Linking salmon and birds: how salmon-derived nutrients influence the diet and density of birds on streams of the Pacific Northwest

By

Katie Christie
B.Sc. University of Victoria, 2000

A thesis submitted in partial fulfillment of the
Requirements for the degree of

MASTER OF SCIENCE

In the Department of Biology

University of Victoria

Abstract

A critical link between marine and terrestrial ecosystems in western North America is the predictable annual spawning of anadromous salmon (*Oncorhynchus spp.*), which results in the deposition of large quantities of marine-derived nutrients (MDN) in coastal streams, lakes and forests. Many vertebrate species, including bears, wolves and gulls congregate around salmon streams in the fall to consume this energy-rich and abundant resource. An important process that occurs on salmon streams involves wildlife-mediated transfer of salmon carcasses into the riparian zone, resulting in the fertilization of otherwise nutrient-deprived soils. This nutrient subsidy, which increases primary productivity and invertebrate biomass in streams and adjacent riparian areas, is likely to increase food availability for vertebrate consumers such as songbirds. In this study I investigated the effect of salmon nutrients on birds by a) quantifying the consumption of salmon carcasses and eggs by gulls; b) testing for the presence of salmon-derived nutrients in feathers and feces of a ground-foraging songbird, and c) determining whether the presence of salmon-derived nutrients affected bird density. Study streams were located on the central coast of British Columbia, and were chosen due to the presence of large waterfalls 1 – 2 km upstream, which blocked the passage of salmon, thus creating a within-watershed control. Several species of gulls (*Larus glaucescens, L. argentatus*, *L. thayeri*, *L. californicus, L. canus, L. philadelphia*) aggregated in large numbers on salmon streams during the fall. Gulls consumed 11-26% of total salmon carcass biomass and 7-36% of all salmon eggs deposited in the system, and re-distributed salmon-derived nutrients via guano to surrounding freshwater, riparian, and marine ecosystems. Salmon-derived nutrients could be detected via stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) into the feathers and feces of Winter Wrens (*Troglodytes troglodytes*) below the falls. Wrens likely obtained salmon-derived nutrients through the consumption of enriched terrestrial and aquatic invertebrates, as well as fly larvae hatched directly from salmon carcasses. Substantial within-population variation in $\delta^{15}N$ (-0.81 to 17.75‰) revealed potential dietary specialization of individual Winter Wrens. The salmon-nutrient subsidy affected breeding densities of Winter Wrens, as well as other songbird species adjacent to salmon streams. Overall songbird density was higher on salmon-bearing reaches than non-salmon-bearing reaches of study streams. This was likely a result of increased food availability and altered forest structure and plant species composition below the falls. These data support previous findings that salmon have cascading effects on multiple trophic levels in terrestrial systems. As a result, the widespread declines in pacific salmon populations may have more serious implications for terrestrial ecosystems than previously understood.

Acknowledgements

I received a huge amount of help while completing this thesis from many people. I am in debt to my supervisor, Dr. Tom Reimchen, for inspiration, support, and guidance throughout this project. I thank my committee for allowing me to do this project, and I would like to thank my colleagues Chris Darimont, Dan Klinka, Blake Matthews and Mark Spoljaric for intellectual discussion, moral support and much-needed comedic relief. I would like to thank Morgan Hocking for help in the field, analysis, and writing phases of this thesis. This project would not have been possible without the many people who helped in the field; I would like to thank Janine Arnold and Karen Petkau for working very hard on this project, as well as Jocelyn Akins, Jesse Beaudin, Sara Steinke, Bob Wilkerson, Mike Windsor, and Buddy Windsor. I would like to thank Dr. Alan Burger, and Dr. Jamie Smith for much needed comments on individual chapters. I thank Don Phillips for help with the isotopic mixing model, and Myles Stocki at the Stable Isotope Facility at University of Saskatchewan. I owe many thanks to Eleanore Floyd at the University of Victoria for her organizational skills. I thank Larry Jorgensen and Raincoast Conservation Society for accommodation in the field, and the Heiltsuk Nation for allowing this research to take place in their territory. Financial aid was provided by the Natural Sciences and Engineering Research Council of Canada, Friends of Ecological Reserves, The David Suzuki Foundation, Bird Studies Canada, The Environment Canada Science Horizons Program, and the Mountain Equipment Co-op Environment Fund. I owe many thanks to Kim Everett for accommodation, and Tyler Lewis for support and advice during the last writing stages of the thesis. I heartily thank friends and family for supporting me throughout this project.

Table of Contents

Abstract..ii

Acknowledgements..iv

Table of Contents..v

List of Tables..vii

List of Figures..viii

General Introduction..1

Chapter 1. Post-reproductive salmon as a major nutrient source for large aggregations of gulls..6

- 1.1. Abstract..6
- 1.2. Introduction..7
- 1.3. Methods..8
- 1.4. Results..10
    - Foraging behaviour..10
    - Abundance..11
    - Consumption of carcasses and eggs..12
    - Guano production and nutrient dispersal..12
- 1.5. Discussion..13
    - Foraging behaviour..13
    - Abundance..14
    - Consumption of carcasses and eggs..15
    - Guano production and nutrient dispersal..15
- 1.6. Acknowledgements..17

Chapter 2. Tracing salmon-derived nutrients in the feathers and feces of a ground foraging passerine..23

- 2.1. Abstract..23
- 2.2. Introduction..24
- 2.3. Methods..27
    - Study sites..27
    - Collection methods - Wrens..28
    - Collection methods - Invertebrates..29
    - Isotope analysis..30
    - Statistical analysis..31
    - Isotopic mixing model..31
- 2.4. Results..33
    - Winter Wrens..33

Invertebrates.....35
Mixing Model.....35
Dietary Shift.....36
2.5. Discussion.....37
Comparisions across the waterfall barrier.....37
Mixing model.....38
Isotopic variation within populations of Winter Wrens.....40
2.6. Acknowledgements.....44

Chapter 3. Effects of salmon derived nutrients on the density of breeding songbirds.....**52**

3.1. Abstract.....52
3.2. Introduction.....53
3.3. Methods.....55
Study area.....55
Songbird density estimates.....56
Vegetation surveys.....57
Statistical analysis.....57
Comparisons among rivers.....62
3.4. Results.....63
General linear models and AIC.....63
Songbird density estimates.....63
Comparisons among rivers.....65
3.5. Discussion.....66
3.6. Acknowledgements.....71

General Discussion.....**79**
Literature Cited.....**82**

List of Tables

Table 1.1. Average body mass (Dunning 1993), calculated field metabolic rate, and daily consumption of eggs or carcasses for large gulls (Glaucous-winged, Herring, Thayer's, California Gulls) Mew Gulls, and Bonaparte's Gulls..20

Table 1.2. Wet mass of salmon carcasses (M. D. Hocking, personal communication) and wet mass of eggs (Beacham and Murray 1993) deposited by pink and chum salmon at the Clatse and Neekas Rivers. Salmon escapement (Department of Fisheries and Oceans) was used to calculate total mass of carcasses and eggs deposited in each watershed in 2002 and 2003..21

Table 1.3. Total consumption of salmon carcasses and eggs during the 60-day study period and proportion of the total salmon and egg biomass in the system consumed by gulls. Shown are consumption estimates basted on original data from the 7-8 surveys per year, as well as interpolated estimates of consumption, where gull abundance was calculated for each day of the 60-day study period..22

Table 2.1. Mean isotopic signatures of feathers and feces collected from wrens captured above and below the falls at Clatse Creek and Neekas River on the central coast of British Columbia. T-tests were used to determine whether isotopic signatures differed significantly across the waterfall barrier. 46

Table 2.2. Isotopic signatures for prey sources used in the mixing model. Invertebrates were obtained from above (AF) and below (BF) the waterfalls on three salmon-bearing watersheds. Values for aquatic invertebrates were obtained from Chaloner et al. (2002). Values shown have been adjusted for fractionation by 4‰ for $\delta^{15}N$ and 2.7‰ for $\delta^{13}C$. $\delta^{13}C$ values for terrestrial invertebrate groups have been normalized for lipid content based on C/N ratios (McConnaughey and McRoy 1979). 49

Table 2.3. Contributions of fly larvae, Marine-enriched invertebrates (Collembola, millipedes, spiders, aquatic invertebrates collected from below the falls) and non-enriched invertebrates (same groups collected from above the falls) to Winter Wren diets (recently grown feathers only) using the mixing model of Phillips and Gregg (2003). Shown are isotopic signatures of wren feathers and possible contributions of each source to the diet. Minimum (1st percentile), mean, and maximum values (99th percentile) are given, accounting for 98% of all possible solutions. Each row represents an individual wren and values in bold represent model output for the mean of the above individuals. The mixing model was run at increments of 4% and a tolerance of 0.6‰ except for two outlying individuals. 50

Table 3.1. General linear models (top models ($\Delta AIC_c \leq 2.0$) are shown) describing variation in songbird density on salmon streams on the central coast of British Columbia, 2002-2003. 76

Table 3.2. Parameter likelihoods (summed AIC_c weights of models that include parameter) of explanatory variables in linear regression models. Parameter likelihoods

reflect the relative importance of each explanatory variable in models describing variation in songbird density. Explanatory variables are defined in Table 3.2............77

Table 3.3. Model selection and density estimates for five bird species above and below the waterfalls on two salmon-bearing rivers (Clatse and Neekas) located on the central coast of British Columbia. 79

Table 3.4. Mean density (untransformed) and standard deviation of birds surveyed at four watersheds on the central coast of British Columbia. Paired comparisons were made between bird densities up to 1km on Clatse Creek to Ripley Creek and Neekas River to Cheenis Creek, and significant results of independent sample t-tests are indicated......80

List of Figures

Figure 1.1. Map of study sites located north of Bella Bella, on the central coast of British Columbia (inset map). 18

Figure 1. 2 a-d. Change in abundance of gulls over time (day 1 = August 25; day 60 = October 23) at Clatse Creek: (a) 2002 and (b) 2003 and Neekas River (c) 2002 and (d) 2003. Dashed lines represent large gulls (Glaucous-winged Gulls, Herring Gulls, Thayer's Gulls, California Gulls), dotted lines represent Mew Gulls, and solid lines represent Bonaparte's Gulls. 19

Figure 2.1. $\delta^{15}N$ and $\delta^{13}C$ signatures for feathers of Winter Wrens (a,b) and arthropod taxa (c,d) collected from the Clatse (a,c) and Neekas (b,d) rivers, British Columbia. Solid symbols reflect individuals collected below the falls, open symbols represent individuals collected above the falls. Circles represent tail feathers (retrices) and squares represent body feathers (contours). Error bars reflect standard error. *represents data presented in Hocking and Reimchen (2002); † represents a combination of data presented in Hocking and Reimchen (2002) and unpublished data. 45

Figure 2.2. $\delta^{15}N$ and $\delta^{13}C$ values for recently grown Winter Wren feathers collected above (open symbols) and below (solid symbols) the falls at the Clatse (squares) and Neekas rivers (circles). 47

Figure 2.3. $\delta^{15}N$ and $\delta^{13}C$ values of Winter Wren feces collected from above (open symbols) and below (solid symbols) the falls at Clatse (squares) and Neekas rivers (circles). 48

Figure 2.4. Shift in $\delta^{15}N$ and $\delta^{13}C$ signatures for individual wrens collected above (open symbols) and below (solid symbols) the falls at Clatse (squares) and Neekas rivers (circles). Shifts were calculated by subtracting isotopic signatures for summer-grown feathers from fall-grown feathers. 51

Figure 3.1. Diagram of point transects used for breeding bird census. Rectangular vegetation plots were situated at random directions around each point and one sample is shown. 73

Figure 3.2. Figure 3.2. Mean and 95% confidence intervals of bird density at points above and below the falls, close (50m) and far (150m) from the stream at Clatse and Neekas Rivers, British Columbia. Density (ln(number of detections per point + 1) was estimated for the following species: Winter Wren (WIWR), Swainson's Thrush (SWTH), Varied Thrush (VATH), Pacific-slope Flycatcher (PSFL), Golden-crowned Kinglet (GCKI), and Chestnut-backed Chickadee (CBCH). On transects close to the stream, 81 points were surveyed below the falls and 56 were surveyed above the falls. On transects far from the stream, 34 points were surveyed below the falls and 24 were surveyed above the falls....74

Figure 3.3. Mean and 95% confidence intervals of total bird density and number of species detected during point-counts above and below the falls, close (50m) and far (150m) from the stream at Clatse and Neekas Rivers, British Columbia. Same sample sizes as Figure 3.2 apply. 75

General Introduction

Nutrient subsidies are common in natural ecosystems, and play a major role in shaping communities (Polis and Strong 1996). Nutrients, detritus, and prey repeatedly cross ecosystem boundaries and have immediate impacts on consumer populations, as well as cascading effects on organisms throughout food-webs (Duggins et al. 1989, Polis and Hurd 1996). Nutrient inputs from external sources have the potential to increase the complexity and resilience of ecosystems, because they provide important resources that may otherwise be limiting (Polis and Strong 1996). For example, in alpine systems, aeolian inputs of insects subsidize nutrient-deficient tundra ecosystems (Halfpenny and Heffernan 1992). Nutrient pulses have been observed to permeate through multiple trophic levels, causing heightened primary productivity and increased densities of consumer and predator populations. A well-studied example of cross-boundary nutrient subsidies involves the input of seabird guano, fish scraps, and detritus to islands inhabited by seabird colonies. In these systems, marine-derived nutrient subsidies lead to increased densities of secondary consumers such as beetles, lizards, and rodents (Sanchez-Pinero and Polis 2000, Stapp and Polis 2003, Barrett et al. 2005).

In the Pacific Ocean, an organism that repeatedly crosses the marine-terrestrial interface is salmon (*Oncorhynchus* spp.). Pacific salmon spend most of their lives in the ocean where they gain much of their biomass, but return in large numbers to spawn and die in their natal streams, thus transporting substantial quantities of marine-derived nutrients to terrestrial systems. The return of spawning salmon during the fall attracts an abundance of vertebrate species, many of which depend heavily on this resource (e.g.

Ben-David et al. 1997) and has profound long-term effects on aquatic and terrestrial systems (Gende et al. 2002).

On the Pacific coast of North America, the most abundant vertebrate visitors to estuaries and rivers during salmon migration are gulls, yet the utilization of salmon nutrients by these scavengers has not been well documented. Gulls congregate en masse on salmon streams during the fall, where they stay for the duration of the spawning period, consuming large quantities of salmon (Reimchen 1992, Cederholm et al. 2000). The importance of salmon to the gull diet is unknown, but gulls on southward migration likely target salmon streams to feed on the energy-rich and highly abundant resource. Subsequent to consumption of salmon, gulls defecate on the stream, the surrounding riparian zone, and into the ocean, thus distributing unknown quantities of salmon-derived nutrients to marine, estuarine, freshwater and riparian habitats

An important process that occurs on salmon streams involves wildlife-mediated transfer of salmon into riparian forests and the subsequent fertilization of otherwise nutrient-poor systems. Bears, and to a lesser extent wolves, birds, and other animals actively transport salmon carcasses or fragments into the forest, where they frequently leave most to decompose on the forest floor. The accumulation of carcasses in the riparian zone can be extensive (Reimchen 1994), and results in increased plant productivity as well as altered plant and invertebrate community structure (Helfield and Naiman 1998, Hocking and Reimchen 2002, Mathewson et al. 2003). The fertilization of coastal forests by salmon likely has strong implications for organisms at higher trophic levels; however, little is known about the extent to which salmon-derived nutrients travel through the food web.

The principal tool that has been used to trace salmon-derived nutrients in terrestrial systems is stable isotope analysis. Because salmon is enriched in the stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) compared with terrestrial sources, it can be traced into elements of riparian ecosystems such as trees, shrubs, soil arthropods, and aquatic invertebrates (Bilby et al. 1996, Wipfli et al. 1998, Hocking and Reimchen 2002, Mathewson et al. 2003). In terrestrial systems, ^{13}C from salmon can be detected only in organisms that directly consume salmon carcasses, whereas nitrogen is cycled throughout the terrestrial food web and can be traced into organisms that obtain it either directly or indirectly, through plant-mediated pathways.

Stable isotopes can also provide insight about aspects of the dietary niche of an organism. The isotopic signature of an animal's tissues on average reflects that of its diet, with a small degree of isotopic enrichment due to fractionation (De Niro and Epstein 1979, De Niro and Epstein 1981). If isotopic signatures of all potential food sources are known, then it is possible to piece together the diet of an animal, using methods such as isotopic mixing models (Phillips and Gregg 2003). Dietary shifts can be detected using stable isotopes, because a change in the isotopic signature of a consumer's food source is reflected in its tissues (e.g. Thompson and Furness 1995). In addition, the isotopic variation observed within a population can lead to information regarding niche width and potential individual specialization (Bolnick et al. 2003). For example, high isotopic variance within a population suggests that individuals specialize on varied food sources.

In this thesis, I explore the ecology of birds in relation to salmon-derived nutrients entering terrestrial systems on the central coast of British Columbia. Study streams had substantial salmon runs (>20 000) interrupted by waterfalls 1-2 km upstream, thus providing a within-watershed control. Concurrent studies on these streams have shown major enrichment of salmon nutrients in shrubs, trees and insects in riparian habitats (Hocking and Reimchen 2002, Mathewson et al. 2003, Wilkinson et al. 2004).

In the first chapter, I investigate the consumption of salmon carcasses and eggs by gulls. Over the spawning period, I identified and counted gulls consuming salmon and eggs, and estimated the consumption of salmon based on body mass and field-metabolic rates. I also estimated guano production by gulls and discuss the implications of the distribution of nutrients via guano to the surrounding area. In the second and third chapters, I focus on a less obvious benefactor of the salmon-nutrient subsidy: forest songbirds. In chapter two, I trace salmon-derived nutrients into the feathers of a common resident of mature forests in the Pacific Northwest, the Winter Wren (*Troglodytes troglodytes*). I compare the isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$) of Winter Wrens in areas influenced by salmon (below the falls) to those around stream reaches without salmon (above the falls). I determine the contribution of salmon-derived nutrients to the wren diet via indirect and direct pathways using an isotopic mixing model. In addition, I use stable isotopes to explore the extent to which the diet of these birds differs within populations, and whether individuals undergo dietary shifts over time. In the third chapter, I examine the response of forest songbirds to the salmon nutrient subsidy by comparing breeding bird density above and below the waterfall barrier. I test the predictive power of several habitat-related variables including position above or below the falls, proximity to the stream, tree community structure, and shrub cover in determining songbird density. Finally, I conclude my thesis with a discussion of the overall importance of salmon to birds and the potential consequences of the 90% reduction of salmon populations over the past century (Gresh and Lichatowitch 2000).

Chapter 1

Post-reproductive Pacific Salmon, *Oncorhynchus* spp., as a major nutrient source for large aggregations of gulls, *Larus* spp.

1.1. Abstract

On the Pacific coast of North America, the most abundant vertebrate visitors to estuaries and rivers during salmon migration are gulls, yet the utilization of salmon nutrients by these scavengers and subsequent ecological impacts are not well documented. On two watersheds on the central coast of British Columbia, I tracked gull abundance during the autumn spawning period for two consecutive years, and estimated consumption of post-reproductive salmon carcasses and drifting eggs, as well as guano production. At Clatse Creek, gulls (*Larus glaucescens, L. argentatus*, *L. thayeri*, *L. californicus, L. canus, L. philadelphia)* consumed 13-26% of total salmon carcass biomass and 29-36% of all salmon eggs deposited in the system. At Neekas River, gulls consumed 11-19% of salmon carcass biomass and 7-18% of total salmon eggs. Local guano production (dry mass) over the 60 day period ranged from 600 kg to 1190 kg over a 1km stretch of Clatse Creek and from 1200 kg to 2100 kg over a 2.1km stretch of Neekas River, and was distributed to marine, estuarine, freshwater and riparian habitats. The large aggregations of gulls and subsequent nutrient cycling observed on my study watersheds may represent a once widespread phenomenon that is now largely reduced due to recent declines in salmon populations.

1.2. Introduction

In the north Pacific, large runs of spawning salmon (*Oncorhynchus* spp.) contribute substantial quantities of nutrients to aquatic and terrestrial food webs (Bilby et al. 1996, Willson et al. 1998). Nutrients from salmon carcasses are used extensively by many vertebrate species such as bears, marten, wolves, eagles, gulls, and ravens and become incorporated into terrestrial vegetation and invertebrate communities (Reimchen 1994, 2000, Ben-David et al. 1998, Cederholm et al. 2000, Helfield and Naiman 2001, Darimont and Reimchen 2002, Hocking and Reimchen 2002). The most numerous, yet least well-studied vertebrates that feed on post-reproductive salmon are gulls, which congregate in the thousands on streams throughout the north Pacific during their southward autumn migration (Mossman 1958; Campbell et al. 1990; Skagen et al. 1991). Migration and feather molt, both energetically demanding activities, require rapid accumulation of lipids (Jenni and Jenni-Eiermann 1998; Stocker and Weihs 1998; Hamer et al. 2002). These metabolic demands, in addition to potential resource scarcity and harsh weather conditions in the fall and winter can lead to high mortality in gulls, especially for juveniles (Burger 1993; Verbeek 1993; Hamer et al. 2002).

In this chapter, I quantify gull abundance and foraging activity on two salmon streams of coastal British Columbia. I examine temporal shifts in abundance of gulls on salmon streams, salmon and egg consumption by each species of gull, and the recycling of salmon nutrients via guano production.

1.3. Methods

This study was conducted on the on the central coast of British Columbia at Clatse Creek (52° 20.6'N; 127° 50.3'W) and Neekas River (52° 28.4'N; 128° 8.0'W; Figure 1.1), both of which support spawning populations of Chum (*Oncorhynchus keta*) and Pink (*O. gorbuscha*) salmon that spawn from late August until early November. Approximately 1 km from the mouth of Clatse Creek and 2.1 km from the mouth of Neekas River, 5-10 m waterfalls act as barriers to further upstream migration of salmon. These watersheds, both of which support more than 20 000 spawning salmon, are described in detail elsewhere (Hocking and Reimchen 2002; Mathewson et al. 2003).

I conducted 33 surveys to count and identify gulls, comprising 8-9 surveys throughout the salmon spawning period per year at each watershed. All surveys were made by foot during low tide and included both estuary and river habitats. The study period extended from 9 September to 17 October in 2002 and from 25 August to 21 October in 2003. Large gulls were grouped to facilitate identification from a distance and later identified to species in sub-sets. Among foraging gulls, I recorded feeding technique, classified as surface-seizing, surface-plunging, or carcass-scavenging (Ashmole 1971). I recorded food item (carcass or eggs) consumed by sub-sets of foraging Mew Gulls.

Daily consumption of salmon carcasses and eggs was calculated for each gull species. I used the consumption model modified from Bishop and Green (2001) as follows:

$$C = FMR/MEC \times P \times M$$

where C = consumption (g day^{-1}), FMR = field metabolic rate (KJ day^{-1}), MEC = metabolizable energy coefficient of salmon or eggs; P = proportion of salmon or eggs in diet; M = mass of salmon or eggs (g) needed to produce 1 KJ energy. FMR was calculated using the allometric equation for all free-living seabirds from Birt-Friesen et al (1989):

$$FMR = 10^{(3.08+0.667 \log M)}$$

where average body mass (M, in kg) was obtained from Dunning (1993; Table 1.1). MEC was assumed to be 0.75 for both salmon flesh and eggs (Castro et al. 1989, Bishop and Green 2001). Energy density of senescent salmon flesh is 2.95 KJ g^{-1} (wet mass; Hendry and Berg 1999), and for salmon eggs it is 7.60 KJ g^{-1} (wet mass; Jonsson et al. 1998). The proportion of salmon or eggs in the diet was 100% for large gulls, who consumed carcasses only, and 100% for Bonaparte's Gulls, who consumed eggs only. Mew gulls, who consumed both carcasses and eggs, were assigned a P value based on proportionate consumption of each resource based on sub-samples. Total consumption by gulls per day was derived from the mean gull count per day for each watershed. Based on the surveys at each watershed, I estimated mean daily gull abundance using two methods: 1) the mean abundance of gulls derived from only the 8-9 days surveyed; and 2) the interpolated mean, where each day during the study period was assigned an estimated value of abundance based on previous and future counts. Although gulls occupied salmon streams throughout most of the 3-month spawning period, I estimated consumption for a 60-day period, the interval in which I had detailed data.

I calculated the proportion of total salmon biomass consumed by gulls using total consumption estimates relative to number of salmon returning to the river to spawn (escapement). Salmon escapement was obtained for my study streams in 2002 and 2003 from the Department of Fisheries and Oceans (Terry Palfrey, personal communication). Average intact carcass mass for pink and chum salmon at my study sites was obtained from M D. Hocking (personal communication). Fecundity and egg wet mass for pink and chum salmon (northern mainland coast) were obtained from Beacham and Murray (1993). Pink salmon fecundity was 1633 eggs/female and egg wet mass was 0.175 g; chum fecundity was 3173 eggs per female and egg wet mass was 0.278 g. A 1:1 sex ratio was used for both chum and pink salmon (Heard 1991, Salo 1991).

We calculated guano production for each species per day based on Burger et al. (1978) for Kelp Gulls (*Larus dominicanus*): $G = 36.1 \text{ g d}^{-1}\text{kg}^{-1}$, where G = output (dried) per kg body mass per 24 hrs. We adjusted this value to the average mass of each gull species. This estimate is compatible with that of Portnoy (1989) who found that Herring Gulls (*L. argentatus;* mass = 1.1 kg) produced 39.4 g day^{-1}.

1.4. Results

Foraging behaviour

In both watersheds, six gull species were observed to feed on salmon carcasses and eggs: Glaucous-winged (*Larus glaucescens)*, Herring, Thayer's (*L. thayeri),* California (*L. californicus),* Mew (*L. canus),* and Bonaparte's Gull (*L. philadelphia).*

The large-bodied gulls (Glaucous-winged, Herring, Thayer's, and California Gulls) mainly scavenged for salmon carcasses and occasionally consumed drifting eggs. Feeding intensity of large gulls was highest at low tide, when most carcasses in the estuary were exposed. Bonaparte's Gulls consumed eggs exclusively and most often hovered, "surface-plunging" for eggs. Bonaparte's Gulls also floated and "surface-seized" eggs from below the surface. Mew Gulls rarely surface-plunged; most of the time they were observed to surface-seize or occasionally dislodge eggs from gravels with their feet. From behavioural observations of sub-sets of Mew Gulls, approximately 93% consumed eggs and 7% consumed carcasses (*n* = 11 observations). Most eggs consumed were floating downstream but some were taken from carcasses.

Abundance

Gull abundance fluctuated over time at the two watersheds (Figure 1.2). At Clatse Creek, total daily counts of gulls reached a maximum of 1979 birds (13 October 2003), of which approximately 45% were large gulls. At Neekas River, the maximum count was 3594 birds (21 October, 2003) of which 64% were large gulls. At both watersheds, Glaucous-winged and Herring Gulls were the numerically dominant large gulls. Large gulls increased in abundance over the spawning period in both years at both watersheds, and likely continued to increase beyond the 60-day study period. Mew and Bonaparte's Gull abundance, on the other hand, was less predictable (Figure 1.2). At Clatse Creek, Mew and Bonaparte's Gulls peaked in numbers and began to decline in early October 2002 and mid-October 2003 (Figure 1.2 a, b) whereas at the Neekas River they did not follow a discernable pattern (Figure 1.2 c,d). Total numbers of Mew and Bonaparte's

Gulls were similar between watersheds, whereas greater numbers of large gulls occurred at Neekas River compared with Clatse Creek.

Consumption of carcasses and eggs

I estimated the proportion of salmon and eggs consumed by gulls using calculated values of FMR and daily consumption (Table 1.1), and total mass of salmon carcasses and eggs deposited in each watershed, based on total salmon escapement (Table 1.2). Estimates of salmon carcasses and egg consumption by gulls varied between years and watersheds, and 11% to 26% of total salmon carcass biomass and 7% to 36% of salmon egg biomass was consumed by gulls during the 60 day study period (Table 1.3). Carcass consumption was higher, but the proportion of total salmon biomass consumed was slightly lower at Neekas than Clatse Creek. Carcass consumption was higher in 2003 than 2002 for both watersheds. Although egg consumption was similar at the two watersheds, substantially higher proportions of total egg biomass were consumed at Clatse compared to Neekas River (Table 1.3).

Guano production and nutrient dispersal

Based on gull counts and body mass, guano production (dry mass) at Clatse Creek ranged from 596 kg to 748 kg in 2002 and 907 kg to 1192 kg in 2003. At Neekas River, this ranged from 1201 kg to 1463 kg in 2002 and 2006 kg to 2104 kg in 2003. Observations of foraging and resting locations of gulls indicated that guano was distributed into multiple habitats including the river, riparian zone, and estuary, where gulls foraged and rested during the day and marine habitats, where gulls roosted at night.

1.5. Discussion

Foraging behaviour

Gulls were significant consumers of the salmon resource, using at least three foraging techniques and consuming multiple tissue types including eggs and flesh. An energy trade-off exists between consumption of calorie-rich eggs, which require active searching, and the highly available yet less energy-dense carcasses. Bonaparte's Gulls, the smallest of the gulls, are well adapted to aerial foraging and surface-seizing and commonly feed on insects and zooplankton (Baltz and Morejohn 1977, Vermeer et al. 1987, Taylor 1993). Their ability to hover above water for extended periods of time may facilitate their ability to effectively spot and capture eggs in the river. The larger gulls, in contrast, with a greater body mass and wing-loading (Pennycuick 1987), may incur additional energy costs of continuous-flapping flight, which would outweigh the benefits of obtaining the more energy-rich food.

Larger gulls were observed on occasion to surface-plunge for eggs, indicating that at certain times, benefits of capturing eggs outweighed energy costs. Although other food sources such as benthic invertebrates were available in the estuaries, I never observed gulls to forage on foods other than salmon tissues and eggs. Gulls tend to maximize their utilization of temporary resources, focusing on localized concentrations of prey (Shealer 2002), and it is probable that when eggs and carcasses are easily available on salmon streams, gulls feed solely on this resource.

Abundance

Abundance of gulls at Clatse and Neekas Rivers fluctuated over the study period and appeared to correspond with food availability. Large gull abundance increased over time on each watershed in both years, corresponding with the accumulation of spawned-out salmon on the stream banks and in the estuary. Abundance of Bonaparte's Gulls and Mew Gulls, however, was not correlated with carcass accumulation. It is possible that fluctuations in gull abundance at study streams were related to timing of migration of the gulls rather than prey abundance. Mace (1983) observed aggregations of Bonaparte's Gulls feeding on juvenile salmonids in the spring and found gull abundance to be directly related to migration. In addition, I suspect that the rate of egg loss, which is associated with spawning density and flooding events, may be an important predictor of Mew and Bonaparte's Gull abundance. The two watersheds had similar numbers of Mew and Bonaparte's Gulls despite the higher biomass of salmon at Neekas River, indicating that comparable quantities of eggs were being washed from redds (thereby making them available to gulls) at the two watersheds. High stream velocity can result in egg loss, causing eggs to be washed out of redds after being deposited (Vronskii and Leman 1991). Clatse Creek may have higher stream velocities and lower gravel stability compared with Neekas River. Additional differences between the rivers include body mass of salmon (Table 1.2), where chum are heavier on average at Clatse than Neekas River. It is possible that as a result, slightly more eggs are produced at Clatse Creek than at Neekas River. Egg loss from salmon redds can also be linked with high salmon spawning density, which results in redd superimposition and subsequent egg dislodgement (Fukushima et al.

1997). Clatse Creek may have fewer optimal spawning gravels than Neekas, thereby causing congestion of spawning salmon and subsequent loss of eggs from redds.

Consumption of carcasses and eggs

Gulls were major consumers of both salmon carcasses and eggs. My estimates for consumption of carcasses at the Neekas and Clatse Creeks are conservative because the 60-day study period ended before gulls had departed from the stream. Extrapolating abundance throughout the duration of the spawning period might increase consumption by as much as 30%. My results are comparable to those of other studies of gulls feeding on fish or eggs (Gabrielsen et al. 1987; Haegele 1993; Bishop and Green 2001). High numbers of egg-eating gulls at Clatse Creek led to a substantial proportion (29-36%) of eggs deposited in the system to be consumed. Only a small proportion of eggs would have been dislodged from buried redds by gulls; most eggs were already floating downstream before capture by gulls. Most eggs captured by gulls would not have hatched if left un-eaten; therefore, gulls had little if any effect on salmon productivity. It is not unusual for large quantities of eggs to be washed out from salmon redds; for example, average egg loss rates of 48.6% and 56% have been reported for pink salmon (Eniutina 1972, Heard 1991). In general, higher proportions of salmon were consumed in 2003 than 2002, largely because there was less total salmon available in 2003. Between-year differences at the Neekas River must be interpreted cautiously, however, because of the short study period in 2002.

Guano production and nutrient dispersal

Gulls contributed to the cycling of nutrients from salmon into terrestrial and aquatic ecosystems through guano and feather deposition. These materials were deposited into the forest adjacent to salmon streams, into the stream itself, into the estuary (large numbers of gulls congregated here at low tide) and into areas offshore where gulls roosted at night. Seabird guano enriches plants in nitrogen and phosphorus (Anderson and Polis 1999, Garcia et al. 2002), resulting in higher abundance of terrestrial arthropods (Sanchez-Pinero and Polis 2000), and increased primary productivity in the intertidal zone (Bosman and Hockey 1986). Guano from gulls and other avian scavengers on salmon streams likely contributes to the nitrogen and phosphorous content of otherwise nutrient-deprived coastal forests and streams (Waring and Franklin 1979, Kiffney and Richardson 2001). In addition, gulls undergo an annual molt after breeding (Taylor 1993, Vandenbulcke 1989), and their feathers, containing high concentrations of mineral elements and energy (Williams and Berruti 1978) are shed into the riparian zone, stream, and estuary.

Salmon streams are likely to provide an important food resource for gulls, particularly the smaller species such as Mew and Bonaparte's Gulls. Salmon streams offer a highly predictable, nutritional and accessible food source to gulls dispersing from breeding grounds in search of abundant food resources at a time of high energy expenditure (feather molt, migration) and high juvenile mortality (Burger 1993; Hamer et al. 2002). Spawning streams throughout the Pacific Northwest attract aggregations of gulls during the autumn and winter. Assemblages of gulls have been reported to utilize salmon streams in Washington (Skagen et al. 1991), Vancouver Island (pers. obs), the Queen Charlotte Islands (Reimchen 1992) and Alaska (Mossman 1958). The large numbers of gulls observed on the Clatse and Neekas Rivers, which have relatively healthy salmon runs compared with southern counterparts, are representative of an ecological phenomenon that has been greatly diluted throughout the Pacific Northwest. Gresh and Lichatowich (2000) estimated a 93-95% reduction in salmon biomass on the west coast of North America over the last century, which would have reduced the availability of this food source for gulls and numerous other vertebrate species that utilize salmon nutrients (Cederholm et al. 2000). The importance of gull assemblages to the ecology of coastal terrestrial ecosystems is unknown, but gulls are potentially important nutrient vectors and thus may contribute to the primary productivity of nutrient-deprived terrestrial systems.

1.6. Acknowledgments

I would like to thank Alan Burger for his helpful comments on this chapter, Karen Petkau, Morgan Hocking, Janine Arnold, Bob Wilkerson, Sara Steinke and Jocelyn Akins for assistance in the field, Chris Darimont, Raincoast Conservation Society and Larry Jorgenson for providing accommodation in the field, Terry Palfrey at the Department of Fisheries and Oceans for fish escapement data, The Natural Sciences and Engineering Research Council of Canada (NSERC), The Friends of Ecological Reserves, The David Suzuki Foundation, Mountain Equipment Co-op Environment Fund, Bird Studies Canada, and Science Horizons Youth Internship Program for financial support, and The Heiltsuk Nation for allowing this study to take place in their territory.

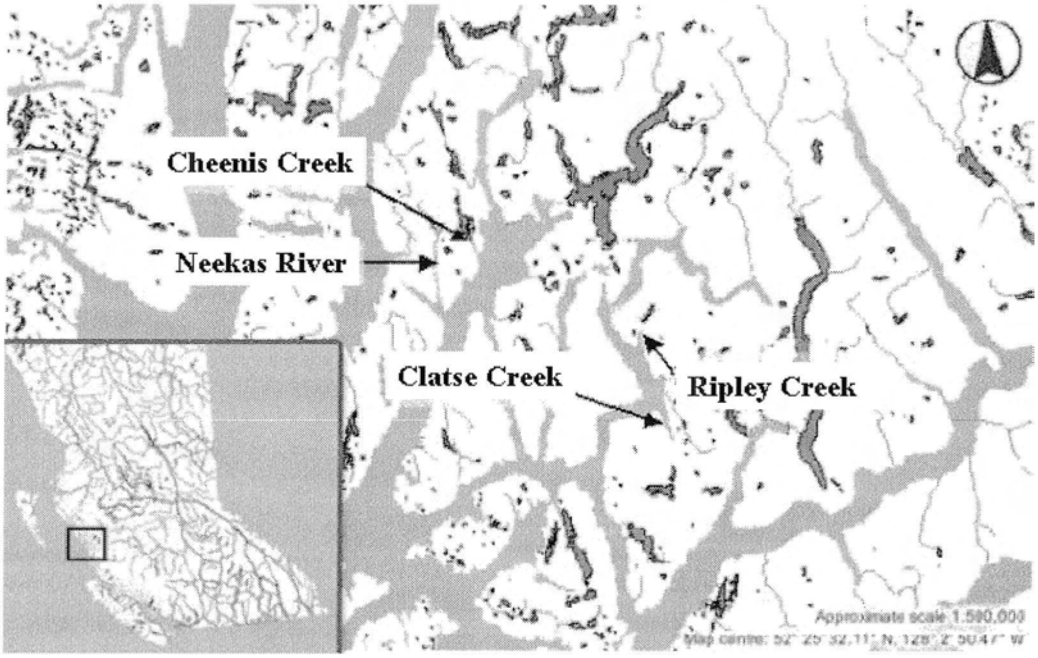

Figure 1.1. Map of study sites located north of Bella Bella, on the central coast of British Columbia (inset map).

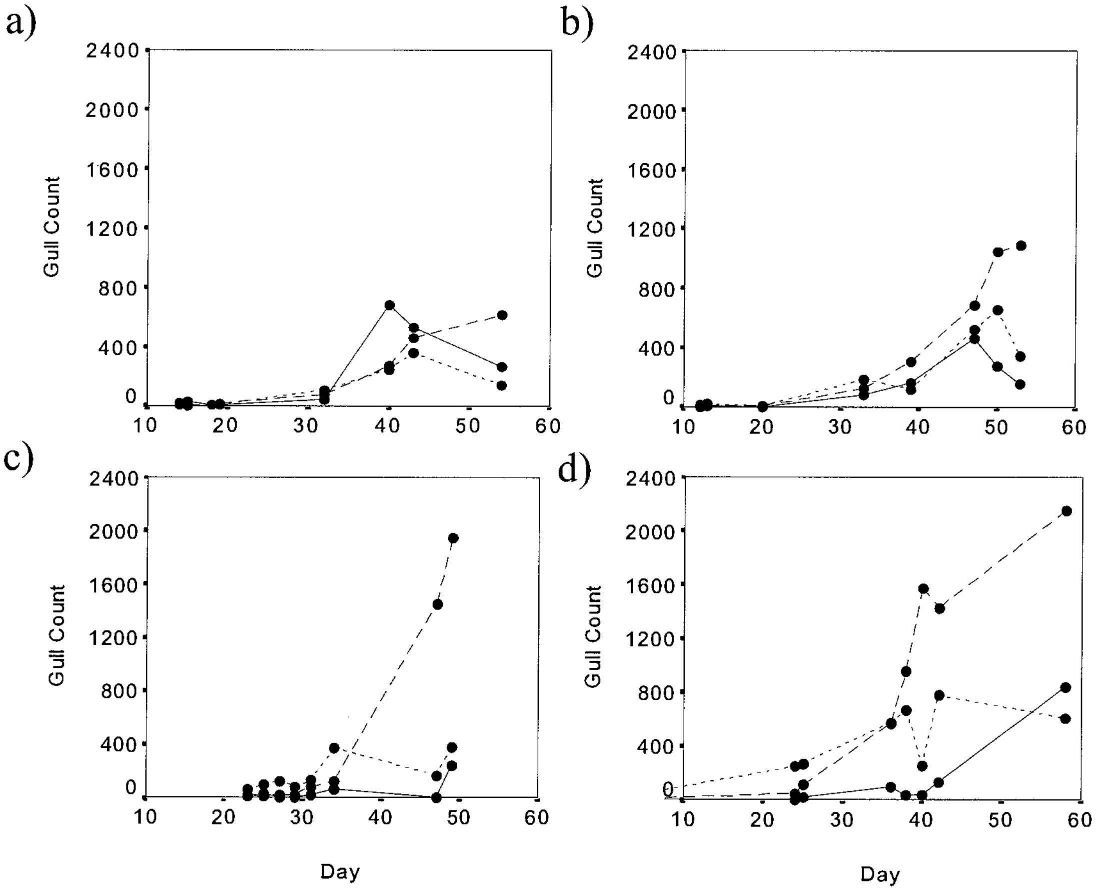

Figure 1. 2 a-d. Change in abundance of gulls over time (day 1=August 25; day 60 =October 23) at Clatse Creek: (a) 2002 and (b) 2003 and Neekas River (c) 2002 and (d) 2003. Dashed lines represent large gulls (Glaucous-winged Gulls, Herring Gulls, Thayer's Gulls, California Gulls), dotted lines represent Mew Gulls, and solid lines represent Bonaparte's Gulls.

Table 1.1. Average body mass (Dunning 1993), calculated field metabolic rate, and daily consumption of eggs or carcasses for large gulls (Glaucous-winged, Herring, Thayer’s, California Gulls) Mew Gulls, and Bonaparte’s Gulls.

Species	Mean body mass (g)	Field metabolic rate (KJ/day)	Consumption of eggs (g/bird/day)	Consumption of carcasses (g/bird/day)
Large gulls	1073.0	1258.9	220.9	569.0
Mew Gull	403.5	656.2	115.1	296.6
Bonaparte's Gull	212.0	426.6	74.9	192.8

Table 1.2. Wet mass of salmon carcasses (M. D. Hocking, personal communication) and wet mass of eggs (Beacham and Murray 1993) deposited by pink and chum salmon at the Clatse and Neekas Rivers. Salmon escapement (Department of Fisheries and Oceans) was used to calculate total mass of carcasses and eggs deposited in each watershed in 2002 and 2003.

Watershed	Species	Mean carcass wet mass (Kg)	Mass of eggs (g/female)	2002 escapement	Total mass of salmon (Kg)	Total mass of eggs (Kg)	2003 escapement	Total mass of salmon (Kg)	Total mass of eggs (Kg)
Clatse	Pink	1.1 +/- 0.1	285.8	25000	27500	3573	25000	27500	3573
	Chum	4.2 +/- 0.2	882.1	4300	18060	1897	6000	25200	2646
	Total			29300	45560	5470	31000	52700	6219
Neekas	Pink	1.3 +/- 0.1	285.8	60000	78000	8574	15000	19500	2144
	Chum	3.4 +/- 0.2	882.1	19000	64600	8380	35000	119000	15437
	Total			79000	142600	16954	50000	138500	17580

Table 1.3. Total consumption of salmon carcasses and eggs during the 60-day study period and proportion of the total salmon and egg biomass in the system consumed by gulls. Shown are consumption estimates basted on original mean from the 7-8 surveys per year, as well as interpolated estimates of consumption, where gull abundance was calculated for each day of the 60-day study period.

River	Year	Total carcass consumption (Kg)		Proportion of total salmon biomass	Total egg consumption (Kg)		Proportion of total egg biomass
		original	interpolated		original	interpolated	
Clatse	2002	6318	7931	0.13 - 0.17	1594	1987	0.29 - 0.36
	2003	14221	10419	0.19 - 0.26	2150	1868	0.30 - 0.34
Neekas	2002	15785	19349	0.11 - 0.14	1311	1515	0.07 - 0.09
	2003	26386	24650	0.18 - 0.19	3012	3168	0.17 - 0.18

Chapter 2

Tracing salmon-derived nutrients in the feathers and feces of a ground-foraging passerine

2.1. Abstract

The predictable annual spawning events of anadromous salmon (*Oncorhynchus spp.)* act as a critical link between terrestrial and marine ecosystems and constitute a substantial food source for many species. An important component of this process involves bear-mediated transfer of salmon into riparian forests and subsequent fertilization of otherwise nutrient poor systems. Using isotopic ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$), I investigate the direct and indirect input of salmon-derived nutrients (SDN) to the diet of a ground-foraging passerine, the Winter Wren (*Troglodytes troglodytes*), above and below a waterfall barrier to salmon migration on two rivers on the Central Coast of B.C., where studies have shown major enrichment of salmon nutrients in shrubs, trees and insects in riparian habitats. During summer and fall of 2001-03, I captured Winter Wrens (n=57) and potential prey items above and below the waterfalls. Feathers of Winter Wrens captured below the falls were enriched in ^{15}N compared with individuals captured above the falls, and this could be largely explained by the enrichment of invertebrate prey below the falls. Certain individuals were highly enriched in both $\delta^{15}N$ and $\delta^{13}C$, suggesting the consumption of fly larvae hatched from salmon carcasses. High variance in $\delta^{15}N$ signatures was observed in Winter Wrens and was likely due to individual variation in diet and direct exploitation of the marine food chain (via maggot consumption) by certain wrens. Nutrients from spawning salmon have

cascading effects on multiple trophic levels of terrestrial ecosystems including top-level consumers.

2.2. Introduction

The movement of nutrients between ecosystems has significant consequences for the productivity, diversity, and structure of communities (Polis and Hurd 1996). Nutrient subsidies, which fluctuate over time, generally flow from regions of high productivity to nutrient-poor systems (Nakano and Murakami 2001). In the Pacific Northwest, where streams are oligotrophic and forests soils are nutrient-limited, the flow of marine-derived nutrients to terrestrial and aquatic systems may be essential to ecosystem functioning (Gende et al. 2002).

The predictable annual spawning of anadromous salmon (*Oncorhynchus spp.*), which deposits large quantities of salmon-derived nutrients (SDN) in coastal streams, lakes and forests, is a critical link between marine and terrestrial ecosystems in western North America (Stockner 2003). Wildlife play an important role in transferring salmon carcasses into the riparian zone, fertilizing otherwise nutrient-deprived soils (Reimchen 2000, Gende et al. 2002). This nutrient subsidy has pronounced effects on aquatic and terrestrial systems including increased plant productivity (Helfield and Naiman 2001), altered plant species composition (Mathewson et al. 2003), and increased aquatic primary productivity and invertebrate biomass (Wipfli et al. 1998; Zhang et al. 2003).

Pacific salmon are enriched in the heavy stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) relative to terrestrial sources, and multiple studies have detected enriched quantities of these isotopes in plants, invertebrates, and mammals occurring near salmon streams (Bilby et al. 1996; Ben-David et al. 1998, Hocking and Reimchen 2002, Darimont and Reimchen 2002). In terrestrial systems, carbon is sequestered by plants from the atmosphere, and therefore ^{13}C from salmon can be detected only in organisms that directly consume salmon carcasses. Nitrogen, on the other hand, is limiting in forests of the Pacific Northwest (Waring and Franklin 1979) and ^{15}N from salmon is sequestered by plants and cycled throughout the terrestrial food web.

The link between salmon-derived nutrients and higher vertebrate consumers, such as songbirds, has been largely unexplored. Qualitative studies have documented the consumption of salmon eggs and flesh by ground-foraging songbirds (Jauquet et al. 2003); however, little is known about the importance of invertebrate scavengers such as fly larvae to songbirds. During the spring, the increased productivity of the stream and riparian zone may lead to higher breeding densities of passerines (Gende and Willson 2001) but the exact pathways through which songbirds obtain SDN are unknown and have not been quantified.

I use the Winter Wren (*Troglodytes troglodytes*), as a representative of higher vertebrate consumers in the riparian food web, to extend investigations of the salmon nutrient subsidy to terrestrial food webs. This builds upon previous isotopic investigations of SDN inputs to terrestrial invertebrates and plants on two salmon-bearing watersheds on the Central Coast of British Columbia, Canada. These watersheds, supporting over 25,000 spawning salmon per year, are representative of many salmon streams in the Pacific Northwest, and were chosen because they have waterfalls 1-2 km from the estuary that prevent further upstream migration of salmon. This presents a unique opportunity to compare the ecology of riparian zones with and without the influence of salmon in a single watershed.

Winter Wrens are generalist insectivores that primarily forage on the forest floor, coarse woody debris, and understory vegetation. This species is a winter resident of coastal forests in the Pacific Northwest, and adults generally maintain territories throughout the year, although territory size increases in the winter (Hejl et al. 2002, Waterhouse et al. 2002). I examine isotopic signatures of Winter Wren feathers and feces, as well as litter invertebrates that likely represent the range of isotopic signatures available to them, including Collembola, spiders, millipedes, and fly larvae, above and below a waterfall barrier to salmon. Unless severely nutrient-deprived, birds synthesize feathers with proteins derived from the immediate diet or from very short-term stores. Feathers therefore incorporate the isotopic signature of foods consumed at the time of moult, after which they become metabolically inert and thus record a discrete period of time (Hobson and Clark 1992, Murphy 1996). I applied an isotopic mixing model adapted from Phillips and Gregg (2003) in order to determine the dietary contribution of a) SDN acquired directly through fly larvae; b) SDN acquired indirectly through enriched invertebrates (collected from below the falls); and c) invertebrates lacking any marine enrichment (collected from above the falls). Because aquatic invertebrates are known to be an important food source for Winter Wrens (Nakano and Murakami 2001), I obtained isotopic signatures for this group (from reaches with and without salmon) from Chaloner et al. (2002) and incorporated them into the model.

In addition to tracing salmon-derived nutrients into wren tissues, I used isotopes to provide information about the dietary niche of the Winter Wren. $\delta^{15}N$ signatures of animal tissues reflect the isotopic content of the diet, plus an additional 3-4‰ due to "fractionation", the discrimination against the heavy isotope during physiological processes (DeNiro and Epstein 1981, Minagawa and Wada 1984). As a result, this isotope achieves greater concentrations in predators than their prey, and thus increases with every level of the food chain. In comparison, $\delta^{13}C$ in animal tissues does not fractionate substantially and is therefore a better predictor of source carbon rather than trophic status (DeNiro and Epstein 1978). Stable isotopes have been used to uncover trophic shifts in diets of consumers (Thompson and Furness 1995) and to determine individual niche breadth (Warburton et al. 1998, Grey 2001). Because the isotopic signature of an individual reflects that of its diet, variation in isotopic signatures within a population can reflect variation in diet among individuals, and thus, individual specialization (Gu et al. 1997, Warburton et al. 1998, Bolnick et al. 2002). Through sampling multiple individuals, as well as multiple feather samples per individual, I examined among and within-individual variation in isotopic signatures of Winter Wren populations above and below the waterfall barrier.

2.3. Methods

Study sites

Study sites were located north of Bella Bella, British Columbia, on the Clatse (52° 20.6'N; 127° 50.3'W) and Neekas Rivers (52° 28.4'N; 128° 8.0'W) (Figure 1.1). On these sites, previous studies investigating SDN inputs to terrestrial invertebrates (Hocking and Reimchen 2002), vascular plants (Mathewson et al. 2003) and bryophytes (Wilkinson et al. 2004). Both rivers have significant runs (over 20,000) of Chum (*O. keta*) and Pink (*O.*

gorbuscha) salmon from late August until early November. Five to ten meter waterfalls act as complete barriers to further upstream migration of salmon 1 and 2.1 km from the mouth of the Clatse and Neekas rivers, respectively. Both watersheds occur in the Coastal Western Hemlock Biogeoclimatic Zone characterized by infrequent, small-scale disturbance, high annual precipitation, and nutrient-poor soils (Meidinger and Pojar 1991).

Collection Methods – Wrens

57 Winter Wrens were captured using 12m x 2m mist-nets from 22 September to 19 October in 2001 (Clatse: number of captures (N)=3, Neekas: N=2), from 10 September to 18 October in 2002 (Clatse: N=5, Neekas: N=7), and from 28 June to 14 October in 2003 (Clatse: N=19, Neekas: N=21, Banding permit # 10429AL, Scientific Permit #59-03-0396). For the first two years, below-falls mist-nets were erected 600 and 1000m downstream from the falls and 250 m and 200 m upstream from the falls at the Clatse River and Neekas Rivers respectively. In these years, three nets were used alternatively above and below the falls. In 2003, a total of 15 mist-nets were open simultaneously above and below the falls in clusters approximately 200-300 m above and below the falls, within 50m of the stream. Mist-net stations above and below the falls were located in areas of similar forest structure and slope. Nets were within 50 m of the river and were open only on days without rainfall or without significant wind.

Upon capture, wrens were aged to hatch year, after-hatch year, or juvenile by degree of skull ossification, plumage, and presence of a yellow commissure (gape) (Pyle 1997). Each bird was banded with a USFWS aluminum leg band, and two retrices (tail feathers) were plucked. If the bird was moulting, new contour (body) or tail feathers (still partially sheathed) were also plucked. For hatch-year birds that were undergoing first pre-basic moult in the fall, retained juvenile feathers representing the summer nestling diet, and newly moulted contour (body) feathers representing the autumn diet were both sampled. Upon capture, birds often defecated. Fecal samples were collected from Winter Wrens in the autumn (September and October) of 2003.

Collection Methods – Invertebrates

Morgan Hocking conducted the collection, identification and isotopic analysis of invertebrate groups. Terrestrial invertebrates were collected in August 2000 (millipedes and spiders: data in Hocking and Reimchen 2002), June 2001 (Collembola and spiders), September 2001 (Collembola, spiders and fly larvae), and September 2002 (fly larvae). Most invertebrates were collected with pitfall traps in small 10 × 10m plots near mist-net stations above and below the waterfalls within 30m of the stream. In 2002, fly larvae were collected from chum and pink salmon carcasses that were experimentally placed in the riparian zone and monitored for invertebrate colonization. I used Collembola, millipedes, spiders, and fly larvae to indicate the isotopic range of food sources available to Winter Wrens. Collembola are abundant soil fungivores and detritivores, representing the base of the litter invertebrate food chain (Addison et al. 2003). The largest and most common Collembola species caught in the pitfall traps (filled with salt water) were *Ptenothrix maculosa* (Dicyrtomidae) and *Tomocerus flavescens* (Tomoceridae). Composite samples of each species representing 44-298 individuals were used as the $\delta^{15}N$ and $\delta^{13}C$ isotopic baseline for the litter community on each watershed. Collembola were caught in both June and September 2001 and were tested for seasonal differences. Millipedes are also common members of forest litter communities and we used an unknown coastal species (F. Parajulidae). Millipedes are enriched in $\delta^{13}C$ relative to insects by several parts per mil due to their carbonate exoskeletons (Ponsard and Arditi 2000; Hocking and Reimchen 2002). Spiders are the apex invertebrate predators of the terrestrial litter community at our sites and feed exclusively on other arthropods. The most common litter spider caught in the pitfall traps, *Cybaeus* spp., was used, as the $\delta^{15}N$ maxima consumed by wrens in the absence of salmon. *Cybaeus* spp. were collected at during the summer and fall (August 2000, June 2001, September 2001). Fly larvae were available only on carcasses below the falls and had the highest known $\delta^{15}N$ and $\delta^{13}C$ signatures of prey available to wrens. Fly larvae sent for isotope analysis were not identified to species or family, but identification of adult flies raised from salmon carcasses indicates that dominant species include *Calliphora terraenovae* (Calliphoridae) and *Dryomyza anilis* (Dryomyzidae).

Isotope analysis

Feathers were stored with silica gel to maintain dryness until brought to the lab, where they were rinsed and soaked in a 2:1 chloroform: methanol solution for 24 hours in order to remove lipids and then dried at 60° for at least 24 hours. Feathers were then chopped into small (<2mm) fragments and both vane and rachis were used. A total of 1mg of feather fragments were randomly chosen and loaded into tin capsules. Fecal samples were stored with silica gel and then frozen. They were then dried for 24 hours at 60°C, powdered by hand, and encapsulated in capsules. 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 and encapsulated in 3.5 by 5mm tin capsules. All samples were analyzed for continuous-flow isotope ratio mass spectrometry (CF-IRMS) of nitrogen and carbon 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). Measurement error was approximately ±0.1‰ for ^{13}C and ±0.3‰ for ^{15}N.

Statistical analysis

I used an ANOVA to test whether variance in feather ^{15}N and ^{13}C (dependant variables) could be explained by the following explanatory variables: location above or below the falls, watershed, feather type, age, and the interaction between location above or below the falls and feather type. This analysis was conducted using all feather samples from the 57 wrens captured. I repeated this analysis twice more, 1) using a subset of the data including recently grown (ie still sheathed) feathers only, and 2) using fecal samples collected from individual wrens. T-tests were used to determine whether $\delta^{15}N$ and $\delta^{13}C$ differed across the waterfall barrier. Furthermore, a Spearman's rank correlation was used to test the relationship between $\delta^{15}N$ and $\delta^{13}C$ in feathers and feces and a Levene's test for equality of variance was used to determine whether variance in feather isotopic signatures differed across the waterfall barrier.

Isotopic mixing model

I used the multi-source mixing model described in Phillips and Gregg (2003) to determine the proportion of marine-enriched invertebrates in the wren diet. Using isotope signatures of both consumer and food sources, isotopic mixing models examine all contributions (0-100%) of potential food sources to the consumers diet, using small increments (e.g. 1%). Feasible combinations of food sources are selected if they match the isotopic signature of the consumer, within a small tolerance (e.g. ± 0.1%). As possible food sources to the Winter Wren, I used mean isotopic signatures of litter invertebrates collected above the falls (Collembola, millipedes, spiders) to represent non-enriched terrestrial invertebrates and used the same groups collected below the falls to represent marine-enriched terrestrial invertebrates. I obtained signatures of multiple taxa of aquatic macro-invertebrates (Nemouridae, Chloroperlidae, Chironomidae) collected on salmon bearing and non-salmon bearing reaches of an Alaskan stream from Chaloner et al. (2002). Invertebrate groups were entered separately into the model and then aggregated *a posteriori* into non-enriched invertebrates (from non-salmon bearing reaches) and marine-enriched invertebrates (from salmon-bearing reaches) (Phillips et al. *in press*). I also included fly larvae (from carcasses) as direct sources of salmon-derived nutrients to the wren diet. Isotopic signatures of prey items were adjusted for diet-tissue discrimination using factors of 2.7‰ for ^{13}C and 4‰ for ^{15}N, which were originally calculated for Garden Warblers (*Silvia borin*; Hobson and Bairlein 2003). Because feathers were lipid-extracted but invertebrates were not, I used an equation from McConnaughey and McRoy (1979) to normalize $\delta^{13}C$ values based on C/N ratios, thus reducing the effect of varying lipid concentrations on $\delta^{13}C$ signatures of invertebrates. This adjustment had the strongest effect on millipedes, increasing $\delta^{13}C$ signatures by a maximum of 1.17‰, which did not have a significant impact on mixing model output. Lipids were not removed from aquatic invertebrates because lipid-extracted and non-extracted samples did not differ isotopically (Chaloner et al. 2002). I used only recently grown feathers in the mixing model and conducted a separate analysis on each wren, and I also analyzed the mean wren signature above and below the falls at each watershed. I used a tolerance of ± 0.6‰ and an increment of 4% in the mixing model. These values are quite high but were necessary to accommodate the high isotopic variability in invertebrate prey groups and within wren populations (Phillips and Gregg 2003). Two individuals with very low $\delta^{13}C$ values were omitted from the mixing model analysis because their signatures fell outside the distribution of source isotopic signatures.

2.4. Results

Winter Wrens

Wrens exhibited a high degree of variation in $\delta^{15}N$ and $\delta^{13}C$, which approximated the variation observed in invertebrate groups (Figure 2.1). $\delta^{15}N$ values for Winter Wren feathers ranged from -0.81 to 17.75‰ at the Clatse River and -0.02‰ to 15.82‰ at the Neekas River. Given a diet-tissue discrimination factor of 4.0‰ for ^{15}N (Hobson and Bairlein 2003), this range spans 4-5 trophic levels. $\delta^{13}C$ values were slightly less variable, and ranged from -25.95 to -18.07‰ at the Clatse River and –25.63 to –20.96‰ at the Neekas River (Figure 2.1).

Feather isotope signatures differed depending on position above and below the waterfall barrier and feather type. When examining all wren feathers, mean $\delta^{15}N$ values were higher below the falls than above the falls at both watersheds, whereas $\delta^{13}C$ values did not differ significantly (Table 2.1). General linear model output indicated that falls, feather type, and the interaction between falls and feather type accounted for significant amounts of variance in feather $\delta^{15}N$ (all $p < 0.05$), whereas $\delta^{15}N$ did not vary depending on watershed or age group (both $p > 0.05$). Variation in $\delta^{13}C$ was predicted by location above or below the falls and the interaction between falls and feather type (both $p < 0.05$), whereas feather $\delta^{13}C$ values did not vary with age, watershed, or feather type (all $p > 0.05$). Contour feathers generally had higher $\delta^{15}N$ and $\delta^{13}C$ values than retrices, and this was more pronounced below the falls (Figure 2.1).

When I considered only recently grown feathers, the isotopic differences between above and below falls birds became even more distinct (Figure 2.2, Table 2.1). Due to the mobility of individual Winter Wrens, especially dispersing juveniles, a subset of feathers collected for isotope analysis may have been grown at locations other than study sites. I attempted to limit spatial variability among individuals by only examining new feathers that had been replaced by recaptured wrens or that were still partially enclosed in sheaths. In the general linear model, position above or below the falls was the only variable to account for significant amounts of variation in $\delta^{15}N$ ($p < 0.001$). Mean $\delta^{13}C$ values appeared to be higher below the falls (Figure 2.2); but this was not significant (Table 2.1), and falls was not a significant predictor of variance in $\delta^{13}C$, nor was watershed, age, or feather type (all $p > 0.05$). There was a significant correlation between $\delta^{15}N$ and $\delta^{13}C$ in birds captured below the falls (Spearman's $R = 0.875$, $p<0.001$, $n = 13$) but not above the falls (Spearman's $R = -0.429$, $p = 0.397$, $n = 6$). Variance in both $\delta^{15}N$ and $\delta^{13}C$ was greater below the falls than above the falls ($\delta^{15}N$: $p = 0.011$; $\delta^{13}C$: $p = 0.023$).

In order to observe variation in the short-term diet of Winter Wrens, I investigated isotopic signatures of fecal samples collected from wrens above and below the falls during the autumn. High isotopic variability was observed at both watersheds, where $\delta^{15}N$ values ranged from –1.95 to 12.53‰ and from 0.43 to 16.58‰ at the Clatse and

Neekas, respectively (Figure 2.3). $\delta^{13}C$ values ranged from –29.11 to –23.04‰ and –29.40 to –22.47‰ at the Clatse and Neekas Rivers, respectively. Both $\delta^{15}N$ and $\delta^{13}C$ values of feces were higher below the falls (Table 2.1), and general linear models indicated that variation in these isotopes was described by position above or below the falls only ($p < 0.05$). $\delta^{15}N$ and $\delta^{13}C$ were positively correlated below the falls (Spearman's R = 0.691, p = 0.003, n = 16) but not above the falls (Spearman's R = 0.200, p = 0.606, n = 9).

Invertebrates

Isotopic differences were detected among invertebrate groups and across the waterfall barrier (Figure 2.1, Table 2.2). With the inclusion of Collembola (Clatse: N = 8, Neekas: N = 8) and fly larvae (Clatse: N = 4, Neekas: N = 24), data from Hocking and Reimchen (2002), and additional specimens of spiders (Clatse: N = 59, Neekas: N = 57) and millipedes (Clatse: N = 9, Neekas: N = 15), the isotopic range of the litter food web was characterized. $\delta^{15}N$ values among all invertebrates ranged from -1.84‰ to 15.30‰ on Clatse and -1.33‰ to 16.30‰ on Neekas, while $\delta^{13}C$ values ranged from -26.62‰ to -18.36‰ at Clatse and -27.48‰ to -17.63‰ at Neekas River. On both watersheds, invertebrate $\delta^{15}N$ differed substantially among groups ($p < 0.001$) and across the waterfall barrier to salmon ($p < 0.001$). $\delta^{13}C$ values differed among invertebrate groups (Clatse: $p < 0.001$; Neekas: $p < 0.001$) but did not differ above and below the falls (Clatse: p = 0.569; Neekas: p = 0.876). Fly larvae from salmon carcasses had highly enriched signatures of both $\delta^{15}N$ and $\delta^{13}C$ relative to other invertebrate groups and were not present above the falls. Of the terrestrial groups, spiders had the highest $\delta^{15}N$ signatures, millipedes had the highest $\delta^{13}C$ signatures, and Collembola typically had the lowest $\delta^{15}N$ and $\delta^{13}C$ signatures (Figure 2.1).

Mixing Model

Wrens consumed varying proportions of salmon-enriched invertebrates and fly larvae, as illustrated by isotopic mixing model (Table 2.3). Higher proportions of marine-enriched invertebrates were observed in the mean wren diet below the falls (Clatse: 44-92%; Neekas: 40-92%) than above the falls (Clatse: 4-52%; Neekas: 4-28%). Extremely low proportions of fly larvae were found in the mean diet of wrens above the falls (Clatse: 0-8%; Neekas: 0-4%), whereas the mean wren diet below the falls was slightly more variable, composed of 4-28% fly larvae at the Clatse and 0-16% at the Neekas (Table 2.3). Up to 76% fly larvae were observed in certain individuals below the falls. On numerous occasions in the autumn, we observed Winter Wrens foraging for larvae on and around salmon carcasses, consuming up to 60 larvae at a time.

Dietary Shift

I examined seasonal shifts in the diet of Winter Wrens by collecting multiple feather samples representing different time periods from individual birds. Substantial isotopic shifts between feathers grown in the summer and autumn were observed in most individuals (Figure 2.4). In most cases where multiple types of feathers were obtained, birds were young of the year and summer feathers therefore represented the nestling diet. Shifts in $\delta^{15}N$ were as high as 14.26‰ for a single individual, and were almost always positive, suggesting that wrens fed at higher trophic levels in the fall than during the summer. Birds captured below the falls had larger shifts in $\delta^{15}N$ than above falls birds, and these shifts often corresponded with shifts in $\delta^{13}C$, suggesting that the presence of SDN may influence these shifts.

2.5. Discussion

The isotopic data gathered in this study provides evidence for the uptake of salmon-derived nutrients by an insectivorous songbird, the Winter Wren. This study advances research documenting the array of aquatic and terrestrial species that incorporate salmon-derived nutrients and furthers our understanding of the ecological consequences of declining salmon on the west coast of North America.

Comparisons across the waterfall barrier

The potential litter invertebrate prey for wrens, including Collembola, millipedes and spiders, were highly enriched in ^{15}N below the falls compared to above the falls on both watersheds. The absence of ^{13}C enrichment in these groups, in concert with observed enrichment of ^{15}N below the falls in vascular and non-vascular plants from these sites (Mathewson et al. 2003, Wilkinson et al. 2004), indicates that these species obtain salmon-derived nitrogen indirectly through soil and plant-mediated pathways rather than by direct consumption of salmon. In contrast, fly larvae collected from salmon carcasses at both watersheds exhibited the highest $\delta^{15}N$ and $\delta^{13}C$ signatures of all invertebrate groups and represent an extension of the marine food chain not available to consumers above the falls. Pink (*O. gorbuscha*) and chum (*O. keta*) salmon have isotope signatures that range from approximately 11‰ to 14‰ for $\delta^{15}N$ and -22‰ to -18‰ for $\delta^{13}C$ and occupy a trophic position of 4-5 in the marine food chain (Welch and Parsons 1993; Kaeriyama et al. 2004). Mean isotopic signatures in fly larvae collected from salmon carcasses were 15.02‰ for $\delta^{15}N$ and -18.70‰ for $\delta^{13}C$ indicating a 5th-6th trophic position in the marine food chain. Insect predators of fly larvae would be expected to be even more enriched in ^{15}N and ^{13}C, thus further expanding the isotopic range of prey available to wrens below the falls.

Despite the mobility of Winter Wrens, I detected clear differences in $\delta^{15}N$ signatures among birds separated by only a few hundred meters above and below the waterfalls, and these differences were accentuated in recently grown feathers and fecal samples. Winter Wrens below the falls were only marginally enriched in ^{13}C. The most likely explanation for the enrichment in ^{15}N but not ^{13}C is that wrens, for the most part, consume invertebrates that are themselves enriched in salmon-derived nutrients through indirect, or plant-mediated pathways. However, certain individuals below the falls with high ^{15}N were also enriched in ^{13}C, indicating that salmon-derived nutrients are acquired by some wrens through direct consumption of fly larvae associated with salmon carcasses enriched in both isotopes. The fact that fecal samples collected during the spawning period below the falls were enriched in both isotopes provides further evidence for the consumption of fly larvae from salmon carcasses.

Mixing Model

Results from mixing models indicated differences in consumption of marine-enriched invertebrates by wrens above and below the falls. Below the falls, marine-enriched invertebrates comprised the majority of the diet for most wrens, and the consumption of fly larvae was low overall except for a few individuals (for example, fly larvae represented between 72% and 76% of the diet of one individual). It is likely that many feathers used in this study were grown before the consumption of fly larvae in the fall and my estimates of the importance of fly larvae to wrens around salmon streams are therefore conservative. Nevertheless, mixing model results indicate that wrens acquire salmon-derived nutrients primarily through indirect (ie, plant-mediated) pathways, and to a lesser extent through the direct consumption of fly larvae.

In this study, the isotopic mixing model employs several major assumptions and therefore should be interpreted cautiously. First, the inclusion of aquatic invertebrates collected from another location brings potential error into the model, as isotopic signatures of consumers can vary geographically (Kelly 2000). However, aquatic invertebrates are likely to be integral to the diet of riparian-dwelling Winter Wrens (Murakami and Nakano 2001) and to omit this group would be to ignore a potentially important food source. Because signatures of aquatic invertebrates fell within the isotopic range of other invertebrate groups, they were unlikely to substantially alter output of the mixing model. An additional assumption is that all possible food sources to Winter Wrens were included in the mixing model. This, in reality, would be extremely difficult as Winter Wrens are generalist insectivores that exploit a huge variety of prey in multiple different forest microhabitats. It is therefore likely that invertebrates groups that were omitted, such as understory herbivores, may have expanded the isotopic range of food sources available to wrens in the mixing model. A third assumption was that feathers from wrens above or below falls sites were grown on-site. The fact that we included only recently grown feathers in mixing models limited, but did not rule out, this possibility and wrens sampled may well have grown their feathers at other locations. The movement of birds across the waterfall barrier if anything would make it more difficult to detect an isotopic difference, and my results are therefore conservative. Lastly, I have assumed that isotopic differences between birds and invertebrates captured above and below the waterfalls are due to the influence of salmon-derived nutrients. Slight differences related to slope, mineral composition of bedrock, and soil decomposition rates, can lead to differences in isotopic signatures of plants and consumers (Nadelhoffer and Fry 1994). Because we used a within-watershed control to compare systems with and without salmon, differences between sites were minimized. To attempt to further minimize potential differences between sites above and below the falls, banding stations were no more than 600m apart and were similar in slope, proximity to the stream, and forest structure.

Isotopic variation within populations of Winter Wrens

The isotopic signatures of Winter Wrens detected in this study provide an example of unusually large intra-specific variation (δ^{15}N ranging from -0.81 to 17.75‰), resulting from an isotopically variable prey base that includes both terrestrial and marine food webs. Wrens captured below the falls had particularly high isotopic variance, and this is likely due to the exploitation of fly larvae, as well as multiple trophic levels of the terrestrial prey base. Other studies of wild birds in non-salmon enriched ecosystems show significantly less within-population variation in feather δ^{15}N (Thompson et al. 1995, Schmutz and Hobson 1998, Herrera et al. 2003). High within-population variability in isotope signatures can reflect dietary specialization within a population (Gu et al. 1997, Vander Zanden et al. 2000, Bolnick et al. 2003, although see Matthews and Mazumder 2004).

Winter Wrens are thought to be generalists that feed on a variety of invertebrate orders including Coleoptera, Aranaea, Diptera, Lepidoptera and Hymenoptera, which range in guild from detritivores and herbivores to scavengers and predators (Van Horne and Bader 1990, Hejl et al. 2002). Individual wrens have been shown to temporarily specialize on certain prey items that are particularly abundant at a given time (Bent 1948, Armstrong and Whitehouse 1977). True generalists are defined as feeding at random on prey from multiple trophic levels (Van Valen 1965). For populations of true generalists, one would expect high isotopic variance in tissues representing the short term, because there is high variance among individual diets over the short term. Conversely, given a longer time period, generalists will have fed on multiple trophic levels, and isotopic signatures of tissues representing the long-term diet will thus have low variance (Bearhop et al. 2004). In Winter Wrens, the large amount of isotopic variance in both feces and feathers, representing the short-term and longer-term diet respectively, suggests that individuals specialize on distinct trophic levels, at least for the duration of feather growth (two to four weeks). Flexibility in specialization may be adaptive in an environment supporting high densities of individuals; generalists often exhibit individual specialization when population niche width is large (Van Valen 1965) and when intra-specific competition exceeds inter-specific competition (Bolnick et al. 2003). This may be the case for Winter Wrens, who feed on a wide array of prey and have relatively little niche overlap with other species in forests of the Pacific Northwest (Shaw and Flick 1999). Winter Wrens are likely to be opportunistically consuming prey according to its relative abundance; for example, when fly larvae are hatching *en masse* out of salmon carcasses, certain wrens with carcasses in their territories likely focus on this resource.

Organisms follow a continuum of foraging strategies, where certain individuals consistently specialize on the same food item over time, and others feed opportunistically based on availability. When isotopic signatures of feathers grown during the summer were compared to those grown during the fall, large temporal shifts in diet were evident. These shifts in the isotopic signatures of individual Winter Wrens indicate that they are not true specialists, but more likely switch their diet opportunistically in accordance with food availabilitiy (Warburton et al. 1998). When feathers grown in the summer were compared with feathers from the same individual grown in the fall, large isotopic shifts (up to 14.26‰ shift in $\delta^{15}N$) reflected significant dietary shifts in wrens from summer to fall. These shifts are substantially higher than individual isotopic shifts recorded in other species in the wild (Thompson et al.1995, Darimont et al. 2002, Cerling et al. 2004).

There are numerous reasons why wrens, particularly those captured below the falls, experienced such dramatic isotopic shifts. Individual shifts in wrens were not likely a function of seasonal isotopic variation in their prey; overall, no seasonal differences were observed in nitrogen or carbon isotope signatures in both Collembola and spiders (Morgan Hocking, personal communication). The observed positive shifts in $\delta^{15}N$ are likely due to wrens feeding higher on the terrestrial food chain in the autumn than in the summer. The birds from which I collected two generations of feathers were mostly hatch-year birds and therefore isotopic shifts represent the difference between the summer nestling diet and the fall diet. It is possible that adults selectively feed nestlings arthropods that occupy low trophic levels, whereas arthropods that occupy higher trophic levels (such as beetles and spiders) are consumed later in the season. Causal factors for this shift in diet likely include changes in relative abundance of different prey items over the season. For example, a high abundance of larval herbivores such as caterpillars in the summer and predators such as spiders in the fall would cause wrens to shift their diet accordingly.

Large shifts in isotopic signatures of wrens captured below the falls may also be a result of dispersal from habitats far from salmon streams into riparian areas bordering salmon streams. For example, many juvenile birds captured below the falls may have hatched in other areas but dispersed to salmon streams where they completed their first pre-basic molt. This would result in the isotopic enrichment of new feathers that were grown in a salmon-influenced habitat compared to depleted summer-grown feathers. In addition, a dietary shift from the terrestrial food chain in the summer to partial exploitation of the marine food chain, ie fly larvae, in the autumn would increase the magnitude of the isotopic shift. The positive shift in $\delta^{15}N$ corresponding with positive shifts in $\delta^{13}C$ in several wrens lends support to this idea. However, more data is required from birds above the falls in order to determine how much of this shift is due to the presence of salmon.

In conclusion, through using stable isotope analysis, I was able to investigate the diffusion of salmon-derived nutrients into a higher vertebrate consumer, the Winter Wren. My results indicate that salmon-enriched invertebrates, and for some individuals, salmon-hatched larvae, are important components of the diet of Winter Wrens that occur around salmon streams. Winter Wrens are probably not unique in their use of salmon-derived nutrients, which likely could be traced in many species of passerine that inhabit riparian areas adjacent to salmon streams. These areas, characterized by an abundance of carcass-consuming insects (Wipfli et al. 1998) and high plant productivity (Helfield and Naiman 2001), may provide increased access to food resources, resulting in greater density of songbirds (Gende and Willson 2001). The annual spawning events of salmon in the Pacific Northwest constitute a large-scale process intrinsic to the terrestrial ecology of this region, and the consequences of widespread declines in salmon populations over the past century (Gresh and Lichatowitch 2000) are poorly understood and may be substantial.

2.6. Acknowledgements

I would like to thank Jocelyn Akins, Janine Arnold, Jesse Beaudin, Chris Darimont, Larry Jorgensen, Karen Petkau, Sara Steinke, Mike Windsor, Buddy Windsor, and Raincoast Conservation Society for assistance in the field, and the Heiltsuk Nation for allowing this study to take place on their territory. Major thanks are owed to Morgan Hocking for providing data, advice, editing, and help in the field. Thanks are also owed to Blake Matthews and Alan Burger for review of the manuscript, Don Phillips for help with the isotopic mixing model, and two anonymous reviewers for valuable comments. We thank Myles Stocki at the Stable Isotope Facility at University of Saskatchewan, and Jan Addison, Rob Bennett, and Monty Wood for invertebrate identification. Financial aid was provided by the Natural Sciences and Engineering Research Council of Canada, Friends of Ecological Reserves, The David Suzuki Foundation, Bird Studies Canada, Environment Canada Science Horizons Program, and the Mountain Equipment Co-op Environment Fund.

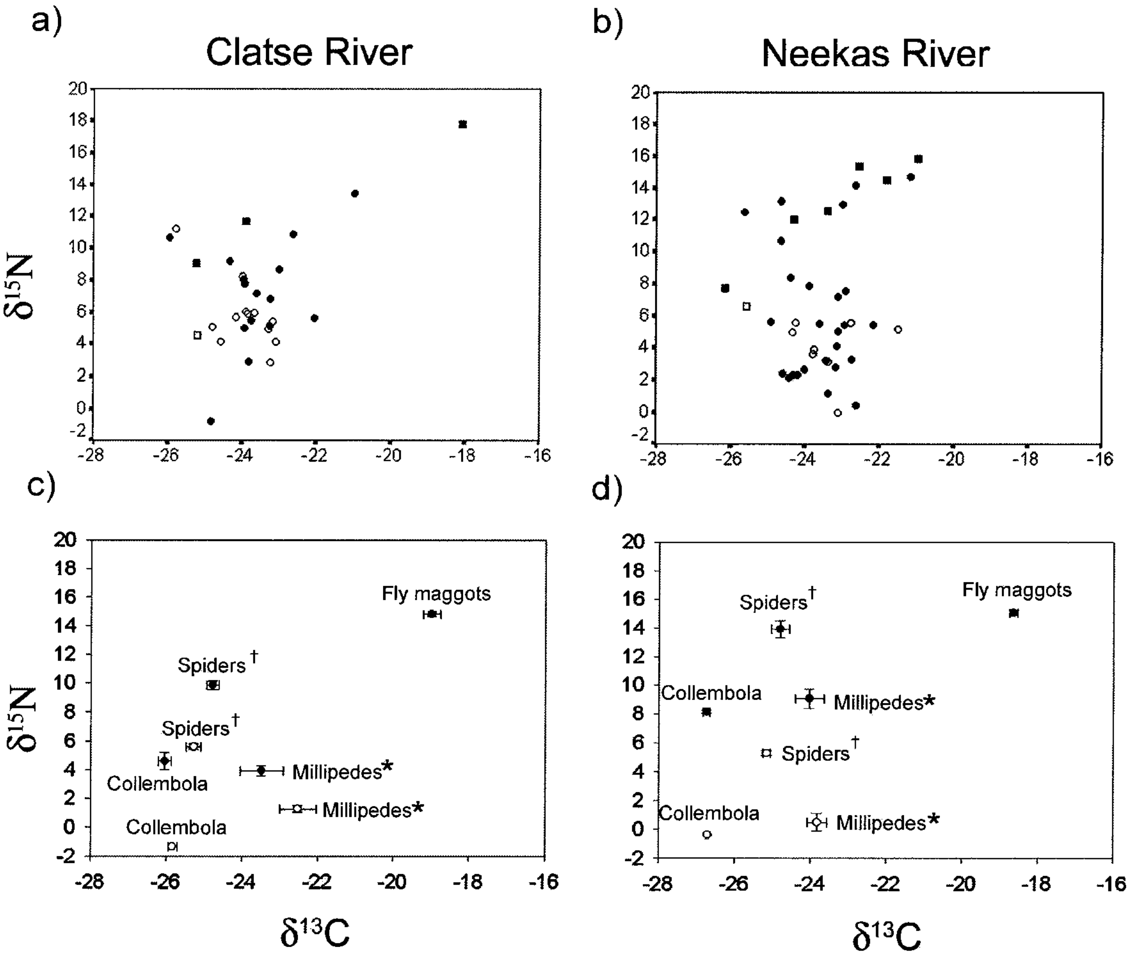

Figure 2.1. $\delta^{15}N$ and $\delta^{13}C$ signatures for feathers of Winter Wrens (a,b) and arthropod taxa (c,d) collected from the Clatse (a,c) and Neekas (b,d) rivers, British Columbia. Solid symbols reflect individuals collected below the falls, open symbols represent individuals collected above the falls. Circles represent tail feathers (retrices) and squares represent body feathers (contours). Error bars reflect standard error. *represents data presented in Hocking and Reimchen (2002); † represents a combination of data presented in Hocking and Reimchen (2002) and unpublished data.

Table 2.1. Mean isotopic signatures of feathers and feces collected from wrens captured above and below the falls at Clatse Creek and Neekas River on the central coast of British Columbia. T-tests were used to determine whether isotopic signatures differed significantly across the waterfall barrier.

Tissue type	River	Location	$\delta^{15}N$	Std. Dev.	Significance	$\delta^{13}C$	Std. Dev.	Significance	N
All feathers	Clatse	Below Falls	8.01	4.14	0.050	-23.35	1.73	0.195	18
		Above Falls	5.67	2.09		-24.04	0.83		13
	Neekas	Below Falls	7.51	4.87	0.005	-23.50	1.16	0.807	32
		Above Falls	4.25	1.94		-23.60	1.14		9
Recently grown feathers	Clatse	Below Falls	12.97	3.66	0.030	-22.03	3.18	0.330	4
		Above Falls	5.86	0.15		-23.88	0.20		4
	Neekas	Below Falls	12.09	3.34	0.005	-23.18	1.71	0.291	9
		Above Falls	4.67	1.64		-24.37	1.05		3
Feces	Clatse	Below Falls	9.18	2.59	< 0.001	-25.05	1.48	0.009	12
		Above Falls	0.67	3.30		-27.27	1.06		5
	Neekas	Below Falls	9.31	4.34	0.001	-25.32	5.28	0.042	8
		Above Falls	1.82	1.40		-27.51	1.20		7

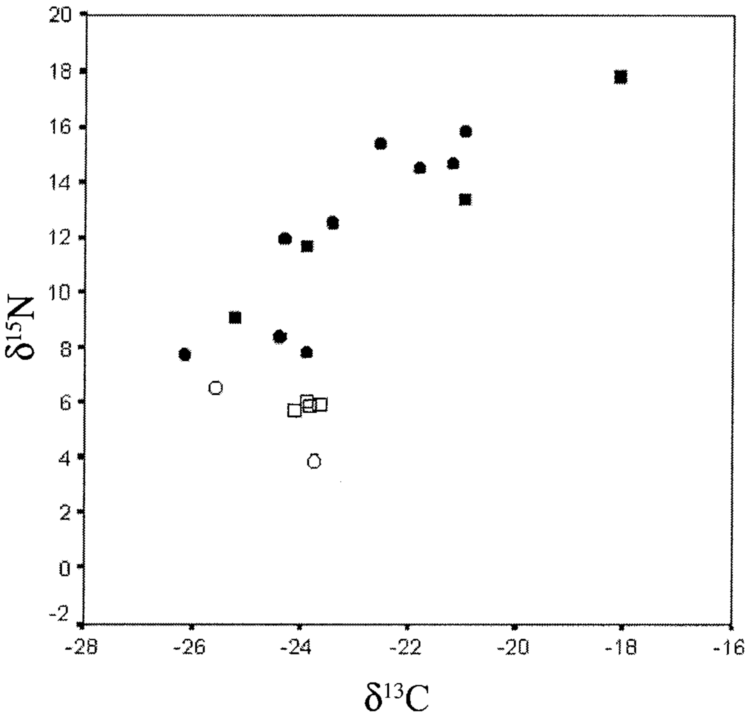

Figure 2.2. $\delta^{15}N$ and $\delta^{13}C$ values for recently grown Winter Wren feathers collected above (open symbols) and below (solid symbols) the falls at the Clatse (squares) and Neekas rivers (circles).

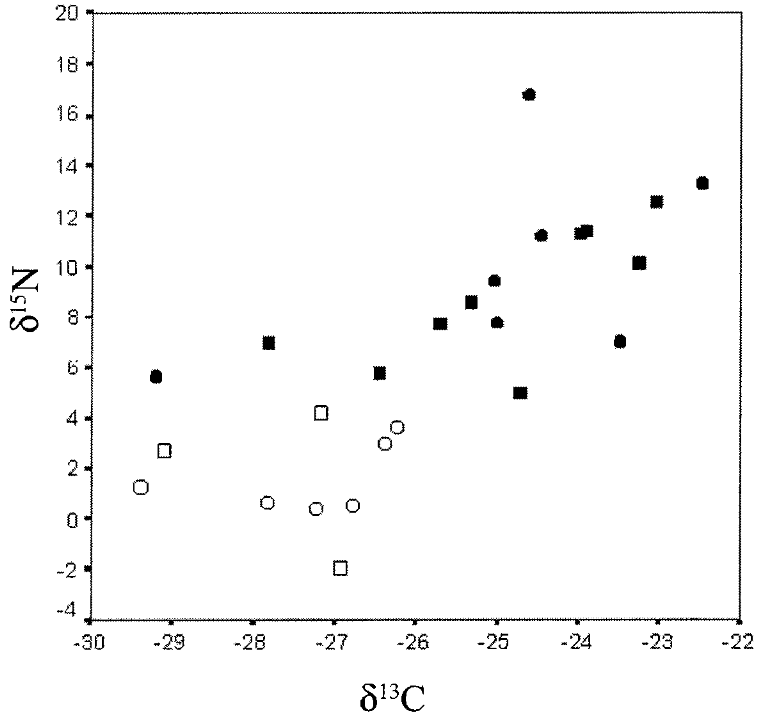

Figure 2.3. $\delta^{15}N$ and $\delta^{13}C$ values of Winter Wren feces collected from above (open symbols) and below (solid symbols) the falls at Clatse (squares) and Neekas rivers (circles).

Table 2.2. Isotopic signatures for prey sources used in the mixing model. Invertebrates were obtained from above (AF) and below (BF) the waterfalls on three salmon-bearing watersheds. Values for aquatic invertebrates were obtained from Chaloner et al. (2002). Values shown have been adjusted for fractionation by 4‰ for $\delta^{15}N$ and 2.7‰ for $\delta^{13}C$. $\delta^{13}C$ values for terrestrial invertebrate groups have been normalized for lipid content based on C/N ratios (McConnaughey and McRoy 1979).

	Clatse Creek		Neekas River		Margaret Creek	
Invertebrate Group	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$
Fly Larvae	18.80	-15.85	19.06	-14.55	-	-
Collembola BF	8.00	-23.99	11.33	-24.56	-	-
Collembola AF	2.62	-23.72	3.32	-24.10	-	-
Millipedes BF	7.93	-19.70	13.06	-20.18	-	-
Millipedes AF	5.26	-18.85	4.50	-19.95	-	-
Spiders BF	13.57	-22.81	17.28	-22.94	-	-
Spiders AF	9.27	-22.78	9.59	-23.02	-	-
Aquatic BF	-	-	-	-	11.50	-23.50
Aquatie AF	-	-	-	-	5.40	-25.70

Table 2.3. Contributions of fly larvae, Marine-enriched invertebrates (Collembola, millipedes, spiders, aquatic invertebrates collected from below the falls) and non-enriched invertebrates (same groups collected from above the falls) to Winter Wren diets (recently grown feathers only) using the mixing model of Phillips and Gregg (2003). Shown are isotopic signatures of wren feathers and possible contributions of each source to the diet. Minimum (1st percentile), mean, and maximum values (99th percentile) are given, accounting for 98% of all possible solutions. Each row represents an individual wren and values in bold represent model output for the mean of the above individuals. The mixing model was run at increments of 4% and a tolerance of 0.6‰ except for two outlying individuals.

Location			Fly larvae			Marine - enriched Invertebrates			Non - enriched Invertebrates		
	$\delta^{15}N$	$\delta^{13}C$	1%	mean	99%	1%	mean	99%	1%	mean	99%
Clatse River Above Falls	6.02	-23.88	0.00	0.01	0.08	0.04	0.27	0.56	0.44	0.72	0.96
	5.91	-23.66	0.00	0.01	0.08	0.04	0.26	0.56	0.44	0.72	0.96
	5.67	-24.14	0.00	0.01	0.08	0.00	0.23	0.48	0.52	0.77	0.96
	5.85	-23.83	0.00	0.01	0.08	0.04	0.25	0.52	0.48	0.73	0.96
	5.86	**-23.88**	**0.00**	**0.01**	**0.08**	**0.04**	**0.24**	**0.52**	**0.48**	**0.75**	**0.96**
Clatse River Below Falls	13.40	-20.96	0.16	0.31	0.44	0.24	0.52	0.76	0.00	0.17	0.40
	9.05	-25.21									
	11.66	-23.89	0.00	0.00	0.04	0.64	0.85	1.00	0.00	0.15	0.32
	17.75	-18.07	0.72	0.75	0.76	0.16	0.23	0.28	0.00	0.02	0.08
	12.97	**-22.03**	**0.04**	**0.17**	**0.28**	**0.44**	**0.70**	**0.92**	**0.00**	**0.13**	**0.32**
Neekas River Above Falls	3.87	-23.75	0.00	0.00	0.04	0.00	0.04	0.12	0.88	0.95	1.00
	6.56	-25.58	0.00	0.00	0.04	0.04	0.16	0.28	0.72	0.84	0.96
	4.67	**-24.37**	**0.00**	**0.00**	**0.04**	**0.04**	**0.16**	**0.28**	**0.72**	**0.84**	**0.96**
Neekas River Below Falls	14.70	-21.19	0.04	0.21	0.32	0.40	0.64	0.88	0.00	0.15	0.32
	7.79	-23.88	0.00	0.02	0.12	0.08	0.31	0.52	0.48	0.67	0.88
	8.37	-24.39	0.00	0.01	0.08	0.12	0.38	0.60	0.40	0.61	0.84
	15.39	-22.55	0.00	0.06	0.16	0.64	0.83	1.00	0.00	0.11	0.24
	11.98	-24.31	0.00	0.00	0.04	0.52	0.77	1.00	0.00	0.23	0.48
	12.55	-23.41	0.00	0.03	0.12	0.48	0.73	0.96	0.04	0.24	0.48
	14.51	-21.80	0.00	0.14	0.28	0.48	0.71	0.96	0.00	0.15	0.32
	15.82	-20.96	0.12	0.24	0.36	0.48	0.66	0.88	0.00	0.10	0.24
	7.72	-26.15									
	12.09	**-23.18**	**0.00**	**0.04**	**0.16**	**0.40**	**0.69**	**0.92**	**0.04**	**0.28**	**0.52**

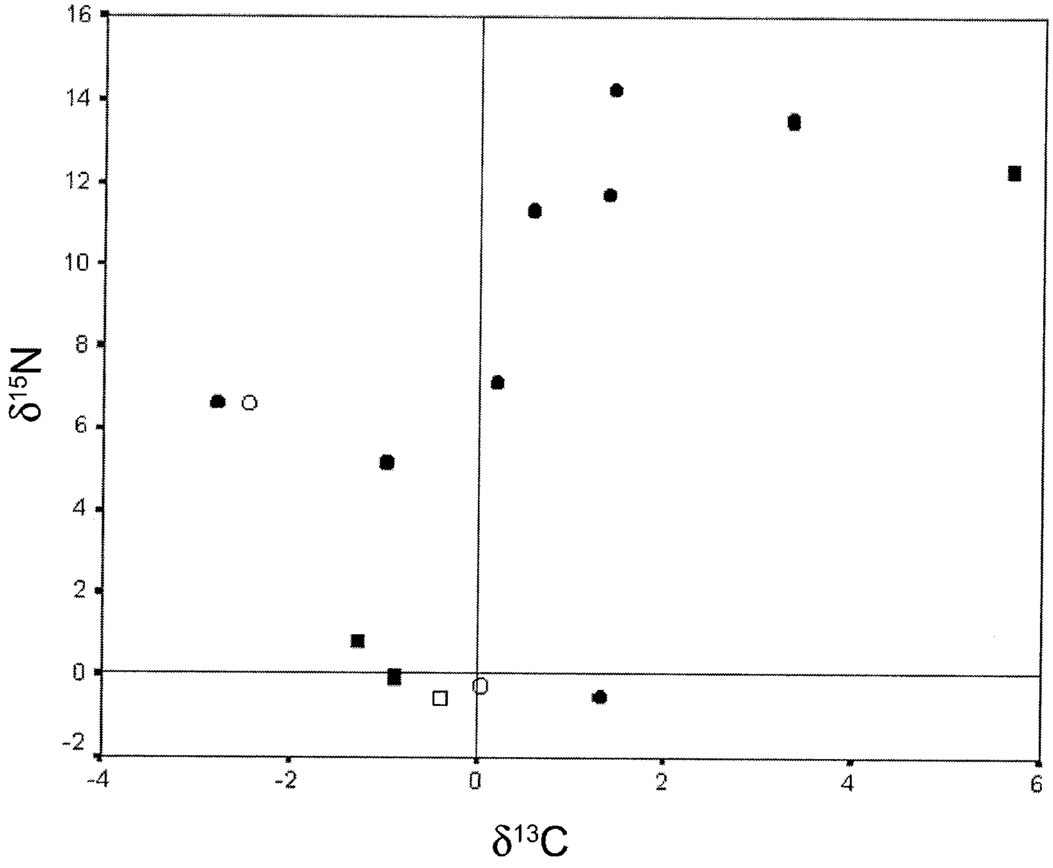

Figure 2.4. Shift in $\delta^{15}N$ and $\delta^{13}C$ signatures for individual wrens collected above (open symbols) and below (solid symbols) the falls at Clatse (squares) and Neekas rivers (circles). Shifts were calculated by subtracting isotopic signatures for summer-grown feathers from fall-grown feathers.

Chapter 3

Presence of salmon increases passerine density on Pacific Northwest streams

3.1. Abstract

The annual migration of Pacific salmon (*Oncorhynchus* spp.) to freshwater streams and lakes provides an important nutrient subsidy to terrestrial systems in North America. Nutrients from salmon enter and fertilize terrestrial systems primarily via wildlife-mediated transfer of carcasses into the riparian zone. As a result, heightened plant productivity and invertebrate biomass have been detected in and around salmon streams, and may have consequences for upper-level consumers such as songbirds. In this study, I investigate differences in breeding songbird density above and below a waterfall barrier to salmon on two streams on the central coast of British Columbia. Significant differences in songbird density were observed across the waterfall barrier, where density was higher in salmon-influenced areas. When assessing the predictive power of various habitat-related variables, position above or below the falls was a good predictor bird density, as was proximity to the stream and to a lesser extent, forest community structure. Increased densities of birds around salmon streams likely result from increased availability of food, as well as forest structure and plant species composition. Salmon-derived nutrients in terrestrial systems have the potential to influence the densities of upper-level consumers and likely have significant implications for overall ecosystem health and stability.

3.2. Introduction

Nutrient subsidies are ubiquitous in natural ecosystems and elevate consumer densities above those that can be derived from in situ resources alone (Polis and Strong 1996). Nutrient subsidies can feed consumers directly or by increasing primary productivity, they can result in effects that cascade throughout the food chain. For example, marine intertidal communities are heavily influenced by nutrient subsidies from detrital kelp, which leads to increased densities of intertidal urchins and limpets (Duggins et al. 1989). Also, guano from nesting seabirds results in greater abundance of terrestrial beetles (Sanchez-Pinero and Polis 2000). Coastlines tend to be highly productive as a result of bi-directional nutrient flow from land to ocean and vice-versa (Ray 1988).

One important nutrient subsidy on the north Pacific coast is the annual spawning of anadramous pacific salmon (*Oncorhynchus* spp.). Salmon spend most of their lives sequestering nutrients from the ocean, but spawn and die in freshwater streams and lakes, thus transporting large quantities of marine-derived nutrients to terrestrial ecosystems. Salmon provide a major food source for vertebrates such as bears, marten, wolves, gulls, ravens, and eagles, which actively transfer salmon carcasses into the forest riparian zone, thus fertilizing otherwise nutrient-limited soils (Waring and Franklin1979, Reimchen 1994, Cedarholm et al. 2000, Darimont and Reimchen 2002, Christie and Reimchen *in press*).

The ecological consequences of salmon-derived nutrients are complex and not fully understood, but they include increased vertebrate density, plant productivity, and aquatic and terrestrial invertebrate biomass (Reimchen 1994, Wipfli et al. 1998, Helfield and Naiman 2001). Researchers have traced salmon-derived nutrients into components of terrestrial systems through the enriched isotopic signatures of plants, invertebrates and vertebrates adjacent to salmon streams (Hocking and Reimchen 2002, Darimont and Reimchen 2002, Mathewson et al. 2003). Although the effects of salmon nutrients on primary producers and consumers has been well documented; little is known about the implications for upper-level consumers such as songbirds, which may benefit from the increased plant and invertebrate productivity adjacent to salmon streams. Landbirds are often more abundant in areas of high productivity such as wetlands and riparian areas due to high abundance of invertebrates and greater structural heterogeneity (Wiebe and Martin 1998, Iwata et al. 2003) and respond positively to nutrient inputs to terrestrial systems (Folklord and Smith 1995, Crozier and Gawlik 2002). Stream biota and riparian bird communities are intricately linked, and the diet of some species, such as the Winter Wren, can be composed largely of aquatic macro-invertebrates (Murakami and Nakano 2001 and Nakano and Murakami 2001). A study by Gende et al. (2001) found songbird density and diversity to be slightly higher adjacent to salmon streams than non-salmon bearing streams in Alaska, suggesting that salmon-derived nutrients indirectly influence breeding birds.

In this study I further investigate the effect of salmon on breeding songbirds by comparing density around salmon and non-salmon bearing reaches of rivers on the central coast of British Columbia. My primary study streams had waterfalls partway upstream that blocked the upstream migration of salmon, thus creating a within-watershed control. My objectives were to (1) estimate whether breeding bird density and number of species varied across the waterfall barrier due to the presence of salmon-derived nutrients, and (2) to investigate the effects of salmon in comparison to other habitat variables known to affect songbird density.

3.3. Methods

Study Area

Songbird density was assessed on two salmon-bearing watersheds north of Bella Bella: the Clatse (52° 20.6'N; 127° 50.3'W) and Neekas Rivers (52° 28.4'N; 128° 8.0'W)(Figure 1.1). Both rivers have large runs (over 20,000) of Chum (*O. keta*) and Pink (*O. gorbuscha*) salmon from late August until early November. These watersheds were chosen largely due to the presence of waterfalls part-way upstream (1000m at Clatse Creek and 2100m at Neekas River) that blocked the upstream migration of salmon, thus producing within-watershed controls where aspects of the riparian zone below the falls could be compared to those above the falls, the major difference being the presence of salmon. Clatse Creek was a second order stream with length of 3.44km, whereas Neekas River was a 5.9km, third order stream. Both watersheds occur in the Coastal Western Hemlock Biogeoclimatic Zone characterized by infrequent, small-scale disturbances, high annual precipitation, and nutrient-poor soils. The most common tree species were Western Hemlock (*Tsuga heterophylla*), Western redcedar (*Thuja plicata*), Sitka Spruce (*Picea sitchensis*), and Amabilis Fir (*Abies amabilis*), with an understory mainly composed of salmonberry (*Rubus spectabilis*), red elderberry (*Sambucus* racemosa), False Azalea (*Menziesii ferruginea*) salal (*Gaultheria shallon*), huckleberry (*vaccinium* spp), and young trees. The only deciduous trees present were Red alder (*Alnus rubrus*) that occurred in a thin band immediately adjacent to the stream. Soils are generally acidic with high organic matter and low rates of decomposition and humus types tend to be mor but become moder/mull in nutrient-rich sites. Logging on study sites was limited to selective harvest of spruce in the early part of the century and a clearcut on Clatse Creek 10-20 years ago, which was not included in point-transect surveys.

Songbird density estimates

Songbird density was assessed on all watersheds using point-transect surveys from 20 June to 16 July in 2002 and from 9 May to 23 July in 2003. Each river was surveyed at least twice throughout the study period, on alternating dates to minimize temporal bias. 8-minute counts were carried out at 100m intervals along transects parallel to the river (Figure 3.1). In 2002, one transect was followed on each side of the river 50m from the riverbank. In 2003, an additional transect 150m from the river was added. Transects continued for 800m above the falls at Neekas River, ending at a lake, and continued for 1km at Clatse Creek. Points at the waterfalls and other points with substantial noise interference were not included in analyses. Each bird seen or heard at any distance during the 8 minutes was identified to species and distance from the observer was also estimated in 2003. Distance estimation was practiced prior to surveys using bird calls or sounds at known distances in order to maximize accuracy. If individual birds were detected at more than one point, the detection at the lowest distance from the observer was counted. Observers were trained in western bird identification and distance sampling during a 1-2 week intensive training period prior to conducting surveys. Surveys began 30 minutes after dawn and continued for no longer than 6 hours. The order that points were visited was rotated so that points were surveyed at varying times in the morning. Point transects were not conducted on rainy or excessively windy days (Beaufort scale > 5).

Vegetation surveys

In order to assess habitat variables that may be associated with bird density and species richness, I carried out vegetation surveys during the spring and summer of 2002 and 2003 at songbird survey points. 30m transects running through the point (15m on either side) were assigned in order to sample shrub cover and tree species composition. The direction of each transect was chosen randomly with a compass. Shrub cover was measured using a visualized 1m^2 quadrat at 5m intervals along the 30m transect to estimate percent shrub cover within the quadrat. Saplings (diameter at breast height (DBH) <10cm) were classified as shrubs. Tree density was measured by counting and identifying to species every tree whose bole fell within 5m on either side of transects, therefore falling within a 300m^2 rectangular area (Figure 3.2). Large trees were identified as those with DBH greater than 55cm. Snags were not identified to species and were counted if height > 2m and DBH > 10cm.

Statistical analysis

I was interested in determining the importance of position above or below the falls in relation to other habitat-relate variables in predicting the density and number of species of songbirds. I therefore used an information theoretic approach (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. When assessing models, it is the relative difference in AIC values among candidate models that is important, rather than absolute AIC values. ΔAIC was calculated as the difference between AIC values of the top-ranked model and all subsequent models. Models with $\Delta AIC \leq 2.0$ are considered to be most strongly supported by the data (Burnam and Anderson 1998). Models were compared to a null model (intercept only). I used the corrected AIC (AIC_c), which adjusts for small sample sizes by balancing the loss of precision when many model parameters are used in a model. I calculated Akaike weights (Burnam and Anderson 1998) for each model, reflecting the probability that the model would be selected as best over repeated samples. In order to assess the relative importance of each explanatory variable, I calculated parameter likelihoods by summing the AIC_c weights of models containing the variable of interest. This was then used to compare the predictive power of different explanatory variables.

General linear models were used to obtain residual sums of squares for AIC_c analysis. Response variables are as follows: density of Winter Wrens (*Troglodytes Troglodytes)*, Varied Thrushes (*Ixoreus naevius*), Swainson's Thrush (*Catharus ustulatus)*, Pacific-slope Flycatchers (*Empidomax difficilis*), Golden-crowned Kinglets (*Regulus satrapa*), Chestnut-backed Chickadees (*Poecile rufescens*), total density including all species, and total number of species detected. Density of individual species was log transformed and expressed as ln(number of detections/point +1). Total density and number of species detected were not transformed because raw data followed a normal distribution. Both years of point-transect data (2002 and 2003) were used in this analysis.

Explanatory variables used in models for all response variables were as follows: river (Clatse vs. Neekas), year (2002 vs. 2003), falls (above vs. below), distance from river (50m vs. 150m), and the interaction term 'falls*distance from river' to determine whether the effect of distance from river varied above and below the falls. In addition, a variable reflecting tree community structure, represented by two principal component factor scores (PC1 and PC2) was used for all response variables.

The original variables used in the principal component analysis were expressed as number of trees (>10cm DBH; >2m height) in the 300m^2 rectangle around each point and were as follows: Western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), Western redcedar (*Thuja plicata*), Red alder (*Alnus rubra*), snags, and number of large trees. I transformed all tree variables to improve normality by adding 1 and taking the natural log of counts. These variables were selected for PC analysis for several reasons. Western hemlock is one of the most common trees on the central coast and was present in most plots. Sitka spruce is a nutrient-rich indicator species that characterizes moist well-drained low elevation sites. Western redcedar has a wide edaphic tolerance, and does not require rich soils (Klinka et al. 1989). Red alder was included because deciduous tree cover has been linked with breeding density of several songbird species (Kirk et al. 1996, Shirley 2004). The number of snags and large trees reflect forest structural attributes that can strongly affect songbird density and species richness (Sharpe 1996, Poulsen 2002). PC1 described approximately 38.04% of total variation, whereas PC2 described 26.55% of total variation in tree variables included (species composition, number of snags, number of large trees). PC1 had positive loadings for Western redcedar (*Thuja plicata*; 0.94) and snags (0.94), whereas PC2 was correlated with positive loadings for Western hemlock (*Tsuga heterophylla*; 0.81), Red alder (*alnus rubrus*; 0.69) and Sitka spruce (*Picea sitchensis*; 0.61). PC1 and PC2 were always kept together in models because I was not interested in the different effects of the two components; moreover, I was interested in the effect of tree community structure as a whole

For certain species (Winter Wren, Swainson's Thrush, and Varied Thrush), percent shrub cover was a useful additional explanatory variable (Campbell et al. 1997, Evans Mack and Yong 2000, Hejl et al. 2002, Shirley et al. 2004). For the response variable 'number of species', I included total number of tree species per plot as an additional possible explanatory variable, because diversity in tree species has been linked with bird diversity (Poulsen 2002).

In all, 20 single model and additive model combinations were tested to account for Winter Wren density, Swainson's Thrush density, Varied Thrush density, and number of species.10 models were used for Pacific-slope Flycatcher density, Golden-crowned Kinglet density, Chestnut-backed Chickadee density, and total density. Sample size was 189 (reflecting number of points surveyed) for all models. To account for variability in year and river, I included these variables in every model. Principal component and linear regression analyses were conducted using SPSS 11.0 (SPSS 2001). For general linear model analyses, assumptions of normality, homoscedascity and collinearity were met (Variance Inflation Factor < 1.5 for all factors).

To conduct a more rigorous test of whether bird density differed over the waterfall barrier, I compared densities above and below the falls within each river, using an independent samples t-test and 95% confidence intervals from Program Distance. Songbird density in 2003 was assessed using the program Distance (version 4.1 release 2;

Buckland et al. 2001). Distance sampling is a useful alternative to traditional point counts because it takes into account differential probability of detection. For example, different species of passerine have varying degrees of detectability depending on behaviour, song frequency and pitch, as well as a host of other variables (Buckland et al. 2001). By modeling the probability of detection at increasing distances from the observer, program Distance is able to account for variability in detection. In contrast, traditional point counts assume constant detectability for different species, observers, habitat types, and distances from the observer. Distance software produces a histogram that models the probability of detection with perpendicular distance away from the observer. A host of key functions (half normal, hazard rate and uniform) and adjustment terms (cosine, simple polynomial, hermite polynomial) are available to model this relationship. I assessed the fits of different combinations of key functions and adjustment terms to the detection curve of each species by using AIC (Akaike's Information Criterion; Burnam and Anderson 1998, Buckland et al. 2001) and Goodness of Fit Chi squared analysis. The area sampled was not fixed; therefore, relative density was estimated instead of absolute abundance. Within years, points were visited multiple (2-4) times by different observers and therefore points were weighted by survey effort.

Detection functions were not estimated separately for observers for a number of reasons. First, sample size was small and I therefore wanted to limit the subdivision of data to maximize the chance of producing unbiased detection probabilities (Buckland et al. 2001). Second, because both observers surveyed each point separately, observer bias was limited. Last, density estimates were generally not different between observers. Songbird data was post-stratified for river and location above or below the falls, to give a total of four density estimates for each species. I assumed that detection functions were similar for both watersheds above and below the falls and therefore pooled detection functions over localities. Only common species (more than 40 observations) were chosen for analysis because rare species with few detections would likely have biased detection functions. 10% of observations at greatest distances from the observer were truncated to improve model fit, and intervals were chosen depending on species to avoid lumping of observations at certain distances (Buckland et al. 2001). I estimated the density of five species (Winter Wren (*Troglodytes Troglodytes*), Swainson's Thrush (*Catharus ustulatus*), Pacific-slope Flycatcher (*Empidomax difficilis*), Golden-crowned Kinglet (*Regulus satrapa*), and Chestnut-backed Chickadee (*Poecile rufescens*) using program Distance. These species were chosen because they were relatively common (over 40 observations) and I was able to fit detection functions to their distributions (GOF tests $p>0.05$). A sub-set of the data was omitted due to small sample size or skewed distributions. For the Varied Thrush (*Ixoreus naevius*), I was unable to obtain a detection function that fit the distribution of data; therefore, no analysis was conducted for this species. Also, analysis was conducted for Swainson's Thrush at Neekas River only because too few birds were detected at Clatse Creek.

Comparisons among rivers

In addition to the above analyses, I compared mean bird density between rivers with and without salmon. Bird abundance in temperate zones is thought to decrease with distance from the mouth of a river and narrowness of the stream channel (Lock and Naiman 1998, Wiebe and Martin 1998), and this phenomenon could potentially bias interpretations of the effect of salmon on bird density, as above-falls sites are further away from the river mouth and may be expected to have fewer birds independent of the effect of salmon. To address this, I sampled 1 kilometer of two additional nearby rivers: Cheenis Creek (128°6'41.79"W; 52°29'37.39"N) and Ripley Creek (127°53'10.84"W; 52°25'56.90"N) on 24 June and 3 June 2003, respectively (Figure 1.1). Both creeks have similar order and magnitude to Clatse and Neekas Rivers; however, both have waterfalls at or close to the mouths, blocking the passage of salmon. This enabled me to compare patterns of bird density with distance upstream on salmon bearing to nearby non salmon-bearing streams. Independent t-tests were used to compare transformed density (ln(number of detections/point +1)) as well as total density and number of species between salmon and non-salmon bearing streams.

3.4. Results

General Linear Models and AIC_c

Position above or below the falls was a highly important predictor of density for all species except for the Chestnut-backed Chickadee. Top models (where $\Delta AIC_c \leq 2.0$) explained between 21% and 49% of the total variation in bird density. In candidate model sets for all analyses except for one (Chestnut-backed Chickadee), all top models included 'falls' as an explanatory variable (Table 3.1). Of the explanatory variables used to model bird density (falls, distance from stream, principal component factor scores, shrub cover and number of tree species), 'falls' had parameter likelihoods between 0.92 and 1.00 in all but one analyses, indicating that only models including this variable were well supported (Table 3.2). The importance of location above or below the falls in predicting songbird density suggests that the presence of salmon in a watershed strongly influences patterns of avian abundance. The variable 'distance from stream' was also present in most top models (Table 3.1) and had high parameter likelihood's, ranging from 0.39 to 1.00 (Table 3.2). For Winter Wren and Swainson's Thrush density, 'falls' and 'distance from stream' were equally important.

The variables 'PC1 + PC2' and 'F*CF' were slightly less important than the above variables in predicting bird density. The combined tree community structure variable (PC1 + PC2) was present in top models for most analyses (Table 3.1), and was reasonably well supported for Winter Wren, Swainson's Thrush, Golden-crowned Kinglet, number of species, and total density (Table 3.2). The interaction term (F*CF) was only well supported in models predicting Swainson's Thrush density, indicating that the effect of distance from stream may have varied above and below the waterfall barrier for this species. Other variables (shrub cover, number of tree species) were largely ineffective in predicting density (Table 3.2). Chestnut-backed Chickadee density was not well explained by any variables, and the null model was the only model supported well by the data.

Songbird density estimates

The density of most species analyzed, as well as total density and number of species detected per point were consistently higher below the falls than above the falls. On transects 50m from the stream, songbird density was 9-230% higher below the falls than above the falls, with an average increase of 100% (Figure 3.2). At transects 150m away from the stream, density increased by 4-292%, where average density increased by 62% below the waterfall barrier (Figure 3.2). Total number of species detected increased below the falls by 54% at 50m from the stream and 24% at 150m from the stream, and total number of detections increased by 83% at 50m from the stream and 39% at 150m from the stream (Figure 3.3). Density differed between transects close and far from the stream, where, except for Winter Wrens, birds tended to be more abundant far from the stream than close to the stream (Figure 3.2, 3.3).

Density estimates using Program Distance were higher below the falls than above the falls for most species; however, for certain species, the effects were small and were only statistically significant at one watershed and not the other (Table 3.3). Winter Wrens had significantly higher densities below the falls at both rivers, whereas Golden-crowned Kinglets and Pacific-slope Flycatchers were higher in density only at Clatse and not Neekas River. Chestnut-backed Chickadee density did not differ over the waterfall barrier at either watershed.

Comparisons among rivers

In addition to the within-watershed control provided by the waterfalls at Clatse and Neekas Rivers, nearby rivers (Cheenis and Ripley Creeks) with obstacles to salmon at the mouths provided additional comparisons. Total bird density decreased with distance away from the mouth of the stream on Neekas (R^2=0.31, n=106) and Clatse (R^2=0.42, n=65) rivers. In contrast, both control streams had very weak relationships between bird density and distance upstream (Cheenis R^2=0.07, n=15; Ripley R^2=0.09, n=28). When mean bird density (birds detected per point) for the first kilometer of Clatse was compared to that of nearby Ripley Creek, the former had greater density for all species except for Chestnut-backed Chickadee (Table 3.4). Total density and number of species was also greater at Clatse Creek than Ripley Creek. Differences between Neekas River and Cheenis Creek were not so obvious. Neekas River had greater numbers of

Winter Wrens, Varied Thrushes, and more species overall; however Pacific-slope Flycatchers were actually more abundant on Cheenis Creek, and all other species did not differ in density between the two watersheds (Table 3.4). When comparing the two salmon streams, overall differences in density and number of species were small. Neekas River had slightly greater densities of all species except for Pacific-slope Flycatcher compared with Clatse Creek. Total density and number of species were also higher at Neekas than Clatse River (Table 3.4).

3.5. Discussion

Data collected from two salmon-bearing streams on the central coast of B.C. demonstrated a distinct change in songbird density over a natural barrier to salmon migration. Songbird density was on average 62-100% higher below the falls than above the falls. Gende and Willson (2001) also found higher densities of passerines on small salmon-bearing streams compared to non-salmon bearing streams in Alaska. The difference in density observed over a sharp ecological barrier indicates that upper-level consumers respond numerically to the presence of salmon-derived nutrients in riparian areas.

Model selection using AIC indicated that position above or below the falls was the most important predictor of songbird density for almost all species analyzed. For the Winter Wren, Varied Thrush, Swainson's Thrush and Golden-crowned Kinglet, the variable "falls" was the best predictor of density in relation to other habitat variables. For total number of species and total density, the variable "falls" was also the best predictor. Further analysis of density above and below the falls using program Distance indicated that for four out of five species analyzed, densities were significantly higher below the falls than above the falls at at least one watershed.

Winter Wrens may be particularly responsive to the presence of salmon-derived nutrients due to their dietary reliance on aquatic macro-invertebrates (Murakami and Nakano 2001, Hejl et al. 2002), which have high densities in and near salmon streams (Wipfli et al. 1998, Minakawa and Gara 1999). In addition, Winter Wrens actively forage on fly larvae hatched from salmon carcasses in the fall (*see Chapter 2.*) and the abundance of this energy- rich resource may influence wren density during the breeding season. Winter Wrens tend to be positively associated with riparian habitat (Waterhouse et al. 2002) and therefore it is not surprising that wrens were more abundant at points close to the stream.

Salmon-bearing reaches may attract Swainson's and Varied Thrushes due to increased availability of arthropods in the riparian zone, and potentially due to increased productivity of berry-producing shrubs. Berry-producing plants produce more fruit after nitrogen fertilization (Penney et al. 2003, Momoh et al. 2004) and fertilization from salmon carcasses may result in heightened fruit production. Fruit production by shrubs such as *vaccinium* spp. and salmonberry (*Rubus spectabilis*) occurs in from May to July (Pojar and MacKinnon 1994), which overlaps with the breeding period and time of counts. Swainson's Thrushes were found in higher densities far from the stream than close to the stream, suggesting that habitat immediately adjacent to the stream is avoided by this species. This may be due to increased chance of nest predation close to the stream (Gates and McKearnan 2003). The importance of the interaction between proximity to the stream and position above or below the falls implies that Swainson's Thrushes may avoid the immediate area next to the stream below the falls but not above the falls, perhaps due to increased predation risk below the falls. Both species of thrush were surprisingly unresponsive to shrub cover, in contrast to findings by Shirley et al. (2004). It may be that the effect of shrub cover on density is masked by the stronger effect of location above or below the falls, or alternatively, that shrub species composition and berry production are more important factors in determining density.

Golden-crowned Kinglets and Pacific-slope Flycatchers forage for arthropods in the upper canopy of mature conifer-dominated forests and likely benefit from the greater biomass of terrestrial and aquatic insects below the falls. Pacific-slope Flycatchers were more abundant at points 150m from the stream, suggesting an avoidance of habitat immediately adjacent to the stream. This species prefers riparian habitat in interior British Columbia but may not be so selective in the wet rainforests of coastal British Columbia, as long as there is adequate mature forest (Lowther 2000, Brand and George 2001).

The Chestnut-backed Chickadee was the only species that did not show a difference in density over the waterfall barrier, reflecting a lack of preference for salmon-bearing reaches by this upper-canopy dwelling insectivore. Unlike other species analyzed, variance in chickadee density was not predicted by proximity to the stream, tree community structure, or falls. This species is an obligate cavity nester (Campbell et al. 1997), and the availability of stumps and snags may be a better predictor of density.

Tree community structure (PC1 + PC2) was a reasonably good predictor of density for several species, including Winter Wren, Swainson's Thrush, and Golden-crowned Kinglet, and was also present in top models for total bird density and number of species. Tree community structure was likely to be partially shaped by the salmon nutrient subsidy, as found by Bartz (2002). The increased availability of soil nutrients below the falls resulted in greater densities of nutrient-rich indicator plants, such as Sitka spruce and salmonberry, whereas higher densities of nutrient-poor indicators were found above the falls at both Clatse Creek and Neekas River (Mathewson et al. 2003, Wilkinson et al. 2005). Shrub and tree species adapted to nutrient-rich soils tend to put fewer resources into secondary metabolites, thus increasing the prevalence of insect herbivores (Witzel and Shevtsova 2004), a potentially important food source to songbirds.

Species richness and overall density were higher below the falls than above the falls, likely due to increased densities of terrestrial and aquatic invertebrates, in conjunction with high plant productivity likely provide favourable habitat for breeding songbirds below the falls, and may even increase habitat carrying capacity for birds. Structural attributes of riparian forests next to salmon streams may favour songbird diversity. High traffic of wildlife traveling to and from the river during the fall causes low-level disturbance of understory plant communities, which potentially leads to greater diversity of plant species and a greater prevalence of gaps in the understory (Bilby et al. 2003). Habitat heterogeneity is directly related to avian richness (Poulsen 2002) and the structural complexity characteristic of salmon streams likely contributes to higher numbers of bird species.

Proximity to the stream was important in predicting total bird density and species richness. Density and number of species were higher at points 150m from the stream compared to 50m from the stream, indicating that most birds avoided habitat immediately adjacent to the stream. Habitats at the stream edge likely have greater rates of nest predation and higher traffic of wildlife. It is likely that predation pressure, whether by mammalian nest predators or by hawks, may be particularly important in shaping avian communities below the falls. Notorious nest predators such as corvids, marten, and red squirrels are also likely to be responding numerically to salmon-derived nutrients and may depress songbird numbers so that they are below habitat carrying capacity.

Gende and Willson (2001) found songbird density and diversity to be strongly correlated with percent deciduous tree cover. Red alder, being the only deciduous tree at my study sites, occurred at extremely low densities on all sites, forming a narrow strip along the stream edge both above and below the falls. Alder was therefore unlikely to strongly influence observed differences in bird density above and below the falls.

Comparisons between salmon streams and nearby streams without salmon showed varying impacts of salmon-derived nutrients on songbird density. The most obvious difference between salmon-bearing and non-salmon bearing streams was the decrease in total bird density with distance upstream that occurred on salmon streams but not non-salmon bearing streams. This result suggests that bird density decreased with distance upstream on the Clatse and Neekas Rivers as a result of the absence of salmon nutrients above the falls. One might suggest that a difference in topography above the falls might be causing declines in bird density; however, on salmon streams, slope if anything decreased with distance from the mouth (Neekas River $R^2 = 0.02$; Clatse Creek $R^2 = 0.28$). Ripley Creek had lower densities for all species except for one (Chestnut-backed Chickadee) when compared with Clatse Creek, as well as lower total density and number of species. Cheenis Creek, on the other hand, had lower songbird densities than Neekas River for some species, such as Winter Wren and Varied Thrush but the reverse was true for other species, such as Pacific-slope Flycatcher. For certain bird species, Cheenis Creek may have equally favorable habitat characteristics to those of a salmon stream, and the benefits of salmon may be superceded in some cases by other forest attributes. Comparisons of multiple streams with and without salmon can be problematic due to major differences that may exist in logging history, topography, and soil dynamics, all of which are likely to affect bird density and diversity. For this reason, emphasis is given in this study to within-watershed as opposed to between-watershed comparisons.

In this study I demonstrate clear differences in songbird density and species richness across a natural barrier to salmon. The central coast of British Columbia has relatively little forest fragmentation, with large expanses of old-growth forest and many still productive salmon streams. This contrasts with southern parts of the province and the U.S., where salmon populations have been decimated (Gresh and Lichatowitch 2000) and forests largely converted to second-growth. Because the central coast is likely to be the focus of resource extraction industries in the near future, it is important to identify and protect areas of high ecological importance. The consequences of large declines in salmon populations to birds are currently unknown, but my findings suggest that the absence of salmon-derived nutrients in riparian areas leads to lower overall songbird density and diversity. As a result, major emphasis should be placed on the protection of salmon populations and spawning habitat. Existing buffer zones around salmon streams are inadequate and only encompass a small proportion of the total area influenced by salmon; therefore, wider buffer zones are required. The conservation of wild salmon populations is critical in maintaining the diffusion of marine-derived nutrients into terrestrial systems, a process that ultimately benefits multiple trophic levels in riparian food chains.

3.6. Acknowledgements

I would like to thank the many people who helped me in the field: Janine Arnold, Morgan Hocking, Karen Petkau, Mike Windsor. Many thanks to Tom Reimchen, Alan Burger, Tyler Lewis, and Jamie Smith for much needed statistical and editorial help. I thank Chris Darimont, Raincoast Conservation Society and Larry Jorgenson for providing accommodation in the field. Thanks to The Natural Sciences and Engineering Research Council of Canada (NSERC), The Friends of Ecological Reserves, The David Suzuki Foundation, Mountain Equipment Co-op Environment Fund, Bird Studies Canada, and Science Horizons Youth Internship Program for financial support, and The Heiltsuk Nation for allowing this study to take place in their territory.

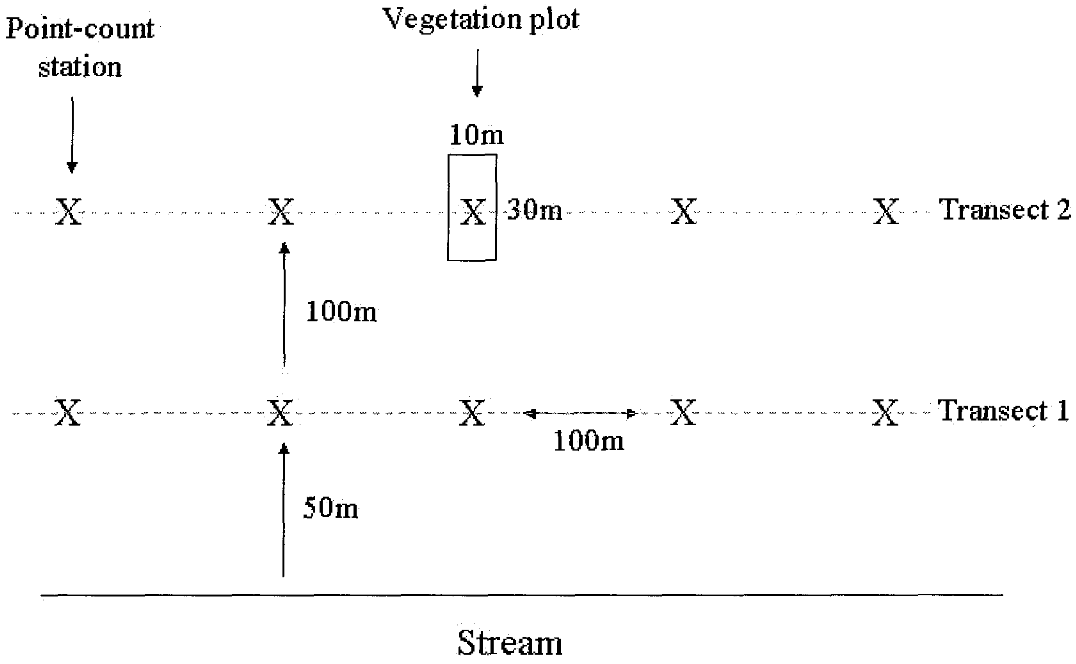

Figure 3.1. Diagram of point transects used for breeding bird census. Rectangular vegetation plots were situated at random directions around each point and one example is shown.

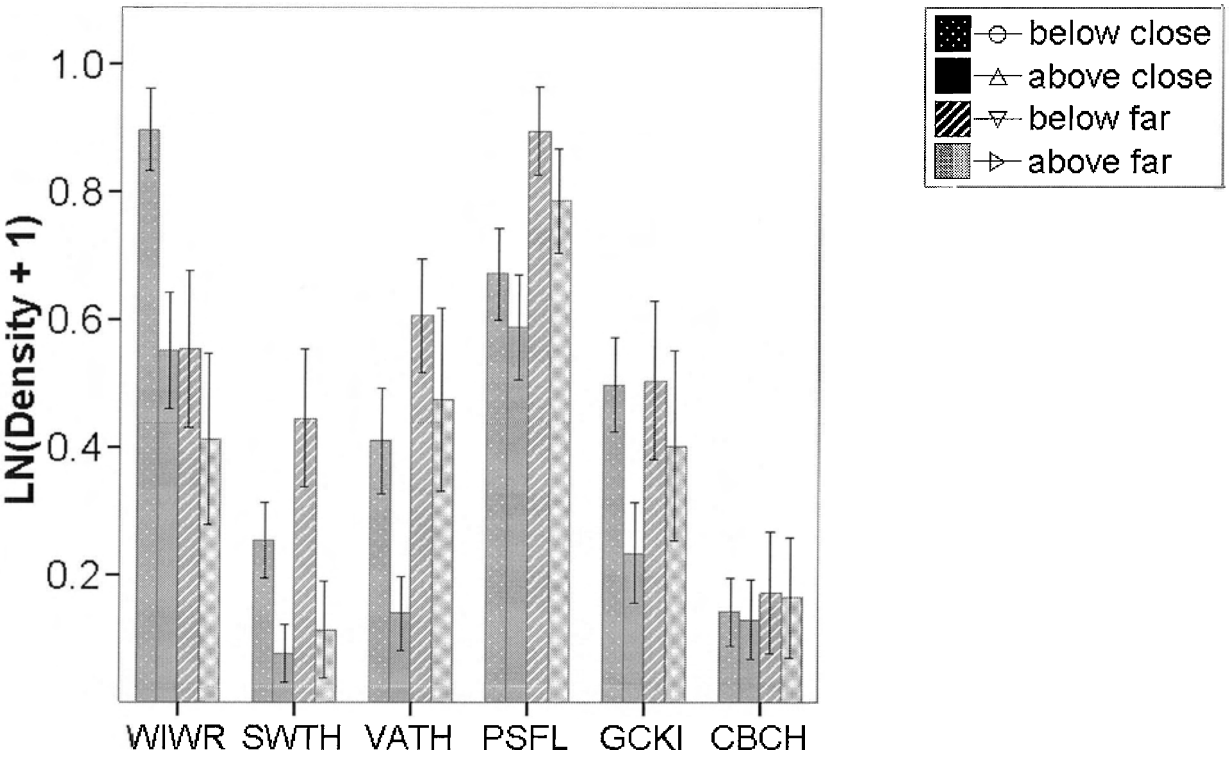

Figure 3.2. Mean and 95% confidence intervals of bird density at points above and below the falls, close (50m) and far (150m) from the stream at Clatse and Neekas Rivers, British Columbia. Density (ln(number of detections per point + 1) was estimated for the following species: Winter Wren (WIWR), Swainson's Thrush (SWTH), Varied Thrush (VATH), Pacific-slope Flycatcher (PSFL), Golden-crowned Kinglet (GCKI), and Chestnut-backed Chickadee (CBCH). On transects close to the stream, 81 points were surveyed below the falls and 56 were surveyed above the falls. On transects far from the stream, 34 points were surveyed below the falls and 24 were surveyed above the falls.

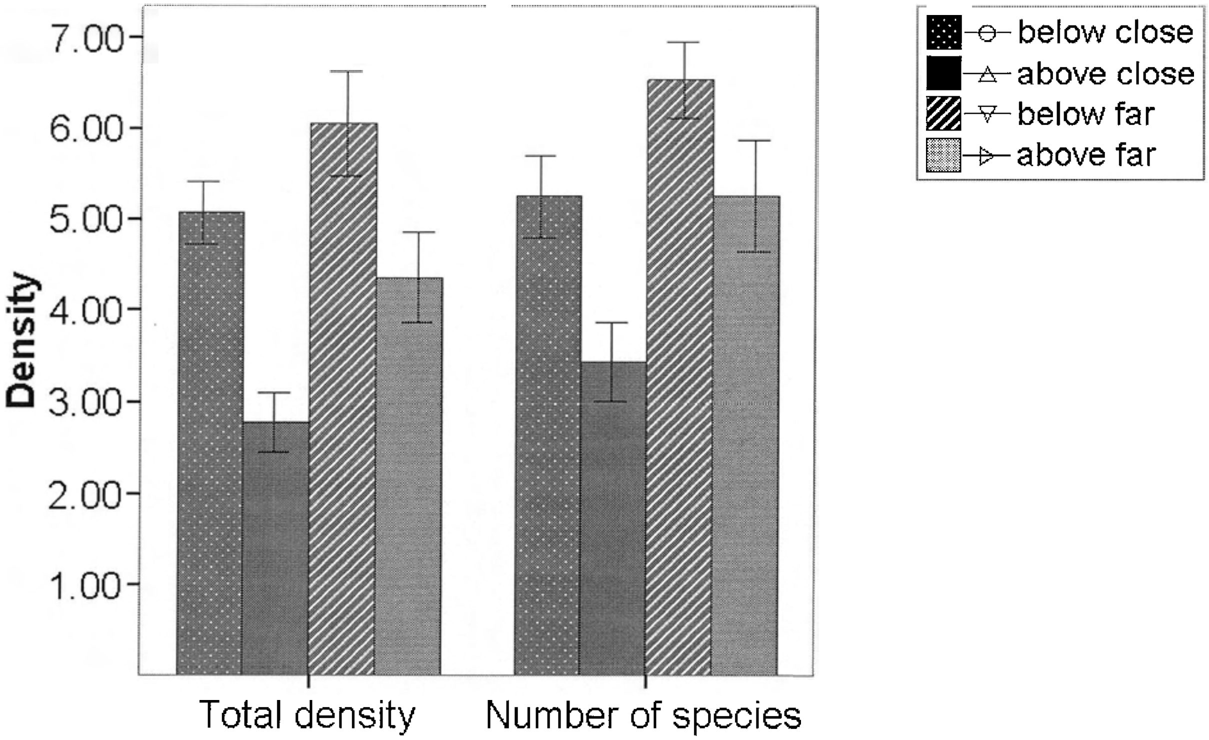

Figure 3.3. Mean and 95% confidence intervals of total bird density and number of species detected during point-counts above and below the falls, close (50m) and far (150m) from the stream at Clatse and Neekas Rivers, British Columbia. Same sample sizes as Figure 3.2 apply.

Table 3.1. General linear models (top models ($\Delta AIC_c \leq 2.0$) are shown) describing variation in songbird density on salmon streams on the central coast of British Columbia, spring, 2002-2003.

Species	Model[a]	K[b]	ΔAICc	AIC weight	R^2
Winter Wren	F + CF + F*CF + PC1 + PC2	9	0.000	0.373	0.311
	F + CF + PC1 + PC2	8	1.088	0.216	0.299
	F + CF + F*CF + SC + PC1 + PC2	10	1.798	0.152	0.312
Varied Thrush	F + CF	6	0.000	0.161	0.462
	F + CF + PC1 + PC2	8	0.012	0.160	0.464
	F + CF + F*CF	7	0.278	0.140	0.467
	F + CF + F*CF + PC1 + PC2	9	0.451	0.129	0.468
	F	5	1.862	0.064	0.451
	F + CF + SC + PC1 + PC2	9	1.877	0.063	0.464
	F + CF + SC	7	1.926	0.062	0.462
	F + CF + F*CF + SC	8	1.964	0.060	0.468
	F + PC1 + PC2	7	2.000	0.059	0.452
Swainson's Thrush	F + CF + F*CF + SC + PC1 + PC2	10	0.000	0.453	0.375
	F + CF + F*CF + PC1 + PC2	9	0.435	0.365	0.367
Pacific-slope Flycatcher	F + CF + PC1 + PC2	8	0.000	0.409	0.307
	F + CF	6	1.014	0.247	0.296
	F + CF + F*CF + PC1 + PC2	9	1.832	0.164	0.308
Golden-crowned Kinglet	F + PC1 + PC2	7	0.000	0.595	0.210
	F + CF + PC1 + PC2	8	2.000	0.219	0.210
Chestnut-backed Chickadee	Null	2	0.000	0.713	
Number of species	F + CF + PC1 + PC2	8	0.000	0.459	0.412
	F + CF + F*CF + PC1 + PC2	9	1.679	0.198	0.413
	F + CF + TS + PC1 + PC2	9	1.941	0.174	0.412
Total density	F + CF + PC1 + PC2	8	0.000	0.609	0.492
	F + CF + F*CF + PC1 + PC2	9	1.382	0.305	0.494

[a] Explanatory variables: F = Falls; CF = Distance from stream (50m vs. 150m); F*CF = Interaction term between falls and distance from stream; PC1 + PC2 = Principal component factor scores relating to tree community structure; SC = % Shrub Cover, TS = number of tree species. River and Year were included as explanatory variables in all models.

[b] Number of parameters used in model.

Table 3.2. Parameter likelihood's (summed AIC_c weights of models that include parameter) of explanatory variables in linear regression models. Parameter likelihood's reflect the relative importance of each explanatory variable in models describing variation in songbird density. Explanatory variables are defined in Table 3.2.

Response Variable	Explanatory variable	Parameter likelihood
Winter Wren	CF	1.000
	Falls	1.000
	PC1 + PC2	0.821
	F*CF	0.647
	SC	0.283
Varied Thrush	Falls	1.000
	CF	0.832
	PC1 + PC2	0.490
	F*CF	0.386
	SC	0.287
Swainson's Thrush	Falls	1.000
	CF	1.000
	F*CF	0.912
	PC1 + PC2	0.896
	SC	0.551
Pacific-slope Flycatcher	CF	1.000
	Falls	0.918
	PC1 + PC2	0.602
	F*CF	0.262
Golden-crowned Kinglet	Falls	0.987
	PC1 + PC2	0.986
	CF	0.387
	F*CF	0.162
Chestnut-backed Chickadee	PC1 + PC2	0.218
	CF	0.154
	Falls	0.102
	F*CF	0.014
Number of Species	Falls	1.000
	CF	0.999
	PC1 + PC2	0.908
	F*CF	0.304
	TS	0.279
Total density	Falls	1.000
	CF	0.998
	PC1 + PC2	0.916
	F*CF	0.339

Table 3.3. Model selection and density estimates for five bird species above and below the waterfalls on two salmon-bearing rivers (Clatse and Neekas) located on the central coast of British Columbia.

Species	Model Selected	GOF *P*[a]	I[b]	TD (m)[c]	River	Location	Density[d]	n	% CV	LCL	UCL
Winter Wren	Half-normal Cosine	0.84	5	70	Clatse	Above Falls	0.86*	22	28.28	0.53	1.42
						Below Falls	1.85*	47	21.6	1.33	2.57
					Neekas	Above Falls	1.29*	50	20.56	0.96	1.74
						Below Falls	2.07*	124	17.99	1.66	2.58
Pacific-slope Flycatcher	Hazard-rate Cosine	0.07	6	70	Clatse	Above Falls	1.71*	39	9.86	1.40	2.08
						Below Falls	2.19*	50	10.24	1.78	2.69
					Neekas	Above Falls	1.78	62	11.07	1.43	2.22
						Below Falls	1.88	101	10.82	1.52	2.32
Swainson's Thrush	Hazard-rate Cosine	0.05	6	90	Neekas	Above Falls	0.08*	7	33.66	0.04	0.16
						Below Falls	0.42*	55	15.06	0.31	0.56
Golden-crowned Kinglet	Hazard-rate Cosine	0.39	7	40	Clatse	Above Falls	1.66*	13	36.11	0.82	3.36
						Below Falls	3.84*	30	29.35	2.17	6.80
					Neekas	Above Falls	3.70	44	25.15	2.27	6.03
						Below Falls	4.35	80	23.01	2.78	6.80
Chestnut-backed Chickadee	Half-normal Cosine	0.49	9	40	Clatse	Above Falls	0.20	2	68.51	0.06	0.72
						Below Falls	0.51	5	51.96	0.19	1.38
					Neekas	Above Falls	0.80	12	31.87	0.43	1.48
						Below Falls	1.07	25	29.05	0.61	1.89

[a] Chi-square goodness-of-fit test to assess whether model fits data

[b] Number of distance intervals

[c] Truncation distance (10% of observations)

[d] Density (number of birds per hectare). Values with an asterix show significant differences in mean density above and below falls.

Table 3.4. Mean density (untransformed) and standard deviation of birds surveyed at four watersheds on the central coast of British Columbia. Paired comparisons were made between bird densities up to 1km on Clatse Creek to Ripley Creek and Neekas River to Cheenis Creek, and significant results of t-tests are indicated.

Species	Clatse Density	Std. Dev.	Ripley Density	Std. Dev.	p<0.05
Winter Wren	1.236	0.802	0.232	0.535	Y
Swainson's Thrush	0.181	0.302	0.000	0.000	Y
Varied Thrush	0.708	0.424	0.500	0.694	Y
Pacific-slope Flycatcher	1.097	0.579	0.393	0.497	Y
Golden-crowned Kinglet	0.690	0.648	0.250	0.518	Y
Chestnut-backed Chickadee	0.116	0.267	0.286	0.535	
Total density	4.990	1.891	1.910	1.401	Y
Number of species	5.139	1.930	1.678	1.090	Y
	Neekas Density	Std. Dev.	Cheenis Density	Std. Dev.	
Winter Wren	1.603	0.641	1.083	0.900	Y
Swainson's Thrush	0.577	0.519	0.833	0.718	
Varied Thrush	1.064	0.663	0.583	0.669	Y
Pacific-slope Flycatcher	0.686	0.430	1.667	0.779	Y
Golden-crowned Kinglet	0.737	0.493	0.833	0.835	
Chestnut-backed Chickadee	0.231	0.432	0.167	0.389	
Total density	6.147	1.550	5.667	2.674	
Number of species	6.269	1.638	4.167	1.642	Y

General Discussion

In this thesis I have explored the importance of the salmon nutrient subsidy to birds, as well as the ecological pathways through which salmon-derived nutrients (SDN) flow to these consumers. Gulls, the most numerous vertebrate on salmon streams during the fall, consumed significant quantities of salmon carcasses and eggs, and re-distributed nutrients acquired from salmon to terrestrial, aquatic, and marine habitats via guano. On my study sites, salmon-derived nutrients moved through the riparian food chain and could be detected in the tissues of Winter Wrens using stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$). Winter Wrens obtained salmon-derived nutrients primarily through indirect pathways by consuming terrestrial and aquatic invertebrates, themselves enriched in SDN, and also through the consumption of salmon carcass-hatched fly larvae during the fall. The presence of SDN in the riparian food web resulted in large shifts in songbird densities, where songbird density increased average by 62-100% below the falls.

Riparian areas around salmon streams may provide important habitat for birds during the breeding season and migration, as evidenced from this study. My results further those of Gende and Willson (2001), who found increased densities of songbirds on salmon streams in Alaska. This indicates that the effect of salmon on birds occurs on a wider geographical scale, and is not restricted to my study sites. The most probable mechanism causing increased breeding bird density and species richness on salmon streams is heightened availability of food, which may increase the carrying capacity of riparian habitat for breeding birds. Increased structural heterogeneity and altered plant species composition of forests adjacent to salmon streams may also provide favorable habitat for songbirds. During the autumn, salmon streams are likely to provide important stopover habitat for migrating songbirds. Songbirds stop at productive sites en route during migration to amass lipid stores (Jenni and Jenni-Eirmann. 1998) and likely benefit substantially by consuming insect larvae that hatch en mass from salmon carcasses.

Inferences can be made about the future of coastal songbird communities based on data collected in this study. The ongoing reduction in salmon populations and subsequent removal of marine nutrients from terrestrial systems is analogous to the conversion of songbird communities below the falls to those found above the falls. If my study streams are representative, the substantially reduced bird density and species richness observed above the falls is likely to characterize areas of the Pacific Northwest not receiving salmon-derived nutrients. Coincident with diminishing marine inputs to terrestrial areas, the carrying capacity of coastal habitats for songbirds may be decreasing. As a result, songbird communities in the Pacific Northwest may be experiencing a shift toward lower density and diversity, and species adapted to nutrient-limiting forests may be favored. Species that showed the most pronounced shifts in density across the waterfall barrier, such as the Winter Wren, Swainson's Thrush and Varied Thrush, are likely to respond most strongly to lowered nutrient inputs to terrestrial systems.

The numerical response of songbirds to salmon-derived nutrients provides evidence for the ecosystem-wide effects of nutrient subsidies. In other terrestrial systems such as boreal forests and wetlands, birds have been shown to respond numerically to nutrient additions (Folklord and Smith 1995, Crozier and Gawlik 2002), largely due to a greater abundance of food. Nutrient subsidies occur commonly in nature, often resulting in higher densities of consumers and increased complexity of foodwebs (Polis and Strong 1996). These subsidies have the potential to increase ecosystem stability, providing alternate resources for consumers when in situ resources are limited, as exemplified in studies of insect inputs to alpine habitats (Halfpenny and Heffernan 1992). The salmon nutrient subsidy may thus enhance the stability of coastal temperate ecosystems in the Pacific Northwest.

The salmon nutrient subsidy is a large-scale process in North America that has significant implications for the maintenance of biological diversity. This process is not limited to coastlines; salmon extend the interface between marine and terrestrial ecosystems by migrating tens to thousands of kilometers inland to spawn. Active transfer of salmon, as well as the deposition of feces and urine into the forest by wildlife further extends this interface hundreds of meters away from streams, ultimately dispersing salmon-derived nutrients over a large geographical area (Reimchen 2000). Given the pronounced effect of salmon-derived nutrients on riparian vegetation, invertebrates, and wildlife, the massive reduction in salmon populations over the past century has undoubtedly had negative effects on overall ecosystem health. Between 6 and 7% of historical levels of salmon biomass now enters streams in North America, such a drastic decline that it has been termed an “ecosystem failure” (Gresh et al. 2000). The long-term effects of this significant removal of nutrients from terrestrial and aquatic systems are unknown but are suspected to be profound (Naiman et al. 2002). Another important factor that contributes to the reduction of salmon nutrients entering coastal forests is the decline in wildlife populations. Large mammals such as the black bear (*Ursus americanus*) play a keystone role in transporting carcasses (up to 70% of the entire salmon run) into the forest (Reimchen 2000). Wolves (*Canus lupus*) also consume large quantities of salmon and transport SDN (via carcasses, urine, and feces) into the forest

(Darimont and Reimchen 2002). Without healthy large carnivore populations in British Columbia, large proportions of salmon nutrients will remain in the aquatic environment instead of fertilizing terrestrial soils. Therefore the protection of habitat for bears and wolves, and the elimination of trophy hunting will contribute to the conservation of this important process.

Coastal forests of the Pacific Northwest are unique amongst other temperate forests due to the massive, regular influx of nutrients via spawning salmon. The importance of the spawning events of Pacific salmon, leading to greater productivity, consumer biomass, and diversity on the west coast of North America, cannot be under-emphasized and is comparable to the migration of ungulates on the plains of eastern Africa or the migration of herring in the Pacific and Atlantic oceans. In order to avoid further deterioration of this process, a multi-faceted approach involving the protection of intact watersheds, effective fisheries management, and maintenance of healthy wildlife populations is needed.

Literature Cited

Addison, J.A., J.A. Trofymow, and V.G. Marshall. 2003. Functional role of Collembola in successional coastal temperate forests on Vancouver Island, Canada. Applied Soil Ecology **24**:247-261.

Anderson, W. B., and G. A. Polis. 1999. Nutrient Fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia **118**: 325-332.

Armstrong, E.A., and H.L.K Whitehouse. 1977. Behavioral adaptations of the wren (*Troglodytes troglodytes).* Biological Reviews **52**:235-294.

Ashmole, N. P. 1971. Sea Bird ecology and the marine environment. Pages 224-271 *in* D.S Farner and J.R. King, editors. Avian Biology, Volume 1. Academic Press, New York, New York.

Baltz, D. M, and G. V. Morejohn. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. Auk **94**: 527-542.

Barrett, K., W.B. Anderson, D. A. Wait, L.L. Grismer, G.A. Polis, M.D. Rose. 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations. Oikos 109: 145-153.

Bartz, K.K. 2002. Impacts of salmon-borne nutrients on riparian soils and vegetation in southwest Alaska. M.Sc. Thesis. University of Washington, Seattle.

Beacham, T., and C. B. Murray. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus).* Journal of Fisheries Biology **42**: 485-508.

Bearhop, S., C.E. Adams, S. Waldron, R.A. Fuller, and H. MacLeod. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology **73**: 1007-1012.

Ben-David, M., T.A. Hanley, and D.R. Klein. 1997. Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. Canadian Journal of Zoology **75**: 803-811.

Ben-David, M., T. A. Hanley, and D. M. Schell. 1998. Fertilization of terrestrial vegetation by spawning pacific salmon: the role of flooding and predator activity. Oikos **83**: 47-55.

Bent, A.C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. National Museum Bulletin. 195.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences **53**: 164-173.

Bilby, R.E., E.W. Beach, B.R. Fransen, and J.K. Walter. 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. Transactions of the American Fisheries Society **132**: 733-745.

Birt-Friesen, V. L., W. A. Montevecchi, D. K. Cairns, and S. A. Macko. 1989. Activity-specific metabolic rates of free-living northern gannets and other seabirds. Ecology **70**: 357-367.

Bishop, M. A., and S. P. Green. 2001. Predation on Pacific Herring (*Clupea pallasi*) spawn by birds in Prince William Sound, Alaska. Fisheries Oceanography **10**: 149-158.

Bolnick, D.I., L.H.Yang, J.A. Fordyce, J.M. Davis, and R. Svanback. 2002. Measuring individual-level resource specialization. Ecology **83**:2936-2941.

Bolnick, D.I., R. Svanback, J.A. Fordyce, L.H. Yang, J.M. Davis, C.D. Hulsey, and M.L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. The American Naturalist **161**:1-28.

Bosman, A. L., and P. A. R. Hockey. 1986. Seabird guano as a determinant of rocky intertidal community structure. Marine Ecology Progress Series **32**: 247-257.

Brand, L.A., and T.L. George. 2001. Response of passerine birds to forest edge in coast redwood forest fragments. Auk **118**: 678-686.

Buckland, S.T., D.R. Anderson, K.P. Burham, J.L. Laake, D.L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling. Oxford University Press, Oxford, England.

Burger, A. E. 1993. Mortality of seabirds assessed from beached-bird surveys in southern British Columbia. Canadian Field-Naturalist **107**: 164-176.

Burger, A. E., H. J. Lindeboom, and A. J. Williams. 1978. The mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. South African Journal of Antarctic Research **8**: 59-70.

Burnam, K.P., and D.R. Anderson. 1998. Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach. Second Edition. Springer-Verlag. New York, NY, USA.

Campbell, W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, and M. C. E. McNall. 1997. The Birds of British Columbia. Volume III. Royal British Columbia Museum, Victoria, British Columbia.

Campbell, W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, and M. C. E. McNall. 1990. The Birds of British Columbia. Volume II. Royal British Columbia Museum, Victoria, British Columbia.

Castro, G., N. Stoyan, and J. P. Myers. 1989. Assimilation efficiency in birds: a function of taxon or food type? Comparative Biochemical Physiology **92**: 271-278.

Cederholm, C. J., D. H. Johnson, R. E. Bilby, L. G. Dominguez, A. M. Garrett, W. H. Graeber, E. L Greda, M. D. Gunze, B. G. Marcot, J. F. Palmisano, R. W. Plotnikoff, W. G. Pearcy, C. A. Simenstad, and P. C. Trotter. 2000. Pacific Salmon and wildlife - ecological contexts, relationships, and implications for management. Special Edition Technical Report, Prepared for D.H. Johnson and T.A. O'Neil (Managing Directors), Wildlife-Habitat Relationships in Oregon and Washington. Washington Department of Fish and Wildlife, Olympia, Washington. 136 pages.

Cerling, T.E., B.H. Passey, L.K. Ayliffe, C.S. Cook, J.R. Ehleringer, J.M. Harris, M.B. Dhidha, and S.M. Kasiki. 2004. Orphan's tails: seasonal dietary changes from Tsavo National Park, Kenya. Paleogeography, Paleoclimatology, and Paleoecology **206**:367-376.

Chaloner, D.T., K.M. Martin, M.S. Wipfli, P.H. Ostram, and G. A. Lamberti. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. Canadian Journal of Fisheries and Aquatic Sciences **59:** 1257-1265.

Christie, K. S., and T. E. Reimchen. 2005. Post-Reproductive Pacific Salmon, *Oncorhynchus* spp., as a major nutrient source for large aggregations of gulls, *Larus* spp. Canadian Field-Naturalist. *In press.*

Crozier, G.E., and D.E. Gawlik. 2002. Avian response to nutrient enrichment in an oligotrophic wetland, the Florida Everglades. The Condor **104**: 631-642.

Darimont, C. T., and T. E. Reimchen. 2002. Intra-hair stable isotope analysis suggests seasonal shift to salmon in gray wolf diet. Canadian Journal of Zoology **80**: 1638-1642.

De Niro, M.J., and S. Epstein. 1979. Influence of diet on the distribution of carbon isotopes in animals. Geochimica Cosmoschimica Acta **42**: 495-506.

De Niro, M.J., and S. Epstein. 1981. Influence of diet on thedistribution of nitrogen isotopes in animals. Geochimica Cosmoschimica Acta **45**: 341-351.

Duggins, D.O., C.A. Simenstad, and J.A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science **245**: 170-173.

Dunning, J. B. 1993. CRC handbook of avian body masses. CRC Press Inc. Boca Raton, FL.

Eniutina, R. I. 1972. The Amur pink salmon (*Oncorhynchus gorbuscha*): a commercial and biological survey. Fisheries Research Board of Canada Translation Series Number 3160.

Evans Mack, D., and W. Yong. 2000. Swainson's Thrush. *In* A.Poole and F. Gill, editors. The Birds of North America; Life histories for the 21st Century. Cornell Laboratory of Ornithology and The Academy of Natural Sciences. No. 540.

Folklord, N.F.G., and J.N.M. Smith. 1995. Evidence for bottom-up effects in the boreal forest: Do passerine birds respond to large-scale experimental fertilization? Canadian Journal of Zoology **73**: 2231-2237.

Fukushima, M., T. J. Quinn, and W. W. Smoker. 1997. Estimation of eggs lost from superimposed Pink salmon (*Oncorhynchus gorbuscha)* redds. Canadian Journal of Fisheries and Aquatic Sciences **55**: 618-625.

Gabrielsen, G. W., F. Mehlum, and K. A. Nagy. 1987. Daily energy expenditure and energy utilization of free-ranging Black-legged Kittiwakes. The Condor **89**:126-132.

Garcia, L. V., T. Maranon, F. Ojeda, L. Clemente, and R. Redondo. 2002. Seagull influence on soil properties, chenopod shrub distribution, and leaf nutrient status in semi-arid Mediterranean islands. Oikos **98:** 75-86.

Gates, J.E., and J.E. McKearnan. 2003. Artificial nest predation across riparian-upland forest ecotones. Southeastern Naturalist **2**: 301-312.

Gende, S.M. and M.F. Willson. 2001. Passerine densities in riparian forests of southeast Alaska: potential role of anadromous spawning salmon. Condor **103**:624-629.

Gende, S.M., R.T. Edwards, M.F. Willson, and M.S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience **52:**917-928.

Gresh, T., and J. Lichatowich. 2000. An estimation of historic and current levels of salmon production in the northeast pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries, **25**: 15-21.

Grey, J. 2001. Ontogeny and dietary specialization in brown trout (*Salmo trutta* L.) from Loch Ness, Scotland, examined using stable isotopes of carbon and nitrogen. Ecology of Freshwater Fish. **10**:168-176.

Gu, B., C.L. Schelske, and M.V. Hoyer. 1997. Intrapopulation feeding diversity in blue tilapia: evidence from stable-isotope analyses. Ecology **78**:2263-2266.

Haegele, C. W. 1993. Seabird predation of Pacific Herring, *Clupea pallasi,* spawn in British Columbia. Canadian Field-Naturalist **107**: 73-82.

Halfpenny, J., and M. Heffernan. 1992. Nutrient input to an alpine tundra - an Aeolian insect component. Southwestern Naturalist **37**: 247-251.

Hamer, K. C., E. A. Schreiber, and J. Burger. 2002. Breeding biology, life histories, and life history-environment interactions in seabirds. Pages 217-261 *in* E.A Schreiber, and J. Burger, editors. Biology of Marine Birds. CRC Press, Florida.

Hawkins, B.A., E.E. Porter, and J.A. Felizola Diniz-Filho. 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology **84**: 1608-1623.

Heard, W. R. 1991. Life history of Pink Salmon (*Oncorhynchus gorbuscha).* Pages 119-230 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. UBC Press, Vancouver, British Columbia.

Hejl, S.J., J.A. Holmes, and D.E. Kroodsma. 2002.Winter Wren. No. 623 *in* A.Poole and F. Gill, editors. The Birds of North America; Life histories for the 21st Century. Cornell Laboratory of Ornithology and The Academy of Natural Sciences..

Helfield, J.M., and R.J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology **82**:2403-2409.

Hendry, A. P., and O. K. Berg. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. Canadian Journal of Zoology **77**: 1663-1675.

Herbers, J.R., R. Serrouya, and K.A. Maxcy. 2004. Effects of elevation and forest cover on winter birds in mature forest ecosystems of southern British Columbia. Canadian Journal of Zoology **82**: 1720-1730.

Herrera, L.G., K.A. Hobson, M. Rodriquez, and P. Hernandez. 2003. Trophic partitioning in tropical rainforest birds: insights from stable isotope analysis. Oecologia **136**:439-444.

Hobson, K.A., and F. Bairlein. 2003. Isotopic fractionation and turnover in captive Garden Warblers (*Sylvia borin):* implications for delineating dietary and migratory associations in wild passerines. Canadian Journal of Zoology **81**:1630-1635.

Hobson, K.A., and R.G. Clark. 1992. Assessing avian diets using stable isotopes I: Turnover of ^{13}C in tissues. Condor **94**:181-188.

Hocking, M. D., and T. E. Reimchen. 2002. Salmon-derived nitrogen in terrestrial invertebrates from coniferous forests of the Pacific Northwest. BMC Ecology **2**: 1-14.

Iwata, T., S. Nakano, and M. Murakami. 2003. Stream meanders increase insectivorous bird abundance in riparian deciduous forests. Ecography **26**: 325-337.

Jauquet, J., N. Pittman, J.A. Heins, S. Thompson, N. Tatyama, and J. Cederholm. 2003. Observations of chum salmon consumption by wildlife and changes in waters chemistry at Kennedy Creek during 1997-2000. American Fisheries Society Symposium **34**:71-89.

Jenni, L., and S. Jenni-Eirmann. 1998. Fuel supply and metabolic constraints of migrating birds. Journal of Avian Biology **29**: 521-528.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1998. The relative role of density-dependent and density independent survival in the life cycle of Atlantic salmon *Salmo salar.* Journal of Animal Ecology **67**: 751-762.

Kaeriyama, M., M. Nakamura, R. Edpalina, J.R. Bower, H. Yamaguchi, R.V. Walker, and K.W. Myers. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (Oncorhynchus spp.) in the central Gulf of Alaska in relation to climate events. Fisheries Oceanography **13**:197-207.

Kelly, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology **78**: 1-27.

Kiffney, P. M., and J. S. Richardson. 2001. Interactions among nutrients, periphyton, and invertebrate and vertebrate (*Ascaphus truei*) grazers in experimental channels. Copeia **2**: 422–429.

Kirk, D.A., A.W. Diamond, K.A. Hobson, and A.R. Smith. 1996. Breeding bird communities of the western and northern Canadian boreal forest: Relationship to forest type. Canadian Journal of Zoology **74**: 1749-1770.

Klinka, K., V.J. Krajina, A.Ceska, and A.M. Scagel. 1989. Indicatory plants of coastal British Columbia. University of British Columbia Press. Vancouver, B.C.

Lock, P. and R.J. Naiman. 1998. Effects of stream size on bird community structure in coastal temperate forests of the Pacific Northwest, U.S.A. Journal of Biogeography **25**: 773-782.

Lowther, P.E. 2000. Pacific-slope Flycatcher. *In* A.Poole and F. Gill, editors. The Birds of North America; Life histories for the 21st Century. Cornell Laboratory of Ornithology and The Academy of Natural Sciences. No. 556.

Mace, P. M. 1983. Bird predation on juvenile salmonids in the Big Qualicum Estuary, Vancouver Island. Canadian Technical Report of Fisheries and Aquatic Sciences Number 1176.

Mathewson, D.D., M.D. Hocking, and T.E. Reimchen. 2003. Nitrogen uptake in riparian plant communities across a sharp ecological boundary of salmon density. BMC Ecology **3**:4.

Matthews, B., and A. Mazumder. 2004. A critical evaluation of intrapopulation variation of δ^{13}C and isotopic evidence of individual specialization. Oecologia **140**: 361-371.

McConnaughey, T. and C.P. McRoy. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Marine Biology **53**: 257-262.

Meidinger, D.V. and J. Pojar. 1991. Ecosystems of British Columbia. Special Report Series No. 6. Ministry of Forests, Victoria, British Columbia.

Minakawa, N. and R.I. Gara. 1999. Ecological effects of chum salmon (*Oncorhynchus keta*) spawning run in a stream of the Pacific Northwest. Journal of Freshwater Ecology **22**: 154-156.

Minigawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and relation between δ^{15}N and animal age. Geochimica Cosmochimica Acta **48**: 1135-1140.

Momoh, E.J., W.J. Song, H.Z. Li, and W.J. Zhou. 2004. Seed yield and quality responses of winter oilseed rape (*Brassica napus*) to plant density and nitrogen fertilization. Indian Journal of Agricultural Sciences **74**: 420-424.

Mossman, A. S. 1958. Selective predation of Glaucous-winged Gulls upon adult red salmon. Ecology **39**: 482-486.

Murakami, M., and S. Nakano. 2001. Species-specific foraging behaviour of birds in a riparian forest. Ecological Research **16**: 913-923.

Murphy, M.E. 1996. Energetics and nutrition of molt. Pages 158-198 *in* C.Carey, editor. Avian energetics and nutritional ecology. Chapman and Hall, NY.

Nadelhoffer, K.J., and B. Fry. 1994. Nitrogen isotope studies in forest ecosystems. Pages 22-44 *in* K. Lajtha and R.H. Michener, editors. Stable Isotopes in ecology and environmental science. Blackwell Scientific, Oxford, UK.

Naiman, R.J., R.E. Bilby, D.E. Schindler, and J.M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems **5**: 399-417.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences **98**:166-170.

Penney, B.G., K.B. McRae, and G.A. Bishop. 2003. Second-crop N fertilization improves lowbush blueberry (*Vaccinium angustifolium Ait.*) production. Canadian Journal of Plant Science **83**: 149-155.

Pennycuick, C.J. 1987. Flight of seabirds. Pages 43-62 *in* J.P. Croxall, editor. Seabirds: Feeding Ecology and Role in Marine Ecosystems. Cambridge University Press, U.K.

Phillips, D.L. and J.W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia **136**:261-269.

Phillips, D.L., S.D. Newsome, and J.W. Gregg. *In press.* Combining sources in stable isotope mixing models: alternative methods. Oecologia.

Pojar, J., and A. MacKinnon. 1994. Plants of Coastal British Columbia. Lone Pine Publishing, Vancouver, British Columbia.

Polis, G.A. and D.R. Strong. 1996. Food web complexity and community dynamics. The American Naturalist **147**: 813-846.

Polis, G.A., and S.D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist **147**:396-423.

Ponsard, S., and R. Arditi. 2000. What can stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) tell about the food web of soil macro-invertebrates? Ecology **81**:852-864.

Portnoy, J. W. 1989. Gull contributions of phosphorous and nitrogen to a Cape Cod kettle pond. Hydrobiologia **202**: 61-70.

Poulsen, B.O. 2002. Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. Biodiversity and Conservation **11**: 1551-1566.

Pyle, P. 1997. Identification Guide to North American Birds. Part I. Slate-Creek Press, Bolinas, California.

Ray, G.C. 1988. Ecological diversity in coastal zones and oceans. *In* E.O. Wilson, editor. Biodiversity. National Academy Press, Washington, D.C.

Reimchen, T. E. 1992. Mammal and bird utilization of adult salmon in stream and estuarine habitats at Bag Harbour, Moresby Island. Canadian Wildlife Service Report. Queen Charlotte City, British Columbia.

Reimchen, T. E. 1994. Further studies of predator and scavenger use of chum salmon in stream and estuarine habitats at Bag Harbour, Gwaii Haanas. Canadian Parks Service Report. Queen Charlotte City, British Columbia.

Reimchen, T. E. 2000. Some ecological and evolutionary aspects of bear - salmon interactions in coastal British Columbia. Canadian Journal of Zoology **78**: 448-457.

Salo, E. O. 1991. Life history of chum salmon (*Oncorhynchus keta).* Pages 231-310 *in* C. Groot and L. Margolis, editors. Pacific Salmon Life Histories. UBC Press, Vancouver, B.C.

Sanchez-Pinero, F., and G. A. Polis. 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. Ecology **81**: 3117-3131.

Schmutz, J.A., and K.A. Hobson. 1998. Geographic, temporal, and age-specific variation in diets of Glaucous Gulls in western Alaska. Condor **100**:119-130.

Sharpe, F. 1996. The biologically significant attributes of forest canopies to small birds. Northwest Science **70**: 86-93.

Shaw, D., and C. Flick. 1999. Are resident songbirds stratified within the canopy of a coniferous old-growth forest? Selbyana. **20**:324-331.

Shealer, D. A. 2002. Foraging behavior and food of seabirds. Pages 137-177 *in* E.A. Schreiber and J. Burger, editors. Biology of Marine Birds. CRC Press, Florida.

Shirley, S. 2004. The influence of habitat diversity and structure on bird use of riparian buffer strips in coastal forests of British Columbia, Canada.Canadian Journal of Forest Research. **34**: 1499-1510.

Skagen, S. K., R. L. Knight, and G. H. Orians. 1991. Human disturbance of an avian scavenging guild. Ecological Applications **1**: 215-225.

SPSS 2001. Version 11.0 for windows. LEAD Technologies Inc. Chicago, Illinois, USA.

Stapp, P., and G.A. Polis. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. Oecologia **134**: 496-504.

Stocker, S., and D. Weihs. 1998. Bird migration - an energy-based analysis of costs and benefits. Journal of Mathematics Applied in Medicine and Biology **15**: 65-85.

Stockner, J.G. 2003. Nutrients in salmonid ecosystems: sustaining production and biodiversity. American Fisheries Society, Symposium 34. Bethesda, Maryland.

Taylor, P. 1993. Migration of Bonaparte's Gull, *Larus philadelphia,* in Southeastern Manitoba. Canadian Field-Naturalist **107**: 314-318.

Thompson, D.R., R.W. Furness, and S.A. Lewis. 1995. Diets and long-term changes in $\delta^{12}C$ and $\delta^{13}C$ values in northern fulmars *Fulmaris glacialis* from two northeast Atlantic colonies. Marine Ecology Progress Series **125**:3-11.

Van Horne, B., and A. Bader. 1990. Diet of nestling Winter Wrens in relationship to food availability. The Condor **92**:413-420.

Van Valen, L. 1965. Morphological Variation and width of ecological niche. The American Naturalist **99**:377-390.

Vandenbulcke, P. 1989. *Larus argentatus ssp* and *Larus cachinnans-michahellis* along the Belgian coast: origin and moulting. Le Gerfaut 79: 3-30.

Vander Zanden, M.J., B.J. Shuter, N.P. Lester, and J.B. Rasmussen. 2000.Within- and among-population variation in trophic position of a pelagic predator, lake trout (*Salvelinus namaycush).* Canadian Journal of Fisheries and Aquatic Sciences **57**:725-731.

Verbeek, N. A. M. 1993. Glaucous-winged Gull (*Larus glaucescens).* Number 59 *In* A. Poole, P. Stettenheim, and F. Gill, editors. The Birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and the American Ornithologists' Union, Washington, D.C.

Vermeer, K., I. Szabo, and P. Greisman. 1987. The relationship between plankton-feeding Bonaparte's and Mew Gulls and tidal upwelling at Active Pass, British Columbia. Journal of. Plankton Research **9**: 483-501.

Vronskii, B. B., and V. N. Leman. 1991. Spawning beds, hydrological regime, and progeny survival in the redds of the chinook salmon, *Oncorhynchus tshawytscha* in the Kamchatka River Basin, Russian SFSR USSR. Journal of Ichthyology **31**: 282-291.

Warburton, K., S. Retif, and D. Hume. 1998. Generalists as sequential specialists: diets and prey switching in juvenile silver perch. Environmental Biology of Fishes **51**:445-454.

Waring, R. H., and J. F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. Science **204**: 1380-1386.

Waring, R.H., and J.F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. Science **204**:1380-1386.

Waterhouse, F.L., A.S. Harestad, and P.K. Ott. 2002. Use of small streams and forest gaps for breeding habitats by Winter Wrens in coastal British Columbia. Northwest Science **76**: 335-346.

Welch, D.W., and T.R. Parsons. 1993. $\delta^{13}C$-^{15}N values as indicators of trophic position and competitive overlap for Pacific salmon (*Oncorhynchus* spp.). Fisheries Oceanography **2**:11-23.

Wiebe, K.L., and K. Martin. 1998. Seasonal use by birds of stream-side riparian habitat in coniferous forest of northcentral British Columbia. Ecography **21**: 124-134.

Wilkinson, C.E., M.D. Hocking, and T.E. Reimchen. 2004. Uptake of salmon-derived nitrogen by mosses and liverworts in Coastal British Columbia. Oikos **108**:85-98.

Williams, A. J., and A. Berruti. 1978. Mineral and energy contributions of feathers moulted by penguins, gulls and cormorants to the Marion Island terrestrial ecosystem. South African Journal of Antarctic Research **8**: 71-74.

Willson, M. F., S. M. Gende, and B. H. Marston. 1998. Fishes and the Forest: Expanding perspectives on fish–wildlife interactions. BioScience **48**: 455-462.

Wipfli, M.S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences **55**:1503-1511.

Witzell, J., and A. Shevtsova. 2004. Nitrogen-induced changes in phenolics of *Vaccinium myrtillus* – Implications for interaction with a parasitic fungus. Journal of Chemical Ecology **30**: 1937-1956.

Zhang, Y.X., J.N. Negishi, J.S. Richardson, and R. Kolodziejczyk. 2003. Impacts of marine-derived nutrients on stream ecosystem functioning. Proceedings of the Royal Society of London **270**:2117-2123.