Assessing the effects of non-native salmonids on Bull Trout (*Salvelinus confluentus*) in Alberta's Rocky Mountain Foothills

by

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Abstract

The rapid decline in global biodiversity threatens the natural resources, food security, health, and livelihoods of current and future generations. Anthropogenic activities, including the introduction of non-native species, habitat fragmentation and alteration, and resource extraction, have exacerbated this decline. One such imperiled species are Bull Trout (*Salvelinus confluentus*), which have exhibited significant declines throughout their range and are expected to decline by >30% over the next 21 years in Alberta. While their decline is attributed to a myriad of threats, the degree to which non-native fishes contribute to their decline is uncertain. The objective of my thesis was to investigate the effects of Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*), two non-native salmonids, on the habitat use and dietary niche of Bull Trout. To address the habitat component, I developed a multi-species N-mixture model using in-stream and land use derived characteristics to assess how Brook Trout and Brown Trout affect Bull Trout abundance in relation to habitat factors. I determined that Brook Trout negatively affect Bull Trout abundance when streams are <11°C and lack habitat complexity. Interactions between Brown Trout and Bull Trout are less certain, but larger, lower elevation streams are likely to see reductions in Bull Trout abundance where Brown Trout invasion is present and likely to occur. To address the dietary component, I employed stable isotope analysis to investigate how Brook Trout and Brown Trout interact with the dietary niche of Bull Trout. I determined that Bull Trout in sympatry with both Brook Trout and Brown Trout undergo a niche shift and are displaced from terrestrial-based resources. Furthermore, potential for competitive exclusion exists when resources are low given all species exhibit a high degree of niche overlap (>80%) when in sympatry and the amount of niche overlap does not decrease between allopatry and sympatry. The findings of my thesis suggest that both Brook Trout and Brown Trout interfere with the resource use of Bull Trout, on multiple levels, and provides practical guidelines for limiting future declines.

Preface

This thesis is an original work by Jacqueline L. Pallard.

Ethics approval for this research project, for which this thesis is a part, was received from the University of Alberta Research Ethics Board, Animal Care and Use Committee “Assessing food web dynamics and niche overlap between Bull Trout and invasive species” AUP00003132_AME2, provincial Fish Research Licenses (20-2208 & 21-2207), and federal Species at Risk Act Permits (20-PCAA-00026 & 21-PCAA-00031).

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Chapter I: General Introduction

The rapid decline in global biodiversity has provoked the current biodiversity crisis, which threatens the natural resources, food security, health, and livelihoods of current and future generations (Costanza et al., 1997; Mannion, 1995; Singh, 2002). This crisis is driven in part by climate change (Bellard et al., 2012; Mantyka-Pringle et al., 2015; Poesch et al., 2016; Rosales, 2008), making the call for bold, transformative action to address these crises extremely urgent. Anthropogenic activities, including the introduction of non-native species, habitat fragmentation and alteration, and resource use, are exacerbating these crises and changing our environment at a rapid rate (Bellard et al., 2012; Pimm et al., 1995; Sala et al., 2000). Consequently, biodiversity is decreasing globally with loss in freshwater systems exceeding the rate of decline in terrestrial ecosystems (Sala et al., 2000). Between 1970 and 2012, freshwater vertebrates declined by 81% (McRae et al., 2017) and are projected to decline by an additional 4% per decade (Ricciardi & Rasmussen, 1999). Salmonids, which are highly sensitive to temperature and flow regimes (Beer & Anderson, 2011; Buisson et al., 2008; Crozier et al., 2008; Pörtner & Farrell, 2008), are at a heightened risk of extirpation and thus their need for conservation is mounting.

Salmonid species require cold, connected, clean, and complex habitat and therefore are indicators for overall ecological functioning and health (Crisp, 2008). With their diverse life cycle, they inextricably link our freshwater, marine, and terrestrial ecosystems, facilitate nutrient flow, and are vital food sources for people and wildlife (Gende et al., 2002; Holtgrieve & Schindler, 2011). This is evident in systems where salmonid populations are thriving, resulting in bear densities that are up to twenty times greater (Reimchen, 2000) and increased scavenger bird abundance (Field & Reynolds, 2013). Subsequently, as predators, salmonids function as top-down control in aquatic ecosystems and their presence is vital to sustaining functioning aquatic food webs and ecosystems (Hammerschlag et al., 2019).

Bull Trout (*Salvelinus confluentus*), a salmonid species native to Western Canada and the Pacific Northwest of the United States, are listed as a species at risk in Canada and the United States and have experienced significant declines in recent decades (COSEWIC, 2012; US Fish and Wildlife Service, 1999). While they can reside from the Pacific Ocean to central Alberta, they are typically restricted to the interior (Haas & McPhail, 1991) with 80% of their global range within western Canada (Rieman et al., 1997). Given their geographical range, Bull Trout have diverse traits and four distinct life histories (McPhail & Baxter, 1996), all of which require returning to headwater or tributary streams in the fall to spawn when stream temperatures are between 5-9°C (Stewart et al., 2007). Given their extensive range, cold spawning temperature requirement, an upper thermal tolerance of 21°C, and an optimal growth temperature of 12-16°C (McMahon et al., 2007; Selong et al., 2001; Stewart et al., 2007), Bull Trout are extremely vulnerable to climatic and environmental changes. In Canada, where there are five recognized Designatable Units of Bull Trout, two are assessed as Special Concern and one as Threatened, the Saskatchewan - Nelson Rivers population (COSEWIC, 2012).

Alberta's Saskatchewan - Nelson Rivers population of Bull Trout extended as far east as Edmonton in the North Saskatchewan River; however, their range is contracting with many downstream populations extirpated (Fisheries and Oceans Canada, 2020; Sinnatamby et al., 2020). It is expected that over the next 21 years, Bull Trout in Alberta will decline by >30% (COSEWIC, 2012; Fisheries and Oceans Canada, 2020). Their decline in Alberta is largely attributed to habitat fragmentation and alteration, exploitation, and competition with non-native salmonids such as Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) (COSEWIC, 2012; Fisheries and Oceans Canada, 2020; M. Rodtka et al., 2009; Sawatzky & Secretariat, 2016). While angling pressure has decreased since 1995, when mandatory catch and release of the species was implemented in Alberta (Sinnatamby et al., 2020), Bull Trout populations continue to decline likely due to the cumulative effect of these threats.

Brook Trout and Brown Trout, two salmonid species native to eastern North America and Europe respectively, were both introduced to Alberta in the early 1900s to improve recreational fishing for arriving European and eastern Canadian settlers (Colpitts, 1997). Since their introduction, both Brook Trout and Brown Trout have established self-sustaining populations and are considered a naturalized species by Alberta Environment and Parks (COSEWIC, 2012). Like Bull Trout, both species are temperature sensitive (MacCrimmon & Campbell, 1969; Smialek et al., 2021), are opportunistic feeders (Lobón-Cerviá & Sanz, 2017; Raleigh, 1982), need in-stream cover (Raleigh, 1982), and use gravel substrate to spawn in the fall (Greeley, 1932). And while there is clear overlap between Bull Trout and these two non-native salmonids, there is conflicting evidence over whether their introduction is a primary cause of Bull Trout decline in Alberta.

Studies in the United States and Canada have identified Brook Trout as a threat to Bull Trout through hybridization (Kanda et al., 2002; Leary et al., 1993), dietary interspecific aggression (Gunckel et al., 2002; McMahon et al., 2007; Warnock & Rasmussen, 2013b), and displacement (Paul & Post, 2001; Rieman et al., 2006; Warnock & Rasmussen, 2013a). However, as displacement was negatively associated with elevation, positively associated with temperature, and highly spatially variable (Rieman et al., 2006; Warnock & Rasmussen, 2013a), it is not easy to differentiate whether Bull Trout are replaced or displaced (J. B. Dunham et al., 2002). While there is considerable evidence of the threats Brook Trout pose to Bull Trout in Canada, there is little research on the effects of Brown Trout when all three species are in sympatry. Yet, in Japan, where both Brook Trout and Brown Trout are introduced, Brown Trout have displaced populations of Whitespotted Charr *(Salvelinus leucomaenis*) and Dolly Varden (*Salvelinus malma*), a close relative of Bull Trout (Hasegawa, 2017; Hasegawa et al., 2004; Hasegawa & Maekawa, 2006; Kitano, 2004; Takami et al., 2002), and are globally recognized as one of the world's top 100 invasive alien species (Lowe et al., 2000).

The overall objective of my thesis was to assess the interactive effects of Brook Trout and Brown Trout on Bull Trout populations where all three species co-exist. In the first chapter, my objective was to determine the in-stream and land use characteristics that best predict Bull Trout abundance when in allopatry and sympatry with Brook Trout and Brown Trout and then see if Brook Trout and Brown Trout have similar habitat preferences that may allude to competition for resources. To do so, I gathered data through electrofishing surveys, habitat surveys, geospatial data, and employed a multi-species N-mixture model that accounts for spatial variance in abundance, overdispersion in count data, imperfect detection, and directional interactions between species. In the second chapter, my objective was to assess how Brook Trout and Brown Trout interact with the dietary niche of Bull Trout. To do so, I assessed the food web dynamics of various streams at five different levels of invasion: (1) Bull Trout dominant, (2) Brook Trout dominant, (3) Brown Trout dominant, (4) Brook Trout and Bull Trout mix, and (5) Bull Trout, Brook Trout, and Brown Trout mix. I then used stable isotope analysis to determine two standard metrics, trophic position, and proportion of terrestrial carbon, and Bayesian analysis to determine the niche width and niche overlap of the three salmonid species. Collectively, this work helps decipher the extent to which Brook Trout and Brown Trout are contributing to Bull Trout declines in Alberta.

Chapter II: Are Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*), displacing Bull Trout (*Salvelinus confluentus*) in Alberta's foothills?

2.1 Introduction

Freshwater biodiversity is undergoing rapid decline from a large number of threats, including climate change, anthropogenic development, infectious diseases, and harmful algal blooms (Dudgeon et al., 2006; Reid et al., 2019). One of the other major threats to freshwater biodiversity is the spread of invasive species (Dudgeon et al., 2006; Gallardo et al., 2016; Moyle & Light, 1996; Reid et al., 2019; Strayer, 2010). Invasive species are species that are not found in their introduced location and cause ecological or economic harm (Mack et al., 2000). Whether released intentionally for recreational fishing (i.e., stocking), to help fight other problem species (i.e. biological control), or accidentally (e.g. bait fish, pet release), the movement of invasive species has altered local flora and fauna globally (Levine & D'Antonio, 2003; Perrings et al., 2005).

Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*), once only native to eastern North America and Europe respectively, are globally introduced and are some of the most pervasive invasive species (Elliott, 1994; Welcomme, 1988). Both species are widely sought after by recreational anglers, which has enhanced their spread through stocking programs to supply anglers with more opportunities (Donald, 1987; MacCrimmon & Campbell, 1969). However, some of the characteristics that make them sought after by anglers (i.e., fast growing and reach maturation quickly) , also make them prolific reproducers and strong competitors with native fishes (Dunham et al., 2002; Lobón-Cerviá & Sanz, 2017; Raleigh, 1982). Globally, Brook Trout have displaced Cutthroat Trout (*Oncorhynchus clarkii*) in North America and pose threats to native charr through hybridization (Adams et al., 2000; J. B. Dunham et al., 2002; Fukui et al., 2021; Kitano et al., 2014; Lobón-Cerviá & Sanz, 2017; Raleigh, 1982). Similarly, Brown Trout have displaced native Brook Trout in eastern United States (Fausch & White, 1981; Waters, 1983), White-spotted Char (*Salvelinus leucomaenis*) and Dolly Varden (*Salvelinus malma*) in Japan (Kitano, 2004; Takami et al., 2002), and pose threats to native fish in many other countries (McDowall et al., 2001; Pascual et al., 2007; Townsend, 1996).

Since Brook Trout and Brown Trout were introduced to western North America both species have established self-sustaining populations and impacted native Bull Trout (*Salvelinus* *confluentus*) populations (Fausch & White, 1981; Rieman et al., 2006; Warnock & Rasmussen, 2013a). Bull Trout, a salmonid species native to Western Canada and the Pacific Northwest of the United States, are a Threatened species in Alberta (Post & Gow, 2012). They are one of the most thermally sensitive salmonids and are geographically limited by this (Kovach et al., 2019; Selong et al., 2001). Although they are limited to cold water streams, they occupy diverse habitats within them depending on their life history and maturity (Haas & McPhail, 1991; McPhail & Baxter, 1996; Rieman et al., 1997). Through interaction with several impacts, including habitat fragmentation and alteration, exploitation, and competition with non-native fishes, many of Alberta's downstream populations are already extirpated (Fisheries and Oceans Canada, 2020; Post & Gow, 2012; Rodtka et al., 2009; Sawatzky & Secretariat, 2016; Sinnatamby et al., 2020).

Although non-native fishes are recognized as threat to Bull Trout populations, how they affect Bull Trout habitat use is unclear. While Brook Trout invasion success appears to generally decrease with elevation and increase with temperature (Paul & Post, 2001; Rieman et al., 2006; Warnock & Rasmussen, 2013a), this result is highly variable between streams, and laboratory studies assessing the effects of temperature on competitive interactions do not fully support this (McMahon et al., 2007; Rieman et al., 2006; Rodtka & Volpe, 2007). To reconcile these conflicting results, many studies have investigated how stream structure affects invasion success. These studies found that streams of smaller size, with lower in-stream cover, smaller substrate, and slower flows increase Brook Trout invasion success (Benjamin et al., 2007; Rich et al., 2003; Warnock & Rasmussen, 2013a; Wenger et al., 2011). Similarly, Brown Trout invasion success is positively associated with temperature. However, it is thought that Brown Trout colonize streams where Bull Trout have already been extirpated as a result of rising stream temperature (Al-Chokhachy et al., 2016). Other studies investigating the invasion success of Brown Trout found that high spring flow, in-stream barriers, smaller streams, and anchor ice limit their upstream invasion success in North America (Bozek & Hubert, 1992; Kirk et al., 2018; Meredith et al., 2017; Wood & Budy, 2009). However, there is no research on how stream structure or landscape effects influence Brown Trout invasion success in Alberta specifically.

The aim of this study is to disentangle whether Brook Trout and Brown Trout are spatially displacing or replacing Bull Trout in Alberta's foothills. Hereafter, we refer to displacement as the local extirpation of a native species due a non-native species. We refer to replacement as the local extirpation of the native species, irrespective of non-native species, followed by local colonization by a non-native species. Our objectives were to (1) develop a multi-species N-mixture model using in-stream and land use derived characteristics to predict Bull Trout abundance when in allopatry and sympatry with Brook Trout and Brown Trout (2) compare the allopatric and sympatric sub-models to identify key characteristics to help guide management efforts. Based on past studies assessing the factors associated with invasion success of Brook Trout and Brown Trout mentioned previously, we hypothesized that the relationship between Bull Trout abundance and individual habitat covariates will depend on whether they are allopatric or sympatric (Appendix A). Specifically, we predict that elevation, stream temperature, wetted width, proportion of pool, proportion of boulder, and large woody debris count will significantly affect allopatric Bull Trout abundance (Al-Chokhachy et al., 2016, p.; Bonneau & Scarnecchia, 1998; Post & Gow, 2012; Rich et al., 2003; Selong et al., 2001; Watson & Hillman, 1997). We predict that sympatric Bull Trout abundance will benefit in streams of higher elevation, with colder temperatures, higher large woody debris count, and higher proportions of pool and boulder (Al-Chokhachy et al., 2016; Bozek & Hubert, 1992; Kirk et al., 2018; Paul & Post, 2001; Warnock & Rasmussen, 2013a; Wood & Budy, 2009).

2.2 Methods

2.2.1 Study area and design

Our study area is located within the Saskatchewan - Nelson Rivers, where Bull Trout is listed as a Threatened species (Fisheries and Oceans Canada, 2020). We selected headwater streams to the Red Deer River and North Saskatchewan River within the range of Bull based on historical electrofishing records (Alberta Environment and Parks, 2022) and local knowledge (K. Kure, personal communication, 2020) to encompass various levels of invasion of Brook Trout and Brown Trout (Figure 2.1). The 12 waterbodies include Yara Creek, Wildhorse Creek, North Burnt Timber Creek, Wilson Creek, Pineneedle Creek, Rocky Creek, Cutoff Creek, Elk Creek, Trout Creek, Rough Creek, Teepee Pole Creek, and Fallentimber Creek.

2.2.2 Data collection

We sampled a total of 44 sites within 12 streams between July and August of 2020 and 2021. Following Alberta's small stream protocol, we divided each site into six 50m transects for a total linear distance of 300m (Alberta Environment and Sustainable Resource Development, 2013). Employing a systematic sampling design, we sampled downstream to upstream using a Smith-Root LR24 backpack unit. Fish were identified, weighed to the nearest gram, and measured for both fork length and total length to the nearest mm. All fish that were not retained we released at least 25m downstream of the start of the next electrofishing transect to avoid recapture and inflated count data.

Immediately following fish sampling, we conducted a habitat survey within each electrofishing transect (T1-T6). At the start of the site (T0) we measured water temperature (°C) and conductivity (uS/cm) using a Pro Plus Multiparameter probe (YSI, Yellow Springs, Ohio) and air temperature with a thermometer (°C). We measured depth, wetted width, and rooted width to the nearest cm using a meter stick and tape measure. Throughout each transect we visually estimated the proportion of pool, riffle, and run to the nearest percent for a total of 100% and the amount of canopy cover as low (<25%), medium (25-75%), or high (>75%) as per Rich et al. (2003). Using a modified Wentworth scale (Cummins, 1962) we visually estimated the amount of silt, sand, gravel, cobble, boulder, and bedrock to the nearest percent for a total of 100%. In stream large wood debris (those >3 m in length and >10 cm in diameter) were counted for the entire transect (Rich et al., 2003) and barriers visible within the transect were noted (i.e., waterfall, culvert, beaver dam, log jam, underground). At the end of each transect we measured wetted width, rooted width, and depth (at 25%, 50%, and 75% of the wetted width) all to the nearest cm with a meter stick and tape measure.

2.2.3 Geospatial covariates

Six geospatial covariates (Table 2.2) were used in our analysis and obtained from geographic information system (GIS) layers. Mean August water temperature was obtained from the West Fraser Stream Temperature Model, which uses temperature data collected over six years and spatial variables to understand the spatial and temporal variability of thermal conditions (MacDonald, 2021). Riparian area was defined as the land with low lying shrubs and lack of stands that lies directly adjacent to a moving stream. Timber harvest area is the net land-base of merchantable timber, which does not include deletions like non forested land, stream buffers, muskeg, pipelines, and other features. Disturbed area includes all other areas disturbed by development (roads, pipelines, powerlines, well sites, and grazing allotments). We measured elevation at T0 and distance to mainstem along the stream polygon from T0 of each site to the confluence of the next larger order stream. To control for spatial autocorrelation between sites within a stream, we ran a multi-ring buffer at 100m intervals from 100-500m around each site location. Using Moran's I, we determined the largest buffer ring that controlled for spatial autocorrelation of each geospatial covariate between sites. Then we clipped each layer to a 300m radius around each site, summarized, and exported to CSV. All analysis was run using ArcGIS Pro (Esri Inc., 2021).

2.2.4 Statistical analysis

i) Data preparation

There are many requirements for developing a N-mixture model. First, missing data needs to be removed and variables need to be scaled relative to one another (Kéry & Royle, 2016; Kéry & Schaub, 2012). To do this, sites with missing habitat observations were removed, depth for each transect was averaged, percentages were converted to proportions, and all continuous variables were scaled to a mean of 0 and standard deviation of 1. Second, variables need to be reduced to a reasonable number relative to the number of observations (Kéry & Royle, 2016). For this, we performed non-metric multidimensional scaling (NMDS) to determine the covariates that contributed to the greatest amount of variation in fish abundance. After using a scree plot to determine the number of dimensions required, we used Bray-Curtis dissimilarity as it is a weighted metric and is preferred over unweighted metrics, like Jaccard dissimilarity, when analyzing abundance data (Schroeder & Jenkins, 2018). To reduce collinearity between the retained covariates and increase model parsimony, we calculated Pearson correlation coefficients and removed those with R^2 values ≥ 0.6 (Møller & Jennions, 2002). All analyses were performed using RStudio (RStudio Team, 2021) and the packages vegan (Oksanen et al., 2020) and Performance Analytics (Peterson & Carl, 2020). Akin to Miller et al. (2011) and Som et al. (2018), subsequent model selection proceeded in two steps. First, we fit single species N-mixture models using maximum likelihood estimations and second, we fit a multispecies static binomial N-mixture model.

ii) Single species N-mixture models

We first fit the single species N-mixture model of Royle (2004) for Bull Trout, Brook Trout, and Brown Trout individually using maximum likelihood estimation with the R package unmarked (Fiske & Chandler, 2021). N-mixture models are a class of hierarchical models that can quantify how abundance changes in response to covariates while also considering imperfect detection and spatial variance (Royle & Dorazio, 2008). A total of 10 habitat covariates were set as fixed effects and two habitat covariates, site and waterbody, were set as random effects to account for spatial autocorrelation in the global model. Holding abundance constant, we used the R package MuMIn (Barton, 2020) to carry out parallel computation to determine the best combination of detection covariates (Miller et al., 2011; Som et al., 2018). Models were ranked by AICc rather than unadjusted AIC due to the small number of observations relative to the number of covariates (Burnham & Anderson, 2002). Models that did not converge were removed from the comparison and the model with the lowest AICc was selected as the top model. We repeated these processes for abundance, holding detection constant. Covariates retained in the top detection and abundance models for each species were carried forward into the multispecies N-mixture model.

iii) Multispecies static binomial N-mixture model with directional interactions

Our multispecies static binomial N-mixture model is an extension of that developed by Kéry and Royle (2020), which adapted the models of Brodie et al. (2018), Clare et al. (2019), and Roth et al. (2016). While there are multi-species occupancy models that provide similar results (i.e., Rota et al., 2016), these models require large sample sizes and do not account for directional interactions between species (Kéry & Royle, 2016). The model uses a log-normal Poisson distribution with the addition of a zero-inflation parameter to account for overdispersion and sparse count data. We added site and waterbody as random effects to account for any residual spatial autocorrelation. For both Brook Trout (1) and Brown Trout (2), we specify two separate static binomial N-mixture models where abundance is a function of observation covariates $(\beta_i \ )$ and detection $(p_{i,j})$ is a function of detection covariates $(\alpha_i \ )$.

(1)

$$z_i^K \sim Bernoulli\ (\omega^K)$$

$$N_i^K \mid zi\ \sim Poisson\ (\ z_i^K\ *\ \lambda^K)$$

$$C_{i,j}^K \sim Binomial\ (N_i^K, p_{i,j}^K\ )$$

$$\epsilon^K \sim normal(0, \tau^K)$$

$$log\ (\lambda_i^K) = \beta_0^K + \beta_1^K * pool + \beta_2^K * riffle + \beta_3^K * depth + \beta_4^K * lwd + \epsilon^K$$

$$logit\ (p_{i,j}^K) = \alpha_0^K + \alpha_1^K * wetwidth + \alpha_2^K * seconds$$

(2)

$$z_i^N \sim Bernoulli\ (\omega^N)$$

$$N_i^N \mid zi\ \sim Poisson\ (\ z_i^N\ *\ \lambda^N)$$

$$C_{i,j}^N \sim Binomial\ (N_i^N, p_{i,j}^N\ )$$

$$\epsilon^N \sim normal(0, \tau^N)$$

$$log\ (\lambda_i^N) = \beta_0^N + \beta_1^N * elev + \beta_2^N * depth + \beta_3^N * timber + \beta_4^N * riparian + \epsilon^N$$

$$logit\ (p_{i,j}^N) = \alpha_0^N + \alpha_1^N * wetwidth + \alpha_2^N * seconds$$

For Bull Trout (3), we specify another static binomial N-mixture model except now abundance (λ_i^L) is also contingent on the interaction effects of Brook Trout (γ_i^K) and Brown Trout (γ_i^N) abundance with the observation covariates (β_i):

(3)

$$z_i^L \sim Bernoulli\ (\omega^L)$$

$$N_i^L \mid zi\ \sim Poisson\ (\ z_i^L\ *\ \lambda^L)$$

$$C_{i,j}^L \sim Binomial\ (N_i^L, p_{i,j}^L\ )$$

$$\epsilon^L \sim normal(0, \tau^L)$$

$$\log(\lambda_i^L) = \beta_0^L + \beta_1^L * temp + \beta_2^L * pool + \beta_3^L * lwd + \beta_4^L * wetwidth + \gamma_0^K + \gamma_1^K * temp + \gamma_2^K * elev + \ldots + \gamma_9^K * wetwidth + \gamma_0^N + \gamma_1^N * temp + \gamma_2^N * elev + \ldots + \gamma_9^N * wetwidth + \epsilon^L$$

$$logit\ (p_{i,j}^L) = \alpha_0^L + \alpha_1^L * wetwidth + \alpha_2^L * seconds$$

We ran the global model and subsequent reductions for 300,000 iterations, with 3 chains, a burn in of 20,000, and a thinning rate of 50 to reach convergence. Akin to Michel et al. (2016) model selection proceeded by sequentially removing covariates if the 95% credible intervals (CrI) of the posterior distribution included zero until the 95% CrI of all habitat covariates excluded zero. Model convergence was visually assessed using trace plots and mathematically using the Rhat statistic (Gelman et al., 2014). Goodness of fit of the final model was assessed using the Bayesian p-value (Kéry & Schaub, 2012). All models were written in the BUGS language and ran in JAGS (Plummer, 2017) through RStudio (RStudio Team, 2021) with the wrapper package jagsUI (Kellner, 2021).

2.3 Results

We captured a total of 1,098 fish within 44 sites and 12 waterbodies, of which 353 were Bull Trout (mean individuals per site = 8; range = 0 - 52), 359 were Brook Trout (mean individuals per site = 8; range = 0 - 39), and 386 were Brown Trout (mean individuals per site = 9; range = 0 - 61). Of the 44 sites sampled, four sites were removed due to missing habitat data. We were unable to sample streams with (1) Brook Trout and Brown Trout only and (2) Bull Trout and Brown Trout only due the current abundance and distribution of the species within the study area.

2.3.1 Local habitat & spatial covariate results

The Moran's I test resulted in clipping all layers to a 300m radius buffer around each site to remove spatial autocorrelation (p-values > 0.05). After clipping, North Burnt Timber had sites with the highest elevation ($\bar{x}$ = 1630m), the greatest amount of riffle ($\bar{x}$ = 75%) and boulder ($\bar{x}$ = 28%), and the least amount of disturbed area ($\bar{x}$ = 0.1ha) and run ($\bar{x}$ = 19%) (Table 2.1). Cutoff sites had the least amount of pool ($\bar{x}$ = 6%) and large woody debris present ($\bar{x}$ = 0.1) but the most amount of gravel ($\bar{x}$ = 37%). While Elk had the highest amount of sand per site ($\bar{x}$ = 12%), it had the lowest amount of boulder ($\bar{x}$ = 3%). Fallentimber had the longest distance to mainstem ($\bar{x}$ = 42.5km), the highest mean august water temperature ($\bar{x}$ = 13.3°C), the largest wetted width ($\bar{x}$ = 15.7m), the greatest amount of riparian area ($\bar{x}$ = 7.2ha), disturbed area ($\bar{x}$ = 19.9ha), run ($\bar{x}$ = 55%), and pool ($\bar{x}$ = 30%), yet the least amount of timber area ($\bar{x}$ = 0ha) and riffle ($\bar{x}$ =15%). Pineneedle had the lowest mean August water temperature ($\bar{x}$ = 8.1°C) and the smallest wetted width (x̄ = 3.1m). Rough had the greatest amount of bedrock (x̄ = 17%) and large woody debris (x̄ = 10.2) per site, the lowest elevation (x̄ = 1243m) and least amount of cobble (x̄ = 27%). While Yara had the shallowest average depth (x̄ = 15cm), Trout had the highest average depth (x̄ = 43cm), the greatest amount of timber harvest area (x̄ = 12.8ha) and silt (x̄ = 38%), and the least amount of riparian area (x̄ = 0ha) and gravel (x̄ = 6%).

2.3.2 NMDS ordination results

Results from the scree plot indicated that three dimensions was adequate for ordination. A final stress value of 0.075 was obtained indicating a stable solution was obtained after 20 random starts. Results from the NMDS ordination identified the following habitat covariates: elevation, water temperature, timber area, wetted width, pool, riffle, depth, large woody debris (Table 2.2). After NMDS ordination Pearson's correlation coefficients showed no colinear or redundant relationships were present.

2.3.3 Single species N-mixture model results

Using AICc to compare the top detection and abundance models for each single species N-mixture model, wetted width and electrofishing seconds were present in the top detection model for all three species. Covariates retained in the top abundance models for Brook Trout were depth, large woody debris count, proportion of pool, and proportion of riffle (Table 2.3). The top Brown Trout abundance model retained depth, elevation, riparian area, and timber area. The top Bull Trout abundance model retained large woody debris count, proportion of pool, mean August stream temperature, and wetted width.

2.3.4 Multi species N-mixture model results

Following covariate reduction, a Bayesian p-value of 0.55 indicated good fit of the final multi species N-mixture model to the data (0.05 < Bayesian p-value < 0.95) (Kéry & Schaub, 2012). Electrofishing seconds was the only detection covariate retained in the model with the probability of detection being positively related to electrofishing seconds for all species (Table 2.4). Brook Trout abundance increases with increasing large woody debris count but decreases with average depth (Table 2.4). Brown Trout abundance increases with average depth but decreases as amount of timber area and elevation increase (Table 2.4). While Bull Trout abundance is positively correlated with Brown Trout abundance, the correlation between Bull Trout abundance and specific habitat covariates varied based on the abundance of the non-native species (Table 2.4).

Water temperature is strongly negatively correlated with Bull Trout abundance with no interaction effects included (posterior mean = -0.726) but has a small positive effect (posterior mean = 0.065) when the Brook Trout interaction term is included (Table 2.4). The model predicts that Bull Trout abundance will be reduced when average August stream temperatures is <11°C when they are in sympatry with Brook Trout versus when they are in allopatry or in sympatry with Brown Trout (Figure 2.2a). This relationship flips when the average August stream temperature is >11°C, with sympatric Bull Trout abundance greater than allopatric Bull Trout. However, the magnitude of the difference between groups is reduced in comparison. Wetted width, which is strongly positively correlated with allopatric Bull Trout abundance (posterior mean = 0.786), becomes slightly negatively correlated when the Brown Trout interaction term is included (posterior mean = -0.059). The model predicts that allopatric Bull Trout abundance increases as wetted width increases but decreases with wetted width when in sympatry with Brown Trout (Figure 2.2b). However, when wetted width is <11m Bull Trout abundance is predicted to be greater when in sympatry with Brown Trout versus when they are in allopatry.

Neither pool nor riffle are correlated with Bull Trout abundance when no interaction terms are included. However, when Brook Trout are present, the abundance of Bull Trout increases with the proportion of both pool and riffle. In contrast, Bull Trout abundance decreases as the proportion of pool increases when in sympatry with Brown Trout (Table 2.4; Figure 2.2c; Figure 2.2d).

Large woody debris, which is strongly negatively correlated with Bull Trout abundance when no interaction effects are included (posterior mean = -2.558), is less strongly correlated and when Brook Trout (posterior mean = -0.217) and Brown Trout (posterior mean = 0.171) interaction effects are included. Interestingly, Brook Trout and Brown Trout result in opposite correlations between Bull Trout abundance of large woody debris. Regardless of their correlation, the model predicts that sympatric Bull Trout will benefit more from high amounts of large woody debris than allopatric Bull Trout (Figure 2.2e). However, this estimate is uncertain given the high standard error for the large woody debris in the allopatry model (Table 2.4).

2.4 Discussion

It is well established that Bull Trout are some of the most temperature sensitive salmonids and much of their distribution is limited by this (Kovach et al., 2019; Selong et al., 2001). As such, we expected stream temperature to be negatively correlated with both allopatric and sympatric Bull Trout. We expected the negative relationship to be affected by the abundance of Brook Trout given the positive correlation between water temperature and Brook Trout invasion success (Paul & Post, 2001; Rieman et al., 2006; Warnock & Rasmussen, 2013a). Our results for allopatric Bull Trout abundance corroborate this, but our results for sympatric Bull Trout do not. Instead, our model predicts sympatric Bull Trout abundance is reduced when Brook Trout are present and the average August stream temperatures is <11°C. While our model cannot confirm the effect of temperature on Brook Trout invasive success, our results show that Bull Trout in these cold water refuges are at risk from invasion pressure (Dunham et al., 2003; Eby et al., 2014; Isaak et al., 2015, 2016). This result also supports the argument that Brook Trout may indeed be displacing Bull Trout in headwater streams, likely aided by their ability to invade higher elevations and their cold water preference (Adams et al., 2000; Kanda et al., 2002; Leary et al., 1993; Nakano et al., 1998; Peterson & Fausch, 2003; Rieman et al., 1997, 2006).

We also expected the negative relationship between Bull Trout abundance and water temperature to be affected by the abundance of Brown Trout given the positive correlation between Brown Trout invasion success and water temperature (Al-Chokhachy et al., 2016; Meredith et al., 2017; Wood & Budy, 2009). Instead, our results show that the relationship between Bull Trout abundance and temperature is not directly affected by Brown Trout. The higher thermal optimum and upper tolerance of Brown Trout compared to Bull Trout and the lack of streams with mean August temperatures of >14°C are likely influencing this relationship (Hari et al., 2006; McMahon et al., 2007; Selong et al., 2001; Stewart et al., 2007). Alike to Al-Chokhachy et al.'s (2016) findings, this suggests that Brown Trout are more likely to replace, rather than displace, Bull Trout in warmer streams and that Bull Trout are likely competitively advantaged in colder streams.

Wetted width is acknowledged as a factor affecting Bull Trout abundance and distribution (Rich et al., 2003; Rieman & McIntyre, 1995), but the magnitude of its effects are often difficult to discern given its relationship with elevation, water temperature, and large-scale landscape effects (Rabeni & Sowa, 1996). Our results indicate that Bull Trout abundance is positively associated with wetted width, which is consistent with observations by Rich et al. (2003). However, Brown Trout abundance shifts this relationship, causing Bull Trout abundance to become negatively correlated with wetted width when the non-native species is present. It is unlikely that temperature is driving this relationship as Bull Trout abundance is positively correlated with wetted width when allopatric. Although model selection removed elevation as a significant covariate in all Bull Trout models, it is retained as a significant covariate in the Brown Trout abundance model. Therefore, it is still difficult to discern whether Brown Trout displace Bull Trout in larger streams specifically or if it is a matter of elevation.

Model selection retained the proportion of pool and riffle as significant covariates depending on which non-native species was present, yet their effects were weak in all model components. However, the positive correlation between proportion of riffle and Bull Trout abundance when in sympatry with Brook Trout supports the observations that complex, fast moving water may reduce competition between salmonids (Blanchet et al., 2006; Warnock & Rasmussen, 2013b). Flow velocity may better capture this relationship and therefore should be included in future studies. Bull Trout demonstrate a preference for pool habitats, particularly for their sit and wait foraging tactics (Bonneau & Scarnecchia, 1998; Nakano et al., 1992, 1998; M. C. Rodtka & Volpe, 2007; Saffel & Scarnecchia, 1994; Warnock & Rasmussen, 2013b; Watson & Hillman, 1997). Because of this, we expected the proportion of pool to be positively correlated with Bull Trout abundance. Yet model selection retained no stream flow habitat features in the allopatric model and showed weak, conflicting results in the sympatry models. Thus, using a single metric, such as in-stream complexity, would be more informative as many stream structure metrics are co-dependent and there is growing evidence for stream complexity to provide refugia for salmonids (McMahon & Hartman, 1989; Pearsons et al., 1992; Rich et al., 2003; Watson & Hillman, 1997).

In-stream large woody debris creates complex in-stream habitat by shaping stream morphology and profile (Keller & Swanson, 1979; Ralph et al., 1994), altering the amount of pool (Beschta & Platts, 1986; Fausch & Northcote, 1992), and providing in-stream cover (Harvey et al., 1999; Keim et al., 2002). While our model cannot confidently predict the degree to which large woody debris influences allopatric Bull Trout abundance, it does result in conflicting correlations depending on which non-native species is present. Our model suggests a negative correlation between large woody debris and Bull Trout abundance when sympatric with Brook Trout. Interestingly, we observe the opposite relationship when Bull Trout are sympatric with Brown Trout. While these correlations are conflicting, sympatric Bull Trout are predicted to benefit more from high amounts of large woody debris (>15) than allopatric Bull Trout. This could be driven by an increase in complex habitat created by large woody debris, which can increase Bull Trout resiliency to Brook Trout invasion and provide Bull Trout with a feeding advantage (Rich et al., 2003; Warnock & Rasmussen, 2013b). Moreover, instream barriers are thought to reduce the invasion success of Brown Trout due to their lesser ability to pass in-stream barriers (Kirk et al., 2018; Lokteff et al., 2013). Therefore, high woody debris counts could provide refuge for Bull Trout from Brown Trout invasion by creating potential barriers.

We designed our collection methods to encompass various levels of invasion, but the study area and current abundance and distribution of the species did not allow us to capture all intended levels. As such, sampling streams that are (1) Brook Trout / Brown Trout only and (2) Bull Trout / Brown Trout only would strengthen the model and help discern these relationships further. Subsequently, creating a model that encompasses three-way interactions and interactions between Brook Trout and Brown Trout would differentiate the population dynamics further. Unfortunately, these models are very data heavy and require much more data than we acquired.

All together, our results suggests that Brook Trout have the potential to displace Bull Trout in Alberta's headwater streams. As high stream temperatures already limit Bull Trout distribution, irrespective of interactions with non-native fish, direct displacement by Brook Trout is most likely to occur in colder streams lacking habitat complexity. The direct interactions between Brown Trout and Bull Trout are less certain, but larger, lower elevation streams are likely to see reductions in Bull Trout abundance where Brown Trout invasion is present and likely to occur. With this, monitoring and management efforts should focus on limiting further invasion of non-native trout into streams of all sizes with complex habitat and average August stream temperatures of <11°C as these provide the greatest potential for Bull Trout recovery and refugia.

2.5 Figures & Tables

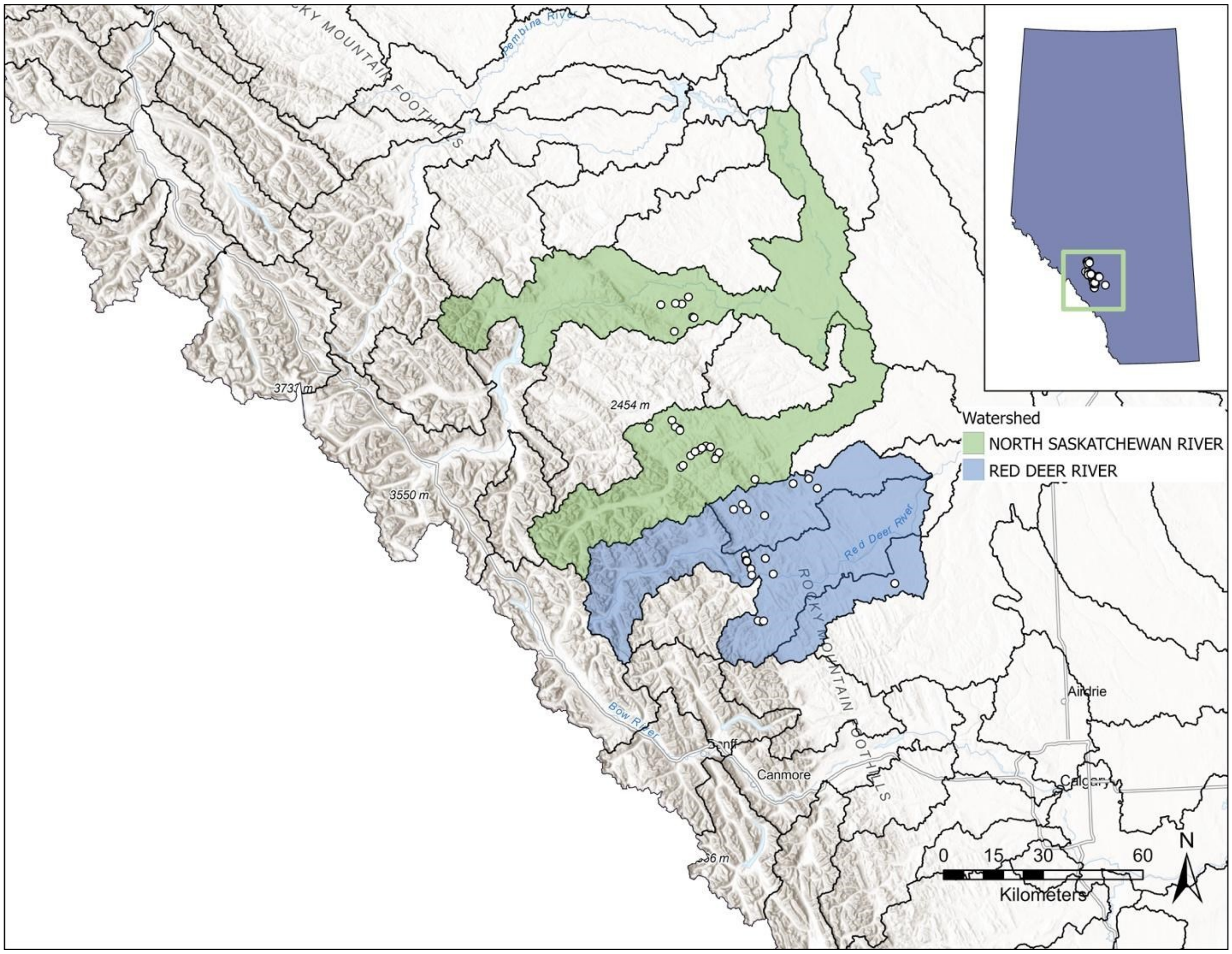

Figure 2.1 - Map of the study area. Individual sites noted by white circles within individual HUC 6 watershed units (black outlines) of the Red Deer River basin (blue) and North Saskatchewan River basin (green).

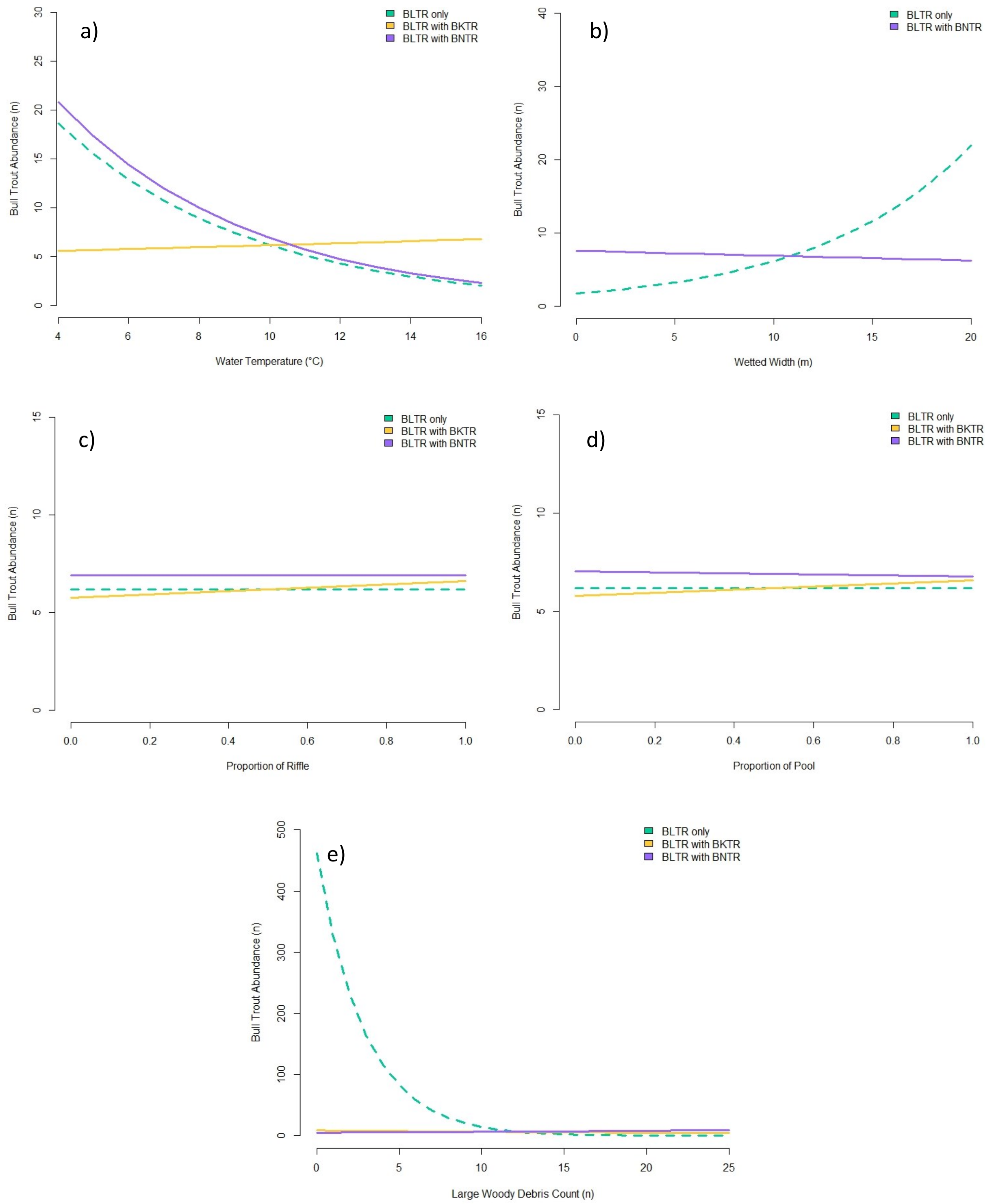

Figure 2.2 – Relationship between Bull Trout abundance (n) and the habitat covariates retained in the final multispecies N-mixture model. Dotted blue line represents Bull Trout abundance when in allopatry whereas the solid lines represent Bull Trout abundance when in sympatry with Brook Trout (yellow) and Brown Trout (purple). The covariates retained include mean August water temperature (°C) (Figure 2.2a), wetted width (m) (Figure 2.2b), proportion of riffle (Figure 2.2c), proportion of run (Figure 2.2d), and large woody debris count (n) (Figure 2.2e).

Table 2.1 – Mean values of recorded habitat covariates for each waterbody. Waterbodies are North Burnt Timber (BT), Cutoff (CT), Elk (EK), Fallentimber (FT), Pineneedle (PN), Rough (RG), Teepee Pole (TP), Trout (TR), Wilson (WS), Wildhorse (WH), and Yara (YR).

Habitat Covariate	**BT**	**CT**	EK	FT	PN	RG	TP	TR	WS	WH	YR
Elevation *(m)*	1630	1453	1504	1260	1435	1243	1295	1261	1493	1614	1495
Distance to mainstem *(km)*	33.8	13.4	15.2	42.5	8.4	17.9	9	8.6	22.2	6.8	5.5
Water temperature *(°C)*	9.5	9.6	10.1	13.3	8.1	10	11	10.4	10.1	9	11.3
Riparian area (*ha)*	2.8	7	5.3	7.2	0.3	2.6	5.5	0	6.1	5.3	1.8
Timber area *(ha)*	1.9	9	0.6	0	11.9	14	10	12.8	9.5	7.5	3.9
Disturbed area *(ha)*	0.1	0.8	16.7	19.9	0.2	0.8	0.8	0.7	14.2	0.8	0.5
Wetted width *(m)*	10.3	7.5	7	15.7	3.1	4.5	7.3	5	8	3.9	4.9
Pool *(%)*	7	6	19	30	14	25	28	23	9	17	10
Riffle *(%)*	75	58	36	15	52	37	46	23	58	56	65
Run *(%)*	19	36	46	55	34	39	25	54	33	27	25
Depth *(cm)*	26	34	25	28	22	24	26	43	24	21	15
Silt *(%)*	1	21	9	7	8	30	17	38	1	20	1
Sand *(%)*	1	2	12	0	2	8	7	0	0	2	3
Gravel *(%)*	10	37	26	34	10	15	16	6	13	9	18
Cobble *(%)*	59	36	50	40	71	27	37	47	71	47	71
Boulder *(%)*	28	4	3	15	10	4	19	8	11	19	7
Bedrock *(%)*	2	0	0	4	0	17	4	0	4	3	0
Large woody debris *(n)*	0.8	0.1	1.1	1.2	1	10.2	5.6	6.3	1.2	2.1	7.3

Table 2.2 - Habitat covariates utilized in the analysis and those retained after the non-metric multidimensional scaling (NMDS) and final model selection. Pr(>r) is the significance level of the multiple regression covariate with alpha levels of <0.1, <0.05, <0.01, and <0.001 (. , * , ** , ***).

Habitat Covariate		Pr(>r)	NMDS Significance	Retained in final model
Spatial				
	Elevation	0.001	***	yes
	Distance to mainstem	0.127		no
	Riparian area	0.522		no
	Disturbed area	0.173		no
	Timber area	0.069	.	no
	Mean August water temperature	0.049	*	yes
Observation				
	Wetted width	0.073	.	yes
	Pool	0.001	***	yes
	Riffle	0.043	*	yes
	Run	0.384		no
	Silt	0.847		no
	Sand	0.502		no
	Gravel	0.867		no
	Cobble	0.906		no
	Boulder	0.691		no
	Bedrock	0.808		no
	Depth	0.017	*	no
	Large woody debris	0.007	**	yes
Detection				
	Seconds	NA	NA	yes
	Wetted width	NA	NA	no

Table 2.3 - Model selection results for the single species N-mixture models. Only models with <5 corrected Akaike information criterion (ΔAICc) values are shown.

Parameter	**Model**	**AICc**	**ΔAIC**
Bull Trout			
Detection	p(INT + seconds + wetwidth)	770.262	0.000
	p(INT + wetwidth)	773.543	3.281
Abundance	λ(INT + lwd + pool + temp + wetwidth)	723.219	0.000
	λ(INT + elev + lwd + pool + wetwidth)	723.536	0.317
	λ(INT + lwd + pool + wetwidth)	724.028	0.809
	λ(INT + lwd + pool + riffle + wet width)	726.816	3.597
	λ(INT + elev + lwd + temp)	728.214	4.995
Brook Trout			
Detection	p(INT + seconds + wetwidth)	777.606	0.000
Abundance	λ(INT + depth + lwd + pool + riffle)	754.396	0.000
	λ(INT + depth + lwd + pool + timber)	754.535	0.139
	λ(INT + depth + lwd + riffle)	757.058	2.663
	λ(INT + depth + lwd + pool)	757.083	2.687
	λ(INT + depth + lwd + riffle + timber)	758.111	3.715
	λ(INT + depth + lwd + pool + temp)	758.704	4.309
	λ(INT + depth + elev + lwd + pool)	758.995	4.599
Brown Trout			
Detection	p(INT + seconds + wetwidth)	624.472	0.000
	p(INT + seconds)	625.920	1.448
Abundance	λ(INT + depth + elev + riparian + timber)	586.463	0.000
	λ(INT + depth + elev + timber + temp)	589.797	3.334
	λ(INT + depth + elev + lwd + timber)	589.924	3.460

Table 2.4 – Significant habitat covariates (predictors) and their relationship (posterior mean) with the abundance and detection of each species in the final multispecies N-mixture model. The Bull Trout abundance model is separated into three components: allopatry (Allopatric Abundance), sympatry with Brook Trout (Abundance with BKTR), and sympatry with Brown Trout (Abundance with BNTR). The posterior standard deviation (posterior SD) and the 95% credible intervals (CrI) of each predictor is noted.

Parameter	**Predictor**	**Posterior mean**	**Posterior SD**	**95% CrI**
Brook trout sub-model				
Abundance	Intercept	1.507	0.098	1.25 to 1.61
	Depth	-0.647	0.268	-1.20 to -0.16
	Large woody debris	0.463	0.191	0.09 to 0.85
Detection	Intercept	-1.818	0.231	-2.3 to -1.39
	Seconds	0.269	0.078	0.12 to 0.42
Brown trout sub-model				
Abundance	Intercept	0.579	0.585	-0.69 to 1.53
	Elevation	-1.580	0.517	-2.70 to -0.64
	Depth	1.028	0.384	0.32 to 1.84
	Timber area	-1.322	0.478	-2.31 to -0.44
Detection	Intercept	-1.861	0.422	-2.78 to -1.14
	Seconds	0.358	0.120	0.13 to 0.60
Bull trout full model				
Abundance	Intercept	1.303	0.271	0.62 to 1.60
	Water temperature	-0.726	0.357	-1.46 to -0.04
	Large woody debris	-2.558	0.953	-4.50 to -0.76
	Wetted width	0.786	0.232	0.32 to 1.24
Abundance with BKTR interaction	Water temperature * *BK*	0.065	0.034	0.01 to 0.14
	Pool * *BK*	0.090	0.027	0.04 to 0.15
	Riffle * *BK*	0.097	0.037	0.03 to 0.18
	Large woody debris * *BK*	-0.217	0.115	-0.46 to -0.02
Abundance with BNTR interaction	*BN*	0.108	0.061	0.02 to 0.26
	Pool * BN	-0.025	0.013	-0.06 to -0.01
	Large woody debris * BN	0.171	0.101	0.03 to 0.42
	Wetted width * *BN*	-0.059	0.032	-0.14 to -0.01
Detection	Intercept	-3.053	0.430	-3.95 to -2.24
	Seconds	0.238	0.097	0.05 to 0.43

Chapter III: Evidence for an isotopic niche shift of Bull Trout *(Salvelinus confluentus*) and competitive exclusion when in sympatry with Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*)

3.1 Introduction

Aquatic ecosystems are under pressure from a multitude of stressors, with invasive species as a leading threat to freshwater biodiversity (Dudgeon et al., 2006; Reid et al., 2019). Successful invasions have resulted in range and abundance contractions of native species (Hill & Lodge, 1999), introduced harmful pathogens (Youngson et al., 1993), altered habitat (Parkos III et al., 2003), and have ultimately contributed to extinctions (Lowe et al., 2000). While these alterations not only reduce biodiversity, they can drastically alter trophic structure and dynamics, which are intrinsic to ecosystem functioning (Eby et al., 2006; Elmqvist et al., 2003; McMeans et al., 2015; Moore & Hunt, 1988; Sakai et al., 2001).

With the potential for invasive species to alter trophic structure and dynamics, stable isotope analysis (SIA) is increasingly being applied to understand diets of co-occurring species. SIA monitors ratios of naturally occurring isotopes in the tissue of organisms and traces their pathways within a food web (Fry, 2006; Peterson & Fry, 1987). Ratios of $^{13}C/^{12}C$ ($d^{13}C$) and $^{15}N/^{14}N$ ($d^{15}N$) are two of the most commonly used isotopes as they have definitive relationships with organic sources (i.e., aquatic vs. terrestrial) and trophic position, respectively, and can be measured to infer changes in diets (Jardine et al., 2012; Vander Zanden et al., 1997; Zeug & Winemiller, 2008). When partnered with computational tools, we can also use $d^{13}C$ and $d^{15}N$ to evaluate the trophic niche of species and their degree of overlap within a system (e.g., Collier et al., 2018; Cucherousset et al., 2020; Hansen et al., 2022). Altogether, SIA results can infer if there is potential for competition, unfilled niche occupancy, displacement, and/or resource partitioning between native and introduced species (Cucherousset et al., 2007, 2020; Gerig et al., 2018; Jensen et al., 2017).

Headwater streams are isolated and easily fragmented, with migratory species within them vulnerable to extinction (Fagan, 2002; Fausch, 2008). Yet when connectivity is high, invasion success of introduced species increases, leaving migratory fishes at risk of invasion pressure (Hess, 1994; Simberloff et al., 1992). Paradoxically, invasion successes in streams are often reciprocal due to the overlap of niche characteristics (Korsu et al., 2007). This is evident between Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*), native to North America and Europe, respectively, where they have replaced each other in their native ranges (Fausch & White, 1981; Korsu et al., 2007; Waters, 1983). Furthermore, both species have been introduced globally and have affected native salmonids in Japan (Hasegawa, 2017; Kitano, 2004; Takami et al., 2002), New Zealand (Jones & Closs, 2017; Townsend, 1996), and elsewhere (e.g., McDowall et al., 2001; Pascual et al., 2007). The Rocky Mountain foothills of Alberta, Canada are no exception as both Brook Trout and Brown Trout have established self-sustaining populations and are threats to native Bull Trout (*Salvelinus confluentus*) (Fisheries and Oceans Canada, 2020; Post & Gow, 2012).

With many of Alberta's downstream populations of Bull Trout extirpated, Bull Trout are of increasing conservation priority (Fisheries and Oceans Canada, 2020; Sinnatamby et al., 2020). Their thermal sensitivity restricts their geographic range (Chapter 2, Haas & McPhail, 1991; Kovach et al., 2019; Rieman et al., 1997; Selong et al., 2001), making them extremely vulnerable to anthropogenic impacts and climate change. While their decline is attributed to a myriad of threats (i.e., climate change, habitat loss, connectivity, exploitation), the introduction of non-native fishes is a likely determinant of their decline in Alberta (Fisheries and Oceans Canada, 2020; J. R. Post & Gow, 2012; M. Rodtka et al., 2009; Sawatzky & Secretariat, 2016). Studies have identified Brook Trout as threats through hybridization (Kanda et al., 2002; Leary et al., 1993), dietary interspecific aggression (Gunckel et al., 2002; McMahon et al., 2007; Warnock & Rasmussen, 2013b), and displacement (Paul & Post, 2001; Rieman et al., 2006; Warnock & Rasmussen, 2013a); however, the interactions between Bull Trout and Brown Trout have not been studied as thoroughly nor have they been studied in tandem with Brook Trout.

Past studies investigating dietary interactions between Bull Trout and Brook Trout have focused on feeding and behavioural interactions. In laboratory settings, sympatric Brook Trout increase interspecific antagonism and display a significant growth advantage over Bull Trout in warmer temperatures (McMahon et al., 2007; Rodtka & Volpe, 2007). Similarly, in-stream experiments observed competitive interactions between Brook Trout and Bull Trout with no indication of either species shifting their niche (Gunckel et al., 2002; Nakano et al., 1998). While Brown Trout have also been introduced to Alberta and occupy a wide range of Bull Trout habitat (MacCrimmon & Campbell, 1969), no studies have investigated feeding or behavioural interactions between the two species. However, experimental studies in Japan indicate that

Brown Trout are competitively superior to two of its native salmonids, White-spotted Charr (*Salvelinus leucomaenis*) and Masu Salmon (*Oncorhynchus masou*) (Hasegawa et al., 2004; Kitano, 2004).

The aim of this study was to assess how Brook Trout and Brown Trout interact with the dietary niche of Bull Trout. To accomplish this, we employed SIA to compare the trophic structure and dynamics in streams over five different levels of invasion: (a) Bull Trout dominant, (b) Brook Trout dominant, (c) Brown Trout dominant, (d) Brook Trout / Bull Trout mix, and (e) Brook Trout / Bull Trout / Brown Trout mix. Our objectives were to (1) use SIA to infer if Bull Trout diet changes in response to varying invasion levels by Brook Trout and Brown Trout, (2) determine the amount of dietary niche overlap between Bull Trout, Brook Trout, and Brown Trout, and (3) infer whether there is potential for competition, unfilled niche occupancy, displacement, and/or resource partitioning between Bull Trout and both introduced species. Hereafter, we refer to competition as a high niche overlap between the native and non-native species with no increase in total niche area or change in resource use. Unfilled niche occupancy as a non-native species using resources that were previously not used by the native species with no change to the niche of the native species. Displacement as a change in resource use from allopatry to sympatry in one species, and niche partitioning as a change in resource use from allopatry to sympatry in both the native and non-native species with reduced niche overlap in sympatry.

Based on previous studies assessing feeding interactions and behaviours between Bull Trout and Brook Trout (Gunckel et al., 2002; McMahon et al., 2007; Rodtka & Volpe, 2007; Warnock & Rasmussen, 2013), we hypothesized that neither Bull Trout nor Brook Trout will shift their niche when in sympatry with each other and will have high niche overlap, resulting in competition. When in sympatry with Brown Trout, however, we hypothesized that Bull Trout and Brown Trout will shift their niche to avoid competitive interactions, resulting in niche partitioning (Hasegawa et al., 2004; Kitano, 2004). Following this, we expected there to be a higher amount of niche overlap between allopatric Brown Trout and Bull Trout than sympatric individuals.

3.2 Methods

3.2.1 Study area and design

Our study area lies within the Saskatchewan - Nelson Rivers, where Bull Trout are listed as a Threatened species (Fisheries and Oceans Canada, 2020). We selected headwater streams to the Red Deer River and North Saskatchewan River watersheds to encompass a vast area of core Bull Trout habitat and various levels of invasion of Brook Trout and Brown Trout (Figure 3.1).The 11 waterbodies include Yara Creek, Wildhorse Creek, North Burnt Timber Creek, Wilson Creek, Pineneedle Creek, Rocky Creek, Cutoff Creek, Elk Creek, Trout Creek, Rough Creek, and Fallentimber Creek.

3.2.2 Field methods

We conducted electrofishing surveys at 48 sites within 11 water bodies between July and August of 2020 and 2021. The goal at each site was to capture 10-30 individuals of each target species within each stream, as this is a statically robust number for stable isotope analysis (Jackson et al., 2011). We divided each site into six 50m transects for a total linear distance of 300m as per Alberta small stream protocol (Alberta Environment and Sustainable Resource Development, 2013). Using a systematic sampling design, we sampled from downstream to upstream with a Smith-Root LR24 backpack unit.

Fish were identified, weighed, and measured for both fork length and total length at the end of each transect. We took a fin clip from the upper lobe of the caudal fin from fish >65mm in fork length using a sterilized scalpel and forceps and stored clips in dry 1mL microcentrifuge tubes. Non-lethal caudal fin clips result in minimal disturbance to species and provide no significant differences in $\delta^{15}N$ and $\delta^{13}C$ isotope measurements than using a more invasive tissue plug (Hanisch et al., 2010 & Sanderson et al., 2009). As a minimum of 0.4 mg of dried tissue is required for analysis, obtaining a non-lethal fin clip large enough for stable isotope analysis was not feasible for fish <65mm and therefore no samples were taken from Bull Trout or Brown Trout <65mm (Sanderson et al., 2009). Brook Trout were the only fish we could retain. We euthanized individuals with a 200ppm buffered solution of Tricaine methane sulfonate (MS222) and then ensured death using single-blow blunt force trauma (Bayans, 2018). Euthanized fish were frozen on-site and store at -20°C until dissected for further analysis. All fish that could not be retained, we released at least 25m downstream of the start of the next electrofishing transect to avoid recapture and inflated count data.

At the start of each site, we set up two pan traps on each stream bank to collect terrestrial invertebrates. After completing electrofishing surveys, we emptied pan traps onto a fine mesh and transferred terrestrial invertebrates to 2.5mL centrifuge tubes. We collected aquatic invertebrates using a 3-minute kick sample from a pool, riffle, and run at each site, for a maximum of three kick samples per site. All samples collected were placed on ice at site, held in portable freezers in the field, and stored at -20°C until they were prepared for stable isotope analysis.

3.2.3 Laboratory methods

For each kick sample, we identified up to 200 individuals down to family, or to the next highest taxonomic rank where family could not be identified, according to Clifford (1991). Repeating families in pool, riffle, and run samples were consolidated into one group per family for each site. We classified aquatic invertebrates into five functional feeding groups (collectors, filterers, scrapers, shredders, and predators) according to Merritt and Cummins (1996). According to Borror and White (1970), we identified all terrestrial invertebrates to order. Due to the large number of samples, all predatory invertebrates were excluded from stable isotope analysis.

Fin clips and invertebrates used for stable isotope analysis were freeze dried for at least 24 hours in microcentrifuge tubes at -55°C and 0.015 Barr in a LABCONCO® FreeZone 1 Liter Benchtop Freeze Dry System. The freeze-dried tissue was homogenized using dissecting scissors and a stainless-steel rod in individual microcentrifuge tubes until a fine powder was reached. We weighed approximately 0.4 mg of each sample into 4 mm x 6 mm tin capsules using a UMX2 Ultra-microbalance (Mettler Toledo). All samples were sent to the Natural Resource and Analytics lab at the University of Alberta, analyzed using the Thermo Delta V Advantage Isotope Ratio Mass Spectrometer, and reported in standard delta notation (δ^{13}C vs. PDB and δ^{15}N vs. Air). Every twelfth sample was repeated for an internal standard as a measure of precision.

3.2.4 Data processing

We categorized streams into five different levels of invasion based on the number of individuals caught electrofishing: (1) Bull Trout dominant streams (>90% of catch), (2) Brook Trout dominant (>90% of catch), (3) Brown Trout dominant (>90% of catch), (4) Bull Trout / Brook Trout mix (10 to 90% of catch per species), (5) Bull Trout / Brook Trout / Brown Trout mix (10 to 90% of catch per species). We visually assessed all data for carbonate contamination using scatter plots of %C and %N and mathematically checked fish tissue for lipid variation using C:N ratios (Hayden, 2021; Logan et al., 2008; D. M. Post et al., 2007). Chitin, a protein common in invertebrates, has a higher C:N ratio than typical proteins (Logan et al., 2008). As such, the assumed C:N ratio of 3 for lipid free muscle does not apply well to invertebrates and the vast majority of published mathematical lipid corrections perform poorly on invertebrates (Kiljunen et al., 2006; Logan et al., 2008). Therefore, we chose not to correct invertebrate tissue for lipids.

3.2.5 Baseline corrections

To account for variation in $\delta^{15}N$ and $\delta^{13}C$ across waterbodies, consumer isotope values should be standardized to a baseline (Newsome et al., 2007; Svanbäck et al., 2015; Syväranta et al., 2013). As our streams lacked long-lived primary consumers, such as native snails and clams, scrapers (Tricoptera, Ephemeroptera) were chosen as the aquatic baseline given their strict algal diet (Finlay, 2001) and their low $\delta^{15}N$ values (Anderson & Cabana, 2007; Jackson & Britton, 2014; Svanbäck et al., 2015). Pooled primary consumer terrestrial invertebrates (Lepidoptera, Thysanoptera, Psocoptera, Homoptera, Plecoptera, Emphemeroptera, Trichoptera) were used as the terrestrial baselines as their $\delta^{13}C$ values mimic those of terrestrial vegetation (Finlay, 2001). Subsequently, $\delta^{13}C$ values were standardized to represent the proportion of carbon derived from terrestrial sources (1- α) using the Post (2002) equation (1) :

$$(1)\ 1 - \alpha = ((\delta^{13}C_{consumer} - TEF) - \delta^{13}C_{baseline2}) / (\delta^{13}C_{baseline1} - \delta^{13}C_{baseline2})$$

Where α represents the proportion of carbon derived from aquatic sources, $\delta^{13}C_{consumer}$ represents the $\delta^{13}C$ of individual fish, $\delta^{13}C_{baseline2}$ represents the average $\delta^{13}C$ of scrapers in each waterbody, and $\delta^{13}C_{baseline1}$ represents the average $\delta^{13}C$ of terrestrial invertebrates in each waterbody. We set the trophic enrichment (TEF) of $\delta^{13}C$ to 2.3‰ as an average reported for trout species in previous studies (Beltrán et al., 2009; McCutchan et al., 2003; Pinnegar & Polunin, 1999). After correction, some α values lie outside of the 0-1 range due to error in source estimation.

$\delta^{15}N$ values were standardized to represent trophic position (TP) using the Post (2002) equation (2):

$$(2)\ TP = ((\delta^{15}N_{consumer} - [\delta^{15}N_{baseline1} * \alpha - \delta^{15}N_{baseline2} * (1-\alpha)]) / (\Delta n)) + \lambda$$

Where $\delta^{15}N_{consumer}$ represents the $\delta^{15}N$ of individual fish, $\delta^{15}N_{baseline1}$ represents average $\delta^{15}N$ of scrapers in each waterbody, and $\delta^{15}N_{baseline2}$ represents the average $\delta^{15}N$ of terrestrial invertebrates in each waterbody. We set the TEF of $\delta^{15}N$, the enrichment in ^{15}N per trophic level, to 3.4‰ as per Post (2002). α represents the proportion of carbon derived from aquatic sources (see equation 1 above) and λ is the trophic level of the baseline organism (2 for primary consumers).

3.2.6 Trophic position and proportion of terrestrial carbon

To determine if the non-native species are affecting the resource use (α) and TP of Bull Trout, we pooled streams by their level of invasion and calculated the mean TP for each species at each respective level. Using a two-way ANOVA, we tested whether there was a significant difference in TP between species within invasion levels and each species between invasion level. In the global model we included species and invasion level as predictors then selected the model with the lowest AICc. The best model was visually assessed for normality and homogeneity and subsequently log transformed to meet the assumptions. Lastly, we used a Tukey HSD post hoc test to test for significant differences (p-value < 0.001) between invasion levels and species. The above process was repeated and used to test the effects of invasion level and species on the proportion of carbon derived from terrestrial sources ($1-\alpha$).

3.2.7 Standard ellipses area and niche overlap

We use standard ellipse area (SEA_B), a Bayesian estimate of isotopic niche width that is suitable for small sample sizes ($n < 30$) (Jackson et al., 2011), to calculate individual species' trophic niche at each invasion level. To calculate SEA_B, we used the R package SIBER (Jackson et al., 2011). TP and proportion of terrestrial carbon were used as proxies for $\delta^{15}N$ and $\delta^{13}C$ to allow for pooling of streams and comparison among invasion levels. We ran the model for 10,000 iterations, with 2 chains, a burn in of 1000, and a thinning rate of 10. To determine if niche width varied between species within invasion levels and for each species between invasion level, we compared the SEA_B 95% posterior credible intervals (Olsson et al., 2009; Syväranta et al., 2013).

If the 95% posterior credible intervals did not overlap, they were considered significantly different from another (Jackson et al., 2011).

To estimate the amount of overlap between species within invasion levels, we used a Bayesian framework in the R package nicheROVER (Lysy et al., 2021). Niche area was calculated at each invasion level for each species as a 95% probability region. The mean overlap was computed directionally and returned as percent overlap, meaning that there is X% of species A in species B's niche and Y% of species B in species A's niche (Lysy et al., 2021; Swanson et al., 2015). We compared percent overlap between levels of invasion to look for evidence of competition, displacement, and resource partitioning.

3.3 Results

3.3.1 Data processing

A total of 610 fin clips were collected from 48 sites within 11 streams (Figure 3.1). Of these were 222 Brook Trout, 224 Bull Trout, and 164 Brown Trout. Before baseline correction, mean stable isotope values ranged from -33.2 to -28.6‰ ($\delta^{13}C$) and 6.9 to 8.2‰ ($\delta^{15}N$) for Brook Trout, -33.5 to -29.2‰ ($\delta^{13}C$) and 6.4 to 8.2‰ ($\delta^{15}N$) for Bull Trout, -31.9 to -25.9‰ ($\delta^{13}C$) and 7.1 to 9.7‰ ($\delta^{15}N$) for Brown Trout (Table 3.1). No effects of carbonate were found and C:N ratios of the fish tissue was near or below 3.5. Baseline isotopic values range from -38.7 to -33.8‰ ($\delta^{13}C$) and 1.4 to 4.4‰ ($\delta^{15}N$) for the aquatic invertebrates and -31.8 to -26.6‰ ($\delta^{13}C$) and 0.4 to 4.4‰ ($\delta^{15}N$) for the terrestrial invertebrates.

3.3.2 Trophic position & terrestrial carbon

Overall, Bull Trout had the lowest TP of the three species (3.38 ± 0.02) (Table 3.2). Comparisons between invasion levels showed that while Bull Trout TP was unchanged in the presence of non-native species, Brook Trout TP significantly increases in all sympatric invasion levels (Figure 3.2). Brook Trout TP was significantly greater when in sympatry with only Bull Trout versus when they were in sympatry with both Bull Trout and Brown Trout (Figure 3.2; Table 3.2). In contrast, Brown Trout TP significantly decreases when both Bull Trout and Brook Trout are present. Comparisons within invasion levels showed that allopatric Brown Trout have a significantly higher TP than allopatric Bull Trout and Brook Trout. Yet when all three species are present, only sympatric Brook Trout have a significantly higher TP than sympatric Bull Trout.

Bull Trout had the lowest proportion of carbon derived from terrestrial sources overall (0.36 ± 0.02) (Table 3.2). Comparisons between invasion levels show that the proportion of carbon derived from terrestrial sources in Bull Trout significantly decreases from allopatry to sympatry with both Brook Trout and Brown Trout (Figure 3.3; Table 3.2). Correspondingly, the proportion of carbon derived from terrestrial sources in Brown Trout significantly increases from allopatry to sympatry with both Bull Trout and Brook Trout (Figure 3.3). There is no significant difference in the proportion of carbon derived from terrestrial sources between the Bull Trout in sympatry with Brook Trout, and Bull Trout in other invasion levels. Brook Trout have no significant change in the proportion of carbon derived from terrestrial sources between invasion levels.

3.3.3 Standard ellipses area and niche overlap

Between invasion levels, there was no significant change in niche width of any of the individual species (Figure 3.4). When comparing total niche width of all species in each invasion level, there was a moderate, yet insignificant, increase in niche width as the number of species increases (Table 3.2). As for niche overlap, there was a high median probability that Brook Trout (88% probability) and Brown Trout (91% probability) will be found in the overall dietary niche of Bull Trout (Figure 3.5; Table 3.3). Similarly, there was a high median probability that Bull Trout will be found in the dietary niche of Brook Trout (89% probability) and Brown Trout (88% probability). When comparing the niche overlap between invasion levels, the likelihood of Brook Trout in the niche of Bull Trout, and vice versa, did not change significantly (Table 3.3). Contrarily, there was a significantly smaller likelihood of allopatric Bull Trout and Brook Trout occupying the dietary niche of allopatric Brown Trout (Table 3.3; Figure 3.6).

3.4 Discussion

The introduction and stocking of Brook Trout and Brown Trout have occurred globally, putting invasion pressure on native fishes (Kitano, 2004; Lowe et al., 2000; Townsend, 1996; Waters, 1983). When top-predator game fish such as these are introduced and naturalized, the number of top predator species increases or the native species are replaced (Eby et al., 2006). In either of these scenarios, trophic structure and dynamics can be altered through changes to top-down control, habitat coupling, or trophic efficiency (Eby et al., 2006; McMeans et al., 2015). If native trout remain after invasion and the number of top-predator species increases, the availability of resources can become limited, forcing one or more species to use less desirable resources (Eby et al., 2006; Kitano, 2004; Nakano et al., 1998; Nakano, Fausch, et al., 1999; Taniguchi et al., 2002). Our results corroborate this process and demonstrate that Bull Trout in sympatry with Brook Trout and Brown Trout undergo a niche shift.

When sympatric with both introduced species, Bull Trout shifted their dietary niche and consumed less terrestrial-based carbon sources. While it appears the niche shift of Brown Trout to consuming more terrestrial-based carbon is driving this, Brook Trout are likely influencing this relationship. When in sympatry with Brook Trout in their native range, European Brown Trout underwent a dietary niche shift, consuming more terrestrial-based carbon than allopatric Brown Trout (Cucherousset et al., 2007). Cucherousset et al. (2007) suggest that the aggressive interference of Brown Trout with Brook Trout for habitat drives the increase in terrestrial-based carbon consumption (Fausch & White, 1981; Nyman, 1970). Our results corroborated this and showed that Bull Trout are excluded from terrestrial resources. While changing foraging tactics can allow for species co-existence (Holbrook & Schmitt, 1989; Nakano, Fausch, et al., 1999), the niche shift did not allow Bull Trout to escape competition with the non-native fishes as there was no significant change in niche overlap between allopatry and sympatry. As a result, Bull Trout are forced to use less desirable resources when in sympatry with Brook Trout and Brown Trout. Consequently, Bull Trout growth and abundance will likely be hindered when terrestrial invertebrates are low and/or usurped, as demonstrated by Dolly Varden (*Salvelinus malma*), a close relative of Bull Trout, when sympatric with non-native Rainbow Trout (*Oncorhynchus mykiss*) (Baxter et al., 2007).

Brook Trout bare fast-to mature young, making them prolific reproducers and strong competitors (Dunham et al., 2002; Lobón-Cerviá & Sanz, 2017; Raleigh, 1982). This is evident in streams they have invaded where they occur in greater densities than the species they replace (Benjamin & Baxter, 2010). With dominance in interspecific interactions mainly determined by size (Nakano & Furukawa-Tanaka, 1994), Brook Trout threaten Bull Trout, given Bull Trout are slower growing and mature later (Dunham et al., 2008; Meyer et al., 2006). Further evidence for the interspecific dominance of Brook Trout is shown in laboratory studies where Brook Trout exhibited a competitive and growth advantage over Bull Trout, particularly in warmer water temperatures (McMahon et al., 2007). Our results showed that Brook Trout TP significantly increases from allopatry to sympatry and that Brook Trout occupied a significantly higher TP than Bull Trout when all three species are in sympatry. This suggests that Brook Trout likely retain their competitive advantage in Alberta's foothills and the presence of Brown Trout may increase their competitive interference. While piscivory is possibly influencing the increase in TP, it is also likely that Brook Trout are selectively feeding on the large to medium sized invertebrates and usurping invertebrates with higher a TP (Bechara et al., 1993). If all the larger invertebrates are usurped by Brook Trout, Bull Trout will be forced to expend more energy to obtain an equal amount of energy intake, thereby decreasing their fitness (Stephens & Krebs, 1987).

The lack of significant change in the total niche width (all species combined) and individual species niche widths combined with the slight increase in percent overlap, provides no evidence of niche partitioning between sympatric Bull Trout and Brook Trout. Our results validated the experimental and observational studies that found no proof of a niche shift when investigating feeding and behavioural interactions between Brook Trout and Bull Trout (Gunckel et al., 2002; Nakano et al., 1998). The lack of niche partitioning and high degree (>84%) of niche overlap between sympatric Brook Trout and Bull Trout leaves a potential for competitive exclusion, mainly when resources are low. The potential for competitive exclusion is likely intensified by the difference in feeding interactions between species. While Bull Trout generally use a sit-and-wait foraging tactic (Bonneau & Scarnecchia, 1998; Nakano et al., 1992, 1998; Saffel & Scarnecchia, 1994; Watson & Hillman, 1997), sympatric Brook Trout are more likely to competitively interfere for resources (Gunckel et al., 2002; McMahon et al., 2007; Rodtka & Volpe, 2007; Warnock & Rasmussen, 2013b). As a result, Bull Trout are likely to be displaced from preferred food sources (i.e., terrestrial invertebrates, and large prey) when resources are scarce and Brook Trout abundance is high.

Although studies have identified terrestrial invertebrates as a key resource for trout (Baxter et al., 2007; Elliott, 1973; Hubert & Rhodes, 1989; Nakano, Kawaguchi, et al., 1999), the degree to which they are incorporated into their diet may depend on the availability of benthic invertebrates (Wilson et al., 2014). While cold water streams are predicted to provide refuge for salmonids in a changing climate (Dunham et al., 2003; L. A. Eby et al., 2014; Isaak et al., 2015, 2016), these streams are often depleted in benthic resources (Huryn & Wallace, 2000). Together with the ability for both Brook Trout and Brown Trout to occupy cold-water streams (MacCrimmon & Campbell, 1969; Smialek et al., 2021), and therefore often low productivity streams, and the competitive interference of Brook Trout, Bull Trout are likely to be excluded from terrestrial invertebrates when resources are limited.

Altogether, our data suggests that Brown Trout and Brook Trout have the potential to competitively exclude Bull Trout in Alberta's headwater streams through two mechanisms. Firstly, Brown Trout are likely to usurp terrestrial invertebrates and displace Bull Trout from a preferred resource. Concurrently, Brook Trout are likely to usurp larger sized prey and displace Bull Trout from high reward resources. Thus, competitive exclusion is most likely to occur in streams where invertebrate abundance is low and all three species are in sympatry. With this, monitoring and management efforts should focus on limiting further invasion of Brook Trout and Brown Trout into streams with healthy Bull Trout populations where resources are already limited by environmental conditions.

3.5 Figures & Tables

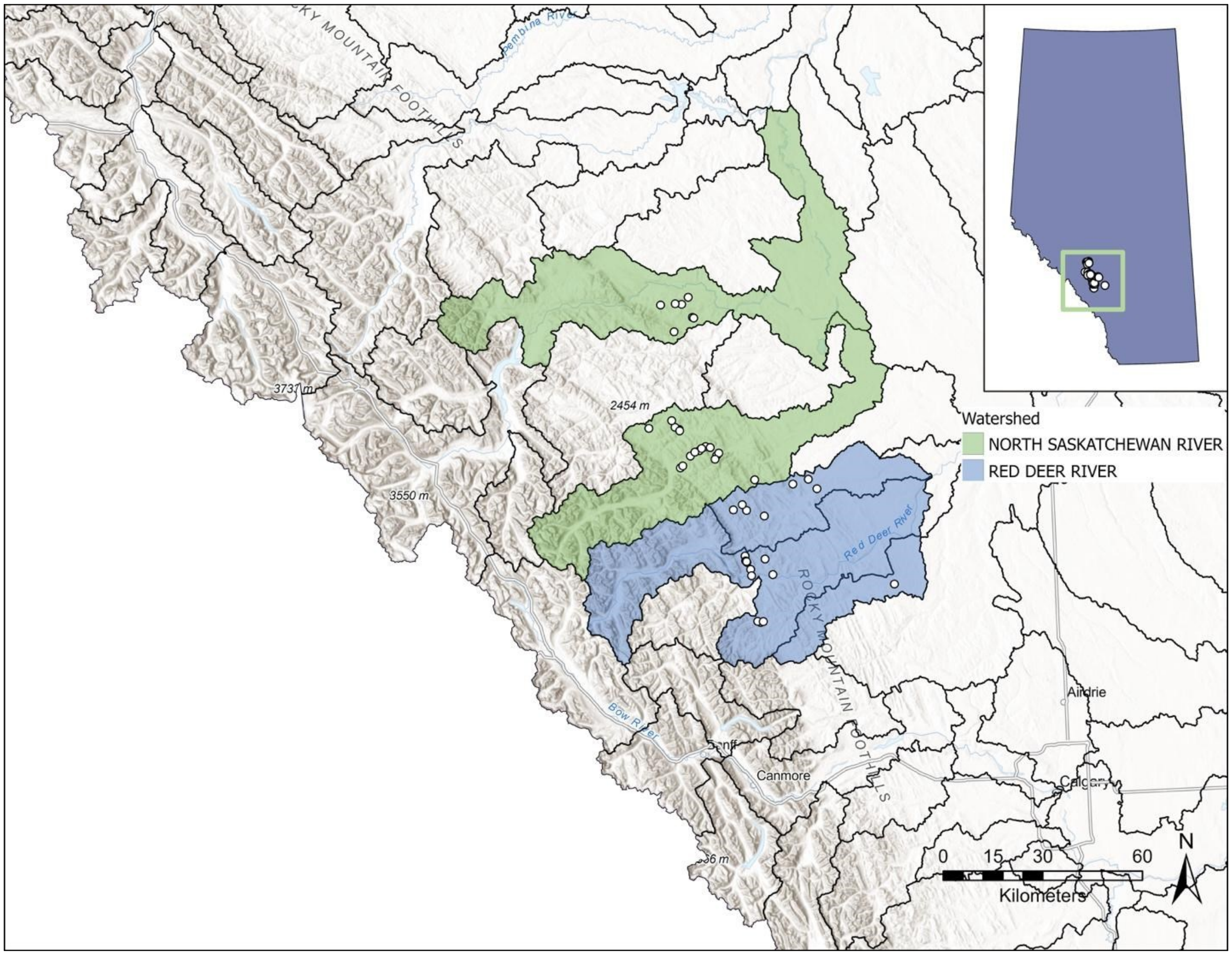

Figure 3.1 - Map of the study area. Individual sites noted by white circles within individual HUC 6 watershed units (black outlines) of the Red Deer River basin (blue) and North Saskatchewan River basin (green)

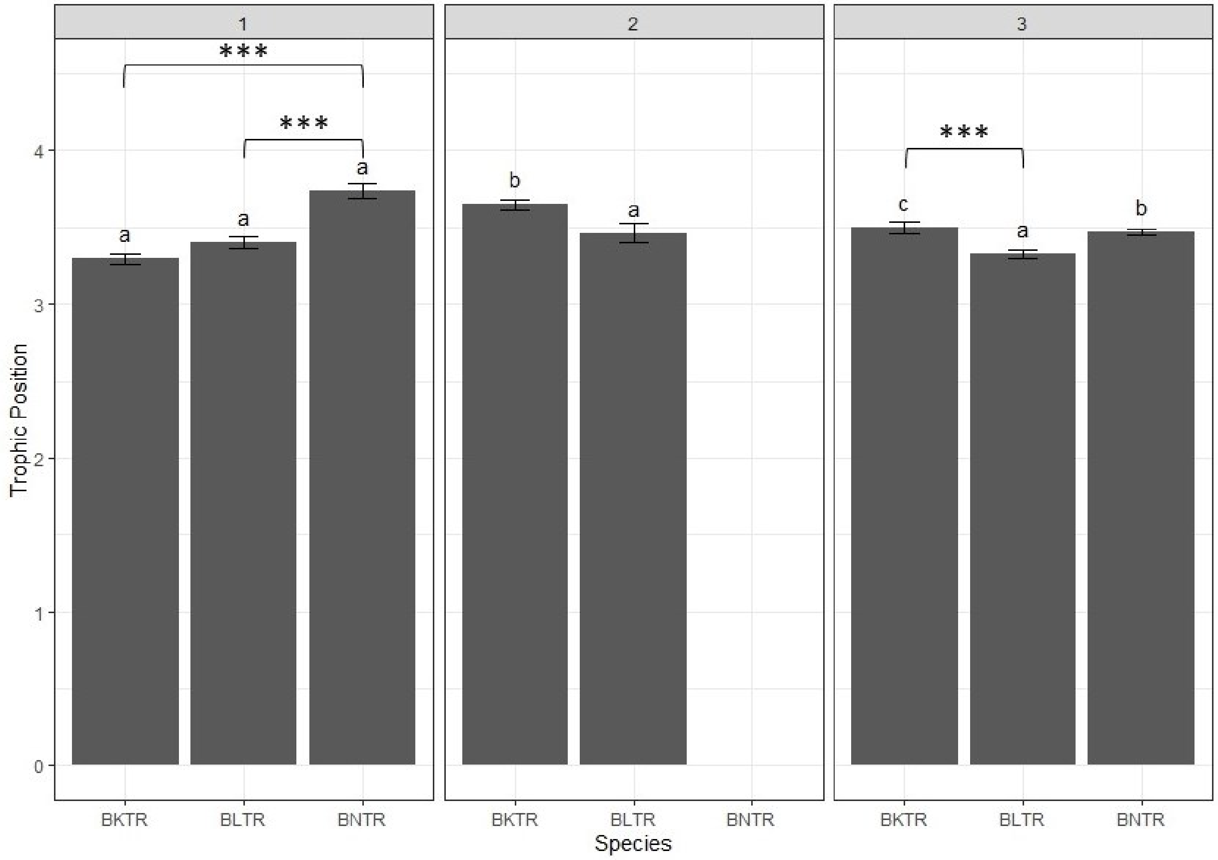

Figure 3.2 – Trophic position of individual species within invasions levels. The first tile includes streams of the Brook Trout dominant, Bull Trout dominant, and Brown Trout dominant streams. The second tile includes streams of the Brook Trout / Bull Trout invasion level, and the third tile includes streams of the Brook Trout / Bull Trout / Brown Trout invasion level. Significant differences (p-value < 0.001) between species indicated by ***. Significant differences within a species denoted by differing letters.

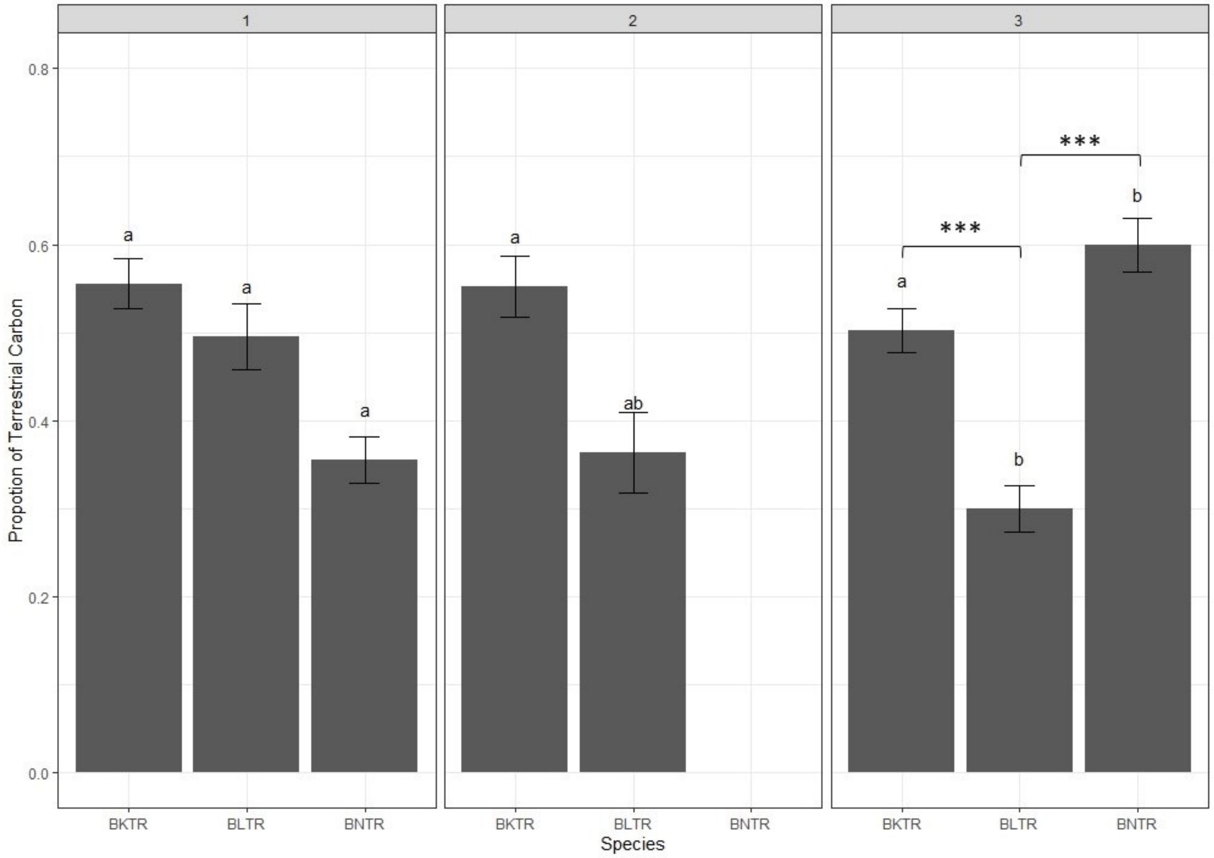

Figure 3.3 – Proportion of terrestrial-based carbon in the diet of individual species within invasions levels. The first tile includes streams of the Brook Trout dominant, Bull Trout dominant, and Brown Trout dominant streams. The second tile includes streams of the Bull Trout / Brook Trout invasion level, and the third tile includes streams of the Bull Trout / Brook Trout / Brown Trout invasion level. Significant differences (p-value < 0.001) between species indicated by ***. Significant differences within a species denoted by differing letters.

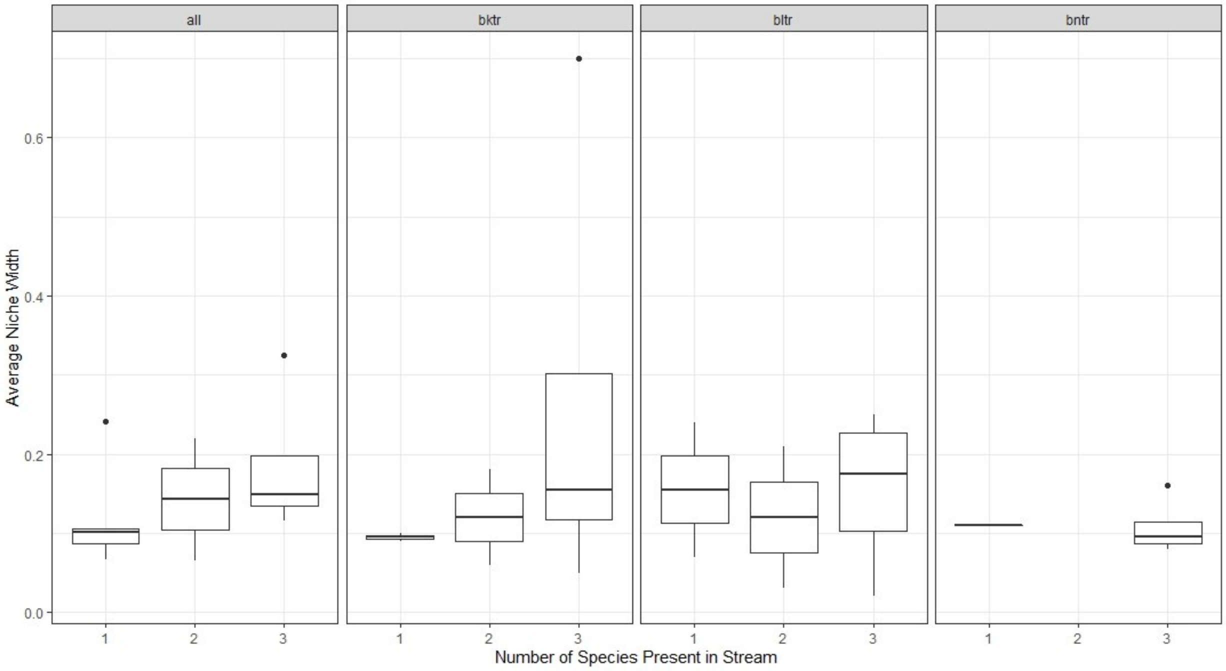

Figure 3.4 – Average niche width (SEA_B) between invasion levels. Individual tiles show the niche width of all species combined (all), Brook Trout (bktr), Bull Trout (bltr), and Brown Trout (bntr).

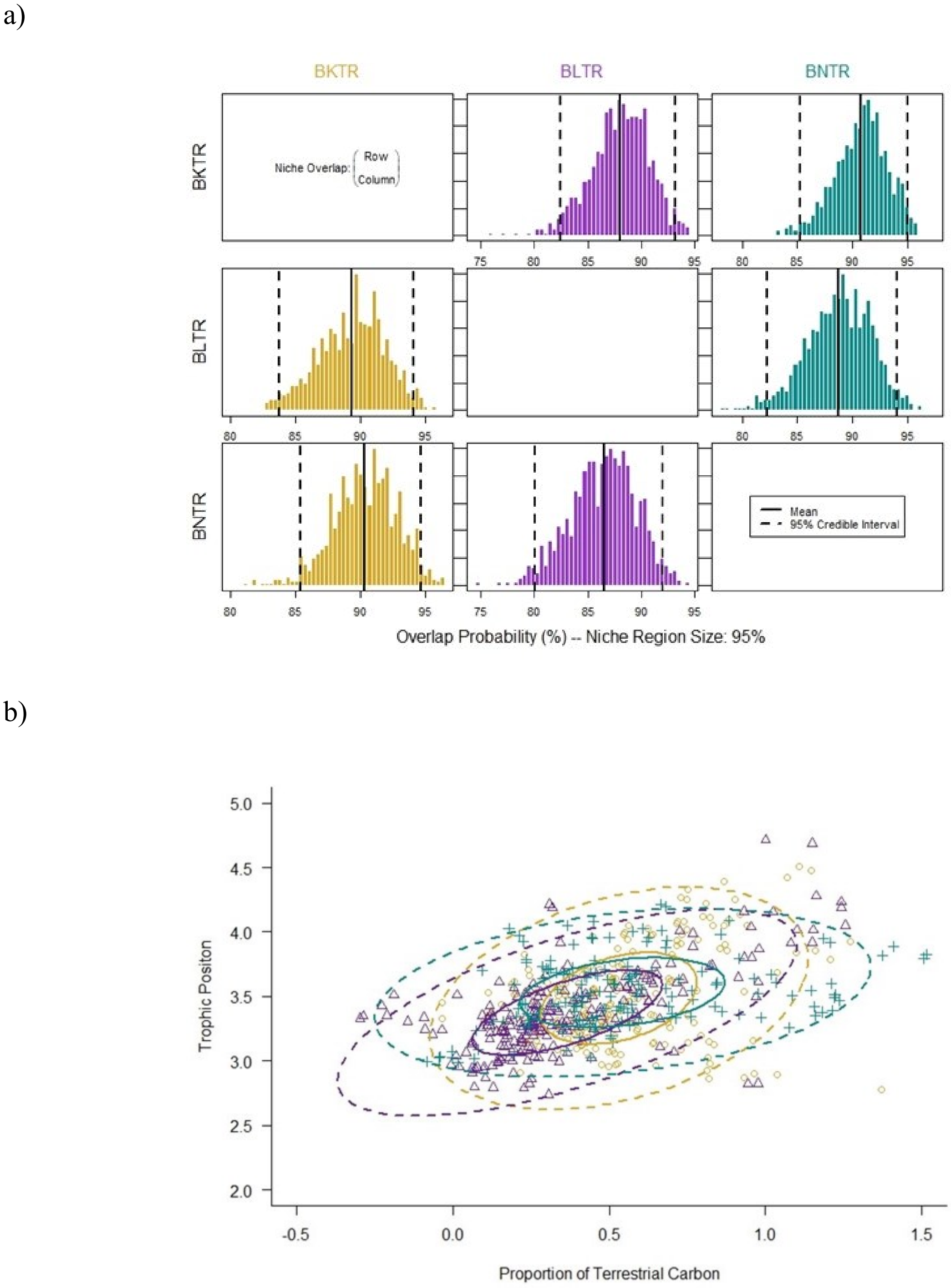

Figure 3.5 – Isotopic niche overlap between Brook Trout (BKTR), Bull Trout (BLTR), and Brown Trout (BNTR) over all invasion levels. Figure 3.5a shows the mean posterior probability (solid line) and the 95% confidence intervals (dotted line) of an individual species from the row being found within the niche of the species in the column. Figure 3.5b shows the standard ellipse area of the core niche (40% confidence interval – solid lines) and the realized niche (95% confidence interval – dotted lines) of Brook Trout (yellow), Bull Trout (purple), and Brown Trout (blue).

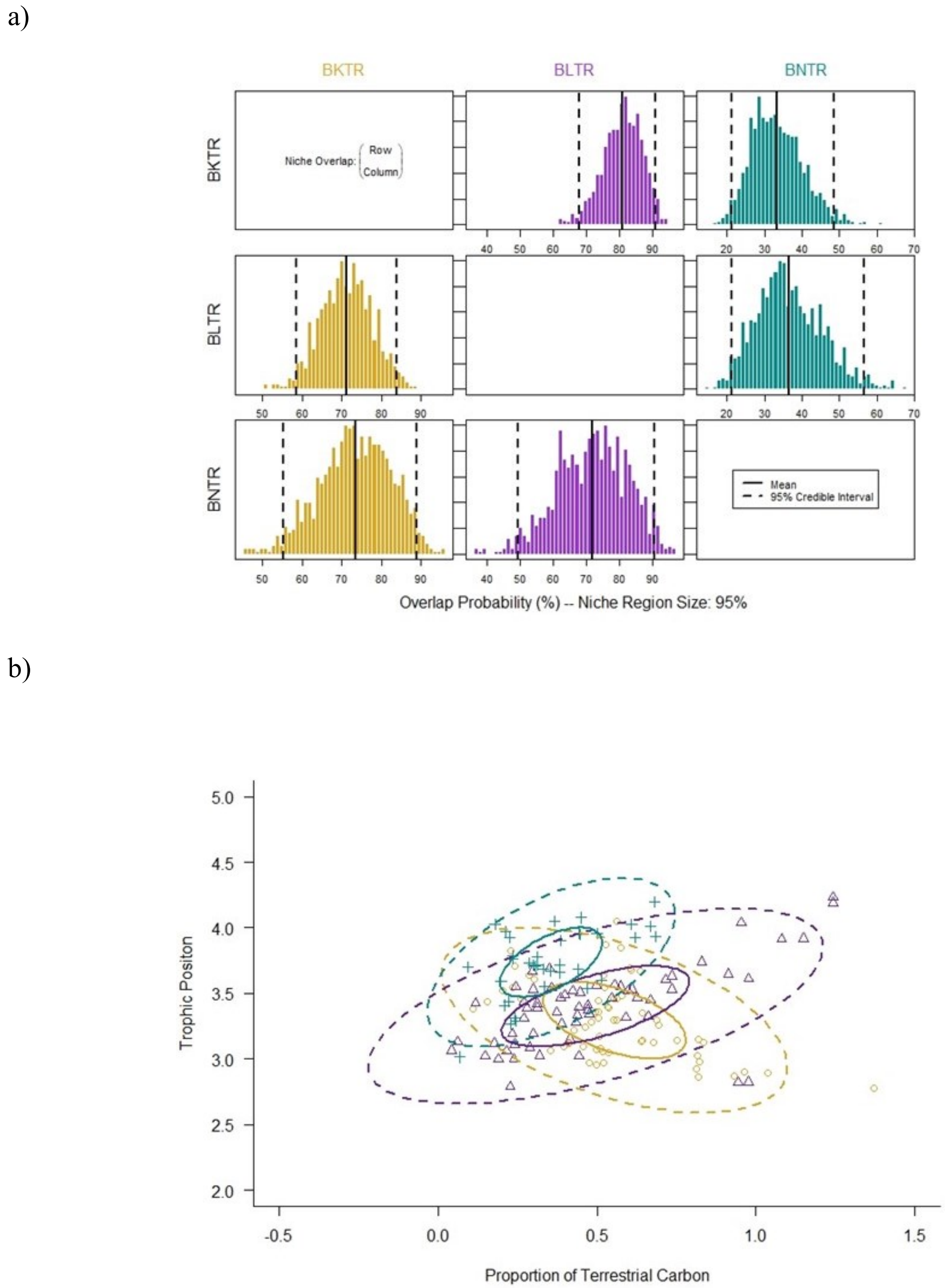

Figure 3.6 – Isotopic niche overlap between allopatric Brook Trout (BKTR), Bull Trout (BLTR), and Brown Trout (BNTR). Figure 3.6a shows the mean posterior probability (solid line) and the 95% confidence intervals (dotted line) of an individual species from the row being found within the niche of the species in the column. Figure 3.6b shows the standard ellipse area of the core niche (40% confidence interval – solid lines) and the realized niche (95% confidence interval – dotted lines) of Brook Trout (yellow), Bull Trout (purple), and Brown Trout (blue)

Table 3.1 – Means and standard deviation of raw δ13C and δ15N values for Brook Trout (BKTR), Bull Trout (BLTR), Brown Trout (BNTR), aquatic invertebrates (Collectors, Filterers, Scrapers, and Shredders), and terrestrial invertebrates (Terrestrial). Streams are separated by the invasion levels of Bull Trout dominant (BLTR), Brown Trout dominant (BNTR), Brook Trout dominant (BKTR), Bull Trout / Brook Trout mix (BLTR/BKTR), and Bull Trout / Brook Trout / Brown Trout mix (BLTR/BKTR/BNTR).

Invasion Level	Waterbody	Isotope	BKTR	BLTR	BNTR	Collectors	Filterers	Scrapers	Shredders	Terrestrial
BLTR	Burnt Timber	δ^{15}N	-	6.4 (0.3)	-	2.5 (0.7)	-	1.4 (0.46)	2.4 (0.5)	2.5 (0.9)
		δ^{13}C	-	-30.9 (0.4)	-	-33.8 (0.5)	-	-35.7 (0.5)	-31.7 (0.5)	-29.1 (0.5)
	Rocky	δ^{15}N	-	7.78 (0.1)	-	3.1 (0.3)	-	3.5 (0.2)	3.1 (0.6)	2.2 (1.2)
		δ^{13}C	-	-31.8 (0.3)	-	-36.1 (1.2)	-	-38.0 (0.6)	-29.7 (2.8)	-30.7 (0.9)
BNTR	Fallentimber	δ^{15}N	-	-	9.7 (0.1)	4.5 (0.2)	-	4.3 (0.3)	5.9 (0.7)	3.0 (3.2)
		δ^{13}C	-	-	-30.0 (0.2)	-34.7 (0.6)	-	-35.5 (1.0)	-32.7 (0.5)	-26.6 (0.3)
BKTR	Pineneedle	δ^{15}N	7.2 (0.1)	-	-	1.8 (0.6)	-	1.8 (0.13)	2.9 (0.8)	4.4
		δ^{13}C	-31.8 (0.2)	-	-	-32.6 (2.8)	-	-36.8 (0.7)	-31.3 (1.9)	-31.8
	Yara	δ^{15}N	7.2 (0.2)	-	-	2.4 (0.5)	-	3.3 (0.3)	3.2 (0.8)	0.5 (0.3)
		δ^{13}C	-31.3 (0.3)	-	-	-36.2 (1.4)	-	-38.2 (0.9)	-31.6 (1.7)	-27.7 (0.4)
BLTR / BKTR	Wildhorse	δ^{15}N	8.2 (0.1)	7.9 (0.3)	-	2.9 (0.2)	-	2.6 (0.1)	3.5 (0.4)	1.7 (0.8)
		δ^{13}C	-29.0 (0.4)	-29.4 (0.6)	-	-33.5 (1.5)	-	-37.8 (0.5)	-32.5 (0.6)	-28.7 (1.1)
	Wilson	δ^{15}N	7.7 (0.1)	7.3 (0.1)	-	2.6 (0.2)	-	3.0 (0.1)	3.3 (0.3)	2.2 (0.9)
		δ^{13}C	-31.5 (0.2)	-33.5 (0.1)	-	-36.4 (0.9)	-	-37.4 (0.5)	-32.0 (0.6)	-27.6 (0.5)
BLTR / BKTR / BNTR	Cutoff	δ^{15}N	6.9 (0.2)	7.1 (0.2)	8.2 (0.1)	2.5 (0.2)	3.8 (0.3)	2.0 (0.2)	2.4 (0.3)	3.1 (0.4)
		δ^{13}C	-29.1 (0.3)	-30.3 (0.3)	-26.0 (0.4)	-31.1 (0.7)	-27.5 (1.2)	-33.8 (0.5)	-30.4 (0.5)	-27.8 (0.5)
	Elk	δ^{15}N	7.9 (0.1)	7.7 (0.2)	8.2 (0.1)	3.6 (0.2)	-	4.1 (0.2)	4.34 (0.3)	3.0 (0.8)
		δ^{13}C	-33.2 (0.3)	-33.0 (0.6)	-30.6 (0.4)	-37.4 (0.8)	-	-38.7 (0.4)	-33.9 (0.7)	-29.4 (1.8)
	Rough	δ^{15}N	7.5 (0.1)	7.0 (0.04)	7.1 (0.2)	2.9 (0.2)	-	3.5 (0.3)	3.3 (0.5)	0.4 (0.3)
		δ^{13}C	-29.4 (0.2)	-31.8 (0.1)	-29.8 (0.2)	-33.9 (0.8)	-	-36.0 (0.4)	-31.4 (1.1)	-28.8 (0.4)
	Trout	δ^{15}N	7.3 (0.2)	8.3 (0.2)	8.5 (0.1)	4.1 (0.2)	4.0 (0.3)	4.4 (0.2)	4.1 (0.3)	1.8 (0.5)
		δ^{13}C	-28.6 (0.6)	-29.2 (0.7)	-31.9 (0.3)	-36.1 (0.5)	-31.8 (1.3)	-37.0 (0.5)	-33.3 (0.6)	-28.3 (0.6)

Table 3.2 – Trophic position (TP), terrestrial-based carbon ($1- \alpha$), and standard ellipses area (SEA$_B$) of Brook Trout (BKTR), Bull Trout (BLTR), Brown Trout (BNTR), and all species together (ALL) by stream. Averages for each species within invasion levels are bolded and significant differences (p-value < 0.001) between invasion levels for each species noted with a *.

	BKTR			BLTR			BNTR			ALL		
	TP	$1-\alpha$	SEA$_B$	TP	$1-\alpha$	SEA$_B$	TP	$1-\alpha$	SEA$_B$	TP	$1-\alpha$	SEA$_B$
Burnt Timber	-	-	-	3.35 (0.08)	0.38 (0.07)	0.24 (0.16, 0.36)	-	-	-	3.35 (0.08)	0.38 (0.07)	0.24 (0.16, 0.36)
Fallentimber	-	-	-	-	-	-	3.74 (0.04)	0.36 (0.03)	0.11 (0.08, 0.15)	3.74 (0.04)	0.36 (0.03)	0.11 (0.08, 0.15)
Pineneedle	3.08 (0.03)	0.67 (0.04)	0.09 (0.06, 0.12)	-	-	-	-	-	-	3.08 (0.03)	0.67 (0.04)	0.09 (0.06, 0.12)
Rocky	-	-	-	3.46 (0.03)	0.54 (0.04)	0.07 (0.05, 0.1)	-	-	-	3.46 (0.03)	0.54 (0.04)	0.07 (0.05, 0.1)
Yara	3.52 (0.04)	0.44 (0.03)	0.1 (0.07, 0.14)	-	-	-	-	-	-	3.52 (0.04)	0.44 (0.03)	0.1 (0.07, 0.14)
Allopatry	**3.29 (0.04)***	**0.56 (0.03)**	**0.1 (0.01)**	**3.4 (0.04)**	**0.5 (0.04) ***	**0.16 (0.09)**	**3.74 (0.04)***	**0.36 (0.03)***	**0.11**	**3.44 (0.03)**	**0.49 (0.02)**	**0.12 (0.03)**
Wildhorse	3.82 (0.04)	0.71 (0.05)	0.18 (0.13, 0.26)	3.74 (0.11)	0.66 (0.06)	0.21 (0.13, 0.34)	-	-	-	3.8 (0.05)	0.7 (0.04)	0.22 (0.17, 0.29)
Wilson	3.44 (0.03)	0.37 (0.02)	0.06 (0.04, 0.08)	3.28 (0.03)	0.16 (0.01)	0.03 (0.02, 0.04)	-	-	-	3.36 (0.02)	0.27 (0.02)	0.07 (0.05, 0.09)
BLTR / BKTR	**3.65 (0.04)***	**0.55 (0.04)**	**0.12 (0.06)**	**3.46 (0.06)**	**0.36 (0.05)**	**0.12 (0.09)**	**-**	**-**	**-**	**3.57 (0.03)**	**0.47 (0.03)**	**0.14 (0.08)**
Cutoff	3.33 (0.05)	0.41 (0.05)	0.17 (0.11, 0.26)	3.45 (0.05)	0.2 (0.05)	0.25 (0.18, 0.35)	3.51 (0.03)	0.93 (0.06)	0.16 (0.11, 0.23)	3.44 (0.03)	0.51 (0.05)	0.33 (0.26, 0.4)
Elk	3.23 (0.03)	0.35 (0.03)	0.05 (0.03, 0.08)	3.17 (0.07)	0.37 (0.07)	0.22 (0.16, 0.32)	3.41 (0.04)	0.62 (0.04)	0.1 (0.07, 0.14)	3.29 (0.03)	0.47 (0.03)	0.14 (0.12, 0.18)
Rough	3.72 (0.06)	0.59 (0.03)	0.14 (0.11, 0.19)	3.27 (0.02)	0.26 (0.01)	0.02 (0.01, 0.02)	3.55 (0.06)	0.54 (0.03)	0.08 (0.05, 0.13)	3.52 (0.03)	0.46 (0.02)	0.12 (0.1, 0.14)
Trout	3.39 (0.06)	0.7 (0.07)	0.06 (0.03, 0.16)	3.62 (0.09)	0.63 (0.08)	0.13 (0.06, 0.27)	3.45 (0.04)	0.33 (0.04)	0.09 (0.07, 0.13)	3.47 (0.04)	0.42 (0.04)	0.16 (0.12, 0.2)
BLTR / BKTR / BNTR	**3.5 (0.04)***	**0.5 (0.02)**	**0.11 (0.03)**	**3.32 (0.03)**	**0.3 (0.02)***	**0.16 (0.05)**	**3.47 (0.02)***	**0.6 (0.03)***	**0.11 (0.02)**	**3.42 (0.02)**	**0.47 (0.02)**	**0.18 (0.05)**
TOTAL	**3.49 (0.02)**	**0.53 (0.02)**	**0.11 (0.02)**	**3.38 (0.02)**	**0.36 (0.02)**	**0.15 (0.03)**	**3.53 (0.02)**	**0.54 (0.03)**	**0.11 (0.01)**	**3.47 (0.01)**	**0.47 (0.01)**	**0.15 (0.02)**

Table 3.3 – Mean isotopic niche overlap between Brook Trout (BKTR), Bull Trout (BLTR), and Brown Trout (BNTR) with 95% confidence intervals. Means represent the probability that a species from the column will be found in the isotopic niche of a species in the row. Percent overlap is separated by allopatric streams (Allopatry), Bull Trout / Brook Trout streams (BLTR / BKTR), Bull Trout / Brook Trout / Brown Trout streams (BLTR / BKTR / BNTR) and overlap within all streams (Total overlap).

		BKTR	BLTR	BNTR
Allopatry	BKTR	-	71.14 (58.49, 83.8)	73.36 (55.29, 88.8)
	BLTR	80.75 (67.9, 91)	-	71.79 (49.5, 90.7)
	BNTR	33.39 (21.3, 48.6)	36.59 (21.2, 56.61)	-
BLTR / BKTR	BKTR	-	84.67 (71.69, 94.6)	-
	BLTR	86.07 (73.79, 95.5)	-	-
	BNTR	-	-	-
BLTR / BKTR / BNTR	BKTR	-	84.66 (75.69, 92.5)	80.69 (71.7, 89.1)
	BLTR	88.57 (80.4, 95.1)	-	81.84 (72.1, 89.61)
	BNTR	83.42 (74.6, 91.1)	84.63 (76.1, 92)	-
Total overlap	BKTR	-	89.18 (83.6, 94.1)	90.43 (85.6, 94.7)
	BLTR	88.11 (82.7, 93.1)	-	86.33 (79.5, 91.8)
	BNTR	90.99 (86, 95.4)	88.47 (82.1, 93.8)	-

Chapter IV: General Conclusions

With Bull Trout (*Salvelinus confluentus*) populations undergoing significant declines from a multitude of stressors (i.e., climate change, introduced species, habitat degradation) (Fisheries and Oceans Canada, 2020; J. R. Post & Gow, 2012; M. Rodtka et al., 2009; Sawatzky & Secretariat, 2016; Sinnatamby et al., 2020), it is imperative to understand the degree to which non-native fishes are implicated in their decline. The overall objective of my thesis was to investigate the effects of Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*), two non-native species, on the resource use of Bull Trout in Alberta's foothills. To do so, I developed a multi-species N-mixture model using in-stream and land use derived characteristics to disentangle whether Brook Trout and Brown Trout are spatially displacing or replacing Bull Trout from habitat (Chapter 2). Subsequently, I investigated how Brook Trout and Brown Trout interact with the dietary niche of Bull Trout using stable isotope analysis to determine if there is potential for competition, unfilled niche occupancy, displacement, and/or resource partitioning when sympatric (Chapter 3).

Brook Trout and Brown Trout are two of the most widely introduced salmonids and have negatively affected native fishes globally, yet how they interact with Bull Trout habitat is unclear. As a result, it is difficult to determine whether Bull Trout are spatially displaced by non-native fishes or if their range contractions are attributed to abiotic conditions. In Chapter 2 we predicted that Bull Trout in sympatry with Brook Trout and Brown Trout would benefit from streams of higher elevation, with colder temperatures, higher large woody debris count, and higher proportions of pool and boulder (Al-Chokhachy et al., 2016; Bozek & Hubert, 1992; Kirk et al., 2018; Paul & Post, 2001; Warnock & Rasmussen, 2013a; Wood & Budy, 2009). However, results from our multi-species N-mixture models only partially supported these hypotheses. Our results confirmed that cold-water streams (<11°C) provide refuge for Bull Trout in a changing climate and from Brown Trout invasion; however, water temperature does not provide refuge from the invasion pressure of Brook Trout. While our model cannot confirm the effect of temperature on Brook Trout invasive success (Paul & Post, 2001; Rieman et al., 2006; Warnock & Rasmussen, 2013a), it corroborated the ability for Brook Trout to invade high elevation streams and their cold water preference (Adams et al., 2000; Kanda et al., 2002; Leary et al., 1993; Nakano et al., 1998; Peterson & Fausch, 2003; Rieman et al., 1997, 2006).

Although cold-water streams limit the invasion pressures of Brown Trout, they pervade in other environments. Our results indicated that Brown Trout shift the relationship between Bull Trout and the wetted width of a stream from positive to negative, irrespective of water temperature. However, given elevation was retained as a model component and its relationship with wetted width and large-scale landscape effects (Rabeni & Sowa, 1996), it is possible that the higher invasion pressure in larger streams is a result of elevation. Although invasion pressure is likely to be present in cold headwater streams from Brook Trout and larger, lower elevation streams from Brown Trout, our result indicated that stream complexity could provide refugia for Bull Trout from invasion pressure. Our model indicated that high large woody debris counts (>15), provides Bull Trout refuge from the invasion of Brook Trout, likely through the creation of complex in-stream habitat, and Brown Trout, likely due impassable in-stream barriers (Beschta & Platts, 1986; Fausch & Northcote, 1992, 1992; Harvey et al., 1999; Keim et al., 2002; Keller & Swanson, 1979; Ralph et al., 1994). These results are consistent with the growing body of evidence that suggests stream complexity will be an important source of refuge for salmonids (McMahon & Hartman, 1989; Pearsons et al., 1992; Rich et al., 2003; Watson & Hillman, 1997). Collectively, our results from Chapter 2 indicate that both Brook Trout and Brown Trout have the potential to spatially displace Bull Trout, but cold-water streams with high stream complexity may help mitigate invasion pressures.

To fully understand the degree to which Brook Trout and Brown Trout contribute to the decline of Bull Trout, we investigated how they interact with the dietary niche of Bull Trout in Chapter 3. We predicted that sympatric Brook Trout and Bull Trout will have a high niche overlap and that we would observe competition because of their feeding behaviour and interactions (Gunckel et al., 2002; McMahon et al., 2007; M. C. Rodtka & Volpe, 2007; Warnock & Rasmussen, 2013b). Our results corroborated our hypothesis, indicated by the high niche overlap (>84%) between sympatric Bull Trout and Brook Trout and the lack of niche shift from allopatry to sympatry. This is consistent with laboratory and in-stream studies that found no evidence for a niche shift in sympatric Bull Trout and Brook Trout (Gunckel et al., 2002; Nakano et al., 1998). Adversely, we predicted that sympatric Brown Trout and Bull Trout would have less niche overlap and would shift their niches to avoid competition (Hasegawa et al., 2004; Kitano, 2004). As hypothesized, sympatric Bull Trout and Brown Trout shifted their niche; however, niche overlap remained high between sympatric Bull Trout and Brown Trout (>80%)

and Bull Trout were displaced from terrestrial resources. These results indicated that a niche shift did not enable Bull Trout to avoid competition while it also displaced them from terrestrial prey, a crucial resource for salmonid growth (Baxter et al., 2007). Taken together, our results from Chapter 3 indicate that both Brook Trout and Brown Trout affect the dietary niche of Bull Trout and that competition for resources is likely to occur in streams where resources are limited, with Bull Trout being the species most negatively affected.

This work has successfully addressed the goal of my thesis which was to assess the effects of Brook Trout and Brown Trout on the resource use of Bull Trout in the Rocky Mountain Foothills of Alberta, Canada. Our findings suggest that both Brook Trout and Brown Trout interfere with the resource use of Bull Trout on a habitat and dietary level. From these works, managers should look to identify streams with high complexity and temperatures <11°C as they provide the greatest potential for Bull Trout refugia from the invasion pressures of non-native fishes in a changing climate. Subsequently, as Bull Trout populations in streams of low productivity are vulnerable to competition for resources, preventing future invasion into streams with healthy Bull Trout populations and low productivity should be prioritized.

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Appendices

Table A2.1 – Hypothesized relationships between habitat covariates and Bull Trout abundance denoted by positive (+) and negative (-) signs. Superscripts denote relationships we expected to be influenced by Brook Trout (K) and Brown Trout (N) presence.

Habitat Covariate	Hypothesis	Literature support
Elevation	$+^{K,N}$	Paul & Post, 2001; Rieman et al., 2006; Warnock & Rasmussen, 2013a; Al-Chokhachy et al., 2016; Wood & Budy, 2009
Distance to mainstem	$-^{K}$	Rich et al., 2003; Wenger et al., 2011
Riparian area	+	McPhail & Baxter, 1996; Nakano et al. 1992
Disturbed area	-	McPhail & Baxter, 1996;
Timber area	-	McPhail & Baxter, 1996;
Mean August water temperature	$-^{K,N}$	Selong et al., 2001; Paul & Post, 2001; Rieman et al., 2006; Warnock & Rasmussen, 2013a; Al-Chokhachy et al., 2016
Wetted width	$+^{K,N}$	Rich et al., 2003; Bozek & Hubert, 1992;
Pool	+	Post & Gow, 2012; Bonneau and Scarnecchia 1998
Riffle	-	Bonneau and Scarnecchia 1998
Run	+	Bonneau and Scarnecchia 1998
Silt	-	Watson & Hillman, 1997
Sand	-	Watson & Hillman, 1997
Gravel	+	Watson & Hillman, 1997
Cobble	$+^{K}$	Warnock & Rasmussen, 2013a; Watson & Hillman, 1997
Boulder	$+^{K}$	Warnock & Rasmussen, 2013a; Watson & Hillman, 1997
Bedrock	-	Watson & Hillman, 1997
Depth	$+^{N}$	Bonneau and Scarnecchia 1998; Heggenes, 1998
Large woody debris	$+^{K,N}$	Rich et al., 2003; Kirk et al., 2018;