



PRESENCE OF SALMON INCREASES PASSERINE DENSITY ON PACIFIC NORTHWEST STREAMS

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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. We investigated the effects of salmon and other habitat variables on abundance of Winter Wren (*Troglodytes troglodytes*), Swainson's Thrush (*Catharus ustulatus*), Varied Thrush (*Ixoreus naevius*), Pacific-slope Flycatcher (*Empidonax difficilis*), Golden-crowned Kinglet (*Regulus satrapa*), and Chestnut-backed Chickadee (*Poecile rufescens*) on the central coast of British Columbia. In our comparisons of salmon-bearing and non-salmon-bearing reaches of two rivers that had waterfall barriers to salmon partway upstream, we found that position above or below the falls and proximity to the stream were the major predictors of songbird abundance. Each species, except for Chestnut-backed Chickadee, had higher densities below the falls at both rivers. Our results suggest that salmon-derived nutrients influence songbird density, and thus benefit multiple trophic levels within riparian ecosystems. Received 9 November 2005, accepted 7 February 2007.

Key words: marine-derived nutrients, *Oncorhynchus* spp., Pacific Northwest, passerines, riparian, salmon.

La présence du saumon augmente la densité de passereaux près des cours d'eau du nord-ouest du Pacifique

RESUME.—La migration annuelle du saumon (*Oncorhynchus* spp.) vers les cours d'eau et les lacs d'eau douce fournit un important apport nutritif aux systèmes terrestres en Amérique du Nord. Nous avons étudié les effets du saumon et d'autres variables de l'habitat sur l'abondance de *Troglodytes troglodytes*, *Catharus ustulatus*, *Ixoreus naevius*, *Empidonax difficilis*, *Regulus satrapa* et *Poecile rufescens* sur la côte centrale de la Colombie-Britannique. Dans nos comparaisons entre les portions avec et sans saumon de deux rivières comportant à mi-chemin des chutes qui empêchent les saumons de remonter plus haut, nous avons trouvé que la position en haut ou en bas des chutes et la proximité au ruisseau étaient les principales variables permettant de prédire l'abondance des oiseaux chanteurs. Toutes les espèces, à l'exception de *P. rufescens*, avaient des densités plus élevées en bas des chutes des deux rivières. Nos résultats suggèrent que les nutriments provenant du saumon influent sur les densités d'oiseaux chanteurs, ce qui profite à de nombreux niveaux trophiques des écosystèmes riverains.

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 they can cascade throughout the food chain via increased primary productivity (Duggins et al. 1989, Sanchez-Pinero and Polis 2000). Coastlines tend to be highly productive as a result of bidirectional 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 anadromous 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 these areas (Bilby et al. 1996, Cederholm et al. 2001). Large quantities of salmon biomass are

transported to forests adjacent to streams and lakes from occasional flooding (Willson et al. 1998) and through the activities of scavengers and predators including bears (*Ursus* spp.), American Martens (*Martes americana*), Gray Wolves (*Canis lupus*), gulls (*Larus* spp.), Common Ravens (*Corvus corax*), and Bald Eagles (*Haliaeetus leucocephalus*) (Reimchen 1994, 2000; Ben-David et al. 1998; Hilderbrand et al. 1999; Gende et al. 2002; Darimont et al. 2003; Reimchen et al. 2003; Christie and Reimchen 2005).

The ecological consequences of salmon-derived nutrients can be far-reaching and include increased vertebrate density, plant productivity, and aquatic and terrestrial invertebrate biomass (Willson et al. 1998, Wipfli et al. 1998, Helfield and Naiman 2001, Chaloner et al. 2002). These nutrients have been detected in plants, invertebrates, and vertebrates adjacent to salmon streams (Ben-David

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1997, 1998; Helfield and Naiman 2002; Hocking and Reimchen 2002; Mathewson et al. 2003; Wilkinson et al. 2005). Although the effects of salmon nutrients on primary producers and consumers have been documented, the implications for upper-level consumers such as songbirds have not been determined. High-productivity areas often have greater biomass of invertebrates, which can result in higher abundance of terrestrial birds. For example, riparian areas have greater abundance of invertebrates than upland areas and therefore tend to support higher densities of landbirds (Stauffer and Best 1980, Iwata et al. 2003). Moreover, terrestrial birds respond positively to nutrient inputs in forests and wetlands (Folkard and Smith 1995, Crozier and Gawlik 2002). Gende and Willson (2001) found that overall songbird density and diversity were slightly higher adjacent to salmon streams than adjacent to streams with no salmon in Alaska, which suggests that salmon-derived nutrients may indirectly influence breeding birds.

We tested the effects of salmon-derived nutrients and other habitat-related variables, including perpendicular distance to the river, tree species composition, and shrub cover, on bird abundance. We hypothesized that the presence of salmon would increase the density of breeding birds on our study sites, and we expected density to be greater at points close to the river on salmon-bearing reaches because of higher concentrations of salmon-derived nutrients close to the stream edge (Ben-David et al. 1998). As an experimental design, we compared salmon-bearing reaches to non-salmon-bearing reaches of two rivers, each with a waterfall barrier to salmon partway upstream. We also compared these rivers to two additional rivers lacking salmon to assess the importance of salmon in relation to upstream distance from the river mouth in predicting bird abundance.

METHODS

Study area.—We assessed songbird density on two salmon-bearing rivers, the Clatse River (52°20.6'N, 127°50.3'W) and Neekas River (52°28.4'N, 128°8.0'W), and on two nearby non-salmon-bearing rivers, the Cheenis River (52°29.4'N, 128°6.4'W) and Ripley River (52°25.6'N, 127°53.1'W), all located north of Bella Bella, British Columbia. Both salmon rivers had large runs (>20,000) of Chum Salmon (*O. keta*) and Pink Salmon (*O. gorbuscha*) from late August until early November. The Neekas and Clatse rivers were chosen because each had a waterfall partway upstream (1 km on the Clatse, 2.1 km on the Neekas) that blocked the migration of salmon. These within-watershed controls allowed comparison of the riparian area below the falls with that above the falls. Both non-salmon-bearing rivers (Cheenis and Ripley) were similar in order and magnitude to the Clatse and Neekas rivers but had waterfalls within 300 m of their mouths. All watersheds occurred in the Coastal Western Hemlock Biogeoclimatic Zone, which is characterized by infrequent, small-scale disturbances, high annual precipitation, and nutrient-poor soils (Pojar et al. 1987). Red Alder (*Alnus rubra*), the only deciduous tree present, occurred in a thin band immediately adjacent to streams. More detailed habitat descriptions of these watersheds are provided in Hocking and Reimchen (2001) and Mathewson et al. (2003).

Songbird abundance estimates.—We assessed songbird abundance using point-transect surveys from 9 May to 23 July

2003. We conducted 8-min counts at a series of points spaced at 100-m intervals along two parallel transects (50 m and 150 m from the riverbank). We used distance-sampling techniques (Buckland et al. 2001), in which we estimated the distance (to nearest 5 m) from the survey point to each bird detected to an unlimited radius. For individuals detected at multiple points, we included only the detection closest to the observer. Each observer participated in a 10-day intensive training period of bird identification and distance-sampling estimation prior to the surveys. Each survey point was assessed on a scale of 0–5 for noise interference, and points >3 on this scale (such as those near the waterfalls) were excluded. We did not conduct surveys during heavy rain. Transects continued for 800 m above the falls at Neekas River, ending at a lake, and continued for 1 km above the falls at Clatse River. Eighty-four points were surveyed at Neekas River, and 40 points were surveyed at Clatse River. Both rivers were surveyed two to four times on alternating dates to minimize temporal bias. For comparison with the salmon-bearing rivers, we surveyed the non-salmon-bearing Ripley and Cheenis rivers once each, on 3 June ($n = 17$ points) and 24 June 2003 ($n = 15$ points), respectively. These surveys consisted of a series of 8-min, unlimited-distance point counts (without distance sampling) at 100-m intervals close to the stream (50 m) over a 1-km stretch of the lower watershed.

Vegetation surveys.—To assess habitat variables that may be associated with bird abundance, we completed vegetation surveys during spring and summer 2003 at bird-survey points on Clatse and Neekas rivers. We sampled shrub cover and tree species composition along 30-m transects running in a randomly selected direction through each point (15 m on either side). We measured percentage of shrub cover, including saplings (diameter at breast height [DBH] <10 cm), within a 1-m² quadrat at 5-m intervals along the 30-m transect. Trees were identified to species and we counted all live trees whose trunks were within 5 m of the transect (300-m² plot). We categorized trees by the following size classes: small (10–30 cm DBH), medium (31–55 cm), or large (>55 cm). We counted separately all snags with height >2 m and DBH > 10 cm.

Habitat modeling.—We used a series of generalized linear models to test the importance of habitat-related variables in predicting songbird abundance, using PROC GENMOD for Poisson-distributed data in SAS (SAS Institute, Cary, North Carolina). Analyses were conducted separately for the six most common species: Winter Wren (*Troglodytes troglodytes*), Swainson's Thrush (*Catharus ustulatus*), Varied Thrush (*Ixoreus naevius*), Pacific-slope Flycatcher (*Empidonax difficilis*), Golden-crowned Kinglet (*Regulus satrapa*), and Chestnut-backed Chickadee (*Poecile rufescens*). The response variable (relative abundance) was measured as number of detections per point. To eliminate the potential bias of the estuarine environment, we excluded from the analysis those points within 400 m from the mouth of the river.

We selected explanatory variables on the basis of their potential influence on bird abundance: salmon (above vs. below falls), perpendicular distance from river (50 m vs. 150 m), the interaction term of salmon and distance from river, shrub cover, and tree species composition. We included river in every model to account for the effects of locality on relative abundance. We tested perpendicular distance from river because it was believed to influence the abundance of several of the species we analyzed (Lowther

2000, Murakami and Nakano 2001, Pearson and Manuwal 2001). We included the interaction term salmon*distance-from-river in the analysis to test whether the effect of distance from river depended on whether or not salmon were present. The influence of salmon on bird abundance may be more pronounced close to the river because of heightened concentrations of salmon-derived nutrients close to the stream edge (Ben-David et al. 1998). Shrub cover and tree species composition are also known to affect bird abundance (Sharpe 1996, Pearson and Manuwal 2001, Hejl et al. 2002, Poulsen 2002, Shirley 2005). Tree species composition, as a single variable based on analysis of numbers of trees, was expressed as a principal component factor score (PC2), and the original variables used in the analysis were as follows: Western Hemlock (*Tsuga heterophylla*), Sitka Spruce (*Picea sitchensis*), Western Red Cedar (*Thuja plicata*), Red Alder, snags, and total number of large trees. PC2, which described 26.55% of total variation, had positive loadings for Western Hemlock (0.81), Red Alder (0.69), and Sitka Spruce (0.61). We included this factor score primarily because of positive loading for Red Alder, which has been strongly correlated with density of breeding birds (Kirk et al. 1996, Gende et al. 2001).

We used an information-theoretic approach (Akaike's Information Criterion; Burnham and Anderson 2002) to assess the explanatory ability of various models in describing relative bird abundance. We used AIC_c , which adjusts for small sample size. We calculated ΔAIC_c as the difference between AIC_c values of the top-ranked model and all subsequent models, and considered models with $\Delta AIC_c \leq 2.0$ to be strongly supported by the data. We tested all possible single and additive combinations of explanatory variables, and also included a null model (intercept only) to assess model fit, for a total of 20 models per species. We calculated Akaike weights, reflecting the weight of evidence supporting a particular model, and weighted parameter estimates, showing overall effect size and direction, using formulas provided by Burnham and Anderson (2002).

Density estimates.—We estimated densities above and below the falls at Clatsop and Neekas rivers using DISTANCE (Thomas et al. 2004), which models the probability of detection at increasing distances from the observer and incorporates detection functions into estimates of density (Buckland et al. 2001). We assessed the ability of various combinations of key functions (half normal, hazard-rate, and uniform) and adjustment terms (cosine, simple polynomial, hermite polynomial) to model detection curves for each species using AIC and goodness-of-fit (GOF) chi-square analysis. Because points were surveyed two to four times each over the season, density estimates were weighted by survey effort. We included in the analysis transects both near (50 m) and far (150 m) from the stream, but excluded all points within 400 m of the river mouth. To improve model fit, we truncated 10% of observations at greatest distances from the observer and grouped observations in distance intervals to avoid heaping. We estimated densities of the five most common species (Winter Wren, Swainson's Thrush, Pacific-slope Flycatcher, Golden-crowned Kinglet, and Chestnut-backed Chickadee), which had sufficient observations (>40) to fit detection functions (GOF tests, $P > 0.05$). We did not estimate detection functions separately for observers, because observers were rotated across sample units. We compared density estimates across the waterfall barrier by calculating confidence limits around the difference between mean densities using formulas appropriate

for either pooled or separate detection functions (Buckland et al. 2001).

Distance-from-shore effects.—Bird abundance is believed to decrease with distance from the mouth of a river (Lock and Naiman 1998, Wiebe and Martin 1998). Because above-falls sites were farther away from the river mouth, distance from the river mouth could potentially influence interpretations of the effect of salmon on bird abundance. Accordingly, we conducted an additional analysis, using all four rivers, to test for the effects of (1) salmon, (2) linear distance from shore, and (3) both salmon and distance from shore on bird abundance. We used generalized linear models (for Poisson-distributed data) and information theoretics to test models containing these variables, as well as the intercept-only model. Total number of birds (for the six most common species) detected per point was used as the response variable, because the small sample size at Cheenis and Ripley rivers prevented separate analyses for each species. Because we visited Cheenis and Ripley rivers only once, we used transects from Neekas and Clatsop rivers that were closest in time to Cheenis and Ripley in analyses. Only transects within 50 m of the river were used in this analysis.

RESULTS

Habitat modeling.—Winter Wren, Swainson's Thrush, Varied Thrush, Pacific-slope Flycatcher, Golden-crowned Kinglet, and Chestnut-backed Chickadee accounted for 83% of all point-transect observations. The explanatory variable "salmon" was present in highly supported models ($\Delta AIC_c \leq 2.00$; Table 1) for all species, and in top-ranked models ($\Delta AIC_c = 0.00$) for Winter Wren, Swainson's Thrush, Varied Thrush, and Chestnut-backed Chickadee. Salmon was present in the second-highest-ranked models for Pacific-slope Flycatcher and Golden-crowned Kinglet. Parameter estimates indicated that bird abundance was always higher below the falls, where salmon spawned, than above the falls, where there were no spawning salmon (Table 2 and Fig. 1).

Distance from river (DR) was also an important explanatory variable and was present, together with salmon, in the highest-ranked models for Winter Wren, Swainson's Thrush, and Varied Thrush (Table 1). For these species, the highest-ranked models had AIC weights more than twice those of other competing models. For Pacific-slope Flycatcher, DR alone constituted the highest-ranked model ($w_i = 0.23$), though the model including salmon and DR received almost as much support ($w_i = 0.22$). Parameter estimates indicated that Winter Wrens were more abundant close to (50 m) than far from (150 m) the river, but the reverse was true for Swainson's Thrush and Pacific-slope Flycatcher (Table 2). For Varied Thrush, the model including the interaction between salmon and DR received the greatest amount of support, and abundance was lowest at points above the falls, close to the stream (Table 2).

The variables PC2 (tree species composition) and shrub cover were less important for most bird species than other variables (Table 1). PC2 was present in top model sets ($\Delta AIC_c \leq 2.00$) for most species, but usually not in highest-ranked models. Golden-crowned Kinglet was the exception, where the top model included this variable only ($w_i = 0.24$). This model, however, had only slightly more support than that which also included salmon ($w_i = 0.20$). Parameter estimates indicated that this species was

TABLE 1. Akaike's Information Criterion (AIC) analysis of generalized linear models (top models [$\Delta\text{AIC}_c \leq 2.00$] are shown) describing variation in songbird abundance in relation to habitat-related variables on streams on the central coast of British Columbia, spring 2003. River (Clatse or Neekas) was included as a variable in all models. A total of 124 points was used in this analysis.

Species ^a	Model ^b	K^c	Log-likelihood	ΔAIC_c	w_i^d
WIWR	Salmon + DR	5	-55.54	0.00	0.36
	Salmon + DR + PC2	6	-55.17	1.47	0.17
	Salmon + DR + SC	6	-55.41	1.94	0.14
SWTH	Salmon + DR	5	-78.73	0.00	0.37
	Salmon + DR + PC2	6	-78.36	1.46	0.18
PSFL	DR	4	-58.43	0.00	0.23
	Salmon + DR	5	-57.40	0.11	0.22
	DR + SC	5	-58.22	1.75	0.09
	Salmon + DR + PC2	6	-57.15	1.83	0.09
GCKI	PC2	4	-110.20	0.00	0.24
	Salmon + PC2	5	-109.28	0.32	0.20
CBCH	Salmon	4	-87.36	0.00	0.13
	DR	4	-87.37	0.02	0.13
	Salmon + DR	5	-86.36	0.18	0.12
	SC	4	-88.02	1.31	0.07
	Null	2	-90.18	1.41	0.06
	Salmon + DR + Salmon*DR	6	-85.99	1.64	0.06
	PC2	4	-88.27	1.83	0.05
	DR + SC	5	-87.24	1.93	0.05
	Salmon + SC	5	-87.25	1.95	0.05
	VATH	Salmon + DR + Salmon*DR	6	-92.45	0.00
	Salmon	4	-95.63	1.99	0.13

^aAbbreviations: WIWR = Winter Wren, SWTH = Swainson's Thrush, PSFL = Pacific-slope Flycatcher, GCKI = Golden-crowned Kinglet, CBCH = Chestnut-backed Chickadee, and VATH = Varied Thrush.

^bExplanatory variables: Salmon = present (below falls) or absent (above falls), DR = perpendicular distance from river (50 m vs. 150 m), Salmon*DR = interaction between salmon and distance from river; PC2 = principal component factor score related to tree species composition; SC = percentage of shrub cover.

^cNumber of parameters used in model.

^dAkaike weight: probability that model is the best approximating model among those considered.

TABLE 2. Weighted parameter estimates \pm unconditional SE from generalized linear models evaluating variance in relative bird abundance (number of birds per point) on salmon streams of the central coast of British Columbia, spring 2003.

Explanatory variable	Winter Wren	Swainson's Thrush	Varied Thrush	Pacific-slope Flycatcher	Golden-crowned Kinglet	Chestnut-backed Chickadee
Intercept	0.316 \pm 0.148	0.151 \pm 0.218	0.433 \pm 0.181	0.751 \pm 0.131	0.220 \pm 0.147	-0.864 \pm 0.297
River ^a	-0.312 \pm 0.159	-1.563 \pm 0.457	-0.740 \pm 0.252	0.130 \pm 0.141	-0.560 \pm 0.223	-0.626 \pm 0.367
Salmon ^b	-0.411 \pm 0.197	-1.442 \pm 0.381	-0.424 \pm 0.388	-0.111 \pm 0.201	-0.131 \pm 0.193	-0.215 \pm 0.228
DR ^c	0.598 \pm 1.020	-0.889 \pm 0.608	0.004 \pm 0.351	-0.733 \pm 0.637	0.012 \pm 0.070	-0.209 \pm 0.197
Salmon*DR	-0.016 \pm 0.074	0.002 \pm 0.186	-0.084 \pm 0.529	0.008 \pm 0.040	-0.010 \pm 0.020	-0.057 \pm 0.088
PC2 ^d	0.022 \pm 0.172	0.053 \pm 0.349	0.006 \pm 0.027	-0.013 \pm 0.199	0.183 \pm 0.191	0.004 \pm 0.081
SC ^e	0.000 \pm 0.006	0.001 \pm 0.013	0.000 \pm 0.002	-0.001 \pm 0.003	0.000 \pm 0.051	-0.001 \pm 0.004

^a"River" has two categories (Neekas and Clatse), with Neekas River as the reference value.

^b"Salmon" has two categories (below falls and above falls), with below falls as the reference value.

^cDR (distance from river) has two categories (50 m and 150 m), with 150 m as the reference value.

^dPrincipal component factor score having positive loadings for western hemlock, red alder, and Sitka spruce.

^eContinuous variable expressed as percentage of shrub cover.

positively associated with PC2 (Table 2). Shrub cover was present in models with $\Delta\text{AIC} \leq 2.00$ for Winter Wren, Pacific-slope Flycatcher, and Chestnut-backed Chickadee, but never in highest-ranked models. For Chestnut-backed Chickadee, many models (including the null) received a high level of support, making any inferences difficult for this species.

Density estimates.—Detectability of Winter Wrens in relation to distance from the observer varied above versus below the falls,

so we used separate detection functions to estimate densities for this species. Detectability of Golden-crowned Kinglets and Pacific-slope Flycatchers did not vary among locations, so we used pooled detection functions for these species as well as for Swainson's Thrushes and Chestnut-backed Chickadees, for which there were too few observations to test for this effect. We were unable to fit any detection function for Varied Thrush, so we could not estimate density for this species. Density estimates incorporating detection

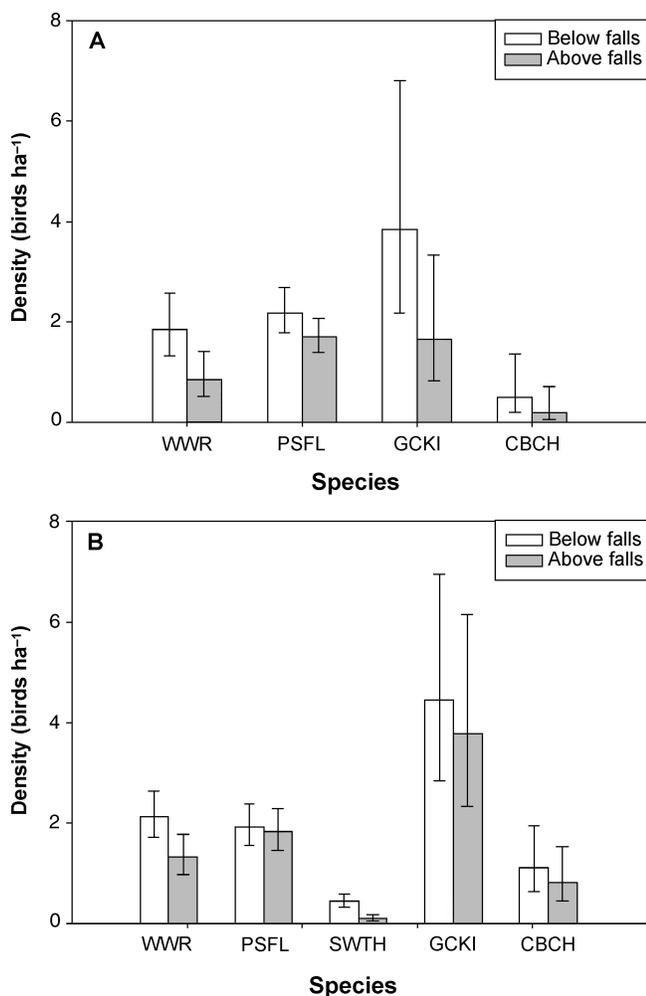


FIG. 1. Density estimates (birds ha⁻¹) and 95% confidence intervals for above and below the falls at (A) Clatse River and (B) Neekas River on the central coast of British Columbia, spring 2003. Bird species analyzed are Winter Wren (WWR), Pacific-slope Flycatcher (PSFL), Swainson’s Thrush (SWTH), Golden-crowned Kinglet (GCKI), and Chestnut-backed Chickadee (CBCH).

probabilities indicated that all species had higher densities below the falls than above the falls, with increases ranging from 6% to 425% at Neekas River and from 28% to 191% at Clatse River (Table 3). There was strong evidence (based on confidence limits) for biologically meaningful differences between below-falls and above-falls sites for Winter Wren, Golden-crowned Kinglet, and Pacific-slope Flycatcher at Clatse River, and for Swainson’s Thrush at Neekas River. Observed increases in density for Chestnut-backed Chickadee were less pronounced and may not be biologically meaningful, given that confidence limits for this species overlapped density differences at zero (Table 3).

Distance-from-shore effects.—When we used AIC_c to rank models that included linear distance from shore and salmon, the model including only salmon received the most support, followed by the model including both salmon and distance from shore

(Table 4). Relative-importance values, calculated by summing Akaike weights across models that contained each parameter, indicated that the weight of evidence in favor of salmon (0.87) was more than twice that of distance from shore (0.42).

DISCUSSION

Salmon was an important predictor of songbird abundance for most species, and large differences in density were detected over the waterfall barrier. The observed differences in abundance over a sharp ecological gradient suggest that upper-level consumers respond numerically to the presence of salmon-derived nutrients. Salmon-bearing reaches of streams may attract songbirds because of increased availability of aquatic and terrestrial invertebrates in the riparian zone. The influence of salmon carcasses on stream invertebrate abundance is complex and depends on the feeding ecology of each species (Chaloner and Wipfli 2002). However, certain aquatic invertebrates, such as chironomid larvae, accumulate in large numbers on salmon carcasses and emerge as adults into terrestrial systems in the spring (Wipfli et al. 1998, Chaloner et al. 2002). Aquatic invertebrates such as chironomid midges are an important component of diets of riparian birds and may provide a food subsidy at a time when terrestrial sources are depressed (Gray 1993, Nakano and Murakami 2001). Salmon deposited in the riparian zone quickly become colonized by flies (Diptera: Calliphoridae and Dryomyzidae) that lay their eggs *en masse* on carcasses (Hocking and Reimchen 2006). The resulting offspring consume the carcass, overwinter as pupae in the soil, and emerge as adult flies in spring, thus providing an additional food source for songbirds. The Winter Wren, a ground-foraging bird that incorporates aquatic invertebrates into its diet in the the spring (Murakami and Nakano 2001) as well as fly larvae hatched from salmon carcasses in the fall (K. S. Christie pers. obs.), may be particularly responsive to the presence of salmon-derived nutrients. Isotopic evidence showing the presence of salmon-derived nutrients in tissues of Winter Wrens further reflects the importance of salmon to this species (Christie 2005). Other species of songbirds that forage for arthropods in the middle and upper canopy likely also benefit from the large biomass of insects that hatch from salmon carcasses.

Songbirds may also benefit from heightened plant productivity around salmon streams (Helfield and Naiman 2001). Nitrogen fertilization increases fruit production and density of fruiting shrubs (Penney et al. 2003, Momoh et al. 2004), which may attract frugivorous birds such as Varied and Swainson’s thrushes. Shrubs such as *Vaccinium* spp. and Salmonberry (*Rubus spectabilis*), which are commonly found around salmon streams, produce fruit from May to July (Pojar and MacKinnon 1994) overlapping with the songbird breeding period.

In addition to the presence of salmon, distance from the river was an important predictor of relative abundance for many of the species analyzed. Winter Wrens were more abundant close to the river and have been associated with riparian habitats in previous studies (Murakami and Nakano 2001, Hejl et al. 2002, Waterhouse et al. 2002). Winter Wrens may concentrate near salmon streams, where they have access to fly larvae and emergent aquatic insects. Contrary to our hypothesis, most of the other

TABLE 3. Model selection and density estimates (using DISTANCE) for five bird species above and below the falls on Clatse River (40 points surveyed) and Neekas River (84 points surveyed) on the central coast of British Columbia. Points close to (50 m) and far from (150 m) the stream were included.

Species	Model selected	GOF P^a	TD (m) ^b	River	Location	Density ^c	n^d	% CV	$D_1 - D_2^e$	LCL, UCL ^f	
Winter Wren	Half-normal cosine	0.99 0.23 0.99 0.23	70	Clatse	Above	0.61	22	28.85	-1.17	-2.23, -0.11	
					Below	1.78	47	28.80			
				Neekas	Above	0.91	50	21.34	-1.09		-2.19, 0.01
					Below	2.00	124	26.20			
Pacific-slope Flycatcher	Hazard-rate cosine	0.07	70	Clatse	Above	1.71	39	9.86	-0.48	-0.86, -0.10	
					Below	2.19	50	10.24			
				Neekas	Above	1.78	62	11.07	-0.10		-0.67, 0.47
					Below	1.88	101	10.82			
Swainson's Thrush	Hazard-rate cosine	0.05	90	Neekas	Above	0.08	7	33.66	-0.34	-0.46, -0.22	
					Below	0.42	55	15.06			
Golden-crowned Kinglet	Hazard-rate cosine	0.39	40	Clatse	Above	1.66	13	36.11	-2.18		-4.11, -0.25
					Below	3.84	30	29.35			
				Neekas	Above	3.70	44	25.15	-0.65	-1.93, 0.63	
					Below	4.35	80	23.01			
Chestnut-backed Chickadee	Half-normal cosine	0.49	40	Clatse	Above	0.20	2	68.51	-0.31		-0.86, 0.24
					Below	0.51	5	51.96			
				Neekas	Above	0.80	12	31.87	-0.27	-0.88, 0.34	
					Below	1.07	25	29.05			

^aChi-square goodness-of-fit (GOF) test to assess whether model fits data.

^bTruncation distance (10% of observations).

^cDensity (number of birds per hectare).

^dNumber of detections (after truncation).

^eDifference in mean density between above and below falls locations (above–below).

^fApproximate 100(1–2 α)% confidence limits for the difference in density above and below the falls.

species in our study were more or equally abundant at points far from the stream, whether above or below the falls. In contrast to arid or agricultural regions, riparian areas of coniferous forests in the Pacific Northwest do not support higher densities of birds than upland areas, because of less pronounced differences in vegetation and microclimate (McGarigal and McComb 1992, Shirley 2005). Some bird species may avoid areas immediately adjacent to the stream because of potentially greater abundance of nest predators in these natural edges (Gates and McKernan 2003). Varied Thrushes seemed to avoid habitats adjacent to the river above the falls but not below the falls, and this is potentially

attributable to increased food availability close to the river in the salmon-influenced habitat. It is possible that we detected fewer birds at points 50 m from the river because the area surveyed at these points was slightly smaller owing to its proximity to the river. This would have only a slight effect, given that most detections were within 50 m of the observer, and would only affect species that were detected more frequently at distances >50 m from the observer, such as Varied and Swainson's thrushes.

PC2 (tree species composition) and shrub cover were present in top model sets for several species but were generally less important than salmon or distance from the stream. PC2 was important for Golden-crowned Kinglets, which responded positively to the presence of Western Hemlock, Red Alder, and Sitka Spruce. Golden-crowned Kinglets breed and forage in spruce–fir forests and glean insects from leaves and twigs (Ingold and Galati 1997). This species may favor spruce- and fir-dominated forests over cedar-dominated forests, which are more prevalent in nutrient-poor soils above the falls (Mathewson et al. 2003). 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), an important food source for songbirds. Percentage of shrub cover was not an important predictor of bird density, in contrast to other studies (e.g., Shirley 2005). Shrub species composition and berry production may be more important factors in determining bird abundance on our study sites than shrub cover alone.

Results of several studies have found songbird density and diversity to be strongly correlated with percentage of deciduous tree cover (Kirk et al. 1996, Gende and Willson 2001). Red Alder, being the only deciduous tree at our study sites, occurred at low

TABLE 4. Akaike's Information Criterion (AIC) analysis of generalized linear models (all models are shown) describing variation in total songbird abundance as it relates to distance from shore and salmon on streams on the central coast of British Columbia, spring 2003. River (Clatse, Neekas, Ripley, or Cheenis) was included as a variable in all models. A total of 113 points was surveyed.

Model ^a	K^b	Log-likelihood	ΔAIC_c	w_i^c
Salmon	6	134.00	0.00	0.58
Salmon + Dshore	7	134.46	1.37	0.29
Dshore	6	132.51	2.98	0.13
Intercept	2	103.11	53.11	0.00

^aModel included the following variables: Salmon = present (below falls at Neekas or Clatse rivers) or absent (above falls at Neekas or Clatse rivers; all points at Ripley and Cheenis rivers), Dshore = linear distance from mouth of river.

^bNumber of parameters used in model.

^cAkaike weight: probability that model is the best approximating model among those considered.

densities, forming a narrow strip along the stream edge both above and below the falls. The principal component factor score used in our models had positive loadings for Red Alder and was not an important predictor of abundance for most species analyzed. Thus, deciduous vegetation apparently was not a driving force determining songbird abundance in our study.

Unlike that of other species analyzed, Chestnut-backed Chickadee abundance was not well explained by any particular model. This resident songbird occurs in the mid- and upper canopy of coniferous forests and is an obligate cavity-nester (Campbell et al. 1997). Density of snags and conifers may be better predictors of abundance for this species, as found by Shirley (2005).

Bird abundance in temperate zones is believed to decrease with distance from the mouth of a river and narrowness of the stream channel (Lock and Naiman 1998, Wiebe and Martin 1998). This phenomenon could potentially bias interpretations of the effect of salmon on bird density, because above-falls sites are farther away from the river mouth and may be expected to have fewer birds, regardless of salmon. However, even after we excluded points within 400 m of the shore to minimize estuarine effects, the comparison between rivers with and without salmon indicated that salmon was a better predictor of songbird abundance than distance from shore. Therefore, we infer that salmon-derived nutrients influence songbird abundance regardless of distance from shore.

The central coast of British Columbia has relatively little forest fragmentation, with large expanses of old-growth forest and many productive salmon streams. This contrasts with southern parts of the province and the contiguous United States, where wild salmon populations have been substantially reduced compared with historical levels (Gresh et al. 2000) and riparian forests have been largely converted to second growth. 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.

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