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ORIGINAL ARTICLE

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The ecology of terrestrial invertebrates on Pacific salmon carcasses

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Abstract In coastal streams throughout the north Pacific region, spawning salmon (*Oncorhynchus* spp.) subsidize terrestrial communities with their nutrients and carcasses. We document the previously unreported composition and ecology of terrestrial invertebrates using salmon carcasses in forest habitats from two high salmon density watersheds in coastal British Columbia. From experimental placement of 186 carcasses, terrestrial Diptera-dominated salmon carcass decay (85.5% of carcasses). Overall, we recorded over 60 species from salmon carcasses, including saprophagous Diptera and Coleoptera (15 spp.), dipteran predators (eight spp.) and parasitoids (four spp.), and opportunistic predators, scavengers, and detritivores (24 spp.). Using stable isotopes of nitrogen and carbon, we reconstruct the dietary niches of select species relative to salmon muscle tissue and previously sampled non-salmon feeding invertebrate species. From comparisons across seasons, sampling locations and larval and adult life stages, we find evidence for a diet of salmon tissue in flies (*Calliphora terraenovae* and *Dryomyza anilis*), and beetles (*Nicrophorus investigator* and *Anthobium fimetarium*). The parasitic wasps *Alysia alticola* and *Atractodes* sp. had the highest levels of enrichment of all species, representing their larval diet of fly larvae that have fed on salmon carcasses 1 year prior to adult wasp sampling. Temporal and spatial isotopic variation in insect indicator species varies by species mobility and the pathway of salmon nutrient uptake. Cataloguing these associations may be useful for developing indices of intact salmon runs, bear foraging, and subsequent nutrient transfer in coastal watersheds.

Keywords Salmon ecosystems · Stable isotopes · Invertebrate assemblage · Spatial and temporal variation · Ecological role

Introduction

Pacific salmon (*Oncorhynchus* spp.) attain the majority of their body mass feeding at sea and, as they return to spawn and die in freshwater habitats, their bodies subsidize terrestrial communities with marine-derived nutrients and energy (Bilby et al. 1996; Ben-David et al. 1998; Gende et al. 2002). In aquatic systems, the retention of salmon carcasses adds nitrogen, phosphorus, and other nutrients, a process that can initiate bottom-up food web effects (Wipfli et al. 1998; Zhang et al. 2003; Yanai and Kochi 2005). Live and dead salmon also support a diverse assemblage of terrestrial scavengers and predators (Reimchen 1994; Willson and Halupka 1995; Cederholm et al. 1999), although continued declines in salmon populations coast-wide threaten these salmon-dependent communities (Finney et al. 2000; Gresh et al. 2000; Stockner 2003).

Brown bear (*Ursus arctos*) and black bear (*Ursus americanus*) are important predators in salmon ecosystems and can transfer >50% of returning salmon biomass into adjacent forest habitats (Reimchen 2000; Gende and Quinn 2004). Based on tradeoffs of optimal foraging, bears will selectively feed on energy-rich portions of the salmon and distribute salmon carcasses to riparian areas in a fashion that is predicted by salmon spawning density, fish size, bear density, and habitat (Quinn and Kinnison 1999; Gende et al. 2001, 2004). Additional vectors of salmon carcasses include foraging by other vertebrates [e.g., river otters (*Lutra canadensis*)

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and wolves (*Canis lupus*)] and physical processes such as flooding (Ben-David et al. 1998).

The addition of salmon carcasses to terrestrial habitats can affect local ecosystem processes. For example, nutrient release from carcasses can influence plant growth and community structure (Wilkinson et al. 2005; Drake and Naiman 2007), while diet shifts to salmon in consumers can alter predator-prey dynamics (Darimont et al. 2008) and rates of detrital processing (Zhang et al. 2003). Terrestrial insect groups such as blowflies (Calliphoridae) and burying beetles (Silphidae) also increase processes of salmon decomposition and nutrient distribution in forest riparian zones (Jauquet et al. 2003; Meehan et al. 2005; Hocking and Reimchen 2006; Hocking et al. 2006). However, the complete composition and ecological role of terrestrial invertebrates using salmon carcasses is poorly known.

We surveyed terrestrial invertebrate use of natural and experimentally placed salmon carcasses in forest habitats on two remote streams on the central coast of British Columbia that support low human disturbance, high densities of spawning salmon and high total biomass of bear-transferred salmon carcasses (Hocking and Reimchen 2006). Our goals were to (1) assess the dominant consumers and principal ecological roles of invertebrates collected on salmon carcasses during autumn spawning, and (2) to test for potential seasonal and spatial variation in the patterns of salmon-nutrient uptake in this assemblage.

To quantify the ecological roles of terrestrial invertebrates, we use naturally occurring stable-isotope ratios (δ^{15}N and δ^{13}C) in select species. Stable-isotope analysis can quantify dietary variation, trophic structure, and sources of nutrients and energy in consumers (Kelly 2000; Post 2002; Vanderklift and Ponsard 2003), including invertebrates (Ponsard and Arditi 2000; Hocking and Reimchen 2002; Langellotto et al. 2006). An important consideration relates to tissue turnover and the seasonality of sampling, particularly when insect diets vary between larval and adult life stages (Tallamy and Pesek 1996). Isotope signatures in adult insects that indicate a salmon diet may be from a current diet of salmon or a larval diet from the previous year (Hocking et al. 2007). Further, differences in species mobility and pathway of salmon nutrient uptake may influence observed isotopic variation. We present new stable isotope findings in flies, parasitic wasps, and litter spiders where we test seasonal and spatial isotopic patterns, carcass-specific variation, and the legacy of a larval diet of salmon in adult individuals.

Materials and methods

Terrestrial invertebrate assemblage on salmon

In separate expeditions from 2000 to 2003, terrestrial invertebrates were surveyed from wildlife-transferred and experimental salmon carcass sites from two watersheds, the Clatse (52°20′15″ N; 127°50′23″ W) and Neekas (52°28′17″ N; 128°9′39″ W) rivers in coastal British Columbia, Canada. The climate of this region is cool and wet, with a mean annual temperature of ~8°C and annual precipitation ranging from 3,200 to 4,200 mm. Both watersheds occur in the Coastal Western Hemlock Biogeoclimatic Zone with forests dominated by Western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and Western red-cedar (*Thuja plicata*) (Green and Klinka 1994). Anadromous chum (*O. keta*) and pink (*O. gorbuscha*) salmon spawn from late August to early November within a 1-km (Clatse) or 2-km (Neekas) distance from the estuary that is terminated by an impassable waterfall. From 2000 to 2003, the average number of spawners (±STD) was 24,250 ± 12,685 pink salmon and 3,950 ± 1,666 chum salmon on the Clatse River and 43,625 ± 19,661 pink salmon and 28,750 ± 6,850 chum salmon on the Neekas River (NuSEDS: Department of Fisheries and Oceans data). From carcass surveys in 2001–2002 (Hocking and Reimchen 2006), black bears and wolves were estimated to transfer 4–6% of the pink salmon run and 16–48% of the chum salmon run into the forest riparian zone and leave >50% of this mass for invertebrate scavengers. This yields an estimated production of 21–42 million (Clatse) and 36–72 million (Neekas) fly larvae from salmon carcasses in each whole watershed (Hocking and Reimchen 2006).

In September of 2002, fresh and post-spawning chum and pink salmon carcasses with variable extent of carcass injuries (e.g., fresh whole fish, and head, brain, dorsal muscle and belly predation) were experimentally placed in the riparian zone within 100 m of the stream channel (Clatse $n = 90$; Neekas $n = 96$). Sites on the Clatse and Neekas Rivers included 36 fresh and 54 post-spawning carcasses (50 pink and 40 chum) and 20 fresh and 76 post-spawning carcasses (40 pink and 56 chum), respectively. The sequence of decay was followed for all carcasses and each were classified by their dominant (or co-dominant) consumer including: 1. Diptera; 2. Vertebrates; 3. Diptera and Vertebrates; or 4. Diptera and Coleoptera. We tested whether spawning condition or watershed influenced the dominant consumer of experimental salmon carcasses (Chi-square tests).

Over the duration of the study, invertebrates collected from salmon were classified according to their ecological role on the carcasses. This was based on field observations, literature sources (Anderson and Peck 1985; Borror et al. 1981; Furniss and Carolin 1977; Hatch 1953, 1957) and on taxonomic support provided by Dr. Monty Wood (Calliphoridae, Dryomyzidae, Drosophilidae), Dr. Steven Marshall (Sphaeroceridae), Dr. Graham Griffiths (Heleomyzidae), Dr. Andrew Bennett (Ichneumonidae), Dr. Henri Goulet (Braconidae), Dr. Matthew Buffington (Figitidae), Dr. Jan Klimaszewski (Staphylinidae), Dr. Stewart Peck (Leiodidae, Hydrophilidae), Dr. David Kavanaugh (Carabidae), Dr. Robb Bennett (Agelenidae) and Dr. Jan Addison (Enchytraeidae, Megascolecidae, Lumbricidae).

Niche variation during salmon spawning

Invertebrate diet was characterized in select species collected in September–October 2001–2003 from the Clatse and Neekas Rivers using stable isotope analysis (SIA) of δ^{15}N and δ^{13}C (Table 1). Whole invertebrate specimens were rinsed with distilled water, dried at 60°C for at least 48 h, and then ground into a fine homogeneous powder using a using a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Ill). Invertebrate subsamples (~1 mg) were assayed for total N, δ^{15}N, total C and δ^{13}C at the University of Saskatchewan Stable Isotope Facility using a Europa Scientific ANCA NT gas/solid/liquid preparation module coupled to a Europa Scientific Tracer 20/20 mass spectrometer. Isotopic signatures are expressed in delta notation (δ) as ratios relative to known isotopic standards of atmospheric N_2 and V-PDB carbon. This is expressed in 'parts per mil' (‰) according to:

$$\delta^{15}\mathrm{N} \text{ or } \delta^{13}\mathrm{C}(‰) = (\mathrm{R}_{\mathrm{sample}}/\mathrm{R}_{\mathrm{standard}} - 1) * 1000 \qquad (1)$$

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

We initially compared stable-isotope ratios in all carrion taxa collected in fall by species and by watershed of collection using analysis of variance (ANOVA) and non-parametric Kruskal–Wallis tests. Watershed variation (Clatse, Neekas) was observed to be minimal for both isotopes ($F_{1,168} < 0.7$, $P > 0.4$) and thus data were pooled across sites for further tests.

We determined guild placement of all salmon carrion species collected in the fall using a hierarchical cluster design of their stable-isotope ratios relative to chum and pink salmon muscle tissue and invertebrates from three terrestrial guilds. We used a single mean (±SE) for chum and pink salmon ($\delta^{15}\mathrm{N} = 12.68 \pm 0.38‰$; $\delta^{13}\mathrm{C} = -19.91 \pm 0.38‰$), which is comparable to other studies (Kaeriyama et al. 2004). Terrestrial guilds included litter-based Collembola (terrestrial detritivore) and *Cybaeus* spiders (terrestrial predator) collected in the fall of 2001 using pitfall traps (Christie et al. 2008), and carrion beetles (terrestrial scavenger: *Nicrophorus defodiens*) predicted to have a diet of shrews and songbirds (Hocking et al. 2007). Cluster classification was based on Euclidean distance from cluster centers using the within-groups linkage method. We chose five clusters (or guilds) as the most parsimonious based on standard distance coefficients in the hierarchical analysis (distance from four to five clusters = 1.010; distance from five to six clusters = 0.004).

We tested for evidence of current consumption of salmon from individual carcasses in fly and beetle larvae and adult Hymenoptera (*Alysia alticola* (Braconidae), *Atractodes* sp. (Ichneumonidae)) collected from separate carcasses (n = 3–4 carcasses; 4–6 individuals per carcass). For each guild, we used a single fixed-factor multivariate ANOVA to predict δ^{15}N and δ^{13}C isotopic variance by carcass of collection.

Seasonal and spatial analysis

Seasonal variation in the timing of invertebrate sampling is a consideration that may affect the isotope signatures of sampled taxa. In two separate years (2001, 2003), we surveyed dominant Diptera and Coleoptera from spring through to the fall in ground-level baited pitfall traps (2001: n = 6 traps) or hanging baited traps (2003: n = 10 traps) in sites below the falls within 20 m of the spawning channel on both the Clatse and Neekas Rivers. In 2001, traps were collected in spring (June), summer (late July and August) and fall (September, October). In 2003, collections were similar except they began earlier in spring (mid-May). We documented seasonal activity patterns of the dominant carrion species including the date of first and last capture. For the dominant Diptera (*Calliphora terraenovae* (Calliphoridae) and *Dryomyza anilis* (Dryomyzidae)), we examined isotopic (δ^{15}N or δ^{13}C) variation by season in separate analyses for individuals collected in 2001 (n = 49: Kruskal–Wallis tests) and 2003 (n = 224: ANOVA). In 2003, season, fly species, and watershed (Clatse, Neekas) were used in a three-way fixed-effect ANOVA of isotope variability. In a companion experiment starting in early October of 2000, we placed six post-spawning chum salmon carcasses in the riparian zone at each watershed. In June 2001, we collected fly pupae and pre-pupae of *C. terraenovae* and *D. anilis* from the soil at these carcass sites and reared them for up to a month until adult emergence. Emergent flies were not given an adult meal and instead immediately sacrificed for isotope analyses.

Spatial proximity to sites with high-density salmon spawning can predict the isotope signatures of sampled riparian consumers (Ben-David et al. 1998; Hocking and Reimchen 2002). We coupled both seasonal and spatial data to examine isotopic variability in two taxa with contrasting life-histories, the litter spider predators *Cybaeus* spp., and the blowfly *C. terraenovae*. *C. terraenovae* data was generated from hanging baited traps described above in 2003, including five traps located above the waterfall barrier to salmon on each watershed. In the spring and fall of 2001 we sampled *Cybaeus* spp. from a grid of passive pitfall traps in 10 × 10 m plots (nine traps per plot, three plots above falls, three plots below falls) within 20 m of the stream on each watershed. For each species, we tested isotope variability using a three-way fixed-effect ANOVA (fixed factors: season, location (above falls, below falls) and watershed (Clatse, Neekas)).

Sample treatment

In this dataset, we did not perform lipid extraction procedures as these can often lead to altered δ^{15}N values (Carabel et al. 2006). As an alternative, lipid normalization equations have been devised to standardize δ^{13}C values to a lipid content indicative of a protein metabolic pathway (Kiljunen et al. 2006). We performed a

Table 1 Terrestrial invertebrates collected from Pacific salmon carcasses on the Clatse and Neekas Rivers, British Columbia

Order	Family	Species	Ecological role
Diptera	Calliphoridae	*Calliphora terraenovae* Macquart	Saprophage
	Calliphoridae	*Lucilia illustris* Meigen	Saprophage
	Dryomyzidae	*Dryomyza anilis* Fallén	Saprophage
	Sphaeroceridae	*Terrilimosina pexa* Marshall	Saprophage
	Heleomyzidae	sp.1	Saprophage
	Phoridae	sp.1	Saprophage
	Muscidae	sp.1	Saprophage
	Muscidae	sp.2	Saprophage
	Drosophilidae	sp.1	Saprophage
	Tipulidae	Various	Unknown
Coleoptera	Silphidae	*Nicrophorus investigator* Zetterstedt	Saprophage/Dipteran predator
	Silphidae	*Necrophilus hydrophiloides* Guérin-Menéville	Saprophage
	Staphylinidae	*Anthobium fimetarium* Mannerheim	Saprophage
	Staphylinidae	*Tachinus maculicollis* Mäklin	Dipteran predator
	Staphylinidae	*Oxytelus niger* LeConte	Dipteran predator
	Staphylinidae	*Bisnius seigwaldi* Mannerheim	Dipteran predator
	Staphylinidae	*Atheta altaica* Bernhauer	Dipteran predator
	Staphylinidae	*A. hampshirensis* Bernhauer	Dipteran predator
	Staphylinidae	*Autalia truncatula* Casey	Dipteran predator
	Staphylinidae	*Oxypoda* sp.	Dipteran predator
	Leiodidae	*Catops basilaris* Say	Saprophage
	Leiodidae	*C. egenus* Horn	Saprophage
	Hydrophilidae	*Cercyon* sp.	Saprophage/Dipteran predator
	Carabidae	*Scaphinotus angusticollis*	Opportunistic predator
		Mannerheim	Opportunistic predator
	Carabidae	*Pterostichus crenicollis* LeConte	Opportunistic predator
	Carabidae	*P. amethystinus* Mannerheim	Opportunistic predator
	Carabidae	*Zacotus mathewsii* LeConte	Opportunistic predator
	Carabidae	*Diplous* sp.	Opportunistic predator
	Ptillidae	Various	Unknown
	Elateridae	sp.1	Unknown
	Dascillidae	sp.1	Unknown
Hymenoptera	Braconidae	*Alysia alticola* Ashmead	Dipteran parasitoid
	Braconidae	*Phenocarpa* sp.	Dipteran parasitoid
	Ichneumonidae	*Atractodes* sp.	Dipteran parasitoid
	Figitidae	*Trybliographa* sp.	Dipteran parasitoid
	Vespidae	sp.1	Opportunistic predator
	Formicidae	sp.1	Opportunistic predator
Microcoryphia	Machilidae	sp.1	Opportunistic predator
Grylloptera	Rhaphidiophoridae	sp.1	Opportunistic predator
Collembola	Tomoceridae	Various	Unknown
	Various	Various	Unknown
Diplura	Various	Various	Unknown
Diplopoda	Parajulidae	sp.1	Detritivore
Chilopoda	Cryptopidae	sp.1	Opportunistic predator
	Geophilidae	sp.1	Opportunistic predator
Araneae	Agelenidae	*Cybaeus reticulatus* Simon	Opportunistic predator
	Agelenidae	*C.eutypus* Chamberlin & Ivie	Opportunistic predator
	Antrodiaetidae	*Antrodiaetus pacificus* Simon	Opportunistic predator
Opiliones	Various	Various	Opportunistic predator
Pseudoscorpiones	Various	Various	Opportunistic predator
Sarcoptiformes	Various	Various	Unknown
Parasitiformes	Parasitidae	Various	Dipteran predator
	Various	Various	Unknown
Isopoda	Oniscidae	sp.1	Detritivore
Systellommatophora	Haplotrematidae	*Haplotrema* spp.	Saprophage
	Arionidae	*Prophysaon* sp.	Saprophage
	Arionidae	*Ariolimax columbianus* Gould	Saprophage
Haplotaxida	Enchytraeidae	*Mesenchytraeus* sp.	Detritivore
	Megascolecidae	*Arctiostrotus perrieri* Benham	Detritivore
	Lumbricidae	*Dendrodrilus rubidus* Savigny	Detritivore

sensitivity analysis to determine the variation in percent lipid among species and the change in δ^{13}C with lipid normalization based on equations derived in McConnaughey and McRoy (1979). Most sampled species showed minimal change in δ^{13}C with lipid normalization (mean change in $\delta^{13}\mathrm{C} < 1‰$), and were not normalized.

Exceptions included fly larvae (−1.3‰), *Nicrophorus investigator* larvae (−2.3‰), *N. investigator* adults (−1.3‰), and *N. defodiens* adults (−1.3‰) owing to their higher lipid contents (34.7, 51.5, 32.3, and 34.6%, respectively). Lipid normalized δ^{13}C data from these species is thus presented. All analysis was conducted using SPSS version 11.0 (SPSS Inc., Chicago, USA).

Results

Terrestrial invertebrate assemblage on salmon

Sixty species of terrestrial invertebrates from 36 families and 17 orders were collected from salmon carcasses on the Clatse and Neekas Rivers, B.C. (Table 1). This assemblage was dominated by the Diptera (ten spp.), Coleoptera (21 spp.) and Hymenoptera (six spp.), and consisted of saprophagous Diptera and Coleoptera (15 spp.), dipteran predators (eight spp.) and parasitoids (four spp.), opportunistic predators and saprophages (19 spp.), detritivores (five spp.) and groups with unknown associations with salmon carrion (nine spp. or groups).

Saprophagous Diptera were the most consistently observed group on salmon carcasses and attracted an array of predators. From experimental carcasses, the Diptera were found to be at least a co-dominant consumer on 159 of 186 carcasses (85.5%) although there were differences in consumer dominance by watershed ($\chi^2_{3,186}$ = 80.2, $P < 0.001$). On the Clatse River, vertebrates wholly consumed 27 of 90 placed carcasses including a significantly greater proportion of fresh versus spawned-out fish ($\chi^2_{2,90}$ = 30.8, $P < 0.001$). On the Neekas River, none of the 96 placed carcasses were consumed by vertebrates. Two fly species, *Calliphora terraenovae* and *Dryomyza anilis*, dominated adult collections in the baited traps. The seasonality of *C. terraenovae* emergence began in mid-May (2003), while the earliest observed emergence for *D. anilis* occurred in late June (2001, 2003). Both species were active through to mid-October. Other collected Diptera from salmon included *Lucilia illustris* (Calliphoridae) and species in the Heleomyzidae, Muscidae, Phoridae Sphaeroceridae, and Drosophilidae. Four species of parasitic wasps from the Braconidae, Ichneumonidae, and Figitidae were documented ovipositing on fly larvae on salmon.

Coleoptera species collected from salmon carcasses included predaceous and saprophagous species in the Staphylinidae, Silphidae, Carabidae, Leiodidae, and Hydrophilidae. From seasonal baited traps, *Nicrophorus investigator* was observed to be active beginning in late June through mid-October while *Nicrophorus defodiens*, a non-salmon carrion species, was first collected in mid-May (2003) and last observed in the first week of September (2001). *N. investigator* was observed as a co-dominant consumer with the Diptera on 14 of the 96 experimental carcasses (14.6%) on the Neekas River, although none of the experimental carcasses on the Clatse River were colonized.

Many litter species were opportunistic scavengers, detritivores, or predators on salmon. Slugs and snails, including *Ariolimax*, *Haplotrema*, *Prophysaon* and *Vespericola*, were commonly collected from fresh carcasses. Millipedes (e.g., Parajulidae) and worms (e.g., Enchytraidae) were common detritivores found within the rich humus underneath carcasses. Other opportunistic predators and scavengers included ants (Formicidae), centipedes (e.g., Geophilidae), spiders (e.g., Agelenidae), bristletails (Machilidae), cave crickets (Rhaphidiophoridae), mites (e.g., Parasitiformes), and springtails (Collembola).

Niche variation during salmon spawning

Niche differentiation in the salmon carrion community was observed within and among species. Invertebrates collected in September and October from salmon carcasses in the Clatse and Neekas watersheds differed in their δ^{15}N and δ^{13}C isotope signatures (Kruskal–Wallis tests for δ^{15}N and δ^{13}C: all $\chi^2 > 55$, all $P < 0.001$) (Table 2). Individuals were classified within one of five guilds (hierarchical clusters) which we define as: 1. Terrestrial: high trophic level; 2. Terrestrial: low trophic level; 3. Marine: salmon saprophage; 4. Marine: dipteran predator or parasitoid; and 5. Transitional marine and terrestrial diet (Fig. 1a; Table 3).

The parasitic wasps *Alysia alticola* and *Atractodes* sp. had the highest isotope signatures of all species (δ^{15}N values 6‰ higher than salmon), and were classified as having a diet of fly larvae consuming salmon (cluster 4) or were transitional between marine and terrestrial food chains (cluster 5). δ^{15}N and δ^{13}C signatures in the parasitic wasps were strongly correlated (Fig. 1b; $R = 0.778$, $P < 0.001$), with no difference in the relationship between δ^{15}N by δ^{13}C by wasp species ($F_{1,36} < 0.5$, $P > 0.5$). δ^{15}N and δ^{13}C values for wasps also did not differ by their carcass of collection ($F_{3,18} < 0.5$, $P > 0.7$).

All fly larvae and beetle *N. investigator* larvae rearing on salmon were grouped in cluster 3, consistent with a salmon diet. Most *N. investigator* adults (85%) were also classified into cluster 3. In contrast to results for parasitic wasps, carcass of collection explained 67 to 94% of the variation in δ^{15}N and δ^{13}C in fly and beetle larvae (Fly larvae: $F_{3,14} > 9.5$, $P < 0.001$; *N. investigator* larvae: $F_{2,11} > 24$, $P < 0.001$). The staphylinid beetle *Anthobium fimetarium* had high but variable signatures within both marine and terrestrial food chains. In comparison, the staphylinid *Bisnius seigwaldi* had signatures indicating a terrestrial predatory diet (cluster 1) overlapping with previously sampled terrestrial species all classified within clusters 1 or 2.

Table 2 $\delta^{15}N$ and $\delta^{13}C$ stable-isotope signatures (±SE) in insect species collected from salmon carcasses in autumn from the Clatse and Neekas Rivers, BC

Species	Watershed	*n*	$\delta^{15}N$	$\delta^{13}C$
Alysia alticola Ashmead	Clatse	6	18.60 ± 0.71	−19.85 ± 0.84
	Neekas	21	18.76 ± 0.30	−20.00 ± 0.32
Atractodes sp.	Neekas	12	18.76 ± 0.39	−20.18 ± 0.30
Anthobium fimetarium Mannerheim	Neekas	3	17.04 ± 1.51	−22.50 ± 0.32
Fly larvae	Clatse	4	14.80 ± 0.17	−18.55 ± 0.24
	Neekas	24	15.06 ± 0.13	−17.25 ± 0.11
Nicrophorus investigator Zetterstedt larvae	Clatse	9	13.97 ± 0.38	−19.09 ± 0.21
	Neekas	5	12.95 ± 0.37	−19.59 ± 0.07
Nicrophorus investigator Zetterstedt adults	Clatse	5	13.12 ± 1.17	−21.07 ± 0.96
	Neekas	8	14.39 ± 0.44	−20.02 ± 0.43
Dryomyza anilis Fallén	Clatse	22	13.49 ± 0.22	−23.62 ± 0.23
	Neekas	10	14.85 ± 0.59	−22.40 ± 0.34
Calliphora terraenovae Macquart	Clatse	25	11.48 ± 0.42	−23.04 ± 0.20
	Neekas	21	11.16 ± 0.61	−23.95 ± 0.28
Bisnius seigwaldi Mannerheim	Neekas	3	11.75 ± 0.89	−26.94 ± 0.30
Salmon[a]	Clatse	12	12.68 ± 0.38	−19.91 ± 0.38
Nicrophorus defodiens Mannerheim	Clatse	50	8.02 ± 0.19	−23.61 ± 0.16
Cybaeus spp.	Clatse	12	9.85 ± 0.30	−24.77 ± 0.16
	Neekas	12	13.91 ± 0.58	−24.80 ± 0.25
Collembola	Clatse	2	4.60 ± 0.59	−26.04 ± 0.17
	Neekas	2	8.14 ± 0.10	−26.75 ± 0.10

For comparison, isotope signatures are presented for salmon muscle tissue and three terrestrial invertebrate guilds (carrion beetles: *Nicrophorus defodiens*, spider predators: *Cybaeus* spp., and litter detritivores: Collembola)

[a] Salmon muscle tissue = mean of chum (n = 6) and pink (n = 6) salmon

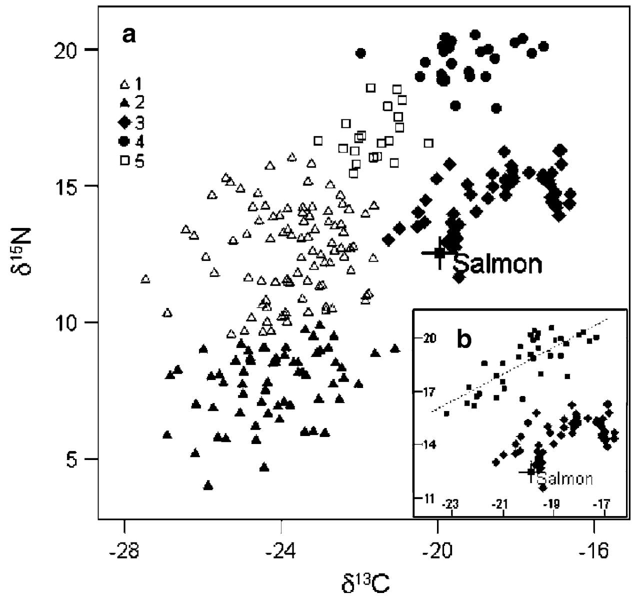

Fig. 1 **a** Hierarchical cluster classification of $\delta^{15}N$ and $\delta^{13}C$ stable-isotope signatures in insect species collected from salmon carcasses from the Clatse and Neekas Rivers, BC (see Table 3). Included are three invertebrate guilds collected in the fall but known previously to have terrestrial-based diets. Cluster membership includes: *1* Terrestrial: high trophic level (*open triangles*); *2* Terrestrial: low trophic level (*closed triangles*); *3* Marine: salmon saprophage (*closed diamonds*); *4* Marine: dipteran predator or parasitoid (*closed circles*); and *5* Transitional marine and terrestrial diet (*open squares*). **b** Correlation between $\delta^{15}N$ and $\delta^{13}C$ in the parasitic wasps *Alysia alticola* and *Atractodes* sp. (*closed squares*) (pooled data: $R = 0.778$, $P < 0.001$) predicted to have a larval diet of fly larvae that have fed on salmon (cluster 3). Shown for comparison is the isotopic signature of salmon muscle tissue (±SE)

Seasonal and spatial diet variation

$\delta^{15}N$ and $\delta^{13}C$ signatures in adult flies *C. terraenovae* and *D. anilis* varied by season of collection with the highest values observed in the spring, followed by individuals collected in the summer and fall (Fig. 2). Similar results were observed across 2 years. A seasonal decline in $\delta^{15}N$ and $\delta^{13}C$ was observed in 2001 (Kruskal–Wallis: all $\chi^2 > 4.6$, all $P < 0.031$), with the highest values observed in flies collected from salmon carcass sites in early spring and raised until adult emergence. In 2003, season was an important predictor of both $\delta^{15}N$ and $\delta^{13}C$ ($F_{2,219} > 27$, $P < 0.001$) with no significant variation observed between watersheds ($F_{1,219} < 2.2$, $P > 0.14$). Adult *D. anilis* had higher $\delta^{15}N$ ($F_{2,219} = 44.5$, $P < 0.001$), but not $\delta^{13}C$ ($P = 0.60$), than *C. terraenovae*. In the fall, adults of both fly species were largely classified into cluster 1, indicating a high trophic level terrestrial diet (Table 3).

Contrasting seasonal and spatial isotopic patterns were observed between two species with different life-histories, the litter spiders *Cybaeus* spp., and the blowflies *C. terraenovae* (Fig. 3). In *Cybaeus* spp., strong spatial variation but no seasonal variation in $\delta^{15}N$ was observed (watershed: $F_{1,86} = 77.2$, $P < 0.001$; falls: $F_{1,86} = 595.1$, $P < 0.001$; watershed*falls: $F_{1,86} = 63.8$, $P < 0.001$; season: $F_{1,86} = 1.7$, $P = 0.2$). $\delta^{13}C$ signatures in *Cybaeus* spp. showed no significant main effects (all $F_{1,86} < 2.2$, $P > 0.13$), but a significant season*falls interaction term ($F_{1,86} = 8.7$, $P = 0.004$). For *C. terraenovae*, no significant spatial variation in $\delta^{15}N$ or $\delta^{13}C$ was observed (watershed or falls $F_{1,128} < 2.3$, $P > 0.13$), but both $\delta^{15}N$ and $\delta^{13}C$ were more

Table 3 Individual cluster membership (1–5) from a hierarchical analysis of δ^{15}N and δ^{13}C stable-isotope signatures in insect species (a–i) collected from salmon carcasses from the Clatse and Neekas Rivers, BC (see Fig. 1a)

Species (total *N*)	1. Terrestrial: high trophic level	2. Terrestrial: low trophic level	3. Marine: salmon diet	4. Marine: diet of fly larvae on salmon	5. Transitional: marine + terrestrial
a. *Alysia alticola* (27)	1	0	0	18	8
b. *Atractodes* sp. (12)	0	0	0	8	4
c. *Anthobium fimetarium* (3)	1	0	0	1	1
d. Fly larvae (28)	0	0	28	0	0
e. *Nicrophorus investigator* larvae (14)	0	0	14	0	0
f. *Nicrophorus investigator* adults (13)	1	1	11	0	0
g. *Dryomyza anilis* (32)	27	0	0	0	5
h. *Calliphora terranovae* (46)	35	8	1	0	2
i. *Bisnius seigwaldi* (3)	3	0	0	0	0
j. *Nicrophorus defodiens* (50)	4	46	0	0	0
k. *Cybaeus* spp. (24)	19	5	0	0	0
l. Collembola (4)	0	4	0	0	0

Included are three invertebrate guilds (j,k,l) collected in the fall but known previously to have had terrestrial-based diets. Clusters 1 and 2 represent individuals with energy sources from the terrestrial food web. Clusters 3 and 4 indicate individuals with energy derived from salmon (3) or fly larvae consuming salmon (4). Cluster 5 indicates individuals with transitional isotope signatures from both marine (salmon) and terrestrial-based sources

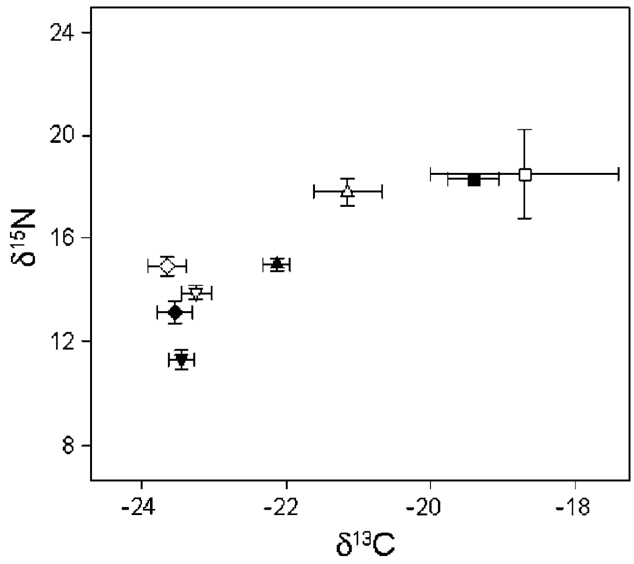

Fig. 2 Seasonal variation of δ^{15}N and δ^{13}C stable isotope signatures (±SE) in two species of flies *Calliphora terranovae* (Calliphoridae) (*filled symbols*) and *Dryomyza anilis* (Dryomyzidae) (*open symbols*) collected from the Clatse and Neekas Rivers, BC. Raised flies (*square symbols*) were collected as pupae from salmon carcass sites in early spring and reared to adult emergence in the lab. Remaining flies were caught using baited traps in May/June (spring: *triangles*), July/August (summer: *diamonds*) and when salmon return to spawn in September/October (fall: *upside-down triangles*). Data pooled across 2 years (2001, 2003) and two watersheds (Clatse, Neekas)

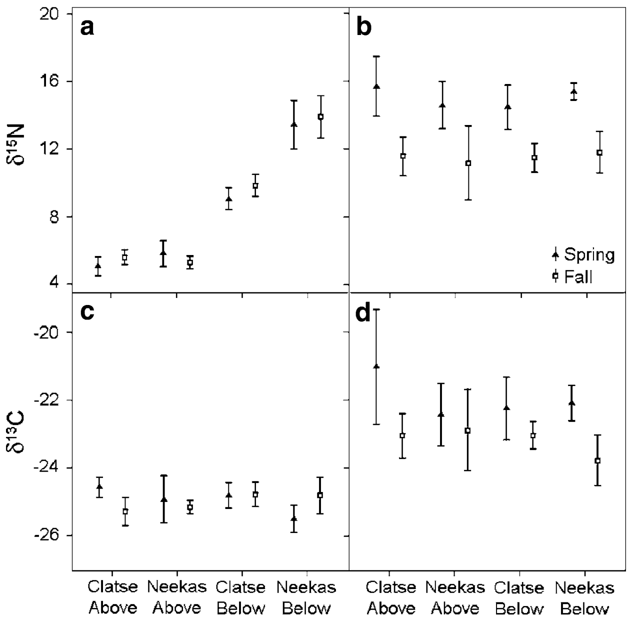

Fig. 3 Temporal and spatial variation in δ^{15}N and δ^{13}C stable-isotope signatures (±95% CI) in litter spiders (*Cybaeus* spp.) (**a**, **c**) and blowfly adults (*Calliphora terraenovae*) (**b**, **d**) collected in spring (*closed triangles*) and fall (*open squares*) from the Clatse and Neekas Rivers, BC. Samples were collected from both above and below waterfall barriers to salmon migration on each watershed within 20 m of the stream channel

enriched in the spring than the fall ($F_{1,128} > 11.2$, $P < 0.001$).

Discussion

Pacific salmon carcasses provide a predictable source of protein for hundreds of species throughout coastal areas of the North Pacific, with most research focusing on consumption of salmon by vertebrates or aquatic invertebrates (Bilby et al. 1996; Ben-David et al. 1997; Wipfli et al. 1998). In this study, over 60 terrestrial invertebrate species from 36 families were documented from salmon carcasses from two watersheds on the central coast of British Columbia with the highest abundance represented within the Diptera, Coleoptera, and Hymenoptera. Many species documented here have also been collected from salmon in watersheds from the

Queen Charlotte Islands (Reimchen 1994; Hocking et al. 2006), Vancouver Island (Reimchen et al. 2003) and Puget Sound (Jauquet et al. 2003). The Diptera, *C. terraenovae*, *D. anilis*, and *L. illustris*, have also been collected from salmon carcasses in Alaska (Meehan et al. 2005), emphasizing their widespread interaction with spawning salmon and their potential importance as a diet resource for further consumers.

Factors responsible for the dominance of flies, carrion beetles, or vertebrates on salmon carcasses likely relate to factors such as salmon spawning density, carcass energy density and size, and features of the environment such as stream habitat and ambient temperature (Reimchen 1994; Gende et al. 2001, 2004; Hocking et al. 2006). When salmon are abundant and accessible, bears can afford to be selective and will feed preferentially on the brain, eggs, and dorsal musculature (Reimchen 2000). In contrast, when salmon are scarce, vertebrates will consume a much larger proportion of individual carcasses. For example, the Neekas River supports higher chum salmon density than the Clatse River and provides higher access for vertebrates to flooded carcasses. In this study, vertebrates consumed none of the experimental carcasses at Neekas compared to 30% of experimental carcasses at Clatse. At Clatse, vertebrates also preferred fresh versus spawned-out fish indicating that carcass condition and energy density are important predictors of vertebrate scavenging (Gende et al. 2004). In the absence of vertebrate scavenging, the Calliphoridae are favored on large carcasses due to their high reproductive output, growth rates, and overall competitive ability, while other fly species are more competitive on smaller remnants (Hocking and Reimchen 2006).

Invertebrate species collected from salmon carrion are partitioned among ecological roles on the carcass including saprophages, dipteran predators and parasitoids, and opportunistic predators, scavengers, and detritivores from the terrestrial food web. Evidence for a diet of salmon or salmon consumers was found in larval flies and larval *N. investigator*, adult parasitic wasps *Alysia alticola* and *Atractodes* sp., and adult beetles *N. investigator* and *A. fimetarium*. In comparison, the staphylinid *B. siegwaldi* was classified as a terrestrial predator based on its stable–isotope composition and, along with groups such as spiders, millipedes, snails and carabid beetles, are likely to be opportunistic predators on the dipteran eggs and larvae or opportunistic scavengers on salmon tissues. The population-level consequences of potential reductions in salmon abundance for these opportunists remain unclear as the annual contribution of salmon to their diet is predicted to be small. For example, no seasonal isotopic variation was observed in the litter spiders *Cybaeus* spp.

In contrast to opportunist species, insects that breed directly on salmon carcasses are predicted to exhibit more seasonal variation in diet (and isotope signatures) comparable to that seen in bears, mustelids, and other vertebrates (Ben-David et al. 1997; Hilderbrand et al. 1999). We observed strong correlations between δ^{15}N and δ^{13}C in flies and parasitic wasps, with some individuals showing transitional isotope signatures (cluster 5) between marine and terrestrial food chains. We suggest that tissue δ^{15}N and δ^{13}C in individuals reared from salmon carcass sites will likely shift from marine to terrestrial signatures over time as adults feed on terrestrial sources. Seasonal shifts in isotope signatures in adult flies *C. terraenovae* and *D. anilis* provide evidence. High δ^{15}N and δ^{13}C values were observed in flies in the spring, with signatures declining through the summer and fall. This implies a legacy of a larval diet of salmon from the previous fall, similar to that observed in burying beetles (Hocking et al. 2007). Further, flies that were raised in our laboratory rearing experiment from pupae at salmon carcass sites and were processed upon emergence (and not given an adult meal) had the highest δ^{15}N and δ^{13}C. δ^{15}N signatures from these individuals may be higher than expected based on a 3‰ trophic shift from salmon because of an ontogenetic shift in δ^{15}N during Diptera metamorphosis (Tibbets et al. 2008).

Individual flies with relatively depleted isotope signatures were likely to have been raised on carrion from terrestrial-based sources such as mammals and birds with δ^{15}N and δ^{13}C ranging from 0 to 10‰ and −30 to −23‰, respectively, rather than salmon (Hocking et al. 2007). This may be particularly true in *C. terraenovae* as ~20 individuals had isotope signatures lower than 10‰ for δ^{15}N (and overlapping with the terrestrial carrion feeder *Nicrophorus defodiens*), while the lowest δ^{15}N signature observed in *D. anilis* across all seasons was 11.10‰.

Spatial variation in δ^{15}N and δ^{13}C is common in biota that feed across environmental gradients (e.g., Anderson and Polis 1998), although this was not observed for the Diptera presented here. Stable-isotope signatures in *C. terraenovae* did not differ from collections above versus below a waterfall barrier to salmon in both spring and fall on two watersheds. In contrast, the litter spider predators *Cybaeus* spp. showed strong spatial variation in δ^{15}N (none in δ^{13}C) and no seasonal variation in either isotope. These patterns highlight the different dispersal abilities and pathways of salmon nutrient uptake in these two consumers. *C. terraenovae* feed directly on salmon and can easily disperse along riparian corridors to alternate sites such as above the falls. In contrast, *Cybaeus* spp. have reduced mobility, do not feed extensively on salmon, and thus are site-specific indicators of the fertilization pathway of salmon-derived nitrogen in riparian zones (Ben-David et al. 1998; Hocking and Reimchen 2002).

The parasitic wasps *Alysia alticola* and *Atractodes* sp. had the highest isotope signatures of all species placing them at trophic positions 5.0–6.0 in the marine food chain (adult salmon are 3.0–4.0), comparable to that of sea lions and orca whales (Hobson et al. 1997; Pauly et al. 1998). Analyses of individuals collected from separate carcasses indicate that fly larvae have carcass-specific signatures, while parasitic wasps do not. This means that the high marine trophic positions of the parasitic wasps originated from their larval diet of flies from salmon carcasses the previous fall (1 year prior to sampling). As a whole, the life-history of these wasps is not well known, and it is possible that local populations extend diapause to time their emergence to the predictable and energy-rich pulse of fly larvae on salmon. This life-history strategy would involve trade-offs as increased diapause duration can reduce fitness (Ellers and van Alphen 2002).

Cataloguing invertebrate associations with salmon may be useful for developing indices of intact salmon runs, bear foraging, and subsequent nutrient transfer in coastal watersheds. Insects are commonly used as indicators (Spellerberg 1993; Rainio and Neimelä 2003), such as in forensic studies (Greenburg 1991). We show that species mobility and the pathway of salmon nutrient uptake influences both seasonal and spatial stable-isotopic patterns and is an important consideration for future analyses. The high marine trophic position of parasitic wasps illustrates their potential as ultimate indicators of salmon-forest nutrient transfers since they rely on larval Diptera that have fed on salmon. In turn, the abundance of the Diptera is directly dependent on the biomass of salmon carcasses transferred to the riparian zone (Hocking and Reimchen 2006), a process that varies with salmon spawning density and bear access to fish (Reimchen 2000; Gende et al. 2001, 2004). Declines in salmon populations may ultimately erode the complex freshwater and terrestrial food webs that act to couple marine and terrestrial ecosystems (Finney et al. 2000; Gresh et al. 2000; Stockner 2003, Christie and Reimchen 2008). Setting conservation targets for wild Pacific salmon that reduce these potential losses in biodiversity remains an important goal.

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