

Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A.

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Abstract: Terrestrial-derived invertebrate (TI) inputs into streams and predation on them by salmonids (40–180 mm fork length) were measured in six coastal Alaska stream reaches from April through October 1993–1994; riparian habitat of three stream reaches contained conifer-dominated old-growth (no timber harvesting) and three were alder-dominated young-growth (31 years postclearcutting). Data from pan-traps placed on stream surfaces showed that TI biomass and nitrogen inputs averaged up to 66 and 6 mg·m⁻²·day⁻¹, respectively, with no significant difference between habitats. Stomach contents from coho salmon (*Oncorhynchus kisutch*), cutthroat trout (*O. clarki*), and Dolly Varden (*Salvelinus malma*) revealed that TI and aquatic-derived invertebrates (AI) were equally important prey. Additionally, salmonids from young-growth systems ingested a greater TI proportion than those from old-growth systems. There were trends but no significant differences between habitats of TI and AI biomass ingested; however, statistical power was <0.30. These results showed that TI were important juvenile salmonid prey and that a riparian overstory with more alder and denser shrub understory may increase their abundance. Riparian vegetation management will likely have important consequences on trophic levels supporting predators, including but not limited to fishes.

Résumé : Les apports d'invertébrés d'origine terrestre (IT) dans les cours d'eau et la prédation exercée sur eux par les salmonidés (longueur à la fourche de 40–180 mm) ont été mesurés dans six tronçons de cours d'eau côtiers de l'Alaska d'avril à octobre 1993–1994; les habitats riverains de trois des tronçons de cours d'eau étaient constitués de forêts mûres (absence de récolte du bois) dominées par des conifères et les trois autres étaient constituées de jeunes forêts (31 ans depuis la coupe à blanc) dominées par l'aulne. Les données obtenues grâce à des pièges à eau placés à la surface des cours d'eau ont montré que la biomasse d'IT et les apports en azote s'élevaient en moyenne à 66 et 6 mg·m⁻²·jour⁻¹, respectivement, sans qu'il y ait de différences statistiquement significatives entre les habitats. Le contenu stomacal de saumons coho (*Oncorhynchus kisutch*), de truites fardées (*O. clarki*) et de Dolly Varden (*Salvelinus malma*) a révélé que les IT et les invertébrés d'origine aquatique (IA) étaient des proies d'égale importance. De plus, les salmonidés des systèmes de jeunes forêts ingéraient une proportion plus grande d'IT que ceux des systèmes de forêts mûres. Il y avait des tendances, mais non des différences significatives, entre les habitats pour ce qui est de la biomasse d'IT et d'IA ingérés; cependant, la puissance statistique était <0,30. Ces résultats ont montré que les IT étaient des proies importantes pour les salmonidés juvéniles et qu'un étage dominant riverain contenant plus d'aulnes et un sous-étage d'arbustes plus denses peuvent accroître leur abondance. La gestion de la végétation riveraine aura vraisemblablement des conséquences importantes sur les niveaux trophiques qui soutiennent les prédateurs, y compris mais non exclusivement les poissons.

[Traduit par la Rédaction]

Introduction

Riparian zones play a major role in regulating nutrient and energy flow in low-order streams (Webster and Benfield 1986; Cummins et al. 1989; Webster et al. 1992). Leaf litter and wood originating from riparian vegetation enters the lotic system and affects associated microbial and benthic macroinvertebrate communities that consume and process this organic material (Sedell et al. 1975; Vannote et al. 1980; Cummins et al. 1989; Hax and Golladay 1993). This allochthonous

material typically constitutes the energy base in low-order forested streams (Minshall 1967; Fisher and Likens 1973; Triska et al. 1982).

While it is understood that stream ecosystems are closely linked to and dependent on their associated riparian zones for organic matter and nutrient inputs, little attention has focused on the terrestrial invertebrate communities associated with riparian vegetation and on how these plants influence terrestrial invertebrates entering streams (e.g., as prey for predators, or as allochthonous material contributing nutrients and organic matter). Southwood (1961) reported that deciduous trees generally have more associated invertebrate species than do conifers. Plant community successional stage also plays a variable role in the associated invertebrate community dynamics by regulating their abundance and species assemblage (Mispagel and Rose 1978). Schowalter et al. (1981) reported lower arthropod mass 1 year after clearcutting but higher mass 2 year

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postclearcutting, relative to an uncut forest. Mundie (1974) indicated that aerial insects were more abundant in a deforested than forested setting in coastal British Columbia, Canada, and that terrestrial insects may be seasonally important salmonid food. Some riparian tree species contribute more terrestrial invertebrate mass to streams than others (Mason and Macdonald 1982).

Little consideration has been given to the role of terrestrial invertebrates in aquatic food web ecology and dynamics, even though their occurrence in fish diets is well documented (Sterba 1962; Hynes 1972; Scott and Crossman 1973; Maitland 1977; Garman 1991). Terrestrial invertebrates often comprise more than 50% of juvenile salmonid diets and associated energy intake during certain times of the year and are often a preferred prey (reviewed by Hunt 1975). Nielsen (1992) reported that the energy contribution of terrestrially derived prey represented from 15 to 28% of the total energy intake for juvenile coho salmon (*Oncorhynchus kisutch*) during summer in a Washington stream. Cada et al. (1987) stated that terrestrial prey were more common in trout stomachs than in the drift, fish had a preference for terrestrial prey over aquatic prey, and riparian vegetation was an important prey source. Cadwallader et al. (1980) indicated that overhanging vegetation was important for terrestrial invertebrate inputs in some Victorian streams and terrestrial prey were more common in diets of fish from sites with overhanging vegetation.

If riparian communities govern terrestrial invertebrate inputs, then riparian management activities that alter plant communities may change food resources within and surrounding the stream. Timber clearcutting in southeastern Alaska across riparian zones of salmonid-rearing streams (pre-1990 timber harvest practices) has given rise to even-aged young-growth riparian communities of various successional stages. Red alder (*Alnus rubra*) often dominates riparian regrowth canopies with variable amounts of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), in addition to some western redcedar (*Thuja plicata*), Alaska yellow-cedar (*Chamaecyparis nootkatensis*), black cottonwood (*Populus trichocarpa*), and willow (*Salix* spp.) in some areas. Influence of these developing riparian communities on stream productivity and fisheries, including energy pathways via terrestrial invertebrate inputs, is unknown. Maintaining productive salmonid fisheries in southeastern Alaska is critical to the economy and quality of life of peoples of this region; preserving riparian and stream productivity is essential for sustaining this resource. Understanding the role of terrestrial invertebrates in stream food webs and how riparian habitat types influence their inputs into streams is crucial for managing these riparian-stream ecotones.

The objectives of this study were to (i) measure terrestrial-derived invertebrate (TI) inputs into streams and predation on them by salmonids (40–180 mm fork length) in six Alaska temperate rainforest stream reaches from April through October 1993–1994 and (ii) contrast these responses between streams containing conifer-dominated old-growth (little to no timber harvesting) riparian habitat and alder-dominated young-growth (31 years postclearcutting) riparian habitat. TI inputs were assessed in terms of biomass and nitrogen they contributed to streams, and predation on them by comparing biomass of TI versus aquatic-derived invertebrates (AI) consumed by salmonids.

Methods

Study site

The study took place on Revillagigedo Island located within the Alexander Archipelago temperate rainforest of the southeastern Alaska panhandle. Climate is maritime: cool and moist; precipitation can exceed 500 cm·year⁻¹ in some areas (Harris et al. 1974).

The study was conducted May–October 1993 and April–May 1994 at Bear, Cedar, Cobble, Spike, Upper Sprout, and Lower Sprout creeks (informally named for study purposes) within or near the 22.6-km² Margaret Lake catchment (55°41'N, 131°36'W) on Revillagigedo Island, Alaska, U.S.A. (Fig. 1). Riparian canopies (mostly closed) contained Sitka spruce, western hemlock, western redcedar, and red alder. Riparian areas of Bear and Sprout creeks contained 31-year-old regrowth of alder or alder–spruce mix; those of Cedar, Cobble, and Spike creeks contained conifer-dominated old-growth canopies. Study reaches of Cedar and Spike creeks were fully contained within old-growth riparian areas. Also, a logging road paralleled Spike Creek 50–100 m away. The Cobble Creek site contained old-growth riparian habitat except for roughly one quarter of its length that received some timber harvesting up to 30 m from the stream banks 30 years earlier. Sprout Creek contained two study reaches with distinctly different riparian habitats: alder-dominated closed-canopy and a partially open mixed alder–spruce canopy. Remaining streams contained single study reaches. Understories were mixtures of blueberry (*Vaccinium ovalifolium* and *V. alaskaense*), salmonberry (*Rubus spectabilis*), devil's club (*Oplopanax horridus*), and elderberry (*Sambucus racemosa*) with other occasional species. Young-growth understories were more dense than those of the old-growth communities (Table 1). Stream channels averaged 2–9 m wide, were generally unrestricted, and contained sand to boulder-sized substrata with frequent coarse woody debris (CWD). Study reaches ranged from 60 to 200 m long with <5% gradients.

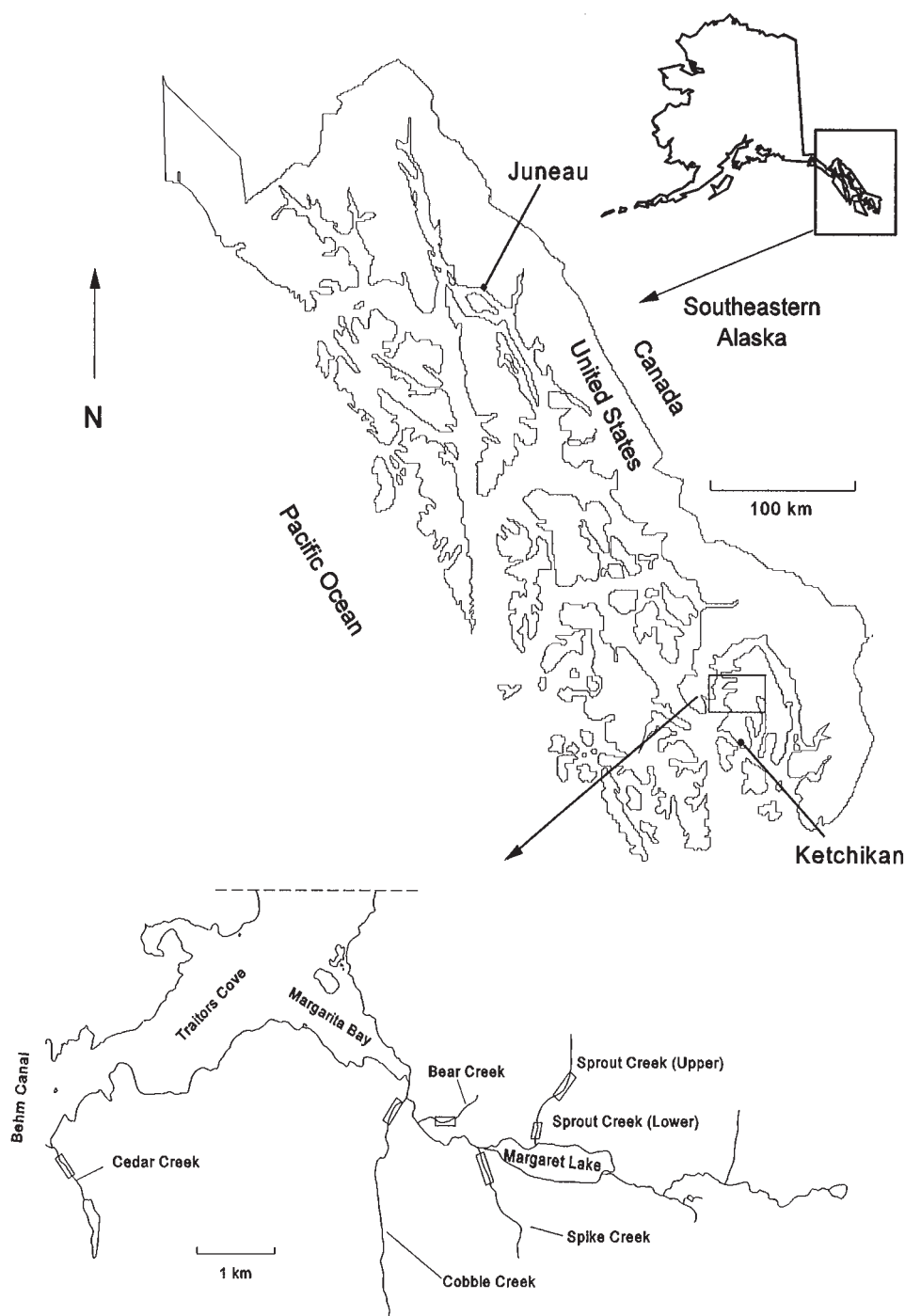
Stream inputs of terrestrial invertebrates

To assess the importance of TI as allochthonous input, I measured number and biomass and determined taxonomic composition of TI and nonwoody plant mass and composition entering streams. Invertebrates were categorized as terrestrial (terrestrially derived) if they were a product of terrestrial secondary production (i.e., terrestrial stages of aquatic production were not classified as TI). The null hypothesis for comparing habitats was that the quantity of TI entering streams was similar between habitats.

Five dark-colored floating pan-traps (930-cm² surface area with 13-cm-high sides) containing ~5 mL of dish soap and 2 L of stream water were placed on stream-water surfaces within each study reach. Traps were approximately evenly spaced and haphazardly placed on pool surfaces throughout stream reaches. The soap helped preserve trap contents and reduced water surface tension within the traps to help retain invertebrates. Traps were designed to catch plant litter and invertebrates landing on the stream surface. Traps were tethered with nylon cord to overhanging tree limbs or other structures and were not positioned according to distance from stream banks.

Trap contents were collected up to every 2 weeks. Invertebrates visible to the unaided eye were removed and remaining nonwoody plant material was strained through a 105-µm-mesh sieve. Invertebrates were placed into 70% EtOH within plastic bags and taken to the laboratory to identify, count, and determine mass. I identified all invertebrates to Order, or Family if necessary, recorded body lengths to the nearest 1 mm, and calculated dry masses with published taxon-specific length–mass conversion equations (Rogers et al. 1976, 1977; Smock 1980). I used these equations because they provided more accurate measurements of original invertebrate mass than did direct weighing of preserved specimens (Meyer 1989), and specimens may have lost mass due to partial decomposition while in traps. Nonwoody plant material was placed into paper envelopes, oven dried, separated into categories (coniferous, alder, nonalder deciduous), and then

Fig. 1. Rectangles enclosing selected stream reaches on bottom map show approximate TI input and salmonid diet study locations during 1993 and 1994 in southeastern Alaska.



ashed to estimate ash-free dry mass (AFDM). I assumed that leaf mass loss due to leaching in trap water was similar to published rates and used published means for coniferous (Short et al. 1980), alder (Kaushik and Hynes 1971; Triska and Sedell 1976; Short et al. 1980), and other deciduous species (Kaushik and Hynes 1971) to correct measured values. Published mean nitrogen content values were used to estimate the amount of nitrogen entering streams via invertebrates and plant litter (Table 2).

Terrestrial invertebrates as salmonid prey

To determine if TI were an important component of these stream food

webs through contributing to predatory fish diets, I compared number and mass of TI versus AI prey ingested by salmonids monthly from May through October 1993. Salmonids 40–180 mm fork length were captured using “minnow” traps (42 cm long \times 23 cm wide), each containing a perforated 7 \times 17 cm plastic bag of salmon eggs as bait. Traps were placed in nonriffle habitats >25 cm deep. Fishes present were coho salmon, cutthroat trout (*Oncorhynchus clarki*), steelhead (*O. mykiss*), Dolly Varden (*Salvelinus malma*), and sculpin (*Cottus* spp.) at various compositions. Sculpin and the relatively uncommon steelhead were excluded from analyses. Traps remained in streams about 1 h. Collected fish were placed in 20-L buckets of

Table 1. Study site characteristics.

Stream	Riparian habitat ^a	Study reach length (m)	Stream width (m) ^b	Canopy composition ^c	Understory composition ^d	Understory density ^e
Cedar Cr.	OG	85	2.6±0.2	H≡C>S>A	BB>DC>SB	L
Cobble Cr.	OG	160	8.6±0.9	H>S>A>C	BB>SB>DC	M
Spike Cr.	OG	200	5.3±0.4	H>S>C>A'	BB>DC>SB	M
Bear Cr.	YG	75	2.1±0.3	A≡S>H>C	SB>BB>DC	H
Lower Sprout Cr.	YG	60	2.6±0.3	A≡S>H>C	SB>BB>DC	H
Upper Sprout Cr.	YG	90	2.5±0.2	A≡S>H>C	SB>BB>DC	H

^aOG, old-growth riparian forest; YG, 31-year-old young-growth riparian forest.

^bMean ± SE.

^cDominant species in order of abundance based on visually estimated foliage composition of trees with stems within 30 m of permanent stream banks: A, alder; C, cedar; H, hemlock; S, spruce.

^dDominant species in order of abundance based on visually estimated foliage composition of the three most common understory shrub species: BB, blueberry; DC, devil's club; SB, salmonberry.

^eRelative shrub density comparison among six sites: L, low; M, medium; H, high.

^fRiparian canopy also contained frequent subdominant alder.

Table 2. Nitrogen levels of invertebrate and leaf^a tissue used to calculate nitrogen inputs into streams.

Tissue type	% nitrogen ^b	Reference
Conifers (general)	0.6	Triska and Sedell 1976
	0.9	Woodwell et al. 1975
Picea (spruce)	1.0	Heilman 1966
	1.4	Iversen 1974
	0.8	Watt and Heinselman 1965
	1.3	Whittaker et al. 1979
	1.4	Yamaya 1968
Alnus (alder)	3.1	Bocock 1964
	2.6	Gessner and Chauvet 1994
	3.3	Hughes et al. 1968
	4.2	Iversen 1974
	3.7	Jacobsen and Sand-Jensen 1994
	2.2	Triska and Sedell 1976
	3.4	Yamaya 1968
Rubus (bramble)	0.8	Bocock 1964
Vaccinium (blueberry)	0.6	Woodwell et al. 1975
Invertebrates	7.7	Iversen 1974
	9.0	Jacobsen and Sand-Jensen 1994
	8.6	Mattson and Scriber 1987

^aMean values of nonwoody plant tissue averaged across plant age, stage, locality, and environmental conditions.

^bBased on dry mass.

water, anesthetized with tricaine methanesulfonate, their stomach contents removed, and then returned to their original habitats. Generally, 10 fish per species were sampled at each site and sampling date. Stomach contents were collected by injecting stream water into fish stomachs using a 10-mL syringe assembly (Meehan and Miller 1978); water pumped into fish stomachs forced contents out of fishes' mouths. Stomach contents and associated water, along with 95% EtOH equal in volume to that of the water, were placed into a 7 × 17 cm plastic bag; bags were labeled and returned to the laboratory where contents were identified and invertebrates counted and their body lengths measured. Invertebrate dry mass was determined with published equations as described above. I estimated lengths of partially digested prey, if actual body measurements were not possible, based on intact individuals of the same taxon that appeared similar in size. Because many prey were partially digested, this procedure apparently estimated actual prey mass ingested more accurately than would direct AFDM or volumetric estimates. It also should have eliminated

bias from specimens with different amounts of sclerotization (that would be digested at different rates), such as chironomid larvae versus coleopteran adults, because head capsules of even the most digested individuals were still discernible.

For contrasting consumption of TI between riparian habitats, the null hypothesis was that the quantity of TI ingested by fish was similar between the two riparian habitats. Cutthroat trout were used as a representative species because only they were common to all sites and sampling dates. I compared salmonid stomach contents between the two forest successional regimes: proportion of TI ingested ($=(\text{mg TI})/(\text{mg TI} + \text{mg AI})$) and mass of AI and TI ingested. Individual fish were subsamples (~ 10) and stream reaches were replicates ($n = 3$). Proportion and mass were calculated for each fish and then averaged across all fish within a study reach.

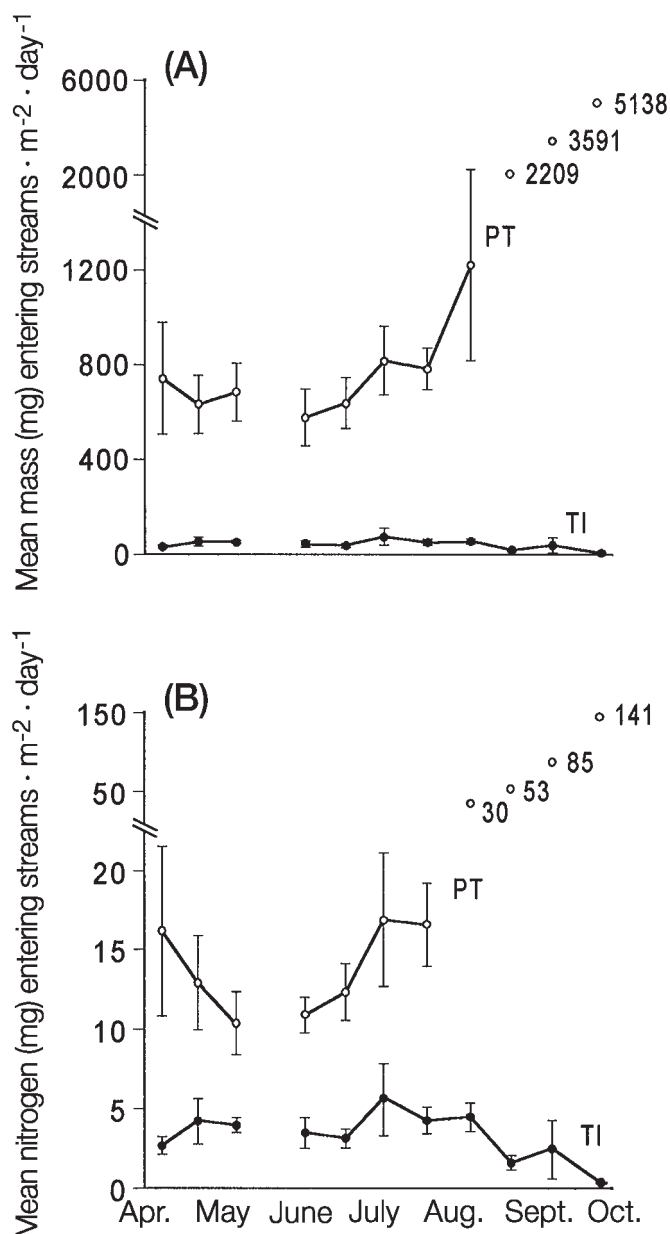
Statistical analyses

The response variable for allochthonous trap data was TI mass. Because some winged Diptera appeared to be attracted to objects placed on stream surfaces (Power 1985; Edwards and Huryn 1995), I analyzed and presented data for habitat contrasts both with and without winged Diptera contributing to input. Response variables for cutthroat trout stomach content data were TI proportion and TI and AI biomass. Statistical analyses of stomach content data were performed for July–October sampling. May–June data were insufficient for analysis. All data were analyzed with PROC-GLM (SAS Institute Inc. 1989) at $p = 0.10$ by two-way factorial (habitat × date) with repeated measure on date ($df = 1,4$). A p -value of 0.10 was chosen because combining low sample size with suspected high within-habitat variability would provide low statistical power. This improved power over a lower p -value. If a significant difference was detected between habitats, an additional ANOVA was performed for each sampling date, again comparing habitats, to determine which dates were significant. Unidentifiable prey, and occasional fish and soil-borne prey that generally comprised <15% of diets, were excluded from these comparisons.

Data were checked for normality, variance homogeneity, and additivity and transformed using $\log_{10}(y + 1)$ for number and mass data and $\arcsin[(y + 1)^{1/2}]$ for proportion data to meet assumptions when necessary. Transformed data were also checked to ensure that assumptions were met. Sample and treatment independence were assumed based on experimental design and protocol used. Statistical power was calculated and reported when H_0 was not rejected (Cohen 1988).

Unfortunately, increasing sample size above three was economically unfeasible. Although I presumed that low sample size ($n = 3$) would provide low statistical power, it was safer to risk low power (and potentially fail to reject null hypotheses) than to falsely conclude

Fig. 2. Mean (A) mass and (B) nitrogen of nonwoody plant tissue (PT) and TI falling into streams ($n = 6$ for all sampling dates except $n = 4$ for early and late September and $n = 2$ for October). Error bars represent 1 SEM.



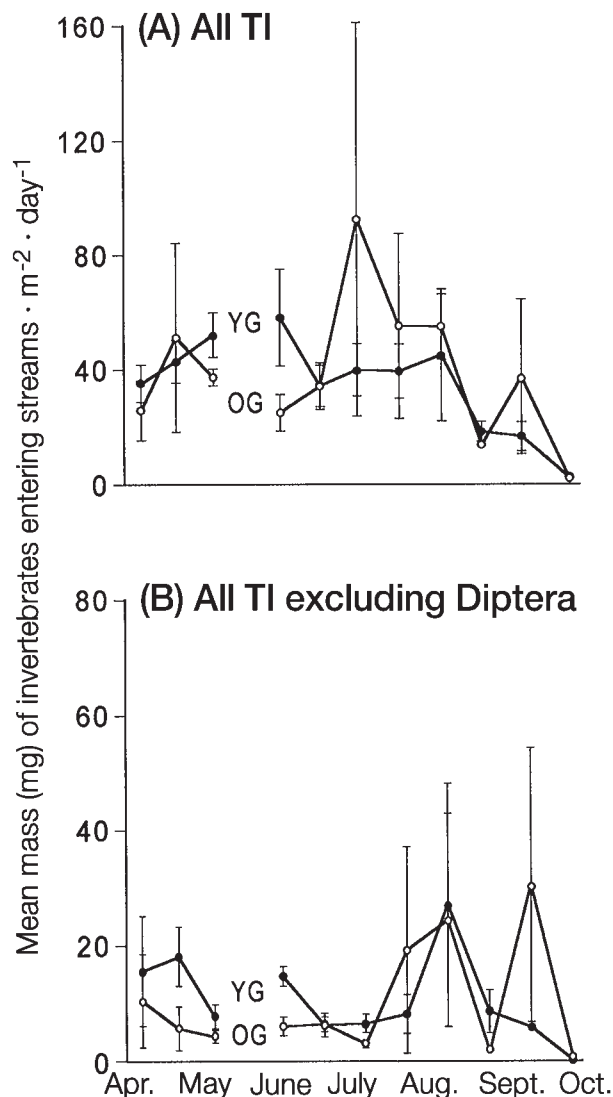
a significant difference in a pseudoreplicated study (i.e., defining fish as experimental units (replicates) and comparing two streams or two reaches within a stream), which unfortunately, still happens with many other natural stream studies. Additionally, the p -value was set at 0.10 instead of 0.05 or 0.01 to help achieve higher statistical power.

Results

Stream inputs of terrestrial invertebrates

TI comprised a small fraction of allochthonous input relative to plant litter: up to 66 versus 5138 mg $\cdot m^{-2} \cdot day^{-1}$ (Fig. 2A). Mean season-long TI input was 37 mg $\cdot m^{-2} \cdot day^{-1}$. Because of

Fig. 3. Mean mass of TI captured in pan-traps in streams within old-growth (OG) and 31-year-old young-growth (YG) riparian habitats (A) including and (B) excluding winged terrestrial Diptera ($n = 3$ for all sampling dates except $n = 1$ for early September OG and October OG and YG and $n = 2$ for late September OG and YG). Error bars represent 1 SEM. Means not significantly different ($p > 0.10$).



their relatively high nitrogen content, they contributed a greater fraction of total nitrogen (than of total biomass), up to 6 versus 141 mg $N \cdot m^{-2} \cdot day^{-1}$, respectively, to these streams (Fig. 2B). Mean season-long nitrogen input from TI was 3 mg $\cdot m^{-2} \cdot day^{-1}$. Their input into streams was not significantly different among habitats for analyses that included (Fig. 3A) and excluded winged terrestrial Diptera (Fig. 3B). Season-long input means including Diptera were 39 and 35 and excluding Diptera were 10 and 11 mg $\cdot m^{-2} \cdot day^{-1}$ in old-growth and young-growth habitats, respectively. Diptera comprised the bulk of TI mass inputs in both habitats, followed by Coleoptera, Lepidoptera, and Araneida (Table 3).

Terrestrial invertebrates as salmonid prey

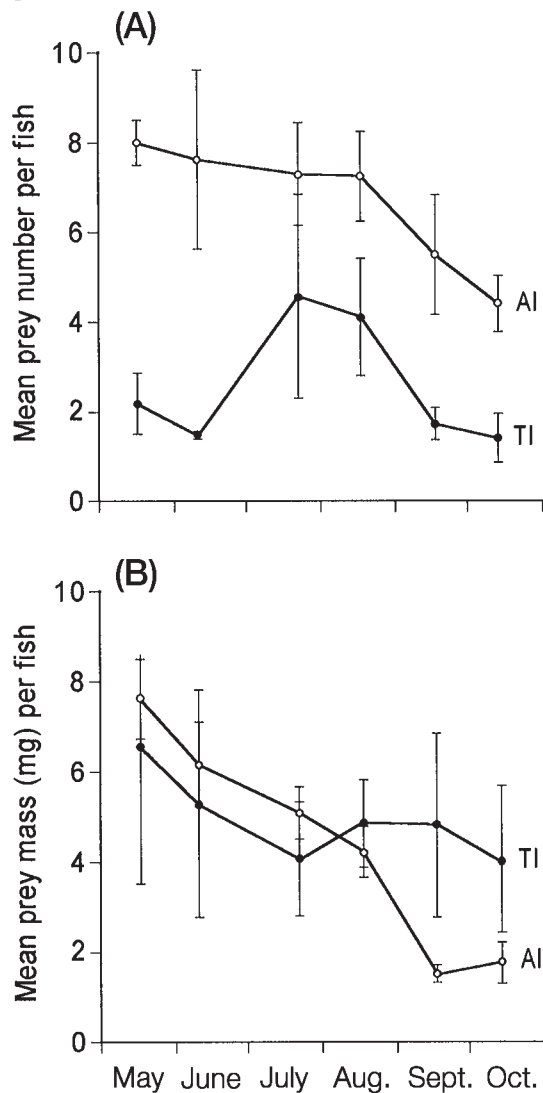
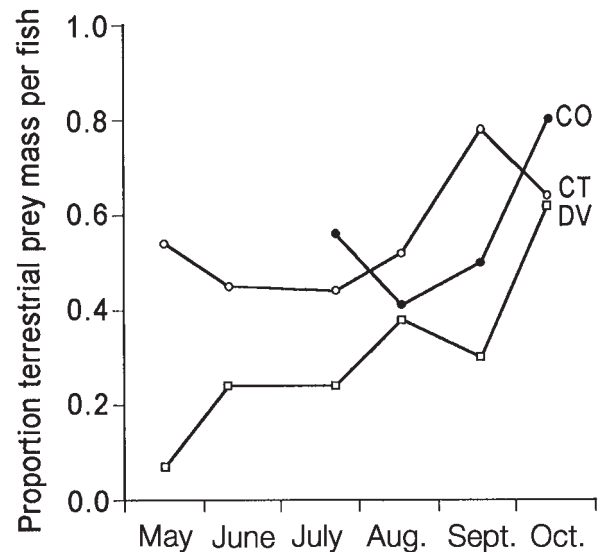
Numerically, TI comprised 30% of invertebrates in fish stomachs

Table 3. Percent composition of TI mass captured in pan-traps.

TI	Riparian forest type ^a	
	OG	YG
Gastropoda	0.0	0.6
Chilopoda	1.3	0.0
Araneida	5.4	6.7
Collembola	0.7	1.5
Hemiptera	0.7	2.6
Coleoptera	7.2	8.0
Lepidoptera	7.8	6.4
Diptera	71.5	60.7
Hymenoptera	0.6	1.7
Other ^b	4.8	11.8

^aOG, old-growth riparian forest; YG, 31-year-old young-growth riparian forest.

^bIncludes unidentifiable invertebrates and taxa that comprised <0.1%.

Fig. 4. Mean (A) number and (B) mass of AI and TI prey ingested by 40–180 mm fork length salmonids, averaged across all six study sites ($n = 3$ for May and June; $n = 6$ for the other months). Error bars represent 1 SEM.**Fig. 5.** Mean proportion of TI prey ingested by the three most common salmonids (coho salmon (CO), cutthroat trout (CT), and Dolly Varden (DV), 40–180 mm fork length) at all six study sites. Values = (TI mass)/(TI mass + AI mass).

(Fig. 4A) but 50% of the biomass (Fig. 4B), for combined fishes. Mass of ingested AI decreased sharply through the season whereas that for TI remained more constant (Fig. 4B). In general, TI were more abundant in fish diets later in the season (Fig. 5). Aquatic taxa (Ephemeroptera, Plecoptera, Trichoptera, and Diptera) and Lepidoptera among TI contributed the greatest masses from individual taxa to food ingested by cutthroat trout over the season (Table 4).

Proportionally, TI were significantly more abundant in cutthroat trout diets through the season in young-growth than in old-growth systems, both numerically ($F = 8.2$, $p = 0.05$) (Fig. 6A) and gravimetrically ($F = 5.8$, $p = 0.07$) (Fig. 6B), with July the only month in which there were significant differences ($F = 10.5$, $p = 0.005$ and $F = 7.4$, $p = 0.015$, proportional number and proportional biomass, respectively). Season-long proportion means were 0.16 and 0.33 for number of terrestrial prey and 0.38 and 0.57 for terrestrial prey mass in old-growth and young-growth habitats, respectively. Although not significant, that trend appeared during all other months. These (terrestrial prey proportion) data appeared lower than what the fish actually ate (i.e., Fig. 5) because they are means of means, summed across fish and streams ($n = 3$) within habitat. (In other words, a fish that ingested one each of AI and TI was given equal “mathematical weight”, for calculating means within habitat, as a fish that ingested one AI and 20 TI.) Statistical power was low ($1 - \beta < 0.30$) because of high within-stream variability and low sample size and subsequently reduced the probability of detecting habitat differences. Taxa that accounted for the most variation between habitats were Chironomidae (Fig. 7A) and Collembola (Fig. 7B). Fish ate significantly more chironomids in old-growth habitats only during July ($F = 6.3$, $p = 0.023$) (Fig. 7A). No significant habitat differences were apparent with ingested collembolans. Again, statistical power was low ($1 - \beta < 0.30$).

Aquatic invertebrate mass ingested was similar for cutthroat trout between habitats (Fig. 8A) and decreased sharply

Table 4. Percent composition of AI and TI mass ingested by cutthroat trout.

	Riparian forest type ^a	
	OG	SG
Aquatic		
Ephemeroptera	11.6	7.3
Plecoptera	12.2	4.5
Trichoptera	15.2	18.0
Diptera	13.0	8.7
Terrestrial		
Gastropoda	0.0	2.1
Diplopoda	3.5	0.0
Chilopoda	4.4	10.7
Isopoda	1.3	0.4
Araneida	4.8	5.9
Collembola	1.1	1.4
Psocoptera	0.1	0.0
Hemiptera	1.7	4.2
Coleoptera	9.3	18.3
Lepidoptera	16.4	13.7
Diptera	0.4	0.6
Hymenoptera	2.0	2.0
Other ^b	3.0	2.2

^aOG, old-growth riparian forest; YG, 31-year-old young-growth riparian forest.

^bIncludes unidentifiable invertebrates and taxa that comprised <0.1%.

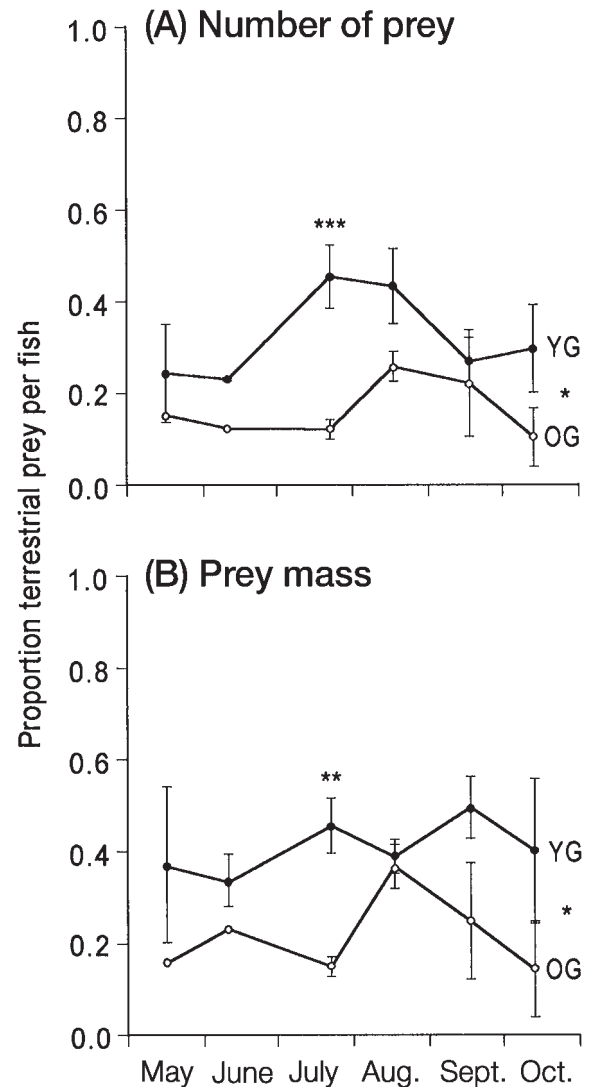
through the season for fish in both habitats; TI mass ingested was also not significant between habitats (Fig. 8B). Season-long means were 4.5 and 4.3 mg·fish⁻¹ for aquatic prey ingested and 3.0 and 6.2 mg·fish⁻¹ for terrestrial prey mass ingested in old-growth and young-growth habitats, respectively. As with previous analyses, power was low ($1 - \beta < 0.30$).

Discussion

These results showed that TI were important food, as important as AI, for young coho salmon, cutthroat trout, and Dolly Varden during spring, summer, and fall in these coastal Alaska streams. The data also suggested that riparian vegetation influences associated TI that fall prey to fishes. This has several implications for riparian forest management and conservation (particularly how it relates to fisheries), stream protection and restoration, and stream ecosystem theory.

Streamside management, including activities that affect riparian vegetation, could have strong influences on stream food web productivity. The 31-year-old alder-dominated young-growth communities in this study appeared to be providing fish with more terrestrial prey (based on diet data) than the old-growth riparian forest. Two obvious characteristics of these young-growth communities, relative to the old-growth communities, were a more dense and diverse understory and a broadleaf-dominated (alder) canopy. This more diverse and possibly productive plant community may support a similarly diverse and productive TI community. Southwood (1961) noted more diverse invertebrate assemblages associated with broadleaf species. Fish in young-growth systems in this study ate a greater proportion of TI than those in old-growth systems

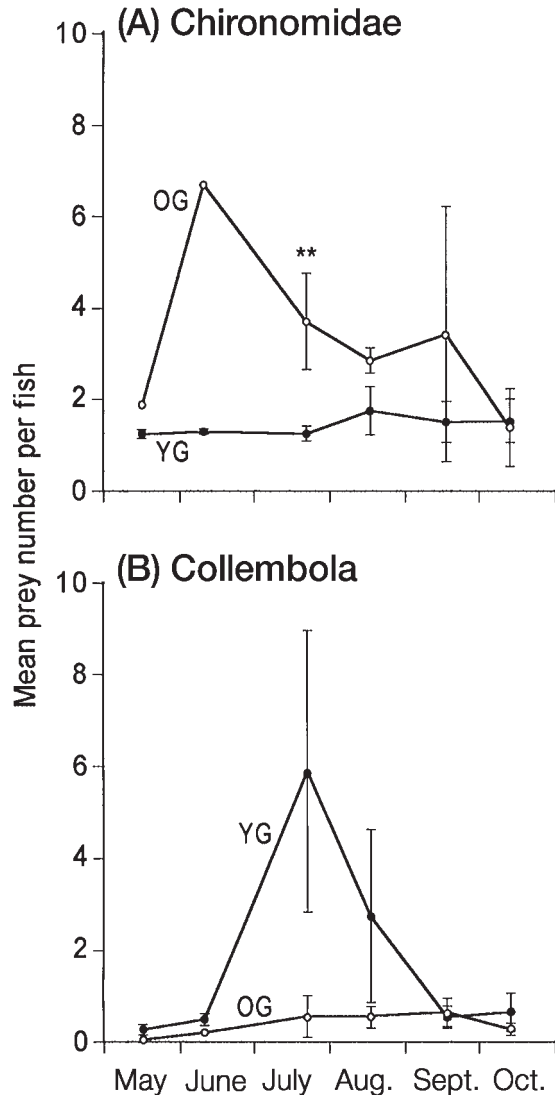
Fig. 6. Mean proportional (A) number and (B) mass of TI prey ingested by 40–180 mm fork length cutthroat trout, contrasting old-growth (OG) and 31-year-old young-growth (YG) habitats ($n = 3$ for all sampling dates except $n = 2$ for May and June YG and $n = 1$ for May and June OG). Values = (TI mass)/(TI mass + AI mass). Error bars represent 1 SEM. Asterisks on the right side of the graph indicate statistically significant season-long (July–October) differences between riparian habitats and those directly above data points indicate month-specific differences (* $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$).



during part of the summer, reflecting possibly higher TI proportions associated with denser broadleaf riparian vegetation. This possibly higher TI abundance in young-growth habitats in this study was probably attributable to the more dense broadleaf-dominated plant community and less related to this habitat simply being young-growth. Less diverse and dense understories seen with 25- to 140-year-old young-growth conifer stands (Franklin and Pechanec 1968; Alaback 1982) may sustain lower invertebrate densities and species richness.

The significant habitat difference seen with diet data did not agree with allochthonous trap data. This may have been a sampling artifact of TI traps. The traps may have been less efficient

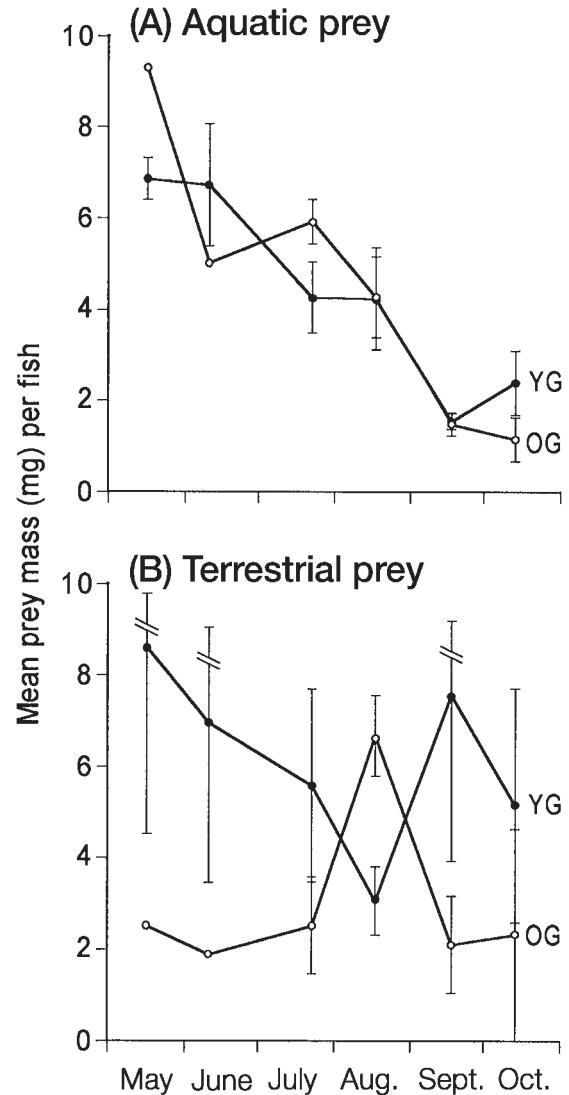
Fig. 7. Mean number of larval and pupal (A) Chironomidae and (B) Collembola ingested by 40–180 mm fork length cutthroat trout, contrasting old-growth (OG) and 31-year-old young-growth (YG) habitats ($n = 3$ for all sampling dates except $n = 2$ for May and June YG and $n = 1$ for May and June OG). Error bars represent 1 SEM. Asterisks indicate month-specific differences between habitats (** $p < 0.05$).



than fish at sequestering certain prey that may have been more abundant in one habitat (e.g., strong crawlers like Coleoptera and Chilopoda may escape from the pans). Traps may also have attracted certain species, particularly winged Diptera (Southwood 1978; Power 1985; Edwards and Huryn 1995). In this study, Diptera comprised an unusually high percentage of pan-trap contents relative to fish stomach contents. However, this should not have compromised habitat comparisons, including when winged Diptera were part of the analysis, because they were about equally abundant in traps from both habitats (i.e., no habitat bias).

Difficulty with accurately measuring TI inputs into aquatic habitats may be one of the reasons quantitative inputs have not been commonly reported in the literature. Trapping methods, including pan-traps, sticky traps, and drift-capture, have their

Fig. 8. Mean mass of (A) AI and (B) TI prey ingested by 40–180 mm fork length cutthroat trout, contrasting old-growth (OG) and 31-year-old young-growth (YG) habitats ($n = 3$ for all sampling dates except $n = 2$ for May and June YG and $n = 1$ for May and June OG). Error bars represent 1 SEM. Means not significantly different ($p > 0.10$).



biases (Southwood 1978; Power 1985; Edwards and Huryn 1995; M.S. Wipfli, personal observation). Pan- and sticky traps may attract certain species, and nets placed in streams will not capture small invertebrates (e.g., Collembola) that pass through netting, nor do they prevent some invertebrates from crawling or flying away. Pan-traps containing a surfactant or sticky traps will help avoid these problems. Drift nets also often become clogged, leading to sample loss. Another possible reason for the paucity of these types of studies may be that aquatic and fishery biologists have traditionally not felt comfortable studying terrestrial ecology, so have ended with simply stating that terrestrial prey are important components of fishes' diets. Another explanation may be that fishery, aquatic, and terrestrial ecologists have historically worked independently. If study objectives are to achieve absolute measures of inputs, nonbiased sampling is crucial (i.e., attractant or

repellent properties of traps are undesirable). Objectives that contrast treatments or habitats, provided that sampling techniques remain consistent across habitats, are less sensitive to errors from biased sampling techniques (i.e., both habitats receive equal bias).

Riparian management will not only affect TI, but aquatic primary and secondary production as well. Riparian vegetation is an important food resource for shredders in streams (Cummins et al. 1989) and may limit shredder communities (Richardson 1991). Broadleaf species, particularly alder, are preferred by aquatic detritivores (Iversen 1974; Friberg and Jacobsen 1994). Higher quality leaf litter increases their growth (Iversen 1974; Anderson and Grafius 1975) and abundance (Sedell et al. 1975), which may increase aquatic prey for fish. In this study, AI were particularly important as prey for fish early in the season, but their relationships to allochthonous inputs were not studied.

Another management consideration is the abundance of terrestrially derived prey for fishes when AI are sparse. Aquatic insect phenology — adult emergence during spring, summer, and fall — will temporarily reduce abundance and availability of many aquatic insects as prey for fishes and other predators. These data showed a rapid decline of AI ingested by fish beginning in May and extending through October, apparently resulting from insect emergence throughout the season. Yet, the quantity of TI ingested remained relatively stable through the season. Late summer/early fall is a critical period for fishes as they sequester lipids and increase body size, providing greater overwinter survivorship (Reimers 1963; Hunt 1969; Hartman et al. 1984). The stable riparian-derived prey supply may be crucial for salmonid survival, especially if fish are already stressed from lack of aquatic prey or suitable habitat, or other stressors.

Reduced water or substrate quality may decrease aquatic prey for fish and other predators. However, loss of all aquatic prey may mean actually only losing up to half of their prey supply if TI are as important as these data have indicated and if their populations have not been reduced. Following disturbance to a stream that substantially reduces aquatic prey abundance, terrestrial prey may help sustain aquatic predators during periods of temporary aquatic prey shortages.

These results provided new insight into the significance of riparian vegetation affecting energy flow in small streams. Aquatic food web models have traditionally often excluded TI as prey for aquatic predators (cf. Minshall 1967; Cummins 1973). This study showed that terrestrially derived prey comprised half of fishes' diets and thus were as important as aquatic prey in these stream food webs. Estimated food consumption of predators has been shown to be higher than what the benthos is believed to provide (Allan 1983; Waters 1988). Allen (1951) reported that benthic invertebrate abundance was far below that needed to support fish production in a New Zealand stream. Waters (1988, 1993) suggested that nonbenthic energy sources may help explain the Allen Paradox. Edwards and Huryn (1995) estimated that TI supported about 5% of trout production in a New Zealand stream. Dedual and Collier (1995) also indicated that TI were present but not a major constituent of trout diets in a New Zealand river whereas McLennan and MacMillan (1984) demonstrated that TI often comprised the bulk of trout diets in several New Zealand rivers. Cloe and Garman (1996) reported that terrestrial arthropod

energy contributions were similar to aquatic contributions in three eastern U.S. streams, with terrestrial inputs being higher in headwater reaches. These results showed that TI comprised half of salmonid diets, suggesting that they may account for much of the presumed energy deficit implicit in the Allen Paradox. However, TI consumption in other years, streams, and ecosystems could be different.

Future stream and riparian zone restoration in southeastern Alaska will probably include managing riparian vegetation. From a salmonid fisheries productivity perspective, both habitat (Bryant 1983; Bisson et al. 1987; Dolloff 1987) and food (Chapman 1966; Mundie 1974; Mason 1976; Richardson 1993) may be important limiting factors in freshwater. Rearing habitat largely depends on in-stream CWD recruited from riparian zones (Bryant 1983; Murphy et al. 1986). Because conifers make better CWD than deciduous trees along the Pacific Northwest coast — they grow larger and decompose more slowly (Harmon et al. 1986) — riparian management may involve selectively thinning less desirable species to promote growth and volume of desirable species (conifers). Thinning the canopy and understory will have dramatic effects on subsequent plant community dynamics: species composition, densities, succession, etc. This should have a dramatic effect on riparian and stream food web productivity, including that of invertebrates. Changes in riparian vegetation will directly influence associated terrestrial arthropods and will affect AI that process allochthonous material. Managers need to consider all possible effects of riparian management activities in this region and other parts of the world, including those on food resources for predators. Vegetation management will influence stream/riparian trophic productivity, thereby affecting fisheries and wildlife.

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References

- Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce – western hemlock forests of southeast Alaska. *Ecology*, **63**: 1932–1948.
- Allan, J.D. 1983. Predator–prey relationships in streams. *In* Stream ecology: application and testing of ecological theory. *Edited by* J.R. Barnes and G.W. Minshall. Plenum Press, New York. pp. 191–229.
- Allen, K.R. 1951. The Horokiwi stream: a study of a trout population. *Bull. N.Z. Mar. Dep. Fish.* **10**: 1–231.
- Anderson, N.H., and Grafius, E. 1975. Utilization and processing of allochthonous material by stream Trichoptera. *Verh. Int. Ver. Limnol.* **19**: 3083–3088.
- Bisson, P.A., Bilby, R.E., Bryant, M.D., Dolloff, C.A., Grette, G.B., House, R.A., Murphy, M.L., Koski, K.V., and Sedell, J.R. 1987. Large woody debris in the Pacific Northwest: past, present, and future. *In* Proceedings of the Symposium Streamside Management: Forestry and Fishery Interactions, Feb. 12–14, 1986, University of Washington, Seattle. pp. 143–190.
- Bocock, K.L. 1964. Changes in the amounts of dry matter, nitrogen,

- carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. *J. Ecol.* **52**: 273–284.
- Bryant, M.D. 1983. The role and management of woody debris in west coast salmonid nursery streams. *N. Am. J. Fish. Manage.* **3**: 322–330.
- Cada, G.F., Loar, J.M., and Cox, D.K. 1987. Food and feeding preferences of rainbow and brown trout in southern Appalachian streams. *Am. Midl. Nat.* **117**: 374–385.
- Cadwallader, P.L., Eden, A.K., and Hook, R.A. 1980. Role of stream-side vegetation as a food source for *Galaxias olidus* Günther (Pisces: Galaxiidae). *Aust. J. Mar. Freshwater Res.* **31**: 257–262.
- Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. *Am. Nat.* **100**: 345–357.
- Cloe, W.W., and Garman, G.C. 1996. The energetic importance of terrestrial arthropod inputs to three warm-water streams. *Freshwater Biol.* **36**: 105–114.
- Cohen, J. 1988. Statistical power analysis for the behavioral sciences. 2nd ed. L. Erlbaum Associates, Hillsdale, N.J.
- Cummins, K.W. 1973. Trophic relations of aquatic insects. *Annu. Rev. Entomol.* **18**: 183–206.
- Cummins, K.W., Wilzbach, M.A., Gates, D.M., Perry, J.B., and Taliaferro, W.B. 1989. Shredders and riparian vegetation: leaf litter that falls into streams influences communities of stream invertebrates. *BioScience*, **39**: 24–30.
- Dedual, M., and Collier, K.J. 1995. Aspects of juvenile rainbow trout (*Oncorhynchus mykiss*) in relation to food supply during summer in the lower Tongariro River, New Zealand. *N.Z. J. Mar. Freshwater Res.* **29**: 381–391.
- Dolloff, C.A. 1987. Seasonal population characteristics and habitat use by juvenile coho salmon in a small southeast Alaska stream. *Trans. Am. Fish. Soc.* **116**: 829–838.
- Edwards, E.D., and Huryn, A.D. 1995. Annual contribution of terrestrial invertebrates to a New Zealand trout stream. *N.Z. J. Mar. Freshwater Res.* **29**: 467–477.
- Fisher, S.G., and Likens, G.E. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecol. Monogr.* **43**: 421–439.
- Franklin, J.F., and Pechanec, A.A. 1968. Comparison of vegetation in adjacent alder, conifer, and mixed alder–conifer communities. I. Understory vegetation and stand structure. *In Proceedings of the Symposium Biology of Alder*, Apr. 14–15, 1967. *Edited by* J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen. Northwest Scientific Association, Pullman, Wash. pp. 37–43.
- Friberg, N., and Jacobsen, D. 1994. Feeding plasticity of two detritivore-shredders. *Freshwater Biol.* **32**: 133–142.
- Garman, G.C. 1991. Use of terrestrial arthropod prey by a stream-dwelling cyprinid fish. *Environ. Biol. Fishes*, **30**: 325–331.
- Gessner, M.O., and Chauvet, E. 1994. Importance of stream micro-fungi in controlling breakdown rates of leaf litter. *Ecology*, **75**: 1804–1817.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **15**: 133–302.
- Harris, A.S., Hutchison, O.K., Meehan, W.R., Swanson, D.N., Helmers, A.E., Hendee, J.C., and Collins, T.M. 1974. The forest ecosystem of southeast Alaska 1. The setting. USDA For. Serv. Gen. Tech. Rep. PNW-12.
- Hartman, G.F., Holtby, L.B., and Scrivener, J.C. 1984. Some effects of natural and logging-related winter stream temperature changes on the early life history of coho salmon (*Oncorhynchus kisutch*) in Carnation Creek, British Columbia. *In Proceedings of the Symposium Fish and Wildlife Relationships in Old-Growth Forests*, Apr. 12–15, 1982. *Edited by* W.R. Meehan, T.R. Merrell Jr., and T.A. Hanley. American Institute of Fishery Research Biologists, Juneau, Alaska. pp. 141–149.
- Hax, C.L., and Golladay, S.W. 1993. Macroinvertebrate colonization and biofilm development on leaves and wood in a boreal river. *Freshwater Biol.* **29**: 79–87.
- Heilman, P.E. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. *Ecology*, **47**: 825–831.
- Hughes, D.R., Gessel, S.P., and Walker, R.B. 1968. Red alder deficiency symptoms and fertilizer trials. *In Proceedings of the Symposium Biology of Alder*, Apr. 14–15, 1967. *Edited by* J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen. Northwest Scientific Association, Pullman, Wash. pp. 225–238.
- Hunt, R.L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. *J. Fish. Res. Board Can.* **26**: 1473–1483.
- Hunt, R.L. 1975. Food relations and behavior of salmonid fishes. 6.1. Use of terrestrial invertebrates as food by salmonids. *In Coupling of land and water systems*. Vol. 10. *Edited by* A.D. Hassler. Springer-Verlag, New York. pp. 137–151.
- Hynes, H.B.N. 1972. The ecology of running waters. 2nd ed. University of Toronto Press, Toronto, Ont.
- Iversen, T.M. 1974. Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of ingested leaves. *Oikos*, **25**: 278–282.
- Jacobsen, D., and Sand-Jensen, K. 1994. Growth and energetics of a trichopteran larva feeding on fresh submerged and terrestrial plants. *Oecologia*, **97**: 412–418.
- Kaushik, N.K., and Hynes, H.B.N. 1971. The fate of the dead leaves that fall into streams. *Arch. Hydrobiol.* **68**: 465–515.
- Maitland, P.S. 1977. The Hamlyn guide to freshwater fishes of Britain and Europe. Hamlyn Publishing Grp. Ltd., New York.
- Mason, J.C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. *J. Wildl. Manage.* **40**: 775–788.
- Mason, C.F., and Macdonald, S.M. 1982. The input of terrestrial invertebrates from tree canopies to a stream. *Freshwater Biol.* **12**: 305–311.
- Mattson, W.J., and Scriber, J.M. 1987. Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral considerations. *In Nutritional ecology of insects, mites, spiders, and related invertebrates*. *Edited by* F. Slansky Jr. and J.G. Rodriguez. 1st ed. John Wiley & Sons, New York. pp. 105–146.
- McLennan, J.A., and MacMillan, B.W.H. 1984. The food of rainbow and brown trout in the Mohaka and other rivers of Hawke's Bay, New Zealand. *N.Z. J. Mar. Freshwater Res.* **18**: 143–158.
- Meehan, W.R., and Miller, R.A. 1978. Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. *J. Fish. Res. Board Can.* **35**: 1359–1363.
- Meyer, E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. *Arch. Hydrobiol.* **117**: 191–203.
- Minshall, G.W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology*, **48**: 139–149.
- Misapagel, M.E., and Rose, S.D. 1978. Arthropods associated with various age stands of Douglas fir from foliar, ground, and aerial strata. Bull. No. 13 Coniferous Forest Biome, Ecosystem Analysis Studies, US/International Biological Program, University of Washington, Seattle.
- Mundie, J.H. 1974. Optimization of the salmonid nursery stream. *J. Fish. Res. Board Can.* **31**: 1827–1837.
- Murphy, M.L., Heifetz, J., Johnson, S.W., Koski, K.V., and Thedinga, J.F. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaska streams. *Can. J. Fish. Aquat. Sci.* **43**: 1521–1533.
- Nielsen, J.L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. *Trans. Am. Fish. Soc.* **121**: 617–634.
- Power, G. 1985. A method for estimating potential insect availability

- at the surface of rivers. Fish. Res. Div. N.Z. Minist. Agric. Fish. Fish. Environ. Rep. No. 53.
- Reimers, N. 1963. Body condition, water temperature, and overwinter survival. Trans. Am. Fish. Soc. **92**: 39–46.
- Richardson, J.S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology, **72**: 873–887.
- Richardson, J.S. 1993. Limits to productivity in streams: evidence from studies of macroinvertebrates. Can. Spec. Pub. Fish. Aquat. Sci. No. 118. pp. 9–15.
- Rogers, L.E., Hinds, W.T., and Buschbom, R.L. 1976. A general weight vs. length relationship for insects. Ann. Entomol. Soc. Am. **69**: 387–389.
- Rogers, L.E., Buschbom, R.L., and Watson, C.R. 1977. Length–weight relationships of shrub–steppe invertebrates. Ann. Entomol. Soc. Am. **70**: 51–53.
- SAS Institute Inc. 1989. SAS-STAT® user's guide, version 6, 4th ed. SAS Institute Inc., Cary, N.C.
- Schowalter, T.D., Webb, J.W., and Crossley, D.A.J. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. Ecology, **62**: 1010–1019.
- Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.
- Sedell, J.R., Triska, F.J., and Triska, N.S. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. Verh. Int. Ver. Limnol. **19**: 1617–1627.
- Short, R.A., Canton, S.P., and Ward, J.V. 1980. Detrital processing and associated macroinvertebrates in a Colorado mountain stream. Ecology, **61**: 727–732.
- Smock, L.A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biol. **10**: 375–383.
- Southwood, T.R.E. 1961. The number of species of insect associated with various trees. J. Anim. Ecol. **30**: 1–8.
- Southwood, T.R.E. 1978. Ecological methods: with special reference to the study of insect populations. 2nd ed. Chapman and Hall, London.
- Sterba, G. 1962. Freshwater fishes of the world. Studio Vista Books, London, England.
- Triska, F.J., and Sedell, J.R. 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. Ecology, **57**: 783–792.
- Triska, F.J., Sedell, J.R., and Gregory, S.V. 1982. Coniferous forest streams. In Analysis of coniferous forest ecosystems in the western United States. Edited by R.L. Edmonds. Hutchinson Ross Publishing Co., Stroudsburg, Pa. pp. 292–332.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37**: 130–137.
- Waters, T.F. 1988. Fish production – benthos production relationships in trout streams. Pol. Arch. Hydrobiol. **35**: 545–561.
- Waters, T.F. 1993. Dynamics in stream ecology. Can. Spec. Publ. Fish. Aquat. Sci. No. 118. pp. 1–8.
- Watt, R.F., and Heinzelman, M.L. 1965. Foliar nitrogen and phosphorus level related to site quality in a northern Minnesota spruce bog. Ecology, **46**: 357–361.
- Webster, J.R., and Benfield, E.F. 1986. Vascular plant breakdown in freshwater ecosystems. Annu. Rev. Ecol. Syst. **17**: 567–594.
- Webster, J.R., Golladay, S.W., Benfield, E.F., Meyer, J.L., Swank, W.T., and Wallace, J.B. 1992. Catchment disturbance and stream response: an overview of stream research at Coweeta Hydrologic Laboratory. In River conservation and management. Edited by P.J. Boon, P. Calow, and G.E. Petts. John Wiley & Sons, New York. pp. 231–253.
- Whittaker, R.H., Likens, G.E., Bormann, F.H., Eaton, J.S., and Siccama, T.G. 1979. The Hubbard Brook ecosystem study: forest nutrient cycling and element behavior. Ecology, **60**: 203–220.
- Woodwell, G.M., Whittaker, R.H., and Houghton, R.A. 1975. Nutrient concentrations in plants in the Brookhaven oak–pine forest. Ecology, **56**: 318–332.
- Yamaya, K. 1968. On the influence of alder (*Alnus inokumae*) on soil properties in northern Japan. In Proceedings of the Symposium Biology of Alder, Apr. 14–15, 1967. Edited by J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen. Northwest Scientific Association, Pullman, Wash. pp. 197–208.