CC	79±15	124±23	na	0.1ns	0.4ns	0.5ns
		OG	130±54	140±75	na			
Piercers	ET	CC	0.3±0.3	2±1	0±0	2.3ns	1.2ns	1.2ns
		OG	0.0±0.0	0.0±0.0	0.0±0.0			
	KN	CC	55.4±33.1	126.2±94.9	na	4.0ns	1.4ns	0ns
		OG	1.1±1.1	2.4±1.3	na			
Total	ET	CC	105±69	46±8	5±4	6.1*	6.3**	2.8ns
		OG	94±17	66±7	71±38			
	KN	CC	634±175	1049±296	na	0.8ns	1.2ns	0.4ns
		OG	961±234	1133±329	na			

**Note:** Means and standard errors are calculated from raw data; analyses are based on appropriate transformations. ns, not significant ( $P > 0.05$ ); \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

<sup>a</sup>No data available.

nity composition (insect families) and stream biophysical characteristics and for over 61% of the variation in the insect data (Fig. 4). The canonical axes significantly explained the relation between aquatic insects and biophysical measures ( $P = 0.025$ , Monte Carlo simulation). Sites clustered primarily by seral stage and by stream persistence classes. The first axis (48% of total variation) described a gradient of increasing light from left to right. The two large perennial old-growth streams were separated from the remainder of the forested streams, probably since more light reached the channel because of their width (Fig. 4). The second axis was related to organic detritus and stream size. Again, the two large old-growth streams were outliers.

The emergence trap samples also showed significant association between aquatic insect and biophysical measures ( $P = 0.015$ , Monte Carlo simulation). The first two axes explained 64% of the total variation. There was strong clustering by stream persistence class along the first axis (Fig. 5). From left to right there was a gradient from perennially flowing to ephemeral streams. The first axis described a gradient of stream size (largest drainage area, substrate size,

and width to the left). The second axis was related to local influences such as light, organic detritus, and elevation. Both persistence classes and seral stages had some influence on the ordination structure, as each group tended to cluster together. The emergence trap data showed a clearer effect of persistence class than the benthic kicknet data, which are clustered primarily by seral stage.

## Discussion

### Influence of seral stage (old growth versus clearcut)

Within flow-persistence classes, we predicted that streams in old growth would have more riparian cover, more organic detritus, and less algae than streams within clearcuts. Consequently, we predicted that old-growth streams would contain more shredders, and that clearcut streams would have more grazers. The ordination of benthos abundance demonstrated the predicted groupings of seral stages along the first axis, and their association with the functional groups was also as predicted. We found that riparian vegetation shaded old-growth streams more and provided more organic detritus, at

**Table 5.** Summary of tests of individual aquatic insect families showing direction of prediction and agreement or disagreement with predictions.

Family	Seral stage effect	Seral stage	Stream persistence effect	Stream size effect	Canopy cover effect	Organic detritus effect	Algal biomass effect
Predictions for shredder families <sup>a</sup>	More in OG		Decrease with increased persistence class	Decrease with increased size	Increase with increased cover	Increase with increased detritus	None
Leuctridae	0 <sup>b</sup> , 0	OG	0, 0	✓, ✓	✓, ✓	0, 0	0, 0
Nemouridae	✓, 0	CC	0, ✓	0, 0	0, 0	✓, ✓	0, 0
Lepidostomatidae	0, 0	OG	0, ✓	0, ✓	✓, ✓	0, 0	0, 0
		CC	0, 0	0, 0	0, 0	0, 0	0, 0
		OG	x, 0	0, 0	0, 0	0, 0	0, 0
		CC	x, ✓	x, ✓	0, 0	x, 0	0, 0
Predictions for scraper and algal piercer families <sup>c</sup>	More in CC		Increase with increased persistence	Increase with increased size	Decrease with increased cover (OG only)	None	Increase with increased algae
Heptageniidae	0, 0	OG	✓, ✓	✓, ✓	0, 0	0, 0	0, 0
		CC	✓, 0	0, 0	0, 0	0, 1	0, ✓
Ameletidae	0, ✓	OG	0, ✓	✓, ✓	✓, ✓	1, 0	0, 0
		CC	0, 0	0, 0	0, 0	0, 0	0, 0
Baetidae	0, 0	OG	✓, 0	✓, 0	0, 0	0, 0	0, ✓
		CC	✓, 0	✓, 0	0, 0	1, 1	0, 0
Ephemereilidae	0, 0	OG	✓	✓	✓	0	0
		CC	✓	✓	1	0	0
Hydroptilidae	✓, ✓	OG	0, 0	0, ✓	0, 0	0, 0	0, 0
		CC	0, 0	0, 0	0, 0	0, 0	✓, 0
Predictions for collector-filterer families	None		Increase with increased persistence	Increase with increased size	None	None	None
Hydropsychidae	0, 0	OG	0, 0	✓, 0	0, 0	0, 0	0, 0
		CC	0, 0	0, 0	0, 0	0, 0	0, 0
Philopotamidae	0, 0	OG	✓, 0	✓, x	0, 1	0, 0	0, 0
		CC	✓, x	✓, x	0, 1	0, 0	0, 0
Rhyacophilidae	0, 0	OG	1, 0	0, 0	0, 0	0, 0	0, 1
		CC	0, 0	0, 0	0, 0	0, 0	0, 0

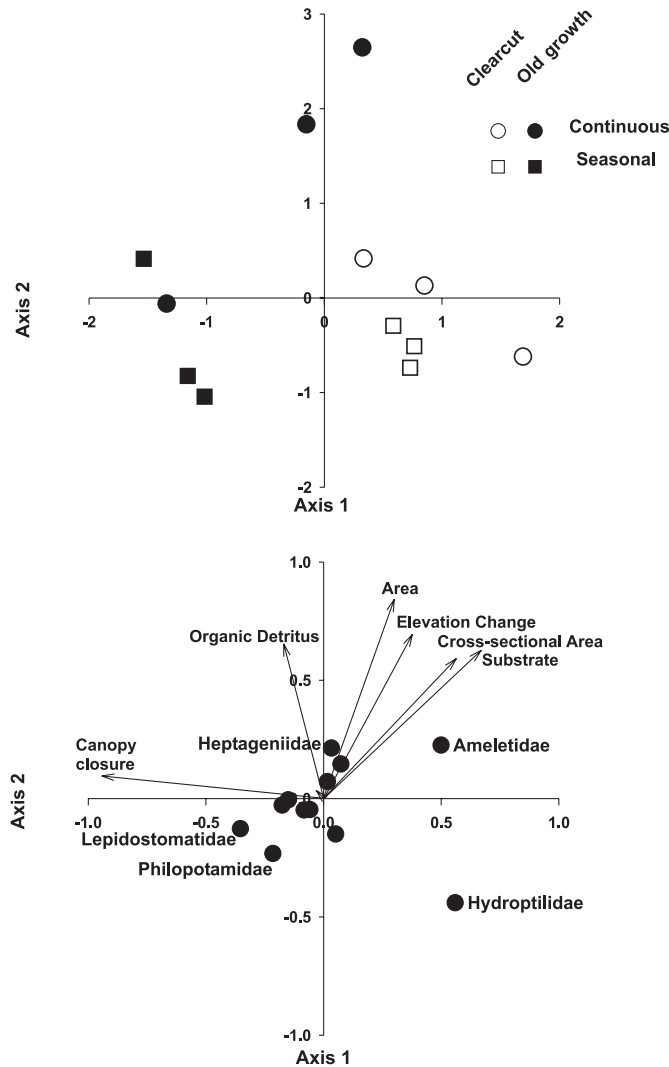
**Note:** Capniidae showed no patterns with respect to treatments and is omitted from this table. There were no specific predictions made for predators (Chloroperlidae, Perlodidae, Polycentropodidae) or for the families Limnephilidae and Leptophlebiidae (a mix of genera in different functional feeding groups). All tests are individual *F* tests with a single independent variable. OG, streams surrounded by old growth; CC, streams surrounded by recent clearcut. Persistence effect uses stream class as independent variable; size effect uses principle component size factor as independent variable.

<sup>a</sup>See introduction for rationale for predictions.

<sup>b</sup>In each column, the first entry represents emergence data and the second represents benthic (kicknet) data. 0, no obvious pattern ( $P > 0.15$ ); ✓, pattern that matches direction of prediction ( $P \leq 0.15$ ); x, pattern opposite to prediction ( $P \leq 0.15$ ); 1 or 1, decreasing or increasing pattern, but no prediction ( $P \leq 0.15$ ); an empty cell denotes family not present in that sample.

<sup>c</sup>Some scraper families also include collector-gatherer genera.

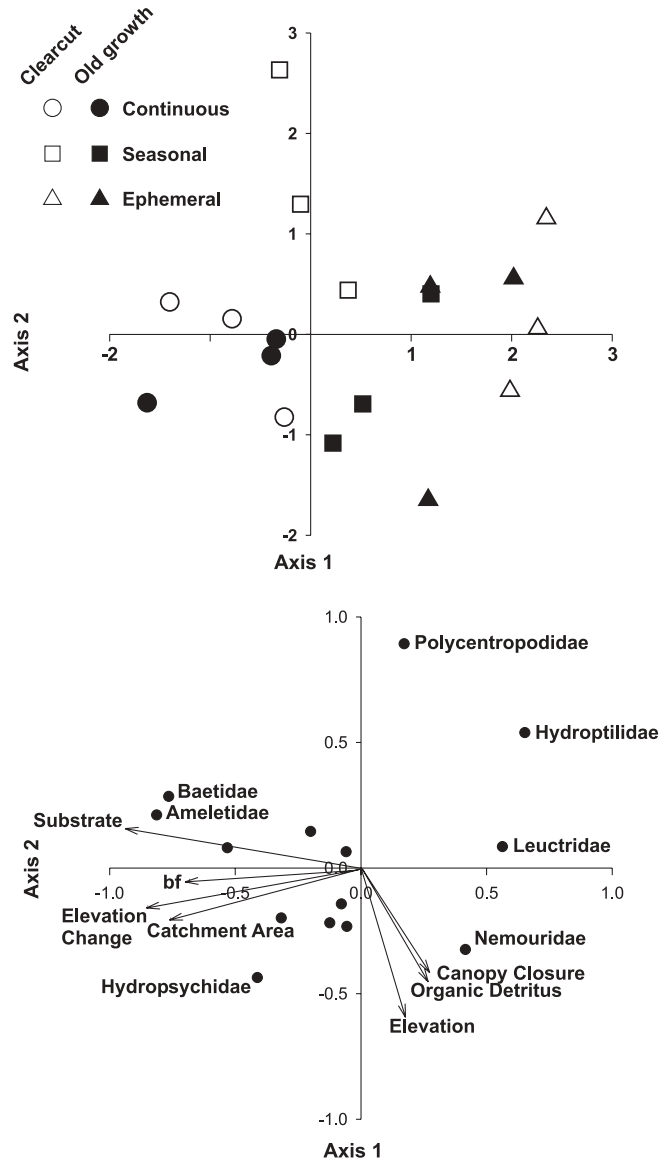
**Fig. 4.** Ordination diagram of site scores for the benthic (kicknet) samples from 12 sites. The top panel shows the position of sites along the first two axes of a canonical correspondence analysis. The bottom panel shows the biplot for the influence of each of the biological and environmental measures on the resulting ordination. The solid circles on the bottom panel represent families, but only those much past the origin are labelled, as these have most influence on the ordination structure.



least as measured in pools. Organic detritus in riffles was not related to seral stage, perhaps because of the limited storage capacity and high patchiness within riffles of the detritus transported from upstream reaches (e.g., Richardson 1992; Wipfli and Gregovich 2002). Matching our predictions, we found a higher abundance of shredders in old-growth than clearcut streams. A single shredder family, Nemouridae accounted for most of this seral stage effect.

Patterns in algal biomass were opposite to our predictions: intermittent and perennial streams in old growth had more algae than those in clearcuts, despite these streams having more cover. Several hypotheses could account for our findings. First, stream depth could be greater in clearcut streams than the slightly smaller old-growth streams, although we found no trend with stream depth. Second, nutrients may

**Fig. 5.** Ordination diagram of site scores for the emergence trap samples from 18 sites. The top panel shows the position of sites along the first two axes of a canonical correspondence analysis. The bottom panel shows the biplot for the influence of each of the biological and environmental measures on the resulting ordination. The solid circles on the bottom panel represent families, but only those much past the origin are labelled, as these have most influence on the ordination structure.



have limited algal growth (Shortreed and Stockner 1983). Third, algal productivity reaches light saturation at relatively low light levels (e.g., Hill et al. 2001), and the light reaching old-growth streams could have been sufficient to saturate algal growth. Fourth, grazers may have depleted the algal crop (Feminella et al. 1989; Wellnitz et al. 1996). In support of this final hypothesis, although algal biomass was lower, some algal grazers (Hydroptilidae and Ameletidae) were more abundant, as predicted, in clearcut streams, while the remaining three grazer families were equally abundant in old-growth and clearcut streams. Experiments would be required to distinguish amongst these hypotheses.

We had no a priori predictions about aquatic insect richness with seral stage, and we found no difference. We found five taxa more often in old-growth streams, and eight taxa more often in clearcut streams; one family was unique to old-growth streams, and two taxa were unique to clearcut streams. These results suggest that in the short term, forest harvesting, even up to the stream banks, may not result in extirpation of genera or families in coastal headwater streams. However, because we did not identify all families to genus, we may have missed the absence of some genera, as well as species, an important consideration for future studies.

### **Influence of stream persistence class (perennial, intermittent, ephemeral)**

Because intermittent and ephemeral streams are subject to periodic drying, we predicted that they would have lower richness of aquatic insects than perennial streams and would contain specially adapted taxa. We found fewer Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, and Megaloptera families in ephemeral streams than in intermittent or perennial streams. We found similar numbers of Plecoptera, Trichoptera, and Coleoptera in perennial and intermittent streams. Another study in coastal British Columbia found that intermittent and perennial streams contained similar richness of Plecoptera species (Muchow and Richardson 2000). There were more Ephemeroptera in perennial streams and more Megaloptera in intermittent streams. Overall, richness was similar between perennial and intermittent streams, and lower in ephemeral streams.

We collected four families or genera in at least two more perennial than intermittent or ephemeral streams, nine in at least two more intermittent streams, and none in more ephemeral streams. Of the taxa present more often in a particular persistence class, intermittent species seemed to show stronger preferences, with four taxa not found elsewhere, and three more found in only one other stream. Only intermittent streams had species not found in streams of other persistence classes. These presence-absence results suggest that intermittent streams may provide a habitat unique from perennial streams, but that ephemeral streams may not. Some species in other studies have adapted to dry periods by having drought resistant eggs or by moving to the hyporheic zone or permanent pools (Delucchi and Peckarsky 1989; Dieterich and Anderson 1995). *Despaxia augusta*, a common stonefly in the Pacific Northwest, was found in our nonperennial streams, despite the fact that it takes 2 years to complete its larval stages (Richardson 2001), suggesting that it can cope with the absence of flowing surface water during summer. These adaptations, however, may not be sufficient to allow survival in ephemeral streams that dry up completely. In the southern United States, for example, streams that were dry from mid-June to mid-November supported half as many taxa as more permanent downstream reaches (Brown and Brussock 1991). We qualify our conclusion somewhat, however, as we were unable to sample the ephemeral benthos because of low flow levels, and we may have missed taxa able to move to the hyporheic zone during dry periods.

In characterizing streams, we found that intermittent streams were smaller than perennial streams and that ephemeral

streams were smaller than intermittent streams. Within a seral stage, we predicted that the smaller ephemeral and intermittent streams would have more riparian cover, more organic detritus, and less algae than perennial streams. Consequently, we predicted that the abundance of shredders would increase with decreasing stream persistence and that the abundance of grazers would decrease.

As predicted, we found a higher abundance of shredders in smaller ephemeral and intermittent streams. One of the taxa that was more common in nonperennial streams in the old growth was the nemourid stonefly *Soyedina*, a shredder genus also found in intermittent streams in Oregon (Dieterich and Anderson 2000). This pattern of higher proportions of shredders in nonperennial streams was also reinforced by the ordination of the data from emergence traps. In clearcuts, we found a similar relative abundance of shredders in intermittent and perennial streams, perhaps because the clearcut intermittent streams resembled clearcut perennial streams in size. Leuctridae and Nemouridae both increased with decreased flow persistence, size, and cover, and Leuctridae increased with increasing organic detritus. Progar and Moldenke (2002) likewise found higher rates of emergence of aquatic insects from temporary streams in Oregon.

Lepidostomatidae, the main Trichopteran shredder, while following the predicted patterns in larval data, exhibited the opposite patterns in emergence data. Emergent Lepidostomatidae increased with increasing stream size and persistence and decreased with increasing organic detritus. Lepidostomatidae are often associated with slower flow, smaller streams, and detritus (Anderson and Wold 1972; Grafius and Anderson 1979; Delucchi 1988; Richardson 1991). Two hypotheses possibly account for this discrepancy. First, emergence traps may provide biased samples as they cover only small patches of stream bottom. However, we found more Lepidostomatidae emerging in perennial than intermittent streams, whereas we may have covered less edge in the perennial streams. Alternatively, we may have missed the main period of emergence for this taxon. Fall emergers may be less abundant than spring emergers in intermittent streams (Delucchi and Peckarsky 1989). It is possible that the intermittent and ephemeral headwater streams in our study contained a different suite of Lepidostomatidae than the perennial streams (i.e., spring rather than late-summer emergers). Hence, our late-summer emergence traps may have caught the summer, but not the spring, emergers. This hypothesis would explain the discrepancy between benthic and emergence sampling data, but requires further testing with spring emergence trapping.

Although algae decreased as stream persistence increased, some grazers were more abundant in perennial streams than in intermittent and ephemeral streams. All four grazer and collector families increased in abundance with increased stream persistence and size. The influence of size was stronger in old-growth streams, perhaps because light is less limiting in clearcuts.

As predicted, Ameletidae and Ephemerellidae decreased with increased riparian cover in the old-growth seral stage, while Heptageniidae, Baetidae, and Hydroptilidae generally increased with increased algae. There are several hypotheses for the relationships between algal biomass and invertebrate abundance, given that grazers may have cropped algae in the

wide clearcut streams (Feminella et al. 1989; Wellnitz et al. 1996; Poff and Nelson-Baker 1997).

In emergence data, collector (filterers and gatherers) and predator feeding groups were significantly less common in intermittent, particularly ephemeral, streams. Examination of individual families, however, revealed that larval Philopotamidae (a collector-filterer) and larval and adult Polycentropodidae (a predator) were more common in the less persistent streams. Both families build nets and some species are adapted to living in low-velocity streams (Dudgeon and Richardson 1988; Wiggins 1996). Emergence sampling may have missed early emerging Philopotamidae from intermittent and ephemeral streams (similar hypothesis as described above for Lepidostomatidae). The difference between benthic and emergence sampling results was further confirmed by the ordinations, which demonstrated different clusters depending on the type of data (clustering by seral stage for the benthic data, but by persistence class for the emergence data).

### Implications for management and future study

The hydrology of intermittent streams may be altered by clear-cutting (e.g., Hicks et al. 1991). We were unable to find intermittent streams in clearcuts to match those common in old growth. In old-growth sites, intermittent streams were intermediate between perennial and ephemeral streams in flow velocity and persistence; in clearcuts, intermittent streams were more similar to perennial streams. This difficulty highlights the importance of studies comparing streams and their communities before and after logging in addition to retrospective studies such as ours.

Intermittent streams support a different suite of organisms and should be treated as providing different habitats rather than as a subset of habitats existing in perennial streams. For example, we found *Soyedina* (Nemouridae) and Corydalidae most often in intermittent streams at old-growth sites. Ephemeral streams, conversely, may not provide unique habitats for aquatic insects, but may rather offer a greater supply of a subset of habitats available in larger, more persistent streams. Because we did not identify organisms beyond genus, however, there may be species specializing in ephemeral channels. For most aquatic insects larvae cannot be identified to species, and keys to adults are not adequate for many faunas, something that requires further work. Our results suggest that forest management should offer protection for intermittent as well as perennial streams.

Communities of aquatic insects are different in streams within 4- to 8-year-old clearcuts than in streams surrounded by old growth. Because the recognition that there are aquatic invertebrate species capable of completing their life cycle in intermittent and ephemeral streams is recent, there are no other studies that examine the effect of clear-cutting adjacent to these systems. There is very little known about the downstream impacts from harvesting. Wipfli and Gregovich (2002) have demonstrated that non-fish-bearing channels, including nonperennial channels, contribute sufficient invertebrate biomass through transport into fish-bearing streams to support up to 2000 juvenile salmonids per kilometre of river annually. The abundance of small headwater streams in wet landscapes suggests that more research is needed on the ef-

fects of forest harvesting on small channels and on the channels they flow into.

Timing of sampling must take into account that species vary in their timing of emergence or other life stages. In particular, animals living in temporary streams likely emerge earlier in summer than insects in perennial streams (Dieterich and Anderson 1995). Our complementary use of emergence trapping and kicknet sampling allowed us to sample streams where low flow prohibited kicknet sampling.

We found that simple measurements of stream size, persistence, and canopy cover were good predictors of invertebrate abundance, while simple measurements of organic detritus and algal biomass (which we had assumed would be more directly linked with invertebrate abundance) were poor predictors.

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