

Consumption and distribution of salmon (*Oncorhynchus* spp.) nutrients and energy by terrestrial flies

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Abstract: Anadromous Pacific salmon (*Oncorhynchus* spp.) subsidize terrestrial food webs with their nutrients and carcasses, a process driven largely by selective foraging by bears (*Ursus* spp.). We quantify wildlife transfer of salmon carcasses to riparian zones on two watersheds in coastal British Columbia and estimate total terrestrial fly production from remnant carcasses. Large-bodied chum salmon (*Oncorhynchus keta*) were transferred into the forest at a greater rate than were pink salmon (*Oncorhynchus gorbuscha*) (chum salmon mass = 6089–11 031 kg, 16%–48% of salmon run; pink salmon mass = 2266–2808 kg, 4%–6% of salmon run). Blow flies (genus *Calliphora*) and other Diptera dominated colonization (>90% of salmon carcasses). Between the two watersheds, 196 and 265 g of *Calliphora* larvae per metre of spawning length (4 and 7 million larvae for whole watersheds) were generated from salmon carcass transfer. Stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of spring-emerging adult *Calliphora* revealed that >80% of individuals had salmon-based signatures. Flies are a dominant consumer and vector of salmon nutrients in terrestrial habitats and supplement the diet of at least 16 vertebrate and 22 invertebrate species. Anticipated further declines of salmon in the North Pacific can be expected to further erode the complex associations coupling marine and terrestrial ecosystems.

Résumé : Les saumons du Pacifique (*Oncorhynchus* spp.) anadromes enrichissent les réseaux alimentaires terrestres avec leurs nutriments et leurs carcasses, un processus grandement contrôlé par l'alimentation sélective des ours (*Ursus* spp.). Nous mesurons le transfert par l'intermédiaire de la faune sauvage des carcasses de saumons aux zones de rivage dans deux bassins versants de la côte de la Colombie-Britannique et nous estimons la production totale de mouches terrestres dans les carcasses abandonnées. Le transfert des saumons kéta (*Oncorhynchus keta*) plus corpulents se fait à un rythme plus élevé que celui des saumons roses (*Oncorhynchus gorbuscha*) (masse des saumons kéta = 6089–11 031 kg; 16–48 % de la montaison; masse des saumons roses = 2266–2808 kg; 4–6 % de la montaison). Les mouches de la viande (le genre *Calliphora*) et les autres diptères sont les principaux colonisateurs des carcasses (>90 %) de saumons. Dans les deux bassins, respectivement 196 et 265 g de larves de *Calliphora* sont produits par mètre de longueur de frayère (4 et 7 millions de larves pour les bassins entiers) à la suite du transfert des carcasses de saumons. Une analyse des isotopes stables de $\delta^{15}\text{N}$ et de $\delta^{13}\text{C}$ faite sur les adultes de *Calliphora* qui émergent au printemps montre que >80 % des individus présentent des signatures associées aux saumons. Les mouches sont les plus grands consommateurs de nutriments de saumons et leurs vecteurs principaux vers les habitats terrestres; elles entrent dans le régime alimentaire d'au moins 16 espèces de vertébrés et 22 espèces d'invertébrés à titre de nourriture d'appoint. Les déclinés additionnels prévus chez les saumons du Pacifique Nord affaibliront encore plus les associations complexes qui relient les écosystèmes marins et terrestres.

[Traduit par la Rédaction]

Introduction

Every year throughout the North Pacific, millions of anadromous salmon (*Oncorhynchus* spp.) return to their natal watersheds to spawn and die (Cederholm et al. 2000; Gende et al. 2002; Stockner 2003). This reverse nutrient flow, from the sea to land, provides a dominant marine subsidy to aquatic and terrestrial systems and regulates the population

dynamics of many wildlife species (Reimchen 1994; Ben-David et al. 1997; Hilderbrand et al. 1999). Historical and continued declines in salmon spawning biomass because of overexploitation, habitat alteration, and climate change threaten salmon-dependent communities coast-wide (Gresh et al. 2000). However, the ecological context of many of these recently described marine–terrestrial associations remains poorly understood.

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Salmon nutrients are distributed from streams and lakes into terrestrial ecosystems mainly through wildlife foraging. Both brown (*Ursus arctos*) and black bears (*Ursus americanus*) consume and distribute salmon carcasses throughout coastal riparian zones of North America and often selectively feed on energy-rich portions of the salmon (Hilderbrand et al. 1999; Reimchen 2000; Gende et al. 2001). The extent of bear predation, carcass consumption, and transfer depends on many factors, the most critical being salmon spawning density, fish size, bear density, and attributes of the habitat that facilitate access (Quinn and Kinnison 1999; Gende and Quinn 2004; Gende et al. 2004a).

Salmon carcasses transferred to riparian areas are consumed by many terrestrial scavengers and saprophages. Previous studies have emphasized the dominant role of the Diptera, particularly blow flies (Calliphoridae), in salmon decomposition (Reimchen 1994; Jauquet et al. 2003; Meehan et al. 2005), although total nutrient flow from salmon into this group has not received much attention. At Bag Harbour, Haida Gwaii, ~4000 of 10 690 kg of salmon tissue transferred to the riparian zone by bears were consumed by fly maggots (Reimchen 1994). Large aggregations of dipteran larvae attract an array of insectivores (Cederholm et al. 2000), and the spring emergence of adult Diptera provides a potential food source for numerous consumers.

Herein, we quantify wildlife transfer of salmon carcasses on two watersheds in coastal British Columbia and estimate total terrestrial Diptera production from remnant carcasses. We compare salmon carcass transfer from two separate years to the department of Fisheries and Oceans Canada (DFO) salmon escapement counts and examine variation in rates of predation and transfer between the dominant salmon species *Oncorhynchus keta* (chum salmon) and *Oncorhynchus gorbuscha* (pink salmon). We further estimate the proportion of each transferred carcass consumed by terrestrial Diptera and the number and biomass of Diptera produced in each watershed. We focus on consumption by blow flies (genus *Calliphora*), although we derive estimates for all Diptera using ecological efficiencies of 10% and 20%.

Because salmon have high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures relative to most terrestrial sources, stable isotopes can be used to trace the fate of salmon nutrients and energy in terrestrial food chains (Bilby et al. 1996; Ben-David et al. 1998; Hocking and Reimchen 2002). Using stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, we assess the frequency of a larval salmon diet in recently emerged adult *Calliphora* as well as the potential for dispersal of flies with salmon signatures to more distant non-salmon habitats.

Materials and methods

Study sites

This study was conducted on two salmon-bearing watersheds, the Clatse (52°20'15"N, 127°50'23"W) and Neekas (52°28'17"N, 128°9'39"W) rivers, on the central coast of British Columbia, Canada. A 5–10 m waterfall truncates spawning at 0.9 km and 2.1 km upstream from the estuary on the Clatse and Neekas rivers, respectively. The climate of this region is cool and wet, with a mean annual temperature of ~8 °C and annual precipitation ranging from 3200 to 4200 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 redcedar (*Thuja plicata*) (Green and Klinka 1994; Hocking and Reimchen 2002).

Pink salmon and chum salmon spawn from late August to early November in both watersheds, with black bears and wolves (*Canis lupus*) as the dominant transfer vectors. From field counts, we estimate that 5 and 10 adult black bears were present on the Clatse and Neekas rivers, respectively, in both years. Wolves were present sporadically on the Clatse River in 2001 and on the Neekas River in both years. In 2002, a wolf pack (five adults and seven pups) established a home site in the Clatse estuary. Transfer by wolves was thus more prevalent in 2002 on the Clatse River, although even in this year the majority of salmon carcasses were transferred by bears (>90%). This was determined by the nature of carcass injuries. Wolf predation was defined by the consumption of the whole salmon head with the rest left untouched (Darimont et al. 2003; M. Hocking, unpublished data).

Salmon carcass transfer

In 2001 and 2002, we surveyed the Clatse (15–16 October 2001; 5–6 October 2002) and Neekas (both years: 11–12 October) rivers for salmon carcasses transferred into the forest by vertebrates. This period corresponds to near the end of the salmon run on both watersheds, and very few additional salmon are likely to return.

On the Clatse River, in both 2001 and 2002, 37 parallel belt transects (19 river left, 18 river right) 10 m wide and 100 m in length were used to enumerate pink salmon and chum salmon carcasses transferred into the forest. Transects were separated by 50 m starting from the estuary up to the base of the falls. Owing to a spawning length of 900 m, this method surveyed 20% of the watershed. Each transect was divided into four distance categories from the stream (0–5, 5–20, 20–50, and 50–100 m). Salmon carcasses were identified to species (chum, pink) and placed into one of several consumption categories: (i) full carcass; (ii) very minor carcass consumption (~95% of fish remains); (iii) minor carcass consumption (~80% of fish remains); (iv) major carcass consumption (~50% of fish remains); (v) nearing complete consumption (~20% of fish remains); and (vi) unknown consumption (i.e., skeleton; estimate ~50% of fish was consumed by vertebrate scavenger). Unidentifiable small carcass remnants (~5% of mass or less) were ignored.

On the Neekas River, we used the same transect and carcass classification methodology, except that transects were separated by 100 m rather than 50 m. In 2001, 33 transects (16 river left, 17 river right) were surveyed up to the base of the falls, and because of a spawning length of 2100 m, this method covered roughly 8% of the watershed. In 2002, 41 transects were surveyed (21 river left, 20 river right), with 10% watershed coverage. The 2001 and 2002 surveys differed in that transects in 2002 were extended through the spawning region in the upper estuary.

To estimate the mass of salmon transferred into the forest, full chum salmon and pink salmon carcasses of both sexes were weighed (Table 1). Pink salmon mass did not differ by watershed for either sex (males: $t_{28} = -0.32$, $p = 0.75$; females: $t_{31} = -1.80$, $p = 0.082$), and thus an aggregate mean

Table 1. Pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) mass (g) (± 1 standard deviation) for both males and females from the Clatse and Neekas rivers, British Columbia.

Watershed	Species	Sex	<i>n</i>	Mass (g)
Clatse	Pink	Male	4	1322.5 \pm 444.6
		Female	15	971.3 \pm 206.4
	Chum	Male	29	4596.6 \pm 999.1
		Female	15	3347.3 \pm 751.3
Neekas	Pink	Male	26	1384.0 \pm 347.2
		Female	18	1124.4 \pm 270.8
	Chum	Male	44	3788.6 \pm 1377.3
		Female	25	2784.8 \pm 810.1

of 1200 g was used. Male and female chum salmon were both larger at Clatse River compared with Neekas River (males: $t_{71} = 2.72$, $p = 0.008$; females: $t_{38} = 2.18$, $p = 0.035$), and thus aggregate means of 3972 and 3287 g were used for chum salmon at the Clatse and Neekas rivers, respectively. This assumes that the sex ratio of spawning salmon transferred into the forest was equal. Since there may be more transfer of males than females owing to their larger size (Reimchen 2000), our carcass mass estimates are likely conservative. Using these aggregate masses, we estimated the mass of salmon remaining after vertebrate foraging for each carcass category (Table 2). An estimate for salmon carcass transfer in the whole watershed was derived by multiplying by 5 on the Clatse River (transect coverage = 20%) and either by 12.7 or 10 on the Neekas River (transect coverage = 8% in 2001 and 10% in 2002). Transfer values were then compared with total salmon escapement determined by DFO (www-heb.pac.dfo-mpo.gc.ca/maps/maps-data_e.htm).

Watershed estimates for salmon transfer and vertebrate consumption were evaluated using two-way analysis of variance (ANOVA), with watershed and salmon species as fixed factors. The variable year (2001, 2002) represented independent replicates for all analyses. The interaction term watershed \times salmon species was removed from all tests. Within watersheds, and for each salmon species and year, salmon transfer values ($\text{kg}\cdot\text{m}^{-2}$) from forest transects were compared by distance category (0–5, 5–20, 20–50, and 50–100 m) using nonparametric Kruskal–Wallis tests.

Diptera consumption and production

From our carcass surveys on the Clatse and Neekas rivers in 2002, we recorded the percentage of carcasses transferred to the forest that showed signs of dipteran activity, including the presence of adults, larvae, or eggs. Observations only included carcasses transferred to the forest and did not include senescent carcasses flooded on the banks.

We investigated Diptera colonization and consumption of thirty-six experimentally placed carcasses in the fall of 2002 (Clatse $n = 16$; Neekas $n = 20$). We estimated the proportion of each salmon carcass consumed by Diptera and the number of blow fly maggots produced as a function of carcass mass. From 8–10 days after initial carcass placement, final instar *Calliphora* maggots were dispersing from these carcasses. At this time, the volume (mL) of *Calliphora* maggots produced from each carcass was estimated using a 30 mL measuring cup. The volume of other dipteran larvae was

visually estimated and likely encompassed the families Dryomyzidae, Heleomyzidae, Muscidae, and Sphaeroceridae. We also reweighed the carcass and determined the change in mass (Δ carcass mass) from initial placement.

To estimate the mass of each individual final instar *Calliphora*, we weighed 30 dispersing larvae from three separate carcasses. *Calliphora* larvae ranged substantially in mass within and between carcasses (overall range: 21.0–118.2 mg; carcass 1: 38.4 ± 11.6 mg (mean ± 1 standard deviation, SD); carcass 2: 49.3 ± 15.3 mg; carcass 3: 85.1 ± 11.2 mg), with an aggregate mean of 57.6 mg. In a separate test, we measured the length and width of 18 *Calliphora* larvae to estimate their volume (volume of cylinder was used), which was compared with measurements of their mass with a paired t test. No difference was observed between the two measurements (paired $t_{17} = 1.46$; $p = 0.164$), and thus we used an approximate mass to volume conversion of 1 g = 1 mL. From each carcass, the mass of *Calliphora* produced (g) is thus equal to the mL estimate, and the number of *Calliphora* produced is described by

$$(1) \quad \text{no. of } Calliphora = \frac{Calliphora \text{ volume (mL)} \times 1 \text{ mL}}{0.0576 \text{ g} \cdot \text{individual}^{-1}}$$

To estimate the number and mass of *Calliphora* produced in each watershed from the salmon carcass transfer data, regression equations were used to predict the proportion of the carcass consumed by all Diptera and the number of *Calliphora* produced as a function of Δ carcass mass. Logistic regression was used to predict proportion consumed by Diptera as a function of initial carcass mass ($F_{[1,34]} = 16.34$, $p = 0.0003$, $R^2 = 0.325$):

$$(2) \quad \ln \frac{Y}{1-Y} = -1.96 + 5.29^{-4} X$$

where Y equals proportion consumed by Diptera, and X equals initial carcass mass. Linear regression was then used to estimate the number of *Calliphora* larvae produced by Δ carcass mass. Two regression equations were generated using the minimum and maximum estimates of *Calliphora* volume produced from each carcass (*Calliphora* low (eq. 3a): $F_{[1,32]} = 77.7$, $p < 0.0001$, $R^2 = 0.708$; *Calliphora* high (eq. 3b): $F_{[1,32]} = 73.2$, $p < 0.0001$, $R^2 = 0.696$):

$$(3a) \quad Y = 224.02 + 2.16X$$

$$(3b) \quad Y = 312.12 + 2.45X$$

where Y equals number of *Calliphora*, and X equals Δ carcass mass. Estimates of mass remaining from carcass categories in carcass transfer data were then used to approximate the number of *Calliphora* produced from carcass transfer on the Clatse and Neekas rivers in 2001 and 2002 (Table 2).

To give an estimate for the average mass of dipteran larvae of all species dispersing from salmon carcasses, we set up a grid of pitfall traps in the fall of 2001 in 10 m \times 10 m plots (nine traps per plot) (Hocking and Reimchen 2002). Dipteran larvae varied widely in size, representing the diversity of species and stages consuming salmon. The wet mass of dipteran larvae from nine separate traps on the Neekas ($n = 6$ –41 maggots per trap) and seven separate traps on the

Table 2. Carcass categories (% vertebrate consumption) and number and mass (g) of *Calliphora* (Diptera: Calliphoridae) larvae produced from pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon carcasses transferred into the riparian zones of the Clatse and Neekas rivers, British Columbia, fall 2001–2002.

% vertebrate consumption	Average mass remaining (g)	Proportion consumed by Diptera	No. of <i>Calliphora</i> maggots produced	<i>Calliphora</i> mass produced (g)
Pink salmon				
0	1200	0.21	768–929	44.3–53.5
5	1140	0.21	728–883	42.0–50.9
20	960	0.19	618–758	35.6–43.7
50	600	0.16	434–550	25.0–31.7
80	240	0.14	296–393	17.0–22.6
Clatse River chum salmon				
0	3972	0.54	4818–5516	277.5–317.8
5	3773	0.51	4375–5014	252.0–288.8
20	3178	0.43	3181–3662	183.3–211.0
50	1986	0.29	1456–1708	83.9–98.4
80	794	0.18	527–655	30.4–37.8
Neekas River chum salmon				
0	3287	0.45	3384–3892	194.9–224.2
5	3123	0.42	3082–3550	177.5–204.5
20	2630	0.36	2278–2639	131.2–152.0
50	1644	0.25	1117–1324	64.4–76.3
80	657	0.17	460–580	26.5–33.4

Clatse ($n = 7$ –18 maggots per trap) rivers was determined to the nearest 0.1 mg. Mass estimates for each trap were then used to calculate a weighted mean mass of individual dipteran larvae caught in each watershed (Clatse $\bar{X} = 21.3$ mg; Neekas $\bar{X} = 22.9$ mg). These masses are lower than the mass estimate for individual *Calliphora* larvae of 57.6 mg.

We estimated the ecological efficiency of *Calliphora* produced from salmon carcasses transferred into the forest by dividing the mass of *Calliphora* produced by the total salmon mass available to invertebrate scavengers for each watershed, year and salmon species. Previous ecological efficiency estimates in the Diptera and other ectotherms have ranged from 7% to 26% (Slobodkin 1960; Putman 1978; Lawton 1981). Using literature values as a guide, we used ecological efficiencies of 10% and 20% to derive estimates of total dipteran larvae production from salmon carcasses that could include all dipteran families on salmon (including Calliphoridae, Dryomyzidae, Spherozeridae, Muscidae, Heleomyzidae, Drosophilidae, and Phoridae). There is often an ecological succession of dipteran species on carrion (Putman 1977), and our empirical observations of *Calliphora* production from salmon carcasses were made early in the decay sequence of the carcass, with an average reduction in mass of $57.9\% \pm 4.2\%$ and $21.5\% \pm 11.8\%$ (mean \pm standard error, SE) for chum and pink carcasses, respectively. This leaves a substantial mass remaining that is likely partially consumed by more *Calliphora* and other dipteran families. To calculate the number of dipteran larvae produced at these ecological efficiencies, we used the Clatse River mean (21.3 mg) or Neekas River mean (22.9 mg) masses estimated from all dispersing Diptera larvae caught in pitfall traps.

Calliphora and total Diptera production at the watershed level was evaluated using two-way ANOVAs with watershed

and salmon species as fixed factors. Upper and lower ranges for *Calliphora* production were averaged, with the variable year (2001, 2002) representing independent replicates for all analyses. The interaction term watershed \times salmon species was removed from all tests.

Many predators and parasitoids predate dipteran eggs and instars on the carcass as well as in their dispersing phase (Putman 1977; Ulrich 1999). From the Clatse and Neekas rivers, we enumerated all vertebrate and invertebrate species observed as predators or parasitoids of dipteran larvae on salmon carcasses. This included direct observations of foraging throughout the 2 years of the study and insect collections from the carcasses. Invertebrates were identified to family, vertebrates to species. We also calculated the number and biomass of adult Diptera emerging in the spring. We assumed a pattern of mortality comparable with that of Putman (1977) (66% mortality of larvae dispersing from carcasses and 30% pupal mortality).

Stable isotope analysis

Stable isotope analysis (SIA) of nitrogen (N) and carbon (C) was conducted on adult *Calliphora* collected in baited traps in May and June 2003. Because the tissues of recently emergent insects were expected to reflect their larval diet sources (Tallamy and Pesek 1996), isotope signatures of adult *Calliphora* were used to evaluate the frequency of a larval diet of salmon from both watersheds and to determine if salmon signatures could be found in individuals caught in non-salmon habitats (i.e., above falls). *Calliphora* specimens were caught in hanging traps placed within 10 m of the stream and baited with ~5 g of rotting beef.

Whole *Calliphora* were rinsed with distilled water and then dried at 60 °C for at least 48 h. Samples were ground into a homogeneous powder using a Wig-L-Bug

Table 3. Salmon escapement (Fisheries and Oceans Canada (DFO) counts) and vertebrate consumption and transfer of salmon carcasses from surveys of wildlife-transferred pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon carcasses on the Clatse and Neekas rivers, British Columbia.

	Clatse River		Neekas River	
	Pink	Chum	Pink	Chum
Salmon escapement (DFO counts)	32 068±9 995	3 150±1 626	57 868±3 016	24 500±7 778
No. of salmon transferred to forest	1 888±1 001	1 533±838	2 340±651	3 356±1 081
Biomass of salmon transferred to forest (kg)	2 266±1 201	6 089±3 329	2 808±781	11 031±3 553
Proportion of salmon run transferred	0.06±0.01	0.48±0.01	0.04±0.01	0.16±0.09
Transferred salmon mass (kg) consumed by vertebrates	897±412	2 969±1 397	1 018±358	4 506±900
Proportion of transferred salmon mass consumed by vertebrates	0.41±0.04	0.50±0.04	0.36±0.03	0.42±0.05
Biomass (kg·m ⁻¹) of salmon available for invertebrates*	1.52±0.88	3.47±2.14	0.85±0.20	3.11±1.27

Note: Data represent mean ±1 standard deviation of 2 years: 2001 and 2002.

*Biomass of transferred salmon remnants available for invertebrate consumption per metre of spawning length.

grinder (Crescent Dental Co., Chicago, Illinois). Samples (~1 mg) were assayed for total N, $\delta^{15}\text{N}$, total C, and $\delta^{13}\text{C}$ at the University of Saskatchewan Stable Isotope Facility by continuous-flow isotope ratio mass spectrometry. Natural abundances of ^{15}N and ^{13}C are given in parts per mil (‰) and are expressed by

$$(4) \quad [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where R is the ratio of $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. Isotopic standards include N_2 in air for N isotope analyses and Pee-Dee Belemnite limestone for C isotope analysis.

Calliphora $\delta^{13}\text{C}$ values were lipid-normalized based on equations derived from McConnaughey and McRoy (1979). This was done because there are large C isotope fractionation differences between proteins and lipids (Tieszen and Boutton 1988), and thus this analysis focuses primarily on diet-tissue fractionation from protein rather than lipid metabolism from the various carrion sources to adult *Calliphora*. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures were compared using two-way ANOVAs with watershed and within-watershed location (above and below waterfalls) as fixed factors.

Isotope signatures were examined relative to possible dietary sources, which include salmon and a variety of terrestrial carrion. The approximate isotopic signatures of pink and chum salmon muscle range from 11‰ to 14‰ for $\delta^{15}\text{N}$ and -22‰ to -18‰ for $\delta^{13}\text{C}$ (Welch and Parsons 1993; Kaeriyama et al. 2004), while terrestrial carrion such as deer and small mammals range from -1‰ to 11‰ for $\delta^{15}\text{N}$ and -30‰ to -21‰ for $\delta^{13}\text{C}$ (Ben-David et al. 1998; Hocking et al. 2006). DeNiro and Epstein (1978, 1981) observed diet-tissue fractionation values of 1.4‰ to 1.8‰ and -0.6‰ to -0.4‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, in *Calliphora* adults on different diets. For *Calliphora* feeding on a 100% salmon diet, $\delta^{15}\text{N}$ signatures may be 1‰–3‰ higher than salmon, while $\delta^{13}\text{C}$ values may be equal to or slightly lower than salmon. As such, we use a cutoff of 12‰ for $\delta^{15}\text{N}$ and -23‰ for $\delta^{13}\text{C}$ as our minimum salmon value.

Results

Salmon carcass transfer

The total transfer of chum salmon generally exceeded that of pink salmon, as chum salmon were transferred much more readily relative to their availability in the stream (16%–48% of chum; 4%–6% of pink; $F_{[1,5]} = 12.9$, $p =$

0.016, $R^2 = 0.720$; Table 3). Both pink and chum salmon showed higher escapement on the Neekas River relative to the Clatse River ($F_{[1,5]} = 30.5$, $p = 0.003$, $R^2 = 0.859$), with pink salmon more abundant than chum salmon on both watersheds ($F_{[1,5]} = 53.3$, $p = 0.001$, $R^2 = 0.914$). Both the total salmon mass (kg) and the proportion of available salmon mass consumed by vertebrates was higher for chum salmon compared with pink salmon ($F_{[1,5]} > 7.8$, $p < 0.038$, $R^2 > 0.612$). Of salmon carcasses transferred into the forest, vertebrate consumption varied from 36% to 41% and from 42% to 50% of the available pink and chum salmon mass, respectively, with total consumption ranging from 897 kg for pink salmon on Clatse River to 4506 kg for chum salmon on Neekas River. Averaged across the length of spawning, the mass of salmon remnants in the forest available for invertebrate consumption varied from 0.85 to 1.52 kg·m⁻¹ for pink salmon and from 3.11 to 3.47 kg·m⁻¹ for chum salmon, depending on watershed.

The biomass (kg·m⁻²) of pink and chum salmon carcasses transferred to the forest was highest within 5 m of the river edge and decreased with increasing distance from the river in both years and on both watersheds (Fig. 1; all $\chi^2_3 > 8.77$; all $p < 0.001$, except for Clatse River 2001 chum salmon, where $p = 0.032$). Highest transfer of pink salmon occurred on the Clatse River in 2001, while chum salmon transfer was highest in 2002 on both watersheds.

Diptera consumption and production

Calliphora and other Diptera were observed as dominant carcass consumers on virtually all naturally occurring and experimentally placed carcasses on the forest floor. From forest-carcass surveys in 2002, 91.7% of carcasses at Clatse River and 94.7% of carcasses at Neekas River showed signs of dipteran activity, including the presence of adults, eggs, or larvae. Carcasses with no activity were mainly small salmon remnants rather than large carcasses. *Calliphora* colonized 94% of experimentally placed carcasses with 100% of these carcasses colonized by the Diptera as a whole.

Calliphora larvae production from experimentally placed carcasses averaged 311.1 ± 48.3 g·carcass⁻¹ (5413 ± 840 individuals) and was strongly predicted by the initial size of the carcass ($F_{[1,34]} = 39.32$, $p < 0.001$, $R^2 = 0.536$). Each *Calliphora* larva consumed an average of 0.70–0.76 g of carcass material (wet mass). This corresponds to an average ecological efficiency of 5.9% ± 2.9% for pink and 7.9% ±

Fig. 1. Average mass ($\text{kg}\cdot\text{m}^{-2}$) (\pm standard error) of (a) pink salmon (*Oncorhynchus gorbuscha*) and (b) chum salmon (*Oncorhynchus keta*) naturally transferred into the riparian forest of the Clatse and Neekas rivers, British Columbia, in 2001–2002. Measurements are derived from carcass surveys on 5 m \times 100 m belt transects perpendicular to the stream and further separated into four distance categories: 0–5 m, solid squares; 5–20 m, open squares; 20–50 m, solid triangles; 50–100 m, open triangles. Numbers below data equal the total number of enumerated carcasses. n = number of transects.

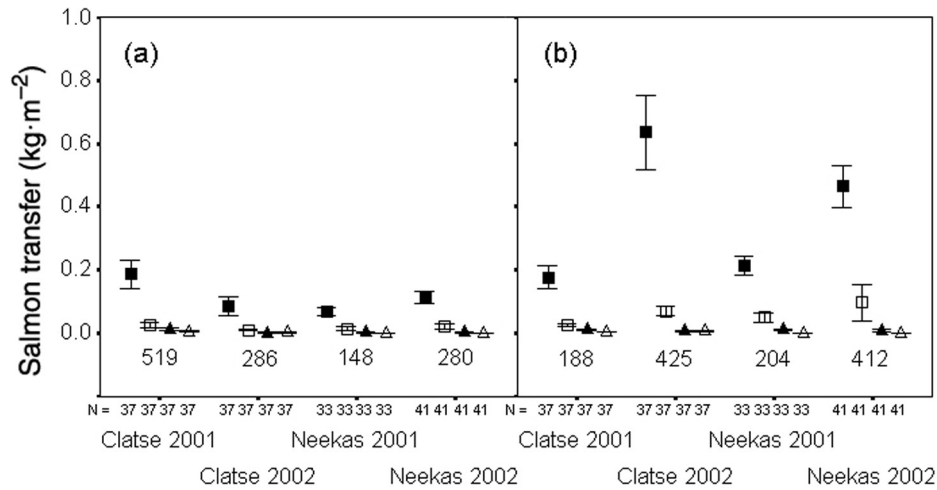
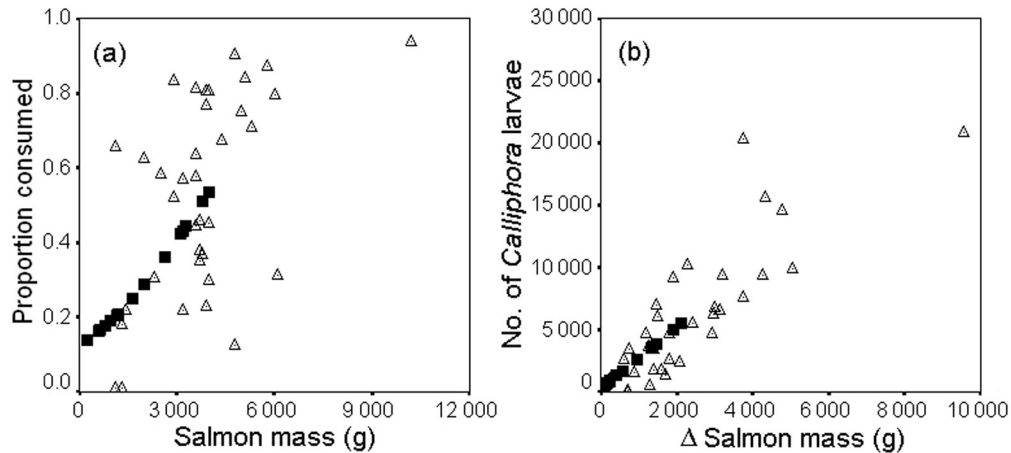


Fig. 2. *Calliphora* (Diptera: Calliphoridae) consumption and production from experimentally placed pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) carcasses on the Clatse and Neekas rivers, British Columbia. Observed (open triangles) versus predicted (solid squares) results are presented for (a) the change in salmon carcass mass (proportion consumed by all Diptera) versus initial salmon carcass mass and (b) the number of *Calliphora* larvae produced versus the change in salmon mass. Observed values were derived from measurements of *Calliphora* consumption and production from experimentally placed salmon carcasses in the riparian zone. Predicted values were determined in (a) by logistic regression ($\ln [Y/(1 - Y)] = -1.96 + 5.29^{-4}X$) and in (b) by linear regression ($Y = 312.12 + 2.45X$) equations derived from observed values and were used to predict the number of *Calliphora* larvae produced from the carcass mass categories from our salmon transfer databases.



1.0% for chum salmon (total range 0%–21%) derived from the initial mass of the carcass. However, when the mass of *Calliphora* produced is divided by Δ carcass mass, this increases to 17.4% for pink (range 0%–26%) and 13.2% for chum (range 0%–28%) salmon.

Excluding the *Calliphora*, dipteran larvae production from remaining fly families on experimental carcasses averaged 53.0 ± 16.6 g for pink and 28.4 ± 4.8 g for chum salmon. Production of these dipteran larvae was negatively predicted by initial carcass mass, as higher productivity occurred on smaller carcasses ($F_{[1,34]} = 8.36, p = 0.007; R^2 = 0.197$).

The percentage of each salmon carcass consumed by Diptera was predicted by initial carcass mass, while the *Calliphora* production from each carcass was predicted by

Δ carcass mass (Fig. 2). Using these predictive equations, we estimated *Calliphora* production from pink and chum carcass categories from our transfer databases in 2001–2002 (Table 2) and then expanded our estimates to include the entire watershed (Table 4). Total *Calliphora* production (in millions of larvae) per spawning season was greater for chum salmon ($3.04\text{--}5.75 \times 10^6$) compared with pink salmon ($1.09\text{--}1.40 \times 10^6$) ($F_{[1,5]} = 7.8, p = 0.038; R^2 = 0.610$; Fig. 3). This translates into $38.2\text{--}69.8$ g of *Calliphora* larvae·m⁻¹ of spawning for pink salmon and $157.6\text{--}194.6$ g·m⁻¹ for chum salmon, depending on watershed.

We calculated total dipteran larvae production (number and biomass) per spawning season from both watersheds using ecological efficiencies of 10% and 20% (Table 4). Com-

Table 4. Estimates of *Calliphora* (Diptera: Calliphoridae) and total dipteran larvae production and ecological efficiencies from pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon carcasses transferred to the forest of the Clatse and Neekas rivers, British Columbia.

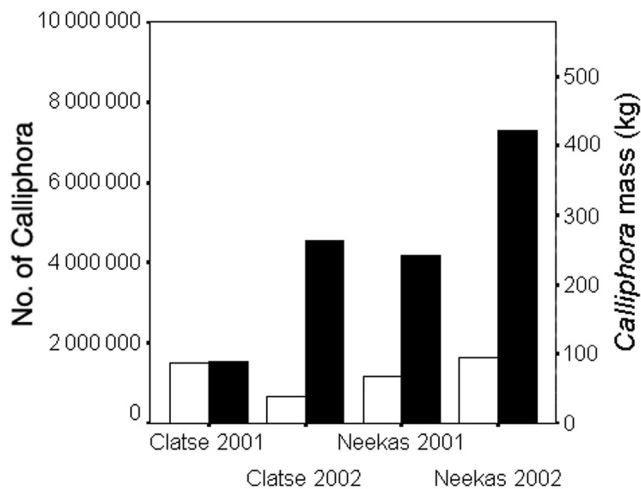
	Clatse River		Neekas River	
	Pink	Chum	Pink	Chum
No. of <i>Calliphora</i> maggots ($\times 10^6$) produced*	1.09 \pm 0.60	3.04 \pm 2.13	1.40 \pm 0.33	5.75 \pm 2.20
Biomass of <i>Calliphora</i> maggots produced ($\text{g}\cdot\text{m}^{-1}$) [†]	69.8 \pm 38.6	194.6 \pm 136.3	38.2 \pm 9.2	157.6 \pm 60.2
Ecological efficiency of <i>Calliphora</i> on salmon (%)	4.6 \pm 0.1	5.5 \pm 0.5	4.5 \pm 0.04	5.1 \pm 0.1
No. of Diptera larvae ($\times 10^6$) at ecoefficiency of 10%*	6.42 \pm 3.71	14.64 \pm 9.07	7.82 \pm 1.85	28.49 \pm 11.59
Biomass of Diptera produced at ecoefficiency of 10% ($\text{g}\cdot\text{m}^{-1}$) [†]	152.0 \pm 87.7	346.5 \pm 214.5	85.3 \pm 20.2	310.7 \pm 126.4
No. of Diptera larvae ($\times 10^6$) at ecoefficiency of 20%*	12.84 \pm 7.41	29.28 \pm 18.13	15.63 \pm 3.69	56.97 \pm 23.18
Biomass of Diptera produced at ecoefficiency of 20% ($\text{g}\cdot\text{m}^{-1}$) [†]	304.0 \pm 175.5	693.0 \pm 429.1	170.5 \pm 40.3	621.3 \pm 252.7

Note: Data represent mean \pm 1 standard deviation of 2 years: 2001 and 2002.

*Total numbers for each watershed ($\times 10^6$).

[†]Diptera biomass production in grams per metre of spawning length.

Fig. 3. Estimated number and biomass of *Calliphora* (Diptera: Calliphoridae) larvae produced from carcasses of pink salmon (*Oncorhynchus gorbuscha*) (open bars) and chum salmon (*Oncorhynchus keta*) (solid bars) naturally transferred into the riparian forest of the Clatse and Neekas rivers, British Columbia, in 2001–2002.



binning pink and chum salmon estimates, these values ranged from 396 g of larval Diptera·m⁻¹ of spawning at Neekas River to 498.5 g·m⁻¹ at Clatse River at an ecological efficiency of 10%. This produces a total of 21 million dipteran larvae at Clatse River and 36 million dipteran larvae at Neekas River (at 10%), with all estimates doubling at an ecological efficiency of 20%.

From Clatse and Neekas rivers, we observed 16 vertebrate and 22 invertebrate species as predators or parasitoids of dipteran eggs or larvae (Tables 5 and 6). Vertebrates included one mammal, two amphibians, and 13 birds. Dominant invertebrates included 13 beetle predators from the Staphylinidae, Silphidae, Hydrophilidae, and Carabidae, and four parasitic wasps from the Ichneumonidae, Braconidae, and Figitidae.

We estimated the biomass and number of adult Diptera emerging in the spring–summer (Table 7). *Calliphora* emergence was greater from chum salmon (0.70–1.33 $\times 10^6$) than pink salmon (0.25–0.32 $\times 10^6$) ($F_{[1,5]} = 7.8$, $p = 0.038$; $R^2 =$

Table 5. Vertebrate species observed feeding on terrestrial dipteran larvae consuming pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon carcasses in forest riparian zones of the Clatse and Neekas rivers, British Columbia.

Order	Species
Mammalia	Montane shrew (<i>Sorex monticolus</i>)
Amphibia	Rough-skinned newt (<i>Taricha granulosa</i>)
	Northwestern salamander (<i>Ambystoma gracile</i>)
Aves	Winter wren (<i>Troglodytes troglodytes</i>)
	Varied thrush (<i>Ixoreus naevius</i>)
	Swainson's thrush (<i>Catharus ustulatus</i>)
	Hermit thrush (<i>Catharus guttatus</i>)
	American robin (<i>Turdus migratorius</i>)
	Song sparrow (<i>Melospiza melodia</i>)
	White-throated sparrow (<i>Zonotrichia albicollis</i>)
	Golden-crowned sparrow (<i>Zonotrichia atricapilla</i>)
	Fox sparrow (<i>Passerella iliaca</i>)
	Savannah sparrow (<i>Passerculus sandwichensis</i>)
	Steller's jay (<i>Cyanocitta stelleri</i>)
	Least sandpiper (<i>Calidris minutilla</i>)
	Spotted sandpiper (<i>Actitis macularia</i>)

0.610), with production ranging from 8.8–16.2 g·m⁻¹ of spawning for pink salmon and 36.5–45.0 g·m⁻¹ for chum salmon. Using an ecological efficiency of 10%, overall dipteran adult emergence ranged from 20–80 g·m⁻¹ or 1.5–6.6 million adults, depending on watershed and fish species. These values double at an ecological efficiency of 20%.

Stable isotope analysis

Stable isotope signatures in spring-emerging adult *Calliphora* varied from 5.0‰ to 19.3‰ for $\delta^{15}\text{N}$ and -27.5‰ to -18.4‰ for $\delta^{13}\text{C}$, with most values indicating a larval diet of salmon (Fig. 4). Both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ did not vary by watershed or by location above and below the falls (ANOVA both isotopes: all $F < 1.5$, all $p > 0.24$). Means for each watershed ranged from 14.82‰ (Clatse) to 15.12‰ (Neekas) for $\delta^{15}\text{N}$ and from -21.94‰ (Neekas) to -21.54‰ (Clatse) for $\delta^{13}\text{C}$. Using a cutoff of 12‰ for $\delta^{15}\text{N}$ and -23‰ for $\delta^{13}\text{C}$, 85.7% of *Calliphora* adults from Clatse River (total $n = 21$) and 81.7% from Neekas River ($n = 60$) were likely raised on salmon carcasses the previous fall.

Table 6. Invertebrate families observed feeding or ovipositing on terrestrial dipteran larvae from pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon carcasses in forest riparian zones of the Clatse and Neekas rivers, British Columbia.

Order	Family	No. of species
Coleoptera	Carabidae	4
	Hydrophilidae	1
	Staphylinidae	7
	Silphidae	1
Hymenoptera	Braconidae	2
	Figitidae	1
	Formicidae	1
	Ichneumonidae	1
Araneae	Agelenidae	1
	Antrodiaetidae	1
Parasitiformes	Parasitidae	1
Chilopoda	Geophilidae	1

Discussion

Salmon carcass transfer

Our analysis of salmon carcass transfer to riparian zones of two coastal rivers highlights two principal findings: (i) the keystone role of riparian predators, in this case black bears, in the distribution of salmon nutrients and energy to adjacent forest habitats and (ii) the increased relative transfer of chum salmon compared with pink salmon.

As salmon return to spawn, bears can predate a large proportion of the available fish, with estimates up to 92% at Bag Harbour, Haida Gwaii (Reimchen 2000), and 100% at the Pedro pond-creek system in Alaska (Quinn and Kinnison 1999). Most observed predation rates, however, are lower, ranging from 2%–70%, and vary by fish species, fish sex, habitat, fish density, and bear density (Gende et al. 2001, 2004a; Gende and Quinn 2004). We estimate that from 4% to 6% of the pink salmon run was transferred into the forest, depending on watershed, while chum transfer was higher, ranging from 16% to 48% of the total salmon run. Several studies have observed size-selective mortality in salmon, as bear-killed fish were larger than those dying of senescence (Quinn and Kinnison 1999; Quinn and Buck 2001). Mass-specific energy and mineral composition of spawning chum and pink salmon are roughly equivalent, although chum salmon have much higher absolute values because of their larger size (Gende et al. 2004b). Bear transfer of the large-bodied chum salmon has been emphasized in several other studies and can range from 40% to 70% (Reimchen 2000; Gende et al. 2004b).

Total salmon transfer declined with distance of placement into the forest. This is comparable with other studies, which have found most salmon transfer to be within 5 m of the stream (Reimchen 2000; Gende et al. 2004b). Both Reimchen (2000) and Gende and Quinn (2004) highlight that carcasses with higher mass-specific and absolute energy contents are transferred further into the forest and that one of the main causes of transfer involves conspecific avoidance by subdominant bears. Since energy intake is closely linked

to overall fitness, bear foraging likely maximizes energy intake per unit of foraging effort (Gende et al. 2004a).

Yearly variation in the rate of salmon transfer was observed in this study, with the most dramatic variation occurring for chum salmon transfer between 2001 and 2002. Yearly variation in transfer is likely linked to yearly variation in salmon escapement and the density of vertebrate predators, as well as environmental factors such as river discharge and flooding (Gende et al. 2001, 2004a). In 2002, low precipitation during spawning resulted in low river discharge and higher access to salmon by vertebrate predators and likely contributed to the higher transfer observed in 2002.

Diptera consumption and production

Flies are a widespread consumer and vector of salmon nutrients and energy in terrestrial habitats, with observations from Washington (Cederholm et al. 2000; Jauquet et al. 2003), Vancouver Island (Reimchen et al. 2003), Haida Gwaii (Reimchen 1994), Alaska (Meehan et al. 2005), and now the mainland midcoast of British Columbia (this study). Blow flies (*Calliphoridae*) typically dominate salmon carrion decomposition, although other families such as *Dryomyzidae*, *Muscidae*, *Spherozeridae*, *Phoridae*, *Heleomyzidae*, *Trichoceridae*, and *Sciomyzidae* have also been observed. The species *Calliphora terranova* has been collected from salmon carrion on Vancouver Island (Reimchen et al. 2003), Alaska (Meehan et al. 2005), and the central coast of British Columbia, emphasizing that this species may be particularly adapted to consume salmon carcasses.

From forest-carcass surveys, flies colonized >90% of naturally occurring salmon carcasses in the forest, with uncolonized carcasses mainly including small remnants. Flies also colonized 100% of experimentally placed carcasses, with *Calliphora* colonizing 94% of these. Colonization values are higher than those reported by Meehan et al. (2005), who found that 57% of forest carcasses were utilized by flies, and are closer to estimates by Reimchen (1994), who found that 85% of transferred carcasses were colonized. An important consideration is temperature. Blow flies are sensitive to cold temperatures (Williams and Richardson 1984), and in cooler years they may be out-competed on salmon carcasses by vertebrates and cold-tolerant flies and beetles (Reimchen 1994).

Competition is highly important in structuring species dominance and diversity within carrion communities (Putman 1977; Hanski 1987; Smith and Wall 1997), a process that appears common in communities of invertebrates on salmon carcasses (Hocking et al. 2006). In favourable conditions, *Calliphora* can out-compete most species and can consume entire carcasses within several days (Meehan et al. 2005). We observed high *Calliphora* production on large carcasses and more production of other dipteran larvae on smaller carcasses. Flies have been shown to partition themselves by carcass size (Kneidel 1984; Hanski 1987), and variable consumption of salmon by bears and variable fish sizes may increase the taxonomic diversity of insect species on salmon.

Another niche dimension along which carrion species are often distributed is the successional stage of the carcass itself (Putman 1977; Anderson and VanLaerhoven 1996). Our

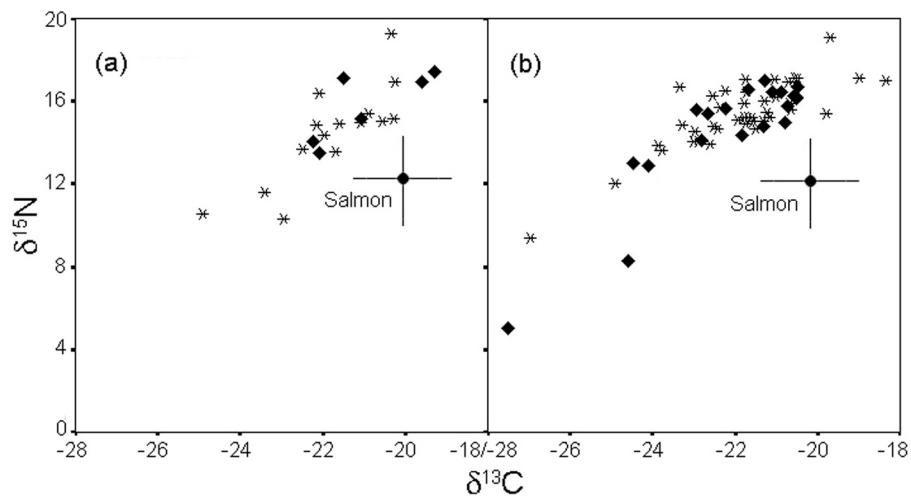
Table 7. Estimates of *Calliphora* (Diptera: Calliphoridae) and total dipteran adult spring–summer emergence from pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon carcasses transferred to the forest of the Clatse and Neekas rivers, British Columbia.

	Clatse River		Neekas River	
	Pink	Chum	Pink	Chum
No. of emerging <i>Calliphora</i> adults ($\times 10^6$)*	0.25 \pm 0.14	0.70 \pm 0.49	0.32 \pm 0.08	1.33 \pm 0.51
Biomass of emerging <i>Calliphora</i> adults ($\text{g}\cdot\text{m}^{-1}$) [†]	16.2 \pm 8.9	45.0 \pm 31.5	8.8 \pm 2.1	36.5 \pm 13.9
No. of emerging Diptera ($\times 10^6$) at ecoefficiency of 10%*	1.49 \pm 0.86	3.38 \pm 2.09	1.81 \pm 0.43	6.58 \pm 2.67
Biomass of emerging Diptera at ecoefficiency of 10% ($\text{g}\cdot\text{m}^{-1}$) [†]	35.1 \pm 20.2	80.1 \pm 49.7	19.7 \pm 4.7	71.8 \pm 29.2
No. of emerging Diptera ($\times 10^6$) at ecoefficiency of 20%*	2.97 \pm 1.71	6.76 \pm 4.19	3.61 \pm 0.86	13.16 \pm 5.35
Biomass of emerging Diptera at ecoefficiency of 20% ($\text{g}\cdot\text{m}^{-1}$) [†]	70.3 \pm 40.5	160.1 \pm 99.1	39.4 \pm 9.3	143.5 \pm 58.4

Note: Data represent mean \pm 1 standard deviation of 2 years: 2001 and 2002.

*Total numbers for each watershed ($\times 10^6$).

[†]Diptera biomass production in grams per metre of spawning length.

Fig. 4. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures in spring-emergent *Calliphora* (Diptera: Calliphoridae) adults from above (solid diamonds) and below (asterisks) the falls on the (a) Clatse and (b) Neekas rivers, British Columbia. *Calliphora* were caught in baited traps and were assumed derived from salmon carrion if isotope signatures are higher than 12‰ for $\delta^{15}\text{N}$ and -23‰ for $\delta^{13}\text{C}$ (solid circle, Salmon).

measurements of *Calliphora* production from salmon carcasses occurred fairly early in the decay sequence, with often a relatively large mass remaining for further consumption. If other Diptera families are more competitive on smaller carcasses, then they may be more prevalent in the later decay stages of larger carcasses.

Of other studies that have emphasized Diptera consumption of salmon carcasses, only Reimchen (1994) and Meehan et al. (2005) attempt to quantify fly maggot production at a watershed level. We found that 4.13 million and 7.15 million *Calliphora* larvae were produced on the Clatse and Neekas rivers, respectively, from salmon carcasses transferred to upland areas per spawning season. These values are lower than Meehan et al. (2005) in terms of overall production (i.e., 10 million larvae), likely because of lower estimates of production per carcass. However, estimates for *Calliphora* production were derived from conservative ecological efficiencies of 4.5%–4.6% for pink and 5.1%–5.5% for chum salmon. If we include other fly families using ecological efficiencies of 10% and 20%, then our estimates for total Diptera production from salmon carcasses becomes higher.

Larval Diptera are important vectors of marine nutrients and energy to numerous vertebrate and invertebrate consumers in terrestrial food webs. Our observation of 16 vertebrate

and 22 invertebrate predators or parasitoids associated with dipteran larvae on salmon carcasses expands on previous observations by Reimchen (1994), Cederholm et al. (2000), and Jauquet et al. (2003) in British Columbia and Washington. Overall, the extent to which these species depend on larval flies derived from salmon carcasses for life history attributes, including reproduction, migration, and overwintering, is relatively unknown. It is possible, for example, that the parasitic wasps observed here have a population life history that is timed to seasonal cycle of salmon, as has been documented for coastal and riverine mink (*Mustela vison*) (Ben-David et al. 1997).

Across all known chum and pink salmon spawning watersheds on the central and north coasts of British Columbia ($n > 500$), total escapement biomass over the last 50 years has averaged roughly 6.5 and 10 million kg for chum and pink salmon, respectively (DFO data available from www.heb.pac.dfo-mpo.gc.ca/maps/maps-data_e.htm). Much of this biomass is either consumed by multiple terrestrial vertebrates or ends up in the form of senescent carcasses that are consumed within aquatic food chains (Bilby et al. 1996; Wipfli et al. 1998). The remaining mass transferred to riparian forests and not consumed by vertebrates is made available for invertebrate scavengers, primarily including the

Diptera. More transfer, less tissue consumption, and consequently more Diptera production is expected when salmon densities are high and salmon are more accessible. Given that the Clatse and Neekas are both small rivers that provide good access to salmon, our estimates of transfer and Diptera consumption may be slightly higher than an average coastal chum and pink salmon run. However, extensive Diptera production from salmon carcasses may also occur in systems supporting sockeye salmon (*Oncorhynchus nerka*), as numerous studies have documented bear predation on sockeye (Quinn and Kinnison 1999; Gende et al. 2001; Quinn and Buck 2001) and Diptera colonization of their carcasses (Meehan et al. 2005).

Stable isotope analysis

Emerging *Calliphora* adults caught in baited traps in the spring indicated a high frequency (>80%) of a larval diet of salmon from both the Clatse and Neekas rivers. The mean isotope signature of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ did not differ by location of collection within each watershed, as high values were also present in individuals collected above the falls. This highlights the further distribution of salmon nutrients to non-salmon habitats in the form of dispersing flies. Riparian corridors are known to be important locations for movement of many animals, including flies (Fried et al. 2005), and emerging *Calliphora* could easily disperse to above the falls in search of mates and carcasses for breeding.

Implications

Spawning salmon provide a dominant source of nutrients and energy to hundreds of aquatic and terrestrial species throughout the North Pacific (Cederholm et al. 2000; Stockner 2003). Salmon have been labelled as “ecosystem engineers” (Schindler et al. 2003) and “intrinsic to ecosystem function” (Zhang et al. 2003) and provide a cross-habitat subsidy that may be thought of as similar in magnitude to the annual migrations of wildebeest (*Connochaetes* spp.) on the Serengeti (Reimchen 2000). We document and quantify a largely unreported yet critical component of this process — the consumption and distribution of salmon-derived nutrients and energy by terrestrial flies. Despite higher escapement of pink salmon, large-bodied chum salmon were preferred prey for bears and were transferred more readily into the forest. The main predictors of total Diptera consumption were linked with carcass size and availability, which is correspondingly linked to the density of fish spawning, the species of fish (chum or pink), bear density, and attributes of the habitat (Reimchen 2000; Gende et al. 2001). Overall this means that the most Diptera production will occur in situations where there is high density spawning of chum salmon, large numbers of bears to transfer carcasses, and streams that facilitate access and selective foraging by vertebrate predators. The presence of flies breeding on salmon carcasses may thus be used as an indicator for not only the presence of bears or other wildlife but adequate salmon escapement to support both vertebrate and invertebrate scavengers.

The ecological implications of this process of salmon transfer by vertebrates and subsequent consumption of carcasses by terrestrial Diptera is most relevant when considering the coast-wide declines in salmon spawning biomass

over the last century (Finney et al. 2000; Gresh et al. 2000). Throughout the coast of British Columbia, it is small chum salmon streams that are experiencing recent declines (Godbout et al. 2004; Spilsted 2004), precisely the watersheds that may be the most critical for preserving the salmon–bear–Diptera linkage. The consumption of salmon carcasses by terrestrial Diptera results in the widespread distribution of salmon nutrients and energy to multiple species, with the potential increases in biodiversity and carrying capacity of these coastal habitats.

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