

Opposing forces: Evaluating multiple ecological roles of Pacific salmon in coastal stream ecosystems

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Abstract. Resource flows and disturbance from species migrations can alter the productivity, structure and function of an ecosystem. Annual mass migrations of Pacific salmon (*Oncorhynchus* spp.) to coastal watersheds import vast quantities of potentially limiting nutrients that have been shown to increase primary and secondary productivity in streams and lakes. Substrate disturbance during spawning can also export nutrients and reduce primary and secondary production. Here we study the impacts of these dual roles of salmon on stream invertebrates. We collected benthic macroinvertebrates in 15 streams prior to and following peak salmon spawning on British Columbia's central coast. Along with other habitat measurements including stream water chemistry, temperature, and watershed size, we investigated the effects of salmon on invertebrate $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and biomass density (mg/m^2) among 15 streams and within 5 streams, upstream and downstream of barriers to spawning salmon. We found that stream invertebrates assimilate salmon-derived nutrients in proportion to availability but invertebrate biomass density declines in both seasons with increasing salmon density. Benthic disturbance appears to be the cause of this decline in the fall, but the decline in the spring may be due to the slow recovery of invertebrates from substrate disturbance the previous fall or salmon nutrients may be indirectly driving declines in spring invertebrate biomass by subsidizing other trophic levels and eliciting a trophic cascade.

Key words: ecosystem-based management; fisheries; freshwater; Great Bear Rainforest; insects; resource subsidy; river.

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INTRODUCTION

Coastal streams and rivers are nutrient highways at the interface between vastly distinct systems (Likens and Bormann 1974). These freshwater networks funnel terrestrial and riverine material downstream and provide passage for species migrating upstream from estuaries and oceans, which can supplement nutrients through their excretion, reproduction or tissue (Willson and Halupka 1995, Flecker 1996). The flow of resources stemming from species migrations provide intense, punctuated periods of

nutrient influx that can have pronounced effects on a recipient ecosystem's productivity, function and structure (Yang and Naeem 2008, Richardson and Sato 2014). However, evaluating the effects of resource pulses on food webs remains a challenge because it involves not only evaluating shifts between consumers and their prey but also other major processes such as disturbance (Ostfeld and Keesing 2000).

Resource subsidies and disturbance can independently have far reaching effects on community structure (Resh et al. 1988, Lake 2000, Ostfeld and Keesing 2000, Yang et al. 2008).

Spiller et al. (2010) found that the abundance of terrestrial predators increased with marine subsidies on islands, while Boucek and Rehage (2014) found that disturbance from two extreme climate events greatly altered fish community composition. However, there is a unique and well-known example in nature where a substantial resource pulse and disturbance occur simultaneously. Pacific salmon (*Oncorhynchus* spp.) have long been recognized as vectors of high quality nutrients to freshwater and terrestrial environments (Juday et al. 1932, Naiman et al. 2002, Janetski et al. 2009) and more recently as a significant source of disturbance to benthic freshwater communities (Moore and Schindler 2008, Janetski et al. 2009, Harding et al. 2014). Mass migrations of salmon can import as much as 266 g/m² of nitrogen to streams on the central coast of British Columbia in high abundance years (Harding et al. 2014), while as much as 55% of nitrogen imported by salmon can be exported out of streams through their spawning behavior (Moore et al. 2007). Consequently, spawning salmon provide an excellent opportunity to simultaneously test hypotheses about the multiple effects of resource pulses and disturbance on consumers in recipient communities.

As primary and secondary consumers, stream macroinvertebrates play a key role in stream food webs, linking riverine and terrestrial production and providing one of the most important food sources for resident fish (Wallace and Webster 1996, Hauer and Resh 2007). They therefore provide a good case study to investigate ecosystem-level responses to subsidies and disturbance at a convenient scale. Invertebrates occupy several functional feeding groups across a wide range of freshwater habitats, with community dynamics affected by stream temperature and pH (Verspoor et al. 2011), chemistry (Allan and Castillo 2007), flow (Minshall and Minshall 1977), watershed size (Vannote et al. 1980), substratum size and stability (Minshall and Minshall 1977, Verspoor et al. 2011), biofilm biomass (Cummins and Klug 1979), riparian vegetation (Fisher and Likens 1973, Vannote et al. 1980), predators (Gilinsky 1984) and salmon density (Wipfli et al. 1999, Chaloner et al. 2004, Moore et al. 2004).

Current research is divided on the multiple

roles of salmon in stream resource and disturbance regimes. Some studies have found that invertebrates from streams with higher salmon density have a more enriched nitrogen and carbon isotope signature (Bilby et al. 1996, Hicks et al. 2005) and are found in greater numbers (Wipfli et al. 1999, Verspoor et al. 2011), while other studies have found fewer invertebrates in the presence of spawning salmon (Moore et al. 2004, Moore and Schindler 2008). These studies seem to contradict each other. However, the effect of spawning salmon is likely mediated by chemical and physical characteristics of streams, including baseline nutrient conditions, and our interpretation of these effects depends on the spatial and temporal range examined (Marczak et al. 2007, Janetski et al. 2009, Tiegs et al. 2011). The aim of this study was to test the net effects of live spawning salmon, in conjunction with key habitat variables, on stream invertebrate stable isotope ratios and biomass density.

To test the concurrent effects of salmon as a source of both nutrients and disturbance, we sampled invertebrates, assessed habitat characteristics, and enumerated salmon from 15 relatively pristine streams from the Great Bear Rainforest on British Columbia's central coast. We predicted that invertebrates would incorporate marine-derived nutrients imported by salmon, which would be shown by enriched nitrogen and carbon isotopes, and that their isotope signature would be highest in the fall when nutrients were readily available for direct uptake. If invertebrates were indeed acquiring these marine-derived resources, we predicted that more invertebrates would be supported in streams with greater salmon density prior to the arrival of salmon. During spawning, however, we predicted that invertebrate biomass density would decline with salmon density due to an increase in substrate disturbance, which would negate any potential subsidy effect in the fall. We also predicted that these results would be mediated by habitat-specific characteristics. For example, in streams with comparable salmon densities, we predicted that invertebrate biomass would be higher in warmer streams that had more neutral pH. Our specific predictions for each variable included in our analyses are in Tables 1 and 2.

Table 1. Hypotheses for salmon and habitat variables for invertebrate $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Response	Variable	Mechanism	Metric	Level	Response	Reference
$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$	Salmon	Salmon have high ^{15}N and ^{13}C due to their largely marine diet. They can subsidize macroinvertebrates directly through consumption in the fall or indirectly by subsidizing macroinvertebrate food sources through salmon-derived nutrient retention year round. Through benthic disturbance, salmon can also dislodge macroinvertebrates during spawning. The effect of salmon will be specific to functional feeding groups.	2007 salmon density (kg/m^2)	Watershed	Enriched	Bilby et al. 1996, Chaloner et al. 2002
$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$	Biofilm and algal biomass	A food source for macroinvertebrates and exhibit a more depleted source of ^{15}N and ^{13}C compared to salmon.	Ash-free dry mass (mg/cm^2) & chlorophyll <i>a</i> ($\mu\text{g}/\text{cm}^2$)	Transect	Depleted	Cummins and Klug 1979, Sullivan 2013, Harding et al. 2014
$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$	Temperature	Temperature affects metabolic and growth rates, which can decrease the discrimination against heavy isotope uptake.	Maximum weekly average temperature ($^{\circ}\text{C}$)	Watershed	Enriched	Finlay 2001, Allan and Castillo 2007, Friberg et al. 2009
$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$	Watershed size	More resources for macroinvertebrates are available in larger more productive watersheds.	Watershed size PC 1	Watershed	Enriched	Harding et al. 2014
$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$	Flow	Higher flow leads to a smaller boundary layer, which reduces carbon and nitrogen stable isotopes in food sources.	Gradient degrees	Transect	Depleted	Finlay et al. 1999, Trudeau and Rasmussen 2003
$\delta^{15}\text{N}$	Alder	Leaves provide food for macroinvertebrates. Alders also fix atmospheric nitrogen and consequently have a $\delta^{15}\text{N}$ approaching 0.	Alder basal area (m^2)	Watershed	Depleted	Cummins et al. 1989, Richardson et al. 2004, Perakis et al. 2012
$\delta^{13}\text{C}$	pH	Streams in our study region have low pH (5.1–7.4). Carbon limitation increases with pH that leads to enrichment of ^{13}C in in situ macroinvertebrate food sources.	pH	Transect	Enriched	Hill and Middleton 2006

METHODS

Study sites

We surveyed 15 streams on the central coast of British Columbia, Canada within 45 km of the Heiltsuk First Nation community of Bella Bella ($52^{\circ}9' \text{ N}$, $128^{\circ}8' \text{ W}$) during the spring (May/June)

and fall (September/October) of 2008 (Fig. 1). This area is in the Wet Submaritime Coastal Western Hemlock Biogeoclimatic subzone, characterized by coniferous forests, nutrient-poor soils, heavy annual rainfall (3,000 mm in our study area), and a mean annual temperature of 5.5°C (Pojar et al. 1991, Price et al. 2009). This is a

Table 2. Hypotheses for salmon and habitat variables for invertebrate biomass.

Variable	Mechanism	Metric	Level	Response	Reference
Salmon	Nutrients from salmon can subsidize the invertebrate community but benthic disturbance during spawning can decrease total macroinvertebrate biomass	2006–2008 mean salmon density for biomass (kg/m ²)	Watershed	Positive in the spring, negative in the fall	Bilby et al. 1996, Chaloner et al. 2004, Moore et al. 2004, Moore and Schindler 2008
Biofilm and algal biomass	An important food source for macroinvertebrates	Ash-free dry mass (mg/cm ²) and chlorophyll <i>a</i> (µg/cm ²)	Transect	Positive	Cummins and Klug 1979
Temperature	Temperature affects metabolic rate and consequently growth rate.	Maximum weekly average temperature (°C)	Watershed	Positive	Friberg et al. 2009
Substrate size	Larger particles provide more stable habitat	Mean pebble size (cm)	Transect	Positive	Allan and Castillo 2007, Verspoor et al. 2011
Watershed size	More resources for macroinvertebrates in larger watersheds	Watershed size PC 1	Watershed	Positive	Lamberti and Steinman 1997
Alder	An important food source for macroinvertebrates.	Alder basal area (m ²)	Watershed	Positive	Cummins and Klug 1979, Richardson et al. 2004
pH	Streams in our study region have low pH (5.1–7.4).	pH	Watershed	Positive	Clenaghan et al. 1998
Nitrogen	Macroinvertebrate food sources have been shown to be nitrogen-limited	Dissolved inorganic nitrogen (µg/L)	Transect	Positive	Rosemond et al. 1993, Wipfli et al. 1998
Phosphorus	Macroinvertebrate food sources have been shown to be phosphorus-limited	Soluble reactive phosphorus (µg/L)	Transect	Positive	Rosemond et al. 1993, Wipfli et al. 1998, Verspoor et al. 2010

relatively pristine area of British Columbia (Green 2007). While selective logging took place throughout the twentieth century and resumed recently, there was no logging upstream of our study reaches during our study. Resident fish species include Coastrange (*Cottus aleuticus*) and Prickly (*C. asper*) sculpins, juvenile coho (*Oncorhynchus kisutch*) and limited numbers of Rainbow trout (*O. mykiss*) and Dolly Varden (*Salvelinus malma*). Chum (*O. keta*) and pink (*O. gorbuscha*) salmon are the dominant species of spawning salmon in these streams but there are also limited numbers of coho in all streams, and Chinook (*O. tshawytscha*) and sockeye (*O. nerka*) in some of the streams. Spawning occurs from late August to early November in densities

ranging from 0 to 6 kg of chum and pink salmon per m² in streams that range from 0.3 km to 5.8 km in spawning length and from 2.7 m to 23.5 m wide. Site-specific data are provided in Table 3.

In addition to spanning a natural gradient in salmon spawning densities, five of these streams also have a barrier to pink and chum migration (waterfall or log jam). We sampled the lower reaches of all streams, immediately upstream of the estuary ($n = 15$) and immediately upstream of the barrier when present ($n = 5$).

Salmon population estimates

Salmon population estimates were derived from stream and bank walks each fall in cooperation with Fisheries and Oceans Canada

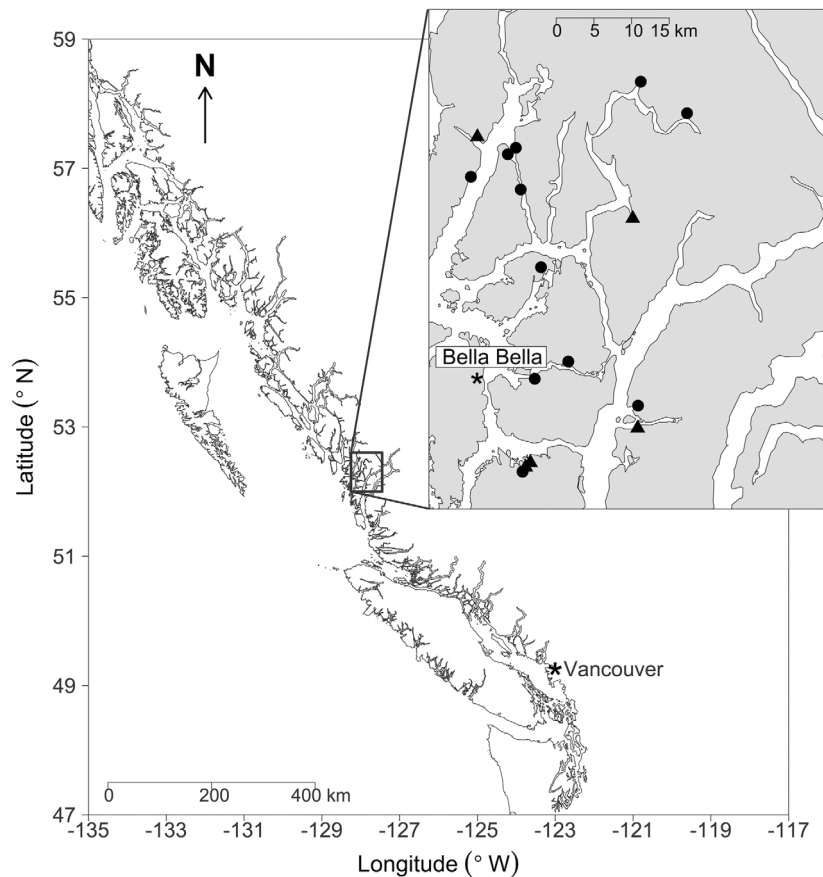


Fig. 1. Streams sampled in spring and fall 2008. Triangles denote streams with a barrier to pink and chum migration used in the within-stream comparison. Circles denote streams along the salmon density gradient used in the among-stream comparison, in conjunction with the five downstream sites from the within-stream comparison. The asterisks indicate the Heiltsuk First Nation village of Bella Bella and Vancouver, British Columbia.

(DFO), the Heiltsuk First Nation and field crews from Simon Fraser University. Hocking and Reynolds (2011) provide a detailed summary. Pink and chum salmon accounted for 90–100% of the Pacific salmon in each stream. We therefore calculated salmon density metrics based on pink and chum abundance that were deemed biologically relevant to assess both salmon as a subsidy and as a source of disturbance. Single- and multiple-year density mean pink + chum mass per unit area for 2006, 2007, 2008 and 2006–2008 were calculated using the following formula,

$$D = \frac{\sum \frac{B_i}{L \times W}}{n}$$

where D is the mass of salmon by unit area, B is the total mass of pink and chum in year i based on mean regional measurements, L is the spawning length (portion of stream where salmon spawning occurs), W is the mean bank-full width based on 12 or more measurements per site and n is the number of years used to calculate D (Verspoor et al. 2010, Harding et al. 2014). We also summed the contribution of salmon over a four-year period by negatively weighting salmon biomass from previous years as follows,

$$D' = \sum D_i \times e^{-\lambda t}$$

where D' is the four-year sum of salmon biomass per unit area, D as calculated in the above

Table 3. Site-specific information for upstream and downstream sampling locations within each stream. The 2007 salmon density was used in the invertebrate isotope analysis while the 2006–2008 mean salmon density was used in the invertebrate biomass density analysis.

Site	Stream location	Catchment area (km ²)	Bankfull width (m)	Spawning length (m)	Salmon density (kg/m ²)	
					2007	2006–2008
Ada	downstream	9.8	11.1	435	0	0.52
Ada	upstream	9.7	10.7	0	0	0
Beales Left	downstream	6.5	10.9	300	0.16	0.78
Bullock Main	downstream	3.3	10.9	622	0.67	0.75
Clatse	downstream	24.3	22.8	900	0.45	0.51
Clatse	upstream	23.9	17.8	0	0	0
Fannie Left	downstream	16.4	12.8	1500	0.20	0.22
Hooknose	downstream	14.8	16.9	1800	0.14	0.26
Jane	downstream	1.3	4.6	500	0	0.01
Jane	upstream	1.3	2.7	0	0	0
Kill Creek	downstream	0.5	3.5	453	1.07	0.51
Kunsoot Main	downstream	4.9	13.1	1280	0.46	0.26
Mosquito Bay Left	downstream	2.1	5.7	250	0.74	1.06
Neekas	downstream	16.0	17.7	2100	0.78	1.60
Neekas	upstream	10.8	12.8	0	0	0
Quartcha	downstream	29.4	21.7	5500	0.09	0.10
Roscoe Main	downstream	33.6	23.5	5800	0.23	0.31
Sagar	downstream	36.6	15.5	180	0.54	0.45
Sagar	upstream	36.6	13.6	0	0	0
Troupe North	downstream	1.6	4.4	332	0	0

equation, for a given year i , λ is the rate of biomass loss and t is time in months from fall 2008 ($t = 2, 6, 12$ and 24) (Verspoor et al. 2010, Harding et al. 2014). We then assessed the individual contribution of each salmon index to the variation in each of our response variables using hierarchical partitioning and Akaike Information Criterion corrected for small sample sizes (AICc) (Akaike 1974, MacNally 2006). Both methods concluded that the 2007 pink + chum biomass density (kg/m²) explained the most variation in invertebrate stable isotope ratios and the 2006–2008 mean kg of pink + chum per m² explained the most variation in our invertebrate biomass density data, which we therefore used in each respective analysis.

Environmental data collection

We prioritized three biotic and seven abiotic variables, in addition to salmon density, which are known to affect aquatic benthic invertebrate isotopes and biomass. These included: chlorophyll a and ash-free dry mass from rock biofilm samples, riparian alder basal area, stream temperature, pH, dissolved inorganic nitrogen and soluble reactive phosphorus, substratum size, gradient and watershed size. Hypotheses for each variable are listed in Tables 1 and 2. A brief

description of how each variable was sampled follows below; more detailed methods are in Harding et al. (2014). Briefly, 12 transects were assigned randomly to study reaches with lengths calculated based on bankfull width in each stream (Bain and Stevenson 1999). Chlorophyll a and ash-free dry mass were used as measures of algal and total biofilm biomass, respectively. Biofilm samples were collected from four cobble-sized rocks (secondary axis <256 mm) across the wetted-width of six transects per stream ($n = 24$ samples per stream per measure of biofilm biomass). Chlorophyll a (median = 0.54 $\mu\text{g}/\text{m}^2$, range = 0.06–8.56 $\mu\text{g}/\text{m}^2$) and ash-free dry mass (median = 1.05 mg/m^2 , range = 0.48–4.03 mg/m^2) were calculated from each sample following Steinman et al. (2007). Alder basal area was calculated from the diameter at breast height of each tree greater than 5 cm in diameter in six 35 m long by 10 m wide belt transects that extended perpendicular from each stream into the riparian zone (median = 0.64 m², range = 0–5.43 m²) (Hocking and Reynolds 2011). We measured stream temperature using waterproofed temperature loggers (iButtons DS1922L) anchored in each stream and set to record every 2 hours (median = 8.8°C, range = 7.0–10.2°C). The mean summer and fall pH were averaged from a

minimum of four spot measurements recorded each season using a YSI Model 63 multi-meter probe (median = 6.08, range = 5.12–7.41). Dissolved nutrients were assayed from water samples taken three months prior to and again following peak salmon spawning. Personnel at the Fisheries and Oceans Canada Cultus Lake Research Facility quantified soluble reactive phosphorus (SRP) (spring, median = 0.4 µg/L, range = below detection to 2.1 µg/L; fall, median = 6.4 µg/L, range = 0.5–244.6 µg/L) and total dissolved inorganic nitrogen (DIN) (spring, median = 17.5 µg/L, range = 4.3–113.4 µg/L; fall, median = 90.5 µg/L, range = 10.5–3,665.8 µg/L), measured separately as ammonium (NH₃⁺) and nitrate (NO₃[−]) following the American Public Health Association methods (APHA 1989). We followed the protocol established by Wolman (1954) to calculate the mean substratum size at each transect (median = 10.8 cm, range = 0.5–400 cm). In the absence of detailed flow data, we used mean gradient degrees measured at 10 transects using a clinometer, as a proxy for variation among streams in flow conditions (median = 1.7°, range = 0.8–4.7°). To quantify watershed size, we used the first principal components analysis axis of bankfull width (mean width of the stream at its highest point before breaching its banks), bankfull height (the mean maximum depth of the stream before breaching its banks), mean depth (mean stream depth measured on sampling dates), and watershed area (calculated from the Government of British Columbia's *iMapBC* website (Government of British Columbia, DataBC 2006, Hocking and Reynolds 2011). The first principal component accounted for 80% of the variation in these four variables, which all loaded positively (0.45–0.53) and were correlated with each other (correlation coefficients ≥ 0.6).

Invertebrate isotopes and biomass

Benthic invertebrates were collected twice from each upstream and downstream site (n = 20 sites); once in the spring prior to the arrival of salmon (May 29 to July 3, 2008) and again after peak salmon spawning in the fall (September 18 to October 28, 2008). We used a Surber sampler (500 µm mesh, metal frame area = 0.09 m²) and combined invertebrates from three riffle habitats within each of three randomly chosen transects

for a total of 120 samples. We disturbed the substrate to a depth of 7 cm for 2 min, excluding the time it took to scrub larger rocks. Samples were stored in 95% ethanol until further processing. Samples were split using a Folsom Plankton Splitter and identified to order to a count of 300 individuals or more. Total counts were calculated by adjusting the number of invertebrates counted by the proportion of the sample picked. We resorted 12 samples to ensure picking accuracy was greater than 90% and re-identified the invertebrates in each of the 12 samples to ensure identification accuracy was greater than 95%. Ephemeropterans, plecopterans, trichopterans and dipterans were further identified to family following Merritt et al. (2008). We broadly categorized each family into the dominant functional feeding group as identified by Merritt et al. (2008) (Table 4). Although a single invertebrate family often represents more than one functional feeding group, for the purpose of this paper we used the dominant feeding group to represent the entire family. For the purpose of our study we focused on grazers (scrapers), shredders, collector-gatherers and predators. The dominant families in each functional feeding group (by biomass) were Lepidostomatidae (Order Trichoptera, shredder, 59%), Heptageniidae (Order Ephemeroptera, grazer, 52%), Chironomidae (Order Diptera, collector-gatherer, 52%) and Chloroperlidae (Order Plecoptera, predator, 84%). When summed together, these four families comprised 67% of the total invertebrate biomass. Total biomass of each functional feeding group was calculated by site using the following equation:

$$B_{\text{FFG}} = \sum_{i=1}^n \frac{N_i \times \bar{m}_i}{A}$$

where B_{FFG} is the biomass of each functional feeding group, N is the adjusted number of individuals within a given family i , \bar{m} is the mean mass of family i , and A is the total stream bed area sampled.

A subset of the most common invertebrate families found in all watersheds was further identified to genus and used for isotope analysis (Table 4). Isotopes have been used in food web studies to infer diet and the assimilation of marine-derived nutrients (Spiller et al. 2010, Rinella et al. 2013, Harding and Reynolds

Table 4. Taxonomic breakdown of invertebrates included in the biomass analysis and isotope (*i*) analysis, including the functional feeding groups assigned based on Merritt et al. (2008).

Order	Family, subfamily or genus	Functional feeding group
Diptera	Ceratopogonidae	predator
	Chironomidae†	collector-gatherer
	Tanypodinae (i)	collector-gatherer
	Psychodidae	collector-gatherer
	Simuliidae	collector-gatherer
	Stratiomyidae	collector-gatherer
Ephemeroptera	Tipulidae	shredder
	Baetidae	grazer
	Ephemerellidae	collector-gatherer
	Heptageniidae†	grazer
	Cinygmula (i)	grazer
	Epeorus (i)	grazer
Plecoptera	Leptophlebiidae	collector-gatherer
	Capniidae	shredder
	Chloroperlidae†	predator
	Swelisa (i)	predator
	Leuctridae	shredder
	Nemouridae	shredder
Trichoptera	Zapada (i)	shredder
	Perlodidae	predator
	Taeniopterygidae	shredder
	Brachycentridae	collector-gatherer
	Glossosomatidae	grazer
	Hydropsychidae	collector-gatherer
	Hydroptilidae	grazer
	Lepidostomatidae†	shredder
	Lepidostoma (i)	shredder
	Limnephilidae	grazer
	Philopotamidae	collector-gatherer
	Polycentropodidae	collector-gatherer
	Rhyacophilidae	predator
	Rhyacophila (i)	predator
	Uenoidae	grazer

† Most common family, by biomass, in each order.

2014). There are natural differences between the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of salmon (12‰, −20‰; Harding et al. 2014) and terrestrial (2‰, −32‰; Hocking and Reynolds 2011) and freshwater sources (3‰, −27‰; Harding et al. 2014), which enable us to infer the contribution of salmon-derived nutrients to freshwater consumers. Ethanol has been shown to affect the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in certain tissue samples within days of preservation (Sarakinos et al. 2002, Sweeting et al. 2004, Ventura and Jeppesen 2009). In a study by Ventura and Jeppesen (2009) on freshwater invertebrates, there was no significant difference from the 1:1 line between control and preserved samples for $\delta^{15}\text{N}$ and a slightly non-significant difference from the 1:1 line for $\delta^{13}\text{C}$. A correction factor can be applied and is strongly recommended when reconstructing food webs with

samples preserved using different methods. We did not apply a correction factor in this case because (1) all of our samples were treated with the same technique, (2) isotopes were analyzed at minimum six months after preservation when any changes in isotopes would have stabilized and (3) if changes occurred to the $\delta^{13}\text{C}$ signature of preserved samples we would expect the effect of salmon to decrease with increasing spawner densities and thus equate to a more conservative effect of salmon in our study (Ventura and Jeppesen 2009). One to four individuals (2.0–3.0 mg) were dried at 60°C, and analyzed for nitrogen and carbon content by the University of California Davis Stable Isotope facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon, Cheshire, UK) (*n* = 140 in spring, 124 in fall). Stable isotopes are expressed as δ , which is the difference between the sample and a standard. Air and Vienna PeeDee Belemnite are the standards used for nitrogen and carbon, respectively. The difference is expressed as parts per thousand according to

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

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

Statistical analyses

Within streams: upstream versus downstream of salmon barriers.—Logjams and waterfalls were present in five of the 15 streams, which blocked pink and chum salmon migration. These sites provided us with the opportunity to compare stream sections with and without salmon, while controlling for watershed-specific characteristics. We assessed the difference between upstream and downstream sections by season using a two-way ANOVA with sampling location (upstream vs. downstream) and stream as factors, including their interaction. We then ran post-hoc Tukey HSD tests of significance to examine stream-level differences between upstream and downstream locations. We inspected our models visually to ensure they met the assumptions of linear regressions and we log transformed invertebrate biomass to satisfy assumptions of normality.

Comparisons among streams.—We compared the effect of salmon and several habitat variables on

invertebrate isotopes and biomass across the 15 streams that spanned a natural gradient in salmon density and habitat characteristics. We first checked for multicollinearity among all variables included in each analysis using variance inflation factors (VIF) and correlation coefficients (Zuur et al. 2010). A VIF score greater than 4 and a correlation coefficient greater than 0.7 were used to eliminate habitat variables considered to have a high degree of collinearity (Zuur et al. 2009). There was a high VIF score and degree of collinearity (0.8–0.9) between DIN, SRP, and salmon density in both seasons. We therefore excluded DIN and SRP from the final analyses. The remaining environmental variables did not significantly correlate with salmon density or each other. Finally, we inspected our models visually to ensure they met the assumptions of linear regressions. We log transformed invertebrate biomass and salmon density to satisfy assumptions of normality.

We generated a list of linear mixed effects models with stream as a random effect and all combinations of two or fewer predictor variables as fixed effects, excluding interactions (Harrell 2001). This generated 22 models for each season for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (model weights, $w_i = 8.23 \times 10^{-5}$ to 0.95) and 37 models for biomass ($w_i = 7.00 \times 10^{-4}$ to 0.14). In instances of lower top model weights and where additional predictors offered little additional information, we used multi-model inference, which helped to account for model uncertainty (Burnham and Anderson 2002, Arnold 2010, Grueber et al. 2011). This method gives less weight to parameter estimates that offer little information about the variance in the response variable (Grueber et al. 2011). We standardized the independent data to a mean of 0 and standard deviation of 2 so that effect sizes of independent variables could be compared (Grueber et al. 2011). Models with $\Delta\text{AICc} < 4$ were retained to form candidate model sets and were averaged using the natural method (Burnham and Anderson 2002, Grueber et al. 2011) in the MuMIn package in R (Barton 2012). We report the un-averaged standardized coefficients from the top model in cases where only one model had a ΔAICc less than 4 ($n = 2$). See Appendices A–C for a list of models used to average coefficients for each response variable. To evaluate the effect of salmon and habitat

variables on invertebrate isotopes and biomass among streams, we considered the magnitude and direction of the averaged coefficient, whether the 95% confidence intervals spanned zero, and the relative variable importance (RVI) of each variable. The latter is calculated as the sum of the model weights of all the models in the final confidence set in which the variable appears (Burnham and Anderson 2002). All analyses were performed in the open-source statistical software R (R Development Core Team 2011).

RESULTS

Within streams: upstream versus downstream of salmon barriers.—As predicted, invertebrates from sites downstream of the barriers had higher $\delta^{15}\text{N}$ than those from upstream sites in both seasons and this difference was more pronounced in the fall (spring, mean difference = 3.1‰, ANOVA, $F_{1,98} = 47.75$, $p < 0.0001$; fall, mean difference = 4.5‰, ANOVA, $F_{1,68} = 81.31$, $p < 0.0001$; Fig. 2A–H). These relationships also varied by functional feeding group. Predators downstream of the barriers in the fall had the most enriched $\delta^{15}\text{N}$ (mean ± 2 SD = 10.06‰ \pm 2.93‰; Fig. 2H), whereas the least enriched invertebrates were collector-gatherers upstream of the barriers in the spring (1.43‰ \pm 1.61‰; Fig. 2C). Similar relationships existed for $\delta^{13}\text{C}$, where invertebrates from downstream sites were more enriched than in sites upstream of the barriers, and this difference was also greater in the fall (spring, mean difference = 2.11‰, ANOVA, $F_{1,98} = 44.73$, $p < 0.0001$; fall, mean difference = 3.09‰, ANOVA, $F_{1,68} = 116.65$, $p < 0.0001$; Fig. 3A–H). Invertebrate biomass density (mg/m^2) was higher upstream of the barriers in eight out of ten stream \times season combinations than downstream of the barrier. However, this difference was only statistically significant in the fall (ANOVA, stream, $F_{8,1943} = 2.47$, $p = 0.01$; location, $F_{1,1943} = 9.29$, $p = 0.002$; Fig. 4A, B).

Comparisons among streams.—The $\delta^{15}\text{N}$ of invertebrates increased with salmon density from the previous spawning year; $\delta^{15}\text{N}$ of shredders and predators became more enriched with salmon density in both seasons, while salmon density had the greatest positive effect on grazers and collector-gatherers $\delta^{15}\text{N}$ in the fall (Fig. 5A, B

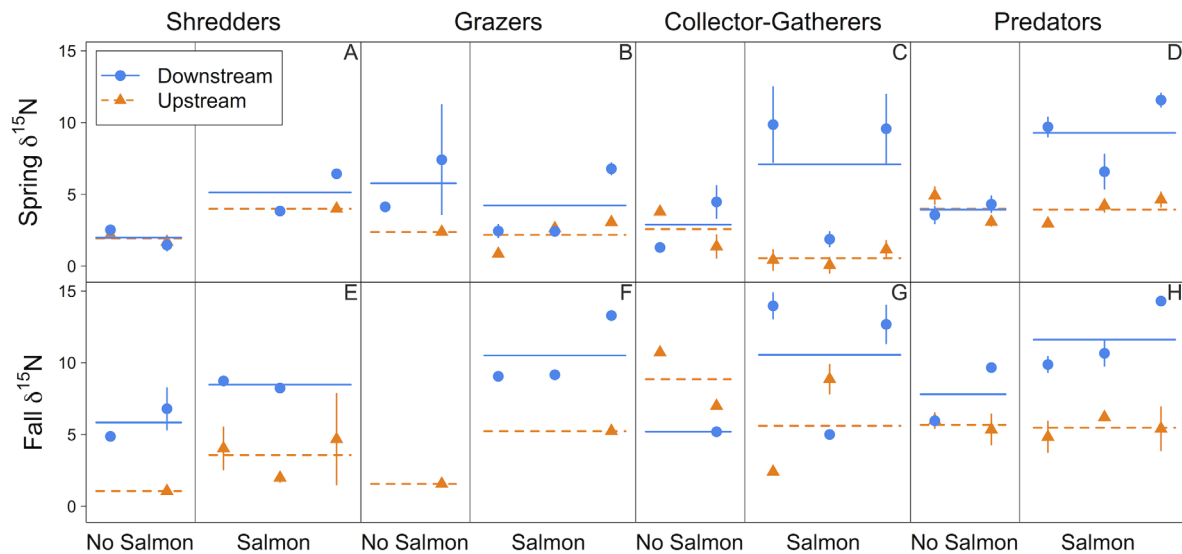


Fig. 2. Mean downstream (blue circles) and upstream (orange triangles) $\delta^{15}\text{N}$ of spring (A) shredders, (B) grazers, (C) collector-gatherers and (D) predators and fall (E) shredders, (F) grazers, (G) collector-gatherers and (H) predators with 95% confidence intervals for the within-stream comparison. “No Salmon” indicates the two streams that did not have salmon downstream of the barrier in the previous fall, while “Salmon” indicates the remaining three sites that did. The solid blue lines are the mean downstream $\delta^{15}\text{N}$ and dashed orange lines are the mean upstream $\delta^{15}\text{N}$ for a given functional feeding group.

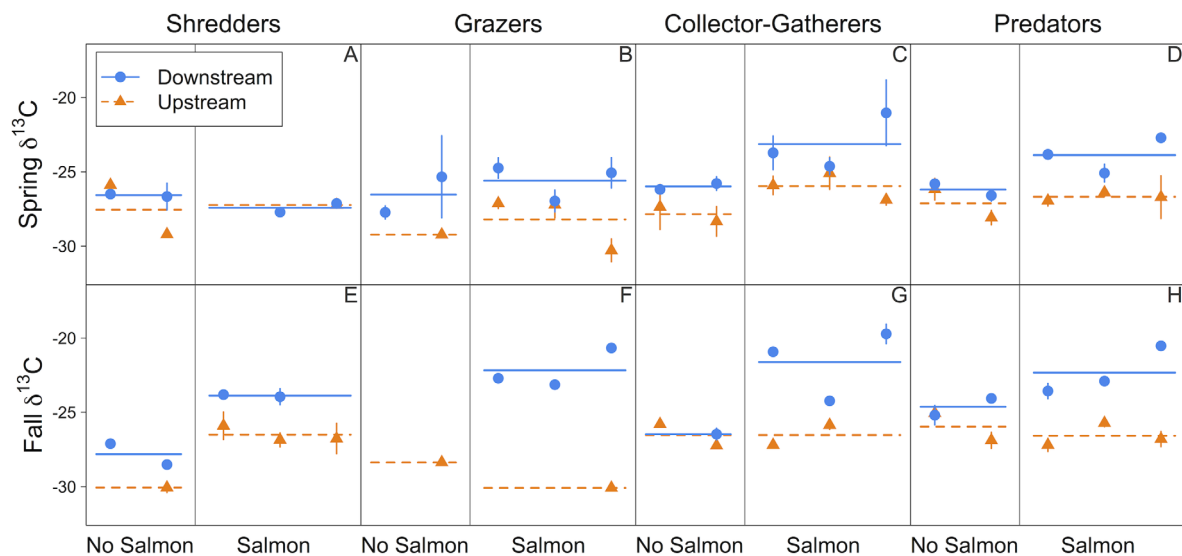


Fig. 3. Mean downstream (blue circles) and upstream (orange triangles) $\delta^{13}\text{C}$ of spring (A) shredders, (B) grazers, (C) collector-gatherers and (D) predators and fall (E) shredders, (F) grazers, (G) collector-gatherers and (H) predators with 95% confidence intervals for the within-stream comparison. “No Salmon” indicates the two sites that did not have salmon downstream of the barrier in the previous fall, while “Salmon” indicates the remaining three sites that did. The solid blue lines are the mean downstream $\delta^{13}\text{C}$ and dashed orange lines are the mean upstream $\delta^{13}\text{C}$ for a given functional feeding group.

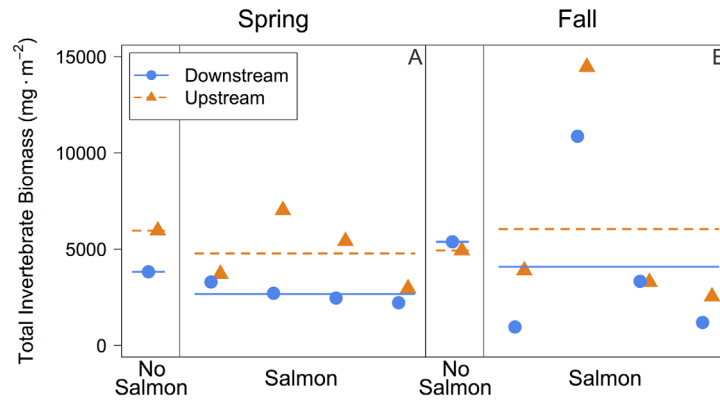


Fig. 4. Total downstream (blue circles) and upstream (orange triangles) spring (A) and fall (B) invertebrate biomass for the within-stream comparison. “No Salmon” indicates the site that did not have salmon downstream of the barrier in the previous fall, while “Salmon” indicates the remaining four sites that did. The solid blue lines are the mean total invertebrate biomass downstream of the barriers while the dashed orange lines are the total biomass upstream of the barriers.

and Fig. 6A–D). The $\delta^{15}\text{N}$ of shredders and predators became more enriched with increasing watershed size in the fall but had the opposite effect on grazer $\delta^{15}\text{N}$ in both seasons (Fig. 6A, B, D). Contrary to our prediction, $\delta^{15}\text{N}$

became more depleted in grazers and predators with increasing stream temperature in the fall (Fig. 6B, D).

Invertebrate $\delta^{13}\text{C}$ became more enriched with salmon density and to a greater extent in fall

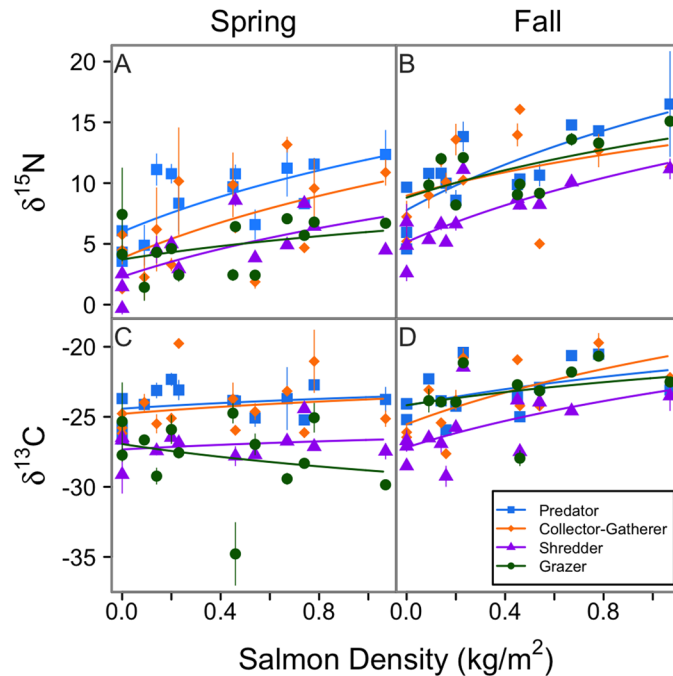


Fig. 5. Relationship between invertebrate spring (A) and fall (B) $\delta^{15}\text{N}$, spring (C) and fall (D) $\delta^{13}\text{C}$ and salmon density. Each data point represents a mean value for each stream with 95% confidence intervals and trend lines reflect the log-salmon density relationship modeled in the among-stream comparison.

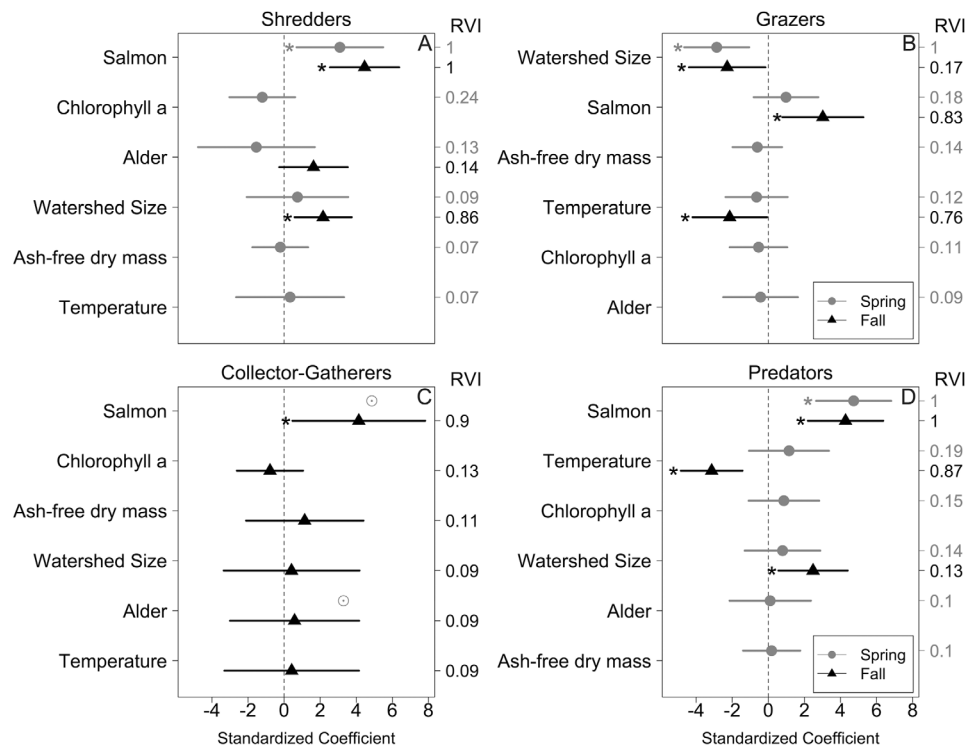


Fig. 6. Standardized coefficients for spring (grey circles) and fall (black triangles) $\delta^{15}\text{N}$ of (A) shredders, (B) grazers, (C) collector-gatherers and (D) predators and each predictor retained in the final confidence model set with $\Delta\text{AICc} < 4$. Results are from the among-stream analysis. The values on the right are the relative variable importance (RVI; colored by season), calculated as the sum of the model weights of all the models in the final confidence set in which the variable appears. The asterisk indicates where 95% confidence intervals do not cross zero. Because only a single model with $\Delta\text{AICc} < 4$ was returned for collector-gatherers in the spring, the unaveraged standardized coefficients are displayed (open circles).

when salmon were present (Fig. 5C, D). The greatest enrichment was in spring collector-gatherers and fall shredders (Fig. 7A, C). The variation in grazer $\delta^{13}\text{C}$ was not well explained by salmon in either season (Fig. 7B). As predicted, invertebrate $\delta^{13}\text{C}$ was most enriched in sites with larger watersheds but this depended on season and functional feeding group. Spring $\delta^{13}\text{C}$ of collector-gatherers and grazers and fall $\delta^{13}\text{C}$ of shredders were the most enriched in larger watersheds compared to other functional feeding group \times season combinations (Fig. 7A, B, C).

As predicted, spring total invertebrate biomass density was higher in warmer streams but generally declined with algal concentration, biofilm biomass and salmon density (Figs. 8 and 9). There were less definitive results for total

invertebrate biomass in fall but generally, invertebrate biomass density increased with the amount of alder in the riparian zone and declined with salmon density and biofilm biomass (Figs. 8 and 9). However, these variables were included in fewer models and their confidence intervals crossed zero to a greater extent than in the spring (Fig. 8).

DISCUSSION

This broad-scale study used a two-fold approach to test hypotheses about the effects of disturbance and resource pulses on stream consumers: the within-stream comparison isolated the effect of Pacific salmon on macroinvertebrates in a presence-absence comparison, and the among-stream approach assessed the consumer-

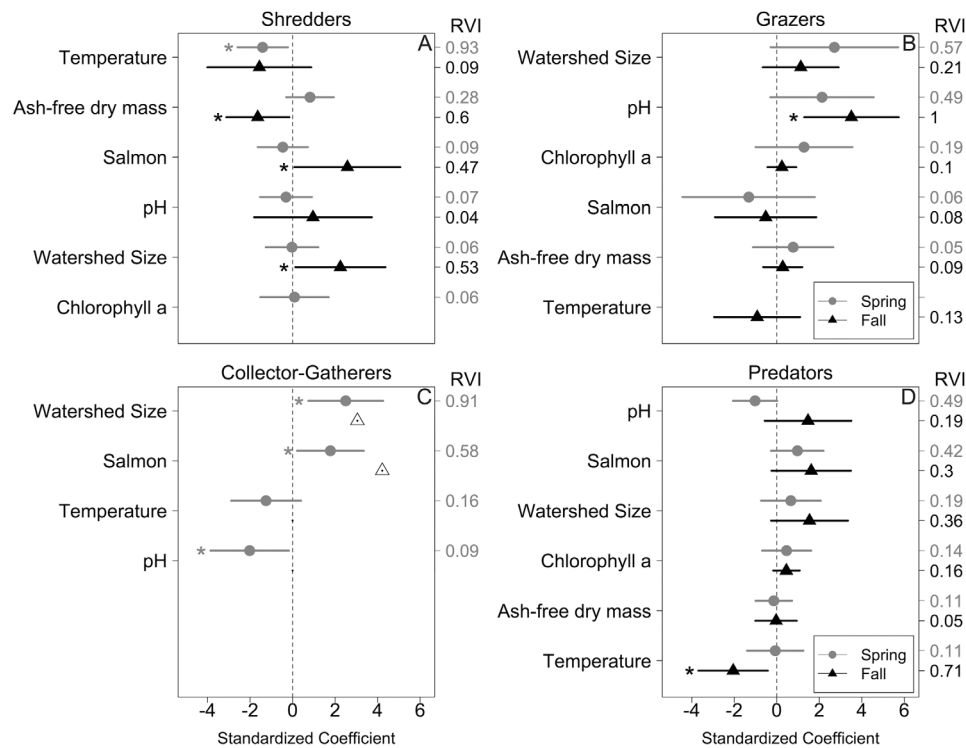


Fig. 7. The standardized coefficients for spring (grey circles) and fall (black triangles) $\delta^{13}\text{C}$ of (A) shredders, (B) grazers, (C) collector-gatherers and (D) predators and each predictor retained in the final confidence model set with $\Delta\text{AICc} < 4$. Results are from the among-stream analysis. The values below each predictor are the relative variable importance (RVI; colored by season) calculated as the sum of the model weights of all the models in the final confidence set in which the variable appears. The asterisk indicates where 95% confidence intervals do not cross zero. Because only a single model with $\Delta\text{AICc} < 4$ was returned for Collector-Gatherers in the fall, the unaveraged standardized coefficients are displayed (open triangles).

level response to salmon while accounting for habitat variation. It is not surprising that no single variable explained all of the variation in our 15-stream study; our results varied by season, functional feeding group, and stream.

As predicted, when we controlled for habitat in the within-stream comparison, we found that all four functional feeding groups of invertebrates had enriched $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures below spawning barriers compared to upstream, particularly in the fall when salmon were spawning. Also, $\delta^{15}\text{N}$ varied by functional feeding group, with predators having the most enriched signature followed by collector-gatherers, shredders and grazers. When we included habitat variation in the among-stream comparison we found that not only did invertebrates have enriched $\delta^{15}\text{N}$ and to a lesser extent $\delta^{13}\text{C}$ in

streams with higher salmon densities, but also in colder streams and in larger watersheds.

Invertebrate $\delta^{15}\text{N}$ increased with salmon density regardless of functional feeding group. This suggests that they assimilated salmon-derived nitrogen, whether by direct consumption of salmon tissue or indirectly through the consumption of enriched resources. Though for some functional feeding groups $\delta^{13}\text{C}$ increased with salmon density, predominantly in fall (i.e., the rate differed between spring and fall), suggesting a change in the abundance of each species and possibly a shift in diet between seasons. Harding et al. (2014) showed that biofilm in the same streams were enriched in both ^{15}N and ^{13}C in spring and fall, which was linked to salmon density. In combination with the current study, these results suggest that grazers were acquiring

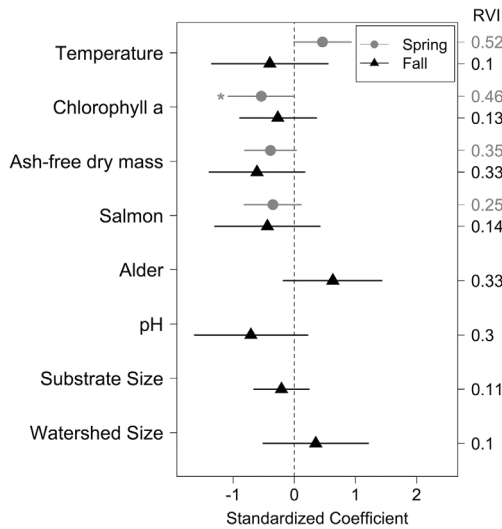


Fig. 8. The standardized coefficients for spring (grey circles) and fall (black triangles) invertebrate biomass and each predictor retained in the final confidence model set with $\Delta AIC_c < 4$. Results are from the among-stream analysis. The values on the right are the relative variable importance (RVI; colored by season) calculated as the sum of the model weights of all the models in the final confidence set in which the variable appears. The asterisk indicates where the 95% confidence interval does not cross zero.

salmon-derived nitrogen indirectly year-round by feeding on enriched biofilm, particularly in fall when salmon nutrients were readily taken up by biofilm (Bilby et al. 1996, Harding et al. 2014). Shredders were probably acquiring salmon-derived nitrogen indirectly through coarse particulate matter from enriched terrestrial sources dropping into streams or enriched riverine material. Riparian plants in this region are more enriched in ^{15}N and have higher percent nitrogen in streams with higher salmon densities (Hocking and Reynolds 2012). Predators could have also acquired salmon-derived nitrogen indirectly by preying on enriched invertebrates. Conversely, the fall $\delta^{15}\text{N}$ of collector-gatherers suggests that they were directly consuming salmon carcasses and switched to indirect sources of salmon-derived material in the spring.

Our results can be used to evaluate support for the two opposing hypotheses on the ecological roles of salmon in stream communities: subsidy vs. disturbance. We found that streams with

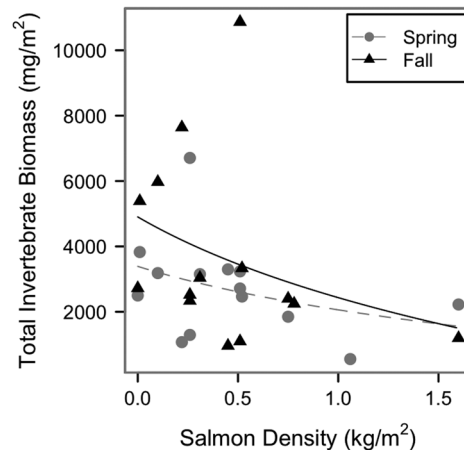


Fig. 9. Total spring (grey circles) and fall (black triangles) invertebrate biomass per unit area by salmon density. Each data point represents a single stream for a given season.

elevated salmon densities had fewer invertebrates in the spring and fall and that invertebrate biomass was higher upstream of salmon spawning barriers compared to downstream, regardless of season. These findings support the disturbance effect (Moore et al. 2004), whereby invertebrate biomass downstream of the barriers might not have had time to recover from spawning the previous fall. Moore and Schindler (2008) found that invertebrate dry mass did not fully recover shortly after spawning but returned to near normal levels the following year prior to spawning. The degree of recovery depended on the density of spawning salmon. Other studies have found that invertebrate richness and density recovered to pre-disturbance levels within 3 to 30 days depending on the frequency and nature of disturbance in the system (Boulton and Lake 1992, Matthaei et al. 1996). It is suggested that the availability of refugia is critical to invertebrate recovery time (Lake 2003). Refugia can include within-generation strategies such as moving to more suitable habitat (e.g., hyporheic zone) or between-generation strategies that involve complex life history adaptations (e.g., egg diapause) (Lake 2003). Without monitoring stream invertebrate populations over the late fall, winter and early spring, we cannot say for certain whether recovery of invertebrates to pre-spawning levels occurred prior to our sampling in May and June.

However, given previous work, it is possible that invertebrates in our system could have recovered to pre-spawning levels within seven months following spawning using either strategy or both. It would also be interesting for future research to test an alternative explanation for the higher density of invertebrates upstream of barriers to salmon: female invertebrates from downstream sections fly upstream (Macneale et al. 2004), and could provide an additional egg supply if salmon-derived nutrients increase female size and fecundity (Tylianakis et al. 2004, Fuller and Peckarsky 2011). However, in our case we do not believe female egg deposition from subsidized reaches were a major source of upstream invertebrate biomass because we did not see an increase in upstream invertebrate biomass per meter squared with downstream salmon density. It is also possible that salmon-derived nutrients elicit a trophic cascade (Polis et al. 1997), whereby stream invertebrates experience elevated predation pressure in the spring by abundant resident fish populations that are subsidized by salmon tissue and eggs the previous fall (Rinella et al. 2012, Swain et al. 2014). This scenario would also explain the negative correlation of invertebrate biomass density with algae and biofilm; depressed invertebrate grazer populations could release algae in the biofilm from grazing pressure (Harding et al. 2014). In combination or isolation, a salmon subsidy, benthic disturbance with slow invertebrate recovery or a trophic cascade could explain the decline in spring invertebrate biomass density, while substrate disturbance during spawning, as shown by others, would explain the decline observed in the fall (Moore et al. 2004, Tiegs et al. 2009, Holtgrieve and Schindler 2011).

While salmon density was an important predictor of invertebrate $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and biomass density, we found that differences in habitat among streams were also important in predicting isotopes and biomass. In cooler streams there were fewer invertebrates per unit area, with more enriched isotope ratios. Metabolism and tissue turnover rates are slower at lower temperatures, which could have led to less biomass and facilitated the retention of ^{15}N and ^{13}C (Rinella et al. 2013). Surprisingly, we found a decline in spring and fall invertebrate biomass density with biofilm and algal biomass. These results likely

reflect the correlation between the potential release from grazing pressure on in situ production caused either by a lack of invertebrate recovery due to benthic disturbance or increased predation pressure on invertebrates by subsidized fish populations. Invertebrates were also more enriched in ^{13}C in larger watersheds, which is consistent with findings from a previous study of biofilm (Harding et al. 2014). There may be a greater reliance on in situ production in larger streams, which have less canopy cover, greater irradiance and enriched $\delta^{13}\text{C}$ (Vannote et al. 1980, Finlay 2001). Larger habitats are also more productive (Lamberti and Steinman 1997), have longer food chains (Spencer and Warren 1996, Vander Zanden et al. 1999, Post et al. 2000) and higher species richness (Vander Zanden et al. 1999, Dodson et al. 2000). We might have therefore expected to see an increase in invertebrate biomass density with watershed size but we did not. By including habitat variables in our analyses, we were able to account for more of the variation in invertebrate isotopes and biomass than if salmon were considered alone.

In summary, we found that regardless of functional feeding group, benthic macroinvertebrate $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ increased with salmon density from the previous fall. While these larvae were directly and indirectly assimilating salmon-derived nitrogen and carbon, this did not translate into higher invertebrate biomass density in either season. If we only consider evidence from this study, it would appear that the disturbance role of spawning salmon prevails and exhibits a net negative effect on invertebrate biomass year round. However, this would imply that invertebrate biomass is decreasing continuously over time. If we consider previous studies in the area (Swain et al. 2014, Harding et al. 2014), salmon-derived nutrients could be subsidizing basal productivity and higher trophic levels, fueling stream communities from the bottom up, and the top-down, eliciting a trophic cascade and striking a balance between primary and secondary production. This would imply that salmon are both a source of limiting nutrients and disturbance at different times of the year.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Invertebrate $\delta^{15}\text{N}$ top models with $\Delta\text{AICc} < 4$ and the confidence set used for model averaging. k is the number of parameters in each model including the intercept and error terms, $\log\text{Lik}$ is the log-likelihood, ΔAICc is the difference between the top model AICc value and subsequent model AICc values and w_i is the model weight for each model.

Season	Functional feeding group	Model	k	$\log\text{Lik}$	ΔAICc	w_i
Spring	Shredders	Salmon	4	-39.71	0.00	0.33
		Salmon + Chlorophyll a	5	-38.49	1.06	0.19
		Salmon + Alder	5	-39.08	2.23	0.11
		Salmon + Watershed size	5	-39.51	3.10	0.07
		Salmon + Ash-free dry mass	5	-39.66	3.39	0.06
		Salmon + Temperature	5	-39.68	3.43	0.06
	Grazers	Watershed size	4	-56.26	0.00	0.33
		Watershed size + Salmon	5	-55.52	1.45	0.16
		Watershed size + Ash-free dry mass	5	-55.77	1.96	0.12
		Watershed size + Temperature	5	-55.88	2.18	0.11
		Watershed size + Chlorophyll a	5	-55.98	2.38	0.10
		Watershed size + Alder	5	-56.14	2.71	0.09
	Collector-gatherers	Salmon + Alder	5	-93.09	0.00	0.80
		Salmon	4	-127.96	0.00	0.33
	Predators	Salmon + Temperature	5	-127.29	1.09	0.19
		Salmon + Chlorophyll a	5	-127.55	1.61	0.15
		Salmon + Watershed Size	5	-127.61	1.74	0.14
		Salmon + Ash-free dry mass	5	-127.93	2.38	0.10
		Salmon + Alder	5	-127.96	2.42	0.10
		Salmon + Watershed Size	5	-56.91	0.00	0.68
Fall	Shredders	Salmon + Alder	5	-58.69	3.55	0.12
		Salmon + Temperature	5	-30.12	0.00	0.42
	Grazers	Salmon	4	-32.72	1.80	0.17
		Temperature + Watershed Size	5	-31.39	2.53	0.12
	Collector-gatherers	Salmon	4	-57.04	0.00	0.31
		Salmon + Chlorophyll a	5	-56.57	2.17	0.11
		Salmon + Ash-free dry mass	5	-56.75	2.52	0.09
		Salmon + Alder	5	-56.96	2.94	0.07
		Salmon + Temperature	5	-57.00	3.02	0.07
		Salmon + Watershed size	5	-57.00	3.03	0.07
	Predators	Salmon + Temperature	5	-82.67	0.00	0.84
		Salmon + Watershed Size	5	-84.61	3.88	0.12

APPENDIX B

Table B1. Invertebrate $\delta^{13}\text{C}$ top models with $\Delta\text{AICc} < 4$ and the confidence set used for model averaging. k is the number of parameters in each model including the intercept and error terms, $\log\text{Lik}$ is the log-likelihood, ΔAICc is the difference between the top model AICc value and subsequent model AICc values and w_i is the model weight for each model.

Season	Functional feeding group	Model	k	$\log\text{Lik}$	ΔAICc	w_i
Spring	Shredders	Temperature	4	-28.81	0.00	0.32
		Temperature + Ash-free dry mass	5	-27.31	0.49	0.25
		Temperature + Salmon	5	-28.40	2.67	0.08
		Temperature + pH	5	-28.62	3.12	0.07
		Temperature + Chlorophyll <i>a</i>	5	-28.80	3.48	0.06
		Temperature + Watershed size	5	-28.81	3.50	0.06
	Grazers	Watershed size + pH	5	-62.74	0.00	0.23
		Watershed size	4	-64.93	1.43	0.11
		pH	4	-65.27	2.10	0.08
		pH + Chlorophyll <i>a</i>	5	-64.25	3.01	0.05
		Watershed size + Chlorophyll <i>a</i>	5	-64.38	3.28	0.05
		Chlorophyll <i>a</i>	4	-65.91	3.38	0.04
	Collector-gatherers	Salmon	4	-65.92	3.41	0.04
		Watershed size + Ash-free dry mass	5	-64.60	3.72	0.04
		Watershed size + Salmon	5	-68.89	0.00	0.40
		Watershed size	4	-71.48	2.47	0.12
		Watershed size + Temperature	5	-70.18	2.58	0.11
		pH	4	-72.14	3.81	0.06
	Predators	pH	4	-93.62	0.00	0.15
		pH + Salmon	5	-92.71	0.62	0.11
		Salmon + Watershed size	5	-92.84	0.87	0.10
		Salmon	4	-94.22	1.19	0.08
		pH + Chlorophyll <i>a</i>	5	-93.48	2.15	0.05
		pH + Ash-free dry mass	5	-93.48	2.15	0.05
		pH + Temperature	5	-93.56	2.31	0.05
		Salmon + Chlorophyll <i>a</i>	5	-93.56	2.32	0.05
		pH + Watershed size	5	-93.58	2.35	0.05
		Watershed size	4	-95.00	2.76	0.04
		Chlorophyll <i>a</i>	4	-95.05	2.86	0.04
		Salmon + Temperature	5	-94.14	3.48	0.03
		Ash-free dry mass	4	-95.41	3.58	0.02
		Salmon + Ash-free dry mass	5	-94.22	3.62	0.02
		Temperature	4	-95.44	3.64	0.02
Fall	Shredders	Salmon + Watershed size	5	-53.70	0.00	0.25
		Ash-free dry mass + Watershed size	5	-53.96	0.53	0.19
		Ash-free dry mass	4	-55.92	1.69	0.11
		Ash-free dry mass + Salmon	5	-54.74	2.08	0.09
		Ash-free dry mass + Temperature	5	-54.92	2.45	0.07
		Salmon	4	-56.66	3.17	0.05
	Grazers	Ash-free dry mass + pH	5	-55.64	3.89	0.04
		pH	4	-28.72	0.00	0.35
		pH + Watershed size	5	-27.64	1.24	0.19
		pH + Temperature	5	-28.10	2.17	0.12
		pH + Chlorophyll <i>a</i>	5	-28.39	2.75	0.09
		pH + Ash-free dry mass	5	-28.49	2.95	0.08
	Collector-gatherers	pH + Salmon	5	-28.58	3.13	0.07
		Salmon + Watershed size	5	-38.26	0.00	0.96
	Predators	Salmon + Watershed size	5	-61.22	0.00	0.17
		Temperature	4	-62.60	0.18	0.15
		Temperature + Chlorophyll <i>a</i>	5	-61.43	0.43	0.14
		Temperature + Watershed size	5	-61.74	1.06	0.10
		Temperature + Salmon	5	-61.91	1.39	0.08
		Temperature + pH	5	-61.92	1.41	0.08
		Temperature + Ash-free dry mass	5	-62.60	2.76	0.04
		pH	4	-63.90	2.78	0.04
		pH + Watershed size	5	-62.68	2.93	0.04

APPENDIX C

Table C1. Invertebrate biomass top models with $\Delta\text{AICc} < 4$ and the confidence set used for model averaging. k is the number of parameters in each model including the intercept and error terms, $\log\text{Lik}$ is the log-likelihood, ΔAICc is the difference between the top model AICc value and subsequent model AICc values and w_i is the model weight for each model.

Season	Model	k	$\log\text{Lik}$	ΔAICc	w_i
Spring	Temperature + Chlorophyll a	5	-28.99	0.00	0.19
	Temperature + Ash-free dry mass	5	-29.44	0.91	0.12
	Salmon + Chlorophyll a	5	-30.19	2.40	0.06
	Salmon + Ash-free dry mass	5	-30.21	2.45	0.06
	Chlorophyll a	4	-31.59	2.57	0.05
	Ash-free dry mass	4	-31.68	2.74	0.05
	Salmon	4	-31.72	2.82	0.05
	Temperature	4	-32.17	3.73	0.03
Fall	pH + Alder	5	-48.88	0.00	0.10
	Ash-free dry mass	4	-50.59	0.81	0.07
	Alder + Ash-free dry mass	5	-49.31	0.86	0.06
	Alder	4	-50.95	1.54	0.05
	pH	4	-50.95	1.55	0.05
	Alder + Salmon	5	-49.86	1.97	0.04
	pH + Ash-free dry mass	5	-49.87	1.98	0.04
	Ash-free dry mass + Substrate size	5	-49.94	2.12	0.03
	pH + Temperature	5	-49.97	2.17	0.03
	Chlorophyll a	4	-51.37	2.38	0.03
	Salmon	4	-51.43	2.50	0.03
	Ash-free dry mass + Watershed size	5	-50.15	2.54	0.03
	Substrate size	4	-51.46	2.55	0.03
	Ash-free dry mass + Salmon	5	-50.23	2.70	0.03
	Alder + Chlorophyll a	5	-50.31	2.87	0.02
	Watershed size	4	-51.67	2.97	0.02
	Temperature	4	-51.73	3.09	0.02
	Ash-free dry mass + Temperature	5	-50.43	3.10	0.02
	pH + Watershed size	5	-50.52	3.28	0.02
	Alder + Substrate size	5	-50.56	3.35	0.02
	Ash-free dry mass + Chlorophyll a	5	-50.56	3.36	0.02
	pH + Chlorophyll a	5	-50.62	3.47	0.02
	pH + Substrate size	5	-50.63	3.49	0.02
	Chlorophyll a + Watershed size	5	-50.76	3.75	0.02
	Salmon + Temperature	5	-50.78	3.80	0.01
	Salmon + Chlorophyll a	5	-50.84	3.93	0.01