CONFRONTING UNCERTAINTIES IN A FRESHWATER RECREATIONAL FISHERY: A CASE STUDY OF FLUVIAL BULL TROUT (*SALVELINUS CONFLUENTUS*) IN CENTRAL BRITISH COLUMBIA

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

October 2021

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Confronting uncertainties in a freshwater recreational fishery: A case study of fluvial bull trout (*Salvelinus confluentus*) in central British Columbia

submitted by Rachel Elizabeth Chudnow in partial fulfillment of the requirements for

the degree of Doctor of Philosophy

in Zoology

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Abstract

Recreational fishery managers operate within complex socio-ecological systems and must balance objectives relating to resource conservation and human use opportunities. Further, agencies have limited resources and often lack high quality ecological and social data to inform decision making. As a result, managers confront considerable uncertainty when faced with management decisions and consequently, recreational fisheries are generally managed passively and/or reactively.

This dissertation addresses several management challenges within a recreational bull trout fishery in the upper Fraser River watershed of British Columbia (UFW) by clarifying uncertainties related to population productivity, fish movement, and the responses of fish and human populations to changing fishery regulations. First, I develop a hierarchical Bayesian meta-analysis to provide the first bull trout specific estimate of recruitment compensation. Second, I use telemetry and genetic assignment data through state-space capture-recapture modeling to estimate seasonal movement patterns for multiple bull trout populations in the UFW. Finally, I use compensation and movement estimates from the first two models to develop a population dynamics model and decision analysis for a bull trout population complex in the UFW.

Stock-recruitment model results indicate bull trout have strong potential for compensatory improvements in juvenile survival when population abundance is reduced, although there is considerable uncertainty in these estimates. This finding suggests habitat quality and quantity likely limit bull trout recovery for many populations across the species range. Movement modeling demonstrates that multiple spawning populations of fluvial bull trout utilize habitats within the UFW in a similar way, using a shared migratory corridor to access favourable spawning, wintering, and foraging habitats. The population dynamics model and decision analysis predict that changing management regulations to permit a low level of retention improves angler satisfaction without measurable impacts on the fishery's conservation objective. However, even under current catch-and-release regulations, the model predicts populations are close to an overfished state. Results and conclusions developed here provide an important management tool within the UFW. Taken separately or together, these models can also reduce uncertainties and improve management decision making for other recreational fisheries both within British Columbia, or more broadly, where data limitations prevent other approaches from being applicable.

Lay summary

Recreational fisheries managers face considerable challenges developing and adjusting fishing regulations that balance the conservation of fish populations while providing angling (recreational fishing) opportunities. Many of these challenges stem from unknowns relating to the biology and ecology of fished species and/or human (angler) behaviour. Within this dissertation, I use a case study of a recreational bull trout fishery in central British Columbia to clarify critical unknowns regarding bull trout biology and ecology (i.e., population productivity, movement, and dispersal) and fish and human behaviour (i.e., how fished and human populations respond to changes in fishing regulations). The results of this dissertation can be applied directly to the fluvial bull trout fishery in the upper Fraser watershed of British Columbia, to bull trout fisheries elsewhere, or can be generalized and used in other similar fisheries.

Preface

The work undertaken within this dissertation was developed from research questions posed by the British Columbia Ministry of Forests, Lands, Natural Resource Operations, and Rural Development (FLNRORD) with the goal of researching questions of relevance to recreational fisheries management in the province of British Columbia. The research questions examined within this dissertation were developed in partnership with representatives from the British Columbia Ministry of Forests, Lands, Natural Resource Operations, and Rural Development (FLNRORD), Dr. Murdoch McAllister (University of British Columbia), Dr. Brett van Poorten (previously of the British Columbia Ministry of Environment and now of Simon Fraser University), and Dr. Scott Hinch (University of British Columbia). No university ethics approval was required for this research.

A version of Chapter 2 has been published as Chudnow, R., van Poorten, B., and McAllister, M. 2019. Estimating cross-population variation in juvenile compensation in survival for bull trout (*Salvelinus confluentus*): A Bayesian hierarchical approach. Canadian Journal of Fisheries and Aquatic Sciences. 74 (4): 1571-1580. I gathered all necessary data, Dr. Brett van Poorten and I developed and programmed the models within JAGs and R, we both performed the analyses, and I wrote the final paper. Dr. Murdoch McAllister provided doctoral supervision and both Dr. Brett van Poorten and Dr. Murdoch McAllister edited the draft and final manuscripts prior to journal submission.

A version of Chapter 3 was submitted to a peer-reviewed journal in June 2021 but has not yet been reviewed or accepted. The manuscript authors are Chudnow, R., van Poorten, B., Pillipow, R., Spendlow, I., Gantner, N., and Hinch, S. The manuscript is titled "Spatial distribution and seasonal movement rate estimates of bull trout (*Salvelinus confluentus*) through a large, uninterrupted river network". The Ministry of Forests, Lands, Natural Resource Operations, and Rural Development (FLNRORD) conducted data collection through fieldwork activities with key work by Ray Pillipow, Ian Spendlow, and John Hagen. I assisted with field sampling within the fall of 2012 and 2013. I conducted data preparation with support of FLNRORD, specifically, Ian Spendlow. Dr. Brett van Poorten and I developed and programed the models within JAGs and R, we both performed the analyses, and I wrote the final paper. Dr. Scott Hinch provided doctoral supervision and all authors (Dr. Brett van Poorten, Dr. Scott Hinch, Mr. Ray Pillipow, Mr. Ian Spendlow, and Dr. Nikolaus Gantner) edited the final manuscript prior to journal submission.

For Chapter 4, Brett van Poorten and I developed and programmed the models. I performed the analyses and wrote the chapter. Dr. Brett van Poorten provided feedback on the analyses. Dr. Brett van Poorten and Dr. Scott Hinch provided chapter editing.

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List of abbreviations

AB	Alberta
BC	British Columbia
CAD	Canadian dollar(s)
CJS	Cormack Jolly Seber
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CPUE	Catch per unit effort
CR	Compensation ratio
DIC	Deviance information criterion
DNA	Deoxyribonucleic acid
FAO	Food and Agriculture Organization of the United Nations
FLNRORD	Ministry of Forests, Lands, Natural Resource Operations, and Rural Development
IOFG	Idaho Fish and Game
JAGS	Just Another Gibbs Sampler
MCMC	Markov chain Monte Carlo
MOE	Ministry of Environment and Climate Change Strategy
MTFWP	Montana Fish, Wildlife, and Parks
n	Number
N/A	Not available / not applicable
ODFW	Oregon Department of Fish and Wildlife
OR	Oregon
SARA	Species at Risk Act
SPR	Spawner potential ratio
UFW	Upper Fraser River watershed
USFWS	United States Fish and Wildlife Service
WDFW	Washington Department of Fish and Wildlife
Yrs.	Years

Regulation Abbreviations:

BL	Harvest (bag) limit
C&R	Catch and release
MaxLL	Maximum size limit
MinLL	Minimum size limit
SC	Spatial closure

Acknowledgements

I would like to thank my committee members: Brett van Poorten, Scott Hinch, Eric B. (Rick) Taylor, and Villy Christensen for their support throughout the development of this dissertation. In particular I would like to thank Brett van Poorten for his endless support, mentorship, and patience. I also owe my gratitude to Scott Hinch for allowing me to join his laboratory late within my dissertation work and for his continued guidance and support through my time under his supervision. I would further like to acknowledge the support of Eric B. (Rick) Taylor for his guidance and expertise surrounding the genetic data used within Chapter 3.

Thank you to the British Columbia Habitat Conservation Trust Foundation (HCTF), Freshwater Fisheries Society of British Columbia (FFSBC), and Mitacs for their generous financial support. I would like to thank the British Columbia Ministry of Forests, Lands, and Natural Resource Operations, and Rural Development (FLNRORD), specifically Ray Pillipow, Ian Spendlow, and Nikolaus Gantner for their knowledge, mentorship, and support throughout this dissertation work. I would further like to thank Ray Pillipow and John Hagen for their patience, generous support, and care during our time conducting field work together, as well as the pilots of Yellowhead Helicopters Ltd., our time together is an experience I will never forget.

My sincerest thanks to my labs: The Quantitative Modeling Group at University of British Columbia’s Institute for the Oceans and Fisheries and Pacific Salmon Ecology and Conservation Laboratory for their support and feedback throughout the course of my dissertation. Extra big thanks to Mairin Deith, Shannon Obradovich, Catarina Wor Lima, Aaron Greenberg, and Sarah

Harper for your help with statistics, coding, course work, and for being there to talk through all of the challenges a PhD can bring, I could not have done it without you.

This work would not have been possible without the endless love and support of my family. Thank you to my parents, David and Beth, for your love and your emotional and financial support which allowed me to pursue my education and my dreams. To my brother, Matthew, for your unwavering support and for always being there to talk shop or distract from it. To Jackie for her ear, her hot home-made meals, and her problem solving. To Mika, Pippin, Tristan, and Holly for their undeniable ability to make every day brighter. Last but not least, to my partner, Larissa. Thank you for your unconditional love and for being my editor, my rock, my sounding board, and my safe place, anything is possible with you by my side.

Dedication

To my family

Chapter 1: General introduction

1.1 Introduction to inland recreational fisheries

Within North America, recreational fisheries have significant socio-economic importance to both local communities and the greater population, as well as intrinsic cultural value (Arlinghaus and Cooke 2009; FAO 2012; Brownscombe et al. 2014). In Canada, recreational fisheries are also considered the dominant extractive sector within freshwater habitats (Arlinghaus and Cooke 2009; Lynch et al. 2017; Brownscombe et al. 2019). In 2015, the date of the most recent national survey, anglers caught over 194 million fish and spent more than 47 million days fishing (Fisheries and Oceans Canada 2015). Direct expenditures by anglers were over $2.5 billion CAD, in addition to indirect economic benefits to local businesses (Fisheries and Oceans Canada 2015).

Recreational fisheries are not inherently self-sustaining systems, and agencies are tasked with developing and implementing regulatory actions that balance a suite of conservation and socio-economic objectives (Post et al. 2002; Lorenzen et al. 2016; Lynch et al. 2017). Agencies operate with limited budgets and capacity, while responsible for management of multiple aquatic species across large spatial areas (Pereira and Hansen 2003; Walters and Martell 2004; Post et al. 2008). Across areas, there can be significant variation in abundance of exploited fish populations (hereafter 'population(s)' or 'stock(s)'), angling effort, and non-fishing related impacts on the natural system (e.g., mining, agriculture, hydroelectric power, and forestry), the specifics of which are often outside of managers' direct control (Pereira and Hansen 2003; Post et al. 2008; Johnston et al. 2011). Beyond uncertainties related to naturally occurring perturbations, agencies must make management decisions for species conservation and provision of ecologically sustainable fishing opportunities despite a multitude of uncertainties about human and natural systems and how they interact (Walters and Martell 2004; Post et al. 2008; Camp et al. 2020).

1.2 Uncertainty

Recognizing and accounting for the impacts of uncertainty is critical for successful fisheries assessment and management (Hilborn and Walters 1992; Zhu et al. 2012). In fisheries, uncertainty can be categorized as three main types: random fluctuations ('noise'), structural uncertainties, and those resulting from imprecise parameter estimates and unknown states of nature (Sissenwine 1984; Hilborn and Walters 1992; Charles 1998). Although unpredictable, random fluctuations (e.g., resulting from biological, physical, or human factors) are recognizable and often easily accounted for (Hilborn and Walters 1992; Charles 1998). In contrast, structural uncertainties (e.g., resulting from spatial complexity or angler behaviour) and uncertainty in parameters and states of nature (e.g., magnitude of system variables such as fish stock size or parameter values such as survival rates) are more difficult to address (Hilborn and Walters 1992; Charles 1998). Key structural uncertainties in recreational fisheries include population productivity, spatial dynamics, and dynamic responses both of fished populations and angling effort to changes in fishing regulations and fish abundance (Hilborn and Walters 1992; Cox et al. 2002; Prévost 2003).

1.2.1 Stock and recruitment

Impacts of naturally occurring stochastic perturbations on survival rates result in continuous fluctuations in population dynamics (Hilborn and Walters 1992; Walters and Martell 2004).

Density-dependent compensatory responses help populations respond to these changing conditions (Hilborn and Walters 1992). Across a species lifecycle, the largest compensatory changes typically occur in juvenile survival (Hilborn and Walters 1992). Traditionally, fisheries scientists have used stock-recruitment relationships to integrate across key compensatory density-dependent processes occurring in stages between the spawning stock and an arbitrary age at recruitment for the next generation (Hilborn and Walters 1992; Walters and Martell 2004).

Understanding the stock-recruitment relationship for a population is crucial, as aspects of this relationship describe how a population will respond when stock size is reduced to low levels (Goodyear 1980; Hilborn and Walters 1992). The rate of sustainable extraction of a renewable resource is dependent on the extent of these compensatory changes in survival rates as abundance declines (Goodyear 1980; Hilborn and Walters 1992). Furthermore, determining the maximum possible improvement in juvenile survival rates helps facilitate assessment of maximum recovery rates for populations at critically low abundances (Myers et al. 1999). Thus, an understanding of stock and recruitment is not only critical to sustainable harvest management, but also for recovery efforts (Koslow 1992; Myers 2002; Forrest et al. 2010).

Our understanding of the stock-recruitment relationship is significantly limited by the presence of uncertainty (Charles 1998; Zhu et al. 2012). Large biases can be introduced to parameter estimates through the impacts of “errors in variables” and/or “time series bias”, which can mask data trends (Hilborn and Walters 1992). When available, stock-recruitment data is often of poor quality, as data sets tend to be noisy and short in timeframe, and are often impacted by measurement error stemming from the effects of spatial heterogeneity and difficulty explicitly defining stock and recruit (Needle 2001; Prévost 2003; Michielsens and McAllister 2004). Bayesian and meta-analytic approaches (described in section 1.3 below) are important tools to reduce impacts of bias, improve parameter estimates, and explicitly account for uncertainties (Gelman et al. 2014).

1.2.2 Movement and dispersal

Fish movement varies significantly in spatial and temporal scale, from localized diel movements associated with foraging and predator evasion, to longer-term seasonal or inter-annual events, in some species including large-scale migrations (Hilborn and Walters 1992; Lucas and Baras 2000). The scale of a population's movements has ramifications for the spatial scale of management that is appropriate, and a spatial mismatch between the population and management regulations could result in regulatory failure (Palumbi 2004; Goethel et al. 2012). When regulations vary across a population's range, spatial considerations are increasingly important as individuals may interact with various management tactics throughout their lifecycle (Palumbi 2004; Goethel et al. 2012). Resolving uncertainties surrounding the specifics of how and where fish move through time is critical for development of fisheries management that adequately accounts for population and community level processes, particularly regarding timing and locations of population aggregations where each individual's susceptibility to exploitation may increase (Hilborn and Walters 1992; Lucas and Baras 2000).

When species exist over a large geographic range, spatial heterogeneity will likely cause variation in population parameters (e.g., growth, natural mortality, and movement rates), which in turn can result in differences in productivity between populations (Goethel et al. 2012; Sippel et al. 2015). This heterogeneity can have impacts across populations (e.g., through source-sink dynamics or variation in different population's ability to sustain harvest) (Kerr et al. 2010a, 2010b; Secor 2014). Fishing will disproportionately affect less productive populations, which can ultimately result in their extinction, lead to loss of genetic diversity, and reduce the population complex's ability to survive naturally occurring or anthropogenic perturbations (Paulik et al. 1967; Thorpe et al. 1995; Secor 2014). Resolving uncertainties surrounding habitat use and spatial structure of population complexes is critical to preservation of these population relationships and weak stocks (Ricker 1958; Nehlson et al. 1991; Secor 2014).

Inclusion of spatial information within population modeling frameworks requires large amounts of time, financial resources, and high-quality data (Maunder 2003; Hulson et al. 2011; Goethel et al. 2012). Even when financially feasible, the ability to collect data with a large enough sample size and with high enough quality for use in spatial modeling can be difficult. Process errors (i.e., underlying unaccounted for stochasticity in population dynamics) within tagging studies can have strong negative impacts on data quality and result in high levels of uncertainty (Caddy and Mahon 1995; Maunder 2003; Goethel et al. 2011). Lack of high-quality raw data often makes it necessary to determine objective weighting schemes for model alternatives (Quinn and Deriso 1998; Chen et al. 2003). The ability to appropriately weight data components is difficult, but failure to do so has large consequences on model accuracy (Quinn and Deriso 1998; Schnute and Richards 2001; Chen et al. 2003).

1.2.3 Dynamics of fish and angler populations

Recreational fisheries are socio-ecological systems that evolve dynamically over space and time in response to changes in fish and angler populations (Hartill et al. 2016; Camp et al. 2020). Uncertainties surrounding the ecology of fished populations and human behaviour can quickly undermine management actions aimed to conserve aquatic resources and maintain or increase angler participation and/or satisfaction (Post et al. 2002; Lynch et al. 2017; Camp et al. 2020; Birdsong et al. 2021). Population dynamics can be impacted by regulations in unexpected ways while drivers of angler behaviour are complex and multifaceted.

Impacts of fishing on fish population dynamics are incredibly context-specific (i.e., determined by the characteristics of the fished and angler populations), and uncertainty in how fish and human populations respond to regulatory change can lead to failure of a management approach (Post et al. 2002; Pereira and Hansen 2003; Walters and Martell 2004). For example, minimum length limits are a common size-based recreational fishery regulation. Imposition of such regulations, which result in removal of large, highly fecund individuals, can reduce a population's compensatory capacity by truncating the population's age and size distribution thus reducing overall egg production (Hilborn and Walters 1992; Birkeland and Dayton 2005; Lorenzen 2008). In contrast, minimum size limit regulations may also increase overall egg production if the number of small, less fecund individuals increases and compensates for the loss of large, highly fecund individuals (Allen et al. 2013).

There are also several depensatory mechanisms that can significantly impact the sustainability of recreational fishing opportunities and can reduce the potential for population recovery when fish abundance is significantly reduced (Hilborn and Walters 1992; Post et al. 2002; Hunt et al. 2011). Uncertainty surrounding the potential for depensatory impacts, or failure to account for depensation, can lead to management failure (Post et al. 2002). Depensatory impacts from inverse density-dependent catchability can result both from a population's life history or angler behaviour (Hilborn and Walters 1992; Hunt et al. 2011). Within modeling frameworks, catchability, the proportion of a population captured by one unit of effort (e.g., angler-hour or angler-day), is often assumed to be constant, with catch rates proportional to population abundance (Ricker 1975; Walters and Martell 2004). The assumption that catch-per-unit-effort (CPUE) and abundance are proportional is true in some instances (Hansen et al. 2000; Pierce et al. 2003; Walters and Martell 2004). However, CPUE can also remain high even when fish abundance is reduced to low levels (termed hyperstability) (Hilborn and Walters 1992; Tsuboi and Endou 2008; Erisman et al. 2011). Such instances can result from individual angler skill (Ward et al. 2013; van Poorten et al. 2016), fishing technology (e.g., fish finders) (Cooke et al. 2021), or specifics of a species' life history (e.g., aggregating behaviour such as schooling or association with specific habitat features) (Hilborn and Walters 1992; Dassow et al. 2020). These life history traits can make the timing and location of individuals predictable, making it easier for anglers to locate and exploit fished populations (Walters and Martell 2004; Erisman et al. 2011; Hunt et al. 2011).

The angler population within a specific recreational fishery is also diverse. Individuals not only differ in their experience levels and angling frequency, which strongly correlates to catch rates, but also their motivations for fishing, what leads to their satisfaction, and their responses to changes in fished populations or regulations (Ward et al. 2013; Hunt et al. 2019; Birdsong et al.

2021). Motivations of where and when anglers choose to fish are complex and can be important factors that prevent self-regulation of angling effort across the landscape of a fishery (Post et al. 2002; Cox et al. 2003; Johnston 2014). Uncertainties surrounding, or failure to account for these motivations, can result in sub-optimal management for social and conservation objectives (Post et al. 2002; Johnston et al. 2010; Hunt et al. 2011).

Angler motivations and drivers of the satisfaction they obtain from fishing are comprised of both catch and non-catch related attributes (Arlinghaus et al. 2008; Hunt et al. 2019). Factors like crowding, travel distance, and financial costs are all important determinants of where anglers choose to fish and how many individuals are active within a fishery at any given time (Hunt 2005; Post et al. 2008; Hunt et al. 2019). If anglers are motivated by, or gain satisfaction from non-catch related fishery attributes, regulations intended to maximize catch rates may not effectively address these motivations and result in decreased angler satisfaction (Arlinghaus 2006; Johnston et al. 2010, 2011).

The relative importance of catch and non-catch related attributes within the angler population's motivations to fish can also impact angler responsiveness to changing catch rates (Johnston et al. 2011; Allen et al. 2013). Clarifying uncertainties surrounding the relative importance of fishery attributes to specific angler populations is critical in developing regulations capable of meeting conservation objectives (Johnston et al. 2010). In instances where angler responsiveness to catch rates is low, effort will remain high even when fish population abundance declines (Johnston et al. 2010; Allen et al. 2013; Hunt et al. 2019).

The ability of regulatory actions to achieve management objectives is also determined in part by angler behaviours relating to regulatory compliance. Uncertainties surrounding the magnitude of, and changes in compliance following regulatory change, can undermine the effectiveness of management actions in achieving conservation goals (Aas et al. 2000). Non-compliance can be unintentional (e.g., resulting from incorrect identification of a species and subsequent retention or lack of understanding of complex regulations) or intentional (e.g., poaching resulting from angler perception that regulations are unfair) (Schmetterling and Long 1999; Page and Radomski 2006). Generally, levels of non-compliance within recreational fisheries are low, however they can vary dramatically within specific contexts (Page and Radomski 2006; Caroffino 2013; Thomas et al. 2015). The complexity and type of regulations used within a fishery's management have been found to significantly influence the rate of noncompliance harvest as a result of failed regulatory understanding for complex management actions or lack of angler buy-in (Sullivan 2002; Caroffino 2013; Thomas et al. 2015). Understanding the drivers of non-compliance within a particular fishery permits correcting actions by managers (e.g., education and stakeholder consultation), which can reduce non-compliance rates and improve management effectiveness (Schmetterling and Long 1999; Page and Radomski 2006).

1.3 Tools to address uncertainty

1.3.1 Bayesian hierarchical meta-analysis

Uncertainty arising from data limitations such as short time series and noisy data sets can undermine parameter estimation and population modeling (Hilborn and Walters 1992; Myers and Mertz 1998; Punt and Dorn 2014). Meta-analyses can confront these uncertainties by pooling information from multiple populations or species with similar characteristics and analyzing them simultaneously (Myers and Mertz 1998; Punt and Dorn 2014). When conducted within a Bayesian hierarchical framework, such analyses are powerful tools in parameter estimation and quantification of uncertainty.

Within a hierarchical meta-analysis, information is incorporated from multiple populations or species within a single model, which can allocate variability in key parameters across populations (termed hyper-priors), which inform prior probability distributions for each population (Myers 2002; Forrest et al. 2010; Goethel et al. 2011). Prior information is then used, in conjunction with the likelihood of the data given the model, to estimate posterior probabilities of parameters for individual populations, which in turn can serve as informative priors for new unstudied populations (Michielsens and McAllister 2004; Forrest et al. 2010). Bayesian hierarchical methods are valuable tools for addressing uncertainty because they provide a framework for formulation of direct probabilistic statements about unknowns (e.g., model parameters, reference points, missing data, inherent differences between populations or groups, and unobservable variables) (Prévost 2003; Michielsens and McAllister 2004; Punt and Dorn 2014).

The approach has gained traction as a method for improving estimation of recruitment parameters in data-limited situations and in studies where data are uninformative (Dorn 2002; Michielsens and McAllister 2004; Forrest et al. 2010). Several authors (e.g., Dorn (2002), Michielsens and McAllister (2004), and Forrest et al. (2010)) have successfully used Bayesian hierarchical meta-analyses to estimate key parameters of stock-recruitment relationships for several populations of their study species of interest. These case studies demonstrate the feasibility of the approach when investigating a population for which no stock-recruitment data are available, or where data across populations are highly limited.

1.3.2 Use of spatial population dynamics modeling and decision analysis

Accounting for all the complexities and uncertainties discussed thus far, management agencies have a choice: Make management decisions relying solely on expert judgement and past experience, or use all available data and tools at their disposal to quantitatively model the state of the system, and use model predictions to assess the efficacy of alternative management actions in meeting fishery objectives (Powers et al. 1975; Hilborn and Walters 1992). Though resource intensive, and not always feasible, population dynamics simulation modeling and decision analyses are invaluable tools for fisheries management. They allow managers to proactively explore the potential impacts of, and inherent trade-offs between, alternative regulatory actions while explicitly accounting for assumptions and uncertainties regarding both natural and human systems (Hilborn and Walters 1992; Irwin et al. 2011; van Poorten and MacKenzie 2020).

The inherent data and computational demands of including spatial information within such modeling frameworks has historically limited its consideration within assessment models, which has led to the failure of some fisheries management initiatives (Maunder 2003; Hutchinson 2008; Goethel et al. 2012). Within the last three decades, there has been increased attention towards including spatial information in assessments through development of spatially explicit population dynamics models (Cadrin and Secor 2009; Goethel et al. 2012; Crossin et al. 2017). Such models can incorporate a variety of spatial population structures, and can thus account for population and community level processes which serves to decrease uncertainty and increase the resolution of a species' key biological characteristics (Hilborn and Walters 1992; Lucas and Baras 2000; Goethel et al. 2012).

Decision analysis is a structured process where alternative regulatory actions are evaluated against fishery objectives through simulation modeling, which explicitly accounts for critical uncertainties (Powers et al. 1975; Peterman et al. 1998; van Poorten and MacKenzie 2020). Through the decision analysis process, management objectives, assumptions, and uncertainties surrounding the dynamics of human and fished populations, and the true states of nature acting upon these populations, are all explicitly identified (Peterman et al. 1998; Robb and Peterman 1998). The approach provides a formalized framework through which managers can explore trade-offs between competing objectives, and clearly identify how alternative management actions perform both relative to one another, and in the face of uncertainty (Robb and Peterman 1998; Jones and Bence 2009; van Poorten and MacKenzie 2020). The formal structure of a decision analysis also aids managers in making management decisions that are robust to uncertainties, defensible, and formulated in a way that can be clearly communicated to stakeholders and rightsholders (Peterman and Anderson 1999; Irwin et al. 2011; van Poorten and MacKenzie 2020).

1.4 Species biology, threats, and management

1.4.1 Bull trout (*Salvelinus confluentus*) biology

Bull trout are relatively long-lived (maximum age 10-20 years), large-bodied, iteroparous salmonids endemic to the northwest United States and western Canada (Haas and McPhail 1991; Post and Johnston 2002; Rees et al. 2012). Populations are subdivided into two evolutionarily and regionally distinct lineages (Haas and McPhail 1991; Taylor et al. 1999). The coastal lineage is found throughout the lower Fraser River below Hells Gate and within the Squamish and upper Skagit river drainages (Hagen and Decker 2011). The interior lineage has an extensive distribution throughout western Canada (i.e., British Columbia, western Alberta, southeast Yukon, and western Northwest Territories) and the northwestern United States (i.e., Washington, Oregon, Idaho, and western Montana) (Haas and McPhail 1991; Hagen and Decker 2011). Historically, this range extended south into California and Nevada, however these populations have since been extirpated (Haas and McPhail 1991; Rieman et al. 1997; Post and Johnston 2002). Within British Columbia, bull trout have a broad distribution encompassing most of the major watersheds east of the Coast Mountains (Hagen and Decker 2011). The species is, however, absent from the Similkameen, Okanagan, and Kettle river drainages (Hagen and Decker 2011).

Bull trout evolution within low productivity, naturally fragmented landscapes resulted in four distinct life history strategies (i.e., resident, fluvial, adfluvial, and anadromy), and development of meta-population structure within many population groupings (Dunham and Rieman 1999; Warnock et al. 2011; Taylor et al. 2021). These different life histories vary substantially in their behaviour, maturity schedules, and maximum size (Rieman and McIntyre 1993). Fluvial and adfluvial bull trout utilize extensive home ranges accessed through annual or interannual seasonal movements (up to approximately 250 km distance) between high elevation, headwater spawning habitats, and larger riverine, lake, or reservoir habitats where increased resource availability improves survival and growth (Gross 1987; Rieman and McIntyre 1993). Both timing and distance travelled for spawning migrations varies between populations, but generally occur in late summer, with spawning in August and early September followed by rapid outmigration to foraging and wintering habitats in early fall (Post and Johnston 2002; Pillipow and Williamson 2004; Hagen and Decker 2011). Bull trout are generally believed to have fidelity to spawning, wintering, and foraging habitats (McPhail and Baxter 1996; McLeod and Clayton 1997; Post and Johnston 2002).

Bull trout play an important role as a top predator in many aquatic communities. Adults have limited predators including mink (*Mustela vison*), bear (*Ursus* spp.), osprey (*Pandion haliaetus*), and river otter (*Lontra canadensis*) (Stelfox and Egan 1995; Stewart et al. 2007). The species becomes increasingly piscivorous with size and are aggressive, opportunistic feeders (McPhail and Baxter 1996; Post and Johnston 2002; Stewart et al. 2007). Fluvial and adfluvial populations are known to be cannibalistic and also prey on trout (*Oncorhynchus* spp.), whitefish (*Prosopium and Coregonus* spp.), Arctic grayling (*Thymallus arcticus*), Pacific salmon (*Oncorhynchus* spp.) spawners, smolts, and eggs, as well as other small finfish, invertebrates, reptiles, and small mammals (McPhail and Baxter 1996; Post and Johnston 2002; Furey and Hinch 2017).

1.4.2 Threats, conservation, and management

Bull trout are thought to be highly susceptible to human impacts and naturally occurring processes. The species requires cold (<15˚C), clean water throughout their life history (Rieman and McIntyre 1993; Post and Johnston 2002). The presence of highly connected, structurally diverse habitats are also critical for maintaining migration pathways and providing access to spatially distinct habitats used for foraging, wintering, spawning, and rearing (Rieman and McIntyre 1993; Post and Johnston 2002; Starcevich et al. 2012). For example, access to mainstem rivers can provide increased foraging opportunities over small headwater systems resulting in increased body size, fecundity, and possibly higher population viability (Schoby and Keeley 2011).

Connectivity, paired with the prevalence of meta-population structure amongst many bull trout populations, also functions to spread risk and support persistence of weak populations (Paulik et al. 1967; Secor 2014; Taylor et al. 2014). Population studies in highly impacted systems have demonstrated bull trout can lose their migratory behaviour (Rieman and McIntyre 1993; Rieman et al. 1997; Jakober et al. 1998). Reductions or loss of migratory behaviour may significantly reduce a meta-population’s potential buffering effects on population fitness through dispersal (e.g., source-sink dynamics), and thus can reduce a population’s capacity to rebuild from depleted states (Hilborn et al. 2003; Kerr et al. 2010b). Anthropogenic impacts resulting in temperature increases, reduced habitat quality, and non-native species introductions are also important drivers within the observed decline of many bull trout populations (Rieman and McIntyre 1993; Post and Johnston 2002; Hagen and Decker 2011).

Bull trout are highly susceptible to overharvest due in part to their life history and behaviour (e.g., adult aggregating, slow growth, late maturity, aggressive feeding, and vulnerability of juveniles to harvest prior to sexual maturity) (Post and Johnston 2002; Post et al. 2003; Erhardt and Scarnecchia 2014). This combination of factors makes it possible to overfish bull trout populations even at low levels of angling effort (Post and Paul 2000; Post and Johnston 2002). Anecdotal evidence also suggests that high exploitation rates prior to the 1980s may have depressed populations accessible to humans, further demonstrating the susceptibility of the species to overexploitation (Hagen and Decker 2011). However, depressed bull trout populations have also been found capable of recovering rapidly when exploitation is reduced (Johnston et al. 2007; Hagen and Decker 2011; Erhardt and Scarnecchia 2014).

Bull trout have designated conservation status of ‘Threatened’ under the United States Endangered Species Act (USFWS 2015). In Canada, the species has been assessed as five conservation units whose status under Canada’s Species at Risk Act (SARA) range from ‘Not at Risk’ to ‘Threatened’ (COSEWIC 2012; Government of Canada 2021). Population declines and local extinctions have occurred across the species range (Post and Johnston 2002; Hagen and Decker 2011; USFWS 2015). Within British Columbia, the first systematic assessment of bull trout conservation status was completed in 2011 and found the majority of populations for which data were available to be stable or increasing over the past three decades (Hagen and Decker 2011). These findings have led to the belief that British Columbia may be the final stronghold of bull trout on Earth (Rieman et al. 1997; Post and Johnston 2002; Hagen and Decker 2011).

Bull trout angling has increased over the past fifty years following improvements to access (Post and Johnston 2002). Management of all bull trout life histories across the species range is highly conservative (Post et al. 2003; Hagen and Decker 2011). Across jurisdictions, the overarching management objective is resource conservation and preservation with the secondary objective of creating and maintaining sustainable use benefits for local user groups (FLNRORD 2017a; IDFG 2019; MTFWP 2021; ODFW 2021; WDFW 2021). Harvest opportunities for the species are extremely limited, and many fisheries employ catch-and-release regulations. Mortality in catch-and-release fisheries, incidental catch in other introduced sports fisheries, and poaching remain problems in fisheries across the species range (Schmetterling and Long 1999; Gutowsky et al. 2011; Joubert et al. 2020).

1.5 Dissertation objectives and structure

This dissertation builds modeling tools to support management decision-making for a fluvial bull trout fishery within the upper Fraser River watershed of British Columbia. The dissertation first characterizes recruitment compensation potential for bull trout as a species; then uses multi-state, capture-recapture modeling to determine movement patterns and natural mortality rate estimates for several bull trout spawning populations contributing to a population complex within the region; and finally, builds an age-, stock-, and spatially-structured population dynamics model and decision analysis to explore the potential effectiveness of alternative regulatory strategies in meeting fishery objectives of resource conservation and maintaining angler satisfaction.

1.5.1 Chapter 2: Estimating cross-population variation in juvenile compensation in survival for bull trout (*Salvelinus confluentus*): A Bayesian hierarchical approach.

This chapter uses a Bayesian hierarchical meta-analysis to integrate stock recruitment information across multiple populations of bull trout spanning the species native range. This analysis estimates key parameters of both the Ricker and Beverton-Holt models of the stock-recruitment relationship and explores variability in these relationships across populations (Ricker 1954; Beverton and Holt 1957). The chapter also generates an estimate of the Goodyear compensation ratio for bull trout, which is a parameter critical to understanding a population's response to reductions in spawning stock size (Goodyear 1977, 1980; Walters and Martell 2004).

This estimate is used within the population dynamics model of Chapter 4 and provides a prior probability density function for study of bull trout populations across the species range.

1.5.2 Chapter 3: Spatial distribution and seasonal movement probability estimates of bull trout (*Salvelinus confluentus*) through a large, uninterrupted river network.

The multi-state Cormack Jolly Seber model (Lebrenton et al. 2009; Kéry and Schaub 2012) developed within this chapter, coupled with genetic information collected during field sampling and analyzed by Taylor et al. (2021), provide a unique opportunity to advance the use of movement models within an inland fisheries context. Within this chapter, seasonal- and stock-specific variation in large-scale movement dynamics are comprehensively assessed for multiple populations of fluvial bull trout within the upper Fraser River watershed of British Columbia. Seasonal- and stock-specific estimates of natural mortality rate are also estimated. State transition probabilities (i.e., movement probabilities between spatial areas) and natural mortality estimates developed in this chapter are used to create the age- and spatially-structured population dynamics simulation model within Chapter 4.

1.5.3 Chapter 4: Evaluating alternative management actions on fluvial bull trout using decision analysis.

This chapter uses the bull trout recruitment compensation estimate derived in Chapter 2 and seasonal transition probability matrices and natural mortality estimates from Chapter 3 to parameterize an age-, stock-, and spatially-structured population dynamics model to represent a fluvial bull trout population complex in the upper Fraser River watershed of British Columbia. This dynamic model is then used through the application of a decision analysis to evaluate the effectiveness of alternative management actions toward the dual fishery objectives of bull trout conservation and maintenance of angler satisfaction within the recreational fishery.

Chapter 2: Estimating cross-population variation in juvenile compensation in survival for bull trout (*Salvelinus confluentus*): a Bayesian hierarchical approach

2.1 Introduction

Bull trout (*Salvelinus confluentus*) are endemic to the northwest United States and western Canada and hold designated conservation status across much of their native range (Post and Johnston 2002; COSEWIC 2012; USFWS 2015). The species expresses four life history types: fluvial, adfluvial, resident, and anadromy (Rieman and McIntyre 1993). Fluvial and adfluvial populations spawn in tributaries and reside in mainstem rivers (fluvial) or lakes and reservoirs (adfluvial), while stream-resident populations remain within their natal tributary for their entire life (Post and Johnston 2002). The anadromous life history is far less common. Fish expressing this life history spawn in tributaries and spend the remainder of their lifecycle within the ocean (Rieman and McIntyre 1993). Life history characteristics (e.g., maturity and growth) vary substantially between bull trout life histories and within life histories across different populations (Rieman and McIntyre 1993; Post and Johnston 2002).

The status of individual populations in different regions varies dramatically. Bull trout were extirpated from much of the southern and eastern portions of their historical range (Rieman and McIntyre 1993). While many populations across much of the species global current distribution have undergone large scale reductions in abundance (Haas and McPhail 1991; Post and Johnston 2002; Hagen and Decker 2011). Within British Columbia, Canada, however, the story is not the same, with the region considered by some to be the last stronghold of bull trout on Earth (Hagen and Decker 2011). The species conservation listing in British Columbia was seen at the time as a precautionary measure (MOE 1994; Hagen and Decker 2011). A more recent systematic assessment of bull trout across the province showed the majority of populations for which data are available to have stable or increasing abundance over the past three decades (Hagen and Decker 2011). Furthermore, sustainable harvest opportunities exist for several adfluvial bull trout populations across the province (Hagen and Decker 2011; FLNRORD 2017a).

Observed declines in bull trout abundance and distribution are believed to have resulted from habitat degradation and fragmentation, non-native species introductions, and warming water temperatures, exacerbated by the species' highly specific habitat requirements for successful spawning and rearing (Rieman and McIntyre 1993; Post and Johnston 2002). Bull trout are also thought to be highly susceptible to overharvest due to a combination of large body size, late maturity, aggressive feeding, and aggregative behaviour (Post and Paul 2000; Post and Johnston 2002; Rees et al. 2012). The species high susceptibility to anthropogenic impacts and fishing pressure has made it a management priority across jurisdictions to develop and deliver management to protect and recover at-risk bull trout populations and preserve healthy populations (COSEWIC 2012; USFWS 2015).

The provision of such management objectives requires estimates of a key population parameter: the Goodyear compensation ratio (*CR*, Goodyear (1977, 1980)); comparable to steepness (Martell et al. 2008). This parameter represents the maximum relative increase in juvenile survival rate when a population's abundance decreases towards zero (Goodyear 1977, 1980;

Walters and Martell 2004). Density-dependent compensation in juvenile survival can enable fish populations to persist when stock size is reduced to low abundances (Goodyear 1980; Walters and Martell 2004). Despite observed reductions in population abundance and geographic range, bull trout appear to have capacity for strong density-dependent compensation in juvenile survival as evidenced by rapid recovery of some populations (Johnston et al. 2007; Erhardt and Scarnecchia 2014). As such, an accurate estimate of bull trout's capacity for density-dependent compensation is an important component in estimating both recovery rates for endangered populations and sustainable harvest rates for fished populations (Goodyear 1980; Walters and Martell 2004). Despite its importance, density-dependent recruitment compensation potential for bull trout is poorly understood, and the relationship has not been quantitatively explored across the species range.

Estimates of *CR* are obtained through analysis of stock-recruitment data. Such analyses have high data needs and are only possible when reliable measures of both spawning stock size and resulting recruitment exist (Hilborn and Walters 1992). In addition, analysis of stock-recruitment data is strongly limited by two types of error known as "errors in variables" and "time series bias", that can introduce large bias into resulting parameter estimates (e.g., α – slope at the origin, and thus *CR*), and mask trends in data (Hilborn and Walters 1992). Bias introduced by both error types can only be limited if data has high contrast in spawning stock size. Or in other words, when data sets contain observations of spawner abundance over a broad range of spawning stock size including estimates near carrying capacity and at very low abundances (Hilborn and Walters 1992). Collecting such data is highly challenging. As a result, the prevalence of uninformative data in combination with structural and observational uncertainties continue to present major challenges within the estimation of key fisheries statistics surrounding population productivity and persistence, including the estimation of *CR* (Walters and Martell 2004).

One approach to limiting the impacts of bias and improving parameter estimates in stock-recruitment analyses is the use of meta-analytic approaches (Gelman et al. 2014). Such analyses can improve estimates of stock-recruitment data through their ability to pool multiple data sets with various ranges of spawning stock abundance within a single model (Gelman et al. 2014). Bayesian hierarchical approaches are typically used to conduct meta-analyses of stock-recruitment and have been shown to improve estimation of stock-recruitment parameters in data-limited situations, demonstrating the approach's feasibility when investigating populations of species such as bull trout, where limited stock-recruitment data are available (Dorn 2002; Michielsens and McAllister 2004; Forrest et al. 2010). Use of a Bayesian approach also facilitates characterization of uncertainty in model structure and key parameters, and permits estimation of posterior predictive distributions, which provide predictions of key parameters (e.g., *CR*) for unsampled populations (Gelman et al. 2014).

In this study, stock-recruitment parameters for bull trout were estimated using a Bayesian hierarchical meta-analysis, with focus on characterizing cross-population variability in bull trout's *CR* (Goodyear 1977, 1980; Walters and Martell 2004). This research is the first attempt to characterize the scope for compensation in bull trout across the species range. Though paired data on spawning stock size and resulting recruitment exist for several isolated populations of bull trout of varied life history, data quantity is limited for most populations, suggesting a robust statistical treatment is necessary. This species-level prediction of *CR* for bull trout is invaluable, as many regions do not collect data on both spawner and juvenile densities. As such, any preliminary information on *CR*, which describes the scope for improvements in juvenile survival at small population size, will benefit regional-level management and conservation efforts.

2.2 Methods

2.2.1 Data collection

Spawner and juvenile abundance estimates were compiled from regional management reports, peer-reviewed literature, and personal communication with experts for 41 populations of fluvial and adfluvial bull trout. Of the data acquired, 27 populations were excluded from this analysis due to short time series duration (i.e., less than five years), incomplete information for either spawner or recruitment estimates, or where substantial changes in productivity or carrying capacity occurred in the system (e.g., strong anthropogenic or natural perturbations and/or enhancement activities). Available data was largely limited to adfluvial populations and streams within British Columbia, Canada. A total of 14 populations were included in the analysis with a median time series length of seven years. Data were available for three fluvial populations, with the remaining 11 data sets coming from adfluvial populations (Table 2.1).

Estimates of the total number of eggs produced by each population in each year were taken to represent the index of spawning stock abundance used within the hierarchical meta-analysis. The majority of spawner data obtained for this study came in the form of redd counts. These data were converted to total number of eggs produced by each population. First, a hierarchical meta-analysis of length-at-age information from a subset of the 14 populations was conducted to generate estimates of von Bertalanffy growth equation parameters ($L_\infty, K,$ and t_0) (Table 2.2). Where length-at-age information was not available for a particular stream, information for a spatially adjacent system was used (e.g., Attichika Creek served as an index stream for all of the tributaries feeding Thutade Lake (e.g., South Pass, Tributary 4, Tributary 12). A list of all model parameters and their description both for the stock-recruitment and length-at-age analyses are given in Table 2.3. Age-specific incidence functions for length-at-age, maturity-at-age, and fecundity-at-age were then calculated (Table 2.4). The resulting fecundity estimate for age 7+ fish in each population was then multiplied by the redd count data to generate the estimated number of eggs produced by each population per year, which were then used as the spawner index data within the system.

In this analysis, recruits were defined as an age 1+ fish. Population specific estimates of recruit abundance came from electrofishing depletion estimates, except for the Metolius River Basin, where recruits were measured from smolt trap counts. Electrofishing depletion estimates in subsections of each stream, for each population, were expanded by best estimates of available stream habitat resulting in a total recruitment estimate for each year, for each population. Smolt trap estimates of juvenile abundance were converted to estimates of age 1+ abundance as follows. A length-age key for the population was first used to assign an age to all fish captured in the smolt trap. Survival rate of these juvenile fish (age 1+ to age 3+) was then calculated by taking the average survival for age 1+ and age 2+ fish as estimated by Bowerman and Budy (2012). The number of age 1+ recruits was then back-calculated based on both estimated age and survival rates. All data sets of recruit abundance were then back-shifted through time by two calendar years to assign each cohort of recruits to the correct spawner abundances (i.e., to account for egg incubation prior to hatching) (Johnston et al. 2007).

2.2.2 Model structure

A hierarchical Bayesian meta-analysis was used to estimate the magnitude of recruitment compensation exhibited by bull trout as a species and to explore population specific variation in the parameter. As the functional form of the stock-recruitment relationship that best represents bull trout is not known, estimates of *CR* were calculated under the assumption of either the Ricker or Beverton-Holt stock-recruitment functions (Ricker 1954; Beverton and Holt 1957). This approach permitted exploration of variation in *CR* between the two models and a preliminary investigation of the functional form of the stock-recruitment relationship for the species.

Analysis of stock-recruitment data served to jointly estimate unfished growth, survivorship, maturity, and fecundity incidence functions, as well as the parameters of either the Ricker or Beverton-Holt models. Both models were parameterized using unfished recruit potential (R_0) and the Goodyear compensation ratio (*CR*) using various incidence functions (see Table 2.4; Botsford 1981a, 1981b; Walters and Martell 2004). Calculated recruitment parameters were then used to predict recruitment in each system based on the observed spawner index in each year (given as total number of eggs) and model fits of each recruitment function to data for each of the 14 populations (Table 2.5). Equations for the Ricker (Equation 2.1) and Beverton-Holt recruitment (Equation 2.2) functions are given by:

$$R_{i,t} = \alpha E_{i,t} e^{\beta_1 E_{i,t} + \Omega_t} \quad \text{Eq. 2.1}$$

$$R_{i,t} = \frac{\alpha E_{i,t}}{1 + \beta_2 E_{i,t}} e^{\Omega_t} \quad \text{Eq. 2.2}$$

2.2.3 Hierarchical hyper-parameter and prior selection

Within the hierarchical model framework, parameters are assumed to come from probability distributions that are shared by all populations (i.e., the prior distribution; Parent et al. (2013)). Hyper-parameters can then be used to describe the distribution of each of these priors (Parent et al. 2013). In this framework, hyper-parameters are assumed to represent all populations and parameters for individual populations are jointly estimated (McCarthy, 2007; Parent et al. 2013). Within the model structure, the parameters of the von Bertalanffy growth equation ($L_\infty, K,$ and t_0) and Goodyear compensation ratio (*CR*) were assumed to be sampled from a common population distribution, conditional on hyper-parameters (Table 2.6).

The hierarchical meta-analysis of length-at-age data discussed in Section 2.1 also served to generate informative priors for the parameters of the von Bertalanffy growth equation ($L_\infty, K,$ and t_0) for each population. This process was integral to the analysis as generation of candidate stock-recruitment models was conditional on population-specific growth rates. Informative hyper-parameters for the mean and precision of the prior probability distributions of *CR* were based on species-specific *CR* estimates provided in Myers et al. (1999). The hyper-parameter for mean of *CR* was assumed normally distributed and based on the mean and precision of log-transformed species-level *CR* estimates reported in Myers et al. (1999). This choice provided a conservative estimate of *CR*. The hyper-parameter for the precision of *CR* was transformed from the standard deviation of each species-level estimate of *CR* used within this analysis. This standard deviation estimate was assumed to be log-normally distributed based on population-level *CR*s reported in Myers et al. (1999).

Unfished recruit density, D_0, was assumed to be log-normally distributed, with mean and precision estimated from observed densities of recruits in various streams, with minimal fishing effort, as reported in Decker and Hagen (2007). To account for low but unknown fishing effort, precision for this prior was expanded by 1.5 times that presented in Decker and Hagen (2007). The prior for unfished abundance (R_0) was obtained by multiplying D_0 by estimates of accessible spawning habitat (*stL*: in kilometers) obtained for each system.

2.2.4 Choice of non-hierarchical priors and parameter values

Estimates of natural mortality rates (*M*) and length-maturity schedules (Υ) for bull trout have not yet been reported in the published literature. A prior for *M* was generated following both the methodology employed by Post et al. (2003), which used bull trout observations from Lower Kananaskis Lake (see Johnston et al. (2007)), as well as estimates of *M* for a similar species, lake trout (*Salvelinus namaycush*). Maturity was calculated as a logistic function with median L_{50} and slope Υ. Length of 50% maturity (L_{50}) was calculated as the product of asymptotic length (L_∞) and an estimated proportion of asymptotic length at 50% maturity (p_{50}), which was given as an informative beta prior with shape parameters of 500 and 1000. This prior was chosen to be consistent with age-at-maturity reported in Johnston et al. (2007). The prior for Υ was determined using a visual examination of Johnston et al. (2007). The beta distribution for p_{50}

was chosen to constrain values of L_{50} to be positive. Finally, the scalar parameter of the length-egg relationship (Γ) and the exponent parameter of the length-age relationship (δ) were set as reported by Johnston (2005).

Time-varying process error (Ω) was assigned a normal distributed prior with mean a mean of zero and precision (τ_t) of 16. Observation error ($\tau_{recruits}$) for the Ricker or Beverton-Holt models was assigned an uninformative gamma prior. Time-varying process error for the von Bertalanffy growth equation (τ_{vbk}) was assigned a beta distribution with shape parameters of 1.5 and 1.5.

2.2.5 Posterior calculation

Posterior density functions for parameters of interest were approximated using the Markov chain Monte Carlo (MCMC) algorithm implemented using JAGS software (Just Another Gibbs Sampler; available from http://mcmc-jags.sourceforge.net/) implemented through R utilizing the R2jags package (Yu-Sung and Yajima 2015; Plummer 2016; R Core Team 2016). Three chains were run for 100,000 iterations after a burn-in of 90,000 and the final posterior estimates were thinned by 10. Convergence was evaluated using the Gelman-Rubin diagnostic tool (Brooks and Gelman 1998) and visual inspection of trace plots of the Markov chains for each parameter.

2.2.6 Bayesian approach to model uncertainty

In this investigation, formal comparison of the stock-recruitment models under the alternative assumptions of the Ricker and Beverton-Holt stock-recruit functions was not conducted. The deviance information criterion (DIC), however, was calculated to provide information regarding goodness of fit (Spiegelhalter et al. 2002). The computed DIC results were not used for model selection, as there is no formal quantitative measure of what scale of difference in DIC values between models should direct model choice, and as the statistically “best” model may still not be the most beneficial for management and policy decisions (Spiegelhalter et al. 2002; Richards 2005; Carruthers et al. 2010).

2.2.7 Sensitivity analyses

A key assumption in the use of hierarchical Bayesian meta-analyses is the concept of exchangeability of data sets (Parent et al. 2013; Gelman et al. 2014). That is, each population-specific parameter (e.g., *CR*) is considered an independent sample from a common distribution, which may be indexed by hyper-parameters (Gelman et al. 2014). To test this assumption for the posterior predictive distribution of *CR*, the hierarchical analyses of the Ricker and Beverton-Holt functions were run an additional 14 times each, systematically excluding one data set in each subsequent run to explore its impacts on the posterior density functions.

2.3 Results

Evaluation of both hierarchical models (i.e., Ricker and Beverton-Holt) using Gelman-Rubin statistics and trace plots showed both models approached convergence. Posterior estimates were insensitive to initial conditions, and there was little to no observed autocorrelation for either model after thinning the posterior MCMC chains. Overall, fits of both models adequately described the mean relationship between spawning stock size and recruit abundance (Figure 2.1). Deviance information criterion for the Ricker and Beverton-Holt models were 390.9 and 386.0, respectively. These DIC results suggest the analyzed bull trout data are best supported by the Beverton-Holt model based on ‘rule of thumb’ in Burnham and Anderson (1998).

Median estimates for the Beverton-Holt model were considerably higher than those obtained for the Ricker model. Further, data sets from several stocks were more informative at estimating *CR* than others (Figure 2.2). No discernable relationship was observed between life history (adfluvial or fluvial) or geographic origin of the stock-recruit data and the estimated values for compensation ratio (Tables 2.7 and 2.8). The posterior predictive distribution for *CR* suggests a median of 384.03 (Beverton-Holt) or 121.45 (Ricker) (Table 2.9). Assessment of the possible impacts of hyper-parameter choice on the posterior predictive estimates of *CR* found the informative priors did not have undue influence on the posterior estimates (Figure 2.3). Finally, posteriors for steepness (Mace and Doonan 1988), which can be calculated directly from *CR* (Martell et al. 2008), were 9.30 (1.04-77.45) for the Ricker and 482.04 (28.69-8295.29) for the Beverton-Holt.

Exchangeability of the data sets was explored by running each of the stock-recruit models (Ricker and Beverton-Holt) an additional 14 times, systematically excluding one population in each run. Posterior predictive distributions for *CR* with each population removed were not noticeably different from the predictive distributions obtained with all populations included. Results of the exchangeability analysis suggest that no specific population data set unduly influenced the results of the hierarchical analysis. It was therefore concluded that the assumption of exchangeability within the analysis was met (Figure 2.4).

2.4 Discussion

Observed large-scale reductions in bull trout abundance and distribution throughout portions of their range, in addition to evidence of the species' susceptibility to anthropogenic impacts has raised conservation concerns surrounding the future of the species (Post and Johnston 2002; Hagen and Decker 2011; Rees et al. 2012). Obtaining an accurate estimate of bull trout's capacity for density-dependent compensation, and thus their ability to respond to population declines, is a crucial step towards evaluating sustainable harvest rates for fished populations and estimating recovery rates and targets for at-risk populations (Walters and Martell 2004; Pine et al. 2013). Using a hierarchical Bayesian approach, this chapter provides the first characterizations of *CR* for bull trout, while accounting for uncertainty within the parameter estimates.

The marginal posterior probabilities for *CR* estimated for each population demonstrate that bull trout have large scope for improvements in juvenile survival at low stock size. This finding is supported by both anecdotal evidence, which has suggested the recovery of multiple unmonitored bull trout stocks following harvest reduction (Hagen and Decker 2011), as well as by the work of Fraley and Shepard (1989) in the Flathead River basin, Johnston et al. (2007) in Lower Kananaskis Lake, and Erhardt and Scarnecchia (2014) in the Clearwater River Basin. High juvenile compensation has also been found in closely related brook trout (*Salvelinus fontinalis*) (de Gisi 1994).

The imprecise nature of both the marginal posterior distributions and the median posterior predictive distributions for *CR* are not surprising. Most data sets used in this analysis were relatively uninformative in that they were characterized by short duration time series and limited ranges of stock abundance over the length of available time series. Only two data sets (Smith-Dorrien Creek and Metolius River Basin) had wide variation in spawner abundances, yet their relatively short duration (time-series length) meant there was still substantial uncertainty in posterior estimates of *CR* for these systems.

CR estimates obtained in this investigation and evidence of rapid recovery of bull trout populations (Johnston et al. 2007; Erhardt and Scarnecchia 2014) suggest the bottleneck for bull trout population recovery is likely habitat quality and quantity, which is assessed through the stock-recruitment β parameter, rather than compensatory response. Bull trout's complex life history and highly specific habitat requirements put them at high risk of population reductions or decreased population persistence as a result of anthropogenic impacts on key habitats (Haas and McPhail 1991; Post and Johnston 2002; Hagen and Decker 2011). A detailed examination of how habitat quality and quantity specifically influence juvenile bull trout survival is necessary to inform future management and recovery efforts focused on habitat improvements and maintenance (Haas and McPhail 1991; Post and Johnston 2002; Hagen and Decker 2011).

Estimating compensation in juvenile survival within population dynamics models is inherently difficult due to high data needs and confounding of compensation with other parameters (i.e., R_0). When estimating such parameters, it is important to include uncertainty and avoid fixed parameter estimates, even if the value is deemed conservative. Failure to account for uncertainty can result in management failure if recovery planning and harvest policies use incorrect conclusions drawn from fixed parameters (Hilborn and Liermann 1998; Morris et al. 2015).

Though this investigation was not able to provide a precise estimate of compensation for specific populations, the posterior predictive estimate developed establishes a distribution for compensation for bull trout that excludes biologically unrealistic values.

The posterior predictive estimate of *CR* calculated within this chapter can be used as an informative prior in future Bayesian models for the species. It serves to restrict the parameter space of this key parameter to one that is biologically realistic for bull trout, reduce uncertainty, and improve inference for populations where stock-recruitment data are scarce or non-existent or where available data lack the contrast necessary to adequately estimate parameters of a population's stock-recruitment relationship. Any future work of this type, which utilizes additional data sets, can build on this investigation, and will further increase precision of the posterior predictive estimates of *CR* provided.

Model comparison conducted using DIC, which provides a formal system to compare the fit of each hierarchical stock-recruitment model to the available bull trout data, supported the model choice of the Beverton-Holt function (Spiegelhalter et al. 2002). This result was not expected ecologically, as bull trout behaviour, notably evidence of adult cannibalism of juveniles and superimposition of redds, coupled with size-dependent predation, would suggest the Ricker function should provide a better fit (Hilborn and Walters 1992; Rieman and McIntyre 1993; McPhail and Baxter 1996). Statistically, however, the finding is expected based on the lack of variation in the available spawner index data. It should be noted that the systems for which highly variable stock-recruitment data were available (e.g., Smith-Dorrien Creek and Metolius River Basin) showed a pattern consistent with the Ricker function. As DIC does not provide a direct mechanism to compare the overall plausibility of each model structure given the data, neither functional form should be ruled out and model uncertainty should be carried forward into any future bull trout stock assessment work (Michielsens and McAllister 2004).

This analysis was negatively impacted by three main factors: a limited quantity of available data, a limited range of spawner abundance within most data sets, and a limited time series within most data sets. During data collection, it became evident that there is a general lack of stock-recruitment data for bull trout. As well, most available information is not at the scale or temporal duration necessary for use in stock-recruitment analyses (i.e., in the form of paired spawning stock biomass and resulting recruit abundance estimates). Twenty-seven populations were excluded from this analysis due to factors including short time series (i.e., less than five years duration) and incomplete information in spawner and/or recruit abundance estimates. Of the systems included, the average length of data set was seven years. Despite best efforts, the analysis' estimates of compensation are understandably uncertain. One key outcome of this work is to direct attention to the need to continue collecting information on both stock and recruitment indices from as many bull trout populations as possible to improve *CR* estimates and therefore improve predictability of models that rely on them.

Data obtained from different regions (i.e., nation, individual state or province) also lacked consistency in data collection approaches. It appears that different regions consistently collect different abundance indices (e.g., redd counts, juvenile estimates, smolt counts, or a combination of these), but rarely collect paired indices of spawners and recruits together over time. This limitation prohibited a more thorough investigation of juvenile compensation across the species range. Gaining an understanding of the recovery potential for bull trout is a key step in population recovery planning and management. Therefore, more rigorous and standardized data collection of bull trout stock-recruitment data across the species range should be a priority.

Only data from two systems (Smith-Dorrien Creek and the Metolius River Basin) had high contrast in spawning stock abundance through time, with spawner abundance estimates ranging from near collapse to near carrying capacity. Generally, data were available for only small ranges of variation in spawning stock size. Data of this kind are challenging to incorporate within stock-recruit analyses because it contributes to biases (i.e., “errors in variables” and “time series bias”), which make it difficult to ascertain the true stock-recruitment relationship (Hilborn and Walters 1992). The inclusion of additional data sets, specifically ones that have large variation in spawner abundances and extend from very low abundance to near carrying capacity (i.e., high contrast), longer than 20 years duration, would serve to improve estimates of recruitment parameters including *CR*, and reduce uncertainty in these estimates (Hilborn and Walters 1992). These data sets are understandably rare and difficult to capture by accident, suggesting a need for an adaptive management experiment on bull trout recruitment. The hierarchical model presented within this analysis was the most appropriate approach to deal with such data, which allowed an estimate of reasonable hyper-parameters for *CR*, which in turn informed the analysis. As additional data become available, particularly if there is high variation in spawner density, posterior predictive estimates will improve over time.

At present, most of what we know about bull trout’s capacity for recovery comes from research on adfluvial fish in Lower Kananaskis Lake, Alberta, where detailed stock and recruit sampling was conducted over a 10-year period and over a population ranging in size from near collapse to near carrying capacity (Johnston et al. 2007). Data could not be obtained for populations across bull trout's migratory life history types and spatial distribution. Stock-recruitment data sets available for use in this study came primarily from British Columbia, Canada, with only three systems from one other Canadian province (Alberta) and only one system from bull trout's range within the United States (Oregon). No difference in *CR* would be expected as a result of geography because of the similarity in conditions required for bull trout recruitment across systems (Post and Johnston 2002).

In addition, most of the available data (11 of 14 systems) were for adfluvial bull trout, with only three systems representing the fluvial life history, and zero data for anadromous or resident life histories. Although bull trout life histories vary significantly in their maximum size, migration patterns, as well as other key statistics, all bull trout life history types rear in similar habitats (Post and Johnston 2002; Rees et al. 2012). Therefore, factors affecting juvenile survival are likely similar, implying findings here are still relevant. Certainly, a noticeable difference between the two life history types examined was not detected.

2.5 Conclusions

Findings of this chapter provide a key first step in establishing a precise estimate of recruitment compensation potential for bull trout. The posterior predictive *CR* estimates obtained within this chapter have broad applications within the management of bull trout across the species range. Notably, these *CR* estimates can be used to establish conservation thresholds for bull trout populations where recreational fishing opportunities exist (e.g., in the development of spawning potential ratios) and in calculating recovery potential for populations of conservation concern (Walters and Martell 2004; Pine et al. 2013). There is still substantial uncertainty in *CR*; however, this work has begun the process of constraining the range of *CR* to one that is biologically realistic for bull trout and provides further evidence that the species is indeed capable of incredible recovery potential if adequate conditions exist.

Table 2.1 Description of bull trout stock-recruitment data sets used within analysis.

System	Province/ state	Major watershed	Life history	Data range (yrs.)	Data series length (yrs.)	Source*
Eunice Creek	AB	Mackenzie River Drainage Basin	Fluvial	1971,1973-1978, 1982, 1983	9	1
Attichika Creek	BC	Mackenzie River Drainage Basin	Adfluvial	2001-2007	7	2
South Pass	BC	Mackenzie River Drainage Basin	Adfluvial	2001-2007	7	2
Tributary 4 Mainstem	BC	Mackenzie River Drainage Basin	Adfluvial	2001-2007	7	2
Tributary 4 Fishway	BC	Mackenzie River Drainage Basin	Adfluvial	2002-2007, 2009-2014	12	2
Tributary 4 Icefalls	BC	Mackenzie River Drainage Basin	Adfluvial	2003, 2007, 2009, 2010, 2012-2015	8	2
Tributary 12	BC	Mackenzie River Drainage Basin	Adfluvial	2001-2007	7	2
Tributary 16	BC	Mackenzie River Drainage Basin	Adfluvial	2001-2007	7	2
Smith-Dorrien Creek	AB	South Saskatchewan River Basin	Adfluvial	1993-2000	8	1
Line Creek	BC	Columbia River Drainage	Fluvial	1991-1999	9	3
Kaslo River	BC	Columbia River Drainage	Adfluvial	2008-2013	6	3
Keen Creek	BC	Columbia River Drainage	Adfluvial	2008-2013	6	3
Lynx Creek	AB	Mackenzie River Drainage Basin	Fluvial	1995-2001	7	3
Metolius River Basin	OR	Columbia River Drainage	Adfluvial	1999-2013	15	2

* Sources: 1. Journal, 2. Research document, 3. Personal communication.

Table 2.2 Description of bull trout length-at-age data sets used within analysis.

System	Province/ state	Major watershed	Life history	Sample size (# of fish)	Data range (yrs.)	Source*
Eunice Creek	AB	Mackenzie River Drainage Basin	Fluvial	N/A	N/A	1
Attichika Creek	BC	Mackenzie River Drainage Basin	Adfluvial	34	1	2
Smith-Dorrien Creek	AB	South Saskatchewan River Basin	Adfluvial	9684	13	1
Line Creek	BC	Columbia River Drainage	Fluvial	63	4	3
Kaslo River	BC	Columbia River Drainage	Adfluvial	2591	16	3
Metolius River Basin	OR	Columbia River Drainage	Adfluvial	N/A	4	2

* Sources: 1. Journal, 2. Research document, 3. Personal communication.

Note: Source for all length-age information comes from personal communication with authors of stock recruitment reports and publications. Length-age-data was provided as length-age-keys.

Table 2.3 Notation of parameter and indices for bull trout stock-recruitment estimation models.

Index or parameter	Value	Description
Indices		
t	(1,2,…,T)	Time (in years)
a	(1,2,…,A)	Age (in years)
A	17	Maximum age (in years)
i	(i,…,I)	Population index
Parameters		
CR	+ +	Goodyear compensation ratio
α	+ +	Slope of the stock-recruit function at the origin
β	+ +	Scaling parameter of the stock-recruit function
R_0	+ +	Unfished recruitment potential
φ_E	+ +	Fecundity incidence function / mean eggs produced at age
lx_a	+ +	Survivorship-at-age
M	+ +	Instantaneous natural mortality rate (year^{-1})
f_a	+ +	Fecundity-at-age (eggs)
s	1.72e^{-3}	Scaler parameter of length-egg relationship
δ	2.31	Exponent parameter of length-egg relationship
L_a	+ +	Length-at-age
L_∞	+ +	Asymptotic length at which growth equals zero
k	+ +	von Bertalanffy metabolic coefficient
t_0	+ +	Hypothetical age when length is zero
m_a	+ +	Maturity-at-age
Υ	+ +	Slope of length-maturity schedule
L_{50}	+ +	Length at 50% maturity as a proportion of L_∞
cv	+ +	Coefficient of variation in length-at-age
τ_t	16.00	Precision of time varying process error for the Ricker and Beverton-Holt stock-recruitment functions
$\tau_{recruits}$	+ +	Precision of observation error for recruitment
Ω	++	Time varying process error

Note: The symbol ++ indicates parameters that are estimated.

Table 2.4 Calculations of age-specific incidence functions used in the bull trout stock-recruitment estimation models.

Parameter	Equation	Conditions
Length-at-age (L_a)	$L_a = L_\infty\left(1 - e^{\left(-K(a-t_0)\right)}\right)$	
Survivorship-at-age (lx_a)	$lx_a = \begin{cases} 1 & a = 1 \\ lx_{a-1}e^{-M} & 1 < a < A \\ \dfrac{lx_{A-1}}{1-e^{-M}} & a = A \end{cases}$	$a = 1$; $1 < a < A$; $a = A$
Maturity-at-age (m_a)	$m_a = \begin{cases} 0 & a \leq 3 \\ \dfrac{1}{1+e^{\left(\frac{-(L_a-(L_{50}*L_\infty))}{\alpha}\right)}} & a > 3 \end{cases}$	$a \leq 3$; $a > 3$
Fecundity-at-age (f_a)	$f_a = \begin{cases} 0 & a \leq 3 \\ sL_a^\delta & a > 3 \end{cases}$	$a \leq 3$; $a > 3$

Table 2.5 Derivation of recruitment parameters of the Ricker and Beverton-Holt stock-recruit functions used within the bull trout stock-recruitment estimation models.

Stock-recruitment function	Parameter	Equation
Ricker	β	$\beta = \frac{\log(\alpha\varphi_E)}{R_0 * \varphi_E}$
Beverton-Holt	β	$\beta = \frac{\alpha\varphi_E - 1}{R_0 * \varphi_E}$
Ricker and Beverton-Holt	α	$\alpha = \frac{CR}{\varphi_E}$
Ricker and Beverton-Holt	φ_E	$\varphi_E = \sum_{a=1}^{A} lx_a m_a f_a$

Table 2.6 Hyper-parameter and prior distributions of parameters used within the analysis of bull trout stock-recruitment and length-at-age.

Estimated parameter	Prior	Hyper-parameter
Compensation ratio (CR)	$L(\mu CR, \tau CR)$	μCR$\sim N(2.287, 0.893)$
		$sdreck \sim L(0.274, 210.786)$
		τCR $= sdreck^{-2}$
Asymptotic length at which growth equals zero ($L\infty$)	$N(\mu L_{\infty,i}, \tau L_{\infty,i})^{*\dagger}$	
von Bertalanffy growth coefficient (k)	$N(\mu k_i, \tau k_i)^{*\,\dagger}$	
Hypothetical age when length is zero (t_0)	$N(0, 0.25)^{*}$	
Unfished recruit density (D_0)	$L(2.87, 0.439)$	
Unfished recruitment potential (R_0)	$R_0[i] = D_0[i] * stL[i]$	
Slope of length-maturity schedule (Υ)	$L(log_e(40), 100)$	
Length at 50% maturity as a proportion of L_∞ (L_{50})	$B(1000{,}600)$	
Natural mortality (M)	$L(log_e(0.2), 100)$	
Precision of observation error for recruitment ($\tau_{recruits}$)	$\Gamma(0.001{,}0.001)$	
Time-varying process error (Ω)	$N(0, \tau_t)$	
Coefficient of variation in length-at-age (cv)	$B(1.5{,}1.5)$	

Note: Priors, hyper-parameters, and likelihood functions are given abbreviated distribution names where L=lognormal (mean, precision), N=Normal (mean, precision), B = Beta (shape parameters), and Γ= Gamma (shape and scale parameters). Mean and precision in text are abbreviated to μ and τ, respectively.

* Prior presented in table was used within hierarchical analysis of stock-recruitment.

† Prior was constrained to be greater than 0.01.

Table 2.7 Population-specific posterior median (95th percentiles) estimates of bull trout compensation ratio (*CR*) obtained from the baseline hierarchical models for the Ricker and Beverton-Holt stock-recruitment functions.

System	Ricker	Beverton-Holt
Eunice Creek	90.98 (14.05-357.82)	182.54 (28.52-1472.00)
Attichika Creek	112.03 (43.09-366.20)	388.55 (70.95-5585.95)
South Pass	165.26 (62.84-445.81)	507.47 (99.24-6970.61)
Tributary 4 Mainstem	1098.66 (421.52-2787.85)	1966.12 (613.79-11177.10)
Tributary 4 Fishway	129.15 (57.07-297.73)	400.13 (89.35-10334.80)
Tributary 4 Icefalls	101.14 (38.94-374.73)	506.22 (74.55-8602.46)
Tributary 12	80.99 (31.12-266.45)	294.83 (48.26-5503.27)
Tributary 16	189.92 (73.77-480.40)	478.98 (115.52-5250.12)
Smith-Dorrien Creek	111.79 (29.45-522.81)	518.85 (66.68-7957.60)
Line Creek	60.11 (15.61-198.91)	210.07 (27.68-7773.40)
Kaslo River	348.7 (71.57-1424.88)	852.16 (117.05-8137.27)
Keen Creek	488.83 (105.17-1948.47)	1069.74 (146.87-10191.67)
Lynx Creek	314.42 (43.18-1449.36)	949.82 (115.69-7405.72)
Metolius River Basin	25.91 (5.72-130.06)	357.94 (26.27-5149.55)

Table 2.8 Population-specific posterior median (95th percentiles) estimates of bull trout R_0 obtained from the baseline hierarchical models for the Ricker and Beverton-Holt stock-recruitment functions.

System	Ricker	Beverton-Holt
Eunice Creek	269.19 (15.7-5219.43)	209.13 (40.06-4065.47)
Attichika Creek	1024.7 (103.69-15166.82)	2615.08 (981.00-17947.29)
South Pass	919.29 (62.64-17173.69)	1530.25 (533.76-13314.03)
Tributary 4 Mainstem	1481.58 (96.41-29984.90)	6777.9 (1899.87-56076.50)
Tributary 4 Fishway	361.55 (19.06-5720.44)	321.6 (125.78-4521.42)
Tributary 4 Icefalls	107.31 (5.78-3905.50)	130.98 (54.16-880.52)
Tributary 12	560.63 (38.22-14405.86)	700.45 (243.09-8004.71)
Tributary 16	937.69 (48.34-15567.56)	1054.79 (337.96-10139.42)
Smith-Dorrien Creek	1203.63 (542.82-24679.94)	8104.24 (3486.26-22514.32)
Line Creek	1493.79 (158.14-19049.16)	1666.29 (618.31-23747.06)
Kaslo River	7684.2 (1030.49-119263.05)	62684.65 (23111.74-282875.57)
Keen Creek	1733.7 (259.88-30340.19)	20755.43 (7445.98-91079.27)
Lynx Creek	1039.69 (117.02-15546.98)	6025.15 (2217.04-26684.33)
Metolius River Basin	841.84 (381.61-7775.83)	1824.28 (1013.68-3460.57)

Table 2.9 Posterior median (95th percentiles) estimates of bull trout compensation ratio (*CR*) obtained from the baseline hierarchical models for the Ricker and Beverton-Holt stock-recruitment functions.

Estimated parameter	**Ricker**	**Beverton-Holt**
μCR	4.75 (3.96-5.02)	5.94 (4.88-7.17)
τCR	0.59 (0.46-0.76)	0.57 (0.43-0.75)
CR posterior predictive	121.45 (7.86-1717.90)	384.03 (22.95-6636.23)

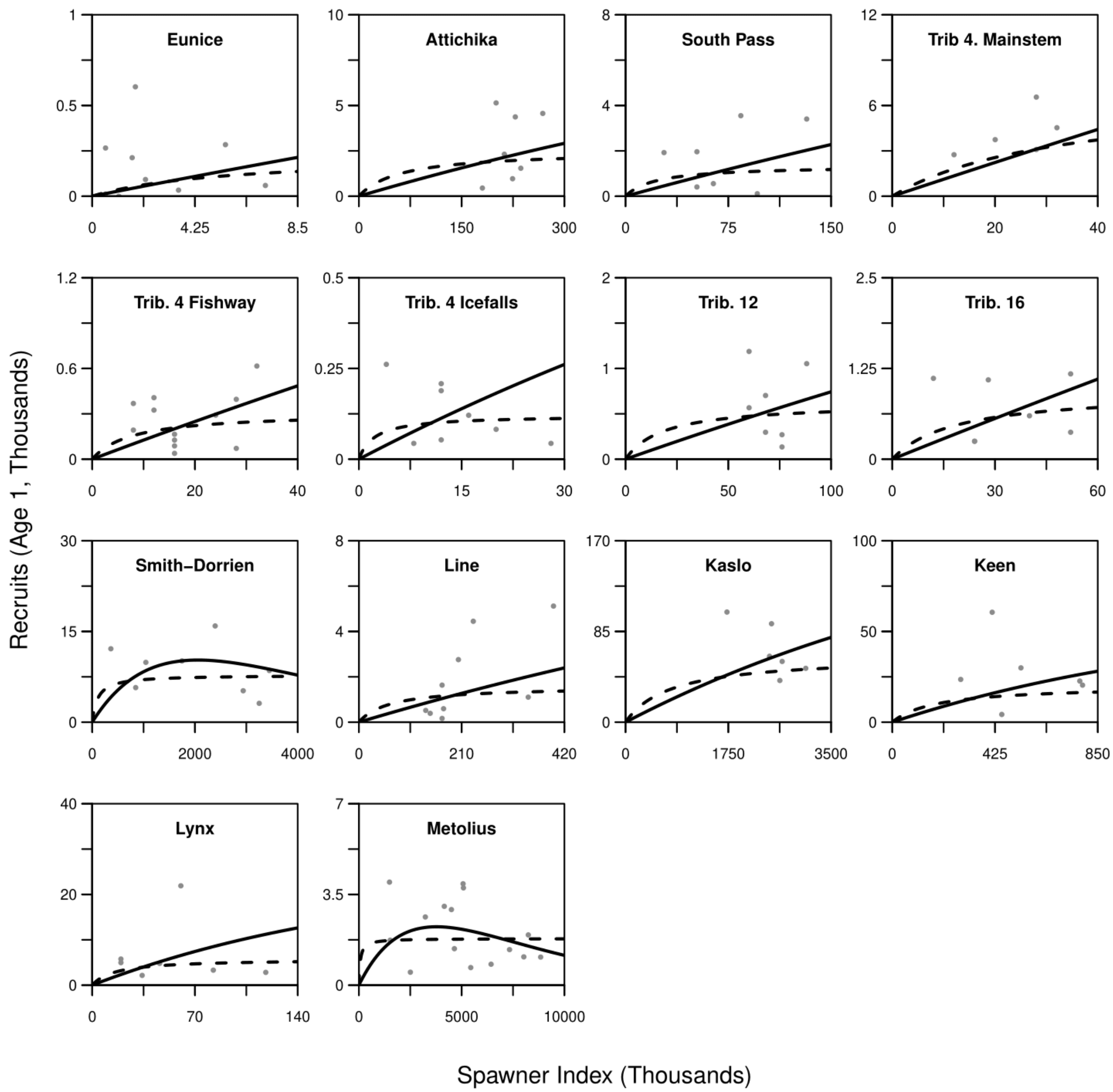

Figure 2.1 Fits to stock-recruitment data obtained for 14 bull trout populations under the assumption of Ricker (continuous lines) and Beverton-Holt (broken lines) stock-recruitment functions.

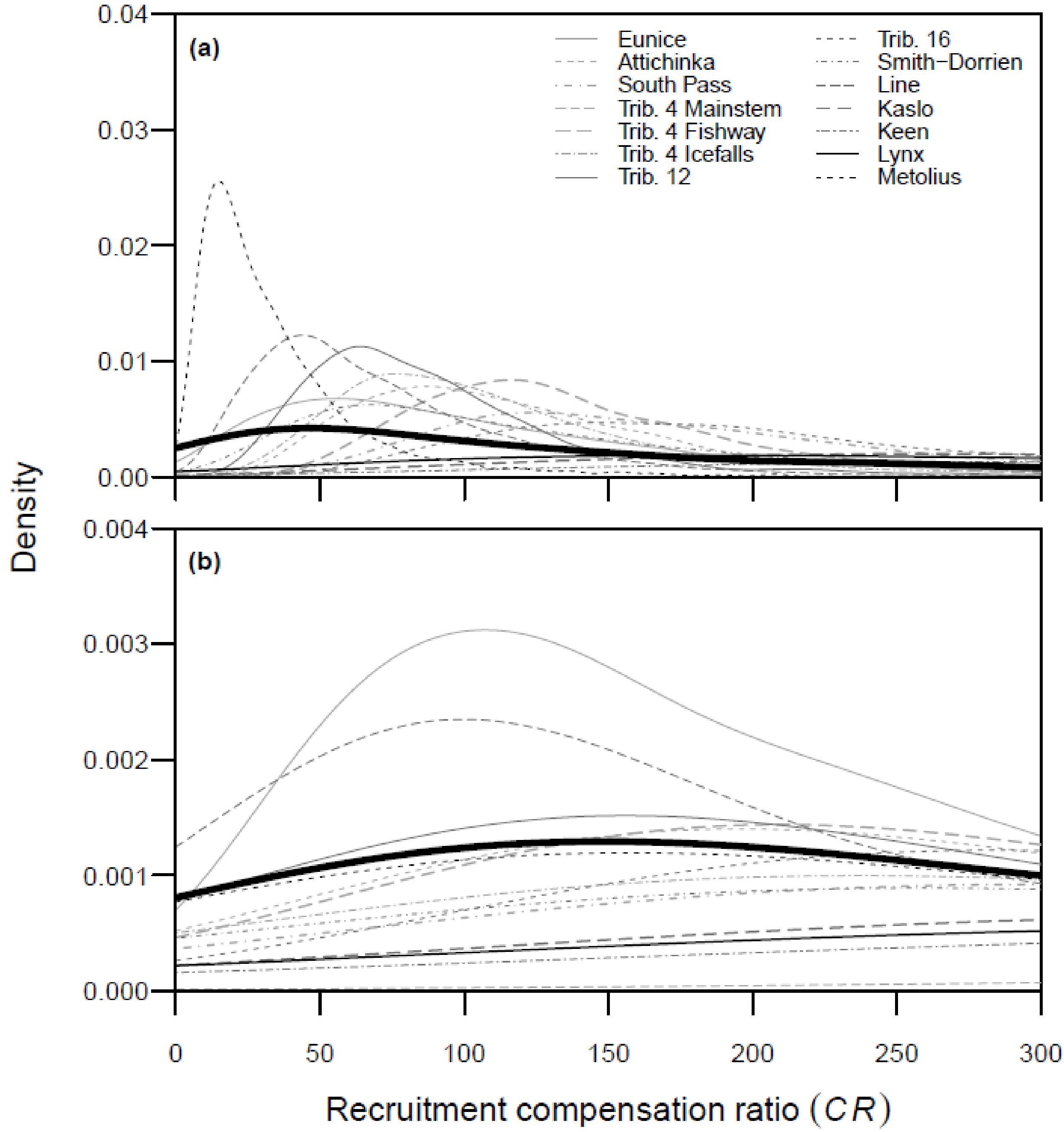

Figure 2.2 Marginal posterior probability distributions of compensation ratio (*CR*) obtained for the 14 bull trout populations under (*a*) Ricker and (*b*) Beverton-Holt hierarchical stock-recruitment models. The posterior predictive distribution for *CR* (thick black line) is also shown.

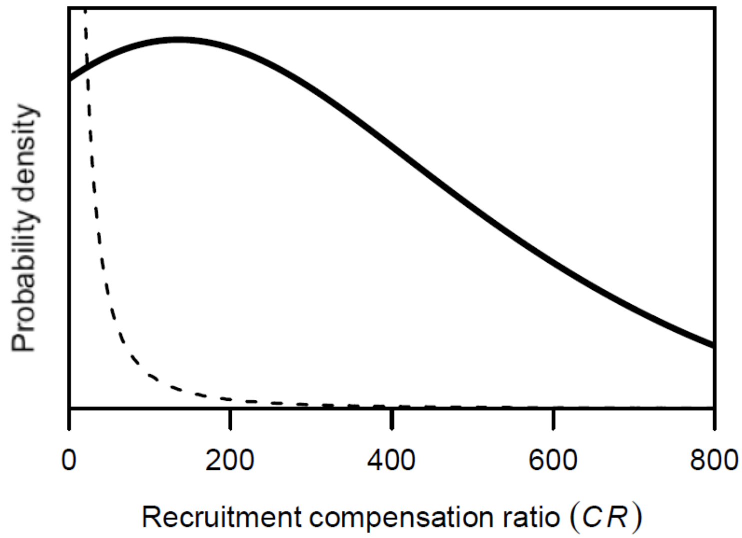

Figure 2.3 Hyper-parameter choice for bull trout compensation ratio (*CR*) (dashed line) with posterior predictive estimate (solid line) superimposed to show potential influence of prior choice on posterior estimate. The two probability density functions are scaled to enable comparison.

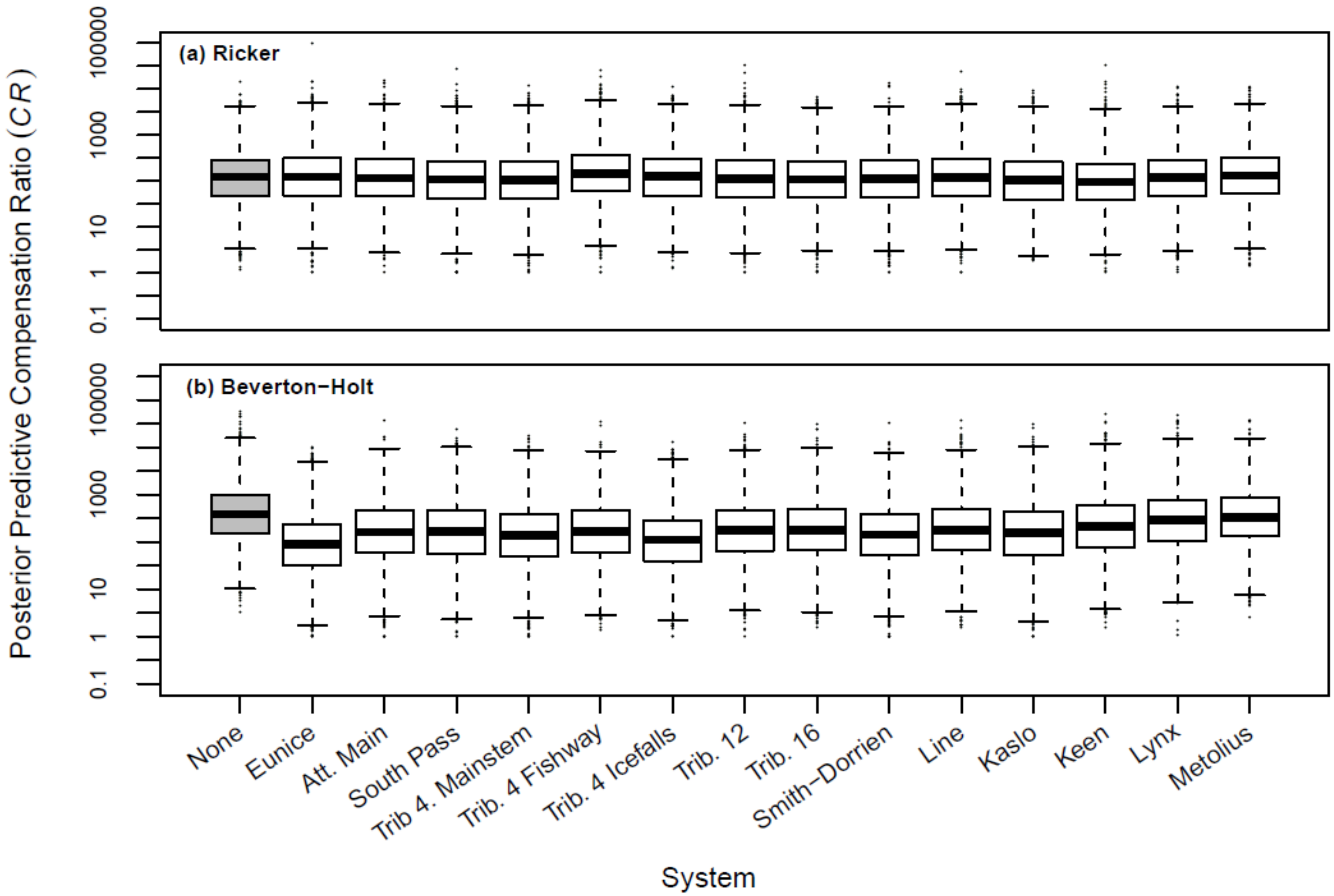

Figure 2.4 Median and quantiles of posterior predictive probability distributions of compensation ratio (*CR*) obtained for the 14 bull trout populations under (*a*) Ricker and (*b*) Beverton-Holt hierarchical stock-recruitment models excluding one population from the analysis at a time. Median estimates are shown as a black bar inside the box showing the interquartile range. Outliers are shown as circles.

Chapter 3: Spatial distribution and seasonal movement probability estimates of bull trout (*Salvelinus confluentus*) through a large, uninterrupted river network

3.1 Introduction

The diverse life history traits expressed by bull trout (*Salvelinus confluentus*), including their ability to migrate long distances to access critical habitats, has enabled their persistence through North America's last glaciation and is fundamental to the stability and long-term persistence of the species (Power 2002). Today, these attributes and their associated behaviours place bull trout at increased risk (Rieman and McIntyre 1993; Post and Johnston 2002; Hagen and Decker 2011). The species has designated conservation status across its historical range within the United States ('Threatened') under the United States *Endangered Species Act* (USFWS 2015). In Canada, bull trout are assessed within five conservation units, whose status under Canada's *Species at Risk Act* (SARA) range from 'Not at Risk' to 'Threatened' (COSEWIC 2012; Government of Canada 2021). In both nations, bull trout populations in many regions are of increased conservation concern due to observed population declines and increased prevalence of local extirpations (COSEWIC 2012; USFWS 2015).

Understanding vital rates, distribution, and movement patterns associated with each bull trout life history strategy (i.e., adfluvial, fluvial, anadromy, and resident) is critical for both conservation and management of this species (Rieman and McIntyre 1993; Rudd et al. 2014). Regardless of watershed, knowing where and when individuals use different habitats is invaluable for prioritizing conservation efforts and ensuring recovery initiatives and harvest management have desired outcomes. Like many highly migratory species, bull trout undertaking large-scale seasonal movements between multiple distinct habitat types encounter a diverse landscape of land use and associated threats (i.e., population and mortality risks) (Rudd et al. 2014). Though meta-population structure present in many systems can function to spread risk and support bull trout's persistence, understanding where and when stock mixing occurs is critical to management and conservation efforts aimed to protect less productive stocks and/or genetic diversity (Paulik et al. 1967; Secor 2014; Taylor et al. 2014).

Much of our understanding of bull trout migratory behaviour has come from research in artificially fragmented systems, where damming or the presence of other obstructions to movement have impacted habitat connectivity (DuPont et al. 2007; Starcevich et al. 2012; Howell et al. 2016). We have less understanding about bull trout behaviour and dynamics where the full life history expression of the species is possible (i.e., in connected systems and where populations have suffered fewer anthropogenic impacts). Clarifying our understanding of where and when bull trout move, and how populations and population complexes distribute in space and time is important for the riverscape-level management of this species. Without this knowledge, it is not possible to ensure population structure is maintained and that the full mosaic of important habitats are incorporated within management and recovery initiatives (Taylor et al. 2014).

Studies aimed to clarify a species spatial distribution or movement dynamics often rely on telemetry, a ubiquitous field technique for investigations in both terrestrial and aquatic systems

(Cagnacci et al. 2010; Hussey et al. 2015; Sippel et al. 2015). Though such analyses are increasingly prevalent for estimation of seasonal movement patterns (e.g., dispersal) and vital population rates (e.g., mortality) in marine systems, lakes, and even linear stretches of river corridors, work in non-linear systems, such as fluvial watershed networks, are relatively rare. Within bull trout literature, telemetry work is often limited to a relatively small sample size (fewer than 70 individuals) and short duration (three years or less) (DuPont et al. 2007; Schoby and Keeley 2011; Howell et al. 2016). Bull trout's late maturity, relatively long life span, and the complex nature of their migratory behaviour in non-resident populations (e.g., presence of skip spawning), make it difficult for these investigations to capture the full extent of behaviours that are important to the long-term management of this species (Rieman and McIntyre 1993).

Within this investigation, radio telemetry detection data is used within a seasonal, multi-state, capture-recapture model to elucidate unknowns regarding seasonal migration patterns, distribution, and survival rates of bull trout in the upper Fraser River watershed of British Columbia. This case study provides a unique opportunity to use such a modeling approach for a migratory, riverine species, and provides estimates of ecological rates to inform spatial-temporal management strategies for bull trout, a species of listed conservation concern.

3.2 Methods

3.2.1 Species background and study area

The study region comprises approximately 98,000 km^2 of the upper Fraser River watershed (UFW) of British Columbia (Figure 3.1). It contains an extensive network of freshwater habitats encompassing Stuart, Fraser, and Francois lakes, the Nechako and Stuart rivers, portions of the upper Fraser River, and multiple low-order, cold water tributaries of the Fraser River. Bull trout habitats across the region are highly interconnected with one another. A major exception, however, is the upstream barrier formed by the Kenny Dam on the Nechako River approximately 160 km upstream of the confluence between the Fraser and Nechako rivers.

Bull trout spawning activity within the region is believed to be confined to tributaries of the upper Fraser River, although anecdotal evidence suggests spawning may also occur within the upper Taka River watershed (Pillipow and Williamson 2004; Pillipow 2012, personal communication). Analyses of UFW bull trout population structure using microsatellite DNA and otolith microchemistry have reported significant genetic differentiation between a number of samples collected from individuals within different spawning tributaries (Taylor and Clarke 2007; Taylor et al. 2021). Past work suggests bull trout spawning migrations in the region occur over an approximately four-week period (late July to late August) with arrival on spawning grounds by the first week of September (Pillipow and Williamson 2004). Spawning then occurs over an approximately three-week period concluding in late September, followed by rapid post-spawning dispersal from tributaries into the Fraser River (Pillipow and Williamson 2004).

Post-spawning dispersal fate of bull trout within the Nechako, Fraser, and Stuart rivers is not well understood. Portions of the mainstem Nechako and Fraser rivers are thought to be important wintering and foraging habitats for some fluvial bull trout populations in the region (i.e., those spawning within the Goat, McKale, and Holmes rivers and Walker Creek) (Pillipow and Williamson 2004; Pillipow 2012, personal communication; Taylor et al. 2021). Regions within the Nechako and Stuart rivers may provide important foraging opportunities for bull trout during outmigration of Chinook (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*) smolts in spring (Pillipow 2021, personal communication). Foraging-related aggregating behaviour has been documented in bull trout elsewhere, including within the Chilcotin watershed of British Columbia (Furey et al. 2016, 2021; Furey and Hinch 2017) and Skagit River in northwestern Washington state (Lowery and Beauchamp 2015).

3.2.2 Data collection

Between 2011 and 2016, 169 mature adult bull trout were radio tagged within both spawning and foraging/wintering habitats of the upper Fraser River watershed (Figure 3.2). Individuals selected were greater than 400 mm fork length and where possible, sexual maturity was confirmed by classifying gonadal maturity at the time of radio tag implantation. All captured fish were sampled for genetic material in the form of an adipose fin punch. Genetic assignments for each tagged fish were obtained from Taylor et al. (2021), who used microsatellite DNA variation across 10 loci to assign individual fish to their most likely population (tributary) of origin. These assignments were used within the multi-stock model to allocate fish of unknown origin to known bull trout populations within the UFW (Figure 3.3).

Sampling within spawning habitat occurred by angling in six tributaries of the upper Fraser River upstream of Prince George during the period of suspected bull trout spawning staging (i.e., July to September). Sampling of wintering and foraging sites occurred via boat electrofishing and angling within the Nechako and Stuart rivers. Fish were captured in habitats capable of supporting wintering and migratory bull trout in early spring following ice-off (i.e., April to June). Sampling in all locations occurred through random site selection, as well as in known aggregation and foraging areas, as determined by prior telemetry observations within the region. Areas holding bull trout were sampled on multiple angling visits and/or several electrofishing passes depending on the technique used.

Individual capture histories for each tagged fish were developed using both fixed and mobile telemetry detections between 2011 and 2016. Fixed telemetry observations occurred through a spatial array of five fixed continuous telemetry monitoring stations (see Figure 3.1). These included three permanent stations (located at Prince George, Vanderhoof, and the upper Stuart River near Stuart Lake) and two seasonal stations (at the confluence of the Stuart and Nechako rivers and confluence of the Nechako and Nautley rivers). Seasonal stations were operated between the months of May to October each year.

The spatial resolution of movement data was extended through use of opportunistic mobile telemetry effort conducted by truck and aircraft using a Lotek model SRX600 receiver (Lotek Wireless Inc.). Within areas 1 to 6, search effort occurred between the months of February and June and again from August to November. Within tributary habitats, mobile effort occurred primarily during capture and tag deployment activities (i.e., within the months of July to September), with additional effort when access was available during fall redd counts. For the duration of the study, for each detection, each individual's unique identification, the time and date of detection, and direction of travel were recorded. Power failures and equipment malfunctions resulted in some periods of data collection gaps at all fixed receiver locations.

3.2.3 State-space Cormack Jolly Seber model

Seasonal, transition (movement) probabilities and survival rates for UFW bull trout were estimated using ‘virtual recaptures’ sourced from radio telemetry (Hightower et al. 2001). Field data were analyzed using a multi-state Cormack Jolly Seber (CJS) model in a Bayesian state-space modeling framework (Table 3.1; Lebrenton et al. 2009; Kéry and Schaub 2012). The study area was split into seven discrete spatial areas based on the location of fixed telemetry receivers (see Figure 3.1). Time was split into two unequal time-blocks to account for seasonal variations in movement. Time-block one spanned from April 15 through October 31 (‘migrating' time-block) and time-block two from November 1 to April 14 (‘wintering/foraging' time-block) of each year. The cut-off for each time-block was determined based on preliminary estimates of bull trout spawning run timing in the region and to account for annual Chinook and sockeye salmon smolt outmigration from Stuart, Francois, and Fraser lakes (Taylor and Bradford 1993; Pillipow and Williamson 2004; Spendlow 2020, personal communication). There were 11 capture occasions within the state-space model and eight possible process model states (1-7 ‘individual alive and in one of the seven spatial areas’ or 8, ‘dead’). There were also eight possible observation model states, where an individual could be ‘detected in one spatial area’ (1-7) or be ‘not detected’ (8).

Modeling was conducted under two alternative assumptions of bull trout stock structure in the UFW: (1) A parametrically concise model where movement probabilities of all tagged individuals was assumed independent of stock (termed the single-stock model); (2) a more complex, multi-stock model that used genetic assignment information obtained from Taylor et al. (2021) to allocate individuals to one of five possible stocks (i.e., Goat River, Milk River, Chalco

Creek, Walker Creek, or a single outgroup), each with its own movement matrix. Choice of tributaries for inclusion within the multi-stock model was based on sample size (i.e., populations where greater than 20 individuals were tagged). Individuals were assigned to one of the five populations based on their probability of genetic assignment to the population based on Taylor et al. (2021). The multi-stock model was repeated three times under 75%, 85%, and 95% assignment confidence to explore the impact of the inclusion cut-off on model results.

3.2.3.1 Model structure

The multi-state capture-recapture model was composed of two components. State equations of the state-space formulation described the true development of state membership through time. While observation equations mapped observed states, recorded through telemetry as individual capture histories, to true states. A four-dimensional state transition matrix (Ω) (dimensions of stock, season, state of departure, and state of arrival) described the true state and was used for both the single stock (i.e., stock fixed at one) and multi-stock (i.e., five stock) models. Each element $\omega_{i,t,a,k}$ of Ω, the probability of an individual's true state (S) at time-t given its state in the previous time-step, was defined by two parameters: the probability of survival ($\emptyset$) and the transition probability between states (ψ).

The probability of transitioning between a living and dead state was $1 - \emptyset$, and it was assumed that once dead, individuals could no longer be encountered (i.e., they remained in the dead state with probability of one and probability of transitioning between dead and alive states was zero). The probability of moving between alive states (i.e., spatial areas) was given by (Equation 3.1):

$$\Omega_{st,se,a,k} = \emptyset * \psi_{st,se,a,k} \qquad \text{Eq. 3.1}$$

Where *a* represents the state at time *t* and *k* represents the state at *t*+1. The probability of survival ($\emptyset$) was an estimated parameter and assumed to be equal across stocks, areas, and sampling occasions. Area dependent transition probabilities (ψ) were calculated using a gravity model whereby the transition probability of an individual moving from area *a* to area *k* ($\psi_{st,se,a,k}$) was calculated by a logit function to constrain all rows of the state transition matrix to sum of 1 (Equation 3.2):

$$\boldsymbol{\psi_{st,se,a,k}} = \frac{\boldsymbol{e^{G_{st,se,a,k}}}}{\boldsymbol{\sum_k e^{G_{st,se,a,k}}}} \qquad \text{Eq. 3.2}$$

The first term in each row of the transition matrix was fixed at zero ($G_{st,se,a,1} = 0$) and not estimated. *G* terms in all subsequent sampling occasions were estimated jointly as (Equation 3.3):

$$G_{st,se,a,k} = \begin{Bmatrix} g_k & a \neq k \\ g_k = v & a = k \end{Bmatrix} \qquad \text{Eq. 3.3}$$

such that state transitions (i.e., from state *a* to state *k*) were proportional to the gravity weight of each area *k*, and the probability of remaining in the same area was proportional to that gravity, with slope *v*.

A four-dimensional observation matrix (Θ), with dimensions true state, observed state, stock, and season, defined the probabilities of observing an individual in each of the possible states. The probability of observing an individual in one of the seven location states was given through the site-specific recapture probability (ρ_{i,t,a_O,k_O}). While the probability of an individual not being observed was given as $1 - \rho_{i,t,a_O,k_O}$. It was assumed that individuals that were observed in the dead state remained so with a probability of one.

3.2.3.2 State-space estimation

The state-space model was conditional on first capture. Initial capture probabilities representing the tagging event for each individual were not estimated. Instead, the vector of first capture f_{s_i} for each individual was taken as the individual's observed state at first capture (i.e., tagging event) such that (Equation 3.4):

$$z_{i,f_i} = f_{s_i} \qquad \text{Eq. 3.4}$$

Where matrix z with elements $z_{i,t}$ denoted the true state of each individual i at time t. Development of state membership of each individual for each subsequent occasion was estimated as (Equation 3.5):

$$z_{i,t+1}|z_{i,t} \sim categorical(\Omega_{zi,t,1\ldots S,i,t}) \qquad \text{Eq. 3.5}$$

With the likelihood estimation linking observed and true states given by (Equation 3.6):

$$y_{i,t}|z_{i,t} \sim categorical(\theta_{zi,t,1\ldots O,i,t}) \qquad \text{Eq. 3.6}$$

The model assumed no additional mortality occurred during transition events and ordered events such that survival occurred prior to movement. Implanted radio telemetry tags were assumed not to be lost during the study, and states were assumed to be recorded by both fixed and mobile telemetry receivers without assignment error. The model assumed independence between all states and all individuals, and the probability of survival was assumed to be uniform across states and individuals. Finally, transition and observation probabilities were assumed to be the same across all individuals within the single stock model, or in the case of the multi-stock model, within stocks.

Posterior density functions for parameters of interest were approximated using the Markov chain Monte Carlo (MCMC) algorithm implemented using JAGS (Just Another Gibbs Sampler; available from http://mcmc-jags.sourceforge.net/) (Plummer 2016) implemented through R (R Core Team 2016) using the R2Jags package (Yu-Sung and Yajima 2015). Three chains were run for 40,000 iterations after a burn-in of 20,000 iterations. Final posterior estimates were thinned by 20. Convergence was evaluated using the Gelman-Rubin diagnostic tool (Brooks and Gelman 1998) and visual inspection of Markov chain trace plots for each parameter.

3.2.4 Sensitivity analysis and model selection

A sensitivity analysis was used to determine the impact of alternative genetic assignment cut-offs of 75%, 85%, and 95% assignment probability on predicted transition matrices. Goodness of fit for model selection between the single and multi-stock model was calculated using the deviance information criterion (DIC) (Spiegelhalter et al. 2002) with the ‘best’ performing model providing the most statistically robust characterization of bull trout in the UFW. This ‘best’ model (i.e., the single stock model) was then used in all further simulations.

3.3 Results

During the six-year study period, 169 unique individuals were tagged within six tributaries of the Fraser River and mainstem Nechako and Stuart rivers. Of these individuals, 78% were tagged within the months of July and August in low-order tributaries (i.e., known spawning habitats) of the Fraser River. The remaining 22% were tagged within the months of April, May, and October within large riverine habitats. Fork length of tagged individuals ranged from 395 to 865 mm with an average length of 596 mm (± 94 mm). Individual weights ranged between 430 and 5500 g with an average weight of 2217 g (± 1041 g). Sex ratio of tagged fish was 70 males to 58 females with sex of the remaining individuals (n= 41) unable to be determined by non-lethal sampling during tagging effort. All tagged individuals for which maturity was determined (n=127) were classified as reproductively mature. Telemetry tracking through a combination of fixed stations and mobile effort resulted in a total of 943 detections over the six-year period. During this time, a total of 148 individuals were detected at least twice while the remaining 21 individuals were never detected again. Further, 94 individuals were detected over a multi-year period (i.e., greater than one-year duration).

The parametrically concise single-stock model was the DIC-preferred model with DIC of 1631 relative to 1676 for the stock-specific (i.e., multi-stock) model. These results suggest the single-stock model is supported by the data, implying no broad differences in movement probabilities between the four stocks or outgroup at the spatial scale investigated. Tagged fish exhibited a fluvial life history strategy (Rieman and McIntyre 1993). Apparent survival rate across populations and seasons was estimated with median $\emptyset = 0.832$ with a 95% credible interval of 0.793 – 0.868. Movement observations and estimated state-transition probabilities between the seven spatial areas demonstrate that bull trout from multiple spawning populations use the upper Fraser River as a migration corridor between spawning habitats within low-order, cold-water tributaries of the Fraser River north of Prince George, and large riverine wintering habitats within both the mainstem Nechako and Stuart rivers. Fish were generally not detected within or predicted to use the lakes monitored (i.e., only 17 individuals were detected within the lakes or lake outlets, for a total of 23 detections).

Bull trout movements within the UFW were strongly seasonally dependent (Figure 3.4; Figure 3.5, Figure 3.6). A large proportion of tagged individuals (74 of 94 individuals (78.7%)) tracked over a multi-year period made directional movements between wintering and foraging habitats within areas 3 to 6 (i.e., mainstem Nechako and Stuart rivers) and spawning habitats within area 7 (i.e., upper Fraser River mainstem and tributaries) during the annual spawning and post-spawning dispersal periods represented by time-block one. In many cases, individuals were also detected in known spawning habitats within low-order tributaries by opportunistic mobile telemetry efforts within the months of August and September. These observations were reflected in model outputs. In time-block one, representing April 15 through October, the multi-state model predicted higher state-transition probabilities area to area in an eastward direction toward area 7 than any other directional movement pattern.

The majority of individuals demonstrated similar post-spawning migration patterns. Across stocks, 80% of individuals detected over a multi-year period initially made post-spawning movements downstream from tributaries into the mainstem Fraser River, then proceeded downstream to the confluence of the Fraser and Nechako rivers. Individuals then migrated upstream within the Nechako and Stuart rivers for distances greater than 190km. For individuals that subsequently returned to known spawning habitats, this post-spawning dispersal pattern of downstream, followed by upstream movements were generally repeated.

Individuals were detected migrating significant distances between known spawning, wintering, and foraging habitats. The furthest migration distance observed was greater than 600 km for an individual tagged within spawning habitat in Chalco Creek and later resighted in area 1; however, travel distances greater than 500km were common among detected fish. Bull trout detected migrating between spawning and wintering habitats over multiple years generally returned to stretches of riverine habitat where they had been previously detected. For example, individuals which migrated upstream into the Stuart River (i.e., area 5) were often detected within the area repeatedly, and individuals detected within the mainstem Nechako River west of its confluence with the Stuart River (i.e., in areas 3 and 4) were generally not detected within the Stuart River (i.e., in area 5). Only five individuals were detected to winter in both the Stuart River and mainstem Nechako River.

Telemetry detections identified 51 individuals as potential repeat spawners. These individuals were identified as spawners due to detections within spawning tributaries on at least one occasion during the spawning period (i.e., September and October), detected movement from wintering habitats (i.e., areas 1 to 6) into spawning habitats (i.e., tributaries within area 7) prior to the spawning period (i.e., June through August), or detected movement from spawning habitats (i.e., tributaries within area 7) into wintering or foraging habitats (area 1 to 6) immediately following spawning (i.e., in September through November). Seventeen of these individuals were detected making repeat movements to the same tributary where they were initially tagged and genetically assigned. A further 13 individuals were detected within a tributary that was not the tributary where they were tagged or assigned. Of individuals tracked over multiple years, an additional 21 individuals were detected making repeated movements past the telemetry receiver in Prince George east into area 7 but were not subsequently encountered within tributary habitat.

Within time-block two, representing November to April 14, individual detections showed bull trout dispersed broadly across the upper Fraser River watershed with detection events occurring in each of the seven areas. Within this time-block, there was increased probability of movement between multiple areas, differing the directional transition patterns observed within time-block one. Individuals that did not appear to move between spawning and wintering habitats within a specific year were considered to be exhibiting ‘station-keeping’ behaviour. These observations were reflected in model-predicted increased probabilities of remaining within a single area (i.e., areas 3 to 7) in both time-blocks.

3.4 Discussion

Understanding the complexity and diversity of bull trout migratory behaviour is critical for prioritizing conservation actions, identifying restoration opportunities, and defining where anthropogenic impacts will have the largest negative effects (Hilborn and Walters 1992; Cadrin and Secor, 2009; Rudd et al. 2014). This investigation demonstrates bull trout populations within the upper Fraser River watershed are dependent on a variety of distinct habitat types, which are spatially segregated over large distances. It also serves to highlight that UFW fluvial bull trout regularly exhibit seasonal, long-distance, migratory behaviours to access favorable spawning, wintering, and foraging habitats. These complex patterns of habitat use are shared across multiple spawning populations, demonstrating the importance of habitat complexity across large contiguous riverscapes in promoting population structure and likely promoting the species persistence in this region.

Bull trout movement patterns within the upper Fraser River watershed occur with high seasonality. Peak movement periods were observed and predicted within time-block one (spring and fall) preceding and subsequent to spawning, similar to observations in other studies (Bahr and Shrimpton 2004; Muhlfeld and Marotz 2005). Individuals regularly travelled significant distances (>500km one way) and used the upper Fraser River as a migration corridor between distinct habitats for spawning, wintering, and foraging. Similar long-distance migrations and spatial segregation between habitats used for specific behaviours (e.g., spawning, wintering, foraging) have been observed in previous, smaller, bull trout studies (i.e., with shorter duration or smaller sample sizes), many of which were focused in artificially fragmented systems (e.g., Swanberg (1997), Bahr and Shrimpton (2004), Schoby and Keeley (2011), and Starcevich et al.

(2012). These observed migratory traits are potentially critical in determining the scale of, and variation in, home range size amongst stream dwelling salmonids, including migratory bull trout life histories (Schoby and Keeley 2011). Within this chapter, past research was extended by tracking migrations, estimating seasonally specific movement probabilities between key habitats, and exploring stock-specific variation in migratory behaviours and habitat use for a relatively large sample size (n=169) of fluvial bull trout composed of several spawning populations, over an extended time (approximately six years), in a system which is highly connected and relatively pristine.

Migratory behaviours (e.g., long-distance migrations, use of migratory corridors, spatial segregation of critical habitats) can put populations at high risk of negative impacts from habitat fragmentation and degradation (Starcevich et al. 2012; USFWS 2015; McIntyre et al. 2016). In bull trout systems across the species' range, populations are regularly impacted by agriculture, mining, forestry, hydroelectric power, and human development, and population declines have been strongly linked to anthropogenic impacts resulting from these human activities (Mace and Doonan 1988; Fraley and Shepard 1989; Hagen and Decker 2011). Taken together, the current investigation and past work, particularly that of Muhlfeld and Marotz (2005) in the Flathead Basin, Starcevich et al. (2012) in the mid Columbia and Snake River basins, and Taylor et al. (2021) within the upper Fraser River watershed, highlight the importance of protecting, restoring, and maintaining a diverse assemblage of complex habitats and the natural connections between them. Critically, such actions must occur over a large enough spatial scale to permit the full expression of bull trout migratory life histories (Muhlfeld and Marotz 2005). These findings are relevant across habitat types where multiple populations, dependent on different spawning tributaries, are all reliant on the same resources for aspects of their life history. As such, negative impacts on these habitats through naturally occurring processes (e.g., landslide events, drought, forest fires) and anthropogenic impacts can affect multiple populations.

Within this investigation, individuals were not generally observed moving between spawning and wintering/foraging habitats on an annual basis. This ‘station keeping’ behaviour within a specific spatial area is likely reflective of individuals that skip spawning for a year, a behaviour that has been well observed in bull trout populations across the species range (Bahr and Shrimpton 2004; Hogen and Scarnecchia 2006; Johnston and Post 2009). In years where individuals did leave wintering and foraging habitats to spawn, they generally returned to the area within wintering and foraging habitat where they had been detected prior to spawning. Although the spatial extent of habitat in each area makes it impossible to investigate finer level fidelity to wintering and foraging habitats within each area, others have observed high site fidelity of bull trout to wintering locations (Swanberg 1997; Bahr and Shrimpton 2004; Starcevich et al. 2012). Significant levels of genetic differentiation among the populations studied here (see Taylor et al. 2021) also implies some spawning site fidelity.

The finding that bull trout representing multiple spawning populations remain within wintering habitat year-round, as well as evidence of fidelity of individuals to specific spawning sites (see Taylor et al. 2021), have implications for both fisheries management and conservation initiatives aimed at identifying and protecting critical habitats. Resolving uncertainties surrounding the specifics of how and where fish move through time is also critical for development of fisheries management that adequately accounts for population and community level processes, particularly regarding timing and locations of population aggregations where each individual's susceptibility to exploitation or anthropogenic impacts may increase (Hilborn and Walters 1992; Rieman and McIntyre 1993; Lucas and Baras 2000). Currently, recreational fishing opportunities for bull trout in the UFW are limited; however, long-term station-keeping behaviour has implications for the effectiveness of spatial-temporal fishing closures both on fishing opportunities for this species as well as for management actions aimed to reduce incidental bull trout capture in other fisheries. Investigations to explore finer scale detail of site fidelity and the spatial scale of bull trout wintering distributions should be considered in the development of management and conservation advice within the UFW (Starcevich et al. 2012). Such work will be critical in ensuring that fishery regulations can limit fishing effort on population aggregations where an individual's susceptibility to exploitation may increase (Rieman and McIntyre 1993; Bahr and Shrimpton 2004; Taylor et al. 2014).

Bull trout in this study demonstrated post-spawning dispersal patterns contrasting those generally observed in iteroparous salmonids, including bull trout in other systems (Quinn 2005; Hogen and Scarnecchia 2006; Schoby and Keeley 2011). Within these species, upstream spawning migrations are generally followed by downstream post-spawning dispersal to access wintering and foraging opportunities, which permit higher growth potential (Quinn 2005; DuPont et al. 2007; Starcevich et al. 2012). Bull trout tracked over a multi-year period within this investigation (~80%), initially dispersed from spawning habitat downstream within the Fraser River, then migrated upstream dispersing broadly within areas 3 to 6. Upstream dispersal toward wintering and foraging habitats has been observed in bull trout elsewhere for populations exhibiting an allacustrine (i.e., outlet spawning, lake rearing) life history (DuPont et al. 2007;

Watry and Scarnecchia 2008; Starcevich et al. 2012). Investigations that have identified this pattern have generally been smaller in sample size (i.e., less than 70 individuals) and observed upstream movements under approximately 50km (e.g., Herman (1997), DuPont et al. (2007) (n=7), Hogen and Scarnecchia (2006) (n=65), Watry and Scarnecchia (2008) (n=71), and Starcevich et al. (2012) (n=25). In contrast, fluvial fish within this study moved longer distances upstream. The ultimate causes of such movements have not been broadly identified in past work; however, they likely relate to either decreased survival for individuals moving further downstream, or increased survival and/or improved foraging opportunities for individuals making upstream migrations (Starcevich et al. 2012). Unfortunately, limitations in the spatial extent of the fixed telemetry receiver network does not permit exploration of the prevalence of bull trout movement south of the Fraser River's confluence with the Nechako River nor consideration of potential variation in survival rates of fish moving within these two regions.

Bull trout migrating upstream into the Nechako and Stuart rivers may encounter improved foraging opportunities not available within the mainstem Fraser River upstream of its confluence with the Nechako River. In portions of their range, bull trout have been identified as important predators on other salmonids, notably sockeye and Chinook salmon (Furey et al. 2015; Lowery and Beauchamp 2015; Furey and Hinch 2017). Upstream bull trout movements into wintering and foraging habitats within the mainstem Nechako and Stuart rivers may permit individuals to exploit seasonal resource pulses in the form of the sockeye or Chinook salmon smolts outmigrating from Stuart, Fraser, and/or Francois lakes. Such opportunities would provide seasonally specific increases in food availability, while presence of deep river sections may offer thermal protection (i.e., cool-water refuges, protection from frazil and anchor ice) in addition to protection from both terrestrial and avian predators (Bahr and Shrimpton 2004; Schoby and Keeley 2011; Furey and Hinch 2017).

Direct observations during tag deployment within the Nechako River mainstem identified the presence of schooling salmon smolts in areas where bull trout were captured (Spendlow 2020, personal communication; Pillipow 2021, personal communication). Opportunistic diet sampling during tagging further supports the idea that bull trout may be using upstream river habitat to prey on Pacific salmon smolts. Of five mortalities where stomach contents were sampled, four out of five bull trout sampled were found with 'stomachs full of smolts' (stomach content smolt counts of 44, 20, two individuals where smolts not enumerated, one empty stomach) (Spendlow 2020, personal communication). Although limited in sample size, these observations are similar to those by Furey et al. (2015, 2016) for bull trout feeding on sockeye smolts within the Chilko River at high rates (i.e., stomachs often containing >20 smolts). Further, Furey and Hinch (2017) found bull trout within the Chilko River preyed on sockeye salmon smolt outmigrations year over year, with individuals making repeated movements to exploit this seasonal resource pulse. If indeed UFW bull trout are exploiting sockeye salmon smolts during their outmigration, it has strong implications for the management and conservation of both species. For example, management actions impacting survival and escapement of sockeye salmon throughout their adult life stages could drive variation in future smolt abundance, which in turn could lead to shifts in bull trout behaviour and distribution within this system (Taylor et al. 2021).

3.5 Conclusions

Unlike the upper Fraser River watershed, bull trout in many regions exist in artificially fragmented systems where their movements are significantly limited. This work builds on that of others to further our understanding of how migratory bull trout life histories behave and spatially distribute when able to access diverse habitats spread across the full extent of a watershed. The combination of stock level mixing across available wintering and foraging habitats, prevalence of similar movement patterns across populations at the watershed scale, and the spatial scale of migrations in this system highlight both the importance of habitat connectivity between tributary spawning and large riverine habitats. Also, anthropogenic impacts through habitat degradation, fishing, etc. have the potential to impact multiple bull trout spawning populations using the same habitats during other stages of their life history, which could reduce the viability of bull trout population complexes within impacted habitats.

Table 3.1 Notation of indices and parameters for bull trout state-space capture-recapture model including prior probability distributions and likelihood functions.

Symbol	Value(s)	Prior	Description
Indices			
i	$(i, \ldots I)$		Individual
st	(1:5)		Stock number
se	(1, 2)		Season (1 = migrating, 2 = wintering)
a_O	(1:8)		Observed state of departure
k_O	(1:8)		Observed state of arrival
a	(1:8)		Estimate state of departure
k	(1:8)		Estimate state of arrival
Parameters			
$\emptyset$	++	B(2,2)	Survival probability
p	++	B(2,2)	Recapture probability
g	++	N(0,0.25)	Gravity
v	++		Viscosity
ψ	++		Transition probability
f_{s_i}	++		Observed state at first capture
z_{i,f_i}	++		True state of individual
Likelihood Estimation		***Likelihood function***	
$z_{i,t+1} \vert z_{i,t}$	++	$C(\Omega_{zi,t,1\ldots S,i,t})$	State membership development
$y_{i,t} \vert z_{i,t}$	++	$C(\Theta_{zi,t,1\ldots O,i,t})$	Estimation linking observed and true states

Note: The symbol ++ indicates parameters that are estimated. Priors and likelihood functions are given abbreviated distribution names as follows: *B* = Beta (shape parameters), *N* = Normal (mean, precision), and *C* = Categorical, respectively.

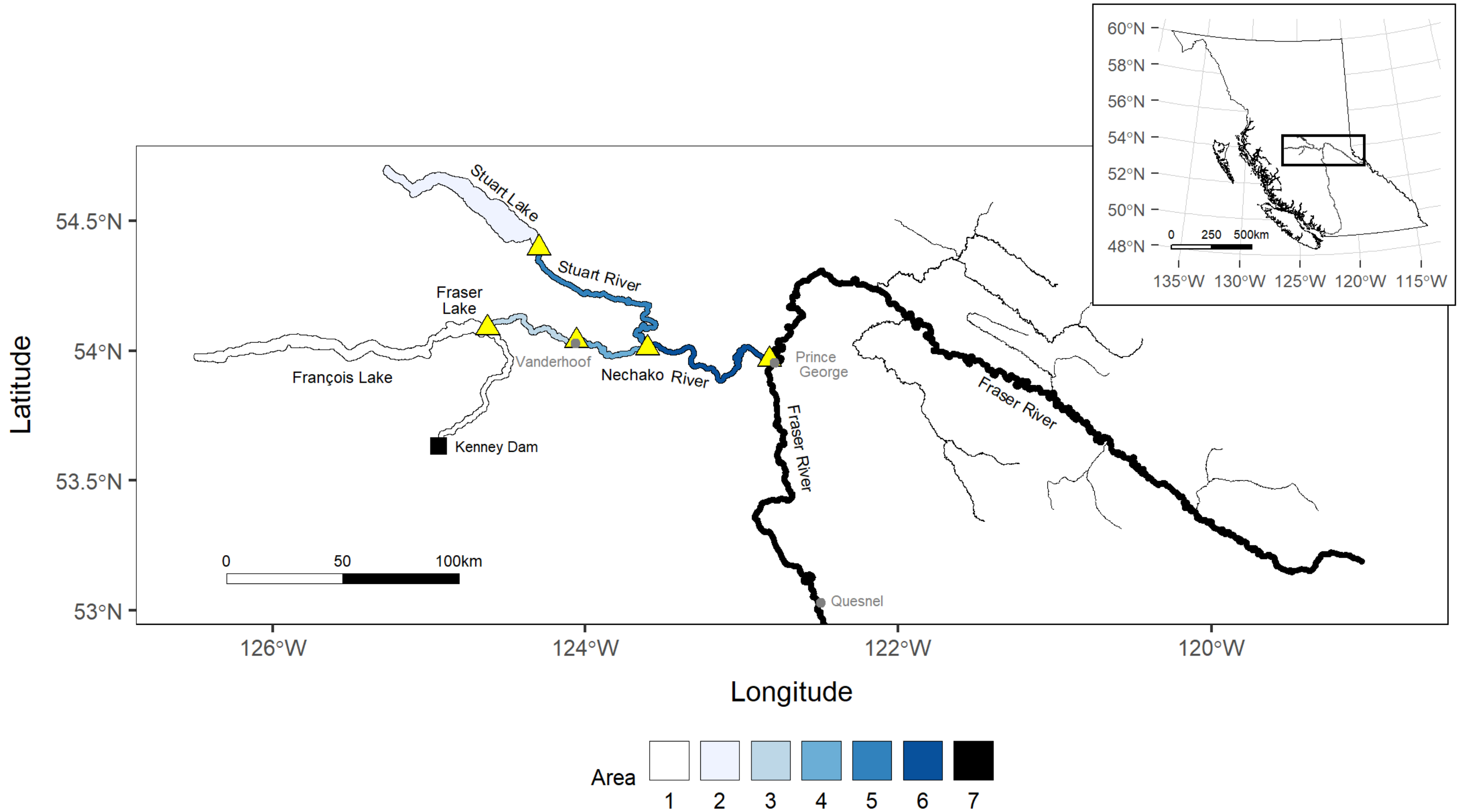

Figure 3.1 Overview map of the study area within the upper Fraser River watershed (UFW). Seven spatial areas modeled within the study area are represented in colour, population centres are identified by grey circles, distribution of fixed receiver array identified by yellow triangles, and the location of Kenney Dam, the only major impediment to movement in the system, is designated with a black square.

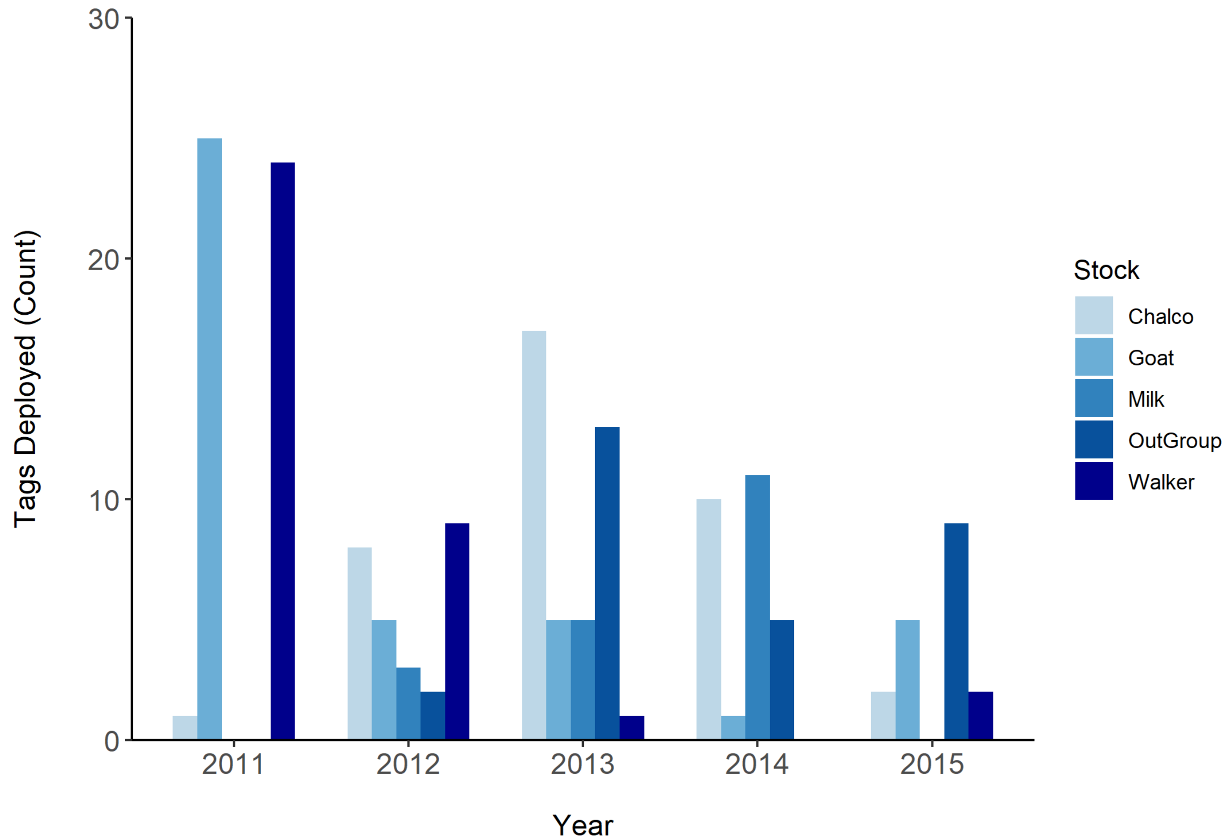

Figure 3.2 Tag deployment (number of bull trout, grouped by genetic assigned of tagged fish to one of four modeled stocks) within the upper Fraser River watershed. Genetic assignments were performed in Taylor et al. (2021).

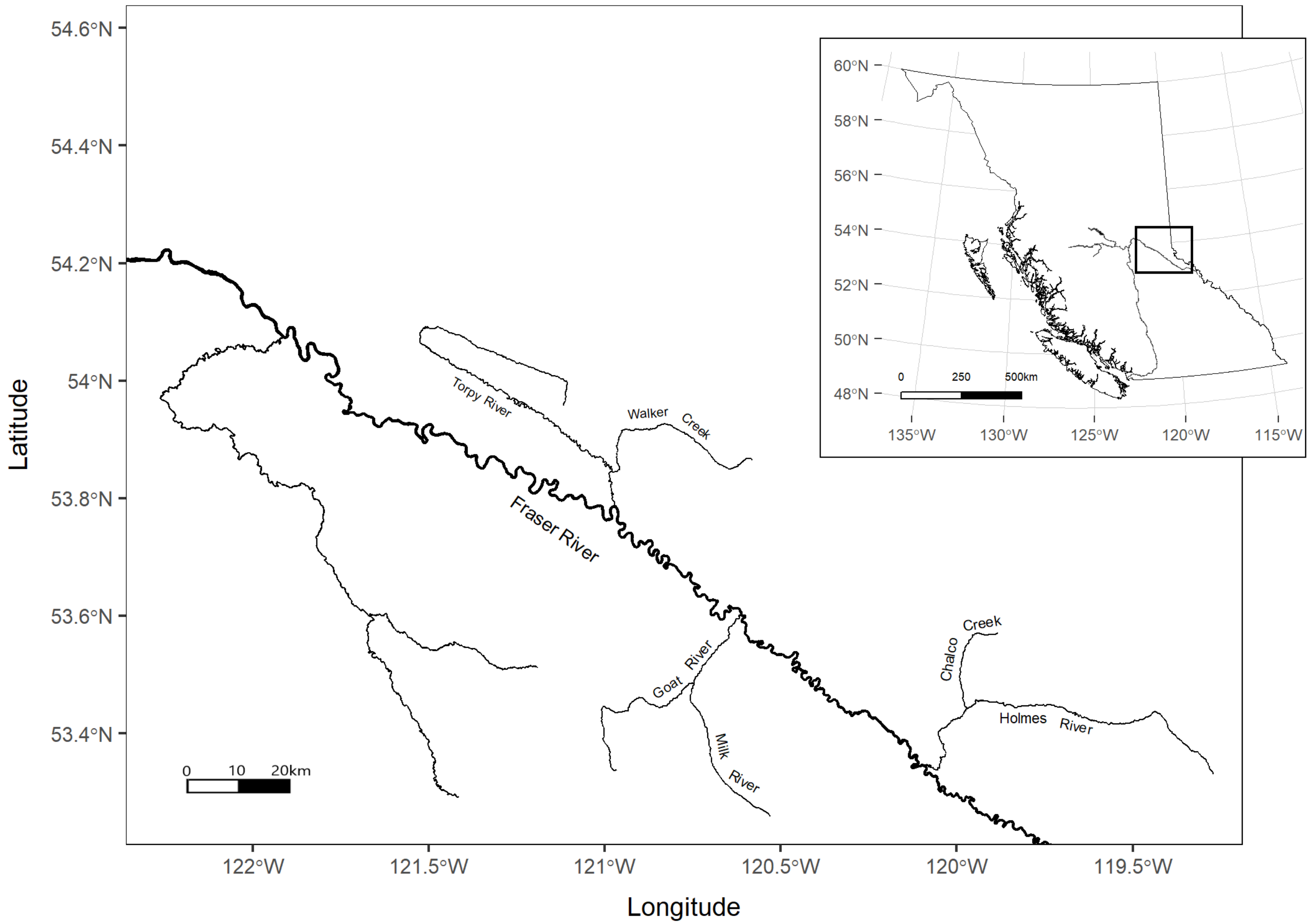

Figure 3.3 Location of null bull trout natal spawning tributaries for modeled populations, outgroup not shown.

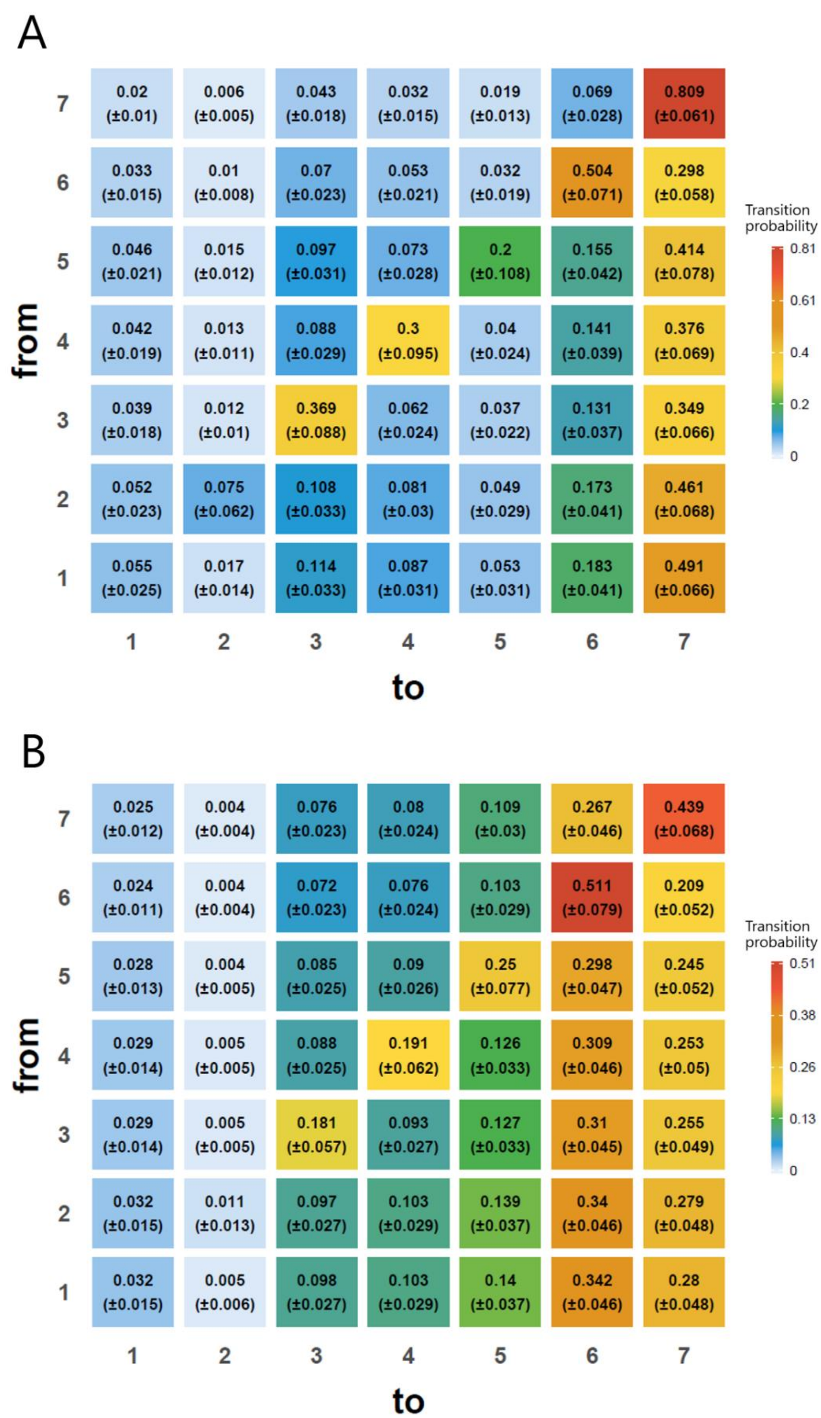

Figure 3.4 Seasonally-specific heatmap ('migration' time-block; panel A and 'wintering' time-block; panel B) of area-to-area estimated state transitions (movement probabilities) for bull trout within the upper Fraser River watershed.

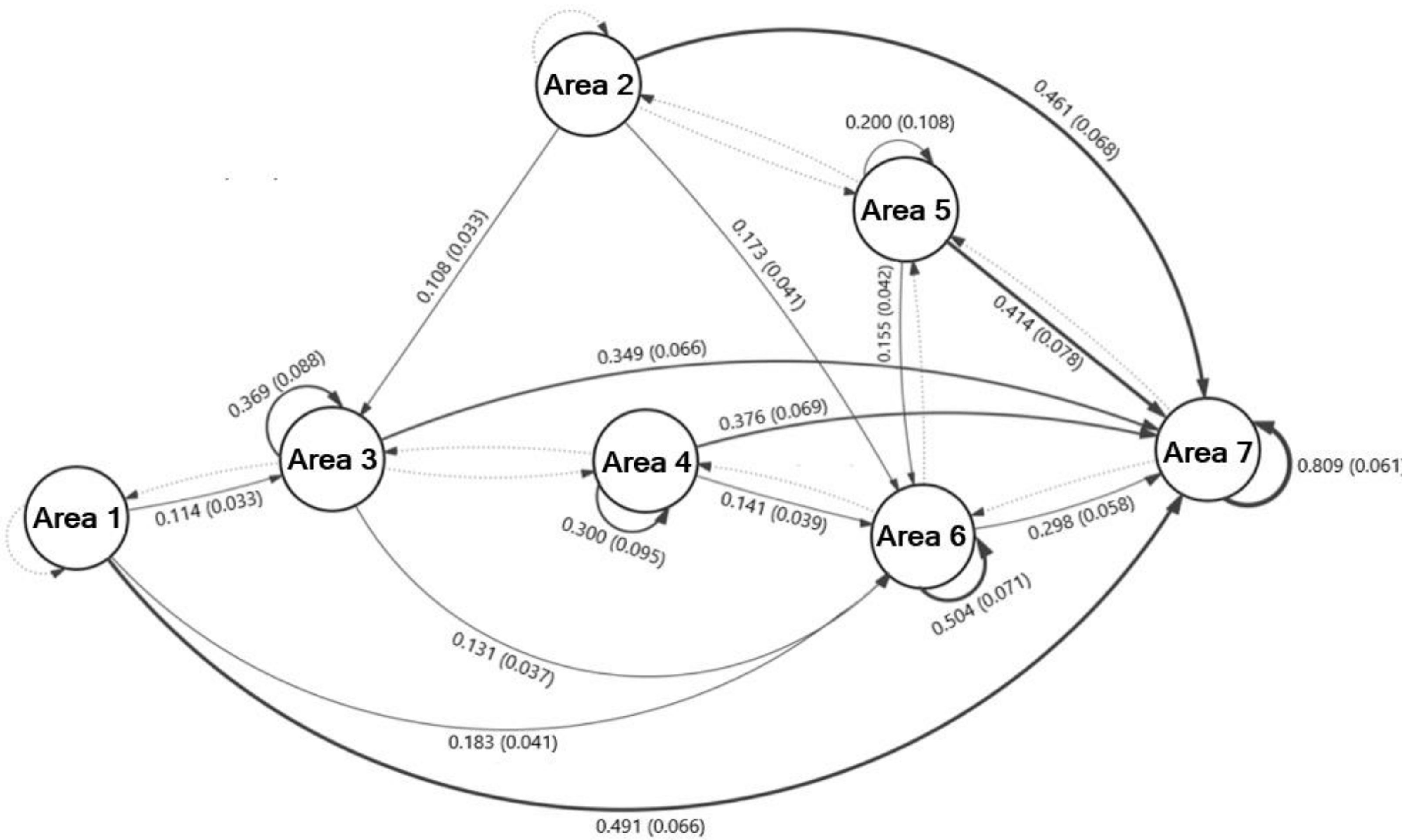

Figure 3.5 Spatial representation of area-to-area estimated state transitions (movement probabilities) for bull trout within the upper Fraser River watershed during the 'migration' time-block. See Figure 3.6. for plot of 'wintering' time-block.

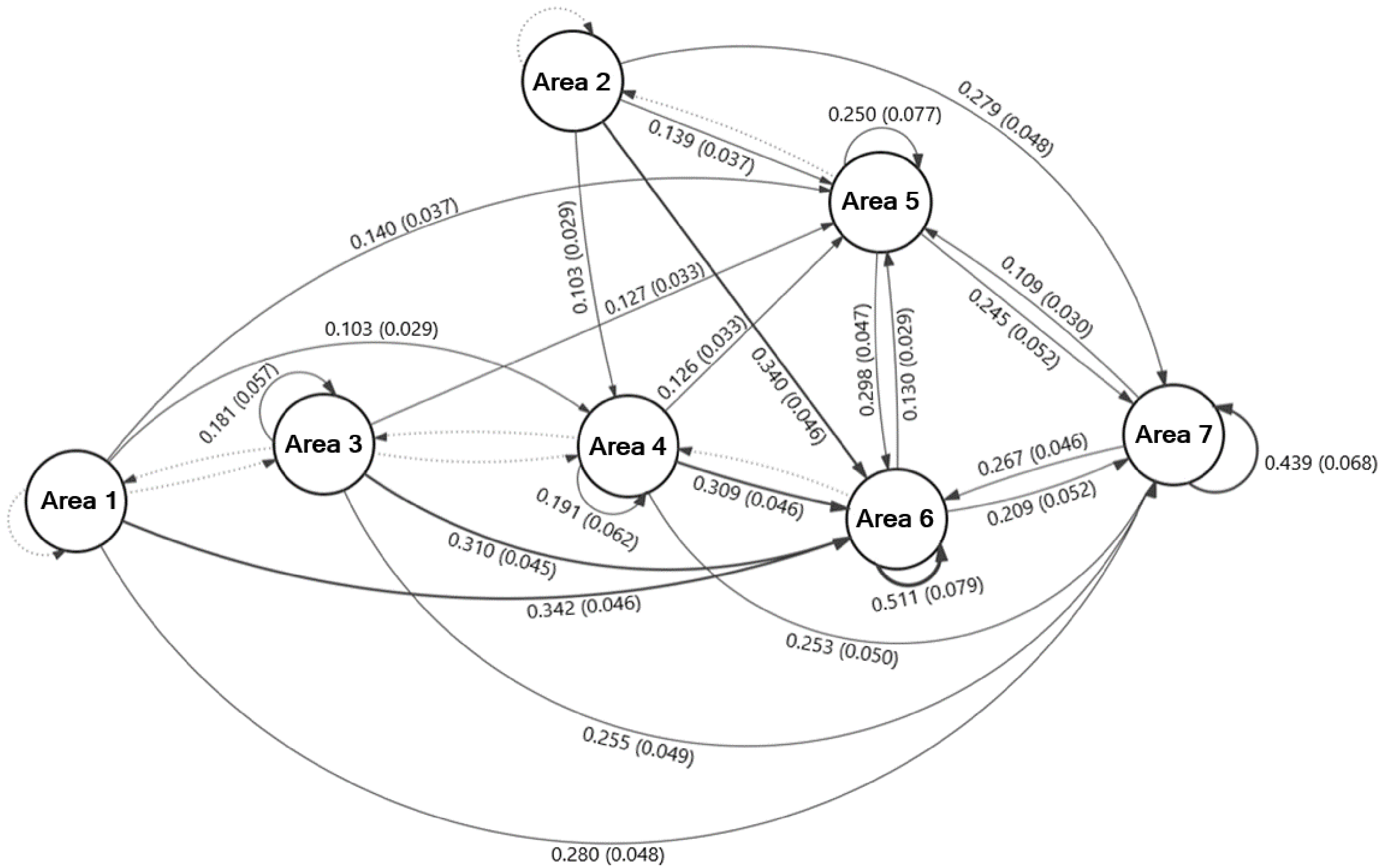

Figure 3.6 Spatial representation of area-to-area estimated state transitions (movement probabilities) for bull trout within the upper Fraser River watershed during the 'wintering' time-block. See Figure 3.5 for plot of 'migrating' time-block.

Chapter 4: Evaluating alternative management actions on fluvial bull trout using decision analysis

4.1 Introduction

Inland recreational fisheries managers must balance multiple, often conflicting objectives related to resource conservation and the social and economic values of fishing opportunities (Lorenzen et al. 2016; Lynch et al. 2017; van Poorten and MacKenzie 2020). They balance these objectives while working within complex natural-human systems, the understanding of which is fraught with uncertainty (Hilborn and Walters 1992; Lyons et al. 2008; Camp et al. 2020). How fished populations respond to management actions or changes in the natural environment can be unpredictable, due to density-dependent effects on survival and growth, changes in population age-structure, and the relationship between spawners and recruits (Hilborn and Walters 1992; Walters and Martell 2004; van Poorten and MacKenzie 2020).

The human dimension of recreational fisheries is equally complex. Angler populations are highly diverse and significant heterogeneity exists both within and between angler types with respect to their preferences, motivations, and what leads to their satisfaction (Johnston et al. 2010; Beardmore et al. 2013; Birdsong et al. 2021). These differences lead to variation in how individuals engage within a fishery system and modify their behaviours (e.g., choices of where and when to fish) in response to changes (Arlinghaus et al. 2008; Johnston et al. 2010; Beardmore et al. 2013). Further, socio-economic influences on angler behaviour and resulting fishing effort can drive considerable uncertainty in both anglers' direct behavioural responses to changing regulations and indirect responses through changes in fishery participation (Hartill et al. 2016; Camp et al. 2020). As a result, fisheries managers are often challenged by considerable uncertainty surrounding how anglers and resulting fishing effort will distribute across a fishery's spatial landscape and how effort and angler participation will fluctuate over time in response to socio-economic changes and changes in fished populations (Johnston et al. 2011; Hunt et al. 2011; Allen et al. 2013).

Within this socio-ecological system, managers make decisions with incomplete knowledge, not only about the current state of the system they are managing, but also how their actions will influence both fish and human populations (Robb and Peterman 1998; Camp et al. 2020). In addition, agencies are often responsible for managing a diverse assemblage of aquatic species across a complex landscape of diverse habitats (e.g., lakes, fluvial systems) (Pereira and Hansen 2003; Ward et al. 2013; Lynch et al. 2017). Non-fishing related human impacts, fishing effort, and fished population habitat use all vary in space and time, may be uncertain, and may be comprised of factors that are outside management control (e.g., anthropogenic change, invasive species introductions, attributes contributing to angler satisfaction) (Pereira and Hansen 2003; Lynch et al. 2017; van Poorten and MacKenzie 2020).

Despite the tremendous socio-economic importance of recreational fisheries to local communities and economies, agencies often have limited capacity and resources for management (Pereira and Hansen 2003; Cooke and Cowx 2006; Lorenzen et al. 2016). Specific fisheries are often managed passively, with the same regulatory scheme (e.g., bait bans, temporal closures, harvest (bag) and/or size limits) implemented broadly across species within the management jurisdiction (Pereira and Hansen 2003; Irwin et al. 2011). Generally, these regulations are modified in a reactionary manner, in response to natural disturbance or stakeholder requests (Walters 1986; Pereira and Hansen 2003; Irwin et al. 2011).

Agencies account for uncertainties by making what they believe to be conservative objectives, using a range of regulations aimed to reduce fishing mortality and responding to reduced fishing quality or observed population declines by imposing more restrictive regulations (Post et al. 2003; Camp et al. 2020; van Poorten and MacKenzie 2020). Such regulatory changes may limit the harvest of individual anglers, but may not account for all the catch and non-catch related attributes that contribute to angler behaviour and participation within a fishery (Post et al. 2008; Beardmore et al. 2015; Hunt et al. 2019). Recreational fisheries rarely regulate total effort. As a result, harvest rates and fishing mortality may still dramatically increase following regulation changes if non-catch related attributes within each angler’s decision-making process keep the fishery sufficiently attractive (Post et al. 2002, 2003; van Poorten and MacKenzie 2020). It is critical that management recommendations are developed in a way that accounts for uncertainties surrounding the many catch and non-catch related attributes that determine a particular angler population’s participation within a fishery and their resulting fishing effort. These aspects of a fishery’s human dimension ultimately determine the optimal regulatory framework within a particular fishery (Johnston et al. 2010; Hunt et al. 2019).

Population dynamics simulation modeling coupled with decision analysis provides a structured framework for evaluation of the relative performance of different management actions while explicitly accounting for the multitude of uncertainties that determine the effectiveness of regulations in meeting fishery objectives (Robb and Peterman 1998; Peterman and Anderson 1999; Harwood 2000). Decision analysis has been applied broadly across several environmental and natural resource fields (e.g., Harwood (2000); Kiker et al. (2005); Mendoza and Martins (2006); Gregory and Long (2009)), including management of commercial fisheries (e.g., Punt and Hilborn (1997); Robb and Peterman (1998); Lackey (1998)), but has received less attention in the management of recreational fishery resources (but see Peterson and Evans (2003); Irwin et al. (2008, 2011); Jones and Bence (2009); Varkey et al. (2016); van Poorten and MacKenzie (2020)).

This chapter develops a population dynamics model to represent a population complex of fluvial bull trout using estimated bull trout recruitment compensation (Chapter 2) and seasonal movement probability matrices and apparent survival estimates (Chapter 3). This dynamic model is then applied through a decision analysis of alternative regulatory actions for a recreational bull trout fishery in the upper Fraser River watershed of British Columbia (UFW). The analysis is designed to provide advice to regional decision-makers for their proactive management of the bull trout resource in the UFW, while specifically accounting for uncertainty in effort response. Thus, providing management advice that is robust to this critical uncertainty. The use of a decision analysis permits evaluation of the potential impacts of alternative management actions on the dual fishery objectives of bull trout conservation and angler satisfaction, given uncertainties about the state of the system, and fish and angler responses to regulatory changes (Peterman and Anderson 1999).

4.2 Methods

4.2.1 Study area

The study region comprises approximately 98,000 km^2 of freshwater habitat within the upper Fraser River watershed (UFW) of British Columbia (Figure 4.1). The watershed provides habitat for several distinct fluvial bull trout populations that migrate between spawning and rearing habitats in tributaries of the Rocky and Cariboo mountains (e.g., Goat, Milk, and Holmes rivers, Walker and Chalco creeks) and large riverine foraging and wintering habitats within the Nechako and Stuart rivers using the upper Fraser River as a migration corridor (see Chapter 3). Human access varies significantly across the region. Some angling opportunities are accessible only by boat or all-terrain vehicle, while other popular angling locations are adjacent to population centres in Prince George and Vanderhoof or immediately adjacent to a highway linking central British Columbia to Alberta (Spendlow 2020, personal communication; Pillipow 2021, personal communication).

Bull trout angling regulations across the species' range are conservation-focused, given the species susceptibility to overharvest due to their late maturity, slow growth, aggressive feeding, and aggregative behaviours (Post and Johnston 2002; Post et al. 2003; Hagen and Decker 2011). Current regulations in the UFW are complex, using a combination of bait bans, temporal and spatial closures, and requirement of single barbless hooks (FLNRO 2017a; FLNRO 2017b). The current fishery occurs seasonally in spring (April and May; following ice-off and prior to bull trout migration to spawning habitats in tributaries of the Fraser River) and to a lesser extent in fall (late September through October; following bull trout spawning within natal tributaries) (Spendlow 2020, personal communication; Pillipow 2021, personal communication). Current regulations limit bull trout harvest to lakes only (e.g., Stuart, Francois, and Fraser lakes) and include a bag limit of one fish per angler per day, within a slot limit of 30-50 cm total length, and seasonal closure (August 15 – October 15). Angling within all fluvial habitat is catch-and-release only. Like lake habitat, there is a seasonal closure between April 1 and June 30 in most locations. The Fraser and Nechako rivers are notable exceptions to this closure and are open to fishing year-round. Anglers in the region have expressed desire for managers to consider regulatory alternatives permitting harvest within fluvial habitats (Pillipow 2012; 2021, personal communications).

4.2.2 Data collection and analysis

A fluvial bull trout population complex within the upper Fraser River watershed was monitored as part of a multi-year radio telemetry study. This work included genetic analysis that permitted the assignment of sampled fish to their population and natal stream of origin (see Taylor et al. 2021) which was used to simulate a multi-stock models within the current investigation. All individuals were measured for total length at the time of tagging, and subset of individuals from each population were sampled for scale tissue used for aging. Resulting length-at-age data were fit to the von Bertalanffy growth equation (Equation 4.1) to provide stock-specific estimates of $L_\infty$and *K*. Table 4.1 provides explanation of all indices, variables, and parameters used within this chapter.

$$L_{st,a} = L_{\infty_{st}}(1 - e^{(-K_{st}*a})$$ Eq. 4.1

State-space capture-recapture modeling within Chapter 3 estimated seasonal- and stock-specific movement probabilities between seven spatial areas within the upper Fraser River watershed (see Figure 4.1) and generated a cross-population estimate of apparent survival. These estimates were used to inform the population dynamics operating model described in the next section. Mark-recapture data collected during telemetry tagging work were used to generate a cross-population estimate of R_0, by estimating cross-population equilibrium abundance under the assumption that annual mortality equaled recruitment.

The number of unmarked and marked fish in the population complex in each year were calculated as (Equation 4.2 and 4.3):

$$\widehat{U_t} = R + \left(\widehat{U_{t-1}} - m_{t-1}\right)^{-M} \quad \text{Eq. 4.2}$$

$$\widehat{M_t} = \left(\widehat{M_{t-1}} - m_{t-1}\right)^{-M} \quad \text{Eq. 4.3}$$

where m_t were observed marks added each year under the assumption that $\widehat{U_t} = N_0$, M was the median estimated natural mortality rate from Chapter 3, and R was constant recruitment, calculated as $N_0 * \left(1 - e^{(-M)}\right)$. Unmarked and marked captures were then predicted as (Equation 4.4 and 4.5):

$$\widehat{u_t} = \widehat{U_{t-1}} * p_t \quad \text{Eq. 4.4}$$

$$\widehat{m_t} = \widehat{M_{t-1}} * p_t \qquad \text{Eq. 4.5}$$

where p was an annual capture probability. Initial abundance and annual capture probability were estimated by assuming observed captures of unmarked and marked bull trout in area 6 were Poisson distributed. Model-predicted fished vulnerable abundance in area 6 ($V_{c_{z=6}}$), under status quo regulations (Equation 4.6) were then compared to estimates of abundance obtained from mark-recapture in that spatial area.

$$V_{c_{y,z=6}} = \sum_{AR}^{A} N^*{}_{s=2,st,a} sc_{st,a} \qquad \text{Eq. 4.6}$$

The model was tuned by varying cross-population R_0 divided across populations according to proportions predicted in Taylor et al. (2021).

4.2.3 Operating model

A stock-, age-, and spatially-structured simulation model was developed to explore effects of different management actions on fishery objectives for stock conservation and angler satisfaction (Table 4.2). The model incorporated parameter estimates derived through past research within this dissertation (T4.2.1), expert judgment of collaborators, and as reported in the literature (T4.2.2). The populations of interest are represented by ages vulnerable to the fishery, with recruitment to the fishery assumed to occur at age 4+ and with individuals attaining a maximum age of 15 years. The study area was split into seven discrete spatial areas as defined within Chapter 3 (see Figure 4.1). As within Chapter 3, time was split into two unequal seasons. Season one, when no fishing activity occurs, was equal to time-block two within Chapter 3 and spanned from November to April 14 each year. Season two, when both fishing opportunities occur, was equal to time-block one within Chapter 3 and spans from April 15 through October of each year.

Life history schedules were first estimated using leading parameters. Length-at-age for each stock was estimated using the von Bertalanffy growth equation (T4.2.3) using estimates of L_∞ and K obtained by fitting length-at-age data collected through field sampling for each of the five stocks (see section 4.2.2. above). Due to the sample size of length-at-age data, a single estimate of L_∞ and K were calculated jointly for two connected systems, Goat and Milk rivers. Length-at-age was then used to estimate stock-specific fecundity-at-age (T4.2.4) and maturity-at-age (T4.2.5). Stock-, age-, and area-specific selectivity to capture was described as a logistic function of length (T4.2.6). Age-specific unfished survivorship (T4.2.7) was calculated assuming natural mortality of recruited fish was independent of age and constant across spatial areas.

Life history schedules were then used to estimate key derived variables. Equilibrium spatial distribution in each season was numerically approximated by repeatedly multiplying a vector, d (across areas, sums to 1) by the transition array, ϴ, over years until the distribution stabilized. Eggs-per-recruit at unfished equilibrium were first calculated for each stock by taking the product of survivorship, maturity, and fecundity incidence functions and multiplying it by survival to the second season and the equilibrium proportion of fish in area 7 (spawning tributaries; T4.2.8) (Walters and Martell 2004). α_R (T4.2.9) and β_R (T4.2.10) parameters of the Beverton-Holt stock recruitment function were then calculated (Botsford and Wickham 1979; Botsford 1981a, 1981b; Walters and Martell 2004). Initial unfished abundance in each area in season one was then calculated as the product of stock-specific unfished recruitment (R_0), survivorship, and equilibrium spatial distribution, d; abundance in season two was estimated by redistributing survivors from season one according to the transition array (ϴ) (T4.2.11).

Unfished abundance vulnerable to capture (whether harvested or released) and harvest (T4.2.12; T4.2.13) were estimated using stock and area specific abundance. Effort and fishing dynamics were calculated based on vulnerable abundance at the start of the fishing season, which occurred within season two. Discussions with regional managers were used to inform the maximum possible catch rate ($CPUE_0$), maximum possible targeted fishing effort (E_{max}) in area 6 (the most popular area of the fishery), and the current perceived distribution of fishing effort across areas (E_{p_z}). $CPUE_0$ and $V_{(0)c_z}$ in area 6 were used to first calculate overall catchability at unfished equilibrium abundance (q) (T4.2.14). Expert opinion from regional managers regarding the current distribution of fishing effort within areas 1-5 and 7 was then used to calculate the maximum possible effort and catch rate in all remaining areas (T4.2.15 and T4.2.16).

The initial unfished equilibrium state was used as a starting point for the time-dynamic simulation model. Recruitment was calculated according to the Beverton-Holt function with lognormal recruitment error (T4.2.17). Abundance in spring (season one) ($N_{y,s=1,z,st,a}$) and fall (season 2) prior to the fishery ($N_{y,s=2,z,st,a}$) were calculated by surviving fish in the past season and redistributing among areas according to the transition array (T4.2.18). Selectivity to harvest length limits in each area were calculated using the logistic approximation to the cumulative normal distribution, assuming a coefficient of variation for length (CV) of 0.1 (T4.2.19). This function accounted for variation in size-at-age as it applies to length limits. Effort and fishing mortality estimates were then calculated based on the area specific abundance of fish at the start of the fishing season within season two.

Abundance of fish vulnerable to capture (T4.2.20) and harvest (T4.2.21) were calculated as a function of selectivity and fish abundance in each area at the start of the fishing season (i.e., season two). Catch importance, a weighted catch per unit effort based on relative abundance of fish vulnerable to capture and harvest was calculated (T4.2.22) and then used to calculate area-specific effort, which was taken as the maximum of either non-directed effort or effort on bull trout within the fishery (T4.2.23). Estimates of non-directed effort in the system come from expert opinion. Density-dependent catchability (T4.2.24) and catch per unit effort of fish vulnerable to legal harvest based on length limits was then calculated (T4.2.25). The proportion of legal-sized fish available to harvest based on the bag limit was calculated assuming a Poisson distribution of catch per day across anglers (T4.2.26). Fishing mortality was a function of catchability, effort, selectivity to catch and harvest, bag limit, and both release and non-compliance mortality (T4.2.27). Fishing mortality was adjusted according to the proportion of the area that was open to harvest (represented as O_z). Abundance at the end of season two after fishing was calculated accounting for fish lost as a result of harvest and incidental fishing mortality (T4.2.28). Finally, stock-specific estimates of egg production during spawning and stock-specific recruits per spawner were calculated (T4.2.29; T4.2.30).

The time-dynamic simulation model was first run to establish current conditions in the fishery by simulating 25 years under current regulations. The model then projected 20 years of fishing under each proposed regulatory scenario. The current management regime (status quo) and all regulatory scenarios are outlined in Table 4.3. Each simulation was run 1,000 times using samples from posterior distributions of compensation ratio (*CR*) from Chapter 2, natural mortality rate, assumed equal to apparent mortality rate, from Chapter 3, and the transition matrices from Chapter 3.

4.2.4 Decision analysis

A Bayesian decision analysis framework was used to evaluate alternative regulatory options identified by managers for the fluvial bull trout fishery in the upper Fraser River watershed (Robb and Peterman 1998; Peterman and Anderson 1999). This approach enabled communication of the relative performance of each management action across a range of hypotheses about unknowns (states of nature), while explicitly accounting for both process and parameter uncertainty (Walters 1986; Peterman and Anderson 1999). Each state of nature hypothesis was assigned a prior probability that reflected the relative degree of belief in that value, relative to all others as a true representation of the system (Morgan and Henrion 1990). Posterior expected values for performance measures under each alternative regulatory action were calculated as the average of the performance measure across states of nature combinations, weighted by priors (Morgan and Henrion 1990; Robb and Peterman 1998). Posterior expected values for each performance measure allow managers to identify management actions that are robust to uncertainties (Morgan and Henrion 1990; Robb and Peterman 1998; Walters and Martell 2004).

This decision analysis management evaluation follows the six steps of decision analysis (modified from Robb and Peterman (1998)): (1) identify alternative management actions; (2)

identify management objectives; (3) identify uncertain states of nature; (4) assign prior probability to each state of nature hypothesis; (5) calculate outcomes for each combination of management action and hypothesis using a simulation model of the fishery; (6) evaluate management actions. The specifics of the application of each step of the decision analysis process are outlined below.

(1) Identify alternative management actions

Possible management actions within the seven spatial areas were identified through consultation with regional biologists and managers as follows (Table 4.3): (1) continuation of current management (i.e., retention of one fish per day between 30-50 cm in areas 1 and 2, catch-and-release in areas 3-7); (2) current regulations in areas 1 and 2; daily harvest (bag) limit of one fish per day in the mainstem Nechako River (areas 3, 4, and 6) with no length limits; (3) current regulations in areas 1 and 2; daily harvest (bag) limit of three fish per day in the mainstem Nechako River (areas 3, 4, and 6) with no length limits; (4) current regulations in areas 1 and 2; daily harvest (bag) limit of one fish over 50 cm per day in the mainstem Nechako River (areas 3, 4, and 6), with catch-and-release in areas 5 and 7; (5) current regulations in areas 1 and 2; closure of area 7 when spawners are present (i.e., season two).

(2) Identify management objectives

The fishery's management objectives were identified to allow the relative efficacy of each identified management action in achieving fishery goals to be ranked (Peterman and Anderson 1999). Recreational fishing management goals in British Columbia are described by MOE (2007) as the dual objectives of resource conservation and maintenance of angler satisfaction.

The conservation objective was represented using spawning potential ratio (SPR), the expected lifetime egg production per recruit in the fished relative to unfished state ($\phi_{(U)0}$) (Equation 4.7) (Walters and Martell 2004).

$$SPR_{y,z} = \frac{\varphi_{(0)E_{st}}}{\varphi_{(F)E_{st}}} \qquad \text{Eq. 4.7}$$

A conservation threshold of maintaining SPR > 0.4 was selected to account for uncertainty around the resiliency of bull trout (Clark 2002).

No fishery-specific information on stated angler preferences was available within the fishery. Therefore, the angler satisfaction objective was represented as a catch-based utility based on literature findings that catch-related attributes are often stated as drivers of satisfaction in specific recreational fisheries (Cox et al. 2003; Arlinghaus 2006; Beardmore et al. 2015). Angler satisfaction was calculated as a linear value function of ‘potential’ catch rate as described in Cox et al. (2003) (Equation 4.8):

$$U_{y,z} = max\left(0, \left(wCPUE_{y,z} - CPUE_{quit}\right)\right) \qquad \text{Eq 4.8}$$

Note that *wCPUE* represented ‘catch importance’, a weighted mean catch rate that accounted for the importance of overall potential catch and harvest to anglers. This resulted in higher satisfaction with higher catch rates overall, and lower catch rates when there were fewer opportunities to harvest.

The conservation and angler satisfaction performance indicators used to measure the relative success of each management action in obtaining fishery objectives in the presence of uncertainty were: (1) The proportion of simulation runs with stock-specific SPR < 0.4 across 1000 simulations and the 20 projected years following regulatory change and (2) the average angler satisfaction over the 1000 simulations and 20 projected years.

(3) Identify unknown states of nature and (4) assign prior probabilities to each hypothesis

The primary uncertainty regarding the state of nature within the system is how angler effort will respond to opening a new retention fishery for bull trout within mainstem river and tributary habitat. This uncertainty was reflected in the model by considering effort response to harvest by modifying w_{keep} as 0.25, 0.5, and 0.75. More prior weight placed on the intermediate hypothesis $p(model)_i$ = (0.25, 0.5, 0.25) based on expert opinion of area managers on the importance of harvest within the fishery.

(5) Calculate outcomes and (6) evaluate management actions

The probability of SPR < 0.4 and average angler satisfaction were calculated across all random draws of the estimated parameter posterior distribution (T1.1), across all years, for each combination of management action and state of nature. Each of the five management actions were then evaluated by calculating the expected values for each of the two performance indicators for each management action, across all states of nature. The expected values for conservation and angler satisfaction objectives were calculated separately to permit managers to evaluate regulatory action performance for each indicator on their own merit and weight the objectives according to management values.

4.2.5 Sensitivity analysis

A one-way sensitivity analysis evaluated the relative influence of each parameter on performance indicators for SPR and angler satisfaction under the baseline assumption of the current state of nature (w_{keep} = 0.5) and current fishery regulations (status quo). Within this analysis, the model was run iteratively with each parameter systematically set ± 10% of the base value. All parameters excluding the parameter of interest remained stochastic within their distribution.

4.3 Results

The stock-, age-, and spatially-structured model simulated the fishery over a 20-year time horizon. Operating model outputs demonstrated significant variability in mean vulnerable abundance, CPUE, effort, and angler satisfaction between the different spatial areas. Visual inspection of temporal predictions for these parameters served as a baseline of the fishery's current state upon which alternative regulations could be compared.

Trends in CPUE and vulnerable abundance were similar between areas and across regulatory scenarios, excluding the status quo scenario. Both estimates were highest in area 6 (Nechako River downstream of Stuart River to Prince George) and area 7 (upper Fraser River north of Prince George and its tributaries; Figures 4.2 and 4.3) across all regulatory scenarios. Model predictions were substantially lower in areas 3 and 4 (Nechako River from confluence with Nautley River to its confluence with the Stuart River), and 5 (Stuart River) and negligible within areas 1 and 2 (lake habitat). Overall, the greatest CPUE and vulnerable abundance estimates occurred under the status quo scenario. In contrast, in all retention scenarios, CPUE and vulnerable abundance declined below levels observed under the status quo scenario within the first five years of the simulation and remained depressed.

The magnitude and pattern of effort response varied between areas and regulatory scenarios (Figure 4.4). Effort was highest in areas 6 and 7, an order of magnitude smaller within areas 3 and 4, and negligible across regulations within areas 1, 2, and 5. Catch importance in areas 1 and 2 was so low that effort was dominated by non-target effort. Areas 5 and 7 showed similar trends in effort through time for all regulations. In scenarios where harvest was introduced, effort in both areas declined over the initial five-year period then remained depressed at levels below predictions under status quo regulations. Effort trends in areas 3, 4, and 6 (i.e., areas permitting harvest in all scenarios excluding status quo) contrasted observations in all other areas. Under regulatory scenarios allowing harvest, effort in areas 3, 4, and 6 increased over an initial five-year period, then declined, but remained higher than effort predicted under the status quo scenario. By area, effort increases were highest in area 6, with the largest increase in effort occurring within the regulatory scenario of one fish over 50 cm per day in areas 3, 4, and 6 with a spatial closure of a portion of area 7.

Across regulatory scenarios, mean angler satisfaction was highest in area 6, followed by area 7, and lower in all remaining areas (Figure 4.5). Under all regulatory scenarios permitting harvest, angler satisfaction was negligible within areas 1, 2, and 5. In areas 3, 4, and 6 (i.e., the areas with harvest opportunity) satisfaction increased relative to the status quo scenario. Satisfaction was highest under the regulatory scenario permitting harvest of one fish over 50 cm per day in areas 3, 4, and 6 with a spatial closure of a portion of area 7. It was lowest under the regulatory scenario of a three fish per day bag limit in areas 3, 4, and 6. In contrast, angler satisfaction in area 7 was below status quo for all harvest regulation scenarios. SPR estimates were lowest under the most liberal harvest regulation (bag limit of three fish per day in areas 3, 4, and 6) ranging from 0.16 to 0.27 and highest under status quo regulations, ranging from 0.25 to 0.44 across stocks.

A decision analysis was used to evaluate the relative performance of five alternative regulatory scenarios in meeting conservation and angler satisfaction objectives over a 20-year time period. Within the analysis, expected values were calculated across all alternative hypotheses of the importance of catch to anglers. The regulatory scenario found to maximize angler satisfaction was insensitive to alternative hypotheses of the importance of catch (Table 4.4). If regulations are maintained at the current status quo, angler satisfaction was estimated as 0.398, the lowest satisfaction level obtained under all regulatory scenarios. Satisfaction was positively impacted by harvest opportunity, however an increase in harvest from one to three fish per day did not further increase satisfaction. Under the baseline assumption of the importance of catch to anglers, $w_{keep} = 0.5$, satisfaction was maximized under regulatory scenario of one fish over 50cm per day with a partial spatial closure within area 7. The lowest satisfaction across regulations allowing harvest was obtained for the bag limit of three per day. Regulatory actions using a bag limit of one fish per day without a spatial closure led to near identical levels of satisfaction.

In contrast to findings for angler satisfaction, the conservation performance indicator (proportion of 1000 simulation runs with SPR < 0.4) was sensitive to alternative hypotheses of w_{keep}. The scale of impact varied between regulatory scenarios (Table 4.5). The regulatory scenario of a bag limit of three fish per day was the least sensitive to variation in w_{keep}, with variation in performance indicator estimates of less than 0.1. The status quo regulatory scenario was most sensitive to variation in w_{keep}. w_{keep} = 0.25 resulted in 85% of simulation runs falling below the conservation threshold, while w_{keep} = 0.75 reduced the proportion to approximately 0.25 across stocks.

Under the baseline catch importance (w_{keep} = 0.5), the proportion of simulation runs where SPR was reduced below 0.4 was lowest under status quo regulations (< 0.65 across stocks). Expected values obtained for this objective under the regulatory scenario of one fish over 50 cm per day with a partial spatial closure, the regulatory action that maximized utility, were only moderately higher (-0.061). All remaining regulatory scenarios resulted in more than 90% of stochastic model runs falling below the conservation threshold, with the highest proportion occurring under the regulatory scenario of a bag limit of three fish per day. Outcomes of regulatory scenarios utilizing a bag limit of one fish per day without a spatial closure were similar, ranging from approximately 0.92 to 0.95 between stocks.

Sensitivity analysis outputs indicated both conservation and angler satisfaction objectives were most sensitive to variation in bull trout hyperstability (Figure 4.6). R_0 was also found to impact both objectives. In contrast, neither objective was sensitive to $CPUE_0$ or E_{max}.

4.4 Discussion

Anglers within the upper Fraser River watershed fluvial bull trout fishery have requested liberalization of current management regulations to permit harvest (Pillipow 2012, personal communication). Within this fishery, critical uncertainties surrounding the state of fished populations, drivers of angler effort, and trade-offs between conservation and user benefit objectives challenge management decision-making (Post et al. 2002; Lynch et al. 2017; Camp et al. 2020). Population dynamics modeling and decision analysis serve as valuable tools providing a framework through which managers can address these challenges (Powers et al. 1975; Peterman and Anderson 1999; van Poorten and MacKenzie 2020). This analysis provided an opportunity for all available information to be brought together to proactively inform management decision-making. The analysis was able to clarify uncertainties surrounding the feasibility of incorporating harvest within the fishery's regulatory framework. Results demonstrate that angler satisfaction could potentially be improved through a shift to regulations that minimally impact bull trout conservation across stocks. It also serves to highlight where additional resources can be best focused to further reduce remaining unknowns.

Regardless of the scale and breadth of uncertainties surrounding a fishery's dynamics, population dynamics modeling and decision analysis are invaluable tools for management decision-making. They provide a framework through which managers explicitly identify objectives and unknowns, and where they can confront trade-offs between different regulatory actions (Powers et al. 1975; Walters 1986; Peterman and Anderson 1999). Such an approach results in management decision-making that best supports objectives, can be clearly communicated to stakeholders, and is robust to uncertainty (Jones and Bence 2009; Irwin et al. 2011; van Poorten and MacKenzie 2020).

Although decision analysis has been broadly applied within natural resource and aquatic science fields (e.g., Robb and Peterman (1998), Harwood (2000), and Kiker et al. (2005)), its application within recreational fisheries management has been limited (but see Peterson and Evans (2003); Irwin et al. (2008, 2011); Jones and Bence (2009); Varkey et al. (2016); van Poorten and MacKenzie (2020)). Decision analysis can shift passive and reactive management toward decision-making that is proactive in its approach (Pereira and Hansen 2003; Lorenzen et al. 2016; van Poorten and MacKenzie 2020). This shift is highly valuable given that recreational fisheries are not inherently self-sustaining and are capable of collapse as demonstrated by the growing body of literature citing failures of passive and reactionary recreational fisheries management (Post et al. 2002; Pereira and Hansen 2003; Lynch et al. 2017).

The results of this analysis have direct applications for the proactive management of a fluvial bull trout fishery in central British Columbia. The species is generally thought to be highly susceptible to angling due to a combination of behaviour (e.g., vulnerability resulting from aggregating, aggressive feeding, capture susceptibility of immature individuals) and life history (e.g., low productivity due to slow growth, late maturity, relatively low eggs-per-female) (Post and Paul 2000; Post and Johnston 2002; Post et al. 2003). Within the upper Fraser River watershed, anglers have requested liberalization of current regulations based on anecdotal evidence of high catch rates and large fish size within the fishery (Pillipow 2012, personal communication). This decision analysis evaluated the performance of alternative regulatory scenarios, four incorporating bull trout harvest within the system and one representing the regulatory status quo, in meeting simplified fishery objectives for resource conservation and social outcomes within this fishery. It is important to recognize that while results presented here are grounded in the best available information, they are still the result of simulations with high uncertainty and due to data limitations, were generated without information regarding many aspects of the current state of the fishery (e.g., catch rates, effort distribution, drivers of angler behaviour and satisfaction). Therefore, any management decision should accompany purposeful monitoring of the fishery before and after action is taken.

Simplified objectives were necessary within this analysis because like many recreational fisheries, the upper Fraser River watershed fluvial bull trout fishery lacks fishery specific quantitative objectives (Lackey 1998; Pereira and Hansen 2003). The objectives and performance indicators chosen were based on the broad management goals specified by the province of British Columbia for all recreational fishing opportunities (MOE 2007). Despite considerable uncertainties surrounding the state of the fishery and the lack of clear quantified objectives, this analysis provides a valuable starting point for the proactive management of this fishery. Future development of specific objectives will be an important next step in quantifying the fishery specific attributes that reflect management success (Pereira and Hansen 2003; Hilborn 2007). Clear, specific objectives will serve both to reduce uncertainty and permit future analyses to evaluate performance outcomes that are more able to reflect the effectiveness of management actions toward achieving specific results toward resource conservation and the human dimension of this fishery (Robb and Peterman 1998).

Model simulations demonstrate that under the current regulatory status quo, SPR is likely below a conservative threshold (i.e., $SPR < 0.4$). Highlighting that current management may not be effective in meeting conservation objectives within this fishery. Within the analysis, expected values for SPR did not vary between stocks. This finding is likely due to significant uncertainty surrounding the relationship between spawners and recruits for each stock rather than a lack of variation between stocks. The estimate of *CR* used for all stocks within this model is a species-specific predictive probability distribution (Chudnow et al. 2018), and does not reflect variation in population productivity across stocks. Further, aspects of recruitment and adult abundance within the model were specified using highly uncertain estimates of R_0 derived from adult abundance as no data to inform R_0 using juvenile abundance are available within the study system. Results of the sensitivity analysis further illustrate the importance of this parameter on performance indicators for both fishery objectives.

If there is substantial variation in *CR* across stocks within the study area, it could lead to different population outcomes as the result of introduced harvest, potentially leading to the collapse of less productive stocks (Ricker 1958; Paulik et al. 1967; Secor 2014). Results of this analysis are robust to uncertainty in *CR* overall, but do not suggest which stocks might be more vulnerable to harvest; this would require population-specific stock and recruitment data. Given bull trout's conservation status, history of overexploitation, and the mixed stock nature of the majority of angling opportunities within the study system, collecting stock-recruitment data to inform stock-specific estimates of *CR*, R_0, and subsequent calculation of SPR is critical (Johnston 2005; Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2012; Erhardt and Scarnecchia 2014; Secor 2014). Without this information, it is not possible to evaluate regulatory actions impacts on less productive stocks within the mixed-stock fishery.

Exploration of alternative, more restrictive regulations may also be warranted if the range of model estimated SPR is of conservation concern to managers.

Within the analysis, the angler satisfaction objective was specified solely based on catch rates. This choice is consistent with stated goals for recreational fisheries both in British Columbia and elsewhere (MOE 2007; van Poorten and MacKenzie 2020). It was also necessary as no fishery-specific information regarding motivations, preference, or satisfaction currently exist. Accounting for the human dimension within this and all recreational fisheries, and clarifying the significant uncertainties surrounding angler behaviour, motivations, and conditions leading to their satisfaction, are critical in developing regulatory actions that can support conservation and maximize angler satisfaction. The choice of objective for angler satisfaction used in this study provides an important starting point that incorporated best available information in the form of expert opinion from area managers. In permitting evaluation of management actions across three alternative hypotheses of the importance of catch to anglers, the decision analysis also serves as a precautionary framework given these uncertainties.

Outputs of this analysis demonstrate angler satisfaction (based on catch rates) could be improved by shifting to a regulatory framework permitting bull trout harvest. An increase in harvest limit from one to three fish per day did not improve angler satisfaction within the model, due to reduced catch rates following significant effort increases and resulting declines in fish abundance. When balancing trade-offs to satisfy both fishery conservation and user objectives, the simulations suggest that angler satisfaction can be maximized without noticeable impact on the conservation objective, based on the SPR performance indicator. If managers choose to move to the regulatory scenario that maximized satisfaction (one fish over 50cm with a seasonal closure within area 7), it will be critical to carry out extensive monitoring to account for catch and effort shifts from the current status quo to new regulations.

Overall, the performance indicator for angler satisfaction was not dramatically impacted by different weighting of the importance of catch to anglers. In contrast, the performance indicator for the conservation objective (SPR) was impacted under most regulatory scenarios. Decreasing W_{keep} to 0.25 resulted in an increase in the proportion of model runs where the performance indicator threshold (SPR < 0.4) was exceeded. This change was minimal across all regulations permitting harvest but had large impacts within the status quo scenario. In contrast, increasing W_{keep} to 0.75 improved SPR across all regulations excluding the bag limit of three fish per day. Again, this shift in SPR was most notable for the status quo regulatory scenario.

The sensitivity of SPR to a catch-related attribute within this fishery, particularly under catch and release regulations, demonstrates that under the right conditions, angler effort can be maintained at a level that has significant conservation impacts even when catch rates are reduced (Post et al. 2002; Hunt et al. 2011; Lenker et al. 2016). Within the upper Fraser River watershed fluvial bull trout fishery, there is no available information to inform estimates relating to drivers of angler effort dynamics (i.e., importance of catch, CPUE at which point anglers stop fishing) or effort distribution across the landscape of available fishing locations. As a result, expert opinion of area biologists and managers was relied on within this analysis. In addition, there is also no information to inform the scale of release mortality and non-compliance mortality resulting from this effort. Surprisingly, the sensitivity analysis showed the area specific maximum effort and maximum possible catch rate in the fishery to have minimal influence on model results.

Future work should consider all parameters identified within the sensitivity analysis to further prioritize reducing uncertainty in the aspects of the fishery and model that had the greatest influence on objectives and optimal management, and thus, where additional data collection will have the greatest impact in further reducing uncertainty. Within the model, both regulatory objectives were most sensitive to the estimate of inverse density-dependent catchability, termed hyperstability. The scale of this parameter, which was informed by expert opinion, has the potential to undermine sustainable management of this species. Bull trout likely exhibit a high level of hyperstability due to their aggregating behaviour during spawning, wintering, and foraging (Fraley and Shepard 1989; Goetz 1989; Rieman and McIntyre 1993). The presence of hyperstability will also significantly impact anglers' perceptions of fishery health as catch rates will remain high even as population abundance is reduced to low levels (Hilborn and Walters 1992; Post et al. 2002; Allen et al. 2013). Within the upper Fraser River watershed, depensation resulting from hyperstability could lead to the extirpation of less productive stocks due to the mixed stock nature of bull trout aggregations and angling opportunities within foraging habitats (Taylor et al. 2021; see Chapter 3).

Despite its importance, clarifying uncertainty regarding the scale of hyperstability within bull trout fisheries is highly challenging. It requires adaptive management whereby a population is fished to low abundance to allow information on catch rates across variable abundances to be collected (Walters 1986; Walters and Martell 2004). For bull trout, such adaptive management may be infeasible due to the species conservation status (COSEWIC 2012; USFWS 2015). The potential impacts of hyperstability also further demonstrate the need for improved understanding of the drivers of angler satisfaction within this fishery, as depensatory impacts will be more significant if there is a strong relationship between catch rates and angler satisfaction (Post et al. 2003; Hunt et al. 2011, 2019).

4.5 Conclusions

Recreational fisheries management requires balancing objectives and accounting for uncertainties inherent within the socio-ecological system in which they operate (Lynch et al. 2017; van Poorten and MacKenzie 2020). This analysis provides a case study where substantial uncertainties surrounding an inland recreational fishery are confronted by integrating best available information into management decision-making. The use of population dynamics modeling and decision analysis enabled alternative regulatory scenarios to be proactively evaluated in a way that demonstrated the relative benefits, risks, and trade-offs between the different potential management actions (Peterson and Evans 2003; Jones and Bence 2009; van Poorten and MacKenzie 2020). Taken together, this analysis is a valuable tool that not only allowed the quantification of objectives, assumptions, and uncertainties, but can serve as a meaningful management tool that can be directly applied to real world management decision-making within the province of British Columbia.

Table 4.1 Fixed parameters used within the bull trout recreational fishery operating model. Index values are presented as a range of values.

Parameter	Value	Description	Source
Indices			
st	1, 2, 3, … 5	Number of stocks	
a	A_R, A_R +1, A_R +2, … A	Age class: A = 15, age of recruitment to fishery, A_R = 5	
z	1, 2, 3…7	Number of spatial areas	
s	1, 2	Seasons	
y	0 - initialization	Years	
	1,2,3… 20 - dynamic model		
d_s		Asymptotic initial population distribution across areas	
j	1, 2, 3, … 7	Transition state of departure	
k	1, 2, 3, … 7	Transition state of arrival	
$\theta_{s,j,k}$	See Chapter 3	Movement / transition matrices	
Parameters estimated from data			
$L_{\infty_{st}}$	$L_{\infty_1=}$ 650.73	Initial stock-specific von Bertalanffy asymptotic length	
	$L_{\infty_2=}$ 578.03		
	$L_{\infty_3=}$ 578.03		
	$L_{\infty_4=}$ 645.04		
	$L_{\infty_5=}$ 622.91		
K_{st}	$K_1 = 0.24$	Stock-specific von Bertalanffy growth parameter	
	$K_2 = 0.31$		
	$K_3 = 0.31$		
	$K_4 = 0.24$		
	$K_5 = 0.25$		
CR	5.94	Goodyear compensation ratio	Chudnow et al. (2018)
M		Instantaneous natural mortality rate	Chapter 3
Parameters on literature and expert opinion			
α_f	$1.72e^{-3}$	Scalar of length-fecundity function	Johnston (2005)
β_f	2.31	Power parameter of length-fecundity function	Johnston (2005)
α_S	20	Slope parameter in logistic selectivity function	Expert opinion
β_S	350	Length at 50% selectivity to angling gear	Expert opinion

Table 4.1 (*Continued*)

Parameter	Value	Description	Source
Indices			
α_m	1.1	Slope parameter for logistic maturity function	Expert opinion
β_m	1.8	Logistic function parameter for maturity	Expert opinion
$CPUE_{O_{z=6}}$	2	Maximum possible catch rate (area 6)	Expert opinion
$CPUE_{quit}$	0.5	Minimum CPUE before angler leaves fishery	Expert opinion
$E_{max_{(z=6)}}$	150	Maximum possible directed fishing effort (area 6)	Expert opinion
E_{grow}		Rate of effort growth	Expert opinion
E_{NT}		Effort directed toward species other than bull trout	Expert opinion
w_{keep}	0.5	Importance of harvest	Expert opinion
h	0.85	Hyperstability	Expert opinion
M_r	0.1	Release mortality rate	Post et al. (2003)
M_{nc}	0.1	Non-compliance mortality rate	Post et al. (2003)
Ω_t	0.6	Recruitment variation	Expert opinion
cv	0.1	Coefficient of variation for length	van Poorten and MacKenzie (2020)
Management controls			
BL_z	1, 3	Bag limit (per day)	
$MinLL_z$	30, 50	Length limit (cm)	
$MaxLL_z$	50	Maximum length limit (cm)	
O_z	1 - all regs. excluding spatial closure 0.25 - spatial closure	Proportion of area that was open to harvest	

Table 4.2 Fishery operating model for generating age-, stock-, and spatially-structured population and harvest dynamics for the fluvial bull trout fishery in the upper Fraser River watershed

Equation number	Description	Equation	Conditions
T4.2.1	Derived from data	$\Theta = \{L_{\infty_{st}}, K_{st}, CR, M\}$	
T4.2.2	Derived from expert opinion or literature	$\varphi = \{\alpha_f, \beta_f, \alpha_s, \beta_s, \alpha_m, \beta_{m,} E_{max_{(z=6)}}, E_{grow}, E_{NT}, w_{keep}, h, M_r, M_{nc}, O_z, CV, \Omega_t\}$	
Initial population			
T4.2.3	Length-at-age	$L_{st,a} = L_{\infty_{st}}(1 - e^{(-K_{st}*a})$	
T4.2.4	Fecundity-at-age (eggs)	$f_{st,a} = \alpha_f L_{st,a}{}^{\beta_f}$	
T4.2.5	Maturity-at-age	$m_{st,a} = \left[1 + e^{\left(\frac{(-(L_{st,a}-\beta_m)}{\alpha_m}\right)}\right]^{-1}$	$A_R \leq$ A
T4.2.6	Capture selectivity-at-age	$sc_{st,a} = \left[1 + e^{\left(-\frac{L_{st,a}-\beta_S}{\alpha_S}\right)}\right]^{-1}$	
T4.2.7	Unfished survivorship-at-age	$lx_{(0)a} = \begin{cases} 1 \\ lx_{(0)a-1}e^{-M} \end{cases}$	$a \leq A_R$ $A_R <$ a $\leq$ A
T4.2.8	Unfished fecundity incidence function	$\emptyset_{(0)_{st}} = d_{s=2,z=7}e^{\frac{-M}{2}}\sum_{a=0}^{A} lx_{(0)a}m_{st,a}f_{st,a}$	

Table 4.2 (*Continued*)

Equation number	Description	Equation	Conditions
Derived parameters			
T4.2.9	Slope of stock-recruit function (Beverton-Holt)	$\alpha_{R_{st}} = \frac{CR}{\emptyset_{(0)st}}$	
T4.2.10	Scaling parameter of stock-recruit function (Beverton-Holt)	$\beta_{R_{st}} = \frac{CR - 1}{R_{0_{st}} \emptyset_{(0)st}}$	
T4.2.11	Initial population distribution	$N_{(0)s,z,st,a} = \begin{cases} R_{0_{st}} lx_{(0)a} d_{z,s=1} \\ \left(R_{0_{st}} lx_{(0)a} e^{-M/2}\right) \theta_{s=2,j,k} \end{cases}$	$s = 1$ $s = 2$
Unfished equilibrium			
T4.2.12	Area specific vulnerable abundance to capture (unfished)	$V_{(0)c_z} = \sum_{AR}^{A} N_{(0)s,z,st,a} sc_{st,a}$	$A_R < a \leq A$
T4.2.13	Area specific vulnerable abundance to harvest (unfished)	$V_{(0)R_z} = \sum_{A_R}^{A} N_{(0)s,z,st,a} sc_{st,a}\, sr_{z,st,a}$	$A_R < a \leq A$
T4.2.14	Catchability	$q = \frac{CPUE_{0(z=6)}}{V_{(0)c_{z=6}}}$	
T4.2.15	Maximum possible targeted fishing effort	$E_{max_z} = \frac{E_{max_{z=6}} E_{p_z}}{E_{p_6}}$	
T4.2.16	Equilibrium CPUE	$CPUE_{0_z} = qV_{(0)c_z}$	

Table 4.2 (*Continued*)

Equation number	Description	Equation	Conditions
Dynamic simulation			
T4.2.17	Recruitment	$R_{y,st} == \begin{cases} R_{0_{st}} \\ \dfrac{\alpha_{R_{st}} * Eggs_{y-A_R-1,st}}{1+\ \beta_{R_{st}} * Eggs_{y-A_R-1,st}} e^{\Omega_t} \end{cases}$	$y < A_R + 1$ $y \geq A_R + 1$
T4.2.18	Abundance	$N_{y,s,z,st,a} = \begin{cases} R_{y,st} * d_{z,s=1} \\ N_{y-1,s=2,k,st,a} e^{-M/2} \theta_{s=2,j,k,} \\ N^*{}_{y,s=1,k,st,a} e^{-M/2} \theta_{s=1,j,k} \end{cases}$	$a = A_R$ $A_R\ \leq$ A $A_R\ \leq$ A
T4.2.19	Harvest selectivity-at-age	$sr_{z,st,a} = \left[1+e^{\left(\frac{-1.7(L_{st,a}-MinLL_z)}{L_{st,a}CV}\right)}\right]^{-1} - \left[1+e^{\left(\frac{-1.7(L_{st,a}-MaxLL_z)}{L_{st,a}CV}\right)}\right]^{-1}$	
T4.2.20	Vulnerability to capture / vulnerable abundance	$V_{C_{y,z}} = \sum_{AR}^{A} N^*{}_{s=2,st,a} sc_{st,a}$	A_R < a ≤ A
T4.2.21	Vulnerability to harvest / vulnerable abundance	$V_{R_{y,z}} = \sum_{AR}^{A} N^*{}_{s=2,st,a} sc_{st,a}\ sr_{z,st,a}$	
T4.2.22	Catch importance	$wCPUE_{y,z} = CPUE_{0_z} \left[\left(\frac{w_{keep} V_{R_{y,z}}}{V_{(0)R_z}}\right) + \left(\frac{(1-w_{keep}) V_{C_{y,z}}}{V_{(0)c_z}}\right)\right]^h$	
T4.2.23	Effort	$E_{y,z} = \max\left(E_{NT}, \left((1-E_{grow})E_{y-1,z}\right) + \left(E_{grow} E_{max_z} (wCPUE_{y,z} - CPUE_{quit})\right)\right)$	

Table 4.2 (*Continued*)

Equation number	Description	Equation	Conditions
T4.2.24	Density-dependent catchability	$q_{y,z} = q\left(\frac{V_{C_{y,z}}}{V_{(0)C_z}}\right)^{h-1}$	
T4.2.25	Catch per unit effort under MLL regulations	$CPUE_{min_{y,z}} = CPUE_{0_z}\left(\frac{V_{R_{y,z}}}{V_{(0)R_z}}\right)^{h}$	
T4.2.26	Probability of retaining a fish	$p_{R_y} = \sum_{y=1}^{20}\left\{\frac{\min(y, BL_z)\left[\frac{\left(CPUE_{min_{y,z}}\right)^{y} e^{\left(-CPUE_{min_{y,z}}\right)}}{y!}\right]}{\left(CPUE_{min_{y,z}}\right)}\right\}$	
T4.2.27	Area-specific total fishing mortality	$F_{st,z,a} = O_z\left[q_{y,z}E_{y,z}sc_{st,a}\left(sr_{z,st,a}p_{R_y} + \left(1 - sr_{z,st,a}p_{R_y}\right)(M_r - M_{nc})\right)\right]$	$O = 1\ (open)$ $O = 0\ (closed)$
T4.2.28	Stock abundance following fishing season	$N_{y,s=2,z,st,a} = N*_{y,s=2,z,st,a}\, e^{-F_{st,z,a}}$	
T4.2.29	Stock-specific egg production	$Eggs_{y,st} = \sum_{a=0}^{A} N_{y,s=2,z=7,st,a}m_{st,a}f_{st,a}$	
T4.2.30	Stock-specific recruits per spawner	$\emptyset_{(F),y,z} = \sum_{a=AR}^{A}\left(\frac{Eggs_{y,st}}{R_{y-(AR:A)+AR,st}}\right)$	

Table 4.3 Possible management controls for recreational bull trout fishery in the upper Fraser River watershed.

	Input controls	*Output controls*	
Scenario	**Spatial / temporal closures**	**Length limits**	**Harvest (bag) limits**
C&R: Maintain status quo	August 15 - October 15 (areas 1 & 2) April 1 – June 30 (area 7, tributaries)	Slot limit (30 - 50cm) (areas 1 & 2)	1 fish per angler per day (areas 1 & 2) Catch-and-release (areas 3 - 7)
BL3: Bag limit of 3 / day (Nechako)	August 15 - October 15 (areas 1 & 2) April 1 - June 30 (area 7, tributaries)	Slot limit (30 - 50cm) (areas 1 & 2)	1 fish per angler per day (areas 1 & 2) 3 fish per angler per day (areas 3, 4, & 6) Catch-and-release (areas 5 & 7)
BL1: Bag limit of 1 / day (Nechako)	August 15 - October 15 (areas 1 & 2) April 1 - June 30 (area 7, tributaries)	Slot limit (30 - 50cm) (areas 1 & 2)	1 fish per angler per day (areas 1 - 4, & 6) Catch-and-release (areas 5 & 7)
LBL: Bag & length limit (Nechako)	August 15 - October 15 (areas 1 & 2) April 1 - June 30 (area 7, tributaries)	Slot limit (30- 50cm) (areas 1 & 2) Minimum length limit (50cm) (areas 3,4, & 6)	1 fish per angler per day (areas 1 - 4, & 6) Catch-and-release (areas 5 & 7)
SC: Spatial closure (tributaries)	August 15 - October 15 (areas 1 & 2) April 1 - June 30 and September - October (area 7, tributaries)	Slot limit (30 - 50cm) (areas 1 & 2)	1 fish per angler per day (areas 1 & 2) Catch-and-release (areas 3 - 7)

Table 4.4 Average angler satisfaction across spatial areas given hypotheses of the relative importance of harvest of bull trout on angler catch per unit effort and resulting effort and regulatory actions taken to achieve management goals (rows). Value in bold indicates the maximum expected value.

Regulatory scenario	**W_{keep} = 0.25**	**W_{keep} = 0.5**	**W_{keep} = 0.75**	**Expected Value**
Prior model weight	0.25	0.50	0.25	
Status quo	0.579	0.398	0.194	0.393
Bag limit (3 / day)	0.491	0.430	0.370	0.430
Bag limit (1 / day)	0.555	0.489	0.429	*0.491*
1 > 50cm / day	0.556	0.488	0.430	0.491
1 > 50cm / day & area closure	0.641	0.546	0.452	**0.546**

Table 4.5 Probability of failing to meet conservation performance indicator threshold (i.e., SPR < 0.4) for each bull trout stock given hypotheses of the relative importance of harvest on angler catch per unit effort and resulting effort and regulatory actions taken to achieve management goals (rows). Values in bold indicate the maximum expected values.

Regulatory scenario	**Stock**	**W_{keep} = 0.25**	**W_{keep} = 0.5**	**W_{keep} = 0.75**	**Expected value**
Prior model weight		0.25	0.50	0.25	
Status quo	Chalco Creek	0.904	0.709	0.267	**0.647**
	Goat River	0.879	0.682	0.242	**0.621**
	Milk River	0.878	0.684	0.243	**0.622**
	Outgroup	0.899	0.714	0.275	**0.650**
	Walker Creek	0.902	0.711	0.271	**0.649**
Bag limit (3 / day)	Chalco Creek	0.987	0.978	0.952	0.974
	Goat River	0.985	0.972	0.905	0.958
	Milk River	0.985	0.971	0.904	0.958
	Outgroup	0.988	0.977	0.944	0.971
	Walker Creek	0.988	0.978	0.948	0.973
Bag limit (1 / day)	Chalco Creek	0.982	0.954	0.764	0.914
	Goat River	0.974	0.926	0.694	0.880
	Milk River	0.974	0.924	0.707	0.882
	Outgroup	0.981	0.949	0.777	0.914
	Walker Creek	0.981	0.952	0.784	0.917
1 > 50cm / day	Chalco Creek	0.981	0.954	0.772	0.915
	Goat River	0.974	0.922	0.699	0.879
	Milk River	0.975	0.921	0.709	0.882
	Outgroup	0.980	0.947	0.784	0.915
	Walker Creek	0.981	0.952	0.788	0.919
1 > 50cm / day & area closure	Chalco Creek	0.822	0.694	0.553	0.690
	Goat River	0.730	0.619	0.513	0.620
	Milk River	0.733	0.627	0.513	0.625
	Outgroup	0.817	0.718	0.578	0.708
	Walker Creek	0.824	0.718	0.579	0.710

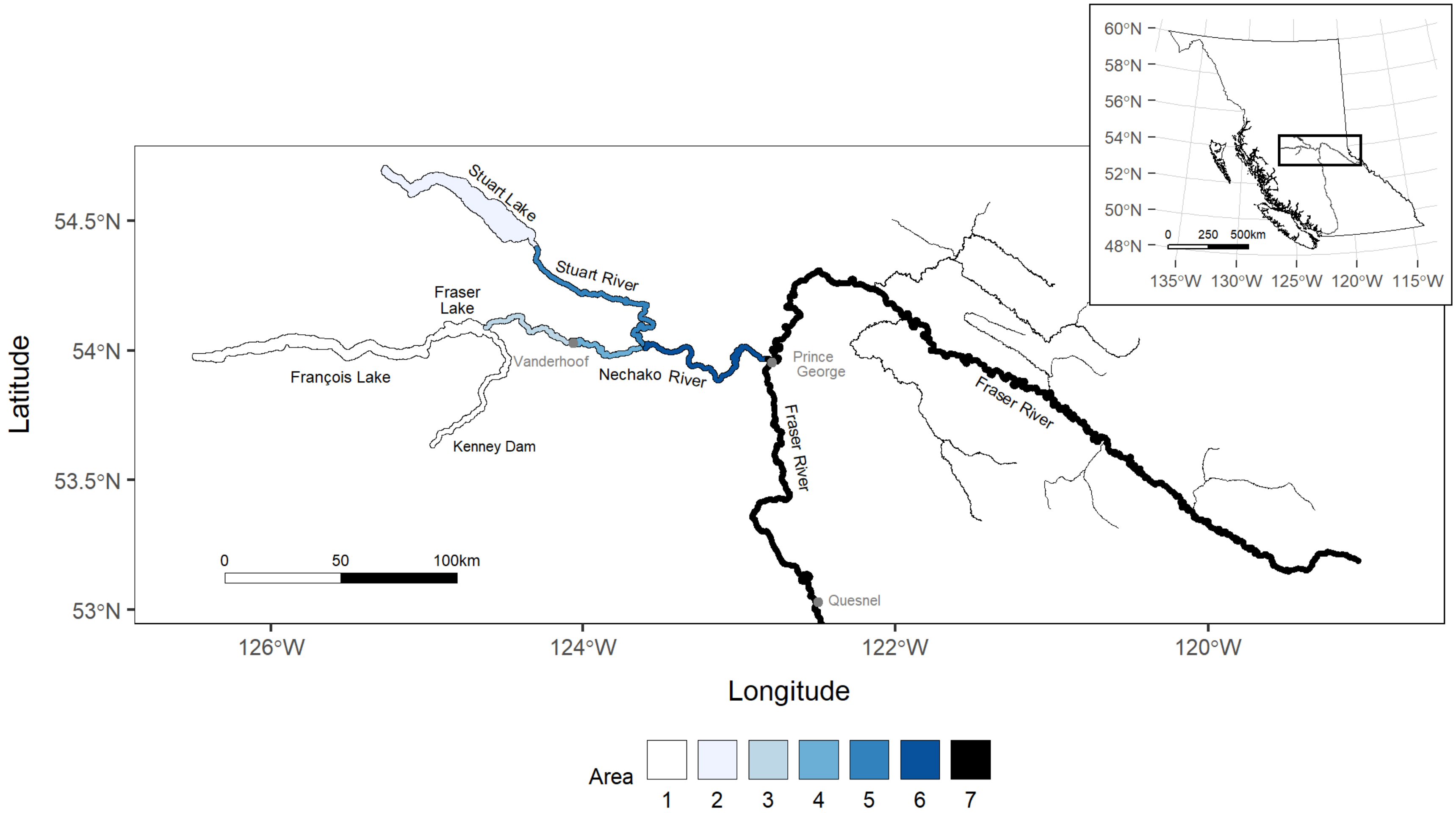

Figure 4.1 Overview map of the bull trout study area within the upper Fraser River watershed (UFW). Seven spatial areas within the study area are represented in colour, population centres are identified by grey circles.

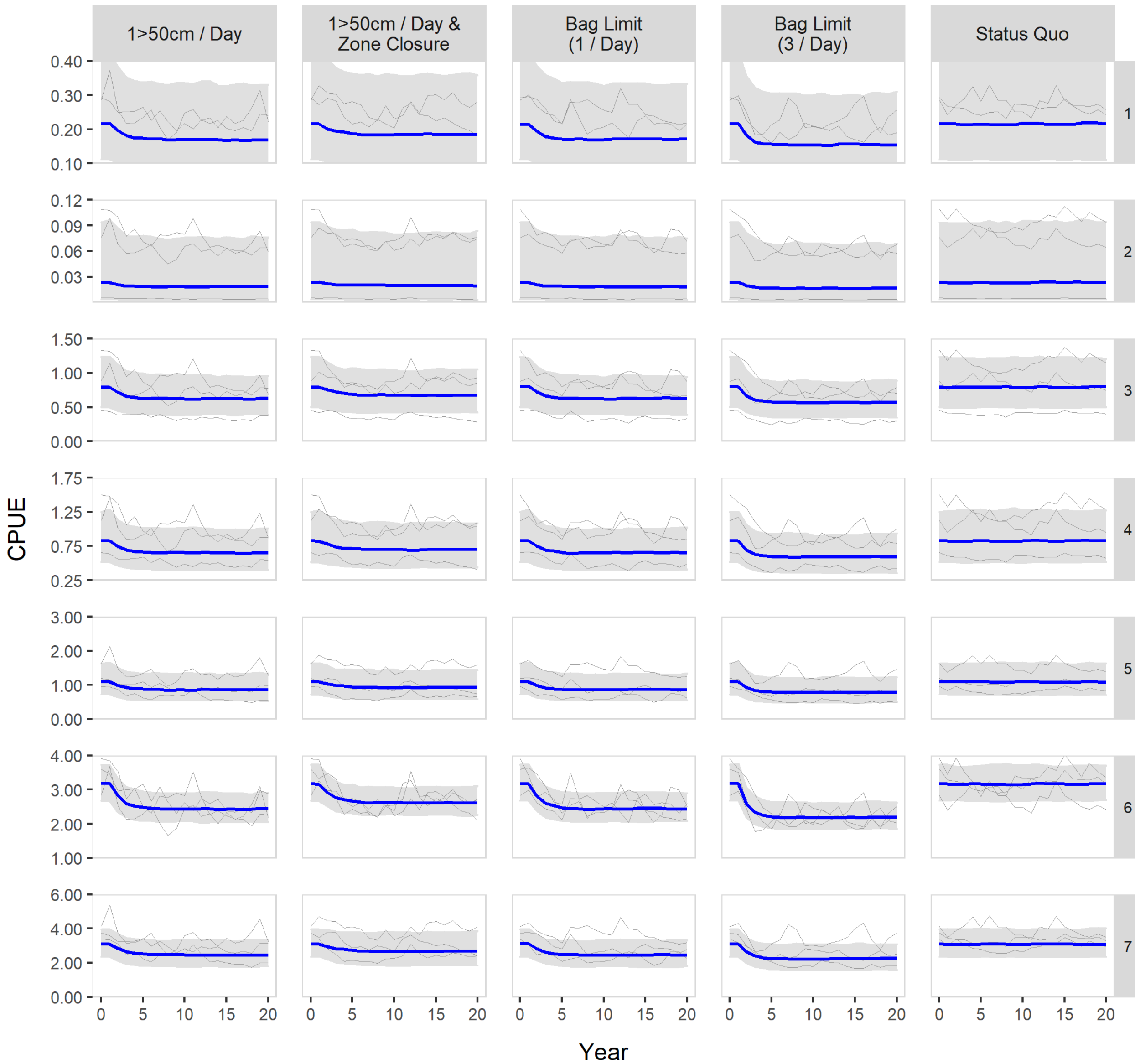

Figure 4.2 Projected time-series of area-specific angling catch per unit effort (CPUE) under alternative regulatory scenarios for the upper Fraser River watershed fluvial bull trout fishery. Columns represent regulatory scenarios and rows represent outputs for each of the seven spatial areas. Note axes ranges differ across areas. Blue lines represent median projections, grey shaded areas represent 80% quantiles, and grey lines represent three of the 1000 simulated model outputs.

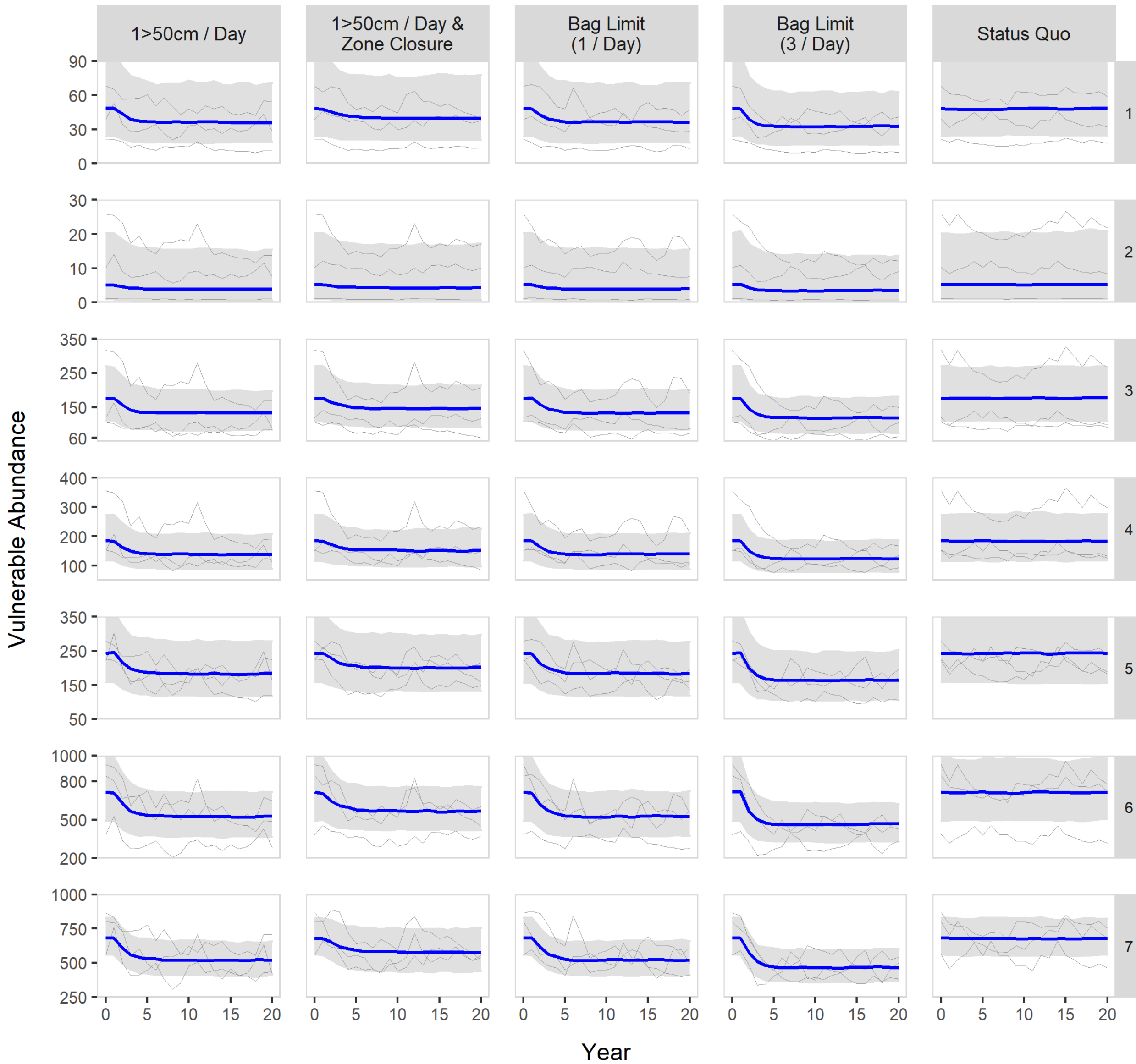

Figure 4.3 Projected time-series of area-specific vulnerable bull trout abundance under alternative regulatory scenarios for the upper Fraser River watershed fluvial bull trout fishery. Columns represent regulatory scenarios and rows represent outputs for each of the seven spatial areas. Note axes ranges differ across areas. Blue lines represent median projections, grey shaded areas represent 80% quantiles, and grey lines represent three of the 1000 simulated model outputs.

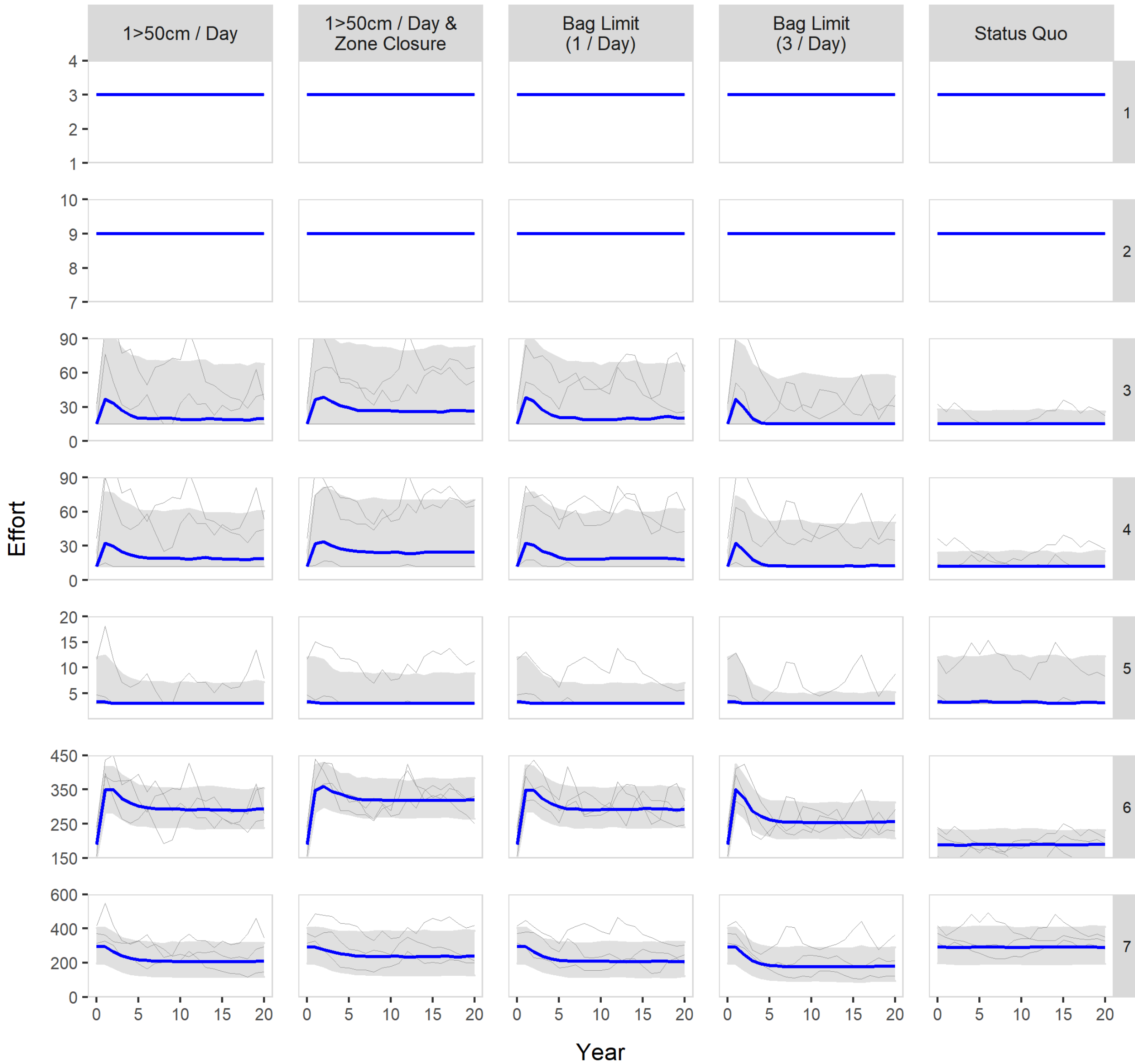

Figure 4.4 Projected time-series of area-specific angling effort under alternative regulatory scenarios for the upper Fraser River watershed fluvial bull trout fishery. Columns represent regulatory scenarios and rows represent outputs for each of the seven spatial areas. Note axes ranges differ across areas. Blue lines represent median projections, grey shaded areas represent 80% quantiles, and grey lines represent three of the 1000 simulated model outputs.

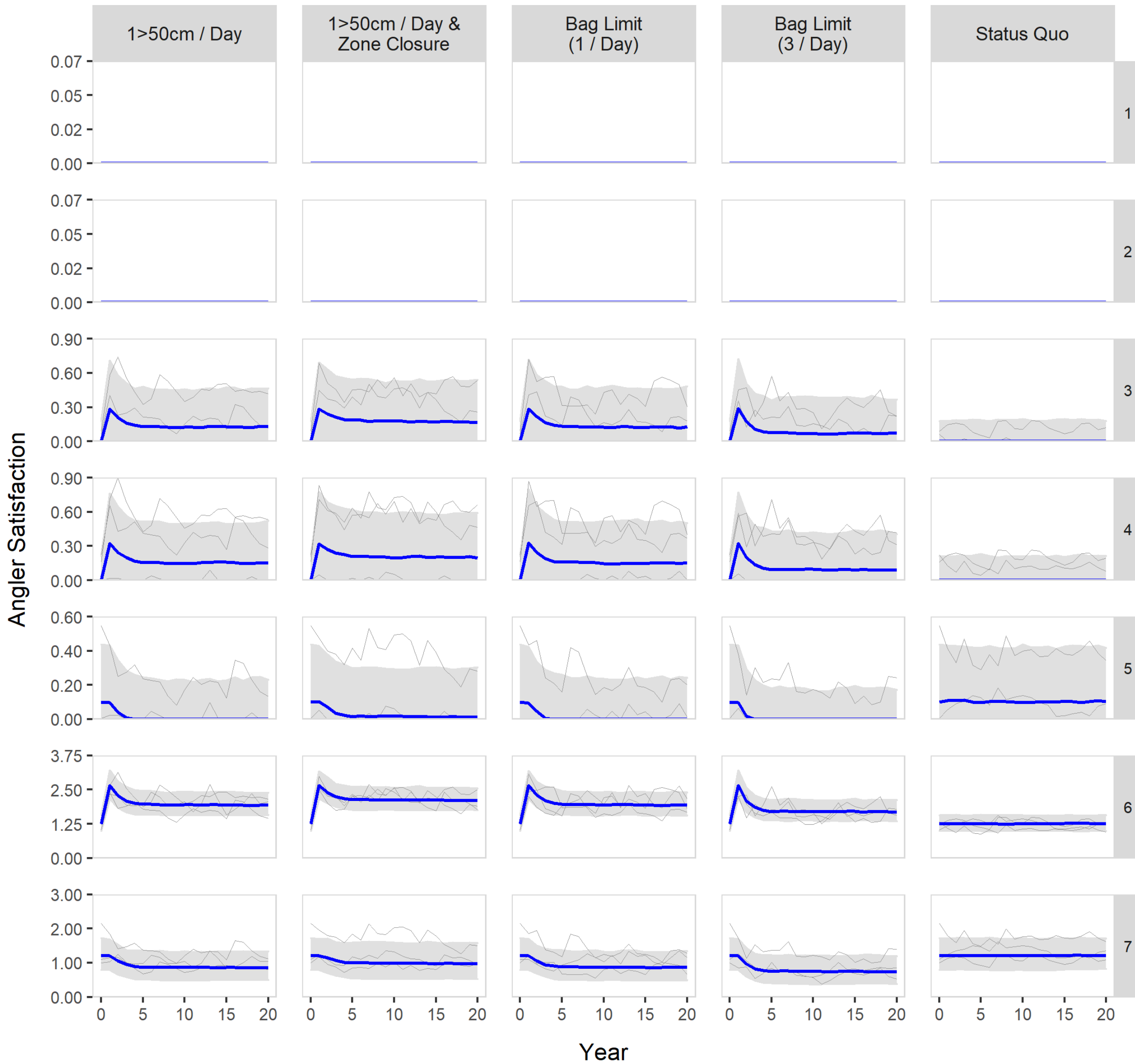

Figure 4.5 Projected time-series of area-specific angler satisfaction under alternative regulatory scenarios for the upper Fraser River watershed fluvial bull trout fishery. Columns represent regulatory scenarios and rows represent outputs for each of the seven spatial areas. Note axes ranges differ across areas. Blue lines represent median projections, grey shaded areas represent 80% quantiles, and grey lines represent three of the 1000 simulated model outputs.

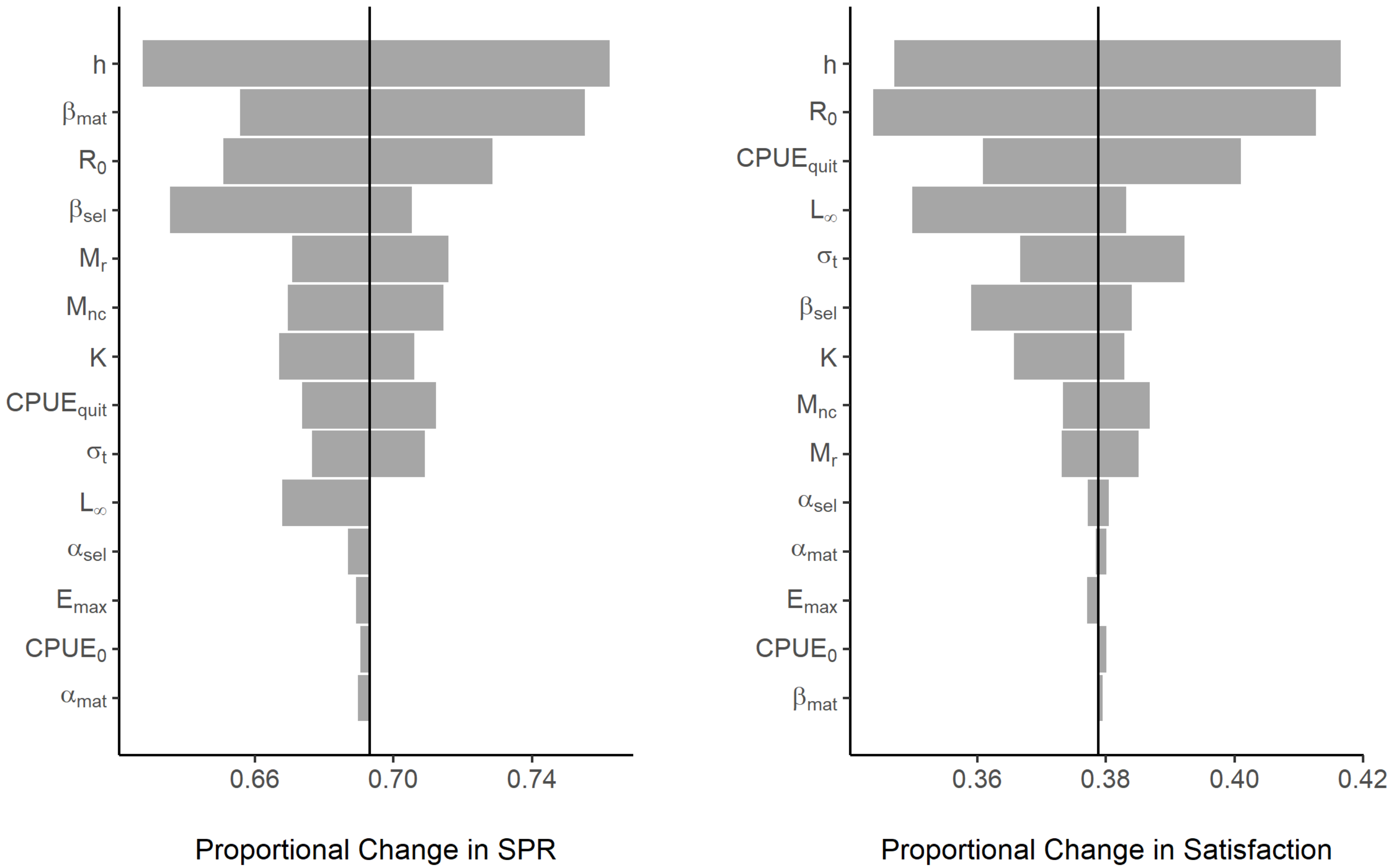

Figure 4.6 Tornado plots showing proportional change in objective functions for the conservation objective (i.e., proportion of 1000 model runs with SPR < 0.4) and angler satisfaction (mean angler satisfaction across spatial areas and the twenty-year time horizon) within a one-way sensitivity analysis for the upper Fraser River watershed fluvial bull trout fishery under the baseline assumption of the current state of nature (w_{keep} = 0.5) and current fishery regulations (status quo). Parameters are listed from greatest (top) to least (bottom) influence on objective functions.

Chapter 5: General discussion and conclusions

Recreational fisheries management operates in complex socio-ecological systems where conflicting objectives relating to resource conservation, provision of angling opportunities, and maintenance of angler satisfaction must be balanced (Walters and Martell 2004; Lorenzen et al. 2016; Lynch et al. 2017). The decision-making process is also confronted by substantial uncertainties surrounding aspects of species biology, the state of the fishery, and how fish and anglers respond to changes in the system due to naturally occurring perturbations, regulatory actions, and anthropogenic impacts outside their control (Walters and Martell 2004; Lorenzen et al. 2016; Lynch et al. 2017). Agencies manage these dynamic natural-human systems for multiple species, across large spatial areas, and with limited budgets and resources to undertake research to inform their decision-making processes (Pereira and Hansen 2003; Lorenzen et al. 2016). As a result, recreational fisheries management often relies heavily on past experience and institutional expertise (Powers et al. 1975; Hilborn and Walters 1992; Pereira and Hansen 2003).

This dissertation comprised a suite of analyses that clarify unknowns surrounding the ecological and fishery dynamics of an inland recreational fishery. These results can be used to actively inform management decision-making. Specifically, this dissertation focused on addressing critical uncertainties surrounding the biology and sustainable recreational fishery management for fluvial bull trout in the upper Fraser River watershed of British Columbia, by:

- Quantifying compensatory capacity of bull trout for improvements in juvenile survival using the Goodyear compensation ratio (Goodyear 1977, 1980);

- Estimating apparent survival and seasonal- and stock-specific spatial-temporal variation in bull trout movement probabilities within the upper Fraser River watershed;

- Predicting population dynamics for a population complex of fluvial bull trout within the upper Fraser River watershed;

- Using decision analysis to evaluate the efficacy of alternative management actions in meeting fishery objectives while explicitly accounting for assumptions as well as parameter and state uncertainties.

5.1 Research summary

5.1.1 Chapter 2: Estimating cross-population variation in juvenile compensation in survival for bull trout (*Salvelinus confluentus*): a Bayesian hierarchical approach

This chapter developed a hierarchical Bayesian meta-analysis to estimate the Goodyear compensation ratio (*CR*) and explore the functional form of the stock-recruitment relationship for bull trout at the species level (Ricker 1954; Beverton and Holt 1957; Goodyear 1980). The relationship between spawning stock abundance and subsequent recruitment is a critical consideration within population dynamics modeling and has significant implications for stock productivity and appropriate management (Myers et al. 1999; Myers 2002; Walters and Martell 2004). Specifically, estimates of juvenile compensation in survival, quantified as compensation ratio (*CR*), are crucial to aid recovery efforts and develop sustainable fisheries policies (Goodyear 1977; Walters and Martell 2004; Hilborn 2007).

As is common in stock-recruitment modeling, the lack of informative data, specifically the prevalence of short duration time series across limited ranges of stock abundances, led to high variance in *CR* estimates (Hilborn and Walters 1992). Despite these limitations, this analysis resulted in the first cross-population estimate of *CR* for bull trout at the species level. This estimate can serve as an informative prior within stock-recruitment investigations for other unstudied populations or be applied within population modeling where stock-specific estimates of *CR* are not available.

The *CR* estimates within this chapter also provide further evidence that bull trout have high scope for density-dependent compensation as suggested elsewhere (Johnston et al. 2007). This finding supports the idea that changes in habitat quality and quantity are likely limiting recovery of many populations and further demonstrates the importance of habitat conservation and preservation in the management and recovery of this species (Post and Johnston 2002; Hagen and Decker 2011).

Model selection to determine the functional form of the stock-recruitment relationship that best characterizes bull trout was inconclusive. Deviance information criterion (DIC) selection of the Beverton-Holt relationship was demonstrated statistically, but not expected ecologically due to aspects of bull trout behaviour described within the chapter. Where data were more informative, visual inspection of stock recruitment data appeared more consistent with the Ricker relationship. The inability to determine which functional form of the stock-recruitment relationship is appropriate for bull trout and the high variance observed within marginal posterior estimates for *CR* within this analysis highlight the importance of collecting additional paired stock–recruitment data to facilitate future investigations and reduce variance in stock-recruitment estimates for bull trout, and more generally across species.

5.1.2 Chapter 3: Spatial distribution and seasonal movement probability estimates of bull trout (*Salvelinus confluentus*) through a large, uninterrupted river network

Within this chapter, radio telemetry detections and genetic assignment information were used to determine stock-specific seasonal transition (movement) probabilities and apparent survival rates for fluvial bull trout within the upper Fraser River watershed. Though telemetry has been used extensively to explore bull trout movement patterns across the species range, past work has generally been of short duration, occurred in artificially fragmented systems, and not included a spatial modeling component (Muhlfeld and Marotz 2005; Schoby and Keeley 2011; Starcevich et al. 2012). This analysis is one of few multi-year telemetry projects that has tracked multiple bull trout populations across a large, uninterrupted, fluvial stream network (but see Starcevich et al. (2012)). It is also the first to apply the demonstrated modeling technique, Bayesian state-space Cormack Jolly Seber (CJS) capture-recapture modeling, to a population complex of bull trout anywhere across the species range and provides the first estimates of movement (as state transitions) between spatially distinct habitats for this species (Hightower et al. 2001; Lebrenton et al. 2009; Kéry and Schaub 2012).

The use of telemetry detections as ‘virtual recaptures’ within a Bayesian state-space CJS modeling framework is also novel in its application to both this species and within a fluvial freshwater system (Hightower et al. 2001). The analysis permitted collection of a substantial quantity of ‘recapture’ data (>900 detections over six years) without reliance on resource intensive traditional mark-recapture techniques. Thus, demonstrating the feasibility of long-term telemetry tracking for elucidating movement patterns through Cormack-Jolly Seber modeling methods, without a large quantity of traditional mark-recapture information.

The results of this investigation clarify critical uncertainties surrounding bull trout movements within the upper Fraser River watershed, building on limited stream-specific work that has previously been conducted in the system, and with important implications for the species management (Pillipow and Williamson 2004). The finding that multiple populations use the upper Fraser River watershed in similar ways (i.e., stocks demonstrated similar state transitions at the spatial scale investigated), demonstrates that fishing opportunities within mainstem river habitats are mixed stock in nature and have the potential to disproportionally impact less productive populations (Secor 2014; Taylor et al. 2014, 2021). The finding that multiple populations use the same habitats and migration corridors also demonstrates the importance of preserving habitat connectivity and quality, not only for spawning and wintering habitats, but also the large-scale migration corridors that connect them.

Bull trout within the upper Fraser River were found to regularly migrate distances exceeding those identified by past telemetry research (Bahr and Shrimpton 2004; Schoby and Keeley 2011; Starcevich et al. 2012). This finding supports the idea that bull trout are dependent on a variety of spatially segregated habitats and highlights the importance of maintaining habitat quality and complexity across large contiguous riverscapes (Schoby and Keeley 2011; Starcevich et al. 2012; Taylor et al. 2021). Observations of tagged individuals also demonstrated upstream post-spawning migratory behaviour which has previously only been observed in allacustrine bull trout populations and which contrasts patterns generally observed for iteroparous salmonids (DuPont et al. 2007; Watry and Scarnecchia 2008; Starcevich et al. 2012). The observed upstream migratory behaviour supports previous evidence that bull trout are important predators of migrating Pacific salmon smolts within this system, as has been identified elsewhere (Furey et al. 2015; Lowery and Beauchamp 2015; Furey and Hinch 2017). This finding has important implications for the management of both bull trout and Pacific salmon and is an important direction for future work within the study system. For example, management actions resulting in shifts in salmon smolt abundance could drive changes in bull trout behaviour and distribution within the upper Fraser River watershed (Taylor et al. 2021).

Results of this chapter further our understanding of bull trout migratory behaviour and movement patterns within the upper Fraser River watershed specifically. More broadly, these results are also important in improving our understanding of how bull trout population complexes behave within relatively pristine, highly connected watersheds. Beyond this, outputs of this analysis form a foundational piece of the spatially structured population dynamics model and decision analysis developed in Chapter 4.

5.1.3 Chapter 4: Evaluating alternative management actions on fluvial bull trout using decision analysis

This chapter used a stock-, age-, spatially-structured population dynamics model and decision analysis to quantify uncertainties, explore trade-offs, and evaluate how alternative regulations affect fishery objectives. Use of such modeling approaches are now commonplace in the management of many commercial fisheries (Peterman et al. 1998; Mardle and Pascoe 1999;

Leung 2006). In contrast, the approach has had limited application within recreational fisheries management (Jones and Bence 2009; Irwin et al. 2011; van Poorten and MacKenzie 2020). Within recreational fisheries, managers balance conflicting and often poorly specified fishery objectives while confronted with significant uncertainties surrounding the state of the socio-ecological system (Post et al. 2002; Pereira and Hansen 2003; Lynch et al. 2017). As a result, recreational fisheries are often managed passively or reactively in response to observed declines in fished populations or as the result of stakeholder requests (Walters 1986; Pereira and Hansen 2003; Irwin et al. 2011).

The population dynamics model and decision analysis within this chapter are a valuable management tool. They provided a mechanism through which all available information from numerous sources (i.e., Chapter 2 and Chapter 3, expert opinion, and established peer-reviewed literature) could be brought together to simulate the current fluvial bull trout fishery within the upper Fraser River watershed (Post et al. 2003; van Poorten and MacKenzie 2020). The inclusion of movement probabilities from Chapter 3 enabled the exploration of spatially distinct regulatory tools within the fishery. While genetic assignment information from Taylor et al. (2021), permitted evaluation of the performance of alternative regulatory actions on specific stocks of management interest. Overall, this decision analysis provided a framework whereby the managing agency could proactively evaluate the efficacy of alternative regulatory actions in meeting fishery objectives, while directly accounting for uncertainties (Peterman and Anderson 1999; Irwin et al. 2011; van Poorten and MacKenzie 2020). The decision analysis also enabled evaluation of the trade-offs between conservation and angler satisfaction objectives under each regulatory scenario (Robb and Peterman 1998; Irwin et al. 2011; van Poorten and MacKenzie 2020).

The chapter results suggest that current regulations may not be providing the conservation benefit that they were designed to. Findings also suggest that improved angler satisfaction can be achieved by selecting a regulatory strategy that has minimal negative impacts on bull trout conservation when compared to current regulations. This analysis also serves to highlight critical uncertainties that remain. Substantial uncertainty still surrounds elements of bull trout stock-recruitment relationships, the prevalence of depensatory impacts within the fishery due to inverse density-dependent catchability, and aspects of the fishery's human dimension. Human dimensions research to resolve uncertainties regarding the impacts of angler motivations on bull trout within the system and the fishery-specific drivers of angler effort and satisfaction will be critical in further identifying regulations that are capable of meeting fishery objectives. Though considerable uncertainty remains, this analysis serves as an important starting point in the proactive management of this important fishery resource. The models are also flexible and able to be iteratively improved as information becomes available, allowing future data collection to further reduce uncertainties.

5.2 Final remarks and future directions

This dissertation serves as foundational work enabling future exploration of questions specific to bull trout within the upper Fraser River watershed, across the species range, and relating to fisheries management more broadly. For bull trout specifically, as with many recreationally important species, population-specific projects to clarify uncertainties surrounding population dynamics (e.g., redd counts, limited duration telemetry tracking) are not uncommon. These projects, however, rarely integrate collected information within a framework that allows it to be used within management (Welcomme 2001; Pereira and Hansen 2003; Cooke et al. 2014; Lorenzen et al. 2016). As a result, agencies make decisions despite critical uncertainties surrounding population dynamics (e.g., stock productivity, spatial distribution, migratory behaviour, and stock mixing) of the targeted stock(s) and the dynamics of how fish and human populations respond to both changes in the natural system and regulatory actions (Post et al. 2008; Lynch et al. 2017; Camp et al. 2020).

This dissertation confronts the general lack of informative data common within inland, recreational fisheries by using estimates derived from numerous sources (e.g., field sampling, existing research on other populations and related species, and expert consultation) to bring together all available information to inform management decision-making (Fitzgerald et al. 2018; Hommik et al. 2020; Shephard et al. 2020). The dissertation focuses on confronting several uncertainties common within fisheries (e.g., stock productivity, seasonal and stock-specific variation in movement patterns, and mortality) surrounding the biology and behaviour of a fished bull trout population complex. By applying a suite of well-established, quantitative methods to generate estimates of key parameters (e.g., Goodyear compensation ratio (Goodyear 1977)), relationships (e.g., shape of the stock-recruitment function), and processes (e.g., seasonal movements), these uncertainties have been further clarified. The methodologies within this dissertation can all serve as valuable case studies which are broadly applicable across both inland and marine species.

The Bayesian hierarchical analysis within Chapter 2 provides a case study of confronting uncertainty within a data poor situation. Chapter 3 provides an example of using a common field technique, radio telemetry, differently through the use of telemetry detections as ‘virtual recaptures’ within a Bayesian state-space Cormack Jolly Seber model (Hightower et al. 2001; Kéry and Schaub 2012). The work demonstrates the applicability of telemetry and ‘virtual recaptures’ in answering management questions where traditional mark-recapture data are limited. The use of Bayesian approaches within these chapters explicitly accounted for uncertainty in parameter estimates (Kéry and Schaub 2012; Parent et al. 2013; Gelman et al. 2014). The Bayesian approaches are also highly valuable because they permit parameter estimates and observed patterns to be incorporated into future work on bull trout and other related species as informative priors that can further reduce uncertainties (Kéry and Schaub 2012; Parent et al. 2013; Gelman et al. 2014).

Chapter 4 provides a valuable case study of how a diverse assemblage of information, from a variety of sources, can be integrated within management decision-making in a way that demonstrates the relative benefits, risks, and trade-offs between different potential management actions. It further serves to demonstrate that such modeling approaches are not only possible, but highly valuable, in situations that may be perceived as too data poor to permit the methodology’s application (Irwin et al. 2011; van Poorten and MacKenzie 2020). The population dynamics model and decision analysis presented within Chapter 4 may be overly simplistic and required the use of assumptions. Despite their limitations, these models provide a valuable tool that permitted quantification of assumptions and uncertainties resulting from unknowns and noisy, small data sets (Powers et al. 1975; Irwin et al. 2008; van Poorten and MacKenzie 2020). The models also serve as a meaningful management tool that can be directly applied to real world management decision-making within the province of British Columbia.

The chosen methodologies of each chapter were able to confront and clarify substantial uncertainty; however, uncertainty also remained a limiting factor in each of the chapters. The explicit statements of assumptions and remaining uncertainties within each chapter can serve as valuable tools in and of themselves. They direct future attention to what is not known and highlight where investment of additional resources towards data collection can be most beneficial. Finally, the analyses presented within each chapter of this dissertation are flexible and can be iteratively improved as more information becomes available. Together they therefore serve not only as valuable tools in the adaptive growth of management for bull trout within the upper Fraser River watershed and can also be modified for application to other systems and species.

Natural and human systems are inherently dynamic. Angler behaviour, demographic changes, and continued urbanization all have the potential to change the dynamics of how anglers interact with fished populations and challenge the sustainability of recreational fishing opportunities (Post et al. 2002; Lynch et al. 2017; Camp et al. 2020). The ability to evaluate the potential impacts of such changes not only requires a comprehensive understanding of the biology and state of fished populations, but also the interactions of management actions, anglers, and fish (Hartill et al. 2016; Lynch et al. 2017; Camp et al. 2020). The analyses presented within this dissertation provide tools to further clarify uncertainties surrounding these dynamic changes. Methodology within Chapters 2, 3, and 4 can be modified to account for shifts in bull trout population dynamics or applied to other species. While the population dynamics model and decision analysis within Chapter 4 can also be extended to account for additional complexity surrounding angler behaviour and drivers of angler satisfaction, as well as to changes to management objectives within the fishery. These models can explore impacts of management actions across a suite of different objectives and performance indicators, which can support management decision-making over both a changing policy and natural landscape.

Taken together, the research presented within this dissertation, including its application to management decision-making through decision analysis, is unique for the management of bull trout as a species and is relatively innovative within inland recreational fisheries management. The approaches used within this dissertation also have broad applications beyond inland recreational fisheries. In Canada and internationally, many recreational and commercial fisheries lack data to support traditional stock assessment methods and operate without fisheries-specific management objectives and regulatory plans (Pereira and Hansen 2003; Lorenzen et al. 2016; Fitzgerald et al. 2018). Even where agencies have access to fishery dependent and independent data, available information is not directly applied through quantitative population modeling or subsequently within management decision-making (Welcomme 2001; Pereira and Hansen 2003; Cooke et al. 2014). Though the reasons for why this occurs are complex and as diverse as the fisheries themselves, there is generally belief that one cannot proactively conduct quantitative modeling and utilize such models through decision analysis without large amounts of high-quality data (Fitzgerald et al. 2018). This dissertation builds on the growing body of existing work showing that with the right analytic tools (e.g., Bayesian hierarchical approaches for data poor situations), such methodologies are highly valuable even in data-limited situations. They permit not only the quantification of assumptions and uncertainties, but also allow proactive decision-making where managers can explore the impacts of various actions before implementation, resulting in regulations that are robust to uncertainty, defensible, and easily communicated.

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