Isotopic Evidence for Enrichment of Salmon-Derived Nutrients in Vegetation, Soil, and Insects in Riparian Zones in Coastal British Columbia

T. E. Reimchen, D. Mathewson, M. D. Hocking, and J. Moran

Department of Biology, University of Victoria,
P.O. Box 3020, Victoria, B.C., Canada V8W 3N5

D. Harris

Stable Isotope Facility, 122 Hunt Hall,
University of California-Davis, Davis, California, USA

Abstract.—Anadromous fishes such as salmonids link marine and terrestrial ecosystems in coastal watersheds of western North America. We examine here the extent of isotopic enrichment of salmon-derived nutrients in soil, vegetation, and terrestrial insects among six watersheds from coastal British Columbia that differ in the density of salmon spawning abundance. Results demonstrate a direct relationship between the salmon spawning density and ^{15}N enrichment in humus soil, in riparian vegetation (*Tsuga heterophylla, Vaccinium parvifolium, Rubus spectabilis*), and in riparian insects including herbivorous and carnivorous Carabidae (*Pterostichus, Scaphinotus, Zacotus*). The results suggest broad cycling of salmon-derived nutrients into multiple trophic levels of terrestrial ecosystems. We also describe for the first time the detection of salmon-derived nitrogen in wood samples extracted from old-growth riparian. This result suggests new opportunities for assessing relative nutrient transfer and salmon abundance in past centuries.

Introduction

Recent studies have begun to quantify the ecological role of salmon to coastal watersheds of western North America. These anadromous fish provide direct nutrients to a diverse assemblage of predators and scavengers in marine coastal waters (Willson and Halupka 1995; Cederholm et al. 2000), ecologically comparable to the migrating herds of wildebeest in the Serengetti (Reimchen 1995). Salmon carcasses, which are considerably enriched in the stable isotopes ^{15}N and ^{13}C, also contribute to primary production in estuaries, freshwater streams, and lakes (Stockner 1987; Cederholm et al. 1989, 2000; Kline et al. 1990, 1993; Bilby et al. 1996; Wipfli et al. 1998) and are incorporated into riparian vegetation (Ben-David et al. 1997, 1998) and terrestrial predators (Hilderbrand et al. 1999a).

Some of the most common and widely distributed large carnivores are bears, and salmon represent a major yearly source of nutrients for these foragers (Gilbert and Lanner 1995, Hilderbrand et al. 1999b). The congregation of bears during the two months of salmon spawning and their extensive diurnal and nocturnal foraging activity results in a major transfer of salmon carcasses from the stream into the forest (Reimchen 1992, 1994, 2000). This can lead to high densities of abandoned carcass remnants reaching 4,000 kg/ha in the near-stream riparian zone and high densities of secondary vertebrate and invertebrate scavengers (Reimchen 1994). Furthermore, there is recent evidence (Hilderbrand et al. 1999a) that the salmon foraging activity of brown bears in Alaska can lead to a major input of nitrogen-enriched urine and feces on bear trails in riparian zones that is subsequently utilized by vegetation.

The extent of the bear-mediated nutrient pulse into forests and the utilization by vegetation and terrestrial insects remains poorly understood. In this paper, we provide preliminary analyses of the ^{15}N levels in soils and three common species of riparian vegetation, as well as ^{15}N and ^{13}C levels in selected terrestrial invertebrates from six British Columbia watersheds varying in salmon density. We also present new evidence that the signature of salmon-derived nutrients is detectable in wood samples extracted from tree cores and this offers new opportunities for historical assessment of nutrient cycling.

Study Area

We studied six coastal watersheds in Clayoquot Sound, on the west side of Vancouver Island, British Columbia. These watersheds, Warn Bay, Bulson, Moyeha, Megin, Watta, and Sidney, are some of the least affected by the extensive deforestation in the region. Up to seven species of salmonids occur in the watersheds comprising chinook *Onchorynchus tshawytscha*, chum *O. keta,* coho *O. kisutch*, pink *O. gorbuscha*, sockeye *O. nerka*, cutthroat trout *O. clarki,* and steelhead *O. mykiss.* The area is located within the Coastal Western Hemlock biogeoclimatic zone (CWHvh1) and is characterized by dense forests of western hemlock *Tsuga heterophylla*, Amabilis fir *Abies amabilis*, and Sitka spruce *Picea sitchensis* (Green and Klinka 1994; Pojar and MacKinnon 1994). Western red cedar *Thuja plicata*, though less common, is also present in the low elevation forests. Shrubs such as salmonberry *Rubus spectabilis*, false azalea *Menziesia ferruginea*, and red huckleberry *Vaccinium parvifolium* dominate understory vegetation along streams. Salal *Gaultheria shallon*, deer fern *Blechnum spicant,* and sword fern *Polystichum munitum* are also locally abundant. The climate of this region is influenced primarily by westerly air masses moving onshore from the Pacific Ocean (Harcombe 1990). It is cool and perhumid, receiving more than 2,500 mm precipitation per year, mainly in the form of rain at lower elevations with an annual temperature range of ca. 10°C (Schaefer 1978). Due to moderate temperatures and high precipitation, soils retain moisture throughout most of the year and rarely freeze, resulting in a prolonged growing season. However, excessive amounts of soil moisture and high leaching lead to low levels of nutrients available for plant growth and a heavy dependence on decomposi-

tion of organic material and nutrient recycling (Harcombe 1990). In a wet, cool climate such as this, decomposition is slow, resulting in large accumulations of deep organic soil horizons (Harcombe 1990).

The soils are ferro-humic podzols (Lord and Valentine 1978) overlying granitic intrusions of Jurassic Age and are characterized by an often substantial, darkly stained organic (humus) layer above siliceous, base-poor mineral horizons. Organic matter, aluminum and iron typically accumulate in the B horizon (Valentine and Lavkulich 1978). This soil type under CWH forest is generally N- and P-deficient (Prescott et al. 1993), and the soil climate is classed as cold cryoboreal (mean annual temperature 2–8°C) and perhumid (i.e., no significant water deficit throughout the year; Lavkulich and Valentine 1978).

Warn Bay Creek (49° 15' 46.14" N, 125° 43' 31.6" W) and Bulson Creek (49° 15' 48.8" N, 125° 43' 40.79" W) are located in adjacent valleys and both feed into Warn Bay through a common estuary. Warn Bay Creek, with a stream length of four km, is a narrow, shallow system, which supports four species of anadromous salmonids (chum, coho, cutthroat, and steelhead). The Department of Fisheries and Oceans escapement counts show an average of 3,700 salmon entering Warn Bay Creek each year during the period 1990–1999. These are primarily chum salmon with a small number of coho. Bulson Creek is 20 km in length and has a high gradient canyon near the mouth of the creek that appears to be impassable to salmon. Although the riparian zones of both Warn Bay and Bulson Creek appeared undisturbed and intact during original field surveys, on subsequent field surveys we observed that the sampling site at Bulson Creek had evidence of past human disturbance (3–4 decades), including localized removal of trees.

Moyeha River (49° 24' 58.62" N, 125° 54' 45.87" W) at the north end of Herbert Inlet is 28 km in length and supports runs of chinook, chum, coho, pink, sockeye, cutthroat, and steelhead. Escapement records show a yearly average of about 9,000 salmon, mainly chum, coho, and sockeye, enter this stream over the period 1990–1999.

Megin River (49° 26' 12.20" N, 126° 5' 5.40" W), located on the north side of Shelter Inlet, is the largest of the six study sites, extending more than 33 km to the southwest from the headwaters. Fish species recorded in this system include

chinook, chum, coho, pink, and sockeye salmon, resident and sea-run cutthroat trout, rainbow trout *O. mykiss*, steelhead, and Dolly Varden *Salvelinus malma*. An average of 6,600 salmon, mainly chum, coho, and chinook, enter the river yearly (1990–1999).

Watta Creek (49° 27' 29.42" N, 126° 1' 38.77" W) flows into the northern end of Herbert Inlet and is 10 km in length, supporting runs of chinook, chum, coho, pink, and steelhead. Average yearly runs during 1990–1999 were approximately 2,400 salmon, with chum comprising the vast majority of these.

Sydney River (49° 30' 47.71" N, 126° 17' 48.28" W) is 11 km long with the majority of spawning activity occurring in a braided region at the lower 2 km. This river supports chinook, chum, coho, pink, and sockeye salmon, as well as cutthroat trout, steelhead, and sculpins (Cottidae). On average, 793 salmon (mainly chum) per year have been recorded in this river between 1990 and 1999.

We observed salmon carcasses or their remnants in the riparian zone of all watersheds apart from the control site (Bulson Creek). As well, black bears were present in each watershed and, based on carcass characteristics, appeared to be the predominant transfer agent of salmon carcasses into the riparian zone. Wolf *Canus lupis*, river otter *Lutra canadensis*, and bald eagle *Haliaeetus leucocephalus* are also present in all watersheds and will be contributing transfer agents. Gulls *Larus* spp. occurred in the estuaries and in the lower reaches of the rivers and, while their fecal droppings were uncommon in the riparian zone, these birds can be expected to also contribute to the nitrogen transfer.

Methods

For each of the rivers where salmon spawning occurred, we made general field notes of the distribution of carcasses, but quantified total carcass abundance only at Warn Bay Creek. We also estimated average salmon density based on average salmon escapement (1990–1999) and total spawning area (m²; Table 1).

We obtained wood samples from five Western Hemlock at Warn Bay Creek and from two hemlocks at the adjacent control site at Bulson Creek. The former were located at 100 m and 500 m upstream from the mouth adjacent to spawning gravels and at variable distances into the riparian zone (4 m to 34 m). Those from Bulson Creek were 600 m upstream from the mouth and 4 m and 28 m into the riparian zone. Trees chosen for augering ranged in size from 30 cm to 50 cm diameter at breast height. Wood samples were extracted using an auger bit (2.5 cm diameter, 12 cm length) drilled at breast height. We collected the wood chips separately from each incremental 1 cm depth into the trees. This yielded 20 to 30 wood samples for each tree. We also used a standard increment borer (5 mm) and extracted a 40-cm core 2 cm above the auger hole, and this allowed us to cross-reference auger depth with an approximate time frame.

Soil sampling was conducted in July and August 1998. At each watershed, collection sites were initially chosen near the stream adjacent to areas of suitable spawning gravel for salmon and where there was evidence of carcass transfer into the forest. At each stream, sampling sites were fairly consistent with respect to general morphological features, slope, and vegetation cover. A 40-m transect was established at each site running perpendicular to the stream edge into the adjacent forest. At 10, 20, 30, and 40 m distance from the stream edge, sampling lines were established perpendicular to the transect line. Ten soil samples, 1 m apart, were collected along each of the four sample lines. The top 10 cm of soil below the litter (L) layer was collected, corresponding to the zone of maximum fine root density

TABLE 1. Average salmon escapement (1990–1999), spawning area and salmon densities for study watersheds in Clayoquot Sound.

Stream	Escapement	Potential spawning area (m²)	Maximum salmon density (salmon/m²)
Bulson Creek	130	65,025	.002
Sydney River	1627	109,000	.015
Megin River	8975	367,200	.024
Moyeha River	7000	264,000	.026
Watta Creek	2683	21,760	.123
Warn Bay Creek	3128	10,400	.301

(and, therefore, maximum potential nutrient uptake). In most cases, the collection zone comprised the humus (F/H) horizon, although the mineral (Ae) horizon and, less frequently, decayed wood from fallen trees, were also included.

Foliar tissues of red huckleberry and salmonberry were sampled in August 1998 and again in April and July 1999 at each watershed. Vegetation sampling sites coincided with soil plots in relatively flat areas, with moderate to dense understory cover and evidence of bear-mediated carcass transfer. Initial collection sites occurred within approximately 15 m of streams and also included steeply sloping sites further into the forest (up to 120 m from stream). Foliage samples were collected from one to five individual plants at each site and stored separately in envelopes.

In May 2000, common carabid beetles (*Pterostichus*, *Scaphinotus*, and *Zacotus*) were collected from all six watersheds through pitfall trapping and hand collection from the forest floor. Five pitfall arrays were constructed on each watershed within a 40 × 40 m area adjacent to the stream. Pitfall arrays were arranged in a three-way branching fashion with a central pitfall connected via three 50 cm by 15 cm aluminum drift fences to a pitfall at the end of each fence. Hand collection occurred more randomly as individual beetles were encountered in the riparian area. All beetles were stored in 70% ethanol. In the spring of 1999, pre-emergent blowfly pupae (Calliphoridae) were hand-collected from the soil and coarse woody debris within five to ten meters of the Moyeha River. Two pupae were dried and the remainder ($N = 5$) was transferred to rearing containers until adult emergence. Adult blowflies were then stored in 70% ethanol until processing in March 2001.

Sample Preparation

Wood samples were oven-dried at 67°C for 3 weeks and then coarsely ground. Foliar samples were oven-dried in their envelopes at 67°C for three days. Soil samples were sieved to remove roots and stones, oven-dried at 105°C for 48 h, then ground and homogenized using mortar and pestle. Whole flies and beetles were dried at 60°C for at least 48 h. All of the samples were ground to a fine homogeneous powder using a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Illinois). Soil and vegetation samples (1 mg) were assayed for total N and ^{15}N, while invertebrate samples (1 mg) were assayed for total N, ^{15}N, to-

tal C, and ^{13}C, at the University of Saskatchewan Stable Isotope Facility, by continuous-flow isotope ratio mass spectrometry (CF-IRMS). Natural abundances of ^{15}N (d^{15}N) and ^{13}C (d^{13}C) are expressed in ppt (‰) and calculated as (R_{sample}/$R_{standard}$)-1) × 1,000, where R = the ratio of ^{15}N/^{14}N or ^{13}C/^{12}C. Isotopic standards include N_2 in air for nitrogen isotope analyses and Pee-Dee Belemnite (PDB) limestone for carbon isotope analysis. Measurement precision is approximately ± 0.35‰ and ± 0.10‰ for ^{15}N and ^{13}C, respectively.

Delta^{15}N values from powdered wood were determined after online combustion of 30 mg samples in an elemental analyzer (PDZEuropa, ANCA-Hydra 20–20). Sample combustion was achieved at 1050°C with a 40 mL oxygen injection and a Cr_2O_3 catalyst. Reproducibility of ^{15}N values on replicated samples averaged ± 1.0‰.

Mean d^{15}N and d^{13}C values in salmon are known to range from +11.2 to +12.3‰ and –23.5 to –19.6‰, respectively, based on variations in species, spawning condition, and body tissue fractionation (Mathisen et al. 1988; Kline et al. 1993).

Statistical Analyses

Analysis of variance (ANOVA) tests were employed to test for differences in d^{15}N values among vegetation and soil samples with varying levels of salmon density and also among carcass categories (i.e., present, absent, control) for vegetation species. Paired and unpaired *t*-tests were used to examine d^{15}N levels in vegetation species. We used Spearman's rank correlation analyses to test whether increasing distance from stream within each watershed and salmon density values among watersheds had significant effects on isotope values in sample types (soil, foliar tissues, and insects). Linear regression was used to examine relationships between d^{15}N values in plants and soil fractions in relation to salmon densities. Assumptions of normality and homoscedasticity were met.

Results

Wood samples extracted from western hemlock yield reproducible isotopic signatures (±1‰) and were highly variable among the seven trees (range minus 2.5‰ to + 2.5‰). The two control trees at Bulson Creek, where salmon were absent, both had d^{15}N values near –2.5‰, and this was

independent of their distance from the stream ($F = 0.0$, $P = 1.0$). Trees from the adjacent watershed at Warn Bay, where salmon are present, have $d^{15}N$ values ranging from –2.4‰ to +2.5‰, dependent on the distance from the stream (Figure 1). The lowest value (–2.4‰) occurs in the tree furthest from the stream (34 m) and intermediate values (–1.5‰ to –0.5‰) occur in the two trees 10–15 m from the stream, while the highest values (1.5‰, 2.5‰) occur in the two trees closest to the stream (7 m, 4 m, respectively; $F = 89.4$, $P < 0.001$).

Delta ^{15}N values for each of the soil fractions and vegetation species differ significantly among watersheds (ANOVA; $P < 0.01$ for each; Table 2). Humus soil, huckleberry, and salmonberry all show highest mean values of $d^{15}N$ at Warn Bay Creek, where salmon carcass density is highest. In contrast, mineral soil has the highest ^{15}N enrichment at Bulson Creek, where salmon are largely absent, although sample size is small ($N = 2$). Sydney River, with a very low salmon density, shows consistently negative $d^{15}N$ values for all species, and Megin River demonstrates positive values for soil fractions and negative values for vegetation samples. Mean values at Moyeha, Watta, and Warn Bay creeks are positive for all samples. Each factor (humus, mineral, huckleberry, salmonberry) shows significant positive relationships between values of $d^{15}N$ and carcass density at each watershed ($P < 0.05$ for each; Figures 2A, 2B). No significant differences in mean $d^{15}N$ values of foliage were detected between spring and summer collections for either of the two species of plants ($P = 0.27$ and 0.15, respectively).

Shrub species, carcass category (i.e., salmon carcasses present or no evidence of carcasses nearby), and distance from stream were tested for associations with $d^{15}N$ values. Species differ in $d^{15}N$, with salmonberry having a higher mean value for all watersheds ($t = 3.51$, df = 247, $P < 0.01$). Within watersheds, the species effect occurs only at Warn Bay ($t = 2.38$, df = 38, $P = 0.02$). Proximity to carcasses is associated with isotopic signature, as both huckleberry and salmonberry collected near carcasses had a marginal but nonsignificant trend of higher $d^{15}N$ values than in plants where salmon carcasses were absent. However, this comparison was only possible at the Sydney and Moyeha rivers, where sample
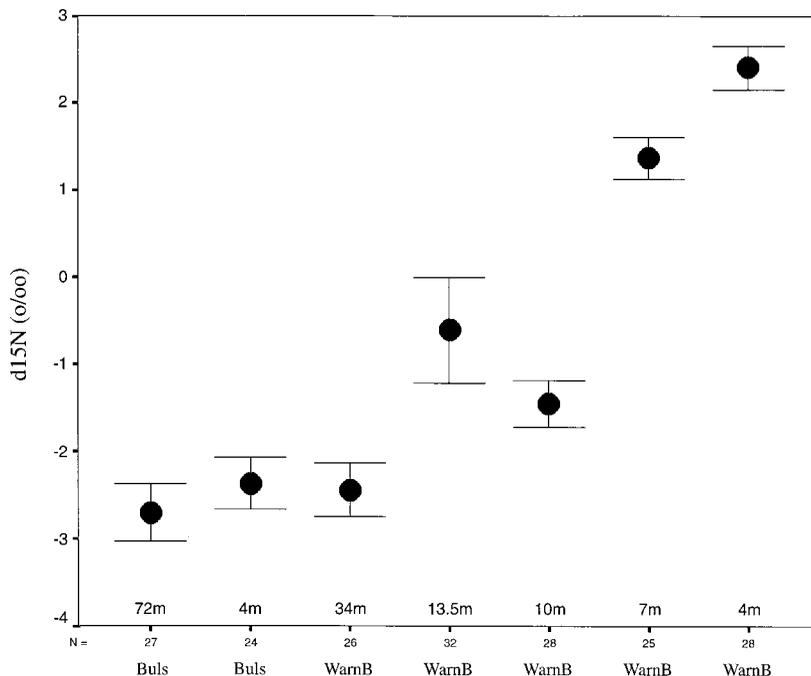

FIGURE 1. Mean $d^{15}N$ values (±1 SE) in wood samples from western hemlock taken at the control site (Bulson Creek–Buls) and the Salmon River (Warn Bay Creek–WarnB) in Clayoquot Sound. Tree distances (m) from stream shown on horizontal axis. N = number of separate wood samples.

TABLE 2. Values of ä^{15}N (mean±SD) of soil fractions and vegetation species from each watershed. Results of ANOVA testing for effects of salmon density on D^{15}N values of each sample type are also shown.

	Mineral		Humus		Huckleberry		Salmonberry	
	n	d^{15}N (‰)	n	ä^{15}N (‰)	n	ä^{15}N (‰)	n	ä^{15}N (‰)
Bulson	2	4.80±1.13	30	0.87±1.33	16	−0.94±1.92	15	−0.10±2.45
Sydney	26	−0.03±1.96	13	−1.95±0.76	21	−0.82±2.05	17	−1.13±1.38
Megin	10	3.79±1.77	29	1.09±0.79	13	−0.38±1.98	14	−0.18±1.12
Moyeha	10	1.57±2.17	30	0.32±1.58	20	1.12±1.89	11	1.30±3.42
Watta	35	2.15±1.97	5	0.60±1.37	7	0.49±2.95	17	1.88±2.90
Warn Bay	1	3.80	35	1.46±1.25	13	1.58±2.89	18	3.18±2.46
df	4		5		5		5	
F	9.62		15.85		3.65		7.55	
P	<0.001		<0.001		<0.01		<0.001	

numbers are high enough for comparisons. Proximity to stream also influences d^{15}N values (Table 3). At Bulson River, which is the control site and has the most depleted d^{15}N values for foliar tissues among watersheds, samples of humus soil, huckleberry, and salmonberry collected near stream have lower ^{15}N values than those collected further from the stream ($P < 0.01$). In contrast, at the adjacent site of Warn Bay, which has high salmon runs and high d^{15}N values in soil and vegetation, humus soil and huckleberry each exhibit a significant reduction in d^{15}N values at increased distances from the stream. The remaining localities show no significant associations apart from Sydney River, which exhibits a reduction in d^{15}N values of mineral soil at increased distance from the stream ($P < 0.05$).

Invertebrates also exhibited isotopic differences with a gradient in salmon density among watersheds. In carabid beetles, d^{15}N was positively correlated to spawning density ($r^2 = 0.43$; $P < 0.001$; Figure 3). Mean d^{15}N values in each beetle species ranged from 3.13‰ in *Scaphinotus* to 4.65‰ in *Pterostichus* to 6.87‰ in *Zacotus*. However, d^{13}C values decreased with increasing salmon spawning density ($r^2 = 0.120$, $P = 0.029$), which was contrary to prediction. Mean d^{13}C values ranged from −26.16‰ in *Zacotus* to −26.04‰ in *Scaphinotus*. Collections of blowfly adults and pupae (Calliphoridae) from the riparian zone at Moyeha River demonstrated substantial isotopic enrichment. Mean d^{15}N and d^{13}C values were +16.55 ± 0.72‰ ($N = 7$) and −20.20 ± 0.37‰ ($N = 5$), respectively.

Discussion

Previous studies of ^{15}N enrichment in salmon watersheds rivers have yielded direct evidence for nutrient cycling between marine and terrestrial habitats (Ben-David et al. 1998; Hilderbrand et al. 1999a). Our results indicate that the levels of ^{15}N enrichment in riparian soils, vegetation, and ground-dwelling insects differ among watersheds and are directly related to the density of salmon in the spawning reaches of each stream. As we observed the greatest extent of bear-mediated transfer of salmon into the riparian zone at Warn Bay, where d^{15}N values were highest, and no transfer at Bulson, where salmon were absent, we infer that salmon is the predominant source of ^{15}N enrichment, at least in the humus soil, vegetation, and insects. We are unable to account for the isotopic enrichment in the mineral soil at Bulson, but this might be associated with human disturbance of the site during the middle part of the 20th century. Additional factors, such as rainfall, have been shown to affect the d^{15}N values in soil and vegetation (Handley et al. 1999), but due to the narrow geographical range of the samples taken in this study, in particular between the adjacent watersheds of Warn Bay Creek and Bulson Creek, differences in precipitation will be negligible. Species differences in d^{15}N levels also occur, as was evident between huckleberry and salmonberry sampled within close proximity to each other. Differences in rooting depths or mycorrhizal associations between co-existing species can lead to different levels of d^{15}N in plant tissues (Schulze et al. 1994; Nadelhoffer and Fry 1994).

As the number of salmon carcasses and scavenger activity decreases with increased distance from the stream, we expected to see a concordant reduction in d^{15}N levels in soil and vegetation. This was observed at Warn Bay among wood samples extracted from western hemlock trees that differed in stream proximity, as well as in foliar tissue of both species of understory vegeta-
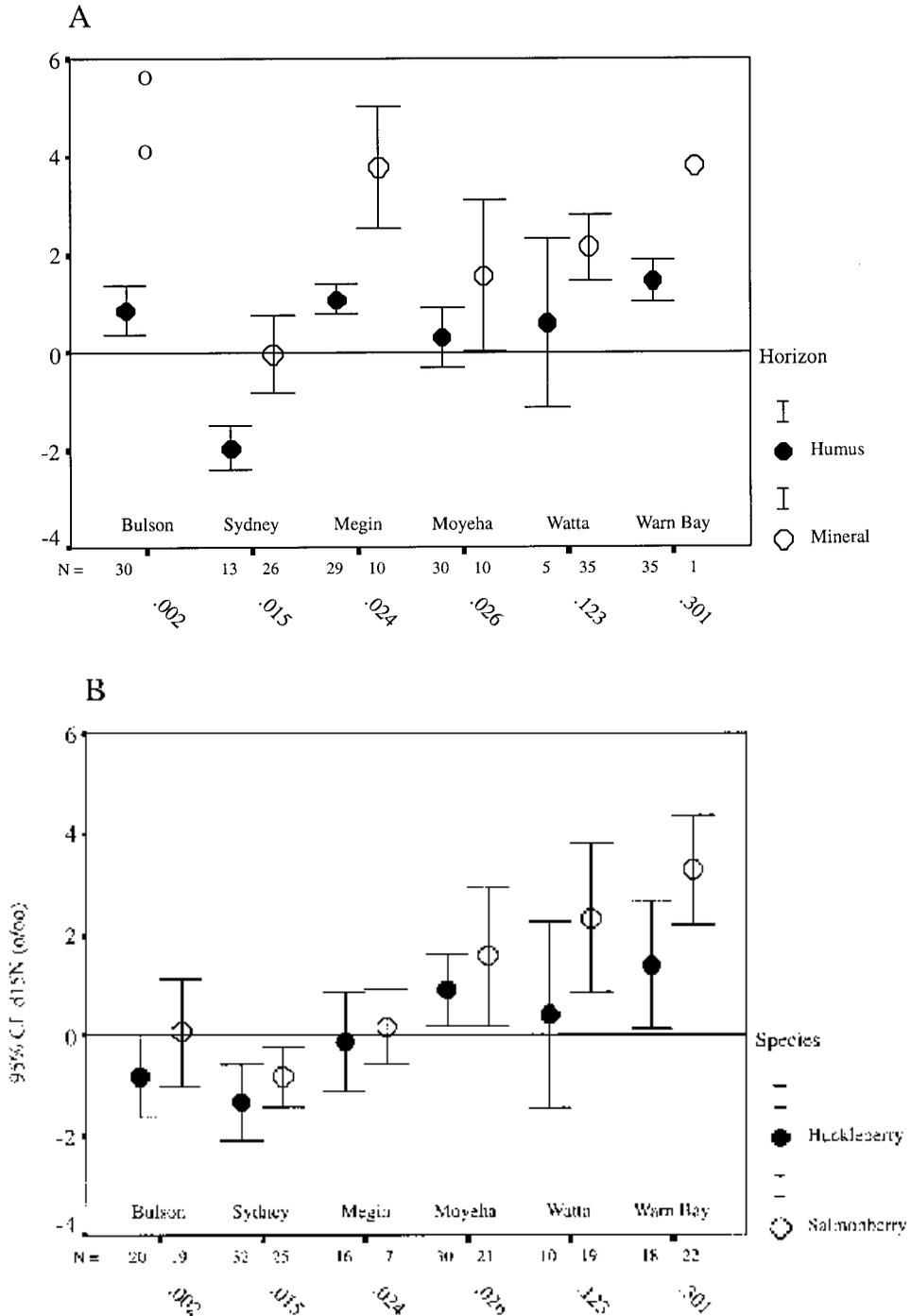
FIGURE 2. Δ^{15}N values of mineral soil and humus (A) and huckleberry and salmonberry (B) plotted against salmon density values for six watersheds. Symbols show mean and 95% confidence intervals. N = number of samples. All sample types show significant positive relationships between d^{15}N values and carcass density. Results of Spearman's rank correlation analyses are HS: $r = 0.23$, $P < 0.01$; MS: $r = 0.26$, $P = 0.02$; HB: $r = 0.39$, $P < 0.001$; SB: $r^2 = 0.48$, $P < 0.001$.

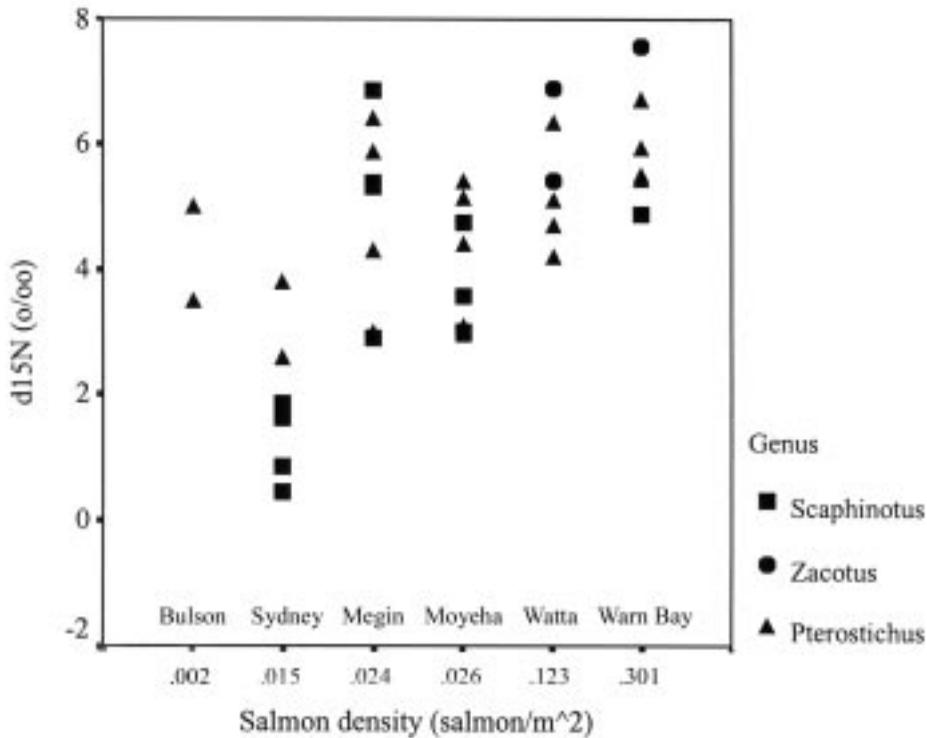FIGURE 3. d[15]N isotopic signatures in three genera of common coniferous forest dwelling carabid beetles (Coleoptera: Carabidae) in six Clayoquot Sound watersheds ranked (left to right) by increasing salmon spawning density ($r^2 = 0.43$, $P < 0.001$).

tion and humus soil. However, within the other watersheds with regular returns of spawning salmon, the decline occurred to a very limited extent in soil and foliar tissues, at least over the 50-m riparian zone that we sampled. One possible explanation for this is that a reduction in levels of ^{15}N with increased distance from stream may be proportional to the density of spawning salmon in the river. Low salmon abundance at the Sydney, Megin, Moyeha, and Watta rivers, relative to Warn Bay, could result in less bear activity and, subsequently, less transfer of carcasses to the streamside forests. Another suggestion is that substantive horizontal cycling of salmon-derived nutrients within forest habitats is occurring through carcass transfers and animal waste, and we may have not sampled over a zone of sufficient width. In Alaska, Ben-David et al. (1998) observed enrichment throughout a 200-m riparian zone for fruits or seeds of *Rubus*, skunk cabbage *Lysichitum americanum*, and devil's club *Oplopanax horridus*. Furthermore, Hilderbrand

et al. (1999a) document ^{15}N enrichment in vegetation 800 m from the stream along bear trails.

It has been well established that higher returns of salmon in coastal streams benefit aquatic organisms through additions of nutrient-rich biomass from decomposing carcasses (Kline et al. 1990, 1993; Bilby et al. 1996). Transfer of salmon carcasses onto the forest floor surrounding coastal streams should, then, also benefit terrestrial organisms where soils are nitrogen deficient. In coastal forests of the Pacific Northwest where precipitation and nutrient leaching rates are high, evidence of utilization of salmon-derived nitrogen by terrestrial vegetation (Bilby et al. 1996, Ben-David et al. 1998, this study) is consistent with this hypothesis. Our results also demonstrate a direct relationship between salmon density and levels of d[15]N in soil and vegetation, suggesting further support for these associations, as plants in N-limited systems utilize virtually every available source of nitrogen (Nadelhoffer and Fry 1994).

The influence of salmon carcass and nutrient pulses may also benefit terrestrial invertebrates, although this has received only limited attention. Dipterans have been found to be dominant carrion consumers in a diverse range of habitats (Lord and Burger 1984; Tomberlin and Adler 1998) and support a wide variety of secondary consumers from predators to parasites (Ulrich 1999). Blowflies (Calliphoridae) dominate salmon carrion communities in forests adjacent to streams, as large numbers of their larvae consume the majority of the salmon carcass tissue and then disperse to the forest floor for pupation (Reimchen 1994; Cederholm et al. 2000; author's personal observations). Blowfly maggots consumed about 90% of the 4,000 kg of salmon carcasses abandoned by bears in the riparian zone of a small chum salmon stream on the Queen Charlotte Islands (Reimchen 1994). Whole insect isotope values in Calliphorids, collected as pupae from the soil adjacent to the Moyeha River in Clayoquot Sound, were enriched by approximately 4.5‰ for $d^{15}N$ and 0.5‰ for $d^{13}C$ over the known isotopic signature of salmon. Blowfly $d^{15}N$ and $d^{13}C$ values are within bounds predicted by the trophic enrichment factor of a single trophic step of 3.4 ± 1.1‰ for $d^{15}N$ (DeNiro and Epstein 1981; Minigawa and Wada 1984) and 0.4 ± 1.4‰ for $d^{13}C$ (DeNiro and Epstein 1978; Gearing et al. 1984), suggesting 100% consumption of salmon carcass tissue. In watersheds with high transfer of salmon biomass into the forest, production of Calliphorid flies may be substantive, representing a significant food source for an unknown array of invertebrate and vertebrate predators and parasites, and requiring further investigation.

Carabid beetles (*Pterostichus*, *Scaphinotus*, *Zacotus*) are common coniferous forest dwelling arthropods and are thought to be generalist forest floor predators on a variety of soil invertebrates, including gastropods, millipedes, isopods, annelids, and springtails (Collembola; Hatch 1953; LaBonte 1998). We observed $d^{15}N$ enrichment in beetles and a positive relationship between enrichment in these litter-based omnivores and salmon spawning density among watersheds, suggesting a direct trophic association between carabids and salmon carcasses. However, the absence of a positive relationship between salmon spawning density and $d^{13}C$ among watersheds suggests that salmon is not a direct component to carabid diets, but rather, that $d^{15}N$ enrichment is derived indirectly through trophic

cycling from the consumption of other $d^{15}N$ enriched invertebrates or vegetation (for example, Ponsard and Arditi 2000; Hocking and Reimchen 2002).

The use of soil, leaves, and invertebrates provides direct information on current or very recent uptake of marine-derived nitrogen, but these results are of limited application to any historical assessment of these processes. Tree rings potentially offer insight into historical trends. Because of the low levels of total nitrogen in wood (ca. 0.05%), natural abundance levels of $d^{15}N$ in tree rings have not been determined apart from Poulson et al. (1995), who were able to characterize $d^{15}N$ values by combusting large quantities of wood from individual rings (400 mg) extracted from two fallen hemlock trees in the eastern United States. Our studies are the first to detect the signature of marine-derived nitrogen in small samples (30 mg) of wood tissues augered from standing trees and show enrichment comparable to that found in the foliar tissues, soil, and insects from the same habitat. There are substantive limitations, such as vertical and horizontal movement of nitrogen in xylem, that may blur any yearly signature of nitrogen isotopes (Sheppard and Thompson 2000). However, our observation that wood $d^{15}N$ values among adjacent trees increase with increased access to salmon suggests new opportunities for assessing the relative transfer of marine-derived nitrogen into riparian zones in past centuries in localities where ancient trees still persist.

We conclude that significant relationships of $d^{15}N$ values in soil, wood, foliar, and insect tissues with salmon density in the streams provide evidence of the influence of salmon on the nutrient budget of riparian habitats and demonstrate the broad-scale ecosystem-level cycling of marine nitrogen from salmon into riparian vegetation and invertebrates occupying multiple trophic levels. This raises the possibility that productivity and carrying capacity in the riparian zone will be directly correlated with the abundance of salmon returning to streams and with the subsequent transfer of these nutrients by bears and other vectors into riparian zones. If so, the widespread decline in salmon abundance throughout most regions of coastal western North America over the last 100 years will translate into ecosystem-level declines in carrying capacity (i.e., cultural oligotrophication; Stockner et al. 2000).

Acknowledgments

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