

The Salmon-Forest

by

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Abstract

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Cross-habitat subsidies of nutrients and prey can structure community processes in receiving ecosystems. Every autumn throughout the northern Pacific region, anadromous salmon (*Oncorhynchus* spp.) return to their natal watersheds to spawn and die, a landward migration that imports marine protein to estuarine, freshwater and terrestrial habitats. Spawning salmon regulate the population dynamics of many wildlife species and fertilize aquatic and terrestrial systems with their nutrients and carcasses. When salmon spawn at high densities, vertebrate predators such as bears (*Ursus* spp.) selectively forage on energy-rich components of the salmon and transfer partially-consumed carcasses to adjacent forests.

Herein, I examine the ecosystem-level consequences of the salmon subsidy in forest food webs, with a primary focus on the role of terrestrial invertebrates in the consumption, distribution and cycling of salmon nutrients and energy in terrestrial habitats. Study watersheds occur throughout coastal British Columbia, with most comparisons from two productive systems on the central coast. Both have high-density salmon spawning and 5-10m waterfalls 1-2km from the estuary that block further upstream salmon migration.

Using stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ I find that there are two principal pathways in which salmon nutrients enter forest food webs: 1) direct consumption of salmon tissue and/or salmon consumers (enrichment in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$); or 2) marine-nitrogen fertilization of soil and vegetation N pools (enrichment in $\delta^{15}\text{N}$ but not $\delta^{13}\text{C}$).

There is a diverse community of terrestrial invertebrates (>60 species) directly associated with the decay of salmon carrion, although from a biomass perspective this is dominated by the terrestrial Diptera. I estimate that from 134-360g of *Calliphora* (Calliphoridae) maggots per meter of spawning length (or 3.5-9 million individuals in whole watershed) were generated from carcass transfer on the Clatse and Neekas, with the majority produced from the large-bodied chum (*O. keta*) relative to pink (*O. gorbuscha*). Processes of competition and predation on salmon-carrion produce temporal dietary shifts in higher-level consumers, and species-specific adaptations, including

communal breeding in burying beetles (*Nicrophorus* spp.). Overall, the insect niche generated by the input of salmon carcasses directly increases the diversity, carrying capacity and food-chain length of riparian food webs.

The bottom-up effects of salmon nutrient fertilization favours plants that are competitive in nutrient-rich soils and structures a community of macro-detritivores as the primary decomposers. Salmon-nutrient fertilization is detectable in multiple trophic guilds in riparian foodwebs, with estimates of %marine-derived nitrogen (%MDN) ranging as high as 78%. Across multiple watersheds, the pattern of %MDN enrichment is most strongly predicted by chum spawning density (kg/m), including the legacy of spawning density from the past. High $\delta^{15}\text{N}$ and %MDN values can be used as indicators for intact ecosystem processes including the presence of wildlife transfer vectors, sufficient spawning densities to facilitate selective foraging, and the further distribution of salmon nutrients and energy by terrestrial insects.

Ongoing declines in salmon escapement throughout the Pacific Rim have far greater ecological context in riparian food webs than previously recognized. The salmon-forest interaction highlights the evolutionary interdependence between marine and terrestrial ecosystems in the North Pacific, and the need for ecosystem-level conservation that includes salmon, their riparian habitats, and their vertebrate and invertebrate scavengers.

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Chapter 1: Introduction

Ecosystem interdependence is best exemplified by the movement of energy and nutrients across habitat boundaries (Moore et al. 2003). Ecological flows can structure recipient communities at multiple scales, including among biomes or within patches of a few meters (Jefferies 2000). Fluxes are often reciprocal, although recipient responses are most dramatic when there is a gradient in productivity between interacting systems (Nakano and Murakami 2001). Inputs of nutrients often increase primary and secondary productivity through bottom-up effects, while consumption of allochthonous prey has direct effects on predator biomass (Polis and Strong 1996). Overall, the biodiversity and productivity in one biogeographic realm is often influenced by ecosystem processes in another (Ray 1988).

Resource subsidies along stream-forest interfaces (Fausch et al. 2002) and aeolian subsidies to alpine communities (Halfpenny and Heffernan 1992; Kaufmann 2001) represent two common examples of terrestrial cross-habitat fluxes. Leaf litter input to streams substantially increases in-stream productivity, while the emergence of aquatic insects supplements the diet of many terrestrial species (Bilby and Bisson 1992; Nakano and Murakami 2001; Sanzone et al. 2003). Alpine habitats tend to be very unproductive and even minor inputs of wind-blown insects and debris can support a community dominated by scavengers and predators (Mani and Giddings 1980).

The ocean-to-land interface along continental shelves is one of the most productive ecosystems in the world and is structured mainly by the upwelling of nutrients from the sea-bottom (Levinton 1995). Coastal upwelling regions support a disproportionate share of global marine productivity and over 50% of total fisheries catch (Jefferies 2000). This juxtaposition of land and sea showcases many marine-terrestrial exchanges, with the most common being land run-off which imports terrestrial nutrients to near-shore waters and increases marine productivity (Ray and Hayden 1992). In the reverse flow, productive marine systems subsidize adjacent terrestrial ones through shore drift of algal wrack and carrion (Polis and Hurd 1996), inputs of guano and carcasses of seabirds (Lord and Burger 1984; Hawke and Newman 2004), and episodic returns of

anadromous fishes (Ray 2005). These fluxes to terrestrial habitats can increase soil nutrient capital, primary productivity and vegetation diversity (Cocks et al. 1998; Leishman and Wild 2001; Hawke and Newman 2004; Wilkinson et al. 2005) as well as the biomass of predators and scavengers at higher trophic levels (Polis and Hurd 1995; Markwell and Daugherty 2002).

A dominant marine subsidy to terrestrial habitats throughout the northern Pacific is the annual spawning of anadromous salmon (*Oncorhynchus* spp.). Every fall, salmon return to their natal watersheds to spawn and die, importing marine protein to estuarine, freshwater and terrestrial habitats (Reimchen 1994; Willson et al. 1998; Gende et al. 2002). Salmon are dominant members of the marine food-chain and have supported human fishers for hundreds or perhaps thousands of years (Chisholm and Schwarcz 1982; Ward et al. 2003). During autumn spawning, many marine and terrestrial species converge to feed on salmon, a process that is critical for species reproduction, migration and overwintering (Ben-David et al. 1997; Hilderbrand et al. 1999a; Cederholm et al. 2000; Christie and Reimchen *in press*). Subsidies of salmon-derived nitrogen, phosphorus and other nutrients fertilize typically nutrient-poor aquatic and terrestrial habitats and can initiate bottom-up effects (Kline et al. 1993; Wipfli et al. 1998; Mathewson et al. 2003; Stockner 2003).

Studies in freshwater habitats, including streams and lakes, have stressed both direct and indirect effects of the salmon subsidy. Nutrient release from salmon carcasses increases aquatic primary productivity and invokes a positive feedback mechanism that can increase juvenile salmon survivorship (Slaney et al. 1994; Bilby et al. 1998; Wipfli et al. 1998; Stockner 2003). Decaying salmon carcasses also directly support an array of aquatic invertebrates in the Amphipoda, Trichoptera, Ephemeroptera, Plecoptera and Diptera (Bilby et al. 1996; Wipfli et al. 1998; Chaloner et al. 2002; Nakajima and Ito 2003). As such, the return of salmon is thought to be intrinsic to aquatic ecosystem functioning (Zhang et al. 2003).

Salmon carcasses and nutrients are distributed from streams and lakes into terrestrial ecosystems mainly through wildlife foraging. Bears (*Ursus* spp.) and other vertebrate species transfer salmon carcasses and nutrients into riparian areas, and often selectively feed on energy-rich portions of the salmon (Reimchen 2000; Gende et al.

2001). The extent of bear predation, carcass consumption and transfer to riparian areas depends on many factors, with the most critical including salmon spawning density, bear density and attributes of the habitat that facilitate access (Reimchen 1994; Quinn and Kinnison 1999; Reimchen 2000; Gende et al. 2004a; Gende and Quinn 2004). Other mechanisms by which salmon nutrients enter terrestrial systems include vertebrate urine, guano and feces deposition (Hilderbrand et al. 1999b; Ben-David et al. 1998a; Christie and Reimchen *in press*), flooding events (Ben-David et al. 1998b) and transfer of nutrients through the hyporheic zone (O'Keefe and Edwards 2003). Overall, carcasses can be transferred over 100m into the forest (Reimchen 2000) while nutrients from salmon can be distributed along wildlife trails up to several km from the spawning beds (Hilderbrand et al. 1999b).

Large salmon carcasses and remnants distributed to riparian forests by vertebrates are consumed by multiple terrestrial scavengers and saprophages, although this community is not well documented (Reimchen 1994; Cederholm et al. 2000). Vertebrate carcasses in terrestrial habitats support many specialized species in distinct communities (Putman 1983; Hanski 1990). Competition for carcasses occurs primarily between necrophagous flies, carrion beetles, ants and vertebrate scavengers, with niche distribution depending on season, habitat, and carcass size, taxon and extent of decomposition (Kneidel 1984; Hanski 1987; Ohkawara et al. 1998). Previous investigations of terrestrial invertebrate use of salmon carcasses have emphasized the dominant role of the Diptera, particularly blowflies (Calliphoridae) (Reimchen 1994; Jauquet et al. 2003; Reimchen et al. 2003; Meehan et al. 2005). However, the number and biomass of maggots produced from salmon and the role of flies in the dispersal of salmon nutrients to terrestrial habitats has not been adequately quantified. Large aggregations of maggots attract an array of consumers including songbirds and small mammals (Cederholm et al. 2000; Christie et al. *submitted*), and overall the addition of carcasses may increase riparian zone diversity and carrying capacity (Reimchen 1994).

As opposed to direct effects, community processes in stream-side forests can also be affected by indirect or bottom-up effects of salmon nutrient fertilization. Nutrient additions can increase riparian primary productivity, vegetation and litter quality, and soil nutrient capital, as well as alter vegetation community structure (Ben-David et al. 1998b;

Hilderbrand et al. 1999b; Helfield and Naiman 2001; Bilby et al. 2003; Mathewson et al. 2003; Wilkinson et al. 2005). Nutrients are often limiting in coastal temperate rainforests (Waring and Franklin 1979), and the input of salmon-derived nitrogen, for example, is thought to contribute to the nitrogen economy of riparian forests. Soil-nutrient conditions can also determine both the dominant humus forms and the dominant detritivores present (Setälä et al. 1991; Green and Klinka 1994; Prescott et al. 2000). Macro-invertebrates of coastal coniferous forests, including insects, arachnids, myriapods, oligochaetes, isopods and gastropods, comprise the base of nutrient and energy pathways from primary producers through to higher vertebrate consumers. They are highly important in ecosystem processes such as herbivory, litter decomposition, and nutrient cycling (Furniss and Carolin 1977; Spiers et al. 1986; Cárcamo et al. 2000), and it is unknown how the salmon subsidy affects their abundance and community organization.

Subsidies of prey and nutrients across habitat boundaries can be quantified with the use of stable isotope analysis (Anderson and Polis 1998; Cocks et al. 1998). Nitrogen and carbon isotopes have been used to estimate dietary variation, trophic structure and sources of nutrients and energy (Peterson and Fry 1987; Kelly 2000; Post 2002b). The ratio of $^{15}\text{N}/^{14}\text{N}$ ($\delta^{15}\text{N}$) in consumer tissues is typically enriched by 3-4 parts per mil (‰) relative to diet (DeNiro and Epstein 1981; Minigawa and Wada 1984) and thus nitrogen isotope ratios are often used to estimate trophic position (Vander Zanden et al. 2000). Carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$ or $\delta^{13}\text{C}$) usually have low diet-tissue fractionation (Deniro and Epstein 1978; Gearing et al. 1984), and thus have been primarily used to determine sources of primary productivity (Tieszen and Boutton 1988). Studies of marine inputs to terrestrial systems benefit from the observation that marine species high on the food chain such as salmon and seabirds have high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures relative to most terrestrial sources. In the salmon-forest system, stable isotopes can identify direct and indirect pathways of salmon nutrient input to multiple consumers (Reimchen et al. 2003). For example, high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in bears and wolves implies a diet of salmon for many individuals (Hilderbrand et al. 1999a; Darimont and Reimchen 2002), while elevated $\delta^{15}\text{N}$ but not $\delta^{13}\text{C}$ suggests an indirect pathway through marine nitrogen enrichment of terrestrial vegetation (Bilby et al. 1996; Ben-David et al. 1998b; Mathewson et al. 2003).

Stable isotope analysis can also be used to measure individual niche (Bearhop et al. 2004). Diets within and among individuals in a population can vary over time, among habitats and prey types, and when the isotopic composition of potential prey is known individual diet variation can be identified (Bolnick et al. 2003; Matthews and Mazumder 2004). For example, tissue separation in bears, wolves and songbirds reveals dietary shifts from terrestrial prey in the spring and summer to at least a partial diet of salmon in the fall for many individuals (Darimont and Reimchen 2002; Christie et al. *submitted*; Klinka and Reimchen *unpublished data*). Stable isotope analysis of individual invertebrates may also indicate dietary shifts to salmon in the fall including differences between larval and adult diets (Tallamy and Pesek 1996).

This project represents a direct extension of several studies initiated by Reimchen (1992, 1994) that investigated vertebrate and invertebrate use of mainly chum salmon (*O. keta*) in a small watershed on Moresby Island, Haida Gwaii. In 1992, chum salmon carcasses transferred to the forest were mainly consumed by vertebrate scavengers while in 1993 much of this biomass was consumed by muscoid flies (Figure 1.1: Reimchen 1994). Overall, terrestrial nutrient cycling through the invertebrate-salmon association represents an unknown and understudied component of the salmon-forest web.

Another important impetus for this project extends from the historical and ongoing reduction in salmon spawning abundance throughout North America and Asia that is causing nutrient deficits that threaten whole communities (Finney et al. 2000; Gresh et al. 2000; Stockner 2003). In California, Oregon, Washington and Idaho it is estimated that there has been greater than a 90% reduction in spawning biomass over the last 100 years, mainly due to commercial fishing and dam construction (Gresh et al. 2000). In Alaska, consistent reductions in sockeye returns to lakes have been observed over the last century (Finney et al. 2000), and on the central coast of British Columbia recent declines in small streams that support chum salmon are prompting concerns (Harvey and MacDuffee 2002; Godbout et al. 2004; Spilsted 2004).

Herein, I document the direct (salmon carcass) and indirect (salmon nutrient fertilization) effects of the salmon subsidy on the terrestrial community, with a principal focus on the litter-based and carrion invertebrates. I collected specimens from 38 watersheds across a wide geographic area in British Columbia including watersheds on

Vancouver Island, the mainland mid-coast and Haida Gwaii (Figure 1.2). Most of my research however occurred on two productive watersheds on the central coast near Bella Bella B.C., the Clatse and Neekas rivers. These watersheds support high density runs of chum and pink salmon and have waterfalls 1-2 km from the estuary that block their further upstream migration. This presents a good within watershed control for the effects of the salmon subsidy in the forest community. My work highlights the interdependence of salmon, bears and forest invertebrates and adds to a diversity of recent publications that have focused on the ecological consequences for coast-wide declines in salmon spawning density (Reimchen 1994; Bilby et al. 1996; Ben-David et al. 1998b; Willson et al. 1998; Wipfli et al. 1998; Cederholm et al. 2000; Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003; Stockner 2003; Zhang et al. 2003; Wilkinson et al. 2005).

Figure 1.1. Summarized flow of salmon biomass (kg) at Bag Harbour, Haida Gwaii (taken from Reimchen 1994).

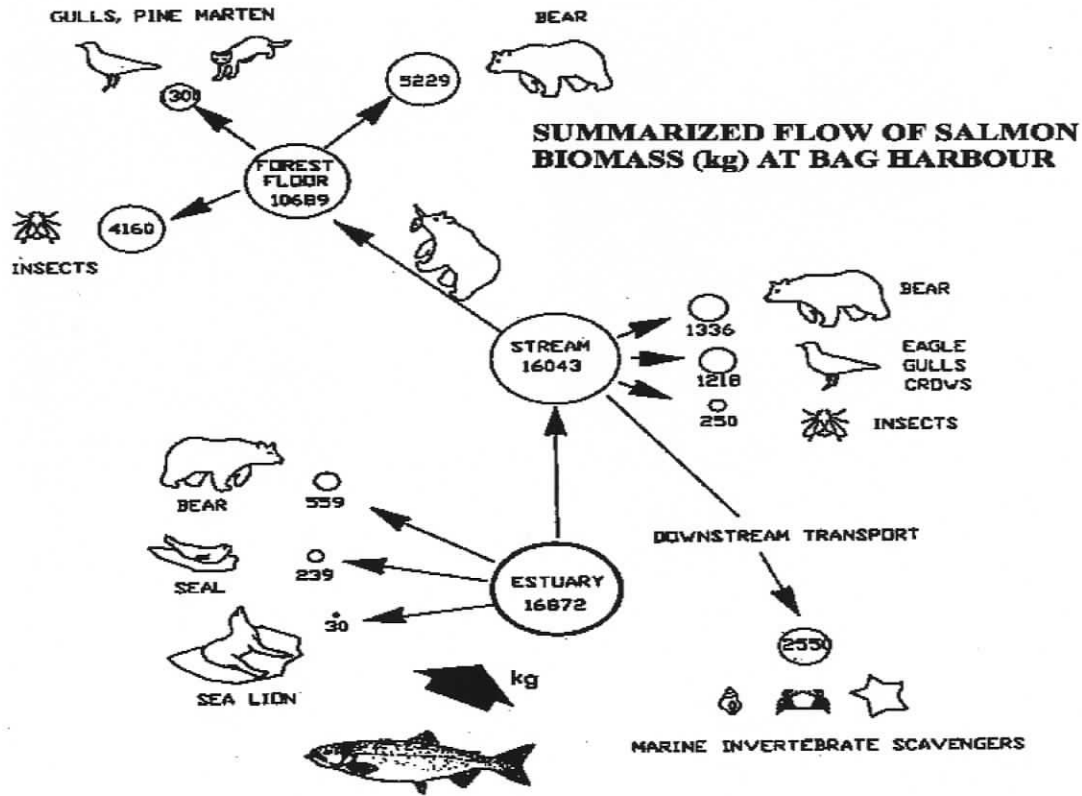


Figure 1.2. Major study locations throughout coastal British Columbia: A – Moresby Island, Haida Gwaii; B – Clayoquot Sound, Vancouver Island; C – the Clatsop and Nekeas rivers, near Bella Bella; D – mainland midcoast near Prince Rupert; E – Goldstream River on Vancouver Island.



Chapter 2:

Study sites of the Salmon-Forest

2.1. Clayoquot Sound, Vancouver Island

Initial collections of terrestrial invertebrates for the salmon-forest project occurred in six coastal watersheds in Clayoquot Sound, on the west side of Vancouver Island, British Columbia, building on previous work by Dr. Thomas Reimchen, Deanna Mathewson, and Dr. Jonathan Moran (Mathewson 2002; Reimchen et al. 2003). In the spring of 1999 and 2000 I visited Warn Bay (49° 15' 46.1"N, 125° 43' 31.6"W), Bulson (49° 15' 48.8"N, 125° 43' 40.8"W), Moyeha (49° 24' 58.62"N, 125° 54' 45.9"W), Megin (49° 26' 12.2"N, 126° 5' 5.4"W), Watta (49° 27' 29.4"N, 126° 1' 38.8"W) and Sidney (49° 30' 47.7"N, 126° 17' 48.3"W) rivers (Figure 2.1), and collected various litter-invertebrate specimens for stable isotope analysis. These watersheds are some of the least affected by the extensive deforestation in the region and are located within the Coastal Western Hemlock biogeoclimatic zone (CWHvh1) characterized by dense forests of western hemlock (*Tsuga heterophylla*), amabilis fir (*Abies amabilis*), sitka spruce (*Picea sitchensis*) and western red cedar (*Thuja plicata*) (Green and Klinka 1994; Pojar and MacKinnon 1994). Shrubs such as salmonberry (*Rubus spectabilis*), false azalea (*Menziesia ferruginea*) red huckleberry (*Vaccinium parvifolium*), salal (*Gaultheria shallon*), deer fern (*Blechnum spicant*) and sword fern (*Polystichum munitum*) dominate understory vegetation along streams. The climate is cool and perhumid, receiving >2500 mm yr⁻¹ precipitation, mainly in the form of rain at lower elevations with an annual temperature range of *ca.* 10 °C (Schaefer 1978). Up to seven species of salmonids occur in these watersheds comprising chinook, chum, coho, pink, sockeye, cutthroat trout, and steelhead. Black bears occur in each watershed and are the dominant transfer agent of salmon carcasses into the riparian zone (Reimchen et al. 2003). Wolves, river otters and bald eagles are also present in all watersheds and will be contributing transfer agents.

Warn Bay Creek and Bulson Creek are located in adjacent valleys and both feed into Warn Bay through a common estuary. Warn Bay Creek, with a spawning length of

1.4 km, is a narrow, shallow system, which supports mainly chum salmon but also coho, pink and chinook. From 1991-2000, Department of Fisheries and Oceans (DFO) escapement counts (Fish Wizard: <http://pisces.env.gov.bc.ca>) show a mean of 4638 chum, 34 pink and 47 coho salmon entering this system each year. Bulson Creek has a high gradient canyon near the mouth of the creek that is impassable to salmon and thus acts as a control watershed.

The Moyeha River is a large system at the north end of Herbert Inlet that supports runs of chinook, chum, coho, pink, and sockeye salmon with a spawning length of approximately 10.6 km. Escapement records from 1991-2000 show a yearly average of about 9600 salmon, mainly chum (mean = 7544) and coho (mean = 1677).

The Megin River, located on the north side of Shelter Inlet, is the largest of the six study sites, with spawning extending for more than 25 km including various tributaries. The Megin supports chinook, chum, coho, pink and sockeye salmon, with an average of 7000 salmon, mainly chum (mean 5345), entering the system annually (1991-2000).

Watta Creek is located at northern end of Herbert Inlet and has a spawning length of 1.7 km supporting runs of chum and coho, with the occasional chinook, pink and sockeye. Average escapement from 1991-2000 was approximately 2200 salmon, with chum comprising the vast majority of these (mean = 2107).

The Sydney River is 11 km long with the majority of spawning activity occurring in a braided region in the lower 2.3 km. This river supports chinook, chum, coho, pink and sockeye, with an average of 600 salmon, mainly chum (mean = 503), returning each year from 1991-2000.

A portion of my data from this region is presented in Reimchen et al. (2003). The rest is presented in Chapter 9.

2.2. Clatse and Neekas rivers

2.2.1. Overview

The majority of my research took place on two salmon bearing streams, the Clatse ($52^{\circ} 20' 15.6''\text{N}$; $127^{\circ} 50' 23.2''\text{W}$) and Neekas ($52^{\circ} 28' 16.8''\text{N}$; $128^{\circ} 9' 38.7''\text{W}$) rivers, on the central coast of British Columbia near the town of Bella Bella (Figure 2.2). The Clatse is located on the mainland below Mt. Keyes in Roscoe inlet, while the Neekas is

located on the Don Peninsula off Spiller Channel. Detailed site descriptions occur throughout the thesis with the climate, vegetation and soils primarily described in Chapter 3 (Hocking and Reimchen 2002) and in Mathewson et al. (2003).

In total I spent ~15 weeks living on each of the Clatse and Neekas rivers from August 2000 to October 2003. This comprised 8 separate expeditions including 4 weeks in August 2000, 1 week in late September 2000, 5.5 weeks in May and June 2001, 5 weeks in September and October 2001, 5 weeks in September and October 2002, 4 weeks in May and June 2003, 2 weeks in July 2003, and 4 weeks in September and October 2003. I worked with many people as co-workers and assistants (see Acknowledgments).

2.2.2. Wildlife observations

Throughout the four years of field work, my colleagues and I observed a total of 87 vertebrate species on the Clatse and Neekas combined, many of which have associations with spawning salmon (Table 2.1). This included at least 14 mammal, 3 amphibian, and 70 bird species. Based on observations in the field by multiple observers I define these vertebrates as either having a direct or indirect association with salmon. Direct uptake of salmon-derived nutrients is indicated by a diet that seasonally includes either live salmon, salmon carcasses, salmon eggs or other animals that have fed directly upon salmon. Examples of the latter include songbirds that feed on fly maggots on salmon carcasses in the forest, and raptors which capture gulls along salmon streams.

Indirect associations with salmon-derived nutrients are more difficult to characterize and may include species that have only passing associations with coastal riparian zones and estuaries with salmon. Salmon-derived nitrogen is detectable in riparian plants (Mathewson et al. 2003: Appendix 2d) and invertebrates (Hocking and Reimchen 2002: Appendix 2a) at Clatse and Neekas, and the salmon nutrient subsidy is associated with increased estuarine, stream and riparian zone productivity (Wipfli et al. 1998; Helfield and Naiman 2001; Gende et al. 2002; Naiman et al. 2002). Thus many vertebrates may use Clatse and Neekas as important feeding areas and obtain salmon-derived nitrogen and other nutrients indirectly. Examples include bears that feed on riparian berries and estuarine grasses in the spring, red squirrels that feed off of Sitka

spruce cones year-round, and migrating and resident songbirds that feed on local plant and invertebrate resources.

Overall, 37 vertebrate species were observed feeding directly on salmon resources (7 mammals, 1 amphibian, 29 birds) with an additional 9 species that may have a direct association with salmon. We also observed 70 species (some overlap with direct species) that may have varying indirect associations with spawning salmon (11 mammals, 3 amphibians, 56 birds) (Table 2.1).

2.2.3. Salmon spawning escapement

The Clatse and Neekas rivers are dominated by high-density returns of pink and chum salmon, with minor runs of coho and the occasional sockeye. On the Clatse from 1991-2000, chum and pink salmon returns averaged 4433 and 14960 individuals respectively. In comparison, average escapement from 1950-59 was almost three times higher for chum (mean = 12700) and twice as high for pink (mean = 29350). Suitable spawning habitat extends for 0.9 km upstream from the estuary whereby a 10 m high waterfall truncates spawning (Manzon and Marshall 1981; DFO Fish Wizard: <http://pisces.env.gov.bc.ca>).

On the Neekas River from 1991-2000, chum and pink salmon returns averaged 29270 and 20738 individuals respectively. In comparison, average escapement from 1950-59 was 33200 for chum and 34950 for pink. Spawning extends for 1.7 km upstream from the estuary on the Neekas whereby an 8m waterfall truncates spawning.

2.2.4. Research plots and vegetation indicator species

In the late summer of 2000 and 2001, I inventoried riparian vegetation in small plots (10 m × 10 m) above and below the waterfalls at both Clatse and Neekas rivers and at two distances from the stream (0-20 m and 90-110 m). These plots were chosen based on similarity in forest structure, canopy cover and slope above and below the falls and were used as my standard sites for my terrestrial invertebrate collections in 2000 and 2001. In total, four habitat blocks were established on each watershed (Above Far; Above Near; Below Near; Below Far) with at least three replicate plots in each block. Most plots ranged from 100 to 250 m above and below the waterfalls on both watersheds. However

on Clatse, plots far from stream above the falls were 400-500m above the falls, and plots far from stream below the falls ranged from 200-500m below the falls. An additional plot close to the stream on Clatse used in 2000 was located 100m upstream from the estuary. Subsets of these plots close to the stream and close to the falls were used in comparisons of plant community structure above and below the falls (Mathewson et al. 2003: Appendix 2d), and in trophic analyses of songbirds (Christie et al. *submitted*). Plots close and far from stream on Clatse were also used to assess moss and liverwort $\delta^{15}\text{N}$ signatures, community structure and diversity (Wilkinson et al. 2005).

Within each plot, understory vascular plant species were identified and percent cover of each visually estimated using two observers. An estimate of cover for each species in each layer (tree, shrub, herb and moss) was agreed. Layers were defined as: 1) Tree layer: all woody species > 10m tall; 2) Shrub layer: all woody species < 10m tall but > 15cm tall; 3) Herb layer: all herbaceous species regardless of height and woody species < 15cm tall; 4) Moss layer: all bryophytes and liverworts (British Columbia Ministry of Environment 1998). On each watershed, I compared the slope, total plant cover of each layer, and plant community richness of each layer among the four habitat blocks (ANOVA's with Tukey post hoc). I also grouped shrub and herb plant species from each plot into soil-nitrogen (poor, rich) and humus-type (Mor, Moder/Mull) indicator categories based on Klinka et al. (1989) (See Chapter 9; Mathewson et al. 2003). Unclassified species, nitrogen-medium indicators, and other humus-indicator species were not included. On each watershed, I compared total cover in each habitat block for each indicator category (ANOVA's with Tukey post hoc). Soil profiles were also dug in representative sites to determine the humus type and original parent material.

All plots close to the stream on both watersheds had negligible slope (5° or less). Mean slope on Clatse far from stream ranged from 20° above the falls to 12.3° below the falls, while at Neekas far from stream blocks averaged 3.2° and 4.7° for above and below the falls respectively. Canopy cover was similar among all habitat blocks on both watersheds (Clatse ANOVA: $F_{3,11} = 0.812$, $p = 0.514$; Neekas ANOVA: $F_{3,14} = 2.136$, $p = 0.141$; Figure 2.3). Shrub cover was higher in blocks above the falls on Clatse (ANOVA: $F_{3,11} = 11.228$, $p = 0.001$), but did not differ among blocks at Neekas (ANOVA: $F_{3,15} = 0.819$, $p = 0.503$) (Figure 2.3). Herb cover was higher on Clatse below the falls near to

the stream than each of the other blocks (ANOVA: $F_{3,11} = 13.610$, $p = 0.001$), while at Neekas, herb cover was marginally higher below falls far from stream than each of the other blocks (ANOVA: $F_{3,15} = 3.614$, $p = 0.038$) (Figure 2.3). Moss cover did not differ among blocks on either watershed (Clatse ANOVA: $F_{3,10} = 2.880$, $p = 0.089$; Neekas ANOVA: $F_{3,15} = 0.946$, $p = 0.443$; Figure 2.3).

A total of 74 vascular and non-vascular plant species including trees and shrubs, herbaceous plants, and mosses and liverworts were inventoried in the riparian plots from the Clatse and Neekas rivers, B.C. (Table 2.2). No predictable differences in species richness were observed for any layer among habitat blocks on each watershed. On the Clatse, the number of species per layer did not differ among habitat blocks (all ANOVA's: $p > 0.05$; Figure 2.4). On the Neekas, tree species diversity was marginally higher below far than in each of the other blocks (ANOVA: $F_{3,15} = 4.474$, $p = 0.020$) while shrub diversity was marginally higher above falls close than in each of the other blocks (ANOVA: $F_{3,15} = 3.716$, $p = 0.035$). Herb and moss layer diversity on the Neekas did not differ among blocks (ANOVA's: $p > 0.05$; Figure 2.4).

At both Clatse and Neekas, percent cover of soil-nitrogen and humus indicator species differed among blocks (Figure 2.5, Figure 2.6). At Clatse, highest coverage of nitrogen-poor species occurred above the falls near to the stream while highest coverage of nitrogen-rich species occurred below the falls near to the stream (ANOVA Poor: $F_{3,11} = 45.804$, $p < 0.001$; ANOVA Rich: $F_{3,11} = 5.708$, $p = 0.013$). On the Neekas, highest coverage of nitrogen-poor species occurred below the falls far from the stream while highest coverage of nitrogen-rich species occurred below the falls near to the stream (ANOVA Poor: $F_{3,15} = 7.161$, $p = 0.003$; ANOVA Rich: $F_{3,15} = 30.823$, $p < 0.001$).

Patterns measured for indicators of humus types were comparable to those found for nitrogen indicators. On Clatse, % cover of Mor-humus indicators was higher above the falls than below (ANOVA: $F_{3,11} = 14.177$, $p < 0.001$), while Moder/Mull-humus indicator species had highest cover below falls near to the stream (ANOVA: $F_{3,11} = 5.684$, $p = 0.013$). On the Neekas, % cover of Mor-humus indicators was highest above the falls far from stream (ANOVA: $F_{3,15} = 5.185$, $p = 0.012$), while Moder/Mull-humus indicator cover was highest below falls near to the stream (ANOVA: $F_{3,15} = 51.662$, $p < 0.001$).

Soil profiles dug in representative plots confirmed the indicator analysis. Mor humus forms predominated on the Clatse and Neekas rivers above the falls with matted LFH (decomposing litter) horizons ranging from 10-25cm thick. Below the falls, ligno-, lepto- and mull-moder humus forms predominated close to the stream with a thin LFH 3-10cm thick and an Ah (mineral horizon enriched in organic matter) 5-20cm thick (British Columbia Ministry of Environment 1998). The parent material at all plots close to the stream was dominated by coarse alluvial sand interspersed with a few large rock fragments. Morrainal silt deposits increased with increasing distance from the stream.

Overall, these preliminary results suggest that there are few predictable differences in vegetation structure or species richness among the habitat blocks on the Clatse and Neekas rivers, but that there are predictable differences in soil types and vegetation community composition. Percent cover of nitrogen-rich and Moder/Mull-humus indicator species was highest below the waterfalls and near to the stream on both watersheds. This suggests that the annual input of nutrients from salmon has favoured plant species that prefer richer soils with higher rates of nutrient turnover over other species found on more typical acidic and nutrient-deficient forest soils (further discussion throughout thesis and Mathewson et al. 2003; Wilkinson et al. 2005).

2.2.5. Ripley Bay Creek control

Ripley Bay Creek (52° 25' 37.5"N; 127° 53' 10.6"W), located in Roscoe inlet near to Clatse Creek, was used sporadically as a control watershed for the Clatse and Neekas rivers (Figure 2.2). The Ripley has 7m falls followed by a cascade at the mouth that prevents Pacific salmon from entering this system. On several occasions I collected representative invertebrate specimens for isotope analysis. Collections for the moss and liverwort study also took place on this watershed (Wilkinson et al. 2005: Appendix 2e). There is a Heiltsuk cabin in the estuary of Ripley and at times we used this as a place of refuge and sanctuary.

2.3. Midcoast watersheds

From September 2nd to 24th 2000, I visited 29 salmon-bearing watersheds as a part of a research expedition through the mainland midcoast and Haida Gwaii (Figures 2.7, 2.8, 2.9). In the mainland midcoast region I collected representative invertebrate specimens from Quartcha Creek (52° 30' 51.3"N; 127° 50' 19.5"W) in Roscoe Inlet, Riordan creek (53° 26' 0.3"N; 128° 57' 29.3"W) on Gribbell Island, Evelyn (53° 35' 3.7"N; 128° 57' 17.3"W) and Little Tillhorn (53° 33' 5.1"N; 129° 10' 3.9"W) creeks on Hawkesbury Island, the Kitkiata (53° 38' 20.3"N; 129° 16' 17.2"W), Kiskosh (53° 34' 33.7"N; 129° 20' 58.7"W) and Hartley Bay (53° 25' 32.6"N; 129° 15' 5.1"W) creeks on the mainland near the community of Hartley Bay, Belowe (53° 28' 32.3"N; 129° 28' 31.9"W) and Kumuleon (53° 52' 17.6"N; 129° 57' 48.9"W) rivers off of Grenville Channel, the Khutzeymateen River (54° 37' 23.6"N; 129° 53' 43.5"W) and Larch Creek (54° 36' 3.8"N; 129° 56' 8.2"W) in Khutzeymateen Inlet, the Ensheshese River (54° 30' 16.4"N; 130° 13' 46.3"W) in Work Channel, and La Hou Creek (54° 29' 55.2"N; 130° 26' 16.8"W) near Prince Rupert (Figure 2.7). I also collected specimens from watersheds in Haida Gwaii including Government (53° 7' 54.8"N; 132° 20' 48.2"W), Salmon (52° 42' 13.6"N; 131° 48' 55.7"W), Echo (52° 41' 30.8"N; 131° 46' 18.3"W), Kostan (52° 34' 45.2"N; 131° 42' 37.3"W), Hutton (52° 29' 58.2"N; 131° 33' 11.5"W), Matheson (52° 26' 27.7"N; 131° 28' 35.7"W), Skaat (52° 22' 45.8"N; 131° 28' 35.7"W), Bag Harbour (52° 20' 38.9"N; 131° 22' 14.7"W), Louscoone (52° 14' 18.3"N; 131° 17' 21.8"W), Sedmond (52° 12' 11.4"N; 131° 9' 11.7"W), Surprise (52° 15' 41.7"N; 131° 13' 8.5"W) and Harriet (52° 17' 28.5"N; 131° 12' 49.6"W) creeks on Moresby Island, Skedans Creek (52° 56' 49.8"N; 131° 38' 31.5"W) on Louise Island, and Windy Bay (52° 41' 29.7"N; 131° 27' 28.9"W) and Gate (52° 39' 46.9"N; 131° 27' 40.3"W) creeks on Lyell Island (Figures 2.8 and 2.9). All of these watersheds lie in the Coastal Western Hemlock Biogeoclimatic Zone, with mean annual temperature of approximately 8°C, and annual precipitation usually above 4000 mm (Green and Klinka 1994). Watersheds on the mainland typically lie in the boundary between the central very-wet hypermaritime (CWHvh2) and the submontane very wet maritime (CWHvm1) subzones, while those on Moresby Island lie in the boundary of the central very-wet hypermaritime (CWHvh2) and submontane wet hypermaritime (CWHwh1) subzones (Green and Klinka 1994). The Khutzeymateen

River is the largest of all watersheds investigated and is characterized as a 4th order system with several salmon-bearing tributaries. All others, with the exception of Evelyn creek (a small 4th order system), are classified as 1st to 3rd order creeks or rivers. Data from this trip are presented in Chapter 9.

2.4. Goldstream River

Goldstream River (48° 29' 1.5"N; 123° 32' 50.8"W) is located close to Victoria at the south end of Saanich inlet on southern Vancouver Island and was used sporadically as a comparison to other sites. While all watersheds in Clayoquot Sound and on the central coast occur in the wet Coastal Western Hemlock zone, Goldstream occurs in the Coastal Douglas Fir zone with yearly precipitation ranging from 700 to 1000 mm (Green and Klinka 1994). Goldstream has spawning populations of chum and coho salmon that spawn from October through early December, but due to human disturbance does not support populations of bears that actively transport carcasses into the forest. Chum salmon dominate this system with mean returns from 1990-1999 of 31 305 fish (DFO Fish Wizard: <http://pisces.env.gov.bc.ca>). Spawning extends for 4km upstream to the base of a waterfall. In 2000, I collected several invertebrate species from experimentally-placed chum salmon carcasses.

2.5. Seabird Colonies

The input of marine-derived nutrients to seabird breeding colonies on islands comprises another example of a marine-terrestrial nutrient subsidy throughout the northern Pacific. As a member of the September 2000 research expedition described above, I visited three seabird colonies in the Midcoast/ Haida Gwaii region. These included Lucy Island (54° 18' N; 130° 37' W) off of Prince Rupert, and Bolkus (52° 19' 26"N; 131° 16' 37"W) and Rankine (52° 15' 29"N; 131° 03' 33"W) islands off of southeast Moresby Island. Lucy Island is 24 ha in size and supports the largest breeding colony of rhinoceros auklets (*Cerorhinca monocerata*) in coastal British Columbia (25,299 ± 1337 pairs: Rodway and Lemon 1991). It also supports colonies of pigeon guillemots, glaucous-winged gulls and black oystercatchers. Rankine and Bolkus islands support breeding populations of ancient murrelets (*Synthliboramphus antiquus*), Cassin's

auklets (*Ptychoramphus aleuticus*) and rhinoceros auklets totalling 132,600 and 22,240 burrow nesters respectively (Hartman and Eastman 1999). Rankine and Bolkus islands are 63.1 ha and 74.5 ha in size. Of the three islands, Lucy has the highest breeding density of at least 2108 burrow nesters per hectare (bn/ha), closely followed by Rankine at 2101 bn/ha, with Bolkus having the lowest density (299 bn/ha).

I collected various terrestrial invertebrates from these islands and conducted stable isotope analysis on several millipede specimens (Parajulidae: $n = 3$ on Rankine and Bolkus; $n = 4$ on Lucy). I compared $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures among the three islands (ANOVA's) and investigated the relationship between breeding bird density and $\delta^{15}\text{N}$ signatures in millipedes (Linear Regression). I also compared $\delta^{15}\text{N}$ signatures on the islands to signatures in parajulid millipedes collected from above and below the waterfall barrier to salmon on the Clatse and Neekas rivers.

$\delta^{15}\text{N}$ signatures in millipedes differed by seabird island (ANOVA: $F_{2,7} = 17.00$, $p = 0.002$) and were positively predicted by breeding bird density (Regression: $F_{1,8} = 6.02$, $p = 0.04$, $R^2 = 0.429$) (Figure 2.10). $\delta^{13}\text{C}$ signatures did not vary by seabird island (ANOVA: $F_{2,7} = 1.57$, $p = 0.274$). $\delta^{15}\text{N}$ signatures on seabird islands were comparable or higher than those observed below the falls from the Clatse and Neekas. On Clatse and Neekas, mean signatures above the falls were 0.71‰ and 0.50‰ respectively, while below the falls, mean $\delta^{15}\text{N}$ signatures varied from 3.93‰ to 8.87‰. Bolkus, Rankine and Lucy averaged 6.62‰, 7.93‰ and 11.59‰ respectively (Figure 2.10).

Elevated $\delta^{15}\text{N}$ signatures have been observed in multiple taxa from seabird colonies elsewhere (for example: Cocks et al. 1998). In that particular study, values in soil were found as high as +26‰. $\delta^{15}\text{N}$ values of bird excreta and carcasses may only occur at near 10‰ with additional enrichment in colony biota occurring by the process of ammonia volatilization. Rapid volatilization of ammonia from guano deposited by seabirds results in the loss of isotopically light nitrogen, with remaining soil highly enriched in $\delta^{15}\text{N}$ (Cocks et al. 1998). For this reason, comparing $\delta^{15}\text{N}$ values from seabird colonies and salmon sites may not accurately represent the extent of marine input to the terrestrial community. Nevertheless, in both marine-terrestrial subsidies, $\delta^{15}\text{N}$ values appear to be largely predicted by the intensity (i.e., density) of the marine flux.

Figure 2.1. Study watersheds for the Salmon-Forest project in Clayoquot Sound, Vancouver Island.

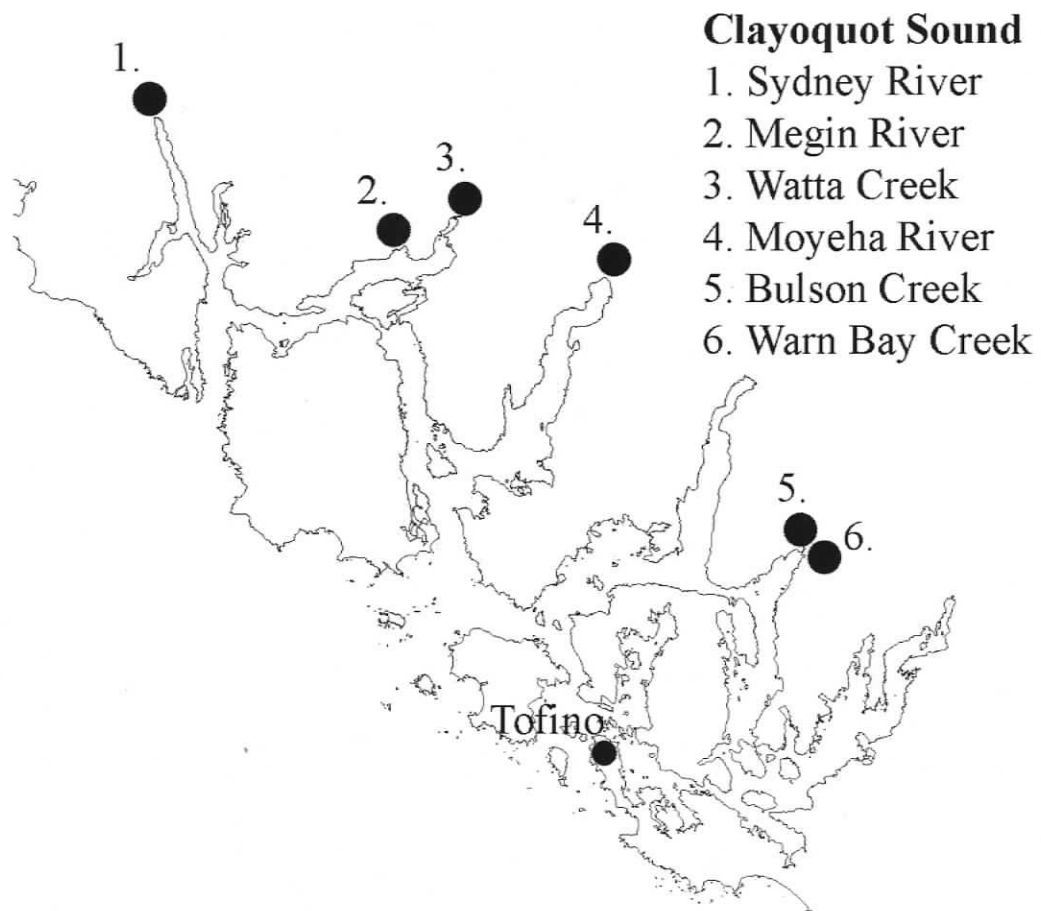


Figure 2.2. Study watersheds near Bella Bella, B.C. for the Salmon-Forest project. The Clatse and Neekas rivers were the two dominant study sites for this project.

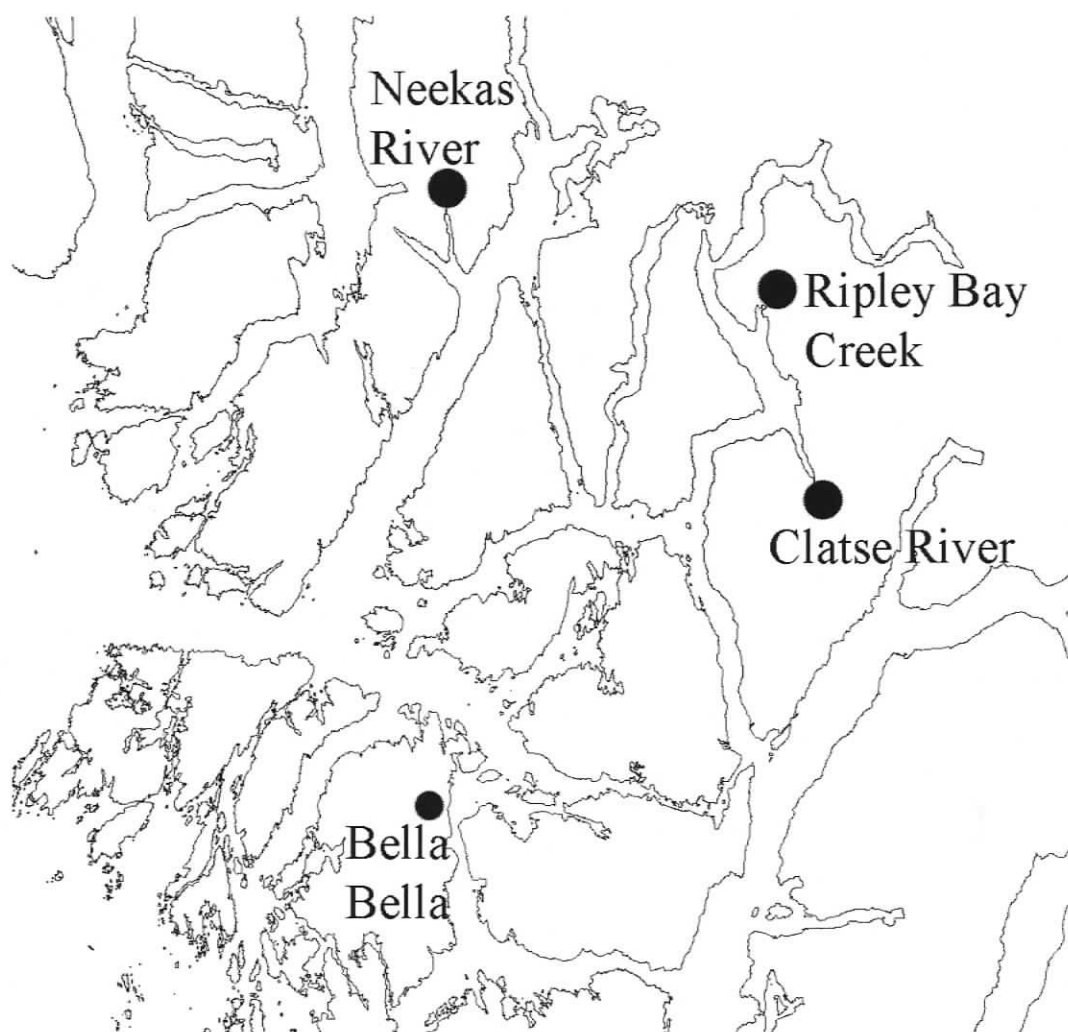


Figure 2.3. Percent cover ($\pm$ SE) of the canopy, shrub, herb and moss layers in research plots on the Clatse and Neekas rivers, B.C. Letters (A,B) indicate homogeneous subsets derived from Tukey's post hoc tests.

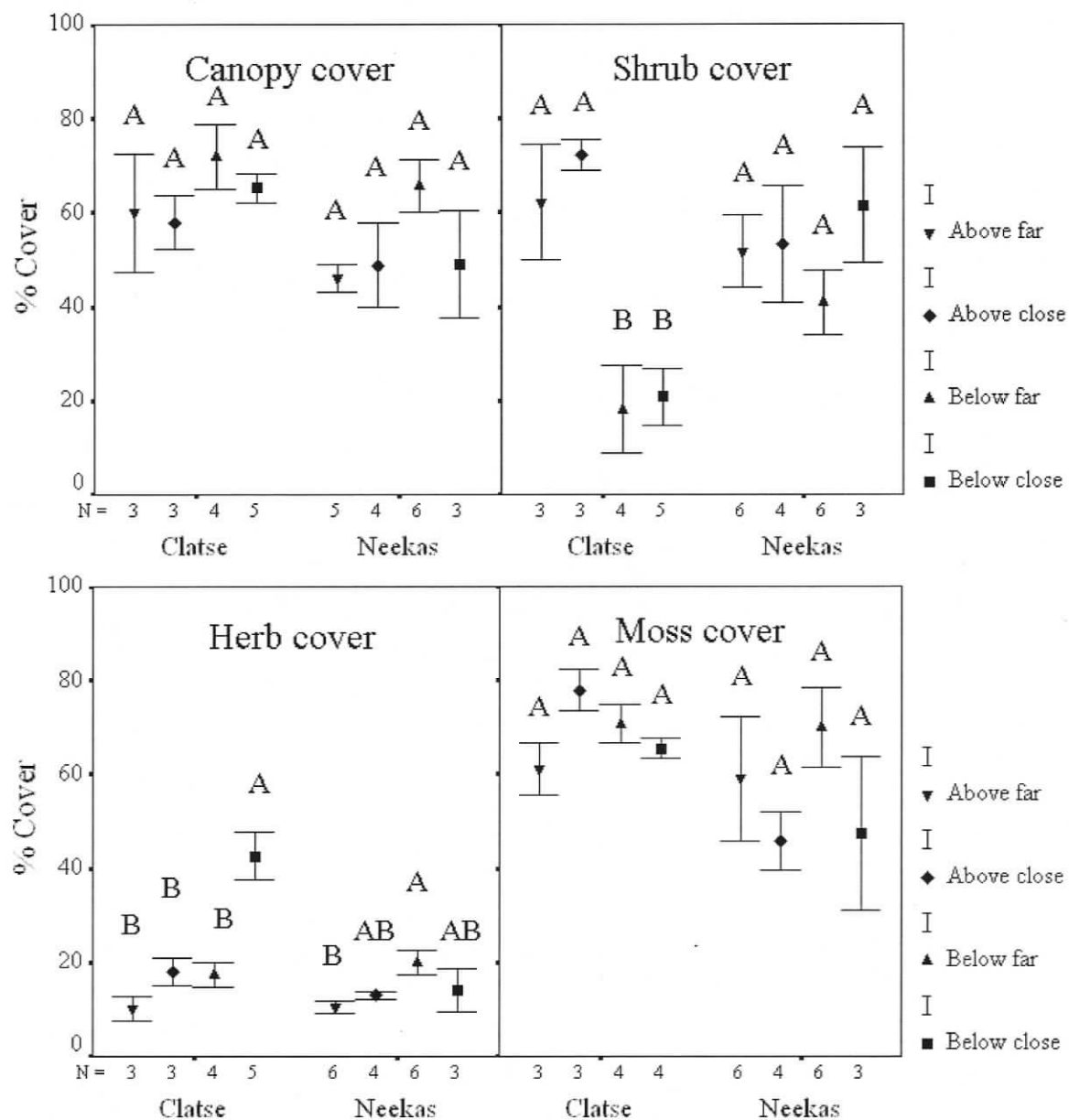


Figure 2.4. Species richness ($\pm$ SE) of the canopy, shrub, herb and moss layers in research plots on the Clatse and Neekas rivers, B.C. Letters (A,B) indicate homogeneous subsets derived from Tukey's post hoc tests.

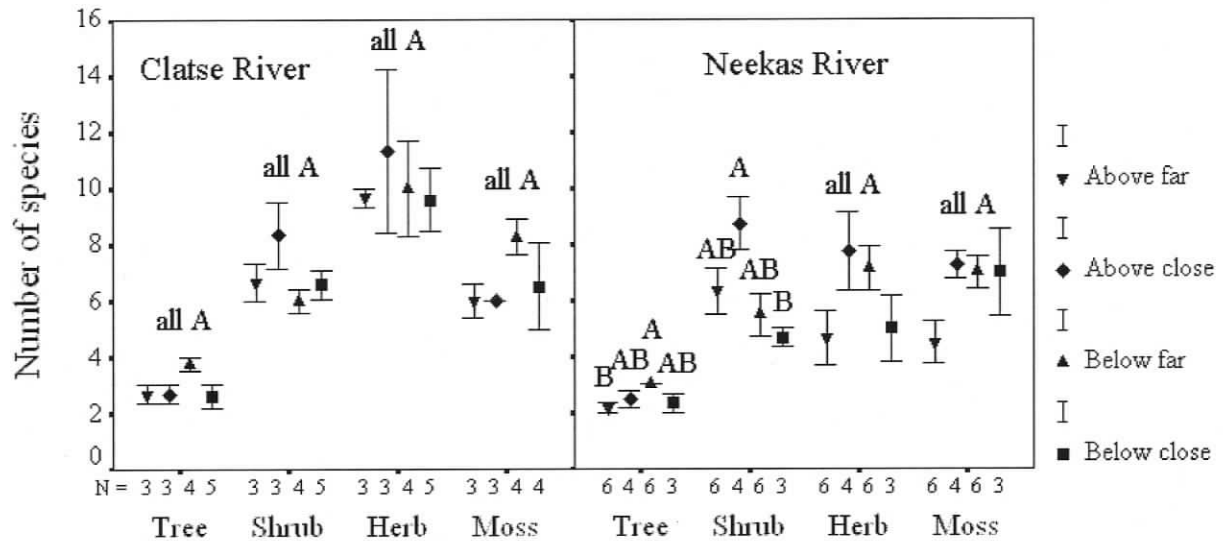


Figure 2.5. Percent cover ($\pm$ SE) of nitrogen-rich and nitrogen-poor soil indicator plant species in research plots on the Clatse and Neekas rivers, B.C. Letters (A,B,C) indicate homogeneous subsets derived from Tukey's post hoc tests.

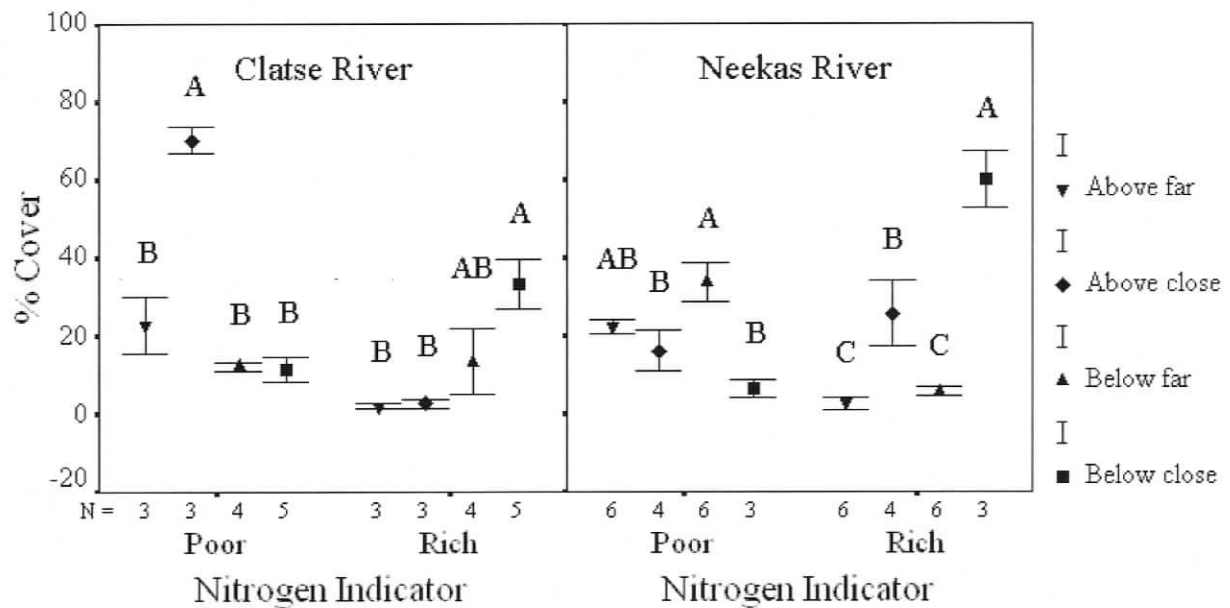


Figure 2.6. Percent cover ($\pm$ SE) of Mor-humus and Moder/Mull-humus indicator plant species in research plots on the Clatse and Neekas rivers, B.C. Letters (A,B,C) indicate homogeneous subsets derived from Tukey's post hoc tests.

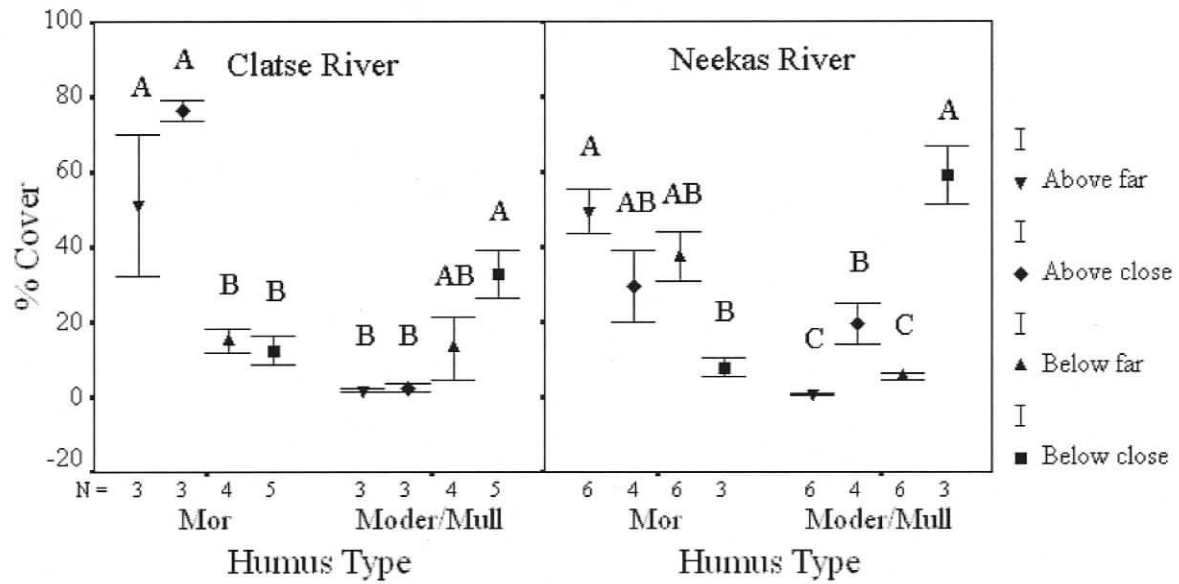


Figure 2.7. Study watersheds visited in the fall of 2000 on the mainland midcoast of B.C. near the community of Prince Rupert.

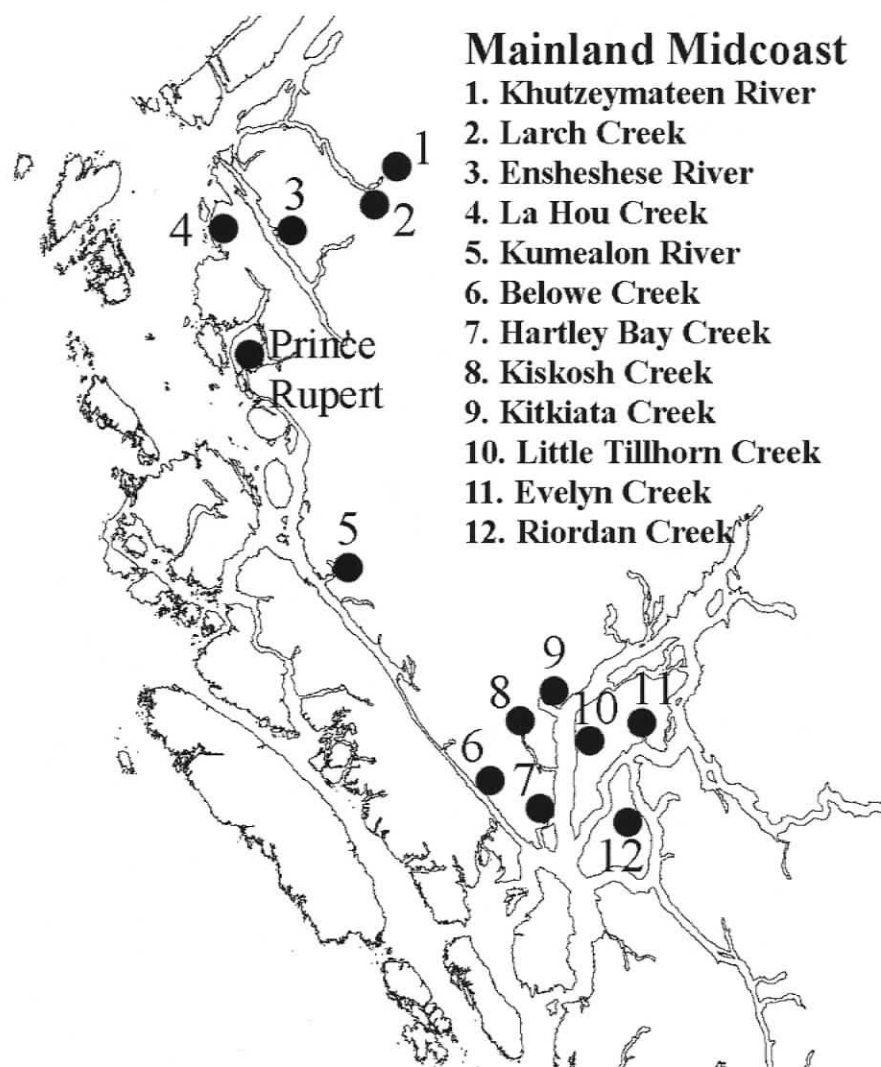


Figure 2.8. Study watersheds visited in the fall of 2000 on North Moresby Island, Haida Gwaii, B.C.

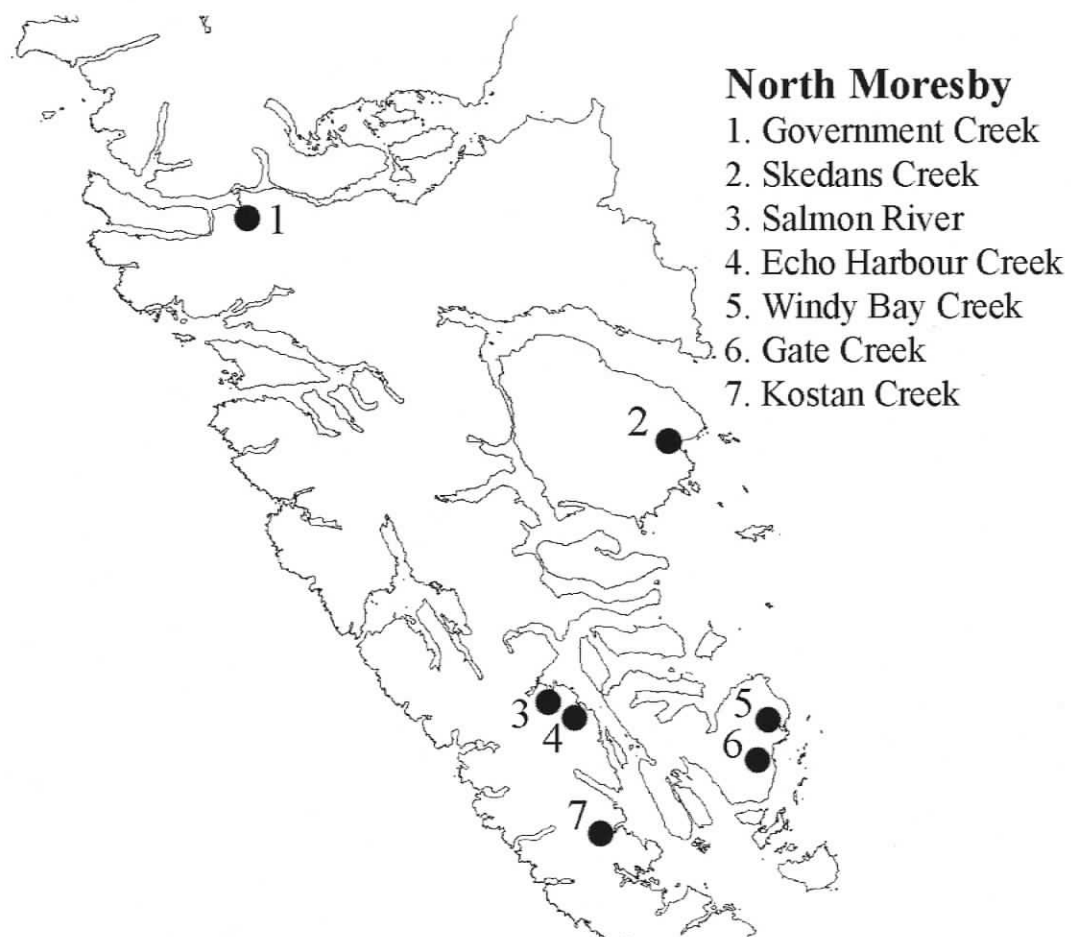


Figure 2.9. Study watersheds visited in the fall of 2000 on South Moresby Island, Haida Gwaii, B.C.

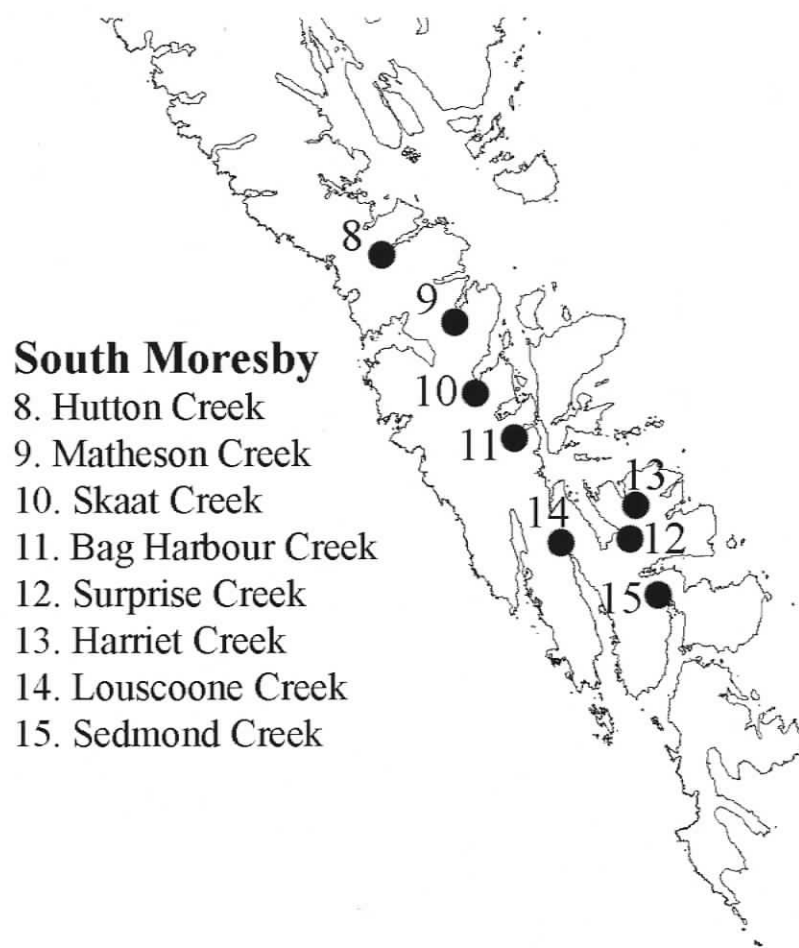


Figure 2.10. $\delta^{15}\text{N}$ stable isotope signatures in millipedes (Parajulidae) collected from three seabird colony islands (Bolkus, Rankine and Lucy), and from above and below waterfall barriers to salmon on two productive watersheds (Clatse and Neekas rivers) in British Columbia. Lucy Island has the highest breeding bird density followed by Rankine and then Bolkus. Neekas has higher spawning density than Clatse. Both demonstrate marine subsidies of nitrogen to terrestrial habitats.

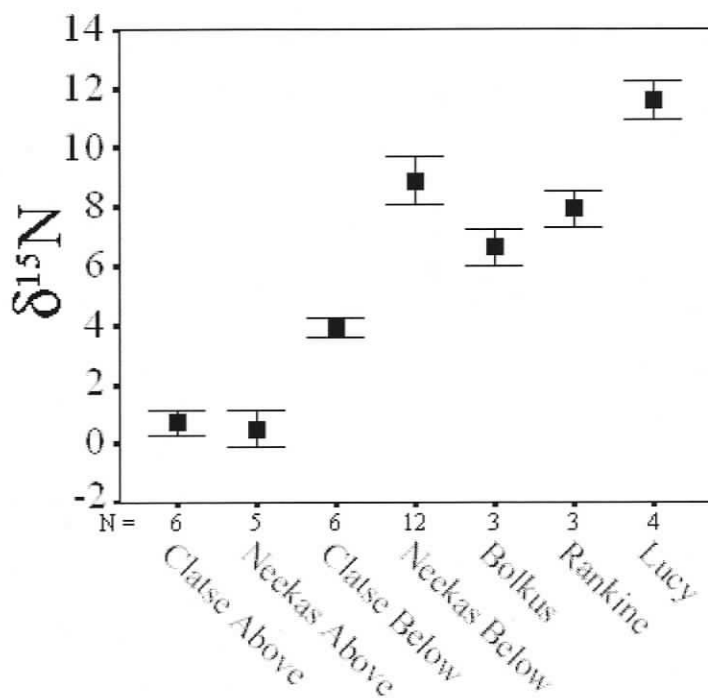


Table 2.1. Vertebrate species observed on the Clatsop and Neekas rivers 2000-2003 and their direct and indirect associations with spawning Pacific salmon.

Vertebrate species:	Direct Effects: diet includes salmon carcasses, eggs, fly maggots or other salmon consumers	Indirect Effects: links with productive riparian zone or estuary	Other notes:
Black bear	live salmon, carcasses, eggs	riparian berries, estuarine plants	primary vector of salmon nutrients into forests
Grizzly bear	historical salmon consumer at these sites	estuarine plants	only observed in spring
Gray wolf	live salmon, carcasses	location for deer predation	consistently observed on both watersheds
American marten	carcasses	riparian fish, songbirds, amphibians, rodents	
Mink	unknown but may consume carcasses	riparian fish, songbirds, amphibians, rodents	
River otter	live salmon, carcasses	other stream and estuarine fish	
Fisher	unknown but may consume carcasses		observed once on Neekas
Bats- <i>Myotis</i> spp.	stream and carcass derived insects	stream and carcass derived insects	
Dusky shrew	carcasses, fly maggots	riparian insects	captured in traps baited with salmon
Deer mouse			common in camp
Porcupine		estuarine plants	common in estuary
Sitka black-tailed deer		riparian and estuarine plants	
Red squirrel		sitka spruce cones	more common below the falls
Harbour seal	live salmon		
Rough-skinned newt	carcasses, fly maggots	riparian insects	observed on salmon carcasses
Northwestern salamander	possibly carcasses, fly maggots	riparian insects	
Western toad	possibly carcasses, fly maggots	riparian insects	
Bald eagle	live salmon, carcasses, gulls feeding on salmon		
Common raven	carcasses, eggs		
Northwestern crow	carcasses, eggs		
Glaucous-winged gull	carcasses, eggs		
Thayer's gull	carcasses, eggs		
Mew gull	carcasses, eggs		
Bonaparte's gull	eggs		interesting social hierarchy on Neekas in fall
Herring gull	carcasses, eggs,		more abundant on Clatsop
			most abundant gull
			more abundant on Clatsop

Table 2.1. continued.

Ring-billed gull	carcasses, eggs		not confirmed
California gull	carcasses, eggs		
Great blue heron	aquatic invertebrates, carcasses		easily spooked on stream
Belted kingfisher	salmon fry		common year-round
Common merganser	salmon fry		very common
Common loon	possibly salmon fry		
Marbled murrelet			
Canada Goose			
Mallard	possibly salmon fry		
Common goldeneye	possibly salmon fry		
Harlequin duck	salmon fry		
Osprey	live salmon		
Sharp-shinned hawk	crows feeding on salmon		
Red-tailed hawk	carcasses, gulls feeding on salmon		
Northern Pigmy-owl	unknown		
Barred owl	unknown		
Western-screech owl	unknown		
Red crossbill			
Winter wren	fly maggots		on Clatsop
Golden-crowned kinglet			on both watersheds
Ruby-crowned kinglet			
Chestnut-backed chickadee			
Varied thrush	maggots, salmon eggs		
Swainson's thrush	maggots		
Hermit thrush	maggots		
American robin	probably maggots but not confirmed		
Townsend's warbler			
Yellow warbler			
Yellow-rumped warbler			
Orange-crowned warbler			
		aquatic invertebrates and fish other stream and estuarine fish other estuarine fish other estuarine fish nesting sites, other estuarine fish estuarine plants	
		aquatic invertebrates and fish aquatic invertebrates and fish other estuarine fish	
		estuarine and riparian invertebrates, mammals estuarine and riparian mammals estuarine and riparian mammals conifer cones	
		riparian invertebrates riparian invertebrates riparian invertebrates riparian invertebrates riparian invertebrates, berries riparian invertebrates, berries riparian invertebrates, berries riparian invertebrates, berries riparian invertebrates riparian invertebrates riparian invertebrates riparian invertebrates	

Table 2.1. continued.

Common yellowthroat		riparian invertebrates	
MacGillivray's warbler		riparian invertebrates	
Song sparrow	maggots	riparian invertebrates, berries, seeds	
Lincoln's sparrow		riparian invertebrates, berries, seeds	
White-crowned sparrow	maggots	riparian invertebrates, berries, seeds	
White-throated sparrow	maggots	riparian invertebrates, berries, seeds	
Golden-crowned sparrow	maggots	riparian invertebrates, berries, seeds	
Fox sparrow		riparian invertebrates, berries, seeds	
Dark-eyed Junco		riparian invertebrates, berries, seeds	
Savannah Sparrow	maggots	riparian invertebrates	rare/migrant
Red-breasted nuthatch		riparian invertebrates	
Cedar waxwing		riparian invertebrates	
Warbling vireo		riparian invertebrates	
Brewer's Blackbird		riparian invertebrates	rare/migrant
Pine Siskin		riparian invertebrates	
Brown creeper		riparian invertebrates	rare
Steller's jay	maggots, salmon eggs		cached salmon bits in trees
Gray Catbird			rare/migrant
Violet-green swallow		riparian invertebrates	
Barn swallow		aquatic invertebrates	
American pipet		aquatic invertebrates	
Pacific-slope flycatcher		aquatic invertebrates	
Hammond's flycatcher		riparian invertebrates	associated with emerging blowflies in spring?
Northern flicker		riparian invertebrates	associated with emerging blowflies in spring?
Red-breasted sapsucker		riparian invertebrates	
Hairy woodpecker		riparian invertebrates	
Rufous hummingbird		nectar	
Western sandpiper		aquatic invertebrates	
Least sandpiper	maggots	aquatic invertebrates	rocky riparian
Spotted sandpiper	maggots	aquatic invertebrates	rocky riparian
Greater yellowlegs		aquatic invertebrates	
American dipper	salmon eggs and fry	aquatic invertebrates	

Table 2.2. Vascular and non-vascular plant species recorded from research plots on the Clatsop and Neekas rivers, B.C.

<i>Abies amabilis</i>	<i>Linnaea borealis</i>	<i>Ribes bracteosum</i>
<i>Alnus rubra</i>	<i>Listera caurina</i>	<i>Riccardia multifida</i>
<i>Athyrium filix-femina</i>	<i>Listera cordata</i>	<i>Rubus parviflorus</i>
<i>Atrichum</i> sp.	<i>Lonicera involucrata</i>	<i>Rubus pedatus</i>
<i>Blechnum spicant</i>	<i>Luzula multiflora</i>	<i>Rubus spectabilis</i>
<i>Bromus</i> sp.	<i>Luzula parviflora</i>	<i>Sambucus racemosa</i>
<i>Carex spectabilis</i>	<i>Lycopodium clavatum</i>	<i>Smilacina stellata</i>
<i>Chamaecyparis nootkatensis</i>	<i>Lysichiton americanum</i>	<i>Sorbus sitchensis</i>
<i>Circaea alpina</i>	<i>Maianthemum dilatatum</i>	<i>Sphagnum capillifolium</i>
<i>Clintonia uniflora</i>	<i>Malus fusca</i>	<i>Sphagnum girgensohnii</i>
<i>Conocephalum conicum</i>	<i>Menziesia ferruginea</i>	<i>Sphagnum squarrosum</i>
<i>Coptis asplenifolia</i>	<i>Oplopanax horridus</i>	<i>Streptopus amplexifolius</i>
<i>Cornus canadensis</i>	<i>Pellia neesiana</i>	<i>Streptopus roseus</i>
<i>Dicranum scoparium</i>	<i>Picea sitchensis</i>	<i>Taxus brevifolia</i>
<i>Dryopteris expansa</i>	<i>Pinus contorta</i> var. <i>contorta</i>	<i>Thelypteris phegopteris</i>
<i>Gaultheria shallon</i>	<i>Plagiochila porelloides</i>	<i>Thuja plicata</i>
<i>Gymnocarpium dryopteris</i>	<i>Plagiomnium insigne</i>	<i>Tiarella trifoliata</i>
<i>Heracleum lanatum</i>	<i>Plagiothecium undulatum</i>	<i>Tsuga heterophylla</i>
<i>Herbertus aduncus</i>	<i>Pogonatum alpinum</i>	<i>Tsuga mertensiana</i>
<i>Hookeria lucens</i>	<i>Pogonatum</i> sp.	<i>Urtica dioica</i>
<i>Hylocomium splendens</i>	<i>Polystichum munitum</i>	<i>Vaccinium alaskaense</i>
<i>Hypnum subimponens</i>	<i>Polytrichum</i> sp.	<i>Vaccinium ovalifolium</i>
<i>Kindbergia oregana</i>	<i>Pteridium aquilinum</i>	<i>Vaccinium parvifolium</i>
<i>Kindbergia praelonga</i>	<i>Rhizomnium glabrescens</i>	<i>Viola glabella</i>
<i>Leucanthemum vulgare</i>	<i>Rhytidiadelphus loreus</i>	

Chapter 3:

Salmon-derived nitrogen in terrestrial invertebrates from coniferous forests of the Pacific Northwest

3.1. Abstract

Bi-directional flow of nutrients between marine and terrestrial ecosystems can provide essential resources that structure communities in transitional habitats. On the Pacific coast of North America, anadromous salmon (*Oncorhynchus* spp.) constitute a dominant nutrient subsidy to aquatic habitats and riparian vegetation, although the contribution to terrestrial habitats is not well established. I use a dual isotope approach of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to test for the contribution of salmon nutrients to multiple trophic levels of litter-based terrestrial invertebrates below and above waterfalls that act as a barrier to salmon migration on two watersheds in coastal British Columbia. Invertebrates varied predictably in $\delta^{15}\text{N}$ with enrichment of 3–8‰ below the falls compared with above the falls in all trophic groups on both watersheds. I observed increasing $\delta^{15}\text{N}$ levels in our invertebrate groups with increasing consumption of dietary protein. Invertebrates varied in $\delta^{13}\text{C}$ but did not always vary predictably with trophic level or habitat. From 19.4 to 71.5% of invertebrate total nitrogen was originally derived from salmon depending on taxa, watershed, and degree of fractionation from the source. Enrichment of $\delta^{15}\text{N}$ in the invertebrate community below the falls in conjunction with the absence of $\delta^{13}\text{C}$ enrichment suggests that enrichment in $\delta^{15}\text{N}$ occurs primarily through salmon-derived nitrogen subsidies to litter, soil and vegetation N pools rather than from direct consumption of salmon tissue or salmon tissue consumers. Salmon nutrient subsidies to terrestrial habitats may result in shifts in invertebrate community structure, with subsequent implications for higher vertebrate consumers, particularly the passerines.

3.2. Introduction

Nutrient cycling between geographically distinctive ecosystems can produce zones of major productivity and biodiversity. It is generally recognized that downstream transport of terrestrial nutrients into marine estuaries produces one of the world's most productive habitats, but recent investigations suggest that the reverse flow, from marine to terrestrial habitats, may also be exceptionally important in structuring highly diverse coastal ecosystems (Wilson et al. 1998; Gende et al. 2002; Reimchen et al. 2003).

Every year in the Pacific Northwest anadromous salmon (*Oncorhynchus* spp.) transport marine-derived nutrients from the North Pacific Ocean into coastal ecosystems. This salmon nutrient subsidy extends from aquatic habitats into riparian forests, and may be ecologically equivalent to the migration of the wildebeest on the Serengeti (Reimchen 1995). Studies in aquatic and terrestrial ecosystems reveal that salmon contribute highly to yearly protein intake for many vertebrates (Wilson and Halupka 1995; Ben-David et al. 1997; Hilderbrand et al. 1999a; Cederholm et al. 2000; Darimont and Reimchen 2002) and invertebrates (Bilby et al. 1996; Reimchen et al. 2003), and provide substantial nutrient inputs to limnetic food webs (Kline et al. 1990; Kline et al. 1993; Bilby et al. 1996; Wipfli et al. 1998), and riparian vegetation (Ben-David et al. 1998b; Hilderbrand et al. 1999b; Helfield and Naiman 2001; Bilby et al. 2003; Mathewson et al. 2003; Reimchen et al. 2003), emphasizing the ecological magnitude of this resource for coastal communities.

Transfer of salmon nutrients into terrestrial habitats occurs primarily through bear (*Ursus* spp.) mediated salmon carcass transfer (Reimchen 1992; 1994; 2000) and urine deposition (Hilderbrand et al. 1999b), but can also occur as a result of flooding events (Ben-David et al. 1998b), hyporheic zone transfer (O'Keefe and Edwards 2003), or the activities of other scavengers and predators (Ben-David et al. 1998a; Cederholm et al. 2000; Darimont et al. 2003). Since nitrogen is often limiting in coastal temperate rainforests of the Pacific Northwest (Waring and Franklin 1979), this salmon nutrient pulse to riparian forests can increase riparian primary productivity, vegetation and litter quality, and soil nutrient capital, and can alter vegetation community structure (Ben-David et al. 1998b; Hilderbrand et al. 1999b; Helfield and Naiman 2001; Bilby et al. 2003; Mathewson et al. 2003).

Most studies in forest ecosystems adjacent to salmon streams have so far been limited to vegetational use of salmon nutrients and have ignored other potential food web beneficiaries, particularly terrestrial invertebrates. Macro-invertebrates of coastal coniferous forests of the Pacific Northwest, including insects, arachnids, myriapods, annelid worms, isopods and gastropods, comprise the base of the myriad of nutrient and energy pathways from primary producers through to higher vertebrate consumers, and are highly important in many ecosystem processes including herbivory, litter decomposition, and nutrient cycling (Furniss and Carolin 1977; Spiers et al. 1986; Cárcamo et al. 2000). There is a diverse community of invertebrates directly associated with the consumption and decay of salmon carcasses. However, most invertebrates of coastal forests and riparian zones have no direct association with salmon, and in this case salmon derived-nitrogen may be incorporated indirectly into the tissues of these invertebrates through consumption of vegetation, litter, soil or other invertebrates enriched in salmon nitrogen.

I use a dual isotope approach of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to assess: a) the extent of utilization of salmon-derived nitrogen and carbon by various trophic groups in a terrestrial invertebrate forest litter community; and b) the mechanism of salmon nutrient utilization by invertebrates; either directly through salmon tissue consumption, or indirectly through utilization of salmon nitrogen sequestered into riparian vegetation or soil N pools. I compare invertebrate isotope values above and below waterfalls at two watersheds as a means of examining ecological discontinuities that may occur in litter-based macro-invertebrates between salmon and salmon-free forest sites, and speculate on possible implications to invertebrate community structure and higher vertebrate consumers. I also discuss components of invertebrate isotopic variability as it relates to microspatial variability in $\delta^{15}\text{N}$, invertebrate trophic structure, and invertebrate niche.

3.3. Methods

3.3.1 Site Description

Two salmon bearing streams were investigated- the Clatse ($52^{\circ} 20.6'\text{N}$; $127^{\circ} 50.3'\text{W}$) and Neekas Rivers ($52^{\circ} 28.4'\text{N}$; $128^{\circ} 8.0'\text{W}$), on the mid-coast of British Columbia, near Bella Bella, Canada. Both watersheds occur in the Coastal Western Hemlock Biogeoclimatic Zone along the boundary between the central very wet

hypermaritime (CWHvh2) and submontane very wet maritime (CWHvm1) subzones (Green and Klinka 1994). Climate is cool and wet, with mean annual temperature of approximately 8°C, and mean annual precipitation above 4000 mm (Environment Canada 2001). Dominant tree species include western hemlock (*Tsuga heterophylla*), sitka spruce (*Picea sitchensis*), amabilis fir (*Abies amabilis*), western red cedar (*Thuja plicata*), and red alder (*Alnus rubra*). Common understory species include Alaskan blueberry (*Vaccinium alaskaense*), red huckleberry (*V. parvifolium*), false azalea (*Menziesia feruginea*), deer fern (*Blechnum spicant*), bunchberry (*Cornus canadensis*), lanky moss (*Rhytidiadelphus loreus*), step moss (*Hylocomium splendens*), and common green sphagnum (*Sphagnum girgensohnii*) on zonal sites, and salmonberry (*Rubus spectabilis*), red elderberry (*Sambucus racemosa*), stink current (*Ribes bracteosum*), and spiny-wood fern (*Dryopteris expansa*) on nutrient rich sites. Deep acidic soils predominate with high organic matter content due to low rates of decomposition. Soil deposits are typically alluvial or glacial in origin, are heavily leached, and often contain iron deposits in the B layer. Mor humus types are most common with a thick layer of moss, but moder/mull humus forms occur in nutrient rich sites along the salmon spawning channel.

Both the Clatse and Neekas watersheds are dominated by high-density returns of pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon, with minor runs of coho (*O. kisutch*) and the occasional sockeye (*O. nerka*). In the last ten years, pink and chum salmon returns on the Clatse River average 17000 and 5000 individuals respectively. Chum salmon constitute the majority of spawning biomass on the Neekas (mean = 30000). Mean pink salmon returns on the Neekas River vary from an average of 33000 on even years to an average of 2700 on odd years (Department of Fisheries and Oceans Escapement data: 1990-1999). Suitable spawning habitat extends for 2.1km on the Neekas River, roughly twice that of the Clatse (1km), whereby both are interrupted by waterfalls that act as a barrier to salmon migration (Manzon and Marshall 1981).

3.3.2. Invertebrate samples

In August of 2000 terrestrial macro-invertebrates were collected on the Clatse and Neekas watersheds through passive pitfall trapping and hand collection from the soil and coarse woody debris. Invertebrate sampling occurred above and below the waterfall

barrier and up to 100 meters from the stream. On the Clatsop River, main invertebrate sampling occurred from 200 to 800 meters upstream from the mouth, and again above the falls at 1200 and 1600 meters. The majority of invertebrate trapping on the Neekas occurred at 1km, and again at 2km, just below the falls. Control samples from the Neekas were collected just above the falls from 2200 to 2400 meters upstream from the mouth.

Pitfall arrays were arranged in a three-way branching fashion. This included a central 10cm diameter pitfall connected via three 24-inch by 6-inch aluminium drift fences (separated by 120°) to a perimeter pitfall at the end of each fence (Reimchen et al. 2003). Pitfall arrays were cleared from four to five days after initial set-up, and to prevent rotting of invertebrate tissue 70% ethanol was used as a field preservative within each pitfall cup. Hand collection of invertebrates occurred more randomly as individuals were discovered in the riparian area. All specimens were stored in 70% ethanol prior to identification and isotopic analysis.

3.3.3. Stable Isotope Analysis

Whole invertebrate specimens were dried at 60°C for at least 48 hours and ground into a fine powder with a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Ill). Approximately 1 mg dry weight per ground specimen was then sub-sampled for continuous-flow isotope ratio mass spectrometry (CF-IRMS) analysis of nitrogen and carbon. Mass spectrometry analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was conducted at the stable isotope facility, University of Saskatchewan, Saskatoon, Canada using a Europa Scientific ANCA NT gas/solid/liquid preparation module coupled to a Europa Scientific Tracer/ 20 mass spectrometer.

Isotopic contents are expressed in 'δ' (delta) notation representing the difference between the isotopic content of the sample and known isotopic standards (atmospheric N_2 for nitrogen and PeeDee Belemnite (PDB) limestone for carbon). This is expressed in parts per mil (‰) according to the formula:

$$1) \left(\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right) \times 1000$$

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

3.3.4. Data Analysis

Individual terrestrial macro-invertebrates processed for $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ were separated into four main groups based on taxonomic similarity and ranked according to degree of animal protein consumption, thus providing a proxy for relative trophic level within the litter based food chain: 1) Root feeders (Coleoptera: Curculionidae) (Hatch 1971; Furniss and Carolin 1977); 2) Detritivores (Julida: Parajulidae) (Hopkin and Reid 1992; Ponsard and Arditi 2000); 3) Omnivores (Coleoptera: Carabidae) (Johnson et al. 1966; Laroche 1972; Thiele 1977; Lovei and Sunderland 1996; LaBonte 1998); 4) Predators (Araneae: Agelenidae, Antrodiaetidae) (Gertsh 1949; Glesne 1998) (Table 3.1).

Curculionid beetles of the genus *Steremnius* feed as larvae and adults on the roots and slash of conifers and are assigned the lowest trophic rank, as there is no current evidence that these beetles utilize animal protein (Hatch 1971; Furniss and Carolin 1977). Millipedes are detritivores, feeding primarily on dead plant material and fragments of organic matter. This potentially includes small amounts of animal protein from faeces, dead animals or microorganisms that occur on the litter material (Hopkin and Reid 1992; Ponsard and Arditi 2000). The Parajulidae are indigenous to the forest ecosystems of the Pacific Northwest but are poorly known at the species level (Shelly 1990). A priori, we assume here that the parajulid millipedes include minor contributions of organic matter derived from animal protein in their diet. Carabid beetles of the genera *Pterostichus*, *Scaphinotus* and *Zacotus* are generalist forest floor predators on a variety of soil invertebrates including snails and slugs (Gastropoda), millipedes (Diplopoda), isopods (Isopoda), worms (Oligochaeta) and springtails (Collembola) (Hatch 1953; Laroche 1972; LaBonte 1998). However, documented observations of carabids feeding on plant material including seeds and fruit suggest that these beetles may be omnivorous rather than purely predaceous (Johnson et al. 1966; Thiele 1977; Lovei and Sunderland 1996). Arachnids of the genera *Cybaeus* and *Antrodiaetus* are known to be funnel-web (Glesne 1998) and trap-door (Gertsh 1949) spiders respectively, feeding exclusively on animals including various insects, myriapods, isopods, other spiders and even small vertebrates (Gertsh 1949; Cloudsley-Thompson 1958).

Independent sample t-tests (two-tailed) were used to test for differences between invertebrate groups collected above and below the falls for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ on each watershed (equal variances not assumed in all tests). All invertebrates collected within 100 meters of the stream were pooled for the analysis, and those collected less than 200 meters from the estuary were removed since these were assumed to possess ambiguous isotopic signatures where marine incursions other than salmon input may particularly obscure soil N pools (Polis and Hurd 1996). F-ratio tests (two-tailed) were conducted for $\delta^{15}\text{N}$ between invertebrate groups collected above versus below the falls under the null hypothesis of equal variances. I also performed separate Nested ANOVA's on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to examine the effects of trophic group, distance from the stream, above and below falls and watershed [model: watershed, watershed(falls), watershed(falls(distance)), watershed(falls(distance (invertebrate group)))]. However, assumptions of normality and homoscedasticity were not met and as such, I place more emphasis on the t-test comparisons. Tukey HSD multiple comparison post hoc tests were performed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ within sites under the null hypothesis that all invertebrate groups were isotopically indistinct. Since inorganic carbon in the form of CaCO_3 , present in the exoskeleton of my millipedes (Hopkin and Reid 1992), is enriched in $\delta^{13}\text{C}$ relative to organic forms (Ponsard and Ardit 2000), I removed millipedes from the post hoc analysis of $\delta^{13}\text{C}$ among feeding groups. Pearson's Correlation Coefficients were used to examine the relationships between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ within trophic groups at different sites to investigate the individual niche variability.

3.3.5. Estimating %MDN

$\delta^{15}\text{N}$ values in animals are influenced by the $\delta^{15}\text{N}$ value of the principal N sources, and fractionation during nitrogen transformations within ecosystems. Principal N sources to riparian ecosystems include atmospheric N_2 with a $\delta^{15}\text{N}$ value of 0‰ (Peterson and Fry 1987), and salmon N with a $\delta^{15}\text{N}$ value of approximately $11.2 \pm 1.0\text{‰}$ (Mathisen et al. 1988). Variations in $\delta^{15}\text{N}$ with trophic level appear to be relatively predictable such that biota are enriched by $3.4 \pm 1.1\text{‰}$ more than their food (Minigawa and Wada 1984), a pattern that seems to hold true for soil macro-invertebrates (Ponsard and Ardit 2000;

Scheu and Falca 2000). Estimates for % marine-derived nitrogen (MDN) in my litter-based macro-invertebrate food chain were obtained based on a combination of a limnetic trophic model proposed by Kline et al. (1990) and a terrestrial vegetation model utilized by Helfield and Naiman (2001) and is expressed mathematically by:

$$2) \%MDN = \left[\frac{Obs - TEM}{MEM_{TL} - TEM} \right] \times 100\%$$

where *Obs* is the observed $\delta^{15}N$ value of a particular taxa below the waterfall barrier to salmon, *TEM* is the terrestrial end-member (the isotopic value obtained for the same taxa above the falls in absence of salmon input), *MEM* is the marine end-member ($\delta^{15}N$ value of salmon of 11.2‰ (Mathisen et al. 1988) which should equal maximum vegetation $\delta^{15}N$ values), and *TL* refers to the trophic level correction factor that applies to the marine end-member in the model. Since variability in utilization of MDN by the various invertebrate groups below the falls might obscure relative trophic level, I used invertebrate $\delta^{15}N$ values above the falls on each watershed to provide an indication of relative trophic position. The trophic level correction factor was thus calculated by subtracting mean $\delta^{15}N$ values in hemlock above the falls, (Mathewson and Reimchen unpublished data: Clatse mean $\delta^{15}N = -1.55\%$; Neekas mean $\delta^{15}N = -3.93\%$) from mean $\delta^{15}N$ values in each invertebrate group above the falls on each watershed. This simplifies the above equation:

$$3) \%MDN = \left[\frac{Obs - TEM}{MEM - VEG_{abv}} \right] \times 100\%$$

where *MEM* equals salmon tissue (Mathisen et al. 1988) and *VEG_{abv}* equals mean vegetation $\delta^{15}N$ values above the falls. I also calculated %MDN for vegetation below the falls (Mathewson and Reimchen unpublished data: Clatse mean $\delta^{15}N = +1.43\%$; Neekas mean $\delta^{15}N = +3.44\%$) as a benchmark comparison to our invertebrate estimates. I was not able to assess the extent of fractionation occurring in the situation of 100% MDN at the level of primary producers (See assumptions in Helfield and Naiman 2001). As such, I calculated two %MDN estimates based on no fractionation (*MEM* = 11.2‰) and maximum fractionation of 4‰ (*MEM* = 7.2‰), which is a typical maximum level of fractionation in vegetation from atmospheric N_2 that is observed in the Clatse-Neekas non-salmon habitats (Mathewson and Reimchen unpublished data). This model assumes

that invertebrate trophic level does not differ above and below the falls and that the marine end-member for vegetation $\delta^{15}\text{N}$ values is represented by salmon tissue.

3.4. Results

Invertebrate trophic groups varied predictably with respect to $\delta^{15}\text{N}$. The nested ANOVA analysis demonstrated that the majority of variance in $\delta^{15}\text{N}$ was due to falls within watersheds ($F = 9.191$; $p = 0.031$; $R^2 = 0.819$) and taxonomic group within all other factors ($F = 13.71$; $p < 0.001$; $R^2 = 0.689$). Variation in $\delta^{15}\text{N}$ that occurred between watersheds or distance of collection from the stream contributed little to total variance and was insignificant in the model (see methods for violations). Invertebrates were enriched by 3-8‰ along salmon spawning reaches compared to similar groups collected above the falls, and showed a gradient of increasing values with increased trophic level at both salmon and non-salmon sites (Figure 3.1). There were highly significant differences in $\delta^{15}\text{N}$ (t-tests: $p < 0.01$) above and below waterfalls for all trophic groups at both watersheds. Multiple comparison tests (Tukey's post hoc) revealed distinct trophic separation in $\delta^{15}\text{N}$ between at least two invertebrate groups depending on site of collection (Table 3.2). Millipede detritivores had higher $\delta^{15}\text{N}$ values than root feeding weevils on all sites but only on the Clatsop above the falls was this trend significant. Carabid beetles demonstrated higher $\delta^{15}\text{N}$ values than millipedes at all sites with significant differences on the Clatsop River below and above the falls and on the Neekas River above the falls. Spider predators were significantly more enriched than carabid beetles on the Neekas River on both salmon and non-salmon sites, but demonstrated only marginally higher $\delta^{15}\text{N}$ values than these beetles on the Clatsop River. Carabid beetle omnivores and spider predators demonstrated significantly higher variance in $\delta^{15}\text{N}$ below the falls than above on both watersheds (Carabidae Clatsop: $F_{14,6} = 14.61$, $p < 0.005$; Carabidae Neekas: $F_{21,6} = 21.94$, $p < 0.001$; Araneae Clatsop: $F_{18,16} = 5.41$, $p < 0.002$; Araneae Neekas: $F_{17,11} = 4.94$, $p < 0.02$) (F-ratio tests).

Invertebrate groups varied in $\delta^{13}\text{C}$ but did not always vary predictably with trophic level or habitat (Figure 3.2). Nested ANOVA analysis using $\delta^{13}\text{C}$ indicated significant variability only in taxonomic groupings ($F = 11.801$; $p < 0.001$; $R^2 = 0.657$),

with all other levels insignificant. Relatively high $\delta^{13}\text{C}$ values were observed in millipedes in both watersheds in salmon and non-salmon sites, most likely a reflection of inorganic carbon content. Multiple comparisons revealed trophic separation for spiders over carabid beetles in all sites (Table 3.3). Spiders were enriched over root feeders on the Clatse River above the falls and on the Neekas below the falls. Carabids and root feeders did not differ in their $\delta^{13}\text{C}$ values. Carabid beetles collected on the Neekas River were the only group to demonstrate isotopic enrichment below the falls ($p = 0.042$). Spiders on the Clatse River were found to be higher in $\delta^{13}\text{C}$ above the falls than below ($p = 0.016$).

I examined isotopic levels in relation to distance upstream from the ocean. At Clatse River, $\delta^{15}\text{N}$ declined with increased distance upstream with the lowest levels occurring above the waterfalls. However, at Neekas River, $\delta^{15}\text{N}$ levels were high but variable throughout the stream channel below the waterfall, above which there was a striking reduction in $\delta^{15}\text{N}$ over short distance delineated by the geological barrier to salmon (Figure 3.3).

In order to assess niche differences within and among groups, I examined the relationships between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Below the falls, there were significant positive correlations between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in spiders on the Clatse ($R = 0.562$; $p = 0.012$) and on the Neekas ($R = 0.741$; $p = <0.001$), and in carabid beetles on the Clatse ($R = 0.682$; $p = 0.005$) and on the Neekas ($R = 0.538$; $p = 0.010$) (Figure 3.4). None of the remaining correlations were significant in groups collected below the falls, and there were no significant correlations between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for any group collected above the falls.

I estimated the contribution of marine-derived nitrogen to the total nitrogen content among invertebrate groups on both watersheds (Table 3.4). At Clatse River, assuming no fractionation, values ranged from 19% in millipedes to 49% in weevils (with fractionation: 28% in millipedes to 71% in weevils). At Neekas River, assuming no fractionation, values ranged from 35% in ground beetles to 51% in spiders (with fractionation 47% in ground beetles to 70% in spiders).

3.5. Discussion

I demonstrate isotopic evidence for substantive incorporation of salmon-derived nitrogen into multiple trophic levels of terrestrial litter-based invertebrates from two salmon bearing watersheds. Enrichment in $\delta^{15}\text{N}$ in terrestrial invertebrates occurs through two possible pathways: 1) direct consumption of salmon tissue and/or predation off of direct salmon consumers such as larval blowflies; or 2) indirect enrichment through $\delta^{15}\text{N}$ enriched soil and vegetation N pools. Here, the use of the dual isotope method provides insight into the mechanism of salmon nitrogen utilization by terrestrial invertebrates. Direct consumption of salmon, with approximate $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of +11.2‰ (Mathisen et al. 1988) and -21‰ (Kline et al. 1993) respectively, would lead to enriched signatures of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in animal tissues. For example, consumption of salmon carcasses by larval blowflies (Calliphoridae) has been documented through the dual isotope method (Reimchen et al. 2003). However, terrestrially derived carbon through C_3 photosynthesis dominates $\delta^{13}\text{C}$ pools in coniferous forest soils and salmon-derived carbon is assumed to contribute little to total carbon in litter and soil. The process of indirect utilization of salmon-derived nitrogen by animals has been observed previously in small mammals (Ben-David et al. 1998b), whereby individuals were enriched in $\delta^{15}\text{N}$ but not $\delta^{13}\text{C}$. Because I found little differences in $\delta^{13}\text{C}$ in all trophic groups collected above versus below the waterfalls, this suggests that the primary mechanism of $\delta^{15}\text{N}$ enrichment is by indirect processes through salmon-derived nitrogen subsidies to soil and vegetation N pools.

$\delta^{15}\text{N} / \delta^{14}\text{N}$ ratios of forest nitrogen pools are influenced by the isotopic values of nitrogen inputs and outputs and fractionation that occurs during nitrogen transformations within ecosystems (Nadelhoffer and Fry 1994). Nitrogen inputs to typical Pacific coast forest ecosystems include atmospheric deposition and biological nitrogen fixation. In the case of forests adjacent to salmon streams there is substantial evidence that marine-derived nitrogen from salmon is transferred to forest ecosystems through predator activity (Reimchen 1992; 1994; Ben-David et al. 1998a; Hilderbrand et al. 1999b; Reimchen 2000), flooding events (Ben-David et al. 1998b) and hyporheic zone transfer (O'Keefe and Edwards 2003), and is incorporated into soil N pools through uptake by vegetation

(Bilby et al. 1996; Ben-David et al. 1998b; Hilderbrand et al. 1999b; Helfield and Naiman 2001; Mathewson et al. 2003; Reimchen et al. 2003).

Vegetation $\delta^{15}\text{N}$ values tend to parallel those in the soil and litter across multiple sites and are typically slightly depleted in $\delta^{15}\text{N}$ relative to the soil source (Nadelhoffer and Fry 1994; Evans 2001). Recent estimates for the contribution of marine-derived nitrogen from salmon in riparian ecosystems to total plant nitrogen have ranged from 15.5-24% (Bilby et al. 1996; Hilderbrand et al. 1999b; Helfield and Naiman 2001). These values may be conservative as they are based on the assumption of no plant fractionation from the original source nitrogen. In the case of high nitrogen inputs from salmon, vegetation may preferentially assimilate isotopically light nitrogen (even though it is also originally from salmon). However, in nutrient rich habitats fractionation from the source is potentially not as marked compared with nutrient poor soils (Hobbie et al. 2000; Evans 2001), making %MDN estimates challenging. %MDN estimates from hemlock (Mathewson and Reimchen unpublished data), possibly constituting a large percentage of litter biomass, vary from 23-34% on the Clatse River and 49-66% on the Neekas River depending on degree of fractionation from the source. These estimates are higher than previously reported, yet remain the baseline for comparison with %MDN estimates in our litter-based invertebrate community.

Ponsard and Ardit (2000) observed substantial site variation in litter and soil $\delta^{15}\text{N}$ due to variations in soil processes and nitrogen sources across small scales (< 1km). Soil and litter $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are not yet available for my sites. However, $\delta^{15}\text{N}$ values in litter-based terrestrial invertebrates are known to parallel the $\delta^{15}\text{N}$ values in the litter and soil (Ponsard and Ardit 2000; Scheu and Falca 2000). I suspect that because vegetation and all invertebrates collected below the waterfall barrier to salmon migration are enriched in $\delta^{15}\text{N}$, that soil and litter $\delta^{15}\text{N}$ are also enriched at these sites. My data demonstrates that terrestrial invertebrates exhibit a substantial shift in $\delta^{15}\text{N}$ over a sharp ecological discontinuity (ca. 250 m) in the source of nitrogen to the forest community, as a consequence of a distinct salmon-derived nitrogen subsidy to litter, soil and vegetation N pools. I estimate that %MDN to multiple trophic levels of litter-based invertebrates ranges from 19-71% on the Clatse River and 34-70% on the Neekas River depending on trophic grouping, and on the extent of fractionation from the original source nitrogen.

These values are similar to %MDN estimates of hemlock and indicate that salmon-derived nitrogen is cycled from primary producers through multiple trophic levels of litter-based terrestrial invertebrates.

Grouping all invertebrate samples over the entire 100m riparian zone may have reduced the extent of statistical differences for $\delta^{15}\text{N}$ in my comparisons above and below falls. This occurs because of a potential isotopic gradient of decreasing $\delta^{15}\text{N}$ from salmon in terrestrial vegetation with increasing distance from the stream over a relatively small scale (< 100 meters) (Ben-David et al. 1998b; Hilderbrand et al. 1999b; Helfield and Naiman 2001). Nevertheless, my %MDN estimates are higher than any other study investigating salmon nutrient transfer into terrestrial ecosystems and emphasizes the magnitude of the discontinuity that occurs across the waterfall barrier to salmon migration in these watersheds.

These %MDN estimates assume salmon tissue $\delta^{15}\text{N}$ as the marine end-member in the model. However, there are other factors that can influence these estimates. Vertebrate urine, particularly from bears (*Ursus* spp.) (Hilderbrand et al. 1999b), faeces and guano deposition may contribute highly to nitrogen inputs during the salmon spawning season. Despite the fact that these inputs are ultimately from salmon tissue consumption, high fractionation during multiple transformation steps prior to nitrogen availability, such as ammonia volatilization (Nadelhoffer and Fry 1994), may lead to unknown shifts in the $\delta^{15}\text{N}$ levels of the source nitrogen. This may increase the microspatial variability in $\delta^{15}\text{N}$ in litter, soil, and vegetation, and subsequently invertebrates, along the salmon spawning channel.

Variation in $\delta^{15}\text{N}$ in carabid beetles and spiders collected below the waterfall barrier was substantially greater than above the falls. It was only marginally higher (non-significant) in root feeding weevils and millipede detritivores, possibly due to low sample sizes. This may indicate higher microspatial variability in $\delta^{15}\text{N}$ in soil, litter and vegetation N pools, increased range of prey resources below the falls, and/ or invertebrate dispersal from other habitats into the zone of substantial salmon transfer.

I detected variation in $\delta^{15}\text{N}$ at different stream reaches, most likely as a function of abundance and species of spawning salmon. On the Clatsop River, $\delta^{15}\text{N}$ values decreased with increasing distance upstream. Potentially, this might result from a gradient

in marine subsidies other than salmon as a function of distance from the estuary (Polis and Hurd 1996). However, this trend was not observed on the Neekas River where $\delta^{15}\text{N}$ values remain high, even at 2 km upstream. The difference between these two watersheds in the distribution of marine-derived nitrogen appears to be due to topography and the species and distribution of spawning salmon. Clatse River is pink salmon dominated, with the majority of spawning, and subsequent predator activity, occurring in the lower 500 meters of the spawning channel (Manzon and Marshall 1981; personal observations). Above 600 meters the stream narrows and the riparian profile becomes increasingly steep on both sides. The Neekas River has high density chum spawning to the base of the falls with high salmon nutrient transfer and predator activity occurring in this region (Manzon and Marshall 1981; personal observations). Chum salmon contain twice the biomass of nitrogen than do pink salmon, and this may partly explain the higher %MDN estimates obtained on the Neekas River compared to the Clatse. The distribution of $\delta^{15}\text{N}$ in these terrestrial invertebrate groups thus appears to be directly correlated to salmon spawning density and biomass, and subsequent predator activity, a pattern that has been observed for $\delta^{15}\text{N}$ in ground beetles (Carabidae) occurring between watersheds on Vancouver Island (Reimchen et al. 2003).

Differences in the variance of isotopic signatures within a population provide insight as to the range of diet available to the individual (Bolnick et al. 2003). For example, this has been found in stable isotope studies of marine mammals and chimpanzees (Schoeninger et al. 1999; Das et al. 2000). In the case of carabid beetles and spiders, high variability in $\delta^{15}\text{N}$ along the salmon-spawning channel compared to above the falls, may indicate higher prey variability in this region. Variance in isotopic signatures can also indicate mobility between habitats (Hobson 1999; Hobson et al. 2001). Carabid beetles, particularly on the Neekas River, exhibited high variance in signatures. The carabid beetle species collected, although brachypterous, can move freely between habitats (LaBonte 1998), and captured individuals may not have obtained their nutrition along the salmon spawning channel for their entire life history.

Correlations between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values provide further resolution into individual niche variability. We observed a significant positive correlation between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in carabid beetles and spiders below waterfalls, with access to salmon

nutrients, but not above falls. Both groups feed on a diverse array of prey including primary and secondary consumers, and in the case of the ground beetles, vegetative matter as well. Individuals within each group that fed at a higher average trophic level would be expected to exhibit more enrichment for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Deniro and Epstein 1978; 1981). Alternatively, individuals that fed on salmon directly or on prey that fed on salmon would also demonstrate isotopic enrichment in both isotopes (Bilby et al. 1996; Ben-David et al. 1997; Hilderbrand et al. 1999a; Cederholm et al. 2000; Reimchen et al. 2003). Positive relationships in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ below the falls and the absence of that relationship above the falls hints that direct consumption of salmon or salmon consumers below the falls may be a factor for some individuals of these species. However, increased range of food resources below the falls would also be consistent with this finding. Furthermore, smaller sample sizes above the falls may have reduced our ability to detect relationships. For the majority of the spiders and ground beetles, direct uptake of the marine isotopes most likely contributes only a minor component to yearly protein intake, as uptake of marine-derived nitrogen occurs by indirect means. The use of dual isotope model becomes most relevant when investigating terrestrial organisms that use salmon protein as a major contributor to diet. This is the case for several terrestrial necrophages including flies (Diptera: Calliphoridae, Dryomyzidae, Heleomyzidae), and beetles (Coleoptera: Silphidae, Leiodidae, Staphylinidae) (Reimchen et al. 2003).

Animals are isotopically enriched in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ relative to their dietary intake as a consequence of preferential excretion of the lighter isotope in metabolism (Peterson and Fry 1987), and this allows insight into relative trophic position within a community. Isotopic enrichment varies widely by body tissue, but there is an approximate stepwise enrichment of $3.4 \pm 1.1\text{‰}$ for $\delta^{15}\text{N}$ (Deniro and Epstein 1981; Minigawa and Wada 1984) and $0.4 \pm 1.4\text{‰}$ for $\delta^{13}\text{C}$ (Deniro and Epstein 1978; Gearing et al. 1984) for each sequential trophic level. Ponsard and Arditi (2000) suggest that there are on average two trophic levels within litter-based invertebrate communities. I also find evidence for two general trophic levels within the litter-based community at Clatse and Neekas Rivers usually consisting of: 1) root feeders and detritivores (weevils and millipedes) as primary consumers of plant material, and 2) predators (carabid beetles and spiders) that feed on these and other presumed plant feeders within the litter community. My data, however,

provides substantial evidence for a gradient in trophic level among our litter-based invertebrates rather than two distinct trophic groupings, a finding that coincides with that of Scheu and Falca (2000). Millipedes, for instance, were often found to be enriched in $\delta^{15}\text{N}$ compared to root feeders, a finding that suggests that either weevils (Curculionidae) feed on roots that are somewhat depleted in $\delta^{15}\text{N}$ compared to litter, or that millipede detritivores utilize some $\delta^{15}\text{N}$ enriched protein food sources such as bacteria in their guts, or both (Ponsard and Arditì 2000). Spiders were enriched in $\delta^{15}\text{N}$ in all cases over those in carabid beetles, and below the falls on the Neekas this constituted a mean difference greater than a single trophic level. Evidence for omnivory is emerging in the carabid beetles (Johnson et al. 1966; Larochelle 1972; Thiele 1977; Lovei and Sunderland 1996; LaBonte 1998) and the observed discrepancy between spiders and carabid beetles is most likely a result of the purely predaceous versus omnivorous life histories of these groups. Spiders also demonstrated trophic enrichment in $\delta^{13}\text{C}$ over carabid beetles at all sites. However, spiders were not consistently enriched over root feeders at each site and carabid beetles exhibited the lowest $\delta^{13}\text{C}$ values. I conclude that, in general, carbon is a poor trophic level indicator (Ponsard and Arditì 2000). This suggests that increased trophic and individual niche resolution in stable isotope studies will more likely extend from a detailed taxonomic separation rather than with guild analyses (Scheu and Falca 2000).

3.5.1. Implications

With the use of stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), spawning salmon have been shown to provide substantial nutrient inputs to limnetic food webs (Kline et al. 1990; 1993; Bilby et al. 1996; Wipfli et al. 1998), with implications for stream primary productivity and subsequent juvenile salmonid survivorship. Young salmon may in fact derive a large proportion of their required nitrogen and carbon from the death and decomposition of their parents, through food web utilization of salmon nutrients by algae and aquatic invertebrates.

Other than inputs to terrestrial vegetation, salmon nutrient effects in forest food webs are poorly known. Input of salmon-derived nitrogen contributes to total available N in the soil and thereby increases forest primary productivity and vegetation and litter

quality (Ben-David et al. 1998b; Hilderbrand et al. 1999b; Helfield and Naiman 2001; Mathewson et al. 2003). Nutrient subsidies (other than salmon) to terrestrial invertebrate communities can result in shifts in invertebrate community structure and abundance as a consequence of bottom-up ecosystem effects (Kytö et al. 1996; Polis and Hurd 1996; Forge and Simard 2001). Soils in coniferous forests of low nutrient status are typically dominated by fungi as the primary decomposers of organic material, and thick humus layers quickly accumulate due to slow rates of nutrient turnover (Prescott et al. 2000). In nutrient-rich conditions, fungi are replaced by bacteria and invertebrates as the dominant decomposers, resulting in higher net rates of nitrogen mineralization and total available nitrogen (Prescott et al. 2000; Forge and Simard 2001). Shifts in invertebrate community structure and abundance due to a nutrient subsidy may have further implications for higher invertebrate and vertebrate consumers such as predaceous beetles, spiders, hymenopteran parasitoids, small mammals, amphibians and passerines. For example, in another form of marine subsidy, spider densities have been reported to be 4-5 times higher on islands with marine bird colonies than those without (Polis and Hurd 1995). Furthermore, avian populations in boreal forests have been observed to respond to experimental nitrogen fertilization (Folkard and Smith 1995), a pattern that also may well be true in the case of nutrient inputs to forest communities along salmon streams (Gende and Willson 2001). Shifts in litter-based invertebrate community structure and abundance could have particular benefits for ground foraging birds such as the resident and migratory sparrows, thrushes and wrens. The widespread enrichment in salmon derived nitrogen among multiple trophic levels also hints at an ecosystem level effect that has further implications for shrub and canopy level invertebrate communities and their various vertebrate consumers (Willson and Halupka 1995; Willson et al. 1998; Cederholm et al. 2000).

3.5.2. Conclusions

The increasing evidence for the coast-wide decline in salmon abundance on the Pacific coast of North America (Finney et al. 2000) may have substantially more ecological implications to terrestrial forest food webs than previously recognized (Cederholm et al. 2000). I present evidence for major uptake of salmon-derived nitrogen

into a terrestrial invertebrate food web, with a sharp reduction in uptake across a waterfall barrier to salmon migration. These results supplement the conclusions of a diversity of recent contributions that have focused on the ecological consequences of the decline of salmon on the west coast of North America (Willson and Halupka 1995; Reimchen 1995; Ben-David et al. 1998b; Wilson et al. 1998; Wipfli et al. 1998; Hilderbrand et al. 1999b; Cederholm et al. 2000; Helfield and Naiman 2001; Gende et al. 2002; Bilby et al. 2003; Mathewson et al. 2003; Reimchen et al. 2003).

Figure 3.1. $\delta^{15}\text{N}$ values in four trophic groupings of litter-based invertebrates collected above and below waterfall barriers to salmon migration on the Clatse and Neekas Rivers, British Columbia. Invertebrates are ranked (left to right) based on increasing consumption of animal protein (see methods). t-test results: ** denotes $p < 0.01$; *** denotes $p < 0.001$.

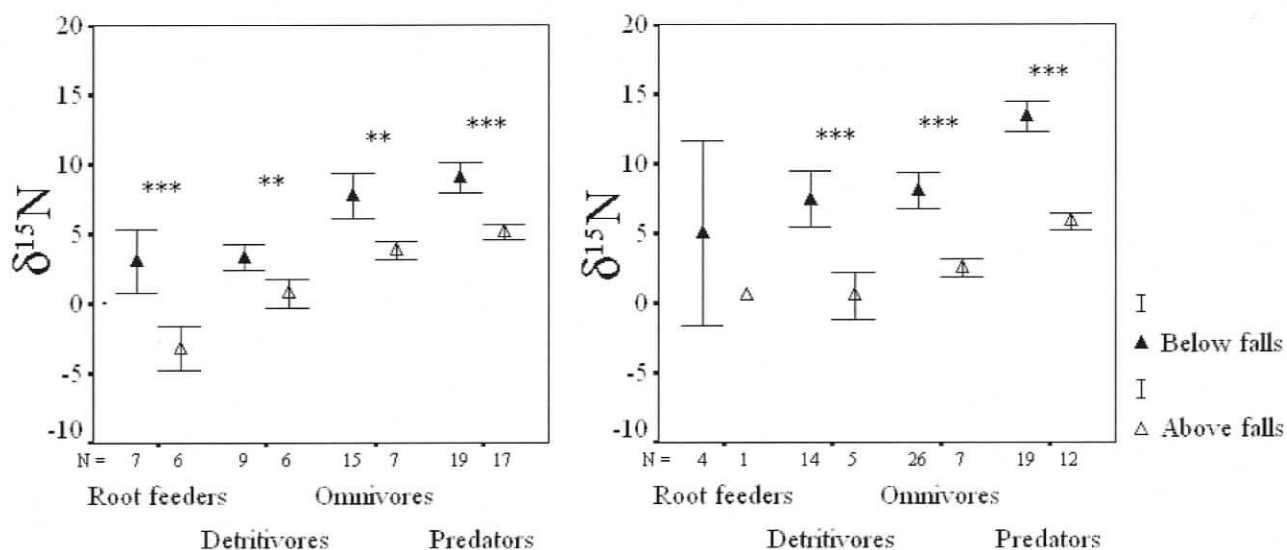


Figure 3.2. $\delta^{13}\text{C}$ values in four trophic groupings of litter-based invertebrates collected above and below waterfall barriers to salmon migration on the Clatse and Neekas Rivers, British Columbia. Invertebrates are ranked (left to right) based on increasing consumption of animal protein (see methods). t-test results: * denotes $0.01 < p < 0.05$

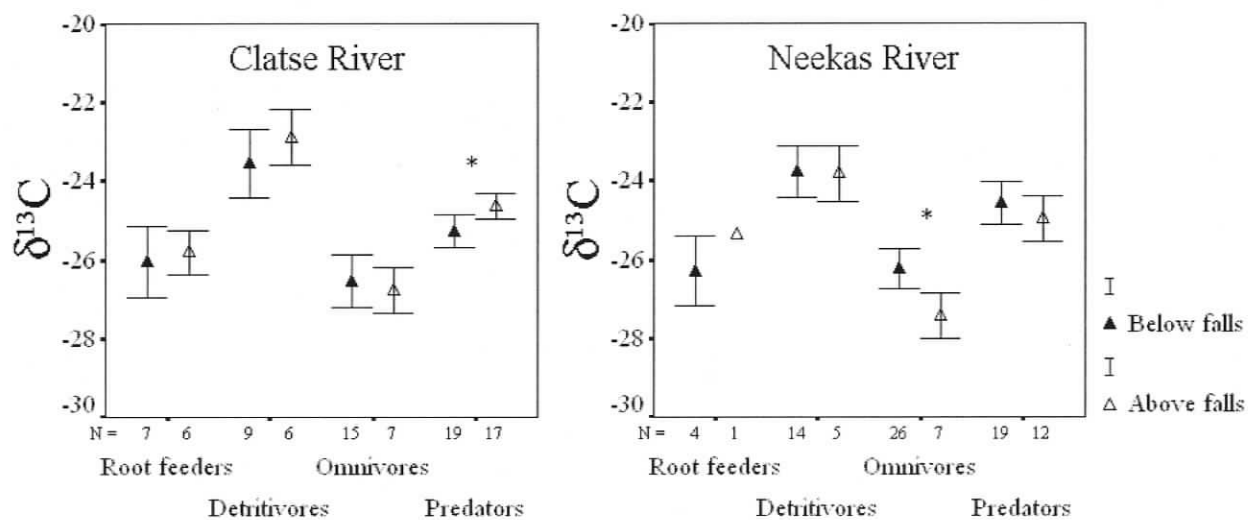


Figure 3.3. $\delta^{15}\text{N}$ values in ground beetles (Carabidae) and spiders (Araneae) with distance of collection upstream from the estuary (m) on the Clatse and Neekas Rivers, British Columbia.

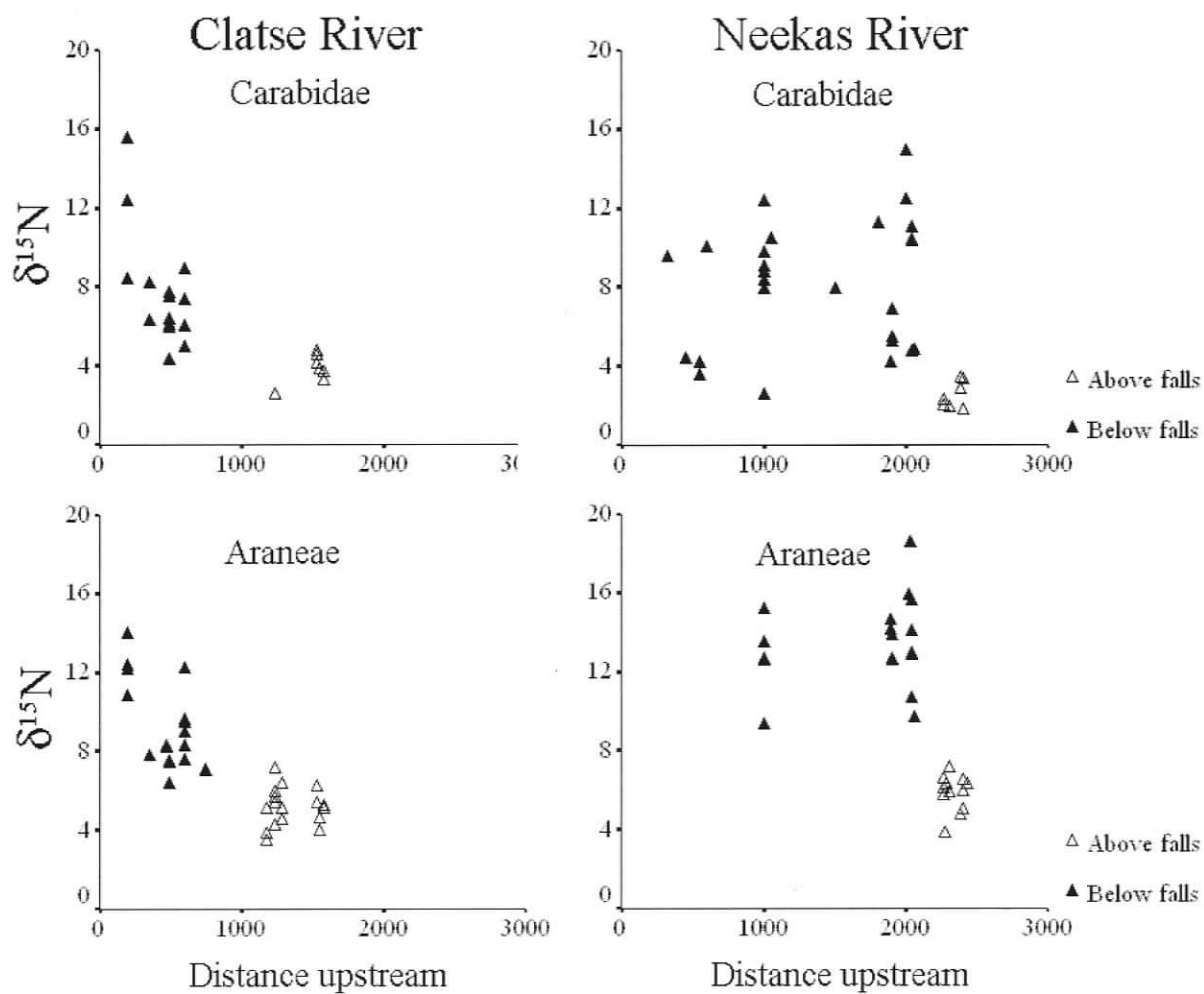


Figure 3.4. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in ground beetles (Carabidae) and spiders (Araneae) below and above waterfalls on the Clatse and Neekas Rivers, British Columbia.

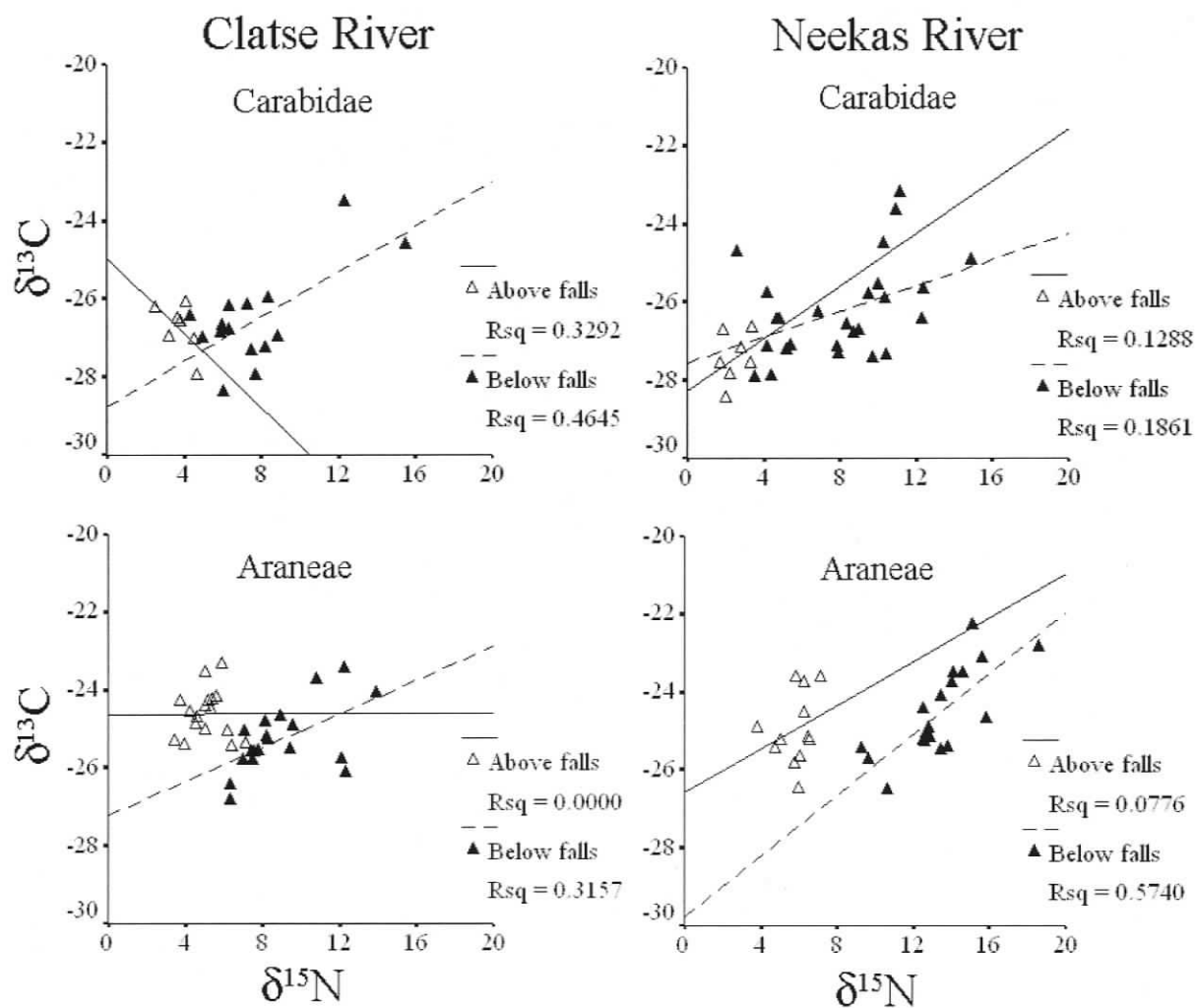


Table 3.1. Family and species level designations by trophic grouping for invertebrates collected on the Clatse and Neekas Rivers, British Columbia, in August 2000.

Trophic grouping	Family	Species
1) Root Feeders	Curculionidae	<i>Steremnius carinatus</i> Boh. <i>Steremnius tuberosus</i> Gyll.
2) Detritivores	Parajulidae	Unknown
3) Omnivores	Carabidae	<i>Pterostichus crenicollis</i> LeC. <i>Scaphinotus angusticollis</i> Mann. <i>Zacotus matthewsii</i> LeC.
4) Predators	Agelenidae	<i>Cybaeus reticulatus</i> Simon
	Antrodiaetidae	<i>Antrodiaetus pacificus</i> Simon

Table 3.2. Tukey's multiple comparison post hoc tests for $\delta^{15}\text{N}$ values in four invertebrate trophic groups collected above and below waterfalls on the Clatse and Neekas Rivers, British Columbia. N/A indicates post hoc tests not possible due to low sample sizes.

		Clatse River			
		Below falls		Above falls	
		Mean		Mean	
Trophic grouping (I)	Trophic grouping (J)	Difference (I-J)	p-value	Difference (I-J)	p-value
Predators	Root Feeders	5.93	<0.001	8.31	<0.001
Predators	Detritivores	5.81	<0.001	4.39	<0.001
Predators	Omnivores	1.28	0.615	1.30	0.123
Omnivores	Root Feeders	4.65	0.002	7.01	<0.001
Omnivores	Detritivores	4.52	0.005	3.09	<0.001
Detritivores	Root Feeders	0.13	1.000	3.92	<0.001

		Neekas River			
		Below falls		Above falls	
		Mean		Mean	
Trophic grouping (I)	Trophic grouping (J)	Difference (I-J)	p-value	Difference (I-J)	p-value
Predators	Root Feeders	8.55	<0.001	5.33	N/A
Predators	Detritivores	6.14	<0.001	5.32	<0.001
Predators	Omnivores	5.84	<0.001	3.34	<0.001
Omnivores	Root Feeders	2.70	0.548	1.99	N/A
Omnivores	Detritivores	0.30	0.999	1.98	0.006
Detritivores	Root Feeders	2.40	0.693	0.01	N/A

Table 3.3. Tukey's multiple comparison post hoc tests for $\delta^{13}\text{C}$ values in four invertebrate trophic groups collected above and below waterfall barriers to salmon migration on the Clatse and Neekas Rivers, British Columbia. N/A indicates post hoc tests not possible due to low sample sizes.

		Clatse River			
		Below falls		Above falls	
		Mean		Mean	
Trophic grouping (I)	Trophic grouping (J)	Difference (I-J)	p-value	Difference (I-J)	p-value
Predators	Root Feeders	0.77	0.555	1.17	0.004
Predators	Omnivores	1.27	0.036	2.14	<0.001
Omnivores	Root Feeders	-0.49	0.847	-0.92	0.058

		Neekas River			
		Below falls		Above falls	
		Mean		Mean	
Trophic grouping (I)	Trophic grouping (J)	Difference (I-J)	p-value	Difference (I-J)	p-value
Predators	Root Feeders	1.80	0.033	0.90	N/A
Predators	Omnivores	2.02	<0.001	2.46	<0.001
Omnivores	Root Feeders	-0.22	0.984	-2.08	N/A

Table 3.4. % Marine-derived nitrogen (MDN) estimates in invertebrates collected above and below waterfall barriers to salmon migration on the Clatse and Neekas Rivers, British Columbia. Estimates of %MDN were made under conditions of no fractionation from the source and maximum fractionation of 4‰ from the source nitrogen by primary producers.

Clatse River		
Invertebrate family(ies)	%MDN (No Fractionation)	%MDN (Fractionation)
Curculionidae	49.1%	71.5%
Parajulidae	19.4%	28.2%
Carabidae	30.6%	44.6%
Agelenidae/ Antrodiaetidae	30.4%	44.3%

Neekas River		
Invertebrate family(ies)	%MDN (No Fractionation)	%MDN (Fractionation)
Parajulidae	45.8%	62.3%
Carabidae	34.8%	47.3%
Agelenidae/ Antrodiaetidae	51.2%	69.6%

Chapter 4:

Consumption and distribution of salmon nutrients and energy by terrestrial flies

4.1. Abstract

Anadromous Pacific salmon (*Oncorhynchus* spp.) subsidize terrestrial food webs with their nutrients and carcasses, a process driven largely by selective foraging and transfer by bears (*Ursus* spp.). In two sequential years, I quantify wildlife-transfer of salmon carcasses to riparian zones on two productive watersheds in British Columbia, and estimate total terrestrial fly production from remnant carcasses. Despite higher escapement of pink salmon, large-bodied chum were transferred more readily into the forest (3.4-6.6% of pink; 9-50% of chum). Blowflies (*Calliphora*) and other Diptera dominated salmon carcass decomposition (>90% of carcasses), with carcass size an important predictor for Diptera production from individual carcasses. From 134-360g of *Calliphora* maggots per meter of spawning length (or 3.5-9 million individuals in whole watershed) were generated from salmon carcass transfer. Using stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in spring-emerging adult *Calliphora*, I find that >80% of individuals had salmon-based signatures. Overall, flies are a dominant consumer and vector of salmon nutrients and energy in terrestrial habitats, and support at least 16 vertebrate and 22 invertebrate species from my study watersheds.

4.2. Introduction

Every year throughout the Pacific Rim, millions of anadromous salmon (*Oncorhynchus* spp.) return to their natal watersheds to spawn and die. 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 (Cederholm et al. 1989; Reimchen 1994; Ben-David et al. 1997; Hilderbrand et al. 1999; Gende et al. 2002; Stockner 2003). Historical and continued declines in salmon spawning biomass due to over-exploitation, habitat alteration and climate change threaten salmon-dependent communities coast-wide (Gresh et al. 2000).

Salmon nutrients are distributed from streams and lakes into terrestrial ecosystems mainly through wildlife foraging. Bears (*Ursus* spp.) and other vertebrate species transfer salmon carcasses and nutrients into riparian areas, and often selectively feed on energy-rich portions of the salmon (Reimchen 2000; Gende et al. 2001). The extent of bear predation, carcass consumption and transfer to riparian areas depends on many factors, with the most critical including salmon spawning density, bear density and attributes of the habitat that facilitate access (Reimchen 1994; Quinn and Kinnison 1999; Reimchen 2000; Gende et al. 2004b; Gende and Quinn 2004).

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

Herein, I quantify wildlife-transfer of salmon carcasses on two productive watersheds in British Columbia, and estimate total terrestrial fly production from remnant carcasses. I compare salmon carcass transfer from two separate years to British Columbia Department of Fisheries and Oceans (DFO) salmon escapement counts, and examine

variation in rates of predation and transfer between the dominant salmon species *O. keta* (chum) and *O. gorbuscha* (pink). I estimate the proportion of each carcass consumed by terrestrial Diptera, and the number and biomass of maggots produced in each watershed. I focus on consumption by blowflies (*Calliphora*), although I use ecological efficiencies of 10 and 20% to expand my estimates to include all Diptera (Slobodkin 1960; Putman 1977, 1978; Lawton 1981).

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; Hilderbrand et al. 1999; Hocking and Reimchen 2002). Using stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, I assess the frequency of a salmon diet in recently emerged adult *Calliphora terranova* (Calliphoridae) as well as the potential for dispersal of flies with salmon signatures to more distant non-salmon habitats.

4.3. Materials and methods

4.3.1. Study sites

This study was conducted on two salmon-bearing watersheds, the Clatse ($52^{\circ}20'15''\text{N}$; $127^{\circ}50'23''\text{W}$) and Neekas ($52^{\circ}28'17''\text{N}$; $128^{\circ}9'39''\text{W}$) rivers, on the central coast of British Columbia, Canada. A 5-10m waterfall truncates spawning at 0.9km and 2.1km upstream from the estuary on the Clatse and Neekas respectively. The climate of this region is cool and wet, with a mean annual temperature of $\sim 8^{\circ}\text{C}$ and annual precipitation ranging from 3200-4200 mm. Both watersheds occur in the Coastal Western Hemlock Biogeoclimatic Zone with forests dominated by Western hemlock, Sitka spruce and Western red-cedar (Green and Klinka 1994; Hocking and Reimchen 2002).

Pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon spawn from late August to early November in both watersheds, with black bears (*Ursus americanus*) and wolves (*Canis lupus*) as the dominant transfer vectors. From field observations, I estimate that five and ten black bears (*Ursus americanus*) were present on the Clatse and Neekas respectively in both years. Wolves were present sporadically on the Clatse in 2001 and on the Neekas in both years. However, in 2002 on Clatse a wolf pack (5 adults and 7 pups) established a home site in the estuary. Transfer by wolves was thus most prevalent on

Clatse in 2002, although even in this year the majority of salmon carcasses were transferred by bears (>90%).

4.3.2. Salmon carcass transfer

In 2001 and 2002 I surveyed the Clatse (2001: Oct. 15th – 16th; 2002: Oct. 5th – 6th) and Neekas (both years: October 11th – 12th) watersheds 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, in both 2001 and 2002, 37 parallel belt transects (19 river left, 18 river right) 10m wide and up to 100m in length were used to enumerate chum and pink salmon carcasses transferred into the forest. Transects were separated by 50m starting from the estuary up to the base of the falls. Due to a spawning length of 900m this method surveyed 20% of the watershed. Each transect was divided into four distance categories from the stream (0-5m, 5-20m, 20-50m and >50m). Salmon carcasses were identified to species (chum, pink) and placed into one of several consumption categories including: 1. Full carcass; 2. Very minor carcass consumption (~95% of fish remains); 3. Minor carcass consumption (~80% of fish remains); 4. Major carcass consumption (~50% of fish remains); 5. Nearing complete consumption (~20% of fish remains); and 5. Unknown consumption (ie-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 I used the same transect and carcass classification methodology except that transects were separated by 100m rather than 50m. In 2001, 33 transects (16 river left, 17 river right) were surveyed up to the base of the falls and due to a spawning length of 2100m this method covered roughly 8% of the watershed. In 2002, 41 transects were surveyed (21 river left, 20 river right), with 10% watershed coverage.

To estimate the mass of salmon transferred into the forest, full chum and pink carcasses of both sexes were weighed (Table 4.1). 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 of 1200g was used. Male and female chum salmon were both larger at Clatse compared to Neekas (males: $t_{71} = 2.72$, $p = 0.008$; females: $t_{38} = 2.18$, $p = 0.035$), and thus aggregate means of 3972g and 3287g were used for chum salmon at the

Clatse and Neekas respectively. This assumes that the sex ratio of spawning salmon transferred into the forest is equal. Since there may be more transfer of males than females due to their larger size (Reimchen 2000), my carcass mass estimates are likely conservative. Using these aggregate masses I estimated the mass of salmon remaining after vertebrate foraging for each carcass category (Table 4.2). An estimate for salmon carcass transfer in the whole watershed was derived by multiplying by 5 on the Clatse (transect coverage = 20%) and either 12.7 or 10 on the Neekas (transect coverage = 8% in 2001, and 10% in 2002). Transfer values were then compared to total salmon escapement determined by Department of Fisheries and Oceans (DFO).

4.3.3. Dipteran consumption and biomass

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

I investigated Diptera colonization and consumption of thirty-six experimentally-placed carcasses in the fall of 2002 (Clatse $n = 16$; Neekas $n = 20$). I estimated the proportion of each salmon carcass consumed by Diptera and the number of blowfly (*Calliphora*) 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 30ml measuring cup. The volume of other dipteran larvae was visually estimated and likely encompassed the families Dryomyzidae, Heleomyzidae, Muscidae and Sphaeroceridae. I also re-weighed the carcass and determined the change in mass from initial placement (Δ carcass mass).

To estimate the mass of each individual final instar *Calliphora*, I weighed 30 dispersing larvae from three separate carcasses. *Calliphora* larvae ranged substantially in mass within and between carcasses (Overall range: 21.0-118.2mg; Carcass 1: 38.4 ± 11.6 mg (mean $\pm$ 1Sd); Carcass 2: 49.3 ± 15.3 mg; Carcass 3: 85.1 ± 11.2 mg) with an aggregate mean of 57.6mg. In a separate test, I measured the length and width of 18 *Calliphora* larvae to estimate their volume (volume of cylinder was used) which was

compared to 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 I use an approximate mass to volume conversion of $1\text{ g} = 1\text{ ml}$. 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:

$$1) \# \text{ Calliphora} = \text{Calliphora volume estimate (ml)} \times \frac{1 \text{ ml}}{0.0576 \text{ g per individual}}$$

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 Diptera and the number of *Calliphora* produced as a function of Δ carcass mass. Logistic regression was used to predict % consumed by Diptera as a function of initial carcass mass ($F_{1,34} = 16.34$, $p = 0.0003$, $R^2 = 0.325$):

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

where Y equals % consumed 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 dipteran volume produced from each carcass (*Calliphora* low (3a): $F_{1,32} = 77.7$, $p < 0.0001$, $R^2 = 0.708$; *Calliphora* high (3b): $F_{1,32} = 73.2$, $p < 0.0001$, $R^2 = 0.696$):

$$3a) Y = 224.02 + 2.16X$$

$$3b) Y = 312.12 + 2.45X$$

where Y equals number of *Calliphora* and X equals the change in 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 Clatsop and Neekas in 2001 and 2002 (Table 4.2).

To give an estimate for the average mass of dipteran larvae of all species dispersing from salmon carcasses, I set up a grid of pitfall traps in the fall of 2001 in $10 \times 10\text{ m}$ plots (9 traps per plot) (see Hocking and Reimchen 2002). Dipteran larvae caught in traps were classified as miscellaneous Cyclorrhaphan larvae. Larvae varied widely in size representing the diversity of dipteran species and stages consuming salmon carcasses. The wet mass of maggots from nine separate traps on the Neekas ($n = 6-41$

maggots per trap) and seven separate traps on the Clatse ($n = 7-18$ maggots per trap) was determined to the nearest 0.1mg. Mass estimates for each trap were then used to calculate a weighted mean mass of individual Cyclorrhaphan larvae caught in each watershed (Clatse mean 21.3mg; Neekas mean 22.9mg). These masses are lower than the mass estimate for individual *Calliphora* larvae of 57.6mg.

I 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. These values were then compared to literature estimates of dipteran and other ectotherm ecological efficiencies that range from 7 to 26% (Slobodkin 1960; Putman 1977, 1978; Lawton 1981). Using ecological efficiencies of 10 and 20%, I then derived estimates of dipteran production from salmon carcasses that could include all dipteran consumers on salmon (including other families Dryomyzidae, Spherozeridae, Muscidae, Heleomyzidae and Phoridae). There is often an ecological succession of dipteran species on carrion (Putman 1977), and my empirical observations of *Calliphora* production from salmon carcasses were made fairly 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 $\pm$ 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, I used two separate masses: the first being the 57.6mg estimate used for *Calliphora*, and the second the Clatse mean 21.3mg or Neekas mean 22.9mg masses estimated from all dispersing larvae caught in pitfall traps.

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, I enumerated all vertebrate and invertebrate species observed as predators or parasitoids of fly maggots on salmon carcasses. Invertebrate taxa are presented in Hocking et al. (*submitted*). Putman (1977) estimates that 66% of larvae dispersing from carcasses are taken by predators, while an additional 30% of the remaining pupae do not emerge as adults. Assuming that this pattern of mortality is representative for my system, I calculated the number and biomass of adult flies emerging in the spring.

Finally, I estimate the mass of Diptera maggots that may be produced for the entire central and north coasts of British Columbia. I averaged Department of Fisheries and Oceans (DFO) counts of both chum and pink salmon over 50 years from 1950-99 on the mid- (DFO statistical areas 7-10) and north coasts (DFO statistical areas 1-6) ($n > 500$ watersheds). I calculated total escapement biomass for each species using regional mean masses of 5.3kg for chum and 1.9kg for pink (Groot and Margolis 1991), and used my minimum and maximum values for percent of the salmon run transferred and percent of the carcass consumed to estimate the total mass of salmon carcass remnants that would be available for invertebrate scavengers. Diptera biomass was then estimated using an ecological efficiency of 10%.

4.3.4. Stable isotope analysis

Stable isotope analysis (SIA) of nitrogen and carbon was conducted on adult *Calliphora terranova* (Calliphoridae) collected in baited traps in May and June 2003 to evaluate the frequency of a larval diet of salmon in adult *Calliphora* from both watersheds, and to determine if salmon signatures could be found in individuals caught in non-salmon habitats (ie- above falls). *Calliphora* specimens were caught in hanging traps baited with ~5g of rotting beef.

Whole Diptera specimens were rinsed with distilled water and then dried at 60°C for at least 48 hours. Samples were ground into a homogeneous powder using a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Ill). Samples (approx 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 (CF-IRMS). Natural abundances of ^{15}N and ^{13}C are given in parts per mil (‰) and are expressed by:

$$4) \left(\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right) \times 1000$$

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

Fly tissue $\delta^{13}\text{C}$ values were lipid normalized based on equations derived from McConnaughey and McRoy (1979). This was done because there are large carbon isotope fractionation differences between protein and lipids (Tiezen 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 ANOVA's with falls (above, below) and watershed as fixed factors.

Isotope signatures were examined relative to possible dietary sources which include salmon and a variety of terrestrial carrion. The isotopic signatures of pink and chum salmon muscle range from approximately 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 unpublished data). Deniro and Epstein (1978; 1981) observe 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 $\delta^{13}\text{C}$ equal to or slightly lower than salmon. As such, I use a cut-off of 12‰ for $\delta^{15}\text{N}$ and -23‰ for $\delta^{13}\text{C}$ as my minimum salmon value.

4.4. Results

4.4.1. Salmon carcass transfer

The total transfer of chum salmon generally exceeded that of pink as chum were transferred much more readily relative to their availability in the stream (Table 4.3). On Clatse, the percent of the run transferred into the forest was consistent among years for both species with an estimated 4.7-6.6% of the pink and 47.0-49.4% of the chum transferred. On Neekas, estimates between years ranged from 3.4-4.7% for pink and 8.6-21.7% for chum. Of salmon carcasses transferred into the forest, vertebrate consumption varied from 33.9-42.8% and 38.0-53.1% of the pink and chum mass, with total consumption ranging from 3169kg on Clatse in 2001 to 6414kg on Neekas in 2002. Averaged across the length of spawning, the mass of salmon remnants in the forest available for invertebrate consumption varied from 0.9 to 2.1 kg per meter for pink and 2 to 5 kg per meter for chum depending on year and watershed (Table 4.3).

The number and biomass of salmon carcasses enumerated in the forest varied by watershed (Clatse, Neekas), year (2001-02), salmon species (pink, chum), distance from

the estuary, and distance into the forest. Greatest transfer of pink salmon occurred on the Clatse River in 2001, while the greatest chum salmon transfer occurred in 2002 on both the Clatse and Neekas (Figure 4.1). In both years and on both watersheds, pink and chum carcass mass was highest within 5m of the stream edge and decreased with increasing distance into the forest (Kruskal-Wallis by distance category: all $\chi^2_3 > 8.77$; all $p < 0.001$ except Chum Clatse 2001 where $p = 0.032$).

4.4.2. Estimates of dipteran consumption and biomass

Blowflies 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 and 94.7% of carcasses at Neekas showed signs of fly 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.

From experimentally-placed carcasses, *Calliphora* larvae production averaged 311.1 ± 48.3 g per carcass (5413 ± 840 individuals) with an average consumption of 0.70-0.76 g of carcass material per maggot (wet mass). This corresponds to an average ecological efficiency of $5.9 \pm 2.9\%$ for pink and $7.9 \pm 1.0\%$ for chum (total range 0-21%) derived from the initial mass of the carcass. However, when the mass of *Calliphora* produced is divided by the change in carcass mass (Δ carcass mass), this increases to 17.4% for pink (range 0-26%) and 13.2% for chum (range 0-28%).

The percent of each salmon carcass consumed by Diptera was predicted by initial carcass mass, while the *Calliphora* production from each carcass was predicted by the change in carcass mass (Δ carcass mass) (Figure 4.2). Using these predictive equations, I estimated *Calliphora* production from pink and chum carcass categories from my transfer databases in 2001-02 (Table 4.2), and then expanded my estimates to include the entire watershed (Table 4.4). Total *Calliphora* production ranged from 28-108 grams per meter of spawning (g/m) for pink, and 90-313 g/m for chum, depending on year and watershed. Over the entire watershed, this translates into 0.59-1.80 and 1.41-7.87 million maggots from pink and chum salmon respectively (Figure 4.3).

Dipteran larvae production from experimentally-placed carcasses, other than *Calliphora*, was visually estimated (in ml) and averaged 53.0 ± 16.6 g for pink and 28.4 ± 4.8 g for chum carcasses. A negative correlation was observed between production of these dipteran larvae and initial carcass mass (Pearson's $R = -0.444$, $p = 0.007$).

I calculated total dipteran larvae production (number and biomass) from both watersheds using ecological efficiencies of 10 and 20% (Table 4.4). These estimates ranged from 292-588 grams of larval Diptera per meter of spawning from all salmon carcasses depending on year and watershed at an ecological efficiency of 10%, to 584-1176 g/m at an ecological efficiency of 20%. This produces a total of 6.4-45.8 and 12.8-91.6 million Cyclorrhaphan maggots at ecological efficiencies of 10 and 20% respectively depending on year, watershed and the mean mass of individual larvae.

From Clatse and Neekas combined, I observed at least 16 vertebrate and 22 invertebrate species as predators or parasitoids of dipteran eggs or larvae. Vertebrates included one mammal, two amphibians and 13 bird species (Table 4.5). Dominant invertebrates included 13 beetle predators (Staphylinidae, Silphidae, Hydrophilidae, Carabidae), and four parasitic wasps (Ichneumonidae, Braconidae, Figitidae).

I estimated the biomass and number of adult flies emerging in the spring/summer (Table 4.6). For *Calliphora*, estimates ranged from 6.5-24.9 g/m for pink and 20.9-72.3 g/m for chum resulting in a total emergence of up to 1.8 million adults depending on year, watershed, and fish species. Using an ecological efficiency of 10%, overall dipteran adult emergence ranged from 67.5-160 g/m or 326,000 to 8.47 million adults depending on year, watershed, fish species and original larval mass. These values double at an ecological efficiency of 20%.

Across all known watersheds with chum and pink salmon spawners on the mid coast and north coast of British Columbia, total escapement biomass has averaged 2.5 and 3.2 million kg on mid coast and 4 and 7 million kg on the north coast for chum and pink respectively from 1950-1999 (Table 4.7). This gives an estimated range of 160 thousand to over 1.4 million kg of salmon mass available for mainly invertebrate scavengers depending on location and the extent of transfer and consumption by vertebrates. At an ecological efficiency of 10% this produces 16-90 thousand kg of fly maggots consuming salmon carcasses on the mid-coast and 22-140 thousand kg on the north coast. Despite

that the average number of pink spawners is 3-4 times higher than the number of chum, the chum carcasses produce up to five times the mass of Diptera than pink.

4.4.3. Stable isotope analysis

Stable isotope signatures in 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 (Figure 4.4). 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 -21.94‰ (Neekas) to -21.54‰ (Clatse) for $\delta^{13}\text{C}$. Using a cut-off of 12‰ for $\delta^{15}\text{N}$ and -23‰ for $\delta^{13}\text{C}$, 85.7% of *Calliphora* adults from Clatse (total $n = 21$), and 81.7% from Neekas ($n = 60$), were likely raised on salmon carcasses the previous fall.

4.5. Discussion

4.5.1. Salmon carcass transfer

My analysis of salmon carcass transfer to riparian zones of two coastal watersheds highlights two principal findings: 1) the keystone role of riparian predators, in this case black bears, in the distribution of salmon-derived nutrients and energy to adjacent forest communities; and 2) the increased relative transfer of chum salmon compared to pink.

The important role of both brown (*U. arctos*) and black bears in the consumption and distribution of salmon carcasses throughout coastal riparian zones of North America has been well documented (Shuman 1950; Frame 1974; Hilderbrand et al. 1999; Reimchen 2000; Gende et al. 2001; Quinn and Buck 2001). As salmon return to spawn, bears can predate a large proportion of the available fish, primarily spawned-out, 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 (Quinn and Kinnison 1999; Reimchen 2000; Gende et al. 2001; Quinn and Buck 2001; Gende et al. 2004b; Gende and Quinn 2004).

I estimate that from 3.4-6.6% of the pink salmon run was transferred into the forest depending on year and watershed while chum transfer was higher ranging from 9-

50% 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 chum and pink salmon are roughly equivalent, although chum salmon have much higher absolute values because of their larger size (Gende et al. 2004a). Bear transfer of the large bodied chum salmon has been emphasized in several other studies and can range from 40-70% (Reimchen 2000; Gende et al. 2004a).

Total salmon transfer declined with distance of placement into the forest. This is comparable to other studies which have found most salmon transfer to be within 5m of the stream (Reimchen 2000; Gende et al. 2004a). 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. 2004b).

4.5.2. Dipteran consumption and biomass

Flies are the most 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 mid-coast of British Columbia (this study). Blowflies (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 B.C. 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. Perhaps when carcasses are surveyed a from single time period, the frequency of colonization is underestimated, in comparison to carcass placements when carcasses are followed for longer time periods. Another important consideration is temperature. Blowflies are sensitive to cold temperatures (Williams and Richardson 1984), and in cooler years they may be out-competed on salmon carcasses by vertebrates and more 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. *in press*). In favourable conditions, blowflies such as *C. terranovae* can out-compete most species and can consume entire carcasses within several days. I observe that an increasing proportion of larger carcasses are consumed by blowflies, and that smaller carcasses are more favourable breeding sites for other fly families. Flies have been shown to partition themselves by carcass size (Kneidel 1984; Hanski 1987) and variable consumption of salmon by bears and other vertebrates likely increases 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). My 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. Based on my forest carcass surveys and *Calliphora* regression equations I estimate that up to 360g of *Calliphora* maggots per meter of spawning length, translating into approximately nine million individuals, were produced from transferred salmon carcasses. This value is comparable to Meehan et al. (2005) in terms of overall production (i.e. ten million maggots) despite that estimates of production

per carcass were substantially lower. Estimates for *Calliphora* production were derived from ecological efficiencies of 4.0-5.2% for pink and 4.6-6.3% for chum. If I include other fly families using ecological efficiencies of 10 and 20% then my estimates for total Diptera production from salmon carcasses becomes much higher.

Carrion communities contain a diverse assemblage of species with a high percentage living as predators of fly eggs, larvae and adults (Ulrich 1999). I observe 16 vertebrate and 22 invertebrate predators or parasitoids associated with fly maggots derived from salmon carcasses on Clatse and Neekas. This includes vertebrate insectivores such as the Winter wren, Varied thrush, Rough-skinned newt and Dusky shrew, predaceous beetles within Staphylinidae, Carabidae and Silphidae, and four species of parasitic wasps (Hocking et al. *submitted*). In the spring, adult flies likely provide a further food source for various canopy-dwelling birds and spiders and disperse salmon nutrients over longer distances (Christie et al. *submitted*).

Across all known chum and pink salmon spawning watersheds on the central and north coasts of B.C. ($n > 500$) total escapement biomass over the last 50 years has averaged roughly 6.5 and 10 million kg for chum and pink respectively (Department of Fisheries and Oceans Salmon Escapement Data). 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 (Reimchen 1994; Bilby et al. 1996; Wipfli et al. 1999; Cederholm et al. 2000; Gende et al. 2002). Herein, I provide an estimate for the remaining mass that is likely transferred to riparian forests and made available for invertebrate scavengers, primarily including the Diptera. Variability in my estimates occurs from variation in the extent of bear transfer and consumption of salmon carcasses. 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 streams that provide good access to salmon, my estimates of transfer may be slightly higher than an average coastal salmon run. If this is true, then my estimates may be more representative of higher spawning densities in the past. Because sockeye (*O. nerka*) salmon transfer to the forest has yet to be explicitly quantified, despite numerous studies which document bear predation on sockeye (Quinn

and Kinnison 1999; Quinn and Buck 2001; Gende et al. 2001), I do not include this species in my coast-wide Diptera estimates.

4.5.3. Stable isotope analysis

Emerging *Calliphora* adults caught in baited traps in the spring indicated a high population frequency (>80%) of a larval diet of salmon from both the Clatse and Neekas watersheds. 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 and energy 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.

4.5.4. Summary and implications

Spawning salmon provide a dominant source of nutrients and energy to hundreds of aquatic and terrestrial consumers throughout the Pacific Rim (Cederholm et al. 2000; Stockner 2003). They 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 on the Serengeti (Reimchen 2000). I 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 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; Gende et al. 2004b). 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 salmon-breeding

flies 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 (Gresh et al. 2000; Finney 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 and increases coastal biodiversity and carrying capacity.

Figure 4.1. Average a) pink and b) chum salmon mass (kg) ($\pm$ SE) transferred into the forest of the Clatse and Neekas rivers, B.C. in 2001-02. Measurements are derived from carcass surveys on $5 \times 100\text{m}$ belt transects perpendicular to the stream further separated into four distance categories (0-5m, 5-20m, 20-50m, >50m).

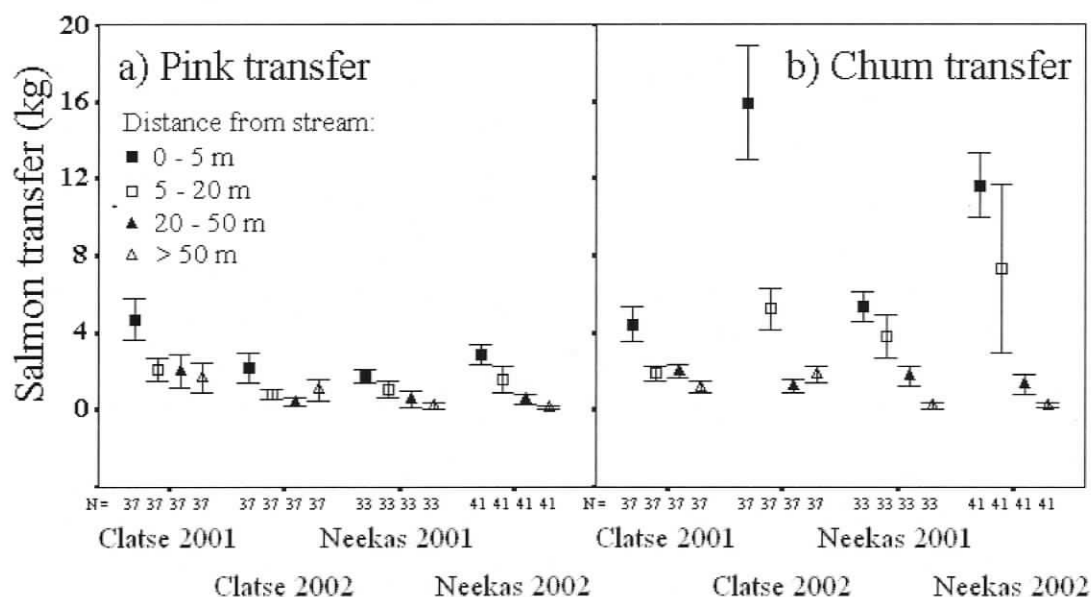


Figure 4.2. Diptera (Calliphoridae) consumption and production from experimentally-placed chum and pink salmon carcasses on the Clatse and Neekas rivers, B.C. Shown are the observed versus predicted results for a) the change in salmon carcass mass (% consumed by Diptera) versus initial salmon carcass mass (g); and b) number of *Calliphora* maggots produced versus Δ salmon mass (g). Observed values were derived from measurements of *Calliphora* consumption and production from experimentally-placed salmon carcasses in the riparian zone. Predicted values were determined by a) logistic regression ($\ln(Y/(1-Y)) = -1.96 + 5.29^{-4}X$) and b) linear regression ($Y = 312.12 + 2.45X$) equations derived from observed values, and were used to predict the number of *Calliphora* maggots produced from carcass mass categories from my salmon transfer databases (see Methods and Table 4.2).

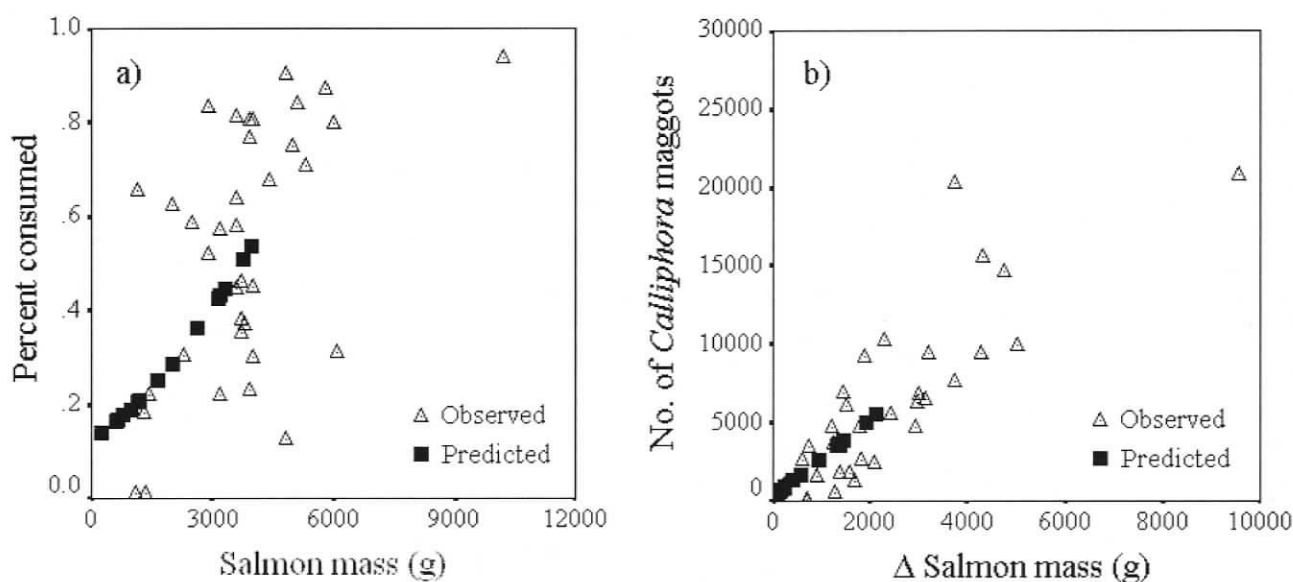


Figure 4.3. Estimated number and biomass (kg) of *Calliphora* maggots produced from pink and chum salmon carcasses naturally transferred into the forest of the Clatse and Neekas rivers, B.C. in 2001-02.

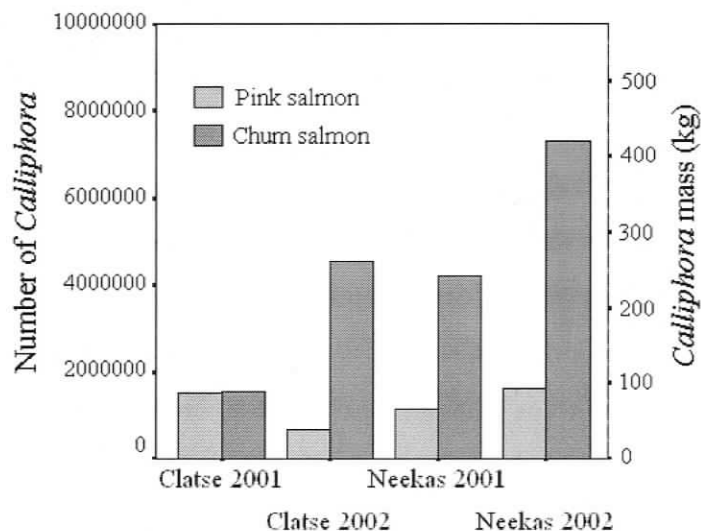


Figure 4.4. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures in recently emerged *Calliphora* (Diptera: Calliphoridae) adults from above and below the falls on the a) Clatse and b) Neekas rivers, B.C. *Calliphora* were caught in baited traps in spring 2003. Flies are assumed derived from salmon carrion if isotope signatures are higher than 12‰ for $\delta^{15}\text{N}$ and -23‰ for $\delta^{13}\text{C}$.

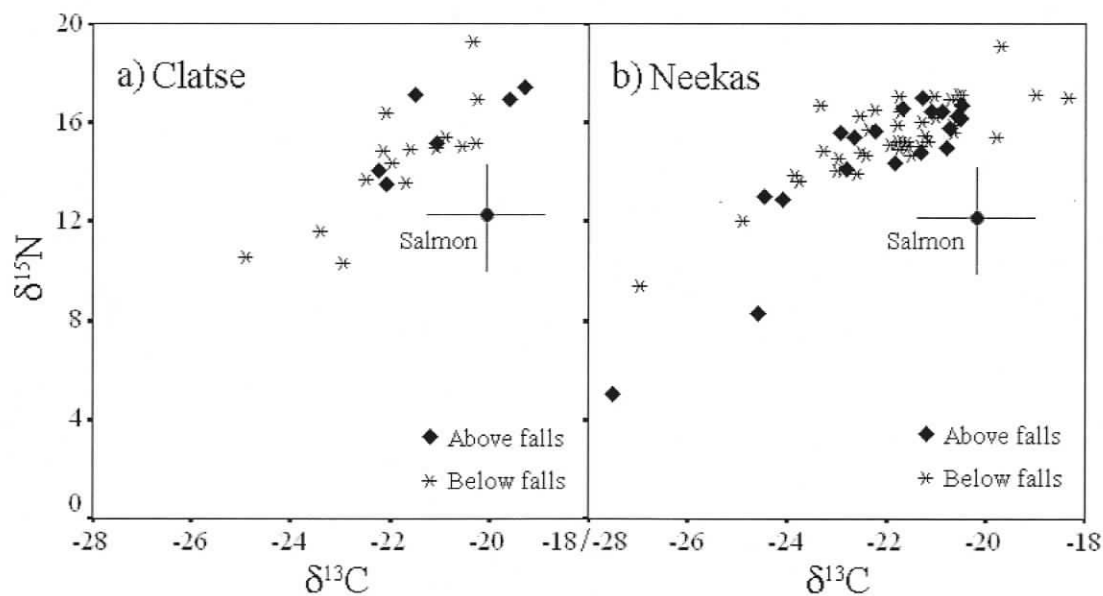


Table 4.1. Chum and pink salmon mass from the Clatse and Neekas rivers, B.C.

Watershed	Species	Sex	N	Mass(g) $\pm$ SD
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 $\pm$ 347.2
		Female	18	1124.4 $\pm$ 270.8
	Chum	Male	44	3788.6 $\pm$ 1377.3
		Female	25	2784.8 $\pm$ 810.1

Table 4.2. Carcass categories, vertebrate consumption and number and mass (g) of maggots produced from salmon carcasses transferred into the riparian zones of the Clatse and Neekas rivers, B.C., fall 2001-02.

Clatse & Neekas Pink Salmon	% vertebrate consumption	Average mass remaining (g)	% consumed by Diptera	No. of <i>Calliphora</i> maggots produced	<i>Calliphora</i> mass produced (g)
Carcass category					
1. Full	0	1200	0.210	768 - 929	44.3 - 53.5
2. Very minor carcass consumption	5	1140	0.205	728 - 883	42.0 - 50.9
3. Minor carcass consumption	20	960	0.190	618 - 758	35.6 - 43.7
4. Major carcass consumption	50	600	0.162	434 - 550	25.0 - 31.7
5. Nearing complete consumption	80	240	0.138	296 - 393	17.0 - 22.6
6. Unknown consumption	50	600	0.162	434 - 550	25.0 - 31.7
Clatse Chum Salmon	% vertebrate consumption	Average mass remaining (g)	% consumed by Diptera	No. of <i>Calliphora</i> maggots produced	<i>Calliphora</i> mass produced (g)
Carcass category					
1. Full	0	3972	0.535	4818 - 5516	277.5 - 317.8
2. Very minor carcass consumption	5	3773	0.509	4375 - 5014	252.0 - 288.8
3. Minor carcass consumption	20	3178	0.431	3181 - 3662	183.3 - 211.0
4. Major carcass consumption	50	1986	0.287	1456 - 1708	83.9 - 98.4
5. Nearing complete consumption	80	794	0.177	527 - 655	30.4 - 37.8
6. Unknown consumption	50	1986	0.287	1456 - 1708	83.9 - 98.4
Neekas Chum Salmon	% vertebrate consumption	Average mass remaining (g)	% consumed by Diptera	No. of <i>Calliphora</i> maggots produced	<i>Calliphora</i> mass produced (g)
Carcass category					
1. Full	0	3287	0.445	3384 - 3892	194.9 - 224.2
2. Very minor carcass consumption	5	3123	0.424	3082 - 3550	177.5 - 204.5
3. Minor carcass consumption	20	2630	0.361	2278 - 2639	131.2 - 152.0
4. Major carcass consumption	50	1644	0.252	1117 - 1324	64.4 - 76.3
5. Nearing complete consumption	80	657	0.166	460 - 580	26.5 - 33.4
6. Unknown consumption	50	1644	0.252	1117 - 1324	64.4 - 76.3

Table 4.3. Salmon escapement (Department of Fisheries and Oceans counts) and vertebrate consumption and transfer of salmon carcasses from surveys of wildlife-transferred pink and chum salmon carcasses on the Clatsse and Neekas rivers, B.C. in 2001 and 2002. † Indicates biomass (kg) of transferred salmon remnants available for invertebrate consumption per meter of spawning length.

	Clatsse River			Neekas River		
	Pink	Chum		Pink	Chum	
	2001	2002		2001	2002	2002
Salmon escapement (DFO counts)	39135	25000	2000	55735	60000	19000
Number of salmon transferred to forest	2595	1180	940	1880	2800	4120
% of salmon run transferred	6.6%	4.7%	47.0%	3.4%	4.7%	21.7%
Transferred salmon mass (kg) consumed by vertebrates	1187.9	605.7	1981.2	764.8	1271.4	5142.6
% of transferred salmon mass consumed by vertebrates	38.1%	42.8%	53.1%	33.9%	37.8%	38.0%
†Biomass (kg/m) of salmon available for invertebrates	2.14	0.90	1.95	0.71	0.99	4.00

Table 4.4. Estimates of *Calliphora* and total Dipteran larvae production (no. and biomass) and ecological efficiencies from pink and chum salmon carcasses transferred to the forest of the Clatse and Neekas rivers, B.C. in 2001-02. *Calliphora* estimates are based on measurements from experimentally-placed carcasses. For total Diptera production I use ecological efficiencies of 10 and 20%, both within the range possible for ectotherms. † Total numbers for each watershed. ‡ Diptera production in grams per meter of spawning length. * Lower limit of the range is defined by the average *Calliphora* mass of 57.6mg, while the upper limit is defined by the mean mass of all Cyclorrhaphan larvae caught in pitfall traps (Clatse mean 21.3mg; Neekas mean 22.9mg).

	Clatse River				Neekas River			
	Pink		Chum		Pink		Chum	
	2001	2002	2001	2002	2001	2002	2001	2002
Number of <i>Calliphora</i> maggots produced	1.35 - 1.68 × 10 ⁶	5.90 - 7.37 × 10 ⁵	1.41 - 1.66 × 10 ⁶	4.21 - 4.89 × 10 ⁶	1.03 - 1.30 × 10 ⁶	1.45 - 1.80 × 10 ⁶	3.86 - 4.53 × 10 ⁶	6.73 - 7.87 × 10 ⁶
Biomass of <i>Calliphora</i> maggots produced (kg)	77.9-96.9	34.0-42.5	81.5-95.4	242.4-281.7	59.5-73.7	83.5-104.0	222.4-260.7	387.7-453.1
Ecological efficiency of <i>Calliphora</i> on salmon	4.0-5.0 %	4.2-5.2 %	4.7-5.5 %	5.4-6.3 %	4.0-4.9 %	4.0-5.0 %	4.8-5.6 %	4.6-5.4 %
Biomass Diptera produced at ecoefficiency of 10% (kg)	192.6	81.0	175.3	448.4	149.1	208.9	464.7	840.0
Biomass Diptera produced at ecoefficiency of 20% (kg)	385.2	162.0	350.6	896.8	298.2	417.8	929.4	1680.0
Number of Diptera maggots produced at ecoefficiency of 10%*	3.34 - 9.04 × 10 ⁶	1.41 - 3.80 × 10 ⁶	3.04 - 8.23 × 10 ⁶	7.79 - 21.05 × 10 ⁶	2.59 - 6.51 × 10 ⁶	3.63 - 9.12 × 10 ⁶	8.07 - 20.29 × 10 ⁶	14.58 - 36.68 × 10 ⁶
Number of Diptera maggots produced at ecoefficiency of 20%*	6.68 - 18.08 × 10 ⁶	2.82 - 7.60 × 10 ⁶	6.08 - 16.46 × 10 ⁶	15.58 - 42.10 × 10 ⁶	5.18 - 13.02 × 10 ⁶	7.26 - 18.24 × 10 ⁶	16.14 - 40.58 × 10 ⁶	29.16 - 73.36 × 10 ⁶

Table 4.5. Vertebrate species observed feeding on fly larvae from salmon carcasses in forest riparian zones of the Clatse and Neekas rivers, B.C.

Order	Species
Mammalia	Dusky 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 macularius</i>)

Table 4.6. Estimates of *Calliphora* and total Dipteran adult emergence (no. and biomass) from pink and chum salmon carcasses transferred to the forest of the Clatsop and Neekas rivers, B.C. in 2001-02. *Calliphora* estimates are based on measurements from experimentally-placed carcasses. For total Dipteran production I use ecological efficiencies of 10 and 20%, both within the range possible for ectotherms. † Total numbers for each watershed. ‡ Dipteran production in grams per meter of spawning length. * Lower limit of the range is defined by the average *Calliphora* mass of 57.6mg, while the upper limit is defined by the mean mass of all *Cyclorhaphan* larvae caught in pitfall traps (Clatsop mean 21.3mg; Neekas mean 22.9mg).

	Clatsop River				Neekas River			
	Pink		Chum		Pink		Chum	
	2001	2002	2001	2002	2001	2002	2001	2002
Biomass of emerging <i>Calliphora</i> adults (kg)	18.0-22.4	7.9-9.8	18.8-22.0	56.0-65.1	13.7-17.0	19.3-24.0	51.4-60.2	89.6-104.7
Number of emerging <i>Calliphora</i> adults	3.12 - 3.88×10^5	1.36 - 1.70×10^5	3.26 - 3.83×10^5	0.97 - 1.13×10^6	2.38 - 3.00×10^5	3.35 - 4.16×10^5	0.89 - 1.05×10^6	1.55 - 1.82×10^6
Biomass of emerging Diptera at ecoefficiency of 10% (kg)	44.5	18.7	40.5	103.6	34.4	48.3	107.3	194.0
Number of emerging Diptera at ecoefficiency of 10% *	0.77 - 2.09×10^6	3.26 - 8.78×10^5	0.70 - 1.90×10^6	1.80 - 4.86×10^6	0.60 - 1.50×10^6	0.84 - 2.11×10^6	1.86 - 4.69×10^6	3.37 - 8.47×10^6
Biomass of emerging Diptera at ecoefficiency of 20% (kg)	89.0	37.4	81.0	207.2	68.8	96.6	214.6	388.0
Number of emerging Diptera at ecoefficiency of 20% *	1.54 - 4.18×10^6	6.52 - 17.56×10^5	1.40 - 3.80×10^6	3.60 - 9.72×10^6	1.20 - 3.00×10^6	1.68 - 4.22×10^6	3.72 - 9.38×10^6	6.74 - 16.94×10^6

Table 4.7. Estimates of total Diptera production from chum and pink salmon carcasses transferred to forest riparian zones on the central and north coasts of British Columbia. ‡ Salmon escapement data are summed Department of Fisheries and Oceans (DFO) counts from the central (DFO statistical areas 7-10) and north coasts (DFO statistical areas 1-6) of B.C. ($n > 500$ watersheds) and averaged over 50 years (1950-99). § Escapement biomass (kg) was calculated using average salmon masses from the North coast (5.3kg for chum and 1.9kg for pink: Groot and Margolis 1991). † The range in the mass of salmon remnants was derived from minimum and maximum estimates of transfer and carcass consumption on the Clatse and Neekas rivers (See Table 4.4).

	Midcoast chum	Midcoast pink	Northcoast chum	Northcoast pink
‡ Salmon escapement	473 149	1 671 703	750 103	3 667 673
§ Escapement biomass (kg)	2 507 690	3 176 236	3 975 546	6 968 579
† Mass salmon remnants (kg)	101 145 - 768 055	61 771 - 138 566	160 350 - 1 217 630	80 320 - 196 848
Diptera mass (kg) at ecoefficiency of 10%	10 115 - 76 806	6 177 - 13 857	16 035 - 121 763	8 032 - 19 685

Chapter 5:

Diversity and ecology of terrestrial invertebrates associated with salmon carcasses in coastal British Columbia

5.1. Abstract

Throughout the north Pacific region, selective foraging by bears and other wildlife on spawning salmon (*Oncorhynchus* spp.) results in a widespread subsidy of salmon nutrients and energy to terrestrial habitats. Using observational and isotopic data, this study documents the diversity and ecology of the forest invertebrate community associated with decaying salmon carcasses. Terrestrial flies (Calliphoridae, Dryomyzidae, and others) dominated salmon carcass decay when carcasses were not disturbed by vertebrates or flooding. At least 60 species from 17 orders were collected from salmon carcasses on two watersheds on the central coast of British Columbia. This community consists of saprophagous Diptera and Coleoptera, dipteran predators and parasitoids, and many opportunistic predators, scavengers and detritivores. Using stable isotopes, evidence for a diet of salmon or salmon consumers was found for adult flies *Calliphora terranova* and *Dryomyza anilis*, larval flies and larval *Nicrophorus investigator*, adult parasitic wasps *Alysia alticola* and *Atractodes* sp., and adult beetles *Necrophilus hydrophiloides* and *Anthobium fimetarium*. High isotope signatures and observations of taxonomic consistency across multiple watersheds highlight the potential for population-level specialization on salmon carrion. Overall, this community is threatened by continued declines in salmon spawning densities throughout the Pacific region and by management practices that do not place enough value on the keystone role of bears and other transfer vectors.

5.2. Introduction

Diversity, competition, and niche specialization are fundamental to the dynamics of carrion communities (Kneidel 1984; Hanski 1987). Every fall throughout the Pacific Rim, anadromous salmon (*Oncorhynchus* spp.) subsidize terrestrial habitats with their nutrients and carcasses (Cederholm et al. 1999; Gende et al. 2002). Hundreds of vertebrate and invertebrate species from both aquatic and terrestrial habitats are associated with this seasonal pulse of marine protein (Reimchen 1994; Cederholm et al. 2000; Jauquet et al. 2003; Nakajima and Ito 2003). Decaying salmon carcasses in streams attract an array of aquatic insects, including Trichoptera, Ephemeroptera, Plecoptera and Diptera (Bilby et al. 1996; Wipfli et al. 1998; Nakajima and Ito 2003). In contrast, the invertebrate community associated with terrestrial-based carcasses is not well known.

Primarily as a consequence of bear foraging (*Ursus* spp.), whole and partially consumed salmon carcasses are transferred to forested areas adjacent to salmon spawning streams (Ben-David et al. 1998; Reimchen 2000). Previous studies have emphasized the dominant role of the blowflies (Calliphoridae) (Reimchen 1994; Cederholm et al. 2000; Jauquet et al. 2003; Reimchen et al. 2003; Meehan et al. 2005) and the activity of burying beetles (Hocking et al. *in press*) in salmon carrion decomposition. This study provides the most complete assessment to date of the diversity and ecology of the terrestrial invertebrate community directly associated with decaying salmon carcasses.

Terrestrial invertebrates were collected from experimentally-placed and naturally-occurring salmon carcasses in forest riparian areas throughout the west coast of British Columbia. Most collections occurred on two watersheds on the central coast near Bella Bella, where previous studies have documented salmon nutrient and energy uptake by terrestrial invertebrates (Hocking and Reimchen 2002; Hocking et al. *in press*). Collections of invertebrate taxa from salmon carcasses documented 1) the dominant consumer of these carcasses; 2) species ecological roles on salmon carrion; and 3) the extent of taxonomic consistency across a wide geographic area.

The ecological role and relationship to salmon was also examined in select carrion species using the stable isotopes $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. This technique has been used in multiple studies to estimate dietary variation, trophic structure and sources of nutrients and energy (reviews in Peterson and Fry 1987; Kelly 2000; Post 2002). In the salmon-forest system,

stable isotopes can determine direct and indirect pathways of salmon nutrient input to terrestrial invertebrates (Hocking and Reimchen 2002; Hocking et al. *in press*). Of particular interest are the isotope findings in flies and two species of parasitic wasps.

5.3. Materials and Methods

5.3.1 Site description and invertebrate collections from salmon carcasses

In September and October of 2000-03 I documented terrestrial invertebrate use of wildlife-transferred and experimentally-placed salmon carcasses on two salmon-bearing watersheds, the Clatse and Neekas rivers, on the central coast of British Columbia, Canada (Hocking and Reimchen 2002) (Figure 5.1). In September of 2000, I visited ~30 watersheds as a part of a biogeographical survey of salmon streams in the central coast - Haida Gwaii region of British Columbia. I collected invertebrate taxa from salmon carrion on the Kiskosh, Tillhorn, Kitkiata, Kumealon, Khutzeymateen and Evelyn watersheds on the mainland mid-coast, Bag Harbour and Government creeks on Moresby Island, Haida Gwaii (Queen Charlotte Islands) and Windy Bay Creek on Lyell Island near Moresby (Figure 5.1). The climate of this region is cool and wet, with a mean annual temperature of approximately 8°C and mean annual precipitation ranging from 3200 to more than 4200 mm (Green and Klinka 1994). Anadromous pink (*O. gorbuscha*), chum (*O. keta*) and coho (*O. kisutch*) salmon spawn from late August to early November in these watersheds, and represent a predictable source of carrion to the terrestrial ecosystem (Manzon and Marshall 1981; Reimchen 2000). The study watersheds support populations of black bears (*U. americanus*) which act as the principal vectors of salmon carcasses into the forest (Reimchen 1994; Reimchen 2000). Grizzly bears (*U. arctos*) and wolves (*Canis lupus*) act as additional vectors on mainland sites.

Throughout the fall of 2002, I experimentally-placed whole and partially consumed salmon carcasses in the riparian zone of the Clatse and Neekas rivers (n = 156 and 135 respectively) and monitored them over a several week period until mid-October. Each fish was weighed, and identified to species (chum or pink) and sex. All carcasses were classified as being primarily consumed/ disturbed by: 1. Diptera; 2. Vertebrates; 3. Coleoptera; or 4. Flooding. Carcasses were transferred to different locations within each

watershed including: 1. 0-20m from stream; 2. ~100m from stream; 3. ~200m from stream (just Clatse); 4. Above falls (just Clatse); and 5. Gravel bank (just Neekas).

In November of 2000, I placed six post spawning chum salmon carcasses in the riparian zone of Goldstream River (48° 29.1' N; 123° 32.9' W) on Vancouver Island near the city of Victoria. After 1 week, carcasses were surveyed for terrestrial invertebrates. This watershed supports populations of chum and coho salmon but due to human disturbance does not support populations of bears that transport carcasses into the forest.

I classified all invertebrates collected from multiple watersheds according to their ecological role on the salmon carcasses. This included: 1) Saprophage – direct consumer of salmon tissue; 2) Dipteran predator – predator of larval Diptera on salmon carcasses; 3) Dipteran parasitoid – parasitoid of larval Diptera on salmon carcasses; 4) Opportunistic predator – predator on various invertebrate taxa on salmon carrion; 5) Detritivore – associated with rich humus/ soil underneath carcasses; and 6) Unknown – unknown association with the salmon carcasses although presence noted. Taxa classified as having unknown associations with salmon carcasses were either due to low numbers of collected individuals or low taxonomic resolution of collected specimens.

5.3.2. Taxonomic identifications

Taxonomic support was 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 (Enchytraidae, Megascolecidae, Lumbricidae).

5.3.3. Dietary characterization using stable isotopes

I characterized invertebrate diet using stable isotope analysis (SIA) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ on individuals reared and collected from salmon carcasses, and from baited and passive pitfall traps on the Clatse and Neekas rivers. Baited traps consisted of 500ml plastic cups buried at ground level with 5-10g of rotting salmon inside with a lid

suspended above the cup to minimize rainwater and debris entry. Passive traps were similar except that they were arranged in a three-way branching fashion (Hocking and Reimchen 2002). In the spring of 2001, Diptera (Calliphoridae, Dryomyzidae) were reared from collections of pupae and pre-pupae from the soil underneath salmon carcasses that had been deposited the previous autumn. Flies were reared for up to a month until adult emergence. All invertebrates were stored in 70% ethanol.

Invertebrate species processed for SIA included unidentified Cyclorrhaphan Diptera larvae ($n = 28$), adult flies *Calliphora terranova* (Calliphoridae) ($n = 31$) and *Dryomyza anilis* (Dryomyzidae) ($n = 18$), adult beetles *Tachinus maculicollis* ($n = 8$), *Anthobium fimetarium* ($n = 3$), *Bisnius seigwaldi* ($n = 3$) (Staphylinidae), *Catops* spp. (Leiiodidae) ($n = 9$), and *Necrophilus hydrophiloides* (Silphidae) ($n = 20$), larvae of the beetle *Nicrophorus investigator* (Silphidae) ($n = 14$), and adult parasitic wasps *Alysia alticola* (Braconidae) ($n = 27$) and *Atractodes* sp. (Ichneumonidae) ($n = 12$).

Whole invertebrate specimens were rinsed with distilled water, dried at 60°C for at least 48 hours and then ground into a fine homogeneous powder using a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Ill). Invertebrate sub-samples (approx 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 (CF-IRMS). Stable isotope ratios of $^{15}\text{N}/^{14}\text{N}$ ($\delta^{15}\text{N}$) and $^{13}\text{C}/^{12}\text{C}$ ($\delta^{13}\text{C}$) are given in parts per mil (‰) deviations from isotopic standards (Peterson and Fry 1987).

5.3.4. Statistical analysis

All stable isotope comparisons were conducted using Analysis of Variance (ANOVA) or t-tests. If the assumption of equal variances was not met, non-parametric approaches such as the Kruskal-Wallis (KW) test were employed. All analysis was conducted using SPSS version 11.0 (SPSS Inc., Chicago, USA).

Isotope signatures can be affected by seasonality of sampling, particularly when diets vary over time or between larval and adult life stages (Tallamy and Pesek 1996). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in the flies *C. terranova* and *D. anilis* were compared across the multiple seasons of collection (raised individuals, and baited traps in spring, summer and fall).

Stable isotope ratios in all carrion taxa collected in late summer and fall were examined relative to literature signatures of pink and chum salmon muscle tissue, and previously measured terrestrial predators (*Cybaeus* spp.) from the Clatse and Neekas. Isotope signatures of salmon vary from approximately 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). *Cybaeus* spp. are spider predators in the litter food chain and, despite having high $\delta^{15}\text{N}$ signatures, have a low direct contribution of salmon to their diet (i.e. – have terrestrial $\delta^{13}\text{C}$ signatures) (Hocking and Reimchen 2002). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in carrion taxa were compared to those of *Cybaeus* spp. collected in pitfall traps in late summer of 2000 and fall 2001 ($n = 18$ on both the Clatse and Neekas) using Dunnett's T3 (non-parametric) post hoc tests.

Isotope signatures that indicate a salmon diet may be from the current diet of salmon or from the larval diet from the previous year (Hocking et al. *in press*). To determine if larval Diptera and adult Hymenoptera had carcass-specific isotope signatures, replicate individuals were collected from multiple carcasses. For larval Diptera, isotope signatures were compared among four separate carcasses and from a single pitfall trap. For the parasitic wasp *A. alticola*, isotope signatures were compared from individuals collected from three separate carcasses and a random collection from multiple carcasses. For *Atractodes* sp., collections from one carcass and one random collection were compared.

5.4. Results

5.4.1 Dominant consumers of salmon carcasses

Flies were the dominant salmon carcass consumer when not disturbed by vertebrates or flooding (Figure 5.2). Of the 156 carcasses experimentally-placed in the riparian zone of the Clatse River, all were consumed by flies and/or vertebrates. 66.6% were wholly or partially consumed by vertebrates while 49.3% were affected by flies. Bears consumed most whole carcasses at sites 100m or 200m from the stream, and thus excluded fly colonization from many carcasses. In comparison, no vertebrate scavenging occurred on the 135 experimentally-placed carcasses on the Neekas. All carcasses in the forest were at least partially consumed by the Diptera. The burying beetle *N. investigator* was observed as a co-dominant consumer with the Diptera on 13.5% of these carcasses.

Despite fly colonization of carcasses placed on gravel banks beside the stream on the Neekas ($n = 31$), all were disturbed by flooding.

5.4.2. Taxonomic diversity and geographic distribution on salmon carcasses

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 5.1). These were dominated by the Diptera (10 spp.), Coleoptera (21 spp.) and the Hymenoptera (6 spp.). The community consisted of saprophagous Diptera and Coleoptera (15 spp.), dipteran predators (8 spp.) and parasitoids (4 spp.), opportunistic predators and saprophages (19 spp.), detritivores associated with the rich humus underneath carcasses (5 spp.) and species or groups with unknown associations with salmon carrion (9 spp. or groups).

Saprophagous Diptera were the most consistently observed group on salmon carcasses. Two species, *C. terranova* (Calliphoridae) and *D. anilis* (Dryomyzidae), dominated salmon carrion decomposition, followed by species in the families Heleomyzidae, Muscidae and Sphaeroceridae. *C. terranova* was also collected from salmon carcasses at Bag Harbour on Haida Gwaii, and Tillhorn and Kiskosh creeks on the mainland midcoast near Hartley Bay. *D. anilis* was also collected from the Bag Harbour, Evelyn, Kumealon, Tillhorn and Khutzeymateen watersheds (Figure 5.1).

A diversity of Coleoptera were collected from salmon carcasses on the Clatse and Neekas rivers, including the saprophagous Silphidae, Staphylinidae, Leiodidae and Hydrophilidae, and the predaceous Staphylinidae and Carabidae. *N. investigator* was collected from salmon carcasses on the Evelyn, Tillhorn, Government and Bag Harbour creeks, while the other silphid, *N. hydrophiloides*, was collected from Clatse, Neekas, Bag Harbour and Goldstream. Apart from Clatse and Neekas, the staphylinid *T. maculicollis* was collected from salmon carcasses on the Kiskosh, Kumealon, and Khutzeymateen watersheds, while *A. fimetarium* was collected from Bag Harbour and Evelyn Creek. Carabid beetles were commonly observed on fresh carcasses as either general predators or scavengers. *Scaphinotus angusticollis* was observed on salmon carrion from the Neekas, Kitkiata, Kiskosh, Kumealon and Khutzeymateen watersheds, while species of the genus *Pterostichus* were observed on Clatse, Neekas, Windy Bay,

Government, Bag Harbour and the Khutzeymateen. The Carabid *Diplous* sp. was collected from gravel bars with decaying carcasses on the Neekas and Kiskosh creeks.

Four parasitic wasp species were observed ovipositing on fly larvae. The two most common species were *A. alticola* (Braconidae), typically associated with early dipteran instars, and *Atractodes* sp. (Ichneumonidae), observed ovipositing on 3rd instar larvae.

A variety of litter fauna were observed as opportunistic scavengers or predators on salmon carcasses or as detritivores associated with the rich humus underneath the carcasses. Millipedes and worms were the most common detritivores on salmon. The millipede Parajulidae and the giant Enchytraidae (*Mesenchytraeus* sp.) were found under carcasses on both mainland and Haida Gwaii watersheds. Slugs and snails, including species in the Genera *Ariolimax*, *Haplotrema*, *Prophysaon* and *Vespericola*, were also common scavengers typically associated with fresh carcasses. Other predators, scavengers or detritivores observed on or underneath salmon carcasses included ants (Formicidae), centipedes (Cryptopidae and Geophilidae), spiders (Agelenidae and Antrodiaetidae), bristletails (Machilidae), cave crickets (Rhaphidiophoridae) and sowbugs (Oniscidae). Groups whose presence was noted included mites (Sarcoptiformes and Parasitiformes), springtails (Collembola), harvestmen (Opiliones), Diplurans and Pseudoscorpions. These groups were not differentiated past the ordinal level.

5.4.3 Stable isotope analysis

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in adult *C. terranova* and *D. anilis* differed by season of collection (Figure 5.3). Highest signatures were observed in raised individuals from salmon carcasses, followed by individuals collected randomly in spring, with lowest signatures in individuals collected in summer and fall (Kruskal Wallis (both isotopes): *Calliphora* Clatse $\chi^2_1 > 4.68$, $p < 0.031$; *Calliphora* Neekas $\chi^2_2 = 10.96$, $p = 0.004$; *Dryomyza* Clatse $\chi^2_3 > 9.68$, $p < 0.022$). Raised flies and flies collected randomly in spring of both species had $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures that likely indicated a larval diet of salmon, as all individuals had $\delta^{15}\text{N}$ values above 12‰ and $\delta^{13}\text{C}$ values above -24‰.

Carrion species collected in late summer and fall differed highly in their $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope signatures at both watersheds (Clatse ANOVA $\delta^{15}\text{N}$: $F_{5,36} = 15.82$, $p < 0.001$;

$\delta^{13}\text{C}$: $F_{5,36} = 27.68$, $p < 0.001$; Neekas Kruskal-Wallis $\delta^{15}\text{N}$: $\chi^2_7 = 69.58$, $p < 0.001$; $\delta^{13}\text{C}$: $\chi^2_7 = 62.75$, $p < 0.001$) (Figure 5.4; Table 5.2). The parasitic wasps *A. alticola* and *Atractodes* sp. had the highest isotope signatures of all species, followed by *N. investigator* larvae, fly larvae, adult flies *D. anilis* and staphylinid beetles *A. fimetarium*. These species had higher $\delta^{13}\text{C}$ and usually higher $\delta^{15}\text{N}$ signatures than those of the litter spider *Cybaeus* (Table 5.2). In comparison, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of adult *C. terranova*, *B. seigwaldi*, *T. maculicollis* and *Catops* spp. did not differ from those of *Cybaeus*.

Carcass of collection had an important influence on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope signatures in collected fly larvae but this was not true for either parasitic wasp species. Fly maggots differed in $\delta^{15}\text{N}$ ($F_{4,23} = 24.59$, $p < 0.001$, $R^2 = 0.810$) and $\delta^{13}\text{C}$ ($F_{4,23} = 9.53$, $p < 0.001$, $R^2 = 0.624$) by carcass. In comparison, isotope signatures in *A. alticola* and *Atractodes* sp. did not differ by carcass of collection (all $p > 0.72$).

Adults of the beetle *N. hydrophiloides* (Silphidae) had isotope signatures indicative of a salmon diet from both Bag Harbour and Goldstream. Mean $\delta^{15}\text{N}$ ranged from 14.91 ± 0.70 ($n = 18$) at Goldstream to 15.24 ± 1.53 ($n = 2$) at Bag Harbour, while $\delta^{13}\text{C}$ ranged from -22.11 ± 0.33 at Goldstream to -20.84 ± 1.22 at Bag Harbour.

5.5. Discussion

5.5.1 Dominant consumers of salmon carcasses

Previous studies have emphasized the dominant role of the blowflies in salmon carrion decomposition (Reimchen 1994; Cederholm et al. 2000; Meehan et al. 2005), observations that are supported by this study. While many carcasses were dominated by the blowfly *C. terranova*, other species from the families Dryomyzidae, Heleomyzidae, Muscidae and Sphaeroceridae were commonly observed. More rarely observed species included *Lucilia illustris* (Calliphoridae) and species within the Phoridae and Drosophilidae. Flies are highly competitive on salmon carrion and can completely consume a carcass within seven days. The carrion beetle *N. investigator* was also observed as a dominant saprophage on many carcasses. This species has been previously documented from salmon carcasses and may breed cooperatively to compete effectively with flies (Hocking et al. *in press*).

Factors responsible for the dominance of flies, carrion beetles and/or vertebrates on salmon carcasses likely relate to salmon spawning density, the extent of salmon transfer, carcass size and decomposition, and features of the environment such as temperature (Reimchen 1994; Reimchen 2000; Gende et al. 2001; Gende et al. 2004; Hocking et al. *in press*). When salmon are scarce there is reduced transfer and vertebrates consume a much larger percentage of the carcasses. For example, the Neekas River has higher chum density than Clatse and has higher access to flooded carcasses. These density differences result in less vertebrate scavenging of carcasses transferred to the forest.

When predation produces carcasses and remnants of various sizes this may not only facilitate colonization (Meehan et al. 2005), but increase carrion community diversity through niche partitioning (Hanski 1987). The Calliphoridae may be particularly favoured on large carcasses due to their high reproductive output, growth rates and overall competitive ability (Williams and Richardson 1984). In comparison, other fly species could be more competitive on smaller remnants (Kneidel 1984).

Cold temperatures may prohibit fly dominance in certain years or sites. For example, Reimchen (1994) observed high dominance of flies on salmon carcasses at Bag Harbour, Haida Gwaii in 1993 but not in 1992 and attributed this difference to cooler night-time temperatures. In the south, salmon spawn in late fall and early winter (Groot and Margolis 1991), and carcasses placed in the riparian zone of Goldstream in November on southern Vancouver Island were primarily consumed by the beetle *N. hydrophiloides* rather than the Diptera. As such, dominance by the Diptera may be restricted to regions or years when temperature is favourable during spawning.

5.5.2 Taxonomic diversity and geographic distribution on salmon carcasses

I document at least 60 invertebrate species from 36 families associated with salmon carcasses from two high spawning density watersheds on the central coast of B.C. These species are partitioned among various ecological roles on the carcass including saprophages, dipteran predators and parasitoids, general predators and scavengers, and detritivores associated with the rich humus underneath carcasses. The highest diversity was represented within the Diptera and Coleoptera, and to a lesser extent within the

Hymenoptera. These findings add to a series of recent publications which have focused on the ecological consequences for declines in salmon abundance throughout the west coast of North America (Reimchen 1994; Bilby et al. 1996; Ben-David et al. 1998; Willson et al. 1998; Wipfli et al. 1998; Cederholm et al. 2000; Gende et al. 2002; Hocking and Reimchen 2002; Stockner 2003; Zhang et al. 2003; Wilkinson et al. 2005).

Many of the most dominant carrion species including *C. terranova*, *D. anilis*, *N. investigator*, *N. hydrophiloides*, *T. maculicollis* and *A. fimetarium* were found from many watersheds throughout a broad geographic region. These observations of taxonomic consistency highlight the potential for population-level specialization on salmon carrion within this community. This may be particularly true for the Diptera as *C. terranova* has been reared from pupae collected in spring along the Moyeha spawning channel on Vancouver Island (Reimchen et al. 2003). Furthermore, *C. terranova*, *D. anilis*, *L. illustris* and species within the Heleomyzidae and Muscidae have been collected from salmon carrion in Alaska (Meehan et al. 2005).

5.5.3 Stable isotope analysis

Stable isotope analysis provides information on individual dietary niche (Peterson and Fry 1987; Kelly 2000; Post 2002) and, in this case, evidence for species' ecological role and relationship to salmon. The stable isotope ^{15}N is a good indicator of trophic position while ^{13}C best indicates sources of primary productivity, including a direct diet of salmon. Evidence for a diet of salmon or salmon consumers was found in adult flies *C. terranova* and *D. anilis*, larval flies and larval *N. investigator*, adult parasitic wasps *A. alticola* and *Atractodes* sp., and adult beetles *N. hydrophiloides* and *A. fimetarium*.

Isotope signatures can be affected by seasonality of sampling, particularly when diets vary over time or between larval and adult life stages (Tallamy and Pesek 1996; Darimont and Reimchen 2002). Seasonal shifts in isotope signatures were observed in the adult flies *C. terranova* and *D. anilis*, with highest signatures in emerging and randomly collected flies in spring, and lower signatures in summer and fall. High signatures in spring imply a legacy of their larval diet of salmon from the previous fall, similar to that found in burying beetles (Hocking et al. *in press*).

Very high isotope signatures were observed in all adult parasitic wasps, *A. alticola* and *Atractodes* sp. Their $\delta^{15}\text{N}$ signatures were on average 3-4‰ higher than fly larvae on salmon carcasses, and their $\delta^{13}\text{C}$ signatures indicated a diet of marine origin. Fly larvae had carcass specific signatures and the parasitic wasps did not. These observations strongly suggest that adults of both species originated from flies consuming salmon carrion the previous fall. Because they were collected in September this means that these species may extend diapause and time their emergence to this rich seasonal pulse of maggots, a life history strategy that would involve trade-offs (Ellers and vanAlphen 2002). What is not known is the extent of adult feeding as well as the duration of their adult life, although both may be quite low (Sisterton and Averill 2002). Overall, these parasitic wasps appear to be partitioned by fly instar (Reznik et al. 1992), and could represent populations of salmon specialists. High isotope signatures in parasitic wasps places them at the 5th-6th trophic position in the marine food chain (salmon are 3rd-4th), comparable to or higher than that of sea lions and orca whales (Hobson et al. 1997; Pauly et al. 1998).

High isotope signatures in the beetles *N. hydrophiloides* and *A. fimetarium* indicate that these species are likely to be salmon saprophages. In comparison, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in the adult beetles *B. seigwaldi*, *T. maculicollis* and *Catops* spp. did not differ from those of *Cybaeus* spiders. *Cybaeus* have an indirect association with salmon through salmon-derived nitrogen enrichment of terrestrial vegetation, although most individuals have little direct influence of salmon in their diet (Hocking and Reimchen 2002). Signatures in *B. seigwaldi*, *T. maculicollis* and *Catops* spp. thus indicate a terrestrial predatory diet, although further seasonal comparisons are needed.

5.5.4. Conclusion

Pacific salmon carcasses provide a predictable source of protein for hundreds of species throughout the west coast of North America and north-eastern Asia (Cederholm et al. 2000; Stockner 2003; Zhang et al. 2003). This study documents over 60 species of terrestrial invertebrates associated with the predictable pulse of salmon carcasses to forest riparian zones in coastal British Columbia. Although this represents the most comprehensive study to date on the subject, these results are likely preliminary with

respect to documenting total diversity, energy flow and specialization within this community. Saprohagous flies within the Calliphoridae and Dryomyzidae are likely to be dominant vectors of salmon nutrients and energy in riparian habitats (Reimchen 1994; Meehan et al. 2005). The magnitude, distribution and predictability of the salmon resource to terrestrial communities should be expected to produce population-level adaptations to salmon in terrestrial invertebrates, as has been documented for bears and other vertebrate wildlife (Hilderbrand et al. 1999). This may be particularly true for flies, parasitic wasps and burying beetles (Hocking et al. *in press*).

The invertebrate community on salmon carrion is threatened by historical and continued declines in salmon spawning densities throughout the west coast of North America (Finney et al. 2000; Gresh et al. 2000), and by frequent removal of bears, the keystone transfer vectors of salmon into riparian forests (Reimchen 2000). If our results are representative, the widespread decline in salmon abundance over the last 100 years will be impacting diversity, competition and niche specialization in carrion communities throughout many northern Pacific watersheds.

Figure 5.1. Study watersheds on the central and north coasts of British Columbia. 1. Clatse River; 2. Neekas River; 3. Evelyn Creek; 4. Tillhorn Creek; 5. Kitkiata River; 6. Kiskosh River; 7. Kumealon River; 8. Khutzeymateen River; 9. Government Creek; 10. Bag Harbour Creek; 11. Windy Bay Creek.

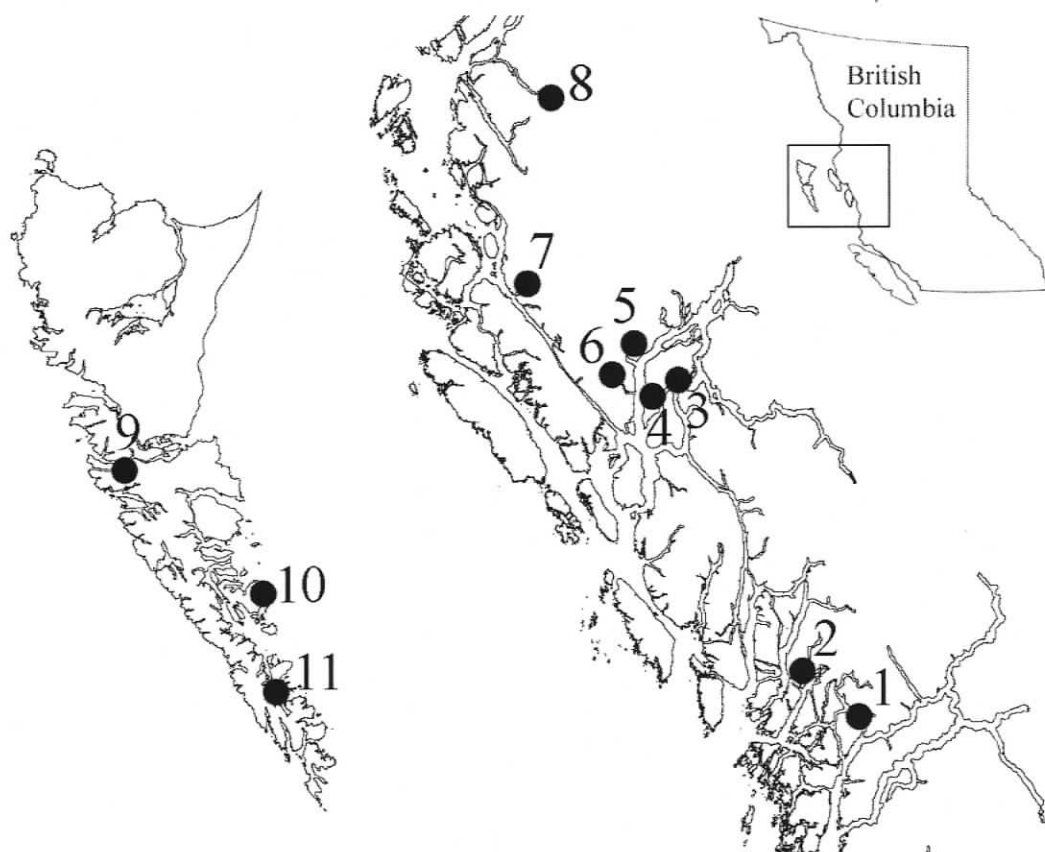


Figure 5.2. Dominant consumers of experimentally-placed chum and pink salmon carcasses from forested sites along the a) Clatse and b) Neekas rivers, B.C. Many carcasses had two dominant consumers (Diptera and vertebrates; Diptera and *Nicrophorus investigator* (Coleoptera: Silphidae)).

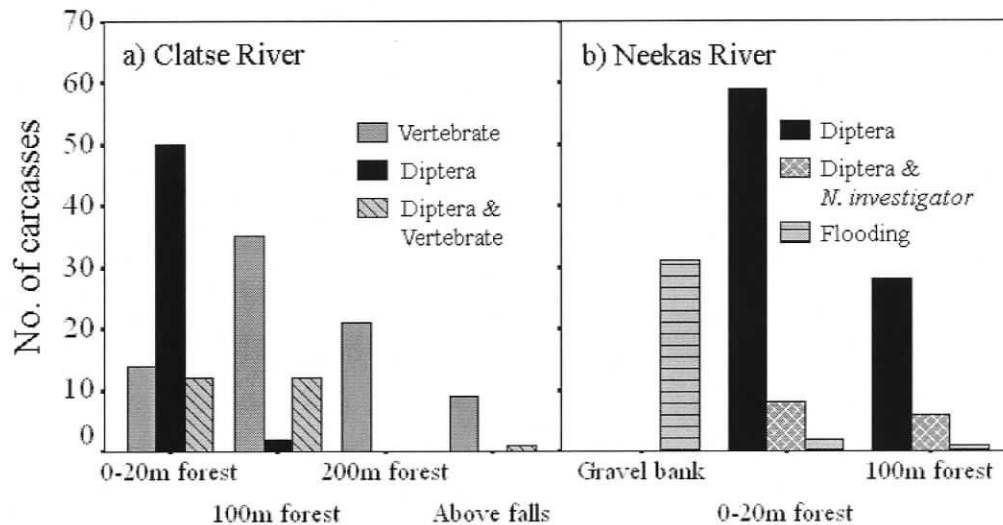


Figure 5.3. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures in the fly adults of the species *C. terranovae* (Calliphoridae) and *D. anilis* (Dryomyzidae) captured in spring, summer and fall from the Clatse and Neekas rivers, B.C. The highest signatures in both species occurred in individuals collected as pupae from salmon carcass sites and raised until adult emergence, followed by those collected randomly in spring.

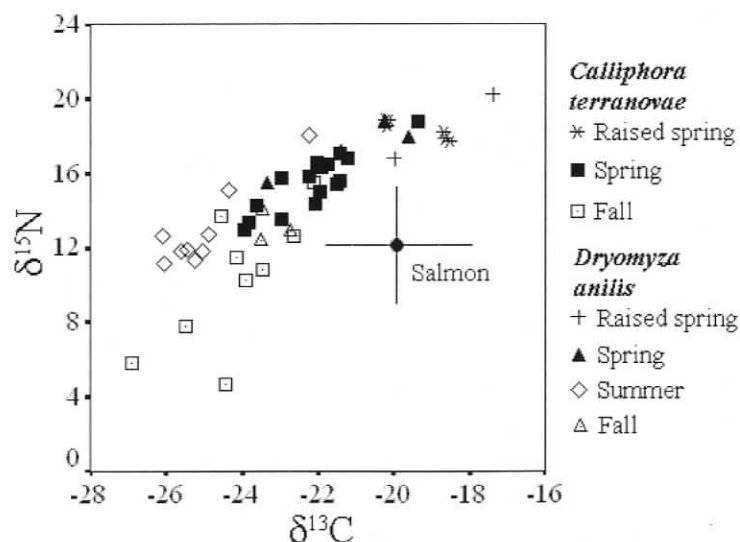


Figure 5.4. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures in carrion invertebrates collected in late summer and fall from a) Clatse and b) Neekas rivers, B.C. Only *Catops* spp. (Leiodidae) and *Tachinus maculicollis* (Staphylinidae) were not collected directly off of salmon carcasses. Shown for comparison are the isotopic range of salmon and the mean signature of a litter predator, *Cybaeus* spp. (Agelenidae).

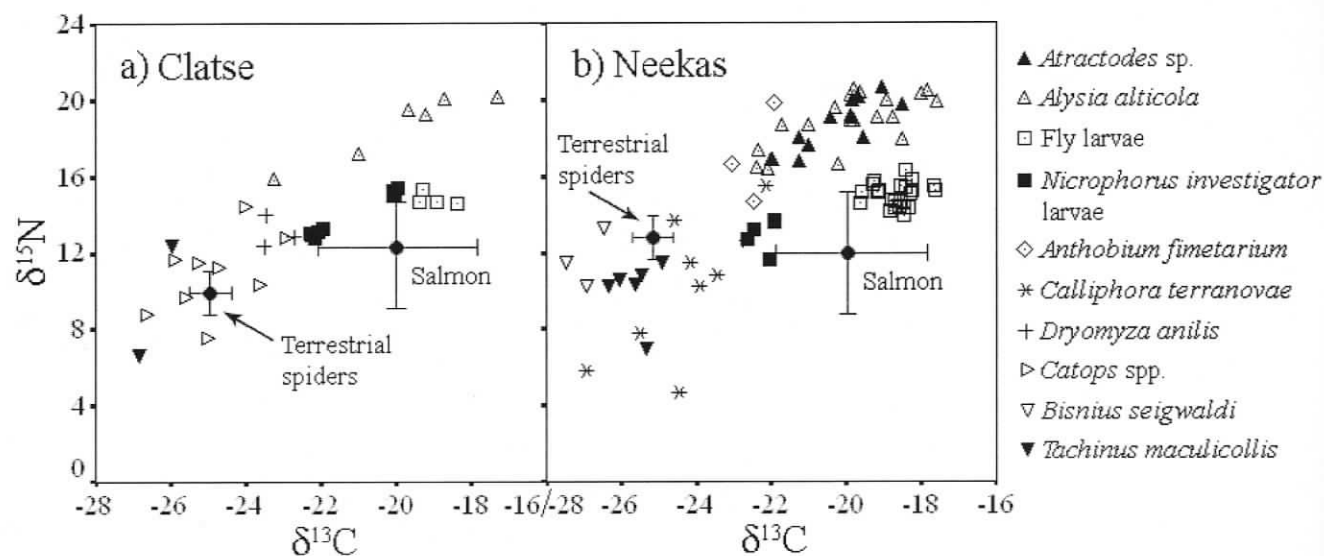


Table 5.1. Taxonomic diversity and ecological role of terrestrial invertebrates observed associated with Pacific salmon carcasses on the Clatse and Neekas rivers, B.C.

Order	Family	Species	Ecological Role
Diptera	Calliphoridae	<i>Calliphora terranova</i>	Saprophage
	Calliphoridae	<i>Lucilia illustris</i>	Saprophage
	Dryomyzidae	<i>Dryomyza anilis</i>	Saprophage
	Sphaeroceridae	<i>Terrilomosina pexa</i>	Saprophage
	Heleomyzidae	sp.1	Saprophage
	Phoridae	sp.1	Saprophage
	Muscidae	sp.1	Saprophage
	Muscidae	sp.2	Saprophage
	Drosophilidae	sp.1	Saprophage
	Tipulidae	various	Unknown
	Tipulidae	various	Unknown
Coleoptera	Silphidae	<i>Nicrophorus investigator</i>	Saprophage / Dipteran Predator
	Silphidae	<i>Necrophilus hydrophiloides</i>	Saprophage
	Staphylinidae	<i>Anthobium fimetarium</i>	Saprophage
	Staphylinidae	<i>Tachinus maculicollis</i>	Dipteran Predator
	Staphylinidae	<i>Oxytelus niger</i>	Dipteran Predator
	Staphylinidae	<i>Bisnius seigwaldi</i>	Dipteran Predator
	Staphylinidae	<i>Atheta altaica</i>	Dipteran Predator
	Staphylinidae	<i>A. hampshirensis</i>	Dipteran Predator
	Staphylinidae	<i>Autalia truncatula</i>	Dipteran Predator
	Staphylinidae	<i>Oxypoda</i> sp.	Dipteran Predator
	Leiodidae	<i>Catops basilaris</i>	Saprophage
	Leiodidae	<i>C. egenus</i>	Saprophage
	Hydrophilidae	<i>Cercyon</i> sp.	Saprophage / Dipteran Predator
	Carabidae	<i>Scaphinotus angusticollis</i>	Opportunistic Predator / Saprophage
	Carabidae	<i>Pterostichus crenicollis</i>	Opportunistic Predator
	Carabidae	<i>P. amethystinus</i>	Opportunistic Predator
	Carabidae	<i>Zacotus mathewsii</i>	Opportunistic Predator
	Carabidae	<i>Diplous</i> sp.	Opportunistic Predator
	Ptillidae	various	Unknown
	Elateridae	sp.1	Unknown
	Dascillidae	sp.1	Unknown

Table 5.1. cont.

Order	Family	Species	Ecological Role
Hymenoptera	Braconidae	<i>Alysia alticola</i>	Dipteran Parasitoid
	Braconidae	<i>Phenocarpa</i> sp.	Dipteran Parasitoid
	Ichneumonidae	<i>Atractodes</i> sp.	Dipteran Parasitoid
	Figitidae	<i>Trybliographa</i> 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
Isopoda	Oniscidae	sp.1	Detritivore
Araneae	Agelenidae	<i>Cybaeus reticulatus</i>	Opportunistic Predator
	Agelenidae	<i>C.eutypus</i>	Opportunistic Predator
	Antrodiaetidae	<i>Antrodiaetus pacificus</i>	Opportunistic Predator
Opiliones	various	various	Opportunistic Predator
Pseudoscorpiones	various	various	Opportunistic Predator
Sarcoptiformes	various	various	Unknown
Parasitiformes	Parasitidae	various	Dipteran Predator
	various	various	Unknown
Systellommatophora	Haplotrematidae	<i>Haplotrema</i> spp.	Saprophage
	Arionidae	<i>Prophysaon</i> sp.	Saprophage
	Arionidae	<i>Ariolimax columbianus</i>	Saprophage
Haplotaxida	Enchytraidae	<i>Mesenchytraeus</i> sp.	Detritivore
	Megascolecidae	<i>Arctiostrotus perrieri</i>	Detritivore
	Lumbricidae	<i>Dendrodrilus rubidus</i>	Detritivore

Table 5.2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures ($\pm\text{SE}$) in insect species observed on salmon carcasses from the Clatse and Neekas rivers, B.C. † Indicates species that were collected in baited pitfall traps in late summer. All remaining species except *Cybaeus* spp. (Agelenidae) were collected directly off of salmon carcasses. Isotope signatures in all taxa were compared to those of *Cybaeus* spp., an apex litter predator not highly associated with salmon carcasses using Dunnett's T3 post hoc tests: * $0.05 < p < 0.001$; ** $p < 0.001$.

Species	Watershed	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<i>Alysia alticola</i>	Clatse	6	$18.60 \pm 0.71^{**}$	$-19.85 \pm 0.84^*$
	Neekas	21	$18.76 \pm 0.30^{**}$	$-20.00 \pm 0.32^{**}$
<i>Atractodes</i> sp.	Neekas	12	$18.76 \pm 0.39^{**}$	$-20.18 \pm 0.30^{**}$
<i>Anthobium fimetarium</i>	Neekas	3	17.04 ± 1.51	$-22.50 \pm 0.32^*$
Fly larvae	Clatse	4	$14.80 \pm 0.17^{**}$	$-18.99 \pm 0.23^{**}$
	Neekas	24	$15.06 \pm 0.13^*$	$-18.65 \pm 0.10^{**}$
<i>N. investigator</i> larvae	Clatse	9	$13.97 \pm 0.38^{**}$	$-21.22 \pm 0.37^{**}$
	Neekas	5	12.95 ± 0.37	$-21.21 \pm 0.14^{**}$
<i>Dryomyza anilis</i>	Clatse	3	$13.08 \pm 0.49^*$	$-23.22 \pm 0.26^*$
<i>Calliphora terranova</i>	Neekas	9	10.29 ± 1.20	-24.19 ± 0.48
<i>Bisnius seigwaldi</i>	Neekas	3	11.75 ± 0.89	-26.94 ± 0.30
<i>Catops</i> spp.†	Clatse	9	10.86 ± 0.70	-24.89 ± 0.39
<i>Tachinus maculicollis</i> †	Clatse	2	9.58 ± 2.89	-26.41 ± 0.44
	Neekas	6	10.13 ± 0.65	-25.61 ± 0.21
<i>Cybaeus</i> spp.	Clatse	18	9.86 ± 0.39	-24.93 ± 0.15
	Neekas	18	13.20 ± 0.49	-24.96 ± 0.19

Chapter 6:

Burying beetle *Nicrophorus investigator* reproduction on Pacific salmon carcasses

6.1. Abstract

In many undisturbed watersheds along the Pacific Rim, anadromous salmon (*Oncorhynchus* spp.) provide a predictable source of carrion to the riparian zone, largely due to horizontal transfer of salmon carcasses by bears (*Ursus* spp.) and other vertebrates. Burying beetles are important members of the North-temperate carrion fauna, and may utilize salmon carcasses and remnants for breeding. In this study, isotopic and observational data are reported that demonstrate previously unrecognized *Nicrophorus investigator* (Zetterstedt) reproduction on large salmon carcasses from five watersheds in coastal British Columbia. Stable isotope signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of adult beetles collected in fall indicate a diet of salmon origin in all but one individual from all watersheds, suggesting that this beetle-salmon association is widespread. Comparison of fall isotope signatures to individuals collected randomly in summer suggests that isotope signatures represent the larval carrion source from the previous fall rather than immediate adult diet. In a survey of *N. investigator* use of salmon carcasses from two watersheds, 35 broods were observed on chum and pink salmon carcasses, including 16 natural brood complexes containing over 100 larvae, and 5 ranging from 250 to 750 larvae. Overall, north-coastal populations of *N. investigator* breed on the rich and reliable salmon resource and may exhibit a system of communal breeding on these carcasses. This is most relevant when you consider the dramatic reduction in salmon spawning biomass over the last century.

6.2. Introduction

Every fall, anadromous Pacific salmon (*Oncorhynchus* spp.) provide a pulse of marine-derived nutrients to terrestrial habitats throughout the Pacific Rim (Gende et al. 2002; Stockner 2003). Primarily as a consequence of vertebrate foraging, salmon carcasses and remnants are distributed up to 150m into the forest adjacent to salmon spawning streams (Reimchen 2000). These carcasses are a predictable source of large carrion to many coastal watersheds and attract an array of invertebrate consumers. Salmon nutrient transfer has indirect implications for litter invertebrate food webs (Hocking and Reimchen 2002), although a detailed assessment of the invertebrate community directly associated with the carcasses is lacking. To date, studies have emphasized the dominant role of blowflies (Calliphoridae) and other Diptera in salmon carrion decomposition (Reimchen et al. 2003; Meehan et al. 2005), but have ignored the potential role of the Coleoptera. Burying beetles (Silphidae: *Nicrophorus* spp.) are important members of the North-temperate carrion fauna, although their association with salmon carcasses has yet to be investigated. Herein, isotopic and observational evidence is presented that demonstrates *N. investigator* (Zetterstedt) reproduction on wildlife-transferred chum (*O. keta*) and pink (*O. gorbuscha*) salmon carcasses from five watersheds in coastal British Columbia.

The stable isotope ratios of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) provide dietary information, including trophic level of feeding (Minigawa and Wada 1984) and sources of primary productivity (Tieszen and Boutton 1988), and, in this case, evidence for direct feeding on salmon (examples: Hilderbrand et al. 1999a; Hocking and Reimchen 2002). Stable isotope signatures were examined in adult beetles collected in the summer and fall from five watersheds to 1) determine the importance of salmon to *N. investigator* diet over a large geographic area and; 2) determine whether observed isotope signatures were derived from the larval diet and/or adult diet on carrion.

Salmon carrion ranges in mass from small remnants to whole carcasses weighing up to 10kg (Reimchen 2000), and it is unknown how carcass size may affect the breeding structure of invertebrates that utilize salmon carcasses. *Nicrophorus* beetles typically bury and prepare small vertebrate carcasses <50g in size, although there have been some reports of breeding on larger carcasses (Milne and Milne 1944; Anderson 1982; Trumbo

1992). In some cases, *Nicrophorus* spp. can develop a strategy of communal breeding on large carcasses due to increased competition with flies, and increased difficulty in burying and defending the carcass (Trumbo and Fiore 1994; Scott 1994, 1998; Trumbo 1995). On two watersheds, adult aggregations and larval brood sizes were surveyed to examine the breeding structure of *N. investigator* on salmon carcasses.

6.3. Materials and Methods

6.3.1 Study sites

This study was primarily conducted on two salmon-bearing watersheds, the Clatse and Neekas rivers, on the central coast of British Columbia, Canada (Figure 6.1; further site description in Hocking and Reimchen 2002). Additional study sites included Government Creek and Bag Harbour Creek on the Queen Charlotte Islands, and Evelyn Creek on Hawkesbury Island near the community of Hartley Bay. Chum and pink salmon spawn from late August to early November in all five watersheds, with populations of black bears acting as the principal vectors of salmon carcasses into the forest (Manzon and Marshall 1981; Reimchen 2000).

6.3.2. Contribution of salmon to diet

The importance of salmon to the diet of *N. investigator* was investigated with simple observations as well as stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ on multiple adults from a broad geographic area. *N. investigator* analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ included adults collected in the fall from salmon carcasses from the Clatse ($n = 5$), Neekas ($n = 8$), Government ($n = 5$), Evelyn ($n = 3$), and Bag Harbour ($n = 2$) watersheds, as well as adults collected in baited traps on the Clatse River in mid-August of 2000 and late-July of 2003 prior to salmon arrival ($n = 80$).

N. investigator adults were stored in 70% ethanol. Whole specimens were dried at 60°C for at least 48 hours and were ground into a fine homogeneous powder using a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Ill). *N. investigator* sub-samples (approx. 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 (CF-IRMS). Stable isotope ratios of $^{15}\text{N}/^{14}\text{N}$ ($\delta^{15}\text{N}$) and $^{13}\text{C}/^{12}\text{C}$ ($\delta^{13}\text{C}$) are given in parts per mil (‰)

deviations from isotopic standards (N_2 in air for nitrogen isotope analyses and Pee-Dee Belemnite (PDB) limestone for carbon isotope analysis). Measurement precision is approximately $\pm 0.16\text{‰}$ and $\pm 0.10\text{‰}$ for ^{15}N and ^{13}C respectively (95% CI).

Isotope signatures were examined relative to possible dietary sources which include salmon and a variety of terrestrial carrion. The isotopic signatures of pink and chum salmon muscle range from approximately 11‰ to 14‰ for $\delta^{15}N$ and -22‰ to -18‰ for $\delta^{13}C$ (Welch and Parsons 1993; Kaeriyama et al. 2004), while terrestrial carrion such as songbirds and small mammals range from 0‰ to 10‰ for $\delta^{15}N$ and -27‰ to -21‰ for $\delta^{13}C$ (Ben-David et al. 1998b; M.D Hocking unpubl. data). Diet-tissue fractionation in animals is typically around +3‰ for $\delta^{15}N$ (Minigawa and Wada 1984) and $\sim 0\text{‰}$ for $\delta^{13}C$, although diets high in lipid content can result in $\delta^{13}C$ isotopic depletion from diet to tissue (Tieszen and Boutton 1988). In the case of *N. investigator* feeding on a 100% salmon diet, $\delta^{15}N$ signatures are expected to be $\sim 3\text{‰}$ higher than salmon while $\delta^{13}C$ equal to or slightly lower than salmon.

To investigate possible seasonal differences in isotopic signatures, the distribution of isotope signatures of adult beetles collected in summer prior to salmon arrival were compared to those collected in the fall directly off salmon carcasses. Since *N. investigator* are univoltine (Smith et al. 2000), this tested whether observed fall signatures likely reflected recent feeding or a legacy of the larval diet from the previous year (ANCOVA with $\delta^{15}N$ as dependent variable, $\delta^{13}C$ as a covariate and season as a fixed factor). All analysis was conducted using SPSS version 11.0 (SPSS Inc., Chicago, USA).

6.3.3. Field survey

In early October 2003, *N. investigator* use of naturally-transferred pink and chum salmon carcasses was surveyed on the Clatse and Neekas rivers. This period corresponds to the peak period of salmon carcass density in each watershed (Manzon and Marshall 1981). A detailed search was conducted for adults and larvae under all carcasses and remnants within 50m of the stream edge on both watersheds. On Clatse this encompassed nearly the entire spawning length ($\sim 1\text{km}$), while on Neekas this covered roughly half of the 2km of spawning. When adults or larvae were discovered on a carcass, the carcass was flagged and monitored until the majority of the larvae reached full size. At this time,

larvae on the carcass were hand-counted by carefully removing them one by one and placing them into a temporary holding container. Throughout all phases of carcass decay all adults in the vicinity of each carcass were captured, counted, sexed and then released. However, due to variation in brood development upon initial discovery of the carcass, the number of initial adults associated with each brood was not determined in all cases.

6.4. Results

6.4.1. Contribution of salmon to diet

Nicrophorus investigator adults were observed breeding on chum and pink salmon carcasses deposited on the forest floor by vertebrate scavengers from all five watersheds across a large geographic region in coastal British Columbia (Figures 6.1, 6.2). Aggregations of 1-18 adults were observed on salmon carcasses in early phases of decomposition, including five aggregations of at least 12 individuals in three of the five watersheds (Clatse, Neekas and Government).

With the exception of one beetle from the Clatse River, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope signatures in adult *N. investigator* collected in fall from all five watersheds indicated a diet of salmon origin (Figure 6.3a). *N. investigator* $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures were similar to or higher than the isotope signatures of salmon and did not differ among watersheds (ANOVA- $\delta^{15}\text{N}$: $F_{4,18} = 1.99$, $P = 0.14$; $\delta^{13}\text{C}$: $F_{4,18} = 2.55$, $P = 0.08$; Tukey's Post Hoc: all $P > 0.14$). The only exception was one individual from Clatse which had an isotope value ($\delta^{15}\text{N} = 8.55$; $\delta^{13}\text{C} = -25.46$) within the range defined by terrestrial carrion.

Since fall $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures were similar across watersheds, all individuals were pooled ($n = 23$). Beetles collected directly from salmon carcasses in the fall were compared to adult beetles collected randomly in summer 2-4 weeks prior to salmon arrival along the Clatse spawning channel ($n = 80$) (Figure 6.3b). $\delta^{13}\text{C}$ values were highly positively correlated to $\delta^{15}\text{N}$ values across both seasons ($F_{1,99} = 70.25$, $P < 0.001$) while no differences were observed by season ($F_{1,99} = 0.21$, $P = 0.65$) or for the interaction term between season and $\delta^{13}\text{C}$ ($F_{1,99} = 0.16$, $P = 0.69$) (ANCOVA of $\delta^{15}\text{N}$ by season with $\delta^{13}\text{C}$). The isotopic variance and the high frequency of a salmon diet was also similar between seasons ($\delta^{15}\text{N}$: Levene's $F_{22,79} = 0.128$, $P = 0.721$; $\delta^{13}\text{C}$: Levene's $F_{22,79} = 0.918$,

$P = 0.340$; Fall frequency of salmon diet = 95.7%; Summer frequency of salmon diet = 88.7-95%; Figure 3b).

6.4.2. Field survey

A total of 35 broods were observed on wildlife-transferred salmon carcasses from the Clatse ($n=15$) and Neekas ($n=20$) rivers (Figure 6.4a). This included 16 broods (or brood complexes) with greater than 100 larvae and five ranging from 250-750 larvae. With the exception of three broods that developed under pink salmon on the Clatse, all remaining broods developed under chum salmon carcasses. The number of adults was counted for both sexes present on each carcass early in brood development (Figure 6.4b,c). Since some broods had larvae that were almost completely developed upon discovery, counts of initial adults include a subset of total number of broods (total adults $n = 19$ carcasses; females $n = 15$ carcasses). Initial number of adults ranged from 0-16 individuals (mean = 3.8), while initial number of females ranged from 0-11 (mean = 2.7). The number of females initially found on a carcass was found to be correlated to brood size (Linear Regression: $F_{1,8} = 48.5$, $P < 0.001$, $R^2 = 0.86$; Figure 6.4d).

Overall, no carcasses were buried. All broods developed underneath the carcass, often in multiple brood centers. The largest brood observed (738 larvae) was from a large male chum carcass, and although it wasn't weighed, likely measured 4-5kg in mass. Several females were breeding in each of the multiple brood centers (in gills and mouth, under belly, and in dorsal muscle region). Nine days after counting 11 adult females and five males on the carcass, larvae of multiple instars were observed scattered throughout the carcass, while four adult females and two males remained.

6.5. Discussion

Pacific salmon carcasses transferred into the forest by bears, wolves, and other vertebrates are a predictable source of carrion to the riparian zone in many coastal watersheds (Reimchen, 2000), and attract an array of invertebrate scavengers (Jauquet et al. 2003; Meehan et al. 2005). Here, isotopic and observational evidence is presented for burying beetle *N. investigator* reproduction on salmon carcasses from the central coast of British Columbia, Canada.

Stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in animal tissues provides information on individual diet integrated over long time periods (Minigawa and Wada 1984; Tieszen and Boutton 1988), and, in this case, evidence for a widespread diet of salmon carrion in *N. investigator*. *N. investigator* is univoltine with reproduction in late summer and fall, with individuals typically surviving for just one breeding season (Smith et al. 2000). Except for one individual at the Clatsop River, all isotope signatures in adult *N. investigator* collected in the fall indicated a diet of salmon origin, with no detectable differences among watersheds. Furthermore, no seasonal differences were observed between adult beetles collected directly off of salmon carcasses in the fall to those collected randomly in summer prior to salmon arrival. This includes the variance of adult isotope signatures and the slope of the relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. The observed frequency of a salmon diet in fall (95.7%) was also similar to that in the summer (88.7-95.0%) with five individuals in summer with intermediate isotope signatures that could not be clearly placed in either category. These intermediate signatures could represent a larval diet from terrestrial carrion that is itself enriched in salmon nutrients (for example a shrew: Ben-David et al. 1998). Alternatively, they could represent individuals that were raised on salmon as larvae but have fed as adults on terrestrial carrion, and thus have intermediate signatures (see Tallamy and Pesek 1996). It seems likely however that observed isotope signatures in adults representing a salmon diet collected in both summer and fall represent a legacy of the larval diet of salmon from the previous fall.

Salmon carcasses range in size from several gram remnants to whole chum carcasses up to 10kg in weight (Reimchen 2000; M.D Hocking unpubl. data). They are often much larger (up to two orders of magnitude) than those known to be accepted by *N. investigator* in several previous studies, which have demonstrated beetle preference for small mammal carcasses 50g or less in size (Smith and Heese 1995; Smith et al. 2000; Smith and Merrick 2001). Overall, *Nicrophorus* spp. display a wide range of behaviours from bi-parental care to communal breeding (Trumbo 1992; Scott 1998), although only a handful of studies have investigated *Nicrophorus* use of large carcasses (Milne and Milne 1944; Peck 1986; Kozol et al. 1988; Trumbo 1992). On the Clatsop and Nekeas rivers a total of 35 brood complexes were observed on salmon carcasses within a two week period, with 17 containing over 100 larvae, and five between 250 and 750 larvae. This

demonstrates a system of possible communal breeding on salmon carcasses. The large chum carcasses most often chosen by *N. investigator* were not buried, but rather mounded at the side with litter to give a sunken appearance. Broods then developed underneath the carcass, often in multiple brood centers, although multiple females (2-3) were often observed sharing these separate brood centers.

Communal breeding in *Nicrophorus* on larger carcasses is thought to have evolved as a consequence of high brood failure due to increased competition with flies, and increased difficulty in burying and preparing the carcass (Scott 1994; Trumbo and Fiore 1994; Trumbo 1995; Scott 1998). Necrophagous flies are excellent competitors for large carrion, and can rapidly detect carcasses and gain priority (Williams and Richardson 1984; Kouki and Hanski 1995). Flies (Calliphoridae, Dryomyzidae, Heleomyzidae, Muscidae, and Sphaeroceridae) are highly competitive for salmon carcasses and have been observed as dominant salmon-carcass consumers in various studies, including this one (Reimchen et al. 2003; Meehan et al. 2005). *N. investigator* is likely competitively excluded from many carcasses, which may favor aggregation and cooperation on a small proportion of available carcasses.

Anadromous salmon spawn in thousands of watersheds throughout the Pacific Rim and are a temporally and spatially predictable source of carrion to the terrestrial ecosystem (Gende et al. 2002; Reimchen et al. 2003). This contrasts with many alternate sources of carrion which are typically much less predictable in time and space (Hanski 1990). Pacific coastal populations of *N. investigator* are known to extend from northern California to Alaska, including Russian Kamchatka and Japan (Katakura and Fukuda 1975; Anderson and Peck 1985; Nishikawa 2000), and reproductive associations with large salmon carcasses, including possible communal breeding, may also occur in these regions where intact salmon runs and their predators remain.

In conclusion, isotopic and observational data suggest a strong association between coastal populations of the burying beetle *N. investigator* and salmon carcasses. Stable isotope analysis indicated that 89-96% of *N. investigator* individuals collected in summer and fall from five watersheds were likely raised on salmon carrion as larvae the previous fall, with 4-11% originating from terrestrial carrion sources. Observations of breeding structure in *N. investigator* revealed large aggregations and brood sizes from

multiple watersheds, suggesting possible communal breeding on these large and predictable carcasses. Overall, the beetle-salmon interaction highlights the dynamic evolutionary interdependence between marine and terrestrial ecosystems in the North Pacific, and the need for ecosystem-level conservation that includes salmon, their riparian habitats, and their vertebrate and invertebrate scavengers. This is most relevant when you consider the dramatic reduction in spawning salmon biomass over the last century (Gresh et al. 2000).

Figure 6.1. Study sites where *N. investigator* burying beetles were collected from Pacific salmon carcasses on the central coast of British Columbia, Canada. A – Neekas River; B – Clatse River; C – Evelyn Creek; D – Government Creek; E – Bag Harbour Creek.



Figure 6.2. a) A male chum salmon carcass (*Oncorhynchus keta*) transferred into the riparian zone of the Neekas River, British Columbia by a black bear attracts adult burying beetles (*Nicrophorus investigator*), and b) a *N. investigator* brood complex developing under the same carcass nine days later. Photos taken by M. Hocking, October 2003.

a



b



Figure 6.3. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures in individual adult *N. investigator* beetles collected in a) the fall from salmon carcasses at five watersheds in coastal British Columbia compared to b) individuals collected at random in summer 2-4 weeks prior to the return of the salmon on the Clatse River, B.C. Fall data are shown in both a) and b). For comparison, the approximate isotope signature of salmon is included. In summer, isotope signatures were derived from salmon (88.7%), terrestrial carrion (5%), or an unknown intermediate (6.3%) (see Methods and Discussion).

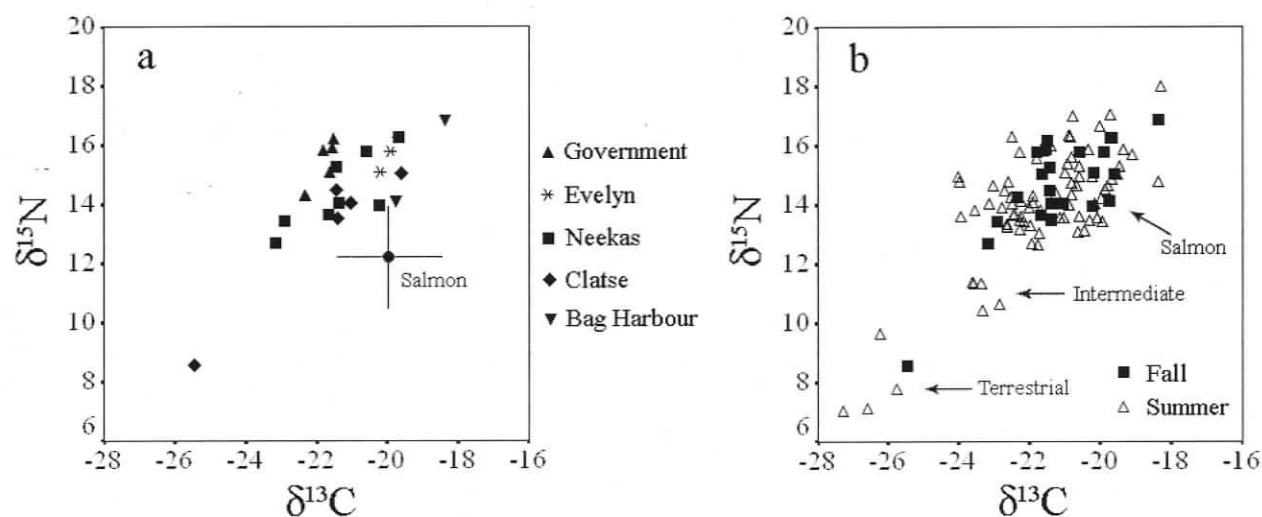
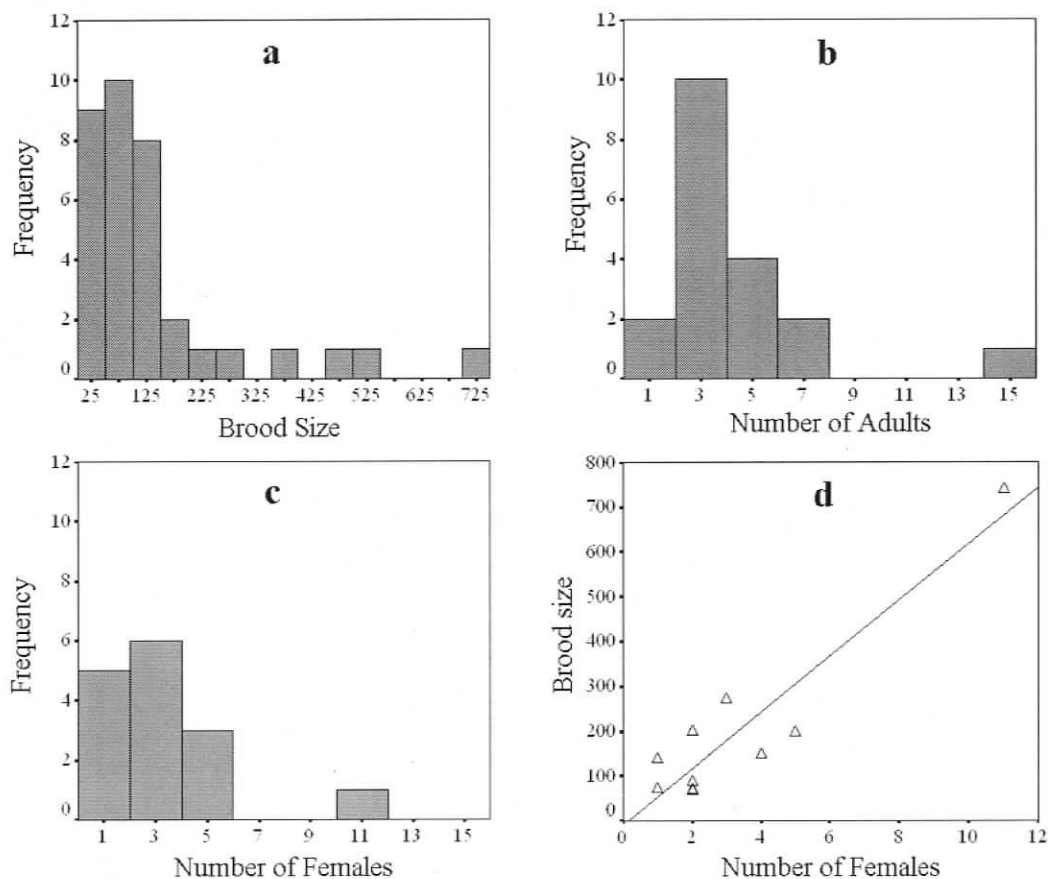


Figure 6.4. Frequency distribution of a) brood size, b) number of initial adults, c) number of initial females, and d) the relationship between brood size and number of initial females, from a survey of *N. investigator* breeding structure on salmon carcasses from both the Clatse and Neekas rivers, British Columbia, October 2003.



Chapter 7:

Insect niches on marine and terrestrial carrion

7.1. Abstract

Niche partitioning in carrion communities typically occurs along dimensions of season, habitat, and the size or extent of decomposition of the carcass, while differentiation by carrion type has received limited attention. In contrast to traditional measures of niche characterization, stable isotope analysis of animal tissues provides a direct and time-integrated measure of dietary niche. Every fall on the central coast of British Columbia, salmon carcasses are distributed to riparian zones by bears where they are consumed by a diverse community of terrestrial invertebrates. Herein, I examine $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in several adult carrion species, including two Coleoptera (Silphidae: *Nicrophorus investigator* and *N. defodiens*) and two Diptera (Calliphoridae: *Calliphora terranova*; Dryomyza: *Dryomyza anilis*) species, and investigate whether individuals were raised on a larval diet of salmon or a range of terrestrial carrion. I demonstrate that most *N. investigator* individuals were raised on a diet of salmon carrion while *N. defodiens* consumed only terrestrial sources. Both fly species exhibited a high population-level frequency of a salmon diet (~90%) after their spring/summer emergence. Seasonal variation in dipteran isotope signatures showed that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ are best predicted by days since first emergence in *Calliphora* and dry weight in *Dryomyza*. This indicates that there may be multiple *Calliphora* generations throughout the season, while *Dryomyza* signatures may be more influenced by terrestrial adult feeding. Overall, flies and beetles represent dominant consumers and vectors of salmon nutrients and energy in terrestrial systems. Stable isotope analysis also offers an alternative technique for investigating carrion preferences and specialization within this and other systems.

7.2. Introduction

Communities based on ephemeral resources, such as those living on carrion, are often structured by competition, a process that can lead to various temporal and spatial niche partitioning (Putman 1983; Shorrocks and Swingland 1990). Carcass specialization has been observed in burying beetles (Silphidae: *Nicrophorus* spp.) and carrion-breeding Diptera, with niche distribution occurring along dimensions of season, habitat, and the size or extent of decomposition of the carcass (Hanski 1987; Ohkawara et al. 1998; Kočárek 2001). In comparison, differentiation by carrion type has received little attention (Kneidel 1984).

Niche separation among species and individuals has been conventionally studied using dietary analyses, habitat choice and phenotypic variation in trophic structures and body size (Grant 1968; Roughgarden 1974; Schoener 1986), although there remain methodological and theoretical limitations to this approach (Bearhop et al. 2004). In carrion-based communities, partitioning among species is typically determined using standard field methods or laboratory experiments (Anderson 1982; Hanski 1987; Smith and Wall 1997). In contrast, stable isotope analysis of animal tissues provides a direct measure of dietary niche, particularly if the isotope signature of potential food sources is known (Bearhop et al. 2004).

Nitrogen and carbon isotopes have been used in multiple studies to estimate dietary variation, trophic structure and sources of nutrients and energy (reviews in Peterson and Fry 1987; Kelly 2000; Post 2002b). The ratio of $^{15}\text{N}/^{14}\text{N}$ ($\delta^{15}\text{N}$) in consumer tissues is typically enriched by 3-4 parts per mil (‰) relative to diet (DeNiro and Epstein 1981; Minigawa and Wada 1984) and thus nitrogen isotope ratios are often used to estimate trophic position (Vander Zanden et al. 2000). Carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$ or $\delta^{13}\text{C}$) usually have low diet-tissue fractionation (DeNiro and Epstein 1978; Gearing et al. 1984), and thus have been primarily used to determine sources of primary productivity (Tieszen and Boutton 1988). For example, in the salmon-forest system, stable isotopes are commonly used to determine direct and indirect pathways of salmon nutrient input to terrestrial organisms (Hocking and Reimchen 2002).

Every fall anadromous salmon (*Oncorhynchus* spp.) subsidize terrestrial habitats throughout the Pacific Rim with their nutrients and carcasses (Cederholm et al. 1999;

Gende et al. 2002). Many terrestrial animals converge on salmon spawning streams to feed, which distributes carcasses into adjacent forests. Bears (*Ursus* spp.) are the primary vectors, but wolves, river otters and other vertebrates, as well as periodic flooding, transfer carcasses (Ben-David et al. 1998b; Reimchen 2000). Salmon remains in riparian zones subsequently attract many invertebrate scavengers and saprophages (Jauquet et al. 2003). This community is dominated by flies (Diptera: Calliphoridae, Dryomyzidae, Muscidae, Heleomyzidae, Spherozeridae) and beetles (Coleoptera: Silphidae, Staphylinidae), as well as parasitic wasps and generalist predators such as carabid beetles (Jauquet et al. 2003; Reimchen et al. 2003; Meehan et al. 2005; Hocking et al. *in press*).

Herein, I examine $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in adults of several dominant members of the carrion guild on the central coast of British Columbia including two Coleoptera (Silphidae: *Nicrophorus investigator* and *N. defodiens*) and two Diptera (Calliphoridae: *Calliphora terranova*; Dryomyza: *Dryomyza anilis*) species. All species except *N. defodiens* have been observed breeding on salmon carcasses. My primary objective was to determine whether individual adults fed as larvae on salmon or a range of terrestrial carrion that span multiple terrestrial trophic levels. Both *Nicrophorus* beetles were caught in highest abundance in mid-summer prior to the arrival of salmon, and I focus my analysis on carcass niche differentiation between these two species on a single watershed. Diptera were caught in baited traps from all seasons from three separate watersheds. I make seasonal comparisons of their isotope signatures and investigate the timing of emergence of different fly generations when salmon are unavailable (spring, summer) and available (fall). My analysis provides a method for evaluating carcass preferences and specialization in carrion communities and provides insight to the importance of carrion species in the consumption and distribution of salmon nutrients in terrestrial systems of coastal British Columbia.

7.3. Materials and methods

7.3.1. Study sites

This study was conducted from 2000-03 on the central coast of British Columbia, Canada. Primary study sites were the Clatse (52° 20.6'N; 127° 50.3'W) and Neekas (52° 28' 16.8"N; 128° 9' 38.7"W) rivers, which had significant runs of salmon (see Hocking

and Reimchen 2002; Mathewson et al. 2003). Chum (*O. keta*) and pink (*O. gorbuscha*) salmon spawn from late August to late October, and represent a predictable source of carrion to terrestrial consumers at this time. Both watersheds support populations of black bears and wolves, which act as the principal vectors of salmon carcasses into the forest. 5-10m waterfalls act as a physical barrier to salmon migration 0.9 and 2.1km upstream on the Clatse and Neekas respectively. A nearby watershed, Ripley Bay Creek (52° 25.6'N; 127° 53.2' W), served as an additional control site because it has a 7m falls followed by a cascade at the mouth which exclude salmon from the system.

7.3.2. Collection methods

In mid-August of 2000 (summer) and late June of 2001 (spring) I set out baited pitfall traps along the Clatse River and captured samples of adult *N. investigator* and *N. defodiens*. Mid-August is at least two weeks before salmon enter the watershed and carcasses begin to accumulate in the forest. Pitfall traps consisted of 500ml plastic cups buried at ground level and baited with 5-10g of decomposing salmon. Adults were stored in 70% ethanol until stable isotope preparation.

In a more detailed survey from May to October 2003, I established and monitored hanging baited traps (~1m) on the Clatse, Neekas and Ripley rivers, and caught adult *C. terranova*, *D. anilis*, *N. investigator* and *N. defodiens*. Traps were 1L clear plastic tubs with lids held up by several cm off of the rim and were baited with ~5g of rotting beef. Bait was wrapped in perforated cloth and suspended into the tub. Water or 70% ethanol was used as a collecting fluid (ethanol if more than 2 days between checks). I established ten traps below the falls and five traps above the falls on both the Clatse and Neekas, and five traps on the control watershed Ripley Bay. All Diptera processed for stable isotopes were identified to sex and were weighed (wet and dry weight). In July, both *N. investigator* and *N. defodiens* were captured in the traps at high frequency on the Clatse River, and additional isotopic analysis was conducted on this collection.

In the fall of 2001, chum and pink salmon dorsal muscle tissue samples (n = 6 for each species) were removed from post spawning carcasses from the Clatse River, and were used to predict the range of isotope values in adult Diptera and Coleoptera that represent a larval diet of salmon. To estimate the isotopic range of terrestrial carrion

available to Diptera and Coleoptera, tissue samples were collected from shrews, songbirds and deer, which span multiple terrestrial trophic levels. Shrews (*Sorex monticolus*) were collected (Clatse n = 19; Neekas n = 6) in passive and baited pitfall traps in the summer of 2000 and the spring and fall of 2001 (Hocking and Reimchen 2002). In the fall of 2003, songbirds were captured using mist-nets adjacent to the Clatse and Neekas rivers (Christie et al. *submitted*). Feathers were collected representing both the summer and fall diet from individual Winter Wrens (*Troglodytes troglodytes*) (Clatse n = 4; Neekas n = 8), Swainson's Thrushes (*Catharus ustulatus*) (Clatse n = 2), and Hermit Thrushes (*Catharus guttatus*) (Clatse n = 6; Neekas n = 1). Deer (*Odocoileus hemionus*) hair (n = 9) was sampled from day beds in late May and early June along random 1 km upslope transects in the Clatse watershed starting at sea-level or low-elevation roads and often terminating in the sub-alpine (up to 800 m) (Darimont et al. *in prep*).

7.3.3. Dietary characterization using stable isotopes

Stable isotope analysis (SIA) of nitrogen and carbon was conducted on adult *Nicrophorus*, adult Diptera, and on potential carrion food sources that include chum or pink salmon, as well as deer, songbirds and shrews (Table 7.1). Overall, little information is known on the carcass preferences of carrion breeding species on the west coast of British Columbia. As such, these terrestrial carrion sources were chosen mainly because they represent prey spanning multiple terrestrial trophic levels. Furthermore, shrews and other small mammals are preferred carrion prey for burying beetles in other regions (Smith et al. 2000), and large carrion such as deer may be favourable breeding sites for many species of flies (Watson and Carlton 2005). Songbirds represent alternative small vertebrate prey that span a wide range of trophic levels and include species that feed directly on salmon carcass resources (Christie et al. *submitted*).

Whole Diptera and Coleoptera specimens and salmon muscle tissue were rinsed with distilled water and then dried at 60°C for at least 48 hours. Samples were ground into a homogeneous powder using a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Ill). Songbird feathers and mammal hair samples were rinsed with distilled water, soaked in a 2:1 chloroform: methanol solution for 24 hours and then dried at 60°

for at least 24 hours. Feathers and hair were then chopped into small fragments and loaded into tin capsules. All samples (approx 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 (CF-IRMS). Natural abundances of ^{15}N and ^{13}C are given in parts per mil (‰) and are expressed by:

$$1) \left(\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right) \times 1000$$

where R = the ratio of $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. Isotopic standards include N_2 in air for nitrogen isotope analyses and Pee-Dee Belemnite (PDB) limestone for carbon isotope analysis. Measurement precision is approximately $\pm 0.35\text{‰}$ for ^{15}N and $\pm 0.10\text{‰}$ for ^{13}C .

Salmon muscle tissue $\delta^{13}\text{C}$ values were lipid normalized ($\delta^{13}\text{C}'$) based on equations derived from McConnaughey and McRoy (1979) (See also Satterfield and Finney 2002):

$$2) L = \frac{93}{1 + (0.246\text{CN} - 0.775)^{-1}}$$

$$3) \delta^{13}\text{C}' = \delta^{13}\text{C} + D \left[-0.207 + \frac{3.90}{(1 + 287/L)} \right]$$

where L is % lipid, CN is the carbon to nitrogen ratio of salmon muscle and D is the depletion of ^{12}C (‰) relative to protein and assigned 6‰. This was done because there are large carbon isotope fractionation differences between protein 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 Diptera and *Nicrophorus* individuals.

Lipid normalization of $\delta^{13}\text{C}$ values was also conducted on all adult Diptera and *Nicrophorus* specimens. I used a Pearson's correlation matrix to examine whether lipid transformation had an effect on the relationships between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, and $\delta^{13}\text{C}$ and C/N ratios. High C/N ratios can indicate high lipid content with depleted $\delta^{13}\text{C}$ values (Tieszen and Boutton 1988). This analysis was conducted on *Calliphora* and *Dryomyza* adults on both the Clatse and Neekas watersheds from the large spring to fall collection in 2003. In *Nicrophorus*, I pooled collections from 2000 to 2003 from Clatse.

Lipid transformation of $\delta^{13}\text{C}$ values increased the strength of the relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in all species. Pearson's R values increased from 0.324 ($p = 0.013$) to 0.489 ($p < 0.001$) in *N. defodiens* for lipid standardized versus unstandardized values, while for *N. investigator*, R values increased from 0.692 ($p < 0.001$) to 0.752 ($p < 0.001$). Unstandardized $\delta^{13}\text{C}$ values were negatively correlated to tissue C/N ratios in both species (*N. defodiens*: $R = -0.407$, $p = 0.002$; *N. investigator*: $R = -0.397$, $p < 0.001$), and lipid transformation reduced these slopes so that they were not significantly different from zero (*N. defodiens*: $R = -0.030$, $p = 0.825$; *N. investigator*: $R = -0.138$, $p = 0.211$).

In the flies, lipid normalization again improved the relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for both *Calliphora* and *Dryomyza* on both watersheds. R^2 values for lipid normalized $\delta^{13}\text{C}$ ranged from 0.20 – 0.77 compared to 0.19 – 0.68 for unstandardized $\delta^{13}\text{C}$. In *Calliphora*, unstandardized $\delta^{13}\text{C}$ values were negatively correlated to C/N ratios ($R = -0.491$ (Clatse) and -0.408 (Neekas); both $p < 0.001$), and lipid normalization decreased the slopes so that they did not differ significantly from zero (Clatse $R = -0.19$, $p = 0.082$; Neekas $R = -0.05$, $p = 0.61$). In *Dryomyza* however, lipid normalization did not reduce the negative correlation between $\delta^{13}\text{C}$ and C/N to a slope equal to zero (Transformed values: Clatse $R = -0.70$, $p < 0.001$; Neekas $R = -0.34$, $p = 0.006$).

Hair and feather samples were not lipid normalized, although several modifications were needed to most accurately reflect the stable isotope signatures of potential resources of sampled consumers. Hair $\delta^{13}\text{C}$ values in shrews were reduced by 1.5‰ to approximate muscle tissue since diet-fur fractionation has been observed to be higher than diet-muscle fractionation by ~1.5‰ in mammalian carnivores (Roth and Hobson 2000). I similarly reduced $\delta^{13}\text{C}$ values in deer hair by 1‰ to approximate muscle tissue (Sponheimer et al. 2003). For birds, diet-to-tissue fractionation of $\delta^{15}\text{N}$ but not $\delta^{13}\text{C}$ is higher (~1‰) in feathers than muscle tissue (Hobson and Clark 1992; Thompson and Furness 1995). Accordingly, I applied a 1‰ correction factor to feather $\delta^{15}\text{N}$ values.

Mammal and bird samples reflected the seasonality of sampling and the schedule of tissue turnover. Sampled winter pelage of deer grows from mid July to the end of October and is carried through the winter. Sampled shrews were from spring, summer and fall and represent the seasonality of sampling. For songbirds, because we had both

summer and autumn-grown feathers, we calculated the mean signature to approximate the average isotopic signature over the period of study.

I estimated diet-tissue fractionation in Diptera and *Nicrophorus* based on previously-reported values. Diet-tissue fractionation in animals is typically around +3‰ for $\delta^{15}\text{N}$ (Minigawa and Wada, 1984) and 0-1‰ for $\delta^{13}\text{C}$ (Tieszen and Boutton, 1988), although there have been only a few studies that have investigated dietary fractionation in adult Diptera or Coleoptera. For *Nicrophorus*, I use values reported in predaceous lady bird beetles (1.2 – 1.7‰ for $\delta^{15}\text{N}$: Scrimgeour et al. 1995; and $2.9 \pm 0.3\%$ for $\delta^{15}\text{N}$, $-0.2 \pm 0.1\%$ for $\delta^{13}\text{C}$: Ostrom et al. 1997) as my best available comparison. From these values I used a fractionation range of 1-4‰ for $\delta^{15}\text{N}$ and -1 to +1 for $\delta^{13}\text{C}$ to reconstruct diet in *Nicrophorus*. DeNiro and Epstein (1978; 1981) observed 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. However, on these same diets, *Musca* adults had $\delta^{15}\text{N}$ diet-tissue fractionation of up to $4.6 \pm 0.5\%$. As such, for both *Calliphora* and *Dryomyza*, I used a range of fractionation of 1-5‰ for $\delta^{15}\text{N}$ and -1 to 0‰ for $\delta^{13}\text{C}$.

Using these estimates of diet-tissue fractionation I constructed expected isotopic ranges for a diet of salmon or terrestrial carrion, and determined the minimum and maximum frequency of salmon diet in the populations of adult *N. investigator*, *N. defodiens*, *Calliphora* and *Dryomyza* (Tables 7.2; 7.3; 7.4). For the flies this included estimates from both watersheds in the spring, summer and fall. Since *Nicrophorus* spp. are often associated with small mammal carrion (Smith et al. 2000), I also constructed an expected range based only on a diet of shrews. Overall, these dietary reconstructions assume that adult feeding is either minimal or contributes little to adult isotope signatures. Since this assumption may be violated, our estimates for the frequency of a salmon diet as larvae are conservative. To try to account for this I compare isotope signatures between the Diptera and *Nicrophorus*. All *N. defodiens* individuals had isotope signatures indicative of a terrestrial carrion diet (see results below). For both *Calliphora* and *Dryomyza* then, the maximum value for *N. defodiens* (11‰ for $\delta^{15}\text{N}$ and -21‰ for $\delta^{13}\text{C}$) was used as a cut-off where it is assumed that all flies with signatures below this value are derived from terrestrial carrion as larvae.

7.3.4 Statistical analysis

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in *N. investigator* and *N. defodiens* were compared using t-tests within three separate sampling periods (spring 2001, summer 2000, summer 2003). If assumptions of equal variances were not met, Welch's t-tests were used. Isotope values were compared among sampling periods using non-parametric Kruskal-Wallis tests.

Collected Diptera were grouped by season (Spring: May – June; Summer: July – August; Fall: September – October) and by the number of days from when the first Diptera were collected (1st Day: Day 1 = May 22nd 2003; Last Day: Day 142 = October 10th 2003). I conducted separate Principal Components Analyses (PCA) on *Calliphora* (n = 222) and *Dryomyza* (n = 140) adults caught in baited traps in 2003 using the variables $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and C/N ratio. I was interested in how watershed, season, falls (ie. above or below), Diptera sex and Diptera dry weight might predict the principal components of variation in isotope signatures (ie. PC1). To do this I used Akaike's Information Criterion (AIC) (Burnam and Anderson 1998) to assess the predictive power of various *a priori* models with different combinations of variables. AIC evaluates models based on the principle of parsimony, balancing optimal model fit with number of parameters used. Thus, the model with the best predictive power using the fewest number of parameters is identified by the lowest AIC value. For *Calliphora* I used uncorrected AIC values, while for *Dryomyza* I used corrected AIC (AIC_c), which adjusts for small sample sizes. ΔAIC was calculated as the difference between AIC values of the top-ranked model and all subsequent models. Models with $\Delta\text{AIC} \leq 2.0$ are considered most strongly supported by the data (Burnam and Anderson 1998). In order to assess the relative importance of an individual variable found within the top models, I summed the weights (W_i) of all models with $\Delta\text{AIC} \leq 4.0$. Models were generated using a general linear model (GLM) approach. Explanatory variables used included all combinations of the main effects of watershed (Clatse, Neekas, Ripley), falls (above, below), season (continuous: days since 1st fly was captured), Diptera sex (male, female) and Diptera dry weight (continuous) (total no. of models = 17 including null). For simplicity, and since none were *a priori* predicted, no interaction terms were included. Since I wanted to account for variation at the watershed level, all models included the variable watershed.

7.4. Results

7.4.1. Carrion sources

Carrion sources differed in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, where chum and pink salmon had the highest values, and deer the lowest (ANOVA both isotopes: $F_{4,66} > 36$, $p < 0.001$; Table 7.1). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in salmon ranged from 10.79 to 14.66‰ and -22.45 to -18.65‰ respectively, with mean values for chum higher than those for pink for both isotopes ($\delta^{15}\text{N}$: $t_{8,42} = -2.85$, $p = 0.020$; $\delta^{13}\text{C}$: $t_{10} = -3.82$, $p = 0.003$). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in terrestrial carrion ranged from -0.29 to 11.23‰ and -30.43 to -20.91‰ respectively, with deer occupying the lowest trophic level followed by shrews and songbirds which displayed high overlap and a fairly wide range of values. The highest values observed for both isotopes in terrestrial carrion occurred in individual Winter Wrens who likely derived a large proportion of their diet from fly maggots feeding directly on salmon carcasses. Terrestrial carrion such as Marten (*Martes americana*), gulls (*Larus* spp.) and River otters (*Lutra canadensis*) not included in this study who may derive a large proportion of their yearly protein from salmon or other marine resources may have similarly high isotopic signatures. Using these various carrion sources, and literature estimates of diet-tissue fractionation, I constructed expected ranges of isotope signatures in adult *Nicrophorus* and Diptera specimens (Table 7.2).

7.4.2. Isotopic signatures in *Nicrophorus*

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope signatures differed highly between *Nicrophorus* species, with a large percentage of *N. investigator* individuals derived from salmon carrion as larvae compared to none for *N. defodiens* (Figure 7.1; Table 7.3). *N. investigator* had higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ than *N. defodiens* in all three collection periods (spring 2001, summer 2000, summer 2003: all $t > 2.8$, all $p < 0.02$), with seasonal means varying from 12.00‰ to 14.27‰ for $\delta^{15}\text{N}$ and -21.97‰ to -20.21‰ for $\delta^{13}\text{C}$ in *N. investigator* and 7.79‰ to 8.45‰ for $\delta^{15}\text{N}$ and -24.38‰ to -23.13‰ for $\delta^{13}\text{C}$ in *N. defodiens*. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures differed by sampling period (Kruskal Wallis: both $\chi^2_2 > 6$, $p < 0.05$) in *N. investigator*, with highest signatures and highest frequency of salmon diet in summer 2003. In *N. defodiens*, $\delta^{13}\text{C}$ signatures differed by sampling period (Kruskal Wallis: $\chi^2_2 = 17.11$, $p < 0.001$), while $\delta^{15}\text{N}$ did not ($p > 0.5$). Of the 84 *N. investigator* individuals

sampled at least 46% were derived from salmon as larvae. Considering that none of the 58 *N. defodiens* individuals had isotope signatures that fell between low salmon values and high terrestrial values (SalmTerr: Table 7.3), it is much more likely that as high as 87% of *N. investigator* individuals fed on salmon as larvae. Most *N. defodiens* (90%) fell within the isotopic range defined by shrews, although this range overlaps highly with that of songbirds.

7.4.3. Isotopic signatures in *Calliphora* and *Dryomyza*

Using data on larval carrion sources, I classified adult *Calliphora* and *Dryomyza* into dietary categories (Table 7.4; Figure 7.2). Due to the uncertainty over the extent of adult feeding as well as partial overlap between salmon and terrestrial prey sources, the range in % salmon diet (max - min) was large in all seasons from all watersheds. Overall, the frequency of a salmon diet as larvae in *Calliphora* adults was lower in the fall relative to the spring and summer, while *Dryomyza* adults showed relatively consistent frequencies across all seasons. In the spring, excluding Ripley (low sample sizes), the frequency of a salmon diet in *Calliphora* ranged from 42-43% (min) to 90-95% (max), while in the fall this range was 0-4% (min) to 62-67% (max). The minimum frequency of a terrestrial diet varied from 5-10% in the spring to 33-38% in the fall. For *Dryomyza*, the frequency of a salmon diet varied from 21-95% in the spring to 0-100% in the fall, while the minimum frequency of a terrestrial diet varied from 0-14% across all seasons on all watersheds. On the control watershed Ripley Bay Creek, salmon signatures were evident in both species.

Factor 1 from the Principal Components Analysis (PCA) of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and C/N ratios in *Calliphora* and *Dryomyza* yielded the strong correlation between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and an associated negative relationship to tissue C/N ratios (Table 7.5). In *Calliphora*, PC1 was most strongly predicted by date of collection as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ decreased with days since first emergence (Figure 7.3). Days since first emergence had the highest AIC weight and was found in all top models, while the parameters sex, falls and dry weight contributed to the top models but to a lesser extent (Tables 7.6 and 7.7). Almost no male *Calliphora* were captured in the fall on either the Clatse or Neekas and thus overall, females had lower PC1 scores than males (Clatse: $F_{1,86} = 5.69$, $p = 0.019$; Neekas $F_{1,129} =$

10.23, $p = 0.002$). On Neekas there was no effect of falls on PC1 scores ($F_{1,129} = 0.61$, $p = 0.437$) while on Clatse PC1 scores were higher above the falls compared to below ($F_{1,86} = 14.49$, $p < 0.001$). In *Dryomyza*, the dryweight of individual adults had the highest AIC_c weight and was found in all top models, with increasing dry weight related to decreasing PC1 scores (Figure 7.4; Tables 7.6 and 7.7). PC1 scores in *Dryomyza* did not differ above or below the falls or by sex on either the Clatse or Neekas (all $F < 1$, all $p > 0.35$). On Clatse, PC1 scores decreased with days since first emergence ($F_{1,67} = 34.55$, $p < 0.001$, $R^2 = 0.344$), while on Neekas there was no major effect ($F_{1,62} = 3.48$, $p = 0.067$, $R^2 = 0.054$).

7.5. Discussion

Spawning Pacific salmon (*Oncorhynchus* spp.) provide a dominant source of marine carrion to terrestrial communities throughout the Pacific Rim (Reimchen 1994; Cederholm et al. 1999; Gende et al. 2002), although a detailed assessment of the insect niches associated with salmon carcasses is lacking. Overall, stable isotope analysis offers an alternative technique for evaluating niche preferences among carrion species, including within the salmon-forest system.

Carrion species on salmon and other carcasses are often subject to high levels of competition, which can lead to species dominance, specialization and niche partitioning in various spatial and temporal dimensions (Hanski 1987; Smith and Wall 1997; Ohkawara et al. 1998; Hocking et al. *in press*). Species are most often distributed along niche dimensions of carcass size, habitat, decay sequence, or temporal activity (Anderson 1982; Kočárek 2001), although flies have been demonstrated to segregate by carcass taxon as well (Kneidel 1984). Burying beetles often partition themselves by time of emergence and seasonal activity, diurnal versus nocturnal activity, and by habitat (Anderson 1982; Ohkawara et al. 1998; Kočárek 2001). In Newfoundland, the species also investigated in this study, *N. investigator* and *N. defodiens*, co-occur on seabird colonies and partition themselves mainly by habitat rather than by seabird carrion type (Wilhelm et al. 2001).

N. investigator and *N. defodiens* are sympatric in coastal forest habitats of Western North America for at least two months in the summer, and, in this case, I provide stable isotope evidence for dietary differences between the two species with segregation

by carrion type (salmon versus terrestrial carrion). I demonstrate that most *N. investigator* adults were derived from salmon carrion as larvae while all *N. defodiens* were not. Most *N. defodiens* individuals, in comparison, had isotope signatures that overlapped highly with those of riparian shrews and songbirds. To my knowledge this is the first time that carcass source preferences have been demonstrated in burying beetle species occurring in sympatry. Whether this is due to differences in seasonal activity, where *N. defodiens* cannot tolerate cooler autumn temperatures, or active exclusion of *N. defodiens* by *N. investigator* on large salmon carcasses, remains unclear. *N. investigator* adults, particularly females, have been observed breeding on salmon carrion until the end of October (Hocking et al. *in press*), while the latest that *N. defodiens* has been observed in all years of the study was early September.

Stable isotope analysis could be used to determine diet and carcass preferences in other carrion communities, including those of burying beetles. For example, recent and historical dietary preferences could be investigated in the endangered American burying beetle (*N. americanus*) using stable isotopes to improve conservation efforts (Lomolino et al. 1995).

Flies of the species *Calliphora terranova* and *Dryomyza anilis* are the dominant consumers of salmon carcasses from my study watersheds and distribute SDN to multiple consumers over a large area (Reimchen 1994; Meehan et al. 2005). Both species displayed high frequencies of a salmon diet after emergence in spring and summer from two separate watersheds, with frequencies declining during the fall spawning run. The observation that isotope signatures in both species did not differ ostensibly above and below the waterfalls as well as among watersheds indicates that these flies can distribute salmon nutrients across a wide geographic area. However, there was some uncertainty surrounding the estimates which was largely due to 1) the overlap between low salmon signatures and high terrestrial ones, and 2) the possibility of mixing of larval salmon diet with adult terrestrial diet. High $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in terrestrial species occur via the consumption of salmon flesh or direct predation of salmon-consumers (for example songbirds that consume fly maggots on salmon carcasses (Christie et al. *submitted*). It is possible that some individual flies fed as larvae on terrestrial sources enriched in salmon-derived nutrients (Hocking and Reimchen 2002).

Although we demonstrate salmon and terrestrial signatures in both fly species, my analysis could more clearly identify sources if isotope values for adult diet were known. Tallamy and Pesek (1996) demonstrate that the elytra of Chrysomelid beetle adults have an intermediate $\delta^{13}\text{C}$ signature between their larval and adult diets only 10 days after emergence. It is likely that many intermediate signatures observed here between the salmon and terrestrial sources occurred because of terrestrial adult feeding. If this is true then all my estimates for the population-level frequency of a salmon diet as larvae are conservative.

Calliphora adults had the highest frequency of a salmon diet after emergence in spring (up to 95%) with frequencies declining during the fall salmon spawning run. AIC analysis revealed that days since first emergence was the best predictor of isotope signatures. This highlights the dominance of salmon as a carrion source in this region as well as the likelihood for multiple generations of flies throughout the summer. Declining signatures could also result from a terrestrial adult diet because longevity is increased when adult blowflies feed on sugars or protein (Peterson et al. 1987). Despite adult feeding, adult life-span may only extend for up to one month (Peterson et al. 1983; Peterson et al. 1987) and individuals emerging in spring are not likely to survive to breed on salmon carcasses in the fall. In autumn, I observed *Calliphora* with both terrestrial and salmon origins breeding on salmon carcasses. This suggests that some individuals extend their diapause and delay emergence until late in the season, a pattern that may be particularly true for females since almost no males were caught in the fall. This may indicate bimodal emergence patterns where males emerge before females, a life-history called protandry (Buck 2001).

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in *Dryomyza* adults were best predicted by individual dry weight rather than seasonal, sex or location effects. The vast majority of isotope signatures fell within the range of uncertainty of either salmon or high terrestrial signatures, with only 3-4 individuals (of 140) with a clearly terrestrial diet. If individual dry weight increases with terrestrial adult feeding then this species may be particularly specialized for a diet of salmon carrion. This species emerges later than *Calliphora* in mid-summer, can tolerate cool late season temperatures and is typically associated with smaller salmon carcass remnants from my study watersheds (pers. obs.).

Strong correlations between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were evident in all species investigated indicating larval development on salmon and terrestrial carrion, as well as trophic variation in their carcass prey from both marine and terrestrial food chains (Hocking and Reimchen 2002). Lipid standardization increased the strength of the relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and decreased the observed negative relationship between $\delta^{13}\text{C}$ and C/N ratios. High C/N ratios can imply high lipid content in body tissues, which have been shown to be more depleted in $\delta^{13}\text{C}$ than other tissue types (Tieszen and Boutton 1988). Based on these results, lipid standardization (McConnaughey and McRoy 1979) is likely a useful methodological approach for SIA of insects, although many of the implicit assumptions (such as a D value of 6‰) need to be tested.

7.6. Conclusion

As an alternative and/or supplement to conventional methods of niche differentiation in carrion-based and other communities, stable isotopes can be used to determine individual- and population-level prey preferences (Bearhop et al. 2004). I use stable isotope analysis of nitrogen and carbon to identify and differentiate larval diets of salmon or terrestrial carrion in two burying beetle (*Nicrophorus investigator* and *N. defodiens*) and two fly (*Calliphora terranova* and *Dryomyza anilis*) species. SIA revealed carcass separation in the two *Nicrophorus* species with *N. investigator* largely associated with salmon carcasses while *N. defodiens* may be associated with riparian shrews. Both fly species showed a close association with salmon carcasses, where season was the best predictor of isotopic variation in the *Calliphora* and dry weight the best predictor in *Dryomyza*. This highlights the likelihood for multiple generations of flies in *Calliphora* and the potential for specialization on salmon carrion within the *Dryomyza*. Further morphological and behavioural studies that are coupled with stable isotope analysis may reveal further population and/or individual-level specialization in these taxa.

Overall, *C. terranova*, *D. anilis* and *N. investigator* are supported by the marine subsidy of salmon carcasses and represent important consumers and further vectors of salmon nutrients in terrestrial systems (Reimchen 1994). They are three of the most dominant insect consumers of salmon carcasses on the central coast of British Columbia,

and contribute to a growing list of terrestrial taxa that utilize this seasonal pulse of marine-derived nutrients and energy (Reimchen 1994; Cederholm et al. 2000; Gende et al. 2001; Jauquet et al. 2003). Individuals with high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures occur high on the marine food-chain at trophic levels that are equivalent to those of pinnipeds and orca whales (Hobson et al. 1997; Pauly et al. 1998). These results are particularly relevant when one considers that bears are the keystone distributors of salmon carcasses to riparian forests, and that salmon have declined dramatically in abundance over the last century (Finney et al. 2000; Gresh et al. 2000).

Figure 7.1. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures in a) larval carrion sources including salmon (chum and pink) and terrestrial carrion (deer, shrews, songbirds) and b) *Nicrophorus investigator* and *N. defodiens* (Coleoptera: Silphidae) adults captured in spring and summer (2000-2003) from the Clatse River, British Columbia.

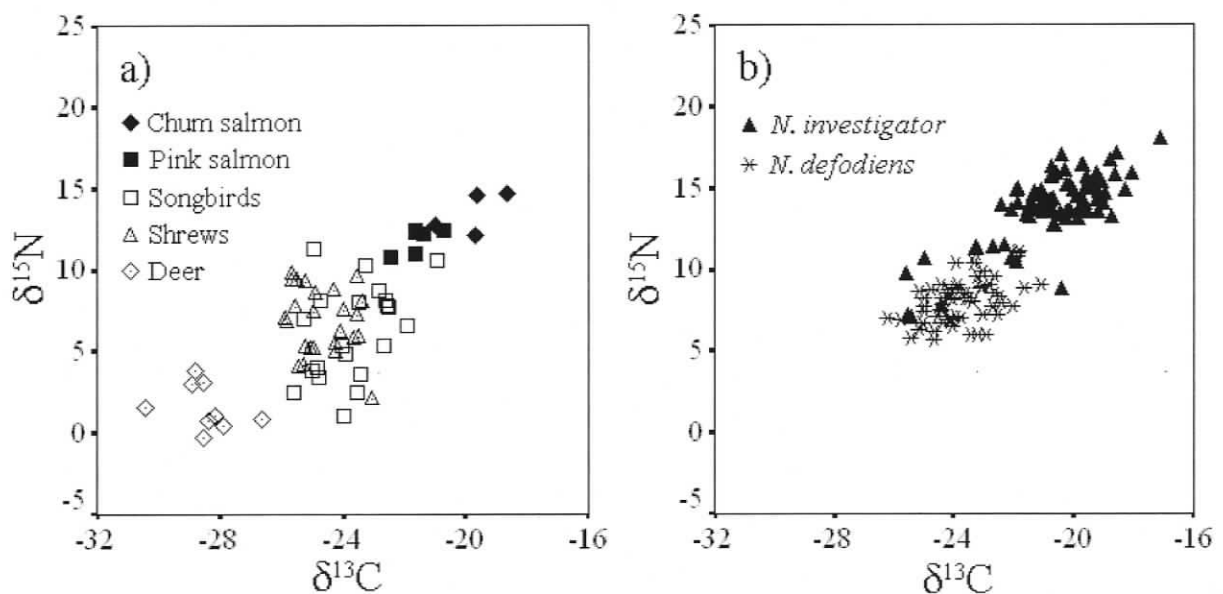


Figure 7.2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures and dietary characterization in a) *Calliphora* (Diptera: Calliphoridae) and b) *Dryomyza* (Diptera: Dryomyzidae) adults caught in baited traps on the Clats, Neekas and Ripley watersheds in 2003 (See Table 7.4). Classification was based on isotope signatures of potential carrion prey including chum and pink salmon and terrestrial songbirds, shrews and deer. Salmon indicates individuals with a salmon diet as larvae with isotope signatures outside the terrestrial range but within the salmon range. Salm/Terr indicates individuals with isotope signatures above a value of 11.0‰ for $\delta^{15}\text{N}$ and/or -22.0‰ for $\delta^{13}\text{C}$ with possible terrestrial larval diet but more likely a larval salmon diet contaminated by terrestrial adult feeding. Terrestrial indicates individuals with likely a terrestrial carrion diet as larvae.

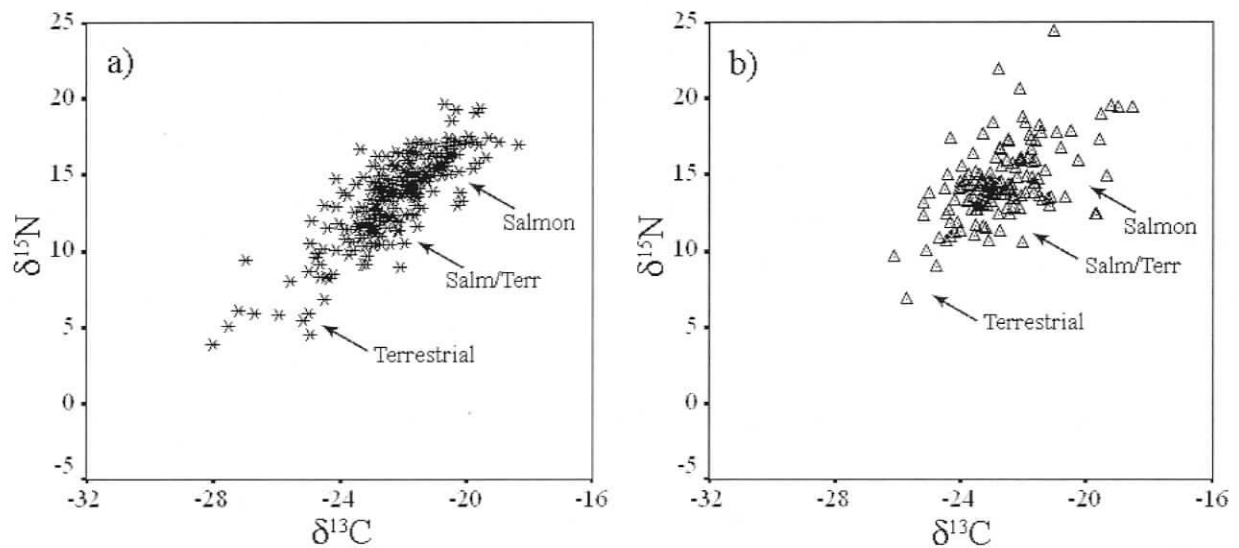


Figure 7.3. Seasonal variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures (here as PC1 scores) in *Calliphora* (Diptera: Calliphoridae) adults captured in baited traps on the Clatse and Neekas rivers, B.C.

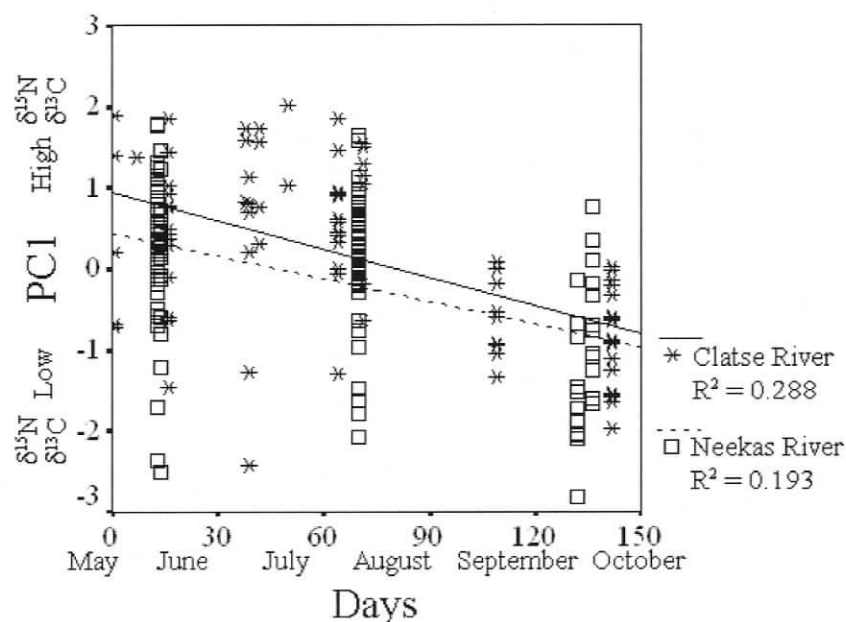


Figure 7.4. Body mass variation and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures (here as PC1 scores) in *Dryomyza* (Diptera: Dryomyzidae) adults captured in baited traps on the Clatse and Neekas rivers, B.C.

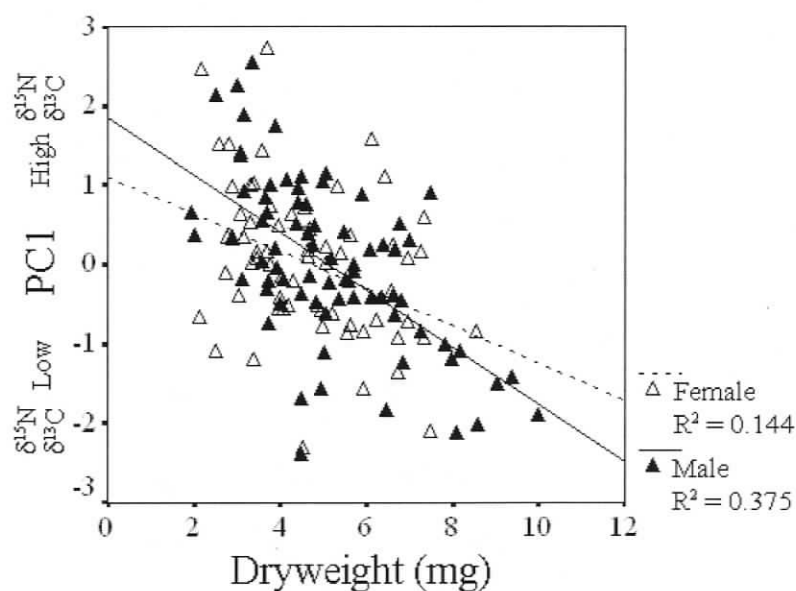


Table 7.1. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope signatures in tissue samples from marine (pink and chum salmon) and terrestrial (songbirds and mammals) animals collected on the Clatse and Neekas rivers, B.C. Minimum and maximum values from salmon and terrestrial groupings were used to construct expected isotopic ranges in adult Diptera that were derived from either a larval diet of salmon or terrestrial carrion.

	N	$\delta^{15}\text{N}(\text{‰})$		$\delta^{13}\text{C}(\text{‰})$	
		Mean $\pm$ SE	Range	Mean $\pm$ SE	Range
Pink salmon (<i>O. gorbuscha</i>)*	6	11.85 $\pm$ 0.31	10.79 to 12.44	-21.58 $\pm$ 0.23	-22.45 to -20.43
Chum salmon (<i>O. keta</i>)*	6	13.52 $\pm$ 0.50	12.05 to 14.66	-19.76 $\pm$ 0.42	-21.01 to -18.65
Dusky shrew (<i>S. monticolus</i>)†	25	6.79 $\pm$ 0.40	2.06 to 9.73	-24.66 $\pm$ 0.18	-25.86 to -23.05
Winter wren (<i>T. troglodytes</i>)‡	12	7.60 $\pm$ 0.74	3.43 to 11.23	-23.41 $\pm$ 0.38	-25.00 to -20.91
Hermit thrush (<i>C. guttatus</i>)‡	7	5.07 $\pm$ 0.70	2.50 to 7.75	-23.76 $\pm$ 0.39	-25.27 to -22.56
Swainson's thrush (<i>C. ustulatus</i>)‡	2	1.78 $\pm$ 0.74	1.05 to 2.52	-24.80 $\pm$ 0.81	-25.61 to -23.99
Black-tailed deer (<i>O. hemionus</i>)#	9	1.59 $\pm$ 0.47	-0.29 to 3.83	-28.47 $\pm$ 0.34	-30.43 to -26.61

* Salmon muscle tissue $\delta^{13}\text{C}$ values were lipid standardized

† Shrew hair $\delta^{13}\text{C}$ samples corrected by 1.5‰ to approximate muscle tissue

‡ Songbird feather $\delta^{15}\text{N}$ samples corrected by 1.0‰ to approximate muscle tissue

Deer hair $\delta^{13}\text{C}$ samples corrected by 1.0‰ to approximate muscle tissue

Table 7.2. Expected isotopic ranges for diets derived from salmon or terrestrial carrion in two species of *Nicrophorus* beetles (Silphidae) and two Diptera species (*Calliphora terranova*, *Dryomyza anilis*) collected from the Clatse and Neekas rivers, B.C.

Source	<i>Nicrophorus</i> spp.		Diptera	
	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
Salmon	11.79 to 18.66	-23.45 to -17.65	11.79 to 19.66	-23.45 to -18.65
All Terrestrial	0.71 to 15.23	-31.43 to -19.91	0.71 to 16.23	-31.43 to -20.91
Shrews only	3.06 to 13.73	-26.86 to -22.05	-	-

Table 7.3. Number and frequency (min, max) of *Nicrophorus investigator* and *N. defodiens* adults (Silphidae) that were raised on a diet of salmon or terrestrial carrion as larvae. Individuals were caught in baited traps on the Clatsop River, British Columbia in spring and summer, with dietary classification based on isotope signatures of potential carrion prey including chum and pink salmon and terrestrial songbirds, shrews and deer.

		Clatsop River			Total
Diet		Spring 2001	Summer 2000	Summer 2003	
<i>N. investigator</i>	Salmon ^	0	2	37	39
	Salm/Terr *	2	8	24	34
	Terrestrial - Shrew †	1	4	4	9
	Terrestrial - Other ‡	1	1	0	2
	Min Salmon	0.00	0.13	0.57	0.46
	Min Terrestrial	0.50	0.33	0.06	0.13
	Max Salmon	0.50	0.67	0.94	0.87
<i>N. defodiens</i>	Salmon ^	0	0	0	0
	Salm/Terr *	0	0	0	0
	Terrestrial - Shrew †	8	19	25	52
	Terrestrial - Other ‡	0	0	6	6
	Min Salmon	0.00	0.00	0.00	0.00
	Min Terrestrial	1.00	1.00	1.00	1.00
	Max Salmon	0.00	0.00	0.00	0.00

^ Individuals with a salmon diet as larvae. Isotope signatures are outside terrestrial range but within salmon range.

* Individuals within salmon range but also within the upper terrestrial range. Likely salmon diet as larvae.

† Individuals falling within the terrestrial range defined by shrews. Note that this range overlaps highly with songbirds.

‡ Individuals within terrestrial range but outside that defined by shrews.

Table 7.4. Number and frequency (min, max) of *Calliphora* (Calliphoridae) and *Dryomyza* (Dryomyzidae) adults that were raised on a diet of salmon or terrestrial carrion. Individuals were caught in baited traps on the Clatse, Neekas and Ripley watersheds in spring, summer and fall of 2003. Classification was based on isotope signatures of potential carrion prey including chum and pink salmon and terrestrial songbirds, shrews and deer.

	Diet	Clatse River			Neekas River			Ripley Creek	
		Spring	Summer	Fall	Spring	Summer	Fall	Spring	Summer
<i>Calliphora</i>	Salmon ^	9	17	0	25	4	1	1	0
	Salm/Terr *	10	15	18	32	35	15	2	1
	Terrestrial ‡	2	5	11	3	7	8	0	1
	Min Salmon	0.43	0.46	0.00	0.42	0.09	0.04	0.33	0.00
	Min Terrestrial	0.10	0.14	0.38	0.05	0.15	0.33	0.00	0.50
	Max Salmon	0.90	0.86	0.62	0.95	0.85	0.67	1.00	0.50
<i>Dryomyza</i>	Salmon ^	-	16	0	-	9	2	-	3
	Salm/Terr *	-	21	25	-	33	17	-	5
	Terrestrial ‡	-	2	4	-	2	0	-	1
	Min Salmon	-	0.41	0.00	-	0.21	0.11	-	0.33
	Min Terrestrial	-	0.05	0.14	-	0.05	0.00	-	0.11
	Max Salmon	-	0.95	0.86	-	0.95	1.00	-	0.89

^ Individuals with a salmon diet as larvae. Isotope signatures are outside terrestrial range but within salmon range.

* Individuals with isotope signatures above 11.0‰ for $\delta^{15}\text{N}$ and/or -21.0‰ for $\delta^{13}\text{C}$ but within the upper range of terrestrial consumers. Diet of either salmon or terrestrial carrion.

‡ Individuals below 11.0‰ and -21.0‰, indicate terrestrial diet.

Table 7.5. Principal components analysis (PCA) scores for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures and tissue C/N ratios in *Calliphora* (Calliphoridae) and *Dryomyza* (Dryomyzidae) adults captured in spring, summer and fall of 2003 from the Clatse and Neekas rivers, B.C.

	<i>Calliphora</i>		<i>Dryomyza</i>	
	PC1 (61.9%)	PC2 (32.2%)	PC1 (65.9%)	PC2 (21.4%)
$\delta^{15}\text{N}$	0.948	0.110	0.774	0.576
$\delta^{13}\text{C}$	0.941	0.165	0.875	-0.013
C/N ratio	-0.270	0.963	-0.782	0.556

Table 7.6. Akaike Information Criterion (AIC) analysis showing top models ($\Delta\text{AIC} < 5$) of GLM analysis predicting the first principal component of variation (PC1) in *Calliphora* (Calliphoridae) and *Dryomyza* (Dryomyzidae) isotope signatures. Parameters include falls (above, below), season (days since 1st fly was captured), Diptera sex and Diptera dry weight. The parameter watershed was used in all models.

Species	Models with $\Delta\text{AIC} < 5.0$	RSS	k	R ²	AIC	ΔAIC	W_i
<i>Calliphora</i>	Wat + Days	178.66	4	0.192	-40.22	-3.67	0.055
	Wat + Days + Sex	174.93	5	0.208	-42.90	-0.99	0.211
	Wat + Days + Falls	176.18	5	0.203	-41.32	-2.57	0.096
	Wat + Days + Falls + Sex	172.59	6	0.219	-43.89	0.00	0.346
	Wat + Days + Sex + Drywt	174.77	6	0.209	-41.10	-2.79	0.086
	Wat + Days + Falls + Sex + Drywt	172.52	7	0.219	-41.98	-1.91	0.133
<i>Dryomyza</i>	Wat + Drywt	98.12	4	0.294	-49.59	-0.10	0.128
	Wat + Drywt + Sex	97.96	5	0.295	-49.69	0.00	0.135
	Wat + Falls + Drywt	98.07	5	0.294	-49.54	-0.15	0.125
	Wat + Drywt + Days	98.12	5	0.294	-49.46	-0.23	0.120
	Wat + Days + Falls + Drywt	98.07	6	0.294	-49.38	-0.31	0.116
	Wat + Falls + Drywt + Sex	97.91	6	0.296	-49.61	-0.08	0.130
	Wat + Days + Sex + Drywt	97.94	6	0.295	-49.57	-0.12	0.127
	Wat + Days + Falls + Sex + Drywt	97.89	7	0.296	-49.46	-0.23	0.120

Table 7.7. Parameter likelihoods (summed AIC_c weights of top models that include parameter) of different explanatory variables in GLM models. Parameter likelihoods reflect the relative importance of each explanatory variable in models describing the first principal component of variation (PC1) in *Calliphora* (Calliphoridae) and *Dryomyza* (Dryomyzidae) isotope signatures.

Species	Explanatory variable	Parameter likelihood
<i>Calliphora</i>	Days	0.927
	Falls	0.575
	Sex	0.776
	Dryweight	0.219
<i>Dryomyza</i>	Days	0.483
	Falls	0.490
	Sex	0.511
	Dryweight	1.000

Chapter 8:

Salmon subsidies to terrestrial communities: implications for invertebrate community structure, diversity and food chain length

8.1. Abstract

Cross-habitat subsidies of nutrients and energy can structure communities in receiving ecosystems. The annual spawning of Pacific salmon (*Oncorhynchus* spp.) directly supports hundreds of terrestrial species and fertilizes riparian forests through carcass and nutrient transfer by bears (*Ursus* spp.) and other vertebrates. I document the direct and indirect community-level implications of the salmon subsidy to a terrestrial invertebrate community on two productive watersheds on the central coast of British Columbia, including analyses of community structure, biomass, diversity and food-chain length. These watersheds have impassable waterfalls to salmon part-way upstream which I use as a within-watershed control for the effects of salmon on forest communities. The most dominant direct effect of the salmon subsidy involves the deposition of the salmon carcasses themselves and the resulting production of fly maggots. Dispersing flies are further vectors of salmon nutrients and energy to terrestrial systems and are consumed by multiple predators and parasitoids. Analyses of diversity in pitfall traps indicate that highest diversity occurs during the autumn spawning run in regions below the falls near to the stream, and that this diversity is best predicted by the biomass of tertiary consumers, such as fly maggots, associated with salmon carcasses. I also observe indirect or bottom-up effects of salmon nutrient fertilization, including shifts in humus forms and increased biomass of macro-detritivores such as earthworms and millipedes. Using stable isotopes I find evidence for multi-channel omnivory in tertiary consumers associated with both marine and terrestrial chains, and overall increases in food-chain length due to a direct diet of salmon. Analyses of the indirect effects on food-chain length were inconclusive and suggest that top-down effects of predation and/or intra-chain omnivory may dampen the effects of increased primary productivity at higher trophic levels. Overall, this study is the most comprehensive analysis to date of the community implications of the salmon subsidy in terrestrial habitats and highlights the widespread value of salmon to this community. This is particularly relevant given the ongoing declines in salmon spawning densities throughout the Pacific Rim.

8.2. Introduction

Exchanges of nutrients and energy across habitat boundaries are common and can result in dramatic shifts in resource availability and community dynamics in receiving ecosystems (Jefferies 2000). Fluxes may be reciprocal (Nakano and Murakami 2001) although recipient responses occur most frequently when there is a gradient in productivity between interacting systems. Inputs of nutrients often increase primary and secondary productivity, either directly or indirectly (Polis et al. 1997), while consumption of allochthonous prey or multi-channel omnivory has direct effects on predator biomass and may ultimately increase community stability and food chain length (Polis and Strong 1996). Resource subsidies can also affect community diversity depending on local productivity and top-down effects (Anderson and Wait 2001; Worm et al. 2002).

Examples of exclusively terrestrial resource subsidies include allochthonous inputs along stream-forest interfaces (Bilby and Bisson 1992; Fausch et al. 2002) and aeolian subsidies to alpine communities (Halfpenny and Heffernan 1992; Kaufmann 2001). In contrast, marine-terrestrial interactions represent important and often reciprocal exchanges that can structure coastal communities (Polis and Hurd 1996). Productive marine systems subsidize adjacent terrestrial ones through shore drift of algal wrack and carrion (Polis and Hurd 1995; 1996), inputs of guano and carcasses of seabirds (Lord and Burger 1984; Hawke and Newman 2004), and episodic returns of anadromous fishes (Ray 2005).

Every year throughout the Pacific Rim millions of salmon (*Oncorhynchus* spp.) return to their natal watersheds to spawn and die. This reverse nutrient flow imports marine protein that directly supports hundreds of terrestrial consumers and provides a dominant nutrient subsidy to nutrient-limited coastal watersheds (Reimchen 1994; Willson and Halupka 1995; Cederholm et al. 2000; Stockner 2003). In watersheds hosting high salmon spawning density, foraging by bears (*Ursus* spp.) and other wildlife actively distributes salmon carcasses and nutrients throughout the adjacent forest (Ben-David et al. 1998b; Hilderbrand et al. 1999b; Reimchen 2000; Gende et al. 2001).

The ecosystem-level implications of the salmon nutrient subsidy are substantial (Reimchen 1994; Gende et al. 2002; Zhang et al. 2003), although many aspects of this

process remain poorly defined. Most studies document direct effects for vertebrates (Reimchen 1994; Willson and Halupka 1995; Ben-David et al. 1997; Hilderbrand et al. 1999a) or aquatic invertebrates (Bilby et al. 1996; Wipfli et al. 1998; Chaloner et al. 2002; Nakajima and Ito 2003). Research in terrestrial systems adjacent to salmon spawning streams typically document uptake of salmon-derived nitrogen or carbon in plants (Bilby et al. 1996; Ben-David et al. 1998b) or invertebrates (Hocking and Reimchen 2002; Reimchen et al. 2003). Some have emphasized shifts in primary productivity and plant community structure (Helfield and Naiman 2002; Mathewson et al. 2003; Wilkinson et al. 2005), but have not examined community implications at multiple trophic levels.

Herein I focus on the community response to the annual pulse of salmon nutrients and carcasses to riparian zones in two productive watersheds on the central coast of British Columbia. Most of my findings center on litter invertebrates and the direct (salmon carcass) and indirect (salmon nutrient fertilization) effects on guild-level biomass and structure, litter diversity and food chain length. This work is a direct extension of previous studies from these same watersheds which have focused on salmon-derived nitrogen and carbon input to invertebrate, plant and songbird communities (Hocking and Reimchen 2002; Mathewson et al. 2003; Wilkinson et al. 2005; Christie et al. *submitted*).

The most dominant direct association of terrestrial invertebrates with salmon occurs from Diptera production from salmon carcasses. This input of prey likely has cascading effects in riparian communities (Reimchen 1994; Meehan et al. 2005; Christie et al. *submitted*), including increased invertebrate diversity. Using pitfall traps, I assess the direct effects of the salmon subsidy on guild-level invertebrate biomass and community structure above and below waterfall barriers to upstream salmon migration, including comparisons of larval Diptera biomass relative to other litter invertebrate groups. I also compare family richness of pitfall-trapped invertebrates and use measures of vegetation community structure and invertebrate biomass to determine the best predictors of family diversity across the waterfall barrier to salmon.

Nutrient subsidies in aquatic and terrestrial habitats are known to initiate bottom-up effects that can indirectly structure communities (Polis and Strong 1996). In temperate

coniferous forests, nutrient availability influences rates of litter turnover (Prescott et al. 2000), vegetation species composition (Turkington et al. 1998) and the community structure of invertebrates (Setälä et al. 1991; Kytö et al. 1996; Forge and Simard 2001), all of which can subsequently affect higher trophic levels such as songbirds (Folkard and Smith 1995). I follow Hocking and Reimchen (2002) and Mathewson et al. (2003) and examine the indirect or bottom-up effects of the salmon nutrient subsidy on the community structure of the litter invertebrate fauna. This includes lumbricid and enchytraid worms, millipedes, isopods and snails whose distribution is tightly linked with the richness of the soil and humus (Haimi and Boucelham 1991; Carcamo et al. 2000).

Finally, inputs of prey and nutrients can affect food-chain length depending on the extent of bottom-up and top-down effects (Power 1992; Polis and Strong 1996). I assess the direct and indirect effects of the salmon subsidy on invertebrate food-chain length using stable isotopes. Stable isotopes have been used in multiple studies to estimate dietary variation, trophic structure and sources of nutrients and energy (reviews in Peterson and Fry 1987; Kelly 2000; Post 2002b), with $\delta^{15}\text{N}$ variation in particular used as a good indicator of trophic position (Vander Zanden et al. 1999). In the salmon-forest system, stable isotopes have determined direct and indirect pathways of salmon nutrient input to terrestrial invertebrates (Hocking and Reimchen 2002; Hocking et al. *in press*). I examined $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in multiple invertebrate guilds and investigate multi-channel omnivory on both marine and terrestrial chains in tertiary consumers, as well as food-chain length of terrestrial chains when tertiary consumers are added. I also test for indirect effects on food chain length using $\delta^{15}\text{N}$ signatures in spiders (apex predator) and Collembola (baseline prey) in an analysis comparable to Vander Zanden et al. (1999). Since these species have little direct association with spawning salmon, this can indicate whether increased riparian productivity affects invertebrate food-chain length.

8.3. Materials and Methods

8.3.1. Site description and trapping methods

This study was conducted on two salmon-bearing watersheds, the Clatse ($52^{\circ}20'15''\text{N}$; $127^{\circ}50'23''\text{W}$) and Neekas ($52^{\circ}28'17''\text{N}$; $128^{\circ}9'39''\text{W}$) rivers, north of Bella Bella, on the central coast of British Columbia, Canada. The mean annual temperature is

~8°C and annual precipitation ranges from 3200-4200 mm. Both watersheds occur in the Coastal Western Hemlock Biogeoclimatic Zone with forests dominated by Western hemlock, Sitka spruce and Western red-cedar (Green and Klinka 1994). Anadromous pink (*O. gorbuscha*) and chum (*O. keta*) salmon spawn from late August to early November, with populations of black bears (*U. americanus*) and wolves (*Canis lupus*) acting as the principal vectors of salmon carcasses into the forest. A five to ten meter waterfall truncates spawning at 0.9km and 2.1km upstream from the estuary at the Clatse and Neekas respectively.

In the spring and fall of 2001 I monitored a grid of pitfall traps on both the Clatse and Neekas rivers in plots that partially overlapped with those previously described in Hocking and Reimchen (2002), Mathewson et al. (2003) and Wilkinson et al. (2005). Three 10m × 10m plots were established in each of four habitat blocks on each watershed: 1) Below falls, near to the stream (<20m) (BN); 2) Below falls, far from the stream (~100m) (BF); 3) Above falls, near to the stream (<20m) (AN); and 3) Above falls, far from the stream (~100m) (AF). Within each plot I placed 9 pitfall traps in a 3 × 3 grid with each trap separated by 5m. To increase the surface area, each pitfall trap had a central 10cm diameter pitfall cup (with 70% ethanol as a field preservative) surrounded by three 8-inch by 6-inch aluminium drift fences separated by 120°. I cleared the pitfall traps every three days for a total of three times over ten days (sampling periods A,B,C in spring and D,E,F in fall). This occurred from June 6th to 16th and September 6th to 16th on the Neekas River, and June 18th to 28th and September 20th to 30th on the Clatse River. To avoid pseudoreplication, diversity, abundance and biomass data were summed within each trap across seasonal time periods, and then averaged to give either mean or total trap catches per plot.

8.3.2. Taxonomic diversity and classification

All invertebrate specimens were returned to the lab and sorted to at least Ordinal level. I identified most invertebrate taxa in the entomology lab of R.A. Ring at the University of Victoria, B.C. Additional taxonomic support was provided by Richard Ring (Diptera and general support), Monty Wood (Diptera: Calliphoridae, Dryomyzidae, Drosophilidae), Steve Marshall (Diptera: Sphaeroceridae), Graham Griffiths (Diptera:

Heleomyzidae), Andrew Bennett (Hymenoptera: Ichneumonidae), Henri Goulet (Hymenoptera: Braconidae), Matt Buffington (Hymenoptera: Figitidae), Jan Klimaszewski (Coleoptera: Staphylinidae), Stuart Peck (Coleoptera: Leiodidae, Hydrophilidae), Dave Kavanaugh (Coleoptera: Carabidae), Goeff Scudder (Hemiptera: Dipsocoridae), Rob Bennett (Araneae) and Jan Addison (Collembola: Tomoceridae, Dicyrtomidae; Haplotaxida: Enchytraidae, Megascolecidae, Lumbricidae).

Due to variation in the level of classification of individual invertebrate specimens, I placed individuals in separate species-code categories (Table 8.1). Emphasis was placed on taxonomic resolution to a level whereby species or groups could be classified into guilds. As such, most taxonomic separation occurred within the Coleoptera, and to a lesser extent within the Diptera and Hymenoptera. Guilds consisted of herbivores, detritivores and fungivores (grouped as primary consumers), omnivores and predators (secondary consumers), and saprophages, blood suckers and parasitic species (tertiary consumers). Individual samples ($n = 1-100$) of each species-code were weighed to give an approximate individual mass (Table 8.1). Biomass of each species-code was then determined by multiplying abundance by individual mass.

8.3.3. Analysis of community structure and biomass

Analyses of community structure data consisted of both parametric and non-parametric approaches. Unequal variances were an issue, particularly for comparisons within tertiary consumers due to the high abundance and biomass of saprophagous fly larvae caught in the fall spawning season below the falls. For some comparisons I used a nested ANOVA design, although some of these tests did not meet the assumptions. I also used multi-way ANOVA's with possible parameters including season (spring, fall), falls (above, below), and proximity to stream ($<20\text{m}$, $\sim 100\text{m}$) within each watershed.

I used non-parametric G-tests (χ^2 distributed) to assess the distribution of total pitfall-trapped biomass among primary, secondary and tertiary consumers among seasons and watersheds. Within primary and secondary consumers, data for biomass comparisons were square-root transformed to meet ANOVA assumptions. For ANOVA's on biomass I excluded the few vertebrates (shrews, amphibians) and large slugs (*Ariolimax* sp.)

captured since their large individual masses biased biomass estimates highly towards these few individuals and resulted in unequal variances for biomass comparisons.

The distribution of biomass among species-code categories within guilds was assessed using non-parametric Wilcoxon and Sign tests. Within each watershed, season and guild (primary, secondary and tertiary consumers), I compared the biomass of species-codes paired above and below falls (only near to stream data used).

Soil-nutrient conditions can determine both the dominant humus forms and the dominant detritivores present (Setälä et al. 1991; Green and Klinka 1994; Prescott et al. 2000). I examined the percent cover of herb and shrub layer plants from my plots that indicated Moder/Mull (nutrient rich) versus Mor (nutrient poor) humus forms (Klinka et al. 1989; Table 8.2), in an analysis similar to that of Mathewson et al. (2003) for nitrogen-rich versus nitrogen-poor soil indicator species. Total cover of Mor humus indicators by plot was subtracted from the cover of Moder/Mull indicators. Coupled with this approach, I separated all soil macro-detritivores from the taxa caught in the pitfall traps, including worms, millipedes and isopods, and compared their total trap catch per plot across all habitat blocks. For both humus-indicators and macro-invertebrate biomass I used nested ANOVA's to test for the effects of watershed, falls within watershed, and proximity to stream within falls within watershed.

I also investigated the distribution of pitfall trap catch in carabid beetles and some of their principal prey, the snails, using nested ANOVA's. These groups represent dominant members of the litter community and have been used as site indicators including the presence of sufficient calcium (Johannessen and Solhoy 2001).

8.3.4. Analysis of diversity

Pitfall trap diversity was analyzed using simple measures of richness including the average number of families or species-codes caught per trap within each plot (ANOVA's – assumptions met). Parameters tested included season (spring, fall), falls (above, below) and proximity to stream (<20m, ~100m) within each watershed. If interaction terms were not significant ($p > 0.05$) they were removed from the models.

Separate from location information, pitfall trap diversity might be caused and predicted by many environmental factors including characteristics of the vegetation and

dominance of different guilds of the invertebrate community. At the plot level, including only plots from near to the stream ($n = 12$), I conducted separate Principal Components Analyses (PCA) to document the principal components of variation in invertebrate community biomass and vegetation community structure. Variables used for the biomass PCA included mean pitfall trap biomass of 1) primary, 2) secondary and 3) tertiary consumers at the plot level. Two PCA's of biomass were conducted, one in spring and one in fall. Vegetation variables measured within each plot that may affect diversity, and included in another PCA, were 1) tree cover, 2) shrub cover, 3) herb cover, 4) vegetation species richness and 5) percent cover of plants that indicate Moder/Mull humus forms (Table 8.2). Standardized z-scores of all variables were used in each PCA, and I report principal components with eigenvalues > 0.5 .

I was interested in how the top principal components of variation from each PCA might predict variation in invertebrate family diversity. To do this I used Akaike's Information Criterion (AIC) (Burnham and Anderson 1998) to assess the predictive power of various *a priori* models with different combinations of variables. Models were generated using a general linear model (GLM) approach which included the following parameters: 1) PC1 biomass; 2) PC2 biomass; 3) PC1 vegetation; 4) PC2 vegetation; 5) PC3 vegetation. Since plot data was collected in two watersheds, the parameter watershed was included in all models. I used a balanced design that included all combinations (just main effects) of the five parameters for a total of 33 possible models (including null). Since no interaction terms were *a priori* predicted, none were included. I used corrected AIC (AIC_c), which adjusts for small sample sizes. ΔAIC was calculated as the difference between AIC values of the top-ranked model and all subsequent models. In order to assess the relative importance of each parameter found within the top models, I summed the weights (W_i) of all models with $\Delta AIC \leq 4.0$. This analysis was conducted twice, for measures of both spring and fall family diversity. I used separate biomass PCA's for each season while the vegetation PCA was used over both seasons.

8.3.5. Food chain length classification and analysis

Food-chain length can be increased when allochthonous prey subsidize recipient communities (Polis and Strong 1996). Nutrient subsidies that increase primary

productivity and alter community structure may also have indirect effects on the food-chain length of receiving ecosystems (Polis and Strong 1996; Post 2002a). A way to test these theories involves the use of stable isotopes. The isotope ^{15}N can indicate trophic position (Vander Zanden et al. 1999), while ^{13}C gives the source of primary productivity (Tieszen and Boutton 1988). I assessed the effects of direct consumption of salmon tissue on food chain length in multiple taxa from the Clatse and Neekas analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Table 8.3). Many of these taxa have been described in detail in previous studies (Hocking and Reimchen 2002; Hocking et al. *in press*). Taxa were classified into trophic guilds including primary, secondary and tertiary consumers (as above). I determined the range in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from the most enriched to least enriched individual above and below the falls on both the Clatse and Neekas rivers. I included species within primary and secondary consumers (terrestrial food chain) and compared the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ range when tertiary consumers (marine food chain) were added for both isotopes. Membership within the marine food chain is best defined by $\delta^{13}\text{C}$ signatures of -18 to -22‰, while terrestrial $\delta^{13}\text{C}$ signatures in invertebrates typically range from -28 to -23‰ (Hocking and Reimchen 2002; Hocking et al. *in press*). Multi-channel omnivory, or feeding within both terrestrial and marine food chains, may be represented by individuals with intermediate isotope signatures ranging from 10 to 14‰ for $\delta^{15}\text{N}$ and -21.5 to -23.5‰ for $\delta^{13}\text{C}$. I also calculated trophic length based on isotope ranges and trophic fractionation of 3.4‰ (Mingawa and Wada 1984).

Indirect effects on food-chain length were tested using two of the most common groups that I collected in the pitfall traps, Collembola (springtails) and predaceous spiders of the Genus *Cybaeus*. These represent reasonable baseline and apex species within the litter community (Ponsard and Arditi 2000) and were collected in a spatially (plot locations) and temporally (spring and fall) controlled fashion. Collembola are one of the most abundant forest soil arthropods and are primarily fungivores, but can also ingest a variety of other organic materials (Addison et al. 2003). The largest and most common species caught in the pitfall traps were *Ptenothrix maculosa* (Dicrytomidae) and *Tomocerus flavescens* (Tomoceridae). Isotopic baselines represented the mean of the two Collembola species and were separated by location above falls near to stream and below falls near to stream, by season of collection (spring, fall) and by watershed. I used the

common litter spiders *Cybaeus* spp., including *C. reticulatus* and juvenile *Cybaeus* spp., as the $\delta^{15}\text{N}$ maxima within this community. *Cybaeus* spp. are apex invertebrate predators of the terrestrial litter community at my sites and feed exclusively on animals including various insects, myriapods, isopods, other spiders and even small vertebrates (Gertsh 1949). Replicate individuals (8-13) were processed for $\delta^{15}\text{N}$ at each location and season where I had established an isotopic baseline. I determined food-chain length by subtracting the $\delta^{15}\text{N}$ value of the appropriate Collembola baseline from the $\delta^{15}\text{N}$ value of each spider. To ensure that age and size were not confounding factors in this analysis, I measured carapace width and length of all *Cybaeus* using an ocular micrometer. Twelve individuals were measured twice with measurement error ranging from 0 to 7.0% (means: length = 2.0% error; width = 2.9% error). I estimated carapace area by multiplying length by width.

Food chain length variation ($\delta^{15}\text{N}$ difference between *Cybaeus* and Collembola) was assessed using ANCOVA's (one for each watershed) with trophic length as the dependent variable, season and falls as fixed factors and carapace area as a covariate. Food chain length was square-root transformed. All non-significant interaction terms were removed. Assuming that each successive trophic level is enriched by 3.4‰ (Minigawa and Wada 1984; Ponsard and Arditi 2000), I used the $\delta^{15}\text{N}$ difference between *Cybaeus* and Collembola to estimate the number of trophic levels between them. I also calculated the trophic position of *Cybaeus* using an approach used by Vander Zanden et al. (1999): $\text{trophic position}_{\text{Cybaeus}} = (\delta^{15}\text{N}_{\text{Cybaeus}} - \delta^{15}\text{N}_{\text{Collembola}}) / 3.4\text{‰} + 2$.

All invertebrates were analyzed for the stable isotopes $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Invertebrate specimens were dried at 60°C for at least 48 hours and ground into a fine powder with a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Ill). For most species this represented whole individuals while for Collembola this represented composite samples of 44-298 individuals. Approximately 1 mg dry weight was then sub-sampled and encapsulated in 3.5 by 5mm tin capsules. All samples were analyzed for continuous-flow isotope ratio mass spectrometry (CF-IRMS) of nitrogen in a Robo prep elemental analyzer interfaced with a Europa 20:20 isotope ratio mass spectrometer at the stable isotope facility, University of Saskatchewan, Saskatoon. Isotopic ratios (heavy isotope / light isotope) are

expressed in δ notation and reflect deviation in parts per mil (‰) from international standards (PeeDee Belemnite for carbon and atmospheric N_2 for nitrogen).

8.4. Results

8.4.1. Community structure and biomass

Near to the stream, total biomass of pitfall-trapped litter invertebrates differed by guild (primary, secondary, tertiary consumers) above and below the falls in both seasons on both watersheds (G-tests: all $\chi^2_2 > 92$, all $p < 0.001$). Tertiary consumers below the falls in the fall showed the highest biomass relative to the other groups, and consisted primarily of fly maggots dispersing from salmon carcasses (Figure 8.1).

On Clatse across all habitat blocks, primary and secondary consumers both had higher biomass below the falls than above (Falls- Primary consumers: $F_{1,20} = 11.10$, $p = 0.003$, $R^2 = 0.357$; Falls- Secondary consumers: $F_{1,20} = 8.22$, $p = 0.005$, $R^2 = 0.334$), with no significant main effects of season or proximity to stream (all $F_{1,20} < 0.9$, all $p > 0.35$) (Figures 8.2 and 8.3). On Neekas, primary and secondary consumers again had higher biomass below the falls than above (Falls- Primary consumers: $F_{1,20} = 10.05$, $p = 0.005$, $R^2 = 0.334$; Falls- Secondary consumers: $F_{1,19} = 17.82$, $p < 0.001$, $R^2 = 0.484$), although this was largely driven by high biomass far from the stream below the falls (Figures 8.2 and 8.3). Primary consumers on Neekas showed no major seasonal or stream proximity effects (both $F_{1,20} < 3.1$, $p > 0.09$), while secondary consumers showed seasonal ($F_{1,19} = 9.22$, $p = 0.007$, $R^2 = 0.327$), proximity to stream ($F_{1,19} = 4.40$, $p = 0.050$, $R^2 = 0.188$), and falls*proximity ($F_{1,19} = 19.99$, $p < 0.001$, $R^2 = 0.513$) effects. Tertiary consumers showed high biomass in fall close to the stream on both watersheds, although data were too non-normal with unequal variances to test using parametric approaches.

Focusing on data just near to the stream, paired comparisons of biomass in separate species-codes classified by guild (primary, secondary and tertiary consumers) highlighted the increased abundance of saprophageous and parasitic taxa below the falls in the fall during the salmon spawning season (Table 8.4). In the spring on Clatse no major differences were observed in biomass among species-codes for all guilds, while on Neekas primary consumers were marginally higher in biomass below the falls, with no differences in the other guilds. In the fall on Clatse and Neekas all guilds showed a trend

towards increased biomass below the falls compared to above, although this was most prominent in the tertiary consumers. Primary consumers showed marginal effects on both watersheds.

Plants that indicated Moder/Mull (nutrient-rich) humus forms dominated below the falls near to the stream on both watersheds, compared to plants that indicated Mor (nutrient-poor) humus (nested ANOVA – watershed(falls): $F_{2,16} = 30.78$, $p < 0.001$, $R^2 = 0.794$; Figure 8.4a). Percent cover of Mor humus indicator species was high in both habitat blocks above the falls and the habitat block far from stream below the falls. No significant effect of watershed was observed (nested ANOVA – watershed: $F_{1,16} = 3.54$, $p = 0.078$, $R^2 = 0.181$), although there was a strong effect of distance from the stream (nested ANOVA – watershed(falls(distance)): $F_{4,16} = 15.38$, $p < 0.001$, $R^2 = 0.794$).

The combined biomass of worms (Lumbricidae, Enchytraidae), millipedes (Parajulidae, Polyxenidae, Nearctodesmidae) and isopods (Isopoda) was highest near the stream below the falls on both watersheds followed by sites far from stream below falls (nested ANOVA – watershed(falls): $F_{2,16} = 8.32$, $p = 0.003$, $R^2 = 0.510$; Figure 8.4b). No distance or watershed effects were observed (nested ANOVA – watershed: $F_{1,16} = 0.01$, $p = 0.912$, $R^2 = 0.001$; – watershed(falls(distance)): $F_{4,16} = 1.28$, $p = 0.320$, $R^2 = 0.242$).

Carabid beetles and snails showed highest pitfall-trapped biomass in sites below the falls far from stream on both watersheds (Figure 8.5). Neekas had higher biomass of both groups, and overall there were strong effects at all levels including falls, distance and watershed (nested ANOVA Carabidae: watershed: $F_{1,16} = 12.51$, $p = 0.003$, $R^2 = 0.439$; watershed(falls): $F_{2,16} = 9.70$, $p = 0.002$, $R^2 = 0.548$; watershed(falls(distance)): $F_{4,16} = 5.40$, $p = 0.006$, $R^2 = 0.575$) (nested ANOVA snails: watershed: $F_{1,16} = 6.69$, $p = 0.020$, $R^2 = 0.295$; watershed(falls): $F_{2,16} = 8.30$, $p = 0.003$, $R^2 = 0.509$; watershed(falls(distance)): $F_{4,16} = 3.67$, $p = 0.026$, $R^2 = 0.479$).

8.4.2. Diversity

Family diversity within the litter community was higher below the falls than above and higher in the fall than in the spring on both the Clatse and Neekas watersheds (Clatse- Season: $F_{1,20} = 5.32$, $p = 0.032$, $R^2 = 0.210$; Falls: $F_{1,20} = 8.07$, $p = 0.010$, $R^2 = 0.288$; Neekas- Season: $F_{1,19} = 15.47$, $p = 0.001$, $R^2 = 0.449$; Falls: $F_{1,19} = 9.10$, $p = 0.007$,

$R^2 = 0.324$; Figure 8.6). Peak diversity occurred in the fall in plots with highest access to salmon carcasses. Proximity to stream was not an important predictor of family diversity on either watershed (both $F < 1.3$, $p > 0.28$), although on Neekas the season*proximity interaction was important ($F_{1,19} = 5.71$, $p = 0.027$, $R^2 = 0.231$). In spring, the highest diversity was observed in plots below falls and far from the stream.

Species-code diversity mirrored the patterns observed for family diversity with an effect of falls on both watersheds (Clatse: $F_{1,20} = 5.25$, $p = 0.033$, $R^2 = 0.208$; Neekas: $F_{1,20} = 10.33$, $p = 0.004$, $R^2 = 0.341$). Proximity to stream was again a poor predictor of diversity (both $F < 1.3$, $p > 0.27$) while the effect of season was apparent on Neekas ($F_{1,20} = 13.78$, $p = 0.001$, $R^2 = 0.408$), but not on Clatse ($F_{1,20} = 0.447$, $p = 0.512$).

Biomass of the litter invertebrate community close to the stream consisted of two principal components of variation in both spring and fall (Table 8.5). In spring PC1 related primarily to high biomass of primary consumers while PC2 related to high biomass of secondary consumers. In the fall, PC1 correlated to high biomass of all groups with an emphasis on tertiary consumers and PC2 indicated high predator biomass relative to low biomass of primary consumers. Measures of vegetation broke down into three principal components including: 1) high tree and herb cover and low shrub cover (PC1); 2) high vegetation diversity (PC2); and 3) high cover of Moder/Mull humus-indicator species (PC3) (Table 8.6).

Family diversity of pitfall-trapped litter invertebrates was best predicted by PC1 of the biomass PCA in both seasons, with almost all best models containing this parameter (AIC analysis: Tables 8.7 and 8.8). Other explanatory parameters with moderate AIC weights included PC1 vegetation (spring) and PC2 biomass and PC3 vegetation (fall). Vegetation diversity (PC2 veg) had low predictive power for invertebrate diversity in both seasons. In summary, this analysis particularly emphasizes the role of tertiary consumers (ie- maggots from salmon carcasses) in the fall for predicting litter invertebrate diversity, with secondary roles of high predator biomass relative to primary consumers and high percent cover of vegetation species that indicate rich Moder/Mull humus forms. In the spring, high biomass of primary consumers best predicts diversity.

8.4.3. Food chain length

Across all major guilds of invertebrates collected in spring, summer and fall on the Clatse and Neekas from 2000-2003, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values ranged from -5.85‰ to 24.37‰ and -29.64‰ to -17.30‰ respectively with individuals falling within terrestrial and/or marine food-chains (Figure 8.7). $\delta^{15}\text{N}$ ranges across all individuals varied from 19.04‰ above the falls on Neekas to 27.73‰ above the falls on Clatse (Table 8.9). Assuming fractionation of 3.4‰ per trophic level, this represents a span of 5.6 to 8.2 trophic levels, although this includes species that occur within terrestrial and marine chains. Many tertiary consumers, including carrion-breeding flies, beetles and parasitic wasps, had high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures indicative of either a marine diet or multi-channel omnivory. Terrestrial food-chain length was longer below the falls compared to above. On the Clatse and Neekas, food-chain length above the falls was 3.81 and 2.69 trophic levels respectively, while below the falls this length increased to 5.10 and 5.79. When tertiary consumers were included the maximum food-chain length above the falls (mean $\delta^{15}\text{N}$ range on Clatse and Neekas) increased by 12.34‰ from 11.05‰ to 23.39‰. Below the falls, food-chain length increased to a lesser extent than above the falls, from 18.54‰ to 23.28‰ (mean difference of 4.74‰). For $\delta^{13}\text{C}$, adding tertiary consumers resulted in a comparable increase of 3-5‰ above and below the falls in the $\delta^{13}\text{C}$ range (mean above: 3.82‰; below: 4.87‰) (Table 8.9).

In a more controlled test of terrestrial food-chain length, the $\delta^{15}\text{N}$ difference between spider predators *Cybaeus* spp. and Collembola did not vary predictably by location above or below falls, season or spider carapace size across each watershed (Table 8.10). Food-chain length varied from 5.25‰ on Clatse below falls in the fall to 6.93‰ on the Neekas below the falls in the spring. This corresponds to an estimated 1.5 to 2.0 trophic levels, with the trophic position of *Cybaeus* varying from 3.5 to 4.0. On the Neekas River there was no predictable variation in food-chain length between *Cybaeus* and Collembola (ANCOVA: Season, Falls and Carapace area – all $F_{1,37} < 1$, all $p > 0.34$). In contrast, on the Clatse, food-chain length was higher above the falls than below (ANCOVA: Falls $F_{1,42} = 5.28$, $p = 0.027$) and there was a significant carapace area*falls interaction term (ANCOVA: $F_{1,42} = 9.67$, $p = 0.003$). The main effects season and carapace area had no effect (ANCOVA: both $F_{1,42} < 1$, $p > 0.36$).

8.5. Discussion

8.5.1. Community structure and biomass

The input of salmon carcasses and nutrients to coastal riparian zones has strong direct and indirect effects for recipient communities. Carcasses and remnants support many terrestrial species (Reimchen 1994; Cederholm et al. 2000; Jauquet et al. 2003; Hocking et al. *in press*), while nutrient addition increases riparian primary productivity and alters vegetation community structure (Helfield and Naiman 2002; Mathewson et al. 2003; Wilkinson et al. 2005). This study is the first to examine the community response to the salmon subsidy at multiple terrestrial trophic levels.

The most dominant interaction observed was the direct contribution of fly maggots hatched from salmon carcasses to the litter community. The total pitfall-trapped biomass of this group alone was higher than the biomass of primary and secondary consumers on both watersheds. On Neekas, Diptera mass from salmon carcasses was roughly four times that of all other invertebrates combined. Despite that pitfall trap catches of larval Diptera were highly variable, indicating a patchy distribution of carcasses and maggots, the addition of larval Diptera biomass represents a major pulse of marine protein to the litter community in the fall along salmon spawning streams. As such, marine input, not terrestrial primary productivity, provides the most energy and biomass to higher trophic levels at this time. This result is supported by previous studies which have emphasized the dominant role of flies, particularly the blowflies (Calliphoridae), in the consumption and distribution of salmon nutrients in terrestrial food webs (Reimchen 1994; Cederholm et al. 2000; Jauquet et al. 2003; Reimchen et al. 2003; Meehan et al. 2005). Maggot production from salmon carcasses supports many terrestrial predators and parasitoids including songbirds (Christie et al. *submitted*). Other studies along the marine-terrestrial ecotone have also found high secondary production from the deposition of carcasses and nutrients of seabirds and onshore drift of sea wrack (Polis and Hurd 1995, 1996; Markwell and Daugherty 2002).

The decomposition of salmon carcasses and the input of vertebrate urine, guano and feces deposits marine-derived nutrients in stream-side forests, and can initiate bottom-up community effects. In coniferous forests, nutrient conditions often predict the

dominance of members of the soil fauna and vice versa (Setälä et al. 1991). Nutrient-poor soils are typically dominated by fungal decomposers, and slow nutrient turnover often results in thick layers of matted Mor humus (Green and Klinka 1994). In nutrient-rich conditions, fungi are replaced by bacteria and invertebrates as the dominant decomposers, resulting in higher nutrient capital and rates of turnover (Prescott et al. 2000; Forge and Simard 2001). Nutrient-rich soils are dominated by Moder or Mull humus forms (Green and Klinka 1994). On the Clatse and Neekas, I find the highest percent cover of plants that indicate Moder/Mull humus forms beside the salmon spawning channel below the falls, while the highest cover of nutrient-poor or Mor-humus indicator species occurred above the falls. Paired with this finding is the dominance of lumbricid and enchytraid worms, millipedes and isopods as the principal decomposers below the falls near the stream on both watersheds. These groups are known to have a strong influence on litter decomposition, nitrogen mineralization and microbial biomass (Haimi and Boucelham 1991; Carcamo et al. 2000), all of which can subsequently impact vegetation communities (Green and Klinka 1994; Prescott et al. 2000; Forge and Simard 2001; Mathewson et al. 2003). Estimates of percent salmon-derived nitrogen in riparian plants have ranged from 12-60% (Bilby et al. 1996; Hilderbrand et al. 1999b; Helfield and Naiman 2001; Mathewson et al. 2003), highlighting that the salmon subsidy provides a major contribution of nutrients relative to available terrestrial sources (Hocking and Reimchen 2002).

Nutrient addition can be counteracted by the top down effects of predation (Power 1992). I find the highest biomass of snails in plots far from the stream below the falls on both watersheds. These plots would have moderate input of salmon nutrients compared to the high input close to the spawning stream and low input above the falls. Carabid beetles were also caught in highest frequency in these same plots and could have populations that are tracking those of their snail prey (Laroche 1972). It may be predicted that snails would show highest densities immediately adjacent to the salmon spawning stream due to the input of nutrients such as calcium which are essential for a range of snail processes (Johannessen and Solhoy 2001). However, songbirds have higher densities along salmon streams than non-salmon systems or reaches (Gende and Willson 2001; Christie and Reimchen *submitted*), and perhaps bird predation is an important limiting factor for local

snail and carabid populations. Overall, the risk of predation is high for many species adjacent to salmon streams (Ben-David et al. 2004) and the coupling of top-down and bottom up effects likely invokes complicated trophic cascades and trade-offs between dietary benefits from profitable patches and predation risk (Power 1992; Polis and Strong 1996).

8.5.2. Diversity

High secondary production from allochthonous inputs of nutrients and prey can initiate trophic cascades and increase diversity (Polis and Hurd 1996; Polis and Strong 1996; Anderson and Wait 2001). Analyses of diversity highlighted both direct and indirect effects as predictors of family richness in pitfall-trapped invertebrates. Family richness was highest below the falls near the stream during the fall spawning season on both the Clatse and Neekas watersheds. In the spring, diversity was again found to be higher below the falls than above but was mainly due to high diversity far from the stream on both watersheds. Species-code diversity mirrored the patterns observed for family diversity, although I place more emphasis on the results for family diversity to reduce potential bias from invertebrate classification.

Using principal components of invertebrate biomass and vegetation community structure, family diversity in the fall was best predicted by high biomass of all guilds (PC1), with highest loading on tertiary consumers. >95% of the biomass of all tertiary consumers consisted of fly maggots from salmon carcasses with other species including adult flies and parasitic wasps. This suggests that the direct input of marine energy supports increased diversity overall although this is particularly true at higher trophic levels. This result is supported by paired comparisons of biomass which indicated that tertiary consumers were particularly abundant below the falls in the fall, although taxa from all guilds, including primary and secondary consumers, showed trends towards higher biomass below the falls compared to above. To date, I have found at least 60 invertebrate taxa that are attracted to the salmon carcasses themselves or are predators/parasitoids of the dispersing fly maggots. This includes saprophageous Diptera (Calliphoridae, Dryomyzidae, Muscidae, Heleomyzidae, Spherozeridae and Phoridae), predaceous and saprophageous Coleoptera (Staphylinidae, Leiodidae, Hydrophilidae,

Carabidae and Silphidae) and predaceous and parasitic Hymenoptera (Formicidae, Vespidae, Ichneumonidae, Braconidae and Figitidae). Vertebrates such as shrews (*Sorex* spp.), songbirds (eg. Winter wren, Sparrows, Thrushes) and amphibians (*Tarisha granulosa*, *Ambystoma gracile*), have also been observed consuming fly maggots on these and other watersheds (Reimchen 1994; Cederholm et al. 2000; Christie et al. submitted). Overall, there are hundreds of species that are directly influenced by spawning Pacific salmon, and changes in salmon spawning density is likely to be the best predictor of carrying capacity for many species (Reimchen 1994; Cederholm et al. 2000).

In spring, the best predictor of family diversity was again PC1, this time with highest loading for the biomass of primary consumers. This observation may point towards the indirect effects of nutrient-rich conditions below the falls in determining the community structure of the decomposers. Total biomass of primary consumers was higher on both watersheds below the falls with no seasonal effects. Paired comparisons of biomass above and below the falls also partially support this conclusion as a higher number of primary consumers were observed below the falls at Neekas but not at Clatse.

8.5.3. Food chain length

Patterns and determinants of food-chain length have been important and long-standing topics in ecology (Vander Zanden et al. 1999 and references therein). Total length can be influenced by many factors including ecosystem productivity and size, and resource subsidies from adjacent food-webs (Polis and Strong 1995; Post 2002a). I find that input of salmon carcasses to coastal riparian zones directly increases food-chain length, although the indirect effects from nutrient addition are more difficult to determine.

Multi-channel omnivory can diffuse the effects of consumption and productivity throughout the food-chain by increasing web connectance, can increase the size of consumer populations through a diet of 'non-normal' or subsidized prey, and ultimately can increase food-chain length (Polis and Strong 1996). Tertiary species, including carrion flies and beetles and parasitic wasps, showed elevated $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures indicative of membership within marine and terrestrial chains. Many individuals had intermediate signatures between the two chains, indicating multi-channel omnivory and a

life-history that likely includes a larval diet of salmon and an adult diet from terrestrial sources. When tertiary consumers were included in trophic calculations, food-chain length increased on both watersheds, particularly above the falls. Flies and beetles with a larval diet of salmon can disperse as adults throughout the watershed, including above the falls, and represent an input of prey high on the marine food-chain. Comparisons of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures to marine taxa suggest that these carrion feeders are equivalent in trophic position to sea lions and orca whales (Hobson et al. 1997; Pauly et al. 1998).

All primary and secondary consumers had isotope signatures indicative of terrestrial-chain membership throughout multiple seasons. $\delta^{15}\text{N}$ signatures were enriched in all taxa below the falls compared to above due to the incorporation of marine nitrogen into terrestrial chains (Hocking and Reimchen 2002). However, high variation in $\delta^{15}\text{N}$ signatures resulted in a wider range below the falls compared to above. On the Clatse and Neekas, assuming trophic fractionation of 3.4‰ (Minigawa and Wada 1984), food-chain length above the falls was 3.81 and 2.69 trophic levels respectively, while below the falls this length increased to 5.10 and 5.79. This may represent an increase in the range of food resources below the falls (Hocking and Reimchen 2002), but could also simply represent increased spatial/ temporal variation in $\delta^{15}\text{N}$ signatures.

To test the indirect effects of the salmon nutrient subsidy on food-chain length more accurately I conducted an experiment using spatially and temporally restricted baseline and apex invertebrate taxa. Using Collembola (springtails) as a baseline and *Cybaeus* spiders as an apex predator, I find no consistent pattern of food-chain length variation across the waterfall barrier to salmon. Collembola and *Cybaeus* are litter species with little to no direct association with salmon carcasses. On Neekas, food-chain length did not differ above and below the falls while on Clatse the $\delta^{15}\text{N}$ difference from Collembola to spiders was slightly greater above the falls compared to below. Perhaps top-down effects from the presence of other predators such as songbirds, beetles (eg. Carabidae, Staphylinidae) and spiders (eg. *Antrodiaetus* spp.) dampen the effects of increased productivity at the trophic position of *Cybaeus* (Christie et al. *submitted*). Another consideration is intra-chain omnivory, which overall tends to shorten food chains (Polis and Strong 1996). I assume that the trophic position of my baseline Collembola is constant (ie. at 2) across the waterfall barrier. An increase in omnivory in Collembola

below the falls, including protein consumption from a diet of bacteria and animal detritus as opposed to fungi, would bias my estimation of food-chain length and trophic position. Finally, ecosystem size is often a better predictor of food-chain length than productivity, particularly when base levels of productivity are high (Post 2002a). Increases in productivity and energy increase food-chain length in impoverished systems such as deserts and alpine tundra, but at sites with intermediate productivities, such as in temperate coniferous forests, nutrient additions may not have noticeable effects.

8.5.4. Conclusion

Salmon spawning density determines the extent of terrestrial transfer and selective foraging on salmon carcasses by vertebrates (Reimchen 2000; Gende et al. 2001). In turn, this facilitates carcass colonization and consumption by many additional species (Cederholm et al. 2000; Meehan et al. 2005), and may ultimately be the best predictor of riparian carrying capacity (Reimchen 1994). The direct and indirect effects of the salmon subsidy in forest habitats are analogous to other marine subsidies along the terrestrial-marine ecotone which have found community-level responses and high secondary production from marine inputs of wrack, carrion and guano (Polis and Hurd 1995, 1996; Markwell and Daugherty 2002). Variation in community-effects across watersheds will likely be largely driven by salmon density, but also local processes such as base riparian productivity, the dominant salmon species, watershed size and human disturbance. Salmon densities have been in decline for the last 100 years and many affected watersheds are already facing nutrient deficits that threaten whole communities (Finney et al. 2000; Gresh et al. 2000; Stockner 2003). Overall, this work adds to a growing literature devoted to preserving wild-salmon ecosystems and shows strongly that in intact systems, such as the Clatsop and Neenah, the salmon subsidy benefits multiple trophic levels and increases total biomass, diversity and food-chain length of the terrestrial invertebrate community. Further implications for riparian-dependent vertebrates such as songbirds are just recently being described (Gende and Willson 2001; Christie et al. *submitted*; Christie and Reimchen *submitted*).

Figure 8.1. Total pitfall trapped biomass of litter invertebrates from multiple trophic levels in the spring and during the fall salmon spawning season on the Clatse and Neekas rivers, B.C. Invertebrates are characterized as primary consumers (herbivores, detritivores, fungivores), secondary consumers (omnivores, predators) and tertiary consumers (saprophages, blood suckers and parasitoids). Tertiary consumers in the fall primarily consist of dipteran larvae dispersing from salmon carcasses.

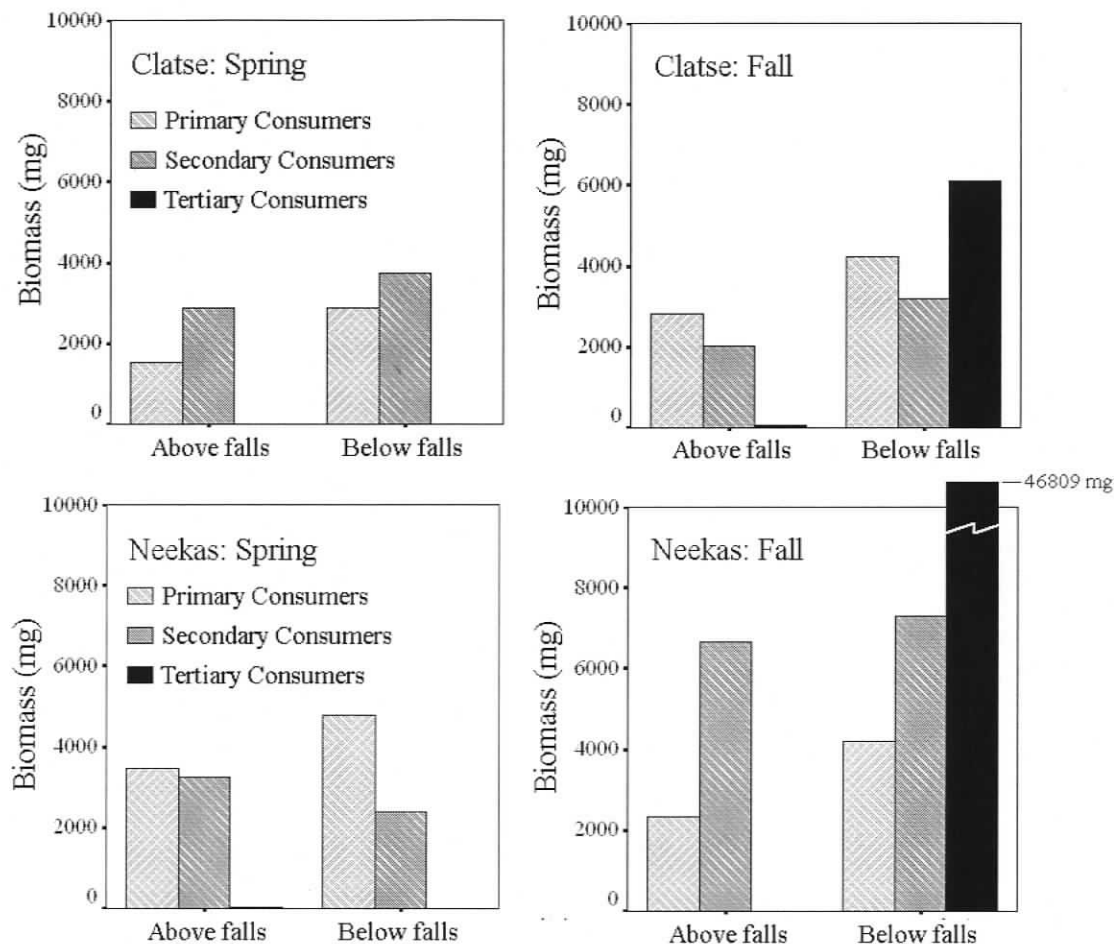


Figure 8.2. Biomass ($\pm$ SE) of primary consumers (herbivores, detritivores, fungivores) caught in pitfall traps in the spring and the fall salmon spawning season on the a) Clatse and b) Neekas rivers, B.C. Data represent the average trap catch (9 traps per plot) in three plots within four habitat blocks on each watershed: 1) Below falls/ Near stream (BN); 2) Below falls/ Far from stream (BF); 3) Above falls/ Near stream (AN); 4) Above falls/ Far from stream (AF). The habitat-block Below/ Near has highest access to salmon nutrients, followed by Below/ Far.

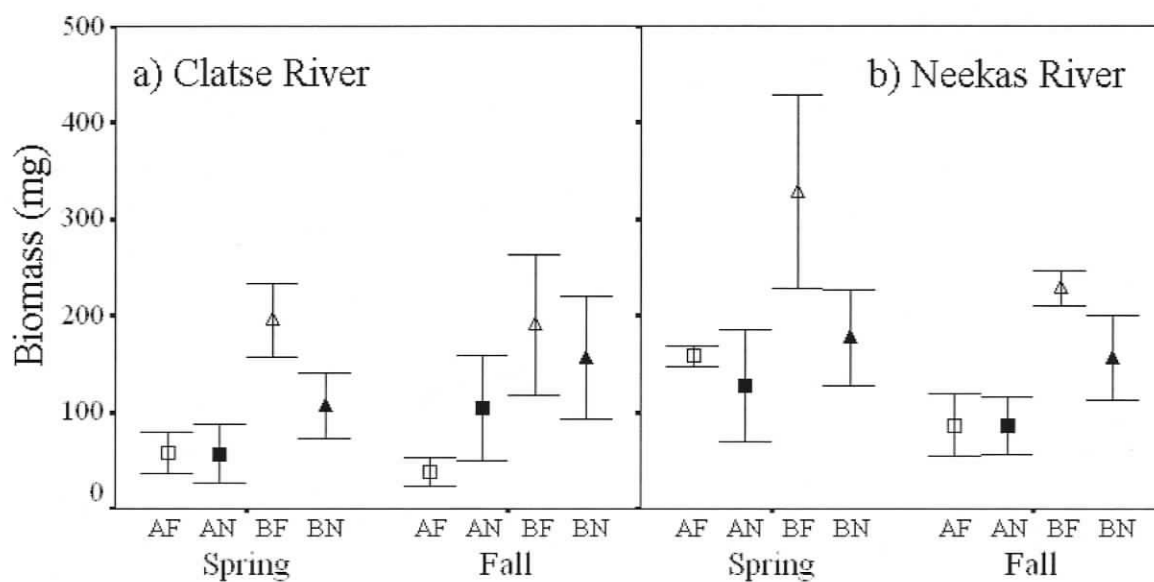


Figure 8.3. Biomass ($\pm$ SE) of secondary consumers (omnivores, predators) caught in pitfall traps in the spring and the fall salmon spawning season on the a) Clatse and b) Neekas rivers, B.C. Data represent the average trap catch (9 traps per plot) in three plots within four habitat blocks on each watershed: 1) Below falls/ Near stream (BN); 2) Below falls/ Far from stream (BF); 3) Above falls/ Near stream (AN); 4) Above falls/ Far from stream (AF). The habitat-block Below/ Near has highest access to salmon nutrients, followed by Below/ Far.

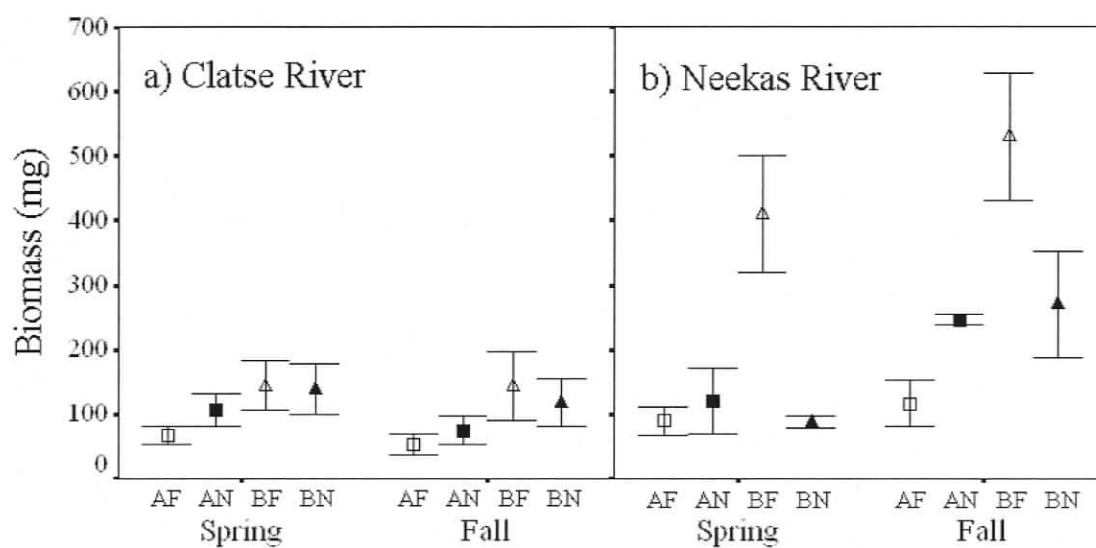


Figure 8.4. Indirect effects of salmon nutrient input to terrestrial litter communities including a) percent cover ($\pm$ SE) of humus-indicator plant species and b) biomass (mg $\pm$ SE) of macro-detritivores (worms, millipedes and isopods). Data collected in 10m*10m plots from four habitat blocks on the Clatse and Neekas rivers, B.C.: 1) Below falls/ Near stream (BN); 2) Below falls/ Far from stream (BF); 3) Above falls/ Near stream (AN); 4) Above falls/ Far from stream (AF). Percent cover data generated by % cover Mor (nutrient-poor) humus-indicators subtracted from % cover of Moder/Mull (nutrient-rich) humus-indicators. Biomass data is from pitfall traps pooled over two seasons of collection (spring, fall). The habitat-block Below/ Near has highest access to salmon nutrients, followed by Below/ Far.

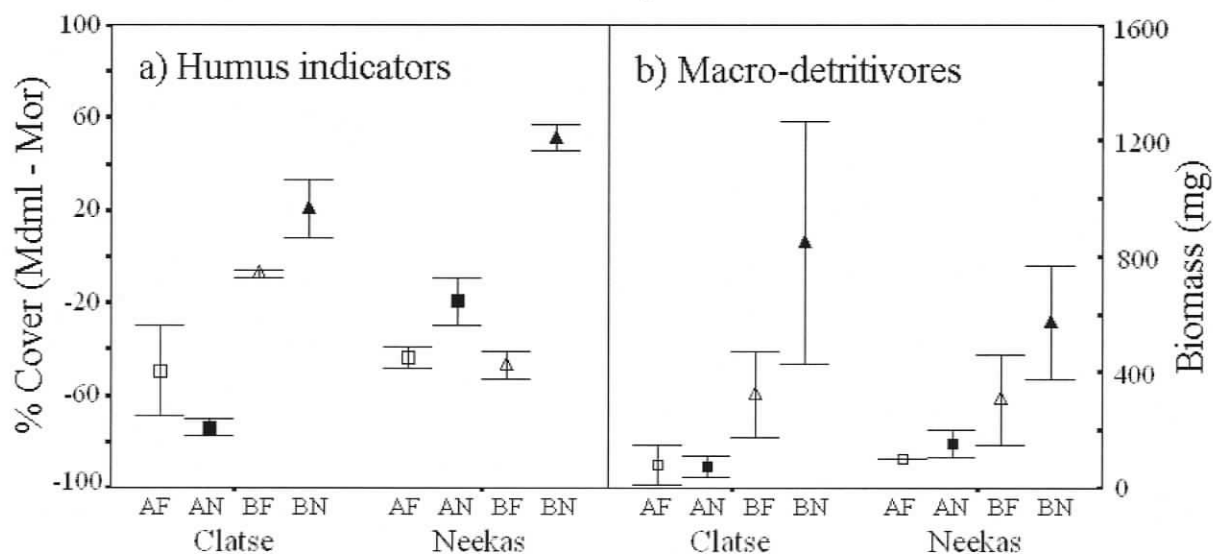


Figure 8.5. Pitfall-trapped biomass ($\text{mg} \pm \text{SE}$) of a) carabid beetles and b) snails from plots within four habitat-blocks on the Clatse and Neekas watersheds, B.C. Habitat blocks include Below falls/ Near stream (BN); Below falls/ Far from stream (BF); Above falls/ Near stream (AN); and Above falls/ Far from stream (AF). The habitat-block Below/ Near has highest access to salmon nutrients, followed by Below/ Far. Data is pooled across seasons of collection.

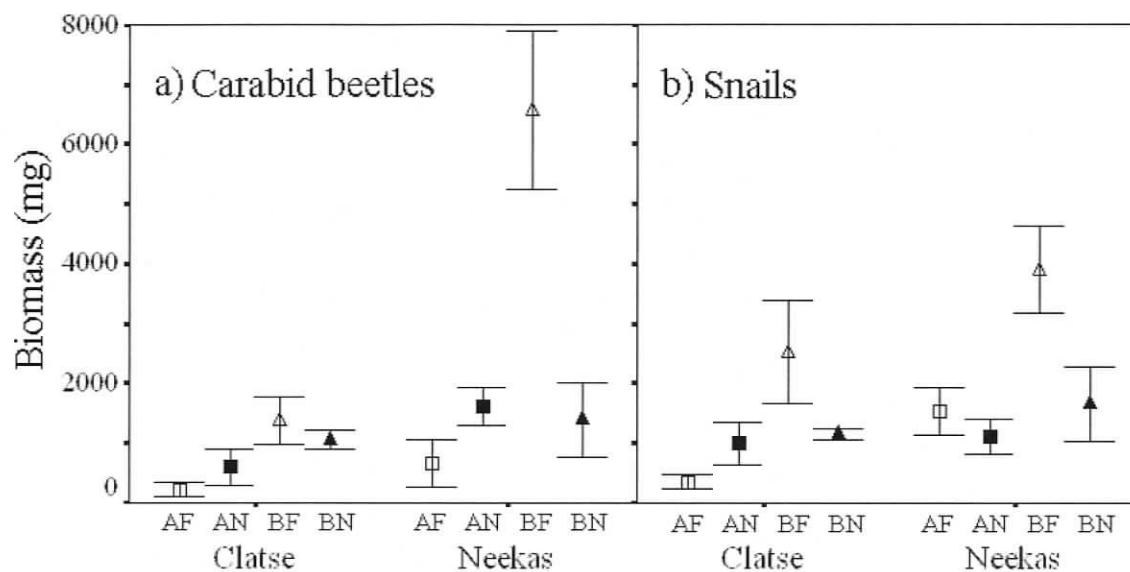


Figure 8.6. Mean family diversity ($\pm$ SE) of invertebrates caught in pitfall traps in the spring and in the fall salmon spawning season on the a) Clatse and b) Neekas rivers, B.C. Data represent the average trap catch (9 traps per plot) in three plots within four habitat blocks on each watershed: 1) Below falls/ Near stream (BN); 2) Below falls/ Far from stream (BF); 3) Above falls/ Near stream (AN); 4) Above falls/ Far from stream (AF). The habitat-block Below/ Near has highest access to salmon nutrients, followed by Below/ Far.

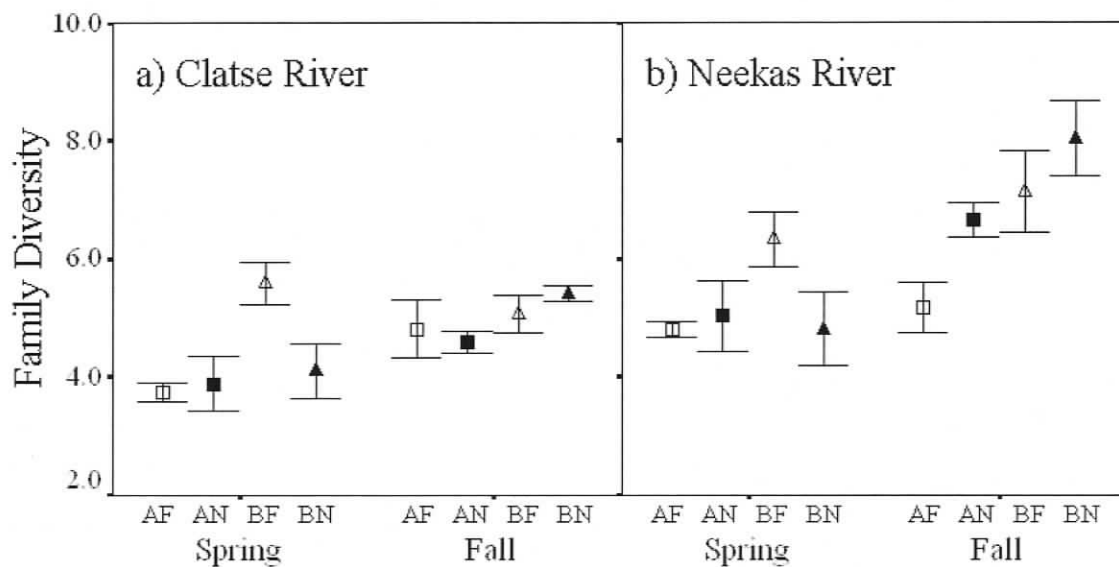


Figure 8.7. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in primary, secondary and tertiary consumers indicate membership within terrestrial and/or marine food-chains on a) Clatsop River above falls; b) Clatsop River below falls; c) Neekas River above falls; and d) Neekas River below falls. Tertiary consumers occur within marine or terrestrial food-chains or are intermediate indicating multi-channel omnivory. Primary and secondary consumers occur within the terrestrial food-chain.

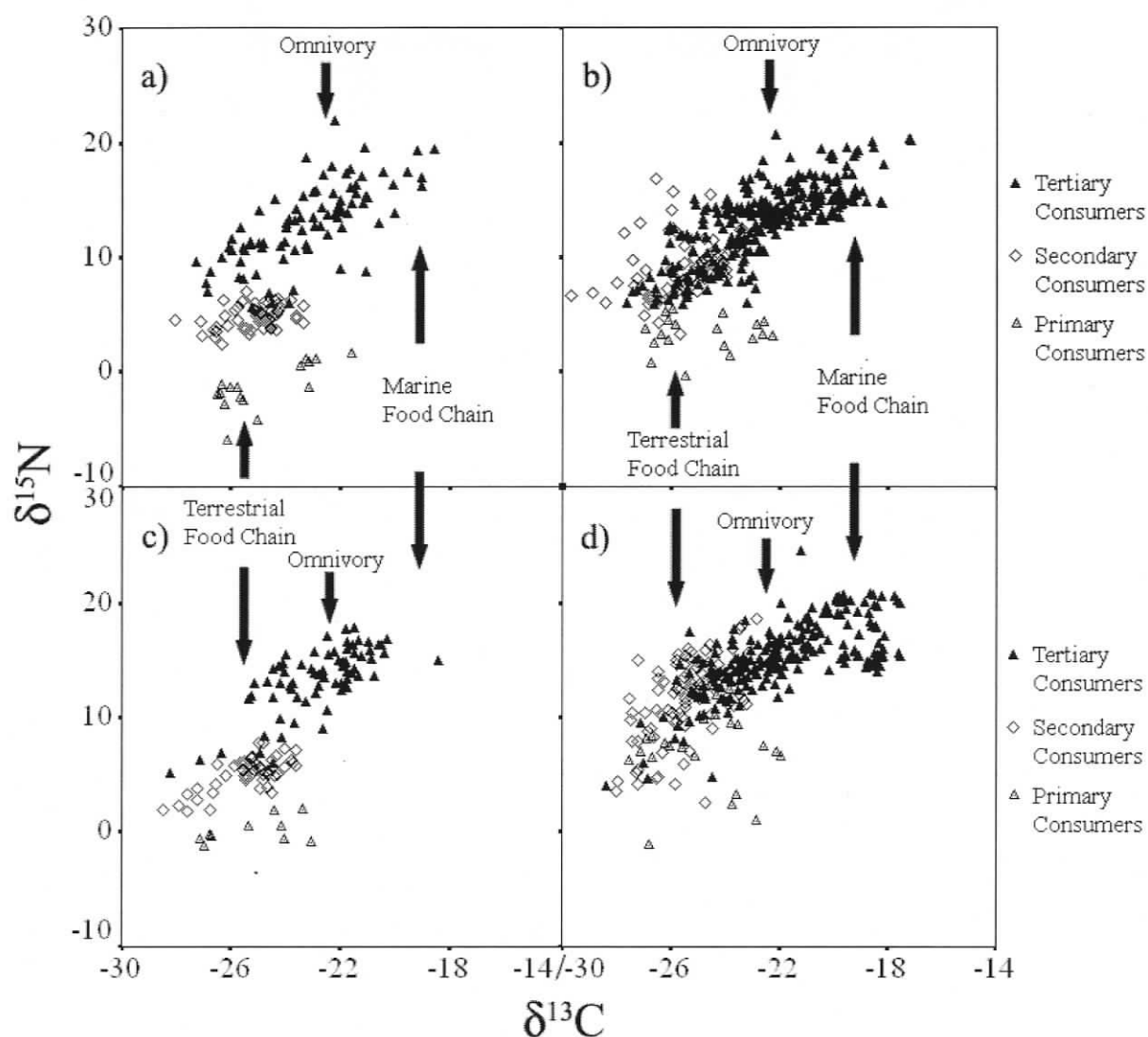


Table 8.1. Classification, abundance, individual mass (mg) and total biomass (mg) of taxonomic groups caught in pitfall traps in spring and fall on the Clatse and Neekas rivers, B.C. (·) Indicates unknown level of classification.

Class	Order	Family	Species	Species code	Guild	Abundance	Mass (mg)	Biomass (mg)
Collembola	Arthropoleona	·	·	misc Collembola	Detritivore	8688	0.1	868.8
Collembola	Arthropoleona	Entomobryidae	·	Entomobryidae	Detritivore	4538	1	4538
Collembola	Symphyleona	Dicyrtomidae	<i>Ptenothrix maculosa</i>	<i>P. maculosa</i>	Detritivore	5207	0.2	1041.4
Insecta	·	·	·	unk Insecta	Unknown	32	1	32
Insecta	Coleoptera	·	·	Coleoptera larva	Predator	10	25	250
Insecta	Coleoptera	·	·	Small Coleoptera larvae	Herbivore	4	0.5	2
Insecta	Coleoptera	Staphylinidae	·	Omalinae	Saprophage	25	2	50
Insecta	Coleoptera	Staphylinidae	·	Aleocharinae	Predator	15	0.2	3
Insecta	Coleoptera	Staphylinidae	<i>Atheta</i> sp.	<i>Atheta</i> sp.	Predator	4	0.2	0.8
Insecta	Coleoptera	Staphylinidae	<i>Tachinus maculicollis</i>	<i>T. maculicollis</i>	Predator	6	8	48
Insecta	Coleoptera	Staphylinidae	·	Oxytelinae	Predator	3	0.5	1.5
Insecta	Coleoptera	Leiodidae	<i>Leiodes</i> sp.	<i>Leiodes</i> sp.	Fungivore	28	5	140
Insecta	Coleoptera	Leiodidae	<i>Catops</i> sp.	<i>Catops</i> sp.	Saprophage	2	5	10
Insecta	Coleoptera	Leiodidae	<i>Catopocerus</i> sp.	<i>Catopocerus</i>	Fungivore	1	0.5	0.5
Insecta	Coleoptera	Silphidae	<i>Nicrophorus investigator</i>	<i>N. investigator</i> larvae	Saprophage	11	25	275
Insecta	Coleoptera	Silphidae	<i>Nicrophorus investigator</i>	<i>N. investigator</i>	Saprophage	6	500	3000
Insecta	Coleoptera	Leptinidae	<i>Leptinus</i> sp.	Leptinidae	Parasitic	1	0.5	0.5
Insecta	Coleoptera	Scydmaenidae	·	Scydmaenidae	Saprophage	19	0.1	1.9
Insecta	Coleoptera	Ptilidae	·	Ptilidae	Fungivore	2	0.1	0.2
Insecta	Coleoptera	Pselaphidae	·	Pselaphidae	Predator	4	0.1	0.4
Insecta	Coleoptera	Pselaphidae	<i>Cupila clavicornis</i>	<i>C. clavicornis</i>	Predator	25	0.1	2.5
Insecta	Coleoptera	Pselaphidae	<i>Sonoma parviceps</i>	Faroninae	Predator	4	0.1	0.4
Insecta	Coleoptera	Curculionidae	·	misc. curculionidae	Herbivore	3	4	12
Insecta	Coleoptera	Curculionidae	<i>Steremnius carinatus</i>	<i>S. carinatus</i>	Herbivore	66	40	2640
Insecta	Coleoptera	Curculionidae	<i>Steremnius tuberosus</i>	<i>S. tuberosus</i>	Herbivore	16	60	960
Insecta	Coleoptera	Byrrhidae	·	Byrrhidae	Herbivore	17	7.5	127.5
Insecta	Coleoptera	Byrrhidae	<i>Exomella pleuralis</i>	<i>E. pleuralis</i>	Herbivore	1	0.5	0.5
Insecta	Coleoptera	Elateridae	·	Elateridae	Herbivore	2	20	40
Insecta	Coleoptera	Cantharidae	·	Cantharidae	Predator	1	40	40
Insecta	Coleoptera	Lycidae	<i>Dictyopetrus simplicipes</i>	Lycidae	Predator	1	20	20
Insecta	Coleoptera	Tenebrionidae	·	Tenebrionidae	Herbivore	1	100	100
Insecta	Coleoptera	Zopheridae	<i>Phellopsis porcata</i>	Zopheridae	Herbivore	1	60	60
Insecta	Coleoptera	Carabidae	<i>Pterostichus crenicollis</i>	<i>P. crenicollis</i>	Omnivore	35	210	7350
Insecta	Coleoptera	Carabidae	<i>Pterostichus amethystinus</i>	<i>P. amethystinus</i>	Omnivore	7	100	700
Insecta	Coleoptera	Carabidae	<i>Pterostichus algidus</i>	<i>P. algidus</i>	Omnivore	1	100	100
Insecta	Coleoptera	Carabidae	<i>Zacotus mathewsii</i>	<i>Z. mathewsii</i>	Omnivore	20	155	3100
Insecta	Coleoptera	Carabidae	<i>Bembidion oblongulum</i>	<i>B. oblongulum</i>	Omnivore	2	10	20
Insecta	Coleoptera	Carabidae	<i>Scaphinotus angusticollis</i>	<i>S. angusticollis</i>	Omnivore	74	290	21460
Insecta	Coleoptera	Carabidae	<i>Scaphinotus angulatus</i>	<i>S. angulatus</i>	Omnivore	4	150	600
Insecta	Coleoptera	Carabidae	<i>Cychnus tuberculatus</i>	<i>C. tuberculatus</i>	Omnivore	12	600	7200
Insecta	Coleoptera	Carabidae	<i>Notiophylus sylvaticus</i>	<i>N. sylvaticus</i>	Predator	3	5	15
Insecta	Coleoptera	Carabidae	<i>Leistus ferruginosus</i>	<i>L. ferruginosus</i>	Omnivore	4	15	60
Insecta	Coleoptera	Dytiscidae	·	Dytiscidae	Predator	2	50	100
Insecta	Diptera	·	·	Nematoceran larvae	Detritivore	21	25	525
Insecta	Diptera	·	·	unk. Nematoceran diptera	Unknown	17	3.12	53
Insecta	Diptera	Chironomidae	·	Chironomidae	Detritivore	99	0.1	9.9
Insecta	Diptera	Simuliidae	·	Simuliidae	Bloodsucker	9	1	9
Insecta	Diptera	Ceratopogonidae	·	Ceratopogonidae	Bloodsucker	50	0.1	4.9
Insecta	Diptera	Cecidomyiidae	·	Cecidomyiidae	Detritivore	2	0.2	0.4
Insecta	Diptera	Tipulidae	·	Tipulidae	Detritivore	580	3.54	2051.5
Insecta	Diptera	Mycetophilidae	·	Mycetophilidae	Fungivore	27	1	27
Insecta	Diptera	Bibionidae	·	Bibionidae	Saprophage	1	1	1
Insecta	Diptera	Psychodidae	·	Psychodidae	Predator	4	0.5	2
Insecta	Diptera	·	·	Cyclorrhaphan larvae	Saprophage	2438	20	48760
Insecta	Diptera	·	·	Acalyptrate muscoid	Saprophage	3	5	15
Insecta	Diptera	Empididae	·	Empididae	Predator	3	1	3
Insecta	Diptera	Empididae	<i>Dolichocephala</i> sp.	<i>Dolichocephala</i>	Predator	6	1	6
Insecta	Diptera	Phoridae	·	Phoridae	Saprophage	42	0.5	21
Insecta	Diptera	Sphaeroceridae	·	Sphaeroceridae	Saprophage	51	0.5	25.5
Insecta	Diptera	Ephydriidae	·	Ephydriidae	Saprophage	3	1	3
Insecta	Diptera	Calliphoridae	<i>Calliphora terranova</i>	<i>Calliphora</i>	Saprophage	2	75	150
Insecta	Diptera	Dryomyzidae	<i>Dryomyza anilis</i>	<i>Dryomyza</i>	Saprophage	4	25	100
Insecta	Diptera	Heleomyzidae	·	Heleomyzidae	Saprophage	2	10	20

Table 8.1. cont.

Class	Order	Family	Species	Species code	Guild	Abundance	Mass (mg)	Biomass (mg)
Insecta	Hymenoptera	.	.	unk Apocrita	Parasitic	1	0.2	0.2
Insecta	Hymenoptera	Ichneumonidae	.	Wingless Ichneumonidae	Predator	10	2.5	25
Insecta	Hymenoptera	Ichneumonidae	<i>Atractodes</i> sp.	<i>Atractodes</i> sp.	Parasitic	8	2.5	20
Insecta	Hymenoptera	Braconidae	<i>Alysia alticola</i>	<i>Alysia alticola</i>	Parasitic	3	2	6
Insecta	Hymenoptera	.	.	Chalcidoidea	Parasitic	1	0.2	0.2
Insecta	Hymenoptera	Mymaridae	<i>Anaphes</i> sp.	Mymaridae	Parasitic	2	0.1	0.2
Insecta	Hymenoptera	Cynipidae	.	Cynipidae	Parasitic	2	0.2	0.4
Insecta	Hymenoptera	Scelionidae	.	Scelionidae	Parasitic	7	0.1	0.7
Insecta	Hymenoptera	Platygastridae	.	Platygastridae	Parasitic	3	0.17	0.5
Insecta	Hymenoptera	Proctotrupidae	.	Proctotrupidae	Parasitic	4	0.2	0.8
Insecta	Hymenoptera	Diapriidae	.	Belytinae	Parasitic	6	0.2	1.2
Insecta	Hymenoptera	Ceraphronidae	.	Ceraphronidae	Parasitic	3	0.1	0.3
Insecta	Hymenoptera	Formicidae	.	Formicidae	Omnivore	19	2.5	47.5
Insecta	Hymenoptera	Vespidae	.	Vespidae	Predator	2	50	100
Insecta	Lepidoptera	.	.	Defoliator larvae	Herbivore	1	25	25
Insecta	Lepidoptera	Geometridae	.	Geometridae	Herbivore	9	50	450
Insecta	Microcoryphia	Machilidae	.	Machilidae	Predator	27	12	324
Insecta	Homoptera	Cicadellidae	.	Cicadellidae	Herbivore	1	2	2
Insecta	Homoptera	.	.	Fulgoroidea	Herbivore	2	0.5	1
Insecta	Homoptera	Aphididae	.	Aphididae	Herbivore	10	2	20
Insecta	Grylloptera	Rhaphidiophoridae	.	Rhaphidiophoridae	Predator	30	50	1500
Insecta	Hemiptera	Dipsocoridae	<i>Ceratocombus vagans</i>	Dipsocoridae	Predator	4	0.5	2
Insecta	Hemiptera	Saldidae	.	Saldidae	Predator	1	4	4
Insecta	Siphonaptera	Ceratophyllidae	.	Siphonaptera	Bloodsucker	4	1	4
Insecta	Psocoptera	Pseudocaeciliidae	.	Psocoptera	Herbivore	4	0.5	2
Diplopoda	Julida	Parajulidae	.	Parajulidae	Detritivore	17	105	1785
Diplopoda	Polyxenida	Polyxenidae	.	Polyxenidae	Detritivore	3	2	6
Diplopoda	Polydesmida	Nearctodesmidae	<i>Nearctodesmus</i> sp.	<i>Nearctodesmus</i>	Detritivore	5	100	500
Chilopoda	Scolopendrida	Cryptopidae	.	Cryptopidae	Predator	25	140	3500
Chilopoda	Geophilida	Geophilidae	.	Geophilidae	Predator	3	10	30
Diplura	Diplura	.	.	Diplura	Predator	4	0.5	2
Arachnida	Araneae	.	.	misc Araneae	Predator	360	2	720
Arachnida	Araneae	Antrodiaetidae	<i>Antrodiaetus pacificus</i>	<i>Antrodiaetus</i>	Predator	46	100	4600
Arachnida	Araneae	Agelenidae	<i>Cybaeus</i> sp.	<i>Cybaeus</i>	Predator	515	40	20600
Arachnida	Pseudoscorpiones	.	.	Pseudoscorpionida	Predator	48	0.2	9.6
Arachnida	Opiliones	.	.	Opiliones	Predator	44	10	440
Arachnida	Acariformes	.	.	Oribatid mite	Detritivore	718	0.1	71.8
Arachnida	Parasitiformes	.	.	Phoretic Mesostigmatid	Predator	521	0.12	62
Arachnida	Parasitiformes	.	.	Mesostigmatid sp.I	Predator	18	1	18
Arachnida	Parasitiformes	.	.	misc Mesostigmatid mite	Predator	243	0.1	24.3
Arachnida	Parasitiformes	Trombididae	.	Trombididae	Predator	44	2	88
Arachnida	Parasitiformes	Bdellidae	.	Bdellidae	Predator	269	1	269
Malacostraca	Isopoda	Oniscidae	.	Isopoda	Detritivore	52	15	780
Gastropoda	Systellommatophora	.	.	misc. Snail	Detritivore	22	40	880
Gastropoda	Systellommatophora	.	.	misc. Slug	Detritivore	16	2000	32000
Gastropoda	Systellommatophora	Haplotrematidae	<i>Haplotrema</i> sp.	<i>Haplotrema</i>	Detritivore	31	800	24800
Gastropoda	Systellommatophora	Polygyridae	<i>Vespericola columbiana</i>	<i>V. columbiana</i>	Detritivore	34	425	14450
Oligochaeta	Enchytraeida	Enchytraeidae	.	Enchytraeidae	Detritivore	34	100	3400
Oligochaeta	Lumbricina	Lumbricidae	.	Lumbricidae	Detritivore	6	150	900
.	.	.	.	Nematoda	Detritivore	8	0.2	1.6
Mammalia	Rodentia	Soricidae	<i>Sorex</i> sp.	<i>Sorex</i>	Predator	14	3000	42000
Amphibia	Caudata	Ambystomatidae	<i>Ambystoma gracile</i>	<i>A. gracile</i>	Predator	2	1500	3000
Amphibia	Caudata	Salamandridae	<i>Tarisha granulosa</i>	<i>T. granulosa</i>	Predator	1	1500	1500

Table 8.2. Understory shrub and herb species of forest research plots on the Clatse and Neekas rivers, B.C. and their associated Ground Surface Material (GSM) indicator status based on Klinka et al. 1989. Only plants that indicate Moder/Mull (nutrient-rich) or Mor (nutrient-poor) humus forms are included.

Understory Species	GSM indicator	Understory Species	GSM indicator
<i>Alnus rubra</i>	Moder/Mull	<i>Rubus parviflorus</i>	Moder/Mull
<i>Athyrium filix-femina</i>	Moder/Mull	<i>Rubus pedatus</i>	Mor
<i>Blechnum spicant</i>	Mor	<i>Rubus spectabilis</i>	Moder/Mull
<i>Clintonia uniflora</i>	Mor	<i>Sambucus racemosa</i>	Moder/Mull
<i>Coptis asplenifolia</i>	Mor	<i>Smilacina stellata</i>	Moder/Mull
<i>Cornus canadensis</i>	Mor	<i>Sorbus sitchensis</i>	Mor
<i>Gaultheria shallon</i>	Mor	<i>Streptopus amplexifolius</i>	Moder/Mull
<i>Gymnocarpium dryopteris</i>	Moder/Mull	<i>Streptopus roseus</i>	Moder/Mull
<i>Heracleum lanatum</i>	Moder/Mull	<i>Thelypteris phegopteris</i>	Moder/Mull
<i>Listera cordata</i>	Mor	<i>Tiarella trifoliata</i>	Moder/Mull
<i>Lonicera involucrata</i>	Moder/Mull	<i>Tsuga heterophylla</i>	Mor
<i>Lycopodium clavatum</i>	Mor	<i>Tsuga mertensiana</i>	Mor
<i>Maianthemum dilatatum</i>	Moder/Mull	<i>Urtica dioica</i>	Moder/Mull
<i>Menziesia ferruginea</i>	Mor	<i>Vaccinium alaskaense</i>	Mor
<i>Oplopanax horridus</i>	Moder/Mull	<i>Vaccinium ovalifolium</i>	Mor
<i>Polystichum munitum</i>	Moder/Mull	<i>Vaccinium parvifolium</i>	Mor
<i>Ribes bracteosum</i>	Moder/Mull	<i>Viola glabella</i>	Moder/Mull

Table 8.3. Sample sizes of terrestrial invertebrate taxa processed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ collected above and below waterfall barriers to salmon on the Clatse (CR-Abv, CR-Bel) and Neekas (NR-Abv, NR-Bel) rivers, B.C. Invertebrates are classified as primary (PC), secondary (SC) or tertiary (TC) consumers. * Samples are composites of >44 individuals.

Family	Species	Guild	Frequency			
			CR-Abv	CR-Bel	NR-Abv	NR-Bel
Curculionidae	<i>Steremnius</i> spp.	PC	6	7	1	4
Tomoceridae	<i>Tomocerus</i> spp.	PC	2*	2*	2*	2*
Dicyrtomidae	<i>Ptenothrix maculosa</i>	PC	2*	2*	2*	2*
Parajulidae	unk.	PC	6	9	5	15
Agelenidae	<i>Cybaeus</i> spp.	SC	37	36	31	29
Antrodiaetidae	<i>Antrodiaetus pacificus</i>	SC	5	15	10	19
Amaurobiidae	<i>Callobius</i> spp.	SC	0	0	0	1
Carabidae	<i>Pterostichus</i> spp.	SC	1	12	2	10
Carabidae	<i>Zacotus mathewsii</i>	SC	6	6	0	4
Carabidae	<i>Scaphinotus angusticollis</i>	SC	0	0	5	9
Carabidae	<i>Cychrus tuberculatus</i>	SC	0	0	0	1
Carabidae	<i>Diplous</i> spp.	SC	0	0	0	3
Aeshnidae	<i>Aeshna</i> spp.	SC	0	0	0	1
Libellulidae	<i>Libellula quadrimaculata</i>	SC	3	3	0	0
Cryptopidae	unk.	SC	1	1	3	6
Staphylinidae	<i>Tachinus maculicollis</i>	SC	0	2	0	6
Staphylinidae	<i>Bisnius seigwaldi</i>	SC	0	0	0	3
Staphylinidae	<i>Anthobium fimetarium</i>	TC	0	0	0	3
Silphidae	<i>Nicrophorus defodiens</i>	TC	14	44	1	0
Silphidae	<i>Nicrophorus investigator</i>	TC	3	81	0	5
Silphidae	<i>N. investigator</i> larvae	TC	0	9	0	5
Leiodidae	<i>Catops</i> spp.	TC	4	5	0	0
Calliphoridae	<i>Calliphora terranova</i>	TC	30	72	44	102
Dryomyzidae	<i>Dryomyza anilis</i>	TC	35	51	26	37
Muscidae	unk.	TC	0	0	0	1
various	Cyclorrhaphan Fly larvae	TC	0	4	0	24
Braconidae	<i>Alysia alticola</i>	TC	0	6	0	25
Ichneumonidae	<i>Atractodes</i> spp.	TC	0	0	0	17

Table 8.4. Biomass of multiple guilds of pitfall-trapped litter invertebrates in the spring and fall from the Clatse and Neekas rivers B.C. Data shown are separate species-codes (Table 8.1) paired by location above and below falls. No. Below indicates the number of taxa with higher biomass below the falls while No. Above indicates the number of taxa with higher biomass above the falls. Associated Wilcoxon and Sign tests are reported.

Watershed	Season	Guild	No. Below	No. Above	Wilcoxon Z	p-value	Sign p-value
Clatse	Spring	Primary Consumers	11	11	-0.244	0.808	1.000
		Secondary Consumers	16	6	-1.510	0.131	0.052
		Tertiary Consumers	3	3	-0.736	0.462	1.000
		All Species	31	20	-0.937	0.349	0.161
	Fall	Primary Consumers	15	6	-1.234	0.217	0.078
		Secondary Consumers	16	11	-0.961	0.337	0.441
		Tertiary Consumers	9	1	-2.497	0.013	0.021
		All Species	42	18	-2.400	0.016	0.003
Neekas	Spring	Primary Consumers	18	6	-1.743	0.081	0.023
		Secondary Consumers	13	11	-0.029	0.977	0.839
		Tertiary Consumers	4	7	-1.604	0.109	0.549
		All Species	36	25	-0.736	0.462	0.200
	Fall	Primary Consumers	19	7	-1.714	0.086	0.031
		Secondary Consumers	18	8	-1.283	0.200	0.078
		Tertiary Consumers	17	5	-3.069	0.002	0.041
		All Species	54	22	-3.174	0.002	<0.001

Table 8.5. Principal components analysis (PCA) scores for measures of litter invertebrate community biomass during the spring and the fall spawning season from 10m by 10m plots on the Clatse and Neekas rivers, B.C.

	Spring		Fall	
	PC1 (43.3%)	PC2 (32.8%)	PC1 (52.2%)	PC2 (33.5%)
Biomass Primary Consumers	0.795	0.020	0.704	-0.606
Biomass Secondary Consumers	-0.483	0.811	0.532	0.799
Biomass Tertiary Consumers	0.660	0.570	0.887	0.003

Table 8.6. Principal components analysis (PCA) scores for measures of vegetation community structure from 10m by 10m plots on the Clatse and Neekas rivers, B.C. MDML cover indicates % cover of vegetation species that indicate Moder/Mull humus forms.

	PC1 (43.7%)	PC2 (23.1%)	PC3 (19.0%)
Veg diversity	0.258	0.847	-0.381
Herb cover	0.868	-0.010	0.206
Shrub cover	-0.842	0.288	-0.296
Tree cover	0.793	0.166	-0.246
MDML cover	-0.171	0.574	0.785

Table 8.7. Akaike Information Criterion (AIC) analysis showing top models ($\Delta AIC < 4$) of GLM analysis predicting family diversity in pitfall-trapped litter invertebrates collected in spring and fall. Parameters include PC1 and PC2 from the biomass PCA (PC1b, PC2b: Table 8.5), and PC1, PC2 and PC3 from the vegetation PCA (PC1v, PC2v, PC3v: Table 8.6). The parameter watershed (Wa) was used in all models.

Season	Top Models	k	RSS	R ²	AIC _c	ΔAIC_c	W_i
Spring	Wa + PC1b	4	3.66	0.623	-8.54	0.00	0.360
	Wa + PC1b + PC2b	5	3.39	0.651	-5.17	3.37	0.070
	Wa + PC1b + PC1v	5	2.57	0.735	-8.49	0.05	0.360
Fall	Wa + PC1b	4	3.69	0.858	-8.44	0.72	0.220
	Wa + PC3v	4	4.71	0.801	-5.51	3.65	0.050
	Wa + PC1b + PC2b	5	2.43	0.897	-9.16	0.00	0.320
	Wa + PC1b + PC1v	5	3.27	0.862	-5.60	3.56	0.050
	Wa + PC1b + PC2v	5	3.18	0.866	-5.94	3.22	0.060
	Wa + PC1b + PC3v	5	2.87	0.878	-7.17	1.99	0.120
	Wa + PC1b + PC2b + PC3v	6	1.86	0.921	-5.57	3.59	0.050

Table 8.8. Parameter likelihoods (summed AIC_c weights of top models that include parameter) of different explanatory variables in GLM models. Parameter likelihoods reflect the relative importance of each explanatory variable in models describing variation in family diversity of pitfall-trapped litter invertebrates in spring and fall at the plot level.

Parameters	ΣW_i spring	ΣW_i fall
PC1b	0.79	0.80
PC2b	0.07	0.37
PC1v	0.36	0.05
PC2v	0.00	0.06
PC3v	0.00	0.22

Table 8.9. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic ranges (‰) in multiple trophic levels of terrestrial invertebrates above and below waterfall barriers to salmon on the Clatse and Neekas rivers, B.C. Ranges are derived from the combination of primary, secondary and tertiary consumers (Range_{P,S,T}) or just primary and secondary consumers (Range_{P,S}). Brackets represent the number of trophic levels within the range assuming fractionation of 3.4‰.

Watershed	Falls	$\delta^{15}\text{N}$ (‰)			$\delta^{13}\text{C}$ (‰)		
		Range _{P,S,T}	Range _{P,S}	Diff	Range _{P,S,T}	Range _{P,S}	Diff
Clatse	Above	27.73 (8.2)	12.95 (3.8)	14.78 (4.3)	9.41	6.41	3.00
	Below	21.01 (6.2)	17.37 (5.1)	3.64 (1.1)	12.34	7.32	5.02
Neekas	Above	19.04 (5.6)	9.14 (2.7)	9.90 (2.9)	10.00	5.36	4.64
	Below	25.54 (7.5)	19.70 (5.8)	5.84 (1.7)	10.68	5.97	4.71

Table 8.10. Trophic length variation in a litter invertebrate community above and below waterfall barriers to salmon on two watersheds (Clatse and Neekas rivers, B.C.) in two seasons (spring and during fall salmon spawning). Shown are $\delta^{15}\text{N}$ values of the spider predator *Cybaeus* spp. (mean $\pm$ SE) and a composite mean of Collembola used as the $\delta^{15}\text{N}$ baseline in this community. Trophic length is calculated as the $\delta^{15}\text{N}$ difference between spiders and Collembola. Trophic position indicates the position of *Cybaeus* in the food chain assuming the trophic position of Collembola = 2.

Watershed	Season	Location	n	$\delta^{15}\text{N}$ values (‰)		Trophic length	Trophic position
				<i>Cybaeus</i>	Collembola		
Clatse	Spring	Above near	13	5.06 $\pm$ 0.26	-1.43	6.49 $\pm$ 0.26	3.9
Clatse	Spring	Below near	10	9.05 $\pm$ 0.29	3.40	5.65 $\pm$ 0.29	3.7
Clatse	Fall	Above near	12	5.59 $\pm$ 0.20	-1.33	6.92 $\pm$ 0.20	4.0
Clatse	Fall	Below near	12	9.85 $\pm$ 0.30	4.60	5.25 $\pm$ 0.30	3.5
Neekas	Spring	Above near	9	5.54 $\pm$ 0.37	-1.00	6.54 $\pm$ 0.37	3.9
Neekas	Spring	Below near	8	13.44 $\pm$ 0.61	6.51	6.93 $\pm$ 0.61	4.0
Neekas	Fall	Above near	13	5.20 $\pm$ 0.17	-0.36	5.56 $\pm$ 0.17	3.6
Neekas	Fall	Below near	11	14.35 $\pm$ 0.41	8.14	6.21 $\pm$ 0.41	3.8

Chapter 9:

Salmon, bears and the legacy of process

9.1. Abstract

Ecosystem properties in one habitat realm can influence community dynamics and diversity in another. Throughout the northern Pacific region, anadromous salmonids (*Oncorhynchus* spp.) link marine and terrestrial habitats through their annual landward migrations. When salmon spawn in sufficient densities, bears (*Ursus* spp.) selectively forage and distribute carcasses into the adjacent forest where they are further consumed by terrestrial invertebrate scavengers. Herein, I use stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to examine patterns of marine-enrichment in seven guilds of plants and invertebrates from multiple watersheds throughout coastal British Columbia that vary in chum (*O. keta*) and pink (*O. gorbuscha*) salmon spawning density (kg fish per meter of stream). Salmon density strongly predicted $\delta^{15}\text{N}$ but not $\delta^{13}\text{C}$ signatures in all riparian guilds, with no difference in the pattern of enrichment by guild or region. In six of the seven guilds analyzed, the density of chum salmon on its own was a better predictor of $\delta^{15}\text{N}$ than pink density or the density of the two species combined. The legacy of spawning density from the past was also an important predictor of $\delta^{15}\text{N}$ as chum density from the 1950's best predicted $\delta^{15}\text{N}$ across all guilds. Chum salmon are larger than pink and provide an energetic reward for bears that facilitates transfer of carcasses to the forest. In many of my study watersheds chum densities have declined from the 1950's to the 1990's and the legacy of community processes generated by historical chum salmon transfer are still detectable in the isotopic signatures of current riparian taxa. Estimates of percent marine-derived nitrogen (%MDN) varied from 0-78% depending on watershed and extent of fractionation used in the %MDN model, and indicated that taxa with no direct association with salmon carcasses can be used as indicators of intact community processes in salmon-bearing watersheds. This study is the first to examine the extent of marine-nitrogen uptake from the salmon-forest subsidy in multiple watersheds across a large geographic area. My results highlight critical processes and watersheds that deserve conservation attention, particularly small chum-bearing streams supporting high bear activity that are coincidentally experiencing recent declines in British Columbia.

9.2. Introduction

The conservation of biodiversity in one biogeographic realm often requires the preservation of ecosystem processes in another (Ray 1988). Coastal ecotones cover approximately 8% of the earth's surface yet host a disproportionate share of global biodiversity and productivity (Ray and Hayden 1992). This is explained by the fact that marine near-shore waters are often supported by adjacent systems, either through upwelling of nutrients from the deep sea or subsidies of terrestrial-based nutrients to coastal bays and estuaries. In the reverse flow, productive marine environments can structure the ecology of adjacent terrestrial ones through various marine-terrestrial resource subsidies. Shore drift of algal wrack and carrion (Polis and Hurd 1996), inputs of guano and carcasses of seabirds (Lord and Burger 1984; Hawke and Newman 2004), and episodic returns of anadromous fishes (Ray 2005) are common examples.

All along the coastlines of the northern Pacific Ocean, salmon (*Oncorhynchus* spp.) return to spawn and die in their natal watersheds. This landward migration imports marine-derived nutrients and energy to terrestrial habitats, and is considered one of the most dominant marine-terrestrial resource subsidies in the Pacific region (Schindler et al. 2003). Spawning salmon regulate the population dynamics of many terrestrial species, as a fall diet of salmon can be critical for species reproduction, migration and overwintering (Reimchen 1994; Ben-David et al. 1997; Hilderbrand et al. 1999; Cederholm et al. 2000; Christie and Reimchen in press; Hocking et al. *in press*). The decomposition of salmon carcasses also adds nitrogen, phosphorus and other nutrients to both aquatic and terrestrial systems, a process that can initiate bottom-up ecosystem effects (Bilby et al. 1998; Wipfli et al. 1998; Helfield and Naiman 2002; Stockner 2003).

Resource fluxes across habitat boundaries can dramatically alter local community dynamics, although the degree of response of spatially subsidized communities depends on the relative amount of input and landscape variables that increase access (Polis et al. 1997). On islands, the abundance of terrestrial prey can be predicted by the density of marine input, such as the density of breeding seabirds (Markwell and Daugherty 2002), and by habitat variables such as the perimeter/area ratio (Polis and Hurd 1996). For example, smaller islands are more dependent on marine resources than larger ones and host higher terrestrial secondary productivity (Polis and Hurd 1996).

The input of salmon resources is thought to increase primary productivity in both aquatic and terrestrial habitats, although the role of salmon spawning density in predicting the response of salmon-dependent communities has surprisingly received fairly limited attention. Comparisons of nutrient inputs and community responses typically have occurred in defined treatments within 1-3 watersheds (eg. Wipfli et al. 1998; Helfield and Naiman 2002; Chaloner et al. 2002; Hocking and Reimchen 2002). Although useful, these studies are limited in the types of coast-wide predictions that can be made, including the carrying capacity of animal populations, diversity-productivity relationships, and areas of highest priority for conservation.

When salmon spawn at high densities, their carcasses and nutrients subsidize forest food-webs. Vertebrate predators such as bears actively distribute carcasses and nutrients into the adjacent forest (Reimchen 1994; Ben-David et al. 1998b; Hilderbrand et al. 1999b), a process that occurs at highest frequency when salmon are abundant and accessible (Reimchen 2000; Gende et al. 2001). In situations where salmon spawn at low densities, or when habitat attributes limit foraging success, vertebrate consumption of carcasses may approach 100% with few remnants distributed to riparian zones (Gende et al. 2001; Gende et al. 2004b).

The importance of the salmon-nutrient subsidy to forest food-webs is just recently being described (eg. Christie et al. *submitted*) although several studies have documented uptake of salmon-derived nitrogen by multiple terrestrial trophic levels (Hocking and Reimchen 2002; Reimchen et al. 2003). Using stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, I expand on these studies and investigate patterns of enrichment of salmon-derived N and C in multiple guilds of plants and animals from 26 watersheds throughout coastal British Columbia that vary in salmon spawning density. Nitrogen isotope ratios are often used to determine plant-nitrogen sources (Nadelhoffer and Fry 1994) or animal trophic position (Vander Zanden et al. 2000), while carbon isotope ratios have been primarily used to determine sources of primary productivity (Tieszen and Boutton 1988). In the salmon-forest system, stable isotopes can identify direct and indirect pathways of salmon nutrient input to multiple consumers. For example, high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in bears and wolves implies a diet of salmon for many individuals (Hilderbrand et al. 1999b; Darimont and Reimchen 2002), while elevated $\delta^{15}\text{N}$ but not $\delta^{13}\text{C}$ suggests an indirect pathway

through marine-nitrogen fertilization of terrestrial vegetation (Bilby et al. 1996; Ben-David et al. 1998b; Mathewson et al. 2003).

Herein, I estimate percent marine-derived nitrogen (%MDN) in multiple guilds of riparian biota that have little to no direct diet of salmon. Taxa were collected from watersheds dominated by runs of chum (*O. keta*) and pink (*O. gorbuscha*) salmon, and I use recent salmon spawning density (kg salmon per m of stream) as my primary predictor of stable isotope signatures. However, the relative role of each salmon species (chum or pink) and the legacy of spawning density from the past may also be important predictors of stable isotope signatures in riparian taxa. Foraging preferences by bears and other wildlife may dictate the extent of transfer and thus fertilization of coastal riparian zones (Reimchen 2000; Bilby et al. 2003; Gende et al. 2004b). Furthermore, the salmon-bear-forest linkage has likely been intact for hundreds or perhaps thousands of years since the last glaciation (Finney et al. 2000; 2002), and spawning densities in the past may be equally likely to predict riparian zone enrichment (Koyama et al. 2005).

Overall, this study is the first to examine the extent of marine-nitrogen uptake from the salmon-forest subsidy in multiple watersheds across a large geographic area. My results highlight critical processes and watersheds that deserve conservation attention, particularly small chum-bearing streams that are coincidentally experiencing recent declines in British Columbia (Godbout et al. 2004; Spilsted 2004).

9.3. Methods

9.3.1. Site description and collection methods

This study took place from 1998 to 2001 in watersheds in Clayoquot Sound, Vancouver Island, on the Queen Charlotte Islands, and on the mainland mid-coast of British Columbia. Collections from Clayoquot Sound occurred in summer 1998-99 and spring 1999-2000 from five salmon-bearing watersheds (Warn Bay, Moyeha, Megin, Watta and Sidney rivers) and one control watershed with an impassable cascade at mouth (Bulson Creek) (Figure 9.1). These watersheds are some of the least affected by the extensive deforestation in the region and are located within the Coastal Western Hemlock biogeoclimatic zone (CWHvh1) characterized by a mild and wet climate (~3300mm/year) and dense forests of western hemlock (*Tsuga heterophylla*), amabilis fir

(*Abies amabilis*), sitka spruce (*Picea sitchensis*) and western red cedar (*Thuja plicata*) (Green and Klinka 1994). Vegetation samples were collected by Deanna Mathewson as a part of her MSc. thesis (Mathewson 2002). An effort was made to collect recently grown foliar samples from plants that were not growing on nurse logs. In the spring of 2000, I collected representative invertebrate samples from sites that coincided with vegetation collections (Reimchen et al. 2003). All samples were collected within 50m of the spawning channel at sites with negligible slope and with some evidence of salmon carcass transfer (bony remnants from previous autumn).

From September 2nd to 24th 2000, I visited multiple salmon-bearing watersheds as a part of a research expedition through the mainland mid-coast and Haida Gwaii (Queen Charlotte Islands). In the mainland mid-coast region I collected invertebrate specimens from Evelyn and Little Tillhorn creeks on Hawkesbury Island, Kiskosh Creek on the mainland near the community of Hartley Bay, Belowe and Kumuleon rivers off of Grenville Channel, the Khutzeymateen River in Khutzeymateen Inlet, and the Ensheshese River in Work Channel (Figure 9.1). I also collected specimens from watersheds in Haida Gwaii including Government, Salmon, Echo, Kostan, Mathieson, Bag Harbour, Louscoone, Sedmond, and Harriet creeks on Moresby Island, Skedans Creek on Louise Island, and Windy Bay Creek on Lyell Island (Figure 9.1). Vegetation samples were collected by Leigh-Anne Isaac and Tom Reimchen in sites that coincided with invertebrate collections. Sites were chosen based on proximity to stream (< 20m), low or negligible slope, and evidence of fresh salmon carcass transfer. Sites also coincided with the coring of large spruce or hemlock trees (Reimchen unpublished data). All of these watersheds lie in the Coastal Western Hemlock Biogeoclimatic Zone, with mean annual temperature of near 8°C, and annual precipitation usually above 4000 mm (Green and Klinka 1994). Watersheds on the mainland typically lie in the boundary between the central very-wet hypermaritime (CWHvh2) and the submontane very wet maritime (CWHvm1) subzones, while those on Moresby Island lie in the boundary of the central very-wet hypermaritime (CWHvh2) and submontane wet hypermaritime (CWHwh1) subzones (Green and Klinka 1994). The Khutzeymateen River is the largest of all watersheds investigated and is characterized as a 4th order system with several salmon-

bearing tributaries. All others, with the exception of Evelyn creek (a small 4th order system), are classified as 1st to 3rd order creeks or rivers.

All invertebrate specimens were collected either in random searches from the forest floor or in ground-level pitfall traps. Pitfall traps were arranged in a three-way branching fashion which included a central 10cm diameter pitfall connected via three 24-inch by 6-inch aluminium drift fences (separated by 120°) to a perimeter pitfall at the end of each fence (Hocking and Reimchen 2002; Reimchen et al. 2003). Invertebrate specimens were stored in 70% ethanol prior to stable isotope analysis. Vegetation samples were dried and stored in small paper bags.

Plant and invertebrate samples were also collected from above and below the waterfall barrier to salmon on the Clatse and Neekas rivers (See Hocking and Reimchen 2002 for thorough site description; Figure 9.1). Vegetation samples were collected by D. Mathewson in fall 1999 in sites within 50m of the top and 50m of the bottom of waterfalls along the stream, and within 15m of the stream edge (data presented in Mathewson et al. 2003). Invertebrate samples were collected in mid- to late August 2000 from random searches or in pitfall traps within 50m of the spawning stream (data presented in Hocking and Reimchen 2002). On the Clatse River, main invertebrate sampling occurred from 200 to 800 meters upstream from the mouth, and again above the falls at 1200 and 1600 meters. The majority of invertebrate trapping on the Neekas occurred at 1km, and again at 2km, just below the falls. Control samples from the Neekas were collected just above the falls from 2200 to 2400 meters upstream from the mouth.

All watersheds listed above support populations of black bears (*U. americanus*) which act as the principal vectors of salmon carcasses into the forest (Reimchen 1994; Reimchen 2000). Grizzly bears (*U. arctos*) and wolves (*Canis lupus*) act as additional vectors on mainland sites (wolves also on Vancouver Island).

9.3.2. Guild classification

I classified individual taxa collected from multiple watersheds into several guild categories based on their physiognomy (plants) and their ecological role and extent of consumption of animal protein (animals). I also included taxa in guilds based on three main criteria: 1) taxa had to be represented in at least four watersheds across a gradient in

salmon spawning density; 2) taxa were not highly mobile and thus likely exhibited site-specific isotope signatures; and 3) taxa did not have a dominant direct relationship with salmon carcasses (based on previous field observations). Vascular plants were subdivided into three guilds: 1) herbs and ferns, 2) shrubs, and 3) tree needles (Table 9.1). The litter animal fauna were separated in a similar fashion to Hocking and Reimchen (2002) in guilds consisting of 1) litter spiders, 2) carabid beetles, 3) millipedes, and 4) root feeders (Table 9.1).

9.3.3. Stable isotope analysis

Whole invertebrate specimens were rinsed with distilled water and then dried at 60°C for at least 48 hours. All foliar samples were also dried completely. Samples were ground into a homogeneous powder using a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Ill). All animal samples were assayed for total N, $\delta^{15}\text{N}$, total C and $\delta^{13}\text{C}$, while plant samples were assayed for total N and $\delta^{15}\text{N}$, at the University of Saskatchewan Stable Isotope Facility, by continuous-flow isotope ratio mass spectrometry (CF-IRMS). Natural abundances of ^{15}N and ^{13}C are given in parts per mil (‰) and are expressed by:

$$1) \left(\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right) \times 1000$$

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

9.3.4. Data analysis

I used salmon spawning density as my primary predictor for isotope signatures in riparian guilds across watersheds. Salmon spawning density was determined by multiplying the average escapement of chum and pink salmon over ten years in the 1990's (Department of Fisheries and Oceans (DFO) Fish Wizard Database) by their regional mass estimates (pink: 1.9kg; chum: 5.3kg; Groot and Margolis 1991), and then dividing by the length of salmon spawning (DFO Fish Wizard Database) (Table 9.2):

$$2) \text{ Spawning density (kg/m)} = \frac{(\text{Mean chum} \times 5.3\text{kg}) + (\text{Mean pink} \times 1.9\text{kg})}{\text{Spawning length (m)}}$$

I used analysis of covariance (ANCOVA) to test for relationships between the dependents $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and the covariate salmon spawning density (kg/m). Guild was used as a fixed factor. Because sample sizes within guilds differed across watersheds ($n = 2-71$), I calculated the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each guild within watersheds for use in ANCOVA's. Some tests did not meet assumptions of equal variances and thus are interpreted with caution. In several companion ANCOVA's for $\delta^{15}\text{N}$, I met assumptions by removing the guild of millipedes.

I conducted separate regional analyses for Clayoquot Sound on Vancouver Island and the central coast watersheds. Clayoquot Sound taxa were collected in spring and summer while taxa from the central coast watersheds, including Haida Gwaii and the mainland, were collected in the fall. To be included in the regional analysis, taxa had to be represented from at least four watersheds (root feeders and spiders absent from Clayoquot; root feeders and carabids absent from the central coast). No $\delta^{13}\text{C}$ values were available for all three vegetation guilds. I also tested for the effects of spawning density on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ across all watersheds of collection (ANCOVA's). For $\delta^{15}\text{N}$ comparisons, all guilds except root-feeders (tree needles, shrubs, herbs, millipedes, carabids and spiders) were represented by at least nine watersheds (root-feeders collected only at Bulson, Bag Harbour, Clatse and Neekas).

Testing for the effects of season on stable isotope signatures are confounded in this study by effects of region of collection. Samples from Clayoquot were collected in spring and summer while samples from the central coast were collected in the fall. To address this issue, I tested for differences in $\delta^{15}\text{N}$ using region/season and guild as fixed factors (ANOVA – assumptions met). I used watershed means for the guilds of tree needles, shrubs, herbs and millipedes, and only included watersheds with salmon spawning densities of less than 10 kg/m. This removed the bias of higher spawning densities on the central coast. From Clayoquot this included Bulson, Sidney, Watta, Moyeha and Megin watersheds, while from the Queen Charlottes this included Skedans, Mathiesen, Harriet, Windy Bay, Louscoone, Kostan and Sedmond. On the mainland mid-coast Khutzeymateen, Belowe, Ensheshese, Kiskosh and Evelyn were included, although no vegetation data was available from these. Spiders were not collected from Clayoquot,

and carabids and root feeders were not collected from watersheds with low spawning densities on the central coast, and so comparisons were not made for these guilds.

I also assessed seasonal variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in the litter spiders *Cybaeus* spp. collected in spring and fall of 2001 from pitfall traps on the Clatse and Neekas watersheds (Christie et al. submitted). Pitfall traps were located in plots held constant across seasons and located above and below the waterfalls on each watershed. I conducted Nested ANOVA's with the levels watershed, watershed(season) and watershed(season(falls)) using either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ as dependents. Both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were square-root transformed to meet assumptions.

Salmon escapement data has been collected from most watersheds in British Columbia since the late 1940's (for example: Manzon and Marshall 1981). To examine trends in salmon abundance across my study watersheds, I compared chum and pink spawning densities in the 1990's and the 1950's (Wilcoxon rank-sum tests). I conducted separate analyses for each region (Vancouver Island, Mainland Midcoast and Haida Gwaii).

Salmon species (chum or pink) and the legacy of spawning density from the past may be important predictors of $\delta^{15}\text{N}$ isotope signatures in riparian taxa. In a separate analysis for each guild, and one for all guilds combined, I conducted Stepwise Linear Regression with six separate predictor variables (all in kg/m): 1) 90's chum density; 2) 90's pink density; 3) 50's chum density; 4) 50's pink density; 5) 90's salmon density (chum + pink); and 6) 50's salmon density (chum + pink). Stepwise Linear Regression chooses models by 1) maximizing the explained variance (R^2 values) of the overall model; and by 2) removing all models that do not uniquely explain additional variance not accounted for by best first model (criteria for rejection: $p = 0.10$).

9.3.5. Estimating %MDN

Across all study watersheds, I estimated percent marine-derived nitrogen (%MDN) in riparian taxa in an analysis that follows that of Hocking and Reimchen (2002). $\delta^{15}\text{N}$ values in forest biota are influenced by the $\delta^{15}\text{N}$ value of the principal N sources, and fractionation during nitrogen transformations within ecosystems (Nadelhoffer and Fry 1994). Predominant sources of nitrogen to typical forest ecosystems

include atmospheric deposition and biological N_2 fixation, both with $\delta^{15}N$ values near 0‰ (Peterson and Fry 1987). Along salmon spawning streams, fertilization of salmon-derived N ($\delta^{15}N \sim 12\text{‰}$) represents an important alternate source of nitrogen for riparian plants and may be cycled through multiple terrestrial trophic levels (Hocking and Reimchen 2002). Variation in $\delta^{15}N$ signatures in vascular plants within habitats is often attributed to differences in the predominant N source, differences in fractionation during N uptake, and variable plant-mycorrhizal interactions (Nadelhoffer and Fry 1994; Schulze et al. 1994; Michelson et al. 1998; Hobbie et al. 2000; Evans 2001). In salmon-free forest sites, plant tissues can be depleted in $\delta^{15}N$ from atmospheric N_2 by 4‰ or more (Mathewson et al. 2003; Wilkinson et al. 2005). In consumer tissues, $\delta^{15}N$ values are typically enriched by 3-4‰ relative to diet (DeNiro and Epstein 1981; Minigawa and Wada 1984), a pattern that holds true for the litter fauna (Ponsard and Ardit 2000; Scheu and Falca 2000). As such, nitrogen isotope ratios in animals are often used to estimate trophic position (Vander Zanden et al. 2000).

I use a model adapted from Kline et al. (1990) and Helfield and Naiman (2001) and used in Hocking and Reimchen (2002) to estimate %MDN in riparian taxa:

$$3) \%MDN = \left[\frac{Obs - TEM_{Guild}}{MEM - TEM_{Veg}} \right] \times 100\%$$

where *Obs* is the observed $\delta^{15}N$ mean of a particular guild from each watershed, TEM_{Guild} equals the terrestrial end-member of that guild, TEM_{Veg} equals the appropriate vegetation end-member for that guild, and *MEM* equals the marine end-member of salmon tissue. The marine end-member was determined through my own $\delta^{15}N$ measurements of salmon muscle tissue from the Clatse and Neekas watersheds ($n = 7$ for both chum and pink: mean = $12.68 \pm 0.32\text{‰}$). This value is comparable to $\delta^{15}N$ values of 11-14‰ observed from other studies (Welch and Parsons 1993; Ben-David et al. 1998a; Kaeriyama et al. 2004). Terrestrial end-members were determined by calculating the guild mean from control sites close to stream with no spawning salmon (ie. Bulson control watershed, Clatse and Neekas above falls control). Values for TEM_{Guild} equalled 5.41‰ for spiders, 3.11‰ for carabids, 2.00‰ for millipedes, -2.67‰ for root feeders, -1.10‰ for herbs and ferns, -0.81‰ for shrubs, and -3.60‰ for tree needles. These are assumed to be representative baseline values for each guild in the absence of salmon influence. The

TEM_{veg} end-member used depended on the guild entered in the model. For all vegetation guilds the TEM_{veg} equalled the TEM_{Guild} used (eg. in tree needles: $TEM_{veg} = TEM_{Guild} = -3.60\text{‰}$). For all animal guilds the TEM_{veg} used equalled the mean of all vegetation terrestrial end-members (mean $TEM_{veg} = -1.84\text{‰}$). This was done because I do not have $\delta^{15}\text{N}$ values for litter at my sites and the $\delta^{15}\text{N}$ baseline of the litter fauna is likely derived from a range of vegetation sources. I do not use a trophic level correction factor for the marine end-member because I assume that the pattern of $\delta^{15}\text{N}$ enrichment from salmon fertilization is constant across all trophic guilds (see results below to confirm assumption). Because it is possible that plants may fractionate nitrogen in the situation of 100% MDN, I calculated two %MDN estimates based on no fractionation ($MEM_{NF} = 12.68\text{‰}$) and maximum fractionation of 4‰ ($MEM_F = 8.68\text{‰}$). However, fractionation is likely not as marked in nutrient-rich sites such as along salmon streams (Nadelhoffer and Fry 1994; Michelson et al. 1998; Hocking and Reimchen 2002), and for most estimates, the estimate with no fractionation may be more representative (possible exceptions: tree needles, root feeders). This model assumes that trophic level does not differ along the salmon fertilization gradient and that the marine end-member for vegetation $\delta^{15}\text{N}$ values is accurately represented by salmon tissue.

I used ANCOVA's to test for differences in %MDN by spawning density and by guild. I also calculated a guild mean %MDN value for each watershed and conducted a preliminary curve-fit analysis to determine if the relationship between %MDN and spawning density could be better explained by a non-linear function. All %MDN values that were slightly negative were assumed to have a %MDN value of zero but were given a value of 0.001 for use in the curve-fit analysis.

9.4. Results

$\delta^{15}\text{N}$ stable isotope signatures in all riparian taxa increased with increasing salmon spawning density (90's chum + pink) in both Clayoquot Sound on Vancouver Island (Figure 9.2) and on the central coast (Figure 9.3). In Clayoquot Sound and on the central coast, both the fixed factor guild and the covariate salmon spawning density were highly significant predictors of $\delta^{15}\text{N}$ signatures (ANCOVA's: Table 9.3). The guild $\times$ salmon spawning density interaction term was not a significant predictor of $\delta^{15}\text{N}$ indicating that

the slopes for the relationship between $\delta^{15}\text{N}$ and spawning density did not differ by guild. All ANCOVA's with millipedes violated assumptions of equal variances (Levene's $p < 0.05$). When millipedes were removed all tests met assumptions and results were highly comparable (Table 9.3). Overall, the central coast watersheds spanned a much larger gradient in recent salmon spawning density (0-115 kg/m) compared to the Clayoquot watersheds (0-17.5 kg/m).

$\delta^{13}\text{C}$ stable isotope signatures varied by invertebrate guild but did not vary by salmon spawning density among the Clayoquot Sound or central coast watersheds (Clayoquot – guild: $F_{1,5} = 25.77$, $p = 0.004$, $R^2 = 0.838$; salmon density: $F_{1,5} = 0.02$, $p = 0.895$, $R^2 = 0.004$; Central coast – guild: $F_{3,35} = 5.35$, $p = 0.004$, $R^2 = 0.315$; salmon density: $F_{1,35} = 2.73$, $p = 0.107$, $R^2 = 0.072$) (ANCOVA's – assumptions met). No significant interaction terms were observed.

Analysis of seasonal data in guilds presented here suggests that season is not an important predictor of $\delta^{15}\text{N}$ isotope signatures. In taxa collected from watersheds with low salmon spawning densities ($<10\text{kg/m}$), $\delta^{15}\text{N}$ signatures varied by guild (among tree needles, shrubs, herbs and millipedes: $F_{3,37} = 12.01$, $p < 0.001$, $R^2 = 0.493$) but did not vary by season / region of collection ($F_{1,37} = 0.44$, $p = 0.511$, $R^2 = 0.012$). In another experiment, *Cybaeus* spiders collected from the Clatse and Neekas in spring and fall showed no dominant seasonal effects for either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$. $\delta^{15}\text{N}$ signatures in *Cybaeus* varied by watershed ($p < 0.001$) and by falls within season within watershed ($p < 0.001$) but not by season within watershed ($F_{2,80} = 2.89$, $p = 0.061$, $R^2 = 0.067$). $\delta^{13}\text{C}$ signatures in *Cybaeus* varied marginally by watershed ($p = 0.051$) but not by season within watershed ($F_{2,80} = 2.59$, $p = 0.082$, $R^2 = 0.061$) or by falls within season within watershed ($p = 0.116$) (Nested ANOVA's).

Chum spawning density has declined from the 1950's to the 1990's in all but two of my study watersheds on the mainland midcoast and Haida Gwaii (Figure 9.4; Midcoast (8 declining, 1 increasing), Wilcoxon $p = 0.015$; Haida Gwaii (10 declining, 1 increasing), Wilcoxon $p = 0.010$). Declines have been substantial (10-50 kg/m) in eight watersheds. In Clayoquot Sound, chum densities have increased in three of five watersheds. Pink salmon show no dominant trends within regions (all $p > 0.15$) and overall have increased in spawning density in 15 of the 25 watersheds.

In all guilds except shrubs, chum spawning density alone was a better predictor of $\delta^{15}\text{N}$ isotope signatures than the sum of chum and pink spawning biomass or pink density alone (Stepwise Linear Regression Analysis: Table 9.4). Shrubs were best predicted by the sum of chum and pink spawning density in the 50's. The legacy of spawning density from the past was also important predictor of $\delta^{15}\text{N}$ isotope signatures. Within spiders and carabids, as well as across all guilds, the best model was 50's chum spawning density. Herbs, tree needles and millipedes were best predicted by 90's chum spawning density. Across all study watersheds, guild and 50's chum density were important predictors of $\delta^{15}\text{N}$ (both $p < 0.001$) with no significant interaction term (ANCOVA: $F_{6,84} = 0.12$, $p = 0.993$, $R^2 = 0.009$) (Figure 9.5).

Estimates of %MDN in riparian taxa varied from a low of zero to a high of 100% in millipedes from Bag Harbour depending on the extent of fractionation from the source nitrogen. %MDN was predicted by salmon density with no differences in the slope or intercept of this relationship by guild. Using the covariate of either 50's chum or 90's chum + pink spawning density, MDN varied by salmon density (ANCOVA: $F_{1,84} > 51.9$, $p < 0.001$, $R^2 > 0.38$), but did not vary by guild ($p > 0.74$) or the interaction between guild and salmon spawning density ($p > 0.97$). Guild means across all watersheds varied from 0% MDN in several watersheds to 56.4-77.8% MDN at Bag Harbour depending on the extent of fractionation (Table 9.5). In a preliminary curve fit analysis, I find that a logarithmic function predicts %MDN better than using a linear approach when 50's chum density is used as the predictor variable (Table 9.6; Figure 9.6). This suggests that the relationship between %MDN and salmon density may be non-linear and asymptotic. However, when recent density (chum + pink) was used the linear function was comparable or more robust than other models (Table 9.6).

9.5. Discussion

I demonstrate isotopic evidence for incorporation of marine-derived nitrogen (MDN) into seven guilds of riparian plants and invertebrates from multiple watersheds in coastal British Columbia. The extent of uptake of MDN was strongly predicted by salmon spawning density (kg salmon per meter of stream length), with no differences in the pattern of enrichment among guilds or regions.

Following Hocking and Reimchen (2002), the two possible pathways whereby salmon-nitrogen could enter terrestrial food-webs include: 1) direct consumption of salmon tissues and/or predation of direct salmon consumers; or 2) indirect enrichment through marine-derived nitrogen fertilization of soil and vegetation N pools. Plants living along salmon streams have been previously demonstrated to take up salmon-nitrogen with estimates of %MDN in foliar tissue ranging from 12-60% (Bilby et al. 1996; Hilderbrand et al. 1999b; Helfield and Naiman 2001; Bilby et al. 2003; Mathewson et al. 2003). In animals, direct consumption of salmon tissues would lead to enriched signatures of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. For example, consumption of salmon carcasses by blowflies (Calliphoridae) and burying beetles (Silphidae) has been documented through the dual isotope method (Reimchen et al. 2003; Hocking et al. *in press*). In this study, I deliberately chose invertebrate taxa that did not have a dominant direct relationship with salmon carcasses. The observation of parallel slopes of $\delta^{15}\text{N}$ enrichment across the salmon density gradient in both plant and animal guilds, coupled with the absence of $\delta^{13}\text{C}$ enrichment in animals, confirms the dominance of the nitrogen fertilization pathway and indirect enrichment in riparian invertebrates. This pathway has been observed in small mammals (Ben-David et al. 1998b) and multiple trophic levels of terrestrial invertebrates (Hocking and Reimchen 2002), whereby individuals were enriched in $\delta^{15}\text{N}$ but not $\delta^{13}\text{C}$. This result is also supported by studies in non-salmon systems where $\delta^{15}\text{N}$ values in litter biota are known to parallel those of the litter and soil across multiple sites (Ponsard and Arditi 2000; Sheu and Falca 2000).

Across multiple watersheds, the subsidy of Pacific salmon to terrestrial habitats likely varies as a consequence of three major factors. This includes the presence of a) vertebrate predators such as bears that actively distribute carcasses and nutrients into the forest (Reimchen 1994; Ben-David et al. 1998a, 1998b; Hilderbrand et al. 1999b; b) high density salmon spawning so that transfer and selective foraging is facilitated (Reimchen 2000; Gende et al. 2001); and c) further consumption and distribution of salmon nutrients by terrestrial invertebrates (Reimchen 1994; Cederholm et al. 2000; Meehan et al. 2005). In situations where salmon spawn at low densities, or when salmon are not easily accessible, vertebrate consumption of captured fish may approach 100% with few 'surplus' remnants distributed to riparian zones (Reimchen 1992, 1994; Quinn and

Kinnison 1999; Gende et al. 2001). In these cases, transfer of marine-derived nutrients to forests may be spatially limited to areas of high wildlife activity; for example, urine and feces deposition along bear trails (Hilderbrand et al. 1999b). When salmon are accessible in small streams and reaches, or when spawning density is high, vertebrate predators selectively forage on energy-rich portions of the fish including the brain and/or head, roe and dorsal musculature (Reimchen 2000; Gende et al. 2001; Gende et al. 2004b). When bear density is also high, this invokes dominant-subdominant relationships among bears and high transfer of carcasses due to conspecific avoidance (Reimchen 2000; Ben-David et al. 2004; Gende and Quinn 2004).

Salmon carcasses and remnants distributed to forest habitats are dominated by many invertebrate scavengers, although from a biomass perspective this primarily includes the terrestrial Diptera (Reimchen 1994; Cederholm et al. 2000; Jauquet et al. 2003; Reimchen et al. 2003; Meehan et al. 2005). Fly maggots are highly competitive on salmon carcasses and represent an important further vector of salmon nutrients and energy to terrestrial habitats. Aggregations of flies and other invertebrates attract an array of predators including songbirds, small mammals, amphibians, predaceous beetles and parasitic wasps, and this ultimately increases the diversity and productivity of the riparian zone (Reimchen 1994; Cederholm et al. 2000; Helfield and Naiman 2001; Gende et al. 2002; Reimchen et al. 2003; Wilkinson et al. 2005; Christie et al. submitted). As a consequence, high $\delta^{15}\text{N}$ signatures in riparian biota are likely a good indicator of important ecological processes within watersheds. For high $\delta^{15}\text{N}$ signatures to occur in species that do not have a dominant direct relationship with the carcasses, transfer vectors such as bears must be present and salmon need to be spawning at densities that are sufficient to facilitate transfer and selective foraging (Reimchen 2000; Gende et al. 2001).

In six of seven guilds, as well as all guilds taken together, chum salmon density was a better predictor of $\delta^{15}\text{N}$ signatures in riparian biota than pink density or the sum of the densities of the two species. In western Washington, Bilby et al. (2003) found higher $\delta^{15}\text{N}$ enrichment in riparian plants along a chum spawning stream compared to a stream dominated by coho salmon. Chum, pink and sockeye salmon tend to spawn in large aggregations which facilitate wildlife predation and transfer, as opposed to steelhead and coho which spawn at lower densities (Bilby et al. 2003). However, the dominance of

chum in predicting $\delta^{15}\text{N}$ in this study is likely due to widespread preferences by bears for chum as potential prey over pink due to higher net energy gain (Reimchen 2000). Several studies have observed size-selective mortality in salmon, as bear-killed fish were larger than those dying of senescence (Quinn and Kinnison 1999; Quinn and Buck 2001). Further evidence for this is that male salmon are often killed at higher frequency than females, an observation that is attributed to their larger size (Quinn and Kinnison 1999; Reimchen 2000). Chum salmon are 3-4 times larger than pink, and have predation rates that can range from 40-70% (Reimchen 2000; Gende et al. 2004a). Large-bodied chum have also been observed to be transferred furthest into the forest (Reimchen 2000).

Another reason why chum salmon density may better predict $\delta^{15}\text{N}$ signatures in riparian biota is that carcass size is an important determinant of the insect community on carrion (Kneidel 1984; Hanski 1987). The blowflies (Calliphoridae) may be particularly favoured on large carcasses due to their high reproductive output, growth rates and overall competitive ability (Williams and Richardson 1984). The deposition of large chum carcasses thus favours colonization by blowflies and the further spread of marine-derived nutrients and energy in terrestrial habitats (Reimchen 1994).

Pacific salmon have been returning to spawn in coastal streams and lakes for hundreds or perhaps thousands of years (Finney et al. 2000; 2002). Given that salmon nutrients have been fertilizing coastal riparian zones year after year, it might be expected that $\delta^{15}\text{N}$ signatures in the local biota reflect some integrated rate of transfer over the past few decades or centuries. Typical terrestrial sources of nitrogen with $\delta^{15}\text{N}$ signatures near 0‰ include atmospheric deposition and biological N_2 fixation (Nadelhoffer and Fry 1994). Continued inputs of these sources would likely decrease riparian $\delta^{15}\text{N}$ signatures if salmon nutrient transfer suddenly fell to zero. However, recent research in central Idaho, where salmon have been in sharp decline for 30 years, has revealed persistent salmon signatures in riparian plants (Koyama et al. 2005). This finding emphasizes that the legacy of spawning density from the past influences current isotopic signatures. I find that chum spawning density in the 1950's best predicts $\delta^{15}\text{N}$ in spiders and carabid beetles, as well as in all guilds taken together. In many of my study watersheds, chum density in particular has declined over the last 50 years. This result is paralleled by recent observations of declines in salmon escapement in small chum-bearing systems on the

central and north coasts of British Columbia (Harvey and MacDuffee 2002; Godbout et al. 2004; Spilsted 2004). Overall, bear transfer of chum salmon to coastal forests was likely higher in the past in many watersheds, a process with a legacy that is still evident in the $\delta^{15}\text{N}$ signatures of riparian biota living today.

Variation in $\delta^{15}\text{N}$ in biota within watersheds may reflect either seasonal or spatial variation in the extent of the salmon subsidy, or individual dietary shifts (Hocking and Reimchen 2002; Hocking et al. *in press*). Seasonal comparisons in this study suggest that season of collection of biota, in spring or fall (in tree needles, shrubs, herbs, millipedes and spiders), is not a strong predictor of $\delta^{15}\text{N}$ signatures. This result supports the previous finding of the historical legacy of spawning density, as one spawning event in the autumn may not immediately or dramatically alter the $\delta^{15}\text{N}$ balance of the watershed as a whole. This contrasts with animals that have a direct diet of salmon, whereby upon prey switch, higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures are detectable in predator tissues (Darimont and Reimchen 2002; Christie et al. *submitted*).

Spatial variation of $\delta^{15}\text{N}$ in plants and litter fauna is widespread at scales of kilometres to a few meters. In non-salmon systems, $\delta^{15}\text{N}$ in the litter fauna covaries with that of the soil and vegetation at the stand scale (Ponsard and Arditi 2000; Sheu and Falca 2000), while in salmon systems, $\delta^{15}\text{N}$ signatures can vary depending on local rates of transfer and sites with high wildlife activity (Hilderbrand et al. 1999b; Hocking and Reimchen 2002; Wilkinson et al. 2005). For example, mosses showed highest $\delta^{15}\text{N}$ enrichment near salmon carcass remnants, followed by bear trails and then random sites (Wilkinson et al. 2005), while invertebrates showed highest $\delta^{15}\text{N}$ along spawning reaches with the highest transfer (Hocking and Reimchen 2002). In fact, patterns of transfer and $\delta^{15}\text{N}$ enrichment across watersheds may also occur within watersheds at small spatial scales. In this study, plant and invertebrate specimens were sampled from fairly discrete sites within watersheds that may not be representative of the spawning density of the watershed as a whole. This helps explain some of the error variance in my %MDN estimates. For example, Bag Harbour specimens were likely collected in sites with very high local transfer (MDN = 56-78%), while specimens collected from Belowe and Kiskosh creeks may have been from sites with no transfer (MDN = 0%).

Because the pattern of $\delta^{15}\text{N}$ enrichment across the salmon density gradient was the same in all guilds (ie. their slopes did not differ), all taxa have similar uptake of MDN. The majority of $\delta^{15}\text{N}$ variation among guilds was thus accounted for by trophic position (animals: Vander Zanden et al. 2000), and by nitrogen source and fractionation processes (plants: Evans 2001). Individual guild means then represented replicate estimates of %MDN within watersheds. Previous estimates of %MDN in riparian biota have ranged to as high as 72% (Hocking and Reimchen 2002), values that are encompassed within this study.

Overall, it is possible that the relationship between %MDN and salmon spawning density is non-linear and asymptotic. For example, %MDN values should never exceed 100%. Furthermore, processes such as density-dependent predation and salmon carcass consumption by bears (Reimchen 2000; Gende et al. 2001; Quinn et al. 2003), and size-dependent colonization of carcasses by invertebrates (Kneidel 1984), may generate non-linear relationships between %MDN (or $\delta^{15}\text{N}$) and salmon density. In a curve-fit analysis, I find that a logarithmic response curve explains more variance in %MDN than a linear model using 50's chum spawning density as the predictor variable. Although determining the ultimate 'best model' requires more data from many additional watersheds, this result suggests that inputs of MDN to terrestrial habitats increase sharply from low to medium densities (0-20kg/m) and saturate at higher densities (>20kg/m).

Because it is likely that high $\delta^{15}\text{N}$ or %MDN values in riparian biota indicate intact ecosystem processes (high spawning density, transfer by predators, invertebrate activity), either currently or in the past, this knowledge can be used for determining watersheds with high priority for conservation. Small chum and pink systems throughout the coast can be easily overlooked because their run-size and watershed-area is small relative to overall regional returns (Harvey and MacDuffee 2002). I demonstrate here that it is small chum-bearing streams which support the highest density of salmon spawning and highest rates of carcass and nutrient transfer into the adjacent forest. This result parallels other marine-terrestrial fluxes where small islands with high perimeter/area ratios support high productivity and biota with a strong dependency on marine resources (Polis and Hurd 1996). Watersheds in this study that currently support medium to strong returns of chum salmon (>6kg/m) and should be considered highest priority for

conservation include Warn Bay and Watta creeks in Clayoquot Sound, the Clatse and Neekas rivers on the mainland midcoast, and Bag Harbour, Salmon, Harriet and Government creeks on Haida Gwaii. %MDN estimates in these watersheds varied from 16.6-22.9% at Watta to 56.4-77.8% at Bag Harbour, and management programs that maintain or increase current chum spawning densities will likely retain critical ecosystem processes generated by the salmon-bear-forest linkage.

Many small systems on the central and north coasts of B.C. have experienced declines in chum escapement, followed by replacement by pink (Godbout et al. 2004; Spilsted 2004; Reimchen pers. comm.). Strongly pink-dominated systems such as the Kumuleon and Kiskosh rivers on the mainland midcoast, and Echo and Skedans creeks on Haida Gwaii, showed low to zero %MDN values in riparian biota despite recent pink spawning densities of 6-29 kg/m. This means that the transfer of salmon nutrients to riparian forests is substantially reduced in pink systems, and emphasizes the keystone role of bears and the interaction between salmon density, bear density and fish size (ie. energetic reward) in predicting transfer (Reimchen 2000). Study watersheds that have reduced chum escapement since the 1950's include Belowe, Kiskosh, Tillhorn and Evelyn creeks on the central coast, and Sedmond, Louscoone, Echo, Mathiesen and Koston creeks on Haida Gwaii. An important focus for these and other comparable systems should be chum recovery.

9.6. Conclusion

I find that salmon-spawning density, and in particular the density of chum spawners, strongly predicts $\delta^{15}\text{N}$ stable isotope signatures and %MDN values in multiple guilds of riparian plants and invertebrates. Patterns of enrichment indicate that this is an indirect process through marine-nitrogen fertilization of coastal riparian zones, although levels of enrichment indicate intact ecosystem processes. These include the presence of wildlife transfer vectors such as bears, sufficient spawning densities to facilitate selective foraging, and the further consumption and distribution of salmon nutrients by terrestrial invertebrates. Although I do not directly demonstrate it here, these processes are known to influence multiple terrestrial trophic levels, including increased primary productivity, shifts in plant, invertebrate and songbird community structure, and increases in overall

riparian diversity and carrying capacity (Reimchen 1994; Willson and Halupka 1995; Cederholm et al. 2000; Gende and Willson 2001; Helfield and Naiman 2001; Hocking and Reimchen 2002; Mathewson et al. 2003; Wilkinson et al. 2005; Christie et al. *submitted*). The observation that small chum-bearing systems support the highest transfer and dependency on marine resources is also comparable to other studies along the marine-terrestrial ecotone which have found high primary and secondary productivities on small islands from the deposition of carcasses and nutrients of seabirds and onshore drift of sea wrack (Polis and Hurd 1995, 1996; Markwell and Daugherty 2002).

If $\delta^{15}\text{N}$ values can be used to indicate intact ecosystem processes then it is possible to set escapement goals that meet system requirements (Bilby et al. 2001). Using data presented here, chum-spawning densities that maximize the flux of marine nutrients and energy to terrestrial habitats occur at values of 20kg/m or more. Systems with densities that are this high should be considered top priority for conservation. In addition, watersheds with densities of 5-10kg/m support rapidly increasing rates of transfer and forest fertilization. As such, densities of 5kg/m or greater could be used as a guideline for future management of salmon escapement and whole-watershed restoration and conservation. If one chum weighs 5kg then this means that 1000 chum per kilometre of spawning may be a minimum value for supporting vertebrate wildlife and ecosystem processes associated with the salmon-forest subsidy. Although I focus on chum and pink dominated systems in coastal British Columbia, this analysis may apply to other salmon species, particularly high density sockeye-grizzly associations throughout British Columbia, Alaska and Russian Kamchatka (Hilderbrand et al. 1999b; Gende et al. 2001; Quinn and Buck 2001).

When the ecological effects of the salmon subsidy in both aquatic and terrestrial habitats are considered, the concept of 'excess salmon production' above which is required to produce the next generation becomes meaningless (Willson et al. 1998). In the southern part of their range, massive reductions in salmon escapement have caused nutrient deficits that threaten whole communities (Gresh et al. 2000; Stockner 2003). In Alaska, consistent reductions in sockeye returns to lakes have been observed over the last century (Finney et al. 2000), while on the central coast of British Columbia recent declines in small streams that support chum salmon represent a concern directly related to

this study (Harvey and MacDuffee 2002; Godbout et al. 2004; Spilsted 2004). In my study watersheds the $\delta^{15}\text{N}$ signatures of current-day riparian taxa indicate a 'legacy of process' directly related to higher chum salmon spawning densities in the past.

Overall, the scope of this marine-terrestrial linkage supports the landscape perspective of food-web dynamics (Polis et al. 1997) and the concept of ecosystem interdependence (Moore et al. 2003). This worldview not only provides insight into global food-web structure and function but gives a clear message for conservation – i.e. the preservation of critical habitats, species and processes.

Figure 9.1. Study watersheds in coastal British Columbia, including Clayoquot Sound on Vancouver Island: 1) Bulson, 2) Warn Bay, 3) Moyeha, 4) Watta, 5) Megin, 6) Sidney; and central coast watersheds including Haida Gwaii: 7) Clatse, 8) Neekas, 9) Evelyn, 10) Tillhorn, 11) Kiskosh, 12) Belowe, 13) Kumuleon, 14) Ensheshese, 15) Khutzeymateen, 16) Government, 17) Skedans, 18) Salmon, 19) Echo, 20) Kostan, 21) Windy Bay, 22) Mathiesen, 23) Bag Harbour, 24) Harriet, 25) Sedmond, 26) Louscoone.

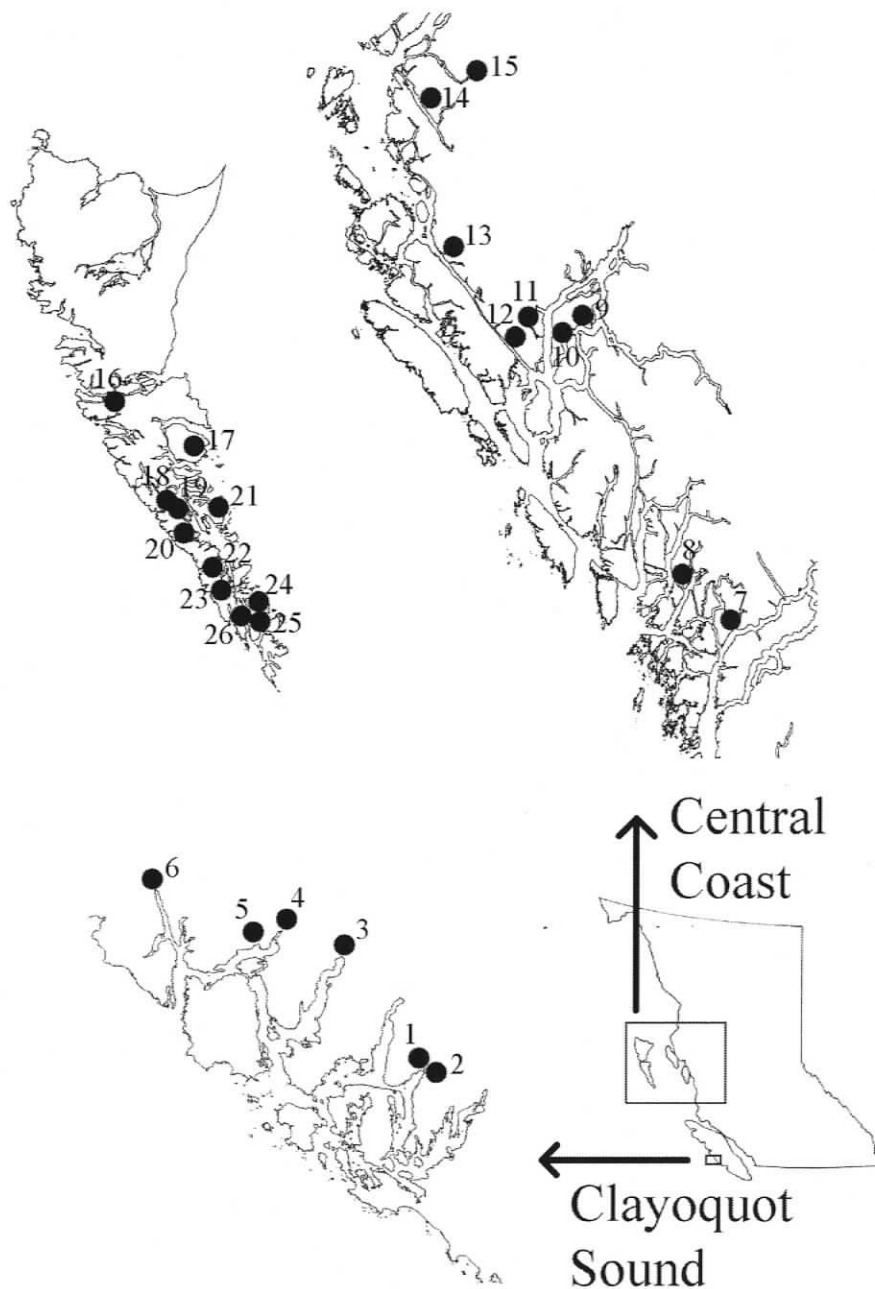


Figure 9.2. $\delta^{15}\text{N}$ stable isotope signatures in riparian taxa are predicted by salmon spawning densities (kg fish/m of stream) from six watersheds in Clayoquot Sound, on Vancouver Island, B.C. Salmon density equals the mean escapement of chum and pink salmon in the 1990's.

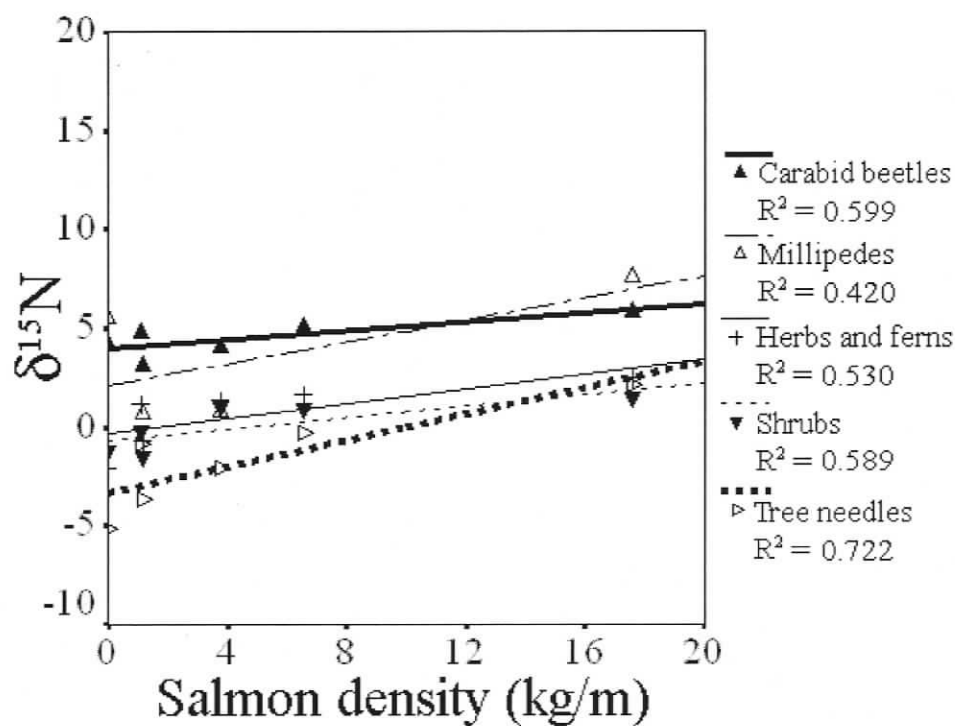


Figure 9.3. $\delta^{15}\text{N}$ stable isotope signatures in riparian taxa are predicted by salmon spawning densities (kg fish/m of stream) from multiple watersheds on the central coast of B.C. including the mainland and Haida Gwaii. Salmon density equals the mean escapement of chum and pink salmon in the 1990's.

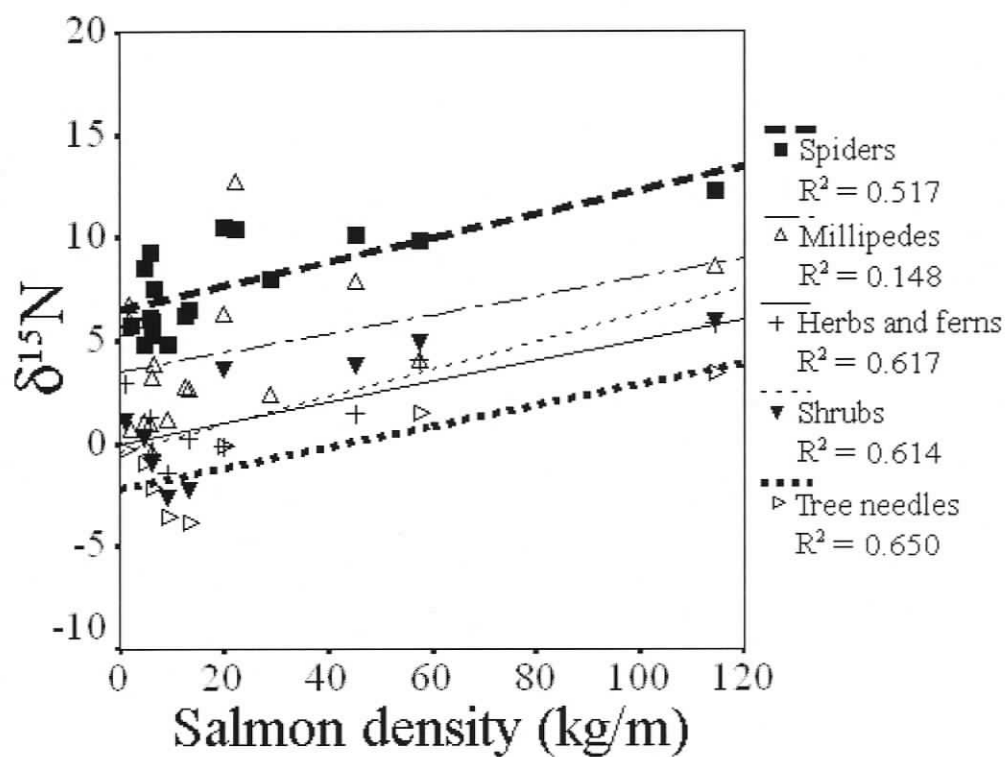


Figure 9.4. Chum salmon spawning density (kg/m) differences in British Columbia study watersheds from the 1950's to 1990's. Watersheds are ranked by spawning density within region of collection.

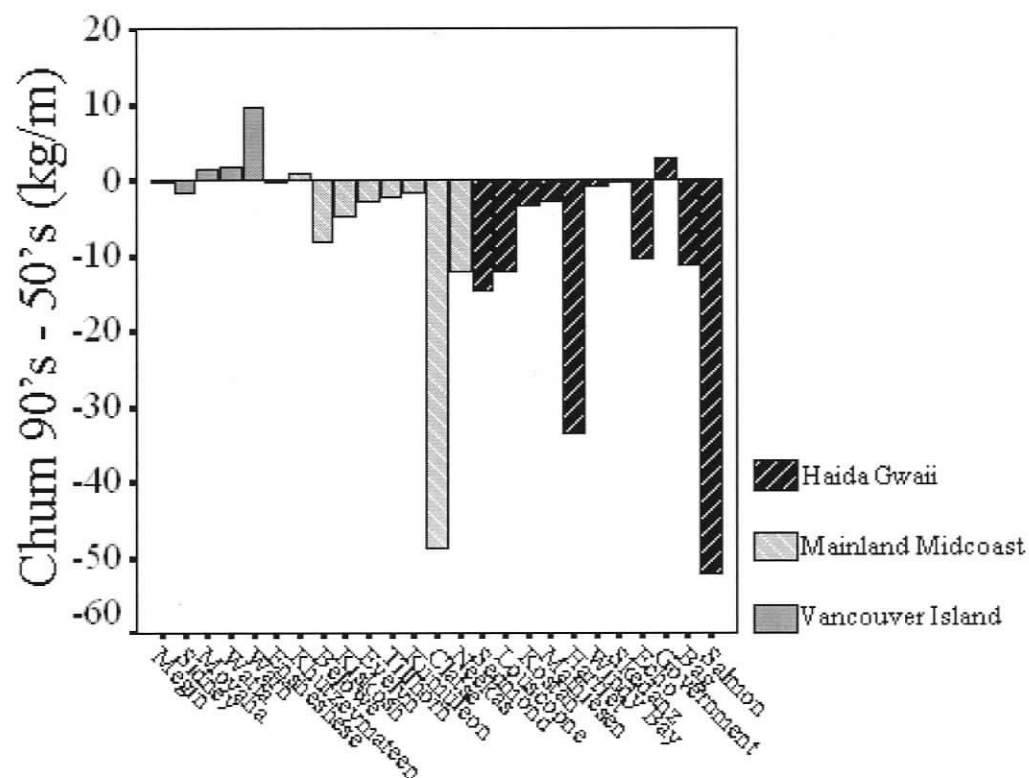


Figure 9.5. $\delta^{15}\text{N}$ stable isotope signatures in riparian taxa as predicted by mean 50's chum spawning densities (kg fish/m of stream) from multiple watersheds in British Columbia, including the Clayoquot Sound on Vancouver Island, the mainland mid-coast and Haida Gwaii.

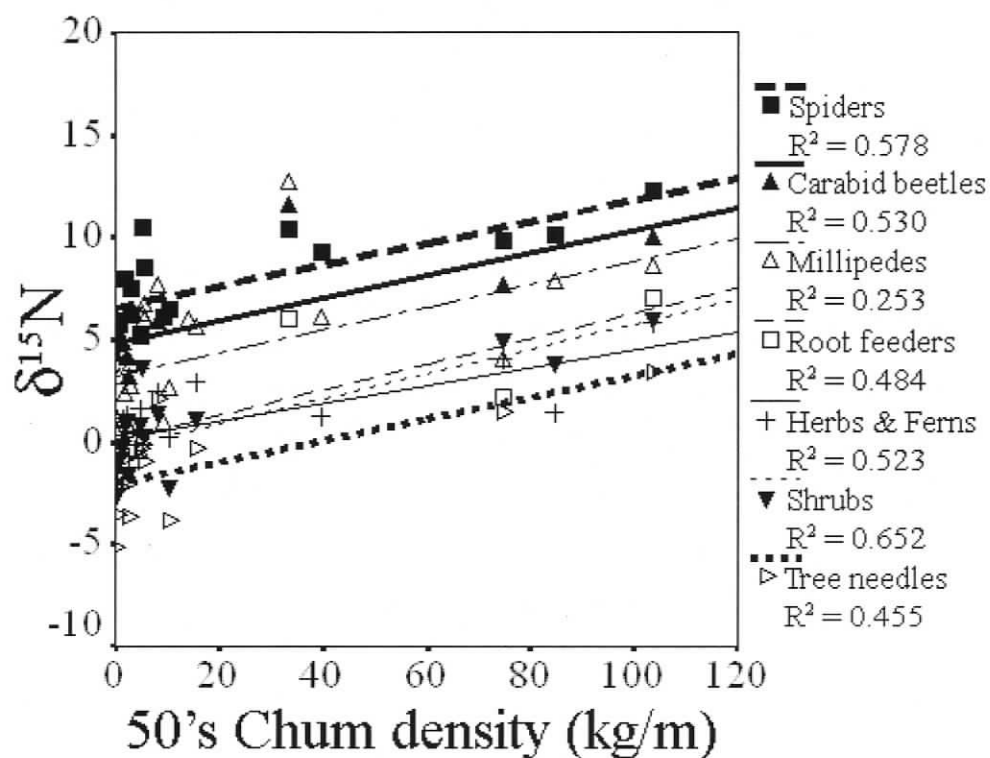


Figure 9.6. Estimates of percent marine-derived nitrogen (%MDN) in riparian plants and invertebrates from multiple watersheds in coastal British Columbia that vary in chum salmon spawning density (kg/m) from the 1950's (see Table 9.5). Individual data points represent guild means from each watershed. Two MDN estimates are shown: a low estimate based on no plant fractionation from the salmon source ($MEM_{NF} = 12.68\text{‰}$); and a high estimate based on plant fractionation of 4‰ ($MEM_F = 8.68\text{‰}$) (see methods). Logarithmic models ($Y = a + b \cdot \ln(X)$) are used to fit the data.

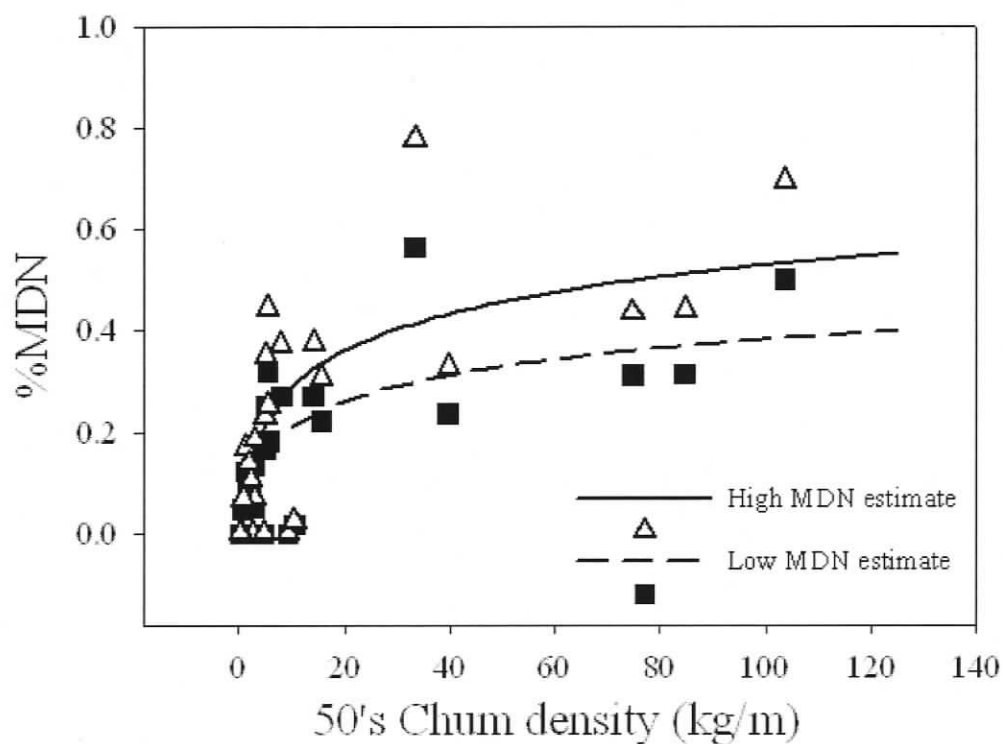


Table 9.1. Guild and species classification within this study.

Guild	Family	Species
1) Spiders	Agelenidae	<i>Cybaeus</i> spp. (<i>C. reticulatus</i> & <i>C. eutypus</i>)
2) Carabids	Carabidae	<i>Pterostichus</i> spp. (<i>P. crenicollis</i> , <i>P. algidus</i> , <i>P. amethystinus</i>)
3) Millipedes	Parajulidae	Unknown
	Xystodesmidae	<i>Harpaphe haydeniana</i>
4) Root Feeders	Curculionidae	<i>Steremnius carinatus</i> <i>Steremnius tuberosus</i>
5) Herbs & Ferns	Aspleniaceae	<i>Athyrium filix-femina</i> <i>Dryopteris expansa</i> <i>Polystichum munitum</i>
	Blechnaceae	<i>Blechnum spicant</i>
	Liliaceae	<i>Maianthemum dilatatum</i>
	Polypodiaceae	<i>Polypodium glycyrrhiza</i>
	Ranunculaceae	<i>Trautvetteria caroliniensis</i>
6) Shrubs	Araliaceae	<i>Oplopanax horridus</i>
	Ericaceae	<i>Gaultheria shallon</i> <i>Menziesia ferruginea</i> <i>Vaccinium alaskaense</i> <i>Vaccinium parvifolium</i>
	Rosaceae	<i>Rubus spectabilis</i>
7) Tree needles	Pinaceae	<i>Picea sitchensis</i> <i>Tsuga heterophylla</i>

Table 9.2. Chum and pink salmon escapement and average spawning densities (kg/m) in the 1990's (Department of Fisheries and Oceans data) from my study watersheds in coastal British Columbia. Watersheds are ranked by spawning density within regions.

Watershed	Region	Distance	Mean Escapement (90's)		Spawning Density (kg/m)	
		Spawning (m)	Chum	Pink	Chum	Pink
Bulson	Vancouver Island	0	0	0	0	0
Megin	Vancouver Island	25300	5345	8	1.12	0
Sidney	Vancouver Island	2300	503	3	1.16	0
Moyaha	Vancouver Island	10600	7544	39	3.77	0.01
Watta	Vancouver Island	1700	2107	4	6.57	0
Warn Bay	Vancouver Island	1400	4638	34	17.56	0.05
Ensheshese	Mainland midcoast	11400	1027	9700	0.48	1.62
Khutzymateen	Mainland midcoast	25200	6250	46500	1.31	3.51
Belowe	Mainland midcoast	1800	388	4517	1.14	4.77
Kiskosh	Mainland midcoast	1500	48	4758	0.17	6.03
Evelyn	Mainland midcoast	1700	54	5807	0.17	6.49
Tillhorn	Mainland midcoast	90	14	567	0.82	11.97
Kumuleon	Mainland midcoast	2100	74	32000	0.19	28.95
Clatse	Mainland midcoast	900	4433	14960	26.11	31.58
Neekas	Mainland midcoast	1700	29270	20738	91.25	23.18
Sedmond	Haida Gwaii	2400	417	392	0.92	0.31
Louscoone	Haida Gwaii	2100	774	30	1.95	0.03
Kostan	Haida Gwaii	900	335	6	1.97	0.01
Mathiesen	Haida Gwaii	2200	1142	2330	2.75	2.01
Harriet	Haida Gwaii	833	934	0	5.94	0
Windy Bay	Haida Gwaii	6000	6	20100	0.01	6.37
Skedans	Haida Gwaii	4800	0	23143	0	9.16
Echo	Haida Gwaii	350	5	2456	0.08	13.33
Government	Haida Gwaii	3100	4721	19502	8.07	11.95
Bag Harbour	Haida Gwaii	800	3340	73	22.13	0.17
Salmon	Haida Gwaii	1600	9813	10640	32.51	12.64

Table 9.3. Analysis of covariance (ANCOVA) of $\delta^{15}\text{N}$ stable isotope signatures (dependent) in multiple guilds of riparian plants and invertebrates (fixed factor) collected from watersheds throughout British Columbia that vary in chum and pink salmon spawning density (kg/m) (covariate). When millipedes are excluded tests meet assumptions of equal variances.

Region	Factor	Millipedes	df	F	P	R ²
Clayoquot	Salmdens (kg/m)	Yes	1,18	20.22	<0.001	0.529
	Guild		4,18	11.55	<0.001	0.720
	Interaction		4,18	0.80	0.540	0.151
Clayoquot	Salmdens (kg/m)	No	1,16	24.90	<0.001	0.609
	Guild		3,16	24.92	<0.001	0.824
	Interaction		3,16	1.62	0.225	0.233
Midcoast	Salmdens (kg/m)	Yes	1,53	33.74	<0.001	0.389
	Guild		4,53	17.80	<0.001	0.573
	Interaction		4,53	0.16	0.959	0.012
Midcoast	Salmdens (kg/m)	No	1,35	48.78	<0.001	0.582
	Guild		3,35	39.49	<0.001	0.772
	Interaction		3,35	0.22	0.881	0.019
All watersheds	Salmdens (kg/m)	Yes	1,84	51.40	<0.001	0.380
	Guild		6,84	19.59	<0.001	0.583
	Interaction		6,84	0.12	0.994	0.008
All watersheds	Salmdens (kg/m)	No	1,62	64.01	<0.001	0.508
	Guild		5,62	31.48	<0.001	0.717
	Interaction		5,62	0.17	0.974	0.013

Table 9.4. Stepwise Linear Regression analysis of $\delta^{15}\text{N}$ stable isotope signatures in multiple guilds of riparian plants and invertebrates collected from watersheds throughout British Columbia that vary in chum and pink salmon spawning density (kg/m). Predictors of $\delta^{15}\text{N}$ included 1) 90's chum density; 2) 90's pink density; 3) 50's chum density; 4) 50's pink density; 5) 90's salmon density (chum + pink); and 6) 50's salmon density (chum + pink). In all cases only one model was retained and five were excluded (criteria for rejection: $p = 0.10$).

Guild	Model retained (kg/m)	df	F	P	R ²
Spiders	50's chum density	1,15	20.56	<0.001	0.578
Carabids	50's chum density	1,7	7.88	0.026	0.530
Millipedes	90's chum density	1,22	8.10	0.009	0.269
Herbs + Ferns	90's chum density	1,13	16.95	0.001	0.566
Shrubs	50's salmon density	1,13	25.68	<0.001	0.664
Tree needles	90's chum density	1,12	12.33	0.004	0.507
All guilds	50's chum density	1,96	25.10	<0.001	0.207

Table 9.5. Chum and pink salmon spawning densities from the 1950's and estimates of % marine-derived nitrogen (%MDN) in riparian forest taxa from watersheds throughout coastal British Columbia. Watersheds are ranked by 50's chum density. %MDN_{NF} refers to estimates with no fractionation while %MDN_F refers to estimates with fractionation from original source of 4‰ (see methods). MDN estimates are an average of guild means from each watershed.

Watershed	Region	50's Spawning Density (kg/m)			% MDN _{NF}	% MDN _F	# of guilds
		Chum	Pink	Sum			
Bulson	Vancouver Island	0.00	0.00	0.00	0.0	0.0	6
Skedans	Haida Gwaii	0.30	11.01	11.31	0.0	0.0	5
Khutzymateen	Mainland midcoast	0.52	1.14	1.66	0.0	0.0	2
Ensheshese	Mainland midcoast	0.68	0.95	1.63	0.0	0.0	2
Windy Bay	Haida Gwaii	0.80	4.82	5.61	5.0	6.8	5
Megin	Vancouver Island	1.42	0.01	1.44	12.4	17.0	4
Kumuleon	Mainland midcoast	1.83	17.91	19.74	10.1	13.9	2
Moyaha	Vancouver Island	2.33	0.03	2.35	7.6	10.6	5
Sidney	Vancouver Island	2.72	0.00	2.72	0.0	0.0	5
Tillhorn	Mainland midcoast	2.94	3.17	6.11	5.1	7.0	2
Evelyn	Mainland midcoast	3.12	9.95	13.06	13.5	18.6	2
Kiskosh	Mainland midcoast	4.89	13.93	18.82	0.0	0.0	2
Watta	Vancouver Island	4.99	0.00	4.99	16.6	22.9	4
Government	Haida Gwaii	5.18	11.36	16.54	25.3	35.0	5
Kostan	Haida Gwaii	5.49	0.09	5.58	32.1	44.3	1
Mathiesen	Haida Gwaii	5.60	1.08	6.68	18.4	25.2	4
Warn	Vancouver Island	8.01	0.00	8.01	27.1	37.3	5
Belowe	Mainland midcoast	9.41	4.54	13.95	0.0	0.0	2
Echo	Haida Gwaii	10.52	0.00	10.52	1.8	2.5	5
Louscoone	Haida Gwaii	14.12	0.68	14.80	27.3	37.6	1
Sedmond	Haida Gwaii	15.62	0.00	15.62	22.2	30.8	4
Bag	Haida Gwaii	33.26	0.00	33.26	56.4	77.8	4
Harriet	Haida Gwaii	39.58	0.09	39.67	23.7	32.9	3
Clatse	Mainland midcoast	74.79	61.96	136.75	31.4	43.5	7
Salmon	Haida Gwaii	84.63	6.90	91.54	31.5	44.0	4
Neekas	Mainland midcoast	103.51	39.06	142.57	50.1	69.3	7

Table 9.6. Curve-fit regression analysis of percent marine-derived nitrogen (%MDN) in riparian taxa as predicted by either 50's chum salmon spawning density or 90's chum + pink spawning density (kg/m).

Model	50's Chum density (kg/m)			90's Chum + Pink density (kg/m)		
	F	P	R²	F	P	R²
Linear	19.13	0.0002	0.454	11.86	0.0022	0.340
Quadratic	11.88	0.0003	0.519	5.87	0.0091	0.348
Cubic	11.16	0.0001	0.615	3.74	0.0269	0.348
Logistic	6.39	0.0188	0.217	4.22	0.0514	0.155
Logarithmic	29.46	<0.0001	0.562	6.21	0.0204	0.212

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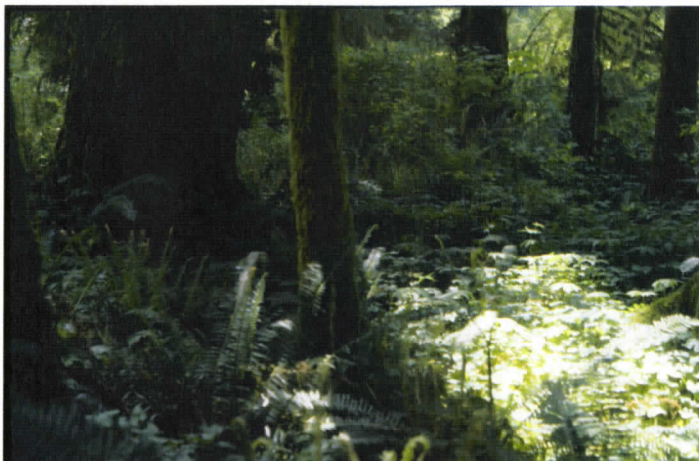
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11. Appendix 1

Sample photographs

1a. Riparian zone of Watta Creek, Clayoquot Sound (May 2000). Some of my first observations of the richness of the Salmon-Forest.



1b. First camp in the Clatse estuary (August 2000).



1c. Transects on the Clatse River (August 2000)



1d. Mike Windsor of the Heiltsuk standing atop the Clatse waterfall (August 2000).



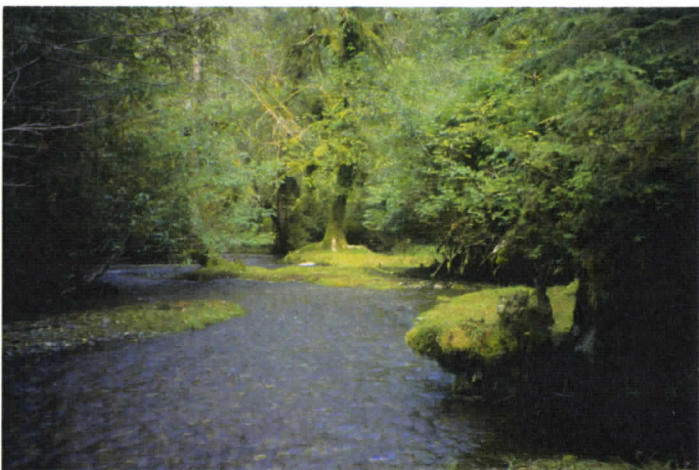
1e. Tom Reimchen and Dan Klinka on the Khutzeymateen River (September 2000).



1f. Morgan Hocking collecting soil invertebrates (boat trip, September 2000).



1g. The beautiful Salmon River, Moresby Island, Haida Gwaii (September 2000).



1h. Maggotized salmon carcass (Fall 2000)



1h. Gulls and salmon carcasses: Neekas River estuary (October 2002)



1i. Spring algae bloom – same spot as above photo, Neekas River estuary



1j. Northern Rice root – Clatsop River estuary. Pollinated by carrion flies and beetles



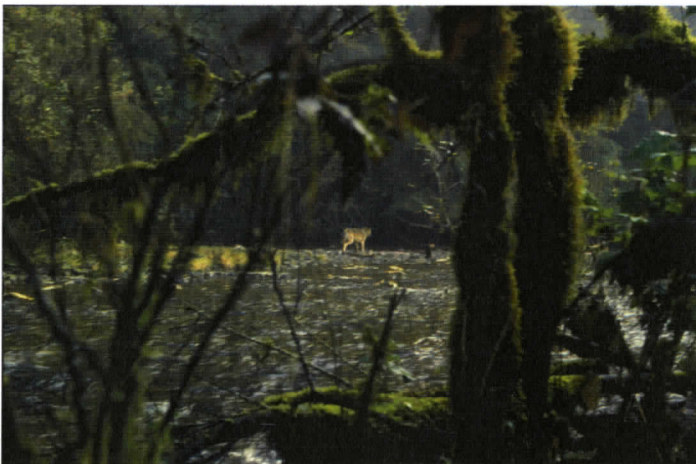
1k. Big pink return – Neekas River (September 2002).



1l. Mike Windsor, Morgan Hocking and a loaded Flatulus – Clatse River estuary



1m. Wolf running away from me after feeding on chum – Clatse River



1n. Fly maggots and a parasitic wasp on a decaying chum salmon – Neekas River



1o. The parasitic wasps *Atractodes* sp. (Ichneumonidae) (left) and *Alysia alticola* (Braconidae) (right)



1p. Body size and elytral colour variation in *Nicrophorus investigator* and *N. defodiens*

