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Observations of Grizzly Bear (*Ursus arctos*) associated with abundance of spawning Kokanee (*Oncorhynchus nerka*) at an inland river, British Columbia, Canada

SAGE RAYMOND^{1,*}, JULIUS STRAUSS², and NANCY FLOOD¹

¹Department of Biological Sciences, Thompson Rivers University, 805 TRU Way, Kamloops, British Columbia V2C 0C8 Canada

²Wild Bear Lodge Ltd., 16420 Highway 31, Meadow Creek, British Columbia V0G 1N0 Canada *Corresponding author: sage.raymond099@gmail.com

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Abstract

Salmon (*Oncorhynchus* spp.) are an important food source for Grizzly Bear (*Ursus arctos*), but many salmon populations are declining. While most research on Grizzly Bear–salmon interactions occurs in coastal ecosystems, declining salmon may also affect Grizzly Bears in inland ecosystems where salmon are also an important part of their diet. We document changes in the number and distribution of observations of Grizzly Bears and changing Kokanee (i.e., landlocked Sockeye Salmon, *Oncorhynchus nerka*) abundance at an inland river. We hypothesized that reduced abundance of Kokanee would limit the number of Grizzly Bear observations at the river. We compared Kokanee abundance and Grizzly Bear observations (n = 535) between 2012 and 2019 at the Lardeau River, British Columbia, Canada. We used a generalized linear mixed model to test if the number of bear observations changed as a function of Kokanee abundance among four river reaches during eight consecutive years of study. Kokanee abundance and reach explained 73% of the variance. Our results suggest that reduced Kokanee abundance also reduces Grizzly Bear presence, likely because bears seek out other, more available food sources, away from Kokanee spawning habitat. This pattern could limit ecosystem services provided by Grizzly Bears adjacent to spawning areas and it could have implications for bear management and conservation.

Key words: Grizzly Bear; Ursus arctos; Kokanee; Oncorhynchus nerka; community science; animal behaviour; dietary plasticity; optimal foraging theory

Introduction

Pacific salmon (Oncorhynchus spp.) represent an important food source for some subpopulations of Grizzly Bear (Ursus arctos; e.g., Hilderbrand et al. 1999; Mowat and Heard 2006). Grizzly Bears that access salmon are larger and occur at higher densities (Hilderbrand et al. 2018). Dietary salmon also increases litter size (Hilderband et al. 1999), decreases cortisol levels (Bryan et al. 2013), and is important for individual and population fitness (Mowat and Heard 2006; Bryan et al. 2013). Unfortunately, many Pacific salmon stocks are declining (Irvine and Fukuwaka 2011), with some runs becoming extinct (Gustafson et al. 2007). A major contributor to salmon declines is ongoing climate change (e.g., Irvine and Fukuwaka 2011; Isaak et al. 2011; Ward et al. 2015; Schoen et al. 2017; Crozier et al. 2021) via increased water temperature (e.g., Martins et al. 2012; Atlas et

al. 2021) and low water levels associated with limited rainfall (e.g., Tillotson and Quinn 2017). Low salmon density may affect the distribution of salmon within spawning areas, for example, via decreased intraspecific competition for spawning sites (Adkison *et al.* 2014; Falcy 2015). Changes in abundance or distribution of salmon in spawning areas may affect the presence and distribution of Grizzly Bears that use them as food (e.g., Quinn *et al.* 2003, 2016; Deacy *et al.* 2016, 2019).

Grizzly Bears exhibit considerable dietary plasticity (e.g., Cristecu *et al.* 2015). Diverse diets that rely on seasonally available foods require Grizzly Bears to travel among habitats (Hamer and Herrero 1987; MacHutchon and Wellwood 2003; Mowat and Heard 2006; Fortin *et al.* 2013). For example, in Banff National Park, Alberta, Canada, seasonal changes in habitat use were related to changes in the phenology

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of forage species, with more use of higher elevations and slopes with a northern aspect as the growing season progressed and snow receded (Hamer and Herrero 1987). They may also change their diet and location annually in response to changing food availability (Schwartz et al. 2013; Costello et al. 2014). Schwartz et al. (2013) found that autumn fat levels in Grizzly Bears did not depend on the quality of Whitebark Pine (Pinus albicaulis Englemann) seed production because bears accessed more meat in years when seed crops were poor. Grizzly Bears also respond to temporal changes in food availability. For example, bears follow resource waves by relocating to areas with abundant spawning salmon, even though the phenology of salmon runs changes among years (Deacy et al. 2016, 2019). Selectivity extends even to individual prey items, with Grizzly Bears consuming a larger proportion of each fish captured and targetting the most energy-rich fish in years with limited salmon abundance. By contrast, in years when salmon are abundant, they consume only the most energy-rich parts of the fish (e.g., eggs, brains; Gende et al. 2001). Dietary changes reflect optimal foraging, which predicts foraging that maximizes energetic intake by selecting foods that provide the greatest energetic reward relative to energy invested (MacArthur and Pianka 1966; Charnov and Orians 1973); this strategy has been observed in Grizzly Bears (e.g., Hamilton and Bunnell 1987; Edwards et al. 2011). For Grizzly Bears, the optimal food may change depending on its abundance and accessibility. For example, when salmon abundance is low, the energetic expenditure of finding and catching fish increases (e.g., Cunningham et al. 2013) and may exceed the energetic benefit of its consumption. The theory of ideal despotic distribution, which postulates that more competitive individuals occupy high-quality habitat with denser resources (Calsbeek and Sinervo 2002), could also affect Grizzly Bear presence in spawning areas. Dominant males would be expected to occupy river sections with abundant and accessible salmon (i.e., high-quality habitat), which could encourage more vulnerable demographics (e.g., mothers with cubs) to seek other food sources (e.g., Nevin and Gilbert 2005). Finally, bears may select mixed diets because consumption of a variety of different foods is nutritionally beneficial (Rode and Robbins 2000; Erlenbach et al. 2014), even if a single food item is most energetically efficient.

While most studies of Grizzly Bear and salmon interactions have occurred in coastal areas, salmon are also an important food source for interior bear populations. Belant *et al.* (2006) found that salmon comprised a large proportion of Grizzly Bear diet and was important for body condition at a site in southcentral Alaska, over 200 km from the coast. Salmon is also an important food source for interior, montane Grizzly Bears in the low Arctic (Sorum et al. 2019; Mangipane et al. 2020). In central British Columbia (BC), landlocked Sockeye Salmon (Oncorhynchus nerka), known as Kokanee, represent an important food source for Grizzly Bears (Mowat and Heard 2006; Herbison 2008). In the Kootenay Lake system of BC, Kokanee have spawned in the Lardeau River since the end of the last ice age (Gayton 2002). Spawning Kokanee in the Lardeau River have been counted annually since 1979 (excepting 1985; Bassett et al. 2018). The number of spawning Kokanee declined dramatically from ~500000 in 2012 (Neufeld 2012) to ~6000 in 2017 (Neufeld 2017). The decline was attributed to increased abundance of piscivorous salmonid predators (Redfish Consulting Ltd. 2016; Bassett et al. 2018), but the impacts of the decline on Grizzly Bear presence and distribution has not been explored.

Our aim was to examine changes in the number and distribution of Grizzly Bear observations in response to changing abundance of Kokanee at an inland river. We hypothesized that reduced Kokanee abundance would decrease the attractiveness of this food source for Grizzly Bears and predicted a positive relationship between the number of Kokanee and the number of Grizzly Bear observations. Understanding density dependent changes in salmon distribution and how Grizzly Bears respond to these changes could be valuable for management, conservation, and bearviewing operations, especially as climate change progresses and salmon populations decline.

Methods

The Lardeau Valley (50.457°N, 117.194°W) is a sparsely human-populated valley in the Selkirk Mountains of southeastern BC (Figure 1). The Lardeau River spans roughly 46 km from the outlet of Trout Lake to the confluence with the Duncan River at the north end of Kootenay Lake. Because the Lardeau River has no flow control structures or dams, its width and depth vary considerably along its length and its numerous side channels and logjams represent excellent spawning habitat (Slaney and Andusak 2003). Along with the Meadow Creek spawning channel, located 6.5 km south of reach 1, the Lardeau River is one of the primary spawning locations for Kootenay Lake Kokanee (Redfish Consulting Ltd. 2016). Riverside ecosystems are classified as the Interior-Cedar-Hemlock biogeoclimatic zone (Herbison 2008). Our study area overlaps the boundaries of both the North Purcells and Central Selkirk Grizzly Bear population units, both of which have been assigned a conservation ranking of 'moderate' by the



FIGURE 1. The study area in the Selkirk Mountains of southeastern British Columbia, Canada. The Lardeau River was divided into four reaches that were used for analysis. Reaches 1 and 4 are the furthest downstream and upstream reaches, respectively. The Meadow Creek spawning channel is located 6.5 km south of reach 1.

province (Environmental Reporting BC 2020). In the study area, Grizzly Bears typically consume vegetation and Yellow Glacier Lily (*Erythronium grandiflorum* Pursh) bulbs upon emerging from hibernation, followed by Mountain Huckleberry (*Vaccinium membranaceum* Douglas ex Torrey) in the subalpine during the summer, moving to valley bottoms to feed on Kokanee prior to hibernating (Mowat and Heard 2006; Herbison 2008).

Salmon abundance

We retrieved spawning Kokanee count data from the BC Ministry of Environment's Ecological Reports Catalogue (https://a100.gov.bc.ca/pub/acat/public/wel come.do). Briefly, from 2012 through 2014, Kokanee were counted once, with a single overland flight resulting in a peak count (Neufeld 2012, 2014a,b). In 2015 (Neufeld 2016a) and 2017 (Neufeld 2017), three counts occurred, and in 2016 (Neufeld 2016b), 2018 (Neufeld 2018), and 2019 (Bassett 2019) fish were counted twice. Flight dates were selected to represent peak Kokanee activity based on observations at the Meadow Creek spawning channel (Bassett *et al.* 2018). Provincial government personnel counted all fish between the Duncan River's outflow into Kootenay Lake and the headwaters of the Lardeau River at Gerrard, BC. They counted fish in six discrete reaches, four of which we used in our study (Figure 1). Reaches were unequal in length and we used ArcGIS Version 10.7 to determine the length of each reach. Counts were not meant to represent absolute abundance of Kokanee, but they provided an index of abundance that allowed comparison among years and locations (Bassett et al. 2018). For brevity, we use the term abundance in our study. Although the number of flights and the complement and number of surveyors varied and may have affected abundance accuracy among years, we used the maximum Kokanee abundance provided in government reports for analysis. Government reports included inflation factors meant to adjust Kokanee counts for factors that affected count accuracy (e.g., shading, water surface conditions, height/speed of aircraft, etc.). We applied this correction factor equally across counts in all reaches.

Bear observations

We compiled records of bear observations from Wild Bear Lodge, a commercial bear viewing company that operates tours along the Lardeau River when Grizzly Bears congregate along the river to consume spawning Kokanee (J.S. unpubl. data). As part of their operational program and to comply with Provincial Park Permits, lodge employees, i.e., 'surveyors', recorded bear observations, including location, time, date, the number of bears, the platform from which the observation occurred (i.e., foot, raft, vehicle), and the bear's response to viewing. We collected records that occurred between 2012 and 2019 during the Kokanee spawning period, which we defined as 1 September to 31 October. Start dates for data collection ranged from 1 to 4 September and end dates ranged from 25 to 31 October. We excluded observations of Black Bear (Ursus americanus), observations that occurred >500 m from the Lardeau River's banks, and any records lacking clear location information, or when bear species was unknown. Overall, we omitted 42 observations, 35 of which occurred in 2012. We omitted between zero and three observations from all other years. We considered family groups (i.e., mother with offspring) as single observations. If surveyors lost sight of a bear and then detected a bear within half an hour and 1 km of where the first bear had been located, we considered it a single observation. Given a lodge policy to leave an area if a bear entered cover or appeared disturbed, such occurrences were rare (n = 11). Surveyors recorded bear locations based on familiar landmarks and kilometre markers along the highway. To facilitate analysis, we reclassified the location of each observation as occurring in one of the four reaches used for Kokanee abundance estimation (Figure 1). If a bear moved among reaches during a viewing, we recorded it as a single observation occurring in the reach where it was originally detected, which rarely occurred (n = 4). We used work logs to calculate daily effort spent searching for bears annually, defining a day of effort as one surveyor spending all daylight hours searching for bears, with or without commercial guests. Surveyors all received the same training and used similar search methods, which involved walking or sitting in high-quality habitat, scanning riverbanks with binoculars, and rafting down the Lardeau River, but some search time was spent in vehicles (typically in transit to a trailhead). Although search methods varied, they were approximately consistent among years and reaches. Surveyors spent time approximately equally along the river's length, however private property adjacent to reaches 1 and 2 somewhat reduced effort in these sections.

Analyses

We used Chi-square goodness-of-fit tests to compare Kokanee abundance among years (assuming equal counts annually) and to compare Kokanee distribution among reaches within years (assuming distribution was proportional to reach length). We also used Chi-square goodness-of-fit tests to compare the number of bear observations among years (with expected values based on effort) and within years but among reaches (assuming observations would be proportional to reach length).

To determine the predictive capacity of Kokanee abundance on bear observations, we used a generalized linear mixed effects model (GLMM) to test the number of bear observations in each reach during each year of the study (n = 32) in relation to annual local Kokanee abundance divided by reach length. Human presence (Gibeau et al. 2002; Schwartz et al. 2010a), spawning habitat (Adkison et al. 2014), and high-quality fishing locations (Luque and Stokes 1976; Gende and Quinn 2004) can affect bear presence and varied along the river's length, so we included reach as a covariate in the model. To address inter-annual variation, we included year as a random effect and included an offset term for the number of days of search effort. We used a negative binomial distribution to accommodate overdispersion in the data (Coxe et al. 2009). We scaled (by 1 SD) and mean-centred Kokanee abundance prior to modelling. To assess model fit and the value of including Kokanee abundance as a covariate, we used AIC weights adjusted for small sample sizes (AICc) and likelihood ratio tests. We assessed the amount of variance explained by the model using an adjusted r^2 metric suitable for GLMMs following negative binomial distributions (Nakagawa et al. 2017). Lastly, we confirmed the absence of collinearity among variables using variance inflation factors. We completed all statistical analyses using R Studio Version 4.2.2. We report averages as mean \pm SD and use a significance level of P = 0.05.

Results

The mean annual abundance of Kokanee summed across the four reaches was 95634 ± 144239 and ranged between 399929 in 2012 and 5210 in 2017 (Table S1). Abundance varied significantly among years ($\chi_7^2 = 1522878$, P < 0.001). In each year, the distribution among the four reaches differed significantly from what would be expected based on distribution proportional to reach length (χ_3^2 ranging from 4906 to 118925, P < 0.001 for all years). Over time, Kokanee abundance in reaches 1 and 2 was relatively constant (Figure 2a). With the exceptions of 2012 and 2019, when the proportion of Kokanee was similar in reaches 3 and 4, most fish were in reach 4 until 2014, after which the greatest proportion of fish was found in reach 3.

There were 535 bear observations that occurred during 487 days of search effort with sufficient information to include in our analysis (Table S2). The number of Grizzly Bear observations/day ranged



FIGURE 2. Distribution of spawning Kokanee (Oncorhynchus nerka) and Grizzly Bear (Ursus arctos) observations among four reaches of the Lardeau River, British Columbia, 2012–2019.

from 0.33 in 2017 to 3.03 in 2012. Compared to what would be expected based on survey effort, the number of observations varied significantly among years $(\chi_7^2 = 208, P < 0.001)$, and distribution of observations among reaches differed significantly from what would be expected based on distribution proportional to reach length for each year $(\chi_3^2, \text{ range } 40-143, P < 0.001$ for each test). The proportion of observations in reaches 1 and 2 was relatively stable over the study period, and most bear observations occurred in reach 4 until 2014, after which most observations occurred in reach 3 (Figure 2b).

The mean rate of Grizzly Bear observations (i.e., number corrected by effort) roughly paralleled annual Kokanee abundance (Figure 3). Model results indicated that local fish abundance was a significant predictor of the number of bear observations ($\beta = 0.52$, P = 0.001, CI = 0.12–0.87). To confirm that Kokanee abundance was an important predictor of bear observations, we conducted a likelihood ratio test between models including and excluding Kokanee abundance as a predictor; the model including Kokanee abundance fit the data significantly better (P = 0.02). Fixed effects (i.e., Kokanee abundance and reach) accounted for 72.7% of the variance in bear observations, while random terms (i.e., year) accounted for only 0.9 % of variance. The \triangle AICc between the null model and our top model was 27.3 AICc points, and likelihood ratio testing indicated the final model had significantly better fit (P < 0.001). Variance inflation factors confirmed the absence of collinearity among variables (VIF \leq 1.18).

Discussion

Consistent with our predictions, Grizzly Bear observations were strongly predicted by Kokanee abundance, suggesting that bears modified their distribution based on food availability, potentially seeking other food sources when Kokanee were limited. Distribution of Kokanee within the Lardeau River appeared to change over time, which is consistent with observations of density-dependent changes in salmon distribution in spawning areas elsewhere (Adkison et al. 2014; Falcy 2015). The observed shift towards reaches further downstream (i.e., from reach 4 to reach 3) in years of low abundance could relate to reduced competition for spawning sites during years with few fish (Adkison et al. 2014; Falcy 2015), with individuals conserving energy by occupying the first suitable site they encounter (Adkison et al. 2014).

The frequency of Grizzly Bear observations was temporally (i.e., among years) and spatially (i.e., among reaches) predicted by Kokanee abundance. This observation is consistent with findings that suggest Grizzly Bears shift their distribution to accommodate the geographic location of food sources (Hamer and Herrero 1987; MacHutchon and Wellwood 2003; Mowat and Heard 2006; Fortin *et al.* 2013). For example, in the Greater Yellowstone Ecosystem, Grizzly Bears moved into Whitebark Pine habitat as seed crops became available (Costello *et al.* 2014), and Grizzly Bears followed resource waves of spawning salmon (Deacy *et al.* 2016, 2019). The predictive capacity of Kokanee abundance on bear observations was also consistent with the work of others who have



FIGURE 3. Kokanee (*Oncorhynchus nerka*) abundance and Grizzly Bear (*Ursus arctos*) observations/day of effort at the Lardeau River, British Columbia, 2012–2019.

found that salmon predation by bears increases with increasing salmon density (Quinn *et al.* 2003, 2016).

Besides reduced bear presence, an explanation for fewer observations in years of Kokanee scarcity could be that reduced Kokanee density promotes behaviour that affected bear detectability. When fish are scarce, bears may become more selective when fishing to compensate for the high energetic cost of locating fish. For example, Cunningham *et al.* (2013) found that Grizzly Bears selectively caught large fish when salmon density was low and Gende *et al.* (2001) observed selection of the most energy-rich fish when salmon were scarce. Because fishing success is higher at night (e.g., Klinka and Reimchen 2002), bears may have selectively fished at night during years of salmon scarcity, reducing detections during daytime surveys.

Lastly, when resources are sparse, individual animals may occupy and defend larger areas to meet resource requirements (Calsbeek and Sinervo 2002). If the most dominant male bears, which are largely nocturnal, occupied larger areas of the river corridor in years of Kokanee scarcity, they may have limited the presence of more vulnerable demographics, such as mothers with cubs, which are more diurnal and therefore easier to detect using our methods (Nevin and Gilbert 2005). In other systems, intraspecific competition and risk of infanticide have been proposed as reasons some Grizzly Bears fail to consume salmon despite its availability in their home ranges (Gende et al. 2001; Deacy et al. 2016), and this effect could increase in years when resources are limited, and competition therefore increases.

When Kokanee were scarce and Grizzly Bears

were largely absent from the Lardeau River, individuals may have switched to other food sources, which has occurred following declines of historically available foods in other ecosystems (e.g., Schwartz et al. 2013; Costello et al. 2014; Cristecu et al. 2015). Although we did not attempt to test if a dietary change occurred, Wild Bear Lodge staff anecdotally observed bears using the subalpine and scats containing Mountain Huckleberry later than average in years of Kokanee scarcity (J.S. unpubl. data). At low fish densities, the energetic cost of fishing may exceed the energetic rewards (Quinn et al. 2003, 2016), even when bears become more selective about the individual salmon they target (Gende et al. 2001; Cunningham et al. 2013). Optimal foraging theory (MacArthur and Pianka 1966; Charnov and Orians 1973) would predict selection of other food sources. In our study area, the primary alternate food source in years of Kokanee scarcity may have been Mountain Huckleberry in the subalpine (e.g., Mowat and Heard 2006), which, given favourable weather, can persist well into the autumn (Minore and Smart 1978). Finding, handling, and consuming berries represents an energetic investment, and the energetic benefits of berry consumption decline if berry density or size is low, or if berry bushes are sparse (Welch et al. 1997). The attractiveness of huckleberries compared to Kokanee could therefore vary among years depending on the quality of the berry crop. Compared to Kokanee, berries are high in carbohydrates and low in protein and lipids (Rode and Robbins 2000; Erlenbach et al. 2014), and the latter may be especially important in the fall prior to hibernation (Erlenbach

et al. 2014). Nutritionally, the optimal Grizzly Bear diet would be mixed (Erlenbach et al. 2014), which would likely mean consumption of both Kokanee and huckleberries. In our study area, the distance and elevation change between the Lardeau River where Kokanee spawn and the subalpine where huckleberries can be found in autumn is considerable, and the energetic investment of travelling between these ecosystems could influence food selection. An important next step in this system could be to better understand the role of Kokanee in the diets of bears and what foods bears use when Kokanee are limited.

Various factors limited the strength of our findings. Multi-year studies can be affected by interannual variation. We controlled for such variation in our models by including year as a random effect; however, inter-annual changes may have affected our results, and we did not study the sources of this variation (e.g., quality of berry crop). We failed to account for the myriad factors besides Kokanee abundance that may have affected Grizzly Bear distribution, such as land cover (e.g., Milakovic et al. 2012) and human presence (e.g., Gibeau et al. 2002; Schwartz et al. 2010a). These factors varied among reaches. For example, reach 4 occurred primarily within Goat Range Provincial Park, where human presence was lower. Spawning habitat (Adkison et al. 2014) and good fishing sites (Luque and Stokes 1976; Gende and Quinn 2004) likely varied among reaches and affected bear presence. We accounted for these factors in our modelling approach by using reach as a covariate. Additionally, we used the number of Grizzly Bear observations as a metric for bear presence, but we did not survey at night, and Grizzly Bears increase nocturnality in response to human presence (Olson 1998; Rode et al. 2006; Ordiz et al. 2011, 2014). Finally, there were several limitations associated with using community science data. Inconsistent data collection in 2012 resulted in the omission of many (n = 35) observations from analysis, but this omission would not have changed the direction of the effects we observed. Surveyors were different among years, and, although they received the same training, their abilities to detect bears could have differed. Upon observing a bear, surveyors typically stopped searching for additional bears, so bears in other reaches may have gone unnoticed. This effect is likely small because most bear observations lasted less than an hour. Although individual bears tolerate human viewers to different extents (e.g., Olson et al. 1998; Nevin and Gilbert 2005), surveyors could not reliably distinguish among individual bears, which may have affected results. For example, the presence of a habituated individual in some years but not others could have inflated viewing rate in some years. Similarly, Kokanee abundance accuracy may have varied among years given variation in the number of flights and the number and complement of surveyors.

Despite these sources of error, our data provide valuable information about the Kokanee–Grizzly Bear dynamics of a system for which there was no existing monitoring, and we made use of publicly available and community-sourced data, which increases efficiencies, democratizes science, and promotes valuable conservation and research outcomes (De Sherbinin *et al.* 2021).

Conclusions

Community science data provided considerable support that changes in Kokanee abundance and distribution was linked to changes in Grizzly Bear observations adjacent to an inland, salmon-bearing river in southeastern British Columbia. These findings are consistent with research from coastal ecosystems, but these principles had not previously been examined in a system with landlocked salmon. The dietary flexibility exhibited by Grizzly Bears may promote resilience as climate change and other factors alter seasonally available foods (e.g., Schwartz et al. 2013; Costello et al. 2014; Cristecu et al. 2015), and this flexibility may be especially valuable given widespread salmon declines (Gustafson et al. 2007; Irvine and Fukuwaka 2011). However, the amount of dietary salmon is functionally related to fitness (Mowat and Heard 2006) and, in coastal systems, bear-salmon interactions culminate in complex and beneficial ecosystem services (Levi et al. 2020). Declines in food sources may promote increased human-bear conflict; for example, in years of Whitebark Pine seed scarcity, Grizzly Bears in the Greater Yellowstone Ecosystem increased use of low-elevation habitat (Mattson et al. 1992), where risk of human-associated mortality increases (Schwartz et al. 2010b). It follows that declines in Kokanee abundance may limit bear fitness and provision of ecosystem services, and could increase human-bear conflict. Lastly, ecotourism businesses that centre operations around salmon-bearing streams (e.g., Rode et al. 2006) may encounter financial difficulties as salmon populations decline and bear distributions change, which could limit the conservation outcomes of wildlife viewing (e.g., Tisdell and Wilson 2001). We recommend future research on how salmon declines affect Grizzly Bear populations, especially as climate change progresses, as well as better understanding the role of Kokanee in the diets of Grizzly Bears.

Author Contributions

Writing – Original Draft: S.R.; Writing – Review & Editing: N.F. and S.R.; Conceptualization: J.S. and

S.R.; Investigation: S.R.; Methodology: S.R.; Formal Analysis: S.R.; Funding Acquisition: N.F. and S.R.

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Literature Cited

- Adkison, M.D., M.B. Ward, and T.P. Quinn. 2014. Nest site preference and intrasexual competition in female sockeye salmon, *Oncorhynchus nerka*. Environmental Biology of Fishes 97: 385–399. https://doi.org/10.1007/s 10641-013-0159-x
- Atlas, W.I., K.M. Seitz, J.W.N. Jorgenson, B. Millard-Martin, W.G. Housty, D. Ramos-Espinoza, N.J. Burnett, M. Reid, and J.W. Moore. 2021. Thermal sensitivity and flow-mediated migratory delays drive climate risk for coastal sockeye salmon. FACETS 6: 71–89. https://doi.org/10.1139/facets-2020-0027
- Bassett, M. 2019. Re: 2019 Lardeau River Kokanee enumeration. Ministry of Environment, Nelson, British Columbia, Canada. Accessed 8 May 2021. https://a100.gov. bc.ca/pub/acat/documents/r59001/LardeauRiverkoka nee2019_1606406953524_6404061406.pdf.
- Bassett, M.C., E.U. Schindler, R. Fox, D. Johner, T. Weir, L. Vidmanic, K.I. Ashley, and K. Peck. 2018. Kootenay Lake nutrient restoration program north arm and south arm 2016 report. Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Nelson, British Columbia, Canada. Accessed 27 May 2020. https://a100.gov.bc.ca/pub/acat/ documents/r54875/Kootenay_2016-FINAL-with RD_1547574424559_7572130131.pdf.
- Belant, J.L., K. Kielland, E.H. Follmann, and L.G. Adam. 2006. Interspecific resource partitioning in sympatric ursids. Ecological Applications 16: 2333–2343. https://doi.org/10.1890/1051-0761(2006)016[2333:irpis u]2.0.co;2
- 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. https://doi.org/10.1371/journal.p one.0080537
- Calsbeek, R., and B. Sinervo. 2002. An experimental test of the ideal despotic distribution. Journal of Animal

Ecology 71: 513–523. https://doi.org/10.1046/j.1365-26 56.2002.00619.x

- Charnov, E.L., and G.H. Orians. 1973. Optimal Foraging: Some Theoretical Explorations. University of Washington, Seattle, Washington, USA. Accessed 25 February 2023. https://digitalrepository.unm.edu/biol_fsp/45.
- Costello, C.M., F.R. van Manen, M.A. Haroldson, M.R. Ebinger, S.L. Cain, K.A. Gunther, and D.D. Njornlie. 2014. Influence of whitebark pine decline on fall habitat use and movements of grizzly bears in the Greater Yellowstone Ecosystem. Ecology and Evolution 4: 2004– 2018. https://doi.org/10.1002/ece3.1082
- Coxe, S., S.G. West, and L.S. Aiken. 2009. The analysis of count data: a gentle introduction to Poisson regression and its alternatives. Journal of Personality Assessment 91: 121–136. https://doi.org/10.1080/00223890802634175
- Cristecu, B., G.B. Stenhouse, and M.S. Boyce. 2015. Grizzly bear diet shifting on reclaimed mines. Global Ecological Conservation 4: 207–220. https://doi.org/10.1016/j. gecco.2015.06.007
- Crozier, L.G., B.J. Burke, B.E. Chasco, D.L. Widener, and R.W. Zabel. 2021. Climate change threatens Chinook salmon throughout their life cycle. Communications Biology 4: 222. https://doi.org/10.1038/s42003-021-01 734-w
- Cunningham, C.J., G.T. Ruggerone, and T.P. Quinn. 2013. Size selectivity of predation by brown bears depends on the density of their sockeye salmon prey. American Naturalist 181: 663–673. https://doi.org/10.10 86/670026
- Deacy, W., W. Leacock, J.B. Armstrong, and J.A. Stanford. 2016. Kodiak brown bears surf the salmon red wave: direct evidence from GPS collared individuals. Ecology 97: 1091–1098. https://doi.org/10.1890/15-10 60.1
- Deacy, W.W., W.B. Leacock, J.A. Stanford, and J.B. Armstrong. 2019. Variation in spawning phenology within salmon populations influences landscape-level patterns of brown bear activity. Ecosphere 10: e02575. https:// doi.org/10.1002/ecs2.2575
- De Sherbinin, A., A. Bowser, T. Chuang, C. Cooper, F. Danielsen, R. Edmunds, P. Elias, E. Faustman, C. Hultquist, R. Mondardini, I. Popescu, A. Shonowo, and K. Sivakumar. 2021. The critical importance of citizen science data. Frontiers in Climate 3: 650760. https:// doi.org/10.3389/fclim.2021.650760
- Edwards, M.A., A.E. Derocher, K.A. Hobson, M. Branigan, and J.A. Nagy. 2011. Fast carnivores and slow herbivores: differential foraging strategies among grizzly bears in the Canadian Arctic. Oecologia 165: 877–889. https://doi.org/10.1007/s00442-010-1869-9
- Environmental Reporting BC. 2020. Grizzly Bear population ranking in B.C. State of Environment Reporting, Ministry of Environment, Victoria, British Columbia, Canada. Accessed 8 May 2021. https://www.env.gov. bc.ca/soe/indicators/plants-and-animals/grizzly-bears. html#:~:text=Conservation%20Ranking%3A%20Of %20the%2055,49%20adults%2F1000%20km2.
- 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. https://doi.org/10.1644/13-mamm-a-161

- Falcy, M.R. 2015. Density-dependent habitat selection of spawning Chinook salmon: broad-scale evidence and implications. Journal of Animal Ecology 84: 545–553. https://doi.org/10.1111/1365-2656.12297
- Fortin, J.K., J.V. Ware, H.T. Jansen, C.C. Schwartz, and C.T. Robbins. 2013. Temporal niche switching by grizzly bears but not American black bears in Yellowstone National Park. Journal of Mammalogy 94: 833–844. https://doi.org/10.1644/12-mamm-a-238.1
- Gayton, D. 2002. Kokanee: the Redfish and the Kootenay Bioregion. New Star Books, Vancouver, British Columbia, Canada.
- Gende, S.M., and T.P. Quinn. 2004. The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. Canadian Journal of Zoology 82: 75–85. https://doi.org/ 10.1139/z03-226
- Gende, S.M., T.P. Quinn, and M.F. Willson. 2001. Consumption choice by bears feeding on salmon. Oecologia 127: 372–382. https://doi.org/10.1007/s004420000590
- Gibeau, M.L., A.P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. Biological Conservation 103: 227– 236. https://doi.org/10.1016/s0006-3207(01)00131-8
- Gustafson, R., R.S. Waples, J.M. Myers, J.J. Hard, G.J. Bryant, O.W. Johnson, and L.A. Weitkamp. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. Conservation Biology 21: 1009–1020. https:// doi.org/10.1111/j.1523-1739.2007.00693.x
- Hamer, D., and S. Herrero. 1987. Grizzly bear food and habitat in the front ranges of Banff National Park, Alberta. Bears: Their Biology and Management 7: 199– 213. https://doi.org/10.2307/3872626
- Hamilton, A., and F. Bunnell. 1987. Foraging strategies of coastal grizzly bears in the Kimsquit River Valley, British Columbia. Bears: Their Biology and Management 7: 187–197. https://doi.org/10.2307/3872625
- Herbison, B. 2008. An assessment of wildlife habitat and conservation priorities along the Lardeau River corridor. Fish and Wildlife Compensation (Columbia Basin), Nelson, British Columbia, Canada. Accessed 7 November 2018. http://a100.gov.bc.ca/appsdata/acat/documents/r23028/ Assessofhab_con_1304955525169_71c2d18b98b5569 b46e6df47cb4f12264069aa81a3a71b58b1dc4d805b11 cb75.pdf?fbclid=IwAR3qfm2vBMosHKtnePJkkQPQu5 rR2fmSQJm9zjg1dn2rS-i4inUVaO6A7ss.
- Hilderbrand, G.V., D.D. Gustine, B.A. Mangipane, K. Joly, W. Leacock, L.S. Mangipane, J. Erlenbach, M.S. Sorum, M.D. Cameron, J.L. Belant, and T. Cambier. 2018. Body size and lean mass of brown bears across and within four diverse ecosystems. Journal of Zoology 305: 53–62. https://doi.org/10.1111/jzo.12536
- 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 Zoo-

logy 77: 132-138. https://doi.org/10.1139/z98-195

- Irvine, J.R., and M. Fukuwaka. 2011. Pacific salmon abundance trends and climate change. ICES Journal of Marine Science 68: 1122–1130. https://doi.org/10.1093/ icesjms/fsq199
- Isaak, D.J., S. Wollrab, D. Horan, and G. Chandler. 2011. Climate change effects on stream and river temperatures across the northwest U.S. from 1980–2009 and implications for salmonid fishes. Climatic Change 113: 499– 524. https://doi.org/10.1007/s10584-011-0326-z
- Klinka, D.R., and T.E. Reimchen. 2002. Nocturnal and diurnal foraging behaviour of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia. Canadian Journal of Zoology 80: 1317–1322. https://doi.org/ 10.1139/z02-123
- Levi, T., G. Hilderbrand, M.D. Hocking, T.P. Quinn, K.S. White, M.S. Adams, J.B. Armstrong, A.P. Crupi, C.T. Darimont, W. Deacy, S.L. Gilbert, W.J. Ripple, Y.N. Shakeri, R.E. Wheat, and C.C. Wilmers. 2020. Community ecology and conservation of bear-salmon ecosystems. Frontiers in Ecology and Evolution 8: 513304. https://doi.org/10.3389/fevo.2020.513304
- Luque, M.H., and A.W. Stokes. 1976. Fishing behaviour of Alaska brown bear. Bears: Their Biology and Management 3: 71–78. https://doi.org/10.2307/3872756
- MacArthur, R.H., and E.R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100: 603– 609. https://doi.org/10.1086/282454
- MacHutchon, G.A., and D.W. Wellwood. 2003. Grizzly bear food habits in the Northern Yukon, Canada. Ursus 14: 225–235.
- Mangipane, L.S., D.J.R. Lafferty, K. Joly, M.S. Sorum, M.D. Cameron, J.L. Belant, G. Hilderbrand, and D.D. Gustine. 2020. Dietary plasticity and the importance of salmon to brown bear (*Ursus arctos*) body size and condition in a low Arctic ecosystem. Polar Biology 43: 825–833. https://doi.org/10.1007/s00300-020-02690-7
- Martins, E.G., S. Hinch, D.A. Patterson, M.J. Hague, S.J. Cooke, K.M. Miller, D. Robichaud, K.K. English, A.P. Farrell, and B. Jonsson. 2012. High river temperature reduces survival of sockeye salmon (*Oncorhynchus nerka*) approaching spawning grounds and exacerbates female mortality. Canadian Journal of Fisheries and Aquatic Sciences 69: 330–342. https://doi.org/10.1139/ f2011-154
- Mattson, D.J., B.M. Blanchard, and R.R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. Journal of Wildlife Management 56: 432–442. https://doi.org/10.2307/3808855
- Milakovic, B., K.L. Parker, D.D. Gustine, R.J. Lay, A.B.D. Walker, and M.P. Gillingham. 2012. Seasonal habitat use and selection by grizzly bears in Northern British Columbia. Journal of Wildlife Management 76: 170–180. https://doi.org/10.1002/jwmg.235
- Minore, D., and A.W. Smart. 1978. Frost tolerance in seedlings of Vaccinium-membranaceum, Vaccinium-globulare, and Vaccinium-deliciosum. Northwest Science 52: 179–185.
- Mowat, G., and D.C. Heard. 2006. Major components of grizzly bear diet across North America. Canadian Jour-

nal of Zoology 84: 473-489. https://doi.org/10.1139/z 06-016

- Nakagawa, S., P.C.D. Johnson, and H. Schielzeth. 2017. The coefficient of determination R² and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. Journal of the Royal Society Interface 14: 20170213. https://doi.org/10.1098/rsif. 2017.0213
- Neufeld, M. 2012. Re: 2012 Lardeau River Kokanee enumeration. Ministry of Forests, Lands and Natural Resource Operations, Nelson, British Columbia, Canada. Accessed 3 November 2018. http://a100.gov.bc.ca/apps data/acat/documents/r43583/LardeauRiverkokanee 2012_1409092446977_9086296733.pdf.
- Neufeld, M. 2014a. Re: 2013 Lardeau River Kokanee enumeration. Ministry of Forests, Lands and Natural Resource Operations, Nelson, British Columbia, Canada. Accessed 3 November 2018. http://a100.gov.bc.ca/apps data/acat/documents/r43584/LardeauRiverkokanee 2013_1409092915577_9086296733.pdf.
- Neufeld, M. 2014b. Re: 2014 Lardeau River Kokanee enumeration. Ministry of Forests, Lands and Natural Resource Operations, Nelson, British Columbia, Canada. Accessed 3 November 2018. http://a100.gov.bc.ca/ appsdata/acat/documents/r49875/LardeauRiverkoka nee2014_1455039411287_5038979637.pdf.
- Neufeld, M. 2016a. Re: 2015 Lardeau River Kokanee enumeration. Ministry of Forests, Lands and Natural Resource Operations, Nelson, British Columbia, Canada. Accessed 14 November 2019. http://a100.gov.bc.ca/apps data/acat/documents/r54970/LardeauRiverkokanee 2015_1541435759867_1434651399.pdf.
- Neufeld, M. 2016b. Re: 2016 Lardeau River Kokanee enumeration. Ministry of Forests, Lands and Natural Resource Operations, Nelson, British Columbia, Canada. Accessed 14 November 2019. http://a100.gov.bc.ca/apps data/acat/documents/r54971/LardeauRiverkokanee 2016_1541435736275_1434651399.pdf.
- Neufeld, M. 2017. Re: 2017 Lardeau River Kokanee enumeration. Ministry of Forests, Lands and Natural Resource Operations, Nelson, British Columbia, Canada. Accessed 3 November 2018. http://a100.gov.bc.ca/apps data/acat/documents/r54972/LardeauRiverkokanee 2017_1541435712406_1434651399.pdf.
- Neufeld, M. 2018. Re: 2018 Lardeau River Kokanee enumeration. Ministry of Forests, Lands and Natural Resource Operations, Nelson, British Columbia, Canada. Accessed 14 November 2019. http://a100.gov.bc.ca/apps data/acat/documents/r56450/LardeauRiverkokanee 2018_1554421746859_4421335626.pdf.
- Nevin, O.T., and B.K. Gilbert. 2005. Perceived risk, displacement and refuging in brown bears: positive impacts of ecotourism? Biological Conservation 121: 611–622. https://doi.org/10.1016/j.biocon.2004.06.011
- Olson, T.L. 1998. Brown bear diurnal activity and human use: a comparison of two salmon streams. Ursus 10: 547– 555.
- Ordiz, A., J. Kindberg, S. Sæbø, J.E. Swenson, and O.G. Støen. 2014. Brown bear circadian behavior reveals hu-

man environmental encroachment. Biological Conservation 173: 1–9. https://doi.org/10.1016/j.biocon.2014.03. 006

- Ordiz, A., O.G. Støen, M. Delibes, and J.E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia 166: 59–67. https://doi.org/10.1007/s00442-011-1920-5
- Quinn, T.P., C.J. Cunningham, and A.J. Wirsing. 2016. Diverse foraging opportunities drive the functional response of local and landscape-scale bear predation on Pacific salmon. Oecologia 183: 415–429. https://doi. org/10.1007/s00442-016-3782-3
- Quinn, T.P., S.M. Gende, G.T. Ruggerone, and D.E. Rogers. 2003. Density-dependent predation by brown bears (*Ursus arctos*) on sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 60: 553–562. https://doi.org/10.1139/f03-045
- Redfish Consulting Ltd. 2016. Kootenay Lake action plan. KL AP2016. Ministry of Forests, Lands and Natural Resource Operations, Cranbrook, British Columbia, Canada. Accessed 3 November 2018. http://www.env.gov. bc.ca/kootenay/fsh/main/pdf/KLAP%20Kootenay%20 Lake%20Action%20PLan%20final%209_May_2016. pdf.
- Rode, K.D., S.D. Farley, and C.T. Robbins. 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. Biological Conservation 133: 70–80. https://doi.org/10.1016/j. biocon.2006.05.021
- Rode, K.D., and C.T. Robbins. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology 78: 1640–1645. https://doi.org/10.1139/z00-082
- Schoen, E.R., M.S. Wipfli, E.J. Trammell, D.J. Rinella, A.L. Floyd, J. Grunblatt, M.D. McCarthy, B.E. Meyer, J.M. Morton, J.E. Powell, A. Prakash, M.N. Reimer, S.L. Stuefer, H. Toniolo, B.M. Wells, and F.D.W. Witmer. 2017. Future of Pacific salmon in the face of environmental change: lessons from one of the world's remaining productive salmon regions. Fisheries 42: 538–553. https://doi.org/10.1080/03632415.2017.13 74251
- Schwartz, C.C., S.L. Cain, S. Podruzny, S. Cherry, and L. Frattatoli. 2010a. Contrasting activity patterns of sympatric and allopatric black and grizzly bears. Journal of Wildlife Management 74: 1628–1638. https://doi. org/10.2193/2009-571
- Schwartz, C.C., J.K. Fortin, J.E. Teisberg, M.A. Haroldson, C. Servheen, C.T. Robbins, and F.T. van Manen. 2013. Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. Journal of Wildlife Management 78: 68–78. https://doi. org/10.1002/jwmg.633
- Schwartz, C.C., M.A. Haroldson, and G.C. White. 2010b. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. Journal of Wildlife Management 74: 654–667. https://doi.org/10.2193/2009-206
- Slaney, P.A., and H. Andusak. 2003. Fish habitat assessments of the Lardeau River (2002) integrated with habitat assessments of the Duncan River. Ministry of Water, Land and Air Protection, Nelson, British Columbia, Canada. Accessed 1 May 2022. https://a100.gov.bc.ca/pub/

acat/documents/r132/Lardeau-DuncanRiversHabitatAss esments2002_1057705108043_38fa5a8e91514cf883d6 91483c259894.pdf.

- Sorum, M.S., K. Joly, and M.D. Cameron. 2019. Use of salmon (*Oncorhynchus* spp.) by Brown Bears (*Ursus* arctos) in an Arctic, interior, montane environment. Canadian Field-Naturalist 133: 151–155. https://doi.org/10. 22621/cfn.v133i2.2114
- Tillotson, M.D., and T.P. Quinn. 2017. Climate and conspecific density triggers pre-spawning mortality in sockeye salmon (*Oncorhynchus nerka*). Fisheries Research 188: 138–148. https://doi.org/10.1016/j.fishres.2016.12.013
- **Tisdell, C., and C. Wilson.** 2001. Wildlife-based tourism and increased support for nature conservation financially and otherwise: evidence from sea turtle ecotourism at

Mon Repos. Tourism Economics 7: 233–249. https://doi. org/10.5367/00000001101297847

- Ward, E.J., J.H. Anderson, T.J. Beechie, G.R. Pess, and M.J. Ford. 2015. Increasing hydrologic variability threatens depleted anadromous fish populations. Global Change Biology 21: 2500–2509. https://doi.org/10.1111/gcb.12 847
- Welch, C.A., J. Keay, K.C. Kendall, and C.T. Robbins. 1997. Constraints on frugivory by bears. Ecology 78: 1105–1119. https://doi.org/10.1890/0012-9658(1997)07 8[1105:cofbb]2.0.co;2

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SUPPLEMENTARY MATERIALS:

TABLE S1. Spawning Kokanee (*Oncorhynchus nerka*) abundance observed by British Columbia provincial government personnel in the Lardeau River, British Columbia, 2012–2019.

TABLE S2. Number of Grizzly Bear (*Ursus arctos*) observations adjacent to four river reaches, effort spent searching for bears, and observations/day of effort at the Lardeau River, British Columbia, 2012–2019.