

Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska?

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Abstract: We assessed the influence of riparian forest canopy type on macroinvertebrate and detritus export from headwater streams to downstream habitats in the Tongass National Forest, southeastern Alaska. Twenty-four fishless headwater streams were sampled monthly, from April to August 1998, across four riparian canopy types: old growth, clearcut, young-growth alder, and young-growth conifer. Young-growth alder sites exported significantly greater count (mean = 9.4 individuals·m⁻³ water, standard error (SE) = 3.7) and biomass (mean = 3.1 mg dry mass·m⁻³ water, SE = 1.2) densities of macroinvertebrates than did young-growth conifer sites (mean = 2.7 individuals·m⁻³ water, SE = 0.4, and mean = 1.0 mg dry mass·m⁻³ water, SE = 0.2), enough prey to support up to four times more fish biomass if downstream habitat is suitable. We detected no significant differences in macroinvertebrate export between other canopy types or in detritus export among different canopy types. Roughly 70% of the invertebrates were aquatic; the rest were terrestrial or could not be identified. Although we do not recommend clearcutting as a means of generating red alder, maintaining an alder component in previously harvested stands may offset other potentially negative effects of timber harvest (such as sedimentation and loss of coarse woody debris) on downstream, salmonid-bearing food webs.

Résumé : Nous avons évalué l'influence du type de couverture forestière de la rive sur l'exportation de macroinvertébrés et de détritit depuis des ruisseaux d'amont vers les habitats d'aval dans la forêt nationale de Tongass dans le sud-est de l'Alaska. Vingt-quatre ruisseaux d'amont dépourvus de poissons ont été échantillonnés tous les mois, d'avril à août 1998, dans quatre types de couverture végétale riparienne: forêt mature, surface coupée à blanc, jeune forêt d'aulnes et jeune forêt de conifères. Les sites de forêt jeune à aulnes exportent significativement plus de macroinvertébrés, en nombre (moyenne = 9,4 individus·m⁻³ d'eau, erreur type (SE) = 3,7) et en biomasse (moyenne = 3,1 mg de masse sèche·m⁻³ d'eau, SE = 1,2) que les sites de forêt jeune à conifères (moyenne = 2,7 individus·m⁻³ d'eau, SE = 0,4; moyenne = 1,0 mg de masse sèche·m⁻³ d'eau, SE = 0,2), soit assez de proies pour subvenir à des biomasses de poissons quatre fois plus grandes, à condition que les habitats d'aval soient convenables. Il n'y a pas de différences significatives décelables d'exportation de macroinvertébrés entre les autres types forestiers, ni de différences d'exportation de détritit entre les quatre types de couverture forestière. En gros, 70 % des invertébrés sont aquatiques; les autres sont terrestres ou impossibles à identifier. Bien que nous ne recommandions pas la coupe à blanc comme moyen de favoriser l'aulne rouge, le maintien d'une composante d'aulnes dans les secteurs déjà coupés pourrait contrebalancer les effets potentiellement négatifs de la coupe du bois, tels que la sédimentation et la perte de débris ligneux grossiers, sur les réseaux alimentaires d'aval qui contiennent des salmonidés.

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Introduction

Headwater habitats play a critical role in the structure and function of downstream ecosystems (Haigh et al. 1998). The headwater streams that drain these habitats transport water,

sediment, debris, and invertebrates (Cuffney and Wallace 1988; Naiman et al. 1992; Wipfli and Gregovich 2002), influencing downstream habitats and food webs. Physical and biological attributes that may influence the productivity of headwater streams and the material available for export in-

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clude catchment size, geology, soil type, aspect, gradient, temperature, precipitation, and plant and animal communities (Naiman et al. 1992). Natural or human-induced disturbances can alter these attributes (Resh et al. 1988), thereby altering productivity in both headwater streams and downstream habitats.

Stone and Wallace (1998) identify clearcut logging as a long-term disturbance that alters stream ecosystems. Their literature review identifies the following effects of clearcutting on stream macroinvertebrate communities: changes in stream temperature, stream flow, primary production, and community structure. The short-term effects of clearcutting may include reduced allochthonous input and increased autochthonous production, which alter macroinvertebrate communities and, consequently, detritus export. The long-term effects of clearcutting on macroinvertebrate export from headwater streams to downstream food webs, however, have not been addressed.

In the temperate rainforest of southeastern Alaska, clearcutting changes terrestrial and aquatic productivity (Alaback 1982; Duncan and Brusven 1985) and the energy flow from terrestrial to aquatic habitats (Wipfli 1997). Canopy removal increases the amount of light reaching the forest floor, increasing the productivity of understory plants (Alaback 1982) and streams (Duncan and Brusven 1985; Hetrick et al. 1998). Following clearcutting, forest succession often includes the development of red alder (*Alnus rubra*) stands in those places where there has been enough surface disturbance to expose mineral soils (Newton and Cole 1994). The establishment of alder may increase understory plant diversity (Deal 1997) and abundance (Hanley and Barnard 1998), and alder-dominated riparian canopies may also provide more terrestrial invertebrates as prey for juvenile salmonids than do conifer-dominated canopies (Wipfli 1997). Although the productivity of terrestrial habitat declines as a dense coniferous canopy develops in later successional stages (Alaback 1982), little information exists on the influence of riparian forest succession on headwater streams and associated export of material.

Forest management plans for southeastern Alaska include timber harvesting in forested headwaters (U.S. Department of Agriculture (USDA) Forest Service 1997). These headwaters contain many small, fishless streams (Swanston 1967), classified by the USDA Forest Service as classes III and IV. Riparian buffer protection during logging operations varies along these streams; most class III streams receive some buffer protection, but few class VI streams do (USDA Forest Service 1997). Many of these streams drain into salmonid-rearing habitats, and it is important to understand how timber harvest and forest regeneration in upland forests influence downstream food webs, including the flow of energy (invertebrates and detritus) to these habitats.

Our objective was to measure the effects of different riparian forest canopy types on macroinvertebrate (aquatic and terrestrial) and organic detritus export from headwater streams to downstream habitats. We tested the null hypothesis that during the salmonid growing season (April–August), headwater streams with old growth, clearcut, young-growth alder, and young-growth conifer riparian canopies do not differ in the amount (number and mass) of macroinvertebrates and detritus they export.

Methods

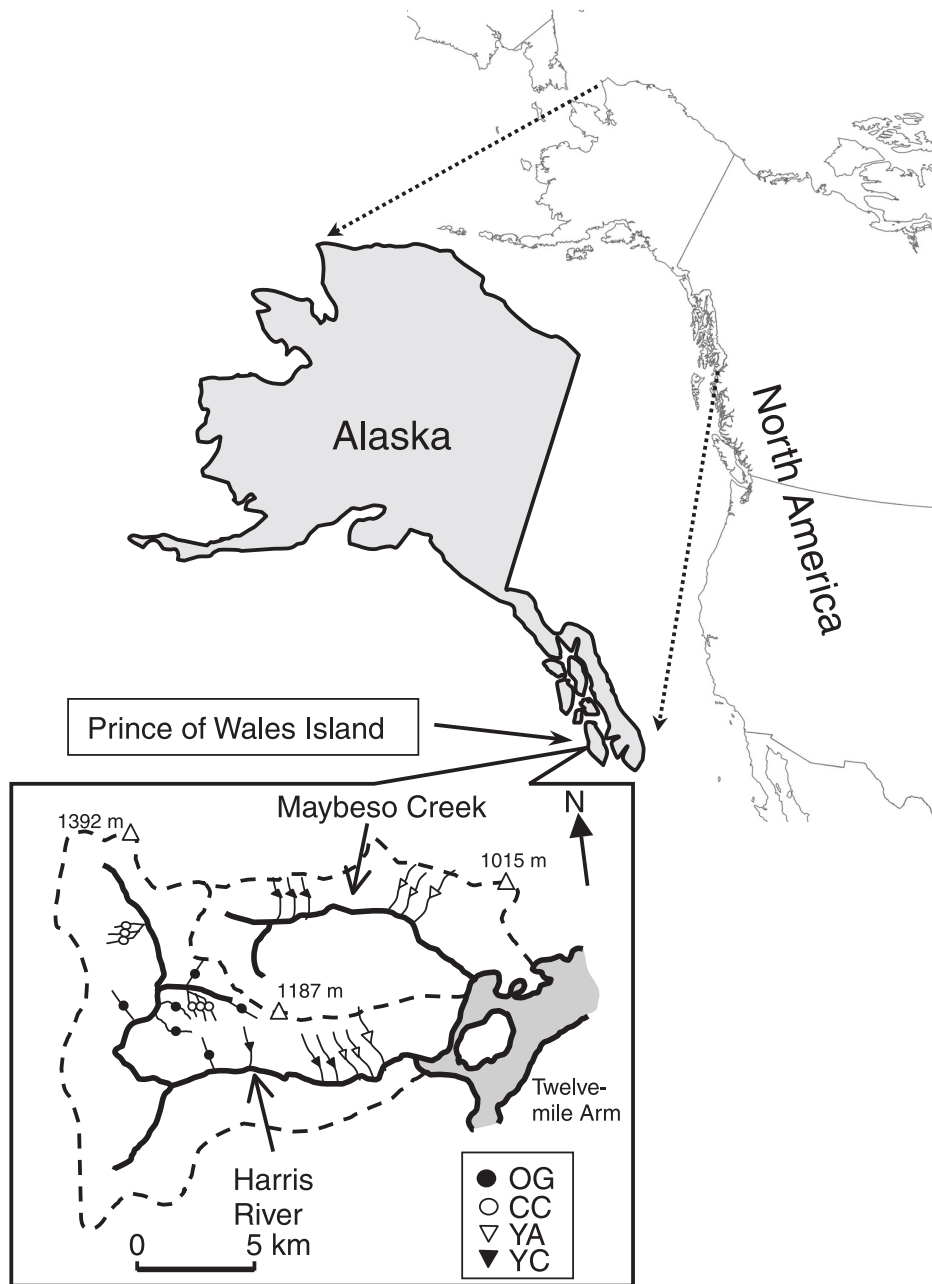
Study site

Research was conducted in small (mean discharge $<3.1 \text{ L}\cdot\text{s}^{-1}$), fishless headwater streams (classified as class III and class IV streams, USDA Forest Service 1997) on Prince of Wales Island in the Tongass National Forest, southeastern Alaska. The climate there is maritime and precipitation can exceed $500 \text{ cm}\cdot\text{year}^{-1}$ (Harris et al. 1974). We sampled macroinvertebrate and coarse detritus ($>250 \mu\text{m}$) export monthly, from April to August 1998, in 24 streams characterized by four distinct riparian canopy types: old growth (OG); clearcut (CC), <5 years post-cut; young-growth alder (YA), 35–40 years post-cut; and young-growth conifer (YC), 35–40 years post-cut. Six replicate streams of similar size and gradient were selected for each canopy type. All streams were within the Harris and Maybeso watersheds (Fig. 1), an area clearcut extensively during the 1950s and 1960s as part of the first large-scale, commercial timber harvest in southeastern Alaska (Swanston 1967). Eighteen sites were selected within the Harris River watershed (3 YA, 3 YC, 6 CC, 6 OG); and six were selected within the Maybeso Creek watershed (3 YA and 3 YC) (Table 1). Because of unusually low precipitation during the sampling season, surface flow became intermittent in nine streams, for which we substituted nearby streams with continuous surface flow to maintain an adequate number of replicates. Because of a scarcity of suitable old-growth headwater streams within these two basins, one OG stream substantially larger than the other study streams (mean discharge $58.2 \text{ L}\cdot\text{s}^{-1}$) was substituted in June–August. Stream temperature for one of each group of three streams (clustered by canopy type and watershed) was monitored continuously with Onset[®] temperature meters (Onset Computer Corp., Pocasset, Mass.), and stream temperature was taken with a hand-held thermometer on each stream at 0, 48, and 96 h during the sampling period.

Macroinvertebrate and detritus export

The density of macroinvertebrate and detritus export from the 24 streams was sampled continuously for 96 h once each month from April through August. Remote location and difficult terrain prevented quick access to sampling sites, so they were divided into two groups of 12 streams each, and sampling start and stop dates were staggered by one day for each group, i.e., 12 streams were sampled on days 0–4 and 12 were sampled on days 1–5. Streams were sampled systematically, based upon their proximity to each other, in the same order each month. Export was sampled by constructing a sandbag dam to divert the entire surface flow of each stream (with the exception of the one larger, old-growth stream) through a polyvinyl chloride (PVC) pipe (1-m long, 10-cm inside diameter), and drift nets (10-cm-diameter mouth, 1–2 m long, 250- μm mesh) were attached to the outflow end of each pipe (Wipfli and Gregovich 2002). Observations from previous studies in streams of this size showed that nets left on for more than 48 h without being emptied can result in occasional overflow (Wipfli and Gregovich 2002), therefore, nets were changed at 48-h intervals to ensure that they did not become clogged. Detritus and macroinvertebrates were washed into a 250- μm sieve and preserved in 95% ethanol, and the two 48-h samples were combined

Fig. 1. Map of Alaska, U.S.A., with inset showing the Harris and Maybeso drainages (132°67'W, 55°49'N) on eastern Prince of Wales Island. The drainage basin boundaries are represented by the dotted line. Both drainages empty into salt water in Twelvemile Arm (shaded area). Study streams are identified by canopy type: old growth (OG), clearcut (CC), young-growth alder (YA), and young-growth conifer (YC).



for data analysis. Discharge was measured by using a stopwatch to count the number of seconds it took for water from the dam outflow pipe to fill a known-volume container. Mean discharge for each stream during each sampling period was calculated by averaging measurements taken at 0, 48, and 96 h (3 replicates at each time). During occasional high flows, discharge sometimes exceeded pipe capacity and we were able to sample only a portion of the stream flow. In these instances, discharge through the pipe was measured as described above, the percentage of total streamflow flowing through the pipe (typically 90% or greater) was visually esti-

mated, and total discharge was calculated using this correction factor.

Samples were sorted under a 7× dissecting microscope. Macroinvertebrates were identified to lowest reliable taxon, measured to the nearest millimetre (total length excluding antennae and cerci), and enumerated. Unusually large samples were subsampled. We used a subsampler that had a large, funnel-shaped container to which we added 16 L of water containing the sample and through which a continuous, vigorous stream of air was injected from the bottom to ensure uniform mixing and distribution of the sample. Part

Table 1. Physical and biological habitat characteristics of headwater study streams on Prince of Wales Island, Alaska, 1998, in old growth (OG), clearcut (CC), young-growth alder (YA), and young-growth conifer (YC) riparian forests.

Parameter	Canopy type			
	OG ^a	CC	YA	YC
Mean				
Stream reach length (m)	250 (260)	237	273	204
Channel width (m)	1.8 (2.7)	1.2	1.9	1.4
Gradient (%)	21.0 (20.4)	22.9	21.7	22.2
Discharge (L·s ⁻¹)	0.4 (3.5)	0.7	1.2	0.9
Stream temperature (°C)	7.7 (7.5)	8.5	9.0	8.2
% open canopy	32 (36)	100	14	26
% alder canopy	<1 (<1)	0	74	20
% conifer canopy	68 (64)	0	12	54
Predominant understory	<i>Vaccinium</i> sp.	<i>Rubus</i> sp.	<i>Rubus</i> sp.	<i>Rubus</i> sp.
Understory density	Moderate	Moderate	Sparse	Low
Sample size (<i>n</i>)	6	6	6	6

^aNumbers in parenthesis include one old-growth stream that was uncharacteristically larger than all other study streams (see Methods, Study site).

of the sample (either 8 L or 4 L) was taken with a smaller known-volume container, and this portion was analyzed. Results were then multiplied by two or four to obtain a full-sample estimate. Macroinvertebrate biomass (mg dry mass) was estimated for individual invertebrates by using either published taxa-specific length–weight regression equations (e.g., Rogers et al. 1977; Sample et al. 1993; Burgherr and Meyer 1997) or our own equations. This was done for a previous study (Wipfli and Gregovich 2002) by drying a sample of known-length invertebrates of a given taxa (at 60°C for 24 h), weighing individuals (nearest 0.1 mg), and developing a length–weight regression (Smock 1980). Detritus was dried (at 60°C for 48 h), weighed, burned to ash (at 500°C for 5 h), and reweighed to determine ash-free dry mass (AFDM), the amount of organic, nonmineral material in the sample.

Physical habitat and riparian canopy measurements

Stream channel gradient, active channel width, canopy coverage, and understory vegetation type and density were surveyed along a 300-m reach of each stream directly upstream from the sample stations. Gradient was measured with a hand-held clinometer and canopy coverage was estimated every 20 m along the stream using a circular viewing tube (10-cm inside-diameter × 30-cm long). To estimate canopy coverage and composition, the observer stood in the center of the stream channel, looked through the vertically held tube, and recorded the percentage of alder, conifer, and open canopy. Foliage density (scale: 0 = none, 1 = sparse, 2 = low, 3 = moderate, 5 = high) and relative abundance (top five plant species in order of abundance) of understory shrubs were estimated visually for a 2-m-wide band along each stream bank (Table 1).

Statistical analysis

A completely randomized design was used incorporating canopy type (OG, YA, YC, CC) as the main factor, and 24 streams were sampled each month (April–August). We used a split-plot analysis of variance (ANOVA) (SAS 1990) to test for significant effects of canopy type, month, and canopy type × month interaction ($\alpha < 0.1$). We used a split-plot

analysis because we were interested in the main effect of canopy type over the entire growing season (five months combined) and because we did not expect any carry-over effects between months (Winer et al. 1991). To further identify what differences might be driving the results of the main effects test, statistical comparisons between individual canopy types were tested using four a priori contrasts: OG vs. CC, OG vs. YA, OG vs. YC, and YA vs. YC. These contrasts were chosen so that we could detect differences between logged and unlogged areas (OG vs. CC, OG vs. YA, OG vs. YC) and differences between canopy types that commonly regenerate after logging (YA vs. YC). Alpha for the contrasts was set-wise at 0.025 (the comparison-wise error divided by a Bonferroni correction factor of four) because the four contrasts were not orthogonal (we did not perform all possible contrasts with the four canopy types) (SAS 1990). We did not contrast individual months, because we were interested in the effects of riparian canopy across the entire 5-month period. Response variables were total count density (number of macroinvertebrates·m⁻³ water), total biomass density (mg dry mass of macroinvertebrates·m⁻³ water), and detritus density (mg AFDM·m⁻³ water). All response variables were logarithmic transformed ($\ln(x + 0.1)$) to meet ANOVA assumptions of normally distributed residuals and equal variances among groups.

Results

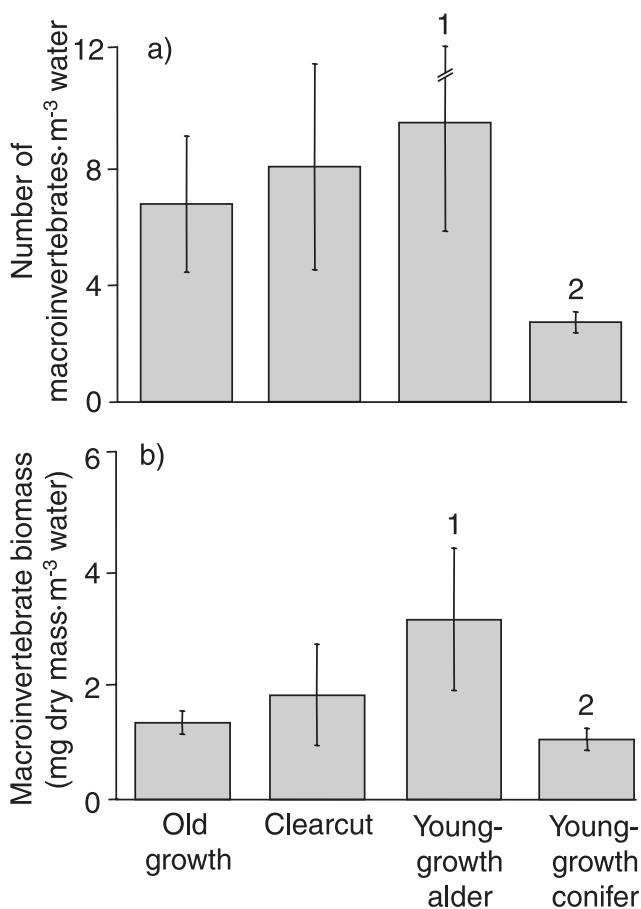
Total count density differed significantly by canopy type ($p < 0.1$; Table 2), and YA sites exported significantly more macroinvertebrates than did YC sites ($p < 0.025$; Fig. 2a, Table 2). There were no significant differences between other contrasted canopy types (OG vs. CC, YA, YC). Total biomass density did not differ significantly among canopy types in the overall test ($p > 0.1$; Table 2), but YA sites exported significantly more total biomass density than did YC sites ($p < 0.025$; Fig. 2b, Table 2). There were no significant differences between other canopy types contrasted (OG vs. CC, YA, YC).

Table 2. Analysis of variance output for comparisons of natural log ($\ln(x + 0.1)$) macroinvertebrate count (individuals·m⁻³ water) and biomass (mg dry mass·m⁻³ water) and detritus densities (mg AFDM·m⁻³ water).

	<i>p</i> values for main effects tests			<i>p</i> values for a priori contrasts of riparian canopy type			
	Canopy effect	Month effect	Canopy × month	OG vs. CC	OG vs. YA	OG vs. YC	YA vs. YC
Count density	0.0601	<0.0001	0.0026	0.4142	0.2939	0.1200	0.0166
Biomass density	0.1419	<0.0001	0.0398	0.9810	0.1661	0.2892	0.0228
Detritus	0.1307	<0.0001	0.1445	0.4261	0.5227	0.0874	0.0292

Note: Output is *p* values for the main effects tests of canopy type, month, and canopy type × month interaction ($p < 0.10$), and the a priori contrasts between canopy types ($p < 0.025$). Riparian forest canopy types are old growth (OG), clearcut (CC), young-growth alder (YA), and young-growth conifer (YC). Significant test results are shown in bold type.

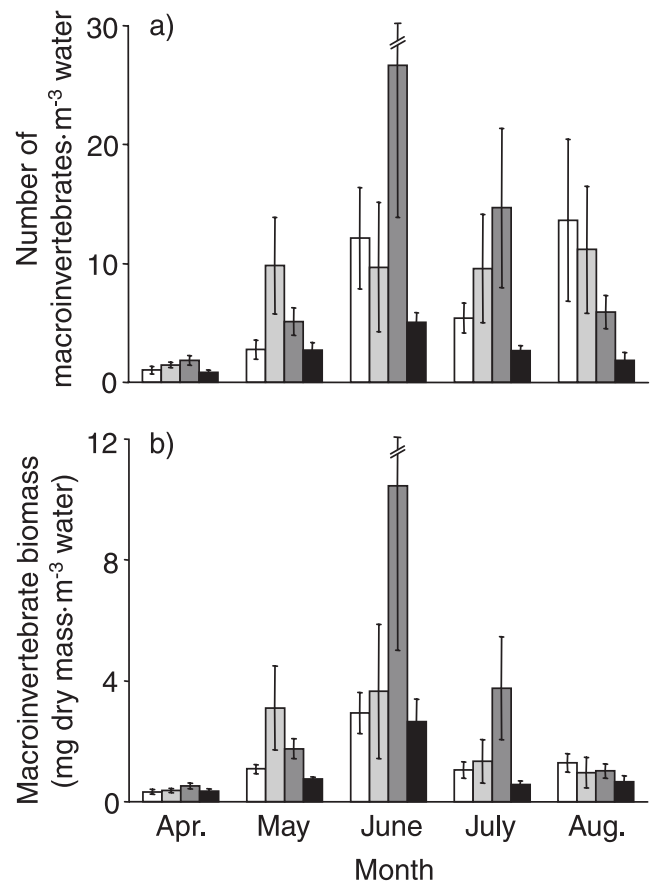
Fig. 2. Mean macroinvertebrate (a) count and (b) biomass densities by riparian forest canopy type, exported from headwater streams on Prince of Wales Island, Alaska. Each bar represents the mean with standard error of six replicate streams over five monthly sampling periods ($n = 6$) in old growth, clearcut, young-growth alder, and young-growth conifer streams. Treatment marked 1 differs significantly from treatment marked 2 ($p < 0.025$).



Both total count and biomass density differed significantly by month, and both displayed a significant canopy type × month interaction ($p < 0.1$; Table 2). Total count density peaked in June and dropped off in July and August, although temporal patterns varied among canopy types (Fig. 3a). Total biomass density peaked in June as well and dropped off sharply by August (Fig. 3b).

Detritus export did not vary significantly by treatment ($p > 0.1$; Table 2), and no significant differences were found

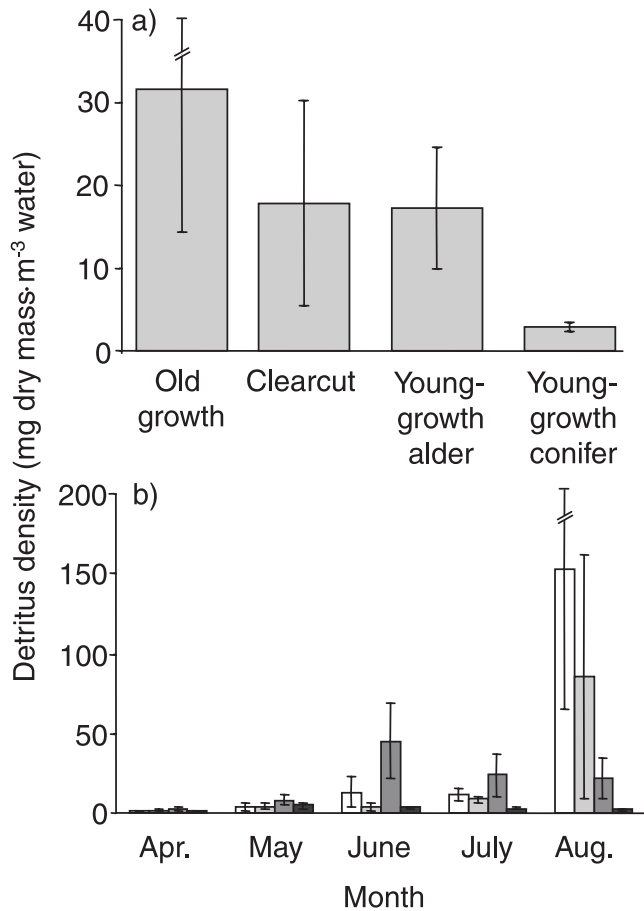
Fig. 3. Mean macroinvertebrate (a) count and (b) biomass densities by riparian forest canopy type and month, exported from headwater streams on Prince of Wales Island, Alaska. Each bar represents the mean with standard error of six replicate streams ($n = 6$) in old growth (open), clearcut (light shading), young-growth alder (dark shading), and young-growth conifer (solid).



between the canopy types contrasted ($p > 0.025$; Fig. 4a, Table 2). Young-growth alder streams exported more AFDM of detritus (mean = 17.2 mg AFDM·m⁻³ water, standard error (SE) = 7.3) than did YC streams (mean 2.9 mg AFDM·m⁻³ water, SE = 0.5), although this difference was not statistically significant ($p = 0.0292$; Table 2). Detritus export did vary significantly by month ($p < 0.1$; Table 2), peaking in August (Fig. 4b). This peak was probably due to a freshet during the sampling period.

All riparian canopy types exported greater count and biomass densities of aquatic versus terrestrial macroinvertebrates

Fig. 4. (a) Detritus density by riparian forest canopy type and (b) canopy type by month, exported from headwater streams on Prince of Wales Island, Alaska. In (a), each bar represents the mean with standard error of six replicate streams over five monthly sampling periods ($n = 6$) in old growth, clearcut, young-growth alder, and young-growth conifer streams; there are no significant differences among canopy types contrasted ($p > 0.025$). In (b), each bar represents the mean with standard error of six replicate streams ($n = 6$) in old growth (open), clearcut (light shading), young-growth alder (dark shading), and young-growth conifer (solid).



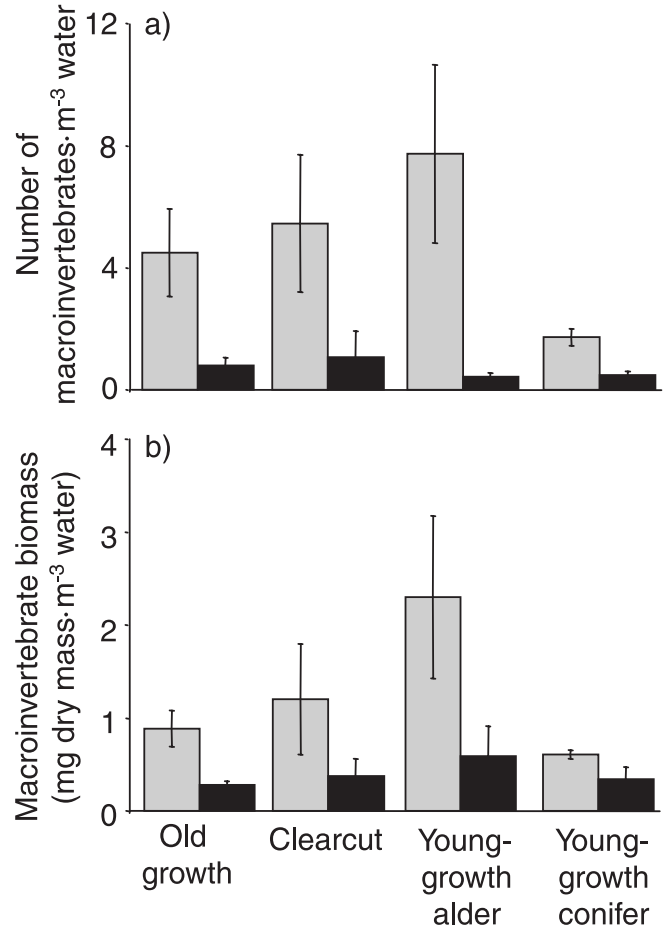
(Figs. 5a, 5b). Export of aquatic macroinvertebrates was greatest in YA streams and lowest in YC streams; terrestrial macroinvertebrate export was similar across all canopy types. Therefore, in YC streams, terrestrial macroinvertebrates made up a considerably larger proportion of total export than they did in YA streams.

More than 50 000 individual macroinvertebrates in at least 55 different taxa were identified and measured. A relatively small number of taxa comprised a large proportion of the total count (Fig. 6) and biomass (Fig. 7) densities. All of the macroinvertebrates exported, with the exception of the Nematophora, would be suitably sized prey (<10 mm long) for juvenile salmonids (Table 3).

Discussion

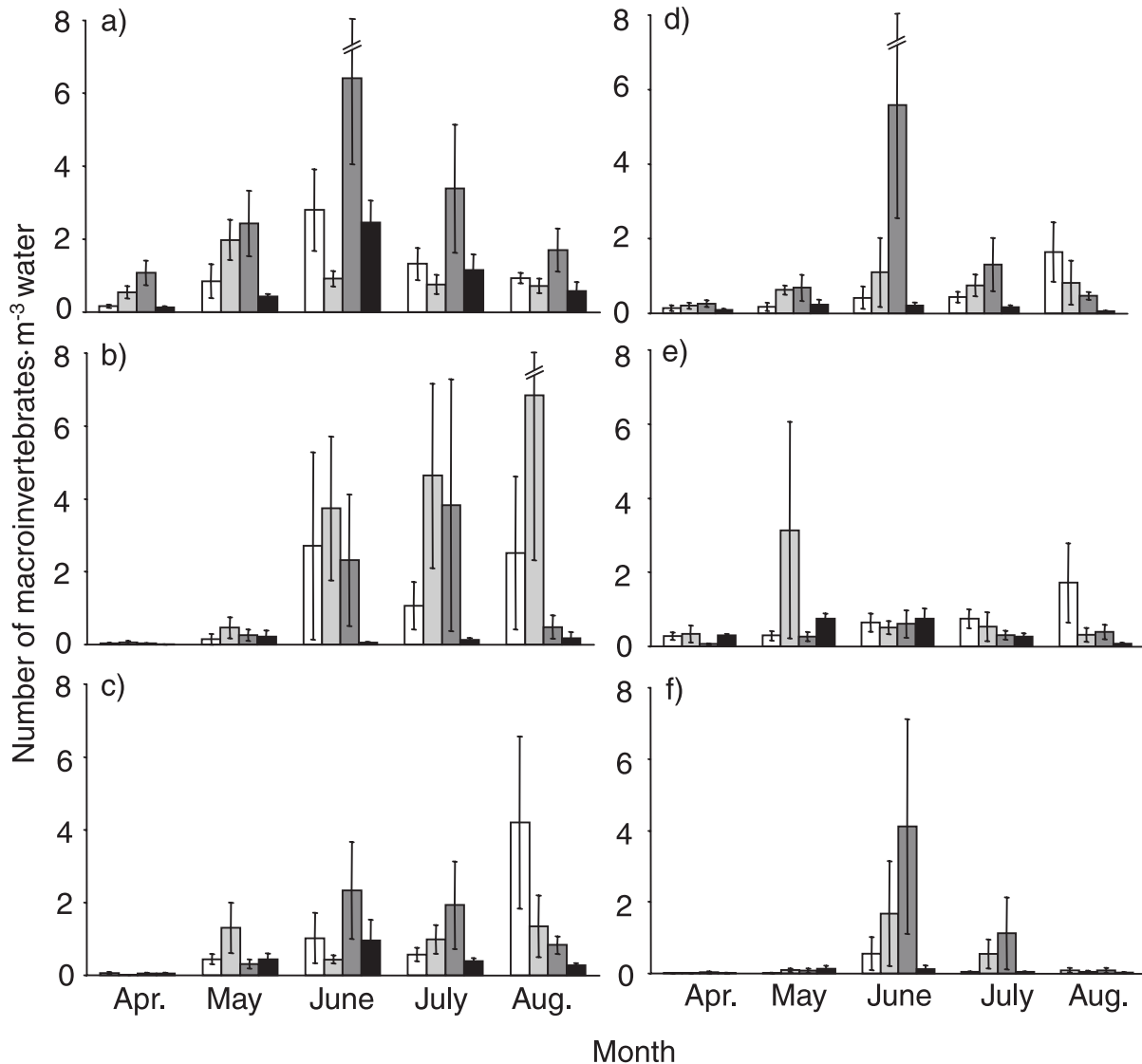
Headwater streams influence the structure and function of downstream habitats through export of organic and inorganic materials (Wallace et al. 1991; Naiman et al. 1992; Wipfli and

Fig. 5. Mean (a) count and (b) biomass densities of aquatic (light shading) and terrestrial (solid) macroinvertebrates by riparian forest canopy type, exported from headwater streams on Prince of Wales Island, Alaska. Each bar represents the mean with standard error of six replicate streams over five monthly sampling periods ($n = 6$).



Gregovich 2002). Because headwater streams can comprise more than 75% of total stream channel length in southeastern Alaska watersheds (Swanston 1967), their contribution to the energy budgets of downstream habitats may be substantial. To illustrate the potential influence of headwater export on fish-bearing foodwebs, Wipfli and Gregovich (2002) presented a trophic model of macroinvertebrate and detritus contribution from headwater streams to downstream, salmonid-producing habitats in southeastern Alaska. The model incorporates the amount of invertebrate biomass and detritus exported from fishless headwater streams that drain into a given length of downstream fish-bearing habitat. It uses these values to predict the number of juvenile salmonids that could be supported by this headwater export. Applying the model, they estimated that each kilometre of fish-bearing habitat receives enough invertebrates (mean = 1210 mg dry mass·day⁻¹) and detritus (mean = 78 g dry mass·day⁻¹) from fishless headwater streams to support 100–2000 young-of-the-year salmonids (equivalent to 0.1–2 fish per metre of fish-bearing stream). Timber harvest in these headwaters is likely to alter allochthonous inputs and is predicted to alter the energy flow and trophic linkages between upland forests and downstream

Fig. 6. Mean count densities of the six most abundant macroinvertebrate taxa by riparian forest canopy type and month, exported from headwater streams on Prince of Wales Island, Alaska. Each bar represents the mean with standard error of six replicate streams ($n = 6$) in old growth (open), clearcut (light shading), young-growth alder (dark shading), and young-growth conifer (solid). Taxa and percent relative abundance (for all canopy types and treatments combined) are as follows: (a) Baetidae, 20.5%; (b) Ostracoda, 19.1%; (c) Acarina, 11.7%; (d) Chironomidae, 9.8%; (e) Collembola, 8.4%; (f) Leuctridae, 5.5%.



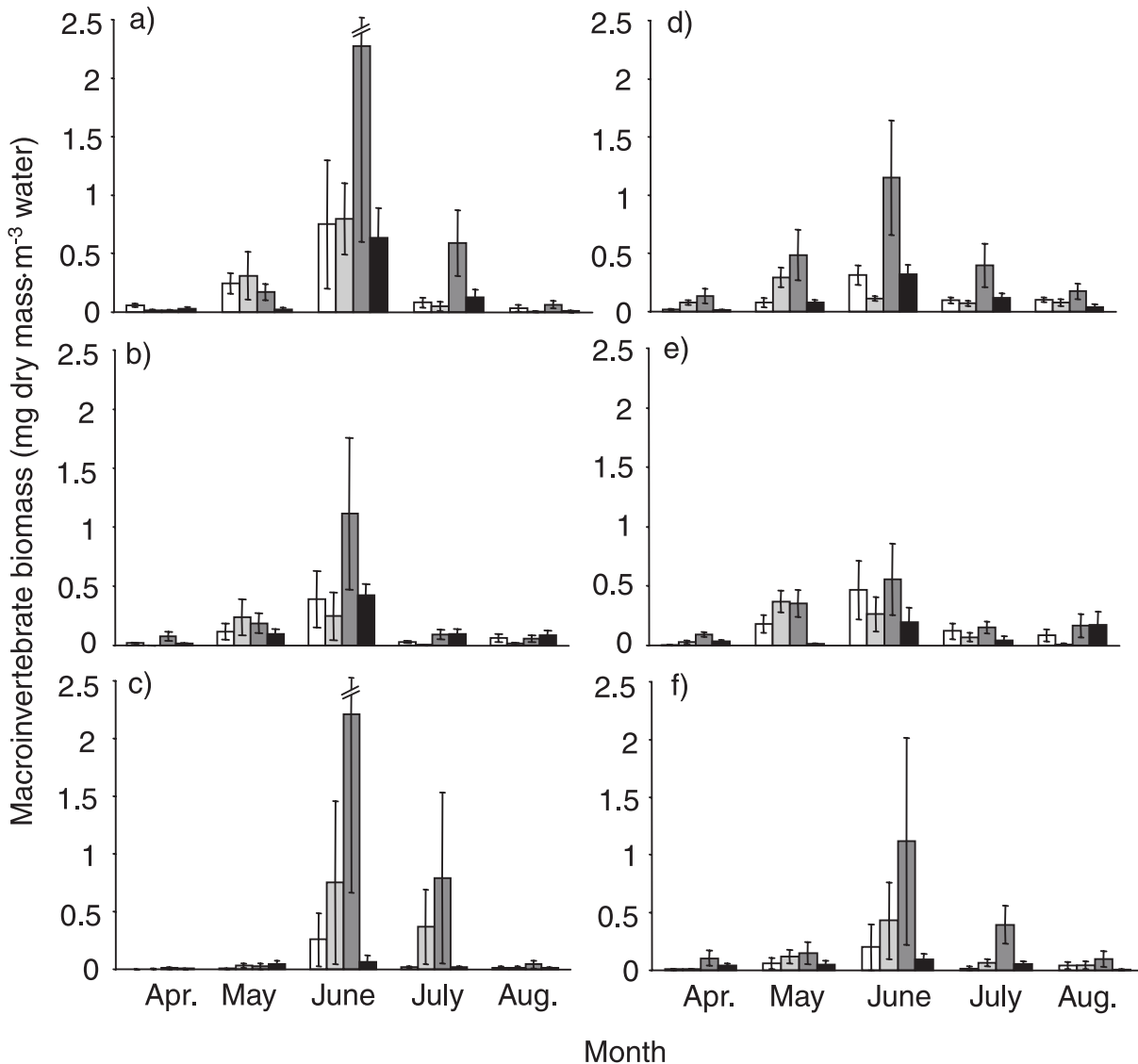
food webs (Wipfli and Gregovich 2002). To determine the long-term effects of timber harvest on the link between headwaters and downstream habitats, we sampled streams with different forest canopy types that commonly develop after clearcutting. Our results indicated that canopy type significantly affected the quantity and biomass of macroinvertebrates exported from headwaters to downstream habitats.

Timber management in the Tongass National Forest includes clearcutting and selective cutting, with stand rotations of 100–200 years between harvests (USDA Forest Service 1997, 1999). Although clearcuts may influence terrestrial and aquatic productivity (Newbold et al. 1980; Alaback 1982), they are a transient stage in forest succession. Greater long-term effects might be expected to result from forest succession following regrowth, which may last for more than 100 years. In southeastern Alaska, forest understory

productivity increases immediately after clearcutting and then decreases below old-growth levels as second-growth conifer stands grow dense and the canopy closes (Alaback 1982). Mixed alder–conifer stands, however, may have greater understory plant diversity (Deal 1997) and abundance (Hanley and Barnard 1998) than do conifer-dominated stands. Further, studies from the Pacific Northwest have shown that alder benefits disturbed riparian ecosystems by fixing nitrogen (Binkley et al. 1994) and adding organic matter (Newton and Cole 1994). Our results indicated that alder and conifer in riparian canopies might have similar respective effects on productivity and on the link between terrestrial and aquatic habitats in upland forests of southeastern Alaska.

We found that in 35- to 40-year-old stands, macroinvertebrate export from streams with young-growth alder

Fig. 7. Mean biomass density of the six most abundant macroinvertebrate taxa by riparian forest canopy type and month, exported from headwater streams on Prince of Wales Island, Alaska. Each bar represents the mean with standard error of six replicate streams in ($n = 6$) old growth (open), clearcut (light shading), young-growth alder (dark shading), and young-growth conifer (solid). Taxa and percent relative abundance (for all canopy types and treatments combined) are as follows: (a) Terrestrial Coleoptera, 13.4%; (b) Heptageiidae, 10.2%; (c) Leuctridae, 9.6%; (d) Baetidae, 9.0%; (e) Rhyacophilidae, 7.5%; (f) Amphizoidae, 7.5%.



canopies was significantly greater than the export from streams with young-growth conifer canopies. By applying the trophic model of Wipfli and Gregovich (2002), we predict that YA streams may export enough invertebrate biomass and detritus to downstream habitats to support approximately four times more juvenile salmonids than will YC streams ($0.8\text{--}11.5\text{ fish}\cdot\text{m}^{-1}$ of fish-bearing stream vs. $0.2\text{--}2.4\text{ fish}\cdot\text{m}^{-1}$ of fish-bearing stream). We apply this model to the data from this study to illustrate the potential influence of headwater canopy type on downstream food webs. Juvenile salmonids typically occupy small streams immediately downstream from headwater habitats and may reside in freshwater for up to 4 years (Groot and Margolis 1991). Headwater streams export prey and detritus to these fish-bearing habitats, potentially subsidizing these downstream food webs. We found that streams that developed al-

der canopies following clearcutting exported more prey to downstream food webs than did streams that developed conifer canopies.

The abundance of invertebrate prey may be important in limiting stream salmonid productivity (Hayes et al. 2000). We found that macroinvertebrate export from headwater streams to downstream habitats varied significantly seasonally and that there was a significant canopy type \times month interaction. This indicates that the relative influence of each canopy type on downstream habitats may change throughout the year. Juvenile salmonids in southeastern Alaska make seasonal upstream migrations into small tributaries to overwinter (Bramblett et al. 2002), and they may be particularly dependent on prey from headwaters during these periods. Our results show that headwater invertebrate export varies seasonally and under different riparian forest canopy types;

Table 3. Macroinvertebrate taxa collected in drift nets on Prince of Wales Island, Alaska, 1998, and their percent relative abundance by count (number·m⁻³ water) and biomass (mg dry mass·m⁻³ water).

Taxon ^a	Percent relative abundance	
	Count	Biomass
Annelida		
Oligochaeta	0.3	0.9
Arthropoda		
Arachnida		
Acari	11.7	0.4
Araneae	0.5	4.5
Pseudoscorpiones	<0.1	<0.1
Amphipoda	<0.1	<0.1
Copepoda	<0.1	<0.1
Isopoda	<0.1	<0.1
Ostracoda	19.1	0.6
Chilopoda	<0.1	0.5
Diplopoda	<0.1	0.4
Insecta	<0.1	<0.1
Collembola	8.4	2.9
Ephemeroptera	0.2	0.3
Ameletidae	<0.1	0.1
Baetidae	20.5	9.0
Ephemerellidae	<0.1	0.1
<i>Drunella</i>	0.2	1.0
Leptophlebiidae	0.4	0.4
<i>Paraleptophlebia</i>	3.1	1.8
Heptageniidae	3.4	10.2
Plecoptera	0.5	0.6
Chloroperlidae	<0.1	0.1
<i>Sweltsa</i>	1.2	1.8
Leuctridae	5.5	9.6
Nemouridae	0.3	0.3
<i>Zapada</i>	0.5	0.4
Perlidae	<0.1	<0.1
Perlodidae	<0.1	<0.1
Psocoptera	<0.1	<0.1
Hemiptera	0.4	0.5
Aphididae	0.2	0.1
Tricoptera	0.6	0.3
Brachycentridae	<0.1	<0.1
<i>Micrasema</i>	0.3	0.2
Glossosomatidae	<0.1	<0.1
<i>Glossosoma</i>	<0.1	<0.1
Hydropsychidae	0.3	0.5
Lepidostomatidae	<0.1	<0.1
Limnephilidae	0.3	1.2
<i>Chyranda</i>	<0.1	0.1
<i>Cryptochia</i>	<0.1	<0.1
<i>Homophylax</i>	<0.1	<0.1
<i>Onocosmoecus</i>	<0.1	<0.1
Philopotamidae	<0.1	0.1
Polycentropodidae	<0.1	<0.1
Rhyacophilidae	0.8	7.5
Lepidoptera	<0.1	<0.1
Coleoptera	0.8	3.0
Misc. terrestrial	0.7	13.4
Amphizoidae	0.4	6.5

Table 3 (concluded).

Taxon ^a	Percent relative abundance	
	Count	Biomass
Elmidae	<0.1	0.5
Dytiscidae	0.2	5.4
<i>Hydroporus</i>	0.2	0.5
Hydrophilidae	<0.1	0.2
Diptera	3.8	4.5
Ceratopogonidae	<0.1	<0.1
Chironomidae	9.8	3.3
Culicidae	<0.1	<0.1
Dixidae	1.3	0.4
Empididae	<0.1	<0.1
Simuliidae	0.5	0.4
Tipulidae	0.2	0.8
Hymenoptera	0.2	0.2
Formicidae	<0.1	<0.1
Mollusca		
Gastropoda	0.3	1.0
Nematomorpha	0.3	1.0
Platyhelminthes		
Turbellaria	1.2	1.5
Unidentified	<0.1	<0.1

^aWe identified macroinvertebrates to lowest reliable taxa (i.e., individuals that could not be positively identified to a certain taxonomic level were assigned to the next higher category). Therefore, percent relative abundance by count or biomass of a higher taxon (i.e., family) does not include those from the taxon or taxa below them (i.e., genus).

the question of how this influences salmonid productivity in downstream habitats remains unanswered.

Terrestrial invertebrates are important prey for stream salmonids and may be particularly so for juvenile salmonids in southeastern Alaska (Wipfli 1997). We found a trend toward greater count and biomass densities of aquatic macroinvertebrates in YA vs. YC streams, whereas export of terrestrial macroinvertebrates was similar across all canopy types. In our YC streams, therefore, terrestrial macroinvertebrates comprised a greater percent of total export (40% by number and 47% by mass) than they did in YA streams (17% by number and 25% by mass). Thus, terrestrial macroinvertebrates may play a greater role in food webs supported by YC streams, where they make up a much greater percentage of total export if aquatic macroinvertebrates are less abundant.

Allochthonous input from alder probably was partly responsible for elevated export of macroinvertebrates and detritus from the young-growth alder streams in this study. We observed accumulations of leaf material from previous years along the banks of YA streams and frequently collected decaying leaves in our samples. Young-growth alder streams exported over five times more detritus than did YC streams, although this difference was not statistically significant. Also, macroinvertebrate shredders prefer alder leaves to birch, willow, or poplar leaves (Irons et al. 1988), and we found that YA streams exported more Leuctridae, the most abundant shredder in our study streams. Processed leaf material may be responsible for the increased count and biomass, as has been shown in other studies (Short and Maslin

1977). We also found a trend towards greater biomass of the most common invertebrate predators, Rhyacophilidae, in YA streams, which suggests that increased production from alder inputs may be influencing upper trophic levels (Wallace et al. 1997, 1999).

Many physical and biological factors may influence the productivity of headwater streams and the invertebrates and detritus available for export (Cuffney and Wallace 1988; Naiman et al. 1992). Our research focused on measuring the effects of riparian forest canopy type on this export. We selected streams similar in size and gradient and located near one another (within an area of 150 km²) to minimize differences in geology, temperature, and precipitation. We sampled the maximum number of replicates that was practical in order to achieve suitable statistical power, although high natural variation greatly reduced statistical power. The high level of significance for the contrast between YA and YC sites, however, indicates that despite the variation added by other factors, these results were robust. Attributes for which we could not control included aspect, soil type, stream substrate, and others; these may have masked treatment effects.

Canopy removal has been reported to increase primary and secondary productivity in fish-bearing streams in southeastern Alaska (Duncan and Brusven 1985; Hetrick et al. 1998) and elsewhere in the Pacific Northwest (Bilby and Bisson 1992). Young et al. (1999) suggested a general model for Pacific Northwest streams of salmonid production initially increasing after clearcutting and subsequently decreasing below old-growth levels as forest canopy closes. Although this may be true for floodplain habitats, productivity in southeastern Alaska headwater streams may be influenced more by allochthonous input than by autochthonous production, as in other systems (Fisher and Likens 1973). Although we did not measure in-stream production, we measured macroinvertebrate and detritus export to assess how headwater streams might influence prey abundance and potentially salmonid production in downstream habitats. We found that clearcut sites did not export significantly more macroinvertebrate numbers or biomass than did old-growth sites, which may be due to low levels of allochthonous input. Also, we observed a trend toward alder-dominated sites exporting more macroinvertebrates than did clearcut sites, although we did not plan an a priori contrast for this pair. Because most nutrients are rapidly transported out of high-gradient streams (Fisher and Likens 1973), headwater productivity may not respond to increased light availability as readily as do lower-gradient streams. Thus, management activities that remove forest canopy along streams should take into account the differences in energy processes in headwater vs. floodplain channels.

Forests in southeastern Alaska are managed for multiple objectives, including sustainable timber harvest, maintenance of biodiversity, conservation of fish and wildlife resources, recreation, and aesthetic values (USDA Forest Service 1997). Successful land management for sustained yield of all of these forest resources depends upon sound knowledge of ecosystem processes for entire watersheds, of which headwaters are an integral part. We found that in areas clearcut 35–40 years ago, alder-dominated sites exported significantly greater numbers and biomass of macroinvertebrates than did conifer-dominated sites. The forest

ecosystem of southeastern Alaska contains an alder component as a consequence of both natural and human-induced disturbance (Deal 1997; Hanley and Barnard 1998). Because present policy extends little or no riparian buffer protection to class IV streams during timber harvest, headwater ecosystems will likely continue to contain an alder component. Although we do not advocate timber harvesting as a means of generating alder to increase productivity in headwater streams, maintaining some alder in existing young-growth stands may help to offset other potentially negative effects of past timber harvest.

Because headwaters are an important component of stream ecosystems, understanding their contribution to downstream habitats holds important management implications. Alder appears to influence the link between terrestrial and aquatic systems in headwaters and between upland forests and downstream habitats. Maintaining an alder component during young-growth forest succession following timber harvest may be beneficial if salmonid productivity is a concern, and we recommend that forest managers consider the potential benefits of alder in stream riparian ecosystems.

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