Assessing the impacts of multiple ecological stressors on an endangered native salmonid, the Athabasca Rainbow Trout, in the foothills of the Canadian Rocky Mountains

by

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Abstract

Freshwater fish face a multitude of ecological stressors, which has resulted in substantial declines in aquatic biodiversity. The loss of aquatic biodiversity can lead to changes in ecosystem function, productivity and food web dynamics. One such imperiled freshwater fish is the Athabasca Rainbow Trout (*Oncorhynchus mykiss*), a unique Rainbow Trout ecotype found in the upper reaches of the Athabasca River watershed, forming the only native Rainbow Trout population in Alberta. Athabasca Rainbow Trout have experienced widespread declines in abundance, with losses of approximately 90% over the last three generation, or approximately 15 years. Two of the main ecological stressors impacting Athabasca Rainbow Trout are competition with invasive Brook Trout (*Salvelinus fontinalis*) and habitat degradation associated with natural resource extraction developments in the region. For example, in 2013 the accidental breach of a tailings dam at the Obed coal mine near Hinton, Alberta, Canada, released 670,000 m^3 of coal tailings material into Athabasca Rainbow Trout habitat. My goal in this thesis was to improve our understanding of ongoing impacts from multiple ecological stressors on Athabasca Rainbow Trout abundance and food resource use, inferred from sampling seven streams in the upper Athabasca River watershed. The specific objectives of this thesis were therefore to: 1) determine how this ecological stressor gradient has influenced Athabasca Rainbow Trout abundance in the foothills of west-central Alberta, and 2) understand how food resource utilization by Athabasca Rainbow Trout populations has been affected along a disturbance gradient associated with habitat degradation from the Obed mine tailings release and competition with invasive Brook Trout.

To meet my first study objective, I compared Rainbow Trout abundance with metrics associated with mining impacts to aquatic systems, landscape level stressors, abundance of invasive species and general stream habitat parameters between waterbodies along a gradient of ecological stressors. I determined that Athabasca Rainbow Trout abundance was not significantly different between groupings of streams impacted by the Obed mine tailings release compared with reference streams but was lowest in streams that were both highly turbid and had high abundance of invasive Brook Trout. To answer my second study objective, I used stable isotope analysis to determine trophic position, carbon source pathways, diet composition, niche width and resource use overlap to infer if food resource use changed along a disturbance gradient. I found that Athabasca Rainbow Trout in tailings disturbed waterbodies were utilizing a wider breadth of dietary resources and had substantially higher niche overlap with Brook Trout than in waterbodies not impacted by the tailings release, indicative of greater competition for food resources.

This thesis contributes to our understanding of how endangered Athabasca Rainbow Trout populations have been impacted by multiple ecological stressors and quantifies important interactions between these stressors with fish abundance and food resource use. Fisheries managers may wish to pursue additional measures to prevent subsequent declines in Athabasca Rainbow Trout populations by minimizing the detrimental impacts associated with landscape level habitat degradation and competition with invasive Brook Trout.

Preface

This thesis is an original work by Nathan A. Medinski.

The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Animal Care and Use Committee "Stream Assessment" AUP 00000757. Field collections were carried out under approved provincial Fish Research Licenses (15-2020 & 16-2018).

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and ellipses = TDI). Figure b shows the 95% Bayesian credibility intervals around the mean estimate of SEA for each of the three disturbance groups when BKTR and RNTR values are combined per disturbance group (NTI = No Tailings and Invaded, NTNI = No Tailings and Not Invaded, TDI = Tailings Disturbed and Invaded).

Chapter 1: General Introduction

Freshwater systems are amongst the most disproportionally impacted ecosystems on earth in terms of declines to native biodiversity (Dudgeon et al. 2006). The main categories of threats facing global freshwater aquatic biodiversity include: overexploitation, water pollution, flow modification, habitat degradation, and the naturalization of invasive aquatic species (Dudgeon et al. 2006). Mining activities, can be classified in the above threat categories as a source of both water pollution and habitat degradation. Some of the negative environmental impacts to aquatic systems commonly associated with coal mining operations include: 1) altered stream hydrology as a result of changes in forest cover and soil compaction, 2) elevated levels of sulphate and other contaminants such as selenium, aluminum and manganese in surface waters from leaching coal wastes, and 3) higher conductivity due to the additive or cumulative elevated concentration of several ions associated with alkaline mine drainage, that can reduce species biodiversity due to ionic toxicity (Bernhardt and Palmer 2011).

It has been well documented that the regular operations of coal mining can have detrimental impacts on aquatic systems. The negative impacts associated with mining on freshwater systems can have both direct and indirect effects on stream fish biomass (Kuchapski and Rasmussen 2015a), fish species richness and total abundance (Hitt and Chambers 2015), salmonid reproductive capacity and recruitment (Holm et al. 2005) and invertebrate food resource availability (Pond et al. 2008, Iwasaki et al. 2009, Kuchapski and Rasmussen 2015b, Kraus et al. 2016). Other impacts associated with natural resource extraction including the construction of infrastructure, such as roads and culverts required for industrial stream crossings, have been shown to negatively impact fish densities and community composition through increased sedimentation and stream turbidity (Ripley et al. 2005, Maitland et al. 2016). Aquatic habitat fragmentation and degradation can also cause changes in prey diversity, leading to alterations of fish diet and resource use (Layman et al. 2007, Kraus et al. 2016) Unintentional mining incidents, such as spills and releases, may further exacerbate these pressures on aquatic ecosystems.

A major mining related ecological disturbance occurred in west-central Alberta on October 31, 2013. A tailings dam at the Obed coal mine failed, resulting in approximately 670,000 m^3 of coal tailings material entering Apetowun Creek and then Plante Creek, tributaries of the Athabasca River approximately 30 km northeast of Hinton, Alberta (Cooke et al. 2016) . The tailings material consisted of a combination of surface water, process water, fine sediments and fine particulate coal material (Cooke et al. 2016). The released tailings plume contained elevated concentrations of several metals, including: Aluminum (Al), Arsenic (As), Barium (Ba), Iron (Fe), Lead (Pb), Manganese (Mn), Selenium (Se), Silver (Ag), Thorium (Th), Uranium (U) and Zinc (Zn) which met or exceeded relevant CCME Canadian Drinking Water Guidelines and Protection of Aquatic Life Guidelines in sample locations closest to the point source (Cooke et al. 2016). Additionally, there were elevated concentrations of several polycyclic aromatic hydrocarbons (PAHs) in both the released water and sediment compared to reference samples (Cooke et al. 2016).

Fish, benthic invertebrates and periphyton within the upper 5 km of Apetowun Creek suffered the most acute impact of the tailings release, resulting in substantial damage to the riparian zone, and substantial scouring of the stream bed and surrounding stream banks (Cooke et al. 2016) (Figure A1.1). The chronic effects of this major ecological disturbance on fish health and habitat use is poorly understood due to uncertainty associated with food resource availability, habitat availability, habitat usage, and impacts associated with contaminant deposition within the watershed (Cooke et al. 2016). This tailings release is of specific concern to fisheries managers because it occurred within the range of the Athabasca Rainbow Trout (*Oncorhynchus mykiss*), which has been designated as "Endangered" by COSEWIC due to substantial declines (> 90%) in abundance over the last three generations, corresponding to approximately 15 years (COSEWIC 2014).

In addition to habitat degradation from this coal tailings release, the Athabasca Rainbow Trout in west-central Alberta face pressures from invasive populations of Brook Trout (*Salvelinus fontinalis*) (COSEWIC 2014). Aquatic invasive species can lead to population declines in native fish species (Hermoso et al. 2011). Competition for food resources between native and invasive freshwater taxa has been shown to have negative impacts on the native species, through decreased growth rates and abundance (Baxter et al. 2007), and changes in resource availability and diet (Vander Zanden et al. 1999, Cucherousset et al. 2007, Olsson et al. 2009). In the upper Athabasca River watershed in west-central Alberta, non-native Brook Trout were stocked from the early 1940's to mid-1960's into several streams and headwater lakes for recreational angling (COSEWIC 2014). Many of these introduced populations of Brook Trout became naturalized and subsequently colonized non-stocked streams by moving through mainstem river networks (COSEWIC 2014).

Brook Trout are a fall-spawning salmonid, which makes their eggs less susceptible to scouring flood events associated with high stream discharge rates during the spring freshet than are those of Rainbow Trout, which typically spawn from late May to early June (Sterling 1992, COSEWIC 2014). Both fine sediment deposition and streamflow during the egg incubation period have been identified as critical factors influencing Athabasca Rainbow Trout fry survival in western Alberta. This seems to indicate that Brook Trout are better adapted to the winter low-flow and summer melt flow regime in the Rocky Mountain region of western North America than are native Rainbow Trout (Fausch 2008). Researchers looking into habitat predictors related to Brook Trout invasiveness in the foothills of western Alberta have also identified warmer average water temperatures (Warnock and Rasmussen 2013) and lower elevation (Paul and Post 2001) stream reaches as being positively associated with Brook Trout occupancy.

It is expected that multiple ecological stressors in the upper Athabasca River drainage will cause further population declines in Athabasca Rainbow Trout. Athabasca Rainbow Trout are not genetically distinct from neighboring Fraser River Rainbow Trout based on both mitochondrial and microsatellite DNA analysis (McCusker et al. 2000, Taylor et al. 2007). They are, however, a unique Rainbow Trout ecotype, which have developed distinct morphological, biological and habitat use differences from adjacent populations of Rainbow Trout in the Pacific drainage (COSEWIC 2014). Athabasca Rainbow Trout are distributed throughout the headwater streams of the upper Athabasca River drainage, including the mainstem Athabasca River, and it's tributary the McLeod River (COSEWIC 2014). The distribution of Athabasca Rainbow Trout is positively associated with higher elevations of approximately 900 – 1500 meters above sea level, reflecting an adaptation to cold water habitats (COSEWIC 2014). Athabasca Rainbow Trout likely colonized the foothills of Alberta through a headwater transfer between the Athabasca and Fraser Rivers following the last glacial period (Taylor et al. 2007). Habitat preferences for the Athabasca Rainbow Trout are thought to include clear and cold lotic systems, which are characterized by low interspecific competition (COSEWIC 2014).

The native Athabasca Rainbow Trout genome also faces pressures from hybridization with stocked non-native Rainbow Trout, though research has shown that limited genetic introgression has occurred in wild populations (Taylor et al. 2007). Recent genetics data, collected following the Obed mine release, shows that there is some genetic introgression in the Rainbow Trout in both Apetowun Creek and Plante Creek (Taylor and Yau 2015). The average admixture coefficient of Rainbow Trout in Apetowun and Plante Creeks were both Qi = 0.92, indicating genetically impure populations (Taylor and Yau 2015). These results need to be interpreted with caution due to small sample sizes (n = 15 and n = 4, respectively), as a proportionally small number of genetically impure individuals are lowering the overall average (Taylor and Yau 2015). Further work resolving the population genetic structuring of Athabasca Rainbow Trout in the Obed region is ongoing, with data collected from this thesis research project.

In this thesis, I address the impacts of multiple ecological stressors on the abundance (Chapter 2) and food resource use (Chapter 3) of Athabasca Rainbow Trout to determine how this species has been impacted by a combination of habitat degradation from the coal mine spill and the presence of invasive Brook Trout. Specifically, in Chapter 2, I studied the impacts of these stressors on Athabasca Rainbow Trout habitat use and abundance two years after the tailings release. To do this, I sampled forty sites in seven different waterbodies within the Obed region, which I classified into three unique treatments based on the types of ecological stressors present. I measured several biotic and abiotic metrics at each sample site and determined how Athabasca Rainbow Trout abundance was impacted by these metrics using both a multivariate analysis and mixed effects modelling approach.

In Chapter 3, I compared if Athabasca Rainbow Trout food resource utilization in streams that were impacted by the tailings release and/or invaded by Brook Trout were different from streams where neither ecological stressor was present. I utilized stable isotope analysis (SIA) to infer dietary habits of both Athabasca Rainbow Trout and Brook Trout in all seven waterbodies. I used standardized metrics such as trophic position and the proportion of diet derived from terrestrial carbon sources to compare differences between species in each sampled waterbody and disturbance group. I also used Bayesian analysis to determine the amount of niche overlap, niche width and contribution of various prey sources to the diet of both Athabasca Rainbow Trout and Brook Trout. This information will be useful to fisheries managers as it provides a description of how Athabasca Rainbow Trout have responded to a major ecological disturbance and provides insight into interspecific competition between native Athabasca Rainbow Trout and invasive Brook Trout in the upper Athabasca River watershed, an interaction that until now was not well understood (COSEWIC 2014).

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1.2 Figures

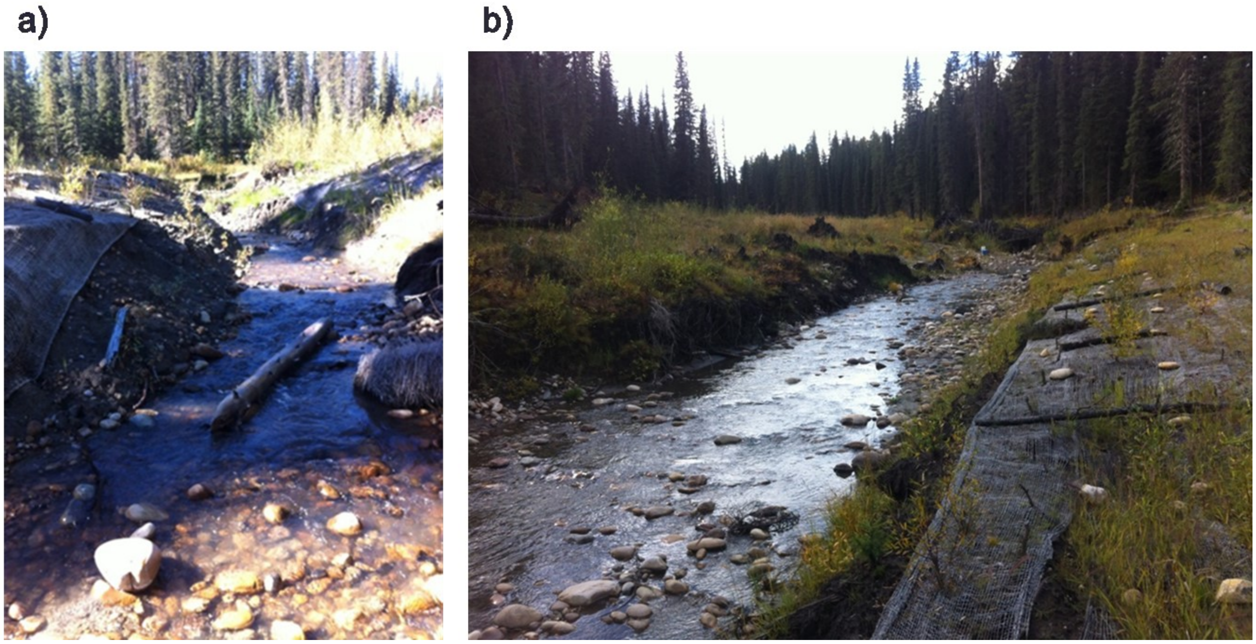

Figure A1.1. Apetowun Creek stream channel within the most disturbed upper 5 km section following the Obed coal mine tailings release of 2013. Both photos illustrate the extent of riparian area and stream bank damage as a result of the force of the tailings release, where approximately 670,000 m^3 of tailings material entered the headwaters of Apetowun Creek, a tributary of the Athabasca River near Hinton, Alberta. Pictures were taken in September 2015 during sampling for this thesis research project.

Chapter 2: Multiple Ecological Stressors Impact Athabasca Rainbow Trout Habitat Use and Abundance

2.1 Executive Summary

Native freshwater salmonids face substantial ecological stressors in the foothills of the Rocky Mountains. Several native salmonids in the foothills of western Alberta are currently listed as Threatened or Endangered either provincially or federally, including Bull Trout, Westslope Cutthroat Trout and Athabasca Rainbow Trout. Athabasca Rainbow Trout are a unique Rainbow Trout ecotype, found only in the upper Athabasca River watershed and form the only native population of Rainbow Trout in Alberta. Athabasca Rainbow Trout have experienced declines in population abundance of approximately 90% over the last three generations due to multiple stressors on the landscape overlapping with their native range. Among the most limiting stressors to native salmonids are associated with invasive species and habitat degradation. In this study, I assess the impacts of a large ecological disturbance, the Obed coal mine tailings release of 2013, on fish community composition, and Athabasca Rainbow Trout distribution and abundance, relative to neighbouring streams in west-central Alberta, Canada. I also measure the impacts that Brook Trout, an introduced salmonid stocked into streams in the region, has on Athabasca Rainbow Trout abundance. My results indicate that Athabasca Rainbow Trout abundance was negatively correlated with both turbidity and Brook Trout abundance. There was no indication that physicochemical parameters associated with the mining impacts, such as elevated conductivity measurements, impacted Athabasca Rainbow Trout abundance more so than landscape level impacts associated with natural resource development. Although there were limited short-term effects of this tailings release on Athabasca Rainbow Trout abundance, there is potential for negative chronic impacts to this threatened Athabasca Rainbow Trout population

associated with habitat degradation in tailings disturbed streams. The longer-term impacts will likely depend on the success of ongoing stream restoration efforts.

2.2 Introduction

Freshwater fish species are among the most imperiled taxa of organisms in North America (Ricciardi and Rasmussen 1999, Dudgeon et al. 2006). Impacts to freshwater fishes are often characterized in five main categories: over-exploitation, water pollution, flow modification, habitat degradation and destruction, and invasive species (Dudgeon et al 2006). Of these impacts, habitat degradation and invasive species are thought to be the most important causes of biodiversity loss, respectively (Light and Marchetti 2007). Habitat degradation can result in the loss of important resources that are required for freshwater fish to complete their life history requirements. For example, stream sedimentation can impair salmonid spawning success, as well as altering food resources available to consumers, resulting in decreased juvenile growth and survival (Suttle et al. 2004). Invasive species impact native freshwater taxa through competition for food and habitat space (Vander Zanden et al. 1999, Baxter et al. 2007), as well as through predation, genetic introgression and disease transmission amongst other impacts (Cucherousset and Olden 2011). In the foothills of the Rocky Mountains, several of these stressors to freshwater fish coincide, particularly habitat degradation associated with industrial development and invasive species (COSEWIC 2014).

The Athabasca Rainbow Trout (*Oncorhynchus mykiss*), found in the upper Athabasca River watershed of Alberta, Canada, is designated as an Endangered species (COSEWIC 2014). The Athabasca Rainbow Trout is a unique Rainbow Trout ecotype, though not genetically distinct from neighboring Fraser River Rainbow Trout based on both mitochondrial and microsatellite DNA analysis (McCusker et al. 2000, Taylor et al. 2007). Athabasca Rainbow Trout likely colonized the foothills of Alberta through a headwater transfer between the Athabasca and Fraser Rivers following the last glacial period (Taylor et al. 2007). Habitat preferences of the Athabasca Rainbow Trout are thought to include clear and cold lotic systems, which are characterized by low interspecific competition (COSEWIC 2014). Some of the major threats facing the future viability of Athabasca Rainbow Trout populations therefore include habitat degradation due to resource exploitation, habitat fragmentation and competition with invasive species (COSEWIC 2014).

Given the sensitivity of Athabasca Rainbow Trout to habitat disturbance and competition with invasive species, understanding the impacts of ecological stressors on the species is crucial for fisheries managers seeking to recover these declining populations. One major ecological disturbance occurred in October 2013, when a tailings dam at the Obed coal mine failed. This event resulted in approximately 670,000 m^3 of coal tailings material entering Apetowun Creek and Plante Creeks, tributaries of the Athabasca River approximately 30 km northeast of Hinton, Alberta (Cooke et al. 2016). This release resulted in substantial damage to the upper 5 km of Apetowun Creek, including the near-complete destruction of the riparian zone, and substantial scouring of the stream bed and surrounding stream banks (Cooke et al. 2016). The tailings plume contained sediment, coal fines, surface and process water, elevated total suspended sediment (TSS), nutrients (nitrogen and phosphorus), total metals concentration (including aluminum, arsenic, lead and selenium) and several polycyclic aromatic hydrocarbons (PAHs) in both the released water and sediment compared to reference samples (Cooke et al. 2016).

Mining has been shown to have widespread adverse impacts on lotic systems, including: increased sedimentation and turbidity in receiving streams (Lloyd et al. 1987, Bailey et al. 1998), increased specific conductivity (Palmer et al. 2010, Cormier et al. 2013, Kuchapski and

Rasmussen 2015b), metal contamination (Holm et al. 2005, Miller et al. 2013, Kuchapski and Rasmussen 2015a), alteration of natural stream flow regimes and degradation of riparian buffer areas (Bernhardt and Palmer 2011), changes to aquatic food web structure (Kraus et al. 2016) and changes to fish and aquatic macroinvertebrate assemblages (Pond et al. 2008, Daniel et al. 2015, Hitt and Chambers 2015, Kuchapski and Rasmussen 2015b). The Obed mine tailings material was shown to have low acute toxicity to Rainbow Trout, however the longer-term impacts due to habitat degradation as a result of channel scouring, contaminant deposition and chronic toxicity, siltation from stream bank erosion and riparian destruction in the upper reaches of Apetowun Creek are harder to assess (Cooke et al 2016). It is possible that this tailings release could lead to increasingly warm and turbid sections of the receiving streams, which would be at odds with the thermal and physical stream properties preferred by Athabasca Rainbow Trout.

In addition to stresses associated with habitat degradation and fragmentation, fisheries managers have long been interested in stocking non-native trout throughout North America, to develop sport and commercial fisheries (Dunham et al. 2002). The introduction of non-native organisms through stocking can causes stress to the receiving freshwater ecosystem (Cucherousset et al. 2007, Strayer 2010). The invasion of non-native salmonids has been shown to alter resource utilization by native species, leading to ecosystem change across multiple trophic levels (Baxter et al. 2004). For Athabasca Rainbow Trout, the introduction of non-native Brook Trout into their range is thought to have contributed to their decline, though this has yet to be quantified (COSEWIC 2014). From approximately the mid 1940's to mid-1990's Brook Trout (*Salvelinus fontinalis*) were stocked into several streams of Alberta's foothills and have since become naturalized (Rasmussen and Taylor 2009). This invasive species has been implicated in contributing to declines in Athabasca Rainbow Trout populations, however the competitive interactions between the two species has not been directly studied, and in general is poorly understood (Fausch 1988, Rasmussen and Taylor 2009).

To further investigate the potential impact of multiple stressors, I designed a multi-comparative study to assess the impacts of the Obed mine tailings release and competition with invasive Brook Trout on Athabasca Rainbow Trout abundance in west-central Alberta. My study goals were to: 1) understand the impacts of the Obed coal mine tailings release on abiotic and biotic conditions in several streams to the upper Athabasca River watershed, including tailings impacted streams, stream indirectly impacted by the coal mine and reference streams, 2) understand which environmental gradients were most influential in structuring fish community composition, and 3) determine which biotic or abiotic variables were most important in explaining Athabasca Rainbow Trout and Brook Trout abundance.

2.3 Methods

2.3.1 Study Area Description

The Obed Coal mine is located within the Upper Athabasca River watershed in the Foothills Natural Region of west-central Alberta (Natural Regions Committee 2006). Elevation in this region ranges from 700 to over 1700 meters above sea level (masl). This region is dominated by upland forests consist primarily of lodgepole pine (*Pinus contorta*) with some aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*), while poorly drained sites are comprised of lodgepole pine, aspen, balsam poplar, paper birch (*Betula papyrifera*), black spruce (*Picea mariana)* and tamarack (*Larix laricina*) (Natural Regions Committee 2006). The region is mostly underlain by sandstone and mudstone bedrock, with medium textured, mildly calcareous glacial till composing the surficial deposits (Natural Regions Committee 2006). In addition to coal mining in the area, additional pressures to the land base from extensive oil and gas exploration and development, forestry and off-highway vehicle recreation affect the natural ecosystems in the Foothills Natural Region (Natural Regions Committee 2006).

2.3.2 Study Design

I sampled 40 sites in 7 waterbodies and grouped these into three distinct treatments: 1) Tailings Disturbed (T.D.), 2) Indirectly Disturbed (I.D.) and 3) Reference (Ref.) (Figure 1.1). The Tailings Disturbed treatment included 17 sites sampled on Apetowun Creek (n = 12) and Plante Creek (n = 5), which directly received inputs of tailings material released in the 2013 Obed mine spill. The Indirectly Disturbed treatment included sites that did not receive coal tailings in the 2013 spill, however they all drain portions of the Obed mine surface lease area and receive discharge water from settling ponds located on the mine site (Hatfield Consultants 2014). Indirectly Disturbed sites included Canyon Creek (n = 6), Baseline Creek (n = 5), and Oldman Creek (n = 6). Reference treatment sites were located outside of the Obed mine area and were chosen to represent areas with minimal habitat disturbance from industrial activities and low Brook Trout invasiveness. Reference sites included McPherson Creek (n = 4) and Trapper Creek (n = 2). All sites were located in either headwater (Strahler order 1-3, n = 23), or medium sized (Strahler order 4-6, n = 17) stream reaches. Sample sites were located at least 300 m upstream or downstream from the nearest sample reach.

2.3.3 Fish Community Composition and Habitat Sampling

Sampling was conducted between mid-July and early October 2015. Previous sampling indicated that 12 species of fish are found in the upper Athabasca River region, including: Athabasca Rainbow Trout (*Oncorhynchus mykiss*), Brook Trout (*Salvelinus fontinalis*), Bull Trout (*Salvelinus confluentus*), Mountain Whitefish (*Prosopium williamsoni*), Arctic Grayling (*Thymallus arcticus*), Burbot (*Lota lota*), Spoonhead Sculpin (*Cottus ricei*), Longnose Dace

(*Rhinichthys cataractae*), Pearl Dace (*Margariscus margarita*), Longnose Sucker (*Catostomus catostomus*), White Sucker (*Catostomus commersoni*) and Northern Pike (*Esox lucius*) (COSEWIC 2014).

Each site was a 300 m reach, as per Alberta small stream protocol (AESRD 2013). Turbidity measurements (NTU) were collected 20 m upstream of each site and analyzed using a LaMotte EPA2020 handheld turbidity meter (LaMotte, Chestertown, MD, USA). Sites were electrofished with a Smith-Root LR24 backpack unit (Smith-Root, Vancouver, WA, USA) from downstream to upstream using a single pass method. All captured fish were identified to species and measured to the nearest millimeter for both total and fork length. Following fish sampling, habitat data were collected from downstream to upstream at seven evenly spaced transects, running perpendicular to the stream channel, at 50 m intervals. At each transect, water parameters were recorded, including: water temperature (ºC), pH, dissolved oxygen (mg/L) and conductivity (µS/cm) using a YSI handheld multiprobe meter (YSI, Yellow Springs, OH, USA). Stream channel width (i.e. wetted width) was measured to the nearest centimeter at each transect using a measuring tape. Depth (cm) and velocity (m/s) measurements were taken at three locations along each transect at 25%, 50% and 75% of the channel width. Velocity measurements were taken at 80% of water depth below the stream surface using a SonTek handheld acoustic Doppler velocimeter (SonTek/Xylem Inc., San Diego, CA, USA). A visual estimate of substrate type was taken at each transect and separated into percentages of fines (< 0.2 cm), gravel (0.2-6.4 cm), cobble (6.4 – 25.6 cm) and boulder (> 25.6 cm), based on a modified Wentworth scale. Finally, the percent of the stream channel between transects consisting of pool, riffle or run habitat was quantitatively estimated to the nearest 5% (AESRD 2013).

2.3.4 Data Analysis

i) Abiotic and Biotic Site Characteristics

Fish abundance at each sample site was standardized as catch per unit effort (CPUE), where abundance of each species was divided by electrofishing effort (seconds). Water depth, wetted width and stream velocity were averaged across transects for each sample site. The average percentage of pool, riffle and run, as well as percent of fines, gravel, cobble and boulder were also averaged from each transect for an overall value representing the 300 m sample reach. Fish species richness, Shannon diversity and a Pielou evenness index were calculated for fish diversity for each sampled stream reach. Permutational ANOVAs (Anderson 2001) were used to analyze treatment-level differences in measured variables, such as fish abundance, richness and environmental habitat variables (Table 2.1). Permutational ANOVAs, using 1000 iterations were conducted in the *lmPerm* package (Wheeler and Torchiano 2016). A Tukey HSD *post-hoc* test was conducted to determine between treatment differences. All analyses for this study were conducted in R version 3.4.1 (R Core Team 2017).

ii) Multivariate Analysis of Environmental Gradients

Redundancy Analysis (RDA) was performed to further determine the correlation between physicochemical habitat parameters and abundance of all fish species that were captured via electrofishing, except Bull Trout, which were only captured at 1 sample location. All fish species were included in the analysis, as the removal of rare species can bias the results of multivariate bioassessment techniques, by removing species that may be sensitive to anthropogenic disturbance (Poos and Jackson 2012). A detrended correspondence analysis (DCA) was first implemented to determine that gradient length, representing species turnover along a measured gradient, was appropriate for the use of RDA. RDA is a form of constrained ordination which combines multi-response regression analysis with principal components analysis, and seeks to form axes that represent linear combinations of predictor variables to explain the most variance in the response data matrix (here fish species abundance) (Borcard et al. 2011).

The most important environmental predictor variables were selected based on a forward stepwise regression procedure from the global model using the *ordiR2step* function in *vegan* (Oksanen et al. 2017), which selects the most important explanatory variables based on maximized adjusted R^2 values. Prior to RDA analysis predictor variables were standardized to z-scores, using the *decostand* function in *vegan* (Oksanen et al. 2017). RDAs were conducted using the *vegan* package in R (Oksanen et al. 2017).The species-site matrix was normalized using a "Hellinger" transformation (Legendre and Legendre 2012) in *vegan* (Oksanen et al. 2017) prior to running the RDA model. This method was chosen as the use of Euclidean distance has been shown to be inappropriate for zero-inflated species abundance data sets (Parris 2004, Borcard et al. 2011). Model terms were retained when the variance inflation factor (VIF) was < 10 to prevent issues associated with multicollinearity (Borcard et al. 2011). To test for significance of the environmental predictors, marginal predictors and RDA axes, permutational ANOVA tests were performed in the package *vegan*, using 999 permutations. Only significant predictor variable at the $p < 0.05$ level were retained in the final model. The correlation between important abiotic predictor variables and the abundance of both Athabasca Rainbow Trout and Brook Trout was further explored using Pearson's product-moment correlation tests. To verify that the RDA analysis included the most important environmental variables in predicting fish abundance, I performed a Procrustes analysis in *vegan*, followed by a PROTEST randomization test comparing site scores in the RDA model to a PCA that included only standardized fish abundance (Peres-Neto and Jackson 2001).

iii) Athabasca Rainbow Trout Mixed Effects Model

I created a linear mixed effects models to determine the importance of selected habitat metrics on Athabasca Rainbow Trout abundance, with treatment (T.D., I.D., Ref.) as the random effect. Treatment was used as a random effect to account for the random variation between waterbodies nested within each Treatment category, and to understand the underlying variation among the treatment groups (Bolker et al. 2009). Linear mixed effects models have been shown to be useful tools for analyzing nested data and dealing with spatial and temporal autocorrelation (Zuur et al. 2009). In this case a mixed effects model is useful to further understand how Athabasca Rainbow Trout abundance varies in response to habitat condition within each of the three distinct treatments in the Obed area. Prior to analysis standardized Athabasca Rainbow Trout abundance was square root transformed to meet the assumptions of a Gaussian error structure (Zuur et al. 2009). Models were constructed in the *nlme* package in R (Pinheiro et al. 2017). All predictor variables were standardized to z-scores prior to running the linear mixed effects model. Only variables with a VIF < 5 were retained for further use, as values above this threshold can indicate multicollinearity issues. Model selection was performed using backwards step selection and validated using $AICc_i$, which is a form of AIC corrected for small sample sizes (i.e., there are fewer than 40 times the number of observations to explanatory variables) (Anderson et al. 2001). Models with $\Delta AICc_i \leq 2$ have been shown to have considerable support (Burnham and Anderson 2004), and the coefficients of these models were explored further. Following model construction residuals were visually assessed for normality and homogeneity of variance using histograms of standardized model residuals and by plotting fitted terms against standardized residuals (Zuur et al. 2009).

2.4 Results

2.4.1 Biotic Differences Between Treatments

A total of 1572 fish were captured in the 40 samples sites. Of this total there were 10 fish species present, including: Athabasca Rainbow Trout (40%), Brook Trout (37%), Spoonhead Sculpin (11%), Burbot (3%), Longnose Sucker (3%), Pearl Dace (2%), Arctic Grayling (1%), Longnose Dace (1%), Mountain Whitefish (0.2%) and Bull Trout (0.0006%). Athabasca Rainbow Trout abundance did not differ between the Reference and Tailings Disturbed treatments ($p = 0.014$), but was higher in both than in the Indirectly Disturbed treatment ($p < 0.001$) (Table 2.1). Brook Trout abundance in the Indirectly Disturbed treatment was 80 times higher than the Reference treatment, and 4 times higher than in the Tailings Disturbed treatment, though these differences were only marginally statistically significant ($p = 0.09$ and $p = 0.08$, respectively) (Table 2.1). Athabasca Rainbow Trout total length (mm) was significantly lower in the Reference treatment than in the Indirectly Disturbed treatment ($p < 0.05$), with no significant differences between other treatment combinations. Brook Trout total length (mm) was not significantly different between the Tailings Disturbed and Indirectly Disturbed treatments. There was no significant difference in fish species richness, evenness or Shannon diversity between any of the treatments (Table 2.1).

2.4.2 Physicochemical Differences Between Treatments

Several physical and chemical stream properties differed significantly between treatments (Table 2.1). Conductivity was significantly higher in the Tailings Disturbed treatment than either the Indirectly Disturbed ($p < 0.001$) or Reference ($p < 0.001$) treatments. Conductivity was also significantly higher in the Indirectly Disturbed treatment than the Reference treatment ($p = 0.01$). Turbidity was significantly higher in the Indirectly Disturbed treatment compared to the

Reference treatment ($p = 0.001$) while the Tailings Disturbed was intermediate between these two. Percent gravel in the Reference treatment was significantly greater than in Tailings Disturbed ($p = 0.03$), and marginally greater than in Indirectly Disturbed ($p = 0.05$). Percent boulder was higher in the Indirectly Disturbed treatment than the Tailings Disturbed treatment ($p = 0.005$) while the Reference treatment was intermediate between the other treatments. There was a significant difference in water temperature (°C) between all three treatments, however this result is difficult to interpret as it represents only a one-time measurement on the day the stream reach was sampled, not a long-term average. None of the other measured physicochemical parameters showed any significant differences (Table 2.1).

2.4.3 Multivariate Analysis Correlating Standardized Fish Abundance with Habitat Characteristics

Four physicochemical terms: elevation (Elevation), average depth (Avg Depth), stream discharge (Discharge) and turbidity (Turbidity), were identified as significant predictors of fish assemblage and relative abundance in the RDA model (Table 2.2, Figure 2.2). The first three RDA axes were found to be significant (RDA Axis 1: $F = 24.6$, $p = 0.001$; RDA Axis 2: $F = 9.1$ $p = 0.001$; RDA Axis 3: $F = 2.4$, $p = 0.05$). The adjusted R^2 value of the model was 0.465, and the first two RDA axes accounted for 41.4% of the explained variance, with RDA axis 1 accounting for 30.1%. All predictor terms were found to significantly contribute to the variance explained on each of the first two significant RDA axes (Table 2.2). There was strong concordance ($m^{1,2} = 0.527$, $P = 0.001$) between the PCA ordination of fish abundance and the RDA model based on PROTEST analysis (Paavola et al. 2006).

Species scores on RDA Axis 1 ranged along a gradient from Athabasca Rainbow Trout dominated sites to Brook Trout dominated sites, with a negative correlation between the two

(Figure 2.2, Table 2.2). The environmental gradient displayed on the first RDA axis ranged from higher elevation sample sites, correlated with Athabasca Rainbow Trout abundance, to higher turbidity sites, which were correlated with Brook Trout abundance (Table 2.2, Figure 2.2). The abundance of Spoonhead Sculpin (SPSC), Burbot (BURB), Longnose Sucker (LNSC), Longnose Dace (LNDC), Pearl Dace (PRDC), Mountain Whitefish (MNWH) and Arctic Grayling (ARGR) were positively correlated with Athabasca Rainbow Trout abundance, and negatively with Brook Trout abundance along RDA axis 1 (Figure 2.2). RDA axis 2 showed an environmental gradient from higher elevation sites, which were correlated with Athabasca Rainbow Trout and Burbot abundance, to sites with greater average depth and stream discharge, correlating with Spoonhead Sculpin and Longnose Sucker abundance (Figure 2.2, Table. 2.2). RDA axis 1 and RDA axis 2 therefore represented environmental gradients from higher elevation sites to sites higher in turbidity, and in average depth and stream flow, respectively.

The correlation between Athabasca Rainbow Trout abundance, Brook Trout abundance and the four most important abiotic predictors identified in the RDA were determined using Pearson's product-moment correlation tests. Athabasca Rainbow Trout abundance was negatively correlated with turbidity ($r = -0.5$, $p < 0.01$), average depth ($r = -0.03$, $p = 0.84$) and Brook Trout abundance ($r = -0.22$, $p = 0.18$). Athabasca Rainbow Trout were positively correlated with both elevation ($r = 0.24$, $p = 0.14$) and weakly correlated with stream discharge ($r = 0.006$, $p = 0.97$). Brook Trout abundance was positively correlated with turbidity ($r = 0.49$, $p < 0.01$), and negatively correlated with elevation ($r = -0.18$, $p = 0.27$), average depth ($r = -0.24$, $p = 0.14$) and stream discharge ($r = -0.18$, $p = 0.25$).

2.4.4 Linear Mixed Effects Model Predicting Athabasca Rainbow Trout Abundance in the Obed Region

Athabasca Rainbow Trout abundance was best explained by three abiotic habitat predictors: turbidity, elevation and average velocity (Table 2.3, Table 2.4). Four models fell within $\Delta AIC_c \leq 2$ and were therefore equally supported as the best performing models. The best-supported models showed that Athabasca Rainbow Trout abundance was positively associated with average velocity in Model 1 (coef = 0.011, $p < 0.05$), Model 3 (coef = 0.0039, $p = 0.14$), and Model 4 (coef = 0.092, $p = 0.05$). Athabasca Rainbow Trout abundance was seen to be negatively associated with turbidity in Model 2 (coef = -0.010, $p < 0.05$), Model 3 (coef = -0.0093, $p < 0.05$) and Model 4 (coef = -0.0054, $p = 0.28$). Athabasca Rainbow Trout abundance was positively associated with elevation in Model 1 (coef = 0.0096, $p < 0.05$) and Model 4 (coef = 0.0070, $p = 0.16$) (Table 2.4). Coefficients for all three models are presented in Table 2.4.

2.5 Discussion

Endangered native freshwater taxa face ecological stressors from both habitat degradation and interactions with invasive species (Baxter et al. 2004, Dudgeon et al. 2006). Athabasca Rainbow Trout are an Endangered ecotype of Rainbow Trout, which are sensitive to anthropogenic stressors, and their substantial population declines over the past several generations have been attributed to impacts associated with habitat degradation, climate change, invasive species, introgression with non-native salmonids, angling pressure and climate change (COSEWIC 2014). In this study I showed that variables associated with both habitat degradation and invasive species were related to lower Athabasca Rainbow Trout abundance in the foothills region of west-central Alberta. Abundance of Athabasca Rainbow Trout was significantly lower in both the Tailings Disturbed and Indirectly Disturbed treatments compared to the Reference treatment. This appeared to be directly related to impacts associated with both landscape level degradation (i.e., turbidity) and invasive species colonization (i.e., Brook Trout abundance). Tailings Disturbed and Indirectly Disturbed streams directly receive surface water discharge from the Obed mine site ponds. Mine runoff into streams is often represented as higher turbidity (Bailey et al. 1998) and higher conductivity values that are associated with leached ions, associated with alkaline mine drainage (Palmer et al. 2010, Kuchapski and Rasmussen 2015b). Turbidity and conductivity were both significantly higher in streams that directly received runoff from the Obed mine than in reference streams where there were relatively few impacts from industrial activity.

Amongst the water quality parameters commonly associated with landscape-level impacts from resource extraction projects, turbidity was most important in predicting both native Athabasca Rainbow Trout and invasive Brook Trout abundance. Turbidity can include several distinct fractions, including dissolved and particulate matter, inorganic and organic materials and suspended materials that result in the scattering and absorption of light particles in a water sample (Henley et al. 2000). Studies have shown there to be measurable negative effects of suspended sediment on Rainbow Trout populations, including reduction in egg viability and development, reduced rates of fry and juvenile survival, reduction in overall population size, decreased growth rate, damage to gill epithelium and increased coughing rate (Newcombe and MacDonald 1991). Elevated turbidity in lotic systems has been shown to result in decreased levels of primary production due to restricted light penetration into the water column, leading to lower abundance of zooplankton, benthic macroinvertebrates and Arctic Grayling abundance in Alaskan streams (Lloyd et al. 1987). Shaw and Richardson (2001) performed a controlled experiment to further understand the mechanisms behind observed negative responses of Rainbow Trout to elevated stream sediment concentration. The authors determined that indirect impacts of increased sediment, such as reduced invertebrate drift, species richness or abundance were less important in explaining reduced trout growth rates than were direct effects, including reduced prey capture efficiency and metabolic stress (Shaw and Richardson 2001).

Interestingly, Brook Trout appear more tolerant of turbid streams than Athabasca Rainbow Trout in the Obed region. Brook Trout abundance was significantly correlated with higher turbidity, largely driven by sites in Baseline Creek and Canyon Creek, where turbidity values (mean ± SE) were 54.3 ± 7.4 NTU and 61.7 ± 4.8 NTU respectively. Research into the impact of turbidity on Brook Trout in eastern North American streams has shown that as stream turbidity increased from 0.3 to >40 NTU, there was no difference in mean daily consumption rate of Brook Trout (Sweka and Hartman 2001a). There was, however, a significant decrease in Brook Trout specific growth rates as turbidity increased, likely due to a shift in foraging to a more energetically costly active searching strategy from a energy conserving drift foraging strategy (Sweka and Hartman 2001a). Other studies have shown that both the reactive distance and probability of reacting to a potential prey source both decreased when Brook Trout were in highly turbid (~ 40 NTU) environments (Sweka and Hartman 2001b). Brook Trout have also been shown to return to spawning areas following habitat disturbance, which resulted in substantial amounts of fine sediment deposited on the stream bed, though the recruitment success of return spawning fish was not documented (Pépino et al. 2012). It is possible that the colonization of Brook Trout into highly turbid streams in the Obed region, may be a result of multiple impacts, including a higher tolerance to turbidity than sympatric Athabasca Rainbow Trout, or their ability to utilize streams impacted by sedimentation for spawning (Rasmussen and Taylor 2009, Pépino et al. 2012).

Additionally, both the Tailings Disturbed and Indirectly Disturbed treatments had higher abundances of Brook Trout than did the Reference treatment. There was a negative correlation between the abundance of Brook Trout and Athabasca Rainbow Trout, likely indicating that these salmonids are competing for resources along one or more niche dimensions, however the trend was not significant. In northern Europe Brook Trout have become successful invaders, often displacing native salmonids (Cucherousset and Olden 2011). Brook Trout have been shown to replace native Brown Trout in small headwater stream reaches, where Brown Trout recruitment had been substantially reduced (Korsu et al. 2007). In lotic systems in France, invasive Brook Trout have caused native Brown Trout to undergo dietary shifts, thereby utilizing more terrestrial prey sources in sympatry, likely as a result of behavioral shifts in feeding patterns (Cucherousset et al. 2007). There are several factors that may confer an advantage to Brook Trout over Athabasca Rainbow Trout in the upper Athabasca watershed. These factors include: pre-adaptation to and selection of small, narrow streams that do not develop anchor ice in the winter due to groundwater upwelling zones used in spawning (Curry and Noakes 1995); faster growth and earlier age at sexual maturity, resulting in greater recruitment to the population (Fausch 2008); fall spawning makes them relatively unsusceptible to scouring high flows associated with the spring freshet, as are Rainbow Trout (Fausch 2008); and relative insensitivity to Selenium contamination in coal mine impacted streams compared to Rainbow Trout (Holm et al. 2005, Kuchapski and Rasmussen 2015a).

Other important habitat metrics associated with Athabasca Rainbow Trout abundance in the Obed region included elevation and average stream velocity. Headwater streams, located in high elevation stream reaches, have been shown to be critically important to aquatic organisms, and create linkages between upstream and downstream stream habitat (Meyer et al. 2007). These uppermost stream segments provide ecosystem services, such as: temperature and streamflow refugia; reduced exposure to competitors, predators and invasive species; provide spawning and nursery habitat; supply food and nutrients to downstream organisms and ecosystems (Meyer et al. 2007). Elevation, which displays a strong negative relationship with stream temperature, has been shown in other studies to be a significant predictor of trout distribution in the eastern slopes of Alberta. In this study I confirmed that Brook Trout abundance is positively correlated with lower elevation, and likely warmer stream reaches, as has been shown in several other studies (Paul and Post 2001, Dunham et al. 2002, Rieman et al. 2006, Warnock and Rasmussen 2013). Alternatively, Athabasca Rainbow Trout are found primarily in the headwater regions of the Athabasca River, and its major tributaries in west-central Alberta (COSEWIC 2014). Their distribution is thought to be strongly influenced by stream temperature and elevation, as they are commonly found in waters ranging from 900-1500 meters above sea level in their native range. These fish are resident of clear and cold waters, which are oligotrophic and characterized by few competitors and predators (COSEWIC 2014).

The final habitat variable in the linear mixed effects model shown to be an important predictor of Athabasca Rainbow Trout abundance was average sample reach velocity. Cunjak and Green (1983) found that in eastern Canada Rainbow Trout utilized habitats with significantly higher stream velocities and less overhead cover than did sympatric Brook Trout of similar size classes. Comparatively Brook Trout were found to prefer slower velocity positions within stream reaches when in sympatry with Rainbow Trout (Cunjak and Green 1983). Similar findings were made in Montana where current velocity was determined to be the most important predictor of Rainbow Trout abundance in pool habitats, likely correlating with increased food availability from drifting sources in faster waters (Lewis 1969).

There was no obvious environmental gradient related to the 2013 Obed mine tailings release seen in my multivariate analysis. The strongest signal of the tailings release was shown by elevated conductivity values in the Tailings Disturbed treatment. One reason for this might be that, as compared to other studies in coal mining regions of western Canada, the conductivity values measured in the Tailings Disturbed sites were relatively low (380.4 ± 23.1 µs/cm), though values up to 631 µs/cm were recorded nearest to the Obed mine site. Kuchapski and Rasmussen (2015b) reported conductivity values of 1099 ± 237 µs/cm (mean ± SE) in mine affected sites, compared with values of 315 ± 14 µs/cm in reference sites not directly impacted by mining in west-central Alberta and southeast British Columbia. Specific conductance concentrations > 500 µS/cm were found to impair invertebrate genus level diversity metrics in the Appalachian mining region (Pond et al. 2008), potentially leading to altered food web dynamics in these systems. Cormier (2013) proposed that a benchmark conductivity of 300 µS/cm may result in the extirpation of approximately 5% of benthic invertebrate genera in Appalachia. However, in the Appalachian mining region the 25th percentile of stream conductivity in reference streams was only 116 µS/cm (Cormier et al. 2013). Background conductivity values in coal mining regions of western Canada are, however, 306 µS/cm at the 25th percentile, indicating that proposed Appalachian benchmark values likely underestimate appropriate benchmark values for western Canada (Kuchapski and Rasmussen 2015b).

2.6 Conclusions

Due to the strong negative association with turbidity found in this study, Athabasca Rainbow Trout populations within Apetowun Creek may face chronic limitations in their abundance, resulting from increasing turbidity as a result of bank erosion and runoff of sediment into the stream. This is most likely to occur in the upper 5 km which was most impacted by the scouring effects of the tailings release and where much of the riparian buffer was lost. Increasing turbidity could potentially result in additional lethal, sub-lethal or behavioural effects that reduce habitat utilization by Athabasca Rainbow Trout, and/or could facilitate further colonization of this waterbody by Brook Trout, which are seemingly more tolerant to the effects of turbidity than Athabasca Rainbow Trout in the Obed region. Bank stabilization and erosion control measures have been undertaken by the mine operator to alleviate these impacts (CVRI 2016), however long term monitoring will be required to ensure these structures adequately remediate the damage caused by this large scale ecological disturbance.

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2.8 Figures and Tables

Table 2.1. Measured biotic and abiotic characteristics of all sample sites separated by treatment type. Values show mean (standard error). Significance testing was done with permutational ANOVA using 1000 iterations, followed by Tukey HSD test for each variable across treatments. The terms F and p denote the permutational ANOVA F-test and p-values, respectively. Significance codes are denoted by asterisks, where * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Letters next to mean values denote significant differences between treatments, as determined by Tukey *post hoc* tests. CPUE indicates Catch Per Unit Effort, measured as fish captured per 100 seconds.

Sampled Variables	Tailings Disturbed (n = 17)		Indirectly Disturbed (n = 17)		Reference (n = 6)		F	p
	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range		
Julian day	237.1 (5.4)	208-271	239.2 (7.2)	201-276	274.7 (1.8)	269-278		
Sampling Effort (s)	4000.5 (333.1)	1082-6688	3831.5 (278.9)	2575-6508	3104.8 (452.5)	1837-4813		
Stream Order	3.7 (0.27)	2.0-5.0	3.4 (0.19)	2.0-5.0	3.2 (0.31)	2.0-4.0		
Elevation (masl)	1118.4 (30.4)	959-1284	1130.8 (25.7)	996-1331	1241.5 (34.3)	1135-1325	2.81	ns
Average velocity (ms^{-1})	0.26 (0.03)	0.09-0.46	0.19 (0.02)	0.07-0.32	0.18 (0.06)	0.04-0.40	2.56	ns
Average depth (cm)	21.7 (1.3)	11-34	21.2 (2.4)	12-44	24.9 (8.4)	11-64	0.27	ns
Average wetted width (cm)	546 (55)	182-853	634.3 (104.5)	269-1709	391 (60)	168-573	1.27	ns
Stream Discharge (m^3s^{-1})	0.34 (0.06)	0.06-0.7	0.37 (0.2)	0.1-2.3	0.14 (0.04)	0.02-0.25	0.61	ns
% Pool	8.5 (1.4)	1.0-22	8.6 (1.1)	2.0-18	12.3 (3.6)	5.0-26	1.05	ns
% Riffle	52.4 (4.6)	29-86	47.1 (5.5)	12-86	40 (5.6)	16-51	0.91	ns
% Run	39.1 (4.3)	13-65	44.4 (4.9)	12-74	47.5 (6.9)	26-78	0.59	ns
% Fines	21.6 (4.1)	3-56	14.3 (3.1)	0-37	18.3 (6.8)	0-43	1.00	ns
% Gravel	**27.2 (1.9)^{b}**	**15-41**	**28.5 (2.8)^{ab}**	**9-47**	**41 (6.5)^{a}**	**24-69**	**3.79**	*****
% Cobble	43.8 (4.2)	11-71	37.6 (3.0)	14-54	27.0 (2.7)	18-38	3.20	ns
% Boulder	**6.9 (1.6)^{a}**	**0-24**	**19.6 (3.5)^{b}**	**1-41**	**13.7 (4.3)^{ab}**	**1-32**	**5.58**	******
Water temperature (^{o}C)	**12.2 (0.9)^{a}**	**6.0-17.0**	**9.1 (0.9)^{b}**	**4.0-14.2**	**4.6 (0.4)^{c}**	**3.1-5.5**	**10.98**	*******
Turbidity (NTU)	**40.2 (1.8)^{ab}**	**28-51**	**49.9 (3.9)^{a}**	**28-76**	**26.6 (6.2)^{b}**	**7-38**	**7.57**	******
Conductivity (µS/cm)	**380.4 (23.1)^{a}**	**265-631**	**266.9 (9.7)^{b}**	**200-326**	**161.3 (28.3)^{c}**	**71-212**	**23.09**	*******
Fish Species Richness	3.2 (0.3)	1.0-5.0	2.5 (0.3)	1.0-6.0	2.7 (0.8)	1.0-5.0	1.32	ns
Shannon Diversity	0.85 (0.07)	0.0-1.23	0.56 (0.1)	0.0-1.48	0.60 (0.3)	0.0-1.6	0.14	ns
Species Evenness	0.58 (0.04)	0.0-0.79	0.40 (0.07)	0.0-0.76	0.37 (0.1)	0.0-0.82	2.73	ns
Athabasca Rainbow Trout CPUE (fish/100s)	**0.52 (0.08)^{a}**	**0.015-1.23**	**0.2 (0.04)^{b}**	**0-0.6**	**0.79 (0.02)^{a}**	**0.27-1.25**	**10.74**	*******
Brook Trout CPUE (fish/100s)	**0.2 (0.09)**	**0-1.4**	**0.8 (0.03)**	**0-3.7**	**0.01 (0.01)**	**0-0.06**	**3.73**	*****

Table 2.2. Outputs from the RDA model showing scores for the most important habitat predictors and Hellinger transformed fish abundances on the first two RDA axis. Species scores are abbreviated as: Athabasca Rainbow Trout (RNTR), Brook Trout (BKTR), Spoonhead Sculpin (SPSC), Burbot (BURB), Longnose Sucker (LNSC), Longnose Dace (LNDC), Arctic Grayling (ARGR), Mountain Whitefish (MNWH) and Pearl Dace (PRDC). Significance testing for environmental predictor variables was performed with a permutational ANOVA, using 999 permutations.

Scores	RDA 1	RDA 2	F	Pr (>F)
Species Scores				
RNTR	-0.482	-0.314	-	-
BKTR	0.972	0.013	-	-
SPSC	-0.239	0.465	-	-
BURB	-0.200	-0.054	-	-
LNSC	-0.130	0.340	-	-
LNDC	-0.005	0.046	-	-
ARGR	-0.085	0.211	-	-
MNWH	-0.008	0.057	-	-
PRDC	-0.074	0.014	-	-
Biplot Scores				
Elevation	-0.621	-0.588	5.05	**
Turbidity	0.904	0.172	20.66	***
Avg Depth	-0.416	0.755	8.05	***
Discharge	-0.270	0.815	4.18	**

Significance codes: ** $p < 0.01$, *** $p < 0.001$

Table 2.3. List of the top candidate linear mixed effects models ($\Delta AIC_c > 7$) predicting Athabasca Rainbow Trout abundance. Models are listed in order from highest to lowest support according to AIC*c* values, which represent Akaike's information criterion with an adjustment for small sample sizes. Candidate models were fit using a maximum likelihood criterion to extract AIC*c* values. The symbol k represents the number of parameters within each model. The symbol *w* represents the Akaike weight of each model, assessing each models' plausibility compared to the top-performing model.

Model	Fixed Effects	*k*	AIC_c	ΔAIC_c	*w*
1	**Avg Velocity, Elevation**	**3**	**-176.2**	**0**	**0.26**
2	**Turbidity**	**2**	**-175.5**	**-0.7**	**0.19**
3	**Avg Velocity, Turbidity**	**3**	**-175.2**	**-1**	**0.16**
4	**Avg Velocity, Elevation, Turbidity**	**4**	**-174.6**	**-1.6**	**0.12**
5	Avg Velocity	2	-173.4	-2.8	0.07
6	Elevation, Turbidity	3	-173	-3.2	0.05
7	Turbidity, BKTR	3	-173	-3.2	0.05
8	Turbidity, Conductivity, BKTR	4	-172.2	-4	0.04
9	Avg Velocity, Elevation, Turbidity, % Fines	5	-171.9	-4.3	0.03
10	BKTR	2	-170.9	-5.3	0.02
11	Elevation	2	-170.6	-5.6	0.02
12	Avg Velocity, Elevation, Turbidity, % Fines, % Boulder	6	-170	-6.2	0.01

Table 2.4. Coefficients and significance values of fixed effects in the four best supported linear mixed effects models predicting Athabasca Rainbow Trout abundance, as supported by AIC*c* ($\Delta AIC_c \geq 2$), representing Akaike's information criterion with an adjustment for small sample size.

	Fixed Effects	Estimate	SE	t value	P
Model 1	(Intercept)	0.062	0.0095	6.5	***
	Elevation	0.0096	0.0041	2.6	*
	Avg Velocity	0.0110	0.0041	2.3	*
Model 2	(Intercept)	0.061	0.0078	7.8	***
	Turbidity	-0.010	0.0042	-2.5	*
Model 3	(Intercept)	0.061	0.0080	7.7	***
	Avg Velocity	0.0058	0.0039	1.5	ns
	Turbidity	-0.0093	0.0042	-2.2	*
Model 4	(Intercept)	0.061	0.0082	7.5	***
	Elevation	0.0070	0.0049	1.4	ns
	Avg Velocity	0.0092	0.0045	2.0	*
	Turbidity	-0.0054	0.0049	-1.1	ns

Significance codes: * $p < 0.05$, *** $p < 0.001$, ns = not significant

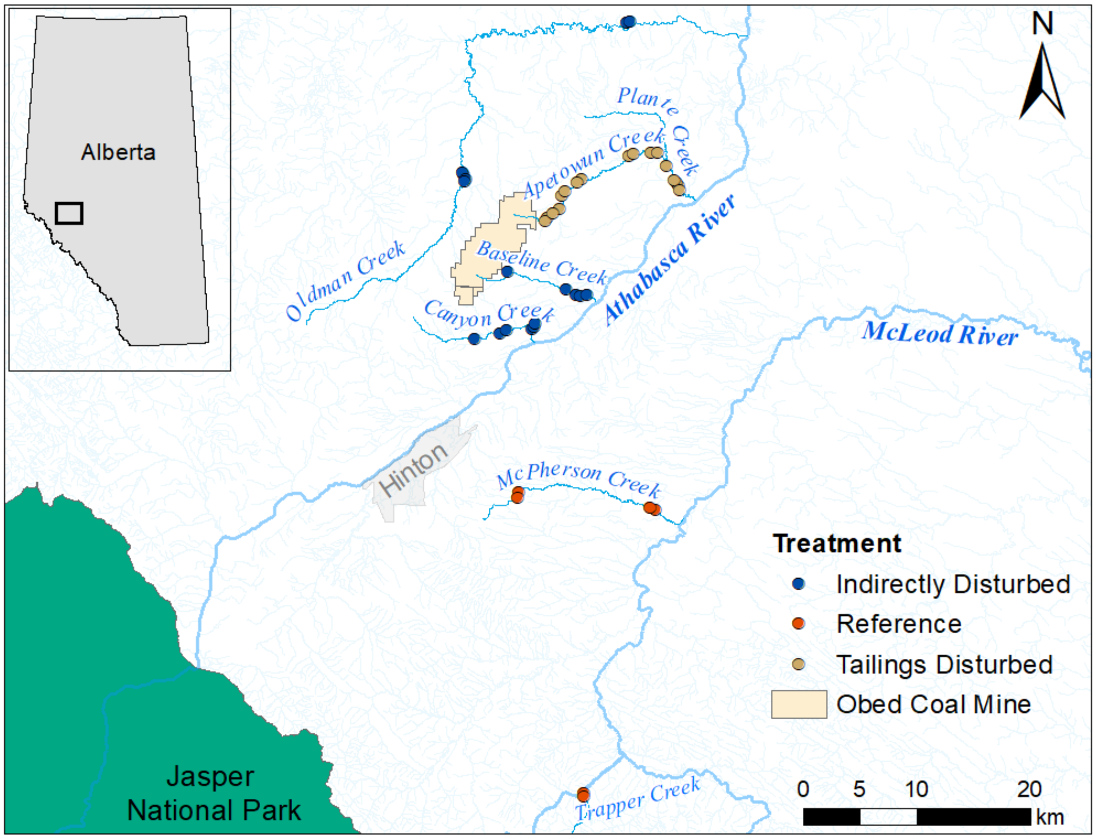

Figure 2.1. Overview of the Obed coal mine area in west-central Alberta showing the sample locations, coloured by treatment, where data were collected for this study from July to October 2015.

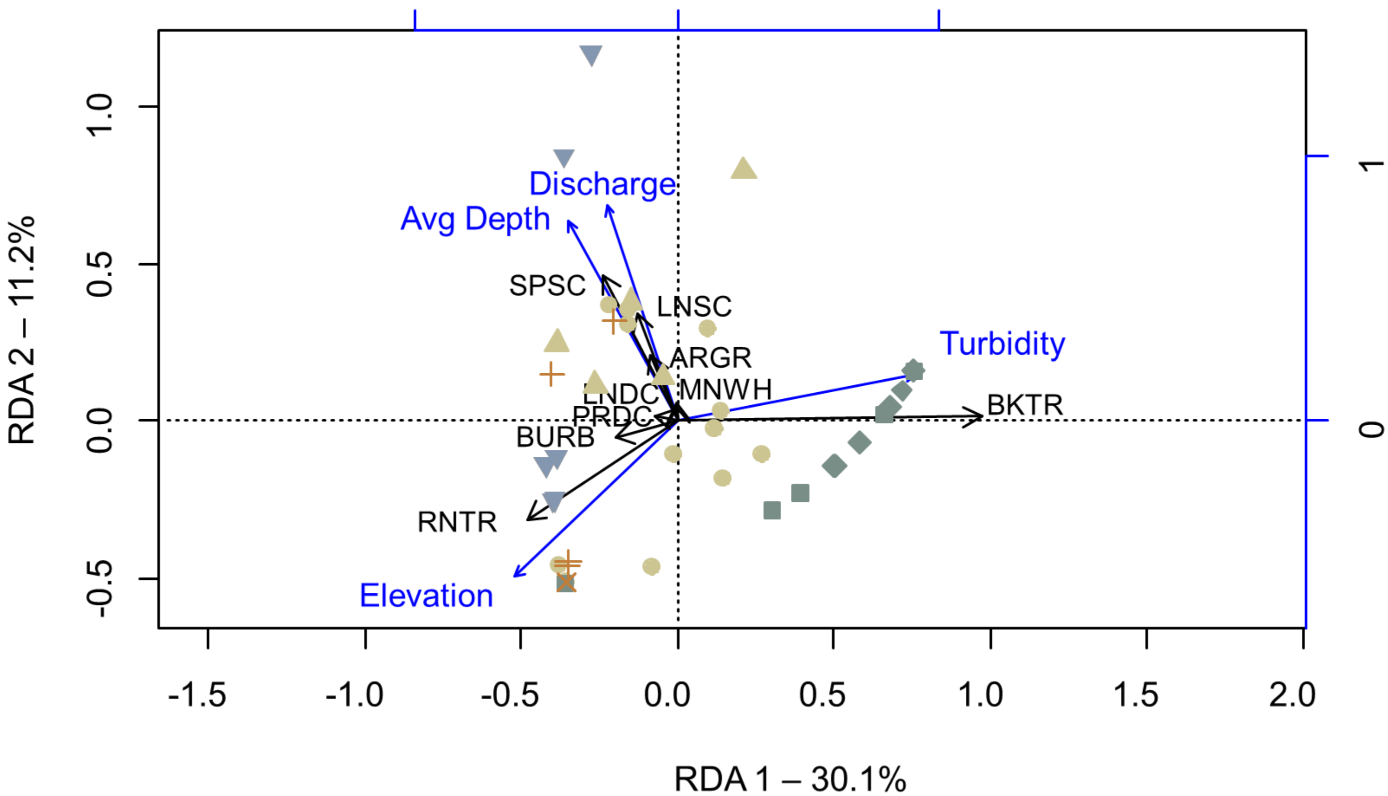

Figure 2.2. RDA triplot showing the correlation between four significant habitat predictors with Hellinger transformed fish abundance for Athabasca Rainbow Trout (RNTR), Brook Trout (BKTR), Spoonhead Sculpin (SPSC), Burbot (BURB), Longnose Sucker (LNSC), Longnose Dace (LNDC), Pearl Dace (PRDC), Arctic Grayling (ARGR) and Mountain Whitefish (MNWH). Sample sites are shown as points (site scores) in ordination space and are distinguished by treatment and waterbody: (orange = Reference (star = MacPherson Creek, cross = Trapper Creek); blue = Indirectly Disturbed (square = Baseline Creek, diamond = Canyon Creek, down triangle = Oldman Creek); grey = Tailings Disturbed (circle = Apetowun Creek, triangle = Plante Creek). Relative angles between arrows show correlation between the environmental predictors (blue arrows) and response variables (black arrows).

Chapter 3: Niche Overlap Between an Endangered Native and an Invasive Salmonid Under Varying Levels of Anthropogenic Disturbance

3.1 Executive Summary

Native freshwater biodiversity faces substantial risk of decline from widespread ecological impacts associated with both habitat degradation and invasive species. In this study, I compared food resource use by the native and Endangered Athabasca Rainbow Trout (*Oncorhynchus mykiss*) in allopatry and in sympatry with invasive naturalized populations of Brook Trout (*Salvelinus fontinalis*) in the foothills of western Alberta, Canada. I also sought to determine if diet differed in stream reaches that were impacted by a major coal mine tailings release that occurred in October 2013. Using stable isotope analysis (SIA), I compared trophic position (TP), proportion of diet derived from autochthonous (α) and allochthonous (1-α) carbon sources, isotopic niche width and isotopic niche overlap in seven waterbodies representing three distinct disturbance groups: 1) Tailing Disturbed and Invaded (TDI) impacted by both stressors, 2) No Tailings and Invaded (NTI) impacted by Brook Trout invasion, and 3) No Tailings and Not Invaded (NTNI) impacted by neither tailings or Brook Trout invasion. Both species showed a significantly larger niche width and more dietary niche overlap in the TDI grouping than in the NTI grouping. These results suggest that Athabasca Rainbow Trout may consume a more generalist diet in tailings disturbed waterbodies than in waterbodies not impacted by the 2013 Obed mine tailings release, likely to compensate for the loss of desirable prey due to the habitat disturbance, in line with optimal foraging theory. These finding provide fisheries managers with further understanding of the mechanisms behind resource competition amongst these often-sympatric salmonids.

3.2 Introduction

Both habitat degradation and invasive species can cause substantial negative impacts to native freshwater taxa (Fausch et al. 2010, Hermoso et al. 2011). Salmonid fishes have been widely introduced around the globe to create food resources and establish recreational fisheries (Cucherousset and Olden 2011). These introductions can lead to declines in native freshwater biodiversity, especially when in combination with interacting ecological stressors (Dudgeon et al. 2006). One of the main impacts that invasive fishes have on native freshwater taxa is through community level effects, including the alteration of food webs through mechanisms such as resource competition (Vander Zanden et al. 1999, Baxter et al. 2007, Cucherousset and Olden 2011). Both competition with invasive species (Vander Zanden et al. 1999, Cucherousset et al. 2007, Olsson et al. 2009) and habitat degradation (Layman et al. 2007, Evangelista et al. 2014, Kraus et al. 2016) have been shown to alter the diet of freshwater organisms, which can result in decreased growth rates and abundance of the native species (Baxter et al. 2007).

The effects of competition between native and invasive species can be explained using classical niche theory, such as the competitive exclusion principle, which states that "complete competitors cannot coexist" (Hardin 1960). The competitive exclusion principle suggests that niche divergence, or resource partitioning must occur when species with similar ecological niches are in sympatry to allow the species to coexist (Schoener 1974). Alternately, species with similar ecological niches can coexist and utilize similar subsets of resources as they become more abundant or scarce seasonally, thereby driving the differential overlap in resource use spatially or temporally, based on competition strength (Wiens 1993).

Changes to a consumer's diet can be inferred from changes in trophic position (Vander Zanden et al. 1999, Cucherousset et al. 2007) or in the proportion of dietary carbon originating from distinct energy pathways (Berglund et al. 2005, Zeug and Winemiller 2008, Jardine et al. 2012). These changes have been widely examined through the use of stable isotope analysis (SIA) metrics (Layman et al. 2012). Common isotopes used in SIA, $^{13}C/^{12}C$ and $^{15}N/^{14}N$ expressed as $\delta^{13}C$ and $\delta^{15}N$, provide a time-integrated estimate of consumer diet. Nitrogen values have been used to derive the trophic position within a food web, while carbon values can be used to infer the ultimate sources of dietary carbon, for example between terrestrial or benthic sources (Post 2002). Determining $\delta^{15}N$ and $\delta^{13}C$ values provides ecologists with a broader understanding of diet, niche width (or breadth) and, in cases of suspected competition, niche overlap in an ecosystem (Jackson et al. 2012).

In the foothills of Alberta, Canada, both habitat degradation and competition with introduced species have been implicated in the population declines of several native salmonids. The Athabasca Rainbow Trout (*Oncorhynchus mykiss*), forms one of only three native Rainbow Trout population to originate east of the Canadian Rocky Mountains, and the only native population in Alberta, Canada. It is a distinct Rainbow Trout ecotype, confined to the cold and unproductive waters of the upper Athabasca River watershed (COSEWIC 2014). Severe documented population decline has resulted in the designation of this ecotype as “Endangered” under the Species at Risk Act in Canada (COSEWIC 2014). Amongst the ecological stressors faced by the Athabasca Rainbow Trout, two of the most important impacts are from competition with invasive species, such as Brook Trout (*Salvelinus fontinalis*), which have become naturalized in many streams in the region following historic stocking practices, and habitat degradation from industrial resource extraction operations (COSEWIC 2014).

In addition to ongoing landscape level impacts of habitat degradation from resource extraction in parts of the range of the Athabasca Rainbow Trout, in October 2013 a major accidental mine tailings release occurred within the range of the Athabasca Rainbow Trout. Approximately 670,000 m^3 of mine tailings breached a tailings pond dam on the Obed mine and flowed directly into the headwaters of Apetowun Creek (Cooke et al. 2016), a tributary supporting Athabasca Rainbow Trout populations. The tailings material consisted of coal slurry, process water, sediment and coal fines, which can be enriched in contaminants such as metals, hydrocarbons and chemicals used in the coal mining process (Cooke et al. 2016). This caused substantial damage to the stream channel and riparian areas in the upper 5 km of Apetowun Creek and impacted the lower reaches of Apetowun Creek and Plante Creek due to the deposition of fine material and flooding from the sheer volume of water entering the stream channels. Due to substantial stream bed scouring, the tailings release impacted benthic invertebrate fauna and periphyton in upper Apetowun Creek (Cooke et al. 2016). Mining related impacts to streams have previously been shown to alter the diet of stream salmonids (Kraus et al. 2016).

The goal of this study was to determine the impacts of both competition with invasive Brook Trout and habitat disturbance from the Obed mine tailings release on food webs of the threatened Athabasca Rainbow Trout. To do this I tested whether native Athabasca Rainbow Trout and invasive Brook Trout compete for resources where they exist in sympatry and sought to understand how the Obed mine tailings release may have impacted resource utilization. The objectives were to examine the effect of each stressor on: 1) Athabasca Rainbow Trout trophic position (TP), 2) proportion of carbon in Athabasca Rainbow Trout diet derived from terrestrial sources ($1 - \alpha$), compared to benthic derived sources (α), 3) Athabasca Rainbow Trout isotopic niche width and diet to determine whether competition and habitat degradation have impacted the breadth of food resources consumed by Athabasca Rainbow Trout, and 4) niche overlap to determine the extent of competition for dietary resources between Athabasca Rainbow Trout and Brook Trout.

3.3 Methods

3.3.1 Study Location

The Obed coal mine is located approximately 30 km northeast of Hinton, Alberta, Canada (Figure 3.1). The area is within the Foothills Natural Region of west-central Alberta. This region is characterized by elevations ranging from approximately 700 – 1700 metres above sea level, with well drained upland forests and poorly drained lowland areas (Natural Regions Committee 2006). The region experiences mean annual precipitation of approximately 630 mm and a mean annual temperature of 1.8ºC (Natural Regions Committee 2006). Samples used for this study came from thirteen distinct reaches in the following seven waterbodies: Apetowun Creek (n = 2), Baseline Creek (n = 2), Canyon Creek (n = 2), McPherson Creek (n = 2), Oldman Creek (n = 2), Plante Creek (n = 2) and Trapper Creek. (n = 1). An upstream and downstream reach were sampled on each waterbody, except for Trapper Creek, where only one reach was sampled (Figure 3.1).

These sampled waterbodies had different disturbance regimes based on the two ecological stressors identified in this study, the Obed coal mine tailings release and invasive Brook Trout colonization. To explore the impacts of both ecological stressors on Athabasca Rainbow Trout resource usage, all waterbodies were categorized into one of three disturbance groupings for analysis of each stressor. The disturbance groupings consisted of: 1) Tailings Disturbed and Invaded (TDI), 2) No Tailings and Invaded (NTI) and 3) No Tailings and Not Invaded (NTNI). The TDI disturbance group consisted of Apetowun Creek and Plante Creek that were impacted by both ecological stressors. In addition to the tailings release, invasive Brook Trout have colonized both of these streams, and are suspected to cause negative biotic interactions with Athabasca Rainbow Trout through competition for food and habitat resources (COSEWIC 2014).

The NTI disturbance group contained Baseline Creek and Canyon Creek that have also been invaded by non-native Brook Trout but did not receive tailings material. McPherson Creek, Oldman Creek and Trapper Creek were categorized into the NTNI grouping as they were not impacted by the Obed mine tailings release, and have not been invaded by Brook Trout, thereby representing a reference grouping where streams are not impacted by either ecological stressor examined in this study. Waterbodies were considered "Invaded" if Brook Trout consisted of more than 20% of the total average salmonid composition (Apetowun Creek, Plante Creek, Baseline Creek and Canyon Creek) and "Not-Invaded" if less than 20% of the total average salmonid composition (McPherson Creek, Trapper Creek and Oldman Creek). A summary of several biotic and abiotic characteristics relating to stream physicochemical parameters and salmonid composition for each sampled waterbody is provided in Table 3.1.

3.3.2 Food Web Data Collection

Food web samples were collected in the field from September to early October 2015. Fish were collected by backpack electrofishing (Smith-Root LR-24, Vancouver, WA, USA), using a systematic single pass sample technique. Each captured individual fish was measured for total length (mm). Caudal fin tissue $\delta^{15}N$ and $\delta^{13}C$ values are similar to dorsal muscle tissue (Hanisch et al 2010; Sanderson et al. 2011), so fin clips from the upper lobe of the caudal fin were collected from Athabasca Rainbow Trout, using a sharp pair of dissecting scissors. Fin clips were stored in a dry 1 mL vial and transferred to a portable freezer in the field and immediately transferred to a -20ºC freezer at the University of Alberta upon return from field sampling.

At each site, a subsample of up to 20 Brook Trout, Longnose Sucker (*Catostomus comersonii*), and Burbot (*Lota lota*) and up to five cyprinids, including Longnose Dace (*Rhinichthys cataractae*), Pearl Dace (*Margariscus margarita*) and Spoonhead Sculpin (*Cottus ricei*) were euthanized for SIA when captured. Terrestrial invertebrates were collected on each sample site using a drift net set 20 m upstream of each sample site, for approximately an 8-hour period. Benthic invertebrates were collected using a three-minute benthic kick sample in a riffle area with a 250 µm mesh D-net. All biological material was stored in a portable -20ºC freezer in the field and immediately transferred to a permanent -20ºC freezer at the University of Alberta upon return from field sampling.

3.3.3 Lab Methods

White muscle tissue from Brook Trout, Spoonhead Sculpin, Longnose Dace, Longnose Sucker and Pearl Dace was dissected from the dorsal region of each individual, and care was taken to avoid bones, scales and skin tissue (Pinnegar and Polunin 1999). Athabasca Rainbow Trout fin clips were rinsed in deionized water and placed in glass vials for freeze-drying. Tissues were freeze dried for a minimum of 24 hours, following which samples were placed in a -20ºC freezer until they were weighed for SIA.

Up to 300 benthic invertebrates were identified to Family from each kick sample (Appendix 1, Table 2); and 100 terrestrial invertebrates were identified to Order from each drift net sample. Following identification, invertebrates were rinsed in deionized water to remove organic particulate matter, and then freeze dried in glass vials for 24 hours. Both fish muscle tissue and invertebrate samples were homogenized using a mortar and pestle or a stainless-steel stirring rod in preparation for SIA, whereas Athabasca Rainbow Trout fin tissue was cut into small pieces using forceps and scissors. Samples were weighed to approximately 0.8 mg into 4 mm x 6 mm tin capsules and analyzed for $\delta^{15}N$ and $\delta^{13}C$ at the Stable Isotope Facility for Ecosystem Research (SIFER) lab at the University of Alberta. Reported values (δ) are referenced against atmospheric N and PeeDee Belemite for $\delta^{15}N$ and $\delta^{13}C$ respectively and reported in parts per thousand (‰) using the formula: δ (‰) = $[R_{sample}/R_{standard} - 1] * 1000$, where $R_{sample} = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

Isotope values were measured with a ThermoFinnigan Delta V Advantage Continuous Flow Isotope Ratio Mass-Spectrometer (CF-IRMS). Internal laboratory standards included protein, wheat flour, sorghum flour, high organic soil and urea. Duplicate samples of homogenized Athabasca Rainbow Trout fin, fish muscle tissue or homogenized whole-body invertebrates were analyzed after every 12th sample to ensure the homogenization procedure was adequate, and to estimate instrument precision. The average difference in $\delta^{15}N$ and $\delta^{13}C$ between duplicate samples within runs was 0.18‰ and 0.13‰, respectively ($n = 61$).

3.3.4 Data Analysis

i. Data processing

Benthic invertebrates were grouped by their functional feeding groups within each waterbody (scraper, shredder, collector, predator) following Merritt and Cummins (1984). Taxa were categorized as Scrapers if genera within the family have been documented as scrapers and their source of primary carbon utilization was dominated by benthic sources (Appendix 3.1, Table A3.1). All terrestrial insect Orders were grouped together as a "Terrestrial" food source, to represent an overall isotopic signature of the allochthonous subsidy available to salmonid consumers. Allochthonous $\delta^{13}C$ signatures in terrestrial invertebrates closely mirrored that of terrestrial C_3 vegetation, which has been determined in other food web studies to be approximately -28‰ (Finlay 2001). Fish prey sources were grouped into juvenile salmonids (< 68 mm total length, both species combined), and small bodied fish (Spoonhead Sculpin, Longnose Dace, Pearl Dace and juvenile Longnose Suckers) (Table 3.2; Figure 3.2). Outliers in Athabasca Rainbow Trout and Brook Trout $\delta^{15}N$ and $\delta^{13}C$ values were identified by visually assessing boxplots and model residuals (Q-Q plots and fitted values vs. residual plots) from linear models of both $\delta^{15}N$ and $\delta^{13}C$ as a function of total length by waterbody. Following the removal of outliers, models met the assumptions of both normality and homogeneity of variance. All analyses for this study were conducted in R version 3.4.1 (R Core Team 2017).

ii. Fin-Muscle isotopic signature correction

Caudal fin tissue is composed of both ray and membrane tissue, and therefore different parts of the fin are variable in their isotopic values (Hayden et al. 2015) and can differ from muscle isotope ratios. In order to calibrate the relationship between fin and muscle tissue, I collected both muscle plugs and fin clips from a subset of 28 Athabasca Rainbow Trout. Fish were anaesthetized in 100 mg/L of clove oil in stream water until stage 4 anaesthesia was reached (Hanisch et al. 2010), then, muscle plugs were collected using a Tru-Cut soft tissue biopsy needle through an approximately 3 mm incision made posterior to the dorsal fin with a sharp scalpel (Hanisch et al. 2010). All surgical tools were rinsed in 95% bleach solution following each sample. Following the surgical procedure, fish were placed in an in-stream flow-through tank and monitored for recovery. Fish were released back into the stream when the effects of the anaesthetic wore off. Samples were frozen in a portable -20ºC freezer in the field and immediately transferred to a -20ºC freezer at the University of Alberta upon return. In the laboratory, samples were freeze dried for a minimum of 24 hours, homogenized, weighed and analyzed for SIA as described in the previous section.

To determine if there were differences in both δ15N and δ13C values between fin clip and white muscle tissue, I performed paired t-tests. Linear regression analysis was conducted to determine the strength of the correlation between the two tissue types for both isotopes of interest and to correct for differences between fin and muscle tissue in further analysis. Samples were not mathematically lipid corrected as all C:N values were < 4, indicative of low tissue lipid content (Logan et al. 2008, Jardine et al. 2011).

iii. Trophic Position and proportion of Terrestrial Carbon in consumer diets

Raw average and standard deviation $\delta^{15}N$ and $\delta^{13}C$ values of all taxa analyzed in this study were plotted to visually assess food web structure in the study area (Figure 3.2; Table 3.2). However, consumer isotopic values should be standardized to ensure that baseline variability is accounted for in $\delta^{13}C$ and $\delta^{15}N$ (Newsome et al. 2007, Syväranta et al. 2013, Svanbäck et al. 2015). To compare $\delta^{15}N$ values amongst consumers in different habitats, raw values need to be corrected to account for shifting baselines in $\delta^{15}N$ in different waterbodies or even within different reaches of the same waterbody (i.e., pelagic vs. littoral) (Post 2002, Anderson and Cabana 2007). Trophic position is used to standardize raw $\delta^{15}N$ values by site specific baselines (Post 2002). The trophic positions of both Athabasca Rainbow Trout and Brook Trout within each sampled waterbody were calculated using equation 1, which accounts for cross-ecosystem linkages, where consumers acquire nitrogen sources from more than one food web (Post 2002):

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

Where $\delta^{15}N_{consumer}$ is the value of each Athabasca Rainbow Trout or Brook Trout individual within each waterbody. $\delta^{15}N_{baseline1}$ is the $\delta^{15}N$ value of the larval life stage of primary consumers in the scraper functional feeding group (*Heptageniidae, Baetidae, Brachycentridae,* *Ephemerellidae and Elmidae*) (See Appendix 1; Table 1) representing the isotopic benthic or autochthonous end member. Scrapers have been documented in previous studies to be the best benthic invertebrates to use as baseline organisms in lotic food web studies in the absence of longer lived primary consumers, such as snails and mussels, as they are widely distributed and generally have low $\delta^{15}N$ values (Anderson and Cabana 2007). $\delta^{15}N_{baseline2}$ is the average $\delta^{15}N$ value of terrestrial invertebrates, representing the terrestrial or allochthonous food web isotopic end member. The symbol α is the proportional contribution of nitrogen that fish consumers obtain from the autochthonous, or aquatic, food webs (see Eqn 2 below in determining α for $\delta^{13}C$). The symbol Δ_n indicates the trophic enrichment factor (TEF), which represents the increase in $\delta^{15}N$ from the diet to the consuming organism (Vander Zanden et al. 1997, Post 2002, McCutchan et al. 2003). I used TEFs derived from McCutchan et al. (2003), who experimentally derived species-specific values for both Rainbow Trout and Brook Trout in a controlled laboratory diet study. The Δ_n values used for this study were, therefore, 3.2‰ and 3.8‰ for Athabasca Rainbow Trout and Brook Trout, respectively. The λ symbol indicates the trophic level of the baseline organism, which in this study was 2, as scrapers are primary consumers (Post 2002).

Similarly, raw $\delta^{13}C$ values can be highly variable between sampling locations as a result of variability in algal values used as a primary carbon source by benthic organisms such as scrapers (Finlay 2001). Raw $\delta^{13}C$ values can be standardized by calculating the proportion of carbon derived from aquatic sources (α) (Eqn. 2), or alternatively, the proportion of carbon derived from terrestrial sources (1- α). To calculate α, the following two-end-member mixing model equation was used (Post 2002):

(Eqn. 2) $\alpha = ((\delta^{13}C_{consumer} - TEF) - \delta^{13}C_{baseline2}) / (\delta^{13}C_{baseline1} - \delta^{13}C_{baseline2})$

Where $\delta^{13}C_{consumer}$ is the individual salmonid $\delta^{13}C$ measurement, TEF is the species specific $\delta^{13}C$ trophic enrichment factor (1.9‰ and 3.3‰ for Athabasca Rainbow Trout and Brook Trout, respectively) (McCutchan et al 2003), $\delta^{13}C_{baseline2}$ is the $\delta^{13}C$ value of scrapers, and $\delta^{13}C_{baseline1}$ is the average $\delta^{13}C$ value of terrestrial invertebrates.

Scrapers are known to feed primarily on autochthonous sources of primary production, including algae (Finlay 2001), thereby allowing their use as a proxy for benthic sources of carbon production. Furthermore, Finlay (2001) showed that there was a significant positive linear relationship between herbivorous invertebrate consumer and epilithic algae $\delta^{13}C$ values. Along with estimates of α for the two focal salmonids, this measure was calculated for all aquatic invertebrate and fish taxa across all waterbodies to gain a better understanding of the importance of each carbon pathway to the various ecosystem compartments. Because we lacked species-specific TEFs for the small bodied fish and aquatic invertebrates, these were set at 0.4‰, which is the mean value reported in previous studies (Post 2002, McCutchan et al. 2003) (Appendix 3.1).

Differences in Athabasca Rainbow Trout and Brook Trout trophic position were analyzed between disturbance groups using a two factor ANOVA, which included an interaction term between species and disturbance group, and compared using a Tukey HSD *post hoc* test. Similarly, a two- factor ANOVA was used to determine if there was a difference in proportional contribution of terrestrial carbon sources between disturbance groups and species.

iv. Mixing models of Athabasca Rainbow Trout food resource utilization

I used the mixSIAR package in R to analyze dietary source contributions to both Athabasca Rainbow Trout and Brook Trout tissue composition (Stock and Semmens 2013). These models incorporate a Bayesian statistical framework and account for uncertainty, prior knowledge and multiple possible prey sources (Moore and Semmens 2008, Phillips et al. 2014). Mixing models for Athabasca Rainbow Trout were specified to use generalist priors on dietary fractions (Stock and Semmens 2016) and models included a residual error structure. Prey sources were included as per section *i*, however Collectors and Predatory Invertebrates were grouped together as their $\delta^{15}N$ and $\delta^{13}C$ values were not significantly different (MANOVA: Wilks' $\lambda = 0.99$, $p = 0.73$). small bodied fish and juvenile salmonids were also grouped together as they form a similar feeding guild based on α and TP values (Appendix 3.1). The values used for Athabasca Rainbow Trout $\delta^{15}N$ and $\delta^{13}C$ TEFs (mean ± SD) were 3.2 ± 0.4‰ and 1.9 ± 1.0‰, respectively, whereas Brook Trout $\delta^{15}N$ and $\delta^{13}C$ TEFs were 3.8 ± 0.5‰ and 3.3 ± 0.8‰, respectively (McCutchan et al. 2003). Prior to running mixing models, isotope biplots were created for all waterbodies to assess if consumers fell within the prey source geometry (Phillips et al. 2014). Due to small sample size there were no mixing models run for Brook Trout in McPherson Creek (n = 2).

Bayesian stable isotope mixing models created in MixSIAR use a Monte Carlo Markov Chain (MCMC) algorithm and were parameterized to discard the initial 200,000 iterations. The posterior probability distribution of prey source contribution to Athabasca Rainbow Trout diet was then derived from a further 100,000 iterations from 3 MCMC chains, with a thinning rate of every 100th sample. Model convergence was assessed using the Gelman-Rubin diagnostic, as has been done by other researchers (Osterback et al. 2015). The mixing model estimates of mean and standard deviation source contributions to both Athabasca Rainbow Trout and Brook Trout diets are presented in Table 3.4.

v. Standard Ellipse Areas and Isotopic Niche overlap

Standard ellipse areas (SEA) use a Bayesian approach to calculate the isotopic niche width of a population or community of organisms, incorporating uncertainties in various parameters into their estimates (Jackson et al. 2011). SEAs are more robust to small sample sizes and provide more accurate estimates of niche width than previously used methods such as convex hull area (Jackson et al. 2011, Syväranta et al. 2013). To accurately compare between populations of both Athabasca Rainbow Trout and Brook Trout in different habitats, I used trophic position and proportion of terrestrial carbon contribution to the diet of Athabasca Rainbow Trout (see Methods Section iii) as proxies for $\delta^{15}N$ and $\delta^{13}C$, respectively (Olsson et al. 2009, Syväranta et al. 2013, Svanbäck et al. 2015). SEA_B values, representing the Bayesian estimate of SEA, as determined using 10,000 replicates (Jackson et al. 2011, Evangelista et al. 2014) were then calculated in the R package SIBER (Jackson et al. 2011) for Athabasca Rainbow Trout and Brook Trout in each disturbance group to compare isotopic niche width amongst these groupings.

To infer the breadth of dietary resources used, I determined the SEA_B of both Brook Trout and Athabasca Rainbow Trout in each of the waterbodies where they were captured, as well as overall species values in each disturbance (Tab 3.3). I also compared the total combined niche widths of both salmonid species in each disturbance group to understand if Brook Trout were displacing Athabasca Rainbow Trout from the subset of total available resources when they were found in sympatry (Appendix 3.1, Fig A3.1). Additionally, I sought to determine if combined niche width differed amongst the three disturbance groups, potentially indicating the incorporation of sub-optimal dietary resources (Appendix 3.1, Fig A3.1).

To quantify the amount of isotopic niche overlap between Athabasca Rainbow Trout and Brook Trout resource use, I used the *nicheROVER* package in R (Swanson et al. 2015). I compared the isotopic niche overlap between Athabasca Rainbow Trout and Brook Trout in the two disturbance groups where they were in sympatry (TDI and NTI). The niche region of each species was quantified as a 95% probability region in multivariate isotope space, and niche overlap was computed as the probability that an individual of one species was present in the niche region of the other species, using a Bayesian framework (Swanson et al. 2015).

3.4 Results

3.4.1 Fin – Muscle Tissue Comparison and Correction

There was a significant difference between fin and muscle $\delta^{15}N$ values ($t_{25} = 3.6$, $p = 0.001$), with fin tissue more enriched in ^{15}N than muscle. A significant relationship existed between fin and muscle $\delta^{15}N$ ($R^2 = 0.92$; $F_{1, 24} = 283$, $p < 0.001$). The following linear equation was used to correct Athabasca Rainbow Trout fin $\delta^{15}N$ values to muscle equivalent: $y = 0.8376x + 1.3406$. A significant difference in muscle versus fin $\delta^{13}C$ was detected ($t_{25} = 7.5$, $p < 0.001$), with muscle tissue significantly more depleted in ^{13}C than fin tissue, with mean values of -27.3‰ and -26.5‰, respectively. Fin tissue had a significantly higher C:N ratio than did muscle tissue ($t_{25} = 13.6$, $p < 0.001$), which corresponds with the higher proportion of bone derived carbonate sources in fin tissue compared to muscle (Jardine et al. 2011). A significant regression relationship existed between fin and muscle $\delta^{13}C$ ($R^2 = 0.86$, $F_{1, 24} = 148$, $p < 0.001$) and the corresponding linear equation ($y = 0.9693x - 2.2615$) was used to convert Athabasca Rainbow Trout fin $\delta^{13}C$ values to muscle equivalent.

3.4.2 Trophic Position

There was no statistically significant interaction term between total length, species and waterbody on trophic position ($F_{3, 281} = 1.3$, $p = 0.28$); therefore, I did not account for size in calculations of trophic position. Athabasca Rainbow Trout trophic position (mean ± SD) ranged from 3.4 ± 0.1 in Canyon Creek to 3.8 ± 0.3 in Oldman Creek (Table 3). Brook trout were at their lowest trophic position in Canyon Creek (2.8 ± 0.2) and had the highest trophic position in McPherson Creek (3.4 ± 0.1), though only two large spawner individuals were caught in this waterbody (Table 3.2). Athabasca Rainbow Trout were at a significantly higher trophic position in the NTNI disturbance group than they were in both the NTI and TDI groups (Table 3.3, Figure 3.4). Brook Trout trophic position was significantly higher in the TDI group than in the NTI group (Table 3.3, Figure3.4). There was also a significant difference between Athabasca Rainbow Trout and Brook Trout trophic position in both the NTI group and the TDI group, with Brook Trout at a significantly lower trophic position in both groups (Table 3.3, Figure 3.4).

3.4.3 Carbon Source Contribution to Athabasca Rainbow Trout and Brook Trout Diet

The majority of both Athabasca Rainbow Trout and Brook Trout diets were composed of terrestrial carbon sources, averaging 52% and 54% respectively. Proportionally, terrestrially derived carbon sources ($1-\alpha$) contributed (mean ± SD) a maximum of 0.66 ± 0.26 to Athabasca Rainbow Trout diet in Apetowun Creek and a minimum of 0.26 ± 0.19 in Trapper Creek (Table 3). The contribution of terrestrial carbon sources to Brook Trout diet was greatest in Canyon Creek (0.62 ± 0.13), and lowest in Plante Creek (0.43 ± 0.18) (Table 3.3). When waterbodies were combined into their respective disturbance groups, there were significant differences in $1-\alpha$

for Athabasca Rainbow Trout, as fish in the TDI groups were utilizing greater proportions of terrestrially derived carbon than in the NTNI group (Figure 3.5; Table 3.3). There was no significant difference in 1-α in Brook Trout diet between TDI and NTI groups (Figure 3.5; Table 3.3). Additionally, 1-α was not significantly different between Athabasca Rainbow Trout and Brook Trout in either the NTI group or TDI group (Figure 3.5).

3.4.4 Prey Source Contribution to Salmonid Consumers

Athabasca Rainbow Trout populations from the three disturbance groups experienced differences in diet composition. Most notably, Athabasca Rainbow Trout in the NTNI group utilized a lower proportion of scrapers compared to both the NTI and the NTNI groups (Table 3.4). Athabasca Rainbow Trout in the NTI group utilized a higher proportion of predatory invertebrates and collectors than they did in the other two disturbance groupings. Additionally, Athabasca Rainbow Trout in the TDI and NTI groups utilized a lower proportion of small fish prey sources than the NTNI group (Table 3.4). Furthermore, differences between Athabasca Rainbow Trout and Brook Trout diets were evident in both groups where they were in sympatry, where Athabasca Rainbow Trout utilized a greater proportion of higher trophic position prey items, such as small fish and predator/collectors than Brook Trout, which utilized more shredders and scrapers (Table 3.4).

3.4.5 Isotopic Niche Width and Niche Overlap

Athabasca Rainbow Trout dietary niche width differed substantially between the sampled waterbodies. Niche width (SEA_B) was substantially larger in Apetowun Creek than any other stream (Table 3.3). Brook trout niche width was greatest in Plante Creek (Table 3.3). When combined into disturbance groups the niche width of Athabasca Rainbow Trout was greatest in the TDI treatment compared with NTI and NTNI groups (Table 3.3). The niche width for Brook Trout was also greater in the TDI group than in the NTI group (Table 3.3).

When comparing the niche overlap between Athabasca Rainbow Trout and Brook Trout amongst the two groups when they were in sympatry (NTI and TDI), there were substantial differences in the amount of overlap within each group (Figure 3.5, Figure 3.6). In the TDI group the median probability that Brook Trout were found within the niche region of Athabasca Rainbow Trout was approximately 77% (61% - 90%: 95% Bayesian credibility interval) (Figure 3.6b). This was in stark contrast to the NTI group, where the median probability of Brook Trout located within the niche space of Athabasca Rainbow Trout was only approximately 4% (0% - 20%: 95% Bayesian credibility interval) (Figure 3.5b).

3.5 Discussion

Both invasive species and habitat disturbance pose major threats to native freshwater biodiversity (Dudgeon et al. 2006). Salmonids are amongst the most widely introduced fish species, due in large part to their value as recreational and food sources (Cucherousset and Olden 2011), which has had widespread impacts on native freshwater species. The ecological impacts of invasive species can be substantial and can lead to changes in native taxa behaviour, substantial food web structural change and species extirpation (Cucherousset and Olden 2011). Studies have shown that invasive fish species can usurp terrestrial subsidies from native taxa, thereby interrupting the flow of important cross-ecosystem subsidies, resulting in native taxa utilizing sub-optimal prey items and leading to reduced growth rates (Baxter et al. 2004, 2007). Invaders can also displace native fishes from their preferred habitats, forcing species that were previously segregated to compete for resources (Fausch et al. 2010). Habitat degradation in turn can result in changes to aquatic consumer diet due to changes in prey availability (Layman et al. 2007, Kraus et al. 2016).

Previous studies have demonstrated that resource use by Rainbow Trout was dominated by terrestrially derived carbon sources. Terrestrial subsidies are highly important to Rainbow Trout (Nakano et al. 1999, Nakano and Murakami 2001, Baxter et al. 2004), providing an important temporal resource that can account for as much as 77% of daily food resource use (Nakano et al. 1999). Alternatively, Brook Trout diet has been shown to be highly variable in terms of allochthonous carbon use. For example, in streams in New Hampshire, Brook Trout diet was influenced by benthic invertebrate biomass, where fewer terrestrial invertebrates were consumed when there was greater availability of benthic invertebrates (Wilson et al. 2014). In lotic systems in eastern Canada, Jardine et al. (2012) showed that Brook Trout diet was largely dependent on allochthonous carbon sources with fish utilizing approximately 95% terrestrially derived carbon sources. Similarly, when in sympatry with Atlantic salmon in Quebec streams, Brook Trout diet consisted of a greater proportion of terrestrial invertebrates (between 50% – 80% of diet) (Mookerji et al. 2004). However, when in allopatry, Mookerji et al. (2004) found that Brook Trout fed more dominantly on abundant benthic invertebrate resources, with terrestrial insects contributing less than 25% of the diet. This dietary shift, leading to increased resource partitioning by Brook Trout when in allopatry compared to sympatry with Atlantic salmon, is thought to promote coexistence, greater overall dietary exploitation, and greater niche breadth in eastern Canadian streams (Mookerji et al. 2004).

Athabasca Rainbow Trout were feeding at a significantly higher trophic position than were Brook Trout in both disturbance groupings where the two were in sympatry. This is likely associated with their greater use of both small fish and predator/collector invertebrate food sources, which were often at higher trophic positions than the benthic invertebrate sources such as scrapers. Rainbow trout have been shown to feed at higher trophic positions than native fishes in streams in the western United States, as large trout (> 150 mm TL) incorporated more large bodied benthic invertebrate predators such as *Corydalus* (Corydalidae) as well as small bodied native fishes into their diets (Whiting et al. 2014). In agreement with my findings, stream resident Rainbow Trout in California, measuring between 280-330 mm total length, were found to prey upon juvenile steelhead Rainbow Trout, thereby feeding at a fourth trophic level in these streams (Finlay et al. 2002). Contrary to my findings, there was no significant difference between Rainbow Trout and Brook Trout trophic position detected in a large ultra-oligotrophic lake in Patagonia where Rainbow Trout and Brook Trout were in sympatry (Arcagni et al. 2013). The differences in findings between Athabasca Rainbow Trout and Brook Trout trophic position in this study compared with those of Arcagni et al. (2013) are not surprising given the differences in average trout size, feeding ecology and habitat type between the two studies.

There were significant differences detected in both trophic position and allochthonous carbon usage ($1-\alpha$) between Athabasca Rainbow Trout in the three different disturbance groups, with trout in the NTNI group different than those in the TDI group for both metrics. Habitat degradation resulting from mining inputs has been shown to result in salmonid consumers using more terrestrial dietary items to compensate for reduced benthic invertebrate availability (Kraus et al. 2016). Elsewhere, stream riparian disturbance that resulted in increased canopy openness did not negatively influence the total biomass of aquatic invertebrate prey in sampled stream reaches; however, as canopy openness increased there was significantly higher inputs of terrestrial herbivorous insects (Evangelista et al. 2014). Canopy openness in turn did not influence native brown trout population density, but trophic specialization was greatest in sites where there were the highest densities of brown trout, indicating increased intraspecific competition for resources, which can lead to resource partitioning (Evangelista et al. 2014). Trophic diversity was also greatest at sites with intermediate canopy openness, where terrestrial invertebrate subsidies were lowest, likely forcing brown trout to incorporate more aquatic invertebrate resources in their diets, thereby expanding their trophic niche width (Evangelista et al. 2014).

In this study, Athabasca Rainbow Trout in the TDI group had the largest niche width, indicating that the largest variety of prey resources were utilized in this treatment. This was mainly driven by the large niche area of Athabasca Rainbow Trout in Apetowun Creek. This result can be explained by optimal foraging theory, where trophic niche widens as a result of consumers incorporating less desirable prey items into their diet to compensate for the loss of more preferable, higher quality food sources (Svanback and Bolnick 2007, Gabler and Amundsen 2010). Alternatively, Athabasca Rainbow Trout in the NTI group had a substantially reduced niche width compared to the other groups. When both Athabasca Rainbow Trout and Brook Trout were combined by disturbance group, indicating the entire breadth of prey resources used by both species, there was no difference in total niche width in the NTNI or NTI groups. The niche width of both combined salmonids was larger in the TDI group than the other groups, further emphasizing that fish in tailings disturbed waterbodies had a broader diet, reflecting the incorporation of sub-optimal prey items.

The amount of niche overlap between Athabasca Rainbow Trout and Brook Trout was substantially higher in the TDI disturbance group than in the NTI group. In addition to changes in prey availability, greater niche width of Athabasca Rainbow Trout and Brook Trout in Apetowun Creek (TDI group) could be explained by competitive interactions for food resources amongst the two species (Svanback and Bolnick 2007). The NTI disturbance group contained the highest abundance of Brook Trout, indicating that there was likely greater interspecific competition for resources in this group than in the TDI or NTNI groups. Interspecific competition is generally thought to be a constraining effect on species niche widths, because of reduced individual resource specialization (Araujo et al. 2011). Waterbodies in the TDI group contained substantially lower abundance of Brook Trout than the NTI group, and intraspecific competition may have been a more important interaction for Athabasca Rainbow Trout resource use than interspecific competition in this group. Intraspecific competition has been shown to increase both individual niche width and individual diet specialization (Araujo et al. 2011). To further understand the role of individual specialization on individual and population niche width, future studies could focus on calculating mean diet overlap and among individual diet variation using stomach content analysis of both Brook Trout and Athabasca Rainbow Trout in tailings disturbed streams (Bolnick et al. 2002, Svanback et al. 2015).

Overall, Athabasca Rainbow Trout in the TDI treatment, and particularly in Apetowun Creek, may be utilizing a wider range of potentially lower quality food resources. This is likely due to the displacement of benthic invertebrate food resources from the mine tailings release in addition to an alteration of the freshwater-terrestrial linkage and terrestrial resource subsidy as a result of riparian vegetation damage in upper Apetowun Creek (Nakano and Murakami 2001, Baxter et al. 2005). This finding is aligned with previous studies which have shown that dietary generalization can facilitate species coexistence under conditions of resource limitation, as would be expected by optimal foraging theory (Gabler and Amundsen 2010). Alternately, Athabasca Rainbow Trout in the NTI treatment have substantially smaller dietary niches than in either the NTNI or TDI groups, likely reflecting the effects of resource partitioning from high interspecific competition (Bolnick et al. 2010, Jackson et al. 2012).

3.6 Conclusion

In this study I determined that Athabasca Rainbow Trout are utilizing food resources differently depending on a gradient of ecological stressors present in several streams in the foothills of western Alberta. In accordance with classical niche theory, Athabasca Rainbow Trout and Brook Trout were partitioning resources in streams where they have co-existed for at least two decades (NTI) and that were not impacted by the 2013 Obed tailings release. In tailings disturbed streams (TDI) there was substantial niche overlap between Athabasca Rainbow Trout and Brook Trout, as well as wider species specific and combined niche width in these streams. The wider isotopic niche width of both Athabasca Rainbow Trout and Brook Trout within these impacted stream reaches indicates that they are incorporating a wider breadth of prey items into their diets, likely to compensate for the loss of more desirable and nutritionally valuable prey items, resulting from habitat alteration associated with the 2013 Obed mine coal tailings release. This hypothesis could be tested widely in other areas where salmonids face dual threats of invasive competitors and habitat disturbance.

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3.8 Figures and Tables

Table 3.1. Abiotic and biotic characteristics relating to stream physical features (Elevation and Stream Discharge), common metrics associated with coal mine related habitat disturbance (Conductivity and Turbidity) and fish capture data (Rainbow Trout CPUE and Brook Trout CPUE) as well as the proportion of Brook Trout captured in each waterbody. Waterbodies are grouped with their respective Disturbance Group, indicating the stressors present in each waterbody (NTI = No Tailings and Invaded; NTNI = No Tailings and Not Invaded; TDI = Tailings Disturbed and Invaded). Data values within the table are presented as mean (SD).

Disturbance Group	Waterbody	Elevation (m)	Stream Discharge (m^3s^{-1})	Conductivity (μScm^{-1})	Turbidity (NTU)	Proportion Brook Trout (%)
NTI	Baseline	1135 (175)	0.15 (0.071)	282 (14)	53 (23)	53 (49)
NTI	Canyon	1150 (37)	0.064 (0.014)	253 (3)	64 (11)	99 (2)
NTNI	McPherson	1183 (75)	0.12 (0.083)	208 (8)	36 (3)	5 (8)
NTNI	Oldman	1181 (110)	1.3 (1.4)	211 (15)	37 (7)	0
NTNI	Trapper	1324 (1)	0.23 (0.022)	72 (1)	7 (0)	0
TDI	Apetowun	1185 (102)	0.29 (0.25)	389 (172)	39 (9)	26 (25)
TDI	Plante	977 (25)	0.68 (0.083)	286 (22)	37 (0)	15 (15)

Table 3.2. Stable isotope values shown as mean (SD) for each group of taxa organized by waterbody and the habitat Disturbance Group they were collected from. The dashed line (-) indicates that no individuals of that group were collected in that waterbody. The Small Bodied Fish grouping was pooled individuals of Longnose Dace, Pearl Dace, juvenile Longnose Sucker and Spoonhead Sculpin. Values of na indicate that sample size was too small to calculate a standard deviation for that group.

Disturbance Group	**Waterbody**	**Isotope**	**Scraper**	**Shredders**	**Collectors**	**Predator Invertebrates**	**Terrestrial Insects**	**Small Bodied Fish**	**Brook Trout**	**Athabasca Rainbow Trout**
		$\delta^{15}N$	1.9 (1.5)	2.8 (1.8)	4.7 (0.6)	4.9 (1.4)	3.2 (1.9)	7.9 (0.5)	-	8.8 (0.9)
NTNI	Oldman Ck.	$\delta^{13}C$	-33.8 (2.6)	-32.3 (2.2)	-31.3 (0.9)	-30.9 (1.7)	-29.1 (3.2)	-29.6 (0.8)	-	-28.7 (1.0)
			n = 9	*n = 7*	*n = 3*	*n = 11*	*n = 9*	*n = 20*	-	*n = 32*
		$\delta^{15}N$	0.5 (0.8)	1.6 (2.3)	2.4 (1.3)	3.1 (0.3)	2.5 (2.9)	-	-	7.1 (0.8)
NTNI	Trapper Ck.	$\delta^{13}C$	-32.6 (0.9)	-30.6 (1.8)	-29.2 (1.7)	-29.4 (0.5)	-28.1 (1.5)	-	-	-29.3 (1.1)
			n = 3	*n = 2*	*n = 3*	*n = 3*	*n = 4*	-	-	*n = 33*
		$\delta^{15}N$	1.8 (0.8)	3.1 (1.6)	4.1 (na)	4.2 (0.7)	5.1 (1.7)	7.4 (0.5)	8.6 (0.1)	8.0 (0.6)
NTNI	McPherson Ck.	$\delta^{13}C$	-35.9 (2.3)	-31.4 (1.7)	-33.4 (na)	-31.5 (1.6)	-27.7 (4.5)	-30.8 (2.2)	-27.8 (1.4)	-28.5 (1.4)
			n = 5	*n = 4*	*n = 1*	*n = 4*	*n = 6*	*n = 18*	*n = 2*	*n = 28*
		$\delta^{15}N$	6.8 (2.0)	6.5 (2.8)	7.6 (1.6)	7.6 (2.2)	4.3 (2.5)	7.8 (0.2)	8.0 (1.1)	9.5 (1.2)
TDI	Apetowun Ck.	$\delta^{13}C$	-33.0 (3.4)	-28.1 (2.7)	-27.5 (2.4)	-28.9 (1.5)	-26.6 (1.1)	-30.4 (1.1)	-27.9 (1.5)	-28.0 (1.5)
			n = 10	*n = 4*	*n = 6*	*n = 15*	*n = 11*	*n = 5*	*n = 22*	*n = 48*
		$\delta^{15}N$	2.5 (0.8)	3.7 (1.4)	6.0 (1.4)	5.4 (1.2)	4.5 (2.6)	8.5 (0.1)	8.2 (0.9)	8.5 (0.7)
TDI	Plante Ck.	$\delta^{13}C$	-35.5 (1.6)	-31.4 (0.7)	-30.3 (2.8)	-30.6 (1.2)	-26.5 (1.4)	-29.5 (1.3)	-28.4 (1.1)	-29.4 (1.4)
			n = 9	*n = 5*	*n = 4*	*n = 10*	*n = 7*	*n = 8*	*n = 14*	*n = 44*
		$\delta^{15}N$	5.5 (1.4)	0.8 (na)	7.1 (na)	6.7 (1.4)	3.9 (2.6)	-	8.1 (0.6)	9.6 (0.6)
NTI	Baseline Ck.	$\delta^{13}C$	-35.6 (0.8)	-27.3 (na)	-31.4 (na)	-30.0 (1.5)	-27.5 (1.5)	-	-27.5 (1.4)	-28.5 (1.3)
			n = 3	*n = 1*	*n = 1*	*n = 3*	*n = 5*	-	*n = 24*	*n = 24*
		$\delta^{15}N$	2.7 (0.3)	1.7 (0.0)	4.2 (0.8)	4.2 (0.1)	3.6 (1.1)	-	6.4 (0.5)	7.7 (0.4)
NTI	Canyon Ck.	$\delta^{13}C$	-37.4 (2.1)	-29.2 (2.0)	-30.7 (0.7)	-29.0 (1.4)	-27.9 (1.6)	-	-27.8 (1.3)	-30.9 (1.2)
			n = 5	*n = 2*	*n = 2*	*n = 3*	*n = 2*	-	*n = 30*	*n = 4*
	Total Average	$\delta^{15}N$	3.4 (2.4)	3.4 (2.3)	5.5 (2.2)	5.7 (2.1)	4.0 (2.3)	7.8 (0.6)	7.5 (1.1)	8.6 (1.2)
		$\delta^{13}C$	-34.6 (2.7)	-30.7 (2.4)	-29.7 (2.5)	-30.0 (1.8)	-27.2 (1.9)	-30.1 (1.6)	-27.8 (1.4)	-28.8 (1.4)
			n = 44	*n = 25*	*n = 20*	*n = 49*	*n = 41*	*n = 51*	*n = 92*	*n = 213*

Table 3.3. Estimates of trophic position (TP), proportion of terrestrial carbon in consumer diet (1-α) along with niche width (SEA_B) for both Brook Trout (BKTR) and Athabasca Rainbow Trout (RNTR) consumers in each waterbody. Group values show the mean values for each consumer in each respective disturbance group (TDI = Tailings Disturbed and Invaded; NTI = No Tailings and Invaded; NTNI = No Tailings and Not Invaded). Values are presented as mean (SD), except for SEA_B, which shows the SEA_C value and 95% Bayesian credibility interval.

	RNTR			BKTR		
	TP	1-α	SEA_B	TP	1-α	SEA_B
Apetowun	3.4 (0.3)	0.66 (0.3)	0.22 (0.2, 0.3)	2.9 (0.2)	0.54 (0.2)	0.11 (0.06, 0.15)
Plante	3.6 (0.2)	0.51 (0.2)	0.11 (0.08, 0.2)	3.4 (0.3)	0.43 (0.2)	0.15 (0.07, 0.23)
TDI Group	3.5 (0.3)	0.59 (0.2)	0.21 (0.17, 0.25)	3.1 (0.3)	0.5 (0.2)	0.17 (0.14, 0.18)
Baseline	3.5 (0.2)	0.57 (0.1)	0.08 (0.07, 0.09)	2.9 (0.1)	0.52 (0.2)	0.07 (0.05, 0.11)
Canyon	3.4 (0.1)	0.46 (0.1)	0.06 (0.01, 0.13)	2.8 (0.2)	0.62 (0.1)	0.06 (0.04, 0.08)
NTI Group	3.5 (0.2)	0.55 (0.1)	0.08 (0.07, 0.09)	2.8 (0.2)	0.57 (0.2)	0.07 (0.06, 0.08)
McPherson	3.5 (0.2)	0.65 (0.2)	0.10 (0.08, 0.11)	3.4 (0.1)	0.61 (0.1)	na
Oldman	3.8 (0.2)	0.46 (0.1)	0.11 (0.07, 0.14)	-	-	-
Trapper	3.8 (0.2)	0.26 (0.2)	0.12 (0.08, 0.17)	-	-	-
NTNI Group	3.7 (0.3)	0.45 (0.2)	0.17 (0.16, 0.18)	-	-	-

Table 3.4. Bayesian isotope mixing model dietary estimates of prey contribution to both Athabasca Rainbow Trout (RNTR) and Brook Trout (BKTR) within each waterbody, organized within their Disturbance Groups (TDI = Tailings Disturbed and Invaded; NTI = No Tailings and Invaded; NTNI = No Tailings and Not Invaded). Salmonid consumer species are abbreviated as BKTR (Brook Trout) and RNTR (Athabasca Rainbow Trout). The Small Fish prey category consists of both small bodied fishes (Longnose Dace, Spoonhead Sculpin, Pearl Dace and juvenile Longnose Sucker), as well as juvenile salmonids less than 68 mm total length.

		TDI		NTI		NTNI		
Species	Prey Group	Apetowun	Plante	Baseline	Canyon	McPherson	Oldman	Trapper
BKTR	Scraper	24.5 (1.5, 61.4)	28.6 (7.0, 45.5)	45.0 (33.9, 59.1)	22.5 (3.0, 40.0)	-	-	-
	Shredder	55.5 (2.6, 83.9)	23.0 (1.5, 68.4)	-	52.6 (35.5, 69.6)	-	-	-
	Predator/Collector	3.6 (0.2, 17.5)	18.4 (0.8, 54.1)	5.4 (0.2, 23.8)	8.3 (0.3, 26.0)	-	-	-
	Small Fish	4.2 (0.1, 19.5)	12.1 (0.7, 29.3)	3.2 (0.1, 13.5)	4.8 (0.3, 15.4)	-	-	-
	Terrestrial	7.2 (0.2, 39.5)	11.0 (0.6, 30.6)	43.9 (8.0, 56.9)	8.3 (0.4, 27.2)	-	-	-
RNTR	Scraper	28.7 (5.3, 52.3)	18.0 (2.6, 32.7)	22.9 (3.0, 40.4)	37.4 (11.2, 54.2)	6.4 (0.3, 19.5)	9.3 (0.6, 26.0)	16.8 (0.8, 42.5)
	Shredder	15.9 (0.7, 53.6)	16.7 (0.6, 54.9)	-	4.9 (0.1, 29.2)	13.1 (0.4, 48.0)	11.2 (0.5, 34.1)	38.9 (1.0, 74.6)
	Predator/Collector	12.8 (0.4, 42.7)	23.2 (0.9, 70.8)	34.3 (1.8, 78.0)	15.2 (0.7, 58.6)	15.4 (0.6, 50.8)	19.2 (0.8, 57.8)	5.9 (0.2, 28.1)
	Small Fish	15.5 (0.7, 47.9)	48.6 (4.9, 43.2)	23.3 (2.0, 46.5)	25.7 (1.7, 49.9)	28.2 (11.4, 41.7)	45.2 (25.0, 58.8)	30.4 (2.4, 56.2)
	Terrestrial	20.0 (1.7, 37.6)	7.3 (0.3, 21.5)	19.1 (2.6, 34.5)	8.7 (0.3, 39.8)	31.1 (8.9, 47.7)	9.9 (0.8, 21.7)	4.1 (0.1, 21.5)

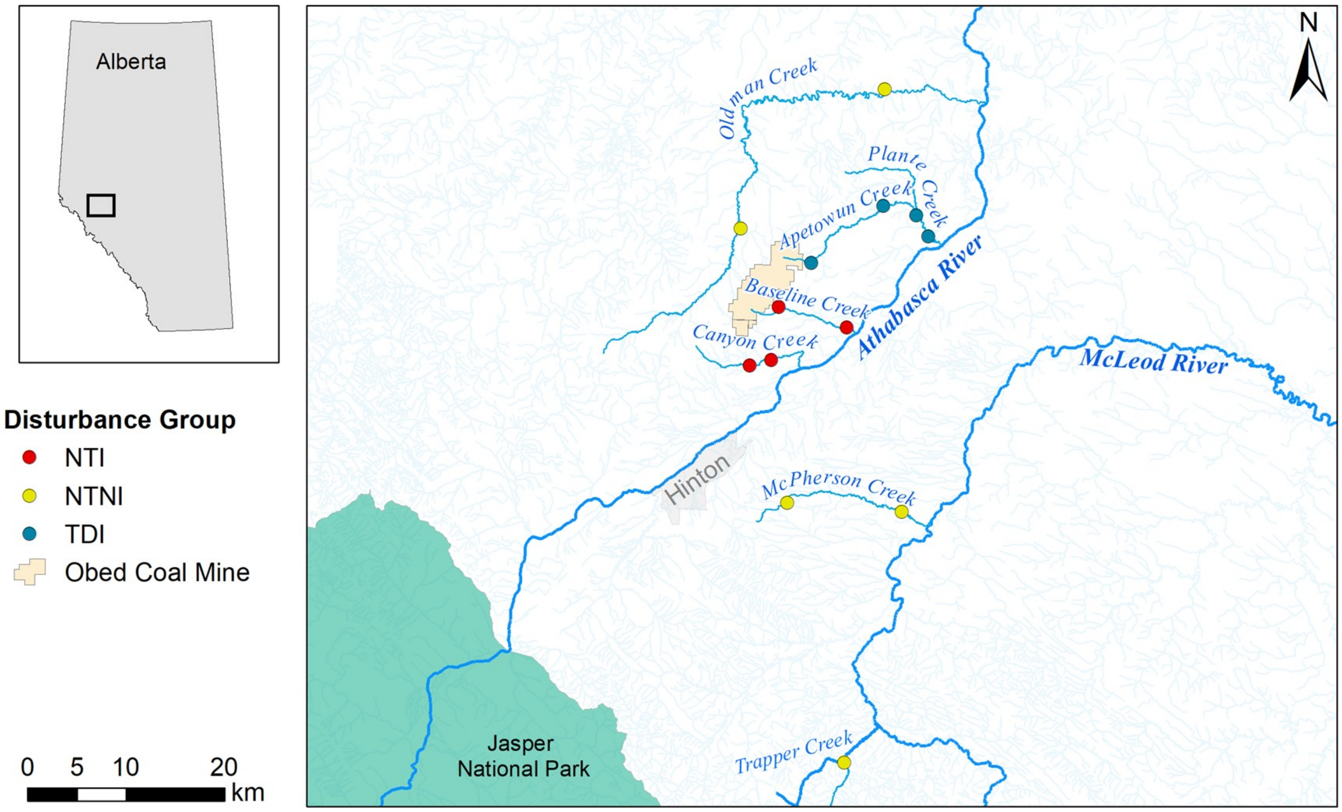

Figure 3.1. Study overview map showing the locations where samples were collected for stable isotope analysis in the 2015 field season. Locations on the map are coloured by Disturbance Group with red circles representing No Tailings and Invaded (NTI) (Baseline Creek and Canyon Creek), yellow circles represent No Tailings and Not Invaded (NTNI) (McPherson Creek, Oldman Creek and Trapper Creek) and blue circles represent Tailings Disturbed and Invaded (TDI) waterbodies (Apetowun Creek and Plante Creek). The Obed mine lease area is indicated by the pink polygon on the map.

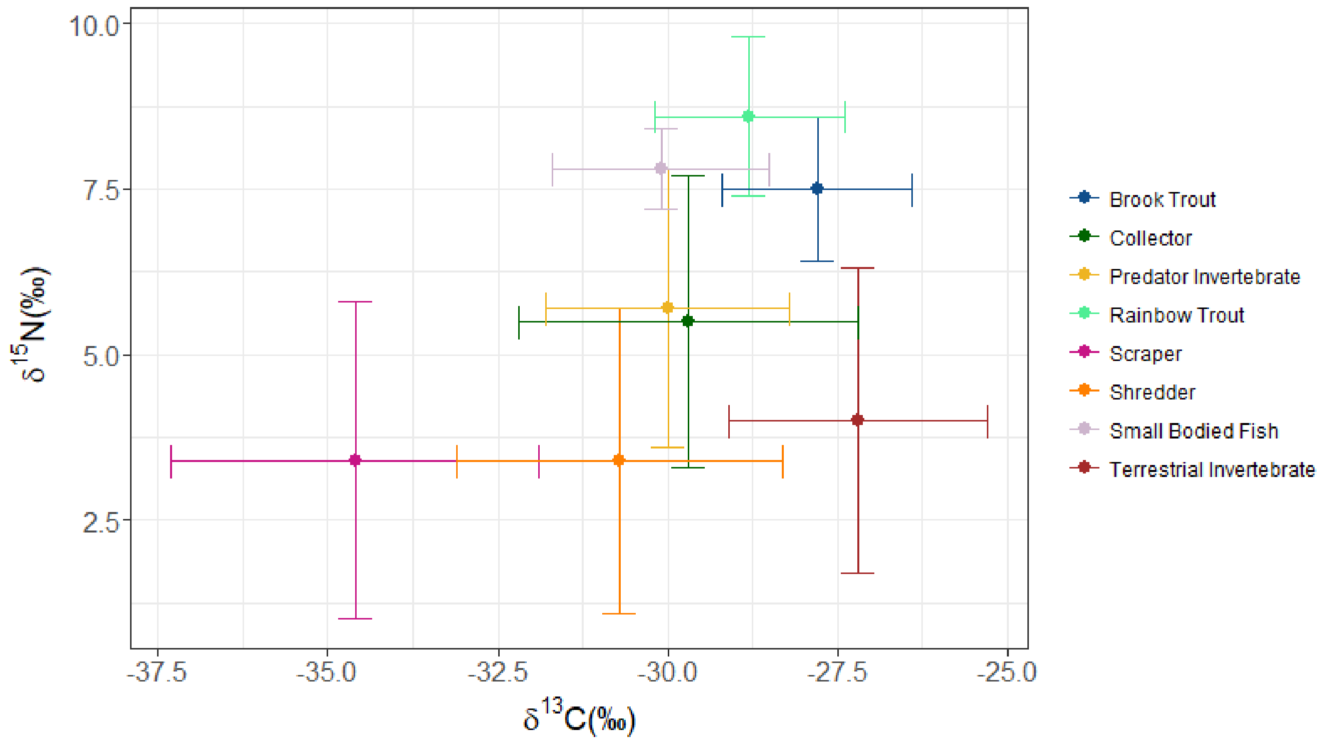

Figure 3.2. Stable isotope biplot of all prey and consumer groups analyzed for stable isotope analysis from the 2015 field season. Values show the mean and SD of $\delta^{15}N$ and $\delta^{13}C$ values for each group from all seven sampled waterbodies.

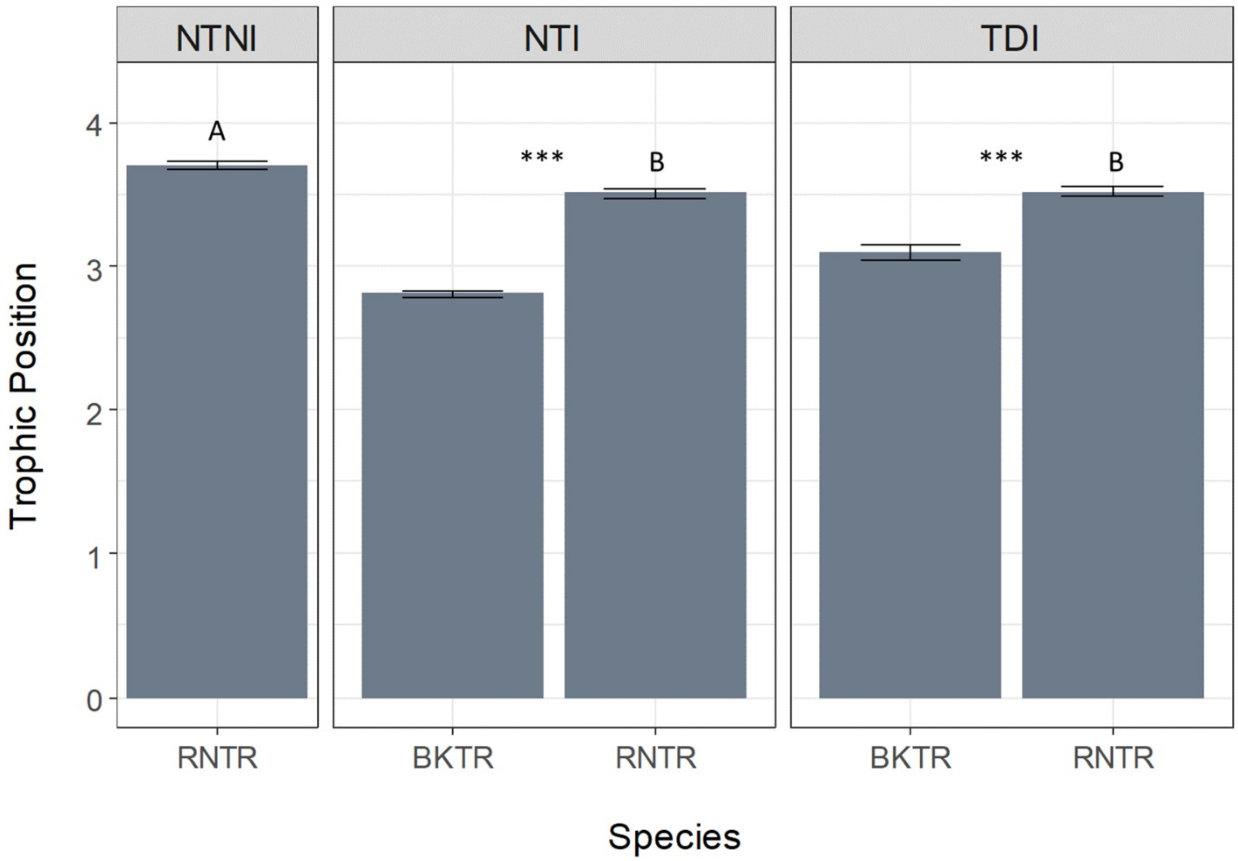

Figure 3.3. Bar plot showing the mean values of both Brook Trout (BKTR) and Athabasca Rainbow Trout (RNTR) trophic position within each disturbance group. Errors bars represent 1 standard error of the mean. Different letters above the error bars indicate statistically significant differences between Athabasca Rainbow Trout in each group, whereas asterisks represent significant differences between Athabasca Rainbow Trout and Brook Trout within each disturbance group (*** $p < 0.001$). In both the NTI and TDI groups there are significant differences in trophic position between RNTR and BKTR, with RNTR at significantly higher trophic position in both groups. RNTR were at a significantly higher trophic position in the NTNI group than they were in either the NTI or TDI groups.

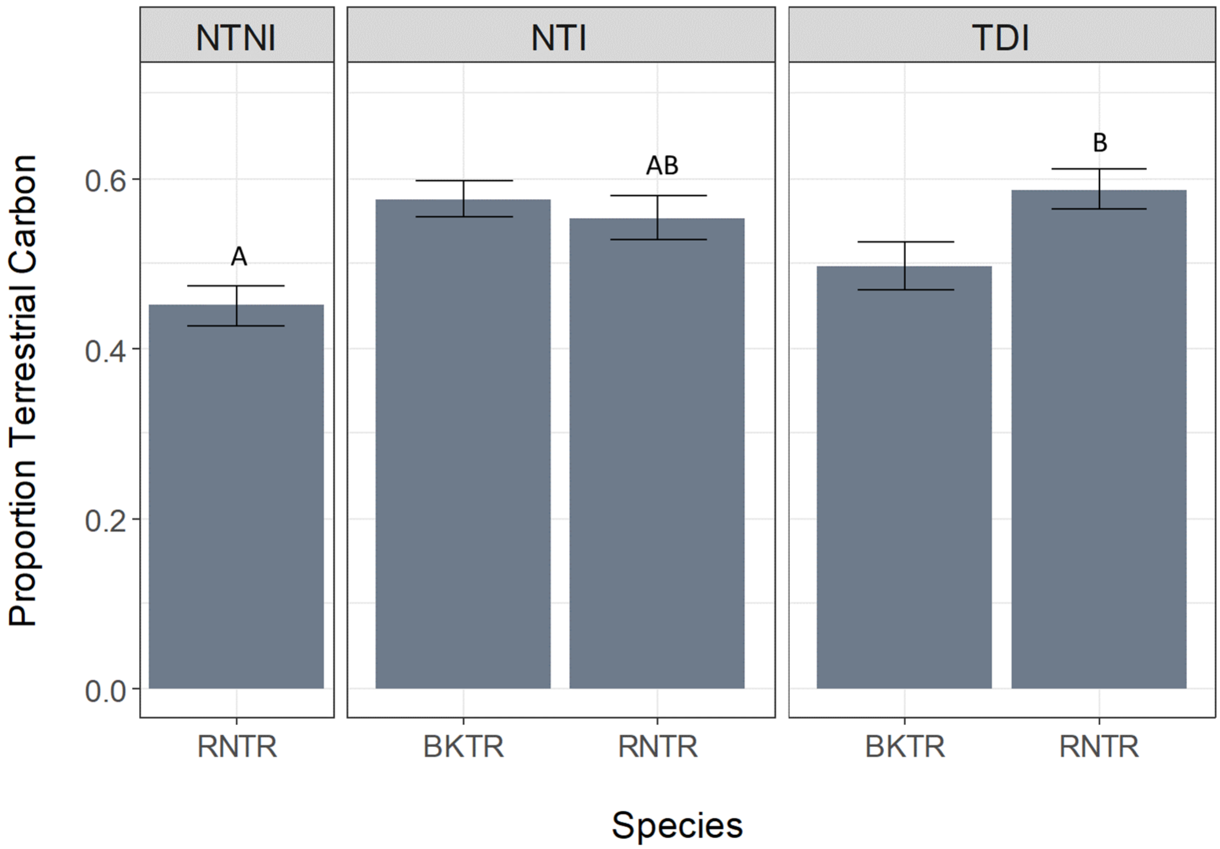

Figure 3.4. Bar plot showing the mean values of both Brook Trout (BKTR) and Athabasca Rainbow Trout (RNTR) proportion of diet derived from terrestrial based carbon sources within each disturbance group. Errors bars represent 1 standard error of the mean. Different letters above the error bars indicate statistically significant differences between Athabasca Rainbow Trout in each disturbance group. There was no significant difference in the proportion of terrestrially derived carbon sources used by RNTR and BKTR in either the NTI or TDI groups. There was a significant difference between RNTR in the NTNI and TDI groups, with Athabasca Rainbow Trout utilizing a significantly lower proportion of terrestrially derived carbon in the NTNI group.

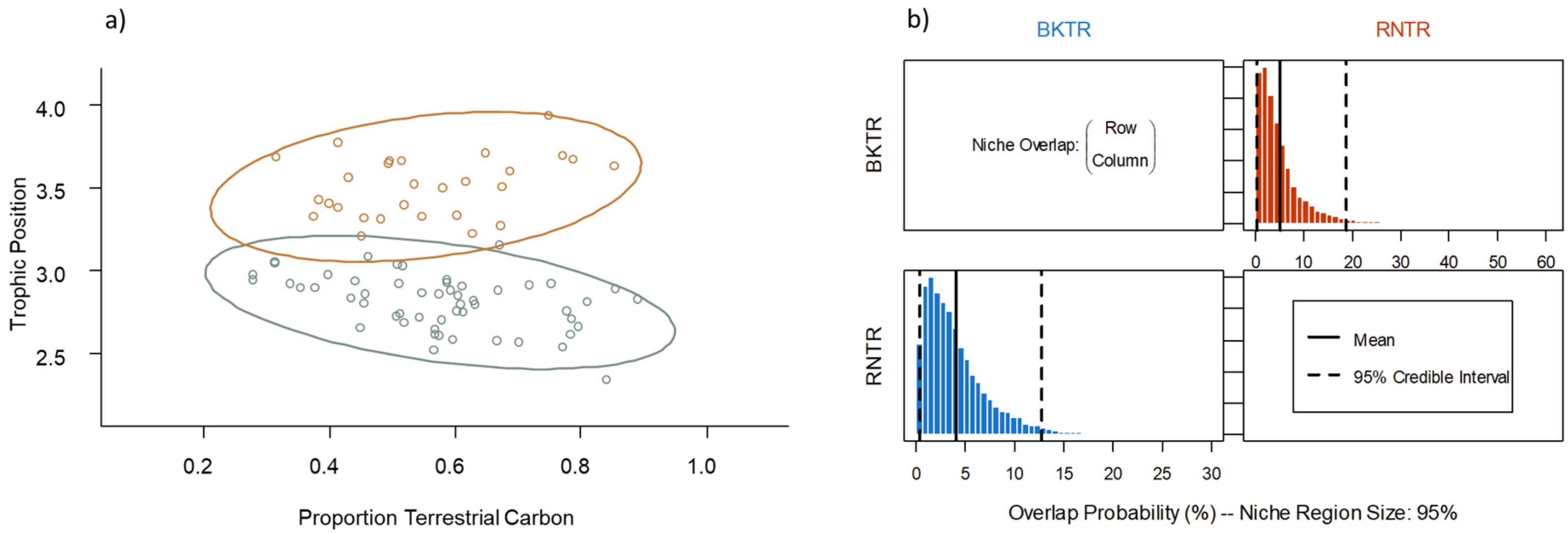

Figure 3.5. Isotopic niche overlap between Athabasca Rainbow Trout (RNTR) and Brook Trout (BKTR) in the NTI disturbance group. Figure 5a shows the 95% confidence intervals around the standard ellipse area (SEA) overlap between RNTR (red points and ellipse) and BKTR (blue points and ellipse). Figure 5b shows the Bayesian derived posterior distributions with 95% niche region overlap between Athabasca Rainbow Trout and Brook Trout in the NTI group. Niche overlap is represented as the probability that the species in each row overlaps with the niche region of the species in the column (Swanson et al. 2015). The probability that Brook Trout are found within the calculated niche region of Athabasca Rainbow Trout is shown in the upper right box, indicating that there was approximately 4% overlap for resources in this treatment.

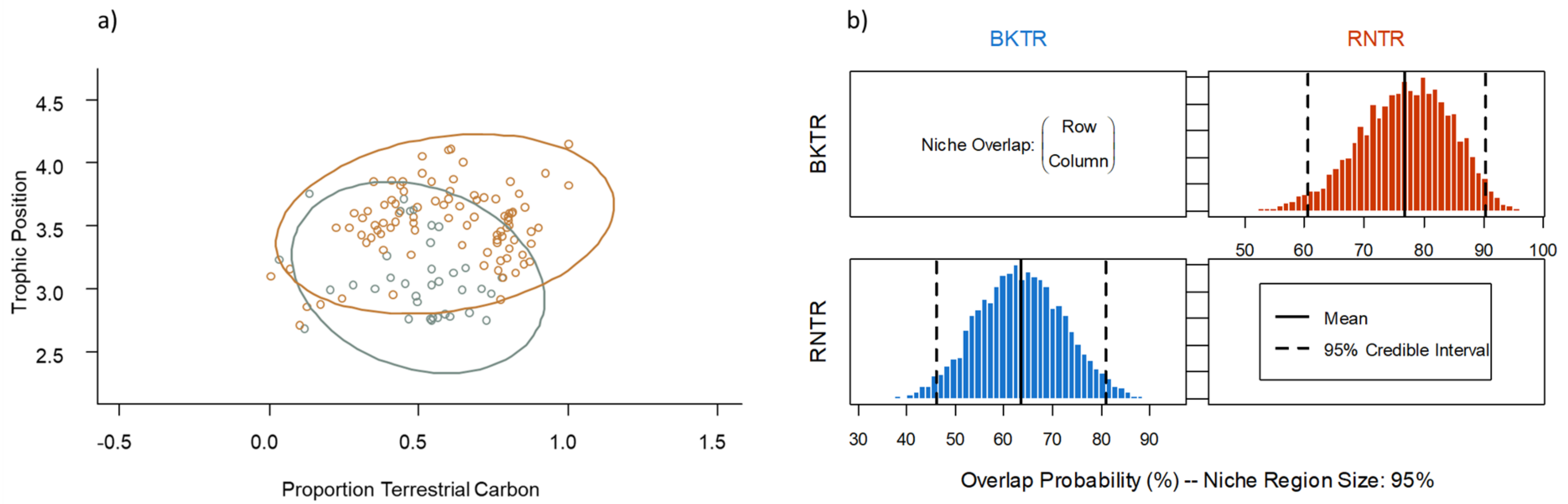

Figure 3.6. Isotopic niche overlap between Athabasca Rainbow Trout (RNTR) and Brook Trout (BKTR) in the TDI disturbance group. Figure 6a shows the 95% confidence intervals around the standard ellipse area (SEA) overlap between RNTR (red points and ellipse) and BKTR (blue points and ellipse). Figure 6b shows the Bayesian derived posterior distributions with 95% niche region overlap between Athabasca Rainbow Trout and Brook Trout in the TDI disturbance group. Niche overlap is represented as the probability that the species in each row overlaps with the niche region of the species in the column (Swanson et al. 2015). The probability that Brook Trout are found within the calculated niche region of Athabasca Rainbow Trout is shown in the upper right box, indicating that there was approximately 77% overlap for resources in this treatment.

3.9 Appendix

Table A3.1. Prey source carbon contribution and invertebrate family groupings. Table values show the functional feeding group classification for analysis purposes in this study. The $\delta^{15}N$ and $\delta^{13}C$ columns show the mean value for all individual samples analyzed for that taxa. The $\%_{Benthic}$ and $\%_{Terrestrial}$ values were calculated using a simple two source isotope mixing model, using the values of Heptageniidae and Terrestrial Invertebrates as $\delta^{13}C$ isotopic end-members. TP indicates trophic position and was calculated using a two-source mixing model (Post 2002).

Group	Taxa	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\%_{Benthic}$	$\%_{Terrestrial}$	TP	*n*
Scraper	Elmidae	2.1	-35.7	100.0	0.0	1.6	8
Scraper	Baetidae	4.5	-35.2	100.0	0.0	2.3	8
Scraper	Brachycentridae	2.4	-34.9	100.0	0.0	1.7	4
Scraper	Ephemerelllidae	3.4	-34.5	100.0	0.0	1.9	11
Scraper	**Heptageniidae**	**3.6**	**-33.5**	**100.0**	**0.0**	**2.0**	**12**
Collector	Leptoceridae	3.5	-32.4	82.3	17.7	1.9	3
Shredder	Pteronarcyidae	3.3	-32.2	79.9	20.1	1.9	2
Juv Salmonid	Rainbow Trout	7.6	-29.9	74.3	25.6	3.2	24
Shredder	Nemouridae	2.8	-31.3	65.3	34.7	1.7	10
Predator	Perlidae	6.1	-31.0	61.6	38.4	2.7	9
Small Bodied	Pearl Dace	7.5	-30.6	61.0	39.0	3.1	9
Juv Salmonid	Brook Trout	6.6	-27.6	59.0	41.0	2.7	9
Predator	Immature Perlidae	5.7	-30.8	58.7	41.3	2.6	6
Collector	Hydropsychidae	6.1	-30.7	56.2	43.8	2.7	10
Small Bodied	Longnose Sucker	7.9	-30.3	56.2	43.8	3.2	17
Small Bodied	Spoonhead Sculpin	7.8	-30.1	53.1	46.9	3.2	20
Predator	Rhyacophilidae	5.9	-30.3	50.2	49.8	2.6	10
Predator	Empididae	6.1	-30.0	45.0	55.0	2.7	3
Predator	Amphizoidae	4.9	-29.9	44.7	55.3	2.3	3
Collector	Chironomidae	4.5	-29.8	42.7	57.3	2.2	4
Predator	Mature Dytiscidae	5.5	-29.7	41.5	58.5	2.5	6
Collector	Tipulidae	4.0	-29.5	37.2	62.8	2.0	9
Small Bodied	Longnose Dace	7.8	-28.7	31.7	68.3	3.2	5
Predator	Corixidae	4.3	-29.1	31.2	68.8	2.1	2
Predator	Chloroperlidae	6.4	-28.8	27.0	73.0	2.7	8
Collector	Simuliidae	5.5	-28.1	16.3	83.7	2.5	2
Collector	Psychodidae	5.0	-27.9	12.7	87.3	2.3	4
Terrestrial	**Terrestrial Invertebrate**	**4.1**	**-27.1**	**0.0**	**100.0**	**2.0**	**41**

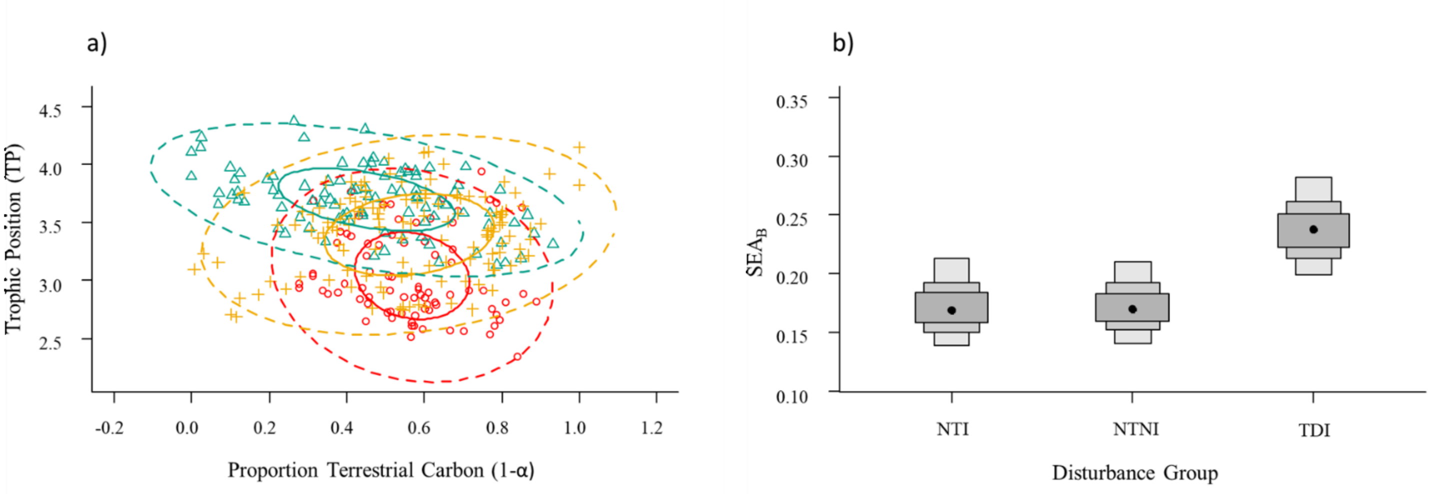

Figure A3.1. Core niche areas (40% confidence interval standard ellipse area (SEA) – solid lines) and broad niche areas (95% confidence interval SEA – dashed lines) for combined BKTR and RNTR values in the three disturbance groups (blue triangles and ellipses = NTNI, red circles and ellipses = NTI, yellow crosses and ellipses = TDI). Figure b shows the 95% Bayesian credibility intervals around the mean estimate of SEA for each of the three disturbance groups when BKTR and RNTR values are combined per disturbance group (NTI = No-Tailings Invaded, NTNI = No-Tailings Not-Invaded, TDI = Tailings Disturbed and Invaded).

Chapter 4: General Conclusion

Given the negative impacts of aquatic pollution, habitat degradation and invasive species on worldwide freshwater biodiversity (Dudgeon et al. 2006), it is critical to understand how these factors are impacting Athabasca Rainbow Trout, an endangered salmonid in the foothills of Alberta, Canada. My results indicate that though there was substantial damage to the stream channel and riparian area in the upper 5 km of Apetowun Creek following the 2013 Obed coal tailings release, Athabasca Rainbow Trout had recolonized the tailings disturbed waterbodies by 2015 (Chapter 2). Turbidity was determined to be the physicochemical parameter that was most limiting to Athabasca Rainbow Trout abundance in the Obed region. Additionally, Athabasca Rainbow Trout abundance was negatively correlated with Brook Trout abundance. Conductivity, a metric commonly associated with coal mining impacts within a watershed (Palmer et al. 2010), was not found to be a significant predictor of Athabasca Rainbow Trout abundance in the Obed region. I found that Athabasca Rainbow Trout abundance was positively correlated with both higher elevation headwater stream reaches, indicative of lower stream temperatures and less competition for resources (Paul and Post 2001, Meyer et al. 2007, Rasmussen and Taylor 2009) and faster water velocities (Lewis 1969, Cunjak and Green 1983). Overall these results seem to suggest that chronic landscape level impacts associated with resource development, such as elevated turbidity and sediment inputs associated with run off from industrial sites and road crossings (Ripley et al. 2005, Maitland et al. 2016), are more limiting to Athabasca Rainbow Trout habitat use and abundance than the residual impacts of this large scale ecological disturbance.

Additionally, I determined that there were significant differences in both the proportion of terrestrially derived carbon sources used and trophic position of Athabasca Rainbow Trout in waterbodies that were impacted by multiple ecological stressors as compared to un-impacted reference streams. There was substantially greater overlap for food resources between Athabasca Rainbow Trout and Brook Trout in tailings impacted and Brook Trout invaded waterbodies than in waterbodies that were invaded by Brook Trout alone. The isotopic niche width of both Athabasca Rainbow Trout and Brook Trout was also substantially greater in tailings disturbed waterbodies compared to waterbodies not impacted by tailings material. These results suggest that both species are incorporating a wider range of prey resources into their diet in tailings disturbed waterbodies. This is likely due to altered food availability following habitat degradation, thereby leading to increased competition for available food resources and a shift in the mechanisms for species coexistence towards greater dietary overlap and generalist food resource use (Bolnick et al. 2010, Gabler and Amundsen 2010, Jackson et al. 2012).

Competition for limiting food resources is the main presumed biotic interaction between Athabasca Rainbow Trout and Brook Trout in this study. This was quantified by determining the isotopic dietary overlap between the two salmonids in streams that were differentially impacted by multiple ecological stressors. Future studies could identify if there are measurable population level effects on Athabasca Rainbow Trout resulting from increased resource use overlap in the tailings disturbed treatment by measuring growth rates, body condition or fecundity in these streams compared to reference streams in the Obed region. Future studies could also explore whether other types of biotic interactions, including predation by Brook Trout on juvenile Athabasca Rainbow Trout is further limiting Athabasca Rainbow Trout population dynamics.

Though Athabasca Rainbow Trout have recolonized the tailings disturbed stream reaches, the long-term viability of these populations is uncertain. Additional deleterious effects may arise from lower food availability, increased resource competition, impaired recruitment, higher water temperatures, and elevated turbidity and sedimentation. All these factors may lead to Brook Trout replacing Athabasca Rainbow Trout in tailings disturbed stream reaches. Due to the extensive damage from the tailings release, the riparian areas are still recovering in upper Apetowun Creek. Riparian areas are important ecosystem linkages between upland and lotic systems, providing organic matter inputs for primary production (Vannote et al. 1980) and important terrestrial food subsidies for trout (Nakano et al. 1999, Baxter et al. 2005).

To fully assess the impact of the Obed mine tailings release on the function of stream food webs in the Tailings Disturbed treatment, long term monitoring will be necessary to determine if these food webs are stable over time. It will be important for fisheries managers to understand the stability of the tailings impacted streams over time to determine their continued suitability in supporting populations of Athabasca Rainbow Trout. Stability in complex food webs has been shown to depend on the maintenance of distinct and heterogeneous energy channels with asynchronous dynamics which are coupled by mobile, higher trophic position consumers (Rooney et al. 2006). Athabasca Rainbow Trout function as a mobile, higher trophic position consumer in these systems, coupling seasonally abundant and important terrestrial invertebrate food resources and promoting food web stability (Nakano et al. 1999, Rooney et al. 2006). An informative further study would be to determine how Athabasca Rainbow Trout resource use changes temporally in tailings disturbed waterbodies and when in sympatry with Brook Trout, compared to when in allopatry in waterbodies not impacted by the tailings release. This could be conducted through winter sampling to determine the effects of seasonality on prey diversity, abundance and fish diet (Nakano and Murakami 2001, McMeans et al. 2015).

An important issue that was outside the scope of this thesis is addressing the potential impacts of residual metal and PAH contaminants to food webs, native fishes and invertebrates in tailings impacted streams (Cooke et al. 2016). Selenium, in particular, has been shown to negatively impact trout reproductive abilities and recruitment in the foothills of Alberta where multiple coal mines operate (Holm et al. 2005, Kuchapski and Rasmussen 2015a). This parameter should be closely monitored in fish tissues, in addition to monitoring juvenile Athabasca Rainbow Trout recruitment in tailings impacted streams. Total mercury and arsenic concentrations were both elevated in the spill material sediment compared to background reference sediment concentrations (Cooke et al. 2016). These metals are of concern due to their toxicity to aquatic organisms and potential to bioaccumulate in aquatic food webs (Cott et al. 2016).

Finally, it is critical to understand if the Athabasca Rainbow Trout which have recolonized Apetowun and Plante Creeks following the Obed mine tailings release are genetically pure Athabasca Rainbow Trout or are genetically hybridized with naturalized stocked populations within the region. Previous work has shown that Rainbow Trout populations in both Apetowun Creek and Plante Creek contain hybridized individuals, however small sample sizes make it difficult to infer larger watershed level trends (Taylor and Yau 2015). Understanding these differences is crucial in order to develop management plans which will help to restore declining populations of native Athabasca Rainbow Trout in the western foothills of Alberta. Data collected in 2015 as part of this thesis research could address this question.

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