Cultural and ecological relationships among consumers, food, and landscapes; implications for stewarding bear-human-salmon systems

by

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B.Sc. (Honours), University of Victoria, 2010

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Abstract

Human activity modifies the behaviour of large vertebrates and their acquisition of key resources. Despite the predation risk and competition for similar food resources that humans impose, wildlife consumers must acquire key foods across the landscape. Predation risk can modify foraging behaviour, yet we know little about the potential consequences, especially on large spatial scales. Humans may also affect food availability for wildlife by competing for shared prey, which most current harvest prescriptions fail to recognize. Against this background of threats to consumer-resource interactions, my research employed new conceptual, analytical, and practical approaches to seek not only new generalizable insight but also applied solutions.

Addressing these goals, I characterized foraging behaviour by grizzly bears (*Ursus arctos horribilis*) on a focal prey, Pacific salmon (*Oncorhynchus* spp.), at multiple spatial scales. I predicted how human activity – both as modifications to landscapes and as salmon harvest – might affect bear-salmon interactions. I co-conceived, designed, and carried out this work through a framework of community engagement, which I crafted in collaboration with Indigenous communities in coastal British Columbia (BC). The framework (Chapter 2) identifies how scientists and communities can engage throughout the research process to work towards shared priorities, despite potential challenges in differences of knowledge systems or capacities. Methodologically, I used ratios of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in bear hair to estimate relative contributions of salmon in the annual diet of bears and employed existing data on landscape modification and salmon fisheries (*i.e.,* escapement and catch) to characterize human activity and to measure associated variation in salmon consumption by bears.

My first empirical contribution (Chapter 3) characterized spatial patterns of annual salmon consumption by grizzly bears across BC. I found substantial differences in salmon consumption within and among grizzly and black (*U. americanus*) bears in a large coastal region and across BC. Visualizing variation in consumer-resource interactions could guide conservation and management efforts that seek to protect predator-prey associations and marine subsidies for terrestrial ecosystems.

I also investigated potential drivers of salmon consumption by bears in interior and coastal watersheds that varied in disturbance (Chapter 4). I found that human footprint in riparian areas of salmon-bearing watersheds affected bear diets more than the amount of salmon biomass available, showing that human activity can disrupt an otherwise strong predator-prey association.

My community-based research occurred at the scale of a single large watershed, where I demonstrated how the Wuikinuxv First Nation might design their salmon management prescriptions according to their cultural values (Chapter 5). Despite a reduced abundance of salmon in the area, I identified harvest options that would trade-off benefits to local people and bears equally.

In general, my dissertation research contributes to our understanding of the role humans increasingly play in mediating consumer-resource interactions. I also highlight how scientific research can support the leadership that local management can provide in mitigating human impacts to sustain an iconic predator-prey interaction of ecological, economic, and cultural importance.

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Co-Authorship Statement

Chapters 2 through 5 of this dissertation were co-authored. The following outlines my contributions, and that of each of the authors. I also provide the publication status of each chapter.

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Adams, M., Service, C.N., Walkus, J., Carpenter, J., Housty, J.A., Neasloss, D., Paquet, P.C., Darimont, C.T., 2015. De-centering the university from community-based research: a framework for engagement between academic and indigenous collaborators in natural resource and conservation research. Pages 7–17 *in*: Gros-Louis McHugh, N., Gentelet, K., Basile, S. (Eds.), Toolbox on the Research Principles in an Aboriginal Context: Ethics, Respect, Equity, Reciprocity, Collaboration and Culture. First Nations of Québec and Labrador Health and Social Services Commission, Centre de recherche en droit public, Université du Québec in Abitibi-Témiscamingue, QC.

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Chapter 1. Introduction

1.1. Ecological framework: consumer-resource interactions in a human-dominated world

Around the world, human activity is increasingly modifying behavioural patterns of large vertebrates. The cumulative impacts of persecution and harvest (Ripple et al. 2014, Darimont et al. 2015) combined with habitat fragmentation and loss (Fahrig 2003, Fischer and Lindenmayer 2007, Barnosky et al. 2012) have resulted in changes to wildlife behaviour (*e.g.,* altered spatial and temporal movement patterns, Tucker et al. 2018, Gaynor et al. 2018; range contraction, Laliberte and Ripple 2004, Crooks et al. 2017) and the availability of their prey (Lacy et al. 2017, Grémillet et al. 2018) across the planet. How individuals navigate the risks of increasingly fragmented or disturbed habitat (Fischer and Lindenmayer 2007) to aggregations of rewarding foods can affect body condition and fitness (Bourbonnais et al. 2013, Lamb et al. 2017, Blecha et al. 2018), scaling up to affect the productivity and persistence of wildlife populations (Estes et al. 2003, Bolnick et al. 2011, Tuomainen and Candolin 2011).

Foraging behaviours are a perceptible expression of a consumer's ecology, representing the acquisition of resources necessary to sustain survival, permit growth, and support reproduction. Foraging decisions by consumers represent a mosaic of costs and benefits accrued while pursuing and handling prey (Stephens and Krebs 1986, Stephens et al. 2007). Consumers exploit variation in ephemeral resources over space and time by tracking prey patches to optimize foraging success and maximize energy gain (Fauchald 1999, Roshier et al. 2008, Furey et al. 2018). The decision to move among prey patches or disperse greater distances in search of food resources can influence numerical population dynamics via immigration and emigration rates (Apte et al. 2000, Vasudev et al. 2015). Habitat selection by a given generation is therefore influenced by the choices of previous generations (McLoughlin et al. 2008, Slagsvold et al. 2013). Taken across individuals, the outcomes of foraging behaviours cumulate to "bottom-up" influences of population size and structure (Holt and Kimbrell 2007, Sih et al. 2012).

Foraging decisions require navigating tensions between rewards and risks on the landscape. Primary among them includes selecting where, when, and on which resources to forage while reducing exposure to predation (Lima and Dill 1990, Godin 1990). This selection occurs at multiple spatial scales, from the distributional range, a home range, patches within a home range, to specific sites or prey items within a patch (Gaillard et al. 2010). The predation risk hypothesis (Lima and Bednekoff 1999) predicts that if external risks are short or infrequent, an individual is more likely to exhibit antipredator behaviour. For example, given infrequent risks, an animal might change the length or location of foraging within a patch, or modify their home range selection (*e.g.*, McLoughlin et al. 2005, Hebblewhite and Merrill 2007). If the duration or frequency of risks increases, the predation risk hypothesis predicts that individuals will engage in risky behaviour, such as foraging near high densities of people in residential areas (*e.g.*, Blecha et al. 2018). Often referred to as the 'landscape of fear' (defined as the spatial variation in the perception of risk by prey; Searle et al. 2008, Laundré et al. 2010), predation risk is a primary structuring element of foraging decisions made by consumers (Gaynor et al. 2019). The disturbance caused by human infrastructure or access on the landscape is an increasingly common form of predation risk for wildlife (Frid and Dill 2002, Wilmers et al. 2013). Although it is clear human-caused predation risk can modify wildlife behaviour (Crooks et al. 2017, Tucker et al. 2018, Gaynor et al. 2018), little is known about its consequences for foraging or subsequent ecological implications, especially over large spatial or temporal scales.

Exploitative competition, whereby the acquisition of food by one individual concurrently deprives others of that same resource, also influences foraging behaviour. Foraging success can be negatively influenced by competition with other inter- and intraspecific consumers (MacArthur and Levins 1967, Case and Gilpin 1974). Competition is intensified through reduced resource availability (Amarasekare 2003). This is especially the case if humans harvest prey species in common with predators. Our technology allows us to travel to and exploit prey at rates that can be orders of magnitude greater than natural predators in both marine and terrestrial environments (Worm et al. 2009, Darimont et al. 2015). For example, fishery catch on potential seabird prey has constrained seabird foraging and subsequent population persistence since the rise of industrial fisheries (circa 1970; Grémillet et al. 2018). Our ability to exploit prey of specific age classes and body sizes has also resulted in changes in prey availability (*e.g.*, Bigler et al. 1996) and shifts in species abundance at different trophic levels as we exploit our way through food webs. A seminal example of this is "fishing down the food chain" in marine systems, where human harvest efforts transition from long-lived, high trophic level catch to short-lived and lower trophic level catch (Pauly et al. 1998, but see Branch et al.

2010 on the potential downfalls of using mean-trophic-level as an adequate biodiversity indicator). Most harvest prescriptions fail to recognize how such impacts might affect also ecological consumers.

The impact of resource use by humans in relation to co-occurring wildlife can vary. The majority of human-wildlife interaction in ecological research focuses on competition with animals for resources (*e.g.*, Happold 1995, Decker and Chase 1997, Grémillet et al. 2018), human predation on animals (*e.g.*, harvest or hunting; Darimont et al. 2009, 2015), human-wildlife conflict (*e.g.*, Valeix et al. 2012, Artelle et al. 2016), or predation risk imposed from human activity (Ordiz et al. 2017b). However, other paradigms occur whereby humans and animals use resources in common and co-occur/coexist (Madden 2004, Peterson et al. 2010). More generalized understanding might emerge from examining how threats to habitat and food security interact in a human-dominated world where spaces for wildlife are becoming riskier and access to foods less reliable. Estimating how human activity alters foraging behaviour over space and time could help in understanding how wildlife might trade off risk and reward and guide mitigation efforts via conservation and management.

1.2. Governing natural resources

Effective governance structures and management approaches are needed to minimize the impact of human activity on foraging behaviour and other ecological process. The sustained availability of natural resources has implications for the well-being and livelihood of people and ecosystems alike. However, governing natural resources use by people can be challenging, especially over large spatial scales. The decline or collapse of natural resources generally occurs where user groups are diverse (*e.g.*, local/subsistence vs. commercial) and disconnected (*e.g.*, do not feel accountable to one another or to ecosystems; Berkes et al. 2006). These conditions are increasingly common under centralized, top-down management approaches (*e.g.*, federal agencies; Holling and Meffe 1996, Ostrom 2009). Given the spatial breadth and ecological complexity of natural resources under their jurisdiction, centralized agencies may be challenged over time to manage natural resources sustainably (Dietz et al. 2003, Berkes et al. 2006). The cost of monitoring and sanctioning resource use can be high. In addition, the consequences of policy changes may be slow to materialize, often before large agencies have time to react and prevent resource collapse (*e.g.*, the collapse of the Atlantic cod (*Gadus morhua*) fishery; Hutchings and Myers 1994). These management challenges can have widespread ecological and socio-economic consequences.

The efficacy of natural resource management for human and wildlife alike can be improved through more comprehensive, ecosystem-based approaches. Ecosystem-based approaches to management seek to sustain healthy ecosystems and resource use by balancing costs and benefits for ecological, economic, and social well-being (Pikitch et al. 2004). This generally involves using indicators of ecosystem status (*e.g.,* monitoring of a focal species) and accounting for the ecological requirements of other species proximal to human resource use (*e.g.,* habitat considerations, non-target and protected species, trophic interactions) (Botsford et al. 1997, Zabel et al. 2003, Long et al. 2015). Many governments and agencies are investing in the development of ecosystem-based approaches, especially in fisheries (*e.g.*, Fisheries Ecosystem Plans in U.S. fisheries management) (Levin et al. 2018). While ecosystem-based management strategies may help address ecological complexities in natural resource use, implementation and enforcement may still be challenging due to lack of engagement of or buy-in from local socio-economic and cultural user groups (Dietz et al. 2003, Loring 2013, Bennett 2018).

Self-organized local governance reflects the general premise of ecosystem-based management applied at small spatial scales. Local people are generally well-positioned to regulate resource use because they hold local knowledge, are socially accountable to other users, and can observe the ecological impacts of their harvest, such that they can adjust their harvest effort accordingly (Armitage 2005). We note that local people may be spatially disconnected from distant or dispersed processes that affect the abundance or health of a resource (*e.g.*, climate or disease that affects the productivity of a migratory species in a prior region). However, small-scale harvesters are also well-positioned to enforce localized governance strategies (*e.g.,* higher levels of local timber harvest enforcement are associated with a greater probability of forest regeneration; Chhatre and Agrawal 2008). Therefore, localized natural resource management can address both environmental and socioeconomic goals while balancing exploitation and conservation (Cox et al. 2015). Centralized agencies can support the inclusion of such self-organized groups in developing and implementing resource management strategies in their region and can connect networks of neighbouring local user groups in management strategies across broader spatial scales (Dietz et al. 2003, Ostrom 2009). This approach requires some transfer of decision-making power and authority over natural resource management to communities (Armitage et al. 2010). Redundancy in governance agencies in management, also known as 'polycentric governance', might address the challenges of governing natural resource use and the implementation of ecosystem-based management better than that of a centralized governance approach (Ostrom 2009, Cox et al. 2015).

The potential for polycentric governance approaches to ecosystem-based management are growing in (what is now known as) Canada. Indigenous people in Canada have rights and authority to access resources (*R. v. Sparrow* 1990). The authority of Indigenous Nations to govern their territories is becoming increasingly recognized by Canadian federal and provincial governments, who are engaging with Nations in resource management and beyond (*e.g.*, in British Columbia: Housty et al. 2014, Coastal First Nations and Province of British Columbia 2016, Ban and Frid 2018). It is important to note that although colonial Canadian legal traditions have recently recognized Indigenous rights and title, from the perspective of many Indigenous Nations, authority to govern their territories was never relinquished. Canadian governments consider federal and provincial/territorial agencies responsible for fisheries and wildlife management, respectively, but they are increasingly overextended (Price et al. 2008, 2017, Hoberg and Malkinson 2013) or challenged to manage harvest or habitat quality sustainably (Wittmer et al. 2007, Moore et al. 2015). In addition, although marine and terrestrial ecosystems across the Pacific Northwest are linked through many ecological, cultural, and socioeconomic systems, they are currently separated by jurisdictional management boundaries (Darimont et al. 2010, Artelle et al. 2016, Adams et al. 2017). Emerging ecosystem-based management approaches could address these challenges. Many principles of ecosystem-based management also reflect the values and principles of many Indigenous resource management systems, including socio-ecological connectivity, intergenerational equity, and reciprocity for the non-human world (Turner and Berkes 2006, Turner 2014, Artelle et al. 2018). As Indigenous governments regain decision-making authority in the governance of their territories in Canada, there is new potential for powerful synergies between local decision-making and ecosystem-based management.

This political context presents ecological scientists in Canada with a unique opportunity to provide tools and information to Indigenous decision-makers in localized natural resource management. In doing so, it is critical that scientists consider how their research process could match priorities, principles, or capacities of Indigenous governments – from the conception of research hypotheses and design of monitoring methodologies, to the inclusion of local ecological knowledge, to the dissemination and application of research findings (Chapter 2). Such engagement would allow for community-driven research that could be acutely applied to local management that could minimize the impact of human activity on foraging behaviour and other ecological process (Chapter 5, Ban and Frid 2018, Salomon et al. 2018, Ban et al. 2018).

1.3. Socio-ecological lens: bear-salmon-human systems

The encroachment of human footprint and its effects on wildlife behaviour is of particular conservation concern where areas of intact habitat still support populations of large predators and their prey (Laliberte and Ripple 2004). As a wide-ranging omnivore of ecological, socioeconomic, and cultural concern that is sensitive to human activities, the grizzly bear (*Ursus arctos horribilis*, also referred to as the 'brown bear') is an excellent model species to examine the potential effect of human activity on consumer-resource interactions (Nielsen et al. 2017, Shackelford et al. 2018).

In this dissertation, I characterize foraging behaviour by grizzly bears at various spatial scales throughout their distribution in British Columbia (BC), Canada, using a community-engaged approach with local Indigenous leaders and managers. I examine how human activity – both as human footprint on the landscape and as harvesters of a common prey – affects foraging behaviour by bears and subsequent implications for ecological and social outcomes of what our research group refers to as '*bear-salmon-human systems*'. We use this term to highlight the common use of resources, such as habitat or foods, among bears and people across ecosystems (Turner 2014).

Bears require many of the same landscapes and food resources people use, but are sensitive to human activity. Like many mammalian carnivores, bears have relatively low population densities and fecundity rates (Hatler et al. 2008), making their populations vulnerable to fragmentation across their large home ranges (Carroll et al. 2001, Crooks 2002). Bears make foraging decisions based on nutritional requirements and food quality and availability (Robbins et al. 2007, Erlenbach et al. 2014) while balancing the risk of encounters with other competitors (Ben-David et al. 2004) or increasingly, humans (Artelle et al. 2016). Grizzly bears require large home ranges to meet their nutritional requirements while contending with intraspecific competition (home ranges for males range from 130 km^2 to 916 km^2, for females from 52 km^2 to 384 km^2; Appendix C, Hatler et al. 2008). Grizzly bear habitat selection is strongly affected by human infrastructure or access as a function of road networks, proximity to human settlements, and human population density (Apps et al. 2004, Stewart et al. 2012). At finer temporal and spatial scales, bears adjust their daily movement and foraging behaviour in response to human activity (Ordiz et al. 2014, Lodberg-Holm et al. 2018), avoiding areas associated with high risk of human-induced mortality from conflict, hunting, or transportation strikes (Nielsen et al. 2004b, Boulanger and Stenhouse 2014, McLellan et al. 2018). As such, remaining North American grizzly bear distribution following European colonization is negatively correlated to cumulative impacts of human activity (Shackelford et al. 2018), where grizzly bears have been extirpated from areas of high human disturbance (Proctor et al. 2012).

Access to ample and nutritious sources of prey is critical to grizzly bear survival, reproduction, and dispersal. Bears rely on fat- and protein-rich food sources annually to accumulate body mass during hyperphagia prior to winter sleep (Robbins et al. 2004, 2007, McDonough and Christ 2012). Where bear and salmon distributions overlap, salmon (*Oncorhynchus* spp.) are among the most important prey for bears because of their high fat and protein content (Hilderbrand et al. 1999a, Gende et al. 2001). Access to salmon supports greater body masses, body condition, litter sizes (Kovach and Powell 2003, Zedrosser et al. 2007, Bryan et al. 2013) and higher population densities in grizzly bears (Hilderbrand et al. 1999a). Unlike the availability of other important foods for bears, such as emergent vegetation, fruit, roots, nuts, insects, or mammals, salmon availability is constrained temporally and spatially by when and where fish return annually to spawn (Quinn 2005). Salmon abundance fluctuates dramatically over years due to natural cycling, flow regimes, and fishing pressure (Groot and Margolis 1991). Social dominance among bears structures foraging success for salmon, especially in years with low salmon abundance when dominant male bears displace subdominant males and females, particularly those with cubs (Gende and Quinn 2004, Ben-David et al. 2004). Bears and other consumers track salmon availability across the landscape, monitoring when and where different runs return to watersheds (Schindler et al. 2013, Levi et al. 2015). These foraging opportunities are extended and stabilized by the diversity of salmon species, habitats, and spawning phenologies (Schindler et al. 2010, Service et al. 2018, Deacy et al. 2019).

Eating salmon has implications for bear populations densities and the ecosystems they subsidize. Bears are critical transporters of marine nutrients via faeces, urine, and salmon carcasses deposited into terrestrial ecosystems (Quinn et al. 2009, Van Daele et al. 2013). This process inadvertently subsidizing plant and animal communities (Reimchen 2000, Hocking and Reynolds 2011, Quinn et al. 2018), and ultimately freshwater biota that feed juvenile salmon (Schindler et al. 2003). Salmon-supported bear populations are then fueled to perform other activities in terrestrial ecosystem at greater rates, such seed dispersal or root propagation via disturbance from digging (Turner 2014, Harrer and Levi 2018, Shakeri et al. 2018).

Human activity can disrupt bear-salmon interactions through landscape alteration in salmon-bearing watersheds, and with it, the subsequent ecosystem interactions of the bear-salmon association. Along valley-bottom routes where bears congregate to forage on salmon, humans often have permanent and significant access and infrastructure, such as roadways, resource extraction development, settlements, or agriculture (Waples et al. 2009), which are associated with increased human-caused mortalities in bears (McLellan and Shackleton 1988, Nielsen et al. 2004a, Boulanger and Stenhouse 2014). Predation risk imposed by human activity in salmon-bearing watersheds could make foraging patches (*i.e.,* riverbanks for predation and consumption) or the corridors connecting foraging patches (*i.e.,* riparian areas and surrounding valley sides) riskier and/or less permeable to bear movement or foraging.

People also compete with bears for salmon as a resource. Salmon are a disproportionately important socioeconomic and cultural species for many peoples of the Pacific Northwest (Quinn 2005). Commercial fisheries intercept salmon in marine environments before they can reach terrestrial consumers, such as bears (Levi et al. 2012). Where salmon populations are in decline (*e.g.,* many populations in British Columbia, Holt 2010, Collie et al. 2012, Peterman and Dorner 2012, Price et al. 2017), commercial harvest may affect abundance or biomass of salmon available for bears and other consumers (Bigler et al. 1996, Levi et al. 2012, Lacy et al. 2017). Conversely, Indigenous peoples of the Pacific Northwest from California to Alaska have harvested salmon for food, social, and ceremonial purposes in local, small-scale terminal fisheries for millennia (Garibaldi and Turner 2004, Campbell and Butler 2010), where the biomass of their catch remains in the system and the scale of harvest likely does not affect long-term salmon availability for bears and other wildlife (Gresh et al. 2000, Housty et al. 2014).

1.4. Research Objectives

Wildlife are motivated to seek critical food resources they require across the landscape in spite of predation risk or competition that other consumers, and increasingly humans, can impose. Access to salmon, a spatially and temporally constrained food source, is integral to persistence of coastal bear populations. This fact is well-recognized by Indigenous communities now increasingly charged with their stewardship in an era of cumulative anthropogenic and environmental pressures.

As the recognition of Indigenous governance authority grows in Canada, scientists have the opportunity to contribute methodologies and knowledge towards applied research questions and informed decision-making for environmental management. The conceptual contributions of my dissertation are centered on investigating spatial patterns of salmon consumption by bears and how human activity affects this consumer-resource interaction. Specifically, I focus on characterizing bear-salmon interactions at multiple spatial scales and predicting how human footprint on the landscape and salmon harvest might affect bear-salmon interactions. I do this work through a framework of community engagement, crafted with input from applied scholars and leaders within Indigenous governments in coastal British Columbia.

1.4.1. General Methods

I used data from two spatial scales in this dissertation. First, data for coastal bear populations were collected between 2010 and 2018 in the territories of the Wuikinuxv, Haíɫzaqv (Heiltsuk), Nuxalk, Kitasoo/Xai'xais, and Gitga'at First Nations as part of a collaborative grizzly and black bear monitoring program throughout the central coast of BC, Canada. Broadly, this collaboration focuses on the ecology and stewardship of coastal bear grizzly and black bear (*U. americanus*) populations, with opportunities for applied conservation and management through the policies and programs of the five Indigenous governments involved (Bryan et al. 2013, 2014, Service et al. 2014, 2018, Adams et al. 2017). I contributed to this project by working with staff from the Wuikinuxv Nation Integrated Stewardship Department to manage their node of this collaborative research effort. Second, data for bear populations across British Columbia were collected between 1994 and 2003 from multiple research projects and compulsory inspections of hunted grizzly bears. These data first appeared in Mowat and Heard (2006). I augmented these data with the coastal dataset in Chapters 3 and 4.

My research process was built upon principles of community engagement, whereby communities participated in designing the scope of the research questions, implementing the data collection, and communicating and applying the findings of the research (see below; Chapter 2). As trust was built through this process, my research questions throughout the dissertation adapted to additional research and management priorities identified by collaborators in local Indigenous governments (see below; Chapter 5).

Congruent with Indigenous law of the collaborating Nations, my field research methods were non-invasive. I identified individual bears by species and sex using genetic approaches from hair samples collected from non-reward hair snag stations distributed roughly every 25 km^2 throughout the territories of collaborating Nations (over 22,000 km^2) (Woods et al. 1999, Shardlow and Hyatt 2013). I used stable carbon and nitrogen ratios from hair samples (reported as $\delta^{13}C$ and $\delta^{15}N$) to estimate annual contributions of salmon and other foods to individual diets with Bayesian mixing models (Darimont et al. 2009b, Semmens et al. 2009, Ben-David and Flaherty 2012, Stock and Semmens 2013). I use these estimated contributions as proxies for foraging behaviour in Chapters 3, 4, and 5 (hereafter 'salmon consumption').

I represented human activity in this dissertation with two approaches. In Chapter 4, I used data presented by Venter et al. (2016a, 2016b) that summarize human infrastructure and access on Earth since 1993 (Sanderson et al. 2002) to characterize potential impacts of human activity in bear-salmon-human systems. In Chapter 5, I account for human harvest of salmon using catch records and estimates of current and future harvest goals at the scale of a single fishery for which I also have data on salmon consumption by bears.

1.4.2. Scope of research

Chapter 2: Towards increased engagement between academic and Indigenous community partners in ecological research (Adams et al. 2014 *Ecology and Society*)

Ecological research, especially related to conservation and resource management, increasingly involves social dimensions. Concurrently, social systems, composed of human communities that have direct cultural connections to local ecology and place, may draw upon environmental research as a component of knowledge (Berkes 2004, Ostrom 2009). As decision-making agency is (re)shifted increasingly to Indigenous governments in Canada, abundant opportunities exist for applied ecological research at the community level. Despite this opportunity, however, current approaches by scholars to community-engaged ecological research often lack a coherent framework that fosters a respectful relationship between research teams and communities (Schnarch 2004, Armitage 2005, Gearhead and Shirely 2007). In Chapter 2, I reflected on the process of academic–community engagement with input from applied scholars and leaders from the Haíłzaqv, Kitasoo/Xai'xais, and Wuikinuxv Nations and emerged with a generalizable framework to guide the research presented in this dissertation and beyond (Adams et al. 2014). At its core, our engaged research process is built upon a consideration of how research questions are framed, the consequences of research outcomes at local scales, and respect for place.

Chapter 3: Intrapopulation diversity in isotopic niche over landscapes: spatial patterns inform conservation of bear–salmon systems (Adams et al. 2017 *Ecosphere*)

Characterizing variation in foraging over time and across space can offer insight into patterns of consumer-resource interactions and associated ecological processes, with important implications for conservation planning. In Chapter 3, I used kernel-weighted regression to examine spatial patterns in salmon consumption between grizzly and black bears at a coastal scale, and among grizzly bears across British Columbia. To assess the efficacy of current protected area designation accounting for this ecological interaction, I compared spatial patterns of salmon consumption inside and outside protected areas for coastal bear populations, and across British Columbia by comparing salmon consumption in the 'Great Bear Rainforest' conservation area to salmon consumption in a provincially-designated coastal eco-region (Adams et al. 2017). This work supports previous findings that male bears consume more than females and grizzly bears outcompete black bears (Ben-David et al. 2004, Service et al. 2018). These results demonstrate that salmon consumption by female grizzly bears was concentrated in coastal regions, while males had relatively high amounts of salmon in their diet in watersheds hundreds of kilometres from the marine-terrestrial interface. The resulting analysis also provided a level of spatial detail to examine the siting of protected areas in novel ways. Salmon are managed as a marine resource, yet their influence on terrestrial ecosystems is far-reaching and must be accounted for across jurisdictional boundaries in management and development. Broadly, this work highlights the importance of considering the spatial connectivity of marine-terrestrial interactions, especially for grizzly bears, in ecosystem-based management.

Chapter 4: Human footprint in salmon-bearing watersheds unravels predator-prey interactions between grizzly bears and salmon

Risk associated with human activity influences movement and behaviour of many species (*e.g.*, Tucker et al. 2018, Gaynor et al. 2018), but little is known about the impact of perceived risk of human activity on the use of key food resources by consumers. In Chapter 4, I used the focal lens of the bear-salmon consumer-resource interaction to examine how the consumption of salmon by grizzly bears corresponded to variation in salmon abundance, proxies for alternative food abundance, and human footprint in 22 salmon-bearing watersheds across 88,000 km^2 in British Columbia. Accounting for supply of salmon and other foods, I detected a strong negative effect of human footprint on annual salmon consumption. These results demonstrate that human footprint can disrupt an otherwise strong predator-prey association, highlighting the potential impacts of human land uses and activities to interrupt consumer-resource interactions, in addition to the well-known effects of disturbance, alienation, and increased mortality for wildlife.

Chapter 5: Culturally-guided ecosystem-based fisheries management: local values and data empower reciprocity in the management of the Wuikinuxv (Rivers Inlet) bear-salmon-human system

Humans can alter resource availability for wildlife through competition for valuable foods. In many commercial fisheries, including salmon, contemporary management systems do not account for how this competition might affect non-human ecological consumers, such as bears (Levi et al. 2012, Lacy et al. 2017). Ecosystem-based fisheries management (EBFM) is an emerging management paradigm that recognizes fisheries as systems with interacting biophysical and human components (Pikitch et al. 2004, Marshall et al. 2017). However, EBFM can be limited in scope or in practice by the exclusion of local peoples (Cox et al. 2015, Bennett 2018). In Chapter 5, I used grizzly bears to assess harvest-ecosystem trade-offs for a sockeye salmon (*O. nerka*) fishery in the bear-salmon-human system of Wuikinuxv Lake, Rivers Inlet, BC through an EBFM framework. Local people here have coexisted with bears in their common use of salmon for millennia. I incorporate Wuikinuxv Nation values of *Na na kila* – to look ahead for someone, to watch out for – to interrogate how current and future sockeye salmon harvest in Wuikinuxv territory affects predicted densities of local bear populations under various scenarios of sockeye stock dynamics. I emerge with EBFM escapement goals, defined where trade-offs between fishers and bear densities are equal, that can guide future harvest by the Nation in the territory while balancing continued salmon abundance for bears.

Chapter 6: Conclusion

Finally, I present concluding remarks and a summary of my contributions to the understanding of consumer-resource interactions in an increasingly human-dominated world. I highlight the key findings of my dissertation and opportunities for future research. I discuss how human activity may continue to modify consumer-resource interactions in the future, and how locally-driven ecosystem-based management could mitigate these impacts. Finally, I discuss the opportunities and challenges of doing ecological research through a community-engaged framework to contribute relevant information for decision-makers in natural resource management.

Chapter 2. Towards increased engagement between academic and Indigenous community partners in ecological research

Adapted from: Adams, M., Carpenter, J., Housty, J., Neasloss, D., Paquet, P., Service, C., Walkus, J., and Darimont, C. 2014. Towards increased engagement between academic and indigenous community partners in ecological research. Ecology and Society 9(3): 5.

2.1. Chapter Summary

Ecological research, especially work related to conservation and resource management, increasingly involves social dimensions. Concurrently, social systems, comprised of human communities that have direct cultural connections to local ecology and place, may draw upon environmental research as a component of knowledge. Such research can corroborate local and traditional ecological knowledge and empower its application. Indigenous communities and their interactions with and management of resources in their traditional territories can provide a model of such social-ecological systems. As decision-making agency is shifted more and more to Indigenous governments in Canada, abundant opportunity exists for applied ecological research at the community level. Despite this opportunity, however, current approaches by scholars to community engaged ecological research often lack a coherent framework that fosters a respectful relationship between research teams and communities. Crafted with input from applied scholars and leaders within Indigenous communities in coastal British Columbia, we present here reflections on our process of academic-community engagement in three Indigenous territories in coastal British Columbia, Canada. Recognizing that contexts differ among communities, we emerge with a generalizable framework to guide future efforts. Such an approach can yield effective research outcomes and emergent, reciprocal benefits such as trust, respect and capacity among all, which maintains enduring relationships. Facing the present challenge of community engagement head-on by collaborative approaches can lead to effective knowledge production towards conservation, resource management and scholarship.

2.2. Introduction

Ecological research increasingly focuses on applied and integrated approaches to resolve complex issues of conservation and management of natural resources. Many ecologists now recognize that local perspectives and the implications of their research should be considered. Despite this realization, ecological research often lacks a consideration of the potential costs and benefits of the research process and its outcomes on local residents. Multidisciplinary approaches to ecological research that incorporate social dimensions can provide an increasingly effective approach by which to consider the impacts of research for local people (Berkes 2004, Deur and Turner 2005, Drew 2005, Trosper 2009, Housty et al. 2014).

Such applied ecological research is often conducted alongside human communities within the broader natural, ecological community. The people, organizations and governments within and among these communities constitute socio-ecological systems; they maintain direct experiences, dynamic relationships and governance systems tied to local ecology through economic, social and cultural connections (Berkes 2004, Brown and Brown 2009, Ostrom 2009). Such communities may be Indigenous or non-Indigenous. Indigenous communities, however, often serve as the center of local governance within large landscapes (*e.g.,* villages, or "reserves" within traditional territories since the passage of the *Indian Act* of 1876 in Canada). We hereafter refer to these autonomous, Indigenous nationhoods as Nations. The intimate and ancient relationships with the natural environment within the territories of Nations far precede the recent claims of colonial governments.

Residents of these communities hold dynamic local or traditional ecological knowledge. A combination of adaptively evolving practice, belief and knowledge of natural systems, this knowledge is transmitted culturally through generations over millennia (Johnson and Ruttan 1993, Heiltsuk Tribal Council 2001, Berkes 2012). This multi-dimensional knowledge provides an understanding of local and interconnected patterns and processes over large spatial and temporal scales, such as insight into effects of harvesting, cycles of resource availability, and shifts in climate or ecosystem structure and function (Heiltsuk Tribal Council 2001, Haggan et al. 2006, Turner and Berkes 2006, Parrotta and Trosper 2011). Local ecological knowledge differs from traditional ecological knowledge in that it is not values-based, but instead, is built on years of empirical observations. As a result of this collective local and traditional knowledge among members, communities represent focal points for information that can help shape strategies for active conservation and land management (Pretty 2003, Gutiérrez et al. 2011).

Despite the experience within communities to employ local socio-ecological management systems of their own making, the current paradigm of western science-influenced resource management and conservation planning dominates in Canada and beyond. This practice relies on the scientific process to generate information to inform management policies that are applied over large geographical and temporal scales. Plans are typically implemented through centralized bureaucracies such as provincial or federal governments (Dietz et al. 2003, Armitage 2005). Conservation and resource management strategies often comprise the end results, which can protect or restore key areas and species from further exploitation or otherwise harmful human activities.

Notwithstanding potential ecosystem benefits, this centralized, science-based model faces increased scrutiny when communities and local governments do not share common land-use goals with outside institutions, or when they are not considered equal stakeholders in the planning process. Broadly, and across sectors from fisheries to land management, communities have shown dissatisfaction with the external influence of centralized, colonial bureaucracies in the process and outcomes of resource management (Armitage 2005, Loring 2013). For example, despite the fishing industry of Alaska being touted as a model of sustainable scientific management, many people and fishing communities consider themselves marginalized or disenfranchised in their ability to participate in government-managed fisheries (Loring 2013). Moreover, in any system, western scientists may conceive questions and conduct research without considering how traditional or local ecological knowledge could inform their research, or how the application of research outcomes could compromise local conservation and management strategies (Schnarch 2004, Gearheard and Shirley 2007). To address these conflicts, academic practitioners can collaborate with local communities towards common objectives toward the conservation for both natural and local human systems.

Such a partnered approach appears to occur more commonly now, at least in theory. Ecologists and policy makers increasingly recognize that community-based approaches and/or co-management can achieve relevant, sustainable outcomes in resource management (Ban et al. 2008, Ostrom 2009, Gutiérrez et al. 2011, Leys and Vanclay 2011). This realization was derived in part due to the scale of community governance over socio-ecological systems, which is localized or heterogeneous, quintessentially de-centralized, and one shown to be increasingly effective compared with, or when coupled with, larger scales of governance (Johannes 2002, Dietz et al. 2003, Armitage 2005). For example, recent empirical tests of which behaviours best predicted successful (*i.e.,* sustainable) fisheries were almost exclusively expressed at the local level (Gutiérrez et al. 2011). Such evidence, and the strong theory on which it rests, presents academic ecologists with an opportunity to engage with communities. Correspondingly, research supported by academics may provide community leadership with information that can be valuable for governance and conservation of local resources (*e.g.,* Ban et al. 2008).

Community engaged research provides a method by which these opportunities can be realized. It occurs when members of communities and research-based institutions collaborate throughout the research process towards shared outcomes. For example, Huntington et al. (2011) recognized the immense value of collaborative fieldwork and input from local experts in their investigations of ecological factors and harvesting techniques in population dynamics of black leather chitons (*Katharina tunicata*) in south-central Alaska. Alternatively, Indigenous governments now commonly employ academics to summarize ecological information or analyze existing data for their benefit (*i.e.,* OOGRG 2004), either to inform management decisions or to understand effects of resource extraction and development on local socio-ecological systems. Regardless of direction, community engaged research requires that each party seeks to enhance individual strengths and cultivate benefits from research by respecting and working together throughout the process. Despite this potential, current approaches to academic ecological research may not recognize opportunities for collaborative engagement (Huntington et al. 2011). For example, in our experience, visiting scholars may not involve communities in the conception of ecological research, respect cultural protocols when operating on the landscape, or communicate information and research outcomes in a manner that is understandable.

To enable engagement in future research endeavors, ecologists can seek guidance from others. For example, individual leaders within communities and local protocols (*e.g.,* Heiltsuk Tribal Council 2001) can provide direction. Other academic disciplines that have training and exposure to contemporary social science practice and that work towards an ethic of community engagement can also be important. For example, the fields of geography, anthropology, and health have developed ethical guidelines for engagement in their research process (Cochran et al. 2008, Bull 2010, Castleden et al. 2012).

Here, as members of a collaborative research team consisting of academic ecologists and community experts, we present a working model for engagement between academics and Indigenous communities, based on our past and present experiences. We start by identifying the contemporary political context in which communities and ecologists are situated in Canada and beyond. We then identify current limitations towards community engagement. Finally, we provide a framework of key principles and roles within the research process that can yield new knowledge and a mutually beneficial process by which research can occur. Although we focus on the ecological experience, we recognize the principles, process, and limitations of community engagement could be applicable across disciplines, especially those within the natural sciences.

2.3. The case for community engaged research

Contemporary and rapid changes to governance structures in Canada, and elsewhere, provide a need for community engaged research. Abundant evidence suggests that centralized bureaucracies have not effectively governed natural resources, in part by disregarding complexities of socio-ecological systems (Holling and Meffe 1996, Folke et al. 2002). This can be reflected in the collapse of global fisheries or mismanagement of forest and water resources (Ostrom 2009). Meanwhile, the capacity of large, centralized bureaucracies to manage resources is waning (*e.g.,* Hoag 2012, Reynolds et al. 2012). Environmental legislation may also face erosion if it presents an impediment to industry or development (Lemos and Agrawal 2006, Todorovich and Schned 2012). As a consequence, environmental legislation might be ineffectually enforced and inadequately address the inherent complexities in the management of natural resources. These conditions are now prominent in Canada (*e.g.,* the dismantling of the *Fisheries Act* under the Harper government; Favaro et al. 2012, de Kerckhove et al. 2013).

This gap in effective governance created by retreating or neutered centralized government agencies provides opportunities for the resurgence of Indigenous communities and their own governments. Co-management, formalized acknowledgement, and state legitimization of Indigenous governance systems, such as land claims arrangements in Canada, Australia, New Zealand and elsewhere, are being bolstered by rapidly changing legal landscapes (Houde 2007, Berkes 2009, Weiss et al. 2013). For example, Canada's *Constitution Act* of 1982 recognizes that Indigenous people hold rights to areas and resources within their recognized territories. Moreover, government processes that propose resource extraction must consult and accommodate Indigenous governments (Canada 1982). To acknowledge these rights and avoid legal conflicts, recent policy agreements have shifted regional decision-making agency towards Indigenous governments in both co-management and government-to-government processes (Wyatt 2008, Berkes 2009, Housty et al. 2014).

This transition can be illustrated with the Reconciliation Protocol in British Columbia, Canada, where we live and work. This agreement was negotiated between a group of Nations collectively referred to as "Coastal First Nations" and the Province to address duality of title and a process for joint decision-making in governance over land and resource use (Coastal First Nations and Province of British Columbia 2016). The Protocol recognizes Coastal First Nations authority and provides a collaborative government-to-government platform to implement land- and marine-use planning, apply ecosystem-based management and oversee economic development in the coastal region, popularly referred to as the 'Great Bear Rainforest' (GBR; McGee et al. 2010, Coastal First Nations and Government of British Columbia 2016).

Despite recent policy developments that recognize regional authority like this, however, Indigenous governance and regional capacity to manage resources has yet to be implemented broadly. Although decision-making agency is being shifted to Indigenous governments, we note that authority cannot be endowed to Nations whose authority is considered inherent. In addition, western-based governance systems within which Indigenous governments must operate, such as laws and negotiation processes, are neither of Indigenous design or contribution and often the products of ineffective or failed management approaches of the past. Implementing such processes and reconciling these governance paradigms requires enormous financial and skill-based capacity, sustained support as this capacity builds, and information about resources and land-use. Consequently, the capacity to conduct resource management-related research at a territorial scale is still developing for many Indigenous communities (Tobias 2000), including those considered here: Bella Bella, Klemtu, and Wuikinuxv village. In theory, scholars of ecology or applied biology from academic institutions are well situated to provide a level of methodological and logistical capacity that can complement the contributions of local and traditional ecological knowledge. As we explain below, however, such partnerships require careful consideration of current limitations.

2.4. Limitations of current approaches to engaged research

Although not universally the case and recognizing that many individuals span perspectives, several deep cultural differences that stem from different values and beliefs, approaches, and reward systems exist in how academic and Indigenous experts conduct what is labeled "research". Articulating these impediments humbly and openly can cultivate understanding and compassion between collaborators; a critical preliminary step in the engagement process.

Differences in the definitions of ecosystems present one major barrier. Scholars, policy makers, and conservation planners have often framed ecosystems by the western notion that they are pristine, largely unaltered, and independent of interaction with local peoples (Pretty 2003, Deur and Turner 2005, Dent 2013). This conception differs strongly from the values and land-use practices of place-based communities, which are necessarily integrated with local ecology (Berkes 2012). An implication of this divergence (and the recent hegemony of the western-based worldview) has been protected areas that limit or exclude humans from land they have long inhabited (Pretty 2003, Dowie 2009).

Another problem is a culture of distrust of western science, which stems from mismanagement of local resources by science-based institutions. Moreover, prescriptive, quantitative management objectives that allocate resources for maximum economic yield have often not favorably served Indigenous communities or the health of resources on which they depend (Pinkerton 1999, Walter et al. 2000, Pinkerton and Silver 2011). For example, marine resources managed through maximizing harvest quotas for non-local license holders have been substantially depressed in many regions of the Pacific Northwest (Pinkerton 1999).

Scholars and community members also often have divergent approaches towards research. The differences are often driven by their respective knowledge systems. Academic ecological research questions are founded on established theory and relevant literature and pursued by empirical or experimental methods (Weiss et al. 2013). In contrast, Indigenous approaches are contextualized by local and traditional knowledge of biodiversity and sustainable resource management as part of complex socio-ecological systems (Brown and Brown 2009, Turner 2014). Although ample attention has been given to these differences (Ingold and Kurttila 2000, Cruikshank 2001, Houde 2007), few studies explore establishing productive relationships that bridge these different knowledge systems and/or knowledge holders (but see Parrado-Rosselli 2007, Huntington et al. 2011, Kimmerer 2012, Housty et al. 2014). Moreover, commonly Indigenous communities have often not been included in the research process adequately. Instead, communities can be solely perceived as a source of local knowledge for the sake of extraction and integration into research design or resource management. Ultimately, such research outcomes serve the state or researchers rather than local or traditional knowledge holders (Nadasdy 2003, Davidson-Hunt and O'Flaherty 2007, Castleden et al. 2010, Bohensky and Maru 2011).

Compounding these problems is that local or traditional knowledge, or the needs of local communities, are often not factored into how and why research is conducted. While some researchers are highly accountable, our observation is that communities may not experience beneficial outcomes (such as compensation or communication of research findings) from participation in the research process. Instead, western notions of information, or evidence, and approaches to its collection have been thrust upon Indigenous Nations.

Capacity barriers, especially those related to funding and timing, may also limit interactions. Community resource managers and academics receive funding to produce deliverables such as policies or publications; upfront funding required for the time to jointly develop the research process (at either universities or in communities) and to cultivate the necessary trust may not be available. This may be compounded by the reality that junior scholars and/or smaller communities generally receive less funding overall. Although policy-based and financial endorsement for community engagement from academic institutions is increasingly evident, recipients may experience tension reconciling their community commitments with the typical academic reward structure (see below; Nicotera et al. 2012). Moreover, whereas research publications often take years to compile, communities may wish results to be communicated more rapidly and directly; the capacity of both parties to translate and interpret information in a timely manner and via suitable means might often be lacking. Finally, Indigenous communities may want to build trustworthy collaborations and be deliberate in the direction of research, which necessarily takes time and may conflict with schedules of academic researchers.

These barriers often relate to different reward systems. Whereas a passion for science and conservation might have originally attracted scholars to their vocation, academic research is in large part motivated by research interests, followed by awarding of degrees, the pursuit of publication and receipt of grants. In contrast, Indigenous resource managers and practitioners often pursue research for the stewardship of single resources and the social and ecological systems within which they are embedded (Haggan et al. 2006, Tobias 2010). Such stewardship is built upon complex connections to ecology, with a view to sustaining such connections for future generations (Brown and Brown 2009).

Finally, these limitations in the traditional model of academic research are further – and ultimately – compounded by a broader lack of trust between Indigenous and non-Indigenous peoples. This stems from a history of imposed assimilation techniques following European contact (*e.g.*, residential schools in Canada). Violence, oppression and discrimination towards Indigenous peoples in the past and present may have potent implications for collaborations (Smith 1999). Many people (or their families) who have endured these abuses are the same community members with whom scholars of colonial ethnicities interact, which can influence day-to-day interactions and the establishment of trust.

Collectively, these limitations conspire so that the design and implementation of ecological research led by either party may not solicit input or participation from other knowledge systems. Outsiders (researchers) have often driven academic research - identifying the scope, methodologies, protocols, pace and meeting of objectives, thus ultimately controlling how information is generated and shared (Davidson-Hunt and O'Flaherty 2007). In addition, without community participation in the forming of the research questions or the methodologies that follow, any inclusion of local and traditional ecological knowledge is often left unexplored or misunderstood and may not fully benefit academic efforts. Academic and community partners can begin to reconcile these limitations by acknowledging cultural differences and working reciprocally towards relevant research goals (Davidson-Hunt and O'Flaherty 2007). An engaged approach to the research process we propose next can provide a means towards realizing shared goals and productive research outcomes.

2.5. Proposed framework for community engaged approaches to ecological research

Confronting these problems and scoping new opportunities, we present our reflections on developing open and communicative approaches to the engagement process. We consider it a work-in-progress for all ecologists and communities in which community members have tangible input to the research process and in which outcomes are jointly determined. Because of the inherent complexity and cross-cultural challenges of such a process, we conceptualize engagement in a framework from both perspectives in three components. We first identify core principles that drive an engaged research process. Second, we outline the suite of possible roles for partners at each research stage. Third, we address the “process benefits” – or tangible, reciprocal benefits of the research process itself, above and beyond the end results of newly generated knowledge. Although not in any sense faultless, prescriptive or a finished product, in our experience this approach can yield productive and enduring relationships between academics and community members for locally driven research.

Our aim is broad applicability. We first note that academics can be part of communities, just as community members can be researchers. While we recognize significant crossover, for the purposes of this paper we have framed the research process through the binary roles of academic and community collaborators. Second, we also note that while this framework has developed through longstanding relationships between Indigenous leaders and applied scholars in coastal British Columbia, its generalizable nature could have broad relevance to other communities and scholars seeking an ethic and practice of engagement anywhere.

2.5.1. Foundational principles

At its core, an engaged research process can be built upon a consideration of how research questions are framed, the consequences of research outcomes at local scales and respect for place. Essential to these principles is acknowledging that Indigenous forms of inquiry and monitoring are most often located in a different cultural context from that of western science and its methods. This necessarily involves an awareness of cultural differences and respectful interpersonal relationships (Davidson-Hunt and O’Flaherty 2007, Gearheard and Shirley 2007, Parrado-Rosselli 2007).

Several local dimensions can provide context for a research question. First, given the rapid legal changes noted above, communities may wish to initially frame their research questions according to their legally-entitled management needs. Second, local and traditional ecological knowledge can inform how research questions are shaped. In this way, the collaborative perspectives of academics and communities can yield productive research questions that reflect local and complex socio-ecological circumstances (Heiltsuk Tribal Council 2001, Housty et al. 2014). Third, we recognize that there will be variation in how questions are framed. For example, communities differ from one another, throughout time. Consideration should therefore be given as to whose voices are being heard, and who is excluded, in framing research questions (Tobias 2010). Clarifying and challenging the assumptions behind the conception of research is critical for all of these dimensions.

The socio-ecological needs of the community in the short and long term can direct the research process (Heiltsuk Tribal Council 2001, Gearheard and Shirley 2007, Huntington et al. 2011). Academics have a responsibility to understand how their short-term research efforts can fall into the broader framework of the community's vision. This can inform the distribution of present and future benefits and costs of the research outcomes for the community, as well as the structure of the research (Tobias 2000). Reconciling the research process to generate information across desired timescales for urgent local management decisions or longer-term monitoring is important for community collaborators. It is also important to consider the implications of research to the political balance among neighbouring communities and/or Nations. Where research takes place in a territory with overlapping claims, working with one Nation (and not with others) can have far reaching and unintended effects in resource management and potential land claims processes that should be carefully considered and discussed.

Finally, respecting the place-based setting and authority of the community is integral to an engaged research approach. By this we mean respect for the landscapes and resources as integral aspects of a community's experience and knowledge systems; not simply a "study site" or a place to conduct "fieldwork" for scholars, but instead, as a part of a complex system to which human communities also belong (Heiltsuk Tribal Council 2001, Castleden et al. 2010). This respect can be demonstrated simply through word choice (*i.e.,* academic partners refraining from possessive pronouns and concepts embodied in, for example, "my study area"). More broadly and deeply, respect can be modeled by engaging with the wider community and giving back to that specific place. For example, researchers could engage with youth and/or cultural events, respecting protocols in the community and on the land, or by visiting community collaborators and friends outside of the field season. These actions signal a longer commitment to, and relationship with, the people and landscapes where research occurs.

2.5.2. Stage-by-stage framework of the research process

To complement these core principles, we provide a framework for engagement at each stage of the research process. While we recognize that engagement does not always follow a simple linear chronology, our model addresses the collaborative experience at each stage (Table 2.1). We identify the contributions academics and Indigenous community members can provide, as well as suggest the process benefits that can emerge at each stage. The latter include: respect, trust, co-capacity building and enduring relationships. Generally, our experience shows us that these outcomes commonly occur in that order (Figure 2.1). We have developed this framework based on our shared experiences and goals for an engaged research process, supplemented with insight from the literature (*e.g.,* Turner and Carpenter 1999, Schnarch 2004, Drew 2006, Davidson-Hunt and O'Flaherty 2007, Gearheard and Shirley 2007, Bull 2010, Huntington et al. 2011, Tobias et al. 2013). Although we aim for generalizability, we recognize this framework might particularly benefit larger projects; they are generally resourced better and operate on time frames over which respect and trust can be more effectively cultivated and maintained. This does not imply, however, that smaller projects cannot incorporate engagement as they occur.

Beyond the direct research process, we believe it is important for the research team to engage with local residents at community events through all stages of the research process. Examples of this include spending time with youth or school groups, feasting together or the witnessing of cultural events. Likewise, scholars can welcome community collaborators to university environments, conferences, or on supervisory committees. Time for experiences such as these is important to build into an otherwise typical 'field season' for academics that usually involves considerable pressure to complete and publish projects in a timely manner (Schnarch 2004).

Stage 1: Conception of research focus and questions. The research process begins with identifying desired outcomes in the application of research. These are often derived through local requirements and informed by local and/or traditional knowledge, typically with applications for resource management or conservation. Both academic and community stakeholders need to identify and examine their assumptions prior to identifying specific research questions. By considering the potential knowledge systems and variables that provide the context of the research focus, collaborators can establish clear and productive research questions.

Communities may identify potentially suitable researchers and engage or hire them towards a research goal. Alternatively, researchers might approach communities, but would do so by considering their potential needs. In addition, academic partners might articulate additional research questions of theirs for communities to consider, even if the questions are of no immediate or direct relevance to local people. Finally, communities with research needs may also opt to not involve academic capacity at all but instead conduct their own research. In our view, the most mutually-beneficial and productive collaborations could satisfy the resource management needs of the communities and their governments while simultaneously providing scholarly opportunity for academics (*e.g.,* Housty et al. 2014). Identifying and negotiating these regions of overlap might require time and thoughtful consideration. Once potential collaborations have been identified, jointly prepared funding could be sought to increase the research and engagement capacity of both parties.

When conceptualizing specific research objectives, respect for each other's context and process can be demonstrated by considering the various approaches and needs of each party. Academic assumptions about a proposed system might differ from traditional or local ecological knowledge. For example, ecologists may see an ecological pattern or process as novel, or understand it through the framework of other ecological research (*e.g.,* a migration pattern shift or switching of prey types by consumer species), whereas traditional or local knowledge may be able to place this observation within a larger perspective, where values are intertwined with site-specific knowledge (*e.g.,* long-term weather processes, large temporal scale population dynamics, and oral histories of human or animal land-use; Berkes 2008). In this way, both academic and local and traditional knowledge provide a broad scale and a strong foundation that can address assumptions inherent to shorter-term research questions. Most importantly, it is crucial to consider the implications of research to communities, whether they be harmful or beneficial (Tobias 2000, Schnarch 2004). For example, if research prompts the conservation or use of an ecological resource, it is important to question how the access and cultural connection to, or governance of, that resource may be altered (and for whom). Openly and thoughtfully entered and navigated, this early stage of the research process can begin to build mutually informed respect and acceptance, which can cultivate trust between collaborators.

Stage 2: Research Design. Once the focus of a research project has been conceived, a research methodology and project plan can be developed that captures and accepts the shared vision of collaborators. Academics can provide expertise in creating approaches to data collection. Importantly, however, these should be consistent with local protocols and guiding principles for operating within the community, on the landscape and with neighbouring communities (*e.g.,* Heiltsuk Tribal Council 2001, Schnarch 2004). This could be done by soliciting direct input from research collaborators or through processes that involve the broader community, such as workshops or information sessions. Inclusive project budgets can cultivate research support and capacity building for collaborators (Heiltsuk Tribal Council 2001). Communities can also suggest how other concurrent projects could support or contribute to proposed research. Negotiating data sharing, communication and storage protocols at the onset of the project is essential to ensuring clear expectations about the ownership, control, access, and possession of information for collaborators (Schnarch 2004, Tobias et al. 2013). Collectively, these steps build and maintain acceptance and respect for both guiding principles and research approaches between collaborators through the learning and observation of scientific and cultural protocols. As capacity is shared and built into the design of research, so too is trust in the engagement process.

Stage 3: Implementation. The research design can be implemented by a collaborative team of scholars, community experts and other participants. Upon beginning a project, the team can consider how to engage and employ community members in research opportunities. Hiring local people for fieldwork can increase logistical safety and ease, while also helping to ensure local protocols are respected. When appropriate, local technicians can also share local ecological knowledge and cultural information about the landscape. Similarly, Nations may hire scientists and technicians for methodological and analytical capabilities. These capacities can be taught and shared between the research team and community (Drew 2006). We also recognize that individuals will bridge both worlds with backgrounds as academically-trained practitioners or scholars and members of Indigenous communities (*e.g.*, White 2006, Moody 2008, Housty et al. 2014).

During implementation, partners develop one another's capacity while also building sincerely collaborative personal and professional relationships. By sincere, we mean respectful; lacking in condescension and/or ulterior motives in forming the relationship. As one example, collaborative fieldwork allows the research team to discuss and envision the ecological questions *in situ* (*e.g.,* Huntington et al. 2011). Sharing observations as a team and with the broader community can have additional benefits, like the conception of alternative hypotheses or improved research methodologies. The mutual trust and respect further cultivated during co-capacity building can allow for a dynamic process that ensures the team is working towards desired outcomes of all collaborators, and that the research team and community can feel a sense of ownership and participation in the research.

Stage 4: Use and dissemination of knowledge. Research ultimately generates information that can have scholarly value and community-based applications. Data sharing protocols will permit appropriate accessibility and dissemination of information while also respecting ownership or confidentiality (Schnarch 2004, Castleden et al. 2010). When information is being synthesized to share with community members (likely in forms and forums different than those intended for scholarly products), it should be crafted to be accessible and informative, as well as conscious of potentially sensitive or confidential material. Communities may apply the information generated towards local governance strategies or an increased understanding of local socio-ecological systems (Tobias 2010), whereas scholars may apply information to test, improve or create theory via the peer-reviewed publication process. Ideally, one reinforces and supports the other in ways that honor an engaged, collaborative process and the complexities of socio-ecological systems.

When preparing scholarly publications, academics may include community members on the review or authorship process. If interest and contributions are consistent with typical publishing expectations, such inclusion is in fact expected (Castleden et al. 2010). At minimum, publications can be reviewed by and respectfully acknowledge the contributions of community collaborators. A collaborative review process involves a careful consideration of the ethics of authorship through direct acknowledgement of the intellectual property of knowledge holders, crediting of community permissions and contributions, and respect for copyright and confidentiality agreements as negotiated at the onset of the research process or as per community protocols (CIHR 2007). For example, academic and community co-authors may acknowledge or include other community members as co-authors given their significant contributions, despite this not being a conventionally academic approach to authorship (*i.e.,* Castleden et al. 2010).

The partnerships built through these stages can lead to enduring relationships and even future collaborations (Figure 2.1). In particular, respect for knowledge systems (acknowledgement of the validity of contributions), data protocols (clear boundaries of possession, ownership and/or confidentiality), and implications of generated knowledge (understanding of where benefits and detriments of the research flow) provides a strong foundation for enduring research partnerships (Turner et al. 2000, Schnarch 2004).

2.6. Conclusions

The meshwork of ecology, socio-economy, culture, and politics in which research is embedded will remain uncertain and difficult to manage if actors and relationships are kept separate with their differences left unspoken. In other words, we believe a central guiding principle of this process is to be open and honest. Integrative approaches that incorporate local and traditional ecological knowledge and focus on the entire human-ecological system can generate productive questions, answers, and solutions to confront socio-ecological challenges and opportunities.

As conventional scientists become more aware of Indigenous knowledge and interactions within traditional territories, the gap between scientific inquiry and Indigenous knowledge systems is narrowing and being bridged. In our case, this emerged out of an ecological and socio-ecological context, but many of these principles could be useful to disciplines outside our domain in areas such geology, physical geography, environmental science as well as to those disciplines of applied, engaged and critical social science. Ecological research and monitoring that involves Indigenous communities as collaborators and/or drivers is inherently social and will involve various cultural and social perspectives. When a knowledge system and worldview does not separate people from place, western science cannot disregard the cultural influence that permeates the ecosystems in which research occurs. In our experience, community engagement, practiced with a sense of humility, respect for place and people as well as an awareness of the complexities of the issues at hand, could present resolutions for current socio-ecological challenges of conservation and resource management for Indigenous communities and beyond.

This journey of learning will involve the academic community divesting its internalized processes and beginning to frame the process from the community context. It will also require direction from communities regarding if and how they wish to be involved or what capacity they require and can offer. This may come as a challenge for academics and communities, but we hope this challenge is balanced by sincere, productive and enduring relationships generated by an increasingly engaged approach.

Table 2.1 Roles and contributions by community and academic collaborators at conception, design, implementation, and dissemination stages of community engaged research. We list a non-exclusive suite of possible roles; in practice, collaborations might take different forms. We also recognize that community members may themselves be academics, but for simplicity we identify binary roles.

Research Stage	Community Partners	Academic Partners
Conception		
• *Identify research focus* • *Examine assumptions* • *Establish research questions beneficial to all parties*	• Formulate research questions within local context of TEK/LEK and research goals	• Situate local context into scholarly framework to shape research focus
Design		
• *Select appropriate scope and methods* • *Organize local logistics* • *Craft data sharing agreements*	• Ensure methodology respects local protocols • Provide clear expectations on research goals and data sharing agreements • Suggest if current project can build from/contribute to other local research	• Provide design expertise in scientific methods • Contribute to shared vision for project goals and data sharing agreements
Implementation		
• *Assemble research team* • *Engage in collaborative fieldwork* • *Consult frequently on progress and challenges*	• Ensure logistically safe and culturally respectful research operations • Contribute local experts on research teams • Share local knowledge • Provide feedback on process	• Share technical expertise • Respect local protocols • Consult regarding project progress with community • Provide feedback on process
Knowledge dissemination		
• *Respect both access to and confidentiality of knowledge* • *Communicate research outcomes*	• Respect data sharing protocols • Make knowledge accessible to community • Potentially use information for resource management decisions • Participate in scholarly publications, if appropriate	• Respect data sharing protocols • Make knowledge accessible for community • Potentially craft academic publications • Offer information for resource management, if appropriate

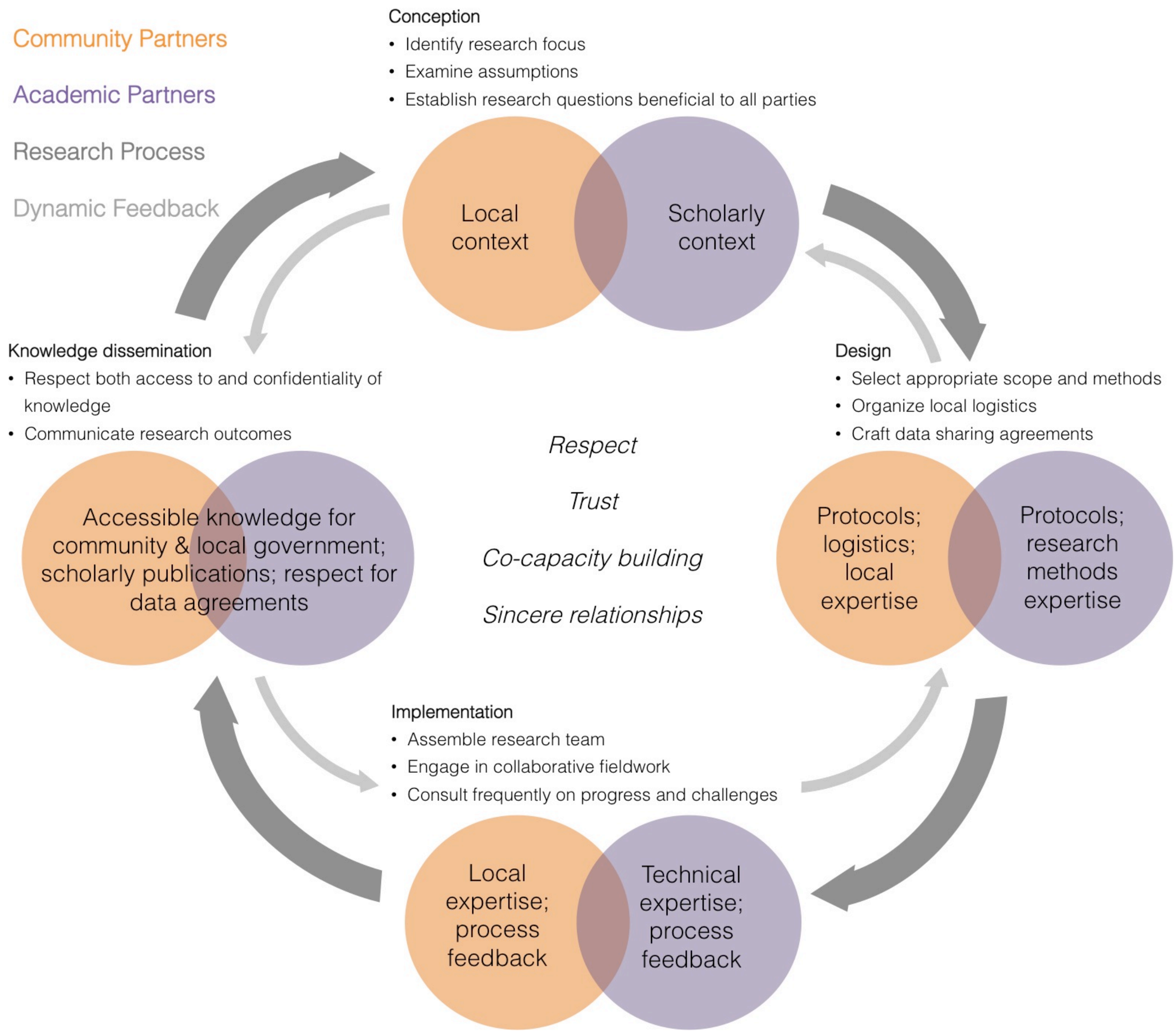

Figure 2.1 Research outcomes, potential collaborative roles, and reciprocal process benefits generated through an engaged research process. Although there will be shared experience among collaborators in the roles (denoted by overlap among circles in figure), knowledge base, and capacity throughout these stages, much of the engaged research process occurs through collaborators working beside one another from their own worldview, knowledge base, and method of inquiry towards shared outcomes (denoted by non-overlap). Throughout each stage, community and academic partners can cultivate process benefits including respect, trust, co-capacity building, as well as open and enduring authentic relationships. The research process can lead to future collaborations, demonstrated by the continuous arrows. Process stages can revisit a previous stage if feedback from within the team or the community suggests that the scope, design, implementation, or dissemination of the process requires modification.

Chapter 3. Intrapopulation diversity in isotopic niche over landscapes: spatial patterns inform conservation of bear–salmon systems

Adapted from: Adams, M., Service, C., Bateman, A., Bourbonnais, M., Artelle, K., Nelson, T., Paquet, P., Levi, T., and Darimont, C. 2017. Intrapopulation diversity in isotopic niche over landscapes: Spatial patterns inform conservation of bear-salmon systems. Ecosphere 8(6):e01843.10.1002/ecs2.1843.

3.1. Chapter Summary

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 *U. 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 ocean, 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.

3.2. 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 behavioural 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.*, behavioural 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). Diet 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, Smith and Blumstein 2008, Biro and Stamps 2008), dietary niche variation across individuals can influence the productivity, stability, and persistence of populations (Sih et al. 2012, Wolf and Weissing 2012, Dall et al. 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, S.D. 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 behaviour 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 *U. arctos horribilis*, respectively) before winter hibernation. 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. 1999a, 2000, Gende et al. 2001, Mowat and Heard 2006, 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 of 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.

3.3. Materials and Methods

3.3.1. 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 British Columbia (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 (Figure 3.1). 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 (Figure 3.1; 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 non-invasive 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 to 14 days. Stations were disassembled between years. Because collection occurred during the shedding phase of the annual moult, isotopic measures in samples represent annual assimilated diet during the entire previous year's hair growth (approximately June through 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 (Figure 3.1; see 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 #2012-018). We conducted research in the traditional territories of the Haíɫzaqv (Heiltsuk), Kitasoo/Xai'xais, Nuxalk, and Wuikinuxv Nations, with whom we partnered in this work. We also had a permit #106703 from BC Parks to sample in conservancies. Agreements for these data with partner governments prohibit us from displaying sample locations.

3.3.2. Dietary contributions

We prepared and processed samples for SIA using established protocols (Darimont and Reimchen 2002, Darimont et al. 2008, 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 (Table A1). 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 (Figure 3.1; Mowat and Heard 2006). Depending on diet model region, these included: terrestrial meat (ungulates), landlocked salmon (kokanee; *O. nerka*), spawning Pacific salmon, intertidal food sources, and plants (Figure 3.1, Table A1). Given our focus on the bear-salmon association, we used the median contribution from salmon to yearly diet (hereafter 'salmon consumption') for spatial analyses.

3.3.3. 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 (LSCV; 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 A 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 post-hibernation bears. 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.

3.3.4. Characterizing interspecific 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.

3.3.5. 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 (Figure A1; 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.

3.3.6. 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 2011) (Figure A2). 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.

3.4. Results

3.4.1. 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 (Figures 3.2 and 3.3). 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 (Figure 3.3). Estimates of salmon consumption were more heterogeneous in male black bears than grizzly bears among years and across space (Figure 3.2). Across the entire dataset, relative variability in salmon consumption was higher for black bears than for grizzly bears (black bears: 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 (Table 3.1). 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 (Figure 3.4). 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.

3.4.2. 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 (Figure 3.5). 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; Figure 3.5). 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; Figure 3.5 insets). Although females with the highest salmon consumption were concentrated in coastal regions, the bear-salmon association extended well into the interior for males (Figure 3.5).

For both sexes of grizzly bears in the coast region, diet models estimated that salmon constituted the largest dietary component (Table 3.1). 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 - 0.63), except in the coast region (medians ranging from 0.06 - 0.12).

Over the provincial area, the coastal regions captured areas where bears have particularly high salmon diets (Figure 3.6). 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.

3.5. 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 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 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 interspecific 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, *personal observation* C. Service 2017). 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 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. 1999a, 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 Great Bear Rainforest 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. 1999a), 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 are 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).

Table 3.1 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 *U. arctos horribilis*, respectively) in British Columbia, Canada. Diet model regions correspond to regions in Figure 3.1.

Food type	Black		Grizzly							
	Coast		*Coast*		*Eastern*		*Central*		*Interior*	
	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

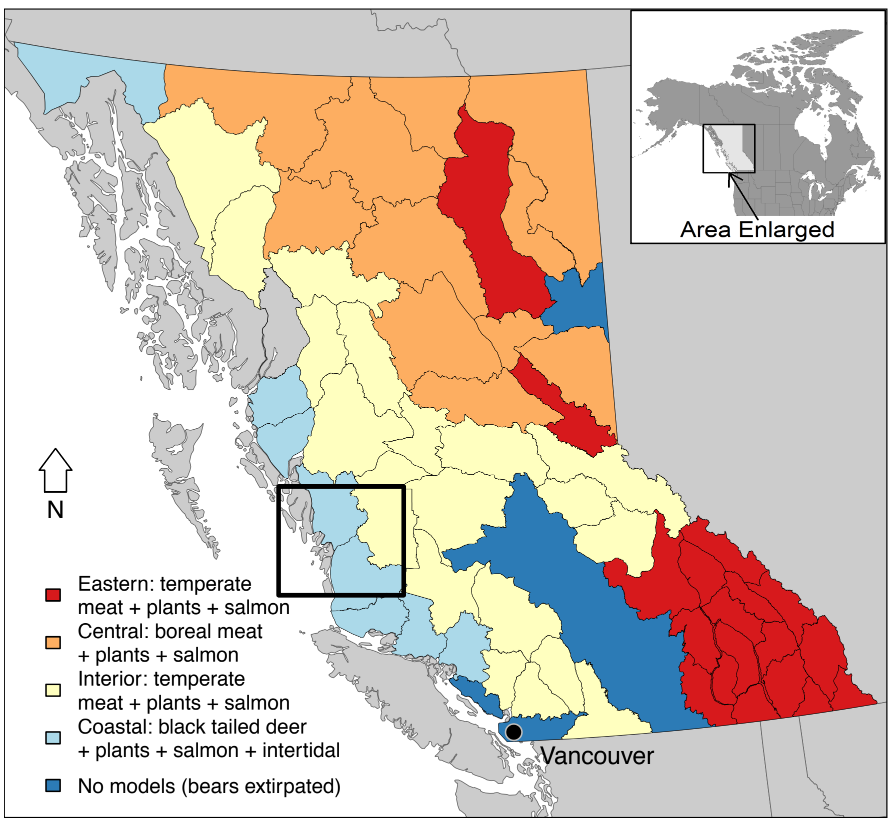

Figure 3.1 Dietary model inputs for grizzly bear (*Ursus arctos horribilis*) population units (n = 57), as designated by the Province of British Columbia, Canada (Province of British Columbia 2012). Potential diet components were informed by Mowat and Heard (2006). We included salmon in each region and intertidal prey for coastal models. Black (*U. americanus*) and grizzly bear data from the 'coastal area' portion of the analysis are contained within the black rectangle.

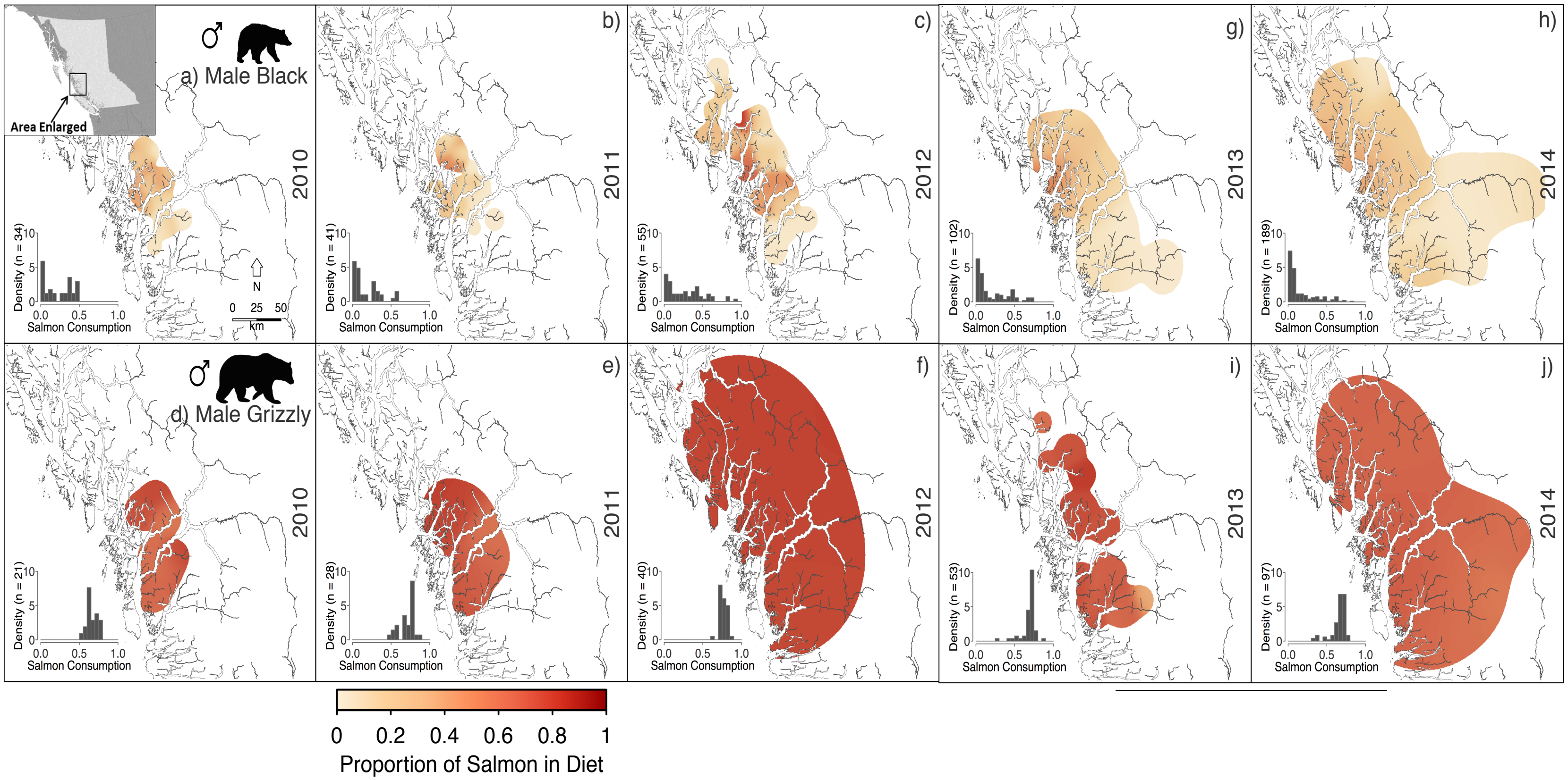

Figure 3.2 Spatial patterns of salmon consumption estimated by kernel regression in male black and grizzly bear (*Ursus americanus* and *U. arctos horribilis*, respectively) diets in coastal British Columbia, 2010 to 2014. Major salmon-bearing rivers are depicted as grey lines. Areas depicted in white 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.

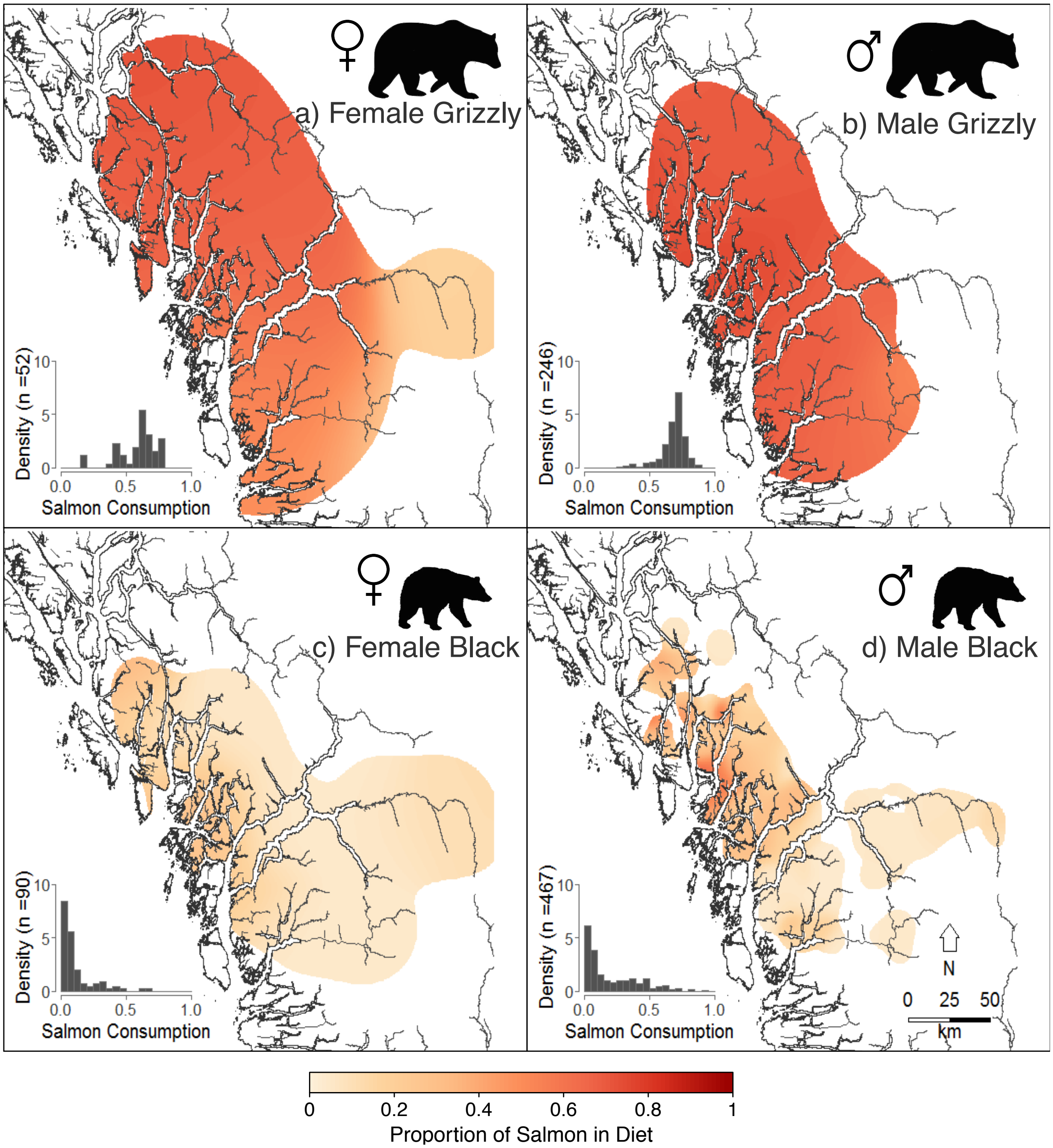

Figure 3.3 Spatial patterns of salmon consumption estimated by kernel regression in female and male black and grizzly bear (*Ursus americanus* and *U. arctos horribilis*, respectively) diets in coastal British Columbia, combined over 2010 to 2014. Salmon-bearing rivers are depicted as grey lines. Areas depicted in white represent regions outside of the models' spatial extent. Histograms represent frequency of individual bears' observed median values of proportional salmon consumption.

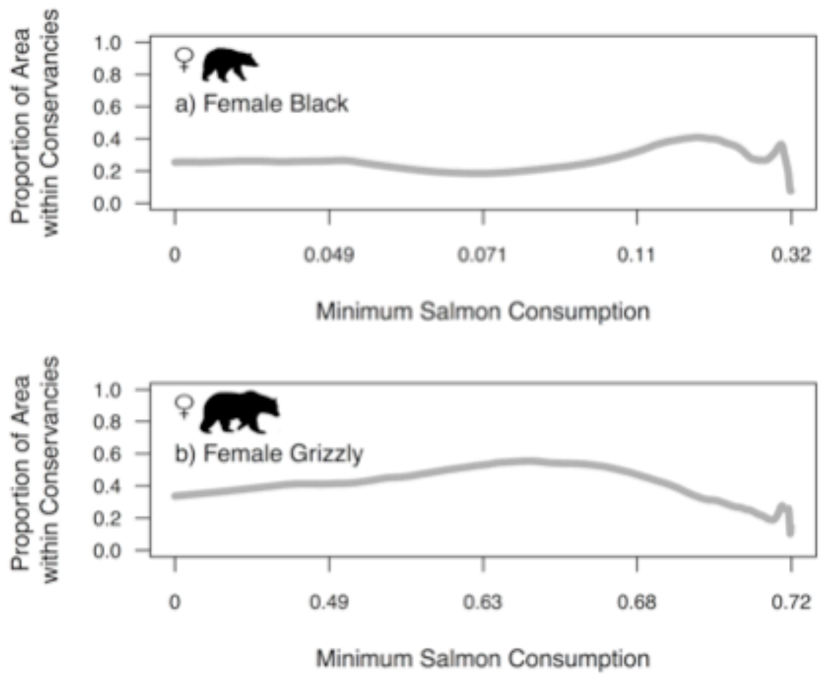

Figure 3.4 Conservancy-protected proportion of coastal area in which median salmon consumption exceeds the given value for female a) black (*Ursus americanus*) and b) grizzly (*U. arctos horribilis*) bears from 2010 to 2014. X-axis based on species-specific quartiles of salmon consumption estimates, whereas minimum salmon consumption within an area (the grey line) based on kernel regression estimates.

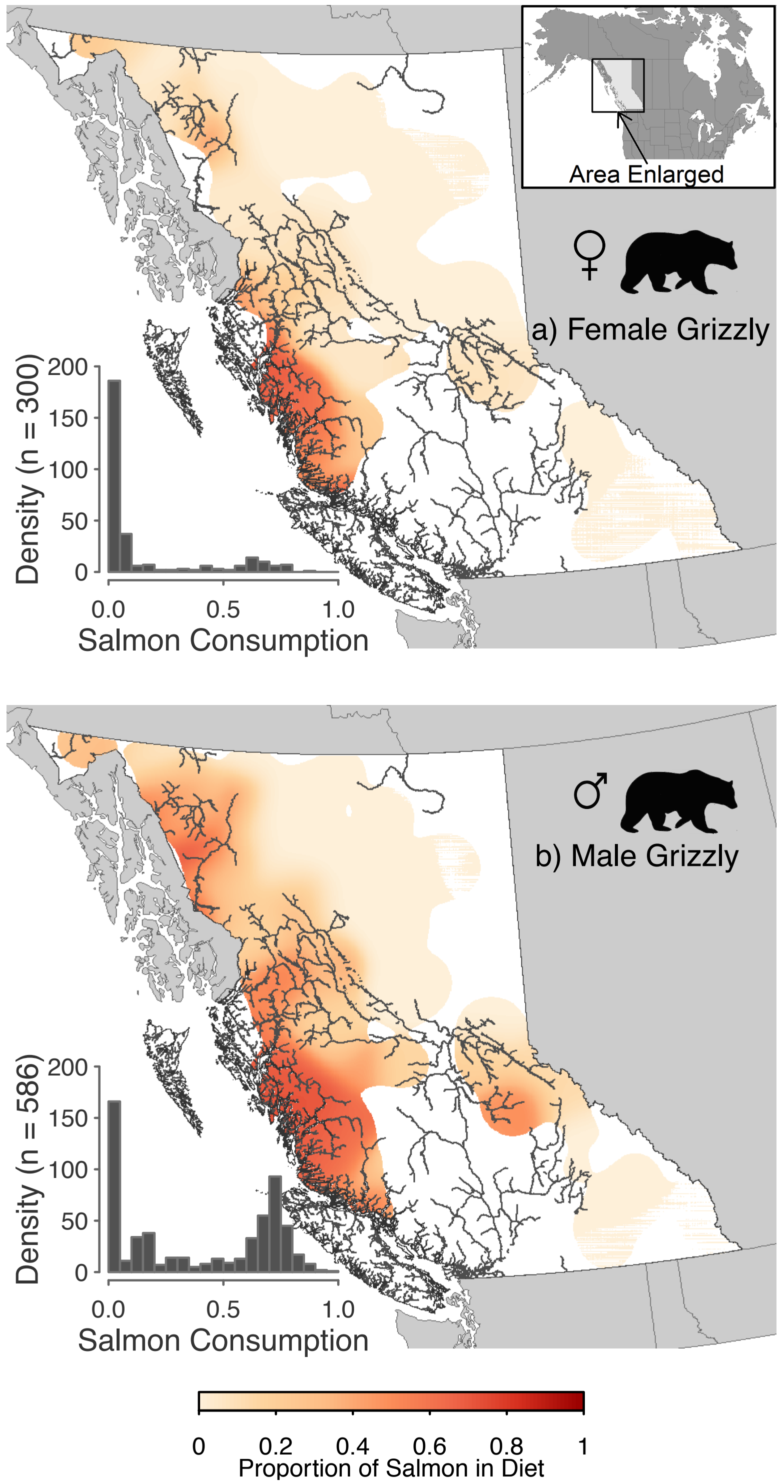

Figure 3.5 Spatial patterns of salmon consumption estimated by kernel regression in a) female and b) male grizzly bear (*Ursus arctos horribilis*) diet across British Columbia, between 1995 to 2014. Major salmon-bearing rivers are depicted as grey lines. Areas depicted in white represent regions outside of the models' spatial extent. Histograms represent frequency of individual bears' observed median values of proportional salmon consumption.

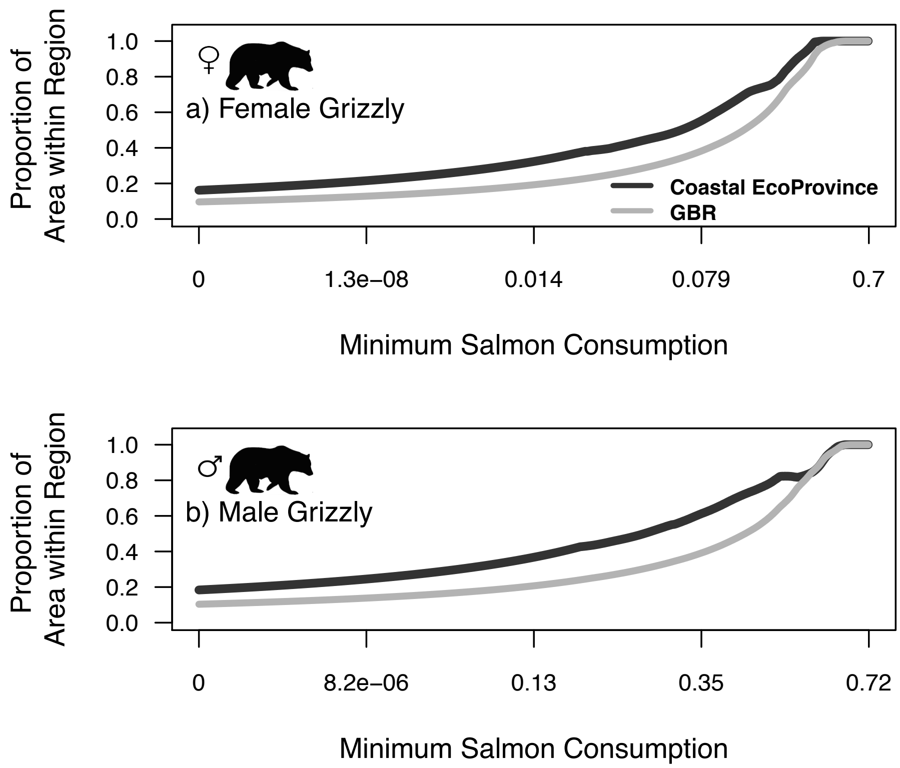

Figure 3.6 Proportion of British Columbia in which salmon consumption estimates exceed the given value contained within the Coastal EcoProvince (black) and Great Bear Rainforest (grey) for a) female and b) male grizzly bears (*Ursus arctos horribilis*), between 1995 and 2014. X-axis based on sex-specific quartiles of salmon consumption estimates, whereas minimum salmon consumption within an area (the grey line) based on kernel regression estimates.

Chapter 4. Human footprint in salmon-bearing watersheds unravels predator-prey interactions between grizzly bears and salmon

Adapted from: Adams, M., Bourbonnais, M., Service, C., Artelle, K., Bryan, H., Paquet, P., Levi, T., Nelson, T., Darimont, C. *In review*. Human footprint in salmon-bearing watersheds unravels predator-prey interactions between grizzly bears and salmon.

4.1. Chapter Summary

Although human activity presents an increasingly common and persistent risk for wildlife, little is known about how the footprint of human activity on the landscape might influence long-term resource use. Using the grizzly bear (*Ursus arctos horribilis*)-salmon (*Oncorhynchus* spp.) predator-prey association across 88,000 km^2 of British Columbia, Canada, we examined how human activity might influence grizzly bear consumption of spawning salmon, a nutritious and fitness-related resource clumped in space and time, and often in human-dominated valley bottoms. Across 22 watersheds, we tested how variation in salmon biomass, alternative food abundance, and the human footprint index (HFI) in riparian areas was associated with annual salmon consumption of individual bears (n = 226 bears, 1995-2014). Our top models revealed strong associations with both HFI and food supply, specifically salmon biomass density and proxies for alternative food. We detected a strong, negative effect of HFI; holding salmon biomass and alternative food variables at their means, predicted salmon consumption by females and males was roughly 52% and 60% lower, respectively, in watersheds with the highest HFI as compared with those with the lowest HFI (90% and 10% quantile, respectively). Unless balanced by restoration, we can expect the ecological and evolutionary interactions between bears and salmon to unravel increasingly as human footprint expands across extant bear-salmon range, and with it the subsequent flow of bear-mediated marine nutrients into terrestrial communities. More broadly, this work illustrates the interaction between habitat modification and food security for wildlife, highlighting the potential for unacknowledged interacting and cumulative effects.

4.2. Introduction

Risk associated with human-caused mortality is now common for the world's wildlife. For many vertebrates, humans account for more adult mortality than any other predator (Estes et al. 2011, Darimont et al. 2015). Risk of predation by humans is particularly acute in human-modified landscapes, which are experiencing unprecedented and accumulating change (Frid and Dill 2002, Barnosky et al. 2012). Anthropogenic features, such as roads, development, and infrastructure (collectively referred to as the 'human footprint'; Sanderson et al. 2002, Venter et al. 2016b) displace wildlife, who avoid disturbed landscapes associated with risk of exploitation or transportation-induced mortality (Torres et al. 2016, Tucker et al. 2018, Gilhooly et al. 2019). Notably, and in contrast to most other threats (like mobile predators, which pose transient risk), human footprint often persists on the landscape (Fischer and Lindenmayer 2007, Crooks et al. 2017).

Confronting risk involves trade-offs for wildlife. The energetic cost of avoiding persistent risk or responding to fear may reduce fitness by restricting access to resources important for reproduction and survival. Existing theory (Lima and Bednekoff 1999, Laundré et al. 2010) suggests that if alternatives are few, animals may tolerate risks of significant duration or frequency (*e.g.,* foraging in areas of reduced security; Blecha et al. 2018), but will avoid risks that are short or infrequent (*e.g.*, changing foraging locations to more secure habitat, length of foraging activity, or home range selection; McLoughlin et al. 2005, Laundré et al. 2010, Ordiz et al. 2014). Despite these apparent trade-offs, emerging evidence suggests that human-mediated risk can lead to persistent spatial or temporal avoidance behaviour at the individual and population level (Polfus et al. 2011, Wilmers et al. 2013, Clinchy et al. 2016, Gaynor et al. 2018). Risk avoidance is also likely mediated by body condition (Lima and Dill 1990, Blecha et al. 2018). Additionally, other case studies show that animals may forage in risky habitats if human activities create opportunities for rewarding foods (Sitati et al. 2003, Lamb et al. 2017). More generalized understanding might emerge when we examine how threats to habitat quality and food security might interact in a human-dominated world in which spaces for wildlife are becoming riskier and access to foods less reliable.

Bear-salmon-human systems provide an opportunity to examine trade-offs between risk and reward. For grizzly bears (*Ursus arctos horribilis*), spawning Pacific salmon (*Oncorhynchus* spp.) offer protein, fat-, and nutrient-rich food sources (Farley and Robbins 1995, Hilderbrand et al. 1999a). Unlike other important foods dispersed over landscapes (*e.g.*, emergent vegetation, fruit, roots, nuts, insects, mammals), salmon occur in clumped resource hotspots (Quinn 2005, Schindler et al. 2013). Moreover, consumption is linked to bear fitness: systems with abundant salmon support larger individuals, increased litter sizes, and denser populations (Hilderbrand et al. 1999a, Van Daele et al. 2013). Despite these benefits, accessing this resource can expose bears to risk. Along valley-bottom routes where bears congregate to forage on salmon, humans often have significant and consistent activities and infrastructure (*e.g.*, roadways, resource extraction, settlements, agriculture; Waples et al. 2009), which are associated with increased human-caused mortalities in bears (Nielsen et al. 2004a, Mowat et al. 2013, Boulanger and Stenhouse 2014).

In British Columbia (BC), Canada, the potential trade-offs between risk and reward are pronounced. Grizzly bears have been extirpated from areas of dense human activity in the province (Proctor et al. 2012) and remaining grizzly bear distribution is negatively correlated to human land use (Shackelford et al. 2018). In areas with salmon, increased conflict kills of grizzly bears are associated with reduced local salmon abundance, and generally occurs after the onset of hyperphagia (early July), after which bears face intense caloric demands (Artelle et al. 2016). Human-induced mortality of grizzly bears is also caused by collisions with vehicles, hunting, and poaching, and collectively accounts for more than 80% of known adult mortality (McLellan et al. 1999, 2018, Artelle et al. 2013, Nielsen et al. 2017). Bears generally avoid areas associated with a high risk of human-induced mortality (Lodberg-Holm et al. 2018), though how bears respond to the risk that human-influenced areas impose differs by sex; avoidance of dangerous habitat is often more pronounced in dominant males than females (especially those with cubs) and sub-adults (Bourbonnais et al. 2013, Kite et al. 2016). Subordinate bears actively avoid dominant males to reduce risk of conflict or infanticide (Ben-David et al. 2004). Collectively, these factors could affect how bears trade-off risk and reward when valuable foods occur in dangerous areas.

Herein we use a large (n = 226 bears), long-term (1995 to 2014) and spatially extensive (22 watersheds, over 88,000 km^2) dataset from BC to explore the potential annual trade-offs between risk and reward in human-dominated environments. Specifically, we assess support for three generalizable hypotheses. The Resource Abundance hypothesis predicts that individuals consume more of a valuable resource where and when it is more abundant (*i.e.*, increased salmon biomass density) and available for longer duration (*i.e.*, increased salmon species diversity, which provides salmon for longer, given spatial and temporal variation in spawning across species). The Alternative Food hypothesis predicts that consumers eat less of a key resource (*i.e.*, salmon) where and when alternative foods are more abundant (*i.e.*, higher mean growing season precipitation and temperature and greater area of early-seral forests, both proxies for alternative food availability). Finally, incorporating risk explicitly, the Human Footprint hypothesis predicts that consumption of a focal resource (*i.e.*, salmon) decreases with increased human footprint. Using data confronting these hypotheses - and interactions among them and sex (see Methods) – we evaluate under which scenarios of risk valuable resources might be forsaken. We did this to better understand how habitat and food security, primary conservation concerns for wildlife, might be related.

4.3. Methods

4.3.1. Study area and sample collection

We used stable isotope signatures of hair samples to assess dietary contributions for individually-identified grizzly bears in salmon-bearing watersheds across British Columbia (BC), Canada (survey methods in detail in Adams et al. 2017). Isotopic data from some of these samples first appeared in (Mowat and Heard 2006) (n = 36 males, n = 14 females) across BC, collected from 1995 to 2003 by provincial representatives as part of inspections of hunter-killed samples, generally aggregated on or near resource-road access. We augmented these data with hair from coastal grizzly bears (n = 135 males, n = 41 females) collected using non-invasive hair snags distributed roughly every 25 km^2 from alpine to estuary environments, sampled in the springs months of 2009 to 2014 (Bryan et al. 2014, Service et al. 2014, Adams et al. 2017, Service et al. 2018). When individuals were detected in multiple years, we considered each bear-year case separately based on detection location (n = 68 recaptured individuals across years). When individuals were detected multiple times within one year, we used the detection location associated with the best hair quality for stable isotope analysis (see below; Service et al. 2018).

Non-invasive hair collection from coastal grizzly bears was approved by the Animal Care Committee at the University of Victoria (permit no. 2012-018), following applicable requirements concerning animal care and wildlife research (Canadian Council for Animal Care 2018, Sikes and Gannon 2011). We conducted coastal research in the traditional territories of the Haíłzaqv (Heiltsuk), Kitasoo/Xai'xais, Nuxalk, and Wuikinuxv Nations. Research protocol agreements with these partnering governments prohibit us from displaying sample locations. We also had a permit (106703) from BC Parks to sample in conservancies.

We linked bear samples to salmon biomass data and other predictor variables based on detection location, only considering hair samples collected within watersheds for which there were also salmon enumeration data (n = 22, Figure 4.1; BCGOV 2011, FOC 2016). We used watersheds as a spatial unit for aggregating annual measures of predictor variables for detected individuals, only considering suitable habitat (see below; Bourbonnais et al. 2017). We used third order basins to define watersheds, as delineated by the Strahler stream order hierarchy of tributaries (Figure 4.1; BCGOV 2011). Unsuitable habitat, including water, rock, and ice, were excluded (Artelle et al. 2016). The total area of the watersheds from which we used samples was 88,622 km^2. The watersheds ranged in size from 1,459 km^2 to 7,674 km^2, with a median of 3,392 km^2. For comparison, the average home range areas for individual grizzly bears are generally an order of magnitude smaller (Table B1), reducing the probability that individual bears spanned multiple large-order watersheds in a given year. Although we selected the location of individuals detected multiple times in a single year based on sample quality, we note that all within-year detections of individuals occurred within the same third order basin. We assumed watersheds were a robust spatial unit for aggregating annual trends in predictor variables at a spatial and temporal scale within potential home ranges of individuals because our response variable is an integrated proxy for foraging behaviour throughout the year (Bourbonnais et al. 2017). Watersheds varied in salmon abundance, both in terms of salmon species available (single species to five species) and length of spawning reach within the watershed (Figure 4.1). To account for behavioural and ecological variation among bears and covariates (see below), we delineated watersheds being in one of two regions – coast (n = 12) or interior (n = 10) – as characterized by the boundary of BC's 'coast and mountain temperate rainforest' eco-province (Demarchi 2011).

4.3.2. Estimating salmon consumption

We used hair collected during the shedding phase of the annual molt (May-June) to assess annual diet of grizzly bears. This ensured that isotopic measures represented the assimilated diet during the entire previous year's hair growth (approx. June through October; Hilderbrand et al. 1996, Deacy et al. 2018). We prepared and processed hair samples for stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio estimation via gas chromatography-mass spectrometry (University of Saskatchewan, Saskatoon, SK, Canada; Bryan et al. 2014, Service et al. 2018). We estimated annual dietary contributions using Bayesian mixing models in MixSIAR in R (version 3.1.7, Stock and Semmens 2013), which use $\delta^{15}N$ and $\delta^{13}C$ in consumer and food resource samples, trophic discrimination values, and associated uncertainties to predict the proportion of a diet comprising of a given resource (Moore and Semmens 2008, Hopkins and Kurle 2016). Depending on foods present in interior or coastal regions in which individuals were sampled (Hopkins and Kurle 2016, Adams et al.

2017), these included: terrestrial meat (ungulates), the five main species of Pacific salmon (modelled as one food group), intertidal food sources, and plants (Table B2). We used the median contribution from salmon to yearly diet (measured as a proportion, hereafter 'salmon consumption') as the response variable in analyses (Moore and Semmens 2008, Bryan et al. 2014, Adams et al. 2017, Service et al. 2018). A complete description of our stable isotope mixing model approach can be found in SI Materials and Methods.

4.3.3. Potential covariates affecting salmon consumption

We modeled spatially- and temporally-explicit covariates expected to influence annual salmon consumption. For each watershed, we accounted for geographic and temporal variation in salmon abundance, proxies of alternative food availability, and human footprint (Figure B1 and B2). We considered each of these factors from the year before each hair sample was collected, because hair-derived isotopic information relates to the preceding year's growth (Adams et al. 2017).

Salmon abundance: We used a geo-referenced database of spawning salmon enumerations across BC (FOC 2016) to estimate annual biomass density ('biomass') and species diversity ('diversity') present in each watershed. This database contains annual abundance estimates of the five Pacific salmon species across their spawning reaches. Estimates from regularly monitored streams, however, are frequently deficient (Price et al. 2008, 2017). Accordingly, we employed an imputation method for missing data points for a given species, year, and watershed developed for this dataset (Appendix B; Bryan et al. 2014). We then calculated salmon biomass in each watershed by multiplying abundance estimates by the average mass of salmon (kg) and summing across species, based on average mass of both sexes and a 1:1 sex ratio (Groot and Margolis 1991). We divided total biomass by the length of spawning area of each salmon-bearing stream contained within the watershed, and summed biomass if multiple salmon streams existed within the watershed. Finally, we divided the total biomass estimate by the useable area of the watershed to compute an estimated salmon density within watersheds. Complementing these estimates of abundance, we used the Shannon diversity index to estimate salmon diversity ('diversity'), weighting the number of salmon species by the proportion of the total estimated salmon biomass comprising each species in each watershed (Appendix B; Service et al. 2018). Accounting for species richness and evenness in species abundance, the Shannon diversity index provides a proxy for salmon resource availability over space and time. Increased species diversity results in spatiotemporal asynchrony of salmon availability that we reasoned would extend foraging opportunities for bears (Schindler et al. 2013, Service et al. 2018).

Salmon enumeration efforts in BC (FOC 2016) vary among watersheds and regions (*e.g.*, greater consistency and effort for commercially valuable populations, such as interior sockeye or Chinook, compared with small populations of other species, which are generally concentrated in coastal rivers) and are eroding over time (Price et al. 2017), all of which may affect the reliability of measurements of salmon abundance. We did not expect, however, for any bias to co-occur from salmon variables with HFI or alternative food proxies (Figure B2, Appendix B).

Alternative food availability: We used growing season climatic variables and area of early-seral forest as proxies for alternative food availability (Mowat et al. 2013, Artelle et al. 2016) because direct and comprehensive spatial and temporal estimates of plant and ungulate availability across BC do not exist. We used mean annual spring and summer (April-September) temperatures (°C) and summer (May-Sep) precipitation (mm) as proxies for food abundance derived from plants. We used the program Climate BC, which assembles climatic variables gathered from weather stations across British Columbia to an 800 m x 800 m resolution with high accuracy ($R^2 > 0.9$ for most predicted and weather-station measurements) (Wang et al. 2015). We created a 4 km x 4 km grid of points within useable habitat across each watershed to extract temperature and precipitation data from Climate BC (Artelle et al. 2016). Temperature and precipitation were then averaged over all points within the watershed for a given year and assigned to bears within each watershed.

Grizzly bears use early-seral forest stands (1-10 years post disturbance, such as fire or harvest) for some of the foraging resources necessary for their diverse macro-nutrient profile (Bourbonnais et al. 2014). Regenerating forest supports high densities of emergent vegetation and berry species (Nielsen et al. 2004b), deer (*Odocoileus* spp.; in spring through autumn months) and moose (*Alces alces;* in spring) when compared with mature forest stands (Schwab 1985, Nielsen et al. 2004b, Fisher and Wilkinson 2005). For areas disturbed greater than 10 years, canopy cover is likely to reduce herbaceous growth that are attractants for ungulates (Swanson et al. 2011, Stewart et al. 2012). Given these patterns, we used a composite dataset of landscape disturbance developed using Landsat imagery (Hermosilla et al. 2015, White et al. 2017) to quantify the proportion of annual area of early-seral habitat within a watershed ('early seral'). We classified early-seral stage habitat as fire disturbances and forest harvest blocks being between greater than or equal to one years of age to less than or equal to ten years of age, relative to the date of bear hair collection.

Human footprint: We used a global human footprint index (HFI; Venter et al. 2016a, 2016b) as a proxy for the indirect effects of human influence (versus hunting prevalence as a proxy for direct effects). The HFI characterizes the extent of built environments from multiple proxies of human influence, including population density, nighttime lights, electric infrastructure, crop lands, pasture lands, roads, navigable waterways, and railways, which were all scaled and weighted according to relative levels of human pressure (Venter et al. 2016a). The full HFI dataset ranged from 0 (natural environments; *e.g.*, unlogged regions of coastal temperate rainforest) to 50 (urban environments; *e.g.*, the city of Vancouver, BC). Composite HFI datasets were compiled for 1993 and 2009 (Venter et al. 2016a). We assigned human footprint data depending on temporal proximity, where bears detected from 1993-2001 were assigned data from the 1993 HFI map, whereas bears detected from 2002-2014 were assigned data from the 2009 HFI map.

We considered the density of human influence within riparian zones of all potential spawning salmon reaches within each watershed (BCGOV 2005, 2006) using a 1,000 m buffer on either side of the river system as a riparian zone estimate, where bear activity during the spawning season is generally concentrated (Figure B1; Titus and Beier 1999, Ben-David et al. 2004). Rivers were also ascribed with an HFI value if navigable (depth >2 m) and had evidence of nighttime lights within 4 km of their banks (Venter et al. 2016a). We summarized mean HFI ('footprint') for all riparian zones of reaches within each watershed (ranging from 0.00 to 10.4).

4.3.4. Analyses

We performed all analyses in R 3.2.1 (R Development Core Team 2018). We used a generalized linear mixed model (GLMM; Bolker et al. 2009) and information-theoretic model selection framework to identify associations among patterns of salmon consumption and salmon abundance, alternative terrestrial foods, and human footprint covariates. We developed a candidate model set from combinations of predictor variables and interactions among them that we considered ecologically plausible for predicting salmon consumption by grizzly bears (Table B4). To account for the proportional and continuous nature of annual contribution of salmon to diet, we assumed the response variable was beta-distributed (Moore and Semmens 2008, Fox 2015). We centered and scaled continuous predictor variables before inclusion in models (Schielzeth 2010). We fit GLMMs using the *glmmADMB* package (Skaug et al. 2013). We used a logit link function with intercept-only random effects for year (to account for temporal variation) and watershed (to account for spatial variation). We ranked models using the Akaike's Information Criterion, correcting for small sample sizes (Burnham and Anderson 2002, Bolker et al. 2009).

Using coefficient estimates from our most parsimonious top model, we considered how the predicted annual proportion of salmon consumption might respond to variation in covariates. Specifically, we predicted consumption for males and females separately across observed variation in salmon biomass density and footprint (*i.e.*, at 10% and 90% observed quantiles of our dataset, ~2 to 432 kg/km^2, ~1 to 8.2 human footprint index, respectively), holding all other covariates at their mean calculated for each region.

4.4. Results

Observed salmon consumption as a proportion of total annual diet ranged from 0.02 to 0.91. Consumption was higher for males than for females in both interior (mean = 0.25 (±0.27 SD), 0.06 (±0.02 SD)) and coastal (mean = 0.83 (± 0.1 SD), 0.66 (± 0.23 SD)) regions, respectively.

We identified three top models among 25 competing models (ΔAIC < 2.0, Table B4). We assessed the strength of predictor variables by comparing parameter estimates of the top models (Figure 4.2, Table B5). Although we found little to no effects of region (coastal vs interior), salmon diversity, or precipitation on salmon consumption in all top models (Figure 4.2), we found that sex was an important predictor; males consumed more salmon than females. Additionally, in all top models, salmon consumption was greater in areas with higher salmon biomass density and higher temperature (Figure 4.2 and 4.3). Salmon consumption was moderately lower with increased proportions of early seral forest in the watershed (Figure 4.2 and 4.3). Finally, salmon consumption decreased strongly with increased human footprint in salmon-bearing reaches of watersheds (Figure 4.3). Standardized coefficient estimates suggest the negative association with footprint was stronger than the positive association with salmon biomass density (Figure 4.2). Although we considered interactions between footprint and salmon abundance and sex, our top models did not include these terms (Table B5).

Using parameter estimates from our top model, we predicted consumption in various regional scenarios. For interior watersheds with lower biomass (10% quantile, ~2 kg/km^2), predicted salmon consumption by males and females was 0.58 and 0.35, whereas in watersheds with higher biomass (90% quantile, ~432 kg/km^2), salmon consumption was higher by roughly 20% and 35% (*i.e.*, 0.7 and 0.48), respectively. In coastal watersheds with lower biomass, predicted salmon consumption by males and females was 0.72 and 0.5, higher by roughly by 12% and 24% (*i.e.*, 0.81 and 0.62), respectively, in watersheds with higher biomass. When considering human footprint, we found among the least affected interior watersheds (10% quantile, ~1 HFI), predicted salmon consumption by males and females was 0.46 and 0.25, whereas among the most affected interior watersheds (90% quantile, ~8.2 HFI), predicted salmon consumption was lower by roughly 52% and 60% (*i.e.,* 0.22 and 0.1), respectively. Among the least affected coastal watersheds, predicted salmon consumption by males and females was 0.85 and 0.68, whereas predicted salmon consumption among the most adversely affected watersheds was lower by roughly 23% and 39% (*i.e.,* 0.68 and 0.41), respectively. The magnitude of the human footprint effect thus reduced salmon consumption substantially more than did a reduction in salmon (Figure 4.2, Table B5).

4.5. Discussion

We inferred that human footprint substantially interferes with use of a highly nutritional, spatially-constrained, and otherwise safe food. Such a pattern suggests that wildlife might forgo profitable fitness-related foods if perceived risks from persistent human activity are too high. Although we lack movement data, we detected distinct patterns in the annual foraging behaviour of bears across an extensive area that related not only to measures of food supply but also to human activity, which disrupted an otherwise strong interaction with salmon. Across a range of observed human footprints, we predicted up to a 60% decrease in yearly salmon consumption with other predictor variables held at their means. Previous investigations that have probed drivers of decreased use of foods by wildlife overwhelmingly identify reductions in available resources (*e.g.*, Chinook salmon (*O. tshawytscha*) and killer whales (*Orcinus orca*), Ford et al. 2010; ungulates prey and lions (*Panthera leo*), Yeakel et al. 2009; sea ice decline and predation by polar bears (*U. maritimus*), Rode et al. 2010). Moreover, most inquiry about the adverse influences of human footprint on wildlife behaviour do not evaluate consequences related to the acquisition of foods (but see Ayres et al. 2012, Wilmers et al. 2013). Our work uniquely illustrates how habitat modification can threaten food security for wildlife.

We found mixed support for our resource abundance hypothesis. Accounting for other factors, salmon consumption increased with higher densities of salmon biomass. Diversity of salmon species in watersheds, however, did not affect salmon consumption. This differs from findings at smaller spatial scales that intraspecific phenological diversity of salmon affects the spatial behaviour by foraging grizzly bears within a watershed (Schindler et al. 2013, Deacy et al. 2018), and that species diversity increases salmon consumption by black bears (*U. americanus*) (Service et al. 2018). Our failure to detect an association might relate to many interior watersheds hosting only sockeye salmon (*O. nerka*).

We found strong associations between alternative food availability and salmon consumption at broad scales. In watersheds with more early-seral forests, less salmon was consumed, supporting the hypothesis that bears may forage on alternative foods (*e.g.*, berries, ungulates) in place of salmon, perhaps as spatially-dispersed and thus less-risky alternatives to salmon. We note that this result accounts statistically only for forest age class at a watershed scale, and not disturbance from human footprint in riparian buffers, which we account for independently in models (see below). Contrary to our alternative food availability hypothesis, however, we found that salmon consumption was positively associated with our other proxy for alternative foods (temperature). We expected higher temperatures to serve a proxy for plant productivity, predicting a negative association with salmon consumption. Recent work in Alaska showed that in warmer years, bears consumed fruit (elderberries, *Sambucus racemosa*) preferentially over sockeye salmon when both were available (Deacy et al. 2017). However, our system spans 22 large watersheds, which host substantial variation in plant diversity not expected to show a uniform response to temperature. Additionally, we postulate that higher temperatures could cause lower river levels and lower body condition or mortality in migrating salmon (Rand et al. 2006), which could make an equivalent spawning biomass more available to bears.

Regardless of abundance, salmon consumption is strongly associated with human footprint in riparian spawning areas. Our top models did not include interaction terms between salmon abundance and footprint variables, suggesting that bears avoided risk no matter how much reward was available. Although we information on the spatial ecology of individual bears during salmon-foraging months, our coarse aggregation of analysis at the watershed scale identified a strong effect of human footprint in riparian areas on annual relative contributions of salmon. Making inferences about spawning events, we note that human activity is likely more pronounced in daytime. Although diel activity of humans could drive bears to forage at night (Ordiz et al. 2014), this potential adaptation to a narrower temporal niche apparently cannot compensate for avoidance owing to risk effects during daytime. Existing resource management guidelines and enforcement regarding fish-bearing streams (*e.g.*, forest harvest, road-building; BCGOV 2018) might not be sufficient in mitigating the interference of human activities on the consumption of this fitness-related food for a sensitive large carnivore. How will human disturbance affect bear-salmon systems into the future? The pattern we detected of reduced salmon consumption where HFI is high occurred in watersheds where human activities will likely continue to alter landscapes at rapid rates (Shackelford et al. 2018). Our data predict continued disruption of this predator-prey association unless focussed management intervention occurs.

Given potential benefits to not only bears but also ecosystems, integrated terrestrial, aquatic and marine management could better safeguard this predator-prey system and its associated ecological processes. Reduction in human activity in fish-bearing riparian areas (*e.g.*, road closures during spawning events, stricter riparian development guidelines; Whittington et al. 2019) might allow bears to increase consumption of salmon, and – potentially – population density (Hilderbrand et al. 1999a). These same interventions might be important to restore grizzly bears previously extirpated by human activities in nearby areas that still host abundant salmon biomass (*e.g.*, Fraser River drainages, Figure 4.1; Proctor et al. 2012). Presumably, with less human disturbance, bears can consume more salmon, and in so doing function as more influential ecological agents. Uneaten carcass remains deposited by bears enter into the surrounding riparian forests where vertebrate and invertebrate scavengers, plants, and ultimately juvenile salmon benefit from these marine-derived nutrients (Schindler et al. 2003, Hocking and Reynolds 2011). Greater densities of salmon-supported bear populations predicted from greater salmon consumption (Hilderbrand et al. 1999a) would also increase seed dispersal of berry species via feces, which in turn increases food supply for granivores and bears (Harrer and Levi 2018, Shakeri et al. 2018). Whereas salmon are generally managed as a marine resource under federal jurisdiction in Canada (see 'Wild Salmon Policy', Canada 2005), regulations that influence their ecosystem benefits in terrestrial and aquatic environments should be accounted for across ecological and jurisdictional boundaries (Levi et al. 2012, Van Daele et al. 2013, Artelle et al. 2016, Adams et al. 2017, Price et al. 2017).

More broadly, our study illustrates that the indirect effects of habitat modification transcend the well-known effects of disturbance, alienation, and increased mortality to include the disruption of consumer access to key resources. Salmon offer bears a hyper-profitable, abundant, and fitness-enhancing resource. Despite this reward, and predictions that persistent risk should encourage risky behaviour, grizzly bears showed strong responses to human footprint. As landscapes become increasingly fragmented, valuable resources become more clumped across the landscape (Fischer and Lindenmayer 2007). How individuals navigate the risks of less secure habitat to travel through or forage among aggregations of rewarding focal foods will affect not only their body condition and fitness (Bourbonnais et al. 2013, Wilmers et al. 2013), but also the productivity of their populations (Tuomainen and Candolin 2011, Crooks et al. 2017). The tolerance to accept such risks will have limits. Accordingly, altering risk regimes wildlife face via intensifying human activity on the landscape will have consequences for their behaviour, populations, and important ecological interactions. Thus, increased consideration of how human footprints might be managed to reduce risk associated with accessing key foods could benefit predator-prey systems globally.

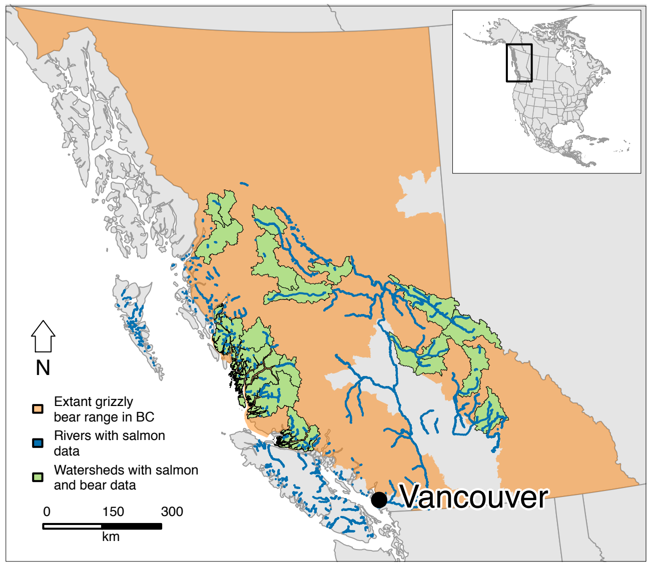

Figure 4.1 Third-order watersheds assessed in analysis (n = 22, in green) within extant range of grizzly bears (*Ursus arctos horribilis*, in orange) in British Columbia, Canada. Salmon-spawning reaches of rivers with enumeration data available are displayed in blue.

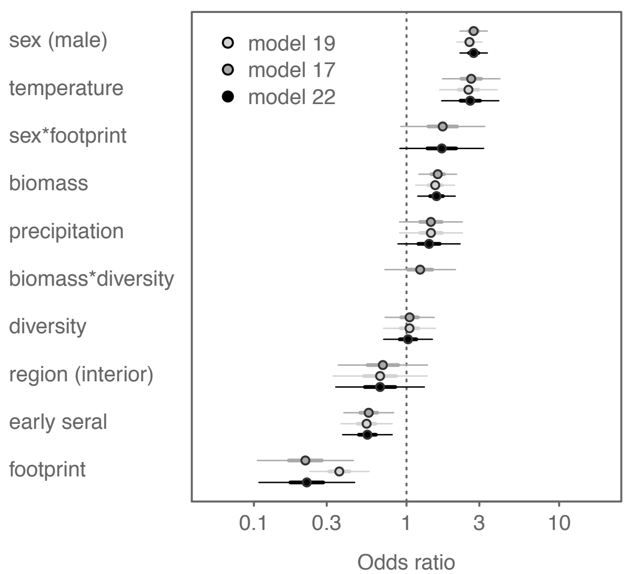

Figure 4.2 Effect sizes of covariates associated with salmon consumption by grizzly bears (*Ursus arctos horribilis,* n = 226) across 22 watersheds in British Columbia, 1995 to 2014. Dots represent parameter estimates as odds ratios, and thick and thin bars represent 50% and 95% confidence intervals, respectively, from the top three models (Table B5). Units are in two standard deviations of each predictor. Parameters are ordered by mean effect size.

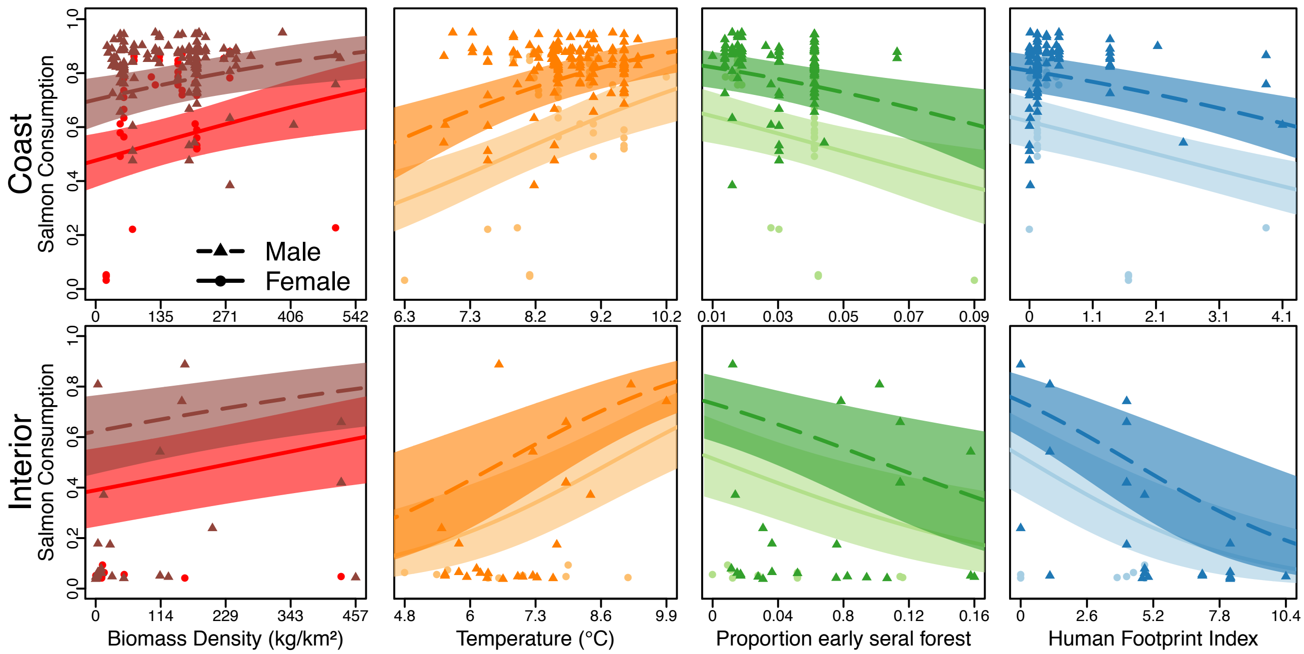

Figure 4.3 Salmon consumption as proportion of total annual diet of grizzly bears (*Ursus arctos horribilis,* n = 226 from 1995 to 2014), as associated with covariates in 22 watersheds. Salmon biomass density, mean annual spring and summer temperature, proportion of early forest area, and riparian human footprint index in watersheds are shown for the simplest model of the top models (model 17), for each factor level of sex and region. The point data represent the raw data associated with each factor level, not accounting for any relationships in the top model (including the covariate modeled on the x axis).

Chapter 5. Culturally-guided ecosystem-based fisheries management: local values and data empower reciprocity in the management of the Wuikinuxv (Rivers Inlet) bear-salmon-human system

5.1. Abstract

Ecosystem-based fisheries management (EBFM) is a comprehensive approach premised on balancing the diverse needs of ecological and socioeconomic beneficiaries. Whereas EBFM has addressed trade-offs between ecological and commercial fishery interests, local social, economic, and cultural recipients have rarely been considered. We illustrate here how harvest goals of an Indigenous fishery and data from their locally-driven wildlife monitoring program align to design and implement EBFM. Grizzly bears (*Ursus arctos horribilis*) hold particular cultural and conservation concern for the Wuikinuxv First Nation in Rivers Inlet, British Columbia, where people and bears have been fishers of sockeye salmon (*Oncorhynchus nerka*) for millennia. The Wuikinuxv Nation's cultural values of respect and reciprocity for wildlife guided our EBFM approach. The region's valuable commercial fishery, active since the late 19th century, has been closed since the sockeye population collapsed in the mid 1990s. In this system, we quantified the predicted trade-offs between long-term fishery yield and ecosystem benefits (*i.e.*, bear densities) in pre- and post-collapse sockeye productivity scenarios. We fit an age-structured state-space spawner-recruitment model before and after the collapse and then estimated the relationship between spawning salmon abundance and relative (1) long-term fishery yield and (2) bear densities. We found that at current levels of productivity the sockeye population had an equilibrium size of roughly 256,190 and could sustain fisheries yields up to 135,350. Before the collapse, we found a population equilibrium size of roughly 1,429,218 and sustainable yields up to 791,650. We found that managing for an EBFM goal, in which fisheries and bears (and by extension, the ecosystem) sustain an equal relative cost, requires foregoing relatively modest amounts of harvest (5-10%), but that the magnitude of the trade-offs is highly dependent on the state of the system (*i.e.*, pre- or post-collapse). Despite large reductions in potential fishery yield after the collapse, we find that Food, Social, and Ceremonial harvest goals of the Wuikinuxv Nation are compatible with an EBFM goal that can simultaneously sustain relatively high bear densities, assuming current productivity remains the same for the foreseeable future. Given the increasing recognition of the stewardship authority held by the Wuikinuxv and other Indigenous Nations in

Canada, a culturally-guided EBFM framework shows much promise for Indigenous and federal managers to implement more holistic approaches to salmon fisheries management.

5.2. Introduction

Moving beyond a single-species focus, ecosystem-based fisheries management (EBFM) aims to sustain healthy ecosystems and resource use by balancing costs and benefits for ecological, economic, and social well-being. Whereas conventional fisheries management has often focused on optimizing long-term commercial catch of single species, EBFM seeks to address cumulative impacts and trade-offs among different ecological and socioeconomic recipients of fisheries (Pikitch et al. 2004, Collie et al. 2016, Marshall et al. 2017). However, the representation of socio-economic recipients in EBFM is typically limited in scope to commercial yield (Marasco et al. 2007, Richerson et al. 2010), despite long-term histories of local subsistence and cultural harvesters also relying on fisheries (Link 2010). The exclusion of local peoples from contemporary fisheries management often leaves communities disenfranchised and marginalized (Read and Hartley 2006, Loring 2013, Bennett 2018). Therefore, while ecosystem-based management strategies may help address ecological complexities in fisheries, implementation may be challenged by lack of engagement or buy-in from local socio-economic and cultural user groups (Bennett 2018).

Local peoples, and their values and knowledge of the land- and seascapes in which they are embedded, can provide additional dimensions to the framework and application of EBFM. Contemporary fisheries are generally managed by centralized agencies over large spatial scales in which harvesters from afar are disconnected from consequences for local communities or ecosystems (Jackson et al. 2001, Berkes et al. 2006, Ostrom 2009). In contrast, local fishers are better positioned to observe ecological consequences and adapt their harvest accordingly, a process made possible by their collective place-based values and knowledge (Wilson et al. 2003, Berkes and Turner 2006). Moreover, fisheries often have prolonged sustainable harvest for human and non-human beneficiaries if they are incentivized and enforced by place-based leadership and the social capital embedded in them (Gutiérrez et al. 2011, Cox et al. 2015, Ban et al. 2017). As such, there is increasing recognition of the benefits of incorporating scientific knowledge with the values, knowledge systems, and decision-making agency held by local peoples to guide EBFM (Armitage 2005, Long et al. 2015, Pinkerton 2018).

Pacific salmon (*Oncorhynchus* spp.) are vital to the culture and economy of local peoples and provide for widespread human and ecological beneficiaries. Indigenous people in the Pacific Northwest harvest salmon for Food, Social, and Ceremonial (FSC) purposes as participants in complex, salmon-driven socio-ecological systems (Brown and Brown 2009, Campbell and Butler 2010, Housty et al. 2014). Common to Indigenous stories, songs, and dances from the region is respect for the plants and animals that also depend on salmon (Turner et al. 2013, Thornton et al. 2015, Artelle et al. 2018). Salmon are also an important nutritional resource for many species of plants and animals (Schindler et al. 2003, Hocking and Reynolds 2011, Levi et al. 2015, Quinn et al. 2018). In addition, commercial salmon fisheries represent vital contributions to settler and Indigenous economies of the Pacific Northwest. However, these economic contributions are waning due to general declines or non-stationarity in many salmon populations attributed to sequential overharvest by commercial fisheries (Slaney et al. 1996, Healey 2009, Price et al. 2017, but see Walters et al. 2018), habitat degradation (Waples et al. 2009), and changing marine conditions (Finney et al. 2000, Peterman and Dorner 2012). Fisheries and Oceans Canada (DFO) is the federal agency responsible for overseeing the conservation of fish populations and management of commercial fisheries in Canada. Under these cumulative stressors, Indigenous communities have much to offer federal managers in the development and implementation of EBFM for salmon (see below) given their local knowledge of fish populations (also referred to as 'stocks'), their adaptive harvesting practices, and their priorities of respect and reciprocity for salmon-driven ecosystems (Healey 2009, Thornton et al. 2015).

Novel opportunities for adaptive salmon management are emerging in the Pacific Northwest. EBFM requires not only quantitative methods but also political will to guide policies and implementation (Levi et al. 2012, Collie et al. 2016). The Wild Salmon Policy in Canada provides a potentially promising opportunity for an integrated approach to salmon management, whereby salmon diversity is to be managed and protected at the level of geographically or genetically distinct populations (Canada 2005). This approach is to be guided by collaboration with Indigenous governments and local stakeholders. A principal tenet of the Wild Salmon Policy is the guarantee of Indigenous fisheries harvest, second only to salmon conservation, followed by commercial harvest (Canada 2005). The policy is under federal review with an increased consideration of ecosystem values and a recent re-commitment to implementation (Price et al. 2017, Walsh et al. 2017). Concurrently, provincial and federal agencies in Canada are increasingly recognizing Indigenous rights and authority not only to access resources (*e.g., R. v. Sparrow* 1990, *Tsilhqot'in Nation v. British*

Columbia 2014), but also to govern resources within their territories (*e.g.*, Coastal First Nations and Province of British Columbia 2016, Adams et al. 2014, Housty et al. 2014, Ban and Frid 2018). We note that from the perspective of many Indigenous Nations, authority to govern territories was never relinquished. Whereas federal agencies responsible for the management of salmon and other species are increasingly overextended (Marshall et al. 2017, Price et al. 2017), the potential for locally-driven monitoring and governance of salmon by Indigenous governments, supported by federal implementation of the Wild Salmon Policy, creates a promising opportunity for novel management approaches.

Grizzly bears (*Ursus arctos horribilis*) are well suited as a focal ecosystem indicator for the EBFM of salmon. Like local Indigenous harvesters, bears are terminal predators that consume salmon in their final life history phase. Sufficient spawner abundances for bear populations may indicate adequate abundance for ocean-based consumers such as seals, seabirds, pinnipeds, and sharks, which access salmon prior to bears (Levi et al. 2012). Bears are a main vector of marine-derived nutrients from salmon carcasses into surrounding ecosystems (Hilderbrand et al. 1999a, Quinn et al. 2009) that benefit many other species (*e.g.,* plants, birds, insects, and other scavengers; Hocking and Reimchen 2009, Hocking and Reynolds 2011, Wagner and Reynolds 2019), and therefore can be considered a surrogate for salmon-influenced ecosystem function (Levi et al. 2012, Van Daele et al. 2013). Salmon-subsidized populations of bears are more dense (Hilderbrand et al. 1999a) and have a greater influence on their surrounding ecosystems (Harrer and Levi 2018, Shakeri et al. 2018). Finally, the charismatic appeal and status as an apex omnivore of conservation concern makes grizzly bears a strong focal species for EBFM for salmon, as people and management agencies may be motivated to account for the ecological requirements of bears alongside those of fisheries.

In the region of Wuikinuxv Territory (Owikeno or Rivers Inlet, BC), people have harvested Pacific salmon alongside bears (*Ursus* spp.) for millennia. Bears are recognized by the Wuikinuxv Nation not only as important ecologically, but also as close cultural relatives that share similar resources on the landscape (F. Hanuse, Elder from Wuikinuxv Nation, pers. comm. 2013). Rivers Inlet sockeye (*O. nerka*) were historically abundant, with upwards of 1.5 million sockeye returning to the system each year (Groot and Margolis 1991, Cox-Rogers and Sturhahn 2005), supporting one of the largest commercial fisheries in British Columbia (Walters et al. 1993, McKinnell et al. 2001). In the mid 1990s, the sockeye population collapsed (to <10,000 returns beginning in 1993), leading to reduced food security for bears. Sharp increases in bear-human conflict ensued, with the destruction of at least fifteen starving grizzly bears in Wuikinuxv village in 1999, when only ~2,000 salmon returned (Boulanger et al. 2004, F. Hanuse, pers. comm. 2013). The decline and eventual collapse of the sockeye population has been attributed to a legacy of overfishing and shifting environmental regimes (McKinnell et al. 2001, Shortreed and Morton 2003, Cox-Rogers and Sturhahn 2005, Ainsworth et al. 2011). The commercial fishery in the region has been closed indefinitely since 1996 following the collapse.

In contrast to previously centralized management by DFO, the Wuikinuxv Nation envisions a new approach to a fishery that sustains their people, provides for bears and the ecosystem, and aligns with their values. Since the closure, the Nation has worked with federal managers to develop in-season monitoring that can inform FSC catch effort (*e.g.*, CPUE, sonar observations). The community communicates regularly amongst themselves and with local decision makers - the Wuikinuxv Stewardship Committee, Wuikinuxv Treaty staff, and Hereditary Leaders - about observed fish conditions or interactions with wildlife and adjusts their effort accordingly. The Nation has harvest goals for future FSC catch (~30,000 salmon) and maintains interest in a small-scale commercial fishery (Wuikinuxv Treaty, pers. comm. 2019). As abundance of the sockeye population has begun to increase (*e.g.*, spawner abundances upwards of 100,000), Wuikinuxv decision makers require more information about the recovery prospects of the population and the potential impacts an increased fishery might have for bears, and by, extension, the ecosystem (Wuikinuxv Stewardship Committee, pers. comm. 2019, T. Walkus/Xvu'sem'da'as, Wuikinuxv Hereditary Leader, pers. comm. 2019). As such, the Wuikinuxv began a locally-driven bear monitoring program that focuses on population monitoring and annual foraging patterns of bears throughout their territory (2013 to ongoing). A research priority for this work was characterizing grizzly diet and population density in response to salmon abundance.

Herein, we examined how salmon catch by both commercial and FSC fishers might be balanced with benefits to grizzly bears, and by extension, to salmon ecosystems. Guided by the Wuikinuxv Nation principle of *Na na kila* – to watch over someone and look ahead for them - we coupled models of fish population dynamics with bear dietary responses to salmon to predict how fishery yield and bear densities respond to increasing abundances of spawning salmon. We then characterized trade-offs between fishery yield and benefits to bears to help understand prospects for the recovery of this salmon population and food security for people and bears alike. Our goal was to identify trade-offs between fishery yield and benefits to bears across a range of spawner abundances to inform Wuikinuxv fisheries managers in harvest decisions. More broadly, our EBFM approach could provide a framework for Indigenous and Western managers to collaborate on increasingly holistic approaches to fisheries management.

5.3. Methods

Following the general method of Levi et al. (2012), we used a multi-stage analysis (see below) to predict how bear population density responded to variation in spawning salmon abundance as influenced by fisheries management in the Wuikinuxv (formerly Owikeno) Lake watershed and adjacent watersheds (3,580 km^2). First, we quantified the shape of the Wuikinuxv sockeye stock-recruitment relationship based on all available data (1948 to 2017), as well as for the periods of pre-collapse (1948 to 1992), and post-collapse (1993 to 2017). Second, we estimated relative dietary contributions of salmon to bears in the study area (n = 68, 2013 to 2017) using stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio estimation from non-invasive hair samples collected from individual bears. We used these data to quantify a relationship between salmon abundance and salmon consumption by bears, as outlined in Levi et al. (2012). Third, we linked this relationship between salmon abundance and consumption by bears to a previously described positive relationship between salmon consumption by bears and their population density (Hilderbrand et al. 1999a). Fourth, holding all other salmon species constant at their median biomass densities (post-collapse, from 1993 to 2017), we quantified the predicted long-term trade-offs between sockeye fishery yields and bear densities across a range of fishery management spawner abundance, also referred to here as 'escapement', targets and stock productivities.

5.3.1. Study area within Wuikinuxv territory

Wuikinuxv (also known as Owikeno) Lake (deep, cold, and oligotrophic, 96 km^2) is located at the head of Rivers Inlet, BC, draining into the inlet via the Waanukv River (5 km) along which Wuikinuxv village is situated (~60 residents; Figure 5.1). Nine salmon-bearing tributaries flow into the lake, all of which host sockeye populations in addition to other salmon species. Local fishers' efforts are generally concentrated in the Waanukv River, and not in the lake's tributaries.

We defined the study area using the lake's watershed (based on the 1:50,000 third order watershed delineation; Province of British Columbia 2018) plus all adjacent neighbouring watersheds to align with the mobility of male grizzly bears within a season of salmon consumption (area = 3,580 km^2 calculated in ESRI Arcmap 10.2, Figure 5.1; Service et al. 2018).

Adult sockeye migrate through the Waanukv River and Wuikinuxv Lake to spawn in nine tributaries (Figure 5.1). Juveniles are primarily lake-rearing (Walters et al. 1993). The tributaries and surrounding systems in the study area (including the Nx-ngvic/Nicknaqueet), Waanukv/Wannock, and C̓àq̌vala/Chuckwalla rivers) also support populations of coho (no consistent enumeration), pink (escapements range from 4300 to 700,700), chum (1,000 to 70,000), and Chinook (1,000 to 70,000) salmon. Median values of these four species collectively comprise ~16% of all salmon biomass in the study area, with remainder biomass contributions from sockeye (ranges presented from 1993 to 2017; FOC 2016).

5.3.2. Estimating spawner abundance

Spawner abundance for the Wuikinuxv Lake sockeye has been annually estimated by Fisheries and Oceans Canada (DFO) since 1948 using stream walks and aerial surveys of clear tributaries, and in recent years by DIDSON and ARIS sonar in the Waanukv River (English et al. 2018). We used the relationship between sonar counts and estimates of spawner abundance on the spawning grounds from 2014 to 2017 to derive an expansion factor (mean = 6.9) for spawning ground surveys from 1948 to 2013 (Appendix C). After applying the expansion factor, average annual reconstructed escapement of Wuikinuxv Lake sockeye from 1948 to 1992 was roughly 974,000 fish (ranging from 195,500 to 3,460,000). Following the collapse in 1993, annual escapements have averaged 273,800 (ranging from 8,300 to 941,100).

We combined sockeye escapements with geo-referenced annual abundance estimates of the four remaining Pacific salmon species from the New Salmon Escapement Database (NuSEDS; FOC 2016) to estimate biomass density. We estimated total salmon biomass in the study area using NuSEDS enumeration data and average-mass estimates for each salmon species, assuming a 1:1 sex ratio (Groot and Margolis 1991, Bryan et al. 2014). Salmon biomass density was calculated as the collective biomass divided by the area of the study area.

5.3.3. Stock-recruitment relationship for Wuikinuxv Lake sockeye

Age composition

We reconstructed annual estimates of population age-structure using scale and otolith samples collected from enumeration efforts between 1960 and 1999 on spawning grounds of Wuikinuxv Lake tributaries (Rutherford and Wood 2000). Age structure varied among years, with five-year-old fish consistently the most abundant age class, comprising on average 68% of spawners. Four-year-old fish comprised on average 31% of spawners, while 3-year-old fish only comprised 1% of spawners. For our stock-recruitment modelling, we applied these average age compositions to years that lacked age-structure data (1948 to 1959, and 2000 to 2017).

Harvest reconstruction

We reconstructed Wuikinuxv Lake sockeye harvest from databases maintained by the Wuikinuxv Nation and DFO. Commercial fishery harvests from 1948 through 1996 are reported in Rutherford and Wood (2000). We updated these harvest records to include Wuikinuxv FSC catch (1964 to 2017; D. Rolston, Wuikinuxv Fisheries Manager, pers. comm. 2019). For years that lacked FSC catch data, we applied a mean FSC harvest rate for years with data to estimate FSC harvests (mean rate = 1% capped at 10,000 rather than a fixed harvest estimate, to reflect Wuikinuxv FSC harvesting practices; D. Rolston, pers. comm. 2019). Prior to the collapse in 1993, commercial harvest rates ranged from 2 to 79%, with an estimated average of 38%. Following the collapse and the closure of the commercial fishery in 1996, reported FSC harvest rates constituted 1% or less of the total run size or less (Figure 5.2).

Stock-recruitment estimation

We used an age-structured state-space stock-recruitment model to estimate the population characteristics of Wuikinuxv sockeye. This approach allows for temporal variability in productivity and age-at maturity, process variation and observation error (Fleischman et al. 2013), and more realistic incorporation of multiple sources of uncertainty than traditional stock-recruitment models fit to salmon data. We fit this model across the entire time series to quantify changes in productivity over time assuming a constant carrying capacity (1948 to 2017; Figure 5.2), and then again for two truncated time series prior to and following the stock collapse (1938 to 1992, 1993 to present; Figure 5.3). Equations 1 through 7 closely follow the model description in Fleischman et al. (2013).

Process model: The process component of the state-space model specified productivity and age-at-maturity by brood year cohort. Returns (R) from 1948-2017 were treated as unobserved states and modeled as a function of spawner abundance (S) assuming a Ricker (1954) stock-recruitment relationship (as is typically used in stationary modelling of Pacific salmon populations (Fleishman et al. 2013) and best reflected the population dynamics within this system (Adams et al. unpublished data)), with serially correlated log-normal process variation:

(1) $$\ln(R_y) = \ln(S_y) + \ln(\alpha) - \beta S_y + v_y$$

where α is productivity (intrinsic rate of growth or recruits per spawner at low population size), β is the magnitude of within brood-year density dependent effects, and v reflects inter-annual variation in survival, which was assumed to be correlated (ϕ) over time:

(2) $$v_y = \phi v_{y-1} + \varepsilon_y\ ,\ \ \varepsilon_y \sim Normal(0, \sigma_R)$$

where ε_y is independent, normally distributed process variation in survival with a standard deviation of σ_R.

The number of sockeye that returned to spawn in year y and age a was the product of the total return in year $y - a$ and the proportion of fish from brood year $y - a$ that returned at age a:

(3) $$N_{y,a} = R_{y-a} p_{y-a,a}$$

where the vector of age-at-maturity proportions were drawn from a common Dirichlet distribution, realized by generating independent gamma variates ($\gamma_{y,a}, a\ \varepsilon\ 3{:}\,5$) and dividing by their sum (Fleischman et al. 2013):

(4) $$p_{y,a} = \frac{\gamma_{y,a}}{\sum_a \gamma_{y,a}}$$

where the gamma variates are drawn from a gamma distribution with shape k_a and inverse scale θ equal to 1. This gamma distribution was parameterized according to Gelman et al. (2013), where the $\gamma_{y,a}$ are the age-specific hyperparameters of the Dirichlet distribution that determine the expected proportions (π_a) of salmon returning at age:

(5) $$\pi_a = \frac{\gamma_a}{\sum_a \gamma_a}$$

Harvest (H) in a given year (y) was then modelled as the product of total run size and the harvest rate (U) experienced:

(6) $$H_y = N_y U_y$$

Data and observation model: Recent sonar observations allowed us to quantify the observation error associated with estimates of spawner abundance based on clear tributaries (CV = 25%; Appendix C). We applied this CV to spawner abundances estimated from clear tributary counts from 1948 to 2013 and assumed sonar observations from 2014 to 2017 were a near-absolute measure of spawner abundance (CV = 0.01, Appendix C). Spawner abundance was assumed to be lognormally distributed with parameters ln($S_{O,y}$) and $\sigma_{S_{O,y}}$, with the CVs converted to lognormal variance (Evans et al. 1993):

(7) $$\sigma^2_{S_{O,y}} = \ln\left[CV^2\left(S_{O,y}\right) + 1\right]$$

We had no direct quantitative estimates of observation error in harvest from the data reported in Rutherford and Wood (2000), but because commercial catch data in this area are considered to be of relatively high precision, we assumed a CV of 15% for years of reported commercial catch, which is similar to estimates applied in other systems (*e.g.*, Fleischman et al. 2013). For the years where cannery pack records contribute to commercial catch (1948-1956), we specified a large observation error (CV of 0.9) to account for the added uncertainty associated with deriving estimates of catch from cannery data. For years where FSC was the only reported harvest, we assumed a large observation error (CV of 0.9 for subsistence harvest as in Fleischman et al. 2013). We assumed harvest observations were log-normally distributed with parameters ln($H_{O,y}$) and $\sigma_{H_{O,y}}$, with the CV converted to log-normal variance as per Equation 7.

Age composition by return year was assumed to be observed with error, where uncertainty in age proportions in a given year was generated by specifying an 'effective sample size' (ESS). For years with age data (1960 to 1999; Rutherford and Wood 2000), we assumed an ESS equal to 100. In years where age composition estimates were unavailable, we used the weighted average proportions from available years as the observed proportions and assumed an ESS of 25 to reflect the higher degree of uncertainty in age composition in those years (pre-1960 and post-1999).

Model fitting: We fit the model (Equations 1-7) for each time series in a Bayesian estimation framework. We constrained the $ln(\alpha)$ prior to follow a uniform distribution between 0 and 3 (Table 5.1). We constrained the β prior to reflect the carrying capacity of the system (as estimated in

Shortreed et al. (2001); Table 5.1). Joint posterior probability distributions for all unknowns in the model were generated using Markov chain Monte Carlo (MCMC) approach in the JAGS sampler in R (Plummer 2017, R Development Core Team 2018). We ran six chains for 300,000 iterations after a burn-in of 50,000 and thinned every 15th iteration. Convergence was assessed by examining the potential scale reduction factor ($\hat{R}$) and assumed to have occurred if $\hat{R}$ was less than 1.1 (Gelman and Rubin 1992).

5.3.4. Estimating Relative Fishery Yield (RFY)

We estimated relative fishery yield (*i.e.*, surplus production relative to MSY, scaled to maximize at 1) across a range of spawning population sizes (S), following Levi et al. (2012):

$$RFY = \frac{\alpha S e^{-\beta S} - S}{\alpha S_{MSY} e^{-\beta S} - S_{MSY}} \tag{8}$$

where α and β are the median estimates of productivity and density dependence (Eqn 1), and S_{MSY} is the spawner abundance predicted to maximize long-term yield from the system under equilibrium conditions (Hilborn 1985). We estimated RFY in pre- and post-collapse scenarios (Table 5.1, Table C2).

5.3.5. Estimating salmon consumption by bears and Relative Bear Density (RBD)

We used hair samples from individual grizzly bears collected in the study area from 2013-2017 (Figure 5.1; survey methods in detail in Adams et al. 2017). Considering the spatial distribution of salmon-bearing watersheds in the area and the mobility of grizzly bears, we considered a watershed region of Wuikinuxv Lake and all adjacent neighbouring watersheds to compromise the study area (Figure 5.1; Service et al. 2018). We collected hair samples from 23 traps located in habitable regions from shore to alpine environments throughout the study area in May and June from 2013 to 2017 (over 575 km^2; Adams et al. 2017). Because collection occurred during the shedding phase of the annual molt (May through June), the stable isotope ratios in samples represent annual assimilated diet during the entire previous year's hair growth (from approximately June through October; Hilderbrand et al. 1996, Deacy et al. 2018).

Non-invasive hair collection from coastal grizzly bears was approved by the Animal Care Committee at the University of Victoria (permit no. 2012-018), following applicable requirements concerning animal care and wildlife research (Canadian Council for Animal Care, Sikes and Gannon 2011). We also had a permit no. 106703 from BC Parks to sample in conservancies.

Estimating dietary contributions

We used estimates of the relative annual proportion of salmon in grizzly bear diet derived from stable isotope analysis (SIA). We preformed SIA on hair samples from 68 grizzly bear detections in the study area collected during the annual moult from 2013 to 2017 (see above). We prepared and processed hair samples and isotope ratio estimation using established SIA procedures (details in Appendix C). We estimated annual dietary contributions from predetermined food groups (see below, Table C4) using Bayesian mixing models in MixSIAR in R (version 3.1.7, Stock and Semmens 2013). These models use the stable nitrogen and carbon isotope ratios in consumer and food resource samples, trophic discrimination values, and associated uncertainties to predict the relative proportion of a diet comprised of given food types (Moore and Semmens 2008, Ben-David and Flaherty 2012, Hopkins and Kurle 2016). We modeled annual proportions of food group contributions by: terrestrial meat (*i.e.*, ungulates), the five main species of Pacific salmon (collectively as one salmon group), intertidal food sources, and plants (Table C4). We used the posterior median contribution from salmon to yearly diet (hereafter 'salmon consumption') in analyses.

Estimating Relative Bear Density (RBD)

We estimated bear density at a particular spawner abundance relative to the spawner abundance at equilibrium (*i.e.*, over the long term in the absence of a fishery), where the spawner abundance in the absence of a fishery, S_{EQ}, is the spawner abundance at the steady state of the Ricker stock-recruitment model,

$$S_{EQ} = \frac{\ln(\alpha)}{\beta} \quad (9)$$

We assumed that long-term spawner abundance at equilibrium would not be affected by the potential for depensatory effects of bear predation, based on the high quality of spawning habitat and the productive nature of sockeye, even at low population densities (Quinn et al. 2014).

Percent salmon in diet for bears, $D(S)$, saturates with salmon abundance, $S\ (kg/km^2)$ (Levi et al. 2012), where h is the half-saturation parameter that determines how quickly bear diets respond to salmon abundance (details in Appendix C, Figure C2):

(10) $$D(S) = \frac{90S}{h+S}$$

Bear density (B) was estimated by linking Equation 10 with a linear relationship between proportion of meat in annual diet and bear population density, assuming a zero intercept (Hilderbrand et al. 1999a, Levi et al. 2012). We assumed the vast majority of meat in the study area was comprised of salmon (Adams et al. 2017). The bear density for a given escapement was therefore,

(11) $$B(S) = b_0 D(S)$$

where b_0 determines how quickly bear densities increase with dietary salmon. Because bear densities increase linearly (Hilderbrand et al. 1999a, Levi et al. 2012), our consideration of bear density cancels out b_0 when considering relative density. Salmon in bear diet saturates with salmon abundance (Equation 10),

(12) $$D(S) = \frac{90\frac{S * m_S + M}{A}}{h + \frac{S * m_S + M}{A}}$$

where m is the mean mass (kg) of an individual sockeye (2.7 kg; Groot and Margolis 1991), M is an estimate of median biomass of other enumerated species present in the study area from 1993 to 2017 (283,108 kg), h is the half saturation parameter estimated in Equation 10 (80.42 kg/km^2; Appendix C), and A is the area of the study area. The relative bear density, RBD, can be written by combining Equations 11 and 12 as,

(13) $$RBD = \frac{B(S)}{B(S_{EQ})} = \frac{D(S)}{D(S_{EQ})} = \frac{S * m_S + M}{S_{EQ} * m_S + M} * \frac{Ah + S_{EQ} * m_S + M}{Ah + S * m_S + M}$$

We compared maximum bear density (over a range of 0 to 1) in pre- and post-collapse conditions with S_{EQ} from the two time periods in Equation 13, assuming pre-collapse conditions as the denominator.

Relative bear density, RBD, and relative fisheries yield, RFY, are now both dimensionless values that can be directly compared. Equations 9 through 13 follow Levi et al. (2012). We solved for an EBFM spawner abundance that aligned with Wuikinuxv values of respect and reciprocity for bears as well as fishers, defined where $RBD = RFY$.

5.4. Results

We estimated the stock-recruitment relationship for the Wuikinuxv sockeye for the full time series, as well as separately before and after the collapse. These estimates and the overall shape of the stock-recruitment relationship, however, are uncertain (Table 5.1, Figure 5.3). Productivity of the stock decreased consistently from the early part of the time series until the collapse in 1993, after which it was highly variable, only recently beginning to rebound (Figure 5.3a; posterior estimates for the full time series in Table C2). Prior to the collapse (1948 to 1992), the stock exhibited greater productivity (median α = 4.26 recruits/spawner, 2.36 – 8.04 95% CIs) with a predicted equilibrium population size more than an order of magnitude larger than at present, at approximately 1,429,218 (Table 5.1). Post-collapse (1993 to 2017), the population demonstrated slightly lower productivity (median α = 4.06 recruits/spawner, 1.25 – 15.17 95% CIs) with a predicted equilibrium population size of roughly 256,194 and an MSY of roughly 102,965 (Table 5.1).

We estimated how bear diet and relative population density responded to increasing salmon abundance in the study area between 2013 and 2017. Male bears consumed more salmon in their annual diet than females (mean = 0.78 ± SD 0.13, mean = 0.53 ± SD 0.27, respectively). Following the sockeye population collapse (mean salmon biomass density sampled in 1998-99 = 77 kg/km^2), the weighted mean of salmon in the annual diet of bears between sexes and among sampled years was 23% (sampled in 1998-99; Levi et al. 2012). In recent years with greater spawner abundance (mean salmon biomass density from 2013 to 2017 = 257 kg/km^2), the weighted mean of annual salmon consumption was 63.6%. Consistent with these observations, predictions of salmon consumption by bears (*i.e.*, predicted by Equation 10) increased with higher spawner abundance (Figure C2). The patterns in this relationship help to explain corresponding increases in predicted bear densities with spawner abundances (*i.e.,* predicted by Equation 13). We found that maximum bear density in post-collapse population equilibrium size was 83% of densities predicted at pre-collapse equilibrium size.

We predicted trade-offs between relative bear density and relative fisheries yields across a range of spawner abundances. Under recent productivities, predicted relative bear density increases and saturates as escapement increases (Figure 5.4b). In contrast, expected fishery yield increases until the escapement that produces MSY (roughly 102,965), and declines thereafter (Figure 5.4b).

We solved for an EBFM spawner abundance where the cost to relative bear densities and fisheries yields were equally reduced from their maxima across a range of system productivities. RBD and RFY were predicted to be reduced by ~10% from their relative maxima at an EBFM escapement of roughly 143,000 (120,000 – 143,000 75% CIs, Figure 5.4b, Table C5), which corresponds to a surplus yield of roughly 123,000 (Figure 5.5). We also assessed RBD and RFY under previous productivities of the system, which were higher and less variable (Table 5.1, Figure 5.4b). We found that under pre-collapse conditions, RBD and RFY were reduced by ~5% from their maxima at an escapement of roughly 735,000 (625,000 – 870,000 75% CIs, Figure 5.4a, Table C5), which corresponds to a surplus yield of roughly 750,000. Changes in population productivity have exacerbated fishery-ecosystem trade-offs in this system, such that the post-collapse trade-off is twice as much loss to maxima relative yield and bear density to meet EBFM goals. However, it is important to note that while the relative trade-off is greater post-collapse, the absolute trade-off for yield is in fact smaller (pre-collapse trade-off = 56,645 vs. post-collapse = 12,352) because the yield declines with declining productivity.

Assuming that recent productivity reflects conditions into the near future, we estimate that maximum sustainable surplus production from the system (*i.e.*, harvest that can occur without causing the population to decline) is approximately 133,000 fish. At the EBFM escapement goal surplus production is approximately 123,000 (Figure 5.5). This EBFM goal and corresponding estimates of production are compatible with the Nation's stated harvest goals for future FSC (30,000) and a modest commercial fishery (*e.g.*, roughly 90,000) (Wuikinuxv Treaty Manager, pers. comm. 2019), although we note the uncertainty associated with these estimates (Figure 5.5).

5.5. Discussion

We quantified the predicted trade-offs between long-term fishery yield and ecosystem benefits (*i.e.*, bear densities) in a salmon system that has undergone a profound regime shift. Cultural values of respect and reciprocity for neighbouring wildlife aligned with, and drove, our EBFM approach. In our design, we fit an age-structured state-space stock-recruitment model to data before and after the regime shift and then estimated the relationship between spawning salmon abundance and relative (1) long-term fishery yield and (2) bear densities. Potential fishery yield from the system declined dramatically post-collapse (MSY = 569,646 and 102,965 pre- and post-collapse, respectively). We found that managing for an EBFM goal, in which fisheries and bears (and by extension, the ecosystem) sustain an equal relative cost, requires foregoing relatively modest amounts of harvest, but that the magnitude of the trade-offs is highly dependent on the state of the system (*i.e.*, pre- or post-collapse). Despite large reductions in potential future fishery yield after the collapse, we find that assuming current productivity remains the same for the foreseeable future, FSC harvest goals of the Wuikinuxv Nation are compatible with an EBFM goal that can simultaneously sustain relatively high bear densities.

Our approach allowed us to consider and account for some of the uncertainty inherent in the data and the system. Specifically, we incorporated uncertainty in the variability of density dependence in the system and observations of spawner abundance, age composition, and catch. Previous assessments of spawner-recruit relationships in Rivers Inlet, and for many systems in the region, assume stationary (*e.g.*, equilibrium) dynamics estimated from stock-recruitment models that assume annual values of spawner abundance and harvest (based on harvest rates and age composition) are measured without error (Walters et al. 1993). In contrast, we used a state-space model framework because it provided a probabilistic approach to population assessment by modeling the stochastic, time-varying nature of population survival and recruitment separately from sampling uncertainty inherent in observations of the population (Fleishman et al. 2013, Holt and Folkes 2015). This approach also allowed us to incorporate prior knowledge of the carrying capacity of the system (Shortreed et al. 2001).

Our approach, however, was limited by a number of assumptions both theoretically and empirically. Despite recent sonar observations, uncertainty in estimates of spawner abundance is quite high in this system (C. Carr-Harris, DFO, pers. comm. 2019). Accurate reporting of FSC catch is highly variable in Wuikinuxv village (D. Rolston, pers. comm. 2019). We also lacked age composition data for 1948 to 1959, and the sample sizes accompanying a subset of years with age composition data (1960 to 1992). Finally, our estimates of relative bear density were limited by our assumption of a linear relationship of salmon in diet and productivity of thirteen grizzly bear populations as reported in Hilderbrand et al. (1999a) without accounting for uncertainty. However, we found that our inference was robust to these assumptions and limitations (see Appendix C for sensitivity analyses with alternative priors and observation errors).

We quantified how bears respond to salmon abundance under alternative salmon population productivity scenarios. We found that under current conditions, predicted grizzly bear density is ~80% of their pre-collapse densities. As spawner abundance increases, bear density will increase and likely saturate, as will the benefits they confer to local systems via salmon foraging (Quinn et al. 2009, 2018, Darimont et al. 2010, Shakeri et al. 2018). While the Wuikinuxv Lake sockeye population may not recover to support previous densities of bears, the dietary contributions we observed and relative bear densities predicted under current conditions suggest that grizzly bears have adequate access to salmon. These results suggest that under current conditions the benefits to surrounding ecosystems from salmon-fed bears (*e.g.*, fertilization, seed dispersal) can be sustained and the risk of potential conflict with Wuikinuxv village residents is low (Artelle et al. 2016).

The opportunity for, and apparent benefits of, values-driven EBFM are illustrated in the Wuikinuxv sockeye system. Here, local Food, Social, and Ceremonial harvest goals and values for ecological well-being support a "triple bottom line" balance between cultural, economic, and ecological goals (Marshall et al. 2017). We found that current and future harvesting goals of the Nation are compatible with an EBFM approach, which accounts for benefits to bears, and by extension, ecosystems. Wuikinuxv's fishery in the Waanukv river is terminal, occurring directly before the spawning area, and is informed by Nation-driven CPUE surveys and sonar observations. In contrast, upper limits of sustainable harvest (*i.e.,* surplus recruitment) are likely not compatible with expected large-scale commercial yield (mean pre-collapse catch (excluding cannery pack) = 521,045 from 1955 to 1993; Figure 5.5). While modest commercial harvest is possible given predicted surplus production (up to 90,000; Figure 5.5), the Wild Salmon Policy specifies salmon conservation and Indigenous access to FSC harvest take precedence to commercial fisheries. Given the high uncertainty in our estimates of EBFM goals (Figure 5.4, Figure 5.5, Table C5) and the importance of long-term sustainable yields to Wuikinuxv harvesters, a prudent approach to management may be the application of the precautionary principle. The local consequences of stock decline are not only reduction in economic and food security for people, but also decreased salmon for bears and subsequent increases in human-wildlife conflict. The consideration of these consequences is reflected in the precautionary approach of Wuikinuxv decision makers and can motivate the implementation and enforcement of management goals.

Non-stationarity in salmon population dynamics is a major challenge for stock assessment and harvest management across the Pacific Northwest (Holt 2010, Collie et al. 2012, Peterman and Dorner 2012). This limitation is compounded by decreased capacity from centralized agencies such as DFO or the Province of British Columbia to monitor and manage fish and wildlife populations (Price et al. 2008, 2017, Loring 2013). Concurrently, however, Indigenous governments are turning their collective efforts towards holistic and increasingly de-centralized monitoring and management to guide their stewardship of marine and terrestrial species (*e.g.,* Coastal Guardian Watchmen Network, the Central Coast Indigenous Resource Alliance, Nation-based Integrated Resource Stewardship Departments or otherwise; Ban et al. 2017, 2018). The bear data we present, which are part of a larger multi-Nation collaborative bear research program, is one such example of the transition to local, Indigenous-led monitoring (Bryan et al. 2013, Service et al. 2014, Adams et al. 2017, Service et al. 2018). In addition to Indigenous Nations' motivations for sustained cultural and economic access to salmon, their values of respect and reciprocity for ecological consumers within socio-ecological systems of which they are part are congruent with the balance among cultural, ecological, and economic goals for which EBFM strives. Locally-driven and executed research, including data on bears and salmon from which we draw, can continue to support place-based and localized decision making. The Wuikinuxv's focus on grizzly bears, from both cultural and coexistence perspectives, makes them an important focal species in an EBFM framework in this system. Although our approach does not recommend specific allocations for bears and other wildlife, we emerge with a spawner abundance goal in a trade-off framework that imposes equal costs to ecological consumers and human fishers. More broadly, the opportunity for locally-driven fisheries management in the system and beyond is timely as the Wild Salmon Policy and Reconciliation Protocol are being implemented in British Columbia. Western scientists are in a unique position to participate as Indigenous Nations increasingly taking the lead on ecosystem-based fisheries management (Adams et al. 2014, Salomon et al. 2018, Ban et al. 2018), which after a recent history of conflict, may actually align with federal management policies.

Future directions of EBFM will have to apply interdisciplinary approaches that draw not only on fisheries science and ecology but also on local values and culture. This approach can more comprehensively and justly account for complexity in socio-ecological systems reliant on fisheries (Bennett 2018). We note that the approach we have taken to quantify fishery yields and evaluate trade-offs with bear densities under an EBFM framework assumes long-term equilibrium conditions. This assumption is limited because it does not fully consider the current state of the system, nor does it account for the imperfect nature of observing a system and managing fisheries that seek to harvest from it (Cenek and Franklin 2017). A closed-loop simulation of stock dynamics and an ecosystem-based management system could be developed to rigorously evaluate the predicted ability of alternative management actions (*e.g.*, fishery management reference points and FSC and commercial harvest goals) to meet ecosystem, Indigenous harvest, and commercial fishery objectives. This would allow the dynamics of the system to be simulated forward in time over a meaningful period (*e.g.*, 20 to 50 years), where the biological state of the system is conditioned on the most recent data. This approach should be undertaken in a collaborative manner with Indigenous titleholders in conjunction with local stakeholders. This group would define the social, economic, and ecological objectives that alternative management actions are evaluated against to be most meaningful and decisions-relevant. This type of approach is commonly referred to as 'Management Strategy Evaluation' in fisheries literature (*e.g.*, Punt et al. 2016). The age-structured state-space stock-recruitment model we developed is well-suited as the basis of the biological model used in such an exercise. These directions have great potential for contributing to ecosystem-based fisheries management efforts focused on delivering sustainable harvest to diverse fishery beneficiaries. The implementation of such efforts can be guided and realized through cultural values and leadership of local governance systems in Canada and beyond.

Table 5.1 Prior distributions for model parameters and marginal parameter estimates of pre-and post-collapse regimes. Alpha posteriors are reported on the natural scale.

Pre-collapse, 1948 to 1992, S_{EQ} = 1,429,218, S_{MSY} = 569,646				
		Posterior		
	Prior	50^{th} percentile	2.5^{th} percentile	97.5^{th} percentile
$ln(\alpha)$	~U(0,3)	4.26	2.36	8.04
β	~N(4.18 E-6, 0.3†)	1.01 E-6	5.72 E-7	1.50 E-6
θ	~U(-1,1)	0.36	0.03	0.70
σ_R	~U(0,100)	0.70	0.22	1.31
γ_3	~Dirichlet(0.33, 0.33, 0.33)	0.016	0.009	0.28
γ_4		0.32	0.28	0.37
γ_5		0.66	0.61	0.71
Post-collapse, 1993 to 2017, S_{EQ} = 256,194, S_{MSY} = 102,965				
		Posterior		
	Prior	50th percentile	2.5th percentile	97.5th percentile
$ln(\alpha)$	~U(0,3)	4.06	1.25	15.17
β	~N(4.18 E-6, 0.3†)	5.47 E-6	1.95 E-6	9.67 E-6
ϕ	~U(-1,1)	0.62	0.23	0.92
σ_R	~U(0,100)	0.85	0.42	2.04
γ_3	~Dirichlet(0.33, 0.33, 0.33)	0.006	0.001	0.016
γ_4		0.28	0.23	0.34
γ_5		0.72	0.66	0.77

† in SD units

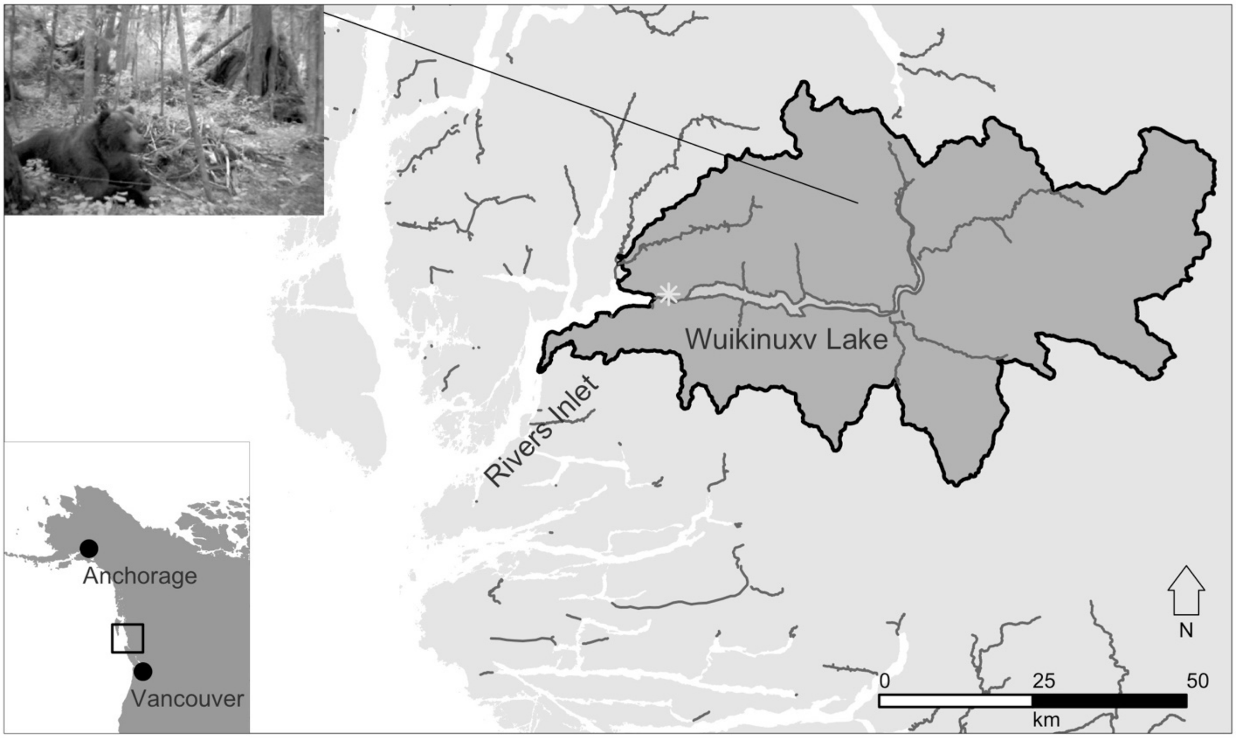

Figure 5.1 Wuikinuxv Lake watershed and neighbouring watersheds (dark grey, 3,580 km²) (Province of British Columbia 2018), located in Wuikinuxv Territory in Rivers Inlet, British Columbia, Canada. Grizzly bears were detected at hair collection traps (n = 23 distributed evenly over 575 km²) throughout the study area from 2013 to 2017 (Adams et al. 2017). The star denotes Wuikinuxv village, where most FSC harvest occurs. Thick grey lines represent salmon-bearing streams and rivers in the region. Sockeye spawn in the Wuikinuxv Lake tributaries and primarily rear in the lake.

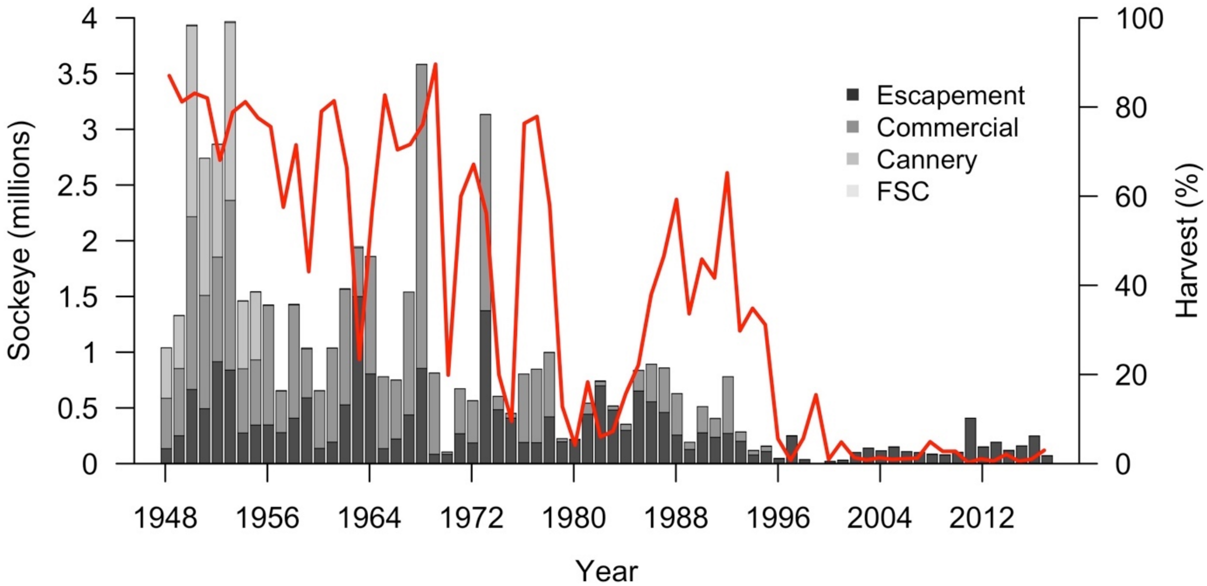

Figure 5.2 Total reconstructed escapement and harvest rate by commercial and FSC fisheries for the Wuikinuxv Lake sockeye 1948 to 2017. Mean FSC harvest rates are less than one percent (range 0.01% to 2.5%), making them undiscernible. Harvest rates are shown in red.

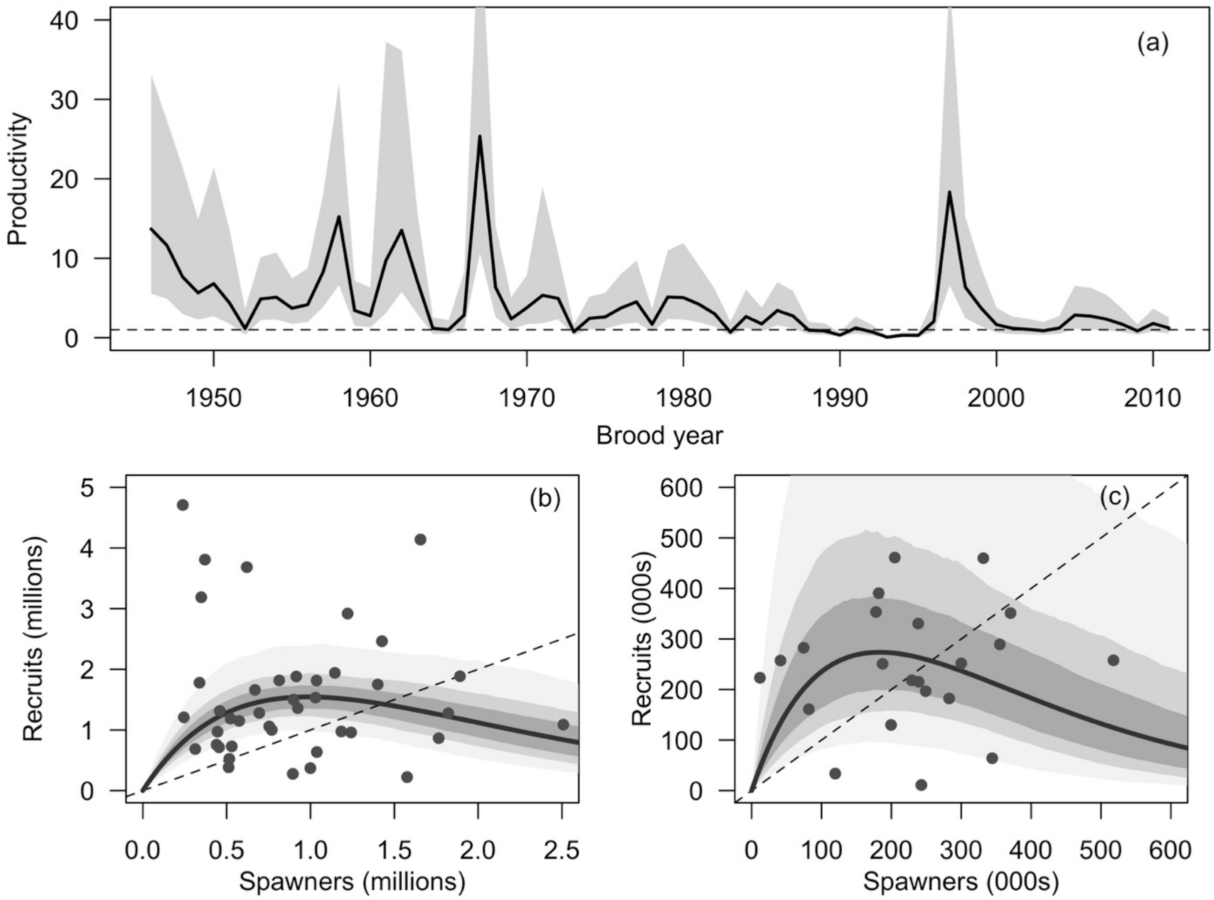

Figure 5.3 (a) Estimated productivity (recruits produced per spawner at small population size) of the Wuikinuxv Lake sockeye (calculated as α + exp(residuals)) with 95% credible intervals from the Bayesian state-space age-structured model over the full time series (1948 to 2018). Relationship between recruitment and spawner abundance for (b) the Wuikinuxv Lake sockeye pre-collapse years (1948 to 1992), and (c) post-collapse years (1993 to 2017). The dashed black line is the 1:1 replacement line. Grey polygons are the 50th (dark grey), 75th (medium grey), and 95th (light grey) credible intervals predicted between spawner abundance and recruitment based on 1000 random draws from the posterior distributions of the stock-recruitment relationship to illustrate uncertainty. Note the difference in magnitude between the y axes in the two time series.

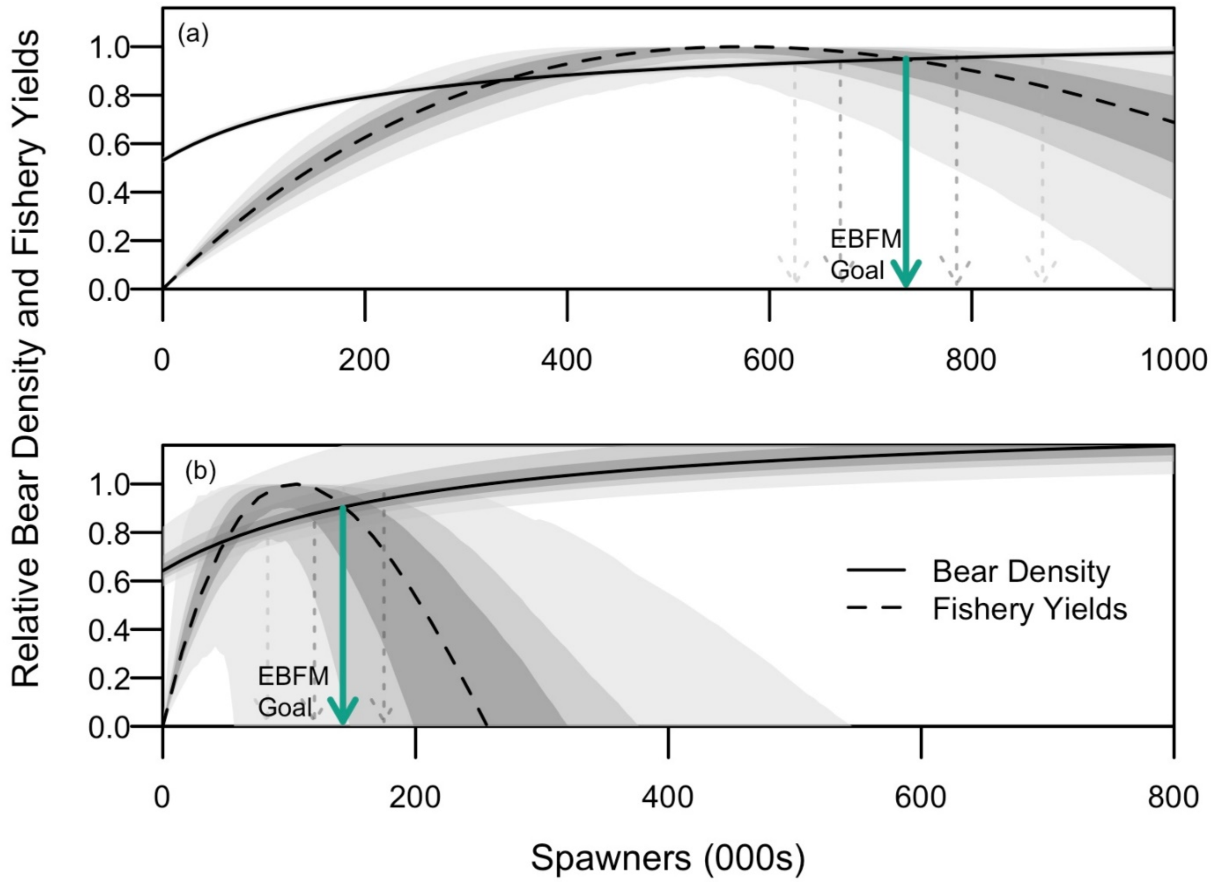

Figure 5.4 The relative bear density (RBD, solid) and relative fisheries yield (RFY, dashed) across a range of escapements in the Wuikinuxv Lake sockeye stock based on median productivity from the (a) pre-collapse stock-recruitment model (median α = 4.26 (2.36-8.04 95% CIs), 1948 to 1992), and median productivity from (b) post-collapse stock-recruitment model (median α = 4.06 (1.25-15.17 95% CIs), 1993 to 2017). Under pre-collapse productivity, ecosystem-based fisheries management (EBFM) is achieved when RBD and RFY are equal, at an escapement goal of ~735,000 (75^{th} and 50^{th} percentiles in dark and medium grey arrows, Table C5). This target would be achieved in post-collapse conditions at an escapement of ~143,000 (75^{th} and 50^{th} percentiles in dark and medium grey arrows, Table C5). Note that biomass from other salmon species in the system was held constant under both calculations of RBD, so as to compare the relative effect of the sockeye biomass on RBD. Grey polygons are the 50^{th} (dark grey), 75^{th} (medium grey), and 95^{th} (light grey) credible intervals predicted for RBD and RFY based on 1000 random draws from the posterior distributions of alpha and beta, and subsequent calculations of S_{MSY} and S_{EQ}, to illustrate uncertainty. Lower ranges of variability in alpha and beta lead to lower CI ranges, especially in RBD, in the pre-collapse period (Table 5.1).

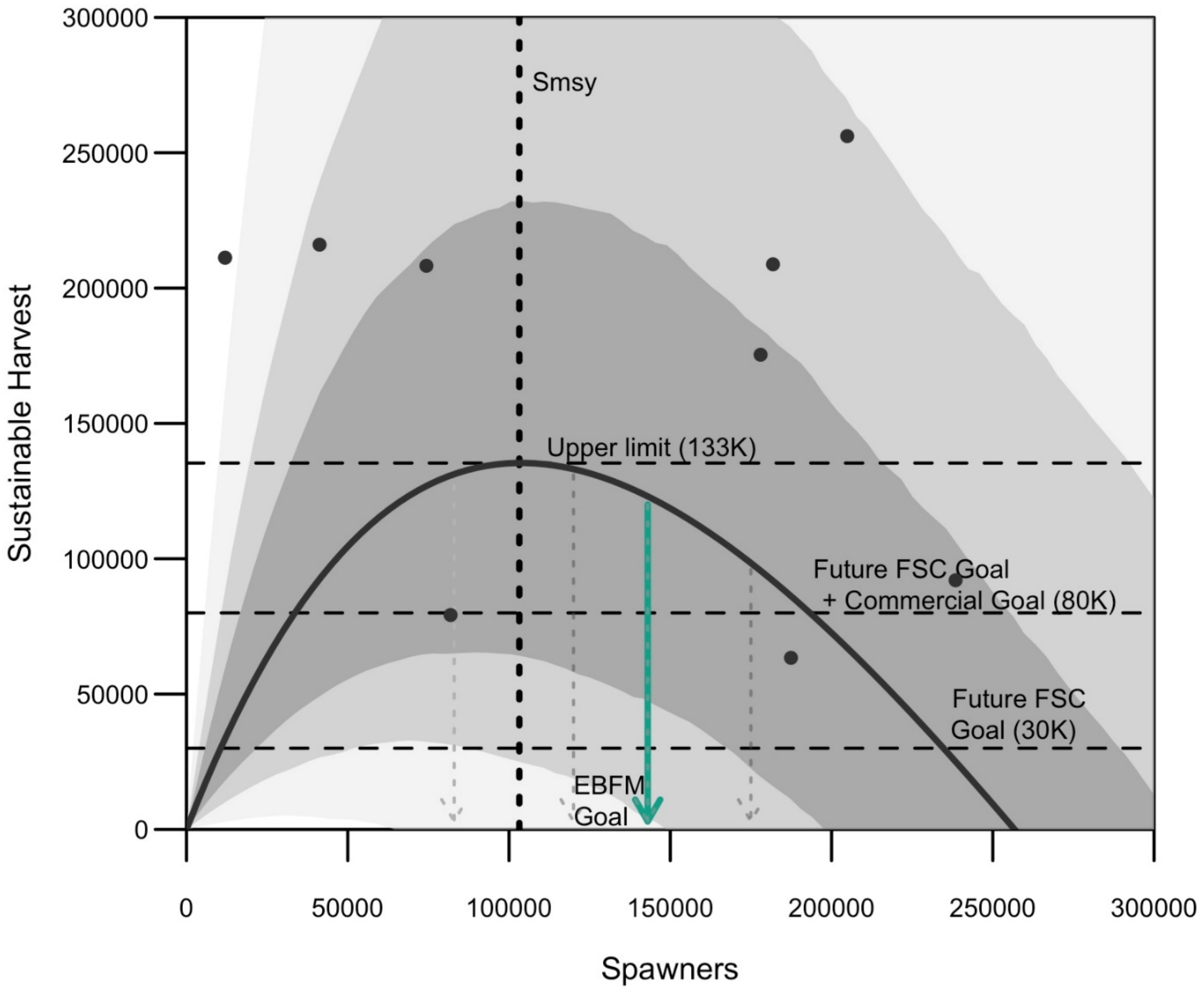

Figure 5.5 Sustainable yield (surplus recruits across the variation in spawner abundance), given alpha and beta parameters of the post-collapse (1993 to 2017) model for Wuikinuxv Lake sockeye. Horizontal dashed lines represent various harvesting levels, where the upper limit occurs at the height of the curve (at MSY). Two future harvesting goals of the Wuikinuxv Nation, including projected future FSC harvest needs and a potential small-scale commercial fishery, are within the upper harvesting limit and the EBFM goal (Figure 5.4b) that corresponds to a yield of approximately 123,000. Grey polygons are the 50th (dark grey), 75th (medium grey), and 95th (light grey) confidence intervals predicted between spawner abundance and recruitment based on 1000 random draws from the posterior distributions of the stock-recruitment relationship to illustrate uncertainty. Dark and medium grey arrows are the 75th and 50th percentiles of the EBFM goal (Table C5).

Chapter 6. Conclusion

6.1. Contributions and opportunities for future research

Considering the needs of wildlife could inform how people use natural resources and mitigate our growing impacts on how, when, and where animals forage. While humans can coexist with wildlife, many of our activities can displace wildlife in shared landscapes or reduce the availability of prey via competition. The cumulative impacts of human activity are altering movement patterns (Tucker et al. 2018, Gaynor et al. 2018), habitat availability and selection (Crooks et al. 2017), and population persistence (Tuomainen and Candolin 2011) for many species. Examples of these impacts exist across taxa, including large cats (Kanagaraj et al. 2013, Wilmers et al. 2013), ungulates (Stankowich 2008), toothed whales (Tosi and Ferreira 2008, Lacy et al. 2017), and migratory birds (Sanderson et al. 2006). Evaluating how human activity affects the acquisition of key foods by wildlife could inform management approaches that are targeted at minimizing impacts to ecological associations.

The impact of human activities on consumer-resource interactions could be moderated by implementing ecosystem-based planning and management approaches. Ecosystem-based approaches promise to balance trade-offs between ecological systems connected to resources that are also culturally, socially, and/or economically important to people (Long et al. 2015, Marshall et al. 2017). These approaches draw on a variety of theory and information from ecology, earth sciences, and remote sensing of human pressures and environmental change on landscapes (Venter et al. 2016b). However, ecosystem-based management approaches are often hard to implement, either for lack of quantitative data or political will (Marasco et al. 2007, Bennett 2018). The involvement of local people in ecological research and in resource management has shown been shown to address these limitations through localized place-based knowledge, small-scale governance systems, and the ability to adapt resource use to management consequences (Armitage 2005, Lemos and Agrawal 2006, Cox et al. 2015). Critical to the success of local management efforts is the transfer of some degree of authority over natural resource decision-making from top-down agencies to local communities (Dietz et al. 2003, Armitage et al. 2010).

My dissertation has focused primarily on quantifying and understanding how foraging behaviour varies across space and time, and how actions by humans via predation risk or competition might affect those behaviours. Using salmon consumption by populations of grizzly bears across British Columbia as a focal consumer-resource interaction, I have made contributions to ecological discourse (Chapters 3 through 5). Specifically, I explore the variation in foraging niche of individuals within species (Bolnick et al. 2003, 2011, Estes et al. 2003), characterize the spatial extent of marine-terrestrial interactions and, by extension, ecosystem subsidies (Willson et al. 2004), and advance theory related to human-mediated predation risk and its effects on consumer-resource interactions (Lima and Bednekoff 1999, Frid and Dill 2002). Broadly, this dissertation contributes to the scientific understanding of human impacts on the ecology of large carnivores, whose persistence is threatened from the cumulative effects of conflict, hunting, fragmentation, and altered food availability in human-dominated landscapes (Laliberte and Ripple 2004, Ripple et al. 2014, Darimont et al. 2015). My research process serves as an example of the opportunities, challenges, and productive synergies for conducting research centered on community priorities (Chapter 2).

I have identified several key findings, opportunities for future research, and management implications for each data chapter:

Chapter 2: Towards increased engagement between academic and Indigenous community partners in ecological research (Adams et al. 2014 *Ecology and Society*)

Complementing local and traditional ecological knowledge, Indigenous communities can draw on scientific research to inform local decision-making and resource stewardship. Given adequate time, funding, and training (*e.g.*, cultural safety, decolonization workshops), scientists are well-positioned to provide capacity towards such research. This requires academics to localize or "center" their research priorities, intentions, and time in communities (Adams et al. 2014, 2015). This chapter provides a framework for the process of community-engaged ecological research from the collective experiences of my academic and community colleagues on the central coast of BC. In this chapter, I outlined how colleagues can collaborate on the conception, design, implementation, and dissemination phases of the research process towards shared priorities (Adams et al. 2014). I showed how respect, trust, co-capacity building, and productive relationship emerge among collaborators throughout the framework stages. While other research disciplines have considered how their knowledge systems and access to academic privilege might be leveraged towards community priorities (*e.g.*, health, geography, anthropology), ecologists and other natural scientists are only just beginning to consider how we might de-center our research process from the academy (Huntington 2010, Huntington et al. 2011). This chapter was a comprehensive 'call to action' for ecologists to engage with Indigenous communities on mutual research priorities, though I recognize this is generally limited in scope to those ecologists doing applied work and for Indigenous communities seeking collaboration.

In addition to outlining why there are mounting motivations to do engaged work, this chapter also provides an honest assessment of how such work can be challenging. Indigenous governments may not have the desire or capacity to engage with many researchers and scientists may not have the desire nor capacity (*e.g.*, funds, time, cultural safety awareness) to conduct research driven by community priorities. Frankly, it is not simple to reconcile timeframes, reward structures, and values among any collaborators that hold different worldviews and knowledge systems. Without addressing these challenges, ecological research collaborations can recreate problematic and extractive academic practices from the past or present (*e.g.,* mapping and geographic research without inclusion of Indigenous peoples or their perspectives, or removal of art and property without consent in historic anthropology; Smith 1999).

Despite these limitations, scientists and Indigenous governments have tools and information that can be shared bi-directionally. More work is required on the part of universities and other research institutions to consider diversifying scholarly reward structures (*e.g.,* beyond the number of publications or citations) to allow for and even encourage greater community engagement capacity. This is important because community-engaged work can be productive (*i.e.*, parties can learn more collectively than the sum of their individual efforts) and can have emergent and unanticipated benefits, such as future research collaborations or capacity building for researchers and community members (Adams et al. 2014, 2015). As Indigenous governments seek diverse tools from the social and natural sciences to support their natural resource governance (*e.g.*, Indigenous knowledge, interview data, ecological monitoring, mathematical modelling, Ban et al. 2017) and investment in community engagement grows in academia, the resulting framework can spur collaborative research among ecologists and Indigenous managers (Salomon et al. 2018, Ban et al. 2018).

Chapter 3: Intrapopulation diversity in isotopic niche over landscapes: spatial patterns inform conservation of bear–salmon systems (Adams et al. 2017 *Ecosphere*)

Understanding hotspots of resource use and how they might change over time can prioritize management actions to mitigate human impacts on consumer-resource systems. In Chapter 3, I characterized spatial variation among male and female grizzly bears in the bear-salmon predator-prey association at a provide-wide scale (~692,000 km^2). At the smaller spatial scale of coastal BC (22,000 km^2), I provided additional resolution and novel visualization of variation in salmon consumption across multiple salmon-bearing watersheds and between species and sex of grizzly and black bears. I demonstrated how these results could evaluate the efficacy of existing protected areas and inform the siting of new protected areas that can specifically target conserving the bear-salmon ecological interaction (Darimont et al. 2010). More broadly, this analysis demonstrates the immense spatial extent of marine subsidies to terrestrial ecosystems, which extends from the coast to nearly the Rocky Mountains.

These findings have limitations as a result of their large spatial scope. Though the data show annual and multi-year cumulative patterns of foraging behaviour at the home range and partial species range scale, they cannot address intra-annual variation in foraging behaviour among or within patches (*i.e.,* within watersheds). In addition, detections of individuals and their diets via hair sampling and stable isotope signatures does not allow for fine-scale assessment of foraging behaviour, especially when samples are collected in months when salmon are not present on the landscape. Instead, isotope ratios in hair samples represent the collective foraging outcomes of an individual bear across a broad spatial scale (*i.e.*, on the order of a home range).

Given cumulative effects of human activities on ecosystems, including climate change (Parmesan and Yohe 2003, Barnosky et al. 2012), future research could characterize interannual shifts in intra- and interspecific spatial patterns of foraging on salmon. This research could focus on stressors affecting salmon availability, such as rising freshwater temperatures (Kaushal et al. 2010), changing marine conditions (Li et al. 2013), and the subsequent implications these stressors have on terrestrial consumers. I did not address underlying drivers of spatial patterns of salmon consumption at a coastal scale (but see Chapter 5 for a provide-wide assessment). However, it is likely that spatial patterns of salmon consumption on the BC coast are driven by salmon species diversity, abundance, phenology, and/or stream characteristics (*e.g.,* depth, flow rate) as bears track salmon availability within and among watersheds (Schindler et al. 2013, Deacy et al. 2018, 2019). At the scale of a single stream, availability and attributes of individual fish may drive bear selection patterns (*e.g.*, entire fish vs. partial, energy-rich body parts; Gende et al. 2001). Foraging by grizzly and black bears on salmon streams is in part also constrained by social dominance (Gende and Quinn 2004, Ben-David et al. 2004, Belant et al. 2006). Additionally, foraging patterns of black bears could be driven by decreased competition with grizzly bears (Belant et al. 2006, Service et al. 2014) or by prolonged foraging opportunities from salmon diversity in the watershed of detection (Service et al. 2018).

If successful foraging outcomes across individuals is ultimately a determining factor for persistence of their populations, then knowing where hotspots of consumer-resource interactions consistently occur in spite of cumulative stressors will be important for prioritizing conservation and management strategies. Identifying hotspots of resource use over space and time could guide allocation of habitat and key foods for wildlife populations, especially across marine and terrestrial ecosystems boundaries (Price et al. 2009, Darimont et al. 2010). For example, this work could contribute to ongoing ecosystem-based management, land-use planning, environmental protection, and wildlife policies of Indigenous Nations in coastal British Columbia. It could also guide land-use planning or multi-species recovery efforts (*e.g.,* Westwood et al. 2018) by accounting for marine and terrestrial connections in ecosystems currently managed separately by federal and provincial agencies (respectively) in Canada.

Chapter 4: Human footprint in salmon-bearing watersheds unravels predator-prey interactions between grizzly bears and salmon

In Chapter 4, I find that the effects of human footprint and proxies for alternative food are more strongly associated with foraging interactions between bears and salmon than the abundance of salmon itself. Although many studies have documented how human activity affects wildlife movement patterns, I demonstrate how these disturbance patterns might reduce foraging of a focal food resource. These results show that in addition to exerting general effects on bear activity and movement (Stewart et al. 2012, Ordiz et al. 2017a, Lamb et al. 2018), predation risk associated with human activity is strong enough to reduce foraging by bears on critical foods such as salmon.

Although human footprint was the most strongly associated predicator variable with salmon consumption in this analysis, mean spring and summer temperature was also strongly associated. We used climate variables as proxies for alternative food availability because we lacked comprehensive estimates of alternative food sources (*e.g.*, berries, ungulates) across the temporal and spatial scope of our dataset (22 watersheds, from 1995 to 2014). While we chose temperature because of its relationship to the primary productivity of plants, fruit production, and food for ungulates (Mowat et al. 2013, Artelle et al. 2016), we cannot offer greater insight from this result. Temperature could be affecting the availability of alternative foods (*e.g.*, productivity or phenology of emergent vegetation or fruit, Deacy et al. 2017), while simultaneously reducing salmon productivity from high water temperatures (Hodgson and Quinn 2002).

Future work could focus on how bear-salmon interactions will change under increasing human impacts to landscapes and climate. To address the limitations presented for Chapter 4, future work will require better estimates of alternative food and salmon availability (*e.g.*, a consideration of access to foraging habitat in salmon-bearing watersheds, in addition to data on salmon abundance and biomass). Phenological shifts in resource pulses, such as the timing of emergent vegetation or the upwelling nutrients in marine environments, are synchronizing foods that were previously available at different times, with widespread repercussions for generalist consumers in many ecosystems (Parmesan and Yohe 2003), including bear-salmon systems (Carlson 2017, Deacy et al. 2017). In essence, phenological synchrony results in the reduced ability of consumers to capitalize on resource pulses that previously occurred at different times (Both et al. 2009, Miller-Rushing et al. 2010). As landscapes become more disturbed and associated predation risk for wildlife from humans increases, synchrony of resource availability may truncate the overall availability of heterogenous food resources and add additional complexity to the decisions animals make on when, where, and what to eat.

Mobile generalist species can better meet nutritional requirements when they can forage on diverse food options in connected landscapes. For the bear-salmon association in British Columbia and beyond, future management should focus on maintaining habitat connectivity and reducing human infrastructure and access in valley-bottoms of salmon-bearing watersheds. This is especially important where bears may not have prolonged access to salmon resources because of low salmon diversity, which often occurs in interior watersheds that also have higher rates of human development. For example, in the upper reaches of the Fraser River, sockeye may be the only species in a watershed (Figure B2). However, intrapopulation salmon diversity, especially in large watersheds, may prolong foraging opportunities as well (Schindler et al. 2010, Nesbitt and Moore 2016). At the watershed scale, future work could characterize how bear movement and/or behaviour responds to human footprint (*e.g.*, Ordiz et al. 2017) with a mechanistic focus on how human infrastructure, access networks, or physical presence might disrupt bears from accessing salmon. In British Columbia, this research could be prioritized in interior watersheds of the Fraser or Skeena rivers where the encroachment of human footprint is higher than more remote coastal watersheds (Figure B2).

Chapter 5: Culturally-guided ecosystem-based fisheries management: local values and data empower reciprocity in the management of the Wuikinuxv (Rivers Inlet) bear-salmon-human system

In Chapter 5, I show how an ecosystem-based fisheries management (EBFM) framework could assess trade-offs between fisheries yield and the stewardship of local bear populations. In this case, local values of coexistence with wildlife were compatible with harvest goals by the Wuikinuxv Nation. In addition to providing an implementable example of EBFM, this is the most comprehensive population assessment for Rivers Inlet sockeye to date. Although productivity and current abundance are lower than historical levels, this research demonstrates that current and future Food, Social, and Ceremonial (FSC) harvest, and modest commercial harvest, are compatible with maintaining stock dynamics while also supporting bear foraging (noting, however, the precautionary approach of the Wuikinuxv Nation given the uncertainty in the stock-recruitment estimation). This work demonstrates the potential for EBFM to be implemented successfully at appropriate spatial scales, especially if it considers and aligns with the values of local peoples. More broadly, it demonstrates the leadership of an Indigenous community choosing to prioritize coexistence with wildlife who use a common resource to people.

I foresee multiple avenues of future research following Chapter 5. First, consistency in observations of spawner abundance is an ongoing concern in this system and elsewhere because of eroding monitoring effort by federal enumeration programs (Price et al. 2008, 2017). Consistent local salmon enumeration in Wuikinuxv territory could provide more certainty and reveal more detail about the abundance and phenology of salmon returning to different tributaries in the Wuikinuxv Lake watershed and other salmon-bearing systems of the territory. Paired with genetic and remote camera approaches to bear monitoring, this could subsequently inform how bears track this diversity (*e.g.*, Quinn et al. 2014, Deacy et al. 2018), and how FSC harvest might affect spawner abundance in tributaries of the system. Second, salmon harvest by bears could exert disproportionate stressors on salmon abundance in small streams where salmon are more readily caught in shallow water (Quinn et al. 2001). These are also the spawning grounds where water temperatures are rising and habitat degradation from logging is more pronounced, compared with the larger tributaries (Wuikinuxv Fisheries, unpublished data). Although sockeye spawn in nine tributaries of Wuikinuxv Lake (three large silted rivers and six clear streams either glacial- or lake-fed), the stock is considered one population (McKinnell et al. 2001). It is yet unclear how bear predation in certain tributaries could affect the natural selection acting on salmon in the population (*e.g.,* Carlson et al. 2007, 2009, Quinn et al. 2017). Finally, it is also unclear how timing of commercial or FSC fisheries could select for sockeye in specific tributaries (or age classes therein) across the stock (Quinn et al. 2007), but current rates of FSC harvest suggest these effects may be negligible.

These results can guide escapement and harvest goals by the Wuikinuxv Integrated Resource Stewardship Department and federal agencies in managing for FSC and commercial sockeye fisheries. The evaluation of different management strategies is important future work for the management of Rivers Inlet and other salmon fisheries in the region. This involves an evaluation of policy options (such as escapement goals or harvest rates on surplus stock) that explicitly considers uncertainty in population and fishery characteristics (Punt et al. 2016).

6.2. Looking ahead: implications for theory and practice

In era of increasing, rapid, and complex environmental change, it is more important than ever to understand how human activities affect ecological associations. As scientists, we can ask ourselves how our knowledge systems and tools can support managers to address challenges ranging from the impact of fragmentation on animal movement to how our activity affects prey availability. Below, I consider the implications of this dissertation for applied science and socio-ecological management in coastal British Columbia and beyond.

6.2.1. Where are the data gaps?

Simply put, long-term ecological monitoring is critical. Without maintaining, extending, and periodically evaluating biotic and abiotic datasets, researchers and managers will be not be able to improve and adapt management to environmental change (Lindenmayer and Likens 2009). In the bear-salmon-human system in British Columbia, there are gaps in the consistency or existence of long-term monitoring datasets for bear populations, salmon enumeration, or other foods.

Bear populations: In the early 2000s, Indigenous governments on the BC Central Coast identified that a lack of information about grizzly and black bear populations was hampering their decision-making process about natural resources development, tenure requests, and conservation planning. They were also concerned about the effect of provincially-managed trophy hunting on bear populations in their territories (Artelle et al. 2013); a hunt that also contravenes Indigenous law in their territories. They sought to fill this gap by organizing an ongoing collaborative long-term bear monitoring program with scientists from the Raincoast Conservation Foundation and the University of Victoria's Applied Conservation Science Lab (Chapter 2), while also monitoring provincially-licenced bear hunting activity. In instances where they needed more information than this relatively recent monitoring could provide (*e.g.,* longer than five years), local knowledge from community members provided a complimentary temporal scope (Sagarin and Pauchard 2012, Service et al. 2014). Given the reduced capacity of many federal or provincial agencies for monitoring or fieldwork, similar collaborative programs could be implemented in other regions of British Columbia and beyond to harness the combined capacity and expertise of multiple parties, such as Indigenous governments, academics, non-profit organizations, and/or centralized agencies.

Salmon enumeration: The effort of collecting salmon enumeration data in British Columbia and the Yukon by Fisheries and Oceans Canada (DFO) (FOC 2016) varies among watersheds and is eroding over time. This is happening concurrently to reductions in spawner abundances for many populations across British Columbia's north and central coast. Price et al. (2017) found that enumeration efforts, which once covered 1,533 streams in the mid 1980s, has declined to 476 streams as of 2014. While the implementation of the Wild Salmon Policy could help address an increase in the number of streams surveyed, more attention needs to be given to methodological consistency and sustained/increased effort in enumeration (Price et al. 2017). Given their expressed interest, local monitoring capacity, and investment in stewarding their territories, Indigenous Stewardship Departments and Guardian Watchmen programs are well positioned to provide capacity or assume leadership of these enumeration efforts (Chapter 5, Atlas et al. 2017).

Alternative foods: Although regional data over small temporal scales (*i.e.*, less than 10 years) exist for some key food resources for bears (*e.g.*, berries in the Kootenay region, mapping of whitebark pine (*Pinus albicaulis*) distribution in the Mountain National Parks), comprehensive estimates or models for many key foods do not exist over the spatial extent of grizzly bear distribution or over long timescales (Mowat et al. 2013, Artelle et al. 2016). Increased application of remote sensing could contribute to estimates of emergent vegetation and primary production and subsequent models of food densities, such as ungulate, berry, nut, or fruit densities. As the phenology of resources shifts with climate change, improved understanding on the factors affecting food availability might become even more important in predicting changes to patterns of foraging behaviours in bears in British Columbia and beyond.

6.2.2. How will human disturbance affect consumer-resource interactions in the future?

Humans can disrupt wildlife access to important food resources by altering 1) wildlife movement patterns either through habitat fragmentation or avoidance behaviour from imposed predation risk and/or 2) food availability either through direct competition or phenological disruption from global environmental change.

The long-term effects that disruptions caused by human activity will have on wildlife and ecosystems are unknown. However, scientists have already documented widespread and accelerated ecological shifts attributed to human cumulative impacts on species persistence (Crooks et al. 2017) and food webs (Bartley et al. 2019). How wildlife foraging behaviours shift to account for cumulative human impacts, how behavioural shifts affect the productivity of consumer populations, and how the selective pressures consumers exert on prey populations shift, are open questions. For example, what will temporal partitioning of wildlife and humans mean for how predators target prey populations or where prey seek refugia? How will pressures of fragmentation and social dominance in predators interact to affect foraging outcomes? If patterns of consumer-resource interactions shift, how will subsequent subsidies or benefits to ecosystems change?

Consumers often compete directly with humans for similar resources. Humans are sometimes referred to as 'superpredators' because our technology allows us to harvest wild prey on land and at sea at rates far greater than natural predators (Darimont et al. 2015). We outcompete other consumers for key foods (Grémillet et al. 2018) and exert selection on prey populations we intercept that differs from natural predators (Darimont et al. 2009a). For example, human harvesters often select for different traits, body sizes, or age classes as compared with wildlife (Fenberg and Roy 2008). By changing prey abundance, traits, and demography, our harvest can alter prey availability for other consumers in a system (Lacy et al. 2017, Grémillet et al. 2018).

In the case of bear-salmon-human systems, humans are altering foraging by bears either through our activities in salmon-bearing watersheds (Chapter 4) or our direct competition with bears for salmon (Chapter 5). Human activity has already effectively extirpated the bear-salmon association in much of southern British Columbia (Chapter 3) – by disturbing landscapes in the southwest along the Fraser River and extirpating bears despite abundant salmon returns, and by nearly ceasing access of salmon to bear populations in the southeast in the Columbia drainage via extensive damming. Where bears and salmon still overlap, commercial salmon fisheries may alter salmon availability for bears via reductions in abundance (Chapter 5, Levi et al. 2012) or available biomass (*e.g.,* reductions in size of salmon; Bigler et al. 1996). Reducing, removing, or re-introducing the bear-salmon association and subsequent nutrient transfer in these interior watersheds (and others similarly impacted) has likely altered interior terrestrial ecosystems (Hilderbrand et al. 1996, Hocking and Reimchen 2009) and the productivity of other consumer populations, such as eagles, gulls, passerines, scavengers, insects, or plants that also utilize salmon (Schindler et al. 2003, Hocking and Reynolds 2011, Levi et al. 2015).

6.2.3. What are the applied management implications?

Human activity is accelerating habitat fragmentation and loss around the world, with wide-ranging implications for access to critical resources that many animals need to survive and reproduce. To mitigate the negative impacts, information from ecological research can inform and guide land-use planning processes and/or the siting of protected areas or interventions that can support connectivity of ecological associations (*e.g.*, Chapter 3, Hilty et al. 2006, Crooks and Sanjayan 2006, Baguette and Dyck 2007, Carroll et al. 2012).

The marine-terrestrial relationship in bear-salmon-human systems highlights something all ecologists know: ecosystems are characterized by connections. My research provides valuable insights for federal and provincial managers who manage salmon and bears, respectively, and has relevance for Indigenous governments who seek to manage interconnected land-use and marine fisheries such that bear populations (and the benefits they confer to ecosystems) are sustained (Chapter 3).

Governing natural resources – within groups and between people and other ecological users – is challenging. Indigenous governments in Canada are well positioned to provide a level of regional expertise, monitoring effort, and governance (Chapter 2, 5). In addition, their leadership and involvement can support larger centralized agencies managing common resources such as water, timber, space on the land, or fisheries over larger spatial scales (Cox et al. 2015). Local knowledge and perspectives from members of Indigenous communities can offer valuable sources of knowledge to developing ecosystem-based approaches to management (*e.g.,* local knowledge extending temporal scope of research documenting a range shift and informing subsequent land-use policy; Service et al. 2014). Indigenous resource governance principles are also premised on adaptive, systems-based management and acknowledge interconnections between people and ecosystems (Turner and Berkes 2006, Turner 2014, Artelle et al. 2018). Including Indigenous governments as actors in governance strategies could also help make it easier to develop and implement broad-scale federal and provincial management policies (Dietz et al. 2003). These efforts can be supported by congruent directives for federal and provincial agencies to uphold broader obligations to Indigenous peoples and engagement of local peoples, such as the Wild Salmon Policy (Canada 2005), Reconciliation Protocol (Coastal First Nations and Province of British Columbia 2016), and UNDRIP (Canada 2017).

In response to the limitations of centralized governance, community-based natural resource management is an emerging approach in socio-ecological systems that can address both environmental and socioeconomic goals, while balancing human resource use with conservation (Cox et al. 2015, Bennett 2018). Community-based approaches in management require some degree of local decision-making power and authority over natural resources. My work with the Wuikinuxv Nation and their Integrated Resource Stewardship Department, who hold such authority, demonstrates we have the data and the scientific capacity to develop management objectives and strategies to moderate human impacts (in our case, competition between people and bears; Chapter 5) and manage for species concurrently at a regional scale. Our case study of locally-driven and values-informed research will contribute to management approaches that seek to effectively balance ecological and human needs, not only through a lens of ecosystem-based management but also by including values in the management process (Artelle et al. 2018).

In the region where I work, Wuikinuxv people and neighbouring Nations have Indigenous law reflecting cultural values of respect and reciprocity for bears and other wildlife. Indigenous decision makers in the region prioritize such cultural directives in their decisions for monitoring programs, policy, and implementation (Housty et al. 2014, Artelle et al. 2018). In her book *Braiding Sweetgrass*, ethnobotanist Robin Wall Kimmerer writes, “One of our responsibilities as human people is to find ways to enter into reciprocity with the more-than-human world.” The deep commitment of the Wuikinuxv people to coexist with bears and to steward salmon populations was an opportunity for me to contribute my skills as an applied ecologist for locally-driven management predicated in respect and reciprocity. I hope this work can highlight the unique leadership of the Wuikinuxv Nation and provide other communities or management agencies with a road map of how to consider other species in governing natural resource use.

6.2.4. Reflections on future engagement with Indigenous communities in ecological research

I see abundant opportunities and challenges for ecologists to contribute to locally-driven decision-making by engaging with Indigenous communities. Many challenges still exist that could limit the potential for engagement, the primary one being the lack of trust in academics by Indigenous governments who may not have time or resources to “get to know” every graduate student who passes through their territory. Māori author Linda Smith wrote that “research is a dirty word” when doing work in her home community, reflecting on how academic research contributed to the process of colonization in many Indigenous cultures (Smith 1999). The first time I read this, her words shocked me. Now I understand that on top of all that has been taken in the process of colonization in Canada (National Centre for Truth and Reconciliation 2015) and elsewhere, modern-day researchers can behave like new-wave colonists extracting more knowledge or samples or data from places that already feel the effects of past and present colonial behaviour (Chapter 2, Salomon et al. 2018). As a starting point, researchers should know whose territories we work and live in (*e.g.*, by using spatial resources such as www.native-land.ca or www.whose.land/en) and consider how our research might contribute to the places that are otherwise serving us on our academic path. To do this, we need to reflect on the resources we might unknowingly demand from community members and government staff during our research and consider if and how our research process is done in service of communities.

If researchers and practitioners are concerned with the ecological consequences of human activity, engaging in applied work with Indigenous governments presents an opportunity for science to directly inform policy change. In Canada, Indigenous Nations are asserting and regaining sovereignty over decision-making in their territories. These Nations have the authority to take care of their land and people, from health and education to natural resource management and economic development. They have the ability to make decisions at local scales and they can manage adaptively because they can see and are directly impacted by the consequences of their decisions (Turner et al. 2013, Turner 2014, Cox et al. 2015). Appropriate information on ecological systems is required for decision-making in natural resource management, and science is one of many knowledge systems that can contribute (Chapter 2, Service et al. 2014, Ban et al. 2017, Salomon et al. 2018). This dissertation provides a small glimpse into how engaged ecological research can be done and how it might contribute information for decision-makers. My findings hint at the potential that such collaborations could hold in a future filled with complex decision-making under global environmental change.

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Appendix A – Supplementary Information for Chapter 3

A.1 Dietary Estimates

We estimated dietary contributions from observed isotope ratios, using fractionation values from the literature (Table A1). We modeled dietary contributions for bears across British Columbia based on their geographic regions and associated regional dietary patterns (Mowat and Heard 2006, G. Mowat personal communication 2015). Specifically, the province of British Columbia uses 57 grizzly bear population units (GBPUs) to characterize the grizzly metapopulation (Province of British Columbia 2012). Depending on which GBPU the sample originated, we used one of four dietary models (Figure 3.1). Each dietary model is based on a classification and analysis as first assigned from Mowat and Heard (2006). These include:

- *Eastern*: temperate meat + plants
- *Central*: boreal meat + plants
- *Interior-salmon*: temperate meat + plants + salmon (including kokanee)

We provided an updated model of coastal diets from Mowat and Heard (2006), which included intertidal prey:

- *Coastal*: plants + salmon + intertidal + black tailed deer

A.2 Spatial Extents of Kernel-weighted Regressions

We presented kernel-regression estimates where summed kernel density exceeds a value, chosen so that 95% of the summed kernel density falls within the corresponding density contour. We refer to the region inside the 95% contour as the 'spatial extent'. Employing the cross-validated bandwidth from our kernel-based nonparametric regression, we used the 'kernelUD' function from the *adehabitatHR* package (Calenge 2015) in R to calculate relevant spatial extents (Kie 2013). In addition, we manually excluded islands that are beyond the current documented range of coastal grizzly bears (Service et al. 2014).

A.3 Regional Maps of Designated Conservation Areas

In the coastal region, we compared coast-wide estimates of salmon consumption for female black and grizzly bears to estimates within designated conservancies (Province of British Columbia 2016). We selected the conservancies within the overlapping spatial extents of female grizzly and black bears (Figure A1). Similarly, in the provincial region, we compared estimates of salmon consumption for female and male grizzly bears from across the province to estimates contained within two different coastal areas based on biogeoclimatic zoning and administrative and management zoning (the 'Great Bear Rainforest' (GBR)) (Figure A2).

Table A1. Isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) and fractionation values (^{13}C frac and ^{15}N frac) used to calculate dietary contributions for black and grizzly bears (*Ursus americanus* and *U. arctos horribilis*, respectively) in coastal British Columbia and for grizzly bears across western North America.

Food type	**$\delta^{13}C$ (‰; SD)**	**^{13}C frac (SD)**	**$\delta^{15}N$ (‰; SD)**	**^{15}N frac (SD)**	**n†**	**Sources**
Terrestrial Meat						
Boreal: moose, caribou	-23.5 (1.0)	2.0 (1.0)	2.1 (1.0)	4.0 (1.0)	35	Szepanski et al. 1999, Ben-David et al. 2001, Kielland 2001, Mowat and Heard 2006
Coast (black tailed deer)	-24.8 (1.0)	2.0 (1.0)	2.5 (1.0)	4.0 (1.0)	107	Jacoby et al. 1999, Szepanski et al. 1999, Ben-David et al. 2004, Mowat and Heard 2006
Eastern (temperate meat, including moose, elk, and white-tailed and mule deer)	-25.3 (1.0)	2.0 (1.0)	3.4 (1.0)	4.0 (1.0)	70	Jacoby et al. 1999, Hobson et al. 2000, Felicetti et al. 2005, Mowat and Heard 2006
Generalized salmon baseline (spawning and landlocked)	-19.9 (1.0)	1.0 (0.3)	12.5 (1.0)	3.8 (0.3)	338	Bilby et al. 1996, Hildebrand et al. 1996, Jacoby et al. 1999, Satterfield and Finney 2002, Ben-David et al. 2004, G. Mowat personal communication 2015
Generalized intertidal baseline	-14.9 (1.41)	0.4 (1.2)	8.67 (1.17)	2.3 (1.6)	16	Ben-David et al. 2004, Fox et al. 2014
Generalized plants baseline	-26.6 (2.0)	2.0 (0.3)	-2.8 (3.0)	5.6 (0.3)	200	Mowat and Heard 2006

n† This sample size applies to both carbon and nitrogen.

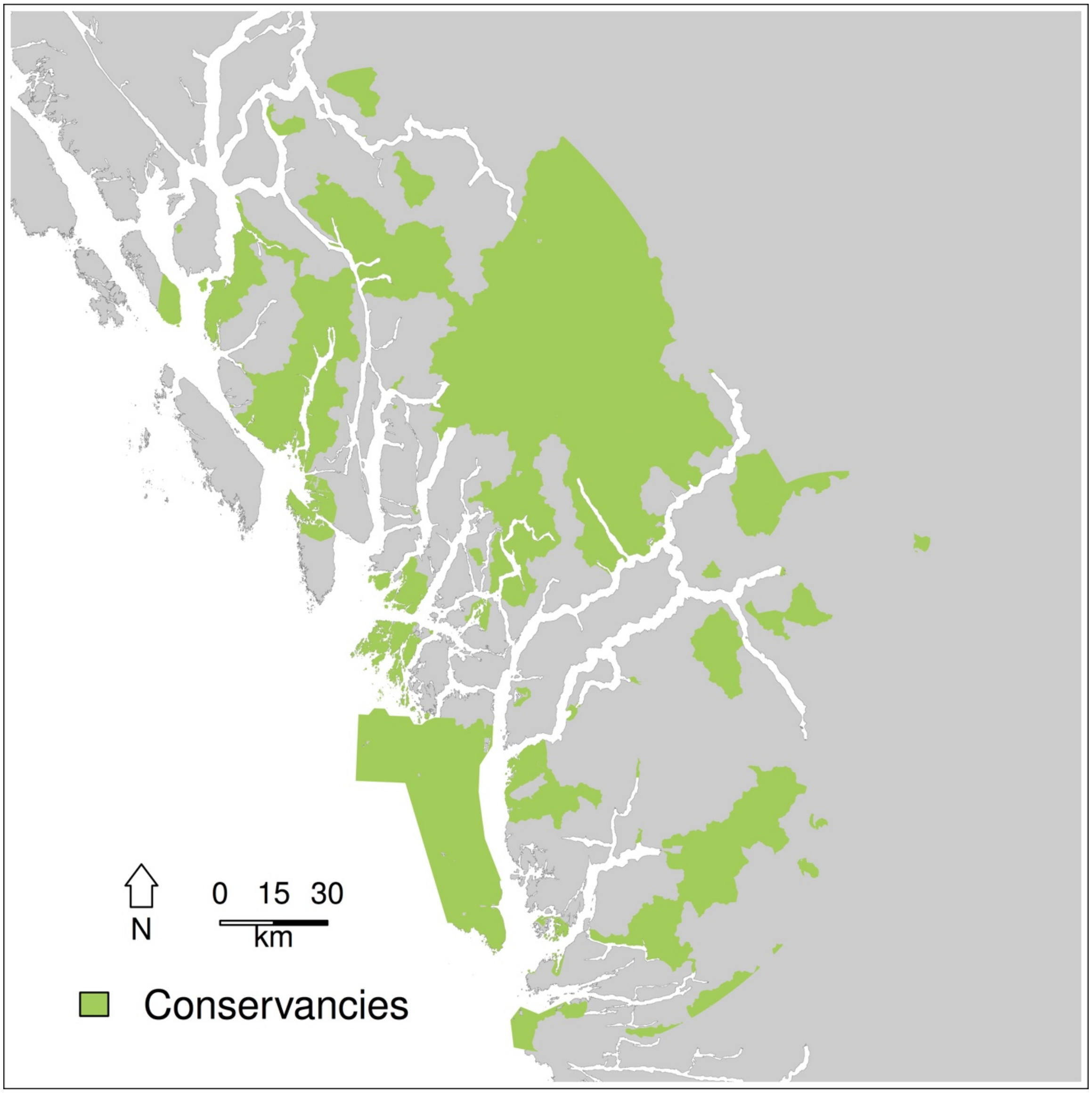

Figure A1. Locations of conservancies in the 'coastal' region of the analysis, on the central coast of British Columbia (Province of British Columbia 2016).

Figure A2. Two representations of coastal areas in British Columbia, based on 1) biogeoclimatic zoning, in the 'Coast and Mountain Temperate Rainforest EcoProvince (Demarchi 2011); and 2) administrative and management zoning, in the 'Great Bear Rainforest' (GBR), where industrial development is limited (DellaSala 2011).

Appendix B - Supplementary Information for Chapter 4

B.1 Overview among and within watersheds

Table B1. Home range sizes for adult male and female grizzly bears in interior and coastal habitats in western North America.

Region	Males (mean area, km^2)	Females (mean area, km^2)	Sources
Flathead valley	446 (n = 5)	200 (n = 5)	LeFranc et al. 1987, Hatler et al. 2008
Interior BC (Revelstoke)	279 (n = 7)	79 (n = 3)	LeFranc et al. 1987, Pasitschniak-Arts 1993, Hatler et al. 2008
NW Montana (Yellowstone)	828 (n = NA)	384 (n = NA)	LeFranc et al. 1987, Pasitschniak-Arts 1993
Jasper National Park	916 (n = 11)	244 (n = 2)	LeFranc et al. 1987, Pasitschniak-Arts 1993
SW Alaska (coastal)	NA	357 (n = 40)	Collins et al. 2005
Khutzeymateen Valley (coastal)	130 (n = 4)	52 (n = 13)	MacHutchon et al. 1993

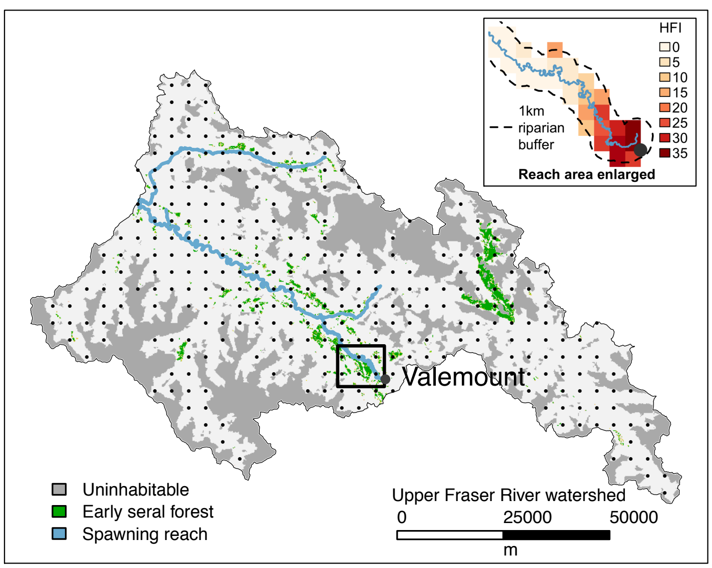

Figure B1. Example watershed (Upper Fraser River watershed basin, containing the town of Valemount, British Columbia, Canada): Spawning salmon reaches are shown in blue, and early seral forest areas are shown in green. Climate variables (mean growing season temperature and precipitation) were sampled annually at 4 km intervals in habitable areas (light grey). The inset shows the area within the rectangle, with a 1 km buffer on either side of the spawning reach that intersects with human footprint index (HFI) raster pixels (1x1 km). See full details and supporting references in Methods.

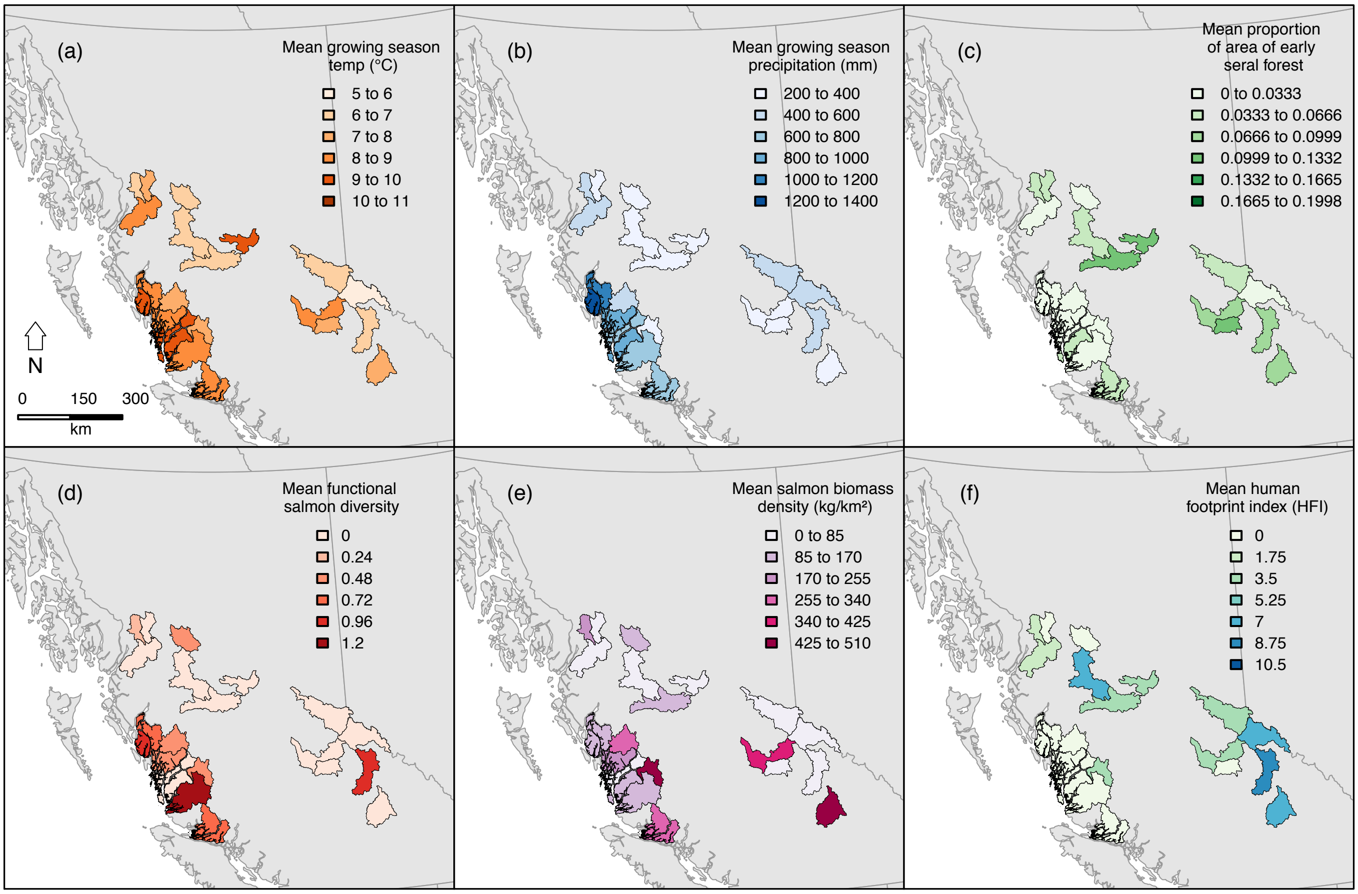

Figure B2. Spatial distribution of covariates within watersheds - (a) growing season temperature, (b) growing season precipitation, (c) proportion of watershed area of early seral (<10 yr. old) forest, (d) salmon species diversity, (e) salmon biomass density, and (f) human footprint index (see full details and supporting references in Methods) - used to predict annual proportions of salmon to grizzly bear (*U. arctos horribilis*) diets across British Columbia, Canada from 1995 to 2014. Means represent covariate data from years in which bear samples were collected.

B.2 Stable Isotope Analysis (SIA) Details

We conducted stable isotope analysis (SIA) and subsequent dietary modeling via the following approach. Specifically, we collected data and performed SIA for 229 grizzly bears. We used the raw stable isotope signatures following Adams et al. (2017). Some isotopic data first appeared in Mowat and Heard (2006) from female and male grizzly bears (n = 14, n = 36, respectively) across BC, collected from 1995 to 2003 by provincial representatives from research projects and inspections of hunter-killed samples. We augmented these data with a dataset of coastal grizzly bears (n = 41 females, n = 135 males) collected using non-invasive hair snags from 2009 to 2014 (Adams et al. 2017). In cases where individuals were sampled in multiple locations within the same year, we attributed the individual's salmon consumption value to the sample location that yielded the most guard hairs (ensuring a sufficient quantity for preparation of samples for isotopic analyses).

Laboratory preparation. Hair samples were washed and rinsed with a 2:1 mixture of chloroform:methanol to remove oils and surficial debris. After the samples were air dried for at least 48 hours, we cut each hair into small segments and subsampled ~1mg into tin capsules for continuous flow isotope ratio mass spectrometry analysis. All isotope analysis was conducted at the stable isotope facility in the Department of Soil Sciences, University of Saskatchewan, Saskatoon, Canada using a Europa Scientific ANCA-NT gas-solid-liquid preparation module coupled to a Europa Scientific Tracer 20-20 mass spectrometer (PDZ Europa, Cheshire, England; Darimont and Reimchen 2002, Reimchen and Klinka 2017).

All isotope ratios are expressed as δ values, which report parts per mil (‰), according to the equation:

$$\delta X = ((R_{sample}/R_{standard}) - 1) \times 1000$$

where X represents ^{13}C or ^{15}N, and R represents the ratio of heavy to light isotopes. Vienna-Pee Dee Belemnite limestone (V-PDB) and atmospheric N_2 are the standard for carbon and nitrogen, respectively. The stable isotope laboratory at the University of Saskatoon estimates their analytical error at 0.05 (SD 0.04) for carbon, and 0.04 (SD 0.05) for nitrogen.

General modeling approach. We estimated annual dietary contributions from predetermined food groups (Table B2) for individuals using MixSIAR (version 3.1.7, Stock and Semmens 2013) in R (version 3.5.1, R Development Core Team 2018). We structured all models with uninformative priors, process error, and included each bear's unique identification number as a random effect. Using Gibbs sampling for each model, we applied a burn-in of 200,000, a thinning interval of 100, and chain length of 300,000 across three chains. Model diagnostics confirmed satisfactory convergence of all models (Stock and Semmens 2013).

While a multiplicative error structure (process * residual) is recommended (Stock and Semmens 2016), our models in the interior region failed to converge with multiplicative error. Given the high degree of individual specialization in bears (Mattson and Reinhart 1995, Lafferty et al. 2015), with the potential for sampling error across a large study area, we structured models with process error (see Deacy et al. (2018), who have a similar model structure in a similar coastal ecosystem). We note that diagnostics and model selection criteria (DIC) supported using process error over residual error (but see Stock and Semmens 2016).

Major food groups and isotope source values. We modeled annual proportions of food group contributions by including only foods consumed in regions in which individuals were sampled (Hopkins and Kurle 2016, Adams et al. 2017). Depending on diet model region, these included: terrestrial meat (ungulates), Pacific salmon, intertidal food sources, and plants (Table B2). We determined prey sample isotope values from the literature. We included values from source samples that were originally collected ecoregions appropriate to the spatial scale and ecological context of our sampled bear hair (Mowat and Heard 2006, Adams et al. 2017). We confirmed suitable isotopic mixing space geometry by plotting raw stable isotope carbon and nitrogen values ($\delta^{13}C$, $\delta^{15}N$) for each grizzly bear hair sample alongside the mean (± 1SD) carbon and nitrogen isotopic source values (corrected for isotopic discrimination: $\Delta^{13}C$, $\Delta^{15}N$) for food groups in interior and in coastal regions (Table B2).

Trophic discrimination factors. As no reliable discrimination factors have been tested for bear hair (Hopkins and Kurle 2016), we used discrimination values from laboratory-controlled feeding experiments of Norway rats - a similarly omnivorous mammal (Table B2; Hopkins and Kurle 2016, Hopkins et al. 2017).

Digestibility. We explored incorporating concentration dependence into our mixing models to account for the omnivorous nature of grizzly bears, which consume a range of food items that vary drastically in C:N ratios (Phillips and Koch 2002). We assessed whether to carry our concentration independent or concentration dependent model results into our main analysis using leave-on-out cross validation (LOO) (Stock and Semmens 2016, Vehtari et al. 2017) and DIC, which has been more broadly applied in Bayesian model selection (Table B3; Hopkins et al. 2017). We applied concentration values derived from digestibility from previous studies that focused on the same food items bears in our system consume (Table B2; Hopkins et al. 2017, Service et al. 2018, Deacy et al. 2018). When concentration dependence was used, we used digestible elemental concentration values (plant matter: = C = 45 $\pm$ 0, N = 5.84 $\pm$ 3.70, n= 43; deer (used for terrestrial meat): C = 51.5 + 0, N = 15.5 +0.54, n = 4; trout: C = 54.8 $\pm$ 0 , N = 11.65 $\pm$ 4.12, n = 6, where the trout value was used for salmon as proven to be identical in a previous study; Rode et al. 2001, Hopkins et al. 2017). As we could find no previously calculated N digestibility in the literature for intertidal animals, we calculated our own values from a subset of our intertidal data (*Hemigrapsus nudis*), for which the required data were available. We applied previously calculated C digestibility values specific to animal sources (n = 18; C = 51.5 $\pm$ 0, N = 15.6 $\pm$ 0.83; Fox et al. 2014).

We determined that our concentration independent model was most appropriate for our data based on both LOO and DIC values, as well a consideration of the inherent uncertainty associated in estimating the relative contributions and digestibility of food groups, especially plants, consumed by bears in interior and coastal study areas using concentration dependent models (Table B3; Deacy et al. 2018). Most important to our main analysis approach of relating salmon consumption values to other predictor values, the individual's salmon consumption values between the concentration independent and dependent model were highly positively correlated (Pearson's r = 0.987 for coastal model, r = 0.997 for interior model). As such, although mean dietary salmon estimates were slightly lower from the concentration dependent model (Table B3), salmon estimates derived from both models should have near identical relationships with the predictor variables. For these reasons, in addition to the added uncertainty in estimating the digestibility and relative contributions of plants to bear diets across our large study over multiple years (Robbins et al. 2002, Deacy et al. 2018), we were confident proceeding with the output from our concentration-independent model. In addition, we wanted to compare our results to previous results in BC and elsewhere that use concentration independent models (*e.g.*, Bryan et al. 2013, 2014, Service et al. 2018, Deacy et al. 2018).

Limitations. We carried forward only median estimates of the proportion of annual dietary salmon contributions into our GLMM framework to test out predictions related to covariates affecting salmon consumption. This approach ignores associated uncertainty from the posterior distribution for each individual estimate. Specifically, in our dataset the mean standard deviation of coast (mean SD = 0.071) and interior (mean SD = 0.077) individual dietary salmon estimates was not accounted for or considered in our analysis structure. We used this simplified approach to reduce modeling complexity but acknowledge the limitations that it may impose on inference. However, we note our median estimate for the coast and interior models were highly correlated to both lower bound of the 95% credible interval estimate from each individual's posterior (Pearson r = 0.980, r = 0.983, respectively) as well as the upper bound (Pearson r = 0.983, r = 0.991, respectively). This high correlation suggests that our main conclusions would hold at both the upper and lower bounds of each individual's posterior distribution of annual dietary salmon consumption.

Table B2. Adapted from Adams et al. (2017). Isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) used to calculate annual proportions of salmon to grizzly bear (*U. arctos horribilis*) diets across British Columbia, Canada (1995 to 2014). Shown are the applied isotopic baselines for food items (*e.g.*, $\delta^{13}C$) and trophic discrimination values from food to bear hair (*e.g.*, $\Delta^{13}C$) (Hopkins and Kurle 2017).

Food type	**δ^{13}C (‰; SD)**	**Δ^{13}C (SD)**	**δ^{15}N (‰; SD)**	**Δ^{15}N (SD)**	**n†**	**Sources**
Terrestrial Meat						
Coast: black tailed deer	-24.8 (1.0)	2.1 (0.1)	2.5 (1.0)	3.9 (0.1)	107	Jacoby et al. 1999, Szepanski et al. 1999, Ben-David et al. 2004, Mowat and Heard 2006
Interior: moose, elk, and white-tailed and mule deer	-25.3 (1.0)	2.1 (0.1)	3.4 (1.0)	3.9 (0.3)	70	Jacoby et al. 1999, Hobson et al. 2000, Felicetti et al. 2005, Mowat and Heard 2006
Generalized salmon baseline	-19.9 (1.0)	2.1 (0.1)	12.5 (1.0)	3.9 (0.3)	338	G. Mowat personal communication 2015, Bilby et al. 1996, Hilderbrand et al. 1996, Jacoby et al. 1999, Satterfield and Finney 2002, Ben-David et al. 2004
Generalized intertidal baseline	-14.9 (1.41)	2.1 (0.1)	8.67 (1.17)	3.9 (0.3)	16	Ben-David et al. 2004, Fox et al. 2014
Generalized plants baseline	-26.6 (2.0)	3.4 (0.5)	-2.8 (3.0)	2.4 (0.2)	200	Mowat and Heard 2006

n† This sample size applies to both carbon and nitrogen.

Table B3. Assimilated dietary estimates and associated model selection criteria (LOO and DIC) of concentration-independent and concentration dependent models for coastal and interior grizzly bears in British Columbia, Canada, from 1995 to 2014. Population level model dietary proportion values include: Mean, 1 SD, Median, and 95% CI (credible interval). Range denotes the range of mean proportion estimates among individual bear-year combinations.

	Concentration Independent					Concentration Dependent				
Dietary Item	**Mean**	**SD**	**Median**	**95% CI**	**Range**	**Mean**	**SD**	**Median**	**95% CI**	**Range**
Coast Model selection criteria: LOO = -12.8, DIC = 8.93						LOO = -31.5, DIC = -28.09				
Intertidal	0.044	0.013	0.044	0.019-0.072	0.019-0.074	0.086	0.018	0.085	0.053-0.125	0.038-0.137
Plants	0.125	0.019	0.126	0.077-0.159	0.022-0.716	0.191	0.028	0.192	0.125-0.235	0.035-0.795
Terrestrial Meat	0.012	0.015	0.007	0.000-0.058	0.002-0.009	0.013	0.013	0.009	0.000-0.048	0.003-0.010
Salmon	0.819	0.020	0.820	0.778-0.858	0.221-0.95	0.711	0.030	0.711	0.654-0.773	0.143-0.917
Interior Model selection criteria: LOO = 20.7, DIC = 35.86						LOO = 44.7, DIC = 54.26				
Plants	0.395	0.083	0.393	0.235-0.561	0.038-0.647	0.530	0.103	0.537	0.315-0.717	0.055-0.804
Terrestrial Meat	0.467	0.101	0.464	0.275-0.667	0.048-0.877	0.362	0.114	0.352	0.166-0.616	0.041-0.786
Salmon	0.138	0.046	0.134	0.057-0.239	0.033-0.900	0.107	0.040	0.104	0.038-0.195	0.027-0.887

B.3 Salmon Biomass Estimates

We estimated yearly biomass available to grizzly bears in each watershed using salmon enumeration data from Fisheries and Oceans Canada (FOC 2016). Geographic coordinates for salmon enumeration points were not included in the 2016 version of the data, so we joined the 2016 data with coordinates from a previous version using a unique stream identifier (FOC 2016). We excluded enumeration points without a geographic location (n =137 of 2137). Although we used the most recent data available at the time of our analyses, with records current to 2013, only 8% of runs are monitored consistently (Price et al. 2008, 2017). To account for missing enumeration data, we applied an imputation method following Ruggerone et al. (2010) and Bryan et al. (2014). This method imputes missing data using the average contribution of a particular stream and salmon species over the 20-year study period relative to the average total abundance for that species across all streams in the same watershed. The missing value is calculated by multiplying the average annual contribution for that species and stream by the average performance of other streams from the same watershed in that year relative to their respective average annual contributions. As such, the imputation method assumes that nearby streams perform similarly relative to their long-term average salmon abundance.

Where possible, we used salmon abundance estimates from other streams in the same 3rd order watershed to impute missing species-year-stream estimates. In watersheds with enumeration points for less than five streams, we grouped streams in adjacent watersheds that were upstream or downstream of the sparsely counted watershed. In coastal areas, if there were no other well-populated watersheds upstream or downstream, we chose the closest adjacent well-populated watershed with the nearest ocean outlet. To be eligible for imputation, we required that each stream and species have estimates for a minimum of 14 (70%) of the 20 years in our study period, with at least 3 (15%) observations occurring in the latter 10 years. For pink salmon with even- and odd-year runs—which we considered separate species due to their distinct two-year lifecycles—we required at least 7 observations in the 20-year study period, with at least one in the latter 10 years. After applying these exclusion criteria, 10% of 15,500 possible abundance species-year-stream estimates were eligible for imputation over the 20-year study period.

Following the imputations, we used ArcGIS 10.2.2 (ESRI, Redlands, California, USA) and Python 2.7.5 (http://www.python.org) to join salmon enumeration points to their corresponding spawning salmon stream line segments. Where possible, we joined enumeration to spawning reaches of streams only (BCGOV 2006). If no corresponding lines existed, we joined enumeration points to line segments from a spatial dataset of streams covering the entire province of BC (BCGOV 2005). We converted abundance estimates to biomass by multiplying fish counts by species-specific average masses (in kg) and summing across all species present in a stream. For the biomass conversion, we used species-specific average masses reported in (Groot and Margolis 1991), and assumed a 1:1 sex ratio. We then intersected watersheds with salmon streams and calculated the length of each stream segment within a watershed. In R, we calculated the total salmon biomass per watershed and year using the ratio of total biomass for a given salmon species to total stream length and multiplying by the length of the stream segment within the watershed. We then summed biomass across all species and stream segments within each watershed in a given year and assigned a salmon biomass estimate to each bear based on its watershed of origin and year hair was grown.

B.4 Salmon Diversity Estimates

Complementing these estimates of abundance, we used the Shannon diversity index to estimate salmon diversity in each watershed:

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

where S is the number of salmon species and p_i is the proportion of the total estimated salmon biomass comprising the i^{th} species. We used biomass estimates instead of enumeration counts to estimate diversity, because we reasoned that total biomass would be more relevant to bear diets (for example, on average even-year pink salmon weigh 1.7 kg, while Chinook salmon weighs 13.6 kg; Groot and Margolis 1991). Accounting for both species richness and evenness in species abundance, the Shannon diversity index provides a proxy for salmon resource availability over space and time (Service et al. 2018).

B.5 Potential impacts of salmon measurement error

We examined potential collinearity among covariates that might occur due to measurement error present in coastal and interior salmon enumeration efforts. Specifically, we were concerned that lower coastal enumeration efforts could create measurement error that other variables which might co-vary with region, such as HFI (less human footprint in remote coastal areas), or temperature and precipitation (generally warmer and wetter in coastal vs. interior environments), could account for in our models. Converting region to a numeric variable, we did not find that strong correlation among un-standardised covariates (Pearson's $r < 0.67$) with the exception of region and HFI (Pearson's $r = 0.81$; see below for further examination of the effects of region). Post-hoc examination for multicollinearity among predictor variables, with the *car* package (version 3.2.0 in R, Fox and Weisberg 2018), also indicated low variance inflation (~ 1 for all parameters).

B.6 GLMM analysis

Table B4. Candidate model set used to assess the effect of ecological variables on annual proportion of salmon in diet of grizzly bears across British Columbia from 1995 to 2014. We predicted that males consume more salmon than females, and coastal bears will consume more salmon than interior bears (Adams et al. 2017), and thus sex and region appear in all our models. All models included year and watershed as random effects. Top models (ΔAIC < 2; Burnham and Anderson 2002) are in grey.

Model	Fixed effects	ΔAIC	Df	Weight
1	Intercept-only	109.0	4	<0.001
H1 – Salmon availability				
2	biomass + diversity	26.1	4	<0.001
3	biomass + diversity + biomass*diversity	27.6	9	<0.001
4	biomass + diversity + biomass*diversity + biomass*sex + diversity*sex	30.8	11	<0.001
H2 – Salmon availability & alternative food				
5	biomass + diversity + precip + temp + earlystage	13.7	11	<0.001
6	biomass + diversity + biomass*diversity + precip + temp + earlystage	15.5	12	<0.001
7	biomass + diversity + biomass*diversity + biomass*sex + diversity*sex + precip + temp + earlystage	18.8	14	<0.001
H3 – Salmon availability & human footprint				
8	biomass + diversity + footprint	18.3	9	<0.001
9	biomass + diversity + footprint + biomass*footprint + diversity*footprint	21.8	11	<0.001
10	biomass + diversity + footprint + sex*footprint	17.8	12	<0.001
11	biomass + diversity + biomass*diversity + footprint	19.9	10	<0.001
12	biomass + diversity + biomass*diversity + footprint + biomass*footprint + diversity*footprint	23.3	12	<0.001
13	biomass + diversity + biomass*diversity + footprint + sex*footprint	19.3	11	<0.001
14	biomass + diversity + biomass*diversity + biomass*sex + diversity*sex + footprint	23.4	12	<0.001
15	biomass + diversity + biomass*diversity + biomass*sex + diversity*sex + footprint + biomass*footprint + diversity*footprint	25.4	13	<0.001
16	biomass + diversity + biomass*diversity + biomass*sex + diversity*sex + footprint + sex*footprint	23.3	13	<0.001
H3 - Salmon availability & alternative food & human footprint				
17	biomass + diversity + footprint + precip + temp + earlystage	1.0	12	0.2252
18	biomass + diversity + footprint + biomass*footprint + diversity*footprint + precip + temp + earlystage	4.0	14	0.0502
19	biomass + diversity + footprint + sex*footprint + precip + temp + earlystage	0.0	13	0.3676
20	biomass + diversity + biomass*diversity + footprint + precip + temp + earlystage	2.5	13	0.1030
21	biomass + diversity + biomass*diversity + footprint + biomass*footprint + diversity*footprint + precip + temp + earlystage	5.5	15	0.0232
22	biomass + diversity + biomass*diversity + footprint + sex*footprint + precip + temp + earlystage	1.4	14	0.1800
23	biomass + diversity + biomass*diversity + biomass*sex + diversity*sex + footprint + precip + temp + earlystage	6.4	15	0.0153
24	biomass + diversity + biomass*diversity + biomass*sex + diversity*sex + footprint + biomass*footprint + diversity*footprint + precip + temp + earlystage	8.1	16	0.0063
25	biomass + diversity + biomass*diversity + biomass*sex + diversity*sex + footprint + sex*footprint + precip + temp + earlystage	5.1	16	0.0284

Table B5. Parameter estimates (with 95% confidence intervals given as ±–2·SE) for top GLMMs (ΔAIC > 2; Table B4) used to predict annual proportion of dietary salmon in diets of grizzly bears (*Ursus arctos horribilis*) across BC (1995 to 2014). Contrast levels for sex and region were female and coast, respectively. Continuous predictors were centered (mean subtracted) and scaled (divided by 2 SD). Bold values indicate estimates with confidence intervals that did not overlap zero; parameter estimates are log odds.

Parameter	**Model 17**	**Model 19**	**Model 22**
Intercept	0.211 (-0.138, 0.559)	0.163 (-0.179, 0.506)	0.148 (-0.196, 0.492)
Sex	**0.950** (-0.760, 1.140)	**1.013** (-0.806, 1.220)	**1.013** (0.807, 1.220)
Region	-0.399 (-1.108, 0.310)	-0.399 (-1.068, 0.269)	-0.357 (-1.032, 0.318)
Biomass	**0.432** (0.138, 0.727)	**0.452** (0.170, 0.735)	**0.471** (0.187, 0.755)
Diversity	0.045 (-0.346, 0.436)	0.023 (-0.345, 0.391)	0.047 (-0.325, 0.418)
Footprint	**-1.014** (-1.461, -0.567)	-**1.504** (-2.227, -0.782)	**-1.526** (-2.251, -0.801)
Temperature	**0.934** (0.502, 1.367)	**0.961** (0.530, 1.392)	**0.976** (0.542, 1.410)
Precipitation	0.369 (-0.104, 0.842)	0.340 (-0.129, 0.808)	0.367 (-0.106, 0.840)
Early-seral	**-0.602** (-0.989, -0.216)	-0.590 (-0.964, -0.216)	**-0.571** (-0.946, -0.195)
Sex * footprint	-	0.5322 (-0.099, 1.164)	0.546 (-0.088, 1.180)
Biomass * diversity	-	-	0.206 (-0.328, 0.739)

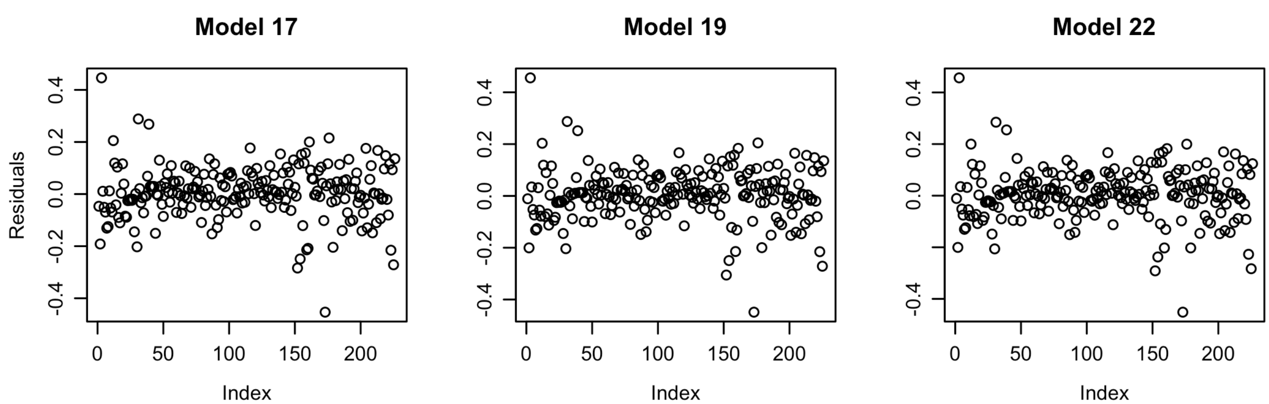

Figure B3. Residuals of top GLMMs (see Table B4 and B5) used to predict annual proportion of dietary salmon in diets of grizzly bears (*Ursus arctos horribilis*) across BC (1995 to 2014).

B.7 Post-hoc model diagnostics

Due to the strong correlation between HFI and region, we considered the full set of candidate models (Table B4) with and without a region factor included. We found the same three top models as our original analysis (Table B5), with a fourth top model (ΔAIC > 2) with the same form as model 19 but excluded region. The direction and magnitude of parameter estimates did not differ with region excluded.

Appendix C – Supplementary Information for Chapter 5

C.1. Stock-recruitment relationship for Wuikinuxv Lake sockeye

C.1.1. Escapement Correction Factor and Observation Error

We used Dual-Frequency Identification Sonar (DIDSON) and ARIS sonar counts deployed in the Waanukv River from 2014 to 2017 to calculate a mean expansion factor for escapement estimates from counts in clear tributaries of Wuikinuxv Lake (Table C1; English et al. 2018). Clear tributary counts were positively correlated to sonar observations across the four years of data (Figure C1). We applied the mean expansion factor (mean = 6.9) to clear tributary counts for the system from 1948 to 2013. We calculated the coefficient of variation of the difference between the sonar observations and clear creek counts (CV = 0.24) to provide an estimate of escapement observation error for our state-space model for spawner abundances estimated prior to years with sonar observations (1948 to 2013). We assumed that sonar observations from 2014 to 2017 were an absolute measure of spawner abundance in the system, though we acknowledge this is problematic because of mortality after the sonar and before the spawning grounds (*e.g.,* seal predation).

Table C1. Sonar counts and estimates of spawner abundance from clear creek counts from 2014 to 2017. The mean expansion factor from four years of data was 6.9.

Year	**2014**	**2015**	**2016**	**2017**
Sonar count	300,000	262,400	482,000	225,400
Clear creek count	40,493	48,800	90,385	23,573
Expansion factor	7.41	5.38	5.33	9.56

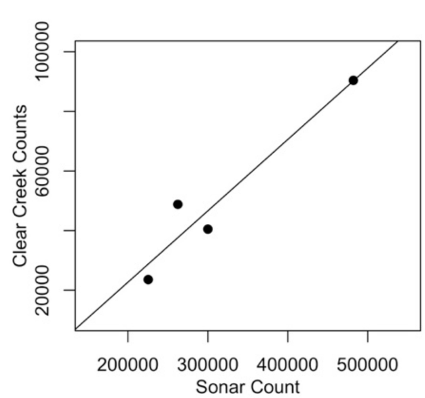

Figure C1. DIDSON sonar counts (English et al. 2018) compared with clear creek counts (Rutherford and Wood 2000) from 2014 to 2017.

C. 1.2. Prior distributions and marginal parameter estimates for full time series

Table C2. Prior distributions for model parameters and marginal posterior estimates for full time series. Alpha posteriors are reported on the natural scale.

Full time series (S_{EQ} =982,976, S_{MSY} =423,568), 1948 to 2017				
		Posterior		
	Prior	50th percentile	2.5th percentile	97.5th percentile
α	~U(0,3)	2.69	1.37	6.20
β	~N(4.18 E-6, 0.3†)	1.00 E-6	5.34 E-7	1.53 E-6
ϕ	~U(-1,1)	0.63	0.39	0.85
σ_R	~U(0,100)	0.82	0.22	1.31
γ_3	~Dirichlet (0.33, 0.33, 0.33)	0.012	0.007	0.020
γ_4		0.305	0.273	0.339
γ_5		0.683	0.647	0.715

† in SD units

C.1.3 Sensitivity Analyses

To determine the sensitivity of our model, we fit alternative prior distributions for β or alternative assumptions about observation error in harvest and age composition for the truncated time series (1993 to 2017) (Table C3).

Table C3. Prior distributions for model parameters and marginal posterior estimates from truncated time series models (1993 to 2017) tested for sensitivity, fit with alternative prior distributions for β or alternative assumptions about observation error in harvest and age composition. Alpha posteriors are reported on the natural scale.

Alternative uniform β prior. S_{EQ} = 255,940, S_{MSY} = 102, 974.				
		Posterior		
	Prior	50th percentile	2.5th percentile	97.5th percentile
α	~U(0,3)	4.04	1.26	14.96
β	~U(0,10)	5.45 E-6	1.99 E-6	9.55 E-6
ϕ	~U(-1,1)	0.62	0.22	0.92
σ_R	~U(0,100)	0.85	0.42	2.02
γ_3	~Dirichlet (0.33, 0.33, 0.33)	0.006	0.002	0.017
γ_4		0.279	0.229	0.339
γ_5		0.715	0.652	0.765

Increased CV for β (SD = 60%) and increased observation error in harvest (30%) and age composition (ESS = 50). S_{EQ} = 248,783, S_{MSY} = 99,441.				
		Posterior		
	Prior	50th percentile	2.5th percentile	97.5th percentile
α	~U(0,3)	4.19	1.26	15.62
β	~N(4.18 E-6, 0.6†)	5.76 E-6	1.97 E-6	1.02 E-5
ϕ	~U(-1,1)	0.62	0.21	0.92
σ_R	~U(0,100)	0.86	0.41	1.96
γ_3	~Dirichlet (0.33, 0.33, 0.33)	0.008	0.019	0.023
γ_4		0.249	0.197	0.315
γ_5		0.742	0.673	0.795

† in SD units

C.2. Bear detections and diet

C.2.1. Stable isotope analysis (SIA)

We collected data and preformed SIA for 68 grizzly bears in the study area collected between 2013 to 2017. We used raw stable isotope signatures following Service et al. (2018) and Adams et al. (2017). In cases where individuals were sampled in multiple locations within the same year, we attributed the individual's salmon consumption value to the sample location that yielded the most guard hairs (ensuring a sufficient quantity for preparation of samples for isotopic analyses).

We prepared and processed hair samples for stable carbon (δ13C) and nitrogen (δ15N) isotope ratio estimation via gas chromatography-mass spectrometry (University of Saskatchewan, Saskatoon, SK, Canada; Bryan et al. 2014, Service et al. 2018). Hair samples were washed and rinsed with a 2:1 mixture of chloroform:methanol to remove oils and surficial debris. After the samples were air dried for at least 48 hours, we cut each hair into small segments and subsampled ~1mg into tin capsules for continuous flow isotope ratio mass spectrometry analysis. All isotope analysis was conducted at the stable isotope facility in the Department of Soil Sciences, University of Saskatchewan, Saskatoon, Canada using a Europa Scientific ANCA-NT gas-solid-liquid preparation module coupled to a Europa Scientific Tracer 20-20 mass spectrometer (PDZ Europa, Cheshire, England; Darimont and Reimchen 2002, Reimchen and Klinka 2017). All isotope ratios are expressed as δ values, which report parts per mil (‰), according to the equation:

$$\delta X = ((R_{sample}/R_{standard}) - 1) \times 1000$$

where X represents ^{13}C or ^{15}N, and R represents the ratio of heavy to light isotopes. Vienna-Pee Dee Belemnite limestone (V-PDB) and atmospheric N_2 are the standard for carbon and nitrogen, respectively. The stable isotope laboratory at the University of Saskatoon estimates their analytical error at 0.05 (SD 0.04) for carbon, and 0.04 (SD 0.05) for nitrogen.

We estimated annual dietary contributions from predetermined food groups (Table C4) for individuals using MixSIAR (version 3.1.7, Stock and Semmens 2013) in R (version 3.5.1, R Development Core Team 2018). Our models were structured with individual identifiers for bears as a random effect, process and residual error, and uninformative priors, and were concentration-independent. Using Gibbs sampling for each model, we applied a burn-in of 200,000, a thinning interval of 100, and chain length of 300,000 across three chains. Model diagnostics confirmed satisfactory convergence of all models (Stock and Semmens 2013).

We modelled annual proportions of food group contributions by including foods consumed by bears in coastal British Columbia following Adams et al. (2017) and Service et al. (2018) (Table C4), including ungulates, salmon, intertidal foods, and plants. We determined prey sample isotope values from the literature, from relevant ecoregions appropriate to the ecological context of our sampled bear hair. As no reliable discrimination factors have been tested for bear hair (Hopkins and Kurle 2016), we used discrimination values from laboratory-controlled feeding experiments of Norway rats - a similarly omnivorous mammal (Table C4; Hopkins and Kurle 2016, Hopkins et al. 2017).

With regard to modeling digestibility, we chose to use the concentration independent models because of the high correlation to dietary salmon between concentration dependent and independent models (Service et al. 2018, Chapter 3), the uncertainty associated in estimating the relative contributions and digestibility of food groups, especially plants, consumed by bears in interior and coastal study areas, and an aim to compare our results to previous results in BC and elsewhere that use concentration independent models (*e.g.*, Service et al. 2018, Deacy et al. 2018). We applied concentration values derived from digestibility from previous studies that focused on the same food items bears in our system consume (Table C4; Hopkins et al. 2017, Service et al. 2018, Deacy et al. 2018). When concentration dependence was used, we used digestible elemental concentration values (plant matter: = C = 45 ± 0, N = 5.84 ± 3.70, n= 43; deer (used for terrestrial meat): C = 51.5 + 0, N = 15.5 +0.54, n = 4; trout: C = 54.8 ± 0 , N = 11.65 ± 4.12, n = 6, where the trout value was used for salmon as proven to be identical in a previous study (Rode et al. 2001, Hopkins et al. 2017). As we could find no previously calculated N digestibility in the literature for intertidal animals, we calculated our own values from a subset of our intertidal data (*Hemigrapsus nudis*), for which the required data were available. We applied previously calculated C digestibility values specific to animal sources (n = 18; C = 51.5 ± 0, N = 15.6 ± 0.83; Fox et al. 2014).

We note that we carried forward only median estimates of the proportion of annual dietary salmon contributions. This approach ignores associated uncertainty from the posterior distribution for each individual estimate.

Table C4. Adapted from Adams et al. (2017). Isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) used to calculate annual proportions of salmon to grizzly bear (*U. arctos horribilis*) diets in the Wuikinuxv Lake watershed and surrounding region (2013 to 2017). Shown are the applied isotopic baselines for food items (*e.g.*, $\delta^{13}C$) and trophic discrimination values from food to bear hair (*e.g.*, $\Delta^{13}C$) (Hopkins and Kurle 2017).

Food type	**$\delta^{13}C$ (‰; SD)**	**$\Delta^{13}C$ (SD)**	**$\delta^{15}N$ (‰; SD)**	**$\Delta^{15}N$ (SD)**	**n†**	**Sources**
Black tailed deer	-24.8 (1.0)	2.1 (0.1)	2.5 (1.0)	3.9 (0.1)	107	Jacoby et al. 1999, Szepanski et al. 1999, Ben-David et al. 2004, Mowat and Heard 2006
Generalized salmon baseline	-19.9 (1.0)	2.1 (0.1)	12.5 (1.0)	3.9 (0.3)	338	Bilby et al. 1996, Hilderbrand et al. 1996, Jacoby et al. 1999, Satterfield and Finney 2002, Ben-David et al. 2004, G. Mowat pers. comm. 2015
Generalized intertidal baseline	-14.9 (1.41)	2.1 (0.1)	8.67 (1.17)	3.9 (0.3)	16	Ben-David et al. 2004, Fox et al. 2014
Generalized plants baseline	-26.6 (2.0)	3.4 (0.5)	-2.8 (3.0)	2.4 (0.2)	200	Mowat and Heard 2006

n† This sample size applies to both carbon and nitrogen.

C.2.2. Estimating salmon consumption by bears

We predicted the relationship between salmon density and salmon consumption. We used annual mean estimates of salmon in diet from our Wuikinuxv territory data (n = 68 individuals detected from 2013 to 2017), deriving annual population means by weighting female estimates to make up 60% of the annual for those years in which we detected females (following Mowat and Heard 2006; Figure C2). We estimated the mean annual salmon biomass potentially available to bears, using spatially explicit escapement data for all five salmon species to estimate the annual salmon returns of the study area. We found the half saturation parameter calculated from our annual weighted means was similar to that of the multi-year population means reported in Levi et al. (2012) as estimated from eighteen grizzly bear populations in BC, Canada (80.42 kg/km^2 and 80.08 kg/km^2, respectively).

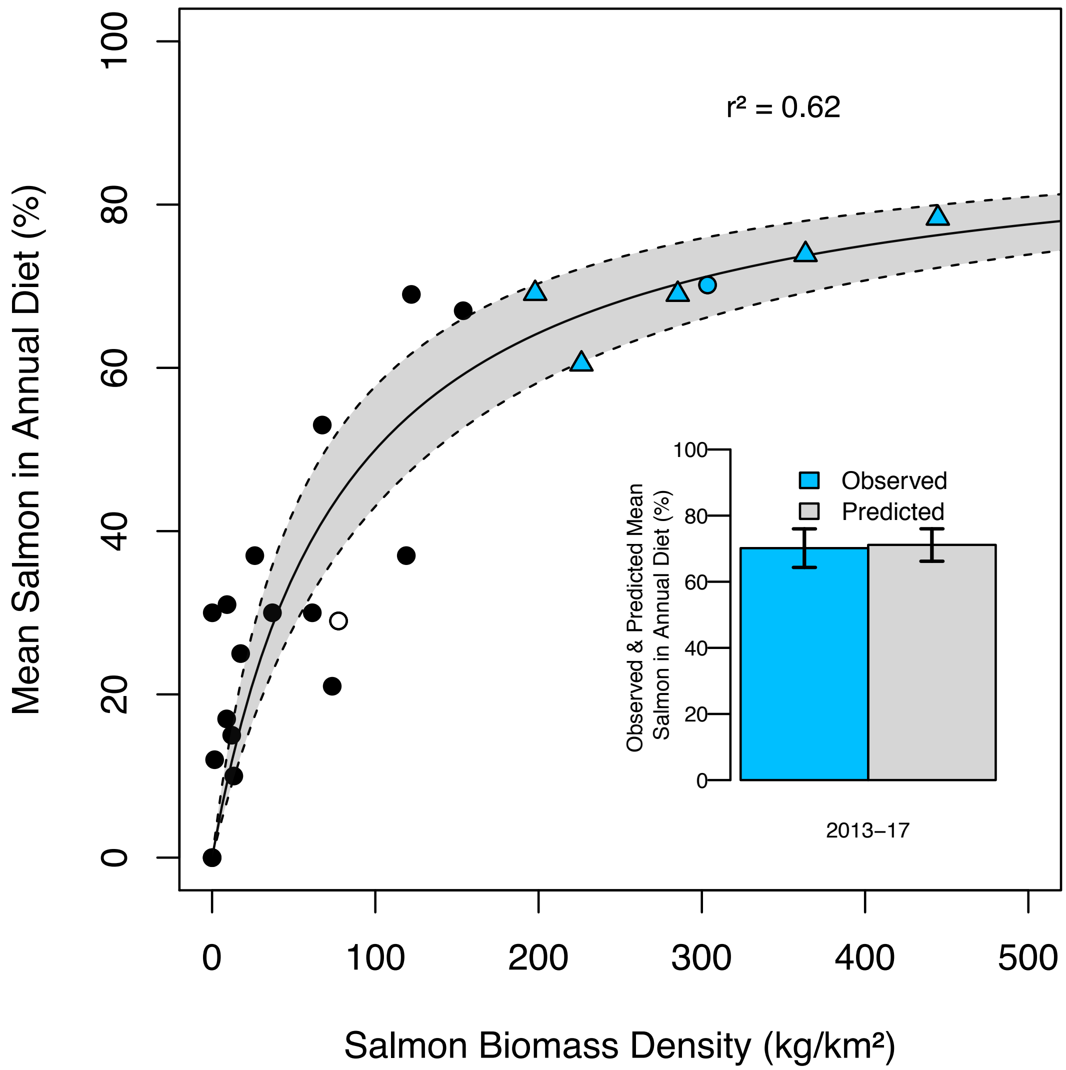

Figure C2. The relationship (with 95% CIs and r^2 value) for salmon density and salmon consumption, as determined by stable isotope analysis of five years of samples from grizzly bears in the study area (blue triangles show annual means made up from detections (n = 68, from 2013 to 2017). This corroborates the relationship for salmon density and salmon consumption used in Levi et al. (2012), as determined by stable isotope analysis of eighteen grizzly bear populations from British Columbia (black points shown for comparison). Multi-year observed mean salmon consumption in the study area during the collapse (1998 and 1999) and in recent years (2013 to 2017) are shown in white and blue dots, respectively (though these did not factor into the relationship we predicted). The barplot depicts predicted mean salmon consumption by bears (light grey bar with 95% confidence intervals) closely matches observed mean salmon consumption (blue bar with 95% confidence intervals) as estimated by stable isotope analysis in bears from the study area.

C.3. Uncertainty in EBFM goals

To characterize and illustrate the uncertainty in pre- and post-collapse EBFM goals, we approximated the spawner abundance where the upper and lower 50th, 75th, and 95th credible intervals of the relative fishery yields and bear density lines intersected (Figure 5.4). Specifically, we used the *locator* function in R (Figure 5.4, Table C5; R Development Core Team 2018). We note that 95th CIs have no solutions in all but one case.

Table C5. Mean and approximate lower and upper 50th, 75th, and 95th credible intervals of spawner abundance at which fisheries yield and bear density are held equally below their maxima during pre-collapse (1948 to 1992) and post-collapse (1993 to 2017) periods. Note that the approximated 75th credible interval is equal to the mean for the post-collapse period and is therefore indistinguishable in Figures 5.4 and 5.5. Relative fisheries yield/relative bear density associated with each spawner abundance is shown in parentheses.

	Mean EBFM Goal	**50th Credible Intervals**	**75th Credible Intervals**	**95th Credible Intervals**
Pre-collapse S_{EQ} = 1,428,548, S_{MSY} = 569,380	735,000 (0.95)	670,000 (0.93), 785,000 (0.96)	625,000 (0.92), 870,000 (0.95)	No solution, 880,000 (0.985)
Post-collapse S_{EQ} = 256,752, S_{MSY} = 103,189	143,000 (0.9)	120,000 (0.84), 175,000 (0.96)	83,000 (0.77), 143,000 (0.98)	No solution, No solution