Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs

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Abstract: Salmonid food webs receive important energy subsidies via terrestrial in-fall, downstream transport, and spawning migrations. We examined the contribution of terrestrially derived invertebrates (TI) to juvenile coho (*Oncorhynchus kisutch*) in streams of southeastern Alaska by diet analysis and sampling of TI inputs in 12 streams of contrasting riparian vegetation. Juvenile coho ingested 12.1 mg·fish^{-1} of invertebrate mass averaged across all sites; no significant differences associated with location (plant or forest type) were detected, possibly because prey are well mixed by wind and water dispersal. Terrestrial and aquatic prey composed approximately equal fractions of prey ingested. Surface inputs were estimated at ~80 mg·m^{-2}·day^{-1}, primarily TI. Direct sampling of invertebrates from the stems of six plant species demonstrated differences in invertebrate taxa occupying different plant species and much lower TI biomass per stem for conifers compared with overstory and understory deciduous plants. Traps placed under red alder (*Alnus rubra*) and conifer (mix of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*)) canopies consistently captured higher biomass of TI under the former. Management of riparian vegetation is likely to influence the food supply of juvenile coho and the productivity of stream food webs.

Résumé : Les réseaux alimentaires des salmonidés reçoivent d'importants apports des chutes depuis le milieu terrestre, du transport vers l'aval et des migrations de reproduction. Nous avons évalué la contribution des invertébrés d'origine terrestre (TI) au saumon coho (*Oncorhynchus kisutch*) dans des cours d'eau du sud-est de l'Alaska par l'analyse du régime alimentaire et un échantillonnage des apports de TI dans 12 cours d'eau à végétation riparienne différente. Les jeunes saumons ingèrent 12,1 mg d'invertébrés par poisson (moyenne de tous les sites); il n'y a pas de différences significatives entre les sites (type de forêt ou de plantes) probablement parce que les proies sont bien dispersées par le vent ou le courant. Les proies terrestres et aquatiques représentent des fractions à peu près égales des proies ingérées. Les apports en surface ont été estimés à ~80 mg·m^{-2}·jour^{-1}, principalement des TI. L'échantillonnage des invertébrés directement sur les tiges de six espèces de plantes révèle des différences entre les taxons d'invertébrés habitant sur les différentes espèces; la biomasse par tige de conifères est beaucoup plus faible que celle observée chez les plantes décidus qui poussent au-dessous ou au-dessus de la canopée. Des pièges placés sous des couvertures d'aulnes rouges (*Alnus rubra*) récoltent toujours une plus grande biomasse de TI que ceux qui sont sous les conifères (mélange de pruches de l'ouest (*Tsuga heterophylla*) et d'épinettes de Sitka (*Picea sitchensis*)). La gestion de la végétation riparienne risque donc d'influencer la nourriture disponible aux jeunes saumons coho ainsi que la productivité des réseaux alimentaires des cours d'eau.

[Traduit par la Rédaction]

Introduction

Subsidies of prey and detritus from one habitat to another can greatly influence communities within receiving habitats, elevating the abundance of consumers and food web produc-tivity (Polis et al. 1997; Wipfli et al. 1998). Freshwater communities commonly receive prey and detritus subsidies from surrounding habitats. For example, riparian vegetation pro-vides terrestrial invertebrates to streams, furnishing prey to fishes (Cadwallader et al. 1980; Nielsen 1992; Wipfli 1997).

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In coastal areas that support salmon or other anadromous fishes, freshwater systems often receive large influxes of detritus from marine ecosystems in the form of fish carcasses and eggs, thereby subsidizing food web productivity (Bilby et al. 1996; Schmidt et al. 1998; Wipfli et al. 1999). River continuum theory illustrates that stream communities are subsidized by allochthonous plant litter and autochthonous production that originates from upstream habitats (Vannote et al. 1980). Studies by Wipfli and Gregovich (2002) and Piccolo and Wipfli (2002) show that upland streams provide substantial invertebrate biomass and organic detritus to downstream habitats, subsidizing salmonid-bearing food webs in Alaska.

Although it is clear that riparian zones play a major role in regulating energy flow in low-order streams (Vannote et al. 1980), less is known of the trophic linkage that terrestrial invertebrates create between riparian and stream food webs, for example, terrestrial invertebrates serving as food for fishes (Wipfli 1997). They can comprise more than 50% of energy intake by stream fishes and are often a preferred prey of juvenile salmonids (see review by Hunt 1975). Nielsen (1992) found that terrestrially derived prey composed up to 28% of the total energy intake of juvenile coho (*Oncorhynchus kisutch*) in Washington, whereas Wipfli (1997) reported that terrestrial prey composed over half of the biomass ingested by Dolly Varden char (*Salvelinus malma*), juvenile coho salmon, and cutthroat trout (*Oncorhynchus clarki*) in several southeastern Alaska streams. By constructing detailed annual budgets of terrestrial inputs and their consumption by salmonids, Kawaguchi and Nakano (2001) demonstrated that terrestrial invertebrates composed 53% of the annual prey consumption in a forested stream and 49% in a grassland stream. Terrestrial inputs were about twice as great in the forested stream than in the grassland stream, but their contribution to fish diet was virtually identical. Conversely, Edwards and Huryn (1995) found that terrestrial invertebrates made only a small contribution to trout diet in a New Zealand pasture stream.

Some evidence indicates that forest management and the species of riparian vegetation and canopy type can greatly influence terrestrial invertebrate abundance and may affect the amount of these invertebrates that enter streams and fall prey to aquatic predators. Deciduous trees generally support more invertebrates than conifers (Southwood 1961). Clearcutting decreased arthropod abundance the following year but increased their abundance the second year in North Carolina (Schowalter et al. 1981). Overhanging vegetation influenced terrestrial invertebrate input in some streams in Victoria, Australia, and terrestrial prey were more common in diets of fish from sites with overhanging vegetation (Cadwallader et al. 1980). Riparian forests with a substantial red alder (*Alnus rubra*) component may provide more terrestrially derived food for juvenile coho salmon, cutthroat trout, and Dolly Varden char than those riparian forests with only conifer (Wipfli 1997).

If plant species or forest type influence terrestrial invertebrate communities, then riparian forest management will likely play a major role in regulating food resources for fishes, especially in small streams. Clearcutting throughout riparian zones of salmonid-rearing streams that occurred from the 1950s through 1990 has given rise to young-growth riparian canopies ranging from 13 to 50 years old in southeastern Alaska (U.S. Department of Agriculture Forest Service (USDA) 1997, 1999). Red alder is often abundant in regenerating young-growth riparian stands of Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Alaska yellow cedar (*Chamaecyparis nootkatensis*); salmonberry (*Rubus spectabilis*), blueberry (*Vaccinium ovalifolium* and *Vaccinium alaskaense*), and currant (*Ribes* spp.) are common understory plants. However, the effect of plant species and forest type on terrestrially derived food resources for fishes is not clear. Knowing the relative contribution that terrestrial invertebrates make to stream food webs and how vegetation cover affects this subsidy should contribute to improved riparian forest and fisheries management in southeastern Alaska and other regions.

Our objectives were to determine (*i*) the importance of terrestrially derived invertebrates (TI) as prey for juvenile coho salmon and (*ii*) the influence of forest and plant type (old growth (OG) versus young growth (YG), deciduous versus coniferous, alder versus spruce–hemlock, and overstory versus understory) on the abundance of TI and their inputs into streams. Our overall goal was to evaluate the flow of prey from riparian forests to stream ecosystems in southeastern Alaska and provide insight into the effects of riparian forest type on the trophic linkages between streams and their associated riparian corridors for improved fish and forest management.

Methods

Study sites

All study sites (12 streams and associated riparian zones) were located on Prince of Wales Island at the southern end of the Alexander Archipeligo temperate rainforest of the southeastern Alaska panhandle, U.S.A. (Fig. 1). Harris et al. (1974) describe the climate and setting. During 1996 and 1997, we studied a total of 12 streams, including six stream reaches in YG forests that were clearcut 35–50 years previously and six reaches in OG catchments. YG sites were selected to represent a range of alder, the predominant overstory deciduous tree found along these streams, and OG sites were chosen to provide reference conditions. Stream reaches were approximately 100–200 m in length, depending on ease of finding suitable locations for invertebrate collection (described below).

Site characterization

Riparian overstory trees >5 cm diameter at breast height (DBH) were surveyed in six pairs of plots (5 × 10 m) spaced evenly along both banks of study reaches, which ranged from 115 to 643 m in length. Length of study reach was determined by the amount of suitable habitat in and along the given reach of stream. Reach boundaries were set once we had enough pools suitable as fish habitat and enough preselected vegetation types under study along the riparian zone. A total area of 600 m² was surveyed, composing 5–26% of the riparian area defined by a 10-m strip on either side of the streams. The basal area for each tree species was estimated using the midpoint DBH of size class (5–10 cm, 10–15 cm,

Fig. 1. Southeastern Alaska and Prince of Wales Island, U.S.A. Study locations are enclosed within a rectangle from 55.00 to 55.30°N and from 132.65 to 133.05°W.
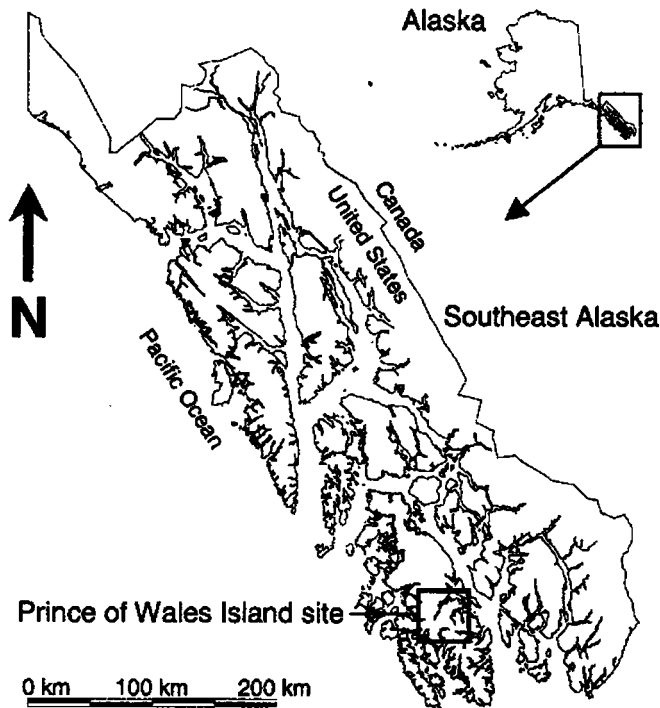
etc.). Understory vegetation was estimated qualitatively to determine the approximate frequency of common taxa.

Physical habitat within each stream reach was characterized following Alaska Region Forest Service protocols that were in draft form at the time (USDA 2001). Channel dimensions (width, depth, and cross-sectional area) were estimated from three transects spaced widely along the study reach. The surface area of principal habitat features (riffles, runs, pools) was measured for a representative 100-m stream section. We estimated wood associated with randomly chosen 50-m sections of stream channel by measuring total length and upper and lower diameters for each piece of wood >2 m in length with 10-cm basal diameter following protocols of Robison and Beschta (1990). This estimate also included wood suspended above the channel and extending laterally from the channel. Stream discharge was measured at each stream once during typical summer flow with a current meter by recording velocity at 10 evenly spaced points across the stream cross-sectional profile (wetted) at 40% depth from the stream bottom.

Invertebrates as salmon prey

Juvenile coho (40–100 mm fork length (FL)) were trapped monthly during June–September 1996 from all pools within the study reach at six YG and six OG sites selected to have either conifer or alder as the dominant (at or near 100%) overhanging vegetation. Fish were removed from minnow traps baited with salmon eggs, usually within <20 min of trap placement, anaesthetized with MS-222® (Argent Chemical Laboratories, Inc., Redmond, WA 98052), measured (mm), and weighed (g), and their stomach contents were flushed with a 10-mL syringe assembly (Meehan and Miller 1978). Three

coho per vegetation type, date, and stream site were treated as subsamples (Table 1). Because streams were the unit of replication in the OG versus YG contrast, with sampling on multiple dates, replication within individual stream reaches was deemed less important. The three fish were haphazardly selected from all trapped fish to represent the full range of size classes (within 40- to 100-mm FL) collected. All invertebrates were preserved in alcohol, and later organisms were identified to order and aquatic or terrestrial origin and were measured to the nearest millimetre for estimating biomass by mass–length regressions (Rogers et al. 1976; Smock 1980; Meyer 1989; Burgher and Meyer 1997; M.S. Wipfli, unpublished data) for this and the other study components.

Stream inputs of aerial invertebrates

Invertebrate composition and abundance falling to the stream surface were assessed using floating pan traps. Wipfli (1997) describes the method and potential limitations. In 1996 we sampled six YG streams to contrast surface inputs associated with locations of predominantly red alder or conifer (spruce and hemlock mix) vegetation ($n = 6$). In 1997, we sampled eight streams to contrast OG and YG forest types (4 YG: Tye, Camp Maybeso, Natzahini; 4 OG: Pass, Trocadero, Three-ten, Upper Fubar; $n = 4$; Table 1). In each year, three surface traps per vegetation type, date, and stream site were treated as subsamples. Clear plastic pans (37 × 25 cm, 13 cm deep) containing a small amount of water and a commercial soap as a surfactant to aid in trapping organisms were tethered in pool areas under vegetation overhanging the stream channel. At monthly intervals, pans were set in place for ~1 week. Low temperatures ensured that decomposition of invertebrates captured over this time period was minimal. Diptera were identified to family where possible to determine if individuals were associated with terrestrial or aquatic habitats. Invertebrates were categorized as terrestrial if they were a product of terrestrial secondary production. Aerial stages of aquatic insects were excluded from the terrestrial category. Because of difficulties with family-level identification of dipterans, our ability to determine aquatic versus terrestrial origin with this group was limited.

Invertebrates associated with terrestrial vegetation

To quantify invertebrate biomass and composition associated with specific vegetation type, we sampled three overstory species (alder, spruce, and hemlock) and three understory taxa (salmonberry, blueberry, and currant) by clipping three haphazardly selected stems within 1 m of the stream bank at each site at approximately monthly intervals (Table 1). Individual stems within a 2 m vertical and 1 m horizontal distance of permanent stream-bank margins were bagged and clipped, and a commercial insecticide (Pyrethrin® strip or aerosol; Schultz Company, Bridgeton, MO 63044-3720) was added to kill invertebrates, which were later identified to order, and body length was determined to the nearest millimetre. All leaves were removed from each stem, dried (60°C, 24 h), and weighed to express invertebrate biomass per leaf biomass sampled. The three stems collected per plant species, date, and stream site were treated as subsamples.

Another estimate of possible differences in invertebrate production between vegetation types was obtained in 1997

Table 1. Data structure and analysis of variance results for the five studies: invertebrates as salmon prey, stream inputs of invertebrates (conifer versus alder, and old growth versus young growth), and invertebrates associated with terrestrial vegetation (stem samples and funnel trap samples).

Source	df (balanced)	df (actual)	F	P
Invertebrates as salmon prey				
Forest type	1	1	0.34	0.574
Error	10	10		
Plant species	1	1	0.56	0.472
Plant species × forest type	1	1	0.19	0.674
Error	10	10		
Month	3	3	4.09	0.011
Month × forest type	3	3	2.03	0.122
Month × plant species	3	3	0.55	0.650
Month × plant species × forest type	3	3	0.94	0.427
Error	60	49		
Total	95	84		
Stream inputs of invertebrates — conifer versus alder				
Stream	5	5		
Plant species	1	1	0.69	0.443
Error	5	5		
Month	3	3	0.68	0.575
Plant species × month	3	3	1.45	0.251
Error	30	26		
Total	47	43		
Stream inputs of invertebrates — old growth versus young growth				
Forest type	1	1	0.64	0.455
Stream (forest type)	6	6		
Month	3	3	3.93	0.026
Forest type × month	3	3	0.31	0.817
Month × stream (forest type)	18	18		
Total	31	31		
Invertebrates associated with terrestrial vegetation — stem samples				
Forest type	1	1	0.54	0.481
Stream (forest type)	10	10		
Plant species	5	5	10.70	<0.001
Plant species × forest type	5	5	1.42	0.232
Error	50	50		
Month	3	3	20.47	<0.001
Month × forest type	3	3	3.38	0.020
Month × plant species	15	15	2.03	0.016
Month × plant species × forest type	15	15	0.91	0.550
Error	180	152		
Total	287	259		
Invertebrates associated with terrestrial vegetation — funnel trap samples				
Stream 1 (Battery)				
Plant species	1	1	2.21	0.163
Site (plant species)	12	12		
Month	3	3	2.30	0.097
Plant species × month	3	3	0.31	0.817
Error	30	30		
Total	49	49		

Table 1 (*concluded*).

Source	df (balanced)	df (actual)	*F*	*P*
Stream 2 (Maybeso)				
Plant species	1	1	5.43	0.042
Site (plant species)	10	10		
Month	3	3	12.00	<0.001
Plant species × month	3	3	1.07	0.378
Error	26	26		
Total	80	80		
Stream 3 (Beaver)				
Plant species	1	1	5.40	0.039
Site (plant species)	12	12		
Month	3	3	2.60	0.066
Plant species × month	3	3	3.30	0.033
Error	36	36		
Total	93	93		

by placing "funnel traps" in dense alder or conifer patches (≥10 m diameter) within the riparian zone (≤10 m from streams) of three YG sites (Upper Beaver, Battery, and Maybeso Branch; Table 1). Each trap consisted of an 11.5-cm-diameter funnel seated on a 1-L bottle containing a small amount of alcohol. Traps were fastened to a wooden dowel and positioned within 1 m of the ground within a dense stand of alder or conifer within 5–10 m of the stream edge and were sampled approximately every 2 weeks. Three traps were arranged in a triangle and placed about 1 m apart under each canopy type.

Statistical analysis

We performed analyses of variance and used a priori contrasts to test hypotheses relating forest type to terrestrial inputs and fish diet (Table 1). Mass and counts of prey ingested per fish were analyzed according to a split–split plot with forest type (OG, YG) assigned to streams (whole plots) and the subfactors of species (alder, conifer) and time (June, July, August, and September) assigned to fishes within a stream. The mass of invertebrates per gram of leaf stem was analyzed according to the same design but with subfactors of species (alder, hemlock, spruce, salmonberry, blueberry, currant) and time. We identified eight a priori contrasts, including deciduous versus conifer and understory versus overstory and pairwise comparisons of species within understory and within overstory classes. This was done to conserve statistical power while still making the most ecologically meaningful comparisons. Mass of stream inputs (1996 pan traps) was analyzed according to a split block with plant species (alder, conifer) assigned to pans within a block (stream) and pans sampled repeatedly over time. Mass of stream inputs for 1997 pan traps was analyzed according to a split-plot experimental design with pans sampled repeatedly over time. Streams (whole units) were nested under the factor of forest type (OG, YG). Mass of invertebrates collected in funnel traps was analyzed separately for each stream according to a split-plot experimental design with traps sampled repeatedly over time. Funnels were nested under species (alder, conifer). Critical value was set to α = 0.05 for all tests except the eight a priori stem comparisons for which the Bonferroni adjustment was used.

Results

Site characteristics

Overstory trees along stream margins consisted primarily of alder, spruce, and western hemlock, with the occasional western red cedar. Spruce was somewhat more common than hemlock at most sites; however, two OG sites, Three-tenth-mile and Twiw, were strongly hemlock-dominated and contained little red alder (Table 2). The total basal area of overstory vegetation was significantly greater in OG compared with YG sites ($p < 0.05$). In addition, the amount of alder generally was greater at YG compared with OG sites ($p < 0.05$).

Line transect surveys of understory shrubs documented that salmonberry was common and abundant at all sites. Currant and blueberry were patchy and uncommon at most sites, with the exception of Old Tom, where currant was common, and Upper Fubar, where blueberry was common.

Active channel widths of the 12 study streams ranged from 1.9 to 11.2 m at YG sites and from 3.6 to 10.5 m at OG sites (Table 2). Discharge during the study varied from <0.01 $m^3 \cdot s^{-1}$ in the smallest streams to nearly 1 $m^3 \cdot s^{-1}$. This encompasses a common range in discharge and drainage area for small streams supporting coho salmon, and the range of stream sizes was similar for both OG and YG sites (Table 2). OG streams averaged about four times the volume of wood associated with the stream channel compared with YG streams when averaged across six streams for both forest types (Table 2). However, variance was high and sample size relatively small, and forest types did not differ statistically in mean volume. Stream surface area that was classified as pool ranged from 25.2 to 75.2%. No relation between wood volume and pool area was discernable. The percentage of stream surface classified as pool was nearly identical when averaged across YG (50.3%) and OG (49.3%) sites.

Invertebrates as salmon prey

Juvenile coho ingested a diverse mix of prey that included both aquatic and terrestrial production. Across all sites, of

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Table 2. Study stream characteristics for young-growth (YG) and old-growth (OG) sites.

Stream	Forest type	Drainage area (km^2)	Discharge (m^3·s^{-1})	Active channel width (m)	Surface area as pool (%)	Wood volume (m^3·50 m^{-1})	Overstory Basal area (cm^2·m^{-2})	Alder (%)
Beaver	YG	96.3	0.18	7.8	76.2	5 585	36.4	70.3
Camp	YG	101.6	0.97	11.2	60.5	6 591	19.8	79.2
Battery	YG	1.1	0.01	1.9	42.3	262	26.5	33.1
Maybeso	YG	4.4	0.01	2.5	32.4	2 214	43.1	43.0
Natzahini	YG	52.9	0.22	9.1	59.8	529	30.4	82.2
Tye	YG	10.2	0.02	2.5	56.4	2 606	30.5	12.1
U. Fubar	OG	68.9	0.11	8.8	27.0	4 129	27.7	35.1
Old Tom	OG	141.2	0.47	11.2	25.2	6 682	96.2	11.7
Pass	OG	46.5	0.54	7.5	43.5	1 223	69.1	5.2
Three-ten	OG	1.4	0.01	3.7	65.1	11 442	103.6	0.5
Trocadero	OG	188.9	0.07	10.5	60.0	46 327	50.1	20.7
Twiw	OG	11.1	0.01	3.6	75.2	3 061	41.2	0.0

the invertebrates that were identifiable, approximately 32% by mass of ingested prey were of aquatic origin and 33% by mass were of terrestrial origin. Roughly one-third of ingested prey, largely Diptera, could not be reliably attributed to either aquatic or terrestrial origin at the level of taxonomic resolution employed here (Table 3). The mean mass of prey ingested per fish averaged across all 12 streams was 12.1 ± 1.4 mg (± standard error of the mean (SEM)).

There were no significant differences for mean invertebrate biomass between forest types (OG vs. YG ; $p = 0.57$), species (alder vs. conifer; $p = 0.47$), and forest type by species interaction ($p = 0.67$) (Table 1). The biomass of terrestrial prey showed significant differences over time ($p = 0.01$), being higher in July and August and lower in June and September. There was no significant interaction between time and forest type or time and plant species (Table 1).

Terrestrial prey were more numerous than aquatic prey in 3 of the 4 months ($p < 0.05$; Fig. 2a), whereas terrestrial and aquatic prey were similar by biomass ($p > 0.05$; Fig. 2b). This indicates that terrestrial prey were more numerous but smaller than aquatic prey, unlike the findings of Wipfli (1997). The Collembola, Aphididae, and Hymenoptera all are small individuals that were ingested in high numbers but comprised relatively little biomass (Table 3). A comparison of OG and YG sites based on the proportion of terrestrial prey did not reveal differences as a result of forest type either by numbers or by biomass ($p > 0.05$). Based on mass, the proportion of terrestrial prey did not differ significantly across months, averaging 49% overall. Prey of coho captured from pools under primarily alder versus conifer vegetation did not differ detectably in the terrestrial versus aquatic component.

Stream inputs of aerial invertebrates

Representatives of 18 orders of invertebrates were collected in surface traps during 1996 and 1997. Diptera made up the largest percentage of total mass captured, varying from 31 to 54% (Table 4). Between 5 and 9% of total invertebrate biomass (between 14 and 23% of the Diptera fraction) was contributed by dipteran families with larvae that rear in streams. The remainder was believed to have originated from terrestrial production, although some semiaquatic taxa may have been included. In total, approximately 20% of the invertebrate biomass captured in surface traps consisted of aerial forms of
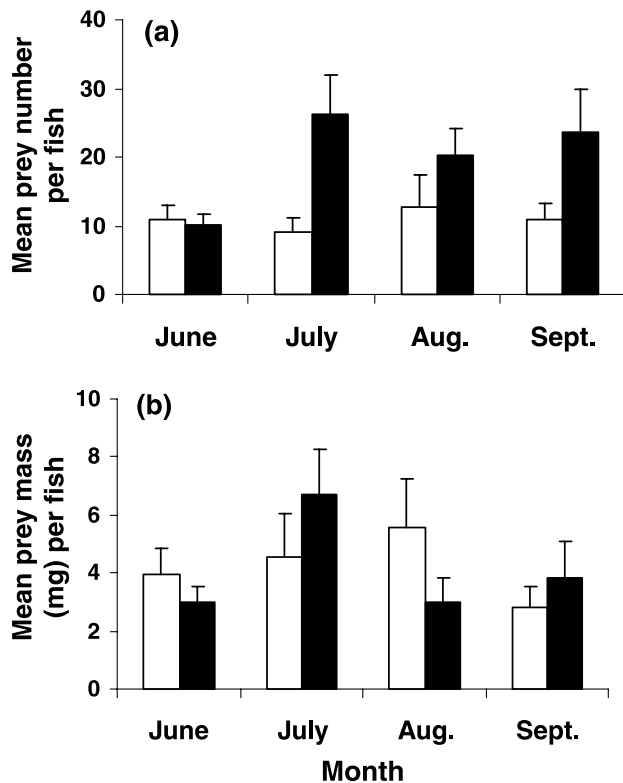
Table 3. Percent composition of invertebrate mass ingested by juvenile coho salmon for young-growth (YG) and old-growth (OG) sites.

	Forest type	
	OG	YG
Aquatic		
Ephemeroptera	5.0	5.1
Plecoptera	10.9	12.0
Trichoptera	9.0	9.7
Diptera	6.4	4.4
Other	1.2	0.5
Terrestrial		
Araneida	0.4	0.4
Coleoptera	7.6	8.3
Collembola	4.1	1.9
Diplopoda	0.1	0.3
Hemiptera	0.5	0.5
Homoptera	4.8	10.3
Hymenoptera	9.0	2.8
Lepidoptera	6.8	8.3
Oligochaeta	2.2	1.0
Psocoptera	0.1	0.1
Other	0.9	1.5
Unknown		
Diptera	28.2	29.4
Other	2.9	3.4

aquatic insects, including Trichoptera, Plecoptera, and Diptera.

The comparison of conifer and alder (1996 pan traps) showed no significant differences in total invertebrate biomass (Fig. 3a; Table 1; $p = 0.44$). When Diptera were excluded from the analysis because of indications that surface traps may attract dipterans and inflate estimates (Wipfli 1997), again no statistical difference between vegetation type was observed (Fig. 3b). Monthly estimates suggest a small, nonsignificant decline in August and September. The estimated input of invertebrate biomass to the stream surface in 1996, averaged across vegetation types, was 75.3 ± 25.5 mg·m^{-2}·day^{-1} in 1996 for total invertebrates and 47.5 ± 17.6 mg·m^{-2}·day^{-1} excluding Diptera.

Fig. 2. Mean (*a*) number and (*b*) mass of aquatic (open bars) and terrestrial (solid bars) invertebrate prey ingested by coho salmon (*Oncorhynchus kisutch*; 40- to 100-mm fork length) averaged across 12 streams. Prey of unknown origin are excluded. Error bars represent +1 SE.

Fig. 3. Mean mass of invertebrates captured in pan traps (1996), averaged across six young-growth streams, for (*a*) all invertebrates and (*b*) all invertebrates excluding Diptera. Alder locations, open bars; conifer locations, solid bars. Error bars represent +1 SE.

The comparison of YG and OG streams (1997 pan traps) revealed a small but not significantly greater total invertebrate biomass captured in surface traps in YG streams (p = 0.45; Table 1). Surface inputs of invertebrate biomass were highest in July, compared with other months, and the time effect was significant (p = 0.03; Table 1). Excluding Diptera from these estimates increased the YG–OG discrepancy in the first 2 months and eliminated it for the last 2 months (J.D. Allan and M.S. Wipfli, unpublished data). The estimated input of invertebrate biomass to the stream surface from 1997 surface traps was very similar to that of 1996 estimates: 83.3 ± 23.4 mg·m^{-2}·day^{-1} for total invertebrates and 43.2 ± 14.9 mg·m^{-2}·day^{-1} excluding Diptera.

Invertebrates associated with terrestrial vegetation

Invertebrates were patchily distributed across stems and plant species. Of the 783 stems sampled, 30% had no invertebrates. The presence/absence of invertebrates across plant species exhibited significant heterogeneity (χ^2 = 21.1, df = 5, p < 0.001). Zero values varied from a low of 19% in alder stems to a high of 40% in hemlock. Perhaps surprisingly, the two conifers were dissimilar in this regard. Spruce had only slightly more unoccupied stems than alder, whereas blueberry had nearly as many unoccupied stems as hemlock.

Thirteen orders of invertebrates were identified from stem samples. The Homoptera, Lepidoptera, and Araneida composed the largest fraction of total biomass (Table 4). Diptera were the major biomass component for hemlock, and Plecoptera were important for both conifers and blueberry. The
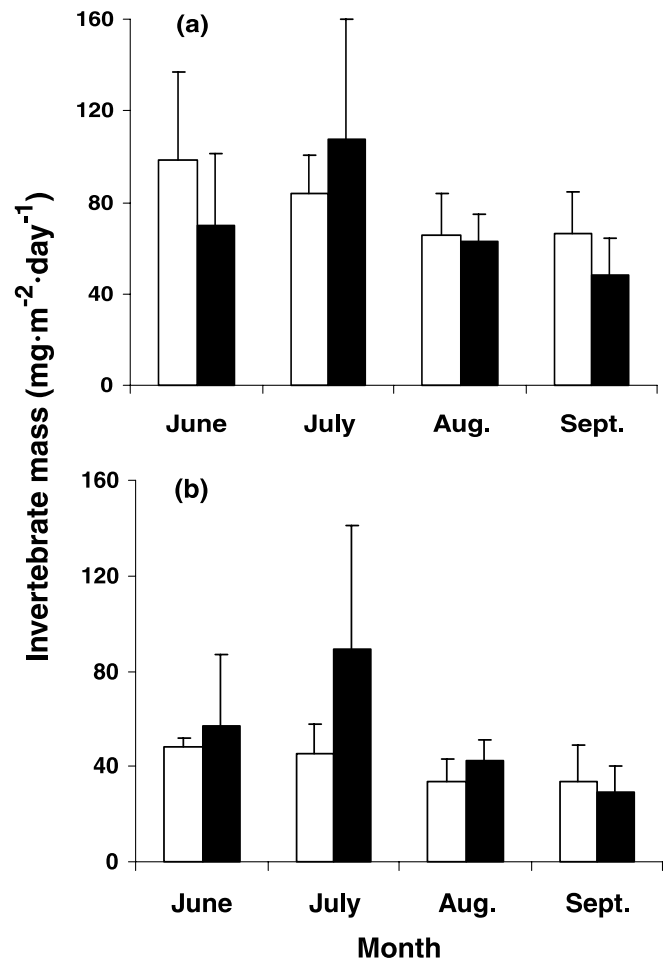
homopteran family Aphididae composed a major percentage of the invertebrate biomass on alder (37.6%), currant (47.7%), and salmonberry (30%) and an even greater fraction by numbers (J.D. Allan and M.S. Wipfli, unpublished data). Very little of the biomass on stems was associated with taxa with aquatic stages, with the exception of the Plecoptera occurring on both conifer species.

Invertebrate biomass per dry leaf mass (mg·g^{-1}) varied substantially based on plant species sampled and date (Fig. 4). Forest type (OG versus YG) was not significant (p = 0.48), although there was a significant (p = 0.02) forest type × month interaction. Effects of plant species (p < 0.001) and month (p < 0.001) were highly significant, and the month × plant species interaction was significant as well (p = 0.02; Table 1). Planned contrasts documented significant differences between individual plant species as well as overstory versus understory and deciduous versus conifer comparisons. The comparison of four deciduous versus two coniferous species was highly significant (p < 0.001), reflecting the much higher invertebrate biomass found on deciduous plant stems compared with either hemlock or spruce. All pairwise comparisons between deciduous plants and conifers were

Table 4. Percent composition of invertebrate mass captured in surface traps, collected from plant stems, and captured in funnel traps.
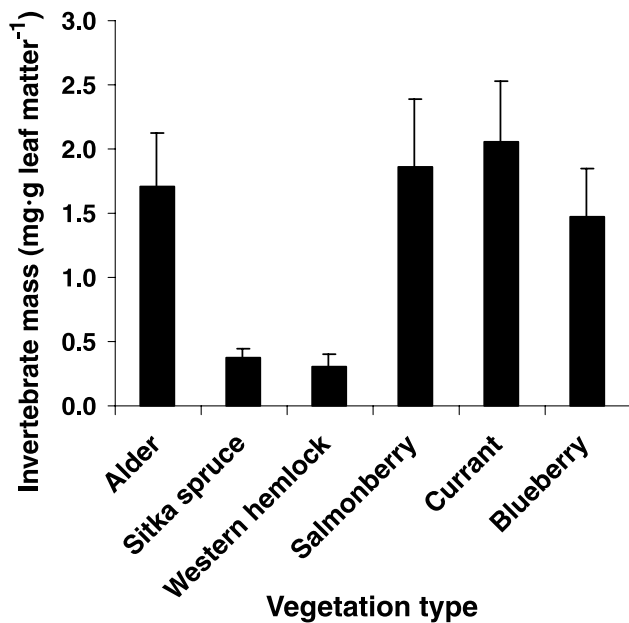
Taxon	Vegetation comparison 1996		Forest type comparison 1997		Funnel trap comparison 1997		Plant stem comparison					
	Alder	Conifer	OG	YG	Alder	Conifer	Alder	Spruce	Hemlock	Salmonberry	Currant	Blueberry
Araneida	3.6	13.1	4.8	2.3	2.9	5.3	1.4	26.0	12.1	9.7	8.6	5.8
Coleoptera	6.8	10.0	10.1	11.6	22.1	18.1	2.4	2.0	1.5	13.6	1.9	3.6
Collembola	4.6	8.1	14.9	15.2	7.9	15.6	0.1	—	—	0.1	0.1	0.1
Diplopoda	0.9	2.1	0.4	1.5	1.7	2.3	—	—	—	—	—	—
Diptera[a]	41.0	31.4	53.8	52.7	29.5	24.1	13.2	11.6	64.9	8.3	3.7	13.8
Ephemeroptera	1.6	1.0	1.1	0.9	0.1	0.0	0.0	0.5	—	—	—	0.2
Gastropoda	0.3	4.7	0.1	0.3	31.9	30.2	—	—	—	—	0.3	0.0
Hemiptera	0.2	0.0	0.1	0.2	0.1	0.0	—	0.5	—	0.1	—	0.7
Homoptera	15.6	10.0	0.6	0.7	0.9	0.9	41.6	25.0	2.8	30.0	52.5	16.5
Hymenoptera	2.1	1.0	0.3	0.2	—	—	0.9	1.0	1.8	1.7	0.7	1.5
Isopoda	0.1	0.2	0.0	0.0	—	—	—	—	—	—	—	—
Lepidoptera	3.6	1.1	1.5	2.9	0.7	0.5	38.1	12.5	2.3	32.8	26.3	42.3
Oligochaeta	4.3	0.0	0.2	0.1	1.2	0.1	—	—	—	—	—	—
Plecoptera	5.4	6.1	5.5	6.1	0.3	0.1	1.7	17.9	13.8	3.4	3.1	13.5
Psocoptera	0.1	0.2	0.0	0.0	0.1	0.3	—	0.1	0.0	—	—	—
Trichoptera	6.9	9.1	4.7	3.6	0.0	0.6	0.1	1.7	0.3	—	—	—
Other[b]	0.0	0.3	1.8	1.5	0.3	1.0	—	—	—	—	—	—
Unidentified	2.9	1.7	0.1	0.2	0.1	0.4	0.4	1.1	0.6	0.3	2.6	2.1

Note: OG = old growth; YG = young growth.

[a] Contribution of Diptera of known aquatic origin: 1996 vegetation comparison, alder 9.3%, conifer 5.4%; 1997 forest type comparison, OG 7.7%, YG 7.7%; funnel traps, alder 4.8%, conifer 5.1%; stem comparison, <0.1%.

[b] Includes Nematoda and Thysanoptera.

Fig. 4. Mean mass of invertebrates per gram of leaf matter sampled for three overstory (alder, hemlock, and spruce) and three understory (salmonberry, currant, and blueberry) plant species common in the riparian vegetation of streams. Error bars represent +1 SE.


Fig. 5. Invertebrate mass captured in funnel traps placed under dense stands of alder (open bars) or conifer (solid bars) at three sites. (*a*) Battery, $n = 24$; (*b*) Maybeso Branch, $n = 23$; (*c*) Upper Beaver, $n = 28$.

highly significant ($p < 0.001$), whereas all comparisons within deciduous plants and between hemlock and spruce were not ($p > 0.05$).

Funnel traps placed in dense stands of either alder or conifer provided further evidence of differences in invertebrate biomass associated with vegetation type. The taxonomic composition of funnel-trap collections at the order level was similar between alder and conifer stands. Gastropoda, Diptera, and Coleoptera dominated the biomass collected (Table 4). More biomass was collected from funnel traps in alder compared with conifer stands over most dates and sites (Fig. 5). Separate analysis of the three stream sites found a significant difference in Maybeso ($p < 0.05$) and Beaver ($p < 0.05$), but not in Battery ($p = 0.16$; Table 1). There were also indications of a time effect, seen as a significant month effect at Maybeso Branch ($p < 0.001$) and a significant month × species interaction at Upper Beaver ($p < 0.05$; Table 1). Biomass capture varied seasonally, peaking in July at two of the sites but later in the season at Battery (Fig. 5).

Discussion

Terrestrial invertebrates are an important trophic link between riparian habitat and stream food webs. In the relatively unproductive small streams of southeastern Alaska, juvenile coho depend on invertebrates of terrestrial origin for roughly half of their energy supply during the growing season. We documented that both TI inputs and their contribution to coho diet were substantial and clearly made a substantial contribution to the energy requirements of young salmonids. Deciduous plants house more invertebrates per unit mass of leaf matter than do conifers, and the taxonomic composition of invertebrates differs among plant species. Our results suggest that invertebrate inputs likely are higher where alder is
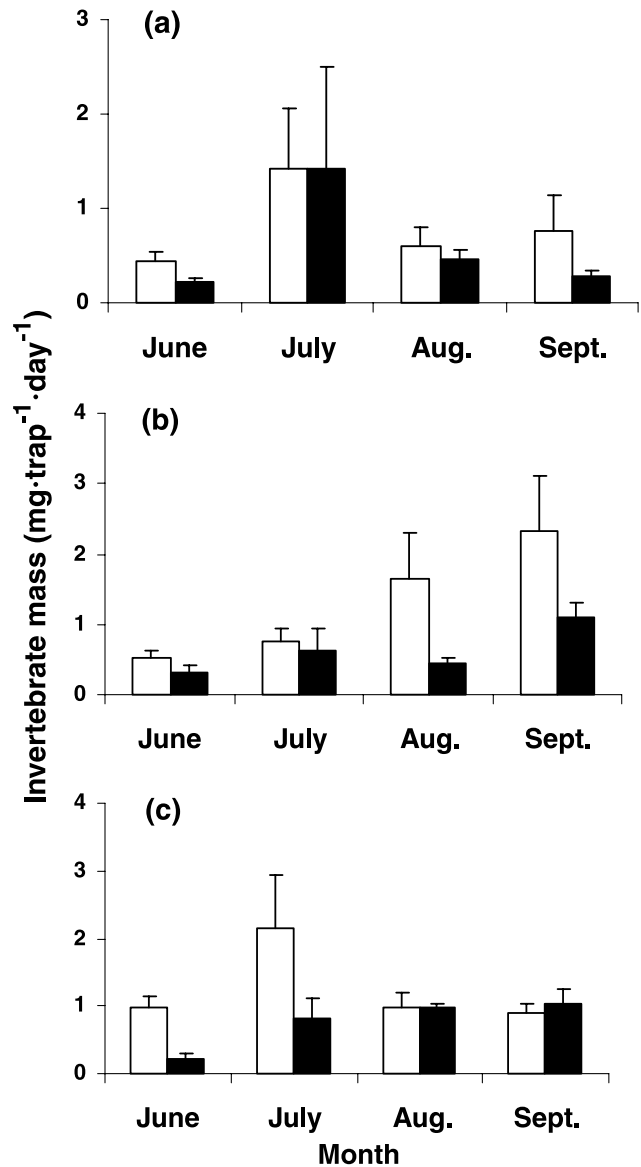
more abundant. Although this was not born out by efforts to quantify coho diet or surface inputs under individual plant clumps, it was supported by sampling within pure stands of alder versus conifer, and so mixing by wind and dispersal may have limited our ability to detect small-scale differences at sites. These findings raise issues that could be considered in forest management of regenerating YG forests after clear-cutting.

Terrestrial invertebrates composed one-third of prey ingested by juvenile coho in this study and one-half of the prey that could be positively assigned to either aquatic or terrestrial origin. Adult Diptera accounted for almost all of the prey of uncertain origin. If the majority of these were found to be of terrestrial origin, the TI component would increase further. In a similar study in southeastern Alaska, Wipfli (1997) also found that terrestrial invertebrates made up

about half of the diet of three species of juvenile salmonids. In a comparison of grassland and forested streams in Japan, terrestrial invertebrates composed 53 and 49%, respectively, of prey consumption by salmonids on an annual basis and fully 77 and 68%, respectively, during summer (Kawaguchi and Nakano 2001). In our study, Diptera, Plecoptera, Trichoptera, and Lepidoptera were the most important prey by mass, whereas by numbers a different picture emerges in which abundant but small Aphididae, Collembola, and Hymenoptera are seen to make up a substantial share of the diet. For small young-of-the-year fish, however, these likely are a critical resource.

Estimates of terrestrial invertebrate infall are in relatively good agreement among studies, with differences that implicate the influence of land use. Our estimates of 75 (1996) and 83 $mg·m^{-2}·day^{-1}$ (1997) are double Wipfli's (1997) estimate of 37 $mg·m^{-2}·day^{-1}$, also in southeastern Alaska. These values are bracketed by Kawaguchi and Nakano's (2001) estimates of ~40–50 mg in grassland and ~80–100 $mg·m^{-2}·day^{-1}$ in second-growth deciduous forest during summer and Nakano et al.'s (1999) estimate of 112 $mg·m^{-2}·day^{-1}$ in June–July, also in second-growth deciduous forest. These comparisons, all based on pan traps, suggest that the terrestrial invertebrate subsidy can differ by at least a factor of two, depending on vegetation type. A study of terrestrial invertebrates in the drift in New Zealand streams found an even greater difference, of the order of five- to ten-fold, between forested and tussock grassland streams versus pasture streams (Edwards and Huryn 1996), suggesting the importance of land-use activities.

A rough approximation suggests that inputs of aerial invertebrates during summer could supply a reasonable portion of the energy needs of juvenile salmon. We observed an average of 12.1 $mg·fish^{-1}$ of prey ingested, and because gut clearance times are ~24 h at these temperatures, this is an approximate estimate of a daily feeding rate (Elliott and Persson 1978). At a maximum sustained consumption rate of 20 $mg·day^{-1}$ at 10°C (Elliott 1975; Dunbrack 1988), terrestrial subsidies in these streams could support about four young-of-the-year coho fry per square metre of stream. As fish grow during summer, the number of fish supported will decrease, especially as water temperature increases. Nevertheless, when compared with our estimate of aerial inputs of 80 $mg·m^{-2}·day^{-1}$ during summer (45 $mg·m^{-2}·day^{-1}$ excluding Diptera), the TI energy subsidy clearly is substantial.

The importance of terrestrial invertebrates to fish and very likely other consumers within stream food webs may be reinforced by the tendency for aquatic prey to become less numerous during summer because of emergence (Hynes 1970). Moreover, the larger aquatic invertebrates preferred by predators are nocturnal in their drift activity (Allan 1978) and thus are less available. It is likely that terrestrial subsidies are an important part of the solution to "Allen paradox" (Hynes 1970), which stems from Allen's (1951) finding that the production of aquatic invertebrates appeared insufficient to support fish production in the Horokiwi Stream, New Zealand. Delivery of aquatic invertebrates from headwaters to downstream reaches may also be part of the solution for many streams (Wipfli and Gregovich 2002). In addition, terrestrial subsidies may influence trophic cascades, as demonstrated by Nakano et al. (1999) who found that experimental

reduction of terrestrial in-fall led to greater predation on aquatic invertebrates and enhanced algal growth.

We detected significant differences between means for some comparisons but not others. Inability to detect treatment effects could be attributable to the absence of a biologically meaningful effect or to low statistical power. A meaningful biological effect size is a difference in the response that would adversely impact prey resources for fishes. Our study attempted to quantify the difference in terrestrial prey abundance between various vegetated treatment conditions (e.g., OG versus YG forest types, alder versus conifer). Extrapolating from these data to fish populations is difficult because of the difficulties in linking prey abundance and availability to fish growth and production. With six streams per treatment group in our experiment (e.g., OG and YG forest types), statistical power to detect changes of 80% of 1 standard deviation (SD) is 0.24 (Cohen 1988). Cohen classifies effects of 80% of 1 SD as large and grossly perceptible to the human eye. It is conceivable that a biologically meaningful effect size is much smaller than 80% of 1 SD, in which case the statistical power of this experiment to detect such a biologically meaningful difference would be lower than 0.24. We conclude that the statistical power in our study was much lower than the conventional standard of 0.80 (Cohen 1988). Nonsignificant results reported in this study should not be interpreted as evidence of an absence of biologically meaningful differences among treatment groups.

Differences in riparian vegetation likely result in variation in quantity, composition, and timing of terrestrial invertebrate subsidies, a topic that merits further study. We found that deciduous trees supported much higher invertebrate mass per stem than did conifers, and alder substantially exceeded either spruce or hemlock. Taxonomic composition of TI also varied markedly among plant species, suggesting a role for plant heterogeneity in providing aerial inputs. Although members of the Homoptera, Lepidoptera, Araneida, and Diptera predominated, spruce and hemlock had high mass of Plecoptera, dipterans were very abundant on hemlock, and lepidopterans were strongly associated with deciduous vegetation. Mason and MacDonald (1982) reported that different riparian tree species contributed different terrestrial invertebrate mass to streams.

Our estimates of input based on pan traps did not detect differences based on YG versus OG streams or alder versus conifer locations within YG sites. Although low statistical power is one explanation, the absence of significant differences may be partly due to design limitations. Our data suggest much greater TI biomass per gram mass of deciduous leaves compared with conifers; however, the total tree volume was considerably greater at OG compared with YG streams, and these may have offsetting effects. It should be noted that Wipfli (1997) did not find significantly greater inputs of TI biomass at YG versus OG sites, and our results also did not show significance. It is possible that no difference was detected between pan traps set under alder versus conifer because of invertebrate dispersal and wind mixing. We placed funnel traps within dense, single-species YG stands of conifer versus alder to circumvent this problem, and these traps collected a significantly greater biomass of TI in alder stands. However, surface traps provided useful informa-

tion, including an estimate of the total input of aerial invertebrates and its taxonomic composition, along a broader stream-reach scale.

Seasonal variation was apparent in several measures of TI, generally because of mid-summer maxima. Significant differences among months were observed in the proportion by counts of TI in coho diet, in 1997 stream inputs, and in funnel traps at two of the three sites. In their study of TI inputs over the annual cycle, Kawaguchi and Nakano (2001) found much greater inputs during summer than in spring and autumn and negligible inputs during winter. Clearly, the importance of TI as a food subsidy for juvenile salmon varies seasonally.

Our methods of estimating TI inputs have several limitations. Pan traps may attract insects seeking oviposition sites, thereby elevating estimates of infall (Wipfli 1997). At the level of taxonomic resolution used (mostly family), it is difficult to determine whether some taxa, particularly dipterans, are the product of aquatic or of terrestrial production.

In conclusion, the evidence that riparian vegetation harbors an important energy subsidy to stream food webs, namely terrestrial invertebrates, draws attention to the influence of riparian vegetation type on the amount and composition of that subsidy. Inputs of terrestrial invertebrates appear to span at least a twofold range based on studies of OG conifer, mixed YG forest (Wipfli 1997; this study), second-growth deciduous forest, and grasslands (Nakano et al. 1999; Kawaguchi and Nakano 2001) and may be greatly reduced in degraded habitat such as pasture (Edwards and Huryn 1996). Based on the evidence that juvenile salmonids receive an important fraction of their food supply from terrestrial in-fall and that the magnitude of this input varies with the type of riparian vegetation, invertebrate subsidy from riparian vegetation appears to be an important consideration in streamside management.

Acknowledgments

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