

Aquatic insects play a minor role in dispersing salmon-derived nutrients into riparian forests in southwestern Alaska

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Abstract: Recent research has highlighted the importance of nutrients derived from Pacific salmon (*Oncorhynchus* spp.) carcasses for coastal freshwater and riparian ecosystems. To investigate the role of emerging aquatic insects in dispersing salmon nutrients from spawning streams to riparian habitats, we quantified the emergence and return rates of mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) on Pick Creek in southwestern Alaska and, using stable isotopes, estimated the associated flux of nutrients derived from sockeye salmon (*Oncorhynchus nerka*) to streamside forests. Between June and September of 2004, 7.6 mg·m⁻² of salmon-derived nitrogen emerged from Pick Creek in the form of aquatic invertebrates, 6.7 mg·m⁻² of which was transferred to the terrestrial ecosystem. Dispersal patterns on four area streams showed that the majority of stream-borne nutrients are deposited within 25 m of the stream. Aquatic insects represent a minor vector for salmon nutrients to terrestrial systems, dispersing less than 0.03% of total nitrogen imported to Pick Creek by spawning salmon. Nevertheless, emerging insects make available salmon-derived resources otherwise inaccessible to some terrestrial consumers.

Résumé : Des recherches récentes soulignent l'importance des nutriments dérivés des carcasses de saumons du Pacifique (*Oncorhynchus* spp.) pour les écosystèmes côtiers d'eau douce et les écosystèmes des rivages. Afin de déterminer le rôle de l'émergence des insectes aquatiques dans la dispersion des nutriments de saumons depuis les cours d'eau de fraye vers les habitats du rivage, nous avons mesuré les taux d'émergence et de retour des éphémères (Ephemeroptera), des perles (Plecoptera) et des phryganes (Trichoptera) à Pick Creek dans le sud-ouest de l'Alaska; nous avons ensuite estimé le flux correspondant de nutriments dérivés des saumons rouges (*Oncorhynchus nerka*) vers les forêts riveraines à l'aide d'isotopes stables. Entre juin et septembre 2004, 7,6 mg·m⁻² de nutriments provenant des saumons ont émergé de Pick Creek sous forme d'invertébrés aquatiques, dont 6,7 mg·m⁻² ont été transmis à l'écosystème terrestre. Les patrons de dispersion dans trois sections du cours d'eau montrent que la majorité des nutriments provenant du cours d'eau sont déposés à moins de 25 m de la rive. Les insectes aquatiques représentent un vecteur peu important pour le transfert des nutriments provenant des saumons vers les systèmes terrestres et sont responsables de la dispersion de moins de 0,03 % de l'azote total importé dans Pick Creek par les saumons en fraye. Néanmoins, les insectes en émergence rendent disponibles des nutriments dérivés des saumons qui autrement seraient inaccessibles à certains consommateurs terrestres.

[Traduit par la Rédaction]

Introduction

Pacific salmon (*Oncorhynchus* spp.) represent an important link between marine and freshwater ecosystems because of their anadromous and semelparous life history. Pacific salmon accumulate over 95% of their body mass in the marine environment (Groot and Margolis 1991), and their nutrient-rich carcasses are deposited in freshwater ecosystems

upon their return migration, spawning, and eventual death. Recent evidence indicates that this seasonal pulse of energy and nutrients is an important subsidy to freshwater systems. Much attention has been drawn to the contribution by spawning salmon of marine-derived nutrients (MDN), including nitrogen (N) and phosphorus, which are incorporated into aquatic biota (Naiman et al. 2002; Schindler et al. 2003). Indeed, lotic organisms across nearly all freshwater trophic levels accumulate MDN relative to biota from streams or reaches inaccessible to salmon, including periphyton (Kline et al. 1990), invertebrates (Kline et al. 1990; Bilby et al. 1996), resident fishes (Wipfli et al. 2003), and juvenile salmonids (Bilby et al. 1998). While there is debate over the impact of MDN on the productivity of aquatic ecosystems, there exists some evidence that salmon carcasses in streams can increase the density of juvenile salmonids (Bilby et al. 1998) and some aquatic invertebrates (Wipfli et al. 1998; Lessard and Merritt 2006) at local scales.

Salmon-derived nutrients deposited in freshwater systems are also incorporated into terrestrial food webs and riparian

Received 6 January 2006. Accepted 29 August 2006.
Published on the NRC Research Press Web site at
<http://cjfas.nrc.ca> on 2 November 2006.
J19091

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forests (Ben-David et al. 1998; Willson et al. 1998; Helfield and Naiman 2001). Numerous terrestrial consumers feed directly on live and dead salmon (Cederholm et al. 1989; Ben-David et al. 1998; Willson et al. 1998). Terrestrial insects along stream reaches accessible to salmon are enriched in MDN relative to their counterparts collected from reaches blocked to salmon (Hocking and Reimchen 2002). Riparian vegetation along salmon-bearing streams or reaches is relatively enriched in ^{15}N compared with upland vegetation and vegetation adjoining reaches inaccessible to salmon (Reimchen et al. 2003; Bartz and Naiman 2005; Koyama et al. 2005), a contrast that suggests an association between spawning salmon and nutrient fluxes to terrestrial ecosystems.

Salmon nutrients are transported to riparian ecosystems via a suite of biotic and abiotic processes (Schindler et al. 2003; Helfield and Naiman 2006). Piscivorous predators carry salmon carcasses into riparian zones for consumption (Ben-David et al. 1998; Hilderbrand et al. 1999). Bears are perhaps the most conspicuous salmon predators and are responsible for the deaths of 5%–95% of salmon in streams (Reimchen 2000; Quinn et al. 2003; Gende et al. 2004). Consumers such as bears deposit salmon nutrients in riparian ecosystems through excretion (Hilderbrand et al. 1999) and often leave behind a substantial amount of unconsumed salmon tissue to decompose and enter riparian nutrient cycles (Reimchen 2000; Gende et al. 2004). Flooding also transports substantial numbers of salmon carcasses out of rivers and streams into adjacent riparian ecosystems (Cederholm et al. 1989). Salmon carcasses in some systems remain in aquatic habitats where they decompose, and riparian vegetation can take up dissolved MDN from both surface and subsurface (hyporheic) flow (Naiman et al. 2000; O'Keefe and Edwards 2003).

Emerging aquatic invertebrates may also be important vectors of MDN to riparian ecosystems. In mesocosms and natural experiments, larval forms of aquatic insects become enriched with salmon nutrients in the presence of salmon carcasses (Johnston et al. 1997; Chaloner and Wipfli 2002; Chaloner et al. 2002). Predatory and omnivorous insects, such as some caddisflies (Trichoptera) and stoneflies (Plecoptera), ingest salmon nutrients through direct consumption of salmon eggs and carcasses (Kline et al. 1993; Minakawa et al. 2002; Winder et al. 2005). Other invertebrates such as mayflies (Ephemeroptera) assimilate salmon nutrients indirectly by grazing on biofilms (Schuldt and Hershey 1995; Bilby et al. 1996). After emerging from streams, some aquatic insects disperse laterally into riparian habitats where they can potentially enter terrestrial food webs. Abundance of aquatic invertebrates generally declines with distance from streams (Griffith et al. 1998; Briers et al. 2002; Petersen et al. 2004), and this lateral dispersal pattern will control the extent to which aquatic invertebrates disperse salmon nutrients into riparian forests.

While it is widely accepted that Pacific salmon can influence terrestrial and aquatic food webs, we do not yet fully understand the extent and mechanisms of MDN movement into riparian habitats. In ecosystems where Pacific salmon have declined, restoration efforts include salmon carcass addition, under the assumption that the salmon-derived nutrients will be taken up in aquatic ecosystems as well as

transferred to riparian habitats. Some of the vectors for nutrient transfer to riparian habitats have been investigated, most notably via the movement of carcasses to streamside areas by bears (Ben-David et al. 1998; Hilderbrand et al. 1999; Helfield and Naiman 2002). Other studies have proposed that emerging aquatic insects may also serve as a vector for the transfer of salmon-derived nitrogen (SDN) to terrestrial habitats (Reimchen et al. 2003; Schindler et al. 2003; Helfield and Naiman 2006; Merz and Moyle 2006). The purpose of this study was to quantify the role of aquatic invertebrates as vectors of MDN to riparian forests. We used N-stable isotopes to estimate the contribution of MDN to the biomass of three benthic invertebrate taxa. To determine the magnitude of the flux of MDN into riparian forests, we quantified emergence and return rates of aquatic insects on one salmon-bearing stream in southeastern Alaska and place our values in a broader context through a comparison with other published emergence rates. Finally, we also measured the lateral dispersal of aquatic insects in four study streams and thereby estimate the extent of transfer of stream nutrients to riparian forests. Our results show that from the perspective of mass flux, emerging aquatic insects play a minor and localized role in dispersing salmon-derived nutrients into terrestrial habitats.

Materials and methods

Study site

We sampled aquatic invertebrates during 2001 and 2004 in the Wood River lake system in the Bristol Bay region of southwestern Alaska ($59^{\circ}20'\text{N}$, $158^{\circ}40'\text{W}$), a system characterized by high densities of sockeye salmon (*Oncorhynchus nerka*) in lakes and streams used as spawning habitat (Hilborn et al. 2003). The 20-year mean sockeye escapement for the Nushagak fishing district, including the Wood River system, was over 2.1 million for 1993–2003, over 60% of which returned to Wood River streams and lakes (Westing et al. 2005).

We sampled invertebrates on Pick Creek, a tributary of Lake Nerka that contains spawning sockeye salmon. The 10-year (1995–2004) mean sockeye salmon escapement to Pick Creek was about 6000 (D. Schindler, University of Washington Alaska Salmon Program, Seattle, Washington, unpublished data). Three additional Lake Nerka tributaries were used to study the spatial extent of invertebrate dispersal or to estimate mean invertebrate N isotopic values: Lynx Creek, with a 10-year mean sockeye salmon escapement of about 3500, and two streams without salmon, Cottonwood and Rainbow creeks (Table 1). Riparian vegetation on Lake Nerka tributaries is dominated by ferns and willow (*Salix* spp.), cottonwood (*Populus* spp.) and alder (*Alnus* spp.) shrubs and trees. Upland forest community is dominated by white spruce (*Picea glauca*).

Invertebrate sampling

To quantify the enrichment in SDN of aquatic insects in salmon-bearing streams of the Wood River system, we collected adult invertebrates during 2004 from Pick Creek and two non-salmon streams, Cottonwood and Rainbow creeks, for reference. Invertebrates were sampled between June and September, before, during, and after salmon spawning, using

Table 1. Physicochemical characteristics of study streams in Bristol Bay, Alaska.

Stream	Total length (km)	Mean channel width (m)	Mean depth (m)	Flow (m·s ⁻¹)	Slope (%) ^a	Mean temperature (°C)	Conductivity (mS·cm ⁻¹) ^d
Pick Creek	4.0 ^a	11.2 ^a	0.7 ^a	0.5 ^b	0.60	7.5 ^b	55.1
Lynx Creek	2.3 ^a	14.2 ^a	0.9 ^a	0.7 ^b	0.82	11.2 ^c	37.5
Cottonwood Creek	2.3 ^e	5.5 ^b	0.24 ^b	0.4 ^b	NA	8.7 ^d	25.0
Rainbow Creek	7.9 ^e	15 ^d	0.23 ^d	1.7 ^d	NA	8.0 ^d	41.9

Note: Flow is calculated as mean flow for June–September 2004, except for Rainbow Creek, where flow was measured on one day in September 2005. Depth and width for Cottonwood and Rainbow creeks are point measurements. Conductivity is corrected to 25 °C. No slope calculations were available for Cottonwood or Rainbow creeks (i.e., NA).

^aG. Pess, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA, unpublished data.

^bJ.W. Moore, unpublished data.

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^dG.W. Holtgrieve, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA, unpublished data.

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emergence traps and settling nets. Specimens were dried at 50 °C and finely ground, and a subsample of between 0.8 and 1.2 mg was used for determination of stable isotope composition. A Europa C/N continuous flow isotope ratio mass spectrometer was used to determine stable N isotopic ratios and total N content at the University of California – Davis Stable Isotope Facility (Davis, California).

The ratio of ¹⁵N:¹⁴N is used to calculate δ¹⁵N as

$$(1) \quad \delta^{15}\text{N} = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000$$

where R_{sample} is ¹⁵N:¹⁴N in the sample, and R_{standard} is ¹⁵N:¹⁴N in the atmosphere (Peterson and Fry 1987). Mean δ¹⁵N and total N content were calculated for the three dominant aquatic invertebrate orders collected, Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies), for Pick Creek and across the two non-salmon streams.

To estimate the proportion of SDN incorporated into individuals of each invertebrate order, we used a two-source mixing model to determine the relative importance of N derived from salmon versus N derived from freshwater sources in insect tissues:

$$(2) \quad \delta^{15}\text{N}_{\text{insect}} = P_{\text{salmon}}(\delta^{15}\text{N}_{\text{salmon}} + \beta L) + (1 - P_{\text{salmon}})(\delta^{15}\text{N}_{\text{insect-ns}})$$

where δ¹⁵N_{insect} is the mean δ¹⁵N of the target insect order collected from salmon-bearing streams; P_{salmon} is the proportion of insect N derived from salmon; δ¹⁵N_{salmon} is the δ¹⁵N of sockeye salmon tissue, assumed to be 11.2 ‰ (standard deviation (SD) = 0.45; Schindler et al. 2005); δ¹⁵N_{insect-ns} is the mean δ¹⁵N of the same insect taxa collected from non-salmon streams, where none of the N is assumed to be derived from salmon; β is the average enrichment in δ¹⁵N between trophic levels (assumed to be 3.4‰; Post 2002); and L is the number of trophic levels between the consumer and the prey source.

Because we did not know the detailed trophic structure of our study streams, we generated scenarios of taxa-specific trophic positions to estimate a range of invertebrate enrichment in salmon nutrients, using the observed mean isotopic values for each insect order and a range of values for L (eq. 2) from 1 to 3. For example, when estimating the enrichment in SDN of stoneflies, we allowed for the possibility that they accumulate SDN either directly from consumption

of salmon carcasses ($L = 1$; Chaloner et al. 2002) or indirectly through consumption of prey that ingest SDN directly. For example, the scenario with $L = 3$ characterizes a system where the stonefly is a secondary carnivore in a system where algae assimilate SDN directly (i.e., algae – grazer – primary carnivore – stonefly). The assumption of direct salmon consumption ($L = 1$) provides the highest estimate of enrichment, whereas assuming several trophic steps between salmon and consumers in the mixing model (i.e., $L = 3$) provides the most conservative estimate of enrichment. In this way, we can account for potential variation in trophic structure between study streams and bound our estimates of SDN enrichment in aquatic insects. Both methods provided similar estimates of the percentage of invertebrate N that was derived from salmon (see Results). A list of the aquatic invertebrate taxa in the four study streams is presented in Table 2.

To quantify the flux of SDN by emerging aquatic insects, we intensively measured emergence and settling rates of adult mayflies, stoneflies, and caddisflies on Pick Creek from June through September 2004. Emergence was measured continuously from 24 June to 10 September using 15 emergence traps at five sites along a 1000 m stretch of the stream, within the area of the stream used by salmon for spawning. Emergence traps were 0.25 m² boxes made of hardware cloth, anchored to the stream beds with rebar, and covered with 1 mm mesh mosquito netting that allowed flow of air and water. At each sampling site, emergence traps were placed along the edge and in the middle of the stream to capture possible variability associated with habitat type. Emergence rates were calculated as the mean number of aquatic insects (Ephemeroptera, Plecoptera, and Trichoptera) emerging per square metre of Pick Creek per day, multiplied by the mean individual mass per taxa. Because of uneven distribution in emergence rates of mayflies (Ephemeroptera) between habitat type (analysis of variance (ANOVA): $p < 0.001$; SYSTAT 11.0, Systat Software Inc., Point Richmond, California), mayfly emergence rates were weighted by the proportion of the stream reach estimated to be composed of open channel (0.9) and edge (0.1).

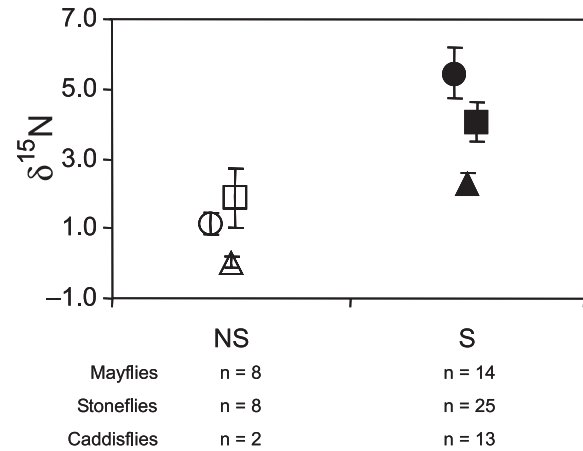
We continuously measured insect return, or settling, on Pick Creek from 26 June to 24 July using 30 settling nets at the same five sites established for measuring emergence. Settling nets were adapted from the design of Jackson and Fisher (1986) and were 39.5 cm diameter conical nets at-

Table 2. Aquatic invertebrate taxa of Wood River system streams, Alaska.

Order	Family	Genus
Ephemeroptera	Baetidae	<i>Baetis</i>
	Ephemerellidae	<i>Drunella</i>
	Heptageniidae	<i>Cinygmula</i>
Plecoptera	Chloroperlidae	
	Nemouridae	
	Perlodidae	
Trichoptera	Limnephilidae	<i>Ecclisomyia</i>

tached to sturdy wire frames suspended 5–8 cm above and parallel to the water. The basket of each net drifted freely downstream, but was weighted down to keep it submerged. Settling nets were also placed in both edge and open channel habitats to capture potential variability in return rates by habitat type. Both emergence traps and settling nets were sampled on average every 48 h. Insects collected were either frozen or preserved in 95% ethanol. Insect return rates were calculated as the mean number of aquatic invertebrates settling per square metre of Pick Creek per day, multiplied by the mean individual weight per taxa. Because settling was measured only until 24 July, whereas emergence was measured until 10 September, to estimate seasonal flux of aquatic invertebrates we calculated a mean per-day settling rate as a percentage of emergence for the period 26 June – 24 July and applied that rate to the period from 24 July to 10 September to estimate total seasonal settling. The proportion of adult aquatic insects returning to the stream is relatively constant over the emergence season, with the exception of a brief period during peak emergence (Stagliano et al. 1998).

To establish a generalizable pattern of lateral aquatic insect dispersal following emergence, we sampled adult aquatic insects on four creeks during July and August of 2001, corresponding to time periods before and after salmon spawning. The majority of invertebrates on all streams emerged during the July sample period, and therefore those data were used to establish dispersal rates. We established sampling points along four transects on Pick, Lynx, Rainbow, and Cottonwood creeks at 0, 5, 10, 20, 50, and 100 m perpendicular to the stream edge. Adult insects were sampled at each sample point using a single sticky trap made of 345 cm² translucent plastic plates sprayed with Tangle-trap Insect Trap Coating (The Tanglefoot Company, Grand Rapids, Michigan) and suspended from vegetation ~1.5 m above ground. Traps were collected after 48 h, wrapped in plastic, and frozen. Insects were removed from sticky traps using Dumonde Tech Citrus Cleaner (Dumonde Design Group, Inc., Seattle, Washington) and rinsed twice in 95% ethanol before being preserved in 95% ethanol. Spatial distributions of aquatic invertebrates were calculated as the mean number of individuals collected per square metre of trap per 48 h period at each distance across all transects per stream. Dispersal results were separated by sample period (July and August) because of differences between sample times on each stream for at least one distance (ANOVA, $p < 0.001$; SYSTAT 11.0). To estimate the lateral extent to which insects disperse nutrients away from each of the four

Fig. 1. Nitrogen isotope signatures of stoneflies (circles), mayflies (triangles), and caddisflies (squares) on streams with no salmon (NS) and with salmon (S) in 2004. Symbols represent means of all individuals collected on each stream type. Error bars are ± 1 standard error. Sample sizes for each taxa are listed below y-axis labels. All NS–S pairs are statistically different (Student's t test; $p < 0.05$).

study streams, we fit a logistic model to the number of insects found at increasing distance from the stream edge for each taxa, stream, and date. The proportion Y_x of insects found at distance X from the stream edge was characterized by the equation

$$(3) \quad Y_x = 1 - \frac{1}{1 + \exp \left[-\ln(19) \left(\frac{X - p_{50}}{p_{95} - p_{50}} \right) \right]}$$

where p_{50} and p_{95} are fitted parameters that define the shape of the logistic model, and correspond to values of X that give 50% and 95% of the cumulative distribution, respectively. The models were fit by minimizing the sums of squares between the model and the observations taken on each of the study creeks. We used the resulting model fits for each insect order in each stream to quantify the distance at which 50% and 95% of insects were dispersed across all streams.

We used Helfield and Naiman's (2006) mass balance model for N flux in the Wood River system to compare emerging aquatic invertebrates against other vectors of SDN to riparian forests. We parameterized the model for Pick Creek stream area (2.4 ha) and salmon density (8200 in 2004). Parameters describing bear predation rate, hyporheic flow, precipitation, proportion of the riparian forest that is alder, and stream discharge were taken from Helfield and Naiman (2006).

Results

We compared enrichment in SDN of aquatic invertebrates collected from Pick Creek with those from two non-salmon streams. Caddisflies, stoneflies, and mayflies from Pick Creek were significantly ($p < 0.05$) enriched in ^{15}N relative to their counterpart taxa on non-salmon streams, as evidenced by their higher $\delta^{15}\text{N}$ values (Fig. 1). These mean $\delta^{15}\text{N}$ values were used in a two-source mixing model (eq. 2)

Table 3. Enrichment of aquatic invertebrates in salmon-derived nitrogen.

Taxa	Proportion salmon-derived N		<i>n</i>
	Direct consumption	Indirect consumption	
Stoneflies	0.32 (0.14)	0.21 (0.09)	25
Mayflies	0.16 (0.04)	0.11 (0.03)	14
Caddisflies	0.17 (0.09)	0.12 (0.06)	13

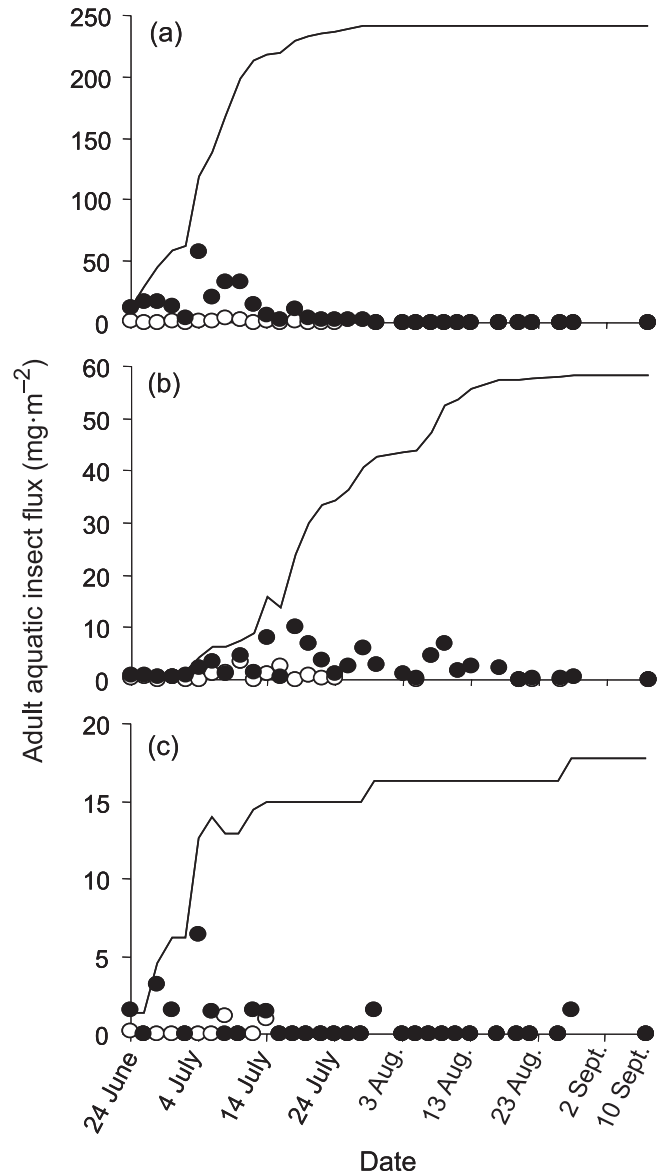
Note: Data shown are taxa-specific means (± 1 standard deviation). Sample sizes (*n*) are the number of insects collected from salmon streams.

to calculate the proportion of N that is salmon-derived for the three insect orders (Table 3). We found that stoneflies on Pick Creek contained 21%–32% SDN, depending on which trophic structure scenario was imposed on the calculation. Enrichment in SDN was similar between mayflies (11%–16%) and caddisflies (12%–17%) on Pick Creek.

We intensively measured emergence and settling rates of three aquatic invertebrate taxa on Pick Creek in 2004. Emergence of mayflies and caddisflies peaked early in the season, on or about 4 July (Figs. 2a, 2c), whereas stonefly emergence peaked 2 weeks later, on or about 18 July (Fig. 2b). Emergence of these taxa from Pick Creek was $361.6 \text{ mg}\cdot\text{m}^{-2}$ over the entire season, or $4.8 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Table 4). Mayflies represented the majority of the measured invertebrate biomass and nutrients emerging from Pick Creek, at over three times the emergence rate of the other two taxa (Table 4). Over the entire stream, $33.4 \text{ mg}\cdot\text{m}^{-2}\cdot\text{season}^{-1}$, or 9.2% of emerging aquatic insect biomass settled back into Pick Creek (Table 4), resulting in a net export of $328.2 \text{ mg}\cdot\text{m}^{-2}\cdot\text{season}^{-1}$ to riparian forests. Adult stoneflies had the highest rate of return to the stream (22.9%), as compared with caddisflies (10.9%) and mayflies (4.7%). Net seasonal flux to riparian forests over the entire season, calculated as the difference between seasonal emergence and seasonal settling, was highest in mayflies, followed by stoneflies and caddisflies (Fig. 2 cumulative line; Table 4). Mean (± 1 standard error (SE)) individual dry mass per taxa was as follows: mayflies = 1.28 mg (0.1 mg); stoneflies = 1.06 mg (0.1 mg); caddisflies = 3.5 (0.9).

Using the stable isotope and mixing model results above, we calculated the flux of total N and SDN from Pick Creek by emerging aquatic insects. Of the $328 \text{ mg}\cdot\text{m}^{-2}$ total invertebrate biomass dispersed to riparian forests in 2004, $35.5 \text{ mg}\cdot\text{m}^{-2}$ of N was exported, of which $6.7 \text{ mg}\cdot\text{m}^{-2}$ was salmon-derived (Table 5). The SDN flux by emerging aquatic insects represented $<0.01\%$ of the 600–673 kg N imported by spawning sockeye salmon to Pick Creek in 2004, based on 8200 salmon returning (D. Schindler, unpublished data) and a conservative estimate of 73 g of N per salmon (Mathisen et al. 1988). Mean (± 1 SD) proportion N by mass for each taxa were as follows: caddisflies = 0.11 (0.04); mayflies = 0.11 (0.04); stoneflies = 0.10 (0.03).

We measured adult insect dispersal on four streams in 2001 to estimate the spatial extent of SDN exported by aquatic insects (Fig. 3). On Pick Creek, for example, dispersal of stoneflies, mayflies, and caddisflies declined exponentially with distance away from the stream edge (Fig. 3). Logistic model fits to cumulative dispersal patterns on all four study streams showed that adult aquatic invertebrate density was

Fig. 2. Emergence (●) and settling (○) rates of adult mayflies (a), stoneflies (b), and caddisflies (c) on Pick Creek. Circles represent mean fluxes of dry mass per square metre of stream per day. Solid lines represent cumulative net flux of dry mass. Dips in cumulative net flux lines represent cumulative net days with greater settling than emergence, resulting in a decline in total net flux to riparian forests.

highest at the stream's edge, 50% of invertebrate biomass was dispersed to within 10 m of the stream, and 95% of invertebrate biomass was dispersed to within 25 m of the stream (Fig. 3). No aquatic invertebrates were collected 100 m away from the edge of any of the four study streams.

Discussion

Relative to estimates of other fluxes of N from salmon streams to riparian systems, we found that emerging aquatic invertebrates represent a minor vector. Many studies have demonstrated that larval aquatic invertebrates become enriched in ^{15}N in salmon-bearing streams (Kline et al. 1990,

Table 4. Emergence and settling rates of aquatic insects on Pick Creek, Alaska.

Taxa	Daily emergence (mg·m ⁻² ·day ⁻¹)	Seasonal emergence (mg·m ⁻² ·season ⁻¹)	Seasonal settling (mg·m ⁻² ·season ⁻¹)	Net seasonal flux (mg·m ⁻² ·season ⁻¹)
Mayflies	3.48 (0.8)	261.1 (62.0)	12.4 (5.9)	248.7 (57.4)
Stoneflies	1.12 (0.2)	84.0 (14.4)	19.2 (8.1)	64.8 (19.5)
Caddisflies	0.22 (0.1)	16.5 (7.8)	1.8 (1.8)	14.7 (8.5)
Total	4.8 (0.8)	361.6 (57.8)	33.4 (9.5)	328.2 (54.0)

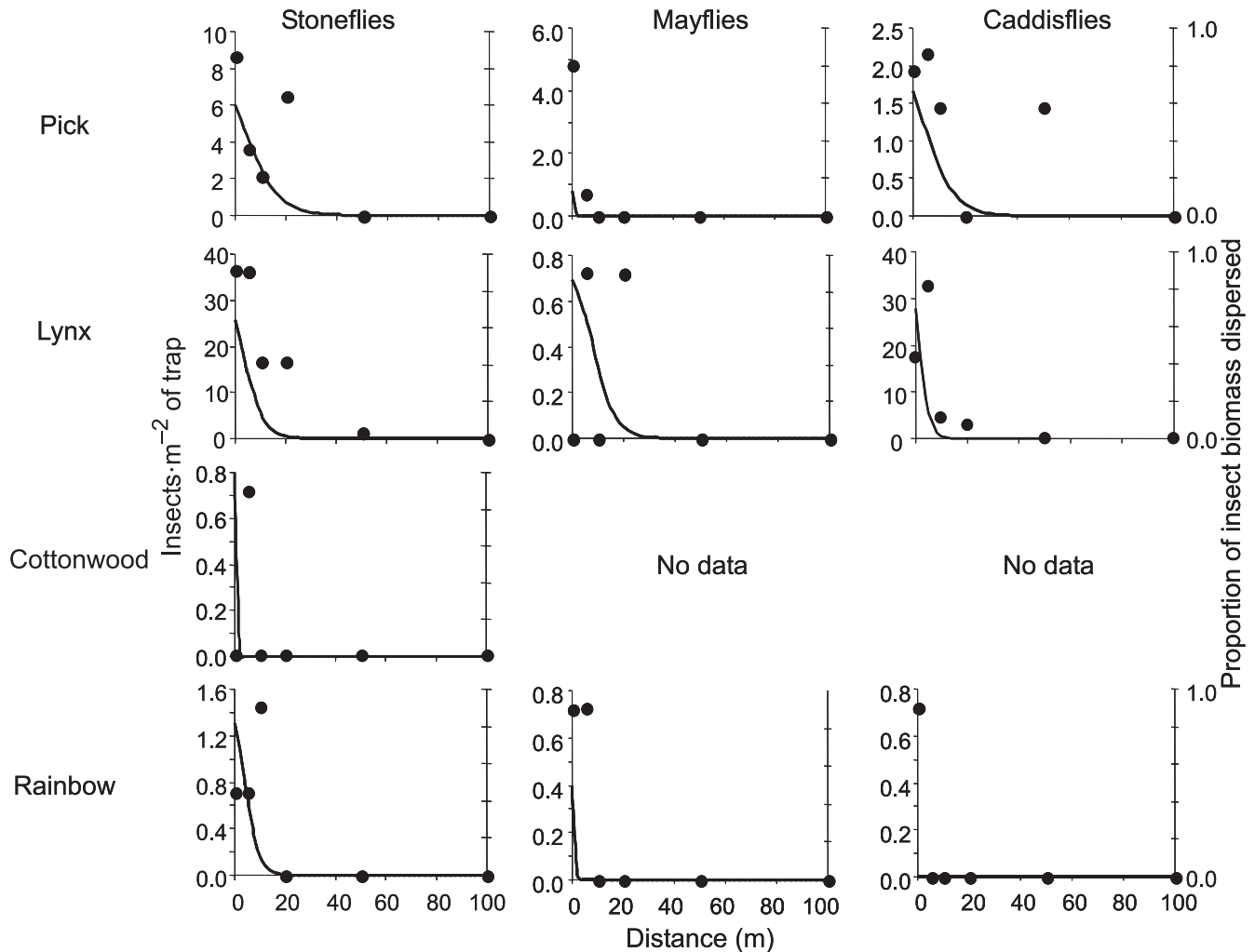
Note: Seasonal values are calculated from 24 June to 10 September. Shown are mean (±1 standard error).

Table 5. Seasonal fluxes of aquatic insect biomass and nutrients on Pick Creek, Alaska.

Taxa	Mass flux (mg·m ⁻² ·season ⁻¹)	N flux (mg·m ⁻² ·season ⁻¹)	SDN flux (mg·m ⁻² ·season ⁻¹)	N imported by salmon (kg·ha ⁻¹ ·year ⁻¹)
Mayflies	248.7 (57.4)	27.4 (6.3)	4.4 (1.0)	
Stoneflies	64.8 (19.5)	6.5 (2.0)	2.1 (0.6)	
Caddisflies	14.7 (8.5)	1.6 (0.9)	0.3 (0.2)	
Total	328.2 (54.0)	35.5 (6.0)	6.7 (0.9)	600–673

Note: Shown are means (±1 standard error). Proportions of N (nitrogen) are given in the text. Proportions of SDN (salmon-derived N) per taxa are as in Table 3.

Fig. 3. Dispersal patterns of emerging aquatic insects into riparian forests of four Wood River streams. Pick and Lynx creeks have salmon (*Oncorhynchus* spp.), Cottonwood and Rainbow creeks do not. Panels show decline in density on sticky traps with distance (●) and modeled (trend line) cumulative dispersal for emerging aquatic insects in July, prior to salmon spawning. No mayflies or caddisflies were caught in traps on Cottonwood Creek.



1993; Bilby et al. 1996), and it has been postulated that the emergence of these enriched invertebrates is a potentially important source of SDN for terrestrial ecosystems (Schindler et al. 2003; Helfield and Naiman 2006). The magnitudes of other biotic and abiotic N vectors to riparian forests, such as precipitation, watershed leaching, fixation by alder, hyporheic flow, and bear activity, have been estimated for Lynx Creek in the Wood River system (Helfield and Naiman 2006). Using the mass balance model of Helfield and Naiman (2006), we calculated that the N exported by emerging aquatic insects to riparian forests is <1% of the total estimated 532.3 kg of N input to the riparian habitats of Pick Creek in 1 year, based on escapement values from 2004 (Table 6). The magnitude of the emerging aquatic insect vector is over 100 times less than inputs from bear activity, 50 times less than the amount of N fixed by alder, and 10 times less than estimated N inputs from precipitation. Further, based on an estimated 600–673 kg SDN imported by salmon per hectare of Pick Creek in 2004, or 1400–1600 kg of SDN imported to the entire stream, we calculated that aquatic insects transfer to riparian systems ~0.16 kg, or 0.01% of the SDN imported to Pick Creek by spawning salmon.

We found that aquatic macroinvertebrates in salmon-bearing streams of the Wood River system had generally lower enrichment in ^{15}N than has been observed in other studies of Pacific salmon ecosystems. We observed a mean mayfly $\delta^{15}\text{N}$ of 2.3 versus a published range of 6.4–8.4 (Bilby et al. 1996); mean stonefly $\delta^{15}\text{N}$ of 5.5 versus a range of 4.8–9.2 (Bilby et al. 1996; Chaloner et al. 2002); and mean caddisfly $\delta^{15}\text{N}$ of 4.0 versus published values of 5.2 (Hicks et al. 2005) and 4–6 (Winder et al. 2005). That the invertebrates in our study have lower $\delta^{15}\text{N}$ signatures than their counterparts in other studies can be explained in part by the lower $\delta^{15}\text{N}$ of sockeye salmon tissue as compared with some other Pacific salmon species. The isotopic signature of sockeye salmon tissue in the Wood River system, which is representative of sockeye salmon generally (S. Johnson, School of Aquatic and Fishery Science, University of Washington, Seattle, WA 98195, USA, unpublished data) is lower than that observed for coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) salmon (Satterfield and Finney 2002), the dominant species in the above-referenced studies (except Winder et al. 2005). Regardless of the pathway by which SDN are incorporated, higher $\delta^{15}\text{N}$ values in the source tissue (i.e., salmon) would be trophically transferred and result in higher $\delta^{15}\text{N}$ in organisms taking up those nutrients. Additionally, each of the above-referenced studies was conducted on nymphal stages of each invertebrate taxa, while we measured enrichment in adults. It is not known what fractionation, if any, occurs during metamorphosis, but any ontogenetic shifts in isotopic ratios may also contribute to variation in isotopic signature between our results and others.

Approximately 9.2% of emerging aquatic invertebrates returned to Pick Creek, a higher rate of return than has been observed in other systems (Jackson and Fisher 1986; Gray 1989). While we do not have reliable emergence rates from other streams within the Wood River lake system to use for comparison purposes, the emergence rates we measured on Pick Creek fall within expected values based on a literature review (Table 7). Jackson and Fisher (1986) calculated that

Table 6. Estimates of nitrogen (N) inputs to the watershed associated with Pick Creek, Alaska.

Vector	Minimum value (kg N·year ⁻¹ ·watershed ⁻¹)
Precipitation	9.1
Leaching from upland soils	328
N inputs by alder	43
Hyporheic flow	46
Bear activity	106
Emerging insects	0.85 (0.14)
Total	532.9

Note: Based on mass balance model from Helfield and Naiman (2006) and adjusted for Pick Creek values.

3% of all invertebrates emerging from a Sonoran desert stream returned, and Gray (1989) estimated 1% return rates for aquatic insects in a prairie stream. However, in heavily vegetated streams and wetlands, Stagliano et al. (1998) observed that return rates may be higher (~25%), perhaps as a function of vegetation structure that restricts dispersal away from streams (Jackson and Fisher 1986; Petersen et al. 1999). Some dispersing invertebrates prefer wooded to open sites (Petersen et al. 1999), and vegetation along Pick Creek may influence the rate of return we observed.

Using the relationship of invertebrate density versus distance for the three aquatic invertebrate taxa on four streams in the Wood River system, it was possible to calculate the total potential biomass dispersed at distance into the riparian forest. Model fits to the data compiled across all four streams indicated that 95% of emergent insect biomass was dispersed to within 25 m of the stream (Fig. 4). This is consistent with other observed patterns of aquatic invertebrate dispersal, for example in the United Kingdom, where a model of exponential decline explained 67%–99% of the variation of stonefly abundance with distance, and many species of stoneflies and caddisflies dispersed no greater than 50 m from their natal stream (Petersen et al. 1999). We observed some variance around the dispersal model fits, and specifically we observed equally high densities of caddisflies at 20 and 50 m on Pick Creek. However, on Pick Creek we caught limited densities of caddisflies in sticky traps, and across all streams caddisflies represented <6% of total emerging biomass. The majority of emerging aquatic invertebrate biomass was represented by mayflies and stoneflies, and therefore the caddisfly dispersal on Pick Creek contributes little to the overall pattern by which stream-borne nutrients are dispersed to riparian forests. Our data show that the influence of stream-borne nutrients on riparian forests due to aquatic insect dispersal is localized to an area within 25 m from the stream edge.

We observed variable aquatic invertebrate emergence patterns that may be relevant for terrestrial consumers reliant on aquatic food resources. When aquatic invertebrates disperse into riparian forests, they can become a key component of terrestrial food webs as a prey source for consumers such as birds and spiders (Nakano and Murakami 2001; Sanzone et al. 2002). Emergence on streams is typically seasonal and spatially organized such that emerging insects are at higher densities near the stream edge (Jackson and Fisher 1986).

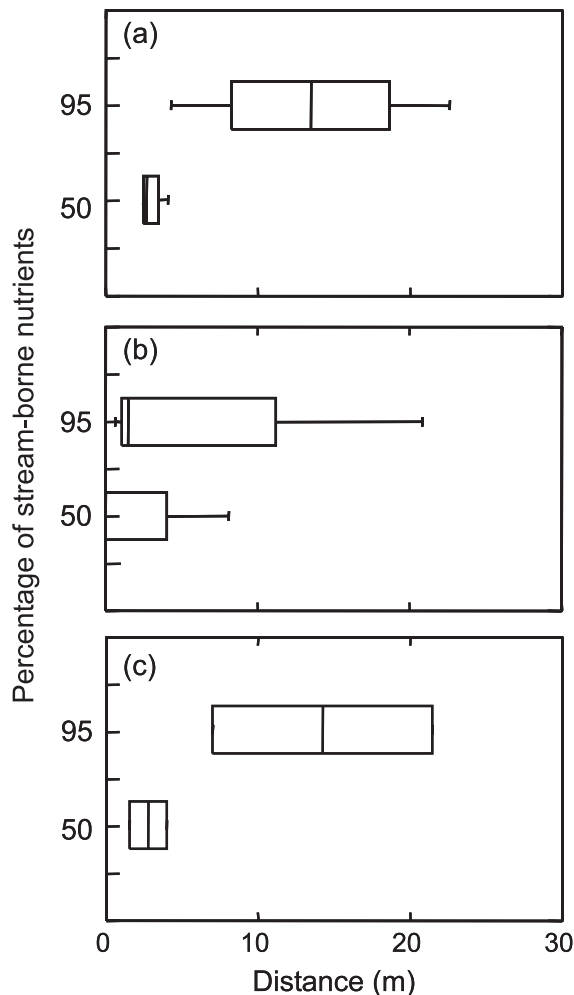
Table 7. Published emergence rates of mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) for various sites worldwide.

Taxa	Site	Location	Stream temperature (°C)	Emergence (mg·m ⁻² ·day ⁻¹)	Reference
Ephemeroptera	Sycamore Creek	33°N, 111°W	15–25	27.3	Jackson and Fisher 1986
	Balsam Hollow Brook	46°N, 63°W	6–17	5.1	Dobrin and Giberson 2003
	Lake Belau	54°N, 10°E	5.5–16	0.21	Poepperl 2000
	Pick Creek	59°N, 158°W	5.5–16	3.41	This study
Plecoptera	Balsam Hollow Brook	46°N, 63°W	6–17	18.5	Dobrin and Giberson 2003
	Broadstone Stream	51°N, 0°E	5–17	3.99	Petersen et al. 1999
	Lake Belau	54°N, 10°E	6–17	0.005	Poepperl 2000
	Central Jutland	56°N, 9°E	5.7–6.4 ^a	1.7–4.3	Thomsen and Friberg 2002
	Pick Creek	59°N, 158°W	5.5–16	1.07	This study
Trichoptera	Balsam Hollow Brook	46°N, 63°W	6–17	2.5	Dobrin and Giberson 2003
	Lake Belau	54°N, 10°E	6–17	2.42	Poepperl 2000
	Pick Creek	59°N, 158°W	5.5–16	0.27	This study

Note: Sites are organized by increasing latitude.

^aRange of mean temperature values over several streams.

Fig. 4. Estimated mean distances to which 50% and 95% of stream-borne nutrients are exported by stoneflies (a), mayflies (b), and caddisflies (c) on Pick, Lynx, Cottonwood, and Rainbow creeks combined. Box plots are calculated from modeled dispersal patterns given in Fig. 3.



This aquatic subsidy can affect spatial aggregations of consumers, in some cases affecting their behavior or growth (Baxter et al. 2005). Insectivorous birds have been shown to be dependent on the subsidy provided by emerging aquatic insects (Gray 1993; Nakano and Murakami 2001), and the response of the insectivore community to this subsidy can be focused on streams that support spawning salmon (Gende and Willson 2001). A review of the phenology of several of the dominant passerine species found near Pick Creek showed that most have initiated fledging by 15 July in higher latitudes (Peck and James 1987; Petersen et al. 1991; Robertson et al. 1992). Emergence across all three insect taxa prior to 15 July equaled 78% of total seasonal emergence. This substantial and early pulse of emergence may result in a focused predatory response by insectivorous birds, whose nesting and rearing periods coincide with the peak emergence of insects, representing substantial quantities of salmon-derived nutrients and energy. More investigation into the taxonomic variability in phenology and emergence, which has been observed in other systems (Huryn and Wallace 2000; Dobrin and Giberson 2003), may demonstrate variable availability of SDN to terrestrial consumers in this system.

While our results suggest that aquatic invertebrates are not substantial vectors of salmon nutrient transfer from streams to riparian ecosystems on a watershed scale, their emergence may still be an important link between aquatic and terrestrial ecosystems in that they provide a prey subsidy for terrestrial insectivores. Emerging insects enriched in SDN make accessible marine nutrients that might otherwise be unavailable to consumers reliant on terrestrial insects. Furthermore, our study did not measure emergence rates or enrichment of aquatic Diptera, which may represent a substantial portion of total emergence from these streams and therefore a key prey item for terrestrial insectivores. Future research to investigate the marine–aquatic–terrestrial linkage in these systems should be conducted with active insectivore communities whose breeding seasons coincide with the presence of spawning salmon, for example passerine birds.

Currently, many runs of Pacific salmon and steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) are either

threatened or endangered, and Pacific salmon stocks have disappeared from over 40% of their historical ranges (National Research Council 1996). The majority of research on Pacific salmon has focused on the salmon themselves. However, recently the ecosystem-level impacts of salmon have become more widely recognized, and research efforts are shifting to include salmon in an ecosystem context. The recent intense focus on salmon as deliverers of nutrients to aquatic ecosystems has identified several routes by which salmon nutrients are incorporated into aquatic biota. However, evidence that this flux of nutrients substantially affects aquatic ecosystem productivity is more equivocal, and in fact salmon may have equal or greater impacts on in-stream production in their role as ecosystem engineers (Moore 2006). As restoration and conservation plans for salmon are developed in areas where their populations have declined or where they have been eliminated, it is important that we clearly understand the linkages that exist between Pacific salmon and riparian and aquatic ecosystems.

Acknowledgements

This is a contribution from the Alaska Salmon Program at the University of Washington. This research was made possible by the Budweiser Conservation Scholarship Program and the National Fish and Wildlife Foundation. T. Francis was supported by the National Science Foundation's Integrative Graduate Education and Research Traineeship Program (IGERT) program in Urban Ecology at the University of Washington and by a National Science Foundation predoctoral grant during the preparation of this manuscript.

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