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Salmonid species diversity predicts salmon consumption by terrestrial wildlife

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Abstract

1. Resource waves—spatial variation in resource phenology that extends feeding opportunities for mobile consumers—can affect the behaviour and productivity of recipient populations. Interspecific diversity among Pacific salmon species (*Oncorhynchus* spp.) creates staggered spawning events across space and time, thereby prolonging availability to terrestrial wildlife.
2. We sought to understand how such variation might influence consumption by terrestrial predators compared with resource abundance and intra- and interspecific competition.
3. Using stable isotope analysis, we investigated how the proportion of salmon in the annual diet of male black bears (*Ursus americanus*; $n = 405$) varies with species diversity and density of spawning salmon biomass, while also accounting for competition with sympatric black and grizzly bears (*U. arctos horribilis*), in coastal British Columbia, Canada.
4. We found that the proportion of salmon in the annual diet of black bears was ≈40% higher in the absence of grizzly bears, but detected little effect of relative black bear density and salmon biomass density. Rather, salmon diversity had the largest positive effect on consumption. On average, increasing diversity from one salmon species to ~four (with equal biomass contributions) approximately triples the proportion of salmon in diet.
5. Given the importance of salmon to bear life histories, this work provides early empirical support for how resource waves may increase the productivity of consumers at population and landscape scales. Accordingly, terrestrial wildlife management might consider maintaining not only salmon abundance but also diversity.

KEYWORDS
black bear, competition, foraging, grizzly bear, resource waves, salmon, stable isotope analysis, *Ursus*

1 | INTRODUCTION

Intra- and interspecific diversity across prey populations can create spatial variation in the timing (phenology) of resource availability for predators (Nesbitt & Moore, 2016; Schindler et al., 2010, 2013). Such variation can comprise *resource waves*—aggregates of food resources that offer ephemeral foraging opportunities at fine spatial scales but exhibit spatial variation in resource timing that prolongs foraging opportunities at larger spatial scales (Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016). Mobile consumers can track the shifting mosaic of foraging opportunities offered by these phenologically diverse resource aggregates to maximize overall intake over time (Lok et al., 2012; Sawyer & Kauffman, 2011).

Data from across taxa and ecosystems show that intra- and interspecific prey diversity can expand foraging opportunities across time and space. Examples of consumers responding to the expanded temporal foraging opportunities afforded by resource waves include mule deer (*Odocoileus hemionus*) that track “green-up” timing of plant forage across elevation in Wyoming (Sawyer & Kauffman, 2011), as well as surf scoters *(Melanitta perspicillata)* that follow waves of migrating Pacific herring (*Clupea pallasii)* along the Pacific coast of North America (Lok et al., 2012). In Alaska, different spawn timing across runs of sockeye salmon (*Oncorhynchus nerka*) is reflected in the movement of foraging grizzly bears (*Ursus arctos;* Deacy, Leacock, Armstrong, & Stanford, 2016) and glaucous-winged gulls (*Larus glaucescens*; Schindler et al., 2013). In addition to such temporal expansion of foraging opportunities, and despite the energetic costs of moving between patches of food (Wirsing et al., 2018), consumers may also benefit from increased spatial variation in food availability, which could reduce intra- and/or interspecific interference competition compared with resources concentrated in space. In this way, mobile consumers may benefit from a diverse interspecific prey portfolio via both the added temporal and spatial foraging opportunities. The magnitude of population-level benefits to consumers of these expanded foraging opportunities may depend on their life-history characteristics (e.g., rate of reproduction), which in turn can also influence indirect ecosystem level impacts such as increased or decreased consumption of in situ resources (Takimoto, Iwata, & Murakami, 2009).

Variation in resource availability is clearly important, but its influence on consumption patterns relative to resource abundance is not well understood. Whereas a consumer’s ability to capitalize on prey availability in a given period of time is generally constrained by a saturating rate of food intake (most simply represented by a Type-II functional response; Holling, 1965), a spatiotemporally diverse portfolio offered by resource waves may extend available foraging time, so that the consumer may realize the saturated components of their functional response curve for longer periods (Armstrong et al., 2016). A simulated consumer–resource model (Armstrong et al., 2016) found that spatial variation in resource phenology could affect consumer energy gain more than total resource abundance. Furthermore, the model suggested that narrower phenological diversity can reduce foraging opportunities—an effect not alleviated by increased resource abundance. These model results provide a set of predictions related to the relative importance of resource abundance and phenology that could be confronted with empirical, landscape-level data.

The effects of prey diversity and abundance may also depend on the inter- and intraspecific competitive environment of the consumer. Theory predicts that the effects of competition will intensify when resource abundance is low (Chesson, 2000), but we hypothesize that diversity in resource phenology might alter this pattern. Dietary resource competition can occur via interference competition (when individuals directly prevent the foraging of others) or exploitative competition (when individuals remove resources from a common pool; Amarasekare, 2003). Typically, larger-bodied animals dominate in interference competition, whereas smaller species can exert exploitative competition, given their reduced resource demands of smaller body sizes (Palomares & Caro, 1999; Peters, 1986). Additionally, given that competing species can coexist via temporal and spatial resource partitioning (Amarasekare, 2003; Chesson, 2000), diverse prey phenologies may provide smaller-bodied species relief from interference competition by distributing resources across the landscape to places and times—and in smaller quantities—that make it difficult or unprofitable for the larger-bodied competitors to exploit. Accordingly, smaller species may be able to benefit from exploitative competition in systems that have high levels of phenological diversity.

Here, we empirically test how spatial and temporal variation in the availability of resources mediates consumption relative to resource abundance and competitive environment. We use the bear–salmon consumer–resource system, consisting of spawning Pacific salmon (*Oncorhynchus* spp.) and highly mobile black bears (*Ursus americanus*) and grizzly bears that compete for these resources (Hilderbrand et al., 1999). Black bears generally are smaller in body size and occupy smaller home ranges, often consuming less salmon than the more dominant, sympatric grizzly bears (Adams et al., 2017). The study region in coastal British Columbia, Canada, hosts five main species of Pacific salmon, each with different spawn timing and habitat-selection characteristics (Fisheries and Oceans Canada 2014; Groot & Margolis, 1991). For bears, such temporal and spatial variation in spawning, as well as differential foraging access (e.g., mediated by spawning depth), contributes to differences in salmon availability over space and time (Table 1). Higher salmon consumption by coastal bears enhances components of fitness (e.g., body condition, mating success, and litter size; Hilderbrand, Schwartz, Robbins, & Thomas, 2000; Kovach & Powell, 2003; Costello, Creel, Kalinowski, Vu, & Quigley, 2009), and supports higher population densities, compared with populations without access to salmon (Hilderbrand et al.,1999). Combined, these characteristics of salmon and their relationship with bears suggest that the diversity of salmon species could extend a resource wave that bears can exploit over space and time with potential benefits to population productivity (Hilderbrand et al., 1999).

TABLE 1 General life-history characteristics of Pacific salmon species (*Oncorhynchus* spp.) in the study area. Mean biomass values were calculated as grand means across populations within the Pacific North West of North America (Bryan et al., 2014; Groot & Margolis, 1991). Spawning channel descriptions are generalized for each species (Groot & Margolis, 1991). Stream length calculations and run timing estimates were calculated from spawning waterways with available data within the study area (Fisheries and Oceans Canada 2014). The data that contribute to these table are coarse and are only suitable for broad illustrative purposes

Species	Mean biomass (kg)	Mean stream length (*n* = 971)	Spawning habitat	Maximum time in freshwater (*n* = 572)
Pink	2.5 kg (odd year); 1.7 kg (even year)	2.7 km	Lower channels below major barriers.	Early July–early November
Chum	5.2 kg	3.2 km	Lower channels below major barriers.	Early July–late October
Coho	3.2 kg	3.5 km	Adaptable to wide variety of spawning habitats from small coastal tributary streams to large main stem rivers.	Mid June–early Feb
Sockeye	2.7 kg	5.2 km	Adjacent to lake rearing areas including lake beaches, tributary creeks, and rivers between lakes.	Late May–late November
Chinook	13.6 kg	7.6 km	Adaptable to wide variety of spawning habitats from small coastal tributary streams to large main stem rivers.	Late April–late December

Building upon previous work that has focused on the movement of consumers, including bears, among patches of prey over time (e.g., Lok et al., 2012; Schindler et al., 2013), we offer an approach that examines the potential ecological importance of a diverse prey portfolio available to mobile predators over greater temporal and spatial scales. Specifically, we use stable isotope analysis to estimate the proportion of salmon in the annual diet of black bears. Although resource waves are sometimes investigated on moderate spatial scales to document phenological tracking by consumers (e.g., along a single waterway or among several; Ruff et al., 2011; Bentley et al., 2012), we use a complementary landscape-scale approach (across ~22,000 km^2) to test for an effect on consumption patterns across many bear home ranges and salmon resource waves. Finally, although the relationship between bear competition and salmon consumption has been examined previously (e.g., Fortin, Farley, Rode, & Robbins, 2007), we aim to better understand the interplay between competition and resource diversity and density.

Using data from a long-term study, we assessed empirical support for several hypotheses of how competition and resource availability might affect consumption of a critical resource. Specifically, we predicted that the proportion of salmon in the annual diet of black bears would be: (a) positively related to densities of spawning salmon biomass, (b) positively related to species diversity of spawning salmon biomass, (c) negatively related to grizzly bear presence and (d) negatively related to relative black bear density.

2 | MATERIALS AND METHODS

2.1 | Overview

We modelled the association between relative black bear density, grizzly bear presence, and salmon biomass density and diversity on the proportion of salmon in the annual diet of black bears. Taking an information-theoretic approach, we compared candidate Generalized Linear Mixed Models (GLMMs) and used model averaging to reveal the best-supported relationship between the predictor variables and dietary proportion of salmon. From an initial dataset of 405 unique bear-year combinations, we performed our main analysis on the 157 bear-year observations for which associated salmon data existed. We used the remaining observations (*n* = 248) to select the most appropriate spatial scale at which to consider intra- and interspecific competition in our main analysis (Appendix S3).

2.2 | Study system

Our remote study area on the central coast of British Columbia is composed of mainland valleys, ocean fjords, and an assemblage of islands (<1 km^2 to >2,220 km^2) separated by tidal waters (Figure 1; Service et al., 2014). Here, black bears are present across the entire landscape. By contrast, grizzly bears are prevalent in mainland watersheds, but are absent from many island watersheds (Service et al., 2014). Grizzly and black bears prey on all five main species of Pacific salmon, which offer varied foraging opportunities in terms of biomass, spawn timing and spawning habitat (Table 1; Quinn, Gende, Ruggerone, & Rogers, 2003; Gende, Quinn, Hilborn, Hendry, & Quinn, 2004). As the spawning habitat for each species is not uniformly distributed across the landscape, different bear home ranges yield access to different portfolios of salmon species, for example, home ranges with only pink (*O. gorbuscha)* and chum (*O. keta*) spawning streams versus home ranges with access to pink, chum, Chinook (*O. tshawytscha*), sockeye and coho (*O. kisutch*) spawning streams. Home range location thus partially determines salmon foraging opportunities in terms of the total number of spawning days and spawning stream length.

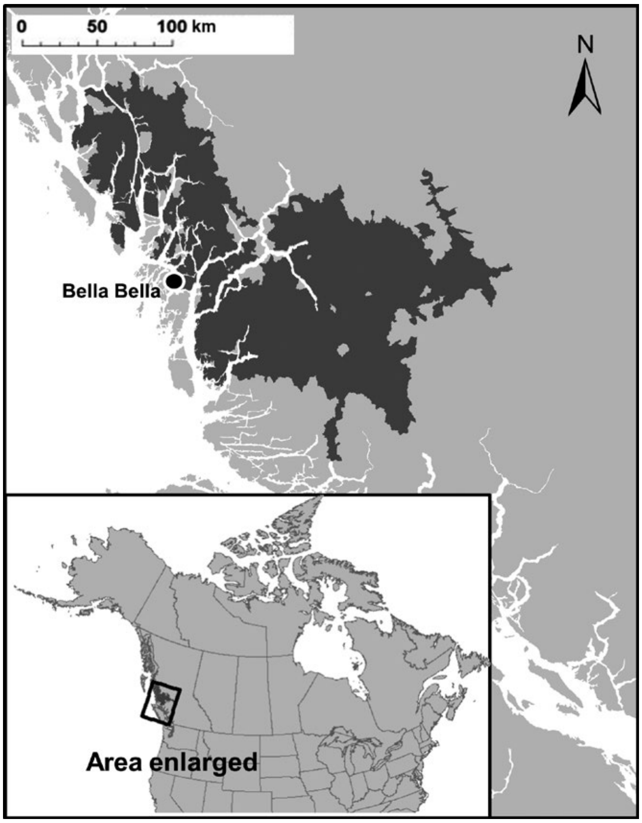

FIGURE 1 Study area in coastal British Columbia, Canada (2009–2014; 22,000 km^2)

2.3 | Field sampling and genetic identification

Using approximately evenly spaced (~1 per 80 km^2) non-invasive hair snagging sites (*n* = 274 per annum) baited with a non-reward bait (Woods et al., 1999, details in Bryan, Darimont, Paquet, Wynne-Edwards, & Smits, 2013, 2014; Adams et al., 2017), we collected bear hair samples across approximately 22,000 km^2, containing 158 watersheds (Figure 1) every ten to fourteen days during May and June from 2009 through 2014. The number of sampling days (n ≈ 30–40 per site per year) was fairly consistent across years.

Information from seven microsatellite loci plus a sex marker revealed species, sex and individual identity from hair samples (Wildlife Genetics International, Nelson, BC, Canada). Our overall dataset included 379 unique male black bears and 122 unique male grizzly bears. The sample size for females, which we captured far less often than males (≈15% of detections), was too small to include in analyses.

2.4 | Proportion of salmon in annual black bear diet

To assess annual diet of black bears, we used hair sampled during the shedding phase of the annual moult. This ensured that the isotopic measures represented the annual assimilated diet during the entire previous year's hair growth (approximately June through October; see experimental work by Hilderbrand et al., 1996 and use by Bryan et al., 2013). Specifically, we measured the stable carbon (13C/12C or δ13C) and nitrogen (15N/14N or δ15N) isotope values from hair collected from black bears via gas chromatography–mass spectrometry (University of Saskatchewan, Saskatoon, SK, Canada). Using these data, we modelled each black bear's annual assimilated diet using Bayesian stable isotope mixing models. Following similar studies of coastal bears in our study area, we used MixSIAR (Stock & Semmens, 2013) to estimate annual dietary contributions from plants, salmon, and intertidal foods by incorporating the δ13C and δ15N values from each of these potential dietary categories with those from the bears. As no reliable trophic discrimination factors (TDFs) exist for bear hair (Hopkins & Kurle, 2016), we followed recent bear hair stable-isotope studies (Hopkins, Ferguson, Tyers, & Kurle, 2017; Hopkins & Kurle, 2016) and used TDF values from laboratory rats fed known diets of plants or animals (Appendix S1, Kurle, Koch, Tershy, & Croll, 2014). Given potential biases possible when not accounting for differences in digestible elemental concentrations in food sources, we evaluated models with and without concentration dependence (Koch & Phillips, 2002). Two separate model-selection approaches suggested that concentration independence provided a better fit to our data (Appendix S1). Accordingly, we proceeded with results from our concentration-independent model. In our subsequent analyses (below), we used the median values from the estimated posterior distributions of proportion of salmon in each individual's diet in each year observed (*n* = 405 individual-years; discussion of limitation of this approach in Appendix S1). A complete description of our stable isotope mixing model approach can be found in Appendix S1.

2.5 | Estimating resource availability

We used geo-referenced annual abundance estimates of the five main Pacific salmon species from the New Salmon Escapement Database (NuSEDS; Fisheries and Oceans Canada 2014) to estimate biomass density and species diversity. To account for data deficiencies, we imputed year-specific missing salmon enumeration data using the estimated total species-specific count for each fisheries management area in combination with long-term relative contribution of each specific watershed. This method was developed specifically for this dataset (*see* Bryan et al., 2014). Even after imputation, owing to incomplete coverage of salmon monitoring, we could only calculate salmon-related predictor variables for a subset of watersheds (*n* = 47 of 158). In these watersheds, we associated salmon data to all bears detected within the watershed in a given year. If bears were detected in multiple watersheds within a season, we used the first watershed of detection. We considered salmon biomass density and diversity from the year before each hair sample was collected, because, given the annual moult of bears, isotopic information in hair collected in the spring relates to the preceding year's growth and associated consumption (Bryan et al., 2014; Felicetti et al., 2004; Hilderbrand et al., 1996).

2.5.1 | Salmon biomass density

We estimated total salmon biomass in each watershed using NuSEDS data and average-mass estimates for each salmon species, assuming a 1:1 sex ratio (Bryan et al., 2014; Groot & Margolis, 1991). Salmon biomass density was calculated as the collective biomass divided by the "functional" area of each watershed, defined as the total land area of watershed minus that of habitat considered unsuitable for bear foraging (i.e., barren rock, snow and ice, and lakes; Carroll, Noss, & Paquet, 2001; Artelle et al., 2016; calculated in ESRI Arcmap 10.2).

2.5.2 | Salmon biomass diversity

We used the Shannon–Weaver (SW) diversity index to estimate salmon diversity:

$$H = -\sum_{i=1}^{S} p_i \ln (p_i) \tag{1}$$

where S is the number of salmon species in the watershed, and p_i is the proportion of the total estimated salmon biomass comprising the i^{th} species. We used biomass estimates instead of counts because we reasoned that total biomass would be more relevant to bears. Accounting for both species richness and evenness in species abundance, the SW diversity index provides a proxy for salmon resource availability over space and time (Appendix S3). Although this metric does not encompass river-specific details, such as correlation between certain species' run timing (e.g., chum and pink) and differences in the ability of bears to fish certain species depending on spawning habitats (e.g., Chinook spawning in large rivers), it is useful for analysing broader scale patterns related to our hypotheses.

2.6 | Estimating the competitive environment

2.6.1 | Black bear relative density

We estimated the relative density of black bears in each watershed in each year as the average number of bears detected per hair-snag sampling station across the watershed. Here, we made the assumption that each hair-snag station attracts bears from a surrounding area that is consistent across watersheds and years. This allowed us to describe density in units of bears per detection area without knowing the specific area involved. As we were only interested in *relative* density across watersheds and years, this measure is well suited to our purposes. It has been applied previously to this dataset to serve as a proxy for bears' intraspecific competitive environment (Bryan et al., 2014).

2.6.2 | Grizzly bear presence

We characterized grizzly bear presence/absence at the same watershed/year scale as above. Likely because grizzly bears kill black bears (Mattson, Knight, & Blanchard, 1992), the presence of a grizzly bear on a salmon stream has been observed to mostly eliminate use of salmon by black bears (Fortin et al., 2007). Given this natural history, and that many watersheds lack grizzly bears, we categorized grizzly bear abundance as present or absent.

2.6.3 | Spatial scale

We considered three possible spatial scales (Figure 1, Appendix S3; British Columbia Ministry of Environment 1996): (a) focal watershed—the watershed containing a given sample location (n = 158 watersheds; mean area = 72 km^2; SD = 94 km^2); (b) the spatial scale in (a) *plus* all adjacent watersheds (average area = 458 km^2; SD area = 606 km^2; n = 554 contributing watersheds); and (c) the spatial scale in (b) *plus* all adjacent watersheds (average area = 1,363 km^2; SD area = 1,825 km^2; n = 765 contributing watersheds). At each scale, we estimated measures of intra- and interspecific competition as the relative density of black bears and categorized grizzly bear presence, as described above.

Because estimates of coastal bear home range sizes vary (Hatler, Nagorsen, & Beal, 2008), we separately analysed a subset of our data (n = 248 bear-year combinations—those without salmon data) to inform the average spatial scale over which we considered the competitive environment could operate. In this supplementary analysis, we fit GLMMs (see below) relating black bear salmon consumption to competitive-environment (but not salmon-related) variables at different spatial scales and compared model performance (Appendix S3). This analysis identified relative black bear density at the scale of focal watershed as the best intraspecific predictor of salmon consumption (Appendix S3). Accordingly, for our main analysis, we used relative black bear density estimates for each bear's focal watershed of detection. This spatial scale also aligns with estimated home range sizes of black bears in similar temperate rainforest habitat (Hatler et al., 2008; Appendix S3). We categorized grizzly bear presence for each black bear's focal watershed of detection plus all adjacent watersheds (i.e., spatial scale b))—a spatial scale that also aligns with grizzly bear home range sizes (Barnes, 1990; Glenn & Miller, 1980; MacHutchon, Himmer, & Bryden, 1993; Schoen, Lentfer, & Beier, 1986).

2.7 | Data analysis

In our primary analysis, we included the subset of bears with associated salmon abundance estimates (n = 157 individual bear–year combinations). We employed an extended version of a Generalized Linear Mixed Model (GLMM) and information-theoretic model selection to examine the effects of salmon biomass density and diversity, as well as measures of intra- and interspecific competition on the proportion of salmon in annual diets of male black bears (n = 157 individual bear–year combinations). To account for the proportional—but continuous—nature of salmon-consumption rates, we assumed that this response variable was beta-distributed (Moore & Semmens, 2008). While a beta error distribution is outside the original definition of GLMMs, this model falls within the broad GLMM family and the format and interpretation are the same (Fox, 2015). For model fitting, we centred and scaled our continuous predictor variables (first subtracting the sample mean from each observation and then dividing by two standard deviations; Gelman, 2008). We fit GLMMs using the *glmmADMB* package (Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2013) in R (R Core Team 2017), employing a logit link function with intercept-only random effects for year (to account for temporal variation—e.g., in precipitation) and watershed (to account for spatial variation—e.g., in topography). We developed a candidate model set from combinations of parameters that estimate resource abundance, resource diversity, and competitive environment (Table 2). Additionally, we modelled interactions between competition parameters and diversity and abundance, reasoning that salmon availability would be more important in the presence of inter- and intraspecific competitors (Table 2). After fitting all models, we ranked models based on differences in Akaike's Information Criterion (AIC), corrected for small sample sizes (ΔAIC_c; Burnham & Anderson, 2002).

To assess the strength of evidence for top models and parameters, we calculated Akaike weights of each model and Relative Variable Importance (RVI) values for each parameter by summing

TABLE 2 Candidate model set with corresponding ΔAIC_c values and rounded model weights used to assess the effect of ecological variables on annual proportion of salmon (*Oncorhynchus* spp.) in diets of male black bears (*Ursus americanus*) in coastal British Columbia, Canada, 2009–2014. Models with "grizzly bear" account for the presence or absence of grizzly bears (*U. arctos horribilis*), and "black bear" represents the relative density estimate of black bears. "Salmon diversity" measure derived from a Shannon–Weaver diversity index, and "salmon biomass density" indicates annual across-species biomass density. All models included year and watershed as random effects. Models that include "salmon biomass density," "salmon diversity," "black bear," and "grizzly bear" as predictors relate to hypotheses i), ii), iii) and iv), respectively (see main text)

Model	Fixed effects	$-2\log\mathcal{L}$	ΔAIC_c	K	Weight	R^2
12	Salmon diversity + grizzly bear	−232.25	0.00	6	0.52	0.206
13	Salmon diversity + grizzly bear + salmon diversity × grizzly bear	−232.49	1.96	7	0.19	0.207
19	Salmon biomass density + salmon diversity + grizzly bear	−232.27	2.17	7	0.17	0.202
20	Salmon biomass density + salmon diversity + black bear + grizzly bear	−232.28	4.39	8	0.06	0.205
3	Grizzly bear	−222.97	7.12	5	0.02	0.090
17	Salmon biomass density + grizzly bear + salmon biomass density × grizzly bear	−226.72	7.73	7	0.01	0.149
4	Black bear + grizzly bear	−223.49	8.76	6	0.01	0.096
16	Salmon biomass density + grizzly bear	−223.40	8.85	6	0.01	0.107
6	Salmon diversity	−220.42	9.67	5	0.00	0.046
11	Salmon diversity + black bear + salmon diversity × black bear	−224.28	10.17	7	0.00	0.116
5	Black bear + grizzly bear + black bear × grizzly bear	−223.52	10.93	7	0.00	0.096
9	Salmon diversity + salmon biomass + salmon diversity × salmon biomass density	−223.42	11.03	7	0.00	0.112
10	Salmon diversity + black bear	−221.03	11.23	6	0.00	0.072
8	Salmon diversity + salmon biomass density	−220.91	11.34	6	0.00	0.057
1	Intercept only	−215.91	12.04	4	0.00	0.000
7	Salmon biomass density	−217.11	12.99	5	0.00	0.026
18	Salmon biomass density + salmon diversity + black bear	−221.35	13.10	7	0.00	0.079
15	Salmon biomass density + black bear + salmon biomass density × black bear	−220.88	13.57	7	0.00	0.096
2	Black bear	−215.97	14.12	5	0.00	0.001
14	Salmon biomass density + black bear	−217.11	15.14	6	0.00	0.028

the weights for individual parameters across all models (Burnham & Anderson, 2002). We considered our top model set to include the top ranked candidate models that together accounted for ≥95% of the total model weight. To combine inference across models, we computed model-averaged predictions from this top model set (Burnham & Anderson, 2002; Grueber, Nakagawa, Laws, & Jamieson, 2011) using the *MuMIn* package (Bartoń, 2015) in R (R Core Team 2017). Simple model-averaged parameter and associated error estimates (i.e., effect sizes and confidence intervals) do not exist for nonlinear models, such as generalized linear models (Cade, 2015). Accordingly, we graphically present model-averaged predictions and associated confidence intervals from our averaged model (Cade, 2015). We also present numerical effect sizes and associated confidence intervals for each individual model that contributes to the averaged model from which we draw inference (Table 3). For all models, we report marginal R^2, calculated as:

$$(SS_{total} - SS_{residual})/SS_{total} \tag{2}$$

where SS_{total} is the sum of squared deviations from the mean and $SS_{residual}$ is the sum of squared deviations from model-averaged predictions (both calculated for the response variable; Merlo, Chaix, Yang, Lynch, & Ra, 2005; Nakagawa & Schielzeth, 2013). We note, however, that there are problems associated with using R^2 in the context of nonlinear and non-normal models (e.g., Cox & Wermuth, 1992), and that marginal R^2 does not account for improved fit due to random effects (e.g., Nakagawa & Schielzeth, 2013). Accordingly, to complement this approach, we provide a graphical indication of model fit (Figure 2, Appendix S4: Figure S1).

TABLE 3 Parameter estimates (with confidence intervals given as ±−2 *SE*) for all top (≥0.95 cumulative model weight) GLMMs (Generalized Linear Mixed Models) that contributed to the final averaged model to predict annual proportion of salmon (*Oncorhynchus* spp.) in diets of male black bears (*Ursus americanus*) in coastal British Columbia (2009–2014). Variables represent (a) spawning salmon biomass density ("salmon biomass"), (b) salmon-species diversity according to the Shannon–Weaver index ("salmon diversity"), (c) relative black bear density ("black bear"), and (d) the presence and absence of grizzly bears ("grizzly bear"; *U. arctos horribilis*). Continuous predictors were centred (mean subtracted) and scaled (divided by 2 *SD*). Bold values indicate estimates with confidence intervals that do not overlap zero

Model	Intercept	Salmon diversity	Grizzly bear	Salmon biomass density	Black bear	Salmon diversity × grizzly bear
12	−**0.698** (−1.170, −0.226)	**0.837** (0.305, 1.369)	−**1.006** (−1.554, −0.458)	–	–	–
13	−**0.649** (−1.159, −0.139)	**1.058** (0.002, 2.114)	−**1.053** (−1.629, −0.477)	–	–	−0.277 (−1.417, 0.863)
19	−**0.690** (−1.176, −0.204)	**0.847** (0.553, 1.402)	−**1.016** (−1.584, −0.448)	−0.027 (−0.386, 0.140)	–	–
20	−**0.689**(−1.178, −0.200)	**0.842** (0.276, 1.409)	−**1.021** (−1.600, −0.438)	−0.025 (−0.444, 0.409)	−0.012 (−0.554, 0.516)	–

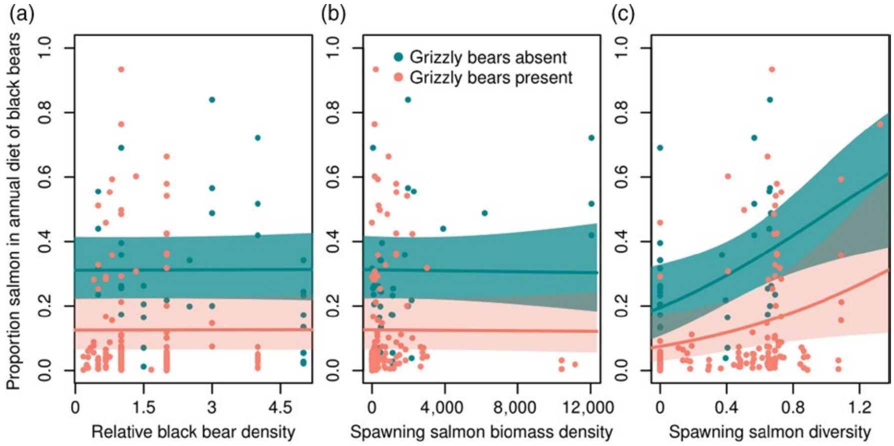

FIGURE 2 Annual proportion of salmon (*Oncorhynchus* spp.) in diets of male black bears (*Ursus americanus*) in coastal British Columbia, Canada as a function of (a) relative black bear density, (b) spawning salmon biomass density, and (c) salmon-species diversity (Shannon–Weaver index) in the presence and absence of grizzly bears (*U. arctos horribilis*). Points show median dietary estimates for unique bear-year combinations (2009–2014; *n* = 157). Curves represent model-averaged predictions from top candidate Generalized Linear Mixed Models (GLMMs) (≥0.95 cumulative model weight), incorporating the effects of competition and salmon, with beta error structure (marginal R^2 = 0.21). Shaded regions represent model-averaged 95% prediction confidence; pink shading representing the model predictions for grizzly bear presence, and blue representing the model prediction for grizzly bear absence. Grey shaded regions represent model prediction overlap between the grizzly presence and absence

To illustrate further the relationship between salmon-species diversity and temporal and spatial foraging opportunities, we computationally reduced species diversity from four to two species in a case-study watershed by removing the two least abundant species, coho and Chinook. From the new data, we recalculated salmon biomass, salmon diversity, and the corresponding change in the number of foraging days and spawning stream length (Figure 3). Using model-averaged parameter coefficients, we compared predicted estimates of the annual proportion of salmon in bear diet across these two scenarios.

3 | RESULTS

The median proportion of salmon in the annual diets of black bears ranged from 0.01 to 0.93 (mean = 0.17; *SD* = 0.20) across individuals and years. Our primary analysis considered the potential influence of salmon biomass density, salmon diversity, grizzly bear presence and relative black bear density on diet, using a dataset with reliable salmon information (n = 157 bear-years). Salmon diversity and grizzly bear presence occurred in all top models, the former consistently positively related and the latter negatively related to salmon consumption (Figure 2, Tables 2 and 3). Relative black bear density, salmon biomass density, and the interaction between salmon diversity and grizzly bear presence also occurred in the top model set, but had modest influence and parameter estimates, which overlapped zero (Figure 2, Tables 2 and 3). Relative Variable Importance (RVI) across our candidate model set suggests that both salmon diversity (0.98) and grizzly bear presence (0.99) are approximately four times as important as salmon biomass density (0.26) and approximately ten times as important as relative black bear density (0.07) in predicting annual proportion of salmon in black bear diets.

Our averaged top model (marginal R^2 = 0.21) suggests that black bears occupying areas with grizzlies consumed about 40% less salmon than those in areas without the larger species (Figure 2). With salmon biomass density held constant, salmon consumption by black bears doubled between the first and third quartiles of observed diversity values, corresponding to the approximate difference between access to one salmon species (Shannon–Weaver = 0.00) and two salmon species with equal biomass (Shannon–Weaver = 0.69; Figure 2c). Additionally, salmon consumption approximately tripled across the range of our observed diversity values (Shannon–Weaver = 0.00–1.32), reflecting the approximate difference between a one-species watershed and a watershed with four species of equal biomass contributions.

When we computationally reduced the number of species from four to two in a case-study watershed by removing the two least abundant species, coho and Chinook, we observed that total biomass dropped by only about 3%. By contrast, the associated reduction in diversity (~48%) lowered the total number of days when salmon were available in the watershed by 28% and the spawning stream length by 62% (Figure 3). This change in diversity corresponded to a ~40% reduction in predicted salmon consumption by black bears.

4 | DISCUSSION

Our work finds a positive association between spawning salmon diversity and dietary contribution of salmon in black bear diets, offering empirical support for a dietary response by a consumer to phenological diversity. Moreover, our data represent the integration of foraging behaviour over a relatively long period (a salmon-spawning season) and on a landscape scale. Earlier research has

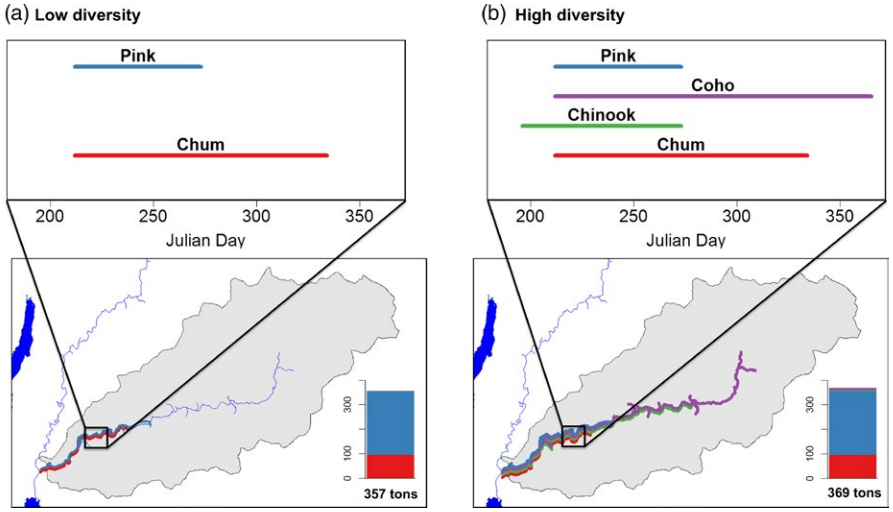

FIGURE 3 Temporal and spatial foraging opportunities afforded by (a) low (Shannon–Weaver diversity = 0.58; two species) vs. (b) high (1.20; four species) species diversity of spawning salmon (*Oncorhynchus* spp.). Actual diversity values from a watershed on the central coast of British Columbia, Canada shown in (b) are predicted to lead to 40% more salmon consumption by black bears (*Ursus americanus*) compared to the artificially reduced diversity shown in (a). Whereas this illustration of increased diversity increased salmon availability by 28% more days and 62% more stream length, total salmon biomass density increased by only 3%

shown consumers tracking prey phenology or increasing their exposure to the resource over smaller spatial and temporal scales (Deacy et al., 2016; Lok et al., 2012; Sawyer & Kauffman, 2011; Schindler et al., 2013). Building off previous research on bear–salmon systems (e.g., Deacy et al., 2016; Schindler et al., 2013), we additionally considered diversity across salmon species, among which we expect substantial spatial and phenological variation, rather than among populations of a single salmon species. Furthermore, we examined resource waves in conjunction with inter- and intraspecific competition, a combination that has not yet been explored theoretically or empirically (Armstrong et al., 2016). We focus on a smaller-bodied, presumably subordinate salmon consumer, offering evidence that the benefits of resource waves might extend beyond the larger-bodied competitor. Our analysis of an integrated dietary measure suggests that a spatially and temporally diverse prey portfolio may provide long-term, measurable benefits to mobile consumers that exploit these resource waves. Finally, these findings complement previously documented observations that salmon diversity can influence salmon consumption by humans (i.e., the maintenance of yields over time; Nesbitt & Moore, 2016).

Past simulation modelling in a generalized resource–consumer system has demonstrated the possibility that resource timing may be more important than abundance under certain conditions (Armstrong et al., 2016), and our study provides empirical support. Although species diversity was important for predicting salmon consumption by bears, total salmon biomass density had only one-fifth as much empirical model-weight support as diversity. Non-informative variables may enter a top model set as a result of the AIC bias correction term being only two; these can be identified by parameter estimates (and corresponding CIs) that overlap zero and unchanged deviance values upon their inclusion in a model set (see discussion from Anderson, 2008). Because the salmon biomass density predictor adds almost no explanatory ability and model likelihoods were nearly identical after its inclusion (Tables 2 and 3), we suspect it to be non-informative (Anderson, 2008). We note, however, that our observations of salmon biomass density occurred in areas with relatively strong salmon runs compared to many areas black bears still inhabit. Indeed, theoretical models predict that foragers might benefit the most from increased phenological diversity when abundance is already high, whereas an increase in abundance might matter more than phenological diversity when abundance is low (Armstrong et al., 2016). Specifically, the apparent lack of evidence for a salmon biomass density effect may be explained by the fact that black bears in our system may be saturated phase of their functional response for the examined salmon runs (Holling, 1965; Quinn et al., 2003).

Given the large spatial scale of our analysis, there were several potential covariates we were unable to explore. Specifically, the conditions that may drive higher interspecific salmon diversity, such as watershed size and habitat complexity (Rogers & Schindler, 2008; Waples et al., 2001), could also contribute to greater intraspecific phenological diversity (Moore, Mcclure, Rogers, & Schindler, 2010). Although we do not have accurate population-level phenological data for salmon that would be required to disentangle these relationships, we address this lack of information by accounting for inherent variability by including a watershed-level random effect in all models. However, it would be informative to explore the relative strength of influence between inter- and intraspecific salmon diversity on black bear salmon consumption in future studies. For example, larger salmon runs often last longer than smaller runs (Davis, 2015; Reimchen, 1994), thereby extending the resource wave—a relationship we did not explore here.

Given that salmon species do not contribute equally to biomass, diversity and biomass need not be tightly correlated (Figure 3a,b). Our model-averaged model suggests that such changes in salmon diversity played a strong role in annual proportion of salmon in diets of black bears, whereas changes in salmon biomass density had little effect. To illustrate, and while holding biomass density constant at its mean, parameter estimates from our top model predicted dietary proportion of salmon in black bears doubled when observed diversity values increased from one salmon species (Shannon–Weaver = 0.00) to two salmon species with equal biomass (Shannon–Weaver = 0.69; Figure 2) and tripled across the range of our observed diversity values (Shannon–Weaver 0.00–1.32), reflecting the approximate difference between a single-species watershed and a watershed with four species each with equal biomass contributions.

Despite the value of salmon diversity to foraging black bears, we suggest that interference competition with larger grizzly bears reduced annual salmon consumption (*see also* Mattson, Herrero, & Merrill, 2005; Fortin et al., 2007; Figure 2). We predicted that the availability of diverse opportunities to forage for salmon across space and time could moderate interference competition (by limiting interaction between competing species at clumped resources). Our results, however, suggest that salmon diversity is no more important for black bears in the absence of grizzly bears than when grizzly bears are present (Figure 2c). Additionally, intraspecific competition, as measured by relative black bear density, had an ambiguous effect on salmon consumption, occurring in several of the top models with a negative association and high uncertainty (Tables 2 and 3). Similar to salmon biomass density, likelihood values and parameter confidence intervals suggest that relative black bear density may be a non-informative variable (Tables 2 and 3; Anderson, 2008). Finally, we were not able to account for the presence or density of wolves (*Canis lupus*) as potential competitors and known salmon consumers (Darimont, Paquet, & Reimchen, 2008), an additional relationship that could be explored in further work.

Together, salmon diversity and the presence of grizzly bears explained more than a fifth of the total variation in estimated proportion of dietary salmon. The overall moderate fit of our final model-averaged model (R^2 = 0.21; Figure 2, Appendix S3: Figure S1) indicates, however, that there remains considerable unexplained variation in black bear salmon consumption patterns. We are not surprised by this moderate explanatory ability. For behaviourally complex vertebrates, like black bears, numerous influences likely affect consumption patterns across a very large and heterogeneous landscape. Although beyond the scope of our analysis, these include an individual's age, body size, and position in its social hierarchy; time devoted to other activities; and especially the availability of other food resources over time and space (Deacy, Armstrong, Leacock, Robbins, & Gustine, 2017; Takimoto et al., 2009). In addition, our estimates of proportion of dietary salmon were inherently noisy, incorporating error from multiple sources (e.g., stable isotope measurement, dietary fractionation estimates; Moore & Semmens, 2008). Although our final model-averaged model demonstrated moderate fit, each individual parameter of interest in our top model explains a reasonable amount of variation. For example, removing the term for salmon diversity reduces our model R^2 by 0.10. Similarly, removing grizzly bear presence reduces R^2 by 0.13. Regardless of limitations in our approach, grizzly bear presence and salmon diversity are evidently important factors that influence black bear salmon consumption.

Several management implications emerge from these findings. The relevance of a diversified salmon portfolio for terrestrial consumers argues for considerations beyond previous ecosystem-based fisheries management recommendations that focussed solely on increasing salmon abundance available to consumers after exploitation by fisheries (Darimont et al., 2010; Levi et al., 2012)—at least for relatively low-density large mammals like bears that satiate (Armstrong & Schindler, 2011). This consideration may be especially relevant for consumers involved in widespread interactions via their roles as vectors of resources to other ecosystem recipients. For example, riparian benefits (e.g., greater insect diversity and biomass, increased songbird diversity and biomass, higher plant diversity) are associated with increased bear-mediated nutrient transfer into temperate rainforest ecosystems (Christie, Hocking, & Reimchen, 2008; Mathewson, Hocking, & Reimchen, 2003; Reimchen, Mathewson, Hocking, Moran, & Harris, 2003; Schindler, Armstrong, & Reed, 2015); these benefits are likely amplified with the increase in consumption associated with greater salmon diversity. Accordingly, if maintaining diversity is important to managers, habitat destruction and other human interference that can reduce salmon diversity should be minimized in riparian areas—the nexus of salmon resource waves. Importantly, these implications of salmon diversity are set against a background of extirpation and reduced phenological diversity of salmon populations (Price, Darimont, Temple, & MacDuffee, 2008; Price, English, Rosenberger, MacDuffee, & Reynolds, 2017; Quinn, McGinnity, & Cross, 2006), efforts to restore lost salmon runs (Lichatowich, Mobrand, Lestelle, & Vogel, 1995), and the conservation of bears that co-evolved with this marine resource.

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AUTHOR CONTRIBUTIONS

C.N.S., C.T.D., P.C.P., and T.E.R. conceived the ideas and designed the work; C.N.S., M.S.A. and K.A.A. collected the data; C.N.S. and A.W.B. analysed the data. C.N.S. and C.T.D. led the writing. All authors contributed to every draft and approved the final version for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.t474mn0 (Service et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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