

Habitat-Mediated Predation and Selective Consumption of Spawning Salmon by Bears

by

Lucas Cale Andersson

B.Sc. (Hons.), University of Ottawa, 2010

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science

in the
Department of Biological Sciences
Faculty of Science

© Lucas Cale Andersson 2016
SIMON FRASER UNIVERSITY
Spring 2016

All rights reserved.

However, in accordance with the *Copyright Act of Canada*, this work may be reproduced, without authorization, under the conditions for Fair Dealing. Therefore, limited reproduction of this work for the purposes of private study, research, education, satire, parody, criticism, review and news reporting is likely to be in accordance with the law, particularly if cited appropriately.

Approval

Name: Lucas Cale Andersson
Degree: Master of Science
Title: *Habitat-mediated predation and selective consumption of spawning salmon by bears*
Examining Committee: Chair: Dr. Michael Silverman
Associate Professor

Dr. John Reynolds
Senior Supervisor
Professor

Dr. Isabelle Côté
Supervisor
Professor

Dr. Lawrence Dill
Supervisor
Professor Emeritus

Dr. Chris Darimont
External Examiner
Associate Professor
Department of Geography
University of Victoria

Date Defended/Approved: April 15, 2016

Ethics Statement



The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

- a. human research ethics approval from the Simon Fraser University Office of Research Ethics

or

- b. advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University

or has conducted the research

- c. as a co-investigator, collaborator, or research assistant in a research project approved in advance.

A copy of the approval letter has been filed with the Theses Office of the University Library at the time of submission of this thesis or project.

The original application for approval and letter of approval are filed with the relevant offices. Inquiries may be directed to those authorities.

Simon Fraser University Library
Burnaby, British Columbia, Canada

Update Spring 2016

Abstract

Predator–prey interactions are key elements of ecosystem functioning and can be mediated by physical characteristics of the environment. To examine this, I studied interactions between bears and spawning salmon on the Central Coast of British Columbia, Canada. I first show how size-biased predation is mediated by stream characteristics that provide refuge for prey, with implications for size-selective pressures acting on salmon in different streams. I then demonstrate that bears feed selectively on energy-rich parts of salmon, depending on characteristics of the stream, with consequences for terrestrial nutrient transfer via uneaten salmon biomass. Overall, I found that bears captured larger salmon in streams with less wood and fewer undercut banks and fed more selectively in narrower, shallower streams with less pool volume. This suggests that habitat characteristics play a role in mediating predator behaviour and, therefore, have implications for the selective pressures faced by salmon, and nutrient subsidies to surrounding habitats.

Keywords: nutrient transfer; *Oncorhynchus* spp.; predator–prey interactions; selective consumption; size-biased predation; *Ursus* spp.

To Sarah Elizabeth Baxter
who encouraged me to skip town and chase my dreams.
I am a better person because of you.

Acknowledgements

What a life-changing journey it has been; I have so many to thank.

First, I would like to thank John Reynolds for taking a big chance on a “chemist”. You truly changed an environmental scientist (with a marketing background) into a caliper wielding, sea navigating, coast exploring, bear dodging ecologist. I would never be here without your trust, valuable input and navigation all along the way. I am forever grateful.

To my committee members Isabelle Côté and Larry Dill: it has been an absolute honour and pleasure getting to know you. Thank you so much for your valuable input on my scattered project and for guiding me back to the underlying biology of it all.

This research was funded by Simon Fraser University, the Natural Sciences and Engineering Research Council of Canada, the W. Garfield Weston Foundation and the Tom Buell BC Leadership Chair endowment funded by the Pacific Salmon Foundation and the BC Leading Edge Endowment Fund. I am extremely grateful to these institutions for their generous support of my research.

I am grateful to the Heiltsuk First Nation for their support of my research in their traditional territory and the Heiltsuk Integrated Resource Management Department for their partnership in data collection. I would like to thank Aaron Gaffney, Howard Humchitt, Jane Pendray, Ben Rabinovich, Mary Vasey, Marlene Wagner, Kirsten Wilcox and Ross Wilcox for field assistance and for making this such an enjoyable project. Thanks to Kyle Artelle, Will Atlas, Andy Cooper, Sean Godwin, Jenny Harding and Joel Harding for their guidance in statistical analyses and project design. Thanks to Lindsay Davidson for feedback and editing my manuscript. Thank you to Sandra Vishloff and Marlene Nguyen for your helpful support throughout my project.

To Michelle Segal: you are a crucial pillar to so many researchers in the Earth to Ocean Research Group both past and present. Your contributions to our projects, to conservation, to conversation (too many tangents!) and to general existence are eternally appreciated. Thank you for all of your advice, support, and friendship. Let your contagious lust for life never die.

To the town of Bamfield and the Bamfield Marine Sciences Centre: thank you for existing. You have changed my life forever. As long as I live, a big piece of my heart will reside in your town, at Brady's Beach and in the Seaside Kitchen. See you again real soon!

To all of my biology family in the Earth to Ocean Research Group, the Reynolds Lab and others I've met through field work, conferences and SFU events: you are all such amazing people! From afar, ecological research looks amazing because of all the wonderful places one can go and wildlife one can see. But what wasn't expected was all of the exceptional people I would encounter on the way. You made it infinitely more enjoyable and rewarding. I know many of these relationships will be for life. And that makes me happy. Thank you all; you know who you are!

Last but certainly not least, to my family: thank you, thank you, THANK YOU for all of your love and support from day one! I am so incredibly lucky to have you all. Your guidance and encouragement have laid the underlying foundation of my whole personality and any success I have is your success too; I owe it all to you! Mom: thanks for always being there and for all of your advice, conversations, and love. Dad: thanks for your guidance through career paths and scientific pursuits and for instilling a love of the outdoors in me from a young age. Lauren: thanks for always being a best friend and for giving me such a perfect nephew! To Aiden James Gallant: keep smiling, keep exploring and keep reaching for the stars!

Table of Contents

Approval.....	ii
Ethics Statement.....	iii
Abstract.....	iv
Dedication.....	v
Acknowledgements.....	vi
Table of Contents.....	viii
List of Tables.....	x
List of Figures.....	xi
List of Acronyms.....	xiii
Glossary.....	xiv

Chapter 1. Introduction	1
--------------------------------------	----------

Chapter 2. Habitat characteristics and stage of season influence size-biased predation on salmon by bears.....	7
---	----------

2.1. Abstract.....	7
2.2. Introduction.....	8
2.3. Methods.....	10
2.3.1. Stream Characteristics.....	11
2.3.2. Spawning Salmon Abundance.....	12
2.3.3. Salmon Measurements.....	12
2.3.4. Predation Intensity.....	13
2.3.5. Statistical Analyses – Habitat-Mediated Predation Models.....	14
2.3.6. Statistical Analysis – Salmon Body-Size Models.....	16
2.4. Results.....	17
2.4.1. Predation Intensity.....	18
2.4.2. Habitat-Mediated Predation.....	19
2.4.3. Salmon Body Size.....	26
2.5. Discussion.....	27

Chapter 3. Habitat-mediated, selective consumption of spawning salmon by bears.....	31
--	-----------

3.1. Abstract.....	31
3.2. Introduction.....	32
3.3. Methods.....	34
3.3.1. Stream Characteristics.....	34
3.3.2. Salmon Characteristics.....	34
3.3.3. Selective Consumption Scoring Systems.....	35
3.3.4. Spawning Salmon Abundance.....	36
3.3.5. Statistics and Modelling.....	36
3.4. Results.....	39
3.5. Discussion.....	45

Chapter 4. General Discussion	50
References	55
Appendix A. Supporting Material for Chapter 3	64
Appendix B. Stream Characteristics.....	68

List of Tables

Table 2.1.	Means (cm), regression slopes and correlation coefficients of jaw-length to body-length relationships of male and female pink and chum salmon.....	17
Table 2.2.	Comparison of mixed effects models of a) habitat-mediated predation with salmon jaw length as the response variable and b) salmon body size with salmon body length as the response variable, using Akaike's Information Criterion (AIC_c), corrected for small sample size. Each model includes a random effect of stream. In section a) only models with AIC_c weights > 0.02 were included (the top 3 totalled 0.98 cumulative weight); in section b) all models are reported. Section a) top model: marginal $R^2 = 0.77$ and conditional $R^2 = 0.78$; Section b) top model: marginal $R^2 = 0.975$ and conditional $R^2 = 0.978$. In section a) "cover" refers to "cover index" and "escape" to "escape index".....	21
Table 3.1.	Models, variables, mechanisms and predictions for original scoring and alternative scoring systems for selective consumption of salmon by bears. A null model and a model that compared only forced variables (sex, species and date) are not shown.	37
Table 3.2.	Comparison of mixed-effects models of selective consumption of salmon carcasses by bears using Akaike's Information Criterion (AIC_c), corrected for small sample size. Each model includes a random effect of site. Sex, species and date are forced fixed effects in each model to control for possible differences in selective consumption patterns by those parameters.	42

List of Figures

Figure 1.1.	Study stream locations (n=12) on the Central Coast of British Columbia, Canada.	5
Figure 2.1.	The number of bear-killed salmon (2014) vs. cover index of study streams (n=12). The regression line is predicted from a linear regression (adj $R^2 = 0.65$, $p < 0.001$) and the grey band is the 95% confidence region.....	18
Figure 2.2.	The mean number of bear-killed salmon vs. mean number of spawning salmon on 12 streams (2009-2014). The regression line is predicted from a linear regression (adj $R^2 = 0.60$, $p < 0.005$) and the grey band is the 95% confidence region.....	19
Figure 2.3.	Mean chum and pink salmon jaw lengths per stream for senescent and bear-killed salmon. Male and female salmon are shown separately. Bars represent 95% confidence intervals. Streams are ordered, per species, by the mean jaw length of male and female, bear-killed and senescent salmon groups per stream.....	20
Figure 2.4.	Standardized (mean=0, SD=2) coefficients (circles) of model parameters with 95% confidence intervals (lines) for top model (as determined by AIC_c) of a) habitat-mediated predation (Table 2.2a) and b) salmon body-size model (Table 2.2b). The coefficients denote the change, in a) (natural-log) salmon jaw-size and b) (natural-log) salmon body-length as each associated parameter increases by 2 standard deviations. Note: Sex: female=0 and male=1, Species: pink=0 and chum=1, Death: senescent=0 and bear-killed=1. In a) each parameter interacts with death to separate senescent and bear-killed salmon jaw size regression estimates and allow for prediction of differences in the intensity of size-biased predation as parameters vary.....	23
Figure 2.5.	The intensity of size-biased predation on delta mean body lengths (cm) of salmon versus date (with 1 = September 11, 2014). Each point represents the difference in bear-killed salmon and senescent salmon body lengths for the corresponding date. Positive values indicate that bear-killed salmon were larger on average than senescent salmon on that sampling date. The regression lines are the top model's prediction (Table 2.2a) of size-biased predation as date increases with cover-index held mid-range.....	24

Figure 2.6.	The intensity of size-biased predation by bears on delta mean body lengths (cm) of salmon versus cover index. Each point represents the difference in bear-killed salmon and senescent salmon body lengths for the corresponding cover index value. Positive values indicate that average bear-killed salmon were larger than average senescent salmon at that level of cover. The regression lines represent the predicted magnitude of size-biased predation from the top ranking model (Table 2.2a) as cover index changes, with date held constant at its mean.	25
Figure 3.1.	Relationships between the proportion of selectively consumed salmon and a) cover index, b) escape index, c) date (1 = 11 September, 2014), d) number of spawning salmon and e) number of bear-killed salmon. Selective consumption by bears is defined as: eggs and/or brain consumed and < 50% of carcass consumed.	40
Figure 3.2.	Probability plots for the top model (see Table 3.2) of selective consumption of salmon carcasses by bears. Lines and circles are predicted probabilities of selective consumption against model variables, with other variables set to their mean value. Bands and error bars are 95% confidence intervals.	44
Figure 3.3.	Standardized (mean=0, SD=2) coefficient values (circles) with 95% confidence intervals (lines) from the top model (see Table 3.2) of selective consumption of salmon carcasses by bears. The positive coefficient for species indicates more selective consumption of chum than pink salmon and the negative value for sex indicates more selective consumption of females than males.	45

List of Acronyms

AIC _c	Akaike's Information Criterion (corrected for small sample size)
AUC	Area-Under-the-Curve (estimation method)
GLMM	Generalized Linear Mixed Model
PC	Principal Component
PCA	Principal Components Analysis
VIF	Variance Inflation Factor

Glossary

Cover index	A principal component consisting of the volume of large wood per 100m and the percentage of bank that is undercut in a stream.
Escape index	A principal component consisting of the volume of pools per 100m and the width and depth of a stream.
Hyperphagia	A pre-hibernation stage for bears which is associated with increased appetite and caloric intake (Nelson 1980; Nelson et al. 1983).
Selective consumption	A metric of selective feeding by bears. Under one scoring system, a salmon carcass was considered selectively consumed if the eggs (in females) and/or brain (both sexes) were consumed and <50% of the overall carcass was consumed. Under an alternative scoring system, a salmon carcass was considered selectively consumed if <50% of the overall carcass was consumed.
Size-biased predation	Predation with a bias for capturing a certain prey-size relative to what is available. In this study, size-biased predation refers to the capture of larger-than-average prey.
Stream complexity	An umbrella term to describe the volume of pools, wood obstacles and percentage of undercut banks as well as the width and depth of a stream. Higher values indicate higher complexity.
Stream size index	A principal component consisting of the width and depth of a stream.

Chapter 1. Introduction

Predator–prey interactions have direct and indirect consequences for ecosystems, influencing far more than the individual predator and prey (Agrawal 2001; Barbosa and Castellanos 2005; Pelletier et al. 2009). For example, hunting and feeding behaviour can govern trophic energy flow and influence pathways of nutrient transfer across ecosystem boundaries (Holtgrieve et al. 2009; Carlson et al. 2011). These interactions can drive trait divergence in both predators and prey, as natural selection favours both the finest hunters and the best escapees (Darwin 1859; Vamosi 2005). Ecosystems are also shaped by non-lethal predator–prey interactions (Lima 1998; Peckarsky et al. 2008; Heithaus et al. 2012) such as fear-induced anti-predator behaviour, which can influence prey feeding success (Lima and Dill 1990; Wirsing et al. 2008) and, therefore, biological productivity (Preisser et al. 2005). As such, understanding these interactions and their impacts is important to a robust comprehension of any ecosystem.

Coastal bears (*Ursus* spp.) and wild spawning salmon (*Oncorhynchus* spp.) are extremely important to North Pacific coastal and inland ecosystem functioning. They are considered to have a “keystone interaction”, i.e., their interaction produces a disproportionately large effect on shaping North Pacific coastal ecosystems (Helfield and Naiman 2006). Spawning salmon provide a massive source of nutrients to inland freshwater and terrestrial systems (Bilby et al. 1996). They spend the majority of their life growing in the ocean and return to their natal freshwater streams to spawn and subsequently die. Thus, their marine-derived nutrients and energy become available to a suite of aquatic and terrestrial organisms, permeating the local food web through a complex series of pathways (Wipfli et al. 1999). Consequently, they are often referred to as a “nutrient conveyor belt”.

During their migration and spawning period, many salmon are killed by terrestrial predators (e.g., Darimont et al. 2003; Quinn et al. 2003). Of these, bears are the leading vector for salmon transfer to terrestrial systems (Hilderbrand et al. 1999). They often abandon partially eaten carcasses (Quinn et al. 2009) on stream banks or, sometimes, at great distances from the stream (Reimchen 2000; Holtgrieve et al. 2009). The nutrients in the abandoned portion of the carcass are then incorporated into the ecosystem through many different pathways (Gende et al. 2002).

The impact of salmon on aquatic and terrestrial ecosystems is substantial and both bear-killed salmon and salmon that die of senescence play important roles (Janetski et al. 2009). Within streams, bear-killed salmon carcasses are favoured by aquatic macroinvertebrates due, in part, to increased tissue accessibility (Winder et al. 2005). The abundance of aquatic invertebrates has been linked to salmon density even months after the spawning period, demonstrating the persistence of the effects of this nutrient input (Verspoor et al. 2011). Furthermore, within streams, metrics of salmon quantity (e.g., density, biomass, abundance) have been shown to be positively associated with sculpin (*Cottus* spp.) condition (Swain et al. 2014), biofilm biomass and accrual rates (Johnston et al. 2004; Harding et al. 2014) and even juvenile coho salmon (*O. kisutch*) body size (Nelson and Reynolds 2015). Within terrestrial ecosystems, a suite of invertebrates benefit from bear-killed salmon tissue (Meehan et al. 2005; Hocking et al. 2009) and may, in turn, benefit higher-level consumers. For example, higher passerine bird densities are associated with salmon-bearing streams (Christie and Reimchen 2008; Field and Reynolds 2011). In estuarine habitats, both the abundance and diversity of scavenging birds are correlated with both spawning salmon biomass and salmon carcass biomass, which provide a high-value, seasonal source of energy (Field and Reynolds 2013). The residual tissue of terrestrial salmon carcasses is ultimately absorbed into surrounding plant-life (Hocking and Reynolds 2012). Salmon influence riparian community composition (Hocking and Reynolds 2011) and are even associated with significantly higher growth rates of riparian trees (Helfield and Naiman 2001). Thus, salmon—bear interactions, or the lack thereof, have far-reaching consequences beyond the simple, obvious implications to individual predator and prey.

Many factors can shape the interactions between bears and spawning salmon. Foraging theory predicts that bears will hunt and feed in a way that maximizes their net energy per unit time/effort (Stephens and Krebs 1986). Targeting larger prey is an example of foraging behaviour that can maximize energy intake as long as the energy costs of this behaviour do not outweigh the benefit of the additional energy gained by capturing larger prey (i.e., as long as the effort of searching for and handling larger prey increases less rapidly, with prey size, than does energy reward) (Sih 1980; Krebs 1978). Bears have a demonstrated preference for both pre-spawned (Gende et al. 2004) and larger-than-average salmon (Quinn and Kinnison 1999) which have more energy per individual than post-spawned and small salmon respectively (Hendry and Berg 1999). I define, and hereafter refer to, “size-biased predation” as predation which is biased towards the capture of larger individuals. Furthermore, bears often abandon carcasses, partially eaten, revealing a preference for energy-rich parts of the fish such as the eggs or brain (Gende et al. 2001), which would maximize calories per stomach space in a prey-saturated stream. I hereafter refer to this type of feeding as “selective consumption”. Size-biased predation and selective consumption complement each other because larger, pre-spawned fish also have higher loads of energy-rich parts like eggs (Quinn et al. 1995) so that even if selective consumption occurs, there is still a greater energy reward in a larger individual. Ultimately, a bear’s diet should be honed to the constraints of the environment in which hunting occurs (MacArthur and Pianka 1966). For example, search time is higher in streams with low salmon abundance and, therefore, all else being equal, bears should be less selective for certain prey traits than in a stream which is saturated with salmon.

There is substantial evidence that salmon–bear interactions are mediated by characteristics of the habitat in which they occur (reviewed in Carlson et al. 2011). Hypothetically, hunting in a narrow, shallow stream may be so effortless, due to the limited escape potential for salmon, that bears are able to consistently catch their desired prey. This scenario would lead to the effective removal, and consumption, of many prized, large, pre-spawned salmon from the breeding population in small streams. On the other hand, hunting in a deep, wide stream may be more difficult since the salmon have more available medium in which to escape and benefit from lower visibility. In deeper, wider streams, bears may be limited to catching the less desirable, less

vigorous, spawned-out salmon and would also be less able to discriminate based on fish size because of lower visibility. In this simplified example, the width and depth of the streams mediate predation by providing refuge for the prey in large streams and, conversely, easier access to prey for the predator in small streams. This hypothetical example is consistent with results demonstrated by Quinn et al. (2001) and Gende et al. (2004).

The date in the spawning season may also mediate these salmon–bear interactions. Near the end of the season, the streams are mainly populated by salmon that have completed spawning and are close to death. As such, their responsiveness and ability to escape is reduced (personal obs.) and, accordingly, prey pursuit times would be reduced. Therefore, I would predict a shift in predator diet. Specifically, at the end of the season, I would expect a higher intensity of size-biased predation, in all streams, relative to the beginning or the middle of the season.

Differences in the size of, and amount eaten from, each salmon has consequences beyond predator diet. First, small but consistent differences in the amount of selective consumption or size-biased predation over multiple salmon kills will have cumulative consequences for biomass/nutrient transfer to the terrestrial habitat (Gende et al. 2002; Carlson et al. 2011). Second, I would expect, all else being equal, to see body size divergence (Carlson et al. 2009) between these genetically isolated salmon populations (Hamon and Foote 2005). This evolutionary response would be a natural consequence of cumulative, consistent, differential selection acting on each population over generations (Fraser et al. 2011).

The aim of this thesis was to examine how habitat characteristics can mediate capture (Chapter 2) and feeding (Chapter 3) behaviour of bears on spawning salmon across a variety of salmon populations. To accomplish this, I measured stream characteristics as well as senescent and bear-killed salmon carcass characteristics on the Central Coast of British Columbia, Canada, in Heiltsuk First Nations Territory (Fig.1.1). I studied 12 streams with a wide, natural gradient of habitat characteristics and spawning salmon abundances. Black bears (*Ursus americanus*) are found at all of the 12 streams and grizzly bears (*U. arctos*) are more likely to be restricted to the four

streams which are located on the mainland and King Island (but may occasionally visit the other streams). The large number of streams and model selection approach are novel ways to evaluate these relationships in this particular field and allowed me to compare the relative contributions of multiple stream characteristics that may provide refuge for prey (i.e., wood obstacles, undercut banks, pool volume, stream width and depth).

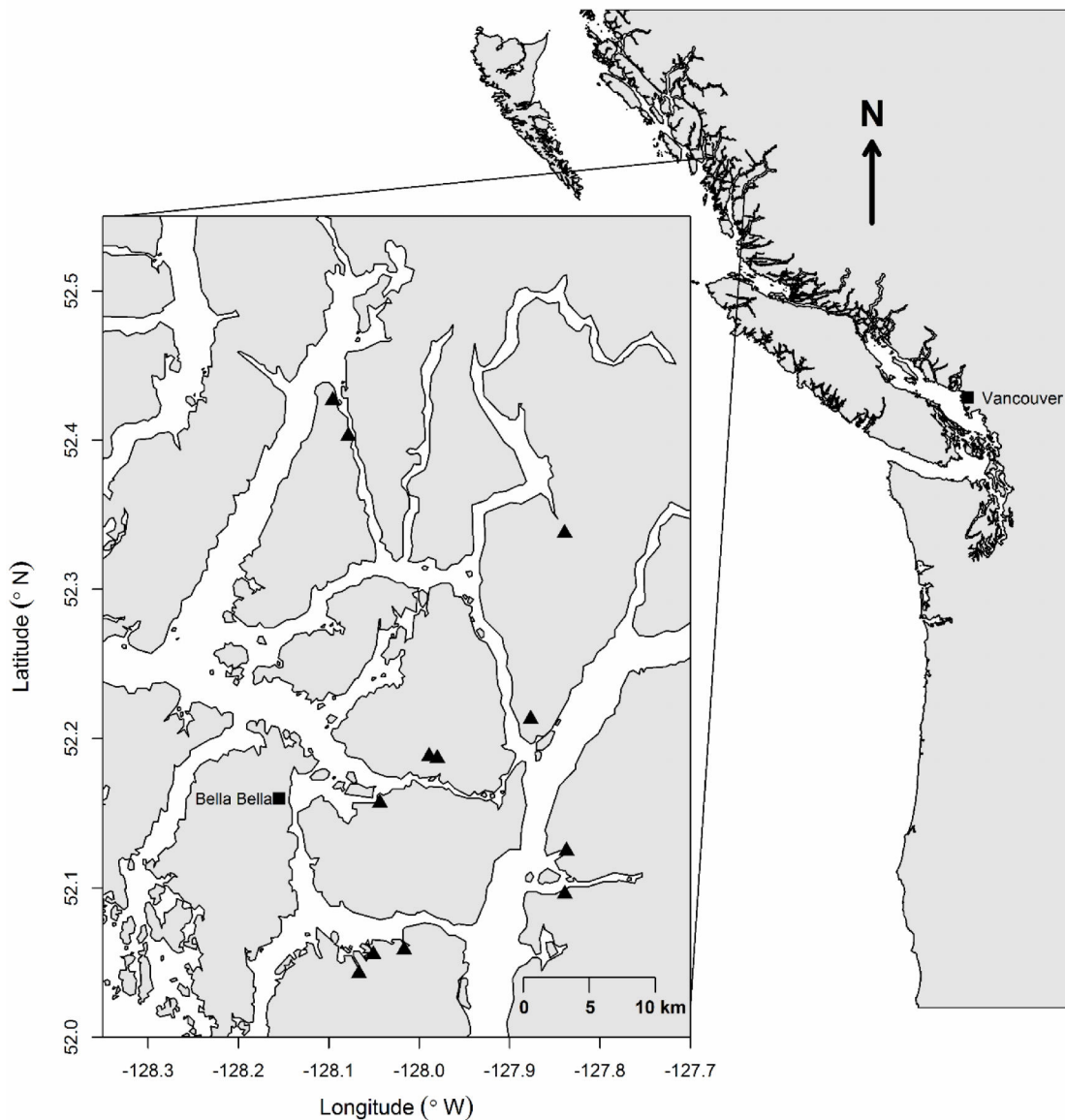


Figure 1.1. Study stream locations (n=12) on the Central Coast of British Columbia, Canada.

First, in Chapter 2, I examine the magnitude of size-biased predation by bears on spawning salmon and I compare multiple hypotheses concerning how stream characteristics mediate the magnitude and directionality of size-biased predation. I specifically test the prediction that more refuge-providing characteristics (for prey) will correlate with less intense size-biased predation. I demonstrate that size-biased predation may be mediated by both habitat characteristics and the stage in the salmon spawning season (i.e., date). I also demonstrate that larger streams have larger salmon.

In Chapter 3, I ask how bears feed, rather than how they hunt. I examine the factors that motivate a bear to abandon a half-eaten carcass, including trade-offs of returning to the stream to hunt for another fish. Specifically, I test if refuge-providing habitat characteristics could predict this behaviour. I predict that the extent of selective consumption should depend on the difficulty of catching prey in each stream and I compare multiple refuge-providing characteristics to determine which best describe patterns in selective consumption. I demonstrate that stream width, depth and pool volume, which are predicted to increase hunting difficulty, are associated with decreased selective consumption and that there is more selective consumption in streams with higher wood volume and higher percentage of undercut banks.

My concluding chapter synthesizes and provides further discussion for some key points in the study. Furthermore, I outline the difficulties of observational studies in ecology, where experiments are less feasible, and how these were overcome in my study.

My results demonstrate the importance of large predators and habitat heterogeneity in salmon-bearing streams. An in-depth understanding of the factors that influence the foraging behaviour of bears on spawning salmon has considerable value for predictions of future ecological and evolutionary impacts on ecosystems. The results also highlight an important mechanism for dissimilarities in salmon nutrient flux between streams and suggest that stream characteristics can mediate the extent of size-biased predation and selective consumption by bears.

Chapter 2. Habitat characteristics and stage of season influence size-biased predation on salmon by bears

2.1. Abstract

Predators can drive trait divergence among populations of prey by imposing selective pressure on certain prey traits. Habitat characteristics can mediate predator selectivity by providing refuge for prey. I aimed to quantify the effects of stream characteristics on biases in the sizes of spawning salmon caught by bears (*Ursus arctos* and *U. americanus*) on the Central Coast of British Columbia, Canada. This involved measuring size-biased predation on spawning chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon in 12 streams with varying habitat characteristics. I tested several hypotheses for how stream characteristics could mediate size-biased predation, and tested for how such size-biases in turn translate into differences among populations in the sizes of the fish. Bears caught larger-than-average salmon as the season progressed and in streams with fewer refugia (i.e., wood and undercut banks) for the fish. Across streams, the mean number of salmon killed by bears was positively correlated with the mean number of spawning salmon (2009-2014). Salmon were marginally smaller in streams with more pronounced size-biased predation but this predictor was less reliable than physical characteristics of streams, with larger fish in wider, deeper streams. These results support the notion that selective forces imposed by predators can be mediated by habitat characteristics, with potential consequences for physical traits of prey.

2.2. Introduction

Predator–prey interactions are important features in the natural functioning of ecosystems (Lima 1998). Over time, they can also drive physical trait divergence among populations via selective pressures imposed on prey (reviewed in Vamosi 2005). These evolutionary responses can then, in turn, influence ecosystem processes such as community structure and ecosystem functioning (Pelletier et al. 2009; Palkovacs et al. 2011).

Predator–prey interactions can be mediated by characteristics of the environment in which they take place (Domenici et al. 2007). These habitat-mediated effects can have strong impacts on predators and prey as well as on other aspects of the ecosystem. For example, a reduction in seasonal sea ice has significant impacts on polar bear hunting opportunities and, therefore, prey survival and biological productivity, among other far-reaching consequences (Stirling and Derocher 1993; Derocher et al. 2004).

Pacific coastal bears and spawning salmon represent excellent model organisms to examine the evolutionary and ecological consequences of predator–prey interactions (Carlson et al. 2011). Bears are a major salmon predator and deposit salmon carcasses, which contain valuable marine-derived nutrients, into the riparian zone (Schindler et al. 2003; Helfield and Naiman 2006) where they become available to terrestrial scavengers and plants (Janetski et al. 2009; Hocking and Reynolds 2011). Furthermore, bears can catch and consume fish non-randomly, with demonstrated preferences for larger-than-average salmon (this behaviour is hereafter referred to as “size-biased predation”) (Reimchen 2000; Ruggerone et al. 2000). Bears may select larger salmon because they have more flesh and more preferred energy-rich parts such as eggs (Quinn et al. 1995; Gende et al. 2001). Similarly, bears may be biased for newly-arrived salmon due to their higher energy content (Gilbert and Lanner 1995; Hendry and Berg 1999; Gende et al. 2004). Size-biased predation may also occur if larger salmon are more visible, more accessible or easier to catch.

Certain stream characteristics may influence bears' ability to successfully capture desirable salmon. Pools, wood obstacles and undercut banks as well as the width and depth of a stream may all affect the difficulty of finding and capturing salmon (Gregory and Ashkenas 1990; Quinn et al. 2001; Gende et al. 2001; Braun and Reynolds 2011). I define stream "complexity" as a combination of all of these habitat characteristics, with higher values indicating higher complexity. In complex streams where prey are harder to catch, bears may be less able to obtain their preferred prey-type. This is supported by previous studies which demonstrate that bears are better able to catch larger (Quinn and Kinnison 1999), newly-arrived salmon (Gende et al. 2004) in narrower, shallower streams than in deeper, wider streams.

The date in the salmon spawning season and abundance of salmon may also modify bear hunting behaviour. During the salmon spawning season, bears may enter a pre-hibernation stage known as "hyperphagia", where they develop a strongly increased appetite (Nelson et al. 1983) which may influence their foraging behaviour. For example, as bears become "hungrier", they may be less discriminate in the types of fish they capture, at all streams. However, I expect this would be counterbalanced by the reduced responsiveness of all the fish near the end of the season, when the stream is only populated with individuals in the post-spawn stage. After fish have spawned, they are noticeably listless and are easily caught by hand (personal obs.). Therefore, I expect that this would decrease pursuit difficulty and afford bears a better ability to capture the desired larger individuals. High abundances of salmon may also influence bear foraging behaviour by decreasing a bear's search time for prey. Positive correlations between the number of bear-killed salmon and salmon abundance have been demonstrated (Quinn et al. 2003) as well as increased selective consumption of the energy-rich body parts of salmon in streams with more fish (Gende et al. 2001).

Size-biased predation on salmon by bears may have important evolutionary consequences. Salmon body size represents a compromise between several selection pressures. Sexual selection favours larger males during competition for mates (Quinn and Foote 1994), and larger females due to larger egg size, higher fecundity (Quinn et al. 1995), ability to dig deeper nests (Steen and Quinn 1999) and greater success competing for prime nest sites (Foote 1990). These effects can be counterbalanced by

predation, which may shift population equilibria towards smaller individuals due to the removal of larger fish before they have spawned (Quinn and Kinnison 1999; Carlson et al. 2009). Strong natal homing results in restricted gene flow between salmon breeding groups (Quinn et al. 1999) and allows adaptive trait divergence between populations under varying selection regimes, including predation.

The goal of this study is to understand how habitats can mediate predation, and potentially, therefore, affect the evolution of salmon body size. Specifically, I examine how size-biased predation is influenced by refugia in spawning habitats. The dynamics of habitat-mediated interactions have been demonstrated, but the effects of specific, refuge-providing characteristics (e.g., undercut banks) and their influence on size-biased predation are not yet well established. Studies in this field have often compared two streams, testing for the role of stream width and depth in size-biased predation. Here, I incorporate a larger suite of stream characteristics, including large wood, pools and undercut banks along with physical dimensions of streams, as well as the abundance of salmon. I also consider a wide gradient of variation in these characteristics across 12 streams, and use information-theoretic methods to assess the relative importance of each. My analyses consider two species of salmon that differ greatly in body size: pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon. Finally, I ask whether the average body sizes of fish in each stream match the magnitude of size-biased predation.

I predict more size-biased predation in streams with 1) more refuge-providing stream characteristics, including undercut banks, wood, pools, depth and width, and 2) higher prey abundance. I also predict size-biased predation will be higher near the end of season than the beginning. These findings lead to predictions about the sizes of the fish in different streams, which I then test in conjunction with analyses of stream characteristics.

2.3. Methods

I studied 12 streams in separate watersheds in the Great Bear Rainforest on the Central Coast of British Columbia (BC), Canada (Fig. 1.1). All of the sites are located in the Heiltsuk First Nation's territory near Bella Bella, BC. These streams are remote,

accessible only by boat, with few contemporary human influences, and represent broad natural gradients of habitat characteristics. Both black (*Ursus americanus*) and grizzly (*U. arctos*) bears are found in this area. However, black bears are likely present at all of the streams whereas grizzlies are more likely to be found at the four mainland/King Island streams. I found no significant trends in predation patterns (e.g., predation rate, number of kills, and intensity of size-biased predation) between the mainland/King Island and the other streams during my exploratory analyses.

2.3.1. Stream Characteristics

Stream characteristics were measured during the summer of 2014 according to standard practices in stream measurement (Bain and Stevenson 1999). I used a stratified random sampling design with the length of the study reach defined as 30 times the average of three bankfull width measurements (i.e., the maximum width of the stream banks that water could reach before flooding). These measurements were taken where the stream meets the estuary. Each study reach was divided into four equal sections and three cross-sectional transects were assigned randomly per section. At each transect, I measured bankfull width and channel height, which indicates the maximum water-level height of the stream.

Measurements in each reach included all pool dimensions, large wood dimensions, and percentage of undercut banks. The length, width, maximum depth and tail depth were measured for all pools within the reach according to Fausti et al. (2004). The tail depth is the pool's deepest location in its downstream break in stream slope; this is the last location that water would flow out of the pool if the stream flow ceased. Pool volume was calculated using maximum depth minus tail depth to control for differences in water levels caused by varied rainfall over the season (Lisle 1987). All wood with diameter > 0.1 m and length > 1.5 m within the reach was measured and transformed to total volume per 100 m for each stream (Fausti et al. 2004). Finally, I measured the percentage of the stream bank that was undercut. Undercut banks are defined as banks that overhang a scoured cavity below the stream water line (Bain and Stevenson 1999). Stream characteristics are listed in Appendix B.

2.3.2. Spawning Salmon Abundance

Spawning salmon abundance was measured concurrently with the salmon carcass measurements during the fall spawning period (11 September to 21 October 2014). Teams walked in the streams and on stream banks to visually estimate the number of live spawning salmon and count bear-killed and senescent salmon carcasses. When possible, streams were counted three times and the Area-under-the-curve (AUC) estimation method was used to calculate total abundance (English et al. 1992) of each species. Pink and chum stream residency times were assumed to be 20 and 10 days, respectively. When fewer than three complete counts were achieved, the peak live + dead estimation method was used to estimate total abundance. This peak count has previously been shown to provide a close match to AUC measurements in the streams we studied (Field and Reynolds 2011; Hocking and Reynolds 2011). This was verified for our 2014 field season (chum AUC mean= 1,172.6 +/- 337, chum peak mean=1,423.1 +/- 421.92, adj R²= 0.911, p<0.001, n=7 streams; pink AUC mean= 1,874.8 +/- 845.17, pink peak mean=1,859.0 +/-976.26, adj R²= 0.988, p<0.001, n=5 streams). Total pink and total chum abundances were combined in all analyses to avoid any collinearity between the species, and to reduce the number of parameters in the models.

2.3.3. Salmon Measurements

During the salmon spawning period in the fall of 2014 we opportunistically measured the first 20 senescent carcasses per sex that we encountered of each species, for a total of 80 senescent fish per stream per visit where possible. Measurement of senescent carcasses establishes a basis for comparing average salmon size, in the population, to the size of bear-killed salmon. The proportion of salmon that are killed by bears is very low in these streams so senescent salmon are good representatives of the population and are not skewed by size-biased predation (see Chapter 2.4.1. Predation Intensity). We measured every bear-killed carcass that we found along a five-metre band into the riparian zone on both banks. Our search distance represents a conservative estimate of the size of bear-killed salmon. Bears may carry some salmon much deeper into the forest and the distance transported can increase with larger salmon size (Reimchen 2000). Therefore, inclusion of carcasses

outside of this search zone would likely only increase the difference in size between bear-killed and senescent fish. We also took opportunistic measurements of salmon that were seen outside of the five-metre riparian boundary when encountered. Though salmon-hunting wolves are present in these streams, bear- and wolf-killed prey have reasonably distinct carcass consumption patterns, which allowed us a considerable degree of confidence when discriminating between kills. Wolves almost exclusively consume the brain and do so quite precisely (Darimont et al. 2003), whereas bear-killed fish are consumed more thoroughly. In our observations, even when the brain case is selectively consumed by bears, the bite marks are larger and less precise (consistent with Reimchen's (1994) observations of bears' salmon consumption behaviour). We clipped the jaw tip of all measured carcasses to prevent duplicate measurements on future visits.

For each measured carcass, we recorded the species, sex, cause of death (senescent or bear-killed) and distance from the stream. We measured, whenever possible, the body dimensions to the nearest mm according to Fleming and Gross (1989, 1994). Body length (postorbital-hypural length) was taken from the back of the eye socket to the beginning of the caudal fin. This measurement avoids difficulties with damaged caudal fins. Jaw length was measured with calipers from the tip of jaw to the posterior point of the maxillary.

We chose jaw size as the proxy for salmon size in our analyses because many bear-killed salmon were so damaged that only jaw measurements could be taken. The jaw was intact in 98.6% of all carcasses (n=2,455). The jaw is also resilient to decomposition and scavenging whereas other measurements become less reliable as the water content of the carcass reduces over time. Most importantly, salmon jaw size is highly correlated with salmon body length (Table 2.1).

2.3.4. Predation Intensity

To examine patterns of predation intensity in 2014, I ran linear models with the number of bear-killed salmon against the cover and escape indices (see next section) as well as the number of spawning salmon (in 2014). Then, to examine broad inter-annual

patterns in predation intensity, I ran the same linear models at these streams but used means of data collected from 2009 to 2014 for both the response variable (number of bear-killed salmon) and for the “number of spawning salmon” explanatory variable. The 2009-2013 bear-killed salmon abundance and spawning salmon abundance data were collected in the same way as our 2014 data (see Chapter 2.3.2. Spawning Salmon Abundance) as part of the Reynolds Research Group’s annual salmon spawning surveys.

2.3.5. Statistical Analyses – Habitat-Mediated Predation Models

All statistical analyses were performed in R (R Core Team 2014). I used Principal Components Analysis (PCA) to create two reduced sets of linearly uncorrelated stream variables. This reduced the number of parameters in the models and eliminated collinearity between habitat variables. For example, wood volume/100 m and % undercut banks variables were positively correlated and are geomorphologically related features of streams (Smith et al. 1993). To account for this, a parameter, named “cover” was created from these two variables; both loaded with coefficients > 0.70 onto the first principal component, which explained 77% of variance in the data. Pool volume/100 m, bankfull width and channel height were also correlated and represent water volume, which translates to escape opportunities from predators and lowers prey visibility. For example, I could easily touch salmon in shallow, narrow streams whereas that was almost impossible in pools or wider, deeper streams. In a separate analysis, I created a new composite variable consisting of these three variables, which I named “escape”. All three variables loaded with coefficients > 0.57 onto the first principal component, which explained 72.5 % of the variance.

I used linear mixed-effects models to account for a lack of independent samples within streams. The random effect allows the intercept of the model to vary depending on the stream, accounting for inherent differences between streams that are not accounted for in the model. The global model was as follows:

$$y = \theta_{\text{stream}} + \beta_0 + \beta_1 X_1 + \sum_{j=2}^7 [\beta_j X_j + \beta_{j:1} X_j X_1] + \varepsilon$$

$$\theta_{stream} \sim Normal(0, \sigma_{stream})$$

$$\varepsilon \sim Normal(0, \sigma_{stream}(x_2x_1))$$

where the response variable γ is salmon jaw size (transformed by the natural logarithm to satisfy assumptions of residual normality) and β_0 is the intercept. To test for size differences between bear-killed and senescent salmon carcasses, I include x_1 as a binary predictor for the cause of death (bear-killed or senescence) which is referred to as “death” in the models. x_2 and x_3 are binary variables for sex and species, respectively and are included in all models, to control for the inherent size differences between the sexes and between species, since both factors change the intercept for each subgroup. I account for the date, cover index, salmon abundance and escape index through the continuous parameters $x_{(4-7)}$. At this point, the model predicts how all combinations of male/female, chum/pink and bear-killed/senescent salmon jaw sizes differ in their intercepts from each other and how they may change, concurrently, along a gradient of the continuous habitat variables. However, the interaction term with the cause of death is crucial to establish if the intensity of size-biased predation changes with stream characteristics. Therefore, each parameter includes an interaction term (x_jx_1) with death, to allow the slopes of the bear-killed salmon regression lines to differ from those of senescent salmon. This provides an estimate of how the magnitude of size-biased predation (i.e., the difference between the two regression lines) changes with respect to each model parameter (e.g., cover index) as the regression lines deviate. To validate model assumptions of equal variance, the models include an error term which allows variances to differ based on sex and death using the “VarIdent” structure (Zuur et al. 2009) and adds four parameters to each model.

To make inferences about the patterns of size-biased predation in the streams, I competed 20 models using Akaike’s Information Criterion (AIC_c), corrected for small sample size, which compares model fit while simultaneously penalizing models with higher numbers of parameters (Burnham and Anderson 2002). All models were calculated using maximum likelihood for AIC_c comparison. The assumption of homoscedasticity was validated in all models. Furthermore, correlation and normality assumptions were validated and Variance Inflation Factors (VIF) were checked with the

top models. All parameter VIF's were less than two, which confirms that multicollinearity between model parameters is not an issue (Zuur et al. 2010). Model covariates were standardized (mean=0, SD=2) to allow for direct comparisons of fixed effects (Gelman 2008; Schielzeth 2010).

The regression slopes of jaw to body-length relationships of male and female pink and chum salmon revealed marginally different ratios between subgroups (Table 2.1). For example, every 1 cm increase in jaw length translates to a 3.02 cm increase in body length for a pink female but only a 2.66 cm increase in chum male's body length. Furthermore, salmon body length is the most visually pertinent feature for hunting bears. To account for this, I standardized jaws by transforming them to respective body lengths using the linear regression results (between body length and jaw length) for each subgroup of salmon (Table 2.1). These standardized body lengths were created after the modelling process and only used in the visual presentation of the results.

2.3.6. Statistical Analysis – Salmon Body-Size Models

I tested predictors of salmon body length in streams in the same way as I tested habitat-mediated predation, i.e., using an information-theoretic approach to compare linear mixed-effects models with stream as a random effect. The response variable was the average body length of all measured senescent salmon ($n=1,585$) by sex and species for each stream. Senescent salmon represent a random sample of the streams' populations because of the way they were sampled (see Chapter 2.3.3. Salmon Measurements). A sample of bear-killed salmon may be biased for larger individuals at certain streams and thus would not represent a random sample of a stream's population. Furthermore, the predation rates are low at these streams (see Chapter 2.4.1. Predation Intensity) and I am, therefore, confident that the removal of salmon by bears, size-biased or not, would not hinder the ability to get a representative sample of the population. Commercial fisheries are size-selective but are not stream-specific and, therefore, these could not have had confounding effects on body-size divergence among these streams, which were in close proximity to one another. I tested two predictor variables for salmon body length: 1) "stream size index", represented by a principal component containing bankfull width and channel height, which both loaded > 0.70 and explain 81% of the

variance in the data, and 2) my metric of size-biased predation: the difference between mean bear-killed salmon jaw length and mean senescent salmon jaw length at each stream, by sex and species in 2014, predicted by the top habitat-mediated predation model. I predicted that salmon body size would be positively associated with stream size (Carlson and Quinn 2007; Quinn and Buck 2001) and I expected to find larger fish in streams that experienced less size-biased predation (Quinn et al. 2001). All model assumptions were validated and VIF's were checked to ensure multicollinearity was not an issue. I also ran linear regression models of average salmon body length per sex and species against average predation rate from 2009-2014 to determine if there was a relationship between body size and predation rate.

2.4. Results

Salmon jaw length proved to be a good proxy for salmon body length, as the two measurements were highly correlated (Table 2.1). It was nearly always possible to measure jaws, whereas heavy consumption by bears precluded many body-length measurements. Linear regressions predicted that differences in 1 cm of salmon jaw length translate to a 2.77 cm increase in average salmon body length, which can translate to approximately a 15% increase in lateral surface area of each individual salmon (Quinn and Kinnison 1999).

Table 2.1. Means (cm), regression slopes and correlation coefficients of jaw-length to body-length relationships of male and female pink and chum salmon.

Subgroup	Mean Jaw Length (cm)	SE	Mean Body Length (cm)	SE	n	r	b	p
Chum Male	10.87	0.06	57.11	0.21	546	0.81	2.66	<0.001
Chum Female	7.92	0.04	56.80	0.17	527	0.72	3.26	<0.001
Pink Male	8.67	0.07	43.8	0.19	313	0.79	2.12	<0.001
Pink Female	5.67	0.03	41.86	0.13	394	0.62	3.02	<0.001

2.4.1. Predation Intensity

The predation rate was low in all the streams. The average predation rate in 2014 was 3.2% (SD = 2.3) and ranged from 0.6% to 7.1%. When using only 2014 data, I found a strong positive correlation between the number of bear killed salmon and the cover index (adj $R^2 = 0.65$, $p < 0.001$, Fig. 2.1). There was no relationship between the number of kills and salmon abundance or stream escape index (both adj $R^2 < 0.16$, $p \geq 0.1$). When using 2009-2014 data, I found that, on average, bears killed more fish in streams that had more spawning salmon (adj $R^2 = 0.60$, $p < 0.005$, Fig. 2.2). There was no relationship between the average number of bear-killed salmon and the cover and escape indices (all adj $R^2 < 0.09$, $p \geq 0.34$). Additionally, there were no significant trends in predation rate vs. the habitat characteristic variables or salmon abundance (all adj $R^2 < 0.14$, $p \geq 0.12$).

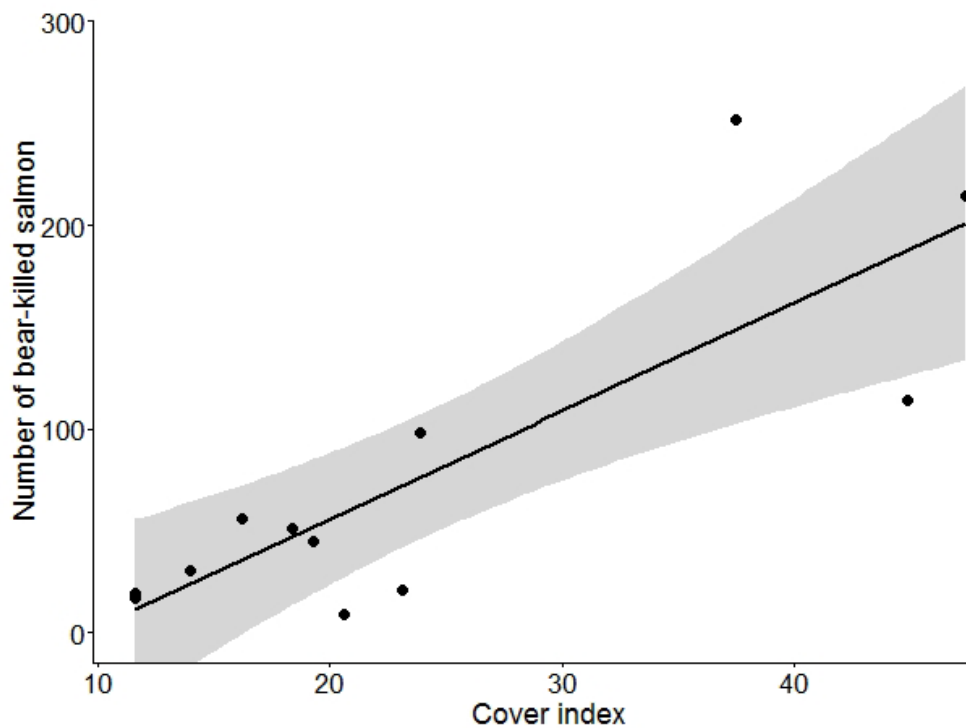


Figure 2.1. The number of bear-killed salmon (2014) vs. cover index of study streams (n=12). The regression line is predicted from a linear regression (adj $R^2 = 0.65$, $p < 0.001$) and the grey band is the 95% confidence region.

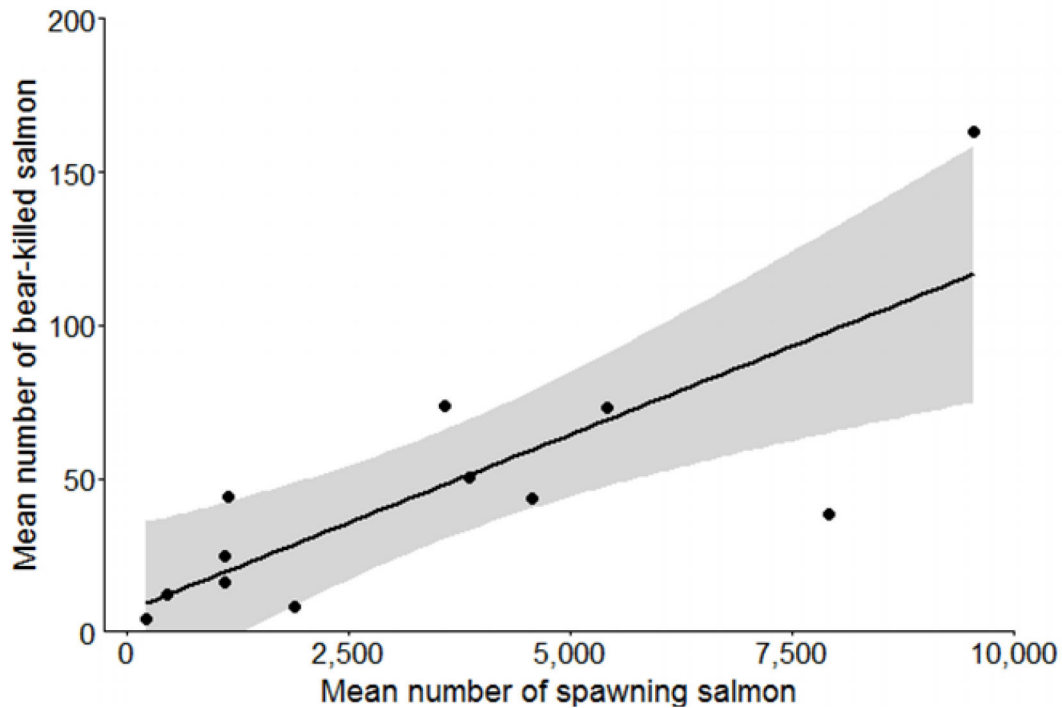


Figure 2.2. The mean number of bear-killed salmon vs. mean number of spawning salmon on 12 streams (2009-2014). The regression line is predicted from a linear regression ($\text{adj } R^2 = 0.60$, $p < 0.005$) and the grey band is the 95% confidence region.

2.4.2. Habitat-Mediated Predation

Size-biased predation was apparent at most of the streams (Fig. 2.3). When broken down by sex, species and stream, 34 out of 46 (74%) subgroup combinations of species and sex had larger mean bear-killed salmon jaws than senescent salmon jaws over the entire season (Fig. 2.3). This figure also reveals the inherent differences in salmon size between streams, which is an observation that I explore further in Section 2.4.3. Salmon Body Size. The tendency of bears to have killed larger fish was also supported by the AIC_c results for the models that included death as a predictor (Table 2.2a). The model that did not include death as a predictor was ranked lowest of all models, which further supports the interpretation that size-biased predation was occurring in these streams.

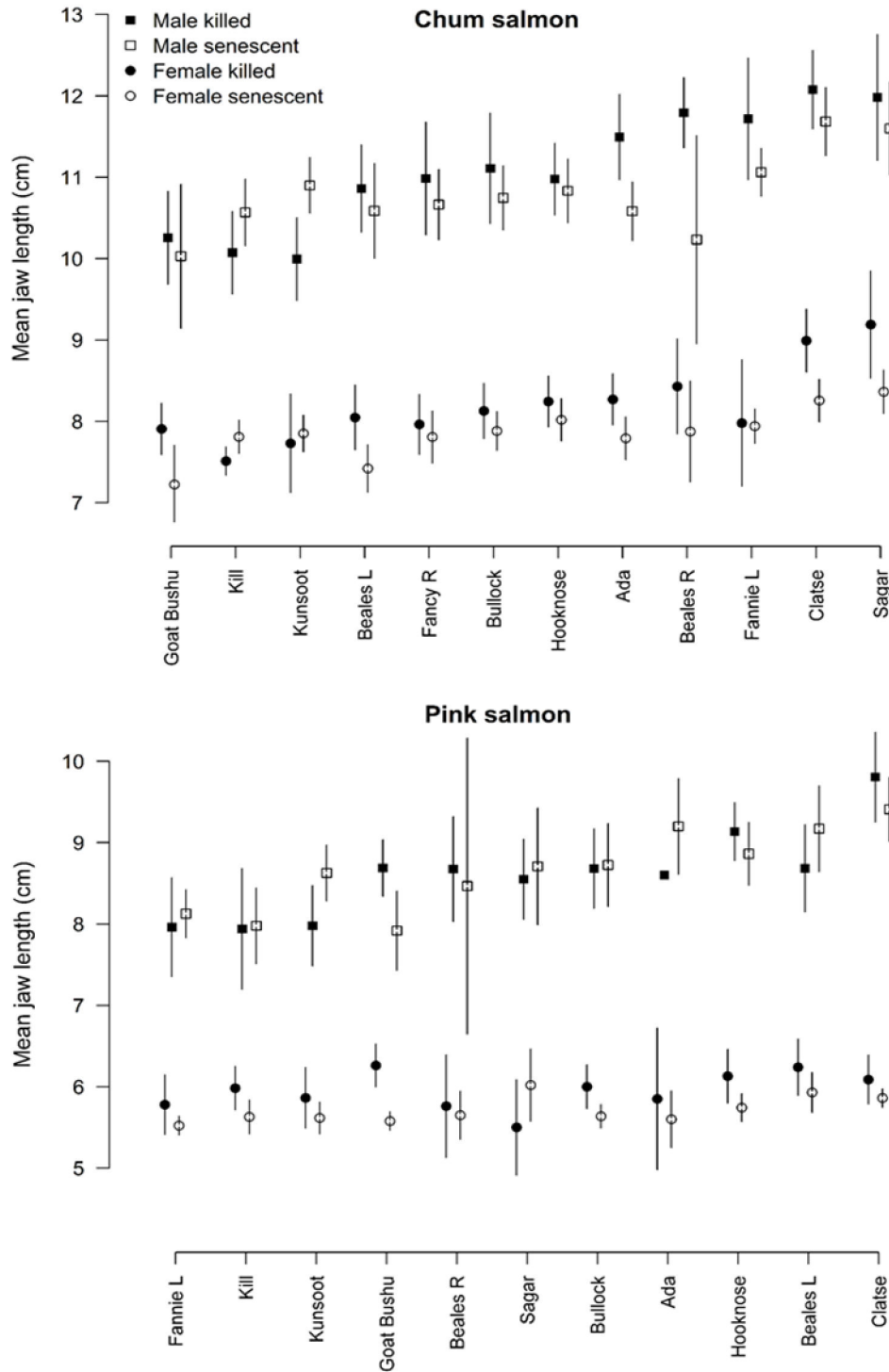


Figure 2.3. Mean chum and pink salmon jaw lengths per stream for senescent and bear-killed salmon. Male and female salmon are shown separately. Bars represent 95% confidence intervals. Streams are ordered, per species, by the mean jaw length of male and female, bear-killed and senescent salmon groups per stream.

Table 2.2. Comparison of mixed effects models of a) habitat-mediated predation with salmon jaw length as the response variable and b) salmon body size with salmon body length as the response variable, using Akaike's Information Criterion (AIC_c), corrected for small sample size. Each model includes a random effect of stream. In section a) only models with AIC_c weights > 0.02 were included (the top 3 totalled 0.98 cumulative weight); in section b) all models are reported. Section a) top model: marginal R² = 0.77 and conditional R² = 0.78; Section b) top model: marginal R² = 0.975 and conditional R² = 0.978. In section a) “cover” refers to “cover index” and “escape” to “escape index”.

Model	K ¹	AIC _c ²	Δ AIC _c ³	w _i ⁴	ER ⁵
a) Habitat-mediated predation models					
sex + species + death + date + cover + sex:death + species:death + date:death + cover:death	15	-3340.2	0	0.738	1.0
sex + species + death + date + cover + escape + sex:death + species:death + date:death + cover:death + escape:death	17	-3336.6	3.6	0.126	5.7
sex + species + death + date + cover + salmon abundance + sex:death + species:death + date:death + cover:death + salmon abundance:death	17	-3336.5	3.7	0.116	6.2
b) Salmon body-size models					
sex + species + stream size + size-biased predation	7	148.3	0	0.86	1.0
sex + species + stream size	6	152.5	4.2	0.10	8.6
sex + species + size-biased predation	6	155.4	7.1	0.02	43
sex + species	5	156.9	8.6	0.01	86
null	3	303.1	154.8	0	-

¹ The number of parameters in the model. ² Value representing the strength of the model relative to other models, with lower values indicating a better fit. ³ The difference between the AIC_c values of the models and the AIC_c value of the best fitting model. ⁴ The Akaike weights evaluate the relative strengths of the models; the probability that it is the top model. ⁵ The evidence ratio (likelihood probability ratios relative to the top model).

As predicted, the magnitude of size-biased predation increased with date and decreased with cover index. This is interpreted by the positive coefficient estimate for the interaction between date and death and the negative coefficient estimate for the interaction between cover index and death, respectively (Fig. 2.4a). There is an

increasing divergence between the size of bear-killed salmon jaws and senescent salmon jaws as the season progresses (Fig. 2.5). Conversely, and as predicted, size-biased predation was lower in more complex streams, as measured by the cover index (a principal component incorporating the volume of wood and % of undercut banks in a stream) (Fig. 2.6). Predation was slightly more size-biased on female salmon than on males, indicated by the negative coefficient value of the interaction between sex and cause of death (Fig. 2.4a). Bears exerted similar intensities of size-biased predation on both species; this is indicated by the parameter estimate for the interaction between species and death (Fig. 2.4a).

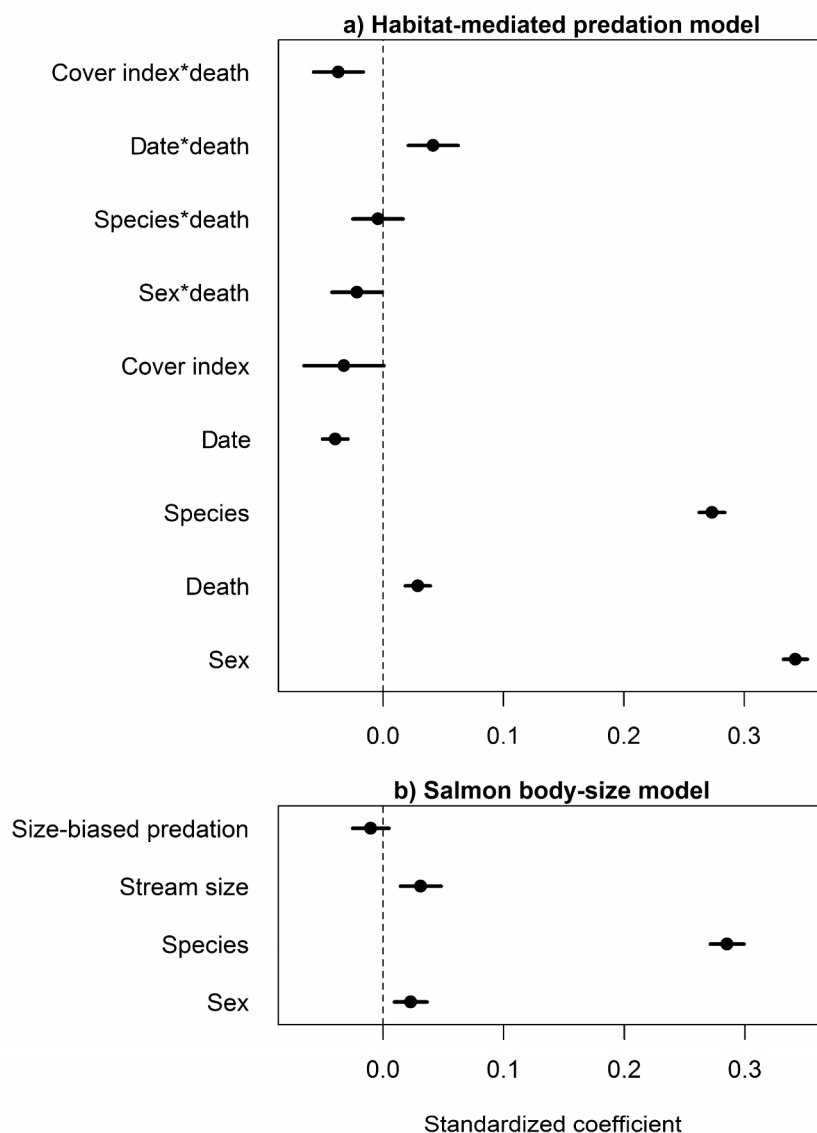


Figure 2.4. Standardized (mean=0, SD=2) coefficients (circles) of model parameters with 95% confidence intervals (lines) for top model (as determined by AIC_c) of a) habitat-mediated predation (Table 2.2a) and b) salmon body-size model (Table 2.2b). The coefficients denote the change, in a) (natural-log) salmon jaw-size and b) (natural-log) salmon body-length as each associated parameter increases by 2 standard deviations. Note: Sex: female=0 and male=1, Species: pink=0 and chum=1, Death: senescent=0 and bear-killed=1. In a) each parameter interacts with death to separate senescent and bear-killed salmon jaw size regression estimates and allow for prediction of differences in the intensity of size-biased predation as parameters vary.

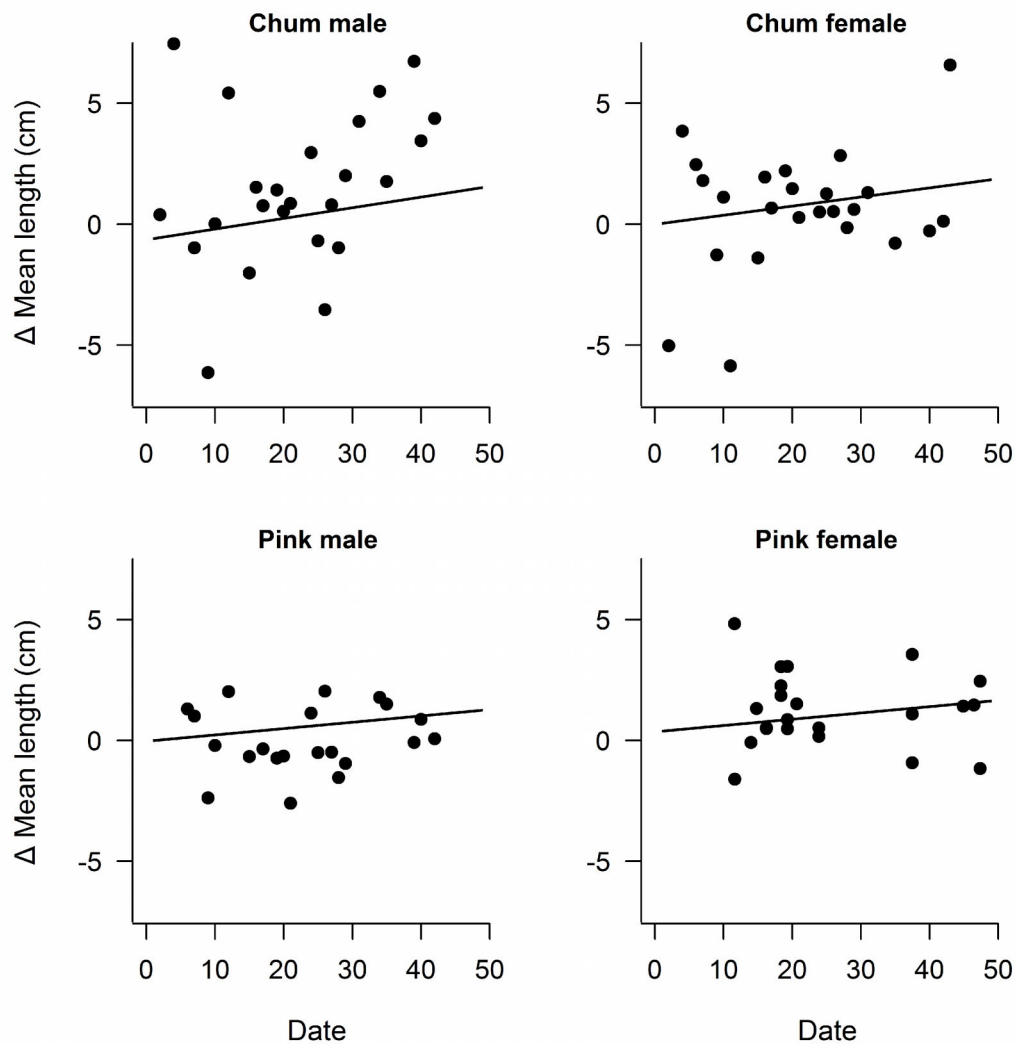


Figure 2.5. The intensity of size-biased predation on delta mean body lengths (cm) of salmon versus date (with 1 = September 11, 2014). Each point represents the difference in bear-killed salmon and senescent salmon body lengths for the corresponding date. Positive values indicate that bear-killed salmon were larger on average than senescent salmon on that sampling date. The regression lines are the top model's prediction (Table 2.2a) of size-biased predation as date increases with cover-index held mid-range.

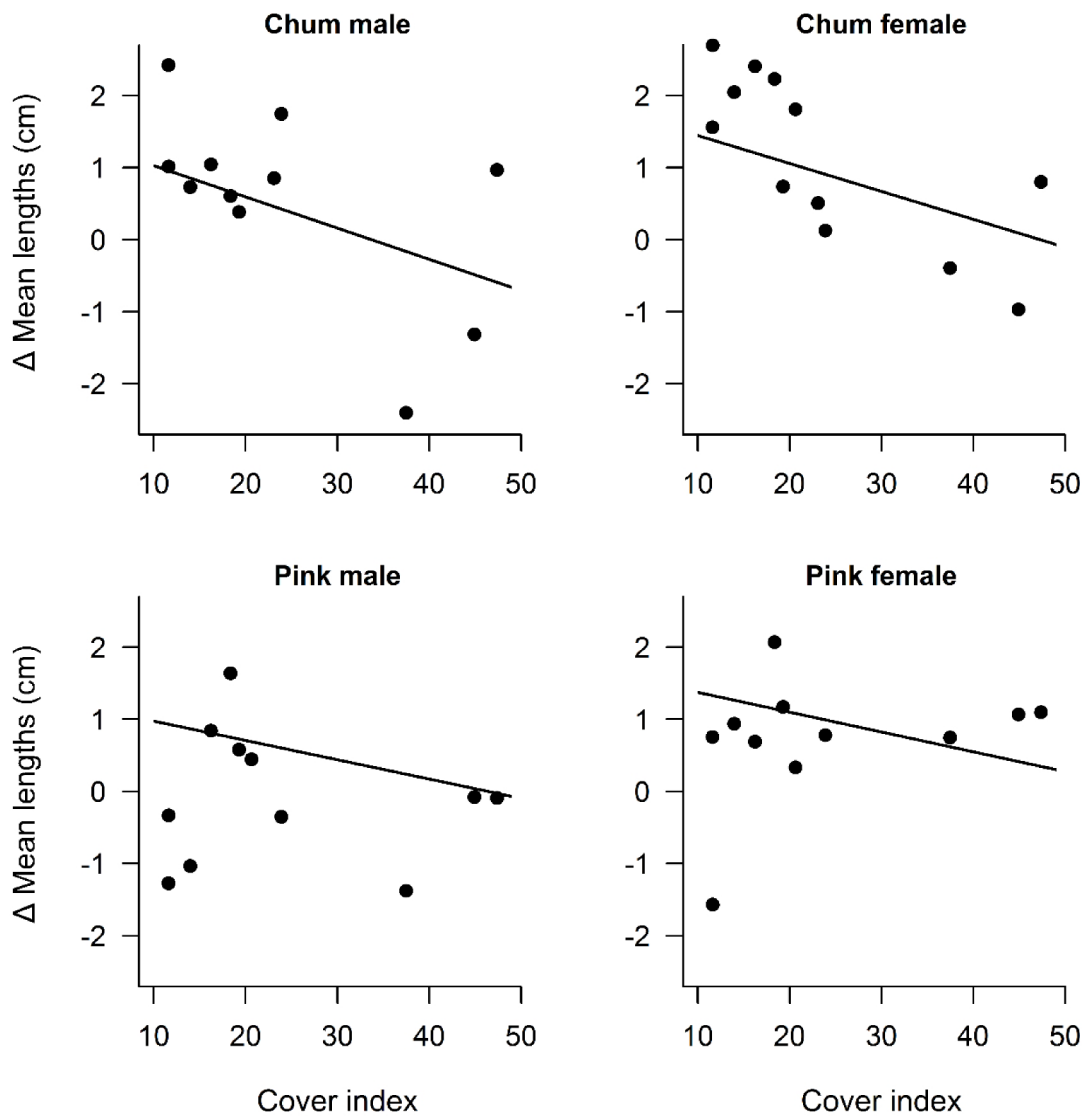


Figure 2.6. The intensity of size-biased predation by bears on delta mean body lengths (cm) of salmon versus cover index. Each point represents the difference in bear-killed salmon and senescent salmon body lengths for the corresponding cover index value. Positive values indicate that average bear-killed salmon were larger than average senescent salmon at that level of cover. The regression lines represent the predicted magnitude of size-biased predation from the top ranking model (Table 2.2a) as cover index changes, with date held constant at its mean.

These results are supported by the top model, with 73.8% of the weighted support, in the AIC_c output (Table 2.2a), which includes date and cover index as predictors, interacting with death. In fact, date, cover index, sex and species are

included in the top 3 of 20 models, which account for 98.0% of the cumulative Akaike weights (i.e., the relative strength of the models), further indicating the importance of these parameters. Escape index and salmon abundance were not included as parameters in the top model and are not considered important predictors of size-biased predation.

Fish arriving at the end of the season experienced more intense size-biased predation (indicated by the positive interaction between date and death) and were also found to be smaller. The interpretation of decreasing size of senescent salmon by date is indicated by the significant negative term for date (with no interaction) which has a small standard error and confidence intervals that do not overlap 0 (Fig. 2.4a). This leads to the inference that the size of salmon (represented by senescent jaws) decreased throughout the season with a considerable degree of confidence.

2.4.3. Salmon Body Size

Salmon were larger in bigger streams, as predicted (Fig. 2.4b). Sex and species were, of course, good predictors of salmon length but were only included to control for the inherent differences in size between these groups. There was also marginal support for the prediction that streams which experience higher intensities of size-biased predation would have smaller salmon. However, this parameter estimate's confidence intervals overlap with 0 and, therefore, this result is less conclusive than the stream-size predictor of salmon body size (Fig. 2.4b). Nevertheless, it was included in the top model, not by necessity or default, but because it added enough explanatory power to better predict the data and outcompete the other models. In fact, the top model had 86% of the support, as indicated by the Akaike weight (Table 2.2b), which strongly supports the notion that body length is associated both with size of the stream as well as marginally associated with the intensity of size-biased predation. Finally, I found no relationship between salmon body length and predation rate with tests of any of the four combinations of sex and species (all $R^2 < 0.17$, and $p > 0.2$).

2.5. Discussion

I found biased predation toward larger pink and chum salmon by bears in most of the 12 streams (Fig. 2.3). As predicted, the intensity of size-biased predation increased as the season progressed (Fig. 2.5) and decreased in streams with more wood and undercut banks, as represented by the “cover index” (Fig. 2.6). The abundance of salmon and the escape index, based on stream width, depth and pool volume variables, were not good predictors of size-biased predation in the streams. As predicted, I also found that salmon were larger in deeper, wider streams and marginally smaller in streams with higher intensity of size-biased predation.

Our strongest predictors of the intensity of size-biased predation were the cover index and the date. The lower intensity of size-biased predation in streams with more cover matches predictions based on the fish being better able to hide, and bears being more impeded physically when hunting (Fukushima and Smoker 1998; Deschênes and Rodríguez 2007; Floyd et al. 2009; Braun and Reynolds 2011). I propose two possible reasons for predation being biased towards larger fish as the season progressed. First, bears may alter their behaviour as they enter hyperphagia, which can occur during the salmon spawning season and corresponds with an increase in caloric intake (Nelson 1980; Nelson et al. 1983). During this stage, bears may become increasingly discriminating while foraging to increase their energy intake per kill. Larger fish contain a higher total mass of energy-rich parts, such as brains or eggs (Quinn et al. 1995; Gende et al. 2001), and bears may attempt to maximize caloric intake with high-value tissues, which can be achieved with fewer kills with larger salmon than small. However, the opposite could be argued as well, where bears may be less discriminate in this stage, opting to indiscriminately capture any individual to satiate their increased hunger. Second, as the season progresses and fewer salmon arrive, the remaining fish may become easier to catch. Hendry and Berg (1999) demonstrated that mass-specific somatic stores decreased during reproduction by approximately 65% and 75% in sockeye males and females, respectively. This post-reproduction stage is also associated with decreased aggression (Quinn and McPhee 1998). I noticed that over the season, the salmon underwent a dramatic change in responsiveness and speed (pers. observation). As the salmon become lethargic, bears become spoiled for choice

and gain an added advantage in their ability to capture their preferred prey-type (i.e., largest fish). I can rule out the possibility that late-arriving salmon are larger by nature because 1) my findings show that the size of salmon in these streams decreased over the season (as indicated by the negative coefficient value for date) (Fig. 2.4a), and 2) the models already account for date by comparing bear-killed salmon with senescent salmon by the date that the carcasses were measured.

I expected less size-biased predation where salmon could escape hunting bears and where fewer spawning salmon were present. The escape index, a combination of width, depth and pool volume, was a predictor of size-biased predation in the 2nd best model (Table 2.2a). However, this model had a low Akaike weight of 0.127 and an evidence ratio of 5.7, indicating that the top model was 5.7 times more likely to be the best model. Therefore, the volume of water in the spawning area, which I used to represent an “escape index”, was not an important predictor of size-biased predation in the streams. Similarly, the number of spawning salmon was not an important predictor of size-based predation as it was only included in the 3rd best model with an Akaike weight of 0.116 and an evidence ratio of 6.2. Interestingly, in a different study, Cunningham et al. (2013) found that size-biased predation was associated with salmon abundance but that the directionality was contrary to their (and my) predictions.

Although the number of salmon was not a good predictor of size-biased predation, my analysis of mean salmon abundance against the mean number of bear-killed salmon across the streams from 2009-2014 revealed a positive correlation (Fig. 2.2, adj $R^2 = 0.60$, $p < 0.005$) and is consistent with the findings of Quinn et al. (2003). My analysis of predation patterns further revealed that predation rate is quite low in these streams, ranging from 0.6% to 7.1%. I expected bears to be more size-biased in streams with higher salmon abundance and less discriminant for prey size in streams with low salmon abundance. However, the low predation rates at these streams suggest that the number of salmon was never a limiting factor for bears. Specifically, none of the streams had a low enough threshold of salmon abundances to encourage indiscriminate capture of prey by bears.

Bears killed more salmon at streams with higher wood volume and higher percentage of undercut banks (Fig. 2.1) where there was a lower intensity of size-biased predation. Capturing more fish may compensate for a lack of ability to capture prized, larger fish in these streams. This is consistent with my results from Chapter 3, where bears ate less flesh from each catch at streams with higher cover index. Together, these results suggest that cover index does not necessarily decrease the ability to capture fish, but instead, influences the ability to discriminate between prey prior to capture. Reimchen (1994) noted that 75% of observed salmon kills by bears in complex streams involved reaching under banks and log jams to pull out prey rather than actively chasing them on the spawning gravels. Though this may be a successful hunting technique in streams with high cover it may limit a bear's ability to discriminate based on prey size.

Predictions about the size of salmon follows from the top "habitat-mediated predation" model and its coefficient estimates for senescent and bear-killed salmon jaw sizes (Fig 2.4.a). Senescent salmon jaw size decreased notably over the spawning season, as indicated by the strong negative coefficient estimate for "date". Though late arriving salmon were smaller, bears increasingly captured larger-than-average fish, relative to what was available at the time, as the season progressed. That is, the size of senescent salmon jaws decreased over time and the size of bear-killed salmon jaws remained relatively stable resulting in an increasing divergence between the two groups as the season progressed. The opposite is true for the cover index parameter. The jaw sizes of senescent salmon did not vary significantly with cover index. However, bears increasingly captured larger-than-average fish, relative to what was available in the stream, as cover index decreased resulting in more size-biased predation at lower cover streams. Cover index is included as a fixed effect for senescent salmon jaw size by necessity because models that include a significant interaction term (e.g., cover index interacting with death), must also include each term independently regardless of its significance (Underwood 1997; Zuur et al. 2009).

The mean body size of salmon in the streams varied with sex, species, stream size and the intensity of size-biased predation. This is supported by the "salmon body-size models" where, the top model carried 86% of the support (Table 2.2b) and included

all four variables as predictors of salmon length in each stream. As predicted, larger streams (i.e., a stream size index PC combining stream width and depth) were occupied by larger salmon and streams with higher intensity of size-biased predation had marginally smaller salmon (Fig. 2.4b). However, the relationship between salmon length and stream size was much greater and more reliable than the relationship between salmon length and size-biased predation, as indicated by comparing their regression coefficients and confidence intervals (Fig. 2.4b). The directionality of the intensity of size-biased predation was consistent with my predictions but the high amount of overlap, with zero, in the parameters estimate's confidence intervals indicates a high degree of uncertainty. Predation can still be an important agent of selection even at the low predation rates observed at these streams. Even though the predation rate is low, the number of unsuccessful predation events may be high. Salmon can survive encounters with bears by escaping or being captured and then rejected. There can be selection for traits that enhance escape ability with unsuccessful predation events as long as the survivors reproduce successfully (Vermeij 1982). If bears keep a higher proportion of larger salmon by rejecting small individuals after capture, this would further drive the evolution of escape traits (i.e. smaller size).

It would be beneficial for future studies to consider multiple years of data to relate bear predation to variation in the size of fish among these streams. It would also be useful to consider differences in spawning habitat conditions (e.g., suitability and size of substrate) and the intensity of sexual selection and competition among individuals within each stream population.

My results suggest that stream characteristics can mediate size-biased predation by bears on salmon. The mean body size of each salmon population should represent a balance between competition and predation. A shift in habitat characteristics (e.g., humans clearing a stream) could result in a shift of habitat-mediated, predator-prey interactions and thus a shift in the selective forces that determine salmon body size.

Chapter 3. Habitat-mediated, selective consumption of spawning salmon by bears

3.1. Abstract

Salmon provide a key source of marine-derived nutrients to aquatic and surrounding terrestrial habitats in coastal areas of the North Pacific. Bears are a major predator of salmon and provide an important pathway for carcass transfer to riparian zones. The amount of salmon transferred depends on the feeding choices of bears, which may be mediated by the abundance of spawning salmon and habitat characteristics that provide refuge for the fish or facilitate their escape. I quantified selective consumption of salmon carcasses by bears (*Ursus arctos* and *U. americanus*) on the Central Coast of British Columbia, Canada. I predicted that bears would select more energy-rich parts, and eat less of each fish (i.e., “selective consumption”), in streams with more prey and simpler habitat (i.e., streams that facilitate capture). I studied 12 streams with a wide range of abundance of chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon. As predicted, there was a higher probability of selective consumption by bears on salmon in narrow, shallow streams with fewer pools, where salmon are easier to catch. However, contrary to my predictions, there was a tendency toward more selective consumption in streams with more wood obstacles and undercut banks, where hunting was predicted to be more difficult. Selective consumption also decreased throughout the salmon spawning season and was higher on chum and female prey. My results suggest that this habitat-mediated selective consumption, whereby bears leave more of each carcass uneaten, leads to streams with the largest amount of wood and percentage of undercut banks receiving an additional subsidy of 70 kg of salmon biomass for every 100 pink and chum salmon killed by bears. This suggests that stream characteristics can have indirect effects on riparian nutrient subsidies to ecosystems through selective feeding by bears.

3.2. Introduction

Pacific salmon are an important source of cross-boundary, marine-derived nutrient delivery to North Pacific coastal ecosystems. Salmon spend most of their lives growing in the sea, gaining mass from marine sources, before migrating to their natal freshwater streams to spawn. After spawning, they die and deliver valuable nutrients to the surrounding aquatic and terrestrial ecosystems (Schindler et al. 2003; Helfield and Naiman 2006). Foraging bears facilitate salmon nutrient transfer to terrestrial habitats, as they pull live fish out of streams and leave their carcasses on land nearby (Hilderbrand et al. 1999; Quinn et al. 2009). Once a salmon carcass is abandoned by a bear, the remains become available to a suite of other species (e.g., insects and scavenging birds) that transfer nutrients (reviewed in Gende et al. 2002 and Janetski et al. 2009). These nutrients are also incorporated into surrounding plant matter (Hocking and Reynolds 2011). Carcasses left in the riparian zone are particularly important to nutrient transfer because they are less likely to be washed downstream into the estuary than the senescent salmon which die in the streams (Cederholm et al. 1989). Even bear-killed salmon abandoned within streams have more value, in nutrient terms, than senescent salmon carcasses, for certain species. For example, caddisfly (Trichoptera) larvae preferentially colonize bear-killed salmon due to increased temporal availability, energetic content and accessibility of tissue (Winder et al. 2005). The amount of salmon biomass abandoned by bears is, therefore, an important component to overall nutrient transfer to both terrestrial and aquatic pathways.

To understand the patterns of salmon consumption by bears, we can turn to classical foraging theory to ask: when should bears stop eating a given carcass and invest the additional time and energy required to catch a new one? A variant on the classical patch model of foraging theory (Charnov 1976) by Sih (1980) treats each prey item as a patch and each bite as a choice. The decision to abandon a partially eaten carcass depends on the diminishing rate of return from continuing to eat a fish after the most energy-rich parts have been consumed versus investing time and energy in catching a new fish. This framework predicts that bears should be more selective for energy-rich parts of salmon in streams where fish are easier to catch. Reimchen (2000) and Gende et al. (2001) demonstrated a preference by bears for high-energy tissues

such as the brain and the eggs. The ease with which bears can catch salmon should depend on the abundance of salmon, as well as habitat characteristics that offer refuge and escape opportunities for the fish, such as wide deep streams with large pools, wood obstacles and undercut banks (Fukushima and Smoker 1998; Gende et al. 2004; Deschênes and Rodríguez 2007; Floyd et al. 2009; Braun and Reynolds 2011, Chapter 2).

Selective consumption patterns by bears may also differ with the sex and species of prey as well as the date in the salmon spawning season. Because of their eggs, females have a higher caloric value per total mass than males (Gilbert and Lanner 1995), which means bears would need to consume more of each male to acquire similar energetic rewards. Chum are larger than pink salmon, with estimated masses of 3.5 kg and 1.2 kg, respectively (Hocking and Reynolds 2011). Therefore, eating an equal amount of biomass of each, before abandonment of the carcass, would result in a lower proportion of consumption of a chum salmon carcass than of a pink salmon carcass. Furthermore, it may be easier to selectively remove and consume energy-rich parts of larger size-classes of salmon because their bodies could allow for more handling dexterity, manoeuvrability and precision of brain removal by bears (Reimchen 1994). Selective consumption patterns may also change through the fall because bears enter hyperphagia, a pre-hibernation stage associated with substantially increased appetite leading to daily caloric intake increases from 8,000 kcal to 15,000 – 20,000 kcal, at some point in the salmon spawning season (Nelson 1980; Nelson et al. 1983). Moreover, the energy-quality of salmon flesh and quantity of eggs decreases throughout salmon migration and reproduction and is, therefore, lower near the end of the season (Hendry and Berg 1999; Reimchen 2000). As the number and quality of salmon decreases toward the end of the spawning period, bears may need to eat more of each kill to acquire similar energy rewards and meet their own energetic requirements.

My objectives were to compare the consumption of salmon carcasses by bears among streams and to quantify relationships with spawning salmon abundance and stream characteristics. I predicted that the proportion of bear-killed salmon that show evidence of selective tissue consumption would be: 1) higher in streams with greater prey abundance, 2) higher in streams with less refuge for prey, 3) higher on chum

salmon than pink, and 4) higher earlier in the salmon spawning season. Predictions relating to salmon sex are less clear. Bears could be more selective when eating females if they target eggs and discard the rest of the carcass, or they could be less selective because females are smaller than males. I studied 12 streams in a remote region along the Central Coast of British Columbia, Canada, where human disturbance to habitats is minimal. The results reveal how patterns in bear consumptive behaviour may be influenced by hunting difficulty caused by physical attributes of the stream, with consequences for the amount of biomass left in the riparian zone, local food webs and overall nutrient transfer in the ecosystem.

3.3. Methods

The 12 streams were located in Heiltsuk First Nation traditional territory in the Great Bear Rainforest on the Central Coast of British Columbia, Canada (Fig. 1.1). Stream characteristics were measured in the summer of 2014 and salmon counts and measurements took place during the salmon spawning season in the fall of 2014.

3.3.1. Stream Characteristics

The stream characteristics measurement protocol is described in Chapter 2.3.1. Stream Characteristics.

3.3.2. Salmon Characteristics

Each site was visited three times throughout the salmon spawning season to quantify patterns of consumption on salmon. A thorough search of the stream reach, as well as a five-metre band of the riparian zone on both banks, was conducted to locate bear-killed salmon. We recorded the sex, species, and consumptive patterns of each bear-killed salmon. Sex was determined by examining the gonads or, if absent, the jaw/snout, teeth, skin colouration and other sexually dimorphic characteristics that readily distinguish the sexes. A categorical spawning status was assigned to each salmon carcass based on a visual inspection of the skin condition, colouration, quantity of eggs, caudal fin damage and other visible decay. The spawning status categories

were: 1) pre-spawned, 2) partially spawned, 3) post-spawned, and 4) heavily decomposed. These “decomposed” individuals were not included in the analysis because heavy decay and scavenging or colonization by maggots made it impossible to quantify consumptive choices by bears or categorize spawning status of the fish at the time of consumption. Furthermore, we excluded measurements of wolf-killed salmon, which are distinguished by their clean, surgical removal of the brain case and abandonment of the rest of the carcass (Darimont et al. 2003). These kills were usually in highly localized regions of estuaries at low tide, rather than along the stream in the forest where we were working (personal obs.). Bear-killed salmon with selective consumption of the brain were identified by their less-surgical removal of the brain, which often damaged the snout, eyes and surrounding tissue (Reimchen 1994) and by the consumption patterns on the surrounding salmon carcasses. We marked each measured carcass by cutting off the tip of the jaw to avoid re-measurement on future visits.

3.3.3. Selective Consumption Scoring Systems

Each carcass was assigned binary categorical values based on the amount of consumption (i.e., whether or not the majority of dorsal and trunk musculature was consumed) and type of body parts consumed (i.e., eggs, brain). A carcass was considered selectively consumed if the eggs (in females) and/or brain (both sexes) were consumed and <50% of the overall carcass was consumed. Otherwise, the carcass was not considered selectively consumed.

To check the robustness of my conclusions to the way in which I scored “selectivity”, I also tried an alternative analysis with a different response variable: 1) <50% of salmon consumed = “selective” consumption, and 2) > 50% of salmon consumed = “non-selective” consumption. That is, I removed the requirement of consumption of an energy-rich part from the response variable and just focused on how much of the carcass was eaten. I used the same statistical methods as for the original models.

3.3.4. Spawning Salmon Abundance

The salmon enumeration protocol and “prey abundance” metric calculation is described in section 2.3.2 –Spawning Salmon Abundance.

3.3.5. Statistics and Modelling

Statistical analyses were performed with R (R Core Team 2015). I competed generalized linear mixed effects models (GLMMs), with a binomial response and logit link, using Akaike’s Information Criterion (AIC_c), corrected for small sample size. The models describe the probability of selective consumption on each bear-killed salmon under varying conditions of prey susceptibility (i.e., stream complexity) and abundance. Mixed-effects models account for a lack of independent samples at the stream level in the study design. I compared five models to evaluate the relative support for each hypothesis (Table 3.1). Care was taken to limit the number of hypotheses to *a priori*, biologically feasible models in order to avoid spurious findings from testing large “all-subsets” models (Burnham and Anderson 2002).

Table 3.1. Models, variables, mechanisms and predictions for original scoring and alternative scoring systems for selective consumption of salmon by bears. A null model and a model that compared only forced variables (sex, species and date) are not shown.

Model	Variables	Mechanisms	Predicted association with selective consumption	Sources
Prey abundance	Number of salmon	Search times for prey are lower in prey-rich patches	Positive	1,2,3,4
Habitat complexity	Escape index <i>[pool vol/100 m]</i> <i>[bankfull width]</i> <i>[channel height]</i> Cover index <i>[wood vol/100 m]</i> <i>[% undercut banks]</i>	Wider, deeper streams with more pools provide salmon with refuge and lower visibility to bears. Wood in the stream and undercut banks decrease prey visibility and are obstacles for bears.	Negative	5,6,7,8,9,10, 11,12
Habitat complexity + prey abundance	All variables combined	All mechanisms above combined	Prey abundance [positive] Habitat complexity [negative]	1,2,3,4, 5,6,7,8,9,10, 11,12

References: 1) Cunningham et al. 2013, 2) Gende et al. 2001, 3) MacArthur and Pianka 1966, 4) Quinn et al. 2003, 5) Gende et al. 2004, 6) Quinn and Buck 2001, 7) Quinn and Kinnison 1999, 8) Deschênes and Rodríguez 2007, 9) Fukushima and Smoker 1998, 10) Braun and Reynolds 2011, 11) Floyd et al. 2009, 12) Roni and Quinn 2001.

In order to deal with collinearity and reduce the number of parameters in the models, I created reduced sets of linearly uncorrelated variables through Principal Components Analysis (PCA). I used the same principal components that were calculated in Chapter 2.3.5. Statistical Analyses - Habitat-Mediated Predation Models. A PC named “cover” represents wood volume / 100 m and percentage of undercut banks and another PC named “escape” represents pool volume / 100 m, bankfull width, and channel height.

The response variable was binomially distributed with 0 = “non-selective” and 1 = “selective” consumption. If the eggs (in females) and/or brain was consumed and the majority of the trunk and dorsal musculature was not consumed, then the carcass was scored as a 1, indicating that selective consumption had occurred (i.e., there was a demonstrated selectivity for the energy-rich parts). Alternatively, if the energy-rich parts had not been consumed and/or if the majority of trunk and dorsal musculature was consumed, then no selectivity for energy-rich parts had occurred and the carcass was assigned a 0. The global model was as follows:

$$Y_i \sim \text{Bin}(1, p_i)$$

$$\text{logit}(p_i) = \beta_0 + \beta_1 \text{sex}_i + \beta_2 \text{species}_i + \beta_3 \text{date}_i + \beta_4 \text{cover}_i \\ + \beta_5 \text{escape}_i + \beta_6 \text{abundance}_i + a_i$$

$$a_i \sim N(0, \sigma_a^2)$$

where logit stands for the logistic link, p_i is the probability that a carcass was selectively consumed for energy-rich parts, β_0 is the intercept and β is a vector that regulates each estimable parameter’s contribution to the probability of selective consumption. Habitat complexity (i.e., cover and escape indices) and salmon abundance are fixed, centered, scaled continuous variables (Schielzeth 2010). Sex, species, and date were included in all models, except the null model, as forced parameters to control for possible differences in predator preferences per type of fish (i.e., due to inherent differences in the amount of flesh and energy-rich parts) or over time in the season. These parameters would also account for differences in sex and species ratios between streams and differences in the actual sampling date between sites. a_i is included as a random intercept, by stream, to control for variability at the stream level and account for a lack of independent sampling within streams. The random intercept is assumed to be normally distributed with mean 0 and variance σ_a^2 and accounts for the lack of information about bear abundance and type or other inherent differences in streams that are not accounted for in the model (Zuur et al. 2009). Variance Inflation Factors (VIF) for each of the models were all less than two, which confirms that the model parameters did not have a multicollinearity issue (Zuur et al. 2010).

3.4. Results

Bears selectively consumed 31% of all measured carcasses across all 12 streams (n=659), with a higher proportion of selective consumption on females (38.6%) than males (20%), and more on chum (35.7%) than pink salmon (25.4%). In species by gender subgroups, selective consumption occurred on 31.2% of pink females, 15.3% of pink males, 44.6% of chum females and 23.7% of chum males.

As predicted, selective consumption was higher at narrower, shallower streams with fewer pools (i.e., low escape index) but contrary to predictions selective consumption was higher at streams with more wood obstacles and undercut banks (i.e., high cover index) (Fig. 3.1 a,b). The bivariate plots revealed no obvious trends in selective consumption over time or with the number of spawning salmon (Fig. 3.1 c,d). The proportion of salmon that were selectively consumed was marginally higher at streams with more bear-killed salmon (Fig. 3.1 e).

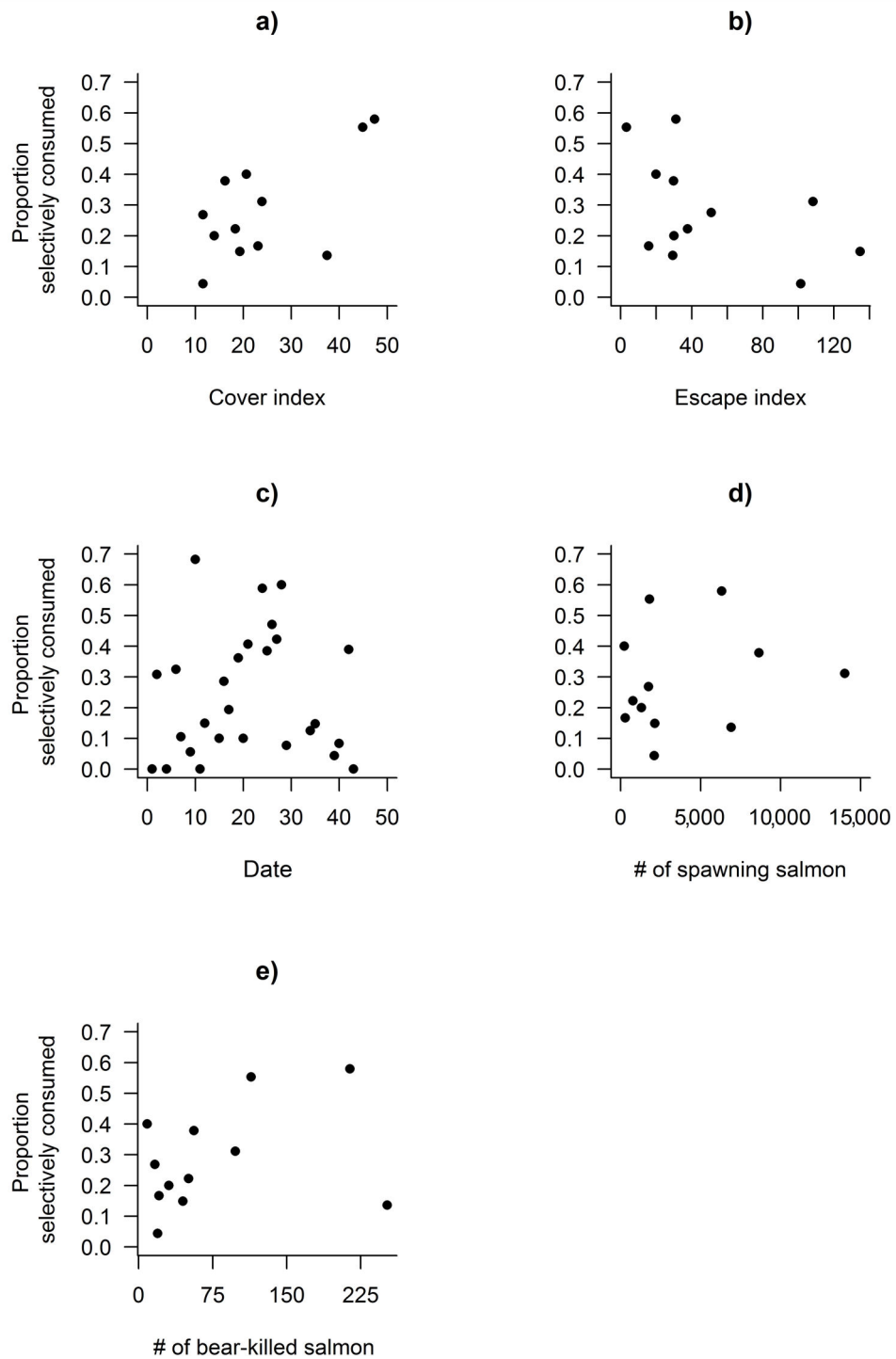


Figure 3.1. Relationships between the proportion of selectively consumed salmon and a) cover index, b) escape index, c) date (1 = 11 September, 2014), d) number of spawning salmon and e) number of bear-killed salmon. Selective consumption by bears is defined as: eggs and/or brain consumed and < 50% of carcass consumed.

The habitat complexity model was the best model for predicting the proportion of selectively consumed salmon among streams, as determined by the AIC_c analyses (Table 3.2). This model had marginal and conditional R² values of 0.15 and 0.21, respectively (Nakagawa and Schielzeth 2013), and likelihood ratio tests confirmed that it fit the data significantly better than the null model (p<0.001). Habitat complexity, which includes both cover and escape indices, was in the top two models which collectively carry 81.0% of the support as calculated by the sum of Akaike weights of both models. The second-best model had 35.2% of the support and was identical to the top model except that it included the number of spawning salmon (Table 3.2). The directionality of the salmon abundance parameter was consistent with my predictions but had less support and overlapped zero (standardized coefficient = 0.22, 95% CI: [-0.11, 0.54]). More importantly, Burnham and Anderson (2002) warn that an identical model which includes one additional parameter and has Δ AIC_c values <2, but similar maximized log-likelihood values to the top model, is not improved by the addition of the extra parameter. The model falls within two units of the top model because of the nature of the AIC_c comparison but does not actually explain the data any better than the simpler, top model. Though it is a common mistake in studies that use AIC_c comparisons, in this scenario the extra parameter should not be interpreted as having a biological effect (Arnold 2010).

Table 3.2. Comparison of mixed-effects models of selective consumption of salmon carcasses by bears using Akaike's Information Criterion (AIC_c), corrected for small sample size. Each model includes a random effect of site. Sex, species and date are forced fixed effects in each model to control for possible differences in selective consumption patterns by those parameters.

Model	Variables	K^1	AIC _c ²	ΔAIC_c^3	w_i^4	ER ⁵
Habitat complexity	cover index escape index sex species date	7	741.18	0	0.458	1.0
Habitat complexity + prey abundance	cover index escape index number of salmon sex species date	8	741.71	0.53	0.352	1.3
Null with forced parameters	sex species date	5	743.78	2.60	0.125	3.66
Prey abundance	number of salmon sex species date	6	745.08	3.90	0.065	7.05
Null	intercept	2	763.90	22.72	0	-

¹ Number of parameters. ² Model strength (lower indicates a better fit). ³ Difference of AIC_c value with top model AIC_c value. ⁴ The Akaike weight; probability that it is the best model. ⁵ Evidence ratio.

The probability plots generated from the top model's predictions further confirmed that bears selectively consumed salmon more frequently in narrower, shallower streams with fewer pools, and in streams with more wood and undercut banks (Fig. 3.2). These plots illustrate the top model's predicted probabilities of selective consumption, holding

all other parameters constant at their means. The predicted probability of selective consumption is higher on females than males, and on chum salmon than on pink (Fig. 3.2). Sex, species and date were included as forced parameters to control for possible differences in patterns with these variables. There is some uncertainty in the date and escape index parameter estimates, which both have 95% confidence intervals that overlap zero (Fig. 3.3). This uncertainty is considerably reduced under the alternative scoring system (Fig. A.3) which is the more relevant measure in terms of implications for nutrient transfer.

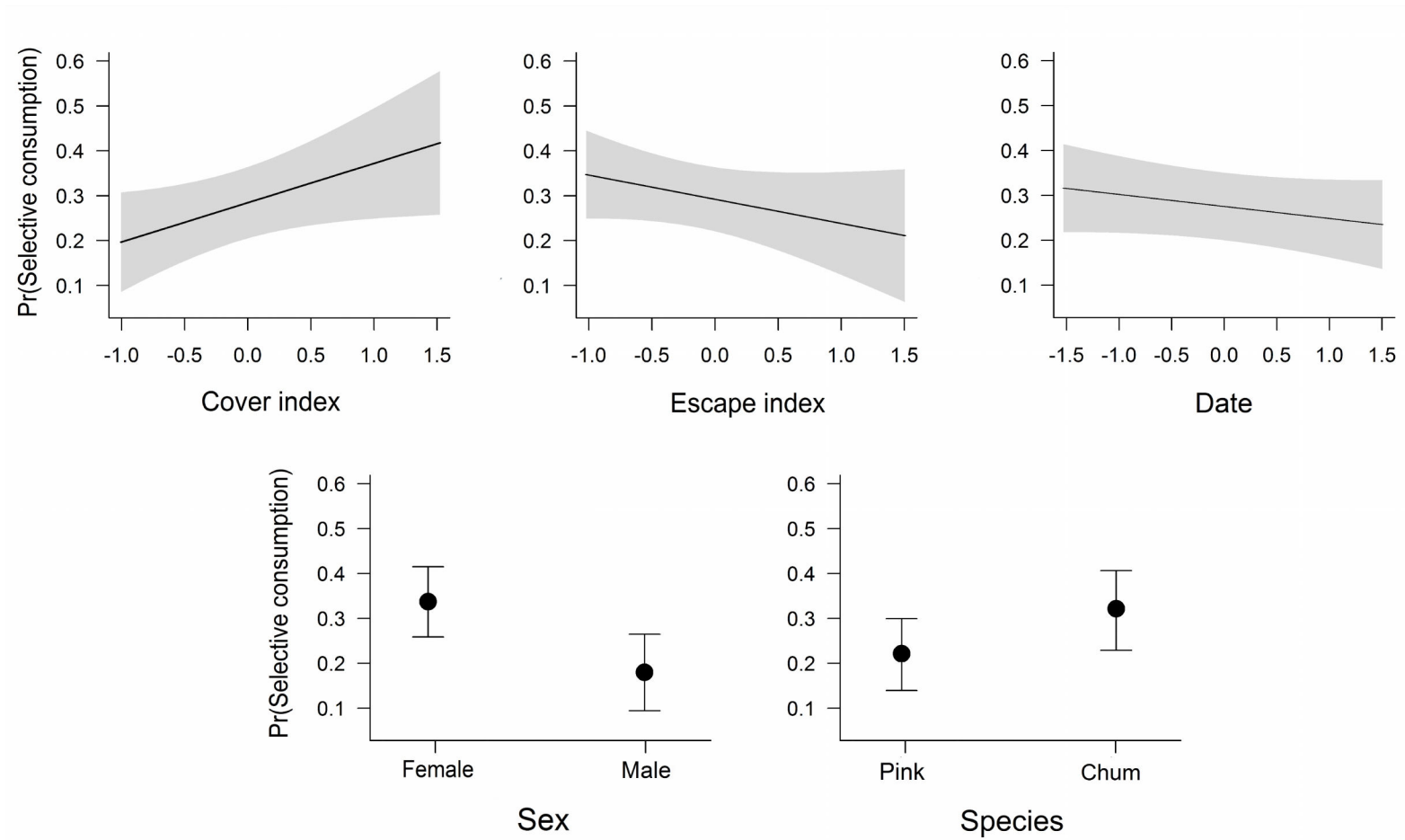


Figure 3.2. Probability plots for the top model (see Table 3.2) of selective consumption of salmon carcasses by bears. Lines and circles are predicted probabilities of selective consumption against model variables, with other variables set to their mean value. Bands and error bars are 95% confidence intervals.

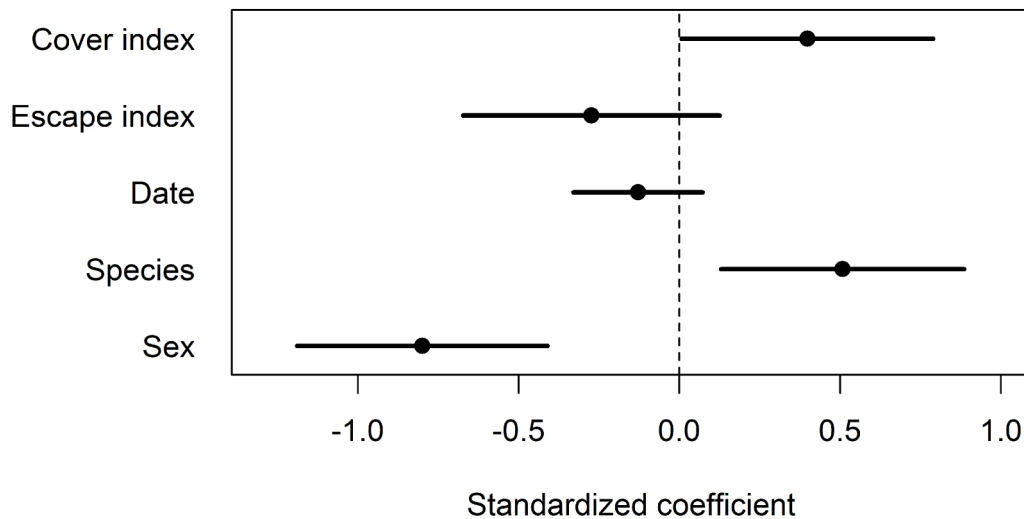


Figure 3.3. Standardized (mean=0, SD=2) coefficient values (circles) with 95% confidence intervals (lines) from the top model (see Table 3.2) of selective consumption of salmon carcasses by bears. The positive coefficient for species indicates more selective consumption of chum than pink salmon and the negative value for sex indicates more selective consumption of females than males.

The results for the alternative scoring system for selective consumption, based only on the amount of flesh eaten, were similar to the original scoring system, including bivariate plots (Fig. A.1), AIC_c competition (Table A.1) and probability plots (Fig. A.2). The only exceptions were a reversal of the effect of sex, whereby males had a higher probability of being selectively consumed (48%) than females (41%) as well as a stronger effect for date, which has parameter coefficient estimates that do not overlap zero, and escape and cover indices (Fig. A.3). The second-best model in this analysis had even less support (Table A.1) and a less reliable estimate for the effect of the number of spawning salmon on selective consumption (standardized coefficient=0.10, 95% CI: [-0.26, 0.47]) than the original scoring system.

3.5. Discussion

These results confirm my prediction that smaller streams (i.e., narrower, shallower and with smaller pool volume) would have more selective consumption of salmon by bears, though the estimate of this effect carried some uncertainty. I was

surprised to find that the opposite appears to be true of streams with less wood volume and fewer undercut banks, where bears tended to eat less selectively on each catch. I discuss these results in light of both the theory that generated the predictions and also the implications for the role of stream habitats and salmon abundance in mediating transfer of salmon-derived nutrients to riparian zones.

The finding that bears ate more of each salmon that they caught on larger streams is consistent with my prediction, based on the trade-off between continuing to consume a given carcass versus hunting for new fish, when hunting is more difficult.

Contrary to my predictions, bears were more likely to be selective in their feeding in streams with higher cover, where I assumed that hunting would be more difficult. A bear's hunting technique (e.g., chasing, wading/plunging, standing at falls) may be determined by topographic features (Luque and Stokes 1974; Klinka and Reimchen 2002; Gill and Helfield 2012) and may differ between "high cover" and "low cover" streams. If bears use these stream features to their advantage (i.e., to trap prey), it is possible that wood and undercut banks decrease the visibility of individual prey but do not necessarily protect them from capture. If so, then the inability to target their desired prey before capture could lead to increased selectivity in consumption after capture, which would explain the results for streams with high cover. This explanation is supported by my results from Chapter 2, where bears were less able to capture preferred larger, higher-quality salmon in streams with higher cover over the same spawning period.

There was no obvious pattern in a bivariate relationship between selective consumption and the number of spawning salmon (Fig. 3.1d). Furthermore, the number of salmon was included in the second model which was an identical but more complex version of the top model, with little additional explanatory power. Therefore, as per the recommendation by Arnold (2010), I report this parameter as having no biologically interpretable effect on selective consumption under either scoring system. This is inconsistent with Gende et al. (2001) who demonstrated that bears selected more energy-rich parts and consumed less of each fish in habitats and years with higher salmon abundance. Abandoning a carcass in pursuit of new prey makes sense when

prey are abundant and easy to catch; low-quality parts can be left uneaten when a surplus of high-quality prey with high-quality parts is still widely accessible (e.g., Goss-Custard 1977). Perhaps the number of spawning salmon was never low enough for bears to compensate in an obvious way by altering their consumption patterns. In Chapter 2, I found that predation rates were relatively low at these streams, ranging from 0.6% to 7.1%. These low predation rates suggest that bears were not limited by the number of salmon.

I considered sex, species, and time of year because these all may influence selective consumption. Even though they were not directly competed in the model selection process (except with the null model), these forced parameters were generally good predictors of selective consumption. As predicted, bears were less selective in their consumption, and ate more of each catch, as the season progressed. This effect was even clearer in the top model of the analysis that used an alternative scoring system (Fig. A.3), where the parameter estimates for date did not overlap zero. Salmon have fewer eggs and lower energy stores after spawning (Hendry and Berg 1999; Reimchen 2000) and bears increase their caloric consumption at the end of the season (Nelson 1980). Salmon that have spawned contain approximately half of the energetic value of pre-spawned salmon (Gilbert and Lanner 1995) and generally are not preferred (Gende et al. 2004). Increased hunger, coupled with lower energy prey, may cause bears to consume more of each carcass near the end of the season when this is all that is available. I also found a higher probability of selective consumption when bears consumed females rather than males. Eggs can comprise as much as 20% of a female's body mass (Hendry and Berg 1999). I found that 89% of the females that were considered selectively consumed were missing eggs whereas 49% were missing brains (these two are not mutually exclusive – many were missing both). The alternative scoring system, which does not include energy-rich parts, revealed that bears were more likely to eat the majority (>50%) of a female carcass than a male carcass, probably because females are smaller. Finally, as predicted, bears were more likely to selectively consume chum than pink salmon. This is likely due to the size difference between the two species. Additionally, and consistent with my findings, Reimchen (1994) proposed that it may be easier for bears to select for energy-rich parts on larger fish (e.g., chum) due to the higher dexterity associated with handling the larger prey.

There is conflicting evidence for whether preference for brains or eggs depends on the spawning status of the fish. Reimchen (2000) demonstrated that bears often ate the brains of newly arrived, unspawned salmon and avoided brains of salmon that had completed spawning and were showing signs of senescence (i.e., spawned-out salmon). Frame (1974) showed the opposite, with a higher preference for brains in salmon that had already spawned. Though I found no trend in selective consumption in relation to spawning status (i.e., pre-spawn, partially spawned or post-spawned salmon), whether I looked at only brain, only eggs or the chosen proxy for selective consumption, I still accounted for this possibility with the additional analysis using the alternative scoring system where “energy-rich part consumption” is excluded from the response variable.

Size-biased predation (i.e., for larger prey) by bears can have significant impacts on the flux of biomass to terrestrial ecosystems (Carlson et al. 2011). Here, I illustrate the impacts of selective consumption on nutrient flux by comparing two streams, at each extreme of the cover index, based on the probabilities of selective consumption (Fig. A.2). The alternative scoring system, which considers the amount of flesh eaten, not contingent on energy-rich parts, is more relevant when investigating terrestrial nutrient inputs. Holding date, escape index, sex and species parameters constant at their means, approximately 60% of carcasses in streams with the highest cover index will be selectively consumed whereas only approximately 30% of carcasses in streams with the lowest cover index will be consumed selectively. I assume that each chum salmon weighs ≈ 3.5 kg, and each pink salmon, ≈ 1.2 kg (Hocking and Reynolds 2011). I further assumed that bears eat 1/4 of each “selectively consumed fish” (i.e., the ones that were <50% consumed) and ate 3/4 of each “non-selectively consumed” fish, which was a typical observation. Thus, for every 100 chum and 100 pink salmon killed by bears at each stream, the stream with highest cover index is subsidized with 192.5 kg (chum) + 66 kg (pink) = 258.5 kg (total) of abandoned carcass biomass that remains uneaten by bears. The stream with lowest cover is subsidized with 140 kg (chum) + 48 kg (pink) = 188 kg (total) of abandoned carcass biomass. This represents a difference of 70.5 kg of salmon biomass, per every 100 fish of each species killed, based only on the differences between the probabilities of selective consumption in streams with little or a lot of wood and undercut banks.

There was also slight positive trend between the number of bear-killed salmon and the proportion of individuals that were selectively consumed by bears (Fig 3.1.e; Fig A.1.e). If bears consume less of each catch, it makes sense that they would need to kill more individuals to fill their stomach and satisfy their hunger. All else being equal, this relationship has further implications for nutrient transfer in these streams. Streams with a high proportion of selectively consumed fish would be subsidized by both more nutrients per killed fish, as well as the additional carcasses that are killed to compensate for selective feeding.

This study emphasizes the importance of habitat characteristics in selective consumption of salmon carcasses by bears, with implications for nutrient transfer to ecosystems. Further multi-year studies in these streams that also quantify patterns in carcass distribution, predator waste excretion and overall nutrient transfer would be valuable for quantifying habitat-mediated nutrient transfer via predation and consumption.

Chapter 4. General Discussion

This thesis aimed to examine how physical characteristics of streams, which could provide refuge for spawning salmon, mediate the hunting and feeding strategies of bears on the Central Coast of British Columbia, Canada.

In Chapter 2, I demonstrated that bears foraging in streams with more wood and undercut banks were less likely to capture larger-than-average salmon, and I proposed that these features effectively protect larger spawning salmon from size-biased predation pressures imposed by bears. Consequently, streams with more wood and undercut banks could allow the size-equilibrium to shift towards larger salmon, which are also favoured by sexual selection (Foote 1990; Quinn and Foote 1994), in the absence of counter-selective pressure by predation (Carlson et al. 2009). At all streams, size-biased predation became more pronounced as the salmon spawning season progressed. Salmon that arrived (to spawn) later in the spawning season were also smaller than those that arrived early. These observations provide further support for the idea that predation intensity can affect body-size, assuming heritability of arrival time (Beacham and Murray 1987; Quinn and Adams 1996; Doctor and Quinn 2009). I also found that salmon were larger in bigger streams and marginally smaller in streams that experienced more intense size-biased predation. These findings are consistent with (but do not prove) an evolutionary response to the selection that I documented. My study was the first to compare such a large number of streams, with broad natural gradients of habitat complexities simultaneously, to evaluate the relative level of support for multiple hypotheses regarding size-biased predation of spawning salmon.

In Chapter 3, I demonstrated that terrestrial nutrient subsidies are associated with habitat characteristics that provide refugia for spawning salmon via predation and selective partial consumption of salmon by bears. Salmon were more likely to be selectively consumed by bears in narrower, shallower streams with fewer pools (i.e.,

lower escape index), which should result in higher nutrient subsidies in the form of abandoned salmon biomass per bear-killed fish in these streams. Contrary to my original predictions, streams with more wood and undercut banks (i.e., higher cover index) were also associated with more selective consumption and, therefore, also received more nutrient subsidies per bear-killed salmon in the form of abandoned biomass. Approximately 70.5 kg of additional salmon biomass is available, for every 100 chum and pink salmon killed by bears, to the streams (and associated riparian zones) with the highest probability of selective consumption (i.e., high cover index) than to those with the lowest probability of selective consumption (i.e., low cover index).

My results suggest that bears capture and feed on prey differently depending on stream characteristics. As predicted and discussed in Chapter 3, bears ate more of each catch in streams with high escape index where hunting was proposed to be more difficult. However, my results for cover index in Chapter 2 and 3 suggest an interesting, cohesive pattern when viewed together. Consistent with findings by Gende et al. (2001), I assume that larger prey are highly prized and that consumption of the majority of a fish is further evidence of a prized catch. Bears were less size-biased (Ch. 2) and they ate less of each captured salmon (Ch. 3) at high cover streams. Both of these observations suggest that there were fewer prized catches at high cover streams. Furthermore, Chapter 2 shows that the number of bear-killed salmon was higher at high cover streams which suggests that hunting was not particularly more difficult. Therefore, cover index may not necessarily increase the difficulty of capturing a fish in a stream, but rather, decreases visibility of prey and, therefore, only increases the difficulty of discriminating, before capture, between prized fish and less desirable fish. In this scenario, bears capture prey indiscriminately, regardless of quality, in high cover streams and only assess the quality of the catch afterwards leading to less prized-catches (e.g., no evidence of size-biased predation) and more abandonment after only partial consumption. That is, capture selectivity cannot be achieved, so selective consumption is implemented to compensate. The bears then return to the stream to gamble again on another catch, ultimately leading to more kills. At low cover streams, bears were size-biased and ate more of each individual which suggests that they were able to discriminate prey quality, prior to capture, and catch (and consume thoroughly) the more prized individuals in these streams. Ultimately, these observations lead to an inference

that streams with more wood and higher percentage of undercut banks receive and retain substantially higher amounts of nutrients, in the form of salmon biomass, than streams with less wood and lower undercut banks. First, senescent salmon carcasses are better retained in streams with more large wood (Cederholm and Peterson 1985). Second, there were more bear-killed salmon in these high cover streams. Finally, there was more selective consumption at high cover streams and, therefore, more abandoned salmon biomass per captured fish.

In the bear-salmon model system, experimental manipulation is rarely feasible and bear behaviour is certain to vary between individuals, habitats and years. As a result, the literature sometimes contains conflicting observations. For example, Frame (1974) showed that bears preferentially ate brains in spawned-out salmon whereas Reimchen (2000) demonstrated that the majority of selective consumption of brains occurred in pre-spawned salmon. Furthermore, the small number of study sites in these types of studies may mask underlying or confounding patterns. Though the model selection approach demanded a high number of study sites ($n=12$), which I consider a major advance on previous studies, I was still limited by the kind of data that could be collected (e.g., bear abundance) during the short salmon spawning season. Furthermore, limitations on which stream characteristics to examine were carefully set a priori to avoid finding spurious results from large, all-subsets models (Burnham and Anderson 2002). However, like all observational studies, some assumptions had to be made about the environment and bear behaviour.

In Chapter 2, I had to assume that scavenging of senescent salmon carcasses was limited. Otherwise, the proposed mechanisms and evolutionary implications are weakened. That is, if bears were scavenging all the salmon that had died of senescence, it would have no evolutionary effect since those fish had already spawned. In that example, the size-bias result still holds true, but its evolutionary implications are weakened substantially. I feel quite confident about this assumption, because I did not see any evidence or indications of scavenging by bears (personal obs.). As a check on this, I ran post hoc models for Chapter 2's findings, using only bear-killed salmon in the "pre-spawn" or "partially-spawned-out" category in the analyses. It was highly unlikely that these salmon died from senescence and were then scavenged since they revealed

no obvious signs of senescence (i.e., damaged caudal fin, cloudy eyes, deteriorated skin, lack of eggs in females). The same models came out as top models with very similar Akaike's weights. Furthermore, the post hoc top model had similar coefficients with the same directionality as the original top model. This confirmed that the original analysis was not biased by possible scavenging of large senescent salmon carcasses by bears.

Due to limitations in time, a consequence of the multi-stream approach, I was not able to quantify the number of bears occupying each stream. Furthermore, bears are wary of humans, and we are wary of bears; both factors make it difficult to observe natural bear behaviour. Fortunately, this information was not required to describe the broad trends between habitat characteristics and foraging patterns of bears across a gradient of habitat complexity. The term "predation" is used broadly to describe the full force of bears acting on salmon per stream (whether that force results from a single bear or a dozen bears). Hypothetically, the stream characteristics may determine how many bears choose to hunt there; and wider streams could attract more bears, leading to less selective consumption of salmon due to competition. Alternatively, perhaps catching fish is indeed harder in wider streams, leading each individual bear to exhibit less selective consumption on each catch. In either case, although I do not know the exact mechanism, the important result is that there is less selective consumption in wider streams, leading to less nutrient inputs, per fish, via uneaten biomass. Another example, of limitation due to lack of direct observations is found in Chapter 2. Bears could be more selective for larger fish because they obtain more energy per fish. Alternatively, larger salmon could be more visible or easier to catch. My data cannot tell us which is correct. However, bears have been shown to be selective for newly-arrived salmon (Gende et al. 2004), despite the increased catch difficulty associated with these higher-energy fish, supporting the foraging theory mechanism for selectivity of pre-spawned salmon. Either way, the selective forces acting on salmon are equal and, therefore, the knowledge of the exact mechanism is not required for the claims made in Chapter 2.

In conclusion, this study contributes to our understanding of cross-boundary, nutrient-transfer pathways and how they can be shaped by characteristics of the stream

in conjunction with the foraging behaviour of bears. The findings of this study suggest how predators could have significant cumulative impacts on salmon population traits as well as nutrient subsidies to aquatic and terrestrial habitats.

References

- Agrawal, A. 2001. Phenotypic plasticity in the interactions and evolution of species. *Science* 294: 321–326.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *The Journal of Wildlife Management* 74: 1175–1178.
- Bain, M. B., and N. J. Stevenson. 1999. *Aquatic habitat assessment: common methods*. American Fisheries Society, Bethesda, Maryland, USA.
- Barbosa, P., and I. Castellanos. 2005. *Ecology of predator-prey interactions*. Oxford University Press, Cary, North Carolina, USA.
- Beacham, T. D., and C. B. Murray. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology chum salmon (*Oncorhynchus keta*) in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 244–261.
- Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 164–173.
- Braun, D. C., and J. D. Reynolds. 2011. Relationships between habitat characteristics and breeding population densities in sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 68: 758–767.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Second edition. Springer, New York, New York, USA.
- Carlson, S. M., and T. P. Quinn. 2007. Ten years of varying lake level and selection on size-at-maturity in sockeye salmon. *Ecology* 88: 2620–2629.
- Carlson, S. M., T. P. Quinn, and A. P. Hendry. 2011. Eco-evolutionary dynamics in Pacific salmon. *Heredity* 106: 438–447.

- Carlson, S. M., H. B. Rich, and T. P. Quinn. 2009. Does variation in selection imposed by bears drive divergence among populations in the size and shape of sockeye salmon? *Evolution* 63: 1244–1261.
- Cederholm, C. J., and N. P. Peterson. 1985. The retention of coho salmon (*Oncoshynchus kisutch*) carcasses by organic debris in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1222–1225.
- Cederholm, C. J., D. B. Houston, D. L. Cole, and W. J. Scarlett. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1347–1355.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129–136.
- Christie, K. S., and T. E. Reimchen. 2008. Presence of salmon increases passerine density on Pacific Northwest streams. *The Auk* 125: 51–59.
- Cunningham, C. J., G. T. Ruggerone, and T. P. Quinn. 2013. Size selectivity of predation by brown bears depends on the density of their sockeye salmon prey. *The American Naturalist* 181: 663–673.
- Darimont, C. T., T. E. Reimchen, and P. C. Paquet. 2003. Foraging behaviour by gray wolves on salmon streams in Coastal British Columbia. *Canadian Journal of Zoology* 81: 349–353.
- Darwin, C. R. 1859. *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. Edited by John Murray. London.
- Derocher, A. E., N. J. Lunn, and I. Stirling. 2004. Polar bears in a warming climate. *Integrative and Comparative Biology* 44: 163–176.
- Deschênes, J., and M. A. Rodríguez. 2007. Hierarchical analysis of relationships between brook trout (*Salvelinus fontinalis*) density and stream habitat features. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 777–785.
- Doctor, K. K., and T. P. Quinn. 2009. Potential for adaptation-by-time in sockeye salmon (*Oncorhynchus nerka*): the interactions of body size and in-stream reproductive life span with date of arrival and breeding location. *Canadian Journal of Zoology* 87: 708–717.
- Domenici, P., G. Claireaux, and D. J. McKenzie. 2007. Environmental constraints upon locomotion and predator–prey interactions in aquatic organisms: an introduction. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 362: 1929–1936.

- English, K. K., R. C. Bocking, and J. R. Irvine. 1992. A robust procedure for estimating salmon escapement based on the area-under-the-curve method. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1982–1989.
- Fausti, K., Dugaw, D., Chambers, J., Dykstra, J., Sedell, T., Moyer, C., Lanigan, S., Anderson, A., Archer, E., and Henderson, R. 2004. Stream channel methods for core attributes. In *Effectiveness monitoring for streams and riparian areas within the Pacific Northwest*. Edited by Multi-federal Agency Monitoring Program, Logan, Utah, and Aquatic and Riparian Effectiveness Monitoring Program and PACFISH/INFISH Biological Opinions (PIBO), Corvallis, Oregon. Available from <http://www.reo.gov/monitoring/reports/watershed-reports-publications.shtml>.
- Field, R. D., and J. D. Reynolds. 2011. Sea to sky: impacts of residual salmon-derived nutrients on estuarine breeding bird communities. *Proceedings of the Royal Society B: Biological Sciences* 278: 3081–3088.
- Field, R. D., and J. D. Reynolds. 2013. Ecological links between salmon, large carnivore predation, and scavenging birds. *Journal of Avian Biology* 44: 9–16.
- Fleming, I. A., and M. R. Gross. 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution* 43: 141–157.
- Fleming, I. A., and M. R. Gross. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution* 48: 637–657.
- Floyd, T. A., C. McInnis, and B. R. Taylor. 2009. Effects of artificial woody structures on Atlantic salmon habitat and populations in a Nova Scotia stream. *River Research and Applications* 25: 272–282.
- Foote, C.J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. *Behaviour* 115: 283–314.
- Frame, G. W. 1974. Black bear predation on salmon at Olsen Creek, Alaska. *Zeitschrift für Tierpsychologie*. 35: 23–38.
- Fraser, D. J., L. K. Weir, L. Bernatchez, M. M. Hansen, and E. B. Taylor. 2011. Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. *Heredity* 106: 404–420.
- Fukushima, M., and W. W. Smoker. 1998. Spawning habitat segregation of sympatric sockeye and pink salmon. *Transactions of the American Fisheries Society* 127: 253–260.
- Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* 27: 2865–2873.

- Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *BioScience* 52: 917–928.
- Gende, S. M., T. P. Quinn, R. Hilborn, A. P. Hendry, and B. Dickerson. 2004. Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. *Oikos* 104: 518–528.
- Gende, S. M., T. P. Quinn, and M. F. Willson. 2001. Consumption choice by bears feeding on salmon. *Oecologia* 127: 372–382.
- Gilbert, B.K., and R.M. Lanner. 1995. Energy, diet selection and restoration of brown bear populations. International Conference on Bear Research and Management. French Ministry of the Environment and the Natural History Museum of Grenoble, France 9: 231–240.
- Gill, I.D., and J.M. Helfield. 2012. Alternative foraging strategies among bears fishing for salmon: a test of the dominance hypothesis. *Canadian Journal of Zoology* 90: 766–775.
- Goss-Custard, J. D. 1977. The energetics of prey selection by redshank, *Tringa totanus* (L.), in relation to prey density. *The Journal of Animal Ecology* 46: 1–19.
- Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84: 2809–2815.
- Gregory, S., and L. Ashkenas. 1990. Riparian management guide: Willamette National Forest. Oregon State University, Department of Fisheries and Wildlife, Portland, Oregon.
- Hamon, T. R., and C. J. Foote. 2005. Concurrent natural and sexual selection in wild male sockeye salmon, *Oncorhynchus nerka*. *Evolution* 59: 1104–1118.
- Harding, J. N., J. M. S. Harding, and J. D. Reynolds. 2014. Movers and shakers: nutrient subsidies and benthic disturbance predict biofilm biomass and stable isotope signatures in coastal streams. *Freshwater Biology* 59: 1361–1377.
- Heithaus, M. R., A. J. Wirsing, and L. M. Dill. 2012. The ecological importance of intact top-predator populations: a synthesis of 15 years of research in a seagrass ecosystem. *Marine and Freshwater Research* 63: 1039–1050.
- Helfield, J. M., and R. J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* 82: 2403–2409.
- Helfield, J. M., and R. J. Naiman. 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. *Ecosystems* 9: 167–180.

- Hendry, A. P., and O. K. Berg. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. *Canadian Journal of Zoology* 77: 1663–1675.
- Hilderbrand, G. V., T. A. Hanley, C. T. Robbins, and C. C. Schwartz. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* 121: 546–550.
- Hocking, M. D., and J. D. Reynolds. 2011. Impacts of salmon on riparian plant diversity. *Science* 331: 1609–1612.
- Hocking, M. D., and J. D. Reynolds. 2012. Nitrogen uptake by plants subsidized by Pacific salmon carcasses: a hierarchical experiment. *Canadian Journal of Forest Research* 42: 908–917.
- Hocking, M. D., R. A. Ring, and T. E. Reimchen. 2009. The ecology of terrestrial invertebrates on Pacific salmon carcasses. *Ecological Research* 24: 1091–1100.
- Holtgrieve, G. W., D. E. Schindler, and P. K. Jewett. 2009. Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. *Ecological Research* 24: 1125–1135.
- Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia* 159: 583–595.
- Johnston, N. T., E. A. Macisaac, P. J. Tschaplinski, and K. J. Hall. 2004. Effects of the abundance of spawning sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 384–403.
- Klinka, D. R., and T. E. Reimchen. 2002. Nocturnal and diurnal foraging behaviour of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia. *Canadian Journal of Zoology* 80: 1317–1322.
- Krebs, J.R. 1978. Optimal foraging: decision rules for predators. In *Behavioural Ecology, an Evolutionary Approach*, edited by J.R. Krebs and N.B. Davies, 22–63. Sinauer Associates, Sunderland, Massachusetts.
- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* 48: 25–34.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619–640.
- Lisle, T. E. 1987. Using 'residual depths' to monitor pool depths independently of discharge. U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment, Berkeley, California.

- Luque, M. H., and A. W. Stokes. 1974. Fishing behaviour of Alaskan brown bear. In *Bears—Their Biology and Management: Proceedings of the Third International Conference on Bear Research and Management*, edited by M.R. Pelton, J.W. Lentfer, and G.E. Folk, 71–78. Binghamton, N.Y., 31 May – 1 June 1974, and Moscow, U.S.S.R., 11 June 1974. International Union for the Conservation of Nature and Natural Resources, Morges, Switzerland.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *The American Naturalist* 100: 603–609.
- Meehan, E. P., E. E. Seminet-Reneau, and T. P. Quinn. 2005. Bear predation on Pacific salmon facilitates colonization of carcasses by fly maggots. *The American Midland Naturalist* 153: 142–151.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142.
- Nelson, M. C., and J. D. Reynolds. 2015. Effects of subsidies from spawning chum and pink salmon on juvenile coho salmon body size and migration timing. *Ecosphere* 6: 1–14.
- Nelson, R. A. 1980. Protein and fat metabolism in hibernating bears. *Federation Proceedings* 39: 2955–2958.
- Nelson, R. A., G. E. Folk Jr., E. W. Pfeiffer, J. J. Craighead, C. J. Jonkel, and D. L. Steiger. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *International Conference on Bear Research & Management* 5: 284–290.
- Palkovacs, E. P., B. A. Wasserman, and M. T. Kinnison. 2011. Eco-evolutionary trophic dynamics: loss of top predators drives trophic evolution and ecology of prey. *PLoS ONE* 6(4): e18879
- Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, et al. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology* 89: 2416–2425.
- Pelletier, F., D. Garant, and A. P. Hendry. 2009. Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364: 1483–1489.
- Preisser, E. L., D. I. Bolnick, and M. E. Bernard. 2005. Scared to death? the effects of intimidation and consumption in predator–prey interactions. *Ecology* 86: 501–509.
- Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology* 77: 1151–1162.

- Quinn, T. P., and G. B. Buck. 2001. Size- and sex-selective mortality of adult sockeye salmon: bears, gulls, and fish out of water. *Transactions of the American Fisheries Society* 130: 995–1005.
- Quinn, T. P., S. M. Carlson, S. M. Gende, and H. B. Rich Jr., 2009. Transportation of Pacific salmon carcasses from streams to riparian forests by bears. *Canadian Journal of Zoology* 87: 195–203.
- Quinn, T. P., and C. J. Foote. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. *Animal Behaviour* 48: 751–761.
- Quinn, T. P., S. M. Gende, G. T. Ruggerone, and D. E. Rogers. 2003. Density-dependent predation by brown bears (*Ursus arctos*) on sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Aquatic Science* 60: 553–562.
- Quinn, T. P., A. P. Hendry, and G. B. Buck. 2001. Balancing natural and sexual selection in sockeye salmon: interactions between body size, reproductive opportunity and vulnerability to predation by bears. *Evolutionary Ecology Research* 3: 917–937.
- Quinn, T. P., A. P. Hendry, and L. A. Wetzel. 1995. The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). *Oikos* 74: 425–438.
- Quinn, T. P., and M. T. Kinnison. 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. *Oecologia* 121: 273–282.
- Quinn, T. P., and M. V. McPhee. 1998. Effects of senescence and density on the aggression of adult female sockeye salmon. *Journal of Fish Biology* 52: 1295–1300.
- Quinn, T. P., E. C. Volk, and A. P. Hendry. 1999. Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology* 77: 766–775.
- Quinn, T. P., L. Wetzel, S. Bishop, K. Overberg, and D. E. Rogers. 2001. Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. *Canadian Journal of Zoology* 79: 1782–1793.
- R: A Language and Environment for Statistical Computing. 2015. R. Core Team, R Foundation for Statistical Computing. <http://www.r-project.org/>.
- Reimchen, T. E. 1994. Further studies of predator and scavenger use of chum salmon in stream and estuarine habitats at Bag Harbour, Gwaii Haanas. – Islands Ecological Research, Queen Charlotte City.

- Reimchen, T. E. 2000. Some ecological and evolutionary aspects of bear-salmon interactions in coastal British Columbia. *Canadian Journal of Zoology* 78: 448–457.
- Roni, P., and T. P. Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in Western Oregon and Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 282–292.
- Ruggerone, G. T., R. Hanson, and D. E. Rogers. 2000. Selective predation by brown bears (*Ursus arctos*) foraging on spawning sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology* 78: 974–981.
- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1: 103–113.
- Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment* 1: 31–37.
- Sih, A. 1980. Optimal foraging: partial consumption of prey. *The American Naturalist* 116: 281–290.
- Smith, R. D., R. C. Sidle, P. E. Porter, and J. R. Noel. 1993. Effects of experimental removal of woody debris on the channel morphology of a forest, gravel-bed stream. *Journal of Hydrology* 152: 153–178.
- Steen, R. P., and T. P. Quinn. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. *Canadian Journal of Zoology* 77: 836–841.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey.
- Stirling, I., and A. E. Derocher. 1993. Possible impacts of climatic warming on polar bears. *Arctic* 46: 240–245.
- Swain, N. R., M. D. Hocking, J. N. Harding, and J. D. Reynolds. 2014. Effects of salmon on the diet and condition of stream-resident sculpins. *Canadian Journal of Fisheries and Aquatic Sciences* 71: 521–532.
- Swain, N. R., and J. D. Reynolds. 2015. Effects of salmon-derived nutrients and habitat characteristics on population densities of stream-resident sculpins. *PLoS ONE* 10(6): e0116090
- Underwood, A. J. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, UK.

- Vamosi, S. M. 2005. On the role of enemies in divergence and diversification of prey: a review and synthesis. *Canadian Journal of Zoology* 83: 894–910.
- Vermeij, G.J. 1982. Unsuccessful predation and evolution. *The American Naturalist* 120: 701-720
- Verspoor, J. J., D. C. Braun, M. M. Stubbs, and J. D. Reynolds. 2011. Persistent ecological effects of a salmon-derived nutrient pulse on stream invertebrate communities. *Ecosphere* 2: 1–17.
- Winder, M., D. E. Schindler, J. W. Moore, S. P. Johnson, and W. J. Palen. 2005. Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? *Canadian Journal of Fisheries and Aquatic Sciences* 62: 2285–2293.
- Wipfli, M. S., J. P. Hudson, D. T. Chaloner, and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 1600–1611.
- Wirsing, A. J., M. R. Heithaus, A. Frid, and L. M. Dill. 2008. Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. *Marine Mammal Science* 24: 1–15.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3–14.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saleliev, A.A. and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York.

Appendix A. Supporting Material for Chapter 3

Table A.1. Comparison of mixed-effects models of selective consumption of salmon carcasses by bears using Akaike's Information Criterion (AIC_c), corrected for small sample size, using the alternative scoring system of selective consumption (<50% of salmon carcass consumed). Each model includes a random effect of site. Sex, species and date are forced fixed effects in each model to control for possible differences in selective consumption patterns by those parameters.

Model	Variables	K^1	AIC _c ²	Δ AIC _c ³	w_i^4	ER ⁵
Habitat complexity	cover index escape index sex species date	7	834.598	0	0.658	1.0
Habitat complexity + prey abundance	cover index escape index number of salmon sex species date	8	836.346	1.749	0.274	2.40
Null with forced parameters	sex species date	5	839.817	5.219	0.048	13.71
Prey abundance	number of salmon sex species date	6	841.680	7.082	0.019	34.63
Null	intercept	2	866.641	32.043	0	-

¹ Number of parameters. ² Model strength (lower indicates a better fit). ³ Difference of AIC_c value with top model AIC_c value. ⁴ The Akaike weight; probability that it is the best model. ⁵ Evidence ratio.

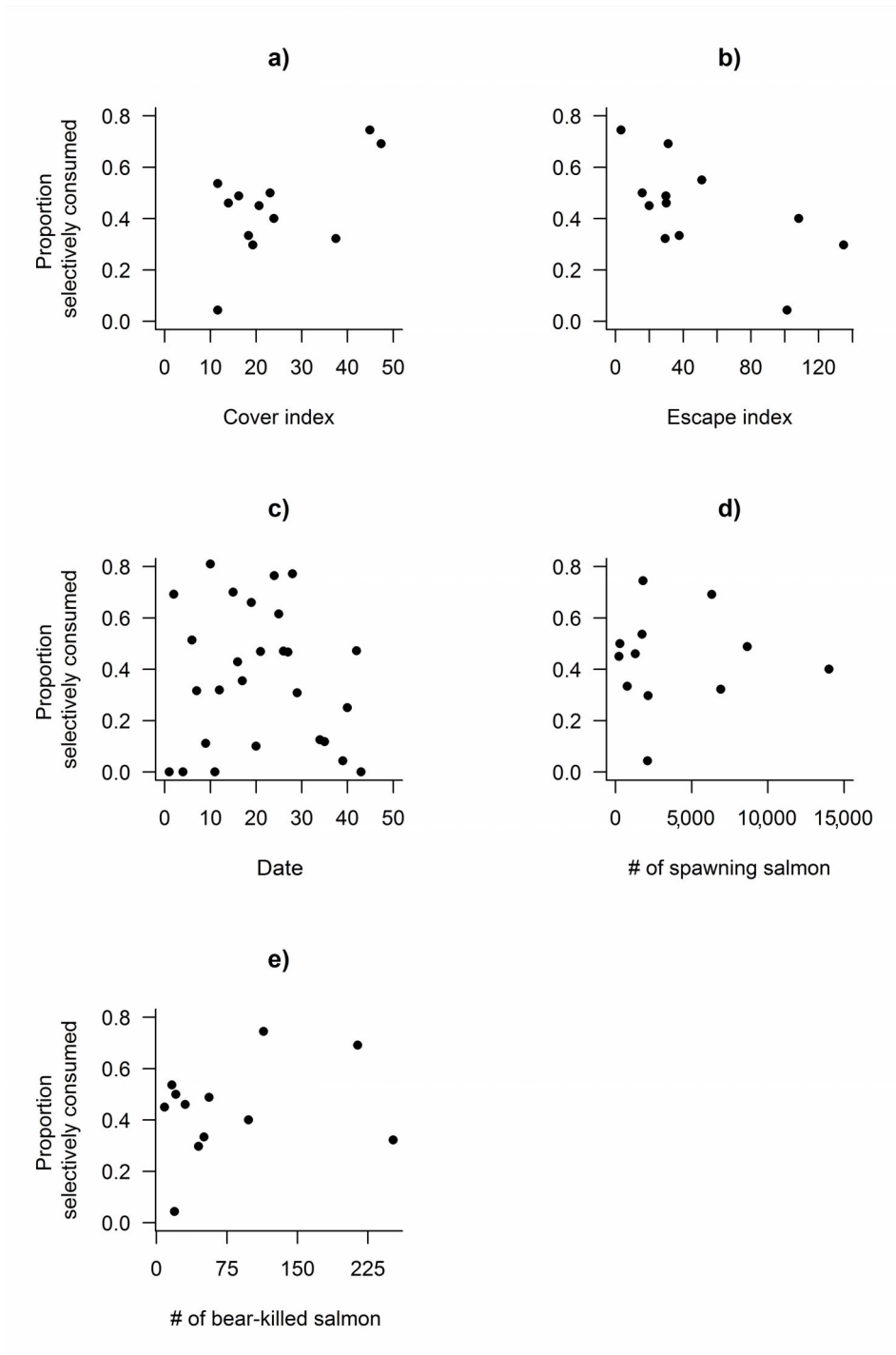


Figure A.1. Relationships between the proportion of selectively consumed salmon and a) cover index, b) escape index, c) date (1 = 11 September, 2014), d) number of spawning salmon and e) number of bear-killed salmon. Selective consumption by bears is defined as <50% of salmon carcass consumed.

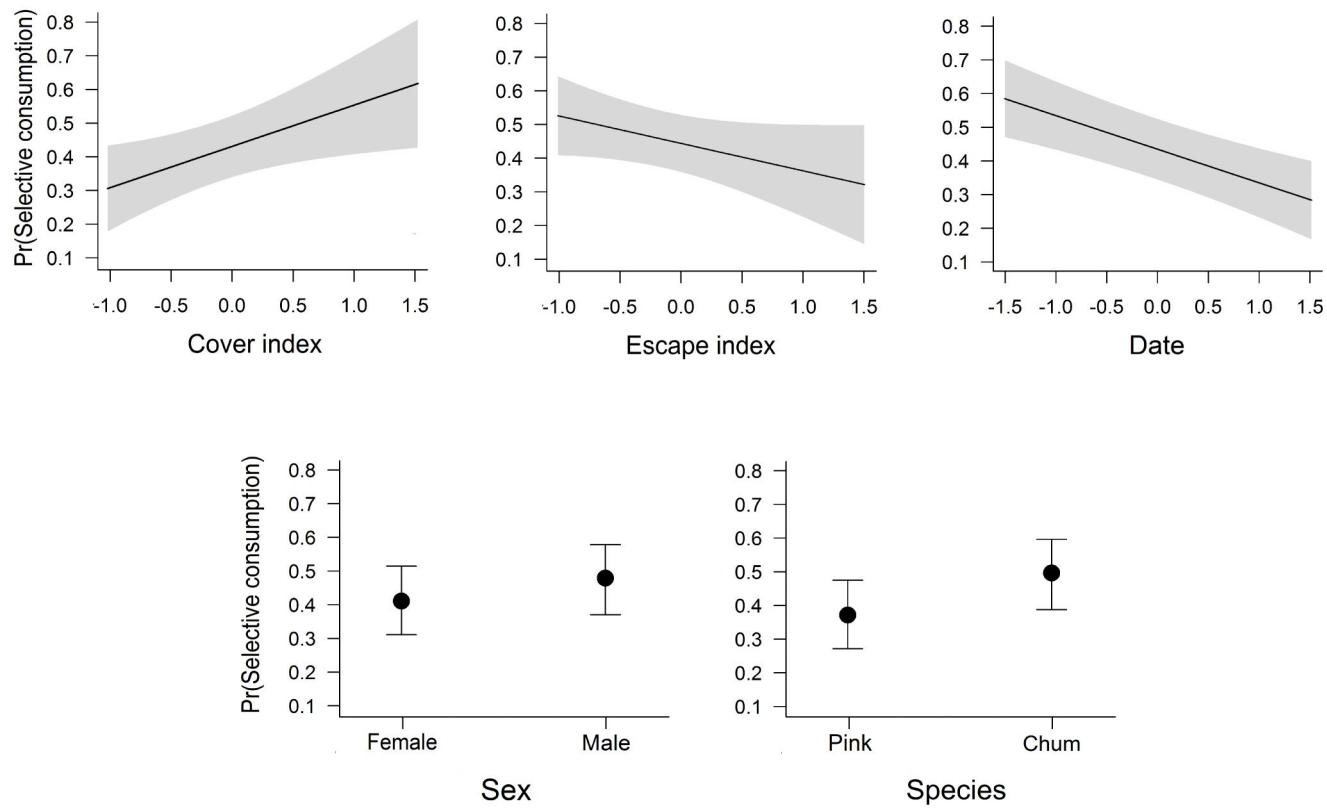


Figure A.2. Probability plots for top model (see Table A.1) of selective consumption of salmon carcasses by bears from competition using the alternative scoring system of selective consumption (<50% of salmon carcass consumed). Lines and circles are predicted probabilities of selective consumption against model variables, with other variables set to their mean value. Bands and error bars are 95% confidence intervals.

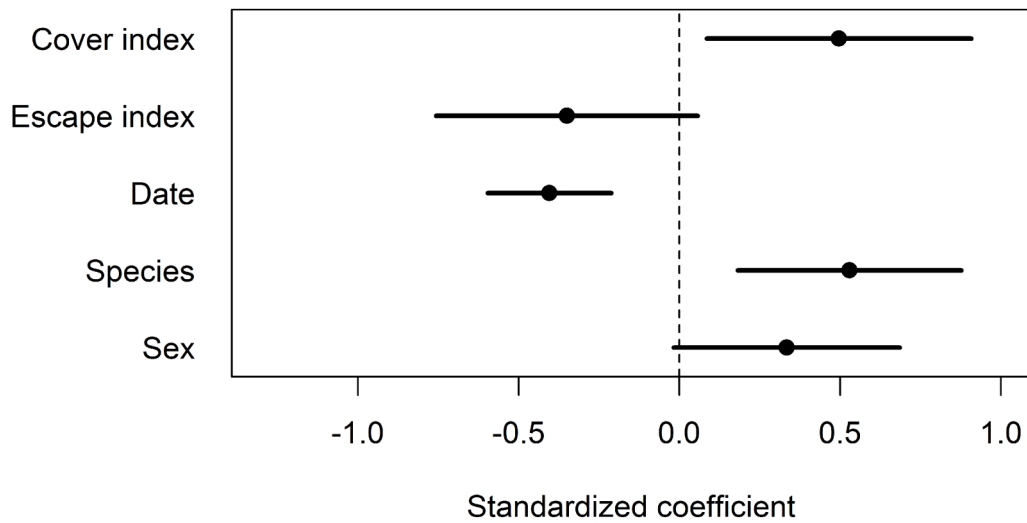


Figure A.3. Standardized (mean=0, SD=2) coefficient values (circles) with 95% confidence intervals (lines) from the top model (see Table A.1) of selective consumption of salmon carcasses by bears using the alternative scoring system for selective consumption. The positive coefficient for species indicates more selective consumption of chum salmon and the positive value for sex indicates more selective consumption of males.

Appendix B. Stream Characteristics

Table B.1. Summary of stream characteristics and locations. Stream characteristics were used to create the principal components: “cover index” (volume of wood per 100 m and percent of bank that is undercut), “stream size index” (mean bankfull width and mean channel height) and “escape index” (mean bankfull width, mean channel height and pool volume per 100 m).

Stream	Latitude	Longitude	2014 Salmon Abundance	Salmon Abundance mean (2009-2014)	Mean Bankfull Width (m)	Mean Channel Height (m)	Pool Volume (m ³) per 100 m	Volume of Wood (m ³) per 100 m	Undercut Bank (%)	Cover Index	Stream Size Index	Escape Index
Ada	52.0553	-128.0507	1,752	1,899	8.8	1.05	79.82	16.19	23	11.61	6.97	50.99
Beales Left	52.1882	-127.9890	1,302	1,102	10.5	1.46	40.64	19.67	10	13.98	8.46	30.07
Beales Right	52.1868	-127.9800	226	220	10.1	1.24	23.32	29.09	11	20.65	8.03	19.92
Bullock Main	52.4029	-128.0785	6,323	5,421	8.6	0.79	45.16	66.75	26	47.38	6.66	31.13
Clatse	52.3377	-127.8391	8,656	8,859	19.6	1.09	31.09	22.85	12	16.24	14.61	29.85
Fancy Right	52.0585	-128.0167	290	468	4.3	0.77	22.71	32.12	56	23.12	3.61	15.86
Fannie Left	52.0426	-128.0668	14,019	7,913	10.7	0.79	179.4	33.49	31	23.90	8.12	108.32
Goat Bushu	52.2132	-127.8767	774	1,156	5.9	0.78	59.61	25.53	46	18.38	4.70	37.66
Hooknose	52.1249	-127.8370	2,147	4,581	11.7	0.99	224.87	26.95	35	19.30	8.98	134.76
Kill Creek	52.4267	-128.0958	1,808	3,868	3.4	0.48	1.86	62.86	66	44.91	2.72	3.33
Kunsoot Main	52.1569	-128.0435	6,910	3,595	14.3	0.66	36.2	52.68	32	37.48	10.55	29.34
Sagar	52.0959	-127.8388	2,100	1,118	15.5	1.39	161.51	16.33	14	11.64	11.95	101.40