



Ecological links between salmon, large carnivore predation, and scavenging birds

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We compared scavenging bird abundance and diversity across 17 estuaries on the Central Coast of British Columbia, Canada in relation to landscape characteristics and biomass of spawning salmon and senescent and depredated salmon carcasses. We discovered that all metrics for spawning salmon and carcass biomasses were strong predictors of scavenger abundance and diversity. Specifically, Shannon's diversity, which emphasizes rare species richness, and total abundances of scavengers, corvids (*Corvus* spp.), and small and large gulls (*Larus* spp.) were most strongly predicted by total biomass of carcasses. In contrast, the abundance of bald eagles *Haliaeetus leucocephalus* was most strongly predicted by biomass of carcasses that had been killed or scavenged by other predators (mostly bears and wolves). Simpson's diversity, which emphasizes evenness of common species, was best predicted by total spawning salmon biomass. Estuary area also featured prominently among top predictors of most scavenger metrics. Our results suggest a link between terrestrial salmon predators and bald eagles, and that available salmon biomass is important for maintaining the abundance and diversity of scavenging birds that congregate at estuaries throughout the spawning season.

Single species can have strong impacts on ecosystems. These species can be essential for the stability and resilience of communities by driving ecosystem processes, such as productivity, which can be heavily influenced by a species' ability to regulate energy flow (Chapin et al. 1997). An example concerns Pacific salmon (*Oncorhynchus* spp.) and their relationships to bird communities. Salmon accumulate >95% of their body mass at sea (Groot and Margolis 1991). When they return to their natal streams to spawn, their energy-rich carcasses and eggs are consumed by a variety of terrestrial vertebrates throughout coastal watersheds, including bears (*Ursus* spp.), wolves *Canis lupus*, and scavenging birds (Reimchen 1994).

A large proportion of salmon carcasses and eggs may become available to scavengers in estuaries through water movement and terrestrial predator activity (Reimchen et al. 2003). However, very few studies have assessed the influence of this food source on estuarine communities. Some of the most abundant vertebrates that assemble in estuaries in the fall are scavenging birds (Willson et al. 1998). Among these are bald eagles *Haliaeetus leucocephalus*, a symbolic raptor in the northeastern Pacific closely linked with salmon. For example, a study on the Skagit River in Washington found that overwintering bald eagle abundance was positively correlated with the number of chum salmon *Oncorhynchus keta* that spawned the previous fall (Hunt et al. 1992). Crows and ravens (*Corvus* spp.) also

eat salmon (Willson et al. 1998). The most abundant but least studied of the salmon scavenging birds are gulls (Christie and Reimchen 2005). They may especially rely on this food source as several species eat salmon during their southward migration, an energetically taxing endeavour that requires substantial fat stores (Schneider and Harrington 1981). One study conducted at two of our study sites (Clatse and Neekas Creeks) explored gull consumption rates of salmon and the potential of gulls to recycle nutrients from salmon back into the surrounding coastal system via guano deposition (Christie and Reimchen 2005). However, no study has quantified the direct influence of salmon on scavenging bird abundance and diversity at sites that vary across a gradient of salmon population sizes. Furthermore, the availability of salmon resources to scavenging birds may be facilitated by other scavengers and predators, such as bears and wolves.

In this study we assess the influence of salmon as food for scavenging bird communities by exploring impacts on bird abundances and diversities in 17 estuaries on the Central Coast of British Columbia, Canada. Study sites vary across a range of salmon population sizes and watershed and estuary sizes. The objectives of this study are 1) to quantify, for the first time, the relationship between salmon biomass and scavenging bird abundance and diversity, while accounting for the effects of landscape variables, migratory timing and inter-annual variability in biomass of fish,

and 2) to determine whether scavenging bird densities are best predicted by depredated estuary carcasses, total estuary carcasses, or total biomass of spawning salmon in the streams. We hypothesize that salmon resources strongly influence the number of scavenging birds that congregate at estuaries during the spawning season and that other terrestrial scavengers and predators may provide improved access to tissues for scavenging birds.

Material and methods

Study sites

We conducted our study in Heiltsuk First Nation traditional territory in the Great Bear Rainforest on the Central Coast of British Columbia (Fig. 1). We surveyed birds in 17 estuaries on coastal islands and mainland inlets. An estuary boundary was associated with the extent of freshwater along the shore, which was defined at the point of termination of the sedge (*Carex* spp.) band that extends from the mouth of the adjacent stream (Stevens and Hoag 1996). Estuary habitats consisted of clumps of trees and shrubs, sedge meadows, rocky intertidal zones, and mudflat zones. Estuaries ranged from 0.003 to 0.171 km² (mean = 0.041 ± 0.020) at low tide (<1.8 m) and watershed catchment areas ranged from 1.03 to 40.90 km² (mean = 14.67 ± 5.84). Our study sites are in the Coastal Western Hemlock Biogeoclimatic Zone, which has high annual precipitation (> 3300 mm yr⁻¹) (Pojar et al. 1987). Study sites varied across a range of salmon abundances representative of the region, from zero to an average of over 59 000 combined chum *Oncorhynchus keta*, pink *O. gorbuscha*, coho *O. kisutch*, and sockeye *O. nerka*. Salmon in this region spawn from late August to early November (Table 1).

Salmon

We surveyed estuary carcasses at each site visit during low tide. For each carcass we recorded percent remaining (100, 75–100, 50–75, 25–50, 0–25%, bones) and predator/scavenger activity (bear, wolf, senescent, unknown). Bear-depredated carcasses characteristically have consumption evidence of brain, dorsal or lateral muscle or ovary tissue (Reimchen 2000), whereas wolf-depredated carcasses only lack the entire head of the salmon (Darimont et al. 2003).

Spawning salmon were counted by people from the Heiltsuk First Nation, the Canadian Dept of Fisheries and Oceans (DFO), and by our field team from Simon Fraser Univ. Surveys were conducted on foot to estimate returning salmon abundance over the August to November spawning season. Where there were at least 3 counts per season, the total number of salmon was calculated using the area-under-the-curve (AUC) method (English et al. 1992). Where there were fewer than 3 counts per season, 'peak' counts were used to estimate total number of salmon. These two estimation methods are highly correlated (peak mean = 1430.4 ± 988.1, AUC mean = 1656.8 ± 906.0, r = 0.88, p < 0.001) (Field and Reynolds 2011, Hocking and Reynolds 2011).

We compared several metrics of salmon nutrient input in our analyses. Total spawning salmon, and estuary carcass and depredated estuary carcass biomasses were calculated from yearly returning salmon abundance estimates and carcass counts, respectively, and from species-specific regional mass estimates: chum = 3.5 kg, pink = 1.2 kg (unpubl.). We excluded coho and sockeye salmon from total spawning salmon biomass estimates because they only account for 2% of the total biomass at our study sites and we never observed their carcasses in estuaries. We quantified salmon according to biomass (kg) rather than

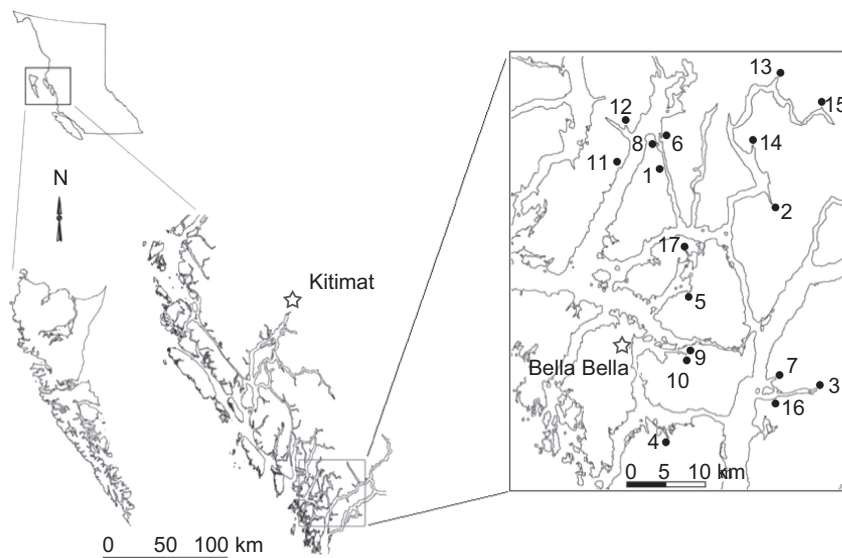


Figure 1. Location of the 17 study estuaries on the Central Coast of British Columbia, Canada (gazetted stream names cited where possible): 1) Bullock Main, 2) Clatse Creek, 3) Evans Inlet no. 2 Creek, 4) East Fannie Cove/Howyete no. 1 creeks, 5) Farm Bay, 6) Fell Creek, 7) Hooknose Creek/Port John, 8) Kill Creek, 9) Kunsoot River, 10) Kunsoot South, 11) Mosquito Bay, 12) Neekas Creek, 13) Quarcha/Lee creeks, 14) Ripley Bay, 15) Roscoe Creek, 16) Sagar Creek, and 17) Troupe Pass North Creek.

Table 1. Two-year mean watershed landscape features, depredated and total estuary carcass biomasses, and spawning salmon biomass for our 17 study sites. See text for how characteristics were measured.

Site	Estuary area (km ²)	Watershed catchment area (km ²)	Stream length (km)	Bankfull width (m)	Depredated carcass biomass (kg)	Total carcass biomass (kg)	Spawning salmon biomass (kg)
Bullock Main	0.018	3.30	2.42	10.9	411	1110	7852
Clatse Creek	0.053	32.10	6.82	22.8	790	4286	18734
Evans Inlet	0.016	22.90	4.20	13.3	33	74	558
Fannie Cove	0.038	35.00	5.92	16.9	109	614	15249
Farm Bay	0.003	2.30	2.52	6.4	0	0	0
Fell Creek	0.025	7.00	1.85	10.9	48	236	539
Hooknose-Port John	0.073	18.40	5.51	20.2	56	171	6101
Kill Creek	0.008	1.03	0.98	3.5	89	148	2233
Kunsoot River	0.032	5.69	3.67	13.1	253	1738	15411
Kunsoot South	0.008	1.50	0.79	1.2	0	3	0
Mosquito Bay	0.028	5.20	6.00	9.7	69	139	3702
Neekas Creek	0.056	17.60	5.90	17.7	1966	9710	102512
Quartcha-Lee	0.101	40.90	12.92	34.1	178	622	18660
Ripley Bay	0.041	16.08	4.32	14.7	0	0	0
Roscoe Main	0.171	33.60	11.03	23.5	490	1770	37134
Sagar Creek	0.033	36.60	5.20	15.5	23	226	2589
Troupe North Creek	0.022	1.60	0.44	4.4	0	0	0

abundance because biomass provides a better gauge of salmon nutrient availability. Mean salmon biomass ranged from zero to 40940 kg (mean = 4151 ± 5273 kg) in 2008, and from zero to 164084 kg (mean = 26043 ± 21745 kg) in 2009 across our study watersheds. Seven sites had two streams entering a common estuary, and spawning salmon biomass estimates were combined where data were available.

Scavenging birds

We recorded all birds seen and heard from a single vantage point with a view of the entire estuary. Surveys were repeated 3 to 4 times over the entire spawning season during low tide (<1.8 m), when feeding is highest due to more estuary carcasses being exposed (Christie and Reimchen 2005). The duration of each survey was standardized to the size of the estuary (1 min 1000 m⁻²). Survey dates ranged from 11 September to 28 October in 2008 and from 16 September to 20 October in 2009. Although 17 estuaries were visited, two sites were only surveyed in 2008 (Farm Bay and Troupe North) and were replaced by two larger sites in 2009 (Quartcha-Lee and Roscoe Main). Survey days were chosen randomly, R. Field was the only observer, and we did not survey birds on days with heavy rainfall or substantial wind (> 10 km h⁻¹).

We focused on birds that feed directly on salmon carcasses and eggs, including gulls, corvids and birds of prey. Six species of gulls forage regularly on salmon tissues during the fall spawning season, including glaucous-winged *Larus glaucescens*, herring *L. argentatus*, California *L. californicus*, Thayer's *L. thayeri*, mew *L. canus*, and Bonaparte's *L. philadelphia*. We divided these gulls into two groups based on foraging preferences: large-bodied gulls, including glaucous-winged, herring, California, and Thayer's, which consume mainly carcasses, and small-bodied gulls, including mew and Bonaparte's, which consume mainly and exclusively eggs, respectively (Christie and Reimchen 2005). One ring-billed gull *Larus delawarensis*

was observed on one survey in 2009 and was excluded from analyses. Northwestern crows *Corvus caurinus* and common ravens *C. corax*, were regularly observed scavenging carcasses. Since their abundances were too low to support individual analyses and because they exhibit similar scavenging behaviour, we combined their abundances for analyses. Only one bird of prey, the bald eagle, was regularly observed scavenging carcasses and this species was investigated separately for some analyses. We also combined all of these species' abundances to assess the impact of salmon on total scavenging bird abundance and diversity. We calculated three measures of diversity: 1) species richness (i.e. total number of species), 2) Shannon's index, which highlights rare species and species richness, and 3) Simpson's index (1-D), which highlights common species and evenness (Shannon and Weaver 1949, Simpson 1949, Nagendra 2002).

Environmental variables

To account for landscape features, exposed estuary areas were sketched on air photos of each study site during each survey. Estuary areas (km²), which depended on tidal height, as well as watershed catchment areas (km²) and mainstem and tributary lengths (m) were then determined using iMapBC, which determines the extent of watershed hydrological features using geographic data (Government of British Columbia 2008). Stream 'bankfull' (m), which is the width of a stream when water flows are highest, was measured at 5 transects randomly placed within the lower reaches of each stream. Bankfull width was multiplied by stream length (m) to obtain approximate stream area (m²) estimates. For sites with more than one stream entering a common estuary, landscape features were summed.

Data analyses

We used principal components analysis (PCA) to extract a reduced set of uncorrelated components from watershed

landscape features. Larger watersheds have higher terrestrial nutrient input, increased access for potential salmon predators, and may provide larger foraging patches for scavenging birds (Flather and Sauer 1996, Polis et al. 1997, Alexander et al. 2000). Larger, more open estuaries may also provide more food and decrease competition and predation risk for scavenging birds. Landscape variables, which included mean site estuary size and watershed catchment and stream areas, were well correlated ($r > 0.76$, $n = 17$, $p < 0.05$) and were scaled prior to PCA (Jolliffe 2002). The first principal component (PC1) accounted for 92% of the variance, with only estuary area weighted highly positively (0.95) while weightings for catchment and stream areas were weak (< 0.23). Therefore, only estuary area was retained for further analyses, though we did also try the analyses using PC1 and found no significant changes in the results.

In the main analyses, the impacts of salmon on scavenging bird abundance and diversity were tested using Akaike's information criterion (corrected for small sample sizes; AICc). This method evaluates models for all combinations of variables based on the principle of parsimony, striving to maximize model fit while minimizing the number of model parameters, and functions optimally when collinearity between all variables included is minimized. Scavenger abundances and salmon metrics were log-transformed ($\log_{10}[\text{variable} + 1]$) to improve residual distribution model assumptions. We used variance inflation factor (VIF) scores to measure how much the variance of an estimated regression coefficient is increased by collinearity among predictors in an ordinary least squares regression. A measure of tolerance for the i th predictor is 1 minus the proportion of variance it shares with other predictors in the model ($1 - R_i^2$), and the VIF is measured as $1/(1 - R_i^2)$. The VIF scores were < 2 for all variables, indicating an acceptably small amount of collinearity among predictors (Zuur et al. 2009a). Due to the repeated measures included in our study design, we used a linear mixed-effects model method. This allowed us to retain our complete dataset while accounting for a lack of independence caused by correlations across repeated surveys, and to calculate parameter estimates which can be used to predict general relationships between birds and salmon (Zuur et al. 2009a, b). We included 'site' as the random effect, which allows the model intercepts to vary by site, as this variable contained the identities of our replicated surveys. A set of 15 candidate models was created for each scavenger response variable, each allowing the model intercept to vary by site. The influence of the total biomass of spawning salmon (kg) was compared with estuary total carcass biomass (kg), estuary depredated carcass biomass (kg), estuary area (km^2), and survey date (Julian day). Year was included as a two-level factor (2008 and 2009) in all candidate models to control for potential inter-annual variability. The diagnostic plots for all candidate models met the assumptions of homoscedacity, normality and independence of residuals (Zuur et al. 2009a). All statistical analyses were computed using R (R Development Core Team).

Results

All six gull species were observed commonly, and foraging preferences for carcass tissues or eggs were consistent with

previous observations, with large-bodied gulls consuming mainly carcass tissues and small-bodied gulls consuming mainly salmon eggs. Gulls accounted for 84% of total scavenging bird abundance. Bald eagles and gulls generally increased in abundance at each site over the salmon spawning season, whereas corvid abundance did not show any clear trend.

Several other bird species were observed in estuaries during fall surveys, but most were never observed consuming salmon tissues. Interestingly, we witnessed several other species consuming insect larvae directly from salmon carcasses, including Swainson's *Catharus ustulatus* and hermit thrushes *C. guttatus*, Pacific wrens *Troglodytes pacificus* and Steller's jays *Cyanocitta stelleri*. These species were not included in analyses because our survey methods were aimed towards large scavengers.

A salmon metric always proved to be the most significant predictor of avian scavengers, appearing in the top-ranked model for all bird response variables (Table 2 and 3). Total estuary carcass biomass was the top-ranked salmon metric for total scavenger abundance and Shannon's diversity and for the numbers of small and large gulls and corvids. Depredated carcass biomass was the top-ranked salmon metric for bald eagles, and total spawning salmon biomass was the top-ranked salmon predictor of Simpson's diversity. Total spawning salmon biomass was still a strong predictor of all bird metrics (e.g. Fig. 2). Total estuary carcass and depredated carcass biomasses were strongly correlated with spawning salmon biomass ($r = 0.65$, $n = 30$, $p < 0.001$; $r = 0.61$, $n = 30$, $p < 0.001$, respectively).

A post-hoc analysis revealed that, although total spawning biomass was always a stronger predictor than individual salmon species biomass, total spawning chum biomass was a better predictor than pink biomass of all bird metrics except large gull and corvid abundance. Summed spawning biomass across all of our sites was greater for chum (45 745 kg) than pink salmon (16 513 kg) in fall, 2008, and pink biomass (204 707 kg) was greater than chum (138 089 kg) in fall, 2009. Further, a post-hoc analysis of the influence of spawning salmon density (biomass m^{-2} of stream) found that this metric was never a better predictor of any bird metric than total spawning or carcass biomasses.

Estuary area was also important for several bird response variables, but it was only significantly related to scavenger species richness and total scavenger and small and large gull abundances. Survey date was also important for bald eagles and for large gulls. There was significant variation among years in total scavenger and bald eagle abundance and for species richness and Shannon's diversity, with greater numbers in 2009 (Table 2, 3). A graphical example of model fits is presented in Fig. 2b.

Discussion

The biomass of salmon carcasses in estuaries and the total biomass of spawning salmon in the streams were important predictors of all measures of scavenging bird density and diversity. Bald eagles were unique because their numbers were tied most closely to carcasses that had been killed or scavenged by bears and wolves, rather than the total number of carcasses available. Furthermore, Simpson's index of

Table 2. Results from AICc model selection analysis of linear mixed-effects models (top models presented: $\Delta AICc < 3$) describing scavenging bird abundance and diversity response variables by salmon, temporal and environmental variables. Model intercepts were allowed to vary by site. K = number of parameters, AICc = Akaike's information criterion adjusted for small sample sizes, $\Delta AICc$ = difference between model AICc and top model AICc, w_i = model AICc weight, the highest w_i associated with the model having the best overall fit using the fewest number of parameters (Anderson 2008). All bird abundances and salmon biomass metrics were ($\log_{10}[variable + 1]$) transformed. AICc values were calculated using maximum likelihood. Year was included in all models but was excluded in the table for clarity of presentation.

Response variable	Model	K	AICc	$\Delta AICc$	w_i
Scavenger abundance	Estuary carcass biomass + Estuary area	6	117.96	0.00	0.71
	Estuary carcass biomass + Estuary area + Survey date	7	120.09	2.13	0.24
Shannon's diversity	Estuary carcass biomass + Estuary area	6	90.92	0.00	0.40
	Estuary carcass biomass	5	92.10	1.18	0.22
	Estuary carcass biomass + Estuary area + Survey date	7	92.17	1.24	0.22
	Estuary carcass biomass + Survey date	6	92.86	1.94	0.15
Simpson's diversity (1-D)	Spawning salmon biomass	5	-29.75	0.00	0.48
	Spawning salmon biomass + Survey date	6	-28.31	1.44	0.23
	Spawning salmon biomass + Estuary area	6	-27.64	2.11	0.17
Species richness	Estuary carcass biomass + Estuary area	6	376.41	0.00	0.68
	Estuary carcass biomass + Estuary area + Survey date	7	378.50	2.09	0.24
Bald eagle abundance	Depredated carcass biomass + Estuary area + Survey date	7	66.70	0.00	0.29
	Depredated carcass biomass	5	67.12	0.42	0.23
	Depredated carcass biomass + Estuary area	6	67.27	0.57	0.22
	Depredated carcass biomass + Survey date	6	67.37	0.67	0.21
Small gull abundance	Estuary carcass biomass + Estuary area	6	168.49	0.00	0.62
	Estuary carcass biomass + Estuary area + Survey date	7	170.41	1.92	0.24
Large gull abundance	Estuary carcass biomass + Estuary area + Survey date	7	155.53	0.00	0.75
Corvid abundance	Estuary carcass biomass + Estuary area	6	127.17	0.00	0.34
	Estuary carcass biomass	5	127.17	0.00	0.34
	Estuary carcass biomass + Estuary area + Survey date	7	128.55	1.38	0.17
	Estuary carcass biomass + Survey date	6	128.84	1.66	0.15

Table 3. Parameter estimates, standard errors (SE), t-values and p-values from the top-ranked linear mixed-effects models evaluating the variance in bird abundance and diversity in estuaries on the Central Coast of British Columbia, fall 2008 and 2009. All bird abundances and salmon biomass metrics were ($\log_{10}[variable + 1]$) transformed. Year was a two-level factor with 2008 as the reference year.

Response	Predictors	Estimate	SE	t	p
Scavenger abundance	Total carcass biomass	0.45	0.05	9.96	0.00
	Estuary area	0.06	0.02	3.09	0.00
	Year	-0.24	0.09	-2.73	0.01
	Intercept	0.56	0.13	4.40	0.00
Shannon's diversity	Total carcass biomass	0.28	0.04	7.39	0.00
	Estuary area	0.03	0.02	1.82	0.07
	Year	-0.19	0.08	-2.36	0.02
	Intercept	0.42	0.09	4.56	0.00
Simpson's diversity (1-D)	Spawning salmon biomass	0.12	0.01	8.50	0.00
	Year	-0.02	0.04	-0.49	0.63
	Intercept	0.16	0.04	3.58	0.00
Species richness	Total carcass biomass	1.38	0.14	9.62	0.00
	Estuary area	0.17	0.06	2.85	0.01
	Year	-0.88	0.28	-3.13	0.00
	Intercept	1.66	0.40	4.14	0.00
Bald eagle abundance	Depredated carcass biomass	0.33	0.05	7.39	0.00
	Estuary area	0.02	0.01	1.67	0.10
	Survey date	0.00	0.00	1.65	0.10
	Year	-0.25	0.07	-3.56	0.00
	Intercept	-0.86	0.60	-1.43	0.16
Small gull abundance	Total carcass biomass	0.35	0.06	6.30	0.00
	Estuary area	0.07	0.02	2.95	0.00
	Year	-0.08	0.11	-0.76	0.45
	Intercept	0.16	0.16	0.96	0.34
Large gull abundance	Total carcass biomass	0.37	0.06	6.31	0.00
	Estuary area	0.06	0.02	2.75	0.01
	Survey date	0.01	0.00	2.46	0.02
	Year	-0.02	0.11	-0.20	0.84
	Intercept	-2.03	0.88	-2.32	0.02
Corvid abundance	Total carcass biomass	0.37	0.04	8.94	0.00
	Estuary area	-0.02	0.01	-1.46	0.15
	Year	-0.05	0.09	-0.48	0.63
	Intercept	0.09	0.08	1.03	0.31

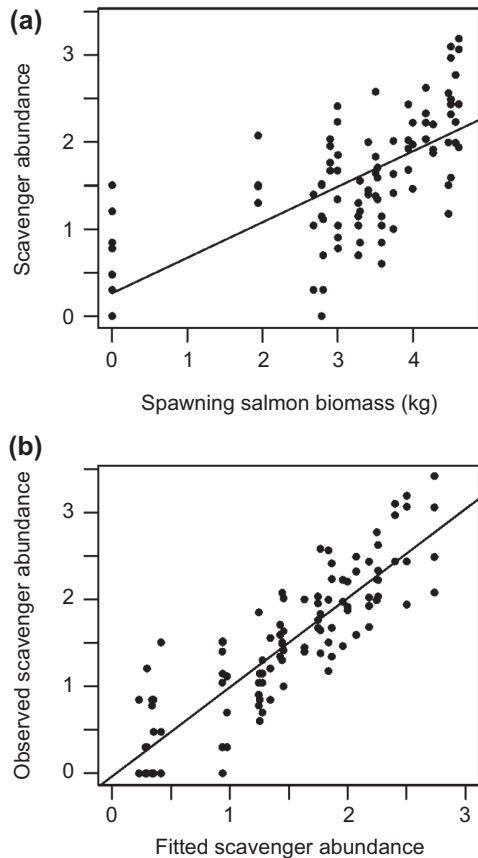


Figure 2. (a) Mixed-effects regression plot for total scavenging bird abundance predicted by total spawning salmon biomass in the stream, using raw data and controlling for multiple observations by allowing the intercept to vary by site. Solid line represents the mean regression line for all sites. (b) Observed total scavenging bird abundance vs fitted total scavenging bird abundance for the model including total spawning salmon biomass and year as predictors. For both plots, scavenging bird abundance and salmon variables were transformed ($\log_{10}[\text{variable} + 1]$).

diversity, which emphasizes evenness of common species, was most influenced by the total number of salmon present over the entire spawning season. Our findings demonstrate quantitatively that salmon support both the abundance and diversity of large numbers of birds at a time when nutrient and fat acquisition is vital to overwinter survival and migration (Stocker and Weihs 1998).

Among the nine scavenging birds that we observed, bald eagles are the only species that regularly kills fish, and this may explain their strong preference for the generally fresher carcasses that have been left by bears and wolves. Salmon killed by predators also have more accessible tissue and eggs and a higher energetic content per volume than fish that have died from senescence after spawning, which tend to be more decayed (Winder et al. 2005). Moreover, another study has found eagles to prefer experimentally placed ‘opened’ over intact salmon carcasses (Knight and Anderson 1990). However, we would expect other species of scavengers to also benefit from higher accessibility and energetic content. They may have been out-competed by eagles in estuaries where there were large numbers of such depredated carcasses. It is not clear whether other

scavenging bird species show similar preferences in the absence of eagles. Although another study has found that bald eagle abundance is positively correlated with the abundance of spawned-out salmon (Armstrong 2008), this is the first demonstration of a link between large terrestrial salmon predators/scavengers and bald eagles.

The total biomass of salmon carcasses in the estuaries, rather than biomass of depredated carcasses, was the best predictor of scavenger richness, Shannon’s diversity, and of all other species of scavenging birds. This suggests that more species may be attracted to estuaries when larger quantities of salmon carcasses are available. A study at two of our sites (Clatse and Neekas Creeks) in 2002–2003 found that abundance of large gulls, but not small gulls, appeared to correspond with food availability (Christie and Reimchen 2005). Accessible egg biomass and/or stream discharge, which can dislodge eggs from spawning beds, could have been correlated with estuary carcass biomass at our sites and influenced egg-consuming small gull abundance. Moreover, scavengers may have been influenced by density-dependent sediment disruption by spawning salmon, which contributes to increased transport of salmon eggs, carcasses, invertebrates, and other nutrients downstream to estuaries (Moore et al. 2008).

Simpson’s diversity, which is driven by common species and highlights evenness, was best predicted by total spawning salmon biomass. This supports the prediction that anadromous fish may support higher diversity of scavengers, likely due to the ease of capture, annual predictability, and high abundance of these fish (Reimchen 1994, Willson and Halupka 1995). This suggests that common species may be attracted to estuaries by spawning salmon. Other site characteristics that we were not able to include in our analysis may have been important, such as proximity to roosting sites. We also considered whether the directional aspect of the estuary or distinctions between mainland and island streams were related to scavenging bird activity, but did not detect any trends.

Total biomass of spawning fish was always a stronger predictor than individual species biomasses, but post-hoc analyses revealed that spawning chum salmon biomass alone was a better predictor of most bird metrics than pink salmon biomass. The larger combined biomass of spawning pink salmon in 2009 suggests that this result did not stem from greater available carcass biomass alone. Chum are the largest salmonid in our study area and have higher fecundity and larger eggs than pink salmon (Beacham and Murray 1993). There could also have been differences among species in downstream transport of carcasses and eggs, which could depend on stream physical characteristics (Janetski et al. 2009). The effect of estuary area was secondary to the effect of salmon. Larger estuaries provide increased foraging space and more non-salmon food sources such as benthic invertebrates.

Seasonal and inter-annual effects on scavenging birds were variable. Survey date was an important predictor of bald eagle and large gull abundance. Bald eagles are known to leave their home range for short time periods to take advantage of seasonally-available food sources (Garrett et al. 1993). The southward migration timing of other birds is governed by the seasonal production of food supplies at

stopover sites (Schneider and Harrington 1981). This appears to be the case at our sites, as the presence of the majority of the local and regional migrants is correlated predominantly with salmon biomass rather than with survey date. Notably, based on data from a companion study at our study sites during the summer avian breeding season in the same two years (May to July; Field and Reynolds 2011), mean site abundance of bald eagles, corvids and gulls increased in the fall by 120, 250, and 7500% respectively in 2008, and by 140, 800 and 17700% respectively in 2009. Most individual species abundances were positively correlated between the summer and fall seasons within each of the 15 sites that were studied in each year ($n = 30$, $r = 0.10-0.89$, $p < 0.05$).

This study suggests that conservation of Pacific salmon populations is important to the persistence of large and diverse assemblages of both resident and migratory scavenging birds. Furthermore, bald eagles particularly benefit from the actions of large carnivores in providing fresh salmon carcasses. In turn, scavengers of salmon are important vectors for cycling salmon nutrients through coastal food webs (Schindler et al. 2003, Christie and Reimchen 2005), a process that benefits many plants and animals year-round (Hocking and Reimchen 2009, Hocking and Reynolds 2011, Verspoor et al. 2011). Understanding the direct interactions between wild salmon and other organisms in the marine-terrestrial interface will benefit coastal conservation and ecosystem-based management (Willson and Halupka 1995, Darimont et al. 2010), and expands our appreciation of the profound impact that a single species can have on recipient communities.

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