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Intrapopulation diversity in isotopic niche over landscapes: Spatial patterns inform conservation of bear–salmon systems

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Abstract. Intrapopulation variability in resource acquisition (i.e., niche variation) influences population dynamics, with important implications for conservation planning. Spatial analyses of niche variation within and among populations can provide relevant information about ecological associations and their subsequent management. We used stable isotope analysis and kernel-weighted regression to examine spatial patterns in a keystone consumer–resource interaction: salmon (*Oncorhynchus* spp.) consumption by grizzly and black bears (*Ursus arctos horribilis*, $n = 886$; and *Ursus americanus*, $n = 557$) from 1995 to 2014 in British Columbia (BC), Canada. In a region on the central coast of BC (22,000 km^2), grizzly bears consumed far more salmon than black bears (median proportion of salmon in assimilated diet of 0.62 and 0.06, respectively). Males of both species consumed more salmon than females (median proportions of 0.63 and 0.57 for grizzly bears and 0.06 and 0.03 for black bears, respectively). Black bears showed considerably more spatial variation in salmon consumption than grizzlies. Protected areas on the coast captured no more habitat for bears with high-salmon diets (i.e., proportions >0.5 of total diet) than did unprotected areas. In a continental region (~692,000 km^2), which included the entire contemporary range of grizzlies in BC, males had higher salmon diets than females (median proportions of 0.41 and 0.04, respectively). High-salmon diets were concentrated in coastal areas for female grizzly bears, whereas males with high-salmon diets in interior areas were restricted to areas near major salmon watersheds. To safeguard this predator–prey association that spans coastal and interior regions, conservation planners and practitioners can consider managing across ecological and jurisdictional boundaries. More broadly, our approach highlights the importance of visualizing spatial patterns of dietary niche variation within populations to characterize ecological associations and inform management.

Key words: bears; dietary niche; geographic information systems; isoscapes; kernel-weighted regression; *Oncorhynchus;* predator–prey systems; salmon; stable isotope analysis; *Ursus.*

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Introduction

Food and other resources are patchily distributed across space and time, creating what Hutchinson (1957) described as the "mosaic nature of the environment." Consumers use multiple behavioral strategies to maximize resource exploitation in the context of this variation (Stephens and Krebs 1986, Fauchald 1999, Weimerskirch et al. 2005). These varied patterns of resource use, constrained by competition within and among species, comprise the spatial and temporal diversity of species' realized niches (Hutchinson 1957, Chase and Leibold 2003, Kearney and Porter 2009). Spatial variation in the realized niche is also a fundamental driver of the distribution and abundance of species (Murdoch et al. 2003, Stephens et al. 2007).

Understanding the spatial variability of resource acquisition within populations can inform conservation planning. Protected areas aim to conserve regions of biodiversity and promote long-term ecological and genetic variation. Yet, they can only represent portions of the habitat of most communities and the populations comprising them (Margules and Pressey 2000, Rodrigues and Gaston 2001, Chape et al. 2005). The spatial configuration of protected areas can be informed and prioritized by the distribution of diverse life history strategies and ecological variation across landscapes (e.g., behavioral variation, Cooke et al. 2014, species diversity, Brooks et al. 2006), such that networks of protected areas prioritize fitness-related resource use within populations (Rodrigues et al. 2004).

Individuals differ in how and where they acquire food resources, often resulting in markedly varied dietary niches within populations. For example, white-chinned petrels (*Procellaria aequinoctialis*) exhibit individual or breeding-pair dietary specialization in the location and depth at which they forage for krill, fish, or squid during nesting and chick rearing (Jaeger et al. 2010). Even within species with limited mobility and home ranges, conspecific diets can differ, owing to specialized habitat use and movement patterns. For instance, differences in foraging-patch use by snappers (*Lutjanus* spp.) relate to differences in prey preferences and movement tendencies among individuals in limited localized habitats (Hammerschlag-Peyer and Layman 2010). Dietary differentiation among individuals can also be driven by competition with other consumers for shared resources (e.g., through interference or exploitation competition; Amarasekare 2002). Given that an individual's foraging directly affects its fecundity and survival (Bolnick et al. 2003, Biro and Stamps 2008, Smith and Blumstein 2008), dietary niche variation across individuals can influence the productivity, stability, and persistence of populations (Dall et al. 2012, Sih et al. 2012, Wolf and Weissing 2012).

Processes to identify candidate protected areas might benefit from measuring intra-population variation, which requires tools to assess how individuals differ in their foraging across space. Spatial variation in resource use within consumer populations can be derived from stable isotope analysis (SIA), which estimates contributions of various food sources to individual consumer diets (Newsome et al. 2007, Moore and Semmens 2008, Ben-David and Flaherty 2012). When SIA data are tied to spatial and temporal information (e.g., island vs. mainland populations, discrete sampling locations), it is possible to characterize realized isotopic niche variation spatially within and among populations (e.g., Darimont et al. 2009, Semmens et al. 2009, Jaeger et al. 2010, Ehrich et al. 2015). Spatial representations of patterns from SIA, often denoted as isotopic landscapes or "isoscapes," have been used in migratory research to visualize geographic origins or movement and behavior patterns across landscapes (Hobson 2005, Hobson et al. 2010, Wunder 2010, Pekarsky et al. 2015). Isotopic landscapes of dietary data can geographically characterize the diversity in realized dietary niche of specific prey contributions, and the corresponding ecological implications of predator–prey systems (Schindler and Lubetkin 2004).

We use a bear–salmon predator–prey system in British Columbia (BC), Canada, to illustrate our isotopic-landscape approach. Pacific salmon (*Oncorhynchus* spp.) provide a critical, energy-rich food for black and grizzly (also referred to as "brown") bears (*Ursus americanus* and *Ursus arctos horribilis*, respectively) before winter sleep. Individual bears exploit variation in salmon availability by tracking spawning events across landscapes to maximize their foraging success (Schindler et al. 2013, Levi et al. 2015). Salmon consumption is closely related to fitness correlates

for both males (e.g., body size, mobility) and females (e.g., cub litter size) (Hilderbrand et al. 2000, Kovach and Powell 2003, Belant et al. 2006, Zedrosser et al. 2007, Costello et al. 2009, Bryan et al. 2014). Moreover, bears with high-salmon diets are physically larger, show decreased levels of stress hormones, exhibit increased reproductive success, and exist at higher population densities than bears without access to salmon (Hilderbrand et al. 1999, 2000, Gende et al. 2001, Belant et al. 2006, Mowat and Heard 2006, Levi et al. 2012, Bryan et al. 2014). Males generally have higher salmon diets than females, with male grizzly bears often competitively excluding sympatric females and black bears (Rode et al. 2006, Fortin et al. 2007). Although salmon and other meat sources are critical for bears, individuals balance their nutritional intake of protein with fruit to maximize fitness (Robbins et al. 2007, Erlenbach et al. 2014). In addition to providing fitness benefits to bears, salmon subsidize coastal ecosystems with marine-derived nutrients, often distributed by bears into terrestrial habitats via the deposition of carcasses, feces, and urine, a process that strongly influences associated food webs (Reimchen 2000, Schindler et al. 2003, Quinn et al. 2009, Hocking and Reynolds 2011).

We demonstrate how isotopic landscapes can characterize variation in dietary contributions and inform conservation planning. Mowat and Heard (2006) broadly described these patterns for grizzly bears at a continental scale; we build on this work by offering spatial approaches to examine variability in the bear–salmon predator–prey association across spatial regions, species, and sexes. First, we characterize and compare spatial variability in salmon consumption by both sexes of coastal black and grizzly bears. Second, we detail the geographic variation in bear–salmon associations across the province of BC. We ask how well conservancies might be protecting the keystone bear–salmon interaction. We illustrate how such a spatial approach can describe ecological associations and support conservation planning.

Materials and Methods

Study areas and sample collection

We used hair samples to estimate dietary salmon and other prey contributions in two regions. In a coastal area of BC, Canada, we used DNA from hair samples to link diet to unique individual bears of known species and sex (Woods et al. 1999, Paetkau 2003, Proctor et al. 2010). The coastal area is nested within a larger continental area, delineated by the province of BC (Fig. 1). Continental (hereafter "provincial") data from grizzly bears first appeared in Mowat and Heard (2006).

Coastal area.—In the central coast region of BC, our sampling efforts focused on a matrix of islands and nearby mainland valleys (Fig. 1; Service et al. 2014). We collected hair samples from female and male black (unique individual–location–year combinations, $n = 90$, $n = 467$, respectively) and grizzly (unique individual–location–year combinations, $n = 52$, $n = 246$, respectively) bears in May and June from 2010 to 2014 at noninvasive hair snagging stations ($n = 71$ in 2010, growing in effort to $n = 265$ by 2014) distributed over approximately 22,000 km^2 (for detailed methods, see Bryan et al. 2013, 2014, Service et al. 2014). We collected hair at intervals of 10–14 days. Stations were disassembled between years. Because collection occurred during the shedding phase of the annual molt, isotopic measures in samples represent annual assimilated diet during the entire previous year's hair growth (~June–October; Hilderbrand et al. 1996).

Provincial area.—Hair samples from female and male grizzly bears (unique individual–location–year combinations, $n = 248$, $n = 340$, respectively) were collected across the 692,000 km^2 of grizzly bear habitat in BC, from 1995 to 2003, by provincial representatives from multiple research projects and inspections (Fig. 1; Mowat and Heard 2006). We augmented these historical data with our own coastal grizzly data for provincial analyses.

Ethics statement.—Black and grizzly bear hair sampling from the coastal area was approved by the Animal Care Committee at the University of Victoria (permit no. 2012-018). We conducted research in the traditional territories of the Heiltsuk, Kitasoo/Xai'xais, Nuxalk, and Wuikinuxv Nations, with whom we partnered in this work. We also had a permit no. 106703 from BC Parks to sample in conservancies. Agreements for these data with partner governments prohibit us from displaying sample locations.

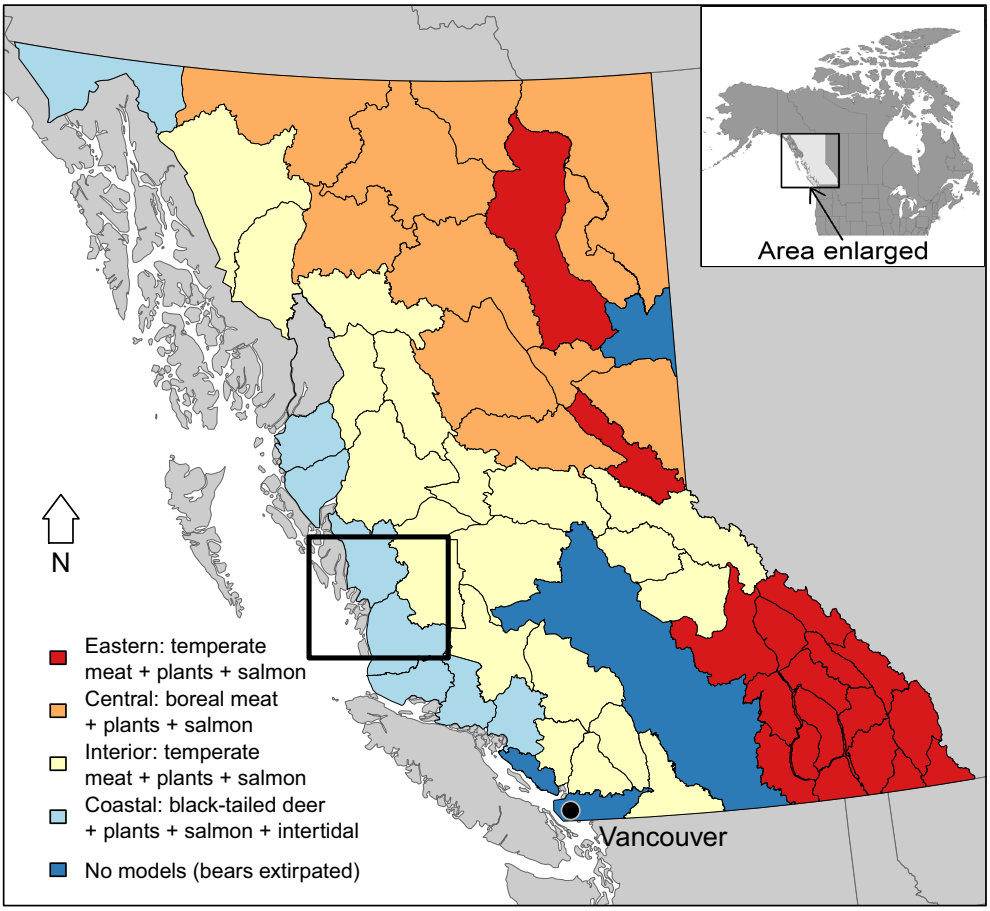


Fig. 1. Dietary model inputs for grizzly bear (*Ursus arctos horribilis*) population units (n = 57), as designated by the Province of British Columbia, Canada (Province of British Columbia 2012). Potential diet components were informed by Mowat and Heard (2006). We included salmon in each region and intertidal prey for coastal models. Black (*Ursus americanus*) and grizzly bear data from the "coastal area" portion of the analysis are contained within the black rectangle.

Dietary contributions

We prepared and processed samples for SIA using established protocols (Darimont and Reimchen 2002, Darimont et al. 2008, and Bryan et al. 2014). We estimated dietary contributions from predetermined food groups for individuals in coastal and provincial areas using Bayesian isotope mixing models (Stock and Semmens 2013), which use the stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope ratios in consumer and food resource samples, fractionation rates, and associated uncertainties to predict the proportion of a diet made up of a given resource (Moore and Semmens 2008, Ben-David and Flaherty 2012). In cases where coastal individuals were sampled in multiple locations within the same year, we attributed the individual's salmon consumption value to the sample selected for measuring the individual's isotope signature (the highest quality sample).

For coastal populations, we estimated the proportion of each bear's yearly diet from salmon, intertidal food sources, ungulates, and plants (Appendix S1: Table S1). Over the provincial area, across which food availability differs, we modeled dietary proportions by including only foods present in areas in which individuals were sampled (Fig. 1; Mowat and Heard 2006). Depending on diet model region, these included terrestrial meat (ungulates), landlocked salmon (kokanee;

Oncorhynchus nerka), spawning Pacific salmon, intertidal food sources, and plants (Fig. 1; Appendix S1: Table S1). Given our focus on the bear–salmon association, we used the median contribution from salmon to yearly diet (hereafter "salmon consumption") for spatial analyses.

Spatial analyses

We estimated continuous isotopic landscapes that characterized salmon consumption using non-parametric kernel-weighted regression (see below; Watson 1964, O'Sullivan and Unwin 2010, Nadaraya 2012). We considered the median salmon consumption value for each individual to be associated with its sample location. When coastal individuals were detected in multiple years, we considered each bear-year case separately (n = 557 black and 298 grizzly), representing 379 black (n = 84 female, n = 295 male) and 122 grizzly (n = 40 female, n = 82 male) unique individuals. If individuals were detected at multiple locations within a year, we considered each individual–location–year combination separately.

Kernel-weighted regression is a locally weighted "smoother" that generates estimates of a response variable across a sampled landscape. Using the spatial location of each observation, kernel-weighted regression affords more importance to nearby observations than to distant observations when estimating the response. Employing a Gaussian kernel, we estimated the model's bandwidth (the smoothing parameter equivalent to the standard deviation of the Gaussian kernel distribution) using the standard least-squares cross-validation technique (Kie 2013). In all models, each empirical observation of salmon consumption contributed to the smoothed prediction of salmon consumption at all other locations in space, as weighted by the two-dimensional Gaussian kernel. We fit models in R 3.2.3 with the kernel regression function "smooth" within the spatstat package (Baddeley and Turner 2005, R Development Core Team 2016; for code and source data, see github.com/megansadams/Isotopic-niche-diversity).

We performed analyses in the coastal and provincial areas. To examine spatial and temporal variation at a coastal scale, we created separate non-parametric kernel-weighted regressions with data for male bears across all years and for each species–year combination (n = 10) from 2010 to 2014, using a unique cross-validated bandwidth in each case. Owing to low sample sizes in each year, we modeled data for female bears by pooling data across all years. In the provincial area, we performed separate non-parametric regressions for female and male grizzly bears, modeling larger-scale patterns in salmon consumption from 1995 to 2014. We present kernel regression estimates in a 95% spatial extent—the region that falls within the 95th-percentile contour of the summed kernel density (see Appendix S1 for details).

Our data represent the spatial and temporal integration of the previous year's foraging. Samples do not represent the exact location of the foraging patterns inferred from isotope analysis. Specifically, samples were collected during spring across varied terrain (from lowland estuaries to alpine meadows), whereas salmon foraging by the same individuals occurs during fall in one to many spawning areas. Accordingly, we describe spatial patterns in annual salmon consumption as exhibited by bear post winter sleep. Given species- and sex-related variability in mobility and home range size, we do this coarsely across large landscapes. We note that the kernels' smoothing parameters (5.4–14.2 km for black, 6.8–38 km for grizzly) align with previously reported home range estimates. Bear home ranges are highly variable, ranging from ~20 km^2 for coastal female black bears to ~900 km^2 for male grizzly bear in interior habitats (Hatler et al. 2008), but these areas are of an order similar to those over which individual bears provide information in our kernel regression models. Although we report estimates of how much salmon (and other foods) bears consumed at an ecologically relevant spatial scale, we cannot specifically predict the watersheds in which consumption occurred.

Characterizing inter-specific and inter-sex niche similarity

We calculated the correlation between species and sexes to assess similarity in coastal black and grizzly salmon consumption estimates across all years using the Spearman's rank correlation coefficient. We calculated the correlation using the kernel regression estimates at grid points (every 250 m, corresponding to widely available landscape data) within the common area of each species' and sex's kernel spatial extent.

Identifying areas of high-salmon diets in conservancies on the coast

Parks and protected areas (here after "conservancies") represent ~28% of the coastal study area (Appendix S1: Fig. S1; Province of British Columbia 2016). To illustrate how well conservancies represent regions with bears of relatively high-salmon diets (and therefore potentially the highest reproductive success), we compared coast-wide estimates of salmon consumption in unprotected areas for female black and grizzly bears to estimates within designated conservancies. We assessed estimates for females because their access to salmon is closely affiliated with fecundity, and is more constrained than males, both by smaller home range size and competition with males (Ben-David et al. 2004, Bryan et al. 2014). For the range of proportional salmon consumption values between zero (no salmon consumed) and one (only salmon consumed), we assessed how well conservancies represent areas where bears consumed salmon at or above each given value. First, for each specified value, we found the spatial region where model-estimated salmon consumption exceeded the value within each model's 95% spatial extent. Next, for each given value, we calculated the proportion of the corresponding spatial region contained within conservancies. We also calculated median estimates of salmon consumption inside and outside of conservancy areas.

Revealing the influence of marine resources on interior regions

Salmon are readily available in coastal watersheds, but they also travel far (i.e., >1000 km) into interior habitats along salmon-bearing rivers (Groot and Margolis 1991). To demonstrate the spatial distribution of bears with relatively high-salmon diets along the salmon–resource gradient from coastal to interior habitats, we compared province-wide estimates of salmon consumption for female and male grizzly bears to estimates from specific coastal areas. We used two representations of coastal areas based on (1) biogeoclimatic zoning (the "Coast and Mountain Temperate Rainforest EcoProvince"; Demarchi 2011) and (2) administrative and management zoning (the "Great Bear Rainforest" (GBR), the popular name for a region of limited industrial development on the coast; DellaSala et al. 2011; Appendix S1: Fig. S2). For the range of proportional salmon consumption values between zero (no salmon consumed) and one (only salmon consumed), we evaluated how well the areas delineated by the EcoProvince and the GBR represent areas where bears consumed salmon at or above each given value as compared with estimates from across the provincial spatial extent. For each specified value, we determined the spatial region where (within each model's 95% spatial extent) model-estimated salmon consumption exceeded the value. For each given value of salmon consumption, we calculated the proportion of the corresponding spatial region contained within both the EcoProvince and the GBR.

Results

Coastal area

Estimates of salmon consumption revealed spatial variation between species and between sexes. For both species at the coastal scale, salmon consumption generally increased from interior to coastal areas (Figs. 2, 3). Grizzlies, both female and male, had higher proportions of dietary salmon (median = 0.57 and 0.62, respectively) than did black bears (median = 0.03 and 0.06, respectively), and males had higher dietary salmon than females in both grizzly and black bears (Fig. 3). Estimates of salmon consumption were more heterogeneous in male black bears than in grizzly bears among years and across space (Fig. 2). Across the entire dataset, relative variability in salmon consumption was higher for black bears than for grizzly bears (black bears: Coefficient of variation (CV) = 1.44 for females, CV = 1.17 for males; grizzly bears: CV = 0.26 for females, CV = 0.15 for males). Despite these differences, estimated levels of salmon consumption were positively correlated across space for species and sexes. Spatial patterns of salmon consumption were particularly similar for male black and grizzly bears (Spearman's $r = 0.83$) and much less so for females of the two species ($r = 0.22$). Salmon consumption patterns were similar for females and males in both black ($r = 0.66$) and grizzly ($r = 0.69$) bears.

The remainder of grizzly diet was made up of similar contributions in females and males by intertidal prey (medians = 0.27) and plant sources (medians = 0.11, 0.06, respectively), with minimal (<0.01) terrestrial meat contributions

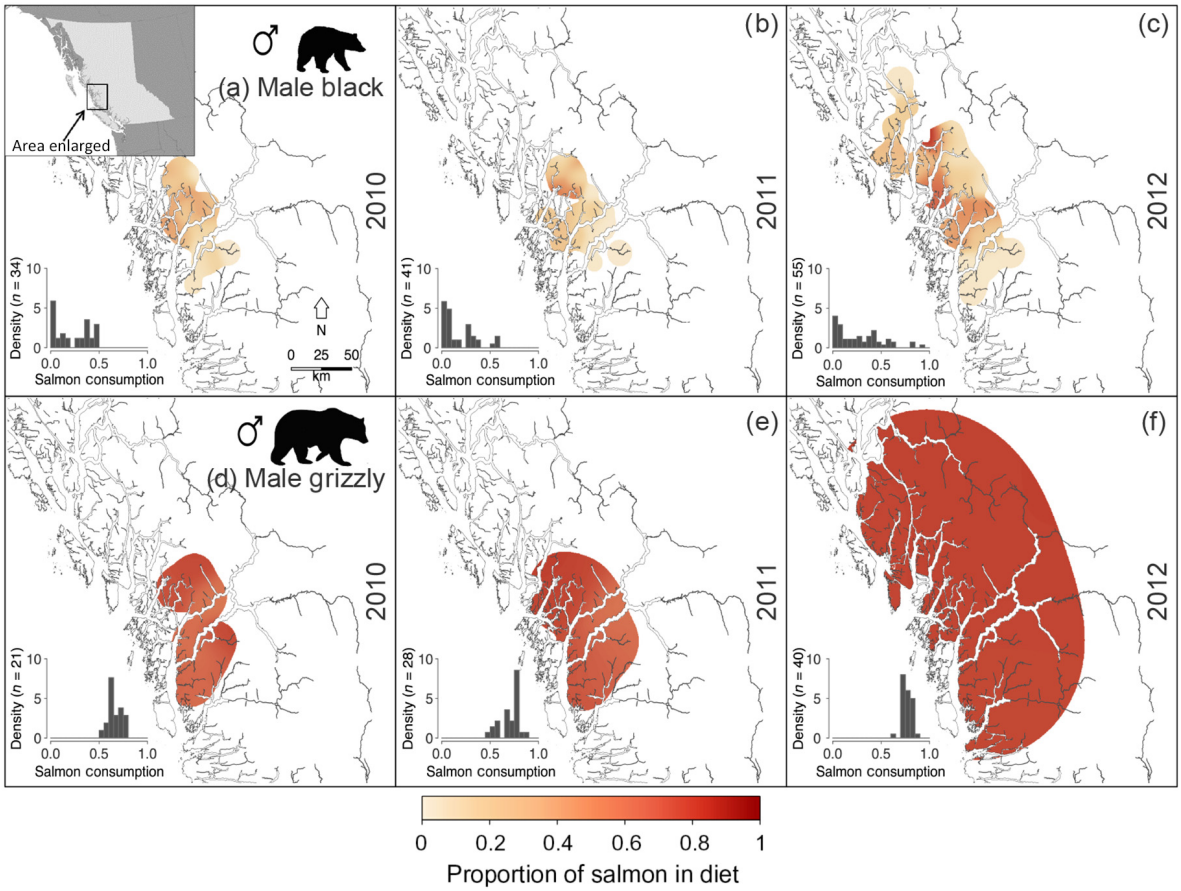


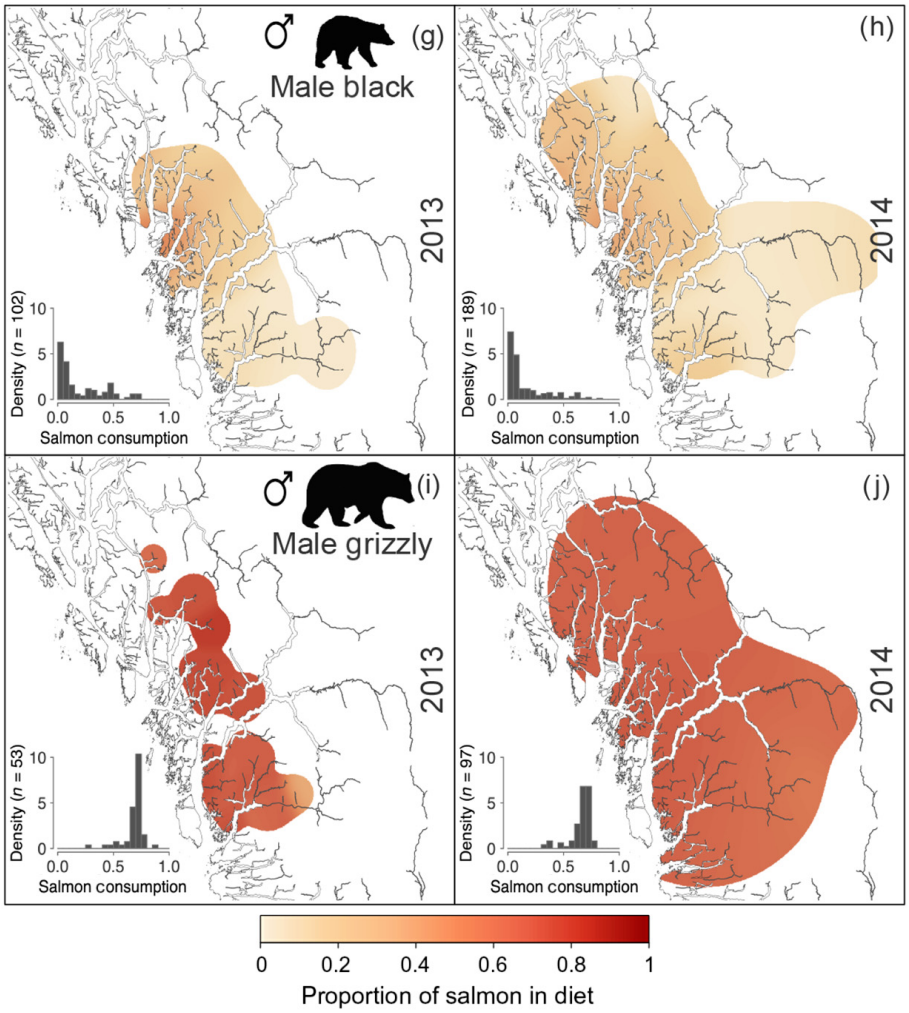
Fig. 2. Spatial patterns of salmon consumption estimated by kernel regression in male black and grizzly bear (*Ursus americanus* and *Ursus arctos horribilis*, respectively) diets in coastal British Columbia, 2010 to 2014. Major salmon-bearing rivers are depicted as gray lines. Areas depicted in white represent regions outside of the models' spatial extent. Note the sampling effort expanded from 2012 to 2014. Histograms represent frequency of individuals' observed median values of salmon consumption.

(Table 1). Female and male black bears had high proportions of plant contributions (medians = 0.89, 0.82, respectively). Following salmon, terrestrial meat was the largest meat source for female and male black bears (medians = 0.03, 0.04), respectively, followed by minimal contributions of intertidal prey.

On the coast, conservancies contained female bears with a similar range of salmon consumption estimates as bears outside conservancies (Fig. 4). Within conservancies, the median estimate of salmon consumption by female black bears was 0.06, and the median estimate for female grizzly bears was 0.67; outside conservancies, median salmon consumption was 0.07 and 0.63, respectively.

Provincial area

Estimates of salmon consumption for bears sampled between 1995 and 2014 reveal the geographic range and variability of grizzly bear diet on a continental scale (Fig. 5). For the entire provincial area, and as expected, salmon comprised a greater proportion of male diet (median = 0.41) than of female diet (median = 0.04; Fig. 5). For both males and females, the distribution of salmon consumption was bimodal, with a large fraction of bears eating almost no salmon and another fraction having high-salmon diets (~0.65 for females and ~0.75 for males; Fig. 5 insets). Although females with the highest salmon consumption were concentrated in coastal



(Fig. 2. *Continued*)

regions, the bear–salmon association extended well into the interior for males (Fig. 5).

For both sexes of grizzly bears in the coast region, diet models estimated that salmon constituted the largest dietary component (Table 1). In the interior, where the Fraser River and associated watersheds flow far inland, females relied on contributions from both plants (median = 0.58) and terrestrial meat (median = 0.31) more than salmon (median = 0.05), whereas males consumed more salmon than terrestrial meat (median = 0.2 and 0.08, respectively). Bears ate considerable quantities of plants in all diet model regions (medians ranging from 0.29 to 0.63), except in the coast region (medians ranging from 0.06 to 0.12).

Over the provincial area, the coastal regions captured areas where bears have particularly high-salmon diets (Fig. 6). In particular, the Coastal EcoProvince contained half of the area in which male estimates of salmon consumption exceed 0.26, and all of the area where estimates exceed 0.67. The same region included half of the area in which female estimates of salmon consumption exceed 0.07, and all of the area where estimates exceed 0.44. The slightly smaller GBR region contained half of the area where male estimates of salmon consumption exceed 0.43, and all of the area where estimates exceed 0.67. For females, the GBR included half of the area where estimates of salmon consumption exceed 0.12, and all of the area where estimates exceed 0.58.

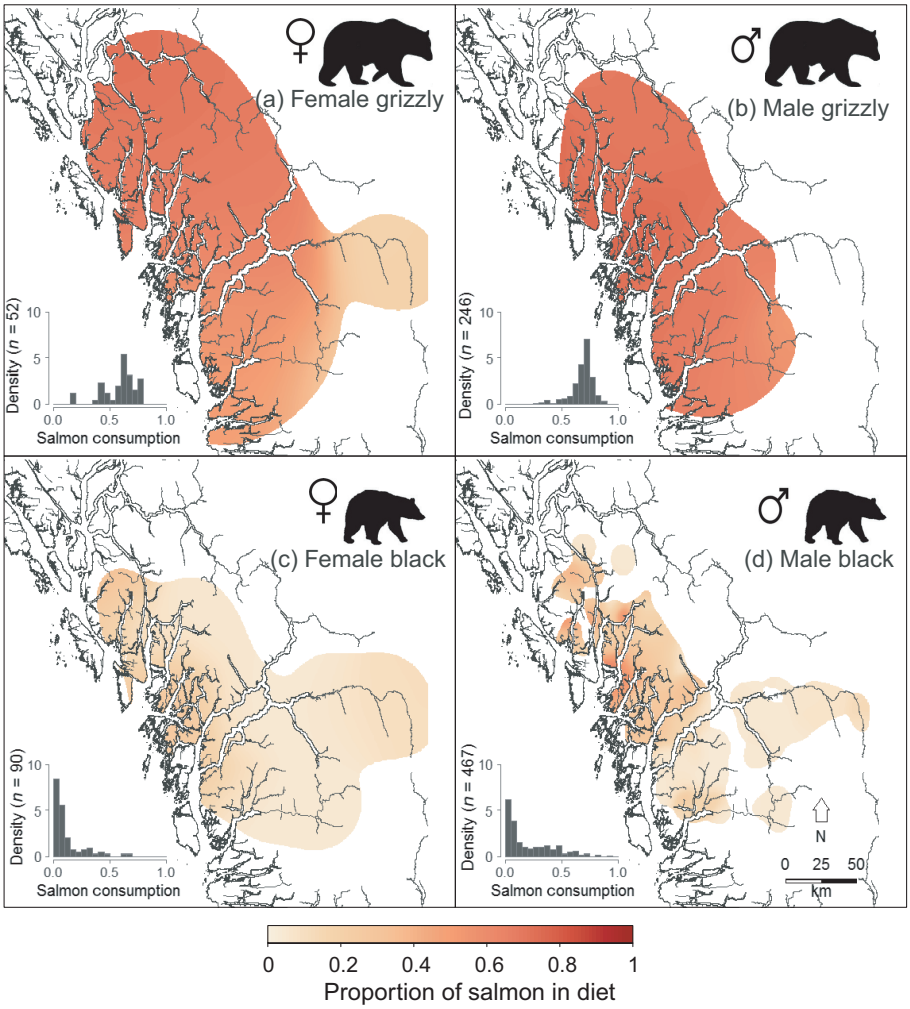


Fig. 3. Spatial patterns of salmon consumption estimated by kernel regression in female and male black and grizzly bear (*Ursus americanus* and *Ursus arctos horribilis*, respectively) diets in coastal British Columbia, combined over 2010 to 2014. Salmon-bearing rivers are depicted as gray lines. Areas depicted in white represent regions outside of the models' spatial extent. Histograms represent frequency of individual bears' observed median values of proportional salmon consumption.

Discussion

We revealed pronounced spatial patterns in salmon consumption by black and grizzly bears using stable isotope signatures from a substantial dataset of sampled individuals across large coastal and provincial areas. Moreover, we revealed new spatial detail about bear–salmon systems and associated ecological implications at a continental scale. We demonstrated differences in the magnitude and variability of salmon consumption between sexes, and within and between bear species from coastal to interior habitats. Salmon consumption by black bears was not only lower, but also more heterogeneous than by grizzly bears. High proportions of dietary salmon were constrained to coastal habitats for female grizzly bears, but extended into interior habitats along major salmon watersheds for males. This level of spatial detail allowed us to examine the geographic siting of conservation areas in a novel way. We detected this detail by developing and applying a generalizable approach to characterize spatial variation in

Table 1. Median proportions of estimated dietary contributions by diet model region and sex of unique individual–year combinations of black and grizzly bears (*Ursus americanus* and *Ursus arctos horribilis*, respectively) in British Columbia, Canada.

	Black		Grizzly							
	Coast		Coast		Eastern		Central		Interior	
Food type	F n = 92	M n = 399	F n = 66	M n = 279	F n = 72	M n = 59	F n = 78	M n = 105	F n = 84	M n = 143
Intertidal	0.01	0.01	0.22	0.27	N/A	N/A	N/A	N/A	N/A	N/A
Plants	0.90	0.82	0.12	0.06	0.62	0.60	0.47	0.40	0.58	0.63
Salmon	0.03	0.06	0.57	0.63	0.02	0.03	0.03	0.02	0.05	0.20
Terrestrial meat	0.03	0.04	<0.01	<0.01	0.36	0.38	0.50	0.58	0.31	0.08

Note: Diet model regions correspond to regions in Fig. 1.

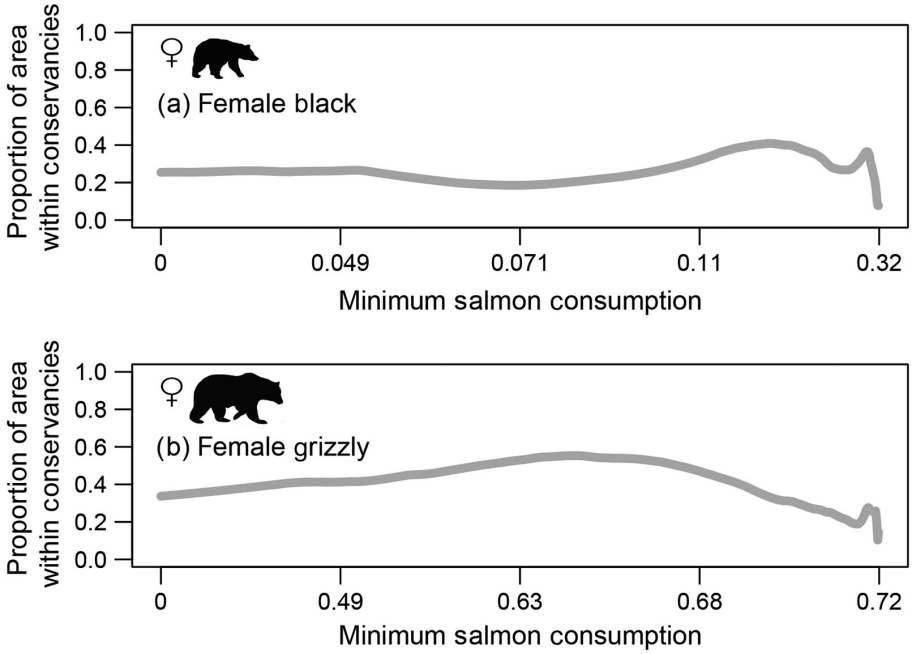


Fig. 4. Conservancy-protected proportion of coastal area in which median salmon consumption exceeds the given value for female (a) black (*Ursus americanus*) and (b) grizzly (*Ursus arctos horribilis*) bears from 2010 to 2014. *X*-axis based on species-specific quartiles of salmon consumption estimates, whereas minimum salmon consumption within an area (the gray line) based on kernel regression estimates.

realized niche of specific prey contributions. Such characterization could provide information key for planning landscape-scale protection of important ecological interactions for wide-ranging carnivores and their prey.

We acknowledge some limitations to our approach. Specifically, our analyses do not incorporate information on age, movement, competition, or resource availability from which we might elucidate the processes driving patterns of dietary variation. We note the scale of movement of these bears, and hence the scale of this analysis, is quite broad and caution against applying the results of this analysis at too fine a scale. Any specific and localized management decisions informed by this model ought to be supplemented with more detailed and scale-appropriate data. Moreover, the spatial extent of our

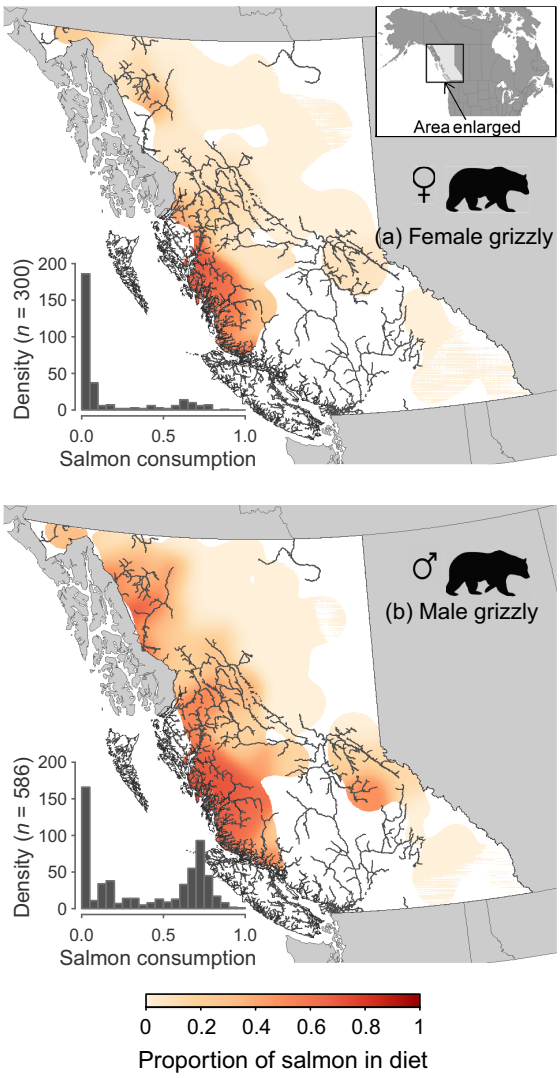


Fig. 5. Spatial patterns of salmon consumption estimated by kernel regression in (a) female and (b) male grizzly bear (*Ursus arctos horribilis*) diet across British Columbia, between 1995 and 2014. Major salmon-bearing rivers are depicted as gray lines. Areas depicted in white represent regions outside of the models' spatial extent. Histograms represent frequency of individual bears' observed median values of proportional salmon consumption.

visualizations of salmon consumption niche is subject to the geographic range of bear detections. Although other dietary sources were accounted for in our model, we did not assess the spatial variation in their consumption patterns across the province, focusing instead only on salmon. Future work could integrate such information to build on our spatial approach.

The patterns we detected in coastal habitats likely arise from intra- and inter-specific bear interactions. Consistent with previous studies, we found pronounced grizzly-over-black and male-over-female patterns for the amount of salmon that coastal bears consume (Rode et al. 2006, Fortin et al. 2007). Although we did not assess competition, where bear species are allopatric (i.e., most island habitats), we suspect black bears consume higher levels of salmon due to a lack of interference competition (Jacoby et al. 1999). A reduced salmon niche in females could be driven by competitive interference with males (or with any sex of grizzly for black bears), especially through females avoiding salmon rivers when accompanied by cubs to reduce the probability of infanticide from males (Ben-David et al. 2004, Rode et al. 2006, Bourbonnais et al. 2014). Work in nearby Alaska shows that male grizzlies often dominate salmon-foraging locations, leaving other bears to feed in less-productive locations or times (Belant et al. 2006, 2010, Fortin et al. 2007). Our results showed that salmon consumption by black bears was more variable than salmon consumption by grizzlies, a pattern that may be driven by interference competition from dominant grizzlies during fluctuations in salmon availability (Hodgson and Quinn 2002) or from competition with salmon-eating coastal wolves (Darimont et al. 2003, 2008). Our results support previous research demonstrating higher dietary contributions of fruit and plants by bears subject to competitive exclusion by male grizzly bears for salmon resources (Fortin et al. 2007).

Analyzing patterns in niche variation across large spatial scales can yield insight into broader ecological implications. The movement of nutrients, prey, and their consumers, for example, can have strong impacts on population and community dynamics (Polis and Hurd 1996, Polis et al. 1997, Yang et al. 2008, McCauley et al. 2012). Mowat and Heard (2006) showed coarse-level geographical variation in the bear–salmon association at a continental scale. We detailed the distribution and degree of salmon consumption, and by extension, patterns of marine–terrestrial nutrient transport. For males, this association appears to reach far beyond the temperate

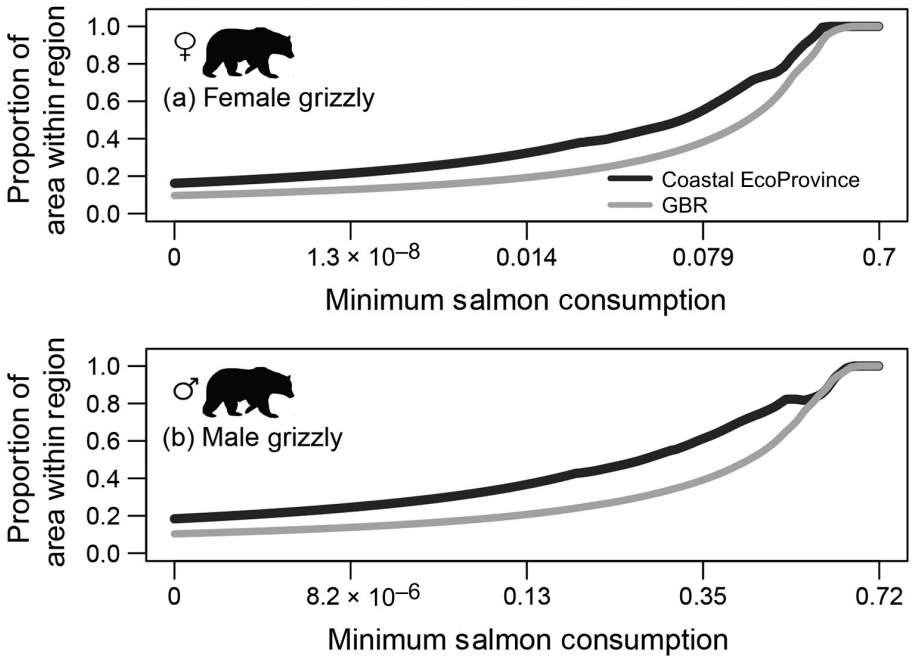


Fig. 6. Proportion of British Columbia in which salmon consumption estimates exceed the given value contained within the Coastal EcoProvince (black) and Great Bear Rainforest (GBR) (gray) for (a) female and (b) male grizzly bears (*Ursus arctos horribilis*), between 1995 and 2014. *X*-axis based on sex-specific quartiles of salmon consumption estimates, whereas minimum salmon consumption within an area (the gray line) based on kernel regression estimates.

rainforest boundary into interior ecosystems along salmon-bearing watersheds, whereas high-salmon diets in females are generally constrained to coastal environments. This is likely driven by competitive interactions with males, whose larger home ranges might also better overlap the sparser locations of salmon availability into interior habitats.

Understanding how individuals make different livings in different areas can inform conservation efforts for bears (Levi et al. 2015). Our approach here highlights variability in consumption of salmon, a food resource tightly coupled to individual and population fitness (Hilderbrand et al. 1999, 2000, Kovach and Powell 2003, Belant et al. 2006, Zedrosser et al. 2007, Costello et al. 2009, Bryan et al. 2014). As variation in resource use can drive population dynamics, understanding spatial and temporal components of such variability at appropriate spatial scales can help to assess the potential ecological relevance of existing protected areas and identify the value of protecting new areas. In the coastal area, within which habitat for salmon and grizzlies putatively played prominent roles in protected-area design (Price et al. 2009, DellaSala 2011), we showed that existing conservancies do no better than unprotected areas at representing habitat where bears exhibit high-salmon diets. This suggests that while future protected areas could be prioritized around high-productivity areas (e.g., river valleys with accessible salmon), current protected areas capture the suite of females' dietary niches at a landscape scale. Whereas lower-productivity areas (with little economic value) are generally designated as protected (Joppa and Pfaff 2009), our results show a suite of dietary niches are captured in these coastal-protected areas. In the provincial area, the GBR region captures the bear–salmon association after which it was in part named (Price et al. 2009, DellaSala 2011).

We speculate that coastal concentrations of salmon-eating grizzly bears may represent source populations. Although beyond the scope of this research, we might expect less-productive

populations (sinks) to be associated with lower meat availability (Hilderbrand et al. 1999), and perhaps additionally with high human-caused mortality (Artelle et al. 2016). Alternatively, contrasting dietary niches driven by some bears' specialization in salmon may create demographic and genetic structure across sub-populations. Our results with males suggest that conservation planners and practitioners can consider this bear–salmon association and the community and ecosystem services it provides to extend far beyond the bounds of the GBR. Whereas salmon are generally managed as a marine resource, their influence on terrestrial communities is widespread and must be accounted for across ecological and jurisdictional boundaries (Price et al. 2009, Darimont et al. 2010, Levi et al. 2012, Artelle et al. 2016).

More broadly, information about geographic and temporal variation in consumer–resource interactions can be used to prioritize conservation and management efforts for any taxa. Visualizing trends in consumer–resource interactions across space allows for insight into the factors that drive niche variation (e.g., spatial variability in critical food resources or important habitats) and facilitate population persistence (Tilman and Kareiva 1997, Roy et al. 2005), although we note that we cannot detect whether the geographic variation is linked to individual specialization in different areas, to resource distribution, or a combination of the two. Understanding spatial variation in ecological patterns, therefore, can inform and empower conservation solutions, such as the configuration of critical habitat, the size of protected areas, and their potential linkages (Crooks and Sanjayan 2006, Bellard et al. 2012). In an era of increasing habitat fragmentation and environmental change, spatial ecology can aid conservation scientists and managers in identifying and safeguarding important areas that remain for wildlife (Polis et al. 2004, Holt 2009).

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Literature Cited

Amarasekare, P. 2002. Interference competition and species coexistence. Proceedings of the Royal Society of London B: Biological Sciences 269:2541–2550.

Artelle, K. A., S. C. Anderson, J. D. Reynolds, A. B. Cooper, P. C. Paquet, and C. T. Darimont. 2016. Ecology of conflict: Marine food supply affects human–wildlife interactions on land. Scientific Reports 6:25936.

Baddeley, A., and R. Turner. 2005. Spatstat: an R package for analyzing spatial point patterns. Journal of Statistical Software 12:1–42.

Belant, J. L., B. Griffith, Y. Zhang, E. H. Follmann, and L. G. Adams. 2010. Population-level resource selection by sympatric brown and American black bears in Alaska. Polar Biology 33:31–40.

Belant, J. L., K. Kielland, E. H. Follmann, and L. G. Adams. 2006. Interspecific resource partitioning in sympatric ursids. Ecological Applications 16: 2333–2343.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

Ben-David, M., and E. A. Flaherty. 2012. Stable isotopes in mammalian research: a beginner's guide. Journal of Mammalogy 93:312–328.

Ben-David, M., K. Titus, and L. R. Beier. 2004. Consumption of salmon by Alaskan brown bears: A trade-off between nutritional requirements and the risk of infanticide? Oecologia 138:465–474.

Biro, P. A., and J. A. Stamps. 2008. Are animal personality traits linked to life-history productivity? Trends in Ecology & Evolution 23:361–368.

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

Bourbonnais, M. L., T. A. Nelson, M. R. Cattet, C. T. Darimont, G. B. Stenhouse, and D. M. Janz. 2014. Environmental factors and habitat use influence body condition of individuals in a species at risk, the grizzly bear. Conservation Physiology 2: cou043.

Brooks, T. M., R. A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, and A. S. L. Rodrigues. 2006. Global biodiversity conservation priorities. Science 313:58–61.

Bryan, H. M., C. T. Darimont, P. C. Paquet, K. E. Wynne-Edwards, and J. E. G. Smits. 2013. Stress and reproductive hormones in grizzly bears reflect nutritional benefits and social consequences of a salmon foraging niche. PLoS ONE 8:e80537.

Bryan, H. M., C. T. Darimont, P. C. Paquet, K. E. Wynne-Edwards, and J. E. Smits. 2014. Stress and reproductive hormones reflect inter-specific social and nutritional conditions mediated by resource availability in a bear–salmon system. Conservation Physiology 2:cou010.

Chape, S., J. Harrison, M. Spalding, and I. Lysenko. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philosophical Transactions of the Royal Society of London B: Biological Sciences 360:443–455.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, Illinois, USA.

Cooke, S. J., et al. 2014. Physiology, behavior, and conservation. Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches 87:1–14.

Costello, C. M., S. R. Creel, S. T. Kalinowski, N. V. Vu, and H. B. Quigley. 2009. Determinants of male reproductive success in American black bears. Behavioral Ecology and Sociobiology 64:125–134.

Crooks, K. R., and M. Sanjayan, editors. 2006. Connectivity conservation. Cambridge University Press, Cambridge, UK.

Dall, S. R. X., A. M. Bell, D. I. Bolnick, and F. L. W. Ratnieks. 2012. An evolutionary ecology of individual differences. Ecology Letters 15:1189–1198.

Darimont, C. T., H. M. Bryan, S. M. Carlson, M. D. Hocking, M. MacDuffee, P. C. Paquet, M. H. H. Price, T. E. Reimchen, J. D. Reynolds, and C. C. Wilmers. 2010. Salmon for terrestrial protected areas. Conservation Letters 3:379–389.

Darimont, C. T., P. C. Paquet, and T. E. Reimchen. 2008. Spawning salmon disrupt trophic coupling between wolves and ungulate prey in coastal British Columbia. BMC Ecology 8:14.

Darimont, C. T., P. C. Paquet, and T. E. Reimchen. 2009. Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. Journal of Animal Ecology 78:126–133.

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

Darimont, C. T., T. E. Reimchen, and P. C. Paquet. 2003. Foraging behavior by gray wolves on salmon streams in coastal British Columbia. Canadian Journal of Zoology 81:349–353.

DellaSala, D. A. 2011. Temperate and boreal rainforests of the world: ecology and conservation. Island Press, Washington, D.C., USA.

Demarchi, D. A. 2011. The British Columbia ecoregion classification. Ecosystem Information Section, Ministry of Environment, Victoria, British Columbia, Canada.

Ehrich, D., et al. 2015. What can stable isotope analysis of top predator tissues contribute to monitoring of tundra ecosystems? Ecosystems 18:404–416.

Erlenbach, J. A., K. D. Rode, D. Raubenheimer, and C. T. Robbins. 2014. Macronutrient optimization and energy maximization determine diets of brown bears. Journal of Mammalogy 95:160–168.

Fauchald, P. 1999. Foraging in a hierarchical patch system. American Naturalist 153:603–613.

Fortin, J. K., S. D. Farley, K. D. Rode, and C. T. Robbins. 2007. Dietary and spatial overlap between sympatric ursids relative to salmon use. Ursus 18:19–29.

Gende, S. M., T. P. Quinn, and M. F. Willson. 2001. Consumption choice by bears feeding on salmon. Oecologia 127:372–382.

Groot, C., and L. Margolis. 1991. Pacific salmon life histories. UBC Press, Vancouver, British Columbia, Canada.

Hammerschlag-Peyer, C. M., and C. A. Layman. 2010. Intrapopulation variation in habitat use by two abundant coastal fish species. Marine Ecology Progress Series 415:211–220.

Hatler, D. F., D. W. Nagorsen, and A. M. Beal. 2008. Carnivores of British Columbia. Royal BC Museum, Victoria, British Columbia, Canada.

Hilderbrand, G. V., S. D. Farley, C. T. Robbins, T. A. Hanley, K. Titus, and C. Servheen. 1996. Use of stable isotopes to determine diets of living and extinct bears. Canadian Journal of Zoology 74:2080–2088.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, and T. A. Hanley. 2000. Effect of hibernation and reproductive status on body mass and condition of

coastal brown bears. Journal of Wildlife Management 64:178–183.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology 77: 132–138.

Hobson, K. A. 2005. Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. Auk 122:1037–1048.

Hobson, K. A., R. Barnett-Johnson, and T. Cerling. 2010. Using isoscapes to track animal migration. Pages 273–298 *in* J. B. West, G. J. Bowne, T. E. Dawson, and K. P. Tu, editors. Isoscapes: understanding movement, pattern, and process on earth through isotope mapping. Springer, New York, New York, USA.

Hocking, M. D., and J. D. Reynolds. 2011. Impacts of salmon on riparian plant diversity. Science 331:1609–1612.

Hodgson, S., and T. P. Quinn. 2002. The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. Canadian Journal of Zoology 80:542–555.

Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences USA 19659–19665.

Hutchinson, G. E. 1957. Pages 415–421 Concluding remarks: the multivariate niche. Cold Spring Harbor Symposium on Quantitative Biology, Spring Harbor, New York, USA.

Jacoby, M. E., G. V. Hilderbrand, C. Servheen, C. C. Schwartz, S. M. Arthur, T. A. Hanley, C. T. Robbins, and R. Michener. 1999. Trophic relations of brown and black bears in several western North American ecosystems. Journal of Wildlife Management 63: 921–929.

Jaeger, A., M. Connan, P. Richard, and Y. Cherel. 2010. Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialization in seabirds. Marine Ecology Progress Series 401:269–277.

Joppa, L. N., and A. Pfaff. 2009. High and far: biases in the location of protected areas. PLoS ONE 4: e8273.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350.

Kie, J. G. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. Animal Biotelemetry 1:1.

Kovach, A. I., and R. A. Powell. 2003. Effects of body size on male mating tactics and paternity in black bears, *Ursus americanus*. Canadian Journal of Zoology 81:1257–1268.

Levi, T., C. T. Darimont, M. MacDuffee, M. Mangel, P. Paquet, and C. C. Wilmers. 2012. Using grizzly bears to assess harvest-ecosystem tradeoffs in salmon fisheries. PLoS Biology 10:e1001303.

Levi, T., R. E. Wheat, J. M. Allen, and C. C. Wilmers. 2015. Differential use of salmon by vertebrate consumers: implications for conservation. PeerJ 3: e1157.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405:243–253.

McCauley, D. J., H. S. Young, R. B. Dunbar, J. A. Estes, B. X. Semmens, and F. Micheli. 2012. Assessing the effects of large mobile predators on ecosystem connectivity. Ecological Applications 22:1711–1717.

Moore, J. W., and B. X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11:470–480.

Mowat, G., and D. C. Heard. 2006. Major components of grizzly bear diet across North America. Canadian Journal of Zoology 84:473–489.

Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 2003. Consumer-resource dynamics. Princeton University Press, Princeton, New Jersey, USA.

Nadaraya, E. 2012. Nonparametric estimation of probability densities and regression curves. Volume 20. Springer Science & Business Media, New York, New York, USA.

Newsome, S. D., C. Martinez del Rio, S. Bearhop, and D. L. Phillips. 2007. A niche for isotopic ecology. Frontiers in Ecology and the Environment 5:429–436.

O'Sullivan, D., and D. J. Unwin. 2010. Geographic information analysis. Second edition. John Wiley & Sons, Hoboken, New Jersey, USA.

Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. Molecular Ecology 12:1375–1387.

Pekarsky, S., A. Angert, B. Haese, M. Werner, K. A. Hobson, and R. Nathan. 2015. Enriching the isotopic toolbox for migratory connectivity analysis: a new approach for migratory species breeding in remote or unexplored areas. Diversity and Distributions 21:416–427.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on

small islands and coastal land communities. American Naturalist 147:396–423.

Polis, G. A., M. E. Power, and G. R. Huxel. 2004. Food webs at the landscape level. University of Chicago Press, Chicago, Illinois, USA.

Price, K., A. Roburn, and A. MacKinnon. 2009. Ecosystem-based management in the Great Bear Rainforest. Forest Ecology and Management 258: 495–503.

Proctor, M., B. McLellan, J. Boulanger, C. Apps, G. Stenhouse, D. Paetkau, and G. Mowat. 2010. Ecological investigations of grizzly bears in Canada using DNA from hair, 1995–2005: a review of methods and progress. Ursus 21:169–188.

Province of British Columbia. 2012. Grizzly bear population units – data catalogue. https://catalogue.data.gov.bc.ca/dataset/grizzly-bear-population-units

Province of British Columbia. 2016. Parks and protected areas regional boundaries - data catalogue. https://catalogue.data.gov.bc.ca/dataset/parks-and-protected-areas-regional-boundaries

Quinn, T. P., S. M. Carlson, S. M. Gende, and J. Rich Harry B. 2009. Transportation of Pacific salmon carcasses from streams to riparian forests by bears. Canadian Journal of Zoology 87:195–203.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Robbins, C. T., J. K. Fortin, K. D. Rode, S. D. Farley, L. A. Shipley, and L. A. Felicetti. 2007. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. Oikos 116:1675–1682.

Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. Ecology 87:2636–2646.

Rodrigues, A. S., and K. J. Gaston. 2001. How large do reserve networks need to be? Ecology Letters 4: 602–609.

Rodrigues, A. S. L., et al. 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428:640–643.

Roy, M., R. D. Holt, and M. Barfield. 2005. Temporal autocorrelation can enhance the persistence and abundance of metapopulations comprised of coupled sinks. American Naturalist 166:246–261.

Schindler, D. E., J. B. Armstrong, K. T. Bentley, K. Jankowski, P. J. Lisi, and L. X. Payne. 2013. Riding the crimson tide: Mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. Biology Letters 9:20130048.

Schindler, D. E., and S. C. Lubetkin. 2004. Using stable isotopes to quantify material transport in food webs. Pages 25–42 *in* G. A. Polis, M. A. Power, and G. R. Huxel, editors. Food webs at the landscape level. The University of Chicago Press, Chicago, Illinois, USA.

Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. Frontiers in Ecology and the Environment 1:31–37.

Semmens, B. X., E. J. Ward, J. W. Moore, and C. T. Darimont. 2009. Quantifying inter-and intra-population niche variability using hierarchical Bayesian stable isotope mixing models. PLoS ONE 4:e6187.

Service, C. N., M. S. Adams, K. A. Artelle, P. Paquet, L. V. Grant, and C. T. Darimont. 2014. Indigenous knowledge and science unite to reveal spatial and temporal dimensions of distributional shift in wildlife of conservation concern. PLoS ONE 9:e101595.

Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioral syndromes. Ecology Letters 15:278–289.

Smith, B. R., and D. T. Blumstein. 2008. Fitness consequences of personality: a meta-analysis. Behavioral Ecology 19:448–455.

Stephens, D. W., J. S. Brown, and R. C. Ydenberg. 2007. Foraging: behavior and ecology. University of Chicago Press, Chicago, Illinois, USA.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.

Stock, B. C. and B. X. Semmens. 2013. MixSIAR GUI user manual, version 3.0. https://github.com/brianstock/MixSIAR, https://doi.org/10.5281/zenodo.56159

Tilman, D., and P. M. Kareiva. 1997. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, New Jersey, USA.

Watson, G. S. 1964. Smooth regression analysis. Sankhyā: The Indian Journal of Statistics Series A 359–372.

Weimerskirch, H., A. Gault, and Y. Cherel. 2005. Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. Ecology 86:2611–2622.

Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology & Evolution 27:452–461.

Woods, J. G., D. Paetau, D. Lewis, B. N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging

of free ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

Wunder, M. B. 2010. Using isoscapes to model probability surfaces for determining geographic origins. Pages 251–270 *in* J. B. West, G. J. Bowne, T. E. Dawson, and K. P. Tu, editors. Isoscapes: understanding movement, pattern, and process on earth through isotope mapping. Springer, New York, New York, USA.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses. Ecology 89:621–634.

Zedrosser, A., E. Bellemain, P. Taberlet, and J. E. Swenson. 2007. Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density. Journal of Animal Ecology 76:368–375.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1843/full