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Trophic linkages between headwater forests and downstream fish habitats: implications for forest and fish management

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Abstract

This study examined the fluvial transport of invertebrates (aquatic and terrestrial) and coarse organic detritus from forested headwaters in alternatives-to-clearcutting (ATC) harvest units to aquatic habitats downstream in the coastal mountains of southeastern Alaska. Fifty small streams (mean discharge $2.7\,\mathrm{L\,s^{-1}}$, range $0.1–128.1\,\mathrm{L\,s^{-1}}$) representing three geographic areas (ATC installations) throughout southeastern Alaska were sampled with $250\,\mu\mathrm{m}$ nets three times per year (April, July, September). Samples were used to assess the subsidy of energy from fishless headwaters to downstream systems containing or potentially containing fish, and to obtain preharvest data on streams for the ATC study. Invertebrates of both aquatic and terrestrial origin were captured, with aquatic taxa averaging roughly 3/4 of the total individuals sampled. Invertebrates and detritus were transported from headwaters during all sampling periods, averaging 163 mg invertebrate dry mass $\mathrm{stream^{-1}\,day^{-1}}$ ($1.7\,\mathrm{mg\,m^{-3}}$ water) and 10 g detritus $\mathrm{stream^{-1}\,day^{-1}}$ ($0.05\,\mathrm{g\,m^{-3}}$ water), respectively. Based on the frequency of headwater streams in the watersheds studied, and the average amount of food delivered to downstream habitats by these streams, every kilometer of salmonid-bearing stream could receive enough energy from fishless headwaters to support 100–2000 young-of-the-year salmonids. These results illustrate that headwaters are source areas of aquatic and terrestrial invertebrates and detritus, linking upland ecosystems with habitats lower in the catchment. ATC activities are predicted to have variable effects on headwater stream productivity, and subsequent food resources for downstream salmonids. Partial canopy removal is expected to increase solar penetration to the stream and primary and secondary production within these partially harvested sites, and full canopy removal will likely reduce allochthonous inputs of leaf litter into the streams, and reduce stream invertebrate abundance.

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1. Introduction

Movements of invertebrate prey and detritus across habitat boundaries often subsidizes receiving food webs, increasing their productivity and elevating local vertebrate and invertebrate population densities (Rose and Polis, 1998; Wipfli et al., 1998; Nakano

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et al., 1999). Stream communities can receive subsidies from both nearby and distant habitats. For example, allochthonous litter from streamside plants often makes up the bulk of the energy assimilated by benthic invertebrates in small forest streams (Fisher and Likens, 1973; Vannote et al., 1980; Cummins et al., 1989; Wallace et al., 1997). River corridors often get substantial energy and nutrient subsidies from marine ecosystems in regions that support salmon or other anadromous fishes (Levy, 1997). Wipfli et al. (1998, 1999) showed that a marine subsidy from salmon carcasses raised invertebrate density by 3–25 times in southeastern Alaska streams. This marine subsidy also dramatically increased the growth rates of resident and anadromous salmonids in Alaska streams (Wipfli et al., 2003). Terrestrial invertebrates originating from riparian forests fall prey to fishes (Hunt, 1975; Cadwallader et al., 1980; Nielsen, 1992) and can form a large portion of the invertebrate mass ingested by salmonids (Wipfli, 1997; Nakano et al., 1999; Kawaguchi and Nakano, 2001). River continuum theory also predicts that stream communities are partially supported by allochthonous plant litter and autochthonous production transported from upstream (Vannote et al., 1980).

Headwater streams are important habitats for invertebrate production (Wallace et al., 1986, 1997; Stone and Wallace, 1998), but the extent to which they subsidize downstream communities, including those containing fishes, is not clear. Aquatic invertebrates are often common in drift (Brittain and Eikeland, 1988), and both aquatic and terrestrial invertebrates can be common prey for stream fishes (Mundie, 1974; Hunt, 1975; Nielsen, 1992; Wipfli, 1997; Nakano et al., 1999; Kawaguchi and Nakano, 2001). However, the supply of invertebrates (both aquatic and terrestrial) transported from fishless headwaters to downstream communities is not understood.

In southeastern Alaska there are many features that may augment the extent to which food from headwaters subsidize downstream fish communities. High rainfall, steep valley walls, and shallow soils provide catchments with extensive networks of small fishless (intermittent and permanent) streams that feed into salmonid streams (Harris et al., 1974; Johnson et al., 2000). Because of their abundance and small size, these headwater streams have a high perimeter-to-area ratio, greatly increasing the stream–land interface (Polis et al., 1997). These same characteristics (i.e., high rainfall, steep valley walls, shallow soils) make the streams vulnerable to sudden and frequent spates, increasing invertebrate drift density and distance traveled (see Brittain and Eikeland, 1988). Further, they compose 70–90% of total stream length within drainages in southeastern Alaska (Swanston, 1967; Benda and Dunne, 1997). Finally, their high gradient produces torrential streams with high mean velocities, even at low flow, facilitating the transport of prey and particulate organic matter downstream.

The objective of this study was to determine the amount of invertebrates and detritus delivered by headwater streams draining alternatives-to-clearcutting (ATC) units (see McClellan et al., 2000) to downstream habitats that contain salmonids. Specifically, the fluvial transport of aquatic and terrestrial invertebrates (i.e., food for fish) and organic detritus (i.e., food for many aquatic invertebrates) from the ATC harvest units to downstream habitats was measured, to evaluate the potential for these streams without fish to serve as sources and conduits of energy to salmonids and other fish species (e.g., cottids) downstream. Secondly, these data would serve as preharvest data to later assess the effects of ATC activities on this fluvial transport of this material after timber harvesting took place.

2. Area description and methods

This study was part of a broader ATC project (McClellan et al., 2000). Fifty streams were sampled across the three ATC study areas: Catherine Island (including three streams on neighbouring Baranof Island) ($n = 17$), Kupreanof Island ($n = 16$), and Prince of Wales Island ($n = 17$). Study streams were small and high gradient (mean grade, 23°). Based on three measurements made during each of two sampling years, streams had a mean wetted width <1 m, depth <20 cm, and averaged 8.7 °C (Table 1 and Fig. 1). The length of stream between its origin and the sampling site was generally less than 0.5 km. All streams contained some surface flow (mean, 2.7 L s^{-1}) during all sampling bouts, albeit negligible for some streams during dry periods (down to <0.1 L s^{-1}). Their high gradient and lack of fish habitat prevented fish from colonizing reaches upstream of our sampling sites, although fish were present below study reaches. Fish species present throughout southeastern Alaska, and in various combinations in streams

Table 1
Study stream characteristics

Study site	n	Latitude/longitude		Mean length[a] (range) (m)	Mean discharge (range) ($L\,s^{-1}$)	Mean gradient (range) (°)	Mean temperature (range) (°C)
Catherine Island	17	57°23.5′N	134°57.7′W	261 (75–629)	3.62 (0.04–35.30)	27 (19–33)	7.4 (2.7–11.4)
Kupreanof Island	16	56°56.4′N	133°10.5′W	360 (63–710)	1.15 (0.01–8.04)	23 (14–31)	9.0 (3.3–12.3)
Prince of Wales Island	17	55°11.1′N	132°5.7′W	268 (42–1140)	3.41 (0.08–128.10)	18 (3–34)	9.6 (5.4–13.6)

[a] Length is of wetted streambed upstream from sampling site during base flow.

in this study depending on site and time of year, included coho (*Oncorhynchus kisutch* Walbaum), pink (*O. gorbuscha* Walbaum), chum (*O. keta* Walbaum), sockeye (*O. nerka* Walbaum), and king (*O. tshawytscha* Walbaum) salmon, cutthroat (*O. clarki* Richardson) and rainbow trout (*O. mykiss* Walbaum), Dolly Varden char (*Salvelinus malma* Walbaum), sculpin (*Cottus* spp.) and stickleback (*Gasterosteus* spp.). Our study streams fell into three broad categories based on their association with downstream fish-bearing habitats: (1) abrupt contact with fish-bearing streams where the high-gradient (typically >15°) headwater streams fed into lower gradient (typically <5°) fish streams at a clearly-defined gradient change, (2) reaches where the gradient break was gradual through a transitional reach and could contain fish at certain times (e.g., high flows), and (3) same as either of the above except streams fed into brackish or saltwater that contained fish. Most streams were in the second category. Sampling sites (points along the stream) were upstream of systems with fish, and were deliberately selected to assess the actual or potential contribution of material from fishless headwaters to salmonid streams. Study streams lacked sufficient water and habitat to consistently support fish.

Transport of invertebrates (aquatic and terrestrial) and organic detritus (i.e., particulate organic matter ≥250 μm) was measured with a 250 μm net attached to one end of a 75 cm long, 10 cm diameter plastic pipe frame, which rested on the stream bottom. The frame with attached net was secured in the middle of each stream with sandbags, one per stream. Because the sampler was placed on the stream bottom, seston (suspended particulate organic matter), and bedload particulate organic matter were both captured, and collectively labeled detritus. Macroinvertebrates in the drift as well as those moving downstream along the streambed were also captured (but were not distinguished between). Stream discharge was measured at the beginning and end of each sampling period; the calculated mean was used to determine the density of invertebrates and detritus. Most of the streams were sufficiently small for the entire streamflow to pass through the pipe. If not, the percentage relative to the total streamflow was estimated. This fraction was used to extrapolate the transport measured through the net for the whole stream.

Streams were sampled over a 72 h period every season (spring, April; summer, July; autumn, September). Invertebrates were sorted from detritus after being preserved in 70% ethanol and identified to the lowest reliable taxon, their body lengths measured, and dry mass determined by using taxon-specific length–mass regression equations (Rogers et al., 1977; Smock, 1980; Meyer, 1989; Sample et al., 1993; Burgherr and Meyer, 1997). Invertebrates were categorized as either aquatic or terrestrial if they were a product of aquatic or terrestrial secondary production, respectively (Wipfli, 1997). The remainder of the sample (detrital component) was oven dried, weighed, ashed (at 500 °C for 5 h), and reweighed to determine ash-free dry mass (AFDM).

3. Results

Study streams showed a wide range in the amount of transported invertebrates (Fig. 2A and B). Invertebrate transport rates averaged 163 mg stream^{-1} day^{-1} (range 2–2460 mg stream^{-1} day^{-1} (Fig. 2A) and <1 to 60 mg m^{-3} water (Fig. 2B)). Both aquatic and terrestrial invertebrates were abundant in the transport throughout the study, but greater numbers of aquatic invertebrates were captured at all locations (averaging roughly 3/4 aquatic and 1/4 terrestrial) (Table 2 and Fig. 3). Mayflies (Ephemeroptera) and stoneflies (Plecoptera) numerically composed the bulk of the aquatic invertebrates (nearly half of all invertebrates), while aquatic beetles composed the bulk of the mass relative

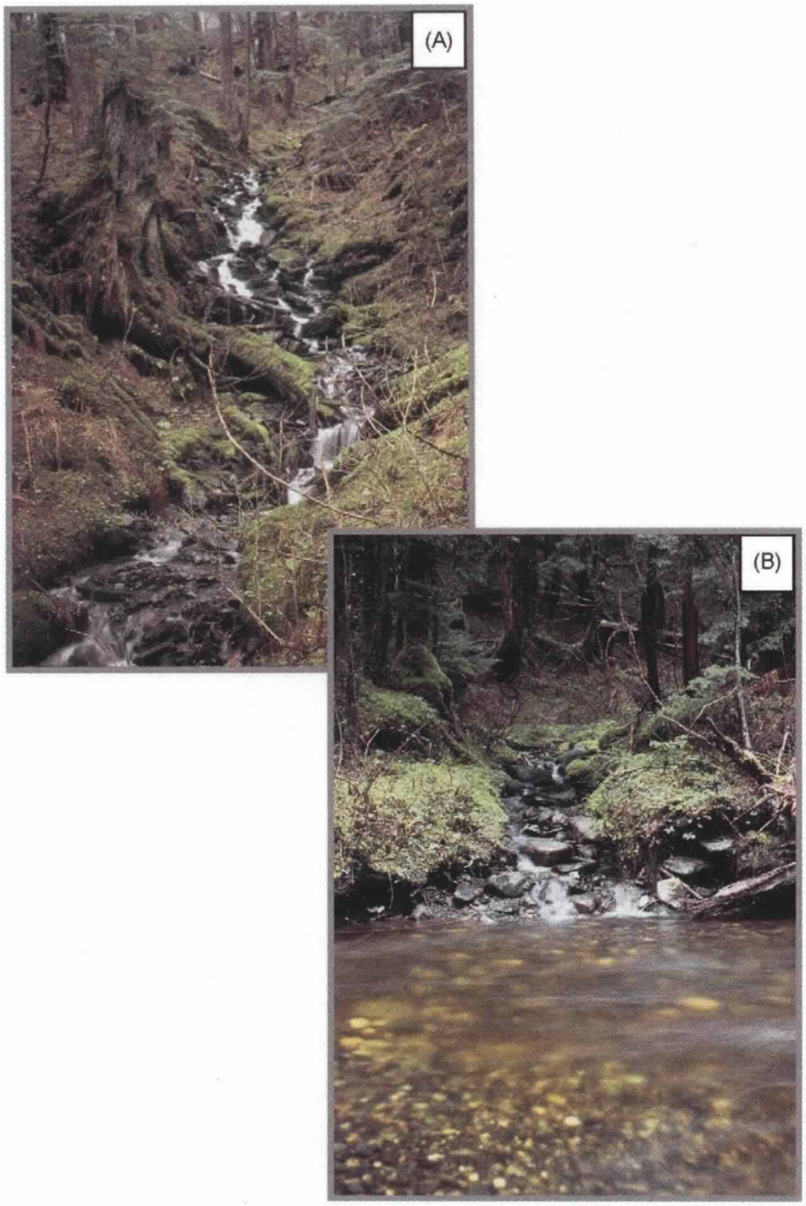

Fig. 1. Example of a typical fishless, headwater stream sampled for fluvial transport of invertebrates and detritus (A), and the junction of a fishless headwater stream with a fish-bearing stream (B).

to other taxa (nearly 1/3 of the total invertebrate mass) (Table 2). Within the terrestrial category, mites (Acari) and springtails (Collembola) were the most numerically abundant at 11 and 10%, respectively, but beetles (10% of total) and Gastropods (4% of total) made up the most mass of any given terrestrial taxa (Table 2).

Organic detritus showed similar patterns for transport (Fig. 4) as those for invertebrates (Fig. 2). Detritus transport rates averaged 10.4 g stream^{-1} day^{-1} (range <1 to 210 g stream^{-1} day^{-1}). Although transport occurred throughout the three seasons, no large differences were observed among seasons for all sites. Inver-

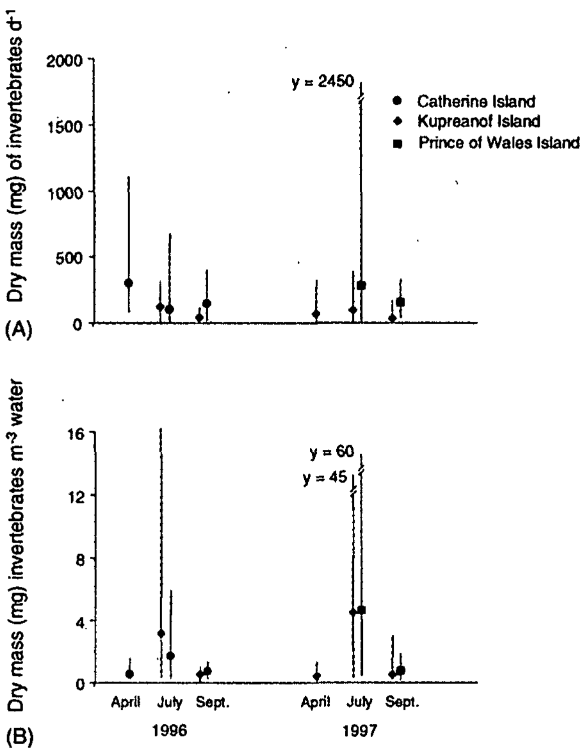

Fig. 2. Invertebrate dry mass transported stream^{-1} day^{-1} (A) and m^{-3} water (B) from study streams in the alternatives-to-clearcutting timber harvest units.

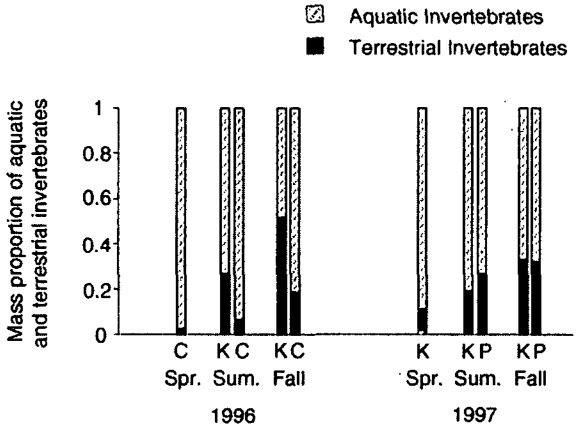

Fig. 3. Proportion of aquatic and terrestrial invertebrates transported from study streams in the alternatives-to-clearcutting timber harvest units (C: Catherine-Baranof Islands, K: Kupreanof Island, P: Prince of Wales Island).

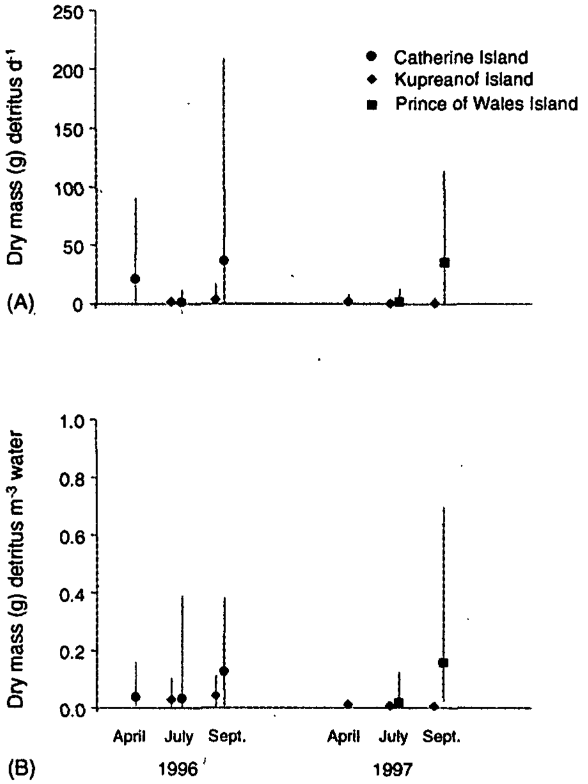

Fig. 4. Amount of detritus transported stream^{-1} day^{-1} (A) and m^{-3} water (B) from study streams in the alternatives-to-clearcutting timber harvest units.

tebrate and detritus transport were not strongly correlated with stream-specific temporal fluctuations in discharge. Correlation coefficients for individual stream discharge versus invertebrate transport, discharge versus detritus transport, and detritus transport and invertebrate transport were 0.53, 0.41 and 0.28, respectively.

4. Discussion

The streams draining the ATC units provided a season-long (spring through fall) source of invertebrates and detritus for habitats downstream. Because of their ability to potentially produce and deliver food to downstream consumers, and their particular abundance across the landscape in southeastern Alaska, these fishless headwaters and associated stream networks may be important food conduits for downstream food

Table 2
Taxonomic composition of invertebrates transported from headwater habitats in southeastern Alaska, alternatives-to-clearcutting study

Taxon	Catherine Island		Prince of Wales Island		Kupreanof Island		Mean across sites	
	Number (%)	Mass (%)	Number (%)	Mass (%)	Number (%)	Mass (%)	Number (%)	Mass (%)
Aquatic taxa								
Ephemeroptera	55.8	31.7	18.6	11.5	25.9	9.8	33.4	17.7
Plecoptera	11.0	12.7	16.9	11.0	9.1	4.7	12.3	9.5
Diptera	9.4	9.0	14.3	6.7	5.8	6.5	9.8	7.4
Ostracoda	2.9	0.1	2.9	0.1	17.4	0.2	7.7	0.1
Trichoptera	2.8	12.0	7.0	6.5	4.3	6.4	4.7	8.3
Coleoptera	2.4	20.2	2.1	31.2	4.5	42.7	3.0	31.4
Hydrachnida	0.4	0.0	1.5	0.5	1.1	0.0	1.0	0.2
Turbellaria	0.3	0.4	0.9	1.3	0.4	0.4	0.5	0.7
Oligochaeta	0.6	1.6	0.4	1.7	0.2	0.3	0.4	1.2
Nematomorpha	0.0	0.0	0.0	0.0	0.6	0.1	0.2	0.0
Amphipoda	0.0	0.0	0.3	0.7	0.0	0.0	0.1	0.2
Total aquatic	85.6	87.7	64.9	70.7	69.3	71.1	73.3	76.5
Terrestrial taxa								
Acari	4.0	0.1	17.2	0.5	12.1	0.2	11.1	0.3
Collembola	6.2	2.3	12.4	3.4	11.0	2.3	9.9	2.7
Diptera	2.5	2.5	1.1	1.3	3.3	1.6	2.3	1.8
Coleoptera	0.5	4.4	0.6	10.3	1.6	14.1	0.9	9.6
Araneida	0.4	1.5	0.9	2.8	0.9	3.3	0.7	2.5
Hemiptera	0.0	0.1	1.1	1.2	0.4	0.2	0.5	0.5
Hymenoptera	0.4	0.3	0.4	0.6	0.7	0.3	0.5	0.4
Gastropoda	0.1	0.1	0.9	6.2	0.2	6.1	0.4	4.1
Other	0.3	1.0	0.5	3.0	0.5	0.8	0.4	1.6
Total terrestrial	14.4	12.3	35.1	29.3	30.7	28.9	26.7	23.5

webs, potentially subsidizing several trophic levels (e.g., biofilm, invertebrates, and fishes) and, in turn, increase aquatic production of larger streams. Simply through their sheer number these streams potentially contribute substantial amounts to downstream aquatic habitats.

From a fisheries perspective, these headwaters may be crucial habitats for producing invertebrates (prey for fish). The invertebrate drift densities in the headwaters in this study (<1 to 22 individuals m^{-3} water) were within the lower range commonly seen in other rivers (<1 to 116 individuals m^{-3} water) throughout the world (O'Hop and Wallace, 1983; Waringer, 1992; see Allan, 1995; Giller and Malmqvist, 1998). Although scant, published evidence supports the hypothesis that salmonid populations along the west coast of North America are often food limited (Chapman, 1966; Mundie, 1974; Ashley and Slaney, 1997). Wipfli (1997) documented that terrestrial invertebrates compose at least half of the prey ingested by salmonids (juvenile salmon, char, and trout) in some southeastern Alaska streams. Although some terrestrial prey come directly from streamside vegetation adjacent to salmonid-bearing habitats, the amount (including aquatic invertebrates) that indirectly enters fish-bearing systems via small fishless permanent or ephemeral feeder streams is unclear. Because these feeder streams are abundant in the ATC units and throughout the southeastern Alaska landscape (Harris et al., 1974) and elsewhere, they may be substantial contributors of invertebrates to whole-catchment energy budgets. The bifurcated stream networks in southeastern Alaska provide numerous points of contact or transition zones between streams with and without fish (USDA, 1995). Conversely, relative to other sources such as instream production and terrestrial invertebrate inputs, these streams may contribute only a small fraction of the prey requirement.

These headwater streams are also conduits for organic detritus from forests upstream. Although the headwater streams in this study individually exported 5–10 times less organic matter (0.05–0.7 g m^{-3} water) than headwaters reported elsewhere, 0.5–4.0 g m^{-3} water (Wallace et al., 1982, 1991), their abundance throughout the landscape in southeastern Alaska makes them a potentially important source of this material. River continuum theory suggests that organic matter is transferred from small to large systems, implying that downstream communities are subsidized by upstream riparian and stream habitats (Vannote et al., 1980). Clearly, the forested headwater streams sampled in this study receive allochthonous input from adjacent riparian vegetation. Timber harvesting in these upland forests is expected to change the riparian plant community composition and structure, in both the understory and overstory (McClellan et al., 2000). The resulting change in allochthonous input may have a large impact on the eventual organic matter transport from these habitats. Although decreased allochthonous inputs should follow timber harvest, more light reaching the streams could increase primary production, which may partially alleviate the predicted reduction in transport of organic matter previously derived from streamside plants (Gregory et al., 1987), provided increased production is not tempered by sedimentation from logging (Waters, 1995). Although the detrital fraction measured in this study represents only a fraction of the entire organic matter suite (Wotton, 1994), it should serve as a useful indicator of relative organic matter abundance among these streams. Thus organic detritus may serve as a practical and reliable tool for assessing relative changes in organic matter transport through time following timber harvest in these plots.

These data suggest that every kilometer of salmonid stream receives enough material (prey and detritus) from the headwaters to support roughly 100–2000 young-of-the-year coho salmon, based on headwater stream frequency in the areas sampled (7.4 streams enter every km of fish-bearing reach). This estimate is based on mean delivery rates of 163 mg invertebrates $stream^{-1}$ day^{-1}, and average consumption rates for young-of-the-year coho salmon fry (2–3 g body mass) ranging from 5 mg to a maximum of 20 mg prey day^{-1} at 10 °C (Elliott, 1975; Dunbrack, 1988; Jobling, 1994), and corrects for contributions from ephemeral streams (by a factor of 1–2), organic matter (factor of 1.5–2), and invertebrates less than 250 μm (factor of 1.5–2) that are also contributing energy to these food webs (i.e., 163 mg invertebrates $stream^{-1}$ day^{-1} × 2.25 to 8 {detritus—250 μm invertebrate—ephemeral stream} correction factor × 7.4 headwater streams km^{-1} fish-bearing reach, with consumption at 5–20 mg invertebrates $fish^{-1}$ day^{-1}). These estimates provide useful insight into the potential dependence of downstream habitats (including salmonid-producing habitats) on upland ecosystems throughout southeastern Alaska including these ATC units, and on the connectivity between these upland and lowland habitats. Stream and catchment-specific physical and biological features (gradient, subsurface flow, catchment geometry, channel roughness and complexity, invertebrate drift distance, spiraling length, riparian vegetation) will probably affect prey and organic matter delivery to salmonid habitats.

5. Conclusion

This study highlights one mechanism that links upland forests, headwater stream margins, headwater streams and larger streams within the valley bottom. It also emphasizes how transport of energy (prey and detritus) from certain habitats or ecosystems may subsidise neighbouring or more distant food webs (Polis and Hurd, 1996; Polis et al., 1997; Wipfli et al., 1998, 1999; Nakano et al., 1999; Kawaguchi and Nakano, 2001). Because fishless headwater streams are abundant in southeastern Alaska, they may contribute substantially to the overall energy budgets of the fish-bearing habitats downstream. The proposed ATC harvesting in these forests could have substantial and variable effects on the energy pathways of these upland streams, and the subsequent flow of material (e.g., invertebrates and detritus) to downstream food webs. Partial or complete riparian forest canopy removal will initially provide less allochthonous inputs and more autochthonous production (due to increased solar radiation) in these small streams (Fisher and Likens, 1973; Gregory et al., 1987; Hetrick et al., 1998). It is also predicted that harvesting strategies that remove fewer trees per stand will cause smaller shifts (less amplitude and shorter duration) in energy pathways than harvesting scenarios that remove more timber. Some of these "intermediate" alternative harvest strategies (i.e., versus no cutting or clearcutting) may actually elevate headwater productivity and downstream material transport, provided the physical integrity of these systems is not compromised, as streams receive increased solar radiation while sustaining some level of allochthonous inputs from the riparian trees and understory plants that remain. However, timber harvesting may also increase soil erosion, temperature, and sedimentation (Waters, 1995), which may ultimately reduce biological responses.

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