



Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs

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Resource subsidies across habitat boundaries can structure recipient communities and food webs. In the northern Pacific region, bears *Ursus* spp. foraging on anadromous salmon *Oncorhynchus* spp. provide a key link between marine and terrestrial ecosystems, with salmon density, fish size and watershed size as potential predictors of the magnitude of marine subsidy to terrestrial habitats. We use nitrogen and carbon stable isotopes to provide an assessment of the patterns of marine-enrichment in riparian plants (11 species, 4 guilds) and litter invertebrates (4 guilds) sampled from 27 watersheds in coastal British Columbia, Canada. Watersheds occurred in three geographical regions (Vancouver Island, mainland midcoast and Haida Gwaii) and varied in size, and in biomass (kg m^{-1} of spawning length) and species of salmon (chum *O. keta*, pink *O. gorbuscha* and coho *O. kisutch*). $\delta^{15}\text{N}$ values in all plant species and invertebrate guilds were positively predicted by total salmon biomass (kg m^{-1}) and negatively predicted by watershed size. We observed replicated parallel slopes among plant species and invertebrate guilds across the gradient in salmon biomass, with differences in means hypothesized to be due to plant fractionation and animal trophic position. As such, we derived a watershed $\delta^{15}\text{N}$ -index averaged across guilds, and using an information theoretic approach we find that the biomass of chum salmon is a much stronger predictor of the $\delta^{15}\text{N}$ -index than either pink or coho salmon, or the sum biomass of all species. The top linear model contained chum biomass and watershed size. Chum salmon biomass independently predicted $\delta^{15}\text{N}$ -index variation in all three regions of British Columbia. Chum salmon are larger than pink or coho and provide an energetic reward for bears that facilitates carcass transfer, tissue selective foraging, and nutrient distribution by insect scavengers. Analyses of biodiversity and habitat data across many watersheds moves towards a long-term goal in fisheries ecology to better integrate ecosystem values in salmon conservation.

A classic theme in ecology is the processes that underpin food webs and structure biodiversity within communities (Hairston et al. 1960). In turn, communities exist within broader ecosystems and among these, spatial subsidies of nutrients, detritus and organisms across habitat boundaries can structure the ecology of recipient systems, particularly when there are strong gradients in site productivity (Polis et al. 1997, Nakano and Murakami 2001). For example, when productive marine environments juxtapose nutrient-poor terrestrial habitats, marine resource subsidies can affect both primary productivity and the populations of top-level consumers (Polis and Hurd 1996, Sánchez-Pinero and Polis 2000). Strong predictors for the degree of response of subsidized communities include the density of flux, the vector and pathway of input, and habitat variables such as relative ecosystem productivity or size (Polis et al. 1997, Marczak et al. 2007).

The landward migration of salmon, *Oncorhynchus* spp., for spawning and subsequent death is one of the most dramatic marine–terrestrial resource subsidies in the north Pacific (Cederholm et al. 1999, Schindler et al. 2003). Temporal and spatial variation in salmon spawning biomass

predicts the occurrence and aggregations of predators and scavengers and regulates the population dynamics of many terrestrial species (Ben-David et al. 1997, Hilderbrand et al. 1999a, Christie and Reimchen 2005, 2008, Hocking and Reimchen 2006). The retention of salmon carcasses in aquatic systems adds nitrogen, phosphorus and other nutrients, a process that can initiate bottom–up dynamics and positive feedback effects for juvenile fish (Wipfli et al. 1998, Zhang et al. 2003, Hicks et al. 2005).

Similar bottom–up processes may subsidize forest food-webs through nutrient enrichment. This occurs primarily through consumption and distribution of salmon carcasses and nutrients by bears, *Ursus* spp., (Reimchen 2000, Hilderbrand et al. 1999b), although there are other pathways (Schindler et al. 2003). Diverse communities of insects are supported by decomposing carcasses (Hocking and Reimchen 2006), while nutrient fertilization from salmon has been linked to bottom–up changes in riparian plant community structure (Mathewson et al. 2003, Bartz and Naiman 2005, Wilkinson et al. 2005) and productivity (Helfield and Naiman 2001, Drake and Naiman 2007).

These findings have led to a more holistic view of salmon and their ecosystems, and the need to develop better tools to integrate ecosystem values in salmon conservation (Janetski et al. 2009). The widespread recent reduction in numbers of salmon returning to coastal rivers potentially compromises coastal ecosystems (Gresh et al. 2000). Surprisingly, the role of salmon biomass in predicting the magnitude of marine enrichment across numerous watersheds has received limited attention (but see Bilby et al. 2001, Nagasaka et al. 2006, Janetski et al. 2009). Comparisons of nutrient inputs and community responses have typically occurred in defined treatments within a few watersheds (Wipfli et al. 1998, Helfield and Naiman 2001, Hocking and Reimchen 2002), and although useful, these studies are limited in their predictive utility.

In the absence of biodiversity data, stable isotopes have been used to model salmon nutrient and energy contributions to biota in lakes, streams and riparian zones (Finney et al. 2000, Hicks et al. 2005). In terrestrial systems, nutrient fertilization from decomposing salmon increases the $\delta^{15}\text{N}$ signatures in local species (Ben-David et al. 1998, Hocking and Reimchen 2002, Bilby et al. 2003), although controversy remains as to the interpretation of observed enrichments (Pinay et al. 2003). Tests using experimental placements of salmon carcasses have demonstrated elevated $\delta^{15}\text{N}$ in soils and vegetation in the vicinity of carcasses and declines to background levels within <1 m (Wilkinson et al. 2005, Gende et al. 2007). However, uncertainty can occur because of plant fractionation of nitrogen during uptake and soil processes such as denitrification that can vary across gradients in site productivity (Pinay et al. 2003, Morris et al. 2005). Here, we test the role of salmon biomass and habitat in predicting watershed-scale nitrogen enrichment in multiple taxa.

In this study, we present an integration of stable isotope data (mainly $\delta^{15}\text{N}$ but also $\delta^{13}\text{C}$) from terrestrial vegetation and litter invertebrates sampled from 27 watersheds in coastal British Columbia as a geographically broad assessment for the relative contribution of marine-derived nutrients to riparian taxa. We test the role of salmon biomass averaged over the stream length of spawning (kg m^{-1}), and an index of watershed size derived from habitat data, in predicting a) $\delta^{15}\text{N}$ in 11 riparian plant species, b) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in eight guilds (mosses, tree needles, shrubs, herbs and ferns, weevils, millipedes, ground beetles and litter spiders), and c) a watershed-level index of $\delta^{15}\text{N}$ enrichment ($\delta^{15}\text{N}$ -index) (Bilby et al. 2001) that removes nitrogen isotopic variation due to plant fractionation and animal trophic position. Carbon isotope analyses are used to determine the pathway of marine nitrogen uptake in sampled invertebrates. Elevated $\delta^{15}\text{N}$ but not $\delta^{13}\text{C}$ in riparian animals implies a marine nitrogen fertilization pathway to terrestrial vegetation and soil nitrogen pools and subsequent cycling to higher trophic levels rather than a diet of salmon (Ben-David et al. 1998, Hocking and Reimchen 2002). Finally, we use model selection criteria to test the relative role of each salmon species in predicting watershed-scale $\delta^{15}\text{N}$ enrichment.

Our sampled watersheds are dominated by chum *O. keta*, pink *O. gorbuscha* and coho *O. kisutch* salmon, with bears and wolves *Canis lupus* as the primary transfer

vectors (Reimchen 1994, Hocking and Reimchen 2006). The transfer of salmon carcasses to riparian areas occurs at the highest frequency when salmon are abundant and accessible (Reimchen 2000, Gende et al. 2001, Quinn et al. 2003, Gende and Quinn 2004). When salmon spawn at low densities, or when habitat attributes limit foraging success, vertebrate consumption of available carcasses may approach 100% with few remnants distributed to riparian zones (Gende et al. 2001, 2004). Salmon body size also influences transfer as larger salmon have higher rates of predation (e.g. chum > pink, male > female), are transferred further into the forest, and have higher rates of colonization by insect scavengers (Quinn and Kinnison 1999, Hocking and Reimchen 2006). We hypothesized that $\delta^{15}\text{N}$ signatures in riparian biota would increase with salmon spawning biomass. However, because subsidies to forests are mediated by vertebrate foraging, we predicted that watersheds supporting a high density of the larger-bodied chum salmon will dominate these relationships (Reimchen 2000, Bilby et al. 2003). Finally, we also hypothesized that $\delta^{15}\text{N}$ would decrease with increasing watershed size, in part because of reduced bear access to salmon in larger streams, but also due to increased water discharge and terrestrial nutrient inputs in larger watersheds (Gende et al. 2001, Bridge 2003).

Methods

Study sites and sampling

We present an integration of foliar and litter invertebrate stable isotope data from collections in 1998 to 2001 from 27 watersheds in coastal British Columbia (regions: 1. Clayoquot Sound, Vancouver Island; 2. mainland mid-coast; and 3. Haida Gwaii (Queen Charlotte Islands); Fig. 1, Table 1). Foliar tissue samples were collected from Clayoquot Sound in spring and summer 1998–2000 from five salmon-bearing watersheds and one watershed with an impassable cascade at the mouth (Bulson Creek). In 2000, litter invertebrates were collected from sites that coincided with vegetation collections (Reimchen et al. 2003). In September of 2000, foliar and litter invertebrate specimens were collected from eight salmon-bearing watersheds on the mid-coast and eleven in Haida Gwaii. From 1999–2001, foliar and litter invertebrate samples were collected from above (control) and below a waterfall barrier to salmon on the Clatsop and Neekas rivers, and from an adjacent non-salmon watershed, Ripley Bay (Hocking and Reimchen 2002, Mathewson et al. 2003, Wilkinson et al. 2005, Christie et al. 2008).

We chose sampling sites for this study based on several criteria: 1) proximity to stream (<20 m), 2) low or negligible slope (<10°), 3) mostly old-growth forest structure, and 4) excluded samples taken directly from salmon carcass microsites (e.g. experimental carcasses in Wilkinson et al. 2005). We sampled upstream of the highest intertidal influence to a maximum of 2 km from the estuary. Because sampled species were not collected from salmon carcass micro-sites, we are confident that seasonal (spring, summer, fall) nitrogen isotope variation was minimal. For example, no seasonal $\delta^{15}\text{N}$ isotopic variation was observed in litter spiders collected in spring, summer

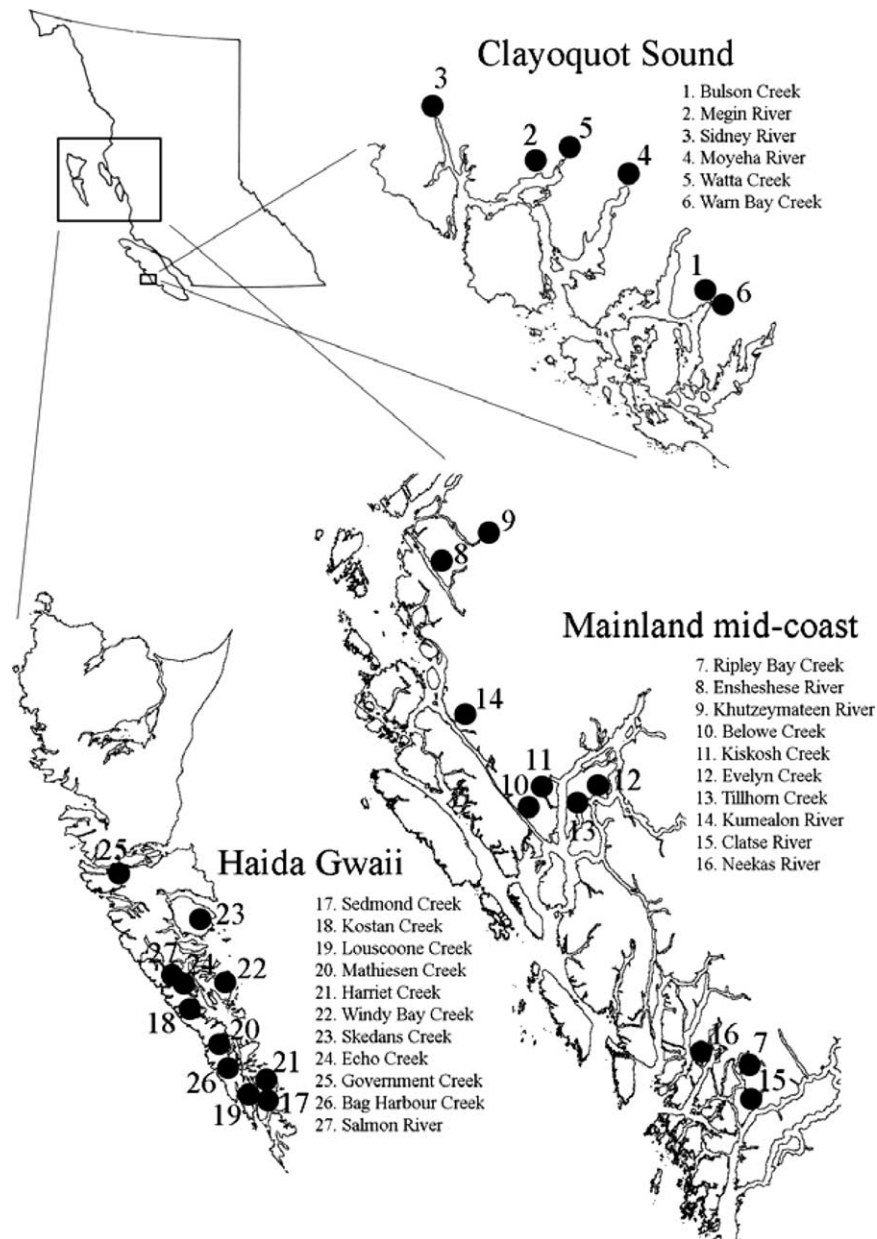


Figure 1. Study watersheds in coastal British Columbia, including Clayoquot Sound on Vancouver Island, the mainland mid-coast and Haida Gwaii. Watersheds are ranked by total salmon spawning biomass (kg m^{-1}) within regions (Table 1).

and fall on the Clatse and Neekas rivers (Christie et al. 2008).

Sampled watersheds occur in the Coastal Western Hemlock biogeoclimatic zone characterized by a cool and wet climate ($>3300 \text{ mm year}^{-1}$) and dense forests of western hemlock *Tsuga heterophylla*, amabilis fir *Abies amabilis*, sitka spruce *Picea sitchensis* and western red cedar *Thuja plicata*. Black bears *U. americanus* occur in all watersheds and act as the principal vectors moving salmon carcasses into the forest. Grizzly bears *U. arctos* and wolves are additional vectors on the mainland (wolves also on Vancouver Island).

Foliar samples were collected from replicate plants per site and were dried for storage. Invertebrate specimens were

collected in random searches or in ground-level pitfall traps and were stored in 70% ethanol. Whole invertebrates were rinsed with distilled water, prior to stable isotope processing. All plant and animal samples were dried at 60°C for at least 48 h, and were then ground into a homogeneous powder using a grinder. Sample size per species by watershed ($\pm \text{SE}$) equalled 7.3 ± 0.7 (range = 1–81).

Guild classification

We classified sampled riparian taxa initially by species and then secondarily into guilds based on their physiognomy (plants) and their ecological role (animals) (Table 2). Sampled species were included in the analysis based on

Table 1. Average chum *Oncorhynchus keta*, pink *O. gorbuscha* and coho *O. kisutch* salmon spawning escapements (mean Dept of Fisheries and Oceans data for the 1990s), salmon spawning lengths (m), total spawning biomass (kg m^{-1}), watershed size indices (PC1 scores of stream length, magnitude and order data) and riparian nitrogen isotope enrichment scores ($\delta^{15}\text{N}$ -index) from study watersheds in coastal British Columbia. Watersheds are ranked by spawning biomass within each region. V.Isl. =Vancouver Island; MidC =Mainland midcoast; H.Gwaii =Haida Gwaii.

Watershed + Region	Spawning length (m)	Salmon Chum	Escapement		Spawning biomass (kg m^{-1})	Watershed size index	Riparian $\delta^{15}\text{N}$ -index
			Pink	Coho			
1. Bulson (V.Isl.)	0	0	0	0	0.00	0.790	0.27
2. Megin (V.Isl.)	25300	5345	8	711	1.21	3.076	1.70
3. Sidney (V.Isl.)	2300	503	3	71	1.26	0.833	-0.34
4. Moyeha (V.Isl.)	10600	7544	39	1677	4.29	2.076	1.04
5. Watta (V.Isl.)	1700	2107	4	96	6.76	0.129	2.51
6. Warn (V.Isl.)	1400	4638	34	47	17.71	-0.253	4.09
7. RipleyBay (MidC)	0	0	0	0	0.00	-0.564	-1.87
8. Ensheshese (MidC)	11400	1027	9700	1700	2.57	0.566	-0.48
9. Khutzeymateen (MidC)	25200	6250	46500	3750	5.30	1.776	-0.80
10. Belowe (MidC)	1800	388	4517	134	6.15	-0.090	-0.24
11. Kiskosh (MidC)	1500	48	4758	56	6.32	-0.289	-0.87
12. Evelyn (MidC)	1700	54	5807	162	6.97	0.187	2.22
13. Tillhorn (MidC)	90	14	567	0	12.79	-0.597	1.24
14. Kumealon (MidC)	2100	74	32000	157	29.38	0.053	1.20
15. Clatse (MidC)	900	4433	14960	33	57.81	-0.494	4.88
16. Neekas (MidC)	1700	29270	20738	69	114.56	-0.026	7.81
17. Sedmond (H.Gwaii)	2400	417	392	51	1.30	-0.979	4.23
18. Kostas (H.Gwaii)	900	335	6	1	1.99	-1.025	4.61
19. Louscoone (H.Gwaii)	2100	774	30	14	2.00	-0.583	4.54
20. Mathiesen (H.Gwaii)	2200	1142	2330	12	4.78	-0.600	3.47
21. Harriet (H.Gwaii)	833	934	0	8	5.97	-1.029	3.80
22. Windy Bay (H.Gwaii)	6000	6	20100	5	6.37	-0.169	1.54
23. Skedans (H.Gwaii)	4800	0	23143	120	9.24	0.130	-0.19
24. Echo (H.Gwaii)	350	5	2456	27	13.66	-0.941	0.27
25. Government (H.Gwaii)	3100	4721	19502	39	20.06	-0.248	3.29
26. Bag (H.Gwaii)	800	3340	73	30	22.42	-0.705	5.65
27. Salmon (H.Gwaii)	1600	9813	10640	147	45.44	-1.024	5.46

three main criteria: 1) taxa had to be represented in at least four watersheds across a gradient in salmon spawning biomass; 2) taxa were not highly mobile (e.g. mobile Diptera excluded) and thus likely exhibited site-specific isotope signatures; and 3) taxa did not have a dominant direct relationship with salmon carcasses (Hocking and Reimchen 2006). Plants were subdivided into four guilds: 1) herbs and ferns, 2) woody shrubs, 3) hemlock needles, and 4) lanky moss. The litter animal fauna were separated into guilds consisting of 1) litter spiders, 2) ground beetles, 3) millipedes, and 4) weevils as in Hocking and Reimchen (2002).

Stable isotope analysis

Ground foliar and invertebrate samples (1–2 mg dry weight) were assayed for $\delta^{15}\text{N}$ (plants) or $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (animals) by continuous-flow isotope ratio mass spectrometry. Isotopic signatures are expressed in delta notation (δ) as ratios relative to known isotopic standards of atmospheric N_2 (nitrogen) and PeeDee Belemnite limestone (carbon). This is expressed in ‘parts per mil’ (‰) according to:

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} (\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

where R is the ratio of the heavy isotope (^{15}N or ^{13}C)/light isotope (^{14}N or ^{12}C).

Analysis: salmon and habitat data

We compiled online Dept of Fisheries and Oceans (Government of Canada) records for salmon escapement data for our sites from records that spanned the decade of the 1990s, and used salmon spawning biomass ($\text{kg} \times \text{m}^{-1}$) averaged over the length of spawning as our primary predictor for isotope signatures in riparian taxa:

$$\text{Salmon spawning biomass} = E_i \times W_i / \text{SL} \quad (2)$$

where E = 1990s mean escapement, i = salmon species (chum, pink or coho salmon), W = species regional mass estimates (chum: 5.3 kg, pink: 1.9 kg, coho: 3.2 kg; Groot and Margolis 1991), and SL = the length of salmon spawning (m) (Table 1). Densities by species were summed to give a total salmon biomass (kg m^{-1}) for each watershed. Because salmon biomass data were skewed towards lower density streams, data were normalized using a natural log transformation ($\ln + 1$).

Watershed size and in situ productivity may influence the isotopic composition of riparian taxa. We obtained stream habitat information from the British Columbia Ministry of Environment’s Habitat Wizard (<www.env.gov.bc.ca/habwiz/>), including data for stream length, stream order and stream magnitude (Table 1). Stream order and magnitude are measures of watershed geometry and branching complexity, with larger values indicative of greater water flow and catchment area (Bridge 2003). We

Table 2. Guild and species classification in this study. Terrestrial end-members (TEM_{Guild}) represent mean $\delta^{15}\text{N}$ stable isotope signatures (‰) for each guild from watersheds or reaches with waterfall barriers that exclude all spawning salmon. n = the number of watersheds represented by each guild.

Guild	TEM_{Guild}	Family	Species
1. Litter spiders n = 17	5.41	Agelenidae	<i>Cybaeus</i> spp. (<i>C. reticulatus</i> and <i>C. eutypos</i>)
2. Ground beetles n = 9	3.11	Carabidae	<i>Pterostichus</i> spp <i>Zacotus matthewsii</i>
3. Millipedes n = 23	2.00	Parajulidae	Unknown sp.1
4. Weevils n = 4	-2.67	Xystodesmidae	<i>Harpaphe haydeniana</i>
5. Shrubs n = 21	-0.81	Curculionidae	<i>Steremnius carinatus</i> <i>Steremnius tuberosus</i>
		Araliaceae	<i>Oplopanax horridus</i>
		Ericaceae	<i>Gaultheria shallon</i> <i>Menziesia ferruginea</i> <i>Vaccinium alaskaense</i> <i>Vaccinium parvifolium</i> <i>Rubus spectabilis</i>
6. Herbs and ferns n = 18	-1.10	Rosaceae	<i>Polystichum munitum</i>
		Aspleniaceae	<i>Blechnum spicant</i>
		Blechnaceae	<i>Maianthemum dilatatum</i>
		Liliaceae	<i>Rhytidiadelphus loreus</i>
7. Lanky moss n = 10	-5.32	Hylocomiaceae	
8. Hemlock needles n = 15	-3.60	Pinaceae	<i>Tsuga heterophylla</i>

used principal components analysis (PCA) on the three stream variables to create an index of watershed size. PC1 explained 87.0% of the variation in stream variables (PC1 extractions: stream length = 0.920, stream order = 0.766, stream magnitude = 0.923). Because we sampled fewer larger watersheds, watershed PC1 data were normalized using a natural log transformation ($\ln + 2$).

Analysis: species and guilds

Plant fractionation processes and animal trophic position can obscure the interpretation of stable isotopic data (mainly $\delta^{15}\text{N}$) used to predict the degree of marine enrichment from salmon. First, for analyses including 11 plant species, we used an ANCOVA design to predict variation in foliar $\delta^{15}\text{N}$ by vegetation species (fixed factor) and salmon spawning biomass (kg m^{-1}) (covariate). We present data using either a) total salmon biomass, b) chum salmon biomass, c) pink salmon biomass, or d) coho salmon biomass as covariates in separate analyses. Second, we used the ANCOVA design to test $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ variation by guild (four plant guilds, four invertebrate guilds: Table 2) and salmon spawning biomass (as above). Guild means were determined by averaging across species within each watershed. To meet assumptions of equal variances, we removed one high $\delta^{15}\text{N}$ outlier in the dataset (millipedes from Bag Harbour: studentized residuals = 3.38). Exclusion of this data point did not alter the ANCOVA results. We also removed weevils from the analysis using coho salmon as the covariate (weevils were sampled in only four watersheds).

Interaction terms in the ANCOVA design (species or guild \times salmon biomass) test the assumption of homogeneity of slopes, and are biologically relevant as they test two principal assumptions in analyses of salmon nutrient uptake in recipient communities. These assumptions are: 1) evidence for diverging slopes by species or guild across the

gradient in salmon biomass may indicate differing pathways or sources of salmon nutrients with potential differences in the residency times of these nutrients in biotic tissues, and 2) because estimates of salmon nutrient contribution to higher trophic levels can be confounded by individual trophic position (particularly for $\delta^{15}\text{N}$), analyses by guild provides a direct test of trophic position variation in the litter invertebrate community across the gradient in salmon productivity (e.g. MDN models in Hocking and Reimchen 2002, Claeson et al. 2006).

Analysis: nitrogen enrichment index

The assumption of homogeneity of slopes was met in all ANCOVA analyses. As such, we derived an index of nitrogen isotopic enrichment ($\delta^{15}\text{N}$ -index) with the aim of creating a simplified marine fertilization score for each watershed that removes nitrogen isotope variation due to plant fractionation and animal trophic position:

$$\delta^{15}\text{N}\text{-index (‰)} = \sum (\text{Obs}_{\text{Guild}} - \text{TEM}_{\text{Guild}}) / \text{N}_{\text{Guild}} \quad (3)$$

where $\text{Obs}_{\text{Guild}}$ = the observed $\delta^{15}\text{N}$ mean for each guild by watershed, $\text{TEM}_{\text{Guild}}$ = the terrestrial end-member for each guild, and N_{Guild} = the number of guilds represented in each watershed. Terrestrial end-members represent mean $\delta^{15}\text{N}$ signatures for each guild from watersheds or reaches with waterfall barriers that exclude all spawning salmon (Bulson and Ripley Bay watersheds, Clatse and Neekas rivers above falls) (Table 2). $\delta^{15}\text{N}$ -index values were tested for potential regional differences in the $\delta^{15}\text{N}$ -index (linear regression for each region followed by ANCOVA).

Analysis: model selection

We used Akaike information criterion (AIC), an information theoretic approach (Burnham and Anderson 1998), to

assess the relative role of each salmon species (chum, pink or coho) and the watershed size index in predicting $\delta^{15}\text{N}$ -index values by watershed. AIC evaluates the predictive power of various a priori models with different combinations of variables based on the principal of parsimony, balancing optimal model fit with the number of parameters used. First, we constructed nine linear regression models, and tested the ability of our watershed size index (PC1) and spawning biomass (kg m^{-1}) split by salmon species (chum, pink and coho) to predict the $\delta^{15}\text{N}$ -index. The model set also included the total spawning biomass (kg m^{-1}) of all salmon species ($k = \text{three parameters}$) and combinations of watershed size with spawning biomass ($k = \text{four parameters}$). We excluded our control watersheds (Bulson, Ripley Bay) from model selection analyses. All AIC values were corrected for analyses using small sample sizes (AIC_c for $n = 25$ watersheds).

Results

Across our 25 salmon spawning watersheds, returns for the 1990s averaged 3327 ± 1214 chum salmon, 8732 ± 2432 pink salmon and 365 ± 169 coho salmon. Total biomass of spawning fish ranged up to 114 kg m^{-1} (mean = 16.3 ± 5.0), with nine of 25 salmon streams supporting densities of greater than 10 kg m^{-1} (Table 1). The spawning biomass of pink salmon differed by region (ANOVA: $F_{2,22} = 9.36$, $p = 0.001$), with highest values on the mid-coast and almost zero recent returns on Vancouver Island. Significant regional variation in spawning biomass was not observed for chum ($F_{2,22} = 0.14$, $p = 0.886$) or coho ($F_{2,22} = 3.17$, $p = 0.062$).

Sampled watersheds varied in size (Table 1). Stream length ranged from 2.12 to 33.46 km (mean = 9.10 ± 1.63 km), while stream magnitude and order ranged from 1 to 153 (mean = 23.3 ± 7.2) and 1 to 5 (mean = 2.63 ± 0.61). Coho salmon biomass (kg m^{-1}) was positively related to the index of watershed size (linear regression: $F_{1,23} = 6.77$, $p = 0.016$, $R^2 = 0.227$), while chum and pink salmon spawning biomass showed no relationship with the watershed size index ($F_{1,23} < 1.05$, $p > 0.32$).

Nitrogen stable isotope variation ($\delta^{15}\text{N}$) in eleven riparian plant species was evaluated in an ANCOVA design using four separate tests with alternate covariates (Table 3: a) total salmon biomass, b) chum salmon biomass, c) pink salmon biomass, and d) coho salmon biomass (kg m^{-1})).

Vegetation $\delta^{15}\text{N}$ signatures were positively related to total salmon, chum salmon and pink salmon spawning biomass, but not to the biomass of coho salmon (Fig. 2a–d). Differences in mean $\delta^{15}\text{N}$ were observed by plant species in models containing total salmon and chum salmon as covariates. In all models, no differences were observed in the slope of the relationship between spawning biomass and $\delta^{15}\text{N}$ by plant species (ANCOVA interaction terms: $p > 0.7$). Model R^2 was greatest using chum salmon biomass as a predictor (Fig. 2b).

We used the ANCOVA design to test isotopic variation in four invertebrate (litter spiders, ground beetles, millipedes and weevils) and four plant guilds (shrubs, herbs and ferns, lanky moss and hemlock needles: Table 2) using the four separate salmon biomass covariates (Fig. 3, Table 4). $\delta^{15}\text{N}$ values were positively predicted by total salmon, chum salmon and pink spawning biomass, but not by the biomass of coho salmon, with the largest model R^2 values observed when chum salmon biomass was used as a covariate (Fig. 3b). Despite the taxonomic and ecological breath of the samples, there was remarkable similarity in slopes among guilds. $\delta^{15}\text{N}$ varied by guild (all $p < 0.001$: e.g. trophic enrichment), with no differences in the slope of the relationship between salmon biomass and $\delta^{15}\text{N}$ among guilds (ANCOVA interaction term for coho: $p > 0.07$; all other interaction $p > 0.45$). $\delta^{13}\text{C}$ stable isotope signatures in invertebrates indicated a terrestrial dietary origin (mean $\delta^{13}\text{C} = -25.01\text{‰}$). $\delta^{13}\text{C}$ variation was observed by invertebrate guild (all $F_{3,48} > 35$; all $p < 0.001$), but not by any of the four salmon biomass covariates (all $F_{1,48} < 3.6$; all $p > 0.06$), indicating that these invertebrate species are not enriched in $\delta^{15}\text{N}$ based on a diet of salmon.

In contrast to salmon biomass, the index of watershed size negatively predicted $\delta^{15}\text{N}$ isotope signatures in all plant species (ANCOVA: $F_{1,116} = 5.91$, $p = 0.017$, $\eta^2 = 0.05$), as well as in all eight riparian guilds (ANCOVA: $F_{1,109} = 16.84$, $p < 0.001$, $\eta^2 = 0.13$). No differences were observed in the slope of the relationship between watershed size and $\delta^{15}\text{N}$ by plant species or riparian guild (both interaction terms $p > 0.25$).

Because regression slopes of $\delta^{15}\text{N}$ by salmon spawning biomass and watershed size were similar for all plant species and invertebrate guilds, we derived an index of nitrogen isotope enrichment ($\delta^{15}\text{N}$ -index) for each watershed that removes nitrogen isotope variation by plant fractionation or animal trophic position. $\delta^{15}\text{N}$ -index values across all guilds were most strongly predicted by the spawning biomass

Table 3. Analysis of covariance (ANCOVA) of foliar $\delta^{15}\text{N}$ stable isotope signatures (dependent) in 11 plant species (fixed factor) collected from watersheds in British Columbia that vary in salmon, *Oncorhynchus* spp., spawning biomass (kg m^{-1}) (covariate). Four separate tests included a) total salmon biomass, b) chum salmon biomass, c) pink salmon biomass, and d) coho salmon biomass as covariates (Fig. 2). $\eta^2 = \text{partial eta-squared}$.

Test	Factor	DF	F	P	η^2
a.	Plant species	10,116	2.34	0.015	0.168
	Total salmon biomass (kg m^{-1})	1,116	99.53	<0.001	0.462
b.	Plant species	10,116	3.49	<0.001	0.231
	Chum salmon biomass (kg m^{-1})	1,116	172.72	<0.001	0.599
c.	Plant species	10,116	1.50	0.15	0.114
	Pink salmon biomass (kg m^{-1})	1,116	20.31	<0.001	0.149
d.	Plant species	10,116	1.32	0.015	0.102
	Coho salmon biomass (kg m^{-1})	1,116	3.28	0.074	0.028

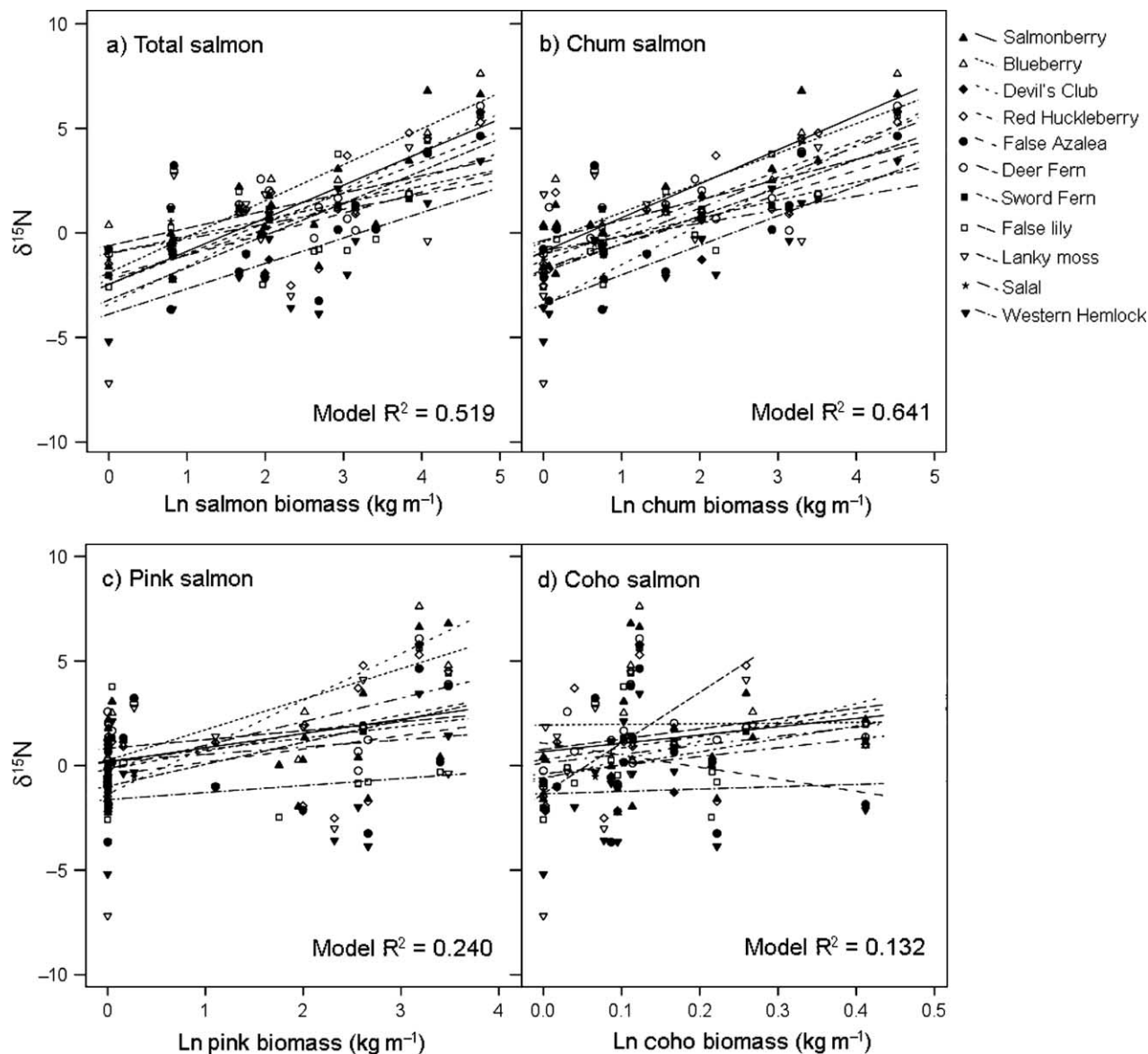


Figure 2. $\delta^{15}\text{N}$ stable isotope signatures in eleven species of riparian plants from 25 salmon-bearing and two non-salmon watersheds in coastal British Columbia using (a) total salmon, *Oncorhynchus* spp., biomass, (b) chum *O. keta* salmon biomass, (c) pink *O. gorbuscha* salmon biomass, and (d) coho *O. kisutch* salmon biomass (kg m^{-1}) as covariates in an analysis of covariance design (Table 2). Salmon data are $\ln + 1$ transformed and represent the 10 year mean escapement (1990s) of chum, pink and coho salmon multiplied by their regional mass estimates (Groot and Margolis 1991) and divided by the stream length of salmon spawning (m).

(kg m^{-1}) of chum salmon (Fig. 4a), which was a much stronger predictor of $\delta^{15}\text{N}$ -index variation than pink or coho salmon biomass or even the sum biomass of all species (AIC model selection: Table 5). Watershed size negatively predicted $\delta^{15}\text{N}$ -index scores (Fig. 4b) and was included as a parameter in the model with the highest AIC weight ($W_i = 0.96$). Chum salmon biomass on its own was ranked second in the model set ($W_i = 0.04$). $\delta^{15}\text{N}$ -index values differed by region ($F_{2,21} = 26.88$, $p = 0.005$), with highest mean values in Haida Gwaii watersheds. When only chum biomass was used to predict $\delta^{15}\text{N}$ -index variation, then all regions independently and positively predicted $\delta^{15}\text{N}$ -index values (linear regression: all $p < 0.05$). High $\delta^{15}\text{N}$ -index values were observed at the site with the highest salmon biomass, the Neekas River (7.8‰) (Table 1). High values were also observed at the Clatse River (4.9‰) on the mid-

coast, and at Bag Harbour Creek (5.7‰) and Salmon River (5.5‰) on Haida Gwaii. Watersheds supporting the highest density on Vancouver Island, Warn Bay and Watta creeks, also had the highest $\delta^{15}\text{N}$ -index values in this region (4.1‰ and 2.5‰, respectively). Several watersheds on Haida Gwaii (Sedmond, Kostan, Louscoone, Matheson, Harriet) had high $\delta^{15}\text{N}$ -index values (3.5–4.6‰) despite low recent salmon returns, while other sites (Echo, Windy Bay, Skedans) with moderate to high pink salmon biomass had low or even negative scores (Table 1).

Discussion

We demonstrate a repeated pattern of nitrogen isotopic enrichment in 11 plant species and four litter invertebrate

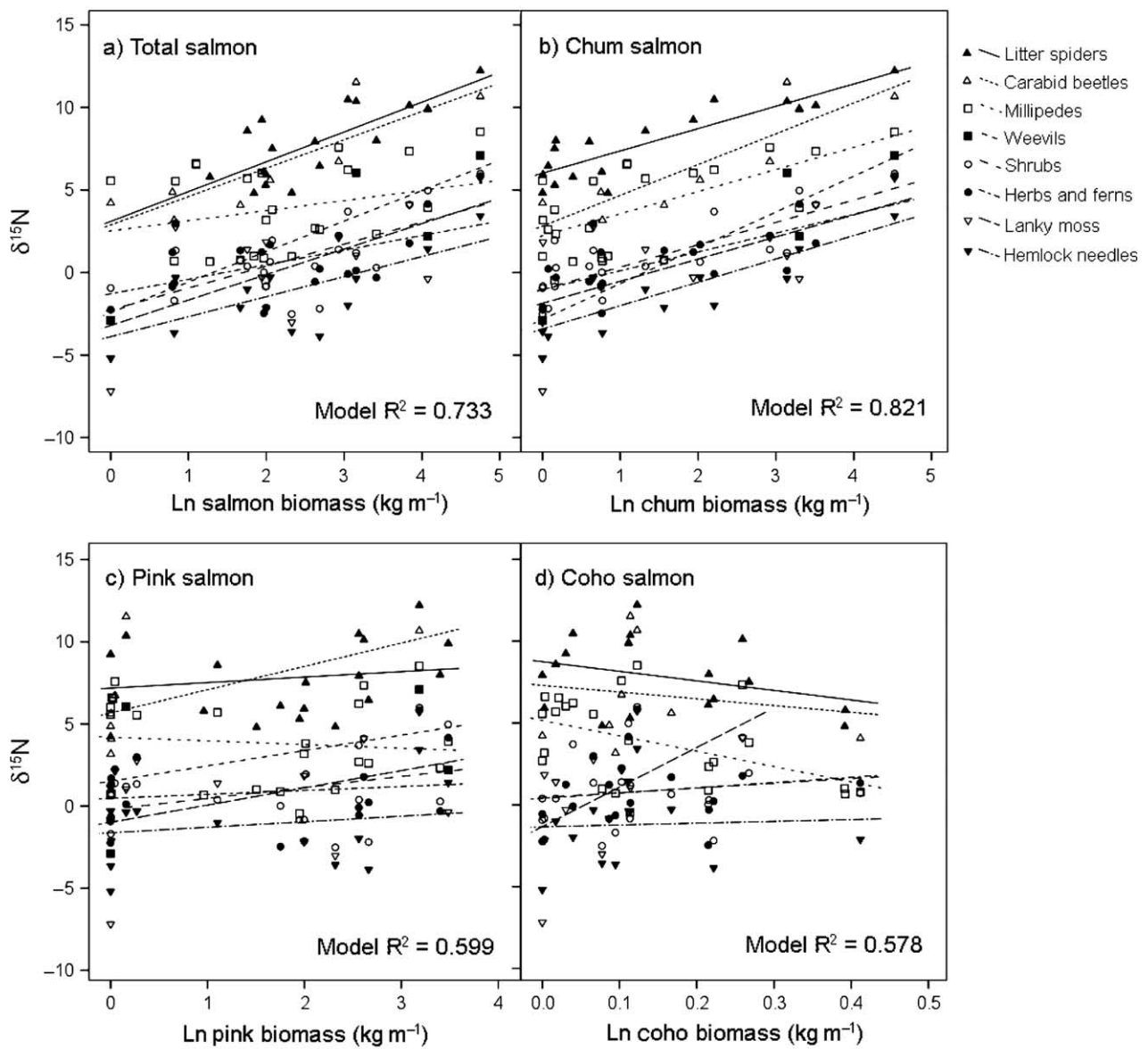


Figure 3. $\delta^{15}\text{N}$ stable isotope signatures in eight guilds of riparian plants and invertebrates from 25 salmon-bearing and two non-salmon watersheds in coastal British Columbia using (a) total salmon, *Oncorhynchus* spp., biomass, (b) chum *O. keta* salmon biomass, (c) pink *O. gorbuscha* salmon biomass, and (d) coho *O. kisutch* salmon biomass (kg m^{-1}) as covariates in an ANCOVA design (Table 2). Salmon data are $\ln + 1$ transformed and represent the 10 year mean escapement (1990s) of chum, pink and coho salmon multiplied by their regional mass estimates (Groot and Margolis 1991) and divided by the stream length of salmon spawning (m).

Table 4. Analysis of covariance (ANCOVA) of $\delta^{15}\text{N}$ stable isotope signatures (dependent) in eight guilds of riparian plants and invertebrates (fixed factor) collected from watersheds throughout British Columbia that vary in salmon, *Oncorhynchus* spp., spawning biomass (kg m^{-1}) (covariate). Four separate tests included a) total salmon biomass, b) chum salmon biomass, c) pink salmon biomass, and d) coho salmon biomass as covariates (Fig. 3). η^2 = partial eta-squared.

Test	Factor	DF	F	P	η^2
a.	Guild	7,108	31.41	<0.001	0.671
	Total salmon biomass (kg m^{-1})	1,108	63.55	<0.001	0.370
b.	Guild	7,108	51.35	<0.001	0.769
	Chum salmon biomass (kg m^{-1})	1,108	148.24	<0.001	0.579
c.	Guild	7,108	21.28	<0.001	0.580
	Pink salmon biomass (kg m^{-1})	1,108	6.22	0.014	0.054
d.	Guild	6,105	26.08	<0.001	0.598
	Coho salmon biomass (kg m^{-1})	1,105	0.87	0.354	0.004

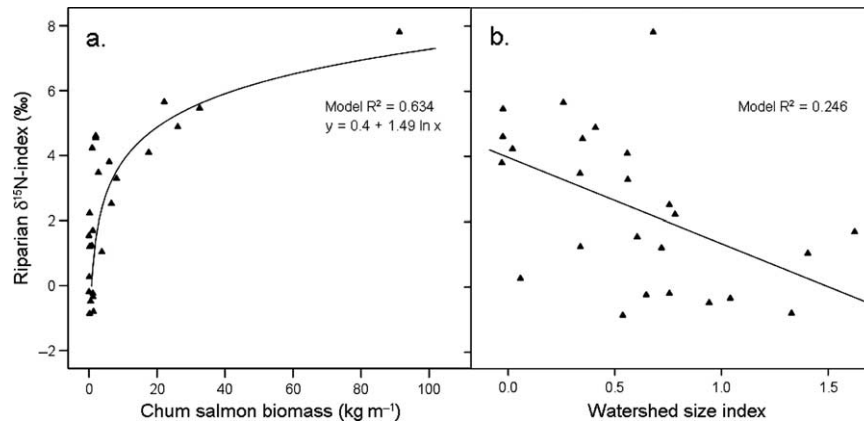


Figure 4. Riparian nitrogen isotope enrichment ($\delta^{15}\text{N}$ -index) values are (a) positively predicted by chum salmon *Oncorhynchus keta* spawning biomass (kg m^{-1}) and (b) negatively predicted by watershed size in 25 watersheds in coastal British Columbia supporting anadromous salmon. $\delta^{15}\text{N}$ -index values represent the mean nitrogen isotope enrichment (‰) of all plant and invertebrate guilds within each watershed relative to control streams/reaches with no spawning salmon. Watershed size scores are $\ln+2$ transformed principal components analysis scores of stream length, stream magnitude and stream order data (PC1 explains 87.0% of variation). The top model predicting $\delta^{15}\text{N}$ -index variation comprised chum biomass (kg m^{-1}) and watershed size (AIC model selection: $W_i = 0.96$).

trophic guilds across a gradient in salmon spawning density in 27 watersheds in three geographical areas in coastal British Columbia. These patterns were largely driven by the biomass and availability of chum salmon (chum density and watershed size), as compared to trends observed for pink or coho salmon or the sum biomass of all salmon species. In western Washington, streams supporting chum salmon have higher marine nutrient transfer than those with coho (Bilby et al. 2003). Chum, pink and sockeye *O. nerka* salmon spawn in large aggregations, which can increase predation by vertebrates, while coho salmon do not (Groot and Margolis 1991). In this study, the separation of chum and pink salmon is likely due to widespread preferences by bears for chum as prey because of their large size and higher net energy gain (Reimchen 2000). Several studies have observed size-selective mortality in salmon, as bear-killed fish were larger than those dying of senescence and male salmon were preyed upon at higher frequency than females (Quinn and Kinnison 1999, Reimchen 2000). In watersheds with explicit counts of salmon carcasses in the forest, chum salmon are transferred at a much greater rate than pink salmon (Reimchen 2000, Hocking and Reimchen 2006), an observation likely explained by size-selective optimal

foraging (Gende and Quinn 2004, Gende et al. 2004). Carcass size is also an important determinant of the insect community on salmon carrion. The blowflies (Calliphoridae) are particularly successful on large chum carcasses due to their high reproductive output, growth rates and competitive ability, and are an important further vector of salmon nutrients in terrestrial habitats (Meehan et al. 2005, Hocking and Reimchen 2006).

Watershed size may influence base productivity or access for predators and thus predict sites with high marine dependency (Polis et al. 1997, Gende et al. 2004). In this study, small chum-bearing streams supported the highest spawning biomass and rates of nutrient transfer. For example, the Clatse, Neekas, Bag Harbour, Salmon and Warn Bay watersheds all have spawning reaches of 2 km or less. This parallels other marine-terrestrial fluxes where small islands with high perimeter/area ratios support high nutrient transfer and biota with a strong dependency on marine resources (Polis and Hurd 1996). In contrast, large watersheds with high salmon returns but a large spawning area (> 10 km) such as the Khutzeymateen, Ensheshese, Megin and Moyeha rivers had low $\delta^{15}\text{N}$ values. The lower reaches of large systems have high water flows and can

Table 5. Model selection using Akaike information criterion (AIC) of nine linear regression models used to predict riparian nitrogen isotope enrichment ($\delta^{15}\text{N}$ -index) scores in watersheds ($n=25$) that vary in size (watershed size index) and spawning biomass (kg m^{-1}) of chum *Oncorhynchus keta*, pink *O. gorbuscha* and coho *O. kisutch* salmon in coastal British Columbia. Total salmon biomass equals the sum biomass of all salmon species. k =number of model parameters; R^2 =model regression coefficient; p =model significance; AIC_c =Akaike information criterion for small sample sizes; ΔAIC =change in AIC score from top model; W_i =AIC model weight.

Model	k	R^2	p	AIC_c	ΔAIC	W_i
1. Chum biomass + Watershed size	4	0.748	<0.001	15.82	0.00	0.96
2. Chum biomass	3	0.634	<0.001	22.31	6.49	0.04
3. Total salmon biomass + Watershed size	4	0.369	0.006	38.81	22.99	0.00
4. Watershed size	3	0.246	0.012	40.40	24.58	0.00
5. Total salmon biomass	3	0.215	0.020	41.42	25.60	0.00
6. Coho biomass + Watershed size	4	0.272	0.030	42.38	26.56	0.00
7. Pink biomass + Watershed size	4	0.254	0.040	43.00	27.18	0.00
8. Coho biomass	3	0.143	0.062	43.60	27.78	0.00
9. Pink biomass	3	0.001	0.905	47.45	31.63	0.00

restrict choice and capture efficiencies for predators such as bears (Gende et al. 2004). In situ productivity is also likely to be high in watersheds with large catchment areas, and lower in small watersheds; for example, increased terrestrial nutrient inputs from large-scale flooding events and greater influence of the nitrogen fixer, red alder *Alnus rubra* (Helfield and Naiman 2002, Bridge 2003).

Nitrogen isotope variation in plants within and among sites can be substantial, reflecting both nutrient sources and soil processes (Evans 2001). Processes such as ammonia volatilization and denitrification with high N fractionations can vary across gradients in site productivity, prompting concern as to the interpretation of elevated $\delta^{15}\text{N}$ along salmon streams (Pinay et al. 2003). Data presented here support a salmon-derived source of nitrogen isotope enrichments rather than by processes such as denitrification. This is because: 1) we directly link nitrogen isotope enrichments at a watershed-scale to the larger bodied chum salmon; 2) despite high total numbers of spawners, large watersheds had low $\delta^{15}\text{N}$; and 3) we excluded samples taken from salmon carcass micro-sites, locations where these processes are more important (Gende et al. 2007). By averaging $\delta^{15}\text{N}$ values among species and guilds we also remove much of the potential small-scale variation present within watersheds, with means representative of larger-scale nutrient transfer.

Parallel slopes of $\delta^{15}\text{N}$ enrichment in our litter food web (plants, invertebrates) show that trophic length and individual trophic position are similar across the gradient in spawning biomass. $\delta^{15}\text{N}$ values in higher trophic levels are ultimately determined by the base or 'background' $\delta^{15}\text{N}$ of the soil, litter and vegetation present within watersheds (Ponsard and Arditì 2000). $\delta^{15}\text{N}$ variation among species and guilds is thus accounted for by trophic position in invertebrates (Ponsard and Arditì 2000, Hocking and Reimchen 2002) and by nitrogen source and fractionation processes in plants (Evans 2001). In contrast, animal species that feed directly on salmon would be predicted to show a) high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicative of a marine diet, and b) more seasonal variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Ben-David et al. 1997, Darimont and Reimchen 2002).

Pacific salmon have been returning to spawn in coastal streams and lakes for thousands of years (Finney et al. 2000), and it might be expected that $\delta^{15}\text{N}$ signatures in soils and plants reflect an integrated rate of salmon subsidy through time. In central Idaho, persistent salmon signatures have been detected in riparian plants where salmon have been absent for 30 years (Koyama et al. 2005). In the last 50 years, many small systems on the central and north coasts of British Columbia have experienced declines in chum returns, followed by pink replacement (Reimchen 1994, Godbout et al. 2004). Watersheds in this study that have reduced chum escapement since the 1950s (Dept of Fisheries and Oceans data) generally exhibited higher $\delta^{15}\text{N}$ -index values than predicted by recent chum salmon returns alone. Transfer of chum salmon to coastal forests by bears was likely higher in the past in many watersheds, a process with a legacy that may be still evident in the $\delta^{15}\text{N}$ signatures of riparian biota living today.

At present, it is relatively unknown whether nitrogen isotope signatures can be used to indicate intact ecosystem processes so that it may be possible to set escapement goals

that consider these values. Similar to Bilby et al. (2001) and Nagasaka et al. (2006), we find a curvilinear relationship between $\delta^{15}\text{N}$ -index values and salmon density indicative of possible $\delta^{15}\text{N}$ saturation at higher salmon densities ($>10\text{ kg m}^{-1}$) in multiple guilds and trophic levels of the riparian zone. Processes such as density-dependent predation and salmon carcass consumption by bears (Gende et al. 2001, Quinn et al. 2003) and carcass size-dependent colonization by invertebrates (Hocking and Reimchen 2006) may generate asymptotic relationships between $\delta^{15}\text{N}$ values and salmon biomass. Under either scenario, the extent of marine flux to terrestrial habitats can be meaningfully inferred from $\delta^{15}\text{N}$ levels when these are well below saturation ($<4\text{‰}$), but higher signatures potentially underestimate the extent of transfer at higher salmon densities ($>10\text{ kg m}^{-1}$) if isotopic saturation is approached. We suggest that densities of 10 kg m^{-1} ($\sim 2000\text{ chum km}^{-1}$) or greater may be used as a guideline for chum salmon escapement and whole-watershed restoration and conservation for vertebrate wildlife and ecosystem processes associated with the salmon-forest subsidy.

Salmon populations and their habitats face numerous anthropogenic impacts (Gresh et al. 2000, Krkosek et al. 2007), particularly when overlaid within the future uncertainty of global climate change (Finney et al. 2000, Battin et al. 2007, Brander 2007). On the north coast of British Columbia, recent declines in small streams that support chum salmon represent a concern directly related to this study (Harvey and MacDuffee 2002, Godbout et al. 2004). Analyses of biodiversity and habitat data across many watersheds moves towards a long-term goal in fisheries ecology to better integrate ecosystem values in salmon conservation.

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