EXAMINING BROOK TROUT INVASION INTO BULL TROUT STREAMS OF THE CANADIAN ROCKIES

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Abstract

Brook trout invasion into bull trout streams is variable, and likely influenced by a suite of biotic and abiotic factors. Field observations revealed that brook trout dominated the fish community over bull trout in warmer sites that had undercut banks; in contrast, bull trout dominated in colder sites that had a high amount of large substrate cover, and where alternate non-native species were present. Laboratory studies of competition between the two species revealed that bull trout use a scramble foraging tactic, whereas brook trout use a territorial tactic. Bull trout outcompeted brook trout when fish density was low and habitat complexity was high, as this scenario reduced the effectiveness of the aggressive territorial foraging strategy of brook trout. Bull trout from a migratory population competed more successfully against brook trout and had higher rates of oxygen consumption than those from a resident population. This combined field-lab study points to some of the abiotic and biotic factors that affect competition between the two species, and may influence the outcome of brook trout invasion into bull trout streams.

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What seemed like never ending series of sleepless nights fretting over issues of sampling design, logistical nightmares, frightening Στατιστιχαλ equations and brilliant (at least to me, anyways) ideas that I simply could not decode from my brain into written English has, in retrospect, been one hell of a fun ride. None of this could have been possible without the generosity of so many friends, colleagues and organizations.

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List of Abbreviations

ACA: Alberta Conservation Association
AIC: An Information Criterion, the value of interest using the information-theortic approach
ANCOVA: Analysis of covariance
ANOVA: Analysis of variance
ASRD: Alberta Sustainable Resources Development
BKTR: Brook trout
BLTR: Bull trout
BNTR: Brown trout
CI: Confidence interval
CP-H Complex pool, high number
CR-H Complex riffle, high number
LGSUB: Percent of stream bottom covered by large substrate (cobbles and boulders)
Li: Livingstone River
Mi: Mill Creek
NONNAT: Presence of rainbow trout or brown trout
NSERC: National Sciences and Engineering Research Council of Canada
OCR: Oxygen consumption rate
OMR: Oldman River drainage
OR: Odds ratio
POOL: Percent pool
RNTR: Rainbow trout
SD: Standard deviation
SEM: Standard error of the mean
SP-H: Simple pool, high number
SP-L: Simple pool, low number
TEMP: Mean daily water temperature for the month of August (°C)
TUC: Trout Unlimited Canada
UCB: Percent undercut bank
VIF: Variance inflation factor
WIDTH: Wetted width of the stream (m)

Chapter 1 Introduction

Species invasions, the ecological niche and salmonids in mountain stream ecosystems

Species invasions are a topic of wide concern that have garnered significant attention in ecology and conservation biology, accelerating through the latter half of the 20th Century. Invasion science can now be considered its own distinct sub-discipline of ecology, and several scientific journals solely devoted to this topic are currently in circulation. Beyond the academic community, broadly applied management and conservation efforts are expended to control the spread of, or eliminate, invasive species, and the topic is commonly addressed in popular media (Simberloff et al. In Press). The impact of invasive species on native ecosystems may be destructive in certain cases, resulting in loss of biodiversity, productivity and ecosystem services, causing devastating economic impacts and long term irreversible damage to native ecosystems (Pimentel et al. 2005). Understanding the mechanisms that influence invasion of non-native species, and how they may interact with and displace or replace native species, are central topics of study in invasion science.

Successful establishment of non-native species is governed by a succession of filters, which prevent most introductions from resulting in an invasion (Williamson and Fitter 1996). The probability that a species will become invasive and have a large effect on the recipient ecosystem increases with the arrival intensity of the invasive species. This is known as propagule pressure and is supported by a large amount of experimental and observational evidence (Lockwood et al. 2005). Propagule pressure is defined as the number of non-native individuals arriving per unit time in an area (Simberloff 2009). Propagule pressure goes a long way as a null model to predicting the establishment of invasive species (Colautti et al. 2006). In-depth knowledge of the ecological attributes of the invasive species, together with niche opportunities provided in the recipient ecosystem, are essential to predicting which introductions will lead to actual invasions, and to predicting the ultimate impact of those invasions (Shea and Chesson 2002; Colautti and MacIsaac 2004). This was initially described by Elton (1958), who argued that invasion would be most prevalent in disturbed or less diverse ecosystems, where biotic resistance is low. Conversely, invasion would be expected to be less successful in ecosystems with high diversity because niche opportunities are filled by specialist native species that are not easily displaced. Indeed, the concept of an ecological niche contains many of the elements required to predict invasion success (Peterson 2003). Despite this, there are many exceptions to Elton’s simple view that diversity in the receiving system predicts the likelihood of successful invasion; however, these can often be explained by an in-depth knowledge of the intrinsic and extrinsic factors of the system (Levine and D'Antonio 1999; Shea and Chesson 2002; Fausch 2008).

In addition to propagule pressure, the factors that influence an invaders’ success include the physical environment (abiotic factors), biotic resistance and resource availability (Shea and Chesson 2002). Physio-chemical attributes of the invaded system, and diseases, predators or competitors in the invaded ecosystem may act as filters that limit the spread and success of invasive species, and their resulting displacement or replacement of native species. Invaders can displace native species through competition, predation, as vectors of pathogens, or through some combination of these mechanisms. In some circumstances, invaders may directly displace native species, and may potentially initiate a cascade of effects that alter whole ecosystems. Zebra mussels (*Dreissena polymorpha*) are perhaps the most well known North American example of such an invasive species. This species directly displaces native benthic invertebrates by competing for space, and indirectly alters whole ecosystems by altering light penetration through water by filtering suspended material. The bottom-up photosynthetic pathways that drive the food web may be disrupted by this aspect of zebra mussel biology in areas that are densely populated (MacIsaac 1996). Physical attachment of mussels has further economic consequences, as they damage submerged infrastructure for transportation, energy generation and water treatment. Most species invasions are benign when compared to the zebra mussel example; however, they may subtly disrupt natural ecosystems that provide services to help sustain the functioning of human society and in fact provide its basic necessities.

Inland western North America has seen a distinct homogenization of its freshwater fish fauna, with species from the eastern portion of the continent, as well as Europe, having been purposefully introduced (Rahel 2000). This came as a result of the prevailing fish management policies of the late nineteenth and early twentieth centuries, following the newly discovered successful rearing programs of salmonids (among other fish species) in hatcheries. Warmwater ecosystems have seen the largest absolute numbers of fish invasions, due to the thermal preferences of introduced sportfishes from the eastern part of the continent and fishes from the aquarium trade (Rahel 2007). Relative to native diversity, however, coldwater ecosystems are also highly invaded, mainly through the introduction of salmonid species across biogeographic barriers to increase sportfish opportunities, both within and between continents (Behnke 2002). As a result of these introductions, cold headwater ecosystems of inland mountainous regions have experienced drastic increases in fish diversity (Dunham et al. 2004). The mountainous topography of western North America make natural colonization across drainages difficult, and relatively short interglacial periods have limited the time for speciation to occur and for new species to colonize from downstream sources (McPhail 2007). The result is that headwater lakes and streams of inland western North America typically contain few native fish species, though many are widely distributed across the previously glaciated landscape. Although these environments are relatively resource poor with harsh abiotic conditions to which few fish species are adapted, the high propagule pressure exerted by intentional introductions, coupled with the fact that many salmonids are pre-adapted by chance to many areas within each others' ranges (Fausch 2008), has led to the rapid homogenization of salmonid fish communities with a few easily cultured cosmopolitan species (Rahel 2002). As previously introduced, the mechanism by which invasive salmonids may displace native species is primarily through competition, resulting in the loss or reduction of many genetically unique populations and subspecies of inland trout, char and grayling (Behnke 2002). In some species interactions, the pathways of displacement may be exacerbated by loss through hybridization and introgression (Rhymer and Simberloff 1996).

From an evolutionary perspective, invasions are conceptually paradoxical because natural selection might be expected to render native species better adapted to their local environment than invaders (Sax and Brown 2000). Nowhere is this better exemplified than in salmonids, as many species become invasive into areas they are introduced at the expense of native species, but are themselves displaced in portions of their own native ranges (Fausch 2008). This paradox may be explained and in fact expected by considering the evolutionary and zoogeographic history of the native and non-native species in the context of adaptations to the niche characteristics and natural disturbance regimes in certain portions of each others' ranges (Korsu et al. 2007; Fausch 2008). In-depth knowledge of the niche requirements of invasive and native species and the opportunities provided in environments that are invaded are therefore especially powerful for explaining patterns of invasion (Korsu et al. 2010). This is especially pertinent in the heterogeneous environments of headwater streams of inland western North America, which are naturally dynamic systems that are often altered further by human land use practices and climate change (Rahel et al. 2008).

Brook trout invasion into bull trout streams of western North America

Bull trout (*Salvelinus confluentus*) are one of the most widely distributed native salmonid species to inland western North America (Figure 1-1). All bull trout require small (second to fourth order) cold streams with significant groundwater input to spawn in, as eggs must overwinter before hatching the following spring (McPhail and Baxter 1996; Baxter and Hauer 2000). During the first several years of life, bull trout remain in small, cold nursery streams. Resident forms remain in these streams for their entire lifecycles, and if the stream does not have barriers (falls, cascades, dams, etc.), migratory life history forms are common. As bull trout reach subadulthood, migratory forms move downstream to larger mainstem rivers, lakes, or in coastal regions, estuarine environments. This is usually accompanied by a trophic shift to piscivory where bull trout often become the apex predator in their ecosystem (McPhail and Baxter 1996). Resident forms may not undergo a trophic shift, and remain primarily non-piscivorous due to the limited productivity of their environments. At five to seven years (in the core regions of the range for most populations), bull trout reach sexual maturity and migratory forms return to their natal streams to spawn.

Bull trout have declined greatly throughout the southern and eastern margins of their range, with the greatest declines occurring for the migratory form (Fitch 1997; Rieman et al. 1997; Dunham et al. 2008). This decline is commonly attributed to four major causes (Dunham et al. 2008; Rodtka 2009; ASRD 2012). Firstly, early management practices failed to understand the population structure of the bull trout; in particular, small units or “demes” of this apex predator are made up of few spawning adults (Warnock et al. 2010). This lack of appropriate management, coupled with their ease of capture and disdain by the angling and management communities of the time resulted in widespread overharvesting of bull trout (Colpitts 1997; Post et al. 2003). Secondly, fragmentation due to in-stream infrastructure that impedes migratory passage, as well as loss of appropriate downstream habitat, has often led to the collapse of whole populations supported by migratory forms or a shift to a less migratory life history (Nelson et al. 2002). Thirdly, loss of suitable physical and thermal habitat in spawning and rearing areas of headwater streams due to land use practices (e.g., clear-cut logging, poorly designed road crossings etc.) has eliminated many appropriate spawning and nursery areas for bull trout (Rieman et al. 1997; Ripley et al. 2005). Finally, the introduction of non-native species has resulted in the decline of bull trout in many areas of their range (Dunham et al. 2008). Of introduced species, the most commonly implicated non-native species in the decline of bull trout are the lake trout (*Salvelinus namaycush*) in lacustrine environments and the brook trout (*Salvelinus fontinalis*) in stream environments.

Brook trout are a species native to eastern North America (Figure 1-1). Intentional introduction into western states and provinces throughout the late-nineteenth and twentieth centuries ensured a high amount of propagule pressure during initial stages of colonization, and has resulted in the successful naturalization of many populations through stream networks (Dunham et al. 2002). Many of these stream networks are, or once were, important habitat for bull trout, and the two species now overlap significantly throughout the bull trout native range (Figure 1-2). In the Canadian Rockies of Alberta, these habitats are often small streams that are characterized as spawning and nursery areas for bull trout (or full lifecycle habitat for resident forms). Brook trout invasion is widespread in the province, with naturalized populations in all six of the major watersheds draining the east slopes of the Canadian Rockies. The only salmonine species native to this entire region is the bull trout. Brook trout have been identified as a major concern to the sustainability and recovery of bull trout populations in Alberta (Rodtka 2009; ASRD 2012).

The outcome of brook trout invasion into bull trout streams appears to be variable, as brook trout displacement of bull trout appears to have mixed support from field studies examining their co-occurrence (Dunham et al. 2008). Brook trout are presumed to potentially exclude bull trout in some habitats by directly competing for limited space or resources, via a competitive pathway (Gunckel et al. 2002), and also by limiting reproductive output through hybridization (Leary et al. 1993). For juvenile fish in particular, bull trout and brook trout may have similar food web roles in nursery streams (Appendix). This may extend to the adult life stage if bull trout are of the stream-resident life history (Chapter 4).

Several studies have attempted to characterize the patterns of brook and bull trout occurrence in the field. Some similarly designed studies have not found a dramatic effect of brook trout presence on the presence of bull trout (Dunham and Rieman 1999; Dunham et al. 2003a; Wenger et al. 2011), whereas others have (Watson and Hillman 1997; Rich et al. 2003). The mechanisms underlying this variable pattern of invasion has been examined further in several studies. When examining the abiotic features of the environment that may influence invasion, brook trout have preferentially colonized downstream areas of bull trout streams (Paul and Post 2001). This has led to Paul's "elevation refuge hypothesis" of invasion (Paul 2000), in which the presence of native and non-native species along an elevation gradient is explained by thermal habitat niche segregation (Taniguchi and Nakano 2000). Experimental studies by McMahon et al. (2007) and Rodtka and Volpe (2007) attempted to test this hypothesis. Both studies confirmed that juvenile brook trout were superior competitors over size-matched bull trout in warm (15-16 °C) water; however, neither were able to demonstrate the reciprocal competitive advantage of bull trout in cold (8° C) water, casting considerable doubt on the elevation refuge hypothesis. Likewise, field observations only provide limited support for the hypothesis, and suggest the involvement of many additional local-scale factors (Rieman et al. 2006). Temperature has therefore failed as a simple panacea for brook trout invasion into bull trout streams, and further research into additional biotic and abiotic factors that may act as filters to brook trout invasion is necessary (Rieman et al. 2006; McMahon et al. 2007; Rodtka and Volpe 2007).

Biotic and abiotic factors that may be important in determining the success of brook trout invasion into bull trout streams have been explored in few studies. Population-level differences in aggression and competitive traits have commonly been observed in salmonid fish (Rosenau and McPhail 1987; Dunbrack et al. 1996; Lahti et al. 2001). It may be reasonable to suspect that this population-level variation influences the success of brook trout over distinct populations of bull trout. Population-level differences in competitive traits are most likely to be seen in populations exhibiting different migratory life histories (Lahti et al. 2001; Lahti et al. 2002). Non-migratory salmonid forms often display slower growth rates and lower aggression, food intake levels and standard metabolic rates than migratory forms (Metcalfe 1998; Lahti et al. 2001; Morinville and Rasmussen 2003; 2006). Therefore, there may be variation among bull trout life history forms in behavioural traits that have a direct effect on competition with an invader, and this variation may have a physiological basis. Abiotic factors have also been proposed to influence brook trout invasion, namely habitat features. Rich et al. (2003) concluded, from a carefully designed field study using co-occurrence data, that bull trout had successfully resisted brook trout invasion in streams exhibiting a high amount of structural complexity and connectivity. In a similarly designed study, Benjamin et al. (2007) also found local-scale habitat factors important in predicting the establishment of brook trout into cutthroat trout (*Oncorhynchus clarkii*) streams. Based on field observations, Nakano et al. (1998) hypothesized that brook trout have a similar ecological niche to bull trout, and that brook trout exhibit competitive superiority over bull trout through interference competition. Rodtka and Volpe (2007) further suggested that bull trout compete for resources with brook trout through exploitation rather than interference, and that this may be beneficial in certain types of habitats that afford visual isolation amongst competitors. Earlier field observations from my own work (Warnock 2008) also suggested that brook trout and bull trout generally inhabited streams with different physical habitat structure. In particular, bull trout appeared to prefer streams with a high amount of in-stream complexity in the form of substrate cover (Warnock 2008), whereas brook trout were most common in small streams with undercut banks, and limited substrate cover (Krimmer et al. 2011). Differences in the physical habitat niche may explain why brook trout have not always successfully invaded bull trout habitat. This stimulated an observational field study, which tests whether physical habitat features can be associated with brook trout invasion into bull trout streams (Chapter 2). To complement this, an experimental study of competition between the two species was conducted to investigate differences in foraging behaviour between the two species and biotic and abiotic conditions under which either species gains a competitive advantage (Chapters 3, 4).

Objectives and organization of thesis

Study design in the biological sciences can be classified as either observational or experimental. In observational research, treatments of an independent variable are naturally occurring, whereas in experimental studies, those treatments are randomly assigned by the researcher (Whitlock and Schluter 2009). Observational studies are associative in nature, and outline potential correlations between an independent variable(s) and a dependent variable(s). In ecology, these studies are usually conducted in the field, and are useful for generating hypotheses about the cause-and-effect relationship between variables in the natural world. While observational field studies therefore never definitively prove associations, and are often significantly confounded by natural variation and "extraneous" variables, they are carried out within a realistic context. On the other hand, experimental studies directly test the cause-and-effect relationships between variables by controlling for confounding factors; however, the often limited and simplistic context provided by the laboratory environment or field enclosures, may limit ecological relevance of their findings (Fausch 1988). Given the advantages and shortcomings of both experimental and observational science, it is apparent that both approaches can be highly complementary when combined under one overarching project (Blanchet et al. 2007; Korsu et al. 2010).

This project is designed to use the advantages of both observational and experimental science to examine brook trout invasion into bull trout streams. Based on the literature described above, several abiotic and biotic factors were identified that may influence brook trout invasion into bull trout streams. These were included as independent variables that were hypothesized to be associated with brook trout invasiveness in an observational field study. An experimental laboratory study was also designed to test some of those variables when brook trout and bull trout were subjected to competition with one another. By combining both approaches, this project makes both ecologically relevant observations of the variables that may be associated with brook trout invasiveness, and provides some experimental evidence as to whether these variables have an underlying cause-and-effect basis.

The remainder of this thesis is organized into three analytical chapters, a synthesis chapter and an appendix. Chapter 2 presents the field portion of the study, in which the relationships between brook trout invasiveness in streams throughout the Canadian Rockies is correlated with a variety of abiotic and biotic features of the environment. Chapter 3 is a laboratory test of competition, and describes the foraging mode of the two species, as well as how habitat and fish density may influence competition between the two species. Chapter 4 is an extension of the laboratory test, and specifically tests whether bull trout collected from a migratory population compete differently against brook trout than those from a non-migratory population. The final chapter synthesizes the information of the three analytical chapters and provides some conservation recommendations based on the observations.

The appendix is divided into two major written sections, but neither is essential for understanding the remainder of the thesis. The first section provides a background and rationale for some of the analytical design chosen for this dissertation. The second section is an additional study that describes some basic biology of juvenile bull trout in the Canadian Rockies. This study provides some important supplemental data that furthers our understanding of juvenile bull trout life history and food web roles in southern Alberta, compared to other areas throughout the bull trout native range.

Figures

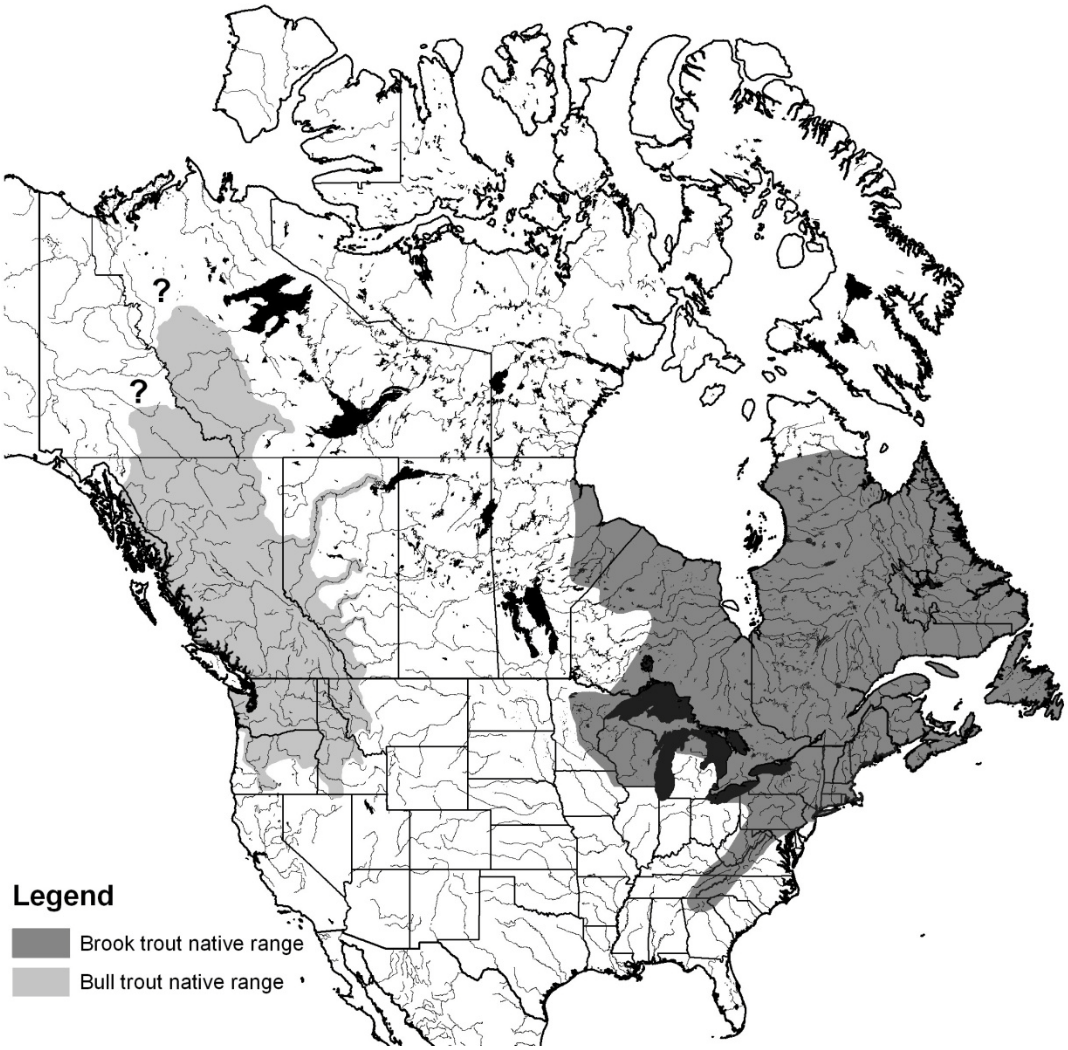

Figure 1-1: Historic native ranges of the bull trout and brook trout in North America. Question marks represent undetermined portions of the bull trout range in its northern periphery (Mochnacz et al. In Press; B. Shonewille, EDI Environmental Dynamics; M. Connor, Taku River Tlingit First Nation; Lars Jessup, Environment Yukon; Joe De Gisi, British Columbia Fish & Wildlife; Nick de Graff, Can-nic-a-nick Environmental Services, personal communication).

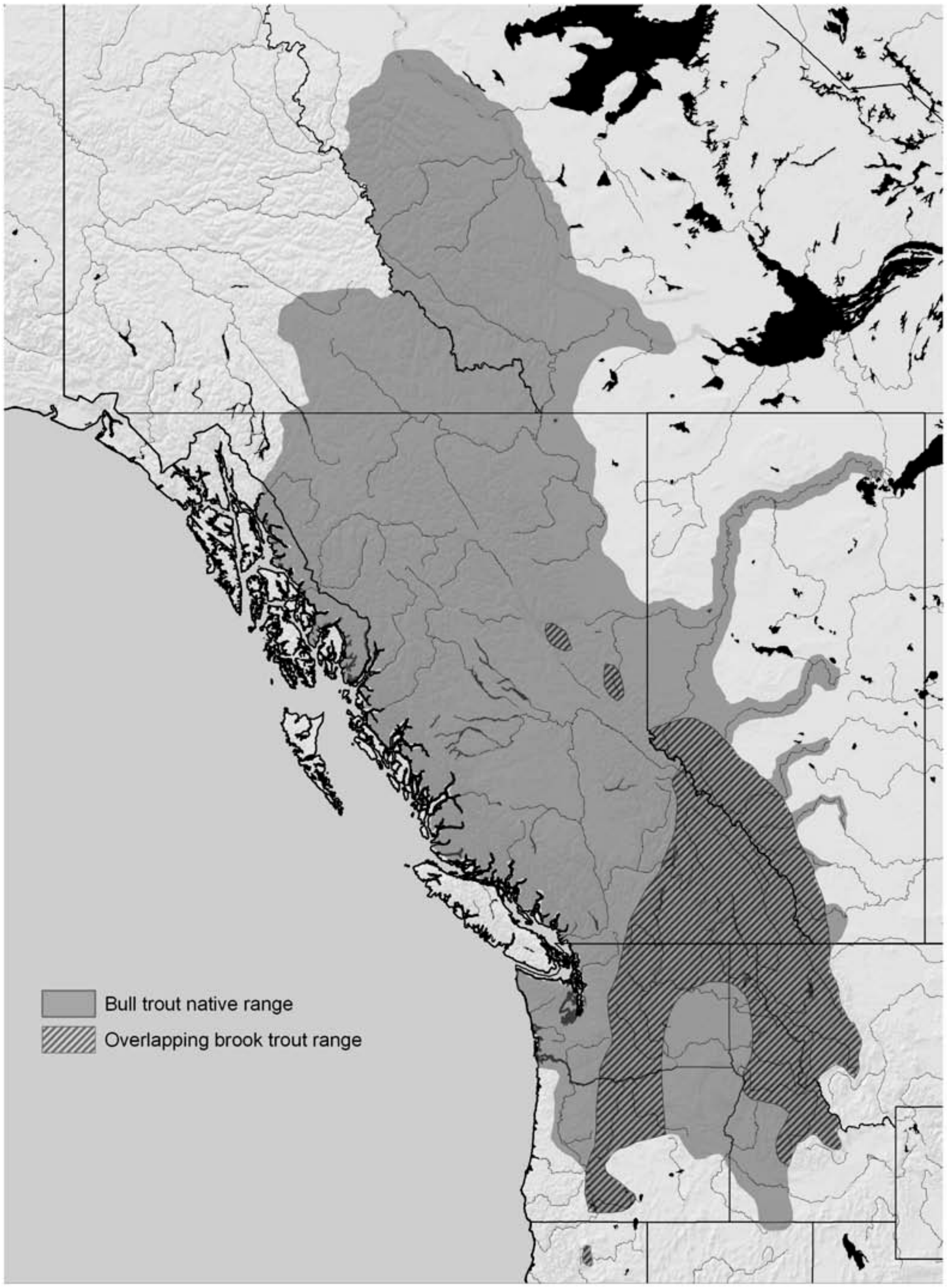

Figure 1-2: Historic range of bull trout into which brook trout have become naturalized.

Chapter 2 Abiotic and biotic factors associated with brook trout invasiveness into bull trout streams of the Canadian Rockies

Abstract

Invasion of brook trout into streams formerly or currently occupied by native salmonid fishes is variable and often associated with a suite of local-scale abiotic and biotic variables. In this study, 80 sites from 51 streams were sampled. These streams had confirmed brook trout invasions, and were identified as current or historical nursery habitat for native bull trout in the Canadian Rockies. Sites were classified as having high brook trout invasiveness (>60% of the community relative to remnant bull trout) or low invasiveness (<40%). Most sites tended to be overwhelmingly or completely dominated (95-100%) by one species or the other. An information-theoretic approach was used to determine the association between brook trout invasiveness and a suite of measured abiotic and biotic features of the site, based on a set of candidate logistic regression models. High brook trout invasiveness was positively associated with stream temperature and undercut bank habitat, but negatively associated with large in-stream substrate (cobbles and boulders). High brook trout invasiveness was also negatively associated with co-occurring rainbow trout or brown trout, two alternate non-native species. Brook trout appear to dominate the community over native bull trout where thermal or habitat niche opportunities are provided for them, although other non-native species may restrict their invasion success into bull trout streams.

Introduction

Invasion success for individual species appear to be spatially variable and difficult to predict (Moyle and Light 1996b; Alpert et al. 2000). In many situations, species invasions result in complete dominance of the invasive species over ecologically similar native species; however, invasions can also be unsuccessful or result in coexistence with native species. This variation in invasion outcome is particularly apparent in spatially heterogeneous environments (Melbourne et al. 2007). Such environments provide a variety of abiotic and biotic conditions that may impart niche opportunities to non-native species (Shea and Chesson 2002). Although it may seem like a paradox, locally adapted native species are often replaced or displaced by non-native species that happen to be pre-adapted by chance to local conditions of the introduced environment (Sax and Brown 2000). This may be understood by an in-depth knowledge of the niche requirements of both the native species and the invader, and the abiotic and biotic environment of invaded habitats (Moyle and Light 1996a; Fausch 2008; Korsu et al. 2010).

Headwater streams in mountainous regions are highly heterogeneous in abiotic conditions, due to spatial variability in geomorphology, landscape cover and climate. There is increasing evidence that invasion patterns of salmonid fish in these areas are shaped by local conditions that favor the foraging strategy, life history or habitat and resource preferences of invading species (Olden et al. 2006; Fausch 2008). Some examples of abiotic conditions that may drive distributions of invading salmonids include temperature (Dunham et al. 2002; Rieman et al. 2006), hydrological regime (Fausch et al. 2001), habitat (Korsu et al. 2007) and presence of migratory barriers (Rahel 2007).

Biotic conditions, for example, competitors or predators (Baltz and Moyle 1993; Harvey et al. 2004), ecosystem productivity (Westley and Fleming 2011) and food web structure and dynamics ("resources", Shea and Chesson 2002), are also variable in mountain stream ecosystems, and may influence invasion success. In fact, the success of an invader may depend on which other invaders are present, since worldwide local salmonid fish community diversities have been rapidly augmented through introductions of non-native species (MacCrimmon and Campbell 1969; Vooren 1972; Fausch et al. 2001; McDowall 2003; Soto et al. 2006).

Brook trout (*Salvelinus fontinalis*) are a salmonid species native to coldwater ecosystems of eastern North America, but have been widely introduced to mountainous regions of western North America (Figure 1-2). Of the native species affected by brook trout establishment, most of the fourteen sub-species of cutthroat trout (*Oncorhynchus clarkii*) and bull trout (*Salvelinus confluentus*) are commonly implicated and studied (Dunham et al. 2002; Rieman et al. 2006; Fausch 2008). The Canadian Rockies represent the largest portion of the non-native range of brook trout in Canada, and include every major watershed draining from the east slopes in Alberta (Figure 1-2).

Cutthroat and rainbow trout (*Oncorhynchus mykiss*) are native to restricted ranges in Alberta, and the bull trout is native to all major watersheds, often being the only native species present in headwater streams. Bull trout have declined greatly throughout their range in Alberta, and this has been attributed to angling-related mortality, land-use practices that have fragmented or altered stream habitat and through competition with introduced species (Rodtka 2009; ASRD 2012). Although many bull trout are large bodied migrants that inhabit large rivers, the species obligatory spawns and rears as juveniles in headwater streams that are typical habitats of invading brook trout (McPhail and Baxter 1996; Rich et al. 2003). Rearing in nursery streams is a critical period for bull trout in the first 1-3 years of their lifecycle (Downs et al. 2006). At the juvenile life stage, migratory bull trout populations therefore often overlap in resource and habitat use with brook trout (Appendix). In addition to this, resident forms of bull trout are common throughout their range, and are the predominant life history in many naturally or artificially fragmented watersheds (Fitch 1997; Nelson et al. 2002; Mogen and Kaeding 2005). These forms do not migrate from headwater streams and remain non-piscivorous as adults (McPhail and Baxter 1996), and therefore may overlap in resource and habitat use with invading brook trout throughout their life-cycle. The outcome of brook trout invasions into bull trout streams is highly variable, ranging from unsuccessful to complete replacement of native bull trout; mixed communities are often numerically dominated by one species or the other.

Observational field studies on bull trout and brook trout occurrence have generally found that bull trout occur in higher elevation reaches of streams, while brook trout are found in lower elevation, warmer reaches (Rieman et al. 2006). This pattern occurrs regardless of their original stocking location (Paul and Post 2001). This association has led to an “elevation refuge hypothesis,” (Paul 2000) explaining trends of native and non-native species occurrence along elevational gradients due to competitive superiority of either species in their preferred thermal niches (Taniguchi and Nakano 2000; Paul and Post 2001; McMahon et al. 2007). This hypothesis has mixed support in the field, as brook trout occurrence and displacement of bull trout appears to be highly context dependent and only weakly predicted (if at all) by such a model (Rich et al. 2003;

Rieman et al. 2006; Wenger et al. 2011). Laboratory studies likewise find incomplete support for this hypothesis. Brook trout are indeed superior competitors over bull trout at warm water temperatures; however, the reciprocal competitive advantage for bull trout at cold temperatures, required by the model, has not been demonstrated experimentally (McMahon et al. 2007; Rodtka and Volpe 2007).

While temperature is no doubt an important abiotic condition in determining brook trout invasion outcome, local-scale habitat conditions have been repeatedly discussed as important variables (Rich et al. 2003; Shepard 2004; Benjamin et al. 2007; McMahon et al. 2007; Rodtka and Volpe 2007). In particular, physical habitat structure has been discussed as important correlates of invasion success, with brook trout preferentially invading smaller streams and streams of low structural complexity in unconstrained valley bottoms (Rich et al. 2003; Benjamin et al. 2007; Wenger et al. 2011). At the local scale, these habitats are usually typified by narrow channels, slow moving meanders with deep pools, small substrate and high bank cover. Such habitats may provide niche opportunities that may favor brook trout over native species. Indeed, in laboratory experiments, brook trout foraging success relative to bull trout increases as habitats become slower, deeper and less structurally complex (Chapter 3). This may reflect the different foraging strategy and habitat-use of the two species when under direct competition in headwater streams (Chapter 3; Nakano et al. 1998; Rodtka and Volpe 2007).

Biotic conditions have occasionally been considered in explaining the patterns of brook trout invasion in field studies (Benjamin et al 2007; Peterson et al. 2004). As the fish community in Rocky Mountain streams has increased in diversity with the introduction of several non-native salmonids, it is reasonable to suspect that competing invaders restrict each others' invasion success. Although biotic resistance of native rainbow trout to brook trout invasion may be weak in some streams (Benjamin et al. 2007), it is possible that in introduced ranges, they and other commonly introduced species such as brown trout (*Salmo trutta*), act as a "biotic barrier" to brook trout invasion. Neither of these alternate non-native species is commonly implicated in competitively excluding bull trout (Donald and Stelfox 1997; ASRD 2012), but both are commonly implicated to interact competitively with brook trout where they co-occur (Dunham et al. 2002; Korsu et al. 2007; Fausch 2008).

In this study, the relationship between brook trout invasiveness and a suite of local-scale abiotic and biotic conditions was examined in bull trout streams of the Canadian Rockies. Specifically, temperature, local-scale physical habitat metrics and presence of alternate non-native species (rainbow and brown trout) were measured on-site, given the evidence from previous studies for these as potential factors influencing brook trout invasion. I predict that several of these abiotic and biotic conditions may provide niche opportunities to brook trout, and will thus be associated with their invasiveness.

Methods

Study area and site selection

Sites were chosen on streams that had current or historical evidence of juvenile or sub-adult bull trout and brook trout occurrence. In essence, only streams that are, or once were, important spawning and/or rearing streams for bull trout that had confirmed brook trout invasions were chosen. Candidate streams were selected based on previous sampling, interviews with local fisheries biologists, consulting literature and provincial fisheries inventory databases (G. Sterling, Alberta Sustainable Resources Development [ASRD]; D. Wig, ASRD; J. Stelfox, ASRD; J. Earle, ASRD; S. Herman, ASRD; M. Rodtka, Alberta Conservation Association [ACA]; K. Fitzsimmons, ACA, personal communication; ASRD 2009; Fitch 1997; Paul 2000) Confirmed brook trout invasions were not recent events. Brook trout were introduced primarily to flowing waters of Alberta in the first half of the 20th century, with rapidly declining efforts in the second half. Although brook trout continue to be stocked in Alberta, the government policy since the late 20th century has limited their stocking to waterbodies with limited chance for escape into flowing waters containing native fish (ASRD 2012). The Crowsnest River drainage was avoided, where bull trout extirpation due to industrial development and angling pressure pre-dated brook trout establishment, and natural-re-establishment of bull trout is impossible due to a major in-stream migratory barrier (Fitch 1997). I also avoided several streams that were significantly altered or impacted by industrial use, including watersheds draining current and historic coal mine sites, and streams of the Kananaskis River Drainage and upper Bow River drainage, which have a long history of industrial and urban development. Multiple sites on the same stream were selected where access allowed, but were separated by at least three linear stream kilometers to reduce the chance of spatial autocorrelation among sites. To avoid over-representing specific streams in the dataset, each stream was represented by a maximum of three sites. Sites on all streams were composed of simple fish communities, being dominated by bull trout, brook trout, cutthroat trout, rainbow trout or brown trout. Occasionally, lower elevation reaches of streams contained whitefish (*Prosopium williamsoni*), suckers (*Catostomus spp*.), sculpins (*Cottus spp*.), burbot (*Lota lota*) and/or longnose dace (*Rhinichthys cataractae*).

One hundred twenty-four sites were sampled from 61 streams that drain the East slopes of the Canadian Rockies in Alberta, Canada (Figure 2-1) in the summers of 2009, 2010 and 2011 (Table A-5). A diversity of streams was selected to represent the range of stream habitats that face brook trout invasion found throughout the east slopes of the Canadian Rockies. Streams were generally of second, third or small fourth order where they were sampled, as these are preferred spawning and rearing habitat for bull trout (Baxter and Hauer 2000). Sites spanned a large range in latitude, from Blakiston Creek in Waterton Lakes National Park (49°04’N 113°52’W) in the south to Wampus Creek near Hinton (53°09’N 117°15’W) in the North, and ranged in elevation from 1137 m to 1970 m. Sites were all sampled in late summer or early fall (July-Oct) in order to represent habitat conditions in base flow, and where electrofishing efficiency is highest.

Brook trout invasiveness

Fish were enumerated by single-pass backpack electrofishing the full length of the sites where habitat data was collected (see subsequent section for a description of sampling length). Relative abundance estimates were the basis of invasiveness, and were made by the observed percent of brook trout in the site, relative to bull trout. These estimates were used to classify a site into one of two categories of brook trout presence, “high” invasiveness (> 60% of brook/bull trout community) or “low” invasiveness (< 40% of community). These two categories were used because most invaded streams were dominated by one species or the other (i.e., approach 100% or 0%), and logistic regression may effectively describe the relationship with measured biotic and abiotic features of the environment. Only fish 75-400 mm were included in the counts. The lower boundary of this size range was chosen in order to reduce bias caused by inefficiency of backpack electrofishing to sample small-bodied young of year fish, which do not typically exceed 75 mm by midsummer in the study area or other areas in the bull trout range (Appendix; McPhail and Baxter 1996). The upper boundary of this size range was an estimate of typical minimum length that may indicate migratory adult bull trout returning to spawn for fluvial and adfluvial bull trout populations (McPhail and Baxter 1996; Rodtka 2009). These fish were not included in the count because their seasonal presence in a community estimate would be biased by the date in which the site was sampled.

In some streams, concurrent fisheries projects were being carried out by a variety of agencies in the years the study was conducted. To avoid excessive electrofishing in these streams, efforts were conducted by only one agency and data were shared. Where possible, sites were repeat sampled in multiple years or additional electrofishing data were obtained from a government fisheries inventory database of sampling efforts within the last five years (ASRD 2009). Multiple year data were available for many sites, and for these, relative abundance estimates were averaged among years. Where only one year of data was available, sites were only included if there was a confident detection of the combined total of either of the two species (≥ 8 75-400 mm bull and/or brook trout per

300 m). This threshold was obtained from a previous study that calculated the maximum number individuals that could go undetected in a single-pass effort according to 95% confidence levels (Paul and Post 2001). The authors calculated this threshold from capture probabilities based on 34 multiple-pass depletion removal studies, many of which were conducted on streams that overlapped with this study area (A. Paul, ASRD, personal communication).

Hybrids between bull trout and brook trout occur in some of the streams sampled, and each hybrid encountered was coded as a half count for each species. Hybrids were identified based on the presence of pale spotting that extended at least past 50% of the height of the dorsal fin (DeHaan et al. 2010), and at least one other of the following intermediate traits: distinct vermiculations on the dorsal side of the fish; bright lateral side spotting with pale haloes; white and pale black anterior borders of ventral fins; intermediate head shape. In-hand identification of hybrids has shown to be highly accurate by experts (Rieman et al. 2006; DeHaan et al. 2010; Popowich et al. 2011). An example photo of a hybrid fish can be seen in Figure 2-2.

Abiotic and biotic variables measured

At each site, measurements were taken to quantify abiotic and biotic variables considered to be potentially important in describing brook trout invasion into bull trout streams. The British Columbia Fish Habitat Assessment Procedure was used as a basis for measurement of several abiotic features related to habitat (Johnston and Slaney 1996). Sampling length at each site was a critical consideration of sampling design, and aimed to achieve an efficient criteria that would not be biased to under or over-represent different major habitat units. Rather than conforming to an arbitrary constant sampling length for each site, sampled reaches were minimally 15 times the wetted width of the stream. In addition to this, stream habitat is recognized as heterogeneous and can be classified coarsely by swift water and slow water major habitat units (Hawkins et al. 1993). Swift water units were characterized by turbulent, broken water surface (riffle) or swift, non-turbulent areas (run/sheet). Slow-water environments (pools) were recognized by a distinct slowing and deepening of the water. In order to properly represent all available habitat types, sampling was stratified to represent an equal number of these major habitat units, and included at least two of each in every site (Rieman et al. 2006). As a result, sites were 180 m +/- 75 in length, an average of 34 times the wetted width.

Swift water and slow water units were only counted if they were least as long as, and occurred over the majority of the wetted width of the channel. The length of each of these major habitat units was measured, and the percent of the slow water habitat along the entire sampled length was calculated for each site (POOL). This variable was selected, as more vigorous competitive traits of brook trout in low velocity, simple pool environments were observed (Chapter 3), but also because previous studies have found brook trout invasion success to be positively associated with the amount of pool habitat (Rich et al. 2003; Shepard 2004). In addition, slow-velocity environments are considered important habitat for juvenile bull trout based on field studies (Al-Chokhachy et al. 2010). Available pool habitat was therefore considered as a potentially important local habitat feature in this species interaction.

The width of the stream was measured at ten randomly selected transects at each site and was used to find the mean wetted width (WIDTH) of the stream. This variable might be associated with brook trout invasion, as previous studies have reported greater invasion success in smaller streams (Rich et al. 2003), and bull trout positive association with wider streams (Dunham and Rieman 1999; Ripley et al. 2005).

Undercut bank (UCB) was an abiotic variable considered to be important, as it represents a cover type that is common in Rocky Mountain streams that are invaded by brook trout (Kozel et al. 1989; Krimmer et al. 2011). This variable was measured according to the % of the total length of the site that was lined by UCB on either bank (possible range of 0-200%). Banks were considered undercut if the bank was cut by > 5 cm.

A modified Wentworth scale was used to classify substrate types, including sand/fines (< 2 mm), gravel (2-15 mm), pebble (16-63 mm), cobble (64-255 mm) and boulder (> 256 mm) classifications. Counts also included bedrock, as this is a commonly encountered substrate type found in Rocky Mountain streams. Ten substrate observations were made by randomly throwing a 1 m long, 10 mm diameter steel bar with 10 cm markings into the wetted portion of the channel and reading the substrate type that lay below each marking. Ten of these throws were taken randomly throughout the site, for a total of 100 substrate observations per site. This was used to calculate the percent of the stream bottom that was covered by large (cobble and boulder) substrate (LGSUB). LGSUB was considered a biologically relevant surrogate for complexity of in-stream substrate cover, as large substrate may afford cover habitat for juvenile bull trout (Al-Chokhachy et al. 2010). In-stream substrate complexity appears to affect competition between these two species, particularly conferring a competitive advantage for bull trout (Chapter 3). In addition, structural complexity in the form of in-stream cover has been associated with bull trout resistance to brook trout invasion in the field (Rich et al. 2003). Fine substrate has been associated with brook trout invasion (Shepard 2004).

Temperature is an abiotic variable that has repeatedly been associated with brook trout invasion success (Paul and Post 2001; Dunham et al. 2002; Rieman et al. 2006; McMahon et al. 2007). Mean august temperature (TEMP) was measured directly at each site in the year it was sampled (with the exception of five sites that were previously monitored in 2006) by in-stream data loggers (Onset™) that continuously recorded hourly temperatures. Loggers were placed in white impact-resistant PVC housings attached to a t-post and installed 15-30 cm deep (base flow) in shallow, swift water habitat directly above the stream bottom. Installation areas were chosen where maximum shading was available, most often flush against banks with overhanging riparian vegetation. Where possible, the t-post was driven in behind in-stream obstacles (e.g., boulders) in the hope that such features would deflect debris during high flow events. Due to theft and vandalism problems early in the study, no flagging tape or markers were used; loggers were subsequently retrieved with GPS marked waypoints and a written description of the installation site. While mean summer temperature (June, July and August) was recorded at most sites, only mean August temperatures were available at others due to spring access and installation issues. To account for inter-annual temperature variation throughout the course of the study, a sub-set of representative sites that were monitored in 2010 also had data taken in 2009 (4) and 2011 (9). This repeat sampling data was used to develop regression equations that standardized temperatures for all sites sampled in 2009 and 2011 to the temperature that would be expected in 2010.

In order to assess whether multicollinearity would present problems in subsequent model selection, individual pairwise regressions were performed for each possible variable combination. Variables were considered highly correlated if they displayed a Pearson correlation coefficient (R) of > 0.7 (Ripley et al. 2005).

Although brook trout have been widely introduced into Rocky Mountain streams in Alberta, several other salmonid species have also been introduced extensively, most commonly including rainbow trout (outside of Athabasca river drainage) and brown trout. Although neither of these species is commonly implicated in the decline of bull trout, they may have substantial niche overlap with introduced brook trout and be negatively associated with them (Kozel and Hubert 1989). Based on electrofishing data, I recorded whether one of these two alternate non-native species was present (NONNAT), and used this as a biotic variable in explaining invasion of brook trout.

Model construction and analysis

An information-theoretic approach was used to model brook trout invasiveness as a function of the measured abiotic and biotic variables (Burnham and Anderson 2002). Rather than using traditional hypothesis tests or searching for the “best” model, this method uses a weight-of-evidence approach to rank competing models according to a principle of parsimony, as well as estimate the relationship between independent and dependent variables (Appendix). The information theoretic approach has emerged over the last decade as the *de facto* process of relating salmonid species occurrence and abundance estimates to a suite of explanatory variables based on a number of potential models (Harig and Fausch 2002; Rich et al. 2003; Ripley et al. 2005; Rieman et al. 2006; Benjamin et al. 2007; Wenger et al. 2011).

A global logistic regression model was first fitted to predict brook trout invasiveness, including every variable in the model (Equation A-2). Logistic regression was chosen as the appropriate statistical model because relative abundance estimates were bounded by 100% and 0%, with most sites tending to approach these bounded values (Figure A-4). The dependent variable was therefore best described as a categorical binary variable (Appendix). The fit of this model was assessed by standard Pearson chi-square and Hosmer-Lemeshow statistics (Hosmer and Lemeshow 2000). The residuals of the global model were then tested for spatial autocorrelation based on Euclidean distances among sample sites in ArcGIS™ 9.3.1. Every possible logistic regression model given the various combinations of available variables were then analyzed and ranked according to Akaike's information criterion with small sample size adjustment (AICc; Equation A-9). AICc was used rather than unadjusted AIC, as this value is recommended only when the number of observations is at least 40 times the number of explanatory variables (Burnham and Anderson 2002). The model with the lowest AICc value was considered the model with the highest support. Akaike weights were calculated for each of the ten most likely models based on their AICc departure (Δ-AICc) from the model with the highest support (Equations A-10, A-11). Weights were used to assess the relative plausibility of models, as well as to calculate multi-model weighted estimates of parameters and their associated uncertainties (Equations A-12, A-13) (Burnham and Anderson 2002).

Parameter estimates were derived for each variable by averaging weighted estimates from the models that had weights within 1/8 (12.5%) of the model with the highest support (Royall 1997). Associated unconditional standard errors for each parameter were likewise derived from the same top-ranked models (Burnham and Anderson 2002). Parameter estimates and associated unconditional standard errors were then used to calculate scaled odds ratios (OR) and associated 95% confidence intervals (CI). These values provide an interpretable estimate of the magnitude, direction and significance of each variable in explaining brook trout relative abundance. An OR = 1 indicates no association between an independent variable and brook trout invasiveness; OR < 1 indicates negative association and OR > 1, a positive association. The magnitude of departure from 1.00 indicates the degree of change in likelihood (or unlikelihood for values < 1) of a site having high brook trout invasiveness for a unit change in the independent variable. To increase biological relevance of associations between continuous variables and brook trout invasiveness, parameter estimates (B_i) were multiplied by a meaningful constant C to calculate a meaningful odds ratio (Hosmer and Lemeshow 2000) (Equation A-4). For example, TEMP was not multiplied by a constant because a change in 1 °C was considered biologically meaningful according to the range of temperatures encountered (4.4-15.3 °C). In contrast, a 1% increase in LGSUB was not considered biologically meaningful over the range of values encountered (0-86%) and was thus scaled up by a factor of 10. 95% confidence intervals were calculated to determine whether variables were significantly associated with brook trout invasiveness.

These were calculated (conforming to a z-distribution) for each independent variable based on model-averaged parameter estimates and unconditional standard error (SE_i) where C is the biological relevant scaling factor for continuous variables (Hosmer and Lemeshow 2000; Rich et al. 2003) (Equation A-5).

Results

Brook trout invasiveness

Of the 124 sites sampled in 61 streams, only 80 sites in 51 streams were appropriate for further analysis (Figure 2-1; Table A-5). Sites were not appropriate for analysis either because less than the established threshold of 8 fish were caught (25 sites; most often for these, no fish were caught), or thermographs were lost (14 sites). Five sites were also discarded because the fish community was not dominated by either species (relative abundance of 40-60%), and thus could not be confidently classified for the logistic regression. Coexistence of the two species was less common than complete dominance over the community, as 53 of the 80 sites were overwhelmingly (>95%) composed of a single species (Figure A-4). Brook trout invasiveness was high in 45 and low in 35 of the 80 sites. Hybridization was rare throughout the province, as hybrids were only caught in four of the 80 sites sampled.

Categories of brook trout invasiveness (high/low) were considered sufficiently precise, as 41 repeat sampling events conducted within 5 years never resulted in a misclassification between these categories at any site. Based on these repeat sampling events, there was only an average of a 5% difference (± 9%) in relative abundance among sampling events in 34 sites for which data were available.

Abiotic and Biotic variables

Mean August water temperatures varied substantially among sites, and the median temperature of brook trout dominated sites was 1 °C higher than sites where brook trout invasiveness was low (Table 2-1). Variability due to instrument differences and logger placement according to the protocol was found to be low, as two instruments placed in similar locations in one site only differed on average by 0.08 °C.

Water temperatures were warmer in 2009 (0.4 °C) and 2011 (0.5 °C) than in 2010. 2009 and 2011 stream temperatures were therefore corrected to the expected temperature in 2010 based on their corresponding regression equations from data at the representative sites. To increase confidence in the validity of these correction equations, the corresponding interannual trends in air temperature were independently considered from nearby locations. This analysis was conducted by examining mean August temperatures (2009, 2010 and 2011) at 20 meteorological stations with a similar spatial and elevational distribution to sites found throughout the study area (ARD 2012). Like stream temperature, mean air temperatures were warmer in 2009 (1.2°C; paired *t*-test: $t_{19} = 12.1$; $P < 0.001$) and 2011 (1.8°C; paired *t*-test: $t_{19} = 9.6$; $P < 0.001$) than in 2010.

Although most sites had temperature measured in 2009-2011, temperatures at five sites were measured in 2006. I did not sufficiently repeat sample to derive a regression equation for correcting the 2006 year; however air temperature from meteorological station data revealed that 2006 and 2009 had similar mean August temperatures (Mean difference = 0.1 °C ± 0.3; paired *t*-test: $t_{11} = 0.37$; $P = 0.72$). The 2009-2010 correction equation was therefore applied to the five sites sampled in 2006.

Median values of all remaining abiotic variables differed substantially between high and low brook trout invasiveness, with the exception of POOL (Table 2-1). UCB values for each site were log-transformed after adding one percent to each value. This was the appropriate transformation to apply to improve model fit for the logistic regression, and appropriately screen for multicollinearity of independent variables. None of the abiotic variables were highly correlated with each other ($R < 0.6$; Table 2-2)

For the biotic variable measured, alternate non-native species were present in 18 of the 80 sites. Of these 18 sites, 6 had high brook trout invasiveness. Alternate non-native species encountered were brown trout (7 sites), and rainbow trout (12 sites).

Model results

A global model was built with the six independent variables considered biologically relevant to brook trout invasion. The global model fit the data well, according to both Pearson chi-square ($\chi^2 = 56.6$; df = 73; $P = 0.92$) and Hosmer-Lemeshow goodness of fit statistics ($\chi^2 = 1.3$; df = 8; $P = 0.99$). Moran's *I* index revealed a random spatial pattern of residuals in the global model ($I = 0.02$; $P = 0.79$), indicating a lack of a spatially dispersed or clustered pattern of autocorrelation.

A candidate set of the 10 most likely models was built, and ranked according to AICc values (Table 2-3) The model containing the five variables TEMP, WIDTH, UCB, LGSUB and NONNAT was the model with the highest support; however, four additional models, including the global model, had sufficiently high Akaike weights (within 1/8 of largest) that precluded them from being discounted as possible models. All variables appeared in at least two of the five possible models, and the parameter estimates and associated standard errors from these five models were averaged based on their Akaike weights. TEMP, LGSUB and NONNAT appeared in all five models and thus were considered important variables with high support, according to the summed Akaike weights of the top four models in which they appeared (Table 2-4).

The sign of the parameter estimates (Table 2-4) provides the direction of the association between the dependent and independent variables. Brook trout invasiveness was positively associated with TEMP and UCB and negatively associated with WIDTH, LGSUB, POOL and NONNAT.

Scaled odds ratios with 95% CIs were calculated from model-averaged parameter estimates to give some indication as to whether any of the variables were significantly associated with brook trout invasiveness, as well as the minimum magnitude of the association (Table 2-4). Highly significant variables did not have scaled odds-ratios of 1 bounded by their 95% CIs. TEMP, UCB and LGSUB were abiotic variables that were significantly associated with brook trout invasiveness. WIDTH was moderately associated with brook trout invasiveness, but the relationship was not significant. POOL was not strongly or significantly associated with brook trout invasiveness. Based on the minimum departure of the scaled odds ratio, a 1 degree increase in temperature was associated with at least a 65% increase (1.65/1) in predicted odds of finding a community dominated by brook trout. A 10% increase in large substrate was associated with at least a 19% decrease (1/0.84) in the predicted odds of finding high brook trout invasiveness. NONNAT was the only biotic variable measured, and was significantly and strongly related to brook trout invasiveness; a site was at least 2.3 times less likely (1/0.43) to be dominated by brook trout if an alternate non-native salmonid species was present.

The interpretation of the odds ratio for UCB was more complicated because of its transformation. To interpret the odds ratio of this log transformed variable, the formulas described in Elswick et al. (1997) were used as follows:

$$\mathrm{OR}(x + C, x) = e^{B_i \ln(b)}$$

Equation 2-1

where $b = \left(\frac{x+C+1}{x+1}\right)$, B is the parameter estimate for the transformed variable, C is a biologically relevant scaling factor, and x is a quantity of interest in the covariate. 95% CIs were also likewise calculated as:

$$95\%\ \mathrm{CI} = e^{B_i * \ln(b) \pm 1.96 * SE_i * \ln(b)}$$

Equation 2-2

According to this formula, there was at least a 2% higher likelihood of a site having high brook trout invasiveness, given a 10% increase (C) in UCB from the overall median value of 39% (x) (Table 2-4).

Discussion

Brook trout invasion into bull trout streams appeared to vary in relative success over the native species, and most invaded sites were either dominated by brook trout or remained dominated by bull trout. This variation of invasion outcome may have been responsible for the mixed results of studies examining the association between brook trout invasion and bull trout occurrence (Watson and Hillman 1997; Dunham and Rieman 1999; Rich et al. 2003; Rieman et al. 2006; Wenger et al. 2011). The results suggest that brook trout invasion into bull trout streams is associated with local-scale abiotic and biotic features of invaded environments. This may reflect the niche opportunities that are provided to brook trout in spatially heterogeneous and changing mountain stream environments (Shea and Chesson 2002).

The results lend partial support to a temperature based hypothesis of brook trout invasiveness into bull trout streams. This corroborates previous observational studies in western North American streams that have found preferential invasion of brook trout into warmer, lower elevation reaches (Paul and Post 2001; Rieman et al. 2006). The positive association between temperature and brook trout occurrence has been experimentally linked to competitive superiority of brook trout over bull trout in warm (15-16 °C) water (McMahon et al. 2007; Rodtka and Volpe 2007), and may point to a thermal niche opportunity for the invasive species along an elevation gradient (Taniguchi and Nakano 2000). This trend of invasion is also apparent in studies considering invasion into cutthroat trout streams (Dunham et al. 2002) and is likewise supported by experimental evidence (De Staso and Rahel 1994); nevertheless, an hypothesis solely based on temperature (or elevation as a surrogate for temperature) does not appear to be a panacea for predicting brook trout invasion (Rieman et al. 2006). A reciprocal competitive advantage of bull trout over brook trout in cold (8 °C) water has not been demonstrated experimentally (McMahon et al. 2007; Rodtka and Volpe 2007), and there are many alternate abiotic and biotic features that appear to be associated with invasion in the field (Watson and Hillman 1997; Rich et al. 2003).

Metrics that quantified the type of structural habitat complexity and cover were significantly associated with brook trout invasiveness. Habitat complexity has been recognized as an abiotic feature that may confer resistance of bull trout to invasion by brook trout in Montana streams (Rich et al. 2003). The results of this study support this finding for in-stream complexity in the form of substrate cover, but not for complexity in the form of bank cover. Bull trout were associated with sites containing large in-stream substrate complexity, while brook trout were associated with sites containing undercut bank habitat. The preference for large substrate cover has long been recognized as a critical habitat feature for juvenile bull trout (reviewed in Al-Chokhachy et al. 2010), and undercut bank habitat has been recognized as an important feature for brook trout (Kozel et al. 1989; Krimmer et al. 2011). Like temperature, this association may indicate pre-adapted niche-segregation into preferred habitat types (Fausch 2008; Korsu et al. 2010), as bull trout and brook trout may have different competitive foraging strategies that are optimal in habitats with different amounts and types of cover (Chapter 3; Nakano et al. 1998; Rodtka and Volpe 2007). Also like temperature, there is experimental evidence suggesting that bull trout foraging success relative to brook trout increases in habitats with in-stream substrate complexity (Chapter 3). Thus, physical habitat structure appears to be an important feature in shaping invasion patterns of brook trout into bull trout streams, and the mechanism may involve the relative success of the two species when competing for resources from their preferred habitat niches. A fruitful avenue for further study would be to examine the microhabitat or mesohabitat characteristics of cover occupied by either species on-site, in streams where they are co-dominant (Korsu et al. 2010).

Pool habitat was found to be a non-significant environmental feature associated with brook trout invasiveness. Although low-velocity habitats are important for juvenile bull trout (Al-Chokhachy et al. 2010), they are important habitat for brook trout as well (Chisholm et al. 1987; Kozel et al. 1989), and both species prefer pools when in sympatry (Dambacher et al. 1992). When brook trout are sympatric with brown trout or Atlantic salmon (*Salmo salar*), they tend to preferentially occupy slow water habitats (Gibson et al. 1993; Korsu et al. 2010). Given the preference for both brook trout and bull trout to occupy slow velocity habitats, it is of no surprise that pool habitat is not significantly associated with brook trout invasiveness.

Invasive brook trout are usually found to occur in smaller tributary streams than native species (Rich et al. 2003; Korsu et al. 2007), and although this relationship was apparent, it was not significant. This discrepancy could have resulted from site selection criteria, as only streams that had confirmed bull trout juvenile (historical or current) presence were included in the analysis. Many smaller streams containing brook trout were present throughout the study range (ASRD 2009), but these were not included in the study design as there is no evidence that they were ever important bull trout habitat. While brook trout probably do have an ecological advantage in smaller streams (Rieman et al. 2006), many such streams are not typical habitat for bull trout (Dunham and

Rieman 1999). Brook trout invasion into smaller streams observed in previous studies may therefore be the result of filling of a habitat niche that is marginal or vacant for native bull trout (sensu Korsu et al. 2007). This may further affect patterns of invasion as small streams may act as propagules from which brook trout can colonize (Peterson et al. 2004).

A common research topic in invasion science is how biotic resistance from native species may influence invasion patterns (Moyle and Light 1996b); however, how multiple invasive species influence each others' invasion success is less commonly addressed, and interactions among invasive species are often in fact positive (Simberloff and Von Holle 1999). Brook trout were found to be negatively associated with alternate non-native species that had become naturalized in bull trout streams. This is not surprising, given that brook trout are themselves often replaced or displaced by rainbow and brown trout in their own native range (Korsu et al. 2007; Fausch 2008). Brook trout are hypothesized to have a resource and habitat use niche that is intermediate to that of bull trout and other stream resident salmonid species such as cutthroat trout (Nakano et al. 1998). The results of this study indirectly support such an hypothesis, and imply that alternate non-native species may restrict the spread of brook trout into some bull trout streams. Rainbow trout and brown trout are not commonly associated with the decline of bull trout, but their presence in bull trout streams may act as a biotic barrier to brook trout dominance over the fish community (Benjamin et al. 2007). Assessing the positive and negative interactions among all introduced species and native species in shaping contemporary stream fish communities is a subject that I encourage further research into.

It should be noted that invasion is a population-level process (Peterson et al. 2004). When considering population demographics, source sink dynamics and movement patterns, there may be alternate influences on invasion patterns that could not be captured in this study. For instance, this study did not quantify side channel habitats or beaver ponds which may be an important source from which brook trout may colonize (Benjamin et al. 2007). More sophisticated modeling procedures that capture such processes at varying spatial scales may be able to better predict patterns of species' invasiveness. Although this study provides features that are associated with relative success of brook trout over bull trout, they do not necessarily imply that brook trout are responsible for the displacement of bull trout in all areas where they were found to be dominant. Many of the streams in Alberta have continuing and historical impacts to bull trout populations in addition to negative interactions with non-native species. These may include impacts from land use practices and historical angling-related harvest. Landscape disturbance, fragmentation and climate change are all known to affect stream habitat, temperature, fish migratory routes and life history. In this sense, the spread of brook trout and their success in some streams may have been facilitated by a changing environment driven by such impacts. Brook trout may have simply replaced or been greatly aided in the competitive displacement of a declining bull trout population in many areas of Alberta. If this bull trout decline was due to degraded habitat features or overharvest, then brook trout may simply be passengers rather than the drivers of further bull trout decline in many of the sites where the native species formerly dominated (*sensu* MacDougall and Turkington 2005). Nevertheless, occupation of these sites by brook trout may be a biotic obstacle for recolonization of bull trout and hence inhibit their recovery.

Knowledge of the abiotic and biotic features that are associated with low brook trout invasion success may be used strategically to rehabilitate habitats that are designed to accommodate the niche requirements of the native species. For bull trout, cold water temperatures and maintenance of in-stream habitat complexity are critical. Some land use practices (forestry, grazing, road networks, etc.) embed large substrate with fine sediment, which may reduce the rearing areas preferred by juvenile bull trout (Al-Chokhachy et al. 2010). The intricate mechanisms controlling the temperature of small mountain streams limits our understanding of how stream temperature might change given the effects of landscape disturbance and climate change (Moore et al. 2005; Arismendi et al. 2012). Further research into these topics are required to predict how potential changes in thermal habitat may drive fish distributions, and how to best restore or conserve habitat in watersheds to maintain the cold water temperatures required for bull trout. To be most effective, conservation efforts in highly invaded habitats should focus on a combination of both brook trout suppression and habitat restoration tailored to the requirements of bull trout (*sensu* Shepard et al. 2003). Knowledge of the niche opportunities for brook trout will also be useful to predict their further spread into bull trout ranges as disturbed habitats change further or novel range expansions occur for unforeseen reasons (Rahel 2007; Rahel et al. 2008).

Generalist native species such as bull trout were incredibly successful at being the first colonizers of cold post-glacial streams of the Canadian Rockies. While they continue to dominate many of these streams, they are now superseded by introduced brook trout in specific environments where niche opportunities for the invasive species appear to be provided (Shea and Chesson 2002). Domination over fish communities may result from pre-adaptation of invading species to specific combinations of the variable abiotic and biotic conditions present in mountain streams (Fausch 2008; Korsu et al. 2010). The conditions that provide niche opportunities to brook trout in the bull trout native range may include warmer waters, type of cover available and whether or not the stream is invaded by an alternate non-native species. Stream thermal regime, physical habitat structure and fish community all fluctuate and change naturally, but this is occurring at an accelerated pace due to shifts in climate and land use practices. Managers need to be particularly cognizant about how this may result in niche opportunities for non-native species in environments currently occupied by native species. Alternatively, managers may use this information for strategic conservation and habitat rehabilitation efforts directed towards the niche requirements of native species.

Tables

Table 2-1: Median values and ranges of encountered for each continuous independent variable (mean August temperature [TEMP], stream wetted width [WIDTH], percent undercut bank [UCB], percent of large stream-bottom substrate [LGSUB], and percent pool [POOL]) for sites containing high (n = 45) and low (n = 35) brook trout relative abundance.

	TEMP (°C)	WIDTH (m)	UCB (%)	LGSUB (%)	POOL (%)
High brook trout	9.1 (5.7-14.2)	4.4 (1.6-9.3)	54.1 (0-194.4)	38.3 (0-75.6)	48.4 (10.5-95.4)
Low brook trout	8.1 (4.4-15.3)	6.2 (1.9-11.9)	21.9 (0-141.7)	55.6 (12.7-86.1)	43.2 (10.3-71.2)

Table 2-2: Correlation matrix (Pearson's *R*) of five abiotic independent variables (mean August temperature [TEMP], stream wetted width [WIDTH], percent undercut bank [UCB], percent of large stream-bottom substrate [LGSUB], and percent pool [POOL]) for inclusion into models predicting brook trout invasiveness.

	TEMP	WIDTH	UCB	LGSUB	POOL
TEMP	-				
WIDTH	0.11	-			
UCB	-0.22	-0.58	-		
LGSUB	-0.17	0.31	-0.37	-	
POOL	0.12	-0.29	0.52	-0.45	-

Table 2-3: List of the 10 most likely candidate logistic regression models for predicting brook trout dominance in sites of bull trout streams, ranked from most plausible to least plausible according to AICc values. Models are named according to the independent variables used , where the global model includes all six variables (mean August temperature [TEMP], stream wetted width [WIDTH], percent undercut bank [UCB], percent of large stream-bottom substrate [LGSUB], percent pool [POOL] and presence of an alternate non-native salmonid species [NONNAT]). *K* refers to the number of parameters estimated in each model, which includes an intercept term. Δ-AIC is the difference between the model AICc value and that of the most plausible model, and is used to calculate Akaike weights for assessing the relative plausibility of each model.

Model	*k*	AICc	Δ-AIC	Akaike weight	% of highest weight
TEMP, WIDTH, UCB, LGSUB, NONNAT	6	58.38	0	0.34	100.0
Global	7	59.06	0.68	0.24	71.2
TEMP, UCB, LGSUB, NONNAT	5	59.69	1.31	0.18	51.9
TEMP, UCB, LGSUB, POOL, NONNAT	6	60.08	1.7	0.15	42.7
TEMP, WIDTH, LGSUB, NONNAT	5	62.49	4.11	0.04	12.8
TEMP, WIDTH, UCB, NONNAT	5	64.48	6.1	0.02	4.7
TEMP, WIDTH, LGSUB, POOL, NONNAT	6	64.71	6.33	0.01	4.2
TEMP, UCB, NONNAT	4	65.6	7.22	0.01	2.7
TEMP, UCB, POOL, NONNAT	5	67.15	8.77	<0.01	1.2
TEMP, LGSUB, NONNAT	4	73.31	14.93	<0.01	0.1

Table 2-4: Logistic regression model-averaged parameter estimates with associated standard errors (Unconditional SE) and summed Akaike weights (Σ weight) for each of the six variables (mean August temperature [TEMP], stream wetted width [WIDTH], percent undercut bank [UCB], percent of large stream-bottom substrate [LGSUB], percent pool [POOL] and presence of an alternate non-native salmonid species [NONNAT]) according to their appearance in the most plausible models. Odds ratios and 95% confidence intervals were calculated from the parameter estimates and associated standard errors, respectively, which were multiplied by a biologically relevant scaling factor for continuous variables.

Parameter	Σ weight	Parameter estimate	Unconditional SE	Scaling factor	Scaled odds-ratio	Confidence interval for scaled odds-ratio
Intercept	0.96	-10.147	4.65			
TEMP	0.96	1.167	0.34	1	3.21	1.65-6.22
WIDTH	0.63	-0.407	0.23	1	0.67	0.42-1.04
UCB	0.91	1.353	0.64	10	1.35	1.02-1.79
LGSUB	0.96	-0.070	0.03	10	0.50	0.29-0.84
POOL	0.39	-0.045	0.04	10	0.64	0.32-1.27
NONNAT	0.96	-2.032	0.61	N/A	0.13	0.04-0.43

Figures

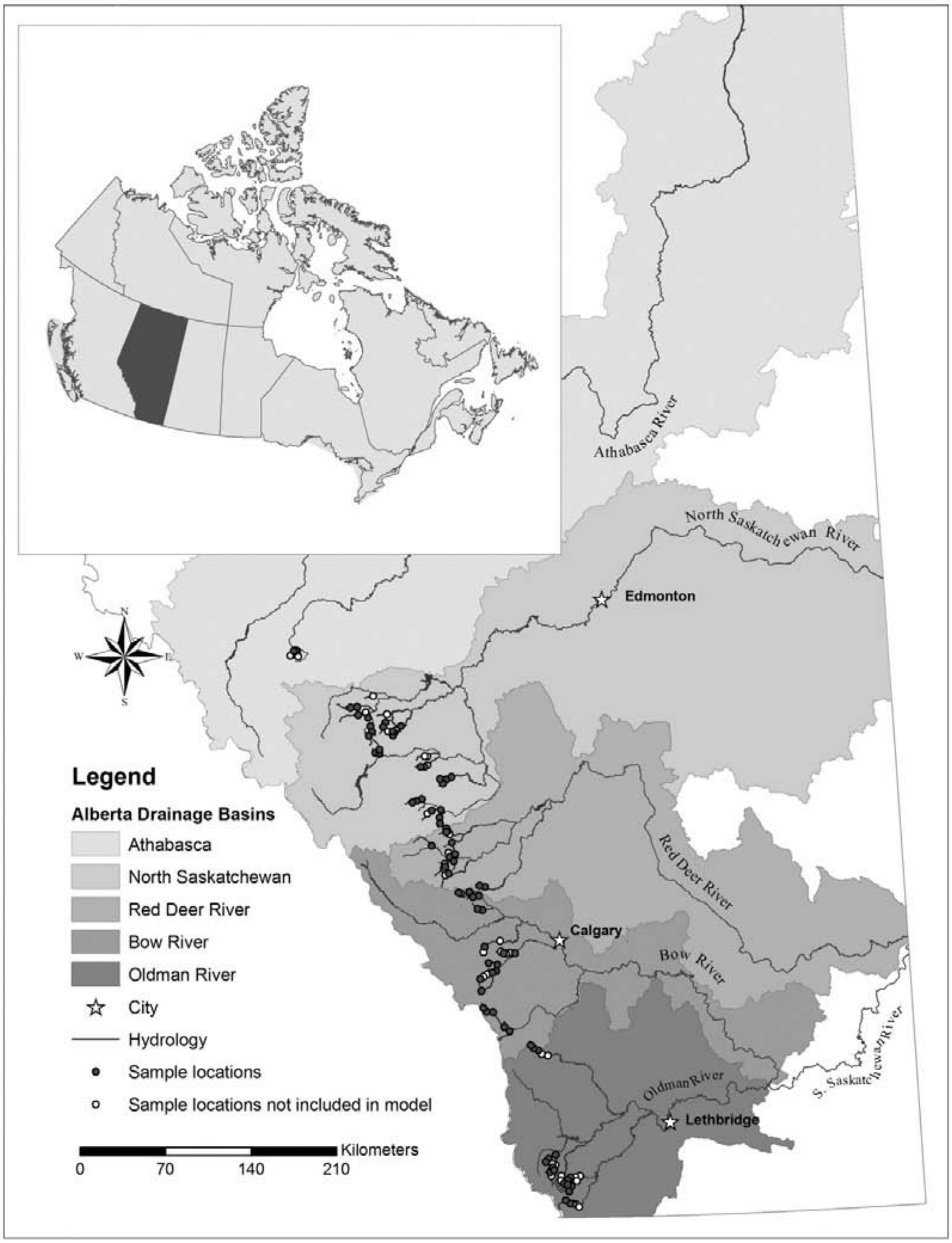

Figure 2-1: Map of sample locations (filled circles) for brook trout invaded bull trout streams of the Canadian Rockies. Several sites that were sampled (open circles) could not be included in the analysis because of temperature logger loss or lack of fish presence.

Figure 2-2: Example of a bull trout X brook trout hybrid. Hybrids were identified based on the presence of pale spotting that extended at least past 50% of the height of the dorsal fin (DeHaan et al. 2010), and at least one other of the following intermediate traits: distinct vermiculations on the dorsal side of the fish; bright lateral side spots with pale haloes; white and pale black anterior borders of ventral fins; intermediate head shape. The fish in the example photograph displayed all of these traits.

Chapter 3 Assessing the effects of fish density and habitat on interference competition between bull trout and brook trout in an artificial stream

Abstract

Territorial, drift foraging salmonids interfere with their competitor for access to resources, but the success and intensity of this tactic may be dependent on the physical environment and number of competitors in close proximity. Within-species and between-species competitions were observed with field-collected native bull trout and non-native brook trout in laboratory streams. In within-species competitions in simple pool habitats, brook trout foraging success was correlated with occupying the lead position in the stream, implying a territorial foraging tactic. In contrast, bull trout foraging success was not correlated with occupancy of the lead position, implying a scramble foraging tactic. In between-species competitions, four stream environments were constructed in which the number of competitors and habitat complexity were altered. Bull trout outcompeted brook trout for food in simple pool environments when the competition involved two competitors (head-to-head; density = 3 fish m^{-2}). When competitor number was doubled in this habitat (density = 5.9 fish m^{-2}), the two became equal competitors. At this higher density, bull trout again outcompeted brook trout for food when the habitat was changed to a complex riffle. Brook trout were more aggressive than bull trout throughout the experiment, and aggression of both species was lowest in head-to-head competitions and in complex riffle environments. The manner in which the scramble foraging tactic of bull trout may allow them to outcompete territorial brook trout in complex or low density environments where interference competition is less intense is discussed.

Introduction

Competitive interactions between invaders and native fishes can be an important determinant of invasion success, and if invaders are to propagate and spread, it is often at the expense of native competitors. It is therefore important to understand the mechanisms that influence both intra and interspecific interactions, if we are to understand why invasive species are in some situations successful and in others not. Laboratory experiments are a common venue for investigating competition between lotic salmonid fishes, allowing both biotic and abiotic conditions to be manipulated and controlled in order to gain insight into the mechanisms of interaction between individuals and species (Fausch 1988). Abiotic features tested often include habitat complexity/type (Hasegawa and Maekawa 2008; Korsu et al. 2010), stream temperature (De Staso and Rahel 1994; McMahon et al. 2007) or current velocity (Cunjak and Green 1984) or a combination thereof (Magoulick and Wilzbach 1998). Biotic features can also affect competitive interactions among fish species, and tested variables include population of origin of competitors (Sabo and Pauley 1997), fish density (Rodtka and Volpe 2007) and fish community (Hasegawa and Maekawa 2006).

Biotic and abiotic factors may interact to determine the intensity of competition, as well as its outcome (Dunson and Travis 1991). While the intensity of competitive interactions among fish usually increase with competitor density (Cole and Noakes 1980; Blanchet et al. 2006; Kaspersson et al. 2010; Wipf and Barnes 2011), habitat complexity and current velocity are often inversely related to interaction intensity (Eason and Stamps 1992; Basquill and Grant 1998; Sundbaum and Naslund 1998; Imre et al. 2002; Danley 2011), suggesting that they may be buffering or dampening the effects of density. Such buffering would be most evident for territorial species that directly interfere with their competitor's ability to access key resources through aggressive interactions. This is because complex, high velocity habitats reduce encounter rates by visual isolation or make it costly to defend large territories (Grant and Noakes 1988; Höjesjö et al. 2004; Hasegawa and Yamamoto 2010). Thus, intense interference competition among fish may be mitigated by increases in habitat complexity or current velocity, even in situations of high density where multiple competitors are in close proximity (Blanchet et al. 2006).

Brook trout (*Salvelinus fontinalis*) are a species native to eastern North America, but have been introduced extensively throughout the native range of bull trout (*Salvelinus confluentus*) in mountainous regions of western North America. The two species now overlap considerably and compete for similar resources, particularly at the juvenile life stage. Several studies have examined juvenile competition under manipulated experimental conditions, and have generally found that brook trout are superior competitors over bull trout, which is especially evident at warmer water temperatures (Gunckel et al. 2002; McMahon et al. 2007; Rodtka and Volpe 2007). All these studies were performed at high fish densities (1.2-20.7 fish m^{-2}) relative to natural densities found in western North American streams (<0.2 fish m^{-2} for bull trout [see references in Rodtka and Volpe 2007] and <0.98 fish m^{-2} for brook trout when species are in allopatry [Johnson et al. 1992; Thompson and Rahel 1996; Benjamin and Baxter 2010]). All studies were also conducted in artificial enclosures that simulated simple pool habitats with predictable sources of drift forage; environments that provide ideal conditions to test which species is a superior territorial forager. The prevalent result, that brook trout outcompete bull trout, is predictable when one considers the interference mode of competition that brook trout generally exhibit when in competition with bull trout, which involves aggressive defense of profitable feeding territories (Gunckel et al. 2002; Rodtka and Volpe 2007). In contrast, bull trout have been observed to forage in a haphazard manner, opportunistically scrambling for food when competing with brook trout, often from behind cover (Nakano et al. 1998; Rodtka and Volpe 2007). Since habitat complexity and high current velocities appear to disrupt the effectiveness of territorial foraging tactics (Rodriguez 1995; Hasegawa and Maekawa 2008; Hasegawa and Yamamoto 2010), there may be reason to suspect that complex or high velocity environments may favor the cover-based scramble foraging mode of bull trout. Such an hypothesis has not been tested under controlled conditions, but there is some field evidence that bull trout may resist invasion of brook trout in streams with high habitat complexity (Chapter 2; Rich et al. 2003).

In this study, the first aim was to test the hypothesis that bull trout and brook trout have different innate foraging strategies by specifically testing whether occupancy of the lead position in the stream is correlated with foraging success. If foraging strategy results in territorial fish occupying the most profitable feeding position, the two are strongly correlated (Grant 1990; De Staso and Rahel 1994). In contrast, a lack of correlation implies that fish may be using alternate tactics to acquire food. Given the previous literature described above, brook trout foraging success is predicted to be correlated with occupying the lead position, whereas bull trout foraging success is not.

Following the first aim, the second aim of this study was to address whether native bull trout outcompete non-native brook trout under different environments where competitor number and physical habitat structure are altered. This aim was chosen to directly test to some variables associated with invasion of brook trout into bull trout streams (Chapter 2). Competition between the two species was observed in four treatments designed to simulate scenarios of altered fish density and habitat structure, and foraging success and interspecific aggression were observed. If brook trout dominate bull trout through territorial aggressive behaviors, they may be more aggressive in low complexity, pool habitats where there are a large number of competitors. This may help explain some of the patterns of brook trout invasion into bull trout streams in wild settings (Chapter 2; McMahon et al. 2007).

Methods

Fish collection, housing and tank design

Juvenile brook and bull trout were collected from wild populations in the fall of 2010 by backpack electrofisher. Non-native brook trout were collected from Beaver Mines Creek (49°22’ N, 114°15’ W). Size-matched native bull trout were collected from nearby Mill Creek (49°22’ N, 114°10’ W) and the upper Livingstone River (50°7’ N, 114°26’ W). Bull trout in these two populations express different migratory life histories, one is resident and the other is migratory. These distinct populations of bull trout were selected to represent opposite ends of the migratory life history spectrum that bull trout display (Warnock et al. 2011). All three selected streams are headwaters of the Oldman River Drainage in southwestern Alberta, Canada.

Upon return to the Aquatic Research Facility at the University of Lethbridge, each species was transferred to separate holding tanks and was gradually adjusted to laboratory conditions. Water temperature was maintained at 8°C, photoperiod was 12:12 hours (light:dark) and fish were fed on a maintenance diet of frozen *Mysis* shrimp at 3% body weight per day. This ration and diet allowed fish to gain weight and maintain their initial condition factor. Tanks were cleaned and 10 % of the water was renewed daily and pH, temperature, ammonia, nitrite and nitrate levels were continuously monitored to ensure optimal housing conditions. Following a two week quarantine period, each fish was anaesthetized and marked with a unique combination of adipose fin clips and colored elastomer tags (NMT technology™) for quick visual individual identification. Fish were allowed three weeks of further acclimation and recovery before experimental trials began.

Experimental trials were carried out in a laminar-flow flume that was divided in the middle to allow simultaneous observation of two replicate chambers. The flume had a flow-through diversion to a filtration unit that continuously cleaned and chilled the water to 8°C. Each experimental area was 135 cm long by 50 cm wide. These areas were divided by medium and low density Matala™ media placed at the upstream and downstream ends (Figure 4-1). This material acts as a sieve to prevent visual contact between fish in different replicates and filter any food and/or waste that would otherwise end up in the downstream experimental area.

Behavioural observations

Before conducting each experimental trial, fish were introduced to the flume and allowed to acclimate to conditions in the artificial stream for 25-26 hours prior to observations. A black polypropylene isolation curtain was suspended around the flume when fish were present to ensure minimal disturbance. Observations were made through viewing windows (20 cm X 20 cm) that were opened during experimental trials.

Behavioural observations of aggression towards an interspecific competitor (nips, chases and lateral displays) were measured continuously throughout the experimental trials (Newman 1956; Keenleyside and Yamamoto 1962). Two periods of observation were conducted in the 24 hours that followed acclimation time. Each replicate was observed for one hour in the daytime (08:00-10:00), and one hour in the night time (20:00-22:00) and the two observational periods were averaged to avoid pseudoreplication. Aggression counts were then square-root transformed for subsequent data analysis. Proportion of time in lead position was measured by observing the fish in the lead position at one-minute intervals throughout each one hour observation period. Foraging success was measured by the proportion of the total number of 20 food items supplied that were successfully captured, relative to the competitor. Night time observations were made with the aid of 4 deep red light bulbs (Rodtka and Volpe 2007). Video cameras recorded the full length of each experiment and were used to review observations.

Foraging strategy of species

In order to test whether bull and brook trout might have innate differences in foraging strategy, the relationship between foraging success and occupying the lead position in the stream was assessed for each species. Fish were placed in head-to-head competition trials, in within-species competitions and between-species competitions. The environment simulated a simple pool habitat, with average current velocities of 7 (+/- 1) cm s^{-1}, a water column depth of 40 cm, and small substrate (gravel, mean particle size = 20 mm) that did not impede visual contact among fish. Nine replicates were run for each species in within-species trials and thirteen replicates in between-species trials. For all between-species replicates, fish of both species were re-used from intraspecific competitions, except for two replicates in which naïve fish were used. Thus, competitors always had the same amount of experience in the flume. Fish were size matched to the nearest mm for both within-species (mean absolute size difference between competitors within a replicate: 1 mm, 1.8 g) and between-species competitions (bull trout: 135 mm [mean], 25.9 g; brook trout: 135 mm, 26.2 g; mean absolute size difference between competitors within a replicate: 2 mm, 2.2 g). Fish were fed via a nylon tube located at the most upstream end of each experimental area. Food was passed down these tubes from a funnel suspended behind the isolation curtain. 25% of the water was continuously renewed daily for the whole unit, and following each trial 75 % of the water was replaced. This ensured that subsequent trials were always conducted in fresh water. Filtration media and substrate were cleaned between each trial and temperature, pH, ammonia, nitrite and nitrate levels were continuously monitored to ensure optimal housing conditions.

The relationship between foraging success and occupancy of the lead position in the streams was analyzed by linear regression. In both within and between-species competitions, only one fish was randomly selected from each replicate for this analysis in order to avoid pseudoreplication.

Effects of fish density and habitat type on between-species competition

In addition to the thirteen head-to-head between-species competitions (fish density = 3.0 fish m^{-2}) described above, three additional experimental treatments were conducted, and interspecific competition was observed. The subsequent three treatments were two-on-two competition experiments (fish density = 5.9 fish m^{-2}) in which the stream habitat was altered, in order to simulate different habitat complexity and density scenarios. The same competitors were used across all treatments. These treatments had more limited sample sizes due to the difficulty in size matching a larger group of fish, and limited numbers of fish that were collected. All four treatments used size-matched fish (bull trout: 142 mm [mean], 29.9 g; brook trout: 142 mm, 30.5 g; mean absolute size difference between competitors within a replicate: 1.5 mm, 2.2 g). The four experimental treatments were thus named as: simple pool low number (SP-L; n = 13), simple pool high number (SP-H; n = 5), complex pool high number (CP-H; n = 5) and complex riffle high number (CR-H; n = 5). Simple pool habitats (Figure 3-1a,b) had average current velocities of 7 (+/- 1) cm s^{-1}, a maximum water column depth of 40 cm, and small substrate (gravel, mean particle size = 20 mm) that did not impede visual contact among fish. The complex pool habitat (Figure 3-1c) had the same velocity and depth characteristics as the simple pool habitat, but visual contact among fish was reduced by adding large substrate (cobble, mean particle size = 165 mm). The complex riffle habitat (Figure 3-1d) had the same substrate characteristics as the complex pool habitat, but water column depth was reduced to 20 cm and average velocity was increased to 14 (+/- 4) cm s^{-1}. Complex habitats were constructed to reduce visual encounter rates and territory size of fish due to increases in substrate size (relative to the depth of the water column) and water velocity (Hasegawa and Yamamoto 2009; Steingrimsson and Grant 2011). Average velocity (+/- s.d.) was calculated by measuring current at 18 equally spaced standardized locations in the stream.

Foraging success of either species was observed in each replicate, and aggression was measured as the average per-capita number of aggressive acts for each species. Foraging success for bull trout was analyzed according to 95% confidence intervals (CI) around each mean estimate of foraging success in each treatment. Since 0.5 is the value in which the both species are equal competitors, one species significantly outcompeted the other if the 95% CI did not overlap with 0.5. The analysis of foraging success was conducted in this manner rather than comparing one species to another, since the value of one is the inverse of the other and thus species effects are not independent. Aggression was compared between species and among the four treatments with a two-way ANOVA.

Results

Foraging strategy of species

For brook trout within-species competitions, successful foraging was predicted by occupying the lead position in the stream (Foraging success = 0.17 + 0.70 Proportion of time in lead position, $R^2 = 0.71$, $F_{1,8} = 17.16$, $P = 0.0043$) (Figure 3-2a). No such pattern was observed in bull trout within-species competitions ($R^2 = 0.02$, $F_{1,8} = 0.13$, $P = 0.73$) (Figure 3-2b).

For between-species trials, foraging success was not significantly correlated with the proportion of time spent in the lead position ($R^2 = 0.15$, $F_{1,12} = 1.87$, $P = 0.20$) (Figure 3-2c). Bull trout were the more successful forager in these trials, consuming a higher proportion of food than brook trout in 10 of 13 replicates. A summary of data can be found in Tables A-6 and A-7.

Effects of fish density and habitat type on between-species competition

According to 95% CIs, in simple pool environments, bull trout captured the majority of presented food (average proportion = 0.70) when the competition was one-on-one, but did not capture the majority of food (average proportion = 0.49) when the fish density was doubled (Figure 3-3). When the pool habitat had complex substrate introduced, bull trout did not capture a higher proportion of food (0.58); however, when the habitat was altered to be a complex riffle environment, bull trout again became the more successful competitor (average proportion = 0.67; Figure 3-3). Aggression of both species appeared to be affected by treatment type ($F_{7,48} = 3.87$; $P = 0.0021$). Effect tests of the two-way ANOVA revealed that brook trout were more aggressive than bull trout overall ($P = 0.010$), and that aggression of both species was different among treatments ($P < 0.001$); however, an interaction term between species and treatment was not significant ($P = 0.48$). A Tukey post-hoc test revealed that aggression of both species was lower in SP-L than in SP-H and CP-H treatments, but not than the CR-H treatment (Figure 3-4)

Discussion

As hypothesized, bull trout and brook trout used different foraging tactics to acquire food resources. In within-species competitions, dominant brook trout were qualitatively observed to defend profitable feeding territories at the upstream end of the stream, while subordinate brook trout generally occupied the rear position in the stream, and foraging success was strongly correlated with the time spent in the lead position. This lends support to the observation that brook trout placed in contest competition (Ward et al. 2006) will defend profitable feeding territories in pools in accordance with their rank in a dominance hierarchy (Fausch and White 1986). In contrast, bull trout did not show the same relationship between foraging success and time spent in the lead position in within-species competition trials. This was also apparent in between-species competitions, as bull trout were the superior forager in most head-to-head trials, yet there was still no relationship of foraging success with time spent in the lead position. The foraging strategy of bull trout was variable. Qualitatively, while bull trout were occasionally observed defending territories at the upstream portion of the stream, they mostly employed scramble behaviours to capture food that could be described as “ambush” or “sit-and-wait” from the stream bottom or behind cover and others that could be described as “active,” “searching” or “cruising” (Hasegawa and Yamamoto 2010; Steingrimsson and Grant 2011). This experiment was not designed to quantify such operationally defined behavioural foraging modes for each individual, but I do hypothesize that bull trout may invoke a variety of flexible foraging tactics to optimally forage when in competition (Nakano et al. 1999). It should be noted that brook trout have also been observed to have variable foraging tactics, and some individuals may sit-and-wait for food, while others will actively search (Grant and Noakes 1987). These different foraging tactics may be temporally flexible even at the individual level (Biro and Ridgway 2008). Therefore, it is important to recognize that the observations in this study should not be taken as evidence that bull trout and brook trout have different, rigidly defined foraging tactics at the whole species level; only that under the conditions tested and for the fish collected, brook trout are more inclined to territorial defense of the lead position to secure resources.

The lack of correlation between foraging success and lead position occupancy for bull trout implies that they were able to successfully compete, both with their own species and against brook trout, by being the first to scramble for food, rather than preventing their competitors' access through territoriality. The hypothesis that bull trout are predominantly scramble foragers, both when in intraspecific competition and with brook trout, is supported by previous observations. In field-based behavioural studies, bull trout have been observed to forage in a mobile, haphazard manner or by intercepting drifting food from behind cover (Nakano et al. 1992; Bonneau and Scarnecchia 1998; Nakano et al. 1998). Laboratory studies have likewise commented on the apparent scramble foraging tactic of bull trout (Rodtka and Volpe 2007). Furthermore, the non-territorial exploitative competition mode has been suggested to account for the density-dependent pattern of survival and growth seen in wild populations of juvenile bull trout (Paul et al. 2000), as size classes do not have growth patterns or survival expected if intercohort interactions were territorial (Post et al. 1999).

Between-species competition was affected by the treatment type. In simple pool environments, bull trout outcompeted brook trout when the competition was head-to-head, but when the number of competitors was doubled there was no clear winner. Previous laboratory studies that have observed competition between bull trout and brook trout in cold (8 degree) water temperatures have generally found that there is no clearly dominant species, and these studies were conducted in simple pool environments with multiple competitors (i.e., not head-to-head) at greater densities than the two-on-two competitions used in this study (Rodtka and Volpe, 2007: 8.2 fish m^{-2}; McMahon et al., 2007: 20.7 fish m^{-2}). When competition was tested with multiple competitors in complex riffle habitats, bull trout again were observed to outcompete brook trout. This may be due to being released from aggressive interference that brook trout were able to display in the pool environments (Nakano et al. 1998).

Aggression was also used to quantify competition between bull trout and brook trout, and increased overall for both species as competitor number was doubled in pool habitats. At these higher fish densities, aggression was again reduced when the habitat was changed to a complex riffle. This supports the observation that aggressive interactions among salmonids in streams increase with fish density, but this can be mitigated in high complexity, swift water environments (Blanchet et al. 2006). When comparing species, brook trout were more aggressive than bull trout. Higher aggression levels in brook trout relative to bull trout are supported by previous studies (Gunckel et al. 2002), especially at high fish densities (McMahon et al. 2007) and warm water temperatures (Rodtka and Volpe 2007) when the two are in direct competition. The higher aggression levels in brook trout are likely associated with their disposition to territorial, foraging behaviour, often in situations of high density (Dunham et al. 2002).

Density is a term that can be thought of more usefully as an adjusted “effective” or “relative” value that fish actually experience when in direct competition (Grant et al. 1998; Berger and Gresswell 2009). Adjusting fish density in a quantitative manner, for visual isolation between competitors or territory size reduction due to high current velocities, may be an informative avenue for further study. This may have widespread use considering that density-dependent processes may be affected by the physical structure of the habitat available for fish in streams (Blanchet et al. 2006), and structurally complex environments may support higher densities of territorial fish (Dolinsek et al. 2007; Venter et al. 2008).

The apparent success of either species according to competitor density or habitat type may be due to inherent costs or benefits of aggressive territoriality in different environments (Grant and Noakes 1988). Territorial behaviour displayed by brook trout in this study may not be an optimal foraging strategy under complex environments where visual contact with competitors is reduced (Sundbaum and Naslund 1998; Höjesjö et al. 2004). Visual contact between competitors was most reduced in the complex riffle environment, as large substrate nearly reached the surface of the water column. Territorial behaviour may be less effective in the higher current velocities of this habitat, as defense becomes more energetically costly (Mcnicol and Noakes 1984). The benefits of territoriality may also be further reduced in this habitat by the chaotic flow patterns created through large substrate, which make the drifting pattern of forage unpredictable (Hasegawa and Yamamoto 2009). In contrast, scramble foraging strategies displayed by bull trout may be advantageous under these complex, higher velocity environments where sources of drift forage are unpredictable and defending a territory is a costly and ineffective strategy to obtain resources (see discussion of Hasegawa and Yamamoto 2010). This highlights the importance of an “arena effect” in testing competition between species that may have different habitat preferences or conditions under which foraging is optimal (sensu Korsu et al. 2010). This may explain why previous studies of competition between bull trout and brook trout have not found the conditions under which bull trout become the superior competitor (Gunckel et al. 2002; McMahon et al. 2007; Rodtka and Volpe 2007).

Unlike previous studies, none of the scenarios tested here showed brook trout to be the superior competitor. This may be due to the fact that all treatments of this experiment were conducted at cold (8°C) water temperatures. Brook trout territorial behaviour has been observed to be especially intense at higher (15-20°C) temperatures, where they will typically dominate bull trout (McMahon et al. 2007; Rodtka and Volpe 2007) and cutthroat trout (De Staso and Rahel 1994) competitors in simple pool habitats. It would be interesting to replicate the higher temperatures tested in these studies in complex, high velocity habitats or in especially low fish densities to assess whether brook trout still hold a competitive advantage.

When examining patterns of brook trout invasion into bull trout streams, warm water temperature appears to largely explain a general trend of invasion at lower elevation reaches of streams (Chapter 2; Paul and Post 2001; Rieman et al. 2006). This may be due to a competitive advantage for brook trout at higher water temperatures (Rodtka and Volpe 2007). In high elevation, cold reaches of streams, the success of brook trout invasion is variable, and likely dependent on a suite of additional abiotic and biotic factors (Chapter 2; McMahon et al. 2007). Brook trout have been observed to occur at greater densities than the native species they replace or displace (Benjamin and Baxter 2010), which may create favorable density situations for the brook trout foraging strategy in the context of interference competition with bull trout (*sensu* Dunham et al. 2002). Quantitative measures of habitat complexity have also been observed to be a possible variable in explaining brook trout occurrence in the field, as brook trout invasion seems to be commonly resisted in environments showing higher structural complexity (Rich et al. 2003). Juvenile bull trout have been shown to be positively associated with in-stream substrate cover and complexity (Al-Chokhachy et al. 2010). Indeed, large in-stream substrate cover is a factor associated with limited success of brook trout invasion into bull trout streams of the Canadian Rockies (Chapter 2). The results of this lab study suggest that limited brook trout invasion in these areas may be due to the foraging disadvantage that they hold relative to bull trout in such environments.

Large in-stream substrate has been recognized as an important habitat feature that bull trout use as cover from which to forage (Watson and Hillman 1997). Rodtka and Volpe (2007) hypothesized that the scramble foraging tactic of bull trout is an advantage over the territorial tactic of brook trout in common environmental conditions of high elevation mountain streams where bull trout resist invasion; as drift forage is unpredictable and less abundant, reducing the profitability of the brook trout territorial foraging strategy. This hypothesis is consistent with the patterns observed in this study, where chaotic flow pattern caused by in-stream obstacles and higher stream velocity simulated such environments. In a similar species interaction, native white-spotted charr (*Salvelinus leucomaenis*; an Asiatic salmonid species that is the closest phylogenetic relative of the bull trout) are inferior interference competitors to exotic brown trout in simply designed experimental tanks (Hasegawa et al. 2004), but the effect can be mitigated in structurally complex environments (Hasegawa and Maekawa 2008). The authors hypothesized that such structural complexity may confer biotic resistance to invasion by releasing the native species from interference foraging interactions with exotic salmonids (Hasegawa and Maekawa 2008). The results of this study support an identical hypothesis in the case of the brook trout and bull trout competitive interaction. This further emphasizes the role that a suite of abiotic and biotic variables may play in determining the relative foraging success invaders hold over native species, which could influence invasion outcome.

Figures

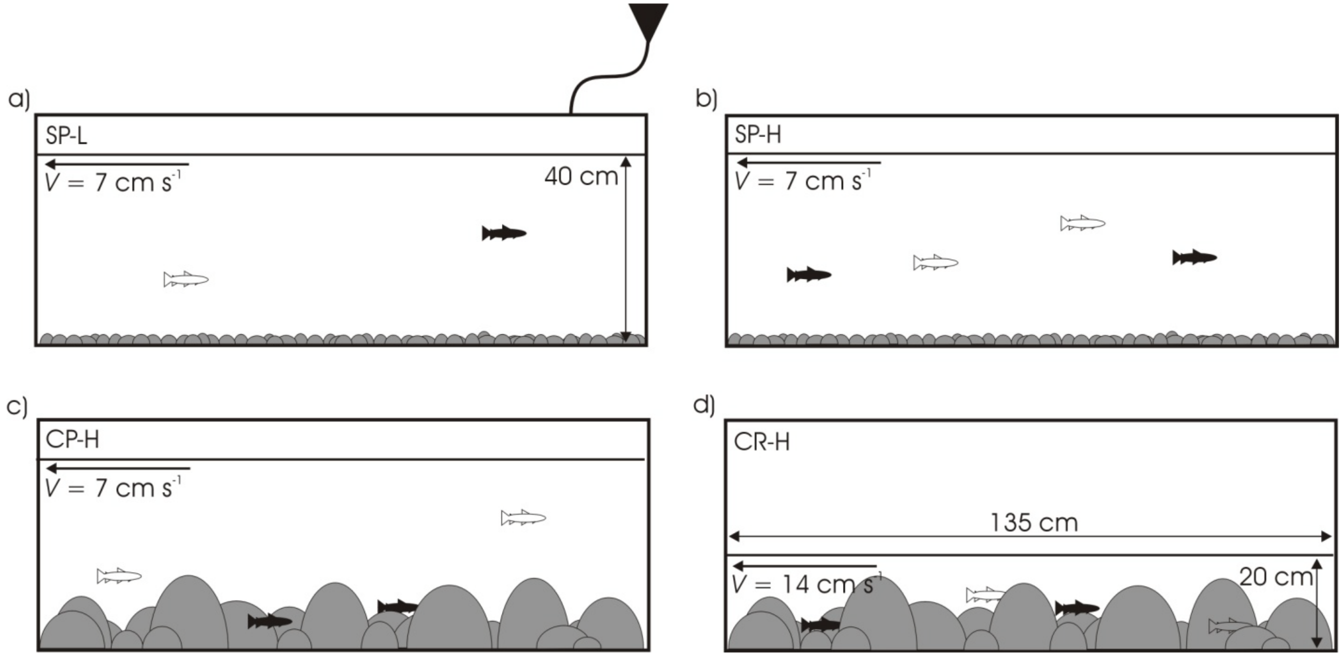

Figure 3-1: Experimental treatments for assessing competition between brook trout (filled fish icons) and bull trout (not filled). Treatments assessed various habitats, including simple pool (SP), complex pool (CP) and complex riffle (CR), either in head-to-head, low number (L) competitions, or two-on-two, high number competitions (H). The stream velocity (*V*) was increased to 14 cm s^{-1} in the CR habitat. Competition for food was assessed by introducing food items through a tube on the upstream portion that was attached to a funnel behind a viewing screen.

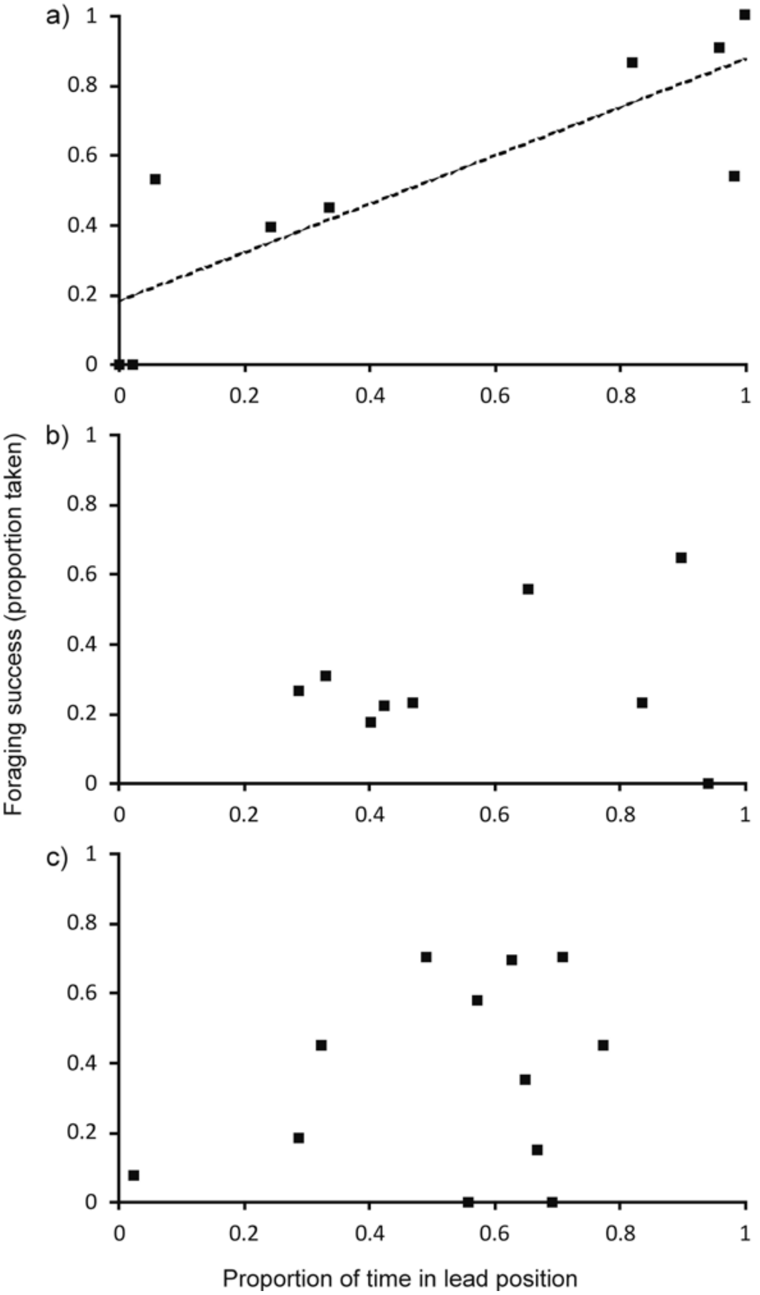

Figure 3-2: Relationships between foraging success and proportion of time spent in the lead position for within-species competitions of brook trout (a; $R^2 = 0.71$) and bull trout (b; $R^2 = 0.02$) and between-species competitions, where one fish was randomly selected from each replicate (c; $R^2 = 0.15$). A regression line indicates a significant relationship.

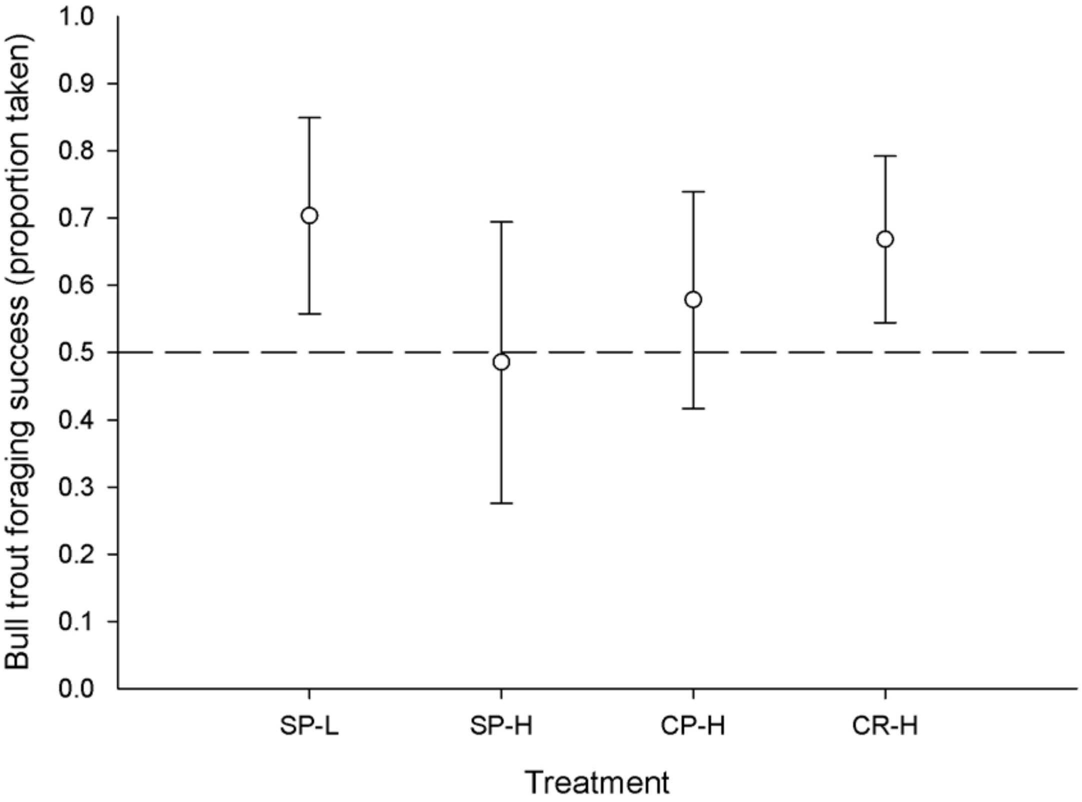

Figure 3-3: Proportion of food captured for bull trout (with 95% CI), relative to total captured when in competition with brook trout through the four treatments. Bull trout outcompeted brook trout in the SP-L and CR-H treatments, as the 95% CI do not overlap with the proportion expected if the two were equal competitors (dashed line).

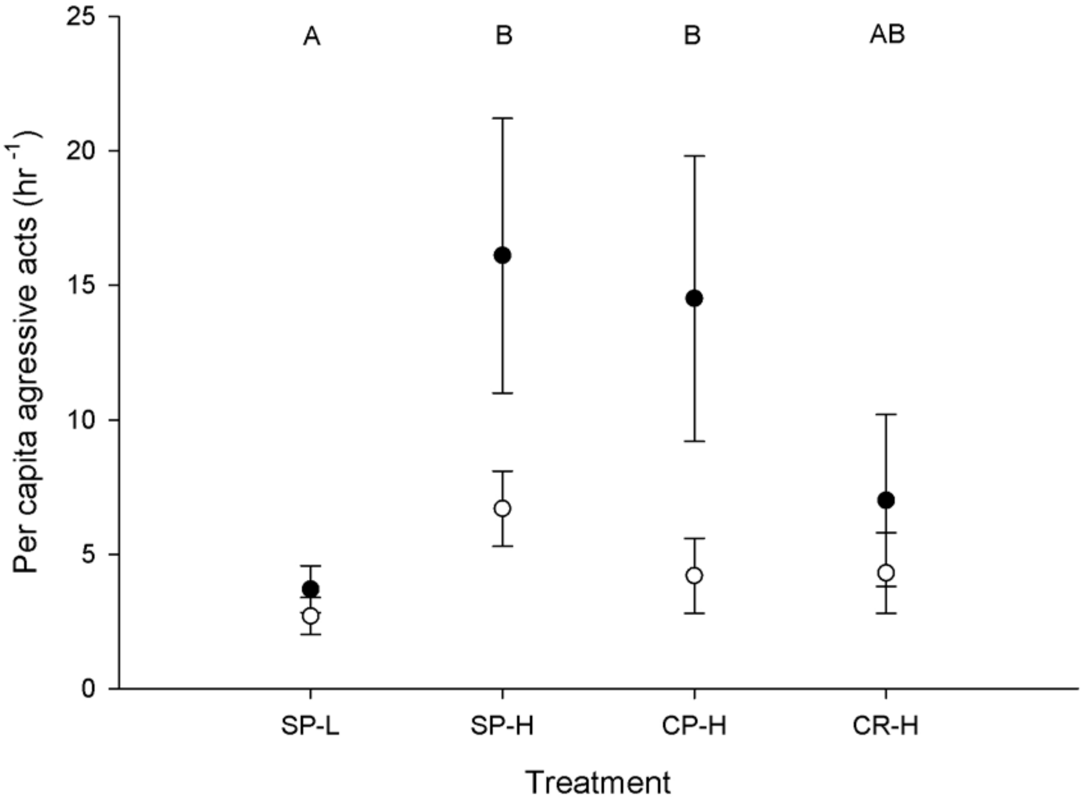

Figure 3-4: Number of aggressive acts per fish of both brook trout (closed circles) and bull trout (open circles), +/- SEM when in competition through the four treatments. Brook trout were more aggressive than bull trout throughout the experiment ($P = 0.010$). Aggression differed among treatments for both species overall ($P < 0.001$). Treatments sharing the same letter are not significantly different in *post-hoc* tests ($P < 0.05$).

Chapter 4 Comparing competitive ability and associated metabolic traits between two populations of bull trout, one migratory and one resident, against brook trout

Abstract

Juvenile bull trout from two geographically and ecologically distinct populations were compared with regard to their ability to compete with invasive brook trout in an artificial stream, and with respect to their rates of oxygen consumption. Bull trout collected from a migratory population competed more effectively against brook trout for food resources and were more aggressive than fish collected from a resident population. The superior competitive ability of the migratory population of bull trout against an invasive species relative to the resident population was positively associated with metabolic rate. Bull trout from the migratory population had a higher oxygen consumption rate (203 mg O_2 $kg{\bullet}hr^{-1}$) in the field than similar sized fish from the resident population (183 mg O_2 $kg{\bullet}hr^{-1}$). These results suggest that these two distinct populations of bull trout compete differently against an invasive species and such competitive ability may be associated with physiology or their migratory life history.

Introduction

Interspecific competition is an important determinant of species' population dynamics and can influence the success of species invasions. As such, experimental observations of interspecific competition are commonplace in ecology and invasion science. Experimental studies often concentrate on variable abiotic factors that influence competition (e.g. temperature, habitat etc.); although variable biotic factors including competitive ability of individuals and populations may also influence interactions among native and invasive species (Leisnham and Juliano 2010; Rossong et al. 2012).

Competitive ability, as commonly measured by food consumption and aggression, varies greatly, both within and among populations of many animal taxa (Reale et al. 2010). This has been well studied and documented in several species of salmonid fishes (Metcalfe et al. 1995; Lahti et al. 2001; Morinville and Rasmussen 2003). Competitive ability is also shown to be positively linked with metabolic rates (Metcalfe et al. 1995; Cutts et al. 2001). Variation in both competitive ability and associated physiology has been attributed to many underlying factors, including artificial selection, predation, resource abundance and migratory status (Biro and Stamps 2008; Reale et al. 2010). Whole populations may therefore be expected to vary in their competitive ability with other species, and this has important implications for interactions among native and non-native species with overlapping niches. For invading species, variation in competitive behavior of founding populations may influence invasion success, severity and competitive dominance over native species (Abbott et al. 2007; Duckworth and Badyaev 2007; Rossong et al. 2012). Alternatively, for native species, variation in competitive ability among populations may determine pathways of successful biotic resistance to invasion (Leisnham and Juliano 2010).

Bull trout (*Salvelinus confluentus*) spawn and rear in headwater streams of mountainous regions of western North America, and display fine-scale genetic population structure that is associated with ecological variation and unique population attributes

(McPhail and Baxter 1996; Costello et al. 2003; Warnock et al. 2010). Bull trout express a variety of migratory life histories (both within and among populations), and occupy a variety of geographically and ecologically diverse watersheds throughout their native range. These diverse aspects of their biology may be reflected in population-level variability in competitive behavior and associated metabolic traits. To this point there have been no attempts to discern whether distinct populations vary in their ability to compete with invasive species, but this may influence the success of invading competitors with overlapping niches (sensu Leisnham and Juliano 2010). Of invading species in headwater streams of mountainous regions of Western North America, brook trout (*Salvelinus fontinalis*) are the most commonly implicated species in the competitive displacement or replacement of bull trout.

The purpose of this study was to assess whether bull trout from two distinct populations compete differently against invasive brook trout in a controlled setting, and if competitive differences can be associated with physiological differences between the two populations.

Methods

Competition experiment

Juvenile bull trout and brook trout were captured from wild populations in September of 2010 by backpack electrofisher. Eleven bull trout (size range: 115-136 mm fork length) were captured from Mill Creek (Mi) (49°22’ N, 114°10’ W; 1400 m elevation), which supports a robust annual spawning run of large-bodied migrant bull trout and high juvenile fish densities (Warnock et al. 2011). Twelve bull trout (size range: 102-121 mm) were caught from the Livingstone River (Li) (50°7' N, 114°26' W; 1700 m elevation), which supports an isolated resident population of bull trout above a migratory barrier. Adult fish in this population live amongst juveniles year-round, rarely exceed 350 mm in length and are not found in downstream migrant fisheries (Warnock et al. 2010; Warnock et al. 2011). Twenty-three size-matched brook trout (size range: 101-138 mm) from a single population were captured in nearby Beaver Mines Creek (49°22' N, 114°15' W; 1350 m elevation). All three streams are situated in the headwaters of the Oldman River watershed in Alberta, Canada. Brook trout were introduced in the 1940s, and bull trout are native to the watershed and exist in an arrangement of unique hierarchical populations among which gene flow can be limited; the Mi and Li populations are genetically distinct (Warnock et al. 2010).

Each species was housed in an isolated, chilled 425 L tank that was gradually adjusted to 8 °C upon transfer of fish to the Aquatic Research Facility at the University of Lethbridge. Photoperiod was set to a 12:12 hr light:dark cycle. After a two week quarantine period, fish were anaesthetized in clove oil and each was tagged with a unique combination of adipose fin clips and colored elastomer tags (NMT technology™) in the caudal, dorsal and anal fins for quick visual individual identification. Fish were acclimated to the lab in two species-specific tanks for another three weeks following tagging before the experiment began. Fish were fed on a maintenance diet of frozen *Mysis* shrimp at 3% body weight per day. This ration was selected during the acclimation period, as every fish gained weight and maintained or gained condition factor according to this ration (data not shown).

Trials of two simultaneous replicates were held in a laminar-flow artificial stream of chilled water (8°C +/- 0.1) (Figure 4-1). Medium and low density Matala™ filtration media was placed at upstream and downstream ends of the experimental areas to prevent fish movement and visual contact between replicates, as well as filter any food and/or waste that would otherwise end up in the downstream experimental area. The substrate used in these trials was smooth round gravels (mean particle size of 20 mm) and the water velocity was calibrated to a mean of 7 cm s^{-1} after measuring in 27 standardized locations throughout the water column in each experimental area (range of 6-9 cm s^{-1}). Water velocity did not differ between experimental areas (*t*-test: $t_{52} = 0.33$; $P = 0.74$). This environment simulated a typical pool habitat in a headwater stream and replicated stream pool characteristics that have often been tested in an artificial setting for salmonid interspecific competition (De Staso and Rahel 1994; Rodtka and Volpe 2007).

An opaque black polypropylene isolation curtain was placed around the steam so that fish could not detect experimenters. A small viewing window was cut into the curtain in front of each experimental area and opened during the experimental periods so that fish could be observed. Feeding was accomplished through nylon tubing attached to a funnel, which was suspended behind the isolation curtain so that fish could not detect experimenter movements during feeding periods. A flow-through supply of fresh water was set so that 25% of the water was made up of new origin every day. In addition to this, 75% of the water was replaced at the end of each experimental trial, so that subsequent trials (conducted at least two days apart) would be conducted in fresh water. The unit was not entirely drained between trials, as a biofilter relying on circulating bacteria was present for ammonia oxidation. Filtration media and gravel were cleaned and ammonia, nitrite and nitrate levels were measured weekly and pH and temperature daily to maintain optimal housing conditions for fish.

Thirteen replicates of interspecific competition were run in head-to-head trials of size matched fish, with population of bull trout as the treatment of interest. This included six replicates where the bull trout competitor was from the Li population treatment and seven replicates where the bull trout competitor was from the Mi population treatment. All fish of both species had equivalent previous experience in a prior competition experiment (Chapter 3; Table A-7) where each species was assessed in intraspecific competitions, except for two replicates (one for each treatment) in which naïve fish were used. This experiment was of roughly the same design, and fish were allowed at least three weeks to recover before the current experiment was conducted. Fish were most often within 1-2 mm of one another, and size differences between fish never exceeded 4 mm in any replicate. Treatments were randomly assigned to either flume section and randomly ordered.

Pairs of fish for each replicate were transferred to the artificial stream between 07:00-08:00. Fish were acclimated to the stream environment for 25-26 hours prior to experimental observations, and feeding was performed at a random time between 09:00-11:00 and again at 21:00-23:00 during this period. Observations began the following day at 09:00-11:00 and nighttime observations at 21:00-23:00 (two hours of total observations per replicate). Nighttime observations were made with the aid of four 60W deep red light bulbs, which turned on automatically during the dark cycle of the photoperiod and provided low ambient lighting in which observations were still possible (Rodtka and Volpe 2007). Observations were made during, 10 min before, and after addition of food, in two separate rounds spaced one hour apart during both day and night periods. Fish were fed 10 *Mysis* shrimp (average size: 17 +/- 5mm [mean +/- SD]; 0.044 +/- 0.017 g), at one-minute intervals in each round. Foraging success was expressed as the total number of food items successfully captured by each bull trout population per hour when competing against brook trout. Behavioural observations of aggression (nips, chases and lateral displays) were measured continuously throughout the experimental rounds and were expressed as the total number of aggressive acts of each bull trout population per hour. Brook trout aggression was also evaluated and compared between treatments. Although direct monitoring of behavior was generally reliable, video cameras recorded the full length of each experiment to ensure that no behaviors were missed.

Oxygen consumption

Oxygen consumption rates (OCR) were measured in the field for both the Mi and Li populations. The procedure used was a non-lethal, simple and repeatable method that examines “routine resting” metabolic rates for comparison purposes, rather than active or basal resting metabolism (described in Rasmussen et al. 2012). Juvenile fish (23 for each population; size: 94-185 mm) were captured by backpack electrofisher on mild settings and transferred to a covered, flow-through enclosure that was placed in the stream. Fish were allowed to recover for approximately 30 minutes before performing oxygen consumption trials. To measure oxygen consumption, fish were placed in a sealed 600 mL bottle filled with stream water. Fish were all simultaneously tested for oxygen consumption, in order to ensure equivalent recovery times from the initial capture effort.

A YSI™ 85 meter was used to measure bottle oxygen concentration (mg L^{-1}) and temperature (°C) before the test began, and once every 10 minutes for a maximum of one hour. A control bottle was also measured at the same intervals to correct for any instrument drift that might occur. Trials were terminated early for some fish that dropped below a threshold bottle oxygen concentration of 2 mg L^{-1} before the 60 minute test period elapsed. After the trials were completed, fish were measured, weighed and allowed to recover in the enclosure for at least 30 minutes before being released.

Results

Competition experiment

Bull trout collected from Mi consumed more food than those collected from Li when competing against brook trout (*t*-test: $t_{11} = 2.25$; $P = 0.046$) (Figure 4-2). Bull trout collected from Mi were more aggressive to brook trout competitors than those collected from Li (*t*-test: $t_{11} = 5.77$; $P < 0.001$) (Figure 4-3). This was not simply an artifact of brook trout aggression differences between treatments, as aggression of this species did not differ when competing with the two populations of bull trout (*t*-test: $t_{11} = 0.79$; $P = 0.44$). For a summary of data, refer to Table A-6.

Oxygen consumption

Analysis of covariance was significant ($F_{3,45} = 321.8$; $P < 0.001$) and revealed significant effects of population and a log-weight covariate on log-OCR; however, an interaction term between population and log-weight was not significant and was discarded from further analyses. Bottle temperature varied little among tested fish (10.3°C +/- 0.6 [mean +/- SD]) and was discarded from further analysss as it was not a significant covariate. While body size explained the majority of the variation in the model ($F = 973.7$; $P < 0.001$), the effect of population was also significant ($F = 16.5$; $P < 0.001$) (Figure 4-3). A *post-hoc* test comparing populations revealed that mean size-standardized fish from Mi had a higher OCR than fish from Li (Figure 4-4).

Discussion

This study provides evidence that juvenile bull trout from the Mi population competed more successfully for resources and were more aggressive against brook trout than bull trout from the Li population. This supports the hypothesis that bull trout exhibit population-level variation in competitive behavior against an invasive species. These differences observed between populations may be associated with metabolic differences, as the Mi population consumed more oxygen than Li population fish when under similar holding conditions. The positive link between food consumption, aggression and metabolic rate supports previous research on a variety of animal taxa and salmonid species, and all these aspects appear to vary at the population level (Lahti et al. 2001; Reale et al. 2010).

Distinct differences in metabolic traits or behaviour between bull trout populations is not surprising, given the strong genetic and life history differences seen between these two populations (Warnock et al. 2010; Warnock et al. 2011). Strong genetic divergence at fine spatial scales is common among bull trout populations, and may be mirrored by differences in locally adapted phenotypes (Costello et al. 2003; Whiteley et al. 2004). Invading salmonids such as brook trout may have different “races,” which may have variable success invading depending on their competitive ability (Fausch 2008). Differences in competitive ability among populations of native species should be considered at least equally important when examining the variable success of non-native species (Leisnham and Juliano 2010).

The higher food acquisition and greater aggression levels observed for the Mi population may reflect a more active or bolder foraging strategy in this population (Stamps 2007). There may be several ultimate factors that are driving the differences in competitive ability and associated metabolic traits between these populations. The most striking ecological difference between these two populations is that Mi is migratory and Li is resident. The positive association between metabolic, feeding and aggression rates and migratory life history is a general phenomenon, having been documented in birds (Duckworth and Badyaev 2007) and a variety of salmonid fish species (Metcalfe et al. 1995; Forseth et al. 1999; Cutts et al. 2001; Lahti et al. 2001; Morinville and Rasmussen 2003). A more active foraging strategy in migratory populations would make sense from an energetic point of view, as these morphs may need higher food consumption rates in order to fuel the high metabolic demands that motivate migration (Forseth et al. 1999; Morinville and Rasmussen 2003). Alternatively, higher food consumption rates and sustained activity in migratory individuals may produce higher metabolisms and therefore the higher oxygen consumption observed is simply a product of rather than the basis of the behavioural differences (Biro and Stamps 2010). Disentagling the cause-and-effect relationship between metabolism, behaviour and migratory life history is clearly an avenue of continuing basic research (Biro and Stamps 2010; Reale et al. 2010); however, the potential association between migratory life history variation and variation in competitive ability against non-native species should be of particular relevance to population-level pathways of biotic resistance to invasion (Leisnham and Juliano 2010).

Along with competitive ability between migratory life histories, there are several other reasons to suspect that resident bull trout are more susceptible to displacement by brook trout. As adults, resident and migratory bull trout are ecologically distinct forms. At 1-3 years of age, migrants outmigrate (potentially long distances) from natal headwater streams (Warnock 2008)) and shift trophic level by becoming piscivorous in downstream mainstem rivers (Appendix); whereas residents exploit a primarily invertebrate food resource base and remain in their natal or closely associated streams throughout their lifecycle (McPhail and Baxter 1996). In their native range, brook trout also display a diversity of migratory life histories and ecological specialization (Ridgway 2008), but this is less variable for introduced populations in the Canadian Rockies. Successfully established brook trout are primarily invertebrate feeders, and although some fish can move several km (Gowan et al. 1994; Gowan and Fausch 1996), the movement patterns and spatial ranges of these invasive populations are generally restricted (Dunham et al. 2002) and are similar to typical stream resident morph bull trout. Brook trout are thus generally restricted to small headwater streams, and are rarely found in downstream mainstem rivers (ASRD 2009). Ecologically, resident bull trout therefore have more of a direct niche overlap with the invasive species which is sustained throughout the entire lifecycle; whereas migrant bull trout are released from competitive interactions once they outmigrate to far downstream areas of higher stream order and undergo a trophic level shift to piscivory. Resident bull trout may therefore be more vulnerable to competitive displacement by brook trout than migrants at adult life stages in particular.

Demographic differences between resident and migratory populations will have perhaps an even greater influence than competitive differences in determining brook trout displacement of bull trout. Relative to migratory forms, resident salmonids may have lower fish densities and recruitment rates (Morita et al. 2009). This is because migrants subsidize their reproductive output with the richer biomass of downstream areas, while resident forms rely on the limited productivity of the headwater stream. Brook trout invasion success has been attributed to additional demographic reasons in other species interactions (Dunham et al. 2002); brook trout mature earlier than the native species they displace (Adams 1999; Paul 2000) and can attain higher densities and biomass than native species (Benjamin and Baxter 2010). If resident bull trout populations have lower recruitment rates, population sizes and densities than migrant populations in general, they may be more susceptible to the reproductive advantage exhibited by invasive brook trout at the population level (Peterson et al. 2004; Rieman et al. 2006). Furthermore, the size at which resident bull trout mature at may theoretically make resident populations more susceptible to displacement via hybridization and backcrossing. Mate choice in salmonids closely related to bull trout is strongly size-selective (Maekawa et al. 1994) which can act as a pre-zygotic hybridization barrier between large bodied migratory bull trout and small brook trout. As resident bull trout reach sexual maturity at much smaller sizes, the chance of successful pairings with brook trout or their hybrids may be greater. Despite this theoretical basis, the observational evidence for this is weak, and hybridization rates observed are probably due more to relative species abundance or spawning time overlap in specific streams (Kanda et al. 2002; DeHaan et al. 2010). Interestingly, there are many populations of bull trout that exhibit patterns of partial migration (Northcote 1992), where resident and migratory forms are sympatric (McPhail and Baxter 1996; Nelson et al. 2002; Homel et al. 2008). Whether one sympatric form is more resilient in an invaded environment is not apparent, but further research should focus on these populations in particular. This is important when considering the potential for invasion to reduce life history variation not only among, but within populations as well.

Although the primary ecological difference between the two populations from which bull trout were sampled is that they express opposite migratory life histories, it is possible that competitive differences between the two populations may have arisen from alternate unrelated reasons. One such possible reason is resource availability. The Mi population comes from a stream of lower elevation and latitude, which could make it a more productive environment with a longer growing season than the Li population stream. Fish with more active and aggressive foraging strategies may be selected for in such environments, as abundant resources ensure less of an energetic tradeoff to these behaviors (Lahti et al. 2002; but see Dunbrack et al. 1996). In contrast, low food abundance may select for fish that have high growth efficiency, but low energetic costs and that do not engage in costly foraging behaviors (Metcalfe et al. 1995). Variation in aggressiveness and foraging strategy may also be affected by predation, as fish with bold foraging strategies and high growth have lower survival under increased predation pressures (Biro et al. 2004). If there is a difference in predation risk between the bull trout populations, it may influence the differences seen in competitive traits. The Li population contains adult bull trout that live amongst rearing juveniles year-round; in contrast, the Mi population hosts adult bull trout for a shorter period of the year during their spawning migration. If the Li population has higher rates of piscivory due to cannibalism from adult fish, it may have a higher pressure of predation and therefore would select against fish with active, bold foraging strategies in the juvenile stage.

In the field, invasive brook trout appear to actively displace native species through aggressive interference (Nakano et al. 1998). If some populations of bull trout are less aggressive in general and cannot compete as effectively for resources then they may be more susceptible to displacement via interference competition from invasive species. Ultimately, the hypothesis of different sensitivities of populations of native species (especially those with different migratory life histories) to displacement by invasive species will need to be subjected to critical testing in the field, among multiple populations. Declines in bull trout abundance have resulted in a decline of population and life history diversity (Nelson et al. 2002). An understanding of potential differences in susceptibility of distinct populations to the threat of species invasions is critical for conserving diversity and thus pathways of biotic resistance to invasion for native species.

Figures

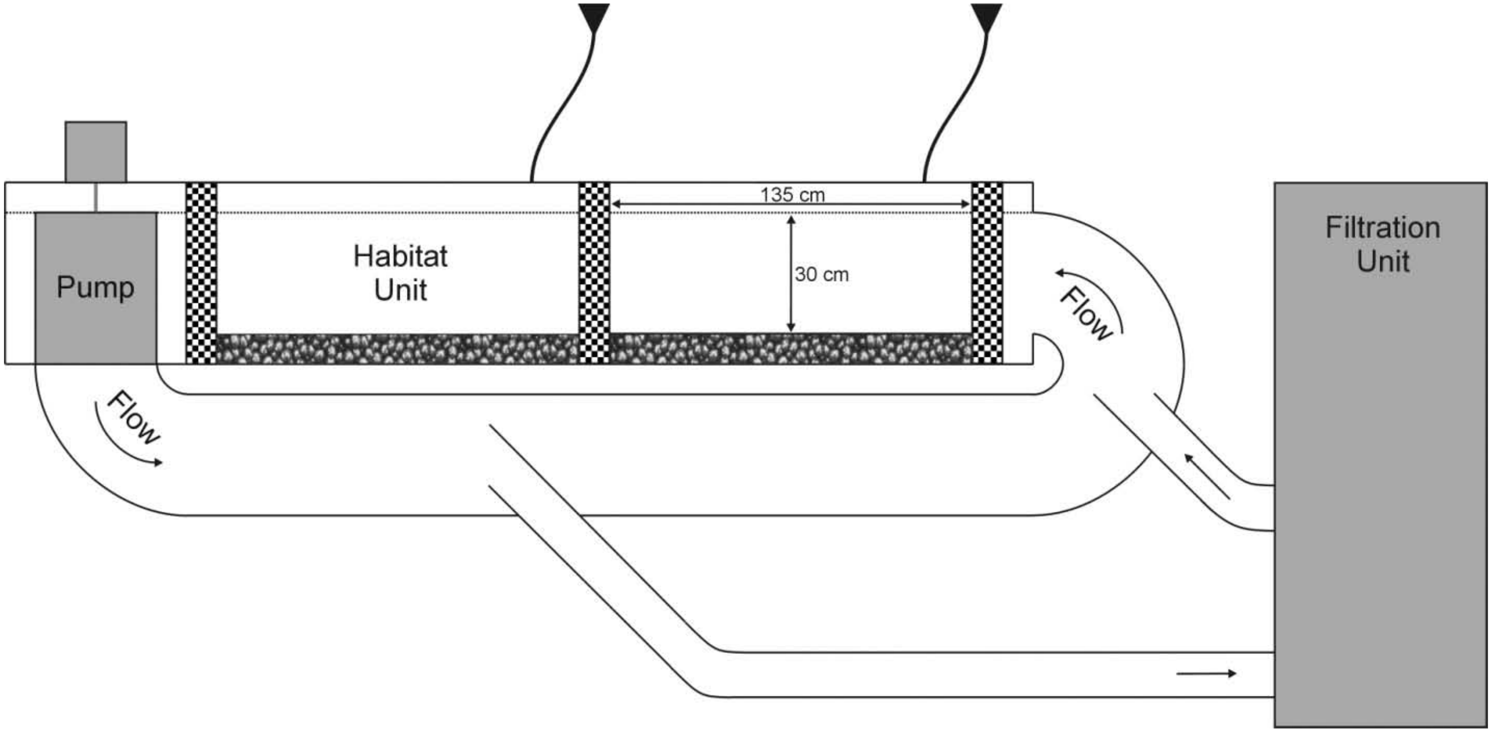

Figure 4-1: Side-view of artificial stream used for experiment (total unit volume of 940 L). The habitat unit was divided into two experimental areas (135 cm l X 50 cm w X 30 cm d) used for competition trials. A flow-through diversion to a filtration unit continuously cleaned and chilled the water. Feeding was performed via feeding tubes attached to funnels that were suspended above the stream.

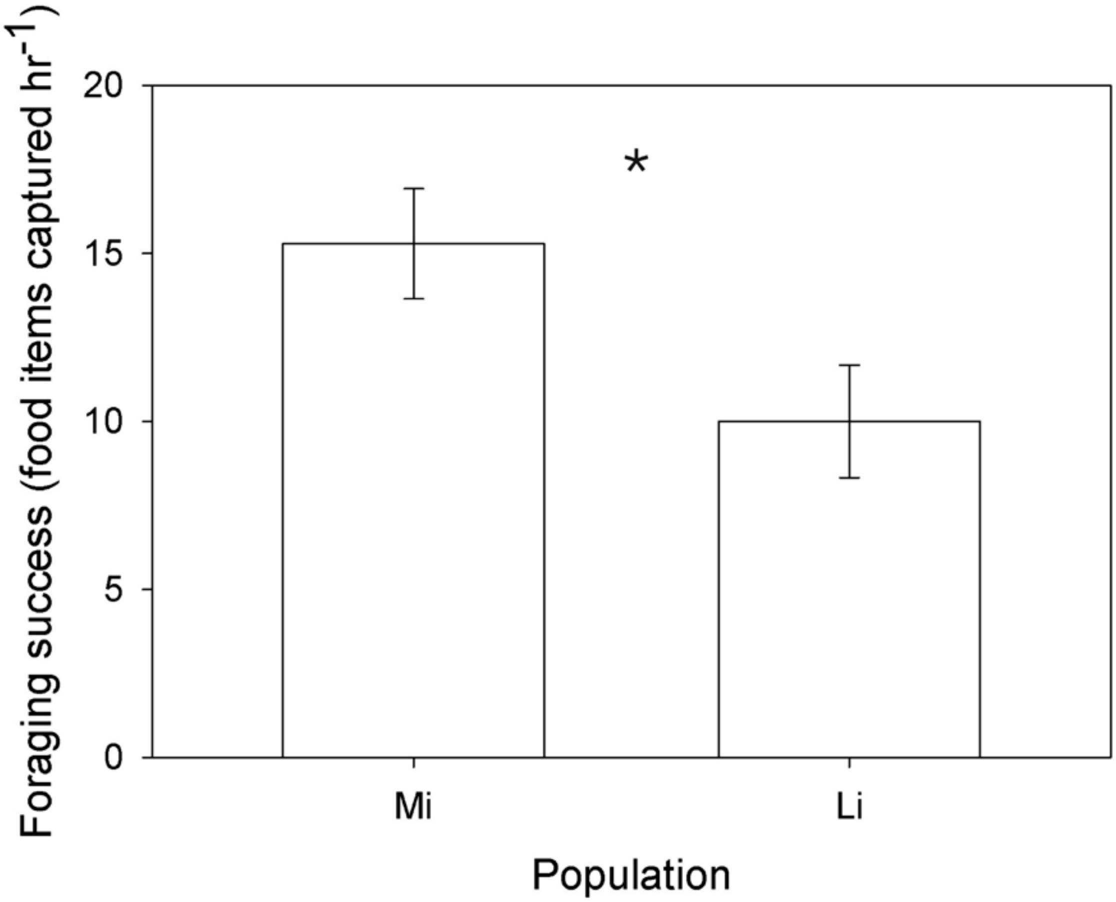

Figure 4-2: Foraging success (+/- SEM) of bull trout from each population when faced with a brook trout competitor. An asterisk indicates a significant difference (*P* < 0.05).

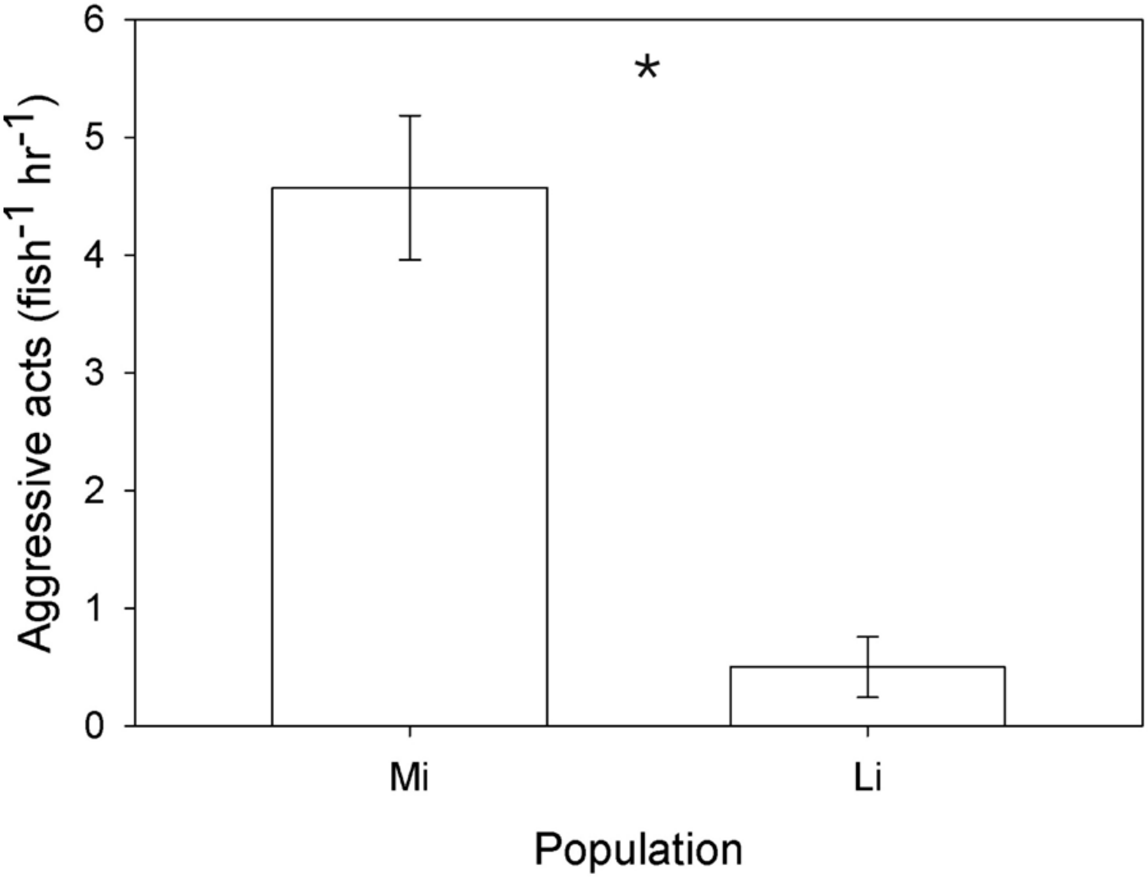

Figure 4-3: Aggression (+/- SEM) of bull trout from each population when faced with a brook trout competitor. An asterisk indicates a significant difference (*P* < 0.001).

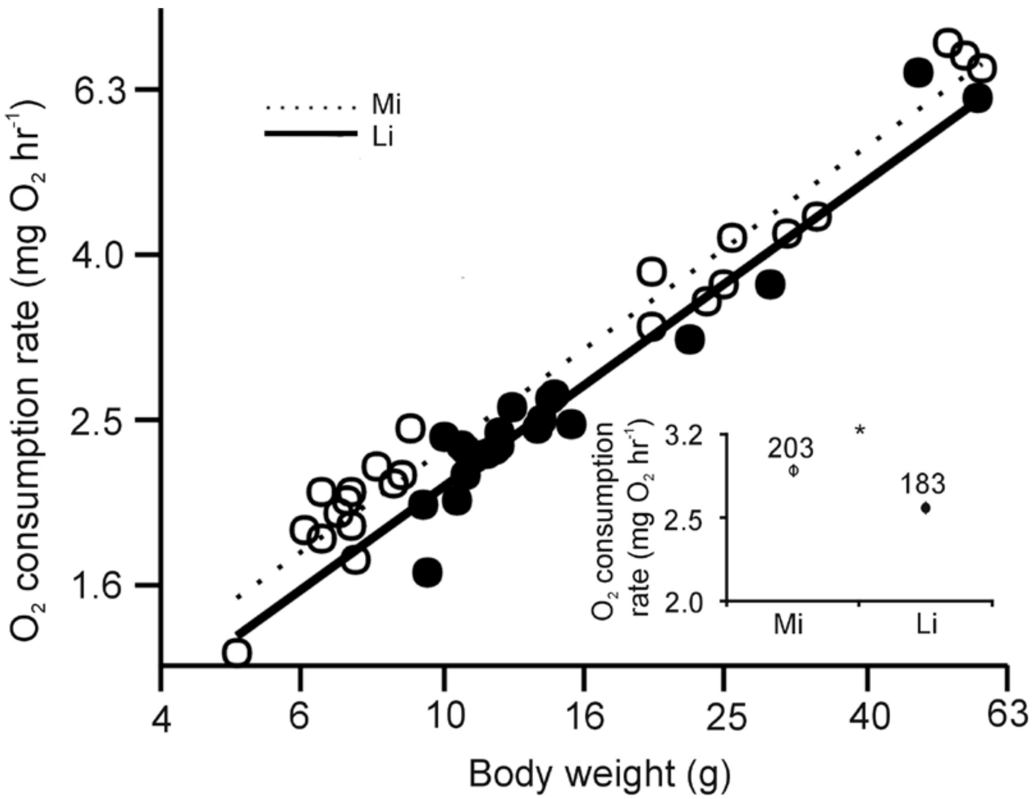

Figure 4-4: Oxygen consumption rates (OCR; mg O_2 hr^{-1}) across body weights of tested fish for the Mi (open circles) and Li (closed circles) bull trout populations determined by analysis of covariance. Both axes are log-transformed.

$$\text{Log OCR} = \text{-}0.278 \ + \begin{bmatrix} -0.023 & \text{Li} \\ 0.023 & \text{Mi} \end{bmatrix} + 0.619 \text{ Log weight}$$

Equation 4-1

Inset plot shows mean OCR of each population (+/- SEM) adjusted to the mean size of the fish tested. Values above each point represent mean OCR expressed in mg O_2 kg^{-1} hr^{-1}. An asterisk indicates a significant difference (t-test: $t_{43} = 4.06$; $P < 0.001$).

Chapter 5 Conclusions

Rocky Mountain stream ecosystems are relatively young. Following the Pleistocene glaciation, bull trout were successful at often being the first colonizers of this aquatic frontier. Following receding glaciers, the adaptations bull trout had to cope with harsh abiotic conditions of the most upstream reaches and migrate long distances, allowed them to rapidly colonize inland western North America. Headwater drainage transfers occurred and continue to occur though low-lying headwater sections across the divide of drainages. These drainages become connected when hydrological conditions are favorable for fish movement. The period of glaciation and deglaciation greatly facilitated such movements, and a combination of stream capture, glacial lakes and isostatic rebound allowed movement across drainages and established new populations (McPhail 2007). In addition, the long distances adult bull trout move through watersheds could result in straying into novel spawning tributaries from their far downstream confluences[1]. The result was that bull trout colonized a larger range in this area than any other salmonine of inland western North America, including in the Canadian Rockies (Behnke 2002). In these novel environments throughout their range, bull trout could maintain a broad ecological niche at the species level, with populations that were locally adapted to the various conditions found in such a heterogeneous landscape. With landscapes that are heterogeneous such as the Canadian Rockies, similar introduced species were also pre-adapted by chance to the various combinations of abiotic and biotic factors present in

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[1] *Salvelinus confluentus*; there is no more fitting name for this species, in capturing the role that watershed connectivity has played as a central factor in their evolutionary history, ecology, and persistence. The fact that George Suckley gave the species such an apt name in 1858 - without any of the current knowledge built upon by generations of hundreds of fisheries scientists - is truly remarkable.

streams that bull trout colonized (Fausch 2008; Korsu et al. 2010). The immature communities in these ecosystems poorly resisted invasion by specialists that exploited local resources more effectively than native generalists (Shea and Chesson 2002). This was facilitated by the myriad of co-occurring negative impacts to native species, including overharvest, habitat alteration and fragmentation. Brook trout appear to now supersede bull trout in much of their former range, and this dissertation provides observational and experimental evidence for several abiotic and biotic factors that may be involved.

Invasive populations of brook trout have passed through a series of filters according to their physio-chemical requirements and interactions with the community, allowing the species to become widespread and dominant in suitable streams throughout the Canadian Rockies (Colautti and MacIsaac 2004). Filters may be thought of as abiotic or biotic aspects of the environment to which a non-native species may be well, or else poorly, adapted. Mountainous regions of Western North America are heterogeneous environments; many streams or reaches within streams have unique communities or physio-chemical attributes that are influenced by factors such as the local climate, elevation, surficial geology, aspect, forest cover, or in-stream movement barriers. In many of these unique environments, introduced brook trout may be pre-adapted by chance based on their evolutionary history within their own native range (Fausch 2008). Bull trout and brook trout both require small streams with groundwater input for parts of their lifecycles, as these streams provide critical spawning and juvenile nursery habitat (Curry and Noakes 1995; Baxter and Hauer 2000). Within such streams that were historically bull trout habitat, this project identified that brook trout now dominated in selected areas, and that these sites had specific attributes that appeared to provide niche opportunities to pre-adapted brook trout (Shea and Chesson 2002; Fausch 2008).

There appears to be a suite of abiotic factors that may influence invasion of brook trout into bull trout streams. In the same way that that low calcium concentrations and pH may provide unsuitable habitats that are resistant to zebra mussel (*Dreissena polymorpha*) invasion (Ramcharan et al. 1992), certain physio-chemical attributes of some rocky mountain stream environments may be unsuitable for brook trout. Bull trout remained the dominant species of the two, in sites that were colder and had a large amount of large in-stream boulder and cobble substrate. Water temperature is clearly an important determinant of species distributions, as fish species are poikilotherms that have narrow, physiologically determined optimal temperature ranges. Brook trout are the warmest adapted of the charrs (Behnke 2002), and they were rarely observed in bull trout streams that were especially cold (average daily temperature of < 7 °C; Chapter 2). The adaptation to different temperature ranges is perhaps the dominant theory invoked in previous literature to explain brook trout invasion into bull trout streams (Paul and Post 2001; Rieman et al. 2006; McMahon et al. 2007; Rodtka and Volpe 2007); however, it is clearly not the only abiotic feature that appears to influence brook trout invasion (McMahon et al. 2007). In the observational study, habitat type was found to be at least as important as temperature in explaining brook trout invasiveness (Chapter 2).

Two types of major in-stream habitat were associated with brook trout invasiveness. Brook trout dominance over bull trout was associated with undercut bank habitat. This specific habitat type may be used by both species (Cunjak 1996; Watson and Hillman 1997), but has been identified as especially important habitat for brook trout outside their native range (Kozel and Hubert 1989; Krimmer et al. 2011). In contrast to undercut bank habitat, the presence of large in-stream substrate cover was negatively associated with brook trout dominance over bull trout (Chapter 2). The success of bull trout over brook trout in sites with large in-stream substrate may be fundamentally based on the two species' foraging behavior, which may be optimal under different habitat types. Experimental evidence in this study suggests that bull trout compete for resources with a competitor primarily by using scramble foraging tactics, rather than by aggressively defending a territory (Chapter 3). This may allow bull trout to outcompete brook trout in stream environments that have a large amount of in-stream substrate complexity (Chapters 2 and 3), as these environments reduce the benefits of aggressively defending a territory (Hasegawa and Yamamoto 2009). Measuring habitat preferences of species *in situ* where they are sympatric and communities are mixed represents a next logical step from this research.

Biotic factors involved in determining invasion success primarily relate to interactions with the community that may facilitate or else inhibit the establishment, spread and abundance of brook trout. In the field, brook trout were negatively associated with alternate non-native species (Chapter 2). Interactions with alternate competitors that have overlapping niches may limit brook trout invasion into some streams. This is the opposite of a phenomenon known as an invasional meltdown, whereby invasive species may facilitate each others' invasion success (Simberloff and Von Holle 1999). In the laboratory, competitive interactions between the two species were affected by fish density (Chapter 3) and population-level variation in bull trout behaviour (Chapter 4). In head-to-head competitions, bull trout outcompeted brook trout, but not when an additional pair of competitors was introduced, whereupon fish became more aggressive. Territorial behaviour of trout and aggressive interactions among competitors increases with increasing fish densities (Blanchet et al. 2006; Hasegawa and Yamamoto 2009). The territorial nature of brook trout and their social behaviour that allows them to compete at such high densities may allow them to effectively outcompete native species in streams in which they achieve much higher densities (Dunham et al. 2002; Benjamin and Baxter 2010). The behaviour that allows these fish to tolerate and compete at such high densities has been invoked to explain possible displacement of cutthroat trout (Schroeter 1998), and may have a similar relationship to bull trout in some situations. Another result of competition experiments was that bull trout outcompeted brook trout and were more aggressive when they were collected from Mill Creek, but not the Livingstone River. The Mill Creek population is migratory, whereas the Livingstone River population is non-migratory (Warnock et al. 2011). These differences in behaviour between these populations expressing different migratory life histories were linked to physiological traits. Population-level differences in competitive ability may explain some of the apparent differences among populations in their biotic resistance to invasion (Leisnham and Juliano 2010); however the generality of this phenomenon requires further investigation. In particular, the possibility that migratory populations are more resistant to invasion (Dunham et al. 2008) may be due to a variety of underlying reasons (Chapter 4) that remain unexplored.

In addition to the abiotic and biotic factors observed and tested that may influence invasion of brook trout into bull trout streams, there are many additional underlying mechanisms that may influence invasion that were not considered. In particular, invasion may be viewed as a population-level process that begins with initial arrival intensity (i.e., propagule pressure) of the non-native species. Because of incomplete documentation in most areas, this study did not examine how historic stocking intensity related to current trends of brook trout invasiveness. Initial propagule pressure, local dispersal and establishment are critical components in the successive stages that determine invasion outcome (Colautti and MacIsaac 2004). Initial propagule pressure was high in Alberta, the result of thousands of introductions throughout the eastern slopes that spanned over half a century, with declining efforts through the 1970s and 1980s (Paul 2000). Brook trout locally dispersed and generally established after several generations into downstream areas that were independent from their stocking location (Adams et al. 2001; Paul and Post 2001), in sites that were suitable to their physical requirements (McMahon et al. 2007). A similar situation was found for cutthroat trout in Colorado and New Mexico, in which stocking intensity was not related to success of establishment (Harig and Fausch 2002). Therefore, it is most likely that the current distribution of brook trout observed is mostly related to occupying suitable niche environments to which they are pre-adapted (Fausch 2008; Korsu et al. 2010).

Additional population-level processes are also likely important to influencing invasion of brook trout, as the species may have reproductive, survival or dispersal advantages that facilitate invasion. Regardless of any asymmetries in competitive abilities at the individual level, outnumbering the competitor is always an advantage. Where they are naturalized in streams of western North America, brook trout tend to mature quickly, at a demographic advantage that allows them to swamp the community over native species (Dunham et al. 2002; Paul et al. 2003; Rodtka 2009; Benjamin and Baxter 2012).

In addition, the local dispersal of brook trout likely contributes to continual invasion in many areas (Adams et al. 2002), and may result in a slow and persistent spread of the species (Westley and Fleming 2011). This may be facilitated by changing mountain stream environments due to human disturbance. When considering brook trout invasion from a biogeographical perspective, further invasion or even current patterns of occurrence of brook trout may be influenced by source-sink dynamics at the population level (Peterson et al. 2004). Brook trout appear to establish especially well in unconstrained valley bottoms, first order streams, and areas showing a high amount of beaver activity (Benjamin et al. 2007). This may again reflect another niche opportunity that brook trout are well adapted to, since beaver density is high in low gradient Canadian Shield streams, and brook trout appear to have well suited adaptations to spawning and carrying out their lifecycles in the highly fragmented, sedimented stream sections that beavers engineer. In western North America, beaver ponds and first order streams may act as sources that provide a continual supply of brook trout into surrounding sink habitats (McCaffery 2009). Therefore, many areas in which brook trout were detected, even in great numbers, may actually be influenced by inputs from nearby sources from which they can colonize. Research into population-level mechanisms that supply continual propagules of brook trout to sink areas may greatly advance our understanding of their pattern of occurrence and spread, and I encourage further research into this topic.

Conservation implications and recommendations

Results of the field study in this project (Chapter 2) and previous literature (Paul and Post 2001; Rieman et al. 2006; McMahon et al. 2007; Rodtka and Volpe 2007) point to water temperature as one of the most important determinants of brook trout invasion into bull trout streams. This is not surprising, given that brook trout have the greatest optimum temperature range and are the most warmwater tolerant of the charrs (Behnke 2002). Maintaining suitable thermal habitat for bull trout is critical (Dunham et al. 2003a), especially as anticipated climate warming may result in range expansions of brook trout into regions formerly occupied by bull trout (Rieman et al. 2007). This is especially pertinent in areas of Alberta that face receding glacial input to streams which keep water temperatures cool (Schindler and Donahue 2006). Other effects of in-stream and landscape disturbance (e.g., logging, wildfire, livestock grazing, road networks) that are shown to increase stream temperature must be carefully considered (Johnson and Jones 2000; Hitt 2003; Webb et al. 2008). Such disturbances may alter stream temperature through the mechanisms that influence the heat budget of streams (e.g., incoming solar radiation, stream flows etc.) (Poole and Berman 2001). Cool stream temperatures may be maintained either by limiting disturbance, or strategic restoration of habitats; however, our understanding of how climate change and disturbance may alter stream thermal regime is limited and sometimes paradoxical in small streams (Moore et al. 2005; Arismendi et al. 2012). Future research is needed to understand the variety of complex underlying mechanisms that govern stream temperature, if we are to apply stream-specific measures to maintain cool stream temperatures.

Both field and laboratory observations from this study revealed that physical habitat structure may influence invasion of brook trout into bull trout streams. Streams with a high amount of habitat complexity are important for juvenile bull trout (Al-Chokhachy et al. 2010), and bull trout appear to resist invasion in sites that have a large amount of in-stream cover (Chapter 2; Rich et al. 2003). Timber harvest, road network construction, livestock grazing and off highway vehicle traffic may increase sediment loading. This may embed substrate that juvenile bull trout use as preferred cover (Watson and Hillman 1997). In addition to landscape disturbance, direct (e.g., altered hydrograph) and indirect effects (e.g., increase of wildfire occurrence and severity) of climate change may alter sediment loading into some streams and reorganize channel structure (Schindler 2001; Rood et al. 2005; Dunham et al. 2007). If disturbed habitats shift to favor the preferred habitat niche of brook trout over bull trout, then this may facilitate their invasion (Dunham et al. 2003b; Gresswell and Vondracek 2010). Maintaining critical habitat components directed to the niche requirements of bull trout should be a goal for sustaining populations, especially those that are currently invaded by brook trout.

Brook trout may continue to spread in Alberta, and this study represents a snapshot in time that has lagged several decades after brook trout have already established (Paul 2000). Most sites tended to be dominated by one species or the other. Sites with mixed communities were not specifically examined, but may have enough environmental heterogeneity to allow niche differentiation of the two species and their coexistence (Nakano et al. 1999); conversely, some of these sites may not be in a state of fixed equilibrium, but rather the initial, or progressive stages of invasion. This may be influenced by ongoing changes in stream habitat structure and migratory connectivity, or further decline of bull trout populations due to human disturbance and climate change. Future trends should be monitored in occurrence and abundance of brook trout, to see if the current distribution changes, and if we are witnessing their slow and persistent spread (Westley and Fleming 2011). In particular, I did not consider any stream environments that drain the west slopes of the Canadian Rockies, or any other drainage basins throughout the Canadian western cordillera that brook trout have invaded. Brook trout are present in the upper Peace, Columbia and Fraser River basins in British Columbia, which represent some core areas for native populations of bull trout. There are concerns with the spread of brook trout and possible displacement of bull trout in these basins (Hagen and Decker 2011). The results of this thesis may be used to identify areas of high risk to further invasion in British Columbia.

Fully integrated remediation efforts to habitat and native species recovery, along with brook trout removal should be prioritized to particular sites that have the highest chances of success (Roni et al. 2002; Gresswell and Vondracek 2010; Kolar et al. 2010; Dunham et al. 2011). Applied conservation efforts to remove brook trout may be most successful in sites that are poor habitat for this species. A successful, extensive brook trout removal project was conducted in a lake-stream system in Banff National Park where the species had been established for decades (Parks Canada 2012: http://www.pc.gc.ca/media/nature_e.asp?video=79). The habitat structure in the stream segment of this system was relatively high gradient, cold, and contained a high amount of large in-stream substrate, with little undercut bank or connectivity to areas from which brook trout could recolonize (C. Pacas, Parks Canada, personal communication). In many other systems, removal of brook trout by electrofishing may be ineffective (Meyer et al.

2006), especially in systems with a large amount of undercut bank habitat (Thompson and Rahel 1996). Alternate methods of brook trout removal may be accomplished by managers using tools that are already at their disposal through engaging the public with strategic angling regulations (Paul et al. 2003). Directed harvest using anglers may provide an efficient, cost effective and continuous source by which brook trout may be controlled, with a resulting recovery of native species (Stelfox et al. 2004). In sites that may have a poor chance of recovery due to unsuitable or degraded native habitat, high densities of brook trout or difficult removal by electrofishing, netting or angling, the use of explosives or piscicides may be the only option available for managers. This may be an appropriate option in densely populated habitats that are marginal for native species (e.g., beaver ponds in side-channels), but supply continual propagules of invading brook trout to adjacent areas inhabited by native species.

Properly identifying priority sites for integrated remediation efforts will benefit from preliminary on-site research and feasibility analysis (Dunham et al. 2011). Temperature data loggers may be placed in-stream and habitat surveys may be conducted as preliminary research to assess the specific requirements and logistics of removal and/or remediation projects. These surveys could identify areas that are associated more closely with the niche requirements of bull trout as having the highest likelihood of success. In areas needing restoration of habitat, surveys before and after could determine whether efforts were successful at altering habitat to target these requirements, providing they are achievable in the first place; follow-up long-term monitoring is critical to assess whether the target of native fish recovery has been achieved (Billman et al. In Press). Restoration efforts may include fencing of stream habitat where livestock grazing occurs, riparian canopy recovery, and limiting watershed disturbance, which are practices that may recover stream temperature and sediment size (Platts et al. 1989; Platts 1991; Moore et al. 2005). In concert with habitat rehabilitation, efforts to re-establish or facilitate the recovery of the native species may then be more successful when combined with direct removal of brook trout. For example, bull trout were extirpated from Willow Creek in the 20th century (Fitch 1997). Attempts to re-introduce bull trout to this watershed were attempted in 2000 and 2007, with the stocking of fingerlings hatched from a wild-stripped stock from a nearby population. Sampling efforts indicate that natural reproduction was unsuccessful in this watershed, as no juvenile bull trout were captured in this study or in any other sampling efforts in the watershed since the initial stocking efforts (ASRD 2009). Willow Creek, and many of its tributaries, are currently dominated by high densities of brook trout. Sites on the stream were found to have smaller substrate, higher temperatures and a large amount of undercut bank habitat relative to the average conditions encountered throughout the study. All these conditions were associated with high brook trout invasiveness. The stream is subject to heavy grazing activity and a large amount of off highway vehicle traffic in all but the highest reaches, which may have altered the stream habitat and thermal regime to its present state. In addition, the watershed is isolated from neighboring bull trout populations, which makes natural supplementation from connectivity unlikely. Recovery potential of a bull trout population in this watershed is low (ASRD 2012), especially considering that the habitat is currently saturated with non-native brook trout, and may no longer be suitable for the native species. Had a feasibility study been conducted prior to re-introducing bull trout (Dunham et al. 2011), it would have been clear that there would be a low chance of success unless efforts were combined with a campaign of both non-native removal as well as habitat rehabilitation. These management objectives can be greatly aided by collaborative partnerships among multiple stakeholders that allow both public and private involvement in the process of native fish recovery and habitat restoration (Gresswell and Vondracek 2010).

In the western United States, artificial barriers are proposed as a management tool to limit further spread of invasive species (Thompson and Rahel 1998; Peterson et al. 2008; Fausch et al. 2009). While clearly of use in many circumstances, there are no areas encountered throughout the Alberta Rockies in this study where I would recommend they be used to limit the further spread of brook trout into bull trout streams. Natural in-stream barriers and steep stream gradients may restrict the spread of brook trout in some stream networks (Adams et al. 2001; Dunham et al. 2002), but artificial barriers would lead to a loss, or limit the recovery of the migratory form of native bull trout (Morita et al. 2009), and connectivity to neighboring populations has in fact been recognized as increasing bull trout resistance to brook trout invasion (Rich et al. 2003). This life history may be more resistant to brook trout invasion for many underlying reasons (Chapter 4), and is a vital component to the long-term genetic and demographic sustainability of many bull trout populations (Swanberg 1997; Dunham and Rieman 1999; Nelson et al. 2002; Warnock 2008). Therefore, while well-intentioned, purposeful fragmentation may cause greater harm than good in most cases for bull trout. Where natural barriers exist, enforcement and public education efforts to curb unauthorized movement of non-native fish above barriers may be undertaken to protect isolated bull trout populations (Rahel 2007).

Former stream habitat restoration or conservation efforts had rarely taken into account future scenarios imposed by climate change or other disturbances, but there is an increasing shift in recent literature to account for potential changes (Rahel and Olden 2008; Jonsson and Jonsson 2009; Milner et al. 2009). By considering future changes, inland managers may be able to strategically implement and prioritize conservation or restoration efforts to targeted areas at greatest risk of deterioration (Battin et al. 2007). Maintaining watershed integrity, habitat complexity, thermal refugia, demographic connectivity and restoring or augmenting particular niche environments of native species may buffer habitat loss and confer biotic resistance to invasion, even as climate change or disturbance may shift stream temperature and habitat in favor of the non-native species (Rieman et al. 2006; Gresswell and Vondracek 2010). Salmonid fishes have an incredible ability to rapidly adapt to local environments (Hendry et al. 2000; Koskinen et al. 2002); it is what has made possible their current diversity and historic success as one of the dominant holarctic fish families since the late cretaceous. Remaining populations of bull trout are no exception, and despite their susceptibility, they can be naturally resilient. Strategic conservation efforts directed to their requirements, and suppression of invasive competitors, may augment this resiliency, and ensure their continued success and diversity in the future.

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Appendix

Analysis of data

All data chapters of this thesis contain a variety of statistical methods to analyze data. While the majority of the analyses used in this thesis are basic statistics that can be easily reviewed in introductory biometry texts, this section introduces two more complicated analytical approaches I took to analyze data. These two approaches are logistic regression, and the information theoretic approach to multiple regressions. I have given these two statistical methods a special description here because the literature base in ecology is recently founded, and most is beyond what might be covered in a basic graduate level university course on statistics for biological data. The majority of the basis for my descriptions of these analyses comes from the books of Hosmer and Lemeshow (2000) and Burnham and Anderson (2002) for logistic regression and the information-theoretic approach, respectively. I have also learned the applied approach to these analyses mainly from a literature base that is related to my own work (Dunham and Rieman 1999; Paul and Post 2001; Harig and Fausch 2002; Rich et al. 2003; Ripley et al. 2005; Rieman et al. 2006; Benjamin et al. 2007; Rasmussen 2007; McCleary and Hassan 2008; Muhlfeld et al. 2009; Kitanishi et al. 2010). For a particularly good example of the use of both of these for field observational studies, you may wish to read the paper of Rich et al. (2003), which provides an excellent but succinct explanation of these analyses in the methods and results.

Logistic Regression

Regression analyses are the mainstay of observational studies in ecology where the aim is to statistically model relationships between variables that are suspected to be dependent. Simple regression is used when there is one independent variable, but the model can easily be extended into a multiple regression to account for more independent variables. In this thesis, simple and multiple regressions are used. The following section provides a little background on the types of regression tests performed, and why they are appropriate for the analyses used in the aforementioned chapters.

If the dependent variable is largely unbounded and continuous (e.g. growth rate, tissue concentration of a metal, time spent foraging etc.), an ordinary least squares regression is appropriate. Ordinary least squares regression is covered in many basic statistics reference books and is a common analysis in the biological sciences (Whitlock and Schluter 2009). Logistic regression is a special consideration when the dependent variable is discrete. This is often the case for fish species presence data, in which presence or absence of a species is modeled as a function of several independent variables (Dunham and Rieman 1999; Paul and Post 2001; Rich et al. 2003; Ripley et al. 2005; Rieman et al. 2006; Benjamin et al. 2007). In this instance, the relationship between the dependent variable and independent variable(s) can be characterized by a sigmoidal relationship between the probability of occurrence and the independent variable(s).

In order to describe this relationship, a logit transformation is applied to the probability p of having an outcome, given a set of k1,…,kx independent variables:

$$\mathrm{logit}\,(p) = \ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \mathrm{k1} + \cdots + \beta_{\mathrm{x}} \mathrm{kx}$$

Equation A-1

by exponentiating both sides, we can model the probability of having a successful outcome in the binary dependent variable by:

$$p = \frac{e^{\beta_0 + \beta_1 \mathrm{k1} + \cdots + \beta_{\mathrm{x}} \mathrm{kx}}}{1 - e^{\beta_0 + \beta_1 \mathrm{k1} + \cdots + \beta_{\mathrm{x}} \mathrm{kx}}}$$

Equation A-2

In ordinary least squares regression, the parameters for the equation (β_0, β_1,…, β_x) would be estimated by the values that minimized the sum of squared deviations of the observed values from those predicted by the model equation. In logistic regression, these parameters are instead estimated by a maximum likelihood method that is calculated by iterative procedures that are automated in statistical software packages.

One assumption of the logistic regression is that the logit is linear in its parameters, that is, the relationship between the logit and covariate(s) are linear. Screening the distributions of each continuous covariate, and their relationship with the logit in advance may allow the most appropriate transformation to be applied and thus model the best linear fit.

Assessing overall model fit is an important step in the modeling procedure, as it provides information on how well the logistic regression describes the relationship between the covariate(s) and the dependent variable, and if data are overdispersed. Two goodness-of-fit values that are commonly used to assess model fit in logistic regression are the Pearson chi-square and Hosmer-Lemeshow statistics. These are both described in greater detail in Hosmer and Lemeshow (2000), and are commonly encountered in output of statistical software packages.

Once an appropriate model has been fit, the next stage is to interpret the coefficients of the independent variables. Coefficients are either positively or negatively associated with the dependent variable, having either positive or negative values, respectively. The most meaningful approach to interpreting the coefficients is through the odds ratio, which is valuable because it provides a biologically meaningful measure of how a change in the independent variable affects the probability of a successful outcome in the binary dependent variable. Like a linear regression, this represents the slope of a change in the logit corresponding to a unit change in the independent variable. In addition, 95% confidence intervals may be calculated for each based on the standard error estimates to ascertain whether coefficients are statistically significant (Rich et al. 2003). How the odds ratio is calculated depends on if the independent variable is binary, ordinal or continuous.

The value of the odds ratio is centered around 1, with a value of 1 corresponding to no relationship between the dependent variable and independent variable (i.e., a slope of 0). Negative relationships take on values that asymptotically approach 0 from 1, while positive relationships take on values that asymptotically approach ∞ from 1. The odds ratio, relative to one, then can be thought of as the likelihood (or unlikelihood for values < 1) of a successful outcome in the dependent variable, given a unit change in the independent variable.

For binary independent variables, odds ratio may be calculated according to:

$$\text{OR} = e^{\beta_i}$$

Equation A-3

where β is the model-estimated coefficient (parameter estimate) of the i^{th} independent variable. This represents how a successful outcome in the binary independent variable affects the probability of a successful outcome in the dependent variable.

For continuous independent variables, odds ratios are calculated by first multiplying β_i by a biologically relevant scaling factor C:

$$\text{OR} = e^{C*\beta_i}$$

Equation A-4

This now represents how an increase of C units in the independent variable affects the probability of a successful outcome in the dependent variable.

In order to test for significance of each variable, we can use the standard error estimate from the model and by assuming a z-distribution we can calculate a 95% confidence interval:

$$95\%\ \text{CI} = e^{C*B_i \pm 1.96*C*SE_i}$$

Equation A-5

where *C* is used as a biologically relevant scaling factor for continuous independent variables. If this confidence interval does not bound 1, then we can assume significance of the variable, as 95% of the predicted observations will not have a slope of 0.

Consider the following hypothetical example where we are trying to model the occurrence of an invertebrate species that are in streams draining aluminum mines in a mountainous coastal region. These mining sites span a wide range in elevation; from previous research, we suspect that the invertebrate prefers higher elevation streams. We design a study to look at the presence or absence of the species in mining and non-mining impacted sites throughout a range of elevations. After collecting the data on occurrence from randomly selected sites (Table A-1), a logistic regression is run predicting species occurrence from both the independent variables of elevation (continuous) and mining impact (discrete and binary). After confirming that the model fits appropriately, we get the following parameter estimates and associated standard errors for each independent variable (Table A-2)

Using Equation A-3, we find that the estimated odds ratio for mining impact is 0.37. This means that sites with mining impact have 2.7 times (1/0.37) higher probability of finding the species absent relative to sites without mining impact. Applying Equation A-5, we find that this impact of mining is significant, as over 95% of the time (based on a z-distribution from the observations) the odds ratio will fall between 0.21 and 0.67.

Unlike mining impact, the positive sign of our parameter estimate indicates that elevation is positively associated with the presence of the invertebrate species. Because elevation is a continuous variable, we must calculate the odds ratio by multiplying the parameter estimate by a biologically relevant scaling factor *C* (in this case, I chose 100m), since an increase in 1m elevation is not conceptually meaningful or useful in making predictions. Using Equation A-4, we find that an increase in 100m elevation results in an odds ratio of 1.23. Thus with every 100m elevation gain, we have a 23% (1.23/1) increase in the odds of the invertebrate species occurring. By applying Equation A-5, we find that this variable is also significant, as 95% of the time, the odds ratio falls between 1.01 and 1.51 for an increase of 100m elevation. From this example, we may conclude that mining activity is negatively associated with the occurrence of the invertebrate species, but elevation also may naturally dictate the species range across longitudinal stream gradients. One could further run an interaction term on the independent variables to determine whether mining has a disproportionately higher negative association with species occurrence, depending on the elevation.

In addition to using logistic regression for a binary dependent variable, there may be special cases in which it can be applied to analyze proportion data (Rasmussen 2007). Since a proportion or percentage is bounded and can never be less than 0 or more than 1 or 0% and 100%, the relationship with the dependent variable is often highly sigmoidal. This type of data is commonly encountered in social sciences, economics and epidemiology but less so in ecology and thus specific techniques for dealing with proportion data is not as well developed (but see Warton and Hui 2011). Logistic regression is an appropriate technique to analyze proportion data in biology, especially when proportions are derived from underlying discrete outcomes in (e.g., presence or absence of a species, presence of one species or the other, death or survival, deformity or no deformity, success or failure at crossing a supposed migration barrier etc.).

How proportion data is best analyzed in regression is dependent on the way the data in which the dependent variable is distributed and can be expressed. There are three approaches I have come across that have dealt with proportion data in regressions, and each may be optimal under different circumstances. Given the nature of the data and research question, the approach that yields the best fitting model may be chosen. This may be objectively assessed by looking at standard goodness of fit tests and examining the distribution of the residuals.

The first, and simplest approach, is to analyze the data as if it is a linear regression. This approach may work if the proportion data is centered around the middle, linear section of the sigmoidal curve (i.e., lots of ~50% values with not many approaching the bounds) and there is no interest in the study to extrapolate the proportions towards extreme values. Such a dataset might be possible, for example, in an ecotoxicological experiment examining the proportion of animals that die due to predation over a realistic gradient of contaminant concentrations (Table A-3). If the sigmoidal shape of the relationship is not pronounced and responds like a linear relationship across the range of values tested, then linear regression might model this relationship well for the realistic gradient tested (Figure A-1). In this example, the realistic range over which the concentration of the contaminant is found happens to itself be bounded to the linear part of the curve and thus may be appropriately modeled by a linear regression.

Unfortunately, most regression models are developed to predict proportions approaching the bounds, or data is very sigmoidally distributed with small sections of the linear portion of the slope. In this instance, linear regression would not optimally model this relationship. Take, for instance, the same situation in our fist example except we now wanted to either predict the proportion that died due to predation at an extreme water concentration value, or the data was highly sigmoidal across the range tested (Table A-4). Linear regression poorly characterizes this relationship, underestimating the slope through the threshold level, and providing nonsensical predictions of the relationship at extreme values (Figure A-2).

This type of data distribution and analysis is far more likely to be encountered in biological datasets. Traditionally, the arcsine transformation was applied to proportion data, as recommended in biometry texts (Sokal and Rohlf 1995; Zar 1999); however, recent literature has cast doubt on the appropriateness of arcsine transformations for proportion data (Warton and Hui 2011), and logit transformations appear to be the preferred approach of logistic regression that characterize the best statistical relationship. This brings us to the second approach of analyzing proportion data. In the previous example (Table A-4), linear regression underestimates the slope for where the threshold occurs, and overestimates the slope towards and beyond the bounded proportion values of 0 and 1. This is because the linear section of the curve happens to fall over a small threshold range in the covariate. Running a best fit linear function through it does approximate, but cannot capture the true sigmoidal relationship (Figure A-2). In addition, the linear regression equation exceeds the bounds rather than approaching them to positive or negative ∞. In order to arrive at the best fit and approximate the sigmoidal relationship, we may logit-transform the dependent variable according to:

$$\operatorname{logit}(p) = \ln\left(\frac{p}{1-p}\right)$$

Equation A-6

The analysis then follows the normal procedure of ordinary least squares regression:

$$\text{logit}\ (p) = \beta_0 + \beta_1 \text{k1} + \cdots + \beta_\text{x} \text{kx}$$

Equation A-7

When the dependent variable is transformed as such, a better fit with the same example dataset (Table A-4) may be achieved (Figure A-3), when we compare to the linear regression approach (Figure A-2). An innovative example where this was used on data in fisheries science was by Muhlfeld et al. (2009), where the dependent variable was the proportion of rainbow trout (*Oncorhynchus mykiss*) admixture into hybridized cutthroat trout populations. The authors found that logit-transformed rainbow trout admixture was positively associated with warm water temperatures and fish density in a multiple ordinary least squares regression.

If we are especially interested in the threshold values, and have a robust dataset with many proportion values falling towards the middle of the distribution, we may describe the least biased relationship of the threshold response by downweighting the values towards the bounds of the distribution:

$$\text{weighting factor} = p * (1 - p)$$

Equation A-8

This is extremely valuable in toxicology studies when there is interest in describing the slope of the threshold response, as there is less skewing introduced from overdispersed values towards the bounds of the distribution (Rasmussen 2007).

An important caveat of the logit transformation, and especially the weighted approach, is that it cannot transform values that are actually on the bounds (i.e., if there are 0 or 1 values), therefore like other log-transformed datasets, one must adjust extreme values of these (for example, by adding 0.01 to 0 values or subtracting 0.01 from 1 values). If boundary values are very common in the dependent variable, this analysis usually provides a poor fit, and the binary logistic regression should provide a much better fit to the data. This is the third approach used, and is the procedure I used in the analysis of the association between brook trout invasiveness and local-scale environmental variables (Chapter 2). As we can see, data was distributed towards the bounds (Figure A-4a), with most relative abundance values of brook trout at either 0 or 1 (Figure A-4b).

In this case, I simply treated the dependent variable as a binary value by discarding the uncommon middle values (those lying between 0.4 and 0.6), and treating all the values around the boundaries as separate categories. In the case of Chapter 2, these are categories of “low” and “high” brook trout invasiveness. This provides a much better fit than any other type of model, and is appropriate when proportions are derived from discrete values, such as presence of one species or the other. Although this does ignore some potentially important values in the middle of the logistic regression, these cannot be expressed by a binary logistic regression. Where values are more common, the logistic regression may be extended to accommodate them by adding “middle” category(s), and running an ordinal polytomous logistic regression (e.g. Harig and Fausch 2002). Such analyses are beyond the scope of this thesis, but may be found in Agresti (1996).

Multiple regression and the information-theoretic approach

Studies that attempt to examine the associations between species occurrence or abundance with several environmental variables at a large spatial scale are confronted with some common analytical issues (Mac Nally 2000). There are a variety of parametric and non-parametric alternatives that may be used to analyze such data (Rahel and Jackson 2007). Parametric approaches generally refer to the use of linear models to examine the association between the dependent variable and independent variables. Non-parametric alternatives that are more recent include decision trees and artificial neural networks, and a good introduction to these methods can be found in Rahel and Jackson (2007).

Multiple regression is a parametric approach that models the association between a single response variable, and any number of multiple predictor variables. This is a common analytical method in large-scale studies concerned with exploring the dependency between fish species occurrence or abundance and a suite of environmental variables that are hypothesized to be important. The goal of such studies is usually to predict how changes in X result in a change of Y, and/or explain the relative importance of a variety of X variables that are hypothesized to affect Y, and their potential interactions (Mac Nally 2000). Complex models are then often constructed, in which many predictor variables (sometimes dozens or even hundreds) are included in the model. As models include more independent variables, the fit of the model is improved simply by mathematical artifact, as R^2 is artificially inflated. Such is an “overfitted” model. This may occur even if explanatory variables are not biologically relevant, possibly leading to spurious conclusions. Interpreting more complicated models also becomes exponentially more difficult with the addition of more variables, especially if interaction terms are involved. The problem is often compounded when few observations are made, relative to the number of variables included. A commonly cited target for sufficiently powerful analysis is to have between 10 and 20 observations per independent variable included in the model (StatSoft 2012). Hence, a simple model is most preferred, in which few but meaningful terms are included as independent variables.

An additional complication of multiple regression is the presence of correlation among the independent variables, termed multicollinearity. This may complicate the interpretation of parameter estimates, which may change dramatically as correlated variables are added or removed from the model. This may be compounded if there is not a high enough sample size, relative to the number of variables (Flack and Chang 1987). Multicollinearity may therefore lead to spurious conclusions about the magnitude or even direction of association between independent and dependent variables (Rahel and Jackson 2007). Multicollinearity is often present if closely related variables are measured, that are not independent from one another. This can often be recognized by the researcher *a priori*, and variables may be chosen accordingly. For example, stream temperature and size are dependent variables with elevation in mountainous environments. Elevation is an easily measured (field data collection is not even necessary) surrogate for temperature and stream size, as temperatures will become lower and streams will become smaller as elevation increases. Elevation is therefore a commonly used independent variable in field studies using multiple regressions (Paul and Post 2001; Rich et al. 2003; Ripley et al. 2005; Rieman et al. 2006; Kitanishi et al. 2010). The problem is that elevation does not carry any biological relevance; species occur in areas according to the physio-chemical environment that fits their fundamental ecological niche. Stream size and temperature are direct measures of these, and including an additional term that is likely to covary with them complicates the model needlessly and may lead to multicollinearity issues. Thus, the number of measures can often be reduced *a priori* by including only the most biologically relevant variables, which fulfils the need both for a simple model, and often reduces multicollinearity. There are several approaches of screening for multicollinearity, with objective methods for determining whether it is a major problem in the analysis (Rahel and Jackson 2007). Three methods are commonly used: Firstly, screening the relationships of all variables with a correlation matrix and using a threshold R value to determine whether any two variables are highly correlated (Ripley et al. 2005). Secondly, multicollinearity can be assessed by using the variance inflation factor (VIF) (Dunham and Rieman 1999; Benjamin et al. 2007). This quantity can be calculated for each variable, based on the amount any predictor variable is correlated with any other variable in the dataset. Threshold VIF values are suggested by Rahel and Jackson (2007), among other authors (Dunham and Rieman 1999). Thirdly, multicollinearity may be detected as variables are included or removed from the model. If the addition or removal of any variables greatly changes the parameter estimate of any other variable, the two are likely dependent (Rahel and Jackson 2007).

In order to select the variables that are most important, and arrive at a simple model for interpreting their association with the dependent variable, a traditionally used approach is stepwise regression. Though widely used, this sequential method suffers from compromised type-1 error rates and artificially inflated R^2 values, and is highly criticized (Mac Nally 2000; Whittingham et al. 2006). Likewise, a researcher cannot perform regressions on each predictor variable (and combination thereof) independently to find the best fitting model, due to multiple comparison issues. These iterative processes of searching for a single “best” model by hypothesis testing generally result in overfitted models that are tailored to the data (a form of data dredging) (Burnham and Anderson 2002). Rather than performing multiple hypothesis tests on all possible models, an alternative approach is to rank models, based on their weight of evidence. Weight of evidence of all models may then be used to arrive at meaningful and unbiased parameter estimates and interpret the relative importance of variables. An approach of ranking multiple regression models according to this framework is the information-theoretic approach (Burnham and Anderson 2002).

The information-theoretic approach is rooted in information theory, and the principle of parsimony. The modeling approach starts with the assumption that every model resulting from every combination of variables may be possible, and provide valuable information. When considering a dataset with *k* independent variables, the number of possible models (not including interaction terms) is $2^k – 1$. A large number of such possible competing models (preferably all of them) are analyzed and ranked according to their maximized log likelihood, while penalizing models for having additional terms due to their artificially inflated fit. Akaike (1973) pioneered this with a resulting ranking value referred to now as AIC (Burnham and Anderson 2002). AIC provides the most weight to the model with the highest explanatory power, which uses the fewest number of terms in the model. In most cases in ecology, AICc should be used, which is an extension of the original method to account for small sample size (Burnham and Anderson 2002). This threshold cutoff of sample size is when the n number of observations is under 40 times the number of k independent variables

$$\text{AICc} = \text{AIC} + \frac{2k(k+1)}{n-k-1}$$

Where

$$\text{AIC} = \text{-2(log-likelihood)} + 2k$$

Equation A-9

The model with the lowest AICc value is deemed as the most parsimonious model (AICc_{min}). As the number of variables increases, the overall term becomes larger, hence we can see the $2k$ term penalizes the addition of further included variables; thus the formula can be seen as a parsimonious balance between model fit and variable number.

After AICc values are derived for each model, the Δ_i value is then calculated, which is the difference between the AICc value of the i^{th} of R possible models, and the most parsimonious model

$$\Delta_i = \text{AICc}_i - \text{AICc}_{min}, \quad \text{for } i = 1, 2, \ldots, R.$$

Equation A-10

Models are then ranked based on their Δ_i values, from smallest to largest for R models. If a model has a value that approaches 0, it has relatively high support as being plausible. Values that are above approximately four to seven are less plausible, and values above 14 are implausible, with little empirical support (Burnham et al. 2011). The actual probability of each model given the data can be estimated from Δ_i by its Akaike weight

w_i, which is a convenient term that assigns a probability to each model so that they sum to 1:

$$w_i = \frac{e^{(-\frac{\Delta i}{2})}}{\sum_{r=1}^{R} e^{(-\frac{\Delta r}{2})}}$$

Equation A-11

in a set of r=1,…,R possible models. Akaike weights can be used to calculate parameter estimates and associated confidence intervals that are averaged across many models, as well as determine which independent variables are the most important. This effectively gives the researcher an option to include as many models as they wish, rather than only using one model, which discards the useful information that may be present in any other plausible model. A commonly used metric to assess whether a model has sufficient support, and should be included for model averaging is the 1/8 cutoff recommended by Royall (1997); whereby all models that have weights of more than 1/8 (>12.5%) of the largest are included (Rich et al. 2003; Benjamin et al. 2007). Model averaged parameter estimates ($\hat{\hat{\beta}}$) may be calculated as a weighted mean from the regression coefficients ($\hat{\beta}$) of all i^{th} of R selected models

$$\hat{\hat{\beta}} = \sum_{i=1}^{R} w_i \hat{\beta}_i$$

Equation A-12

For estimating associated unconditional standard errors of parameter estimates, we also include a term for the conditional variance, given model g_i

$$\text{Unconditional SE} = \sum_{i=1}^{R} w_i \sqrt{\widehat{\text{var}}(\hat{\beta}_i | g_i) + (\hat{\beta}_i - \hat{\bar{\beta}})^2}$$

Equation A-13

from this value, we may now calculate 95% confidence intervals around the parameter estimate of each variable. This can be used to determine the significance of each independent variable, while including all of the plausible models that describe its relationship with the dependent variable (Rich et al. 2003; Benjamin et al. 2007).

The information-theoretic approach has emerged as a commonly used objective way to make inferences about the relationships between fish occurrence or abundance, with a suite of possible explanatory variables (Harig and Fausch 2002; Rich et al. 2003; Ripley et al. 2005; Rieman et al. 2006; Benjamin et al. 2007; Wenger et al. 2011). Its use extends far beyond this, and some authors assert that using this approach to model alternative hypotheses is a foundation of a new paradigm for empirical science (Burnham et al. 2011).

Diet and early growth of juvenile bull trout in headwater streams of the Oldman River drainage, Alberta.

Abstract

Ninety-one bull trout from six streams in the Oldman River drainage were sampled for diet and back-calculation of size-at-age. Bull trout throughout the study area primarily consumed aquatic invertebrates, and only a single case of piscivory was observed from 83 fish that had food in their stomachs. Back-calculated size-at-age one was negatively associated with elevation, and was significantly associated with the year bull trout turned one year of age. Fish that turned one in 2007 and 2008 were significantly larger (76.1 mm and 73.9 mm, respectively; $P < 0.05$) than those that turned one in 2009 (67.6 mm). After reviewing previous literature, diet and size-at-age patterns in the Oldman River drainage were typical of those observed through the core and southern area of the bull trout native range. These results suggest that juvenile bull trout in inland headwater streams overlap in resource use with other invertebrate consuming stream salmonids, including invasive brook trout. Early growth pattern may be heavily dependent on local rearing conditions that affect stream productivity and thermal regime.

Introduction

Bull trout (*Salvelinus confluentus*) are one of the most widely distributed native salmonid species in western North America, once occupying a wide known range in latitude (40°N - 65°N; Behnke 2002; Mochnacz et al. In Press), longitude (133° W – 111° W; McPhail 2007; Rodtka 2009) and elevation (sea level – 2400 m; Allen et al. 2010). Given this large native range, bull trout are present in dramatically different aquatic environments and diverse ecosystems; however, regardless of where they occur in this range, all bull trout must reproduce in cold, second to fourth order headwater streams due to their specialized spawning requirements (McPhail and Baxter 1996; Baxter and Hauer 2000). Migratory adults may occupy downstream areas in rivers, lakes, and estuaries, but headwater streams serve as critical rearing areas for the first few years of life. Stream rearing fish have higher survival to adulthood than fish that migrate early in life, despite the fact that early migrants may be more numerous (McPhail and Murray 1979; Fraley and Shepard 1989; Ratliff 1992; Stelfox 1997; Downs et al. 2006). In this early stage of life, bull trout are an integral part of headwater stream food webs, and their growth trajectories may be influenced by their trophic position and the stream environment.

While adult bull trout ecology is relatively well studied, significant gaps in knowledge are present in juvenile ecology. Most recent work to this end has been conducted on understanding patterns of juvenile habitat use and movement (Homel and Budy 2008; Al-Chokhachy et al. 2010). By comparison, studies on some aspects of basic ecology, including size-at-age, growth and food web roles are difficult to research from the literature. Most information can be found in reports, theses and conference proceedings from local scale studies conducted between the late 1970s and the mid-1990s. Given the wide geographic range over which bull trout occur, and difficult access to such limited circulation documents, it is difficult to assess general patterns of juvenile ecology throughout the species' range. Clearly, such knowledge is important for determining trends in growth and the role of juvenile bull trout in headwater stream food webs.

As adults, bull trout are generally recognized as piscivores where sufficient productivity can support such a trophic position (McPhail and Baxter 1996). Reviews on bull trout biology highlight that the shift to piscivory in these populations begins sometime between 100 and 200 mm in length (Pratt 1992; McPhail and Baxter 1996; Stewart et al. 2007); however, the evidence for this in headwater streams appears to be lacking, with few studies throughout the species' range reporting fish as a common diet item for juveniles (Shepard et al. 1984; Boag 1987; Hagen and Baxter 1992; Nakano et al. 1992; Underwood et al. 1995; Wilhelm et al. 1999; Ben-James 2001; Hagen and Taylor 2001; Mochnacz et al. 2004; Stantec 2004). Whether bull trout are opportunistic generalists on seasonally available prey (Brown 1994), or rapidly become specialized piscivores is essential knowledge when considering their role in food webs of headwater streams. This is particularly important when considering potential competitive or predatory interactions with introduced species, which are now common throughout the bull trout native range (Popowich 2005). Given the large geographic range over which bull trout exist and productivity gradients in headwater streams, there may be variation in diet and incidence of piscivory.

In addition to large scale trends in resource use, there may be geographic gradients in growth of bull trout occupying areas of different elevations. Warmer environments may support higher productivity for growth, longer growing seasons and/or shorter incubation periods for eggs and developing alevins, resulting in earlier fry emergence and more rapid growth trajectories. This in turn may promote piscivory, as bull trout become increasingly piscivorous with increasing size (Stewart et al. 2007). Indeed, bull trout early growth trajectory is variable among populations, and this may be attributed to environmental influences over productivity of the rearing environment (Carl et al. 1989). Generally, growth should be slower and fry emergence later with increasing elevation and latitude (Parra et al. 2009).

In this study, the diet and size-at-age patterns of juvenile (75-200 mm) bull trout are assessed in sites collected throughout a wide elevation range from several Southern Alberta streams, and compared to those documented throughout the species' range. Given that fish community becomes less diverse with increasing elevation, juvenile bull trout were expected to be rarely piscivorous in all but the lowest elevation sites. High elevation sites were expected to have the smallest size-at-age and lowest elevation sites to have the largest size-at-age.

Methods

Study area

Bull trout are one of two salmonine species native to headwater streams of the Oldman River drainage (OMR) in Alberta, Canada (Figure A-5). This area supports several local populations on the easternmost periphery of the bull trout native range (Warnock et al. 2010). Although adult migratory forms are found throughout the drainage in low elevation mainstem rivers, second and third order tributary streams are used for spawning, provided they contain suitable habitat. These streams are also used by juveniles as critical rearing habitat for the first one to three years of life, during which bull trout generally appear to be < 200 mm (Warnock 2008). There are several primary spawning and rearing streams in the OMR above the Oldman River Dam (Warnock 2008), and these span a considerable range of elevation. Spawning areas are found from ~1400 m to ~1750 m (Gerrand and Watmough 1998; Hurkett et al. 2011), and bull trout juveniles are found rearing in tributaries spanning an elevation range between ~1200 m (Mill Creek) and ~1800 m (Livingstone River) (Warnock 2008). All bull trout spawning streams are relatively cold (Chapter 2), with simple fish communities containing a combination of native and introduced salmonid species, including cutthroat (*Oncorhynchus clarkii*), brook (*Salvelinus fontinalis*) and rainbow (*Oncorhynchus mykiss*) trout. Lower elevation reaches of some streams also contain mountain whitefish (*Prosopium williamsoni*), sculpins (*Cottus spp.),* suckers (*Catostomus spp.*) and/or longnose dace (*Rhinichthys cataractae*).

While a growing body of literature exists on basic bull trout ecology in the OMR drainage, like elsewhere throughout the bull trout native range, there is little published work on basic juvenile ecology, including their role in food webs.

Fish sampling

Juvenile bull trout from six spawning and rearing streams were sampled from the OMR in July-October of 2009 (Figure A-5). Sampling in Hidden Creek occurred above a migratory barrier, which may separate a small resident population. Fish from all sites were 75-200mm, in order to not sample young of the year or adult life stages. Previous sampling has shown that bull trout in the OMR fall in between one and three years of age for this size range (Warnock 2008; Warnock unpublished data). Sampling was conducted by single-pass backpack electrofishing on 150-300 m stretches of stream per site, between 09:00 and 17:00. Mill, Lost and Dutch Creek and the Carbondale River contained multiple collection sites. Fish were euthanized in a lethal dose of clove oil, and individually packaged and frozen immediately for future dissection in the laboratory.

Diet analysis

Stomach contents were retrieved from frozen fish, and each individual food item was counted and identified into major groupings, including fish, terrestrial insects and aquatic invertebrates by taxonomic order. Stomachs were flushed with water to ensure all food items were counted. Larval aquatic invertebrates were further identified to family using Clifford (1991). Invertebrates were only counted if a full head was intact. Particular attention was devoted to identifying fish skeletal structures if present, as these are the least easily digested structures that can successfully identify cases of piscivory.

The frequency of occurrence for each major food resource was calculated (Chipps and Garvey 2007) based on the number of fish containing a food item of an aquatic invertebrate order, terrestrial insect or fish (J_i), divided by the total number of fish containing food in their stomachs (P):

$$\frac{J_i}{P}$$

Equation A-14

To further describe the diet of aquatic invertebrates to a finer taxonomic level, the percent of food items by number within each aquatic invertebrate order was calculated:

$$100\% \, \frac{N_f}{N_o}$$

Equation A-15

Where N_f is the total number of food items for each family within an order and N_o is the total number of food items in the taxonomic order (Chipps and Garvey 2007).

Comparing size-at-age among populations

All lethally sampled bull trout had both right and left sagittal otoliths extracted, which were subsequently cleaned and prepared for aging. The otolith displaying the clearest annuli was chosen for aging. With few exceptions, most fish had otoliths that displayed clear annuli, and these were aged fully intact under a compound microscope with reflected light (Figure A-6). Ethanol immersion was used to bring out the contrast between light and dark bands on otoliths. Unreadable otoliths were usually caused by extensive vaterite deposition or broken sections, and these were not used for further analysis. Otoliths were photographed under the microscope lens and aged in the graphics editing program Adobe Acrobat Professional® 9 (Adobe Systems Inc. 2010). The editing program was used to gauge radius length of the whole otolith, as well as the length to the end of the first annulus (winter growth period). Bull trout are fall spawners and emerge from gravels in the spring before high summer flow period. The deposition of the first annulus in this species thus corresponds closely to a full year of growth. This can be used to calculate the size of bull trout starting from their hatch time in the spring of the previous year.

The Fraser-Lee formula (Isely and Grabowski 2007) was employed to back-calculate the size-at-age (L_a) for all fish sampled from the measured radius at the end of each otolith annulus (O_a):

$$L_a = \frac{L_c - \alpha}{O_c} O_a + \alpha$$

Equation A-16

Where L_c and O_c are the length of the fish and whole otolith at the time of capture, repectively, and α is a correction factor derived from the intercept of a regression predicting L_c from O_c from the whole dataset (Isely and Grabowski 2007). Size-at-age was described for each of the back-calculated ages for all streams sampled. Literature values of back-calculated size-at-age were researched for comparative purposes with other studies conducted throughout the species' range. Since size was back-calculated to the time of annulus formation, size-at-age was not confounded by capture date.

An analysis of covariance (ANCOVA) was built to determine the factors that may be associated with size-at-age one from the pooled dataset. Emergence time, growing season and stream productivity are the main pressures that were assumed to control size-at-age one; therefore a model was built based on two predictor variables that would theoretically be a good surrogate to represent the variability caused by these pressures. The covariate used was elevation at the site of capture, since elevation is highly correlated with stream temperature (Rieman et al. 2006) and hence may drive the time of fry emergence, the length of the growing season and the productivity of the stream. Although a similar effect may be expected with latitude, this varied less than a degree through the study area and was not assumed to cause large scale differences among sites. Fish that were captured at higher elevations were predicted to be smaller at age one. In addition to elevation, there may be significant differences in size-at-age between each unique cohort. Bull trout that were different ages were categorized into the year they turned age one, and this was used as a second predictor variable. For example, fish that were caught in 2009 that were aged as one, turned one year of age in the same year, while fish that were aged as three turned one year of age in 2007.

In order to compare interannual differences in size-at-age one with corresponding large trends in climate, time series temperature data was collected from five meteorological stations run by the Government of Alberta (ARD 2012). These stations spanned a similar elevation range to the range tested in this study and were in close geographical proximity to the sites sampled (Figure A-5). Mean daily air temperature was taken from each station for the period spanning the vernal equinox of the previous year (March 20 for 2006-2009 period), to the day before the vernal equinox of the following year. This period was chosen to roughly conform to the full possible growing season of bull trout, and capture the mean temperature for each growing season for sampled bull trout. Data was screened for artifacts or processing errors by examining outliers from minimum and maximum daily temperature values throughout each time series (<-40°C or

>30°C). The mean annual temperature from all five sites were averaged, and plotted with marginal means of size-at-age one for each year (as estimated by the general linear model described above). All statistical analyses were conducted in JMP™ 8.0 (SAS Institute Inc. 2008) and R 2.15 (R Foundation for Statistical Computing 2012).

Results

Of the 91 fish caught, 85 were successfully aged (Table A-8). Sixteen were three year-olds (turned one in 2007), 34 were two year-olds (turned one in 2008) and 35 were one year-olds (turned one in 2009). Of the 91 fish caught, 8 had empty stomachs and were removed from further diet analysis.

Diet

Bull trout stomachs contained four orders of aquatic insects, terrestrial insects and fish. The food resource that was the most frequently encountered was Ephemeroptera, occurring in the majority of stomachs (Figure A-7). Fish was the least commonly encountered food resource, as there was only one case of piscivory. This fish was a two year old (146 mm) caught in the lowest elevation site in the study area (1375 m, Mill Creek; Figure A-5) and was not exclusively piscivorous, as aquatic invertebrates were also found in its stomach.

The four aquatic insect orders encountered included Plecoptera, Tricoptera, Ephemeroptera and Diptera (Tipulidae only). Within these orders, some families were more commonly ingested than others (Figure A-8).

Size-at-age

Back-calculated sizes at each age showed relatively linear growth trajectory in OMR streams throughout the first three years of life (Figure A-9). Mean size-at-age in the populations of the study area spanned a range that was similar to those encountered in other studies that have back-calculated bull trout size-at-age from aging structures (Table A-9).

The overall model predicting size-at-age one from elevation and year was significant (Figure A-10; $R^2 = 0.50$ $F_{3,81} = 26.7$, $P < 0.0001$). An interaction term between year and elevation was not significant ($P = 0.55$) and was dropped from the model. Elevation was negatively associated with size-at-age ($P < 0.001$) and year was significant ($P < 0.01$). A Tukey post-hoc test ($\alpha = 0.05$) on the model-estimated marginal means of the year variable revealed that fish that turned one in 2007 and 2008 were significantly larger (76.1 mm and 73.9 mm, respectively) than fish that turned one in 2009 (67.6 mm). These marginal means and associated standard errors were plotted with the mean air temperatures encountered in the corresponding years (Figure A-11). The warmest year corresponded with the largest size of one year old bull trout, and the coldest year corresponded with the smallest size.

Discussion

As predicted, bull trout fed primarily on aquatic invertebrates, although piscivory was less common than expected (one out of 83 cases where stomachs were not empty), especially at lower elevation sites. Reviews of bull trout biology suggest that bull trout, given sufficient forage, begin to shift to a piscivorous diet as they become larger than 110 mm and move downstream to more productive environments (Pratt 1992; McPhail and Baxter 1996; Stewart et al. 2007). Although some studies report juvenile bull trout as being primarily piscivorous (Horner 1978; Goetz 1997), upon reviewing all available studies conducted on bull trout diets, cases of piscivory in this size and age class are absent or rare (Shepard et al. 1984; Boag 1987; Hagen and Baxter 1992; Nakano et al. 1992; Underwood et al. 1995; Wilhelm et al. 1999; Ben-James 2001; Hagen and Taylor 2001; Mochnacz et al. 2004; Stantec 2004). Therefore, the shift to piscivory for most populations likely occurs when juveniles outmigrate from rearing streams and/or when they attain larger sizes and subadulthood (> 200 mm). Non-migratory populations often never make this shift due to a lack of fish forage in spawning streams, and migratory fish may still continue to supplement their diet into subadulthood with aquatic invertebrates and other available forage (Boag 1987). This was found to be the case in two independently conducted studies of adfluvial populations, where a shift to a predominantly piscivorous diet occurred well into adulthood, at over 500 mm in both cases (Connor et al. 1997; Guy et al. 2011). Piscivory in juveniles may be more common in some headwater streams of the bull trout range that have more abundant food resources and seasonally available fish forage. This supports the notion that juvenile bull trout are opportunistic foragers that will exploit any abundant food resource available that is within their gape limit (Brown 1994; Stewart et al. 2007). For example, juvenile bull trout in coastal headwater systems with stream rearing salmon parr may have greater seasonal piscivory rates than in inland streams, where juvenile fish production is not supplemented by marine productivity. More thorough studies throughout the bull trout range are needed to determine the role of juvenile bull trout in headwater stream foodwebs. Modern foodweb analysis techniques using stable isotope analysis should serve particularly useful for assessing this (Vander Zanden and Rasmussen 1999; Popowich 2005; Meeuwig et al. 2011).

Cold inland headwater stream foodwebs are generally very simple, and limited resources are available for fish in these relatively unproductive environments. Given that most populations of juvenile bull trout are secondary consumers that feed primarily on aquatic invertebrates, they are likely to overlap in resource use with co-occurring non-piscivorous foragers. Bull trout in headwater streams of inland drainages do not usually co-occur with diverse native communities of salmonid fishes; however, introductions of exotic species have greatly increased encounters between juvenile bull trout and a much more diverse fish community. The most commonly occurring non-native salmonid species that is naturalized throughout the range of historic bull trout spawning and rearing streams is the brook trout (Chapter 1). Additional species introduced include rainbow trout, cutthroat trout and brown trout, but these are less commonly implicated in ecological niche overlap with bull trout (Nakano et al. 1998). Streams in the OMR in which this may occur between bull trout and brook trout include Mill Creek and Beaver Mines Creek. Brook trout have been present in these streams for at least 60 years as of the time of this study and have not spread further thus far, although no significant barriers are present that would preclude the further spread of brook trout further throughout the Castle River drainage (Figure A-5). Brook trout are widely introduced through every other major river drainage in the bull trout native range in Alberta. It is a reasonable assumption that all populations of these two species in Alberta overlap in food resource use where they co-occur, at least during the juvenile stage. Despite similar resource use, co-occurring species may have divergent benthic and drift foraging behaviours which lead to capture of distinct prey types, leading to potential co-existence (Nakano et al 1999). More detailed studies are needed to quantify the actual diet overlap and foraging mode between the two species in the field (*sensu* Hagen and Taylor 2001); although stable isotope analysis shows indirect evidence for this, as there is overlap in trophic position between co-occurring stream rearing juvenile bull trout and exotic brook trout in the Elbow River drainage, Alberta (Popowich 2005).

Bull trout size-at-age indicated that juvenile growth during the rearing phase is relatively constant through the first few years of life (Carl et al. 1989). The growth spurt seen in some populations by age three was not seen, further supporting the lack of a trophic shift to piscivory (Stewart 2007). Many studies report size-at-age or growth of juvenile bull trout, but these are usually based on size at the time of capture, with age assigned by length-frequency histograms or aging structures (Dietz 1971; Sterling 1978; McPhail and Murray 1979; Boag 1987; Carl et al. 1989; Hagen and Baxter 1992; Ratliff 1992; Slaney 1992; Connor et al. 1997; Mogen and Kaeding 2005; Allen et al. 2010). Fewer studies that have back-calculated size at the time of annulus formation were available for comparison to this study (Table A-9). Although the aging structures used and methods of back-calculation were not always consistent between studies, bull trout from the OMR fell in between the extremes of mean size reported for one year olds, depending on the stream they were sampled from. Local-scale influences over size-at-age between locations within major watersheds (e.g., elevation, stream productivity etc.) are therefore likely more important influences than large-scale influences between major watersheds (e.g., latitude, surficial geology etc.). Similar results were found in other studies, where bull trout size-at-age and early growth trajectory is markedly different between streams within the same watershed (Fraley and Shepard 1989), and the streams spanning the lowest elevation range have the most rapid growth trajectories (Underwood et al. 1995).

The ANCOVA indicated that bull trout were observed to be smaller at age one as elevation increased. This supports previous work that has found smaller sizes of bull trout and other salmonids early in life at higher elevations and less productive environments (Carl et al. 1989; Underwood et al. 1995; Parra et al. 2009). At the earliest stages of development, hatch time and alevin development and size is thermally dependent (Ojanguren and Brana 2003). In the OMR, the lowest elevation areas in which bull trout spawn may have earlier emergence times, resulting in larger size-at-age by the time of their first annulus formation. Larger size-at-age could also be observed in lower, warmer sites due to longer and more productive growing seasons and/or thermal dependency of metabolic and feeding rates. Of course, there may be an upper thermal limit in which bull trout development is inhibited, leading to a decline in growth in some streams that approach the upper thermal tolerances for developing bull trout (Parra et al. 2012). This may explain the opposite trend seen in Shepard et al. (1984), in which cooler streams were observed to have the fastest bull trout growth rates. Throughout the range of the species, latitude may also play an important role in determining early bull trout growth trajectory. There have been no attempts thus far to generalize the influence of latitude on bull trout growth, but a similar phenomenon could be expected to occur as with elevation.

Further variability in the ANCOVA could be explained by the year in which bull trout turned age one, as bull trout that turned one in 2007 and 2008 were larger than bull trout that turned one in 2009. Interannual variability in size-at-age may be explained by several hypotheses. Since the sampling occurred in a single season, variation in growth among years may be attributed to differences associated with each unique cohort. For example, 2009 may have the smallest observed size-at-age because of intra or intercohort interactions causing more intense situations of intraspecific competition in this season, thus limiting growth (Paul et al. 2000; Parra et al. 2012). If population estimate data were available for each year, this could be included in the model as an additional covariate. Alternatively, fish that do remain in the stream longer may have more rapid growth than younger fish, as they may be more territorial foragers; thus, the fact that three year olds were larger at age one may simply reflect the fact that fish that rear in the stream for the longest period of residency are the most territorial with the fastest growth rates (Hutchison and Iwata 1997; but see Morinville and Rasmussen 2003 and Chapter 4). Given the strong qualitative association between temperature and size-at-age (Figure A-11), I consider inter-annual temperature variation to be the most likely explanation for the variability observed between years. The fact that bull trout were the largest after the warmest growing season may indicate an indirect influence via the same thermally coupled mechanism as elevation. A multiple year study ideally using capture-mark-recapture to measure growth would adequately test this hypothesis.

The year in which bull trout turned age one, as well as the elevation of the collection site predicted bull trout size-at-age; nevertheless, there was a large amount of variability that could not be accounted for by the ANCOVA. Elevation was used as a surrogate in this study to explain differences in the environmental factors (i.e., stream thermal regime, productivity, etc.) considered most likely to influence bull trout size after their first year. Although phenotypic variation is bound to introduce model variability, other environmental factors, including land-use practices, aspect, stream hydrology, inter and intra-specific competition may also directly or indirectly influence bull trout size-at-age, and are no doubt important influences over bull trout emergence time and growth. Another important consideration that cannot be accounted for in the model is the fact that juvenile bull trout move (Homel and Budy 2008; Warnock 2008), and back-calculated size may be a record of growth from an alternate area. Fish that spent an earlier stage of life rearing in an upstream source may underestimate the size at age in lower elevation reaches (or vice-versa). Juvenile fish that move among tributaries (Warnock et al. 2010) would likewise be poor representatives of the stream/site in which they were captured. Studies using stream enclosures and capture-mark-recapture may adequately control for this.

When compared to previous studies conducted at the core and southern range of the bull trout, juveniles rearing in streams of the OMR have fairly typical non-piscivorous food web roles and early growth patterns. Size-at-age appears to be negatively associated with the local elevation of the rearing site at the time of capture. Studies on the coastal and northern periphery of the bull trout range are lacking, and particular attention should be paid to these populations in the future, as the ecology of these populations is poorly documented. This is particularly important given the different food web structure, and physical stream environment in these areas compared with those in the core and eastern periphery of the inland bull trout range.

Tables

Table A-1: Example dataset for logistic regression, examining the effect of both stream temperature and mining impact on the presence of an invertebrate species

Elevation (m)	Number of sites where present, controls	Number of sites where present, impacted	Number of sites where absent, controls	Number of sites where absent, impacted
100	0	0	5	5
200	1	0	4	5
300	2	1	3	4
400	3	1	2	4
500	3	1	2	4
600	4	2	1	3
700	4	2	1	3
800	5	3	0	2
900	5	3	0	2
1000	5	5	0	0

Table A-2: Parameter estimates and errors from a logistic regression examining the relationship between the presence of an invertebrate species and both elevation and mining activity.

Term	Estimate	Std Error
Intercept	-1.1719202	0.5882104
Mining impact	-0.9787228	0.2971716
Elevation	0.00213261	0.0009984

Table A-3: Proportions of an organism that died along a realistic gradient of contaminant water concentrations, with a linear relationship.

Proportion died	Water concentration of contaminant (mg/L)
0.3	3
0.3	3.4
0.34	3.5
0.38	4
0.4	4.1
0.45	3.9
0.46	4.8
0.49	5
0.5	4.9
0.52	5
0.53	5.3
0.54	5.5
0.57	5.9
0.59	6
0.62	6.3
0.64	6.1
0.66	6.5
0.67	6.2
0.68	7.1
0.72	7

Table A-4: Proportions, and logit-transformed proportions of an organism that died along a gradient of contaminant water concentrations, with a sigmoidal relationship.

Proportion died	Water concentration of contaminant (mg/L)	logit-transformed proportion died
0.01	3	-4.60
0.03	3.4	-3.48
0.02	3.5	-3.89
0.04	4	-3.18
0.06	4.1	-2.75
0.04	3.9	-3.18
0.36	4.8	-0.58
0.5	5	0.00
0.45	4.9	-0.20
0.51	5	0.04
0.7	5.3	0.85
0.85	5.5	1.73
0.95	5.9	2.94
0.96	6	3.18
0.97	6.3	3.48
0.96	6.1	3.18
0.98	6.5	3.89
0.96	6.2	3.18
0.99	7.1	4.60
0.99	7	4.60

Table A-5: Locations and characteristics of all sites sampled for field study of brook trout invasiveness into bull trout streams throughout the Alberta Rockies. If caught, species listed for the purposes of this study include bull trout (BLTR), brook trout (BKTR), rainbow trout (RNTR) and brown trout (BNTR). Of the 124 sites listed, 44 were not included in the analysis (sites listed as N/A), most often because temperature data was not successfully collected, or there was an insufficient number of fish caught. Where included in the analysis, sites were categorically classified as high (H) or low (L) invasiveness. For a spatial representation of these sites, refer to Figure 2-1.

Stream	Watershed	Site code	Year sampled	UTM Zone	UTM E	UTM N	Elevation (m)	Species present (BLTR, BKTR, RNTR, BNTR)	Daily temp, Aug (°C)	High or Low BKTR
Baril Creek	Bow	Ba-1	2010	11	668071	5581285	1570	NO FISH CAUGHT		N/A[1]
Beaver Mines Creek	Oldman	Bm-1	2011	11	701138	5478777	1320	BLTR, BKTR, RNTR	7.69	H
Beaver Mines Creek	Oldman	Bm-2	2011	11	699390	5476963	1351	BKTR, RNTR	13.17	H
Blakiston Creek	Oldman	Bl-2	2009	12	289577	5440128	1316	BLTR, BKTR		N/A[2,3]
Blakiston Creek	Oldman	Bl-3	2009	12	286966	5442760	1361	BLTR, BKTR	9.24	N/A[1,2]
Blakiston Creek	Oldman	Bl-4	2009	12	285080	5442960	1381	BLTR		N/A[1,2]
Blakiston Creek	Oldman	Bl-5	2009	12	282578	5443422	1413	BLTR	8.48	L
Blakiston Creek	Oldman	Bl-6	2009	11	716648	5445780	1478	BLTR	7.15	L
Bragg Creek	Bow	Br-1	2009	11	669742	5647113	1331	BLTR, BKTR, RNTR, BNTR	13.68	H
Bragg Creek	Bow	Br-2	2009	11	667024	5647003	1347	BKTR, RNTR, BNTR		N/A[2]
Bragg Creek	Bow	Br-3	2009	11	664867	5647288	1369	BKTR		N/A[2]
Bragg Creek	Bow	Br-4	2009	11	662332	5646640	1410	BKTR		N/A[2]
Bragg Creek	Bow	Br-5	2009	11	660282	5646650	1430	BKTR	11.07	H
Bragg Creek	Bow	Br-6	2009	11	658092	5648024	1468	BKTR		N/A[1,2]

Stream	Watershed	Site code	Year sampled	UTM Zone	UTM E	UTM N	Elevation (m)	Species present (BLTR, BKTR, RNTR, BNTR)	Daily temp, Aug (°C)	High or Low BKTR
Brown Creek	North Saskatchewan	Bn-1	2010	11	533250	5845084	1380	BLTR	9.79	L
Brown Creek	North Saskatchewan	Bn-2	2010	11	529583	5844361	1430	BLTR	9.1	L
Cat Creek	Bow	Ct-1	2010	11	662571	5586555	1579	BLTR, BKTR	7.56	L
Chungo Creek	North Saskatchewan	Ch-1	2010	11	542173	5840965	1315	BLTR		N/A[2]
Chungo Creek	North Saskatchewan	Ch-2	2010	11	535800	5838409	1458	BLTR	9.39	L
Colt Creek	North Saskatchewan	Co-1	2010	11	566964	5826517	1389	BLTR, BKTR	7.68	N/A[3]
Colt Creek	North Saskatchewan	Co-2	2010	11	565706	5824513	1426	BLTR, BKTR	7.82	H
Colt Creek	North Saskatchewan	Co-3	2010	11	564961	5822054	1458	BKTR	7.25	H
Cutoff Creek	North Saskatchewan	Cu-1	2010	11	605750	5762485	1387	BLTR, BKTR, BNTR	8.18	L
Cutoff Creek	North Saskatchewan	Cu-2	2010	11	598433	5761660	1442	BLTR, BKTR, BNTR	8.98	L
Cutoff Creek	North Saskatchewan	Cu-3	2010	11	594842	5759309	1477	BLTR, BKTR, BNTR	6.28	N/A[3]
Deerlick Creek	Athabasca	De-1	2011	11	483665	5889539	1274	BKTR, RNTR	9.96	H
Deerlick Creek	Athabasca	De-2	2011	11	483526	5885913	1342	BKTR, RNTR	8.57	N/A[1]
Dry Creek	North Saskatchewan	Dy-1	2011	11	613870	5789740	1196	BLTR, BKTR	10.83	H
Dry Creek	North Saskatchewan	Dy-2	2011	11	608484	5786756	1296	BLTR, BKTR	8.05	H
Dry Creek	North Saskatchewan	Dy-3	2011	11	606840	5784403	1351	BKTR	7.8	H
Drywood Creek	Oldman	Dr-2	2009	12	291067	5464951	1311	RNTR	13.94	N/A[1]
Drywood Creek	Oldman	Dr-3	2009	12	288171	5464669	1372	RNTR		N/A[1,2]
Drywood Creek	Oldman	Dr-4	2009	12	283854	5464549	1426	BLTR, BKTR	12.07	H
Drywood Creek	Oldman	Dr-5	2009	11	717734	5462713	1492	BKTR	8.55	H
Drywood Creek	Oldman	Dr-6	2009	11	714825	5459925	1565	BLTR, BKTR	9.37	L
Elbow River	Bow	Eb-3	2011	11	643029	5615613	1970	BLTR	5.87	L
Elbow River seepage channel	Bow	ESC	2010	11	654538	5631837	1577	BLTR, BKTR	7.24	H
Elk Creek	North Saskatchewan	El-1	2010	11	590022	5771038	1518	BLTR, BNTR	10.94	L
Elk Creek	North Saskatchewan	El-2	2010	11	585736	5769379	1583	BLTR, BNTR	10.42	L

Stream	Watershed	Site code	Year sampled	UTM Zone	UTM E	UTM N	Elevation (m)	Species present (BLTR, BKTR, RNTR, BNTR)	Daily temp, Aug (°C)	High or Low BKTR
Elk Creek	North Saskatchewan	El-3	2010	11	582525	5767988	1611	BLTR, BKTR, BNTR	8.09	L
Etherington Creek	Bow	Et-1	2010	11	667201	5583286	1520	BLTR, BKTR, RNTR	7.86	L
Eunice Creek	Athabasca	Eu-1	2011	11	484496	5889496	1247	NO FISH CAUGHT	5.85	N/A[1]
Eunice Creek	Athabasca	Eu-2	2011	11	485356	5884867	1395	NO FISH CAUGHT	8.17	N/A[1]
Ford Creek	Bow	Fo-1	2010	11	651839	5630418	1606	BLTR, BKTR	7.59	L
Gladstone Creek	Oldman	Gl-1	2009	11	704680	5475565	1353	RNTR		N/A[1,2]
Gonika Creek	North Saskatchewan	Go-1	2010	11	552425	5808758	1356	BKTR	8.03	H
Hansen Creek	North Saskatchewan	Hn-1	2010	11	544114	5836301	1371	BLTR, BKTR	8.8	H
Haven Creek	North Saskatchewan	Ha-1	2010	11	553884	5808367	1318	BLTR, BKTR	9.3	H
Haven Creek	North Saskatchewan	Ha-2	2010	11	554002	5809260	1325	BLTR, BKTR	10.57	H
James River	Red Deer	Jr-1	2011	11	615494	5735861	1490	BKTR	8.59	H
Johnson Creek	Bow	Jo-1	2011	11	631858	5694547	1586	BLTR, BKTR	9.37	H
Jumpingpound Creek	Bow	Ju-1	2011	11	644664	5651629	1621	BKTR	9.16	H
Jumpingpound Creek	Bow	Ju-2	2011	11	643637	5647260	1730	BKTR	7.02	N/A[1]
Jumpingpound Creek	Bow	Ju-ACA	2011	11	657376	5656724	1394	BKTR, RNTR	9.85	N/A[2]
Leseur Creek	Bow	Le-1	2011	11	641746	5681730	1363	BKTR	13.36	H
Leseur Creek	Bow	Le-2	2011	11	638077	5682636	1462	BKTR	13.34	H
Lick Creek	North Saskatchewan	Lc-1	2011	11	604494	5788019	1341	BLTR, BKTR	6.87	H
Limestone Creek	North Saskatchewan	Lm-1	2011	11	605083	5756421	1475	BLTR, BKTR	10.33	H
Limestone Creek	North Saskatchewan	Lm-2	2011	11	605533	5751638	1543	BLTR, BKTR	9.29	H
Little Elbow River	Bow	Leb-1	2011	11	647269	5629163	1680	BLTR	6.47	L
Little Elbow River	Bow	Leb-2	2011	11	644260	5627311	1750	BLTR		N/A[2]
Little Elbow River	Bow	Leb-3	2011	11	641707	5625357	1803	BLTR		N/A[2]
Little Red Deer River	Red Deer	LRD-1	2011	11	643491	5700667	1388	BKTR	11.12	H
Little Red Deer River	Red Deer	LRD-2	2011	11	639105	5701362	1454	BKTR	12.41	H

Stream	Watershed	Site code	Year sampled	UTM Zone	UTM E	UTM N	Elevation (m)	Species present (BLTR, BKTR, RNTR, BNTR)	Daily temp, Aug (°C)	High or Low BKTR
Lookout Creek	North Saskatchewan	Lk-1	2010	11	546289	5829321	1359	BKTR	10.95	H
Lookout Creek	North Saskatchewan	Lk-2	2010	11	547750	5824634	1402	BKTR	10.72	H
Margaret Creek	Bow	Ma-1	2011	11	630891	5696248	1588	BLTR, BKTR	9.12	H
Meadow Creek	Bow	Me-1	2011	11	638654	5693371	1463	BKTR	10.49	H
Meadow Creek	Bow	Me-2	2011	11	634090	5692057	1532	BLTR, BKTR	10.05	H
Mill Creek	Oldman	Mi-1	2009	11	707604	5483035	1203	BLTR, RNTR	14.59	L
Mill Creek	Oldman	Mi-3	2009	11	707529	5474437	1375	BLTR, RNTR		N/A[2]
Mill Creek	Oldman	Mi-4	2009	11	705215	5472669	1419	BLTR, BKTR, RNTR	9.14	L
Mill Creek	Oldman	Mi-5	2009	11	705238	5469933	1473	BLTR, BKTR	7.22	L
Mill Creek	Oldman	Mi-6	2009	11	704394	5465588	1544	NO FISH CAUGHT		N/A[1,2]
Nordegg River	North Saskatchewan	No-1	2010	11	558514	5832930	1271	BLTR, BKTR	8.85	L
Nordegg River	North Saskatchewan	No-2	2010	11	556550	5829022	1323	BLTR	8.86	L
North Burnt Timber Creek	Red Deer	NBT-3	2011	11	613779	5710730	1688	BLTR	6.33	L
North Burnt Timber Creek	Red Deer	NBT-4	2011	11	610882	5709046	1724	BLTR		N/A[2]
North Drywood Creek	Oldman	NDr-1	2010	11	712298	5462003	1600	BKTR	8.15	N/A[4]
Pincher Creek	Oldman	Pi-1	2009	11	712691	5465936	1543	BLTR, RNTR	9.31	N/A[4]
Prairie Creek	Bow	Pr-1	2010	11	655566	5637349	1516	BKTR	9.52	H
Prairie Creek	Bow	Pr-2	2010	11	648369	5638371	1690	BLTR	4.42	L
Rapid Creek	North Saskatchewan	Ra-2	2010	11	571236	5829934	1322	BKTR	5.73	H
Rough Creek	North Saskatchewan	Ro-1	2010	11	593906	5798554	1278	BLTR, BKTR, BNTR	9.86	N/A[3]
Rough Creek	North Saskatchewan	Ro-2	2010	11	592034	5797508	1333	BLTR, BKTR, BNTR	9.08	L
Rough Creek	North Saskatchewan	Ro-3	2010	11	588265	5797136	1400	BLTR, BKTR	8.08	L
Scalp Creek	Red Deer	Sc-1	2011	11	598990	5732936	1593	BLTR, BKTR	8.17	L
Sheep Creek	Red Deer	Sh-1	2011	11	610041	5718429	1560	BLTR		N/A[2]
Sheep Creek	Red Deer	Sh-2	2011	11	610556	5716402	1620	BLTR	7.58	L

Stream	Watershed	Site code	Year sampled	UTM Zone	UTM E	UTM N	Elevation (m)	Species present (BLTR, BKTR, RNTR, BNTR)	Daily temp, Aug (°C)	High or Low BKTR
Sheep Creek	Red Deer	Sh-3	2011	11	609688	5714664	1664	BLTR		N/A[2]
Spionkop Creek	Oldman	Sp-1	2009	11	718009	5459423	1506	BLTR, BKTR, RNTR	10.93	L
Storm Creek	Bow	St-1	2010	11	652821	5598159	1762	BLTR	8.53	L
Storm Creek	Bow	St-2	2010	11	647974	5598390	1873	BLTR	6.84	L
Storm Creek	Bow	St-3	2010	11	645348	5600770	1956	BLTR	5.84	L
Sturrock Creek	North Saskatchewan	Sk-1	2010	11	545259	5821171	1472	BLTR, BKTR	9	H
Swale Creek	North Saskatchewan	Sw-1	2010	11	565412	5825440	1424	BLTR, BKTR	6.52	L
Swale Creek	North Saskatchewan	Sw-2	2010	11	560894	5825222	1518	NO FISH CAUGHT	4.26	N/A[1]
Trout Creek	North Saskatchewan	Tr-1	2010	11	593569	5805919	1265	BNTR	9.75	N/A[1]
Trout Creek	North Saskatchewan	Tr-2	2010	11	591319	5806117	1247	BNTR	8.9	N/A[1]
Unnamed tributary to Elk Creek	North Saskatchewan	El-t	2010	11	582276	5768152	1607	BLTR, BKTR	9.37	N/A[3]
Unnamed tributary to the Brazeau River	North Saskatchewan	Un-1	2010	11	548792	5454888	1137	BLTR	12.31	N/A[1]
Unnamed tributary to Waiparous Creek	Bow	Wpt-1	2011	11	623121	5694925	1750	BLTR	7.38	L
Unnamed tributary to Willson Creek	Red Deer	Wst-1	2011	11	610773	5744716	1527	BLTR, BKTR	10.72	L
Waiparous Creek	Bow	Wp-1	2011	11	624106	5694816	1717	BLTR		N/A[2]
Wampus Creek	Athabasca	Wm-1	2011	11	482495	5889773	1271	BKTR, RNTR	9.14	H
Wampus Creek	Athabasca	Wm-2	2011	11	479209	5885225	1374	BKTR, RNTR	10.37	N/A[2]
Wawa Creek	North Saskatchewan	Wa-1	2010	11	559517	5839819	1179	NO FISH CAUGHT	11.3	N/A[1]
Whitney Creek	Oldman	Wh-1	2009	11	706468	5470175	1460	BLTR, RNTR	10.66	L
Wigwam Creek	Red Deer	Wg-1	2011	11	617585	5721035	1523	BKTR	9.65	H
Wildhorse Creek	Red Deer	Wd-1	2011	11	614189	5724378	1497	BLTR, BKTR	9.61	H
Wildhorse Creek	Red Deer	Wd-2	2011	11	613105	5727587	1626	BLTR, BKTR		N/A[2]
Willow Creek	Oldman	Wi-1	2009	11	698956	5564193	1302	NO FISH CAUGHT		N/A[1,2]
Willow Creek	Oldman	Wi-2	2009	11	693517	5565266	1376	RNTR		N/A[1,2]
Willow Creek	Oldman	Wi-3	2009	11	691063	5567785	1416	BKTR, RNTR	12.48	H

Stream	Watershed	Site code	Year sampled	UTM Zone	UTM E	UTM N	Elevation (m)	Species present (BLTR, BKTR, RNTR, BNTR)	Daily temp, Aug (°C)	High or Low BKTR
Willow Creek	Oldman	Wi-4	2009	11	687401	5569466	1497	BKTR	10.16	H
Willow Creek	Oldman	Wi-5	2009	11	684571	5571787	1546	BKTR	9.1	H
Willson Creek	Red Deer	Ws-1	2011	11	613616	5743096	1478	BLTR, BKTR		N/A[2]
Willson Creek	Red Deer	Ws-2	2011	11	611431	5745499	1518	BLTR, BKTR	10.61	N/A[3]
Willson Creek	Red Deer	Ws-3	2011	11	610559	5747555	1578	BKTR	7.23	H
Yara Creek	Red Deer	Yr-1	2011	11	618473	5726549	1514	BKTR	9.29	H
Yarrow Creek	Oldman	Ya-2	2009	12	291978	5462825	1304	BLTR, BKTR, RNTR	13.68	N/A[1]
Yarrow Creek	Oldman	Ya-5	2009	12	282020	5453480	1546	BLTR, RNTR	10.09	L
Yarrow Creek	Oldman	Ya-3	2010	12	288870	5461562	1357	BLTR, BKTR, RNTR		N/A[2]
Yarrow Creek	Oldman	Ya-4	2010	12	284610	5457748	1448	BLTR, BKTR, RNTR	10.78	H

[1] Site could not be included in analysis of Chapter 2 because an insufficient number of bull trout and/or brook trout were caught

[2] Site could not be included in analysis of Chapter 2 because temperature data was not successfully collected

[3] Site could not be included in analysis of Chapter 2 because the fish community of bull trout and brook trout was mixed

[4] Site could not be included in analysis of Chapter 2 because the site was deemed inappropriate due to failure to meet suitable site criteria outlined in the methods of Chapter 2

Table A-6: Raw data of night and daytime averaged between-species competitions through four treatments of varying fish densities (H = high density, L = low density) and habitat types (SP = simple pool, CP = complex pool, CR = complex riffle).

Species	Treatment	Replicate	Population of bull trout competitors	Fork length (mm)	Food capture (number captured)	Per capita aggressive acts (number)	Proportion of time spent in lead position
BKTR	SP-H	SP-H-1	Mill	149.25	9	7.75	0.48
BKTR	SP-H	SP-H-2	Mill	153	14.5	22	0.75
BKTR	SP-H	SP-H-3	Mill	144	5.5	11.25	0.18
BKTR	SP-H	SP-H-4	Livingstone	135.5	12	33.25	0.59
BKTR	SP-H	SP-H-5	Livingstone	129.75	10.5	6.25	0.12
BLTR	SP-H	SP-H-1	Mill	148.5	11	4	0.52
BLTR	SP-H	SP-H-2	Mill	153.5	5.5	4.75	0.25
BLTR	SP-H	SP-H-3	Mill	144	14.5	9	0.82
BLTR	SP-H	SP-H-4	Livingstone	135.75	8	11	0.41
BLTR	SP-H	SP-H-5	Livingstone	128.75	9.5	4.75	0.88
BKTR	CP-H	CP-H-1	Mill	151	9.5	10.75	0.24
BKTR	CP-H	CP-H-2	Mill	155	9	8.5	0.69
BKTR	CP-H	CP-H-3	Mill	145.5	7.5	25.25	0.13
BKTR	CP-H	CP-H-4	Livingstone	136	11.5	28	0.78
BKTR	CP-H	CP-H-5	Livingstone	132	4.5	0	0.07
BLTR	CP-H	CP-H-1	Mill	151.25	10.5	4	0.76
BLTR	CP-H	CP-H-2	Mill	156.5	11	2.75	0.31
BLTR	CP-H	CP-H-3	Mill	147.5	12	9.5	0.87
BLTR	CP-H	CP-H-4	Livingstone	136.5	8.5	2.75	0.22
BLTR	CP-H	CP-H-5	Livingstone	131.5	15.5	1.75	0.93
BKTR	CR-H	CR-H-1	Mill	153	9	3.5	0.49
BKTR	CR-H	CR-H-2	Mill	146	6.5	4.75	0.33
BKTR	CR-H	CR-H-3	Mill	157.5	6	3.25	0.33
BKTR	CR-H	CR-H-4	Livingstone	137.75	4	19.75	0.22
BKTR	CR-H	CR-H-5	Livingstone	133	5.5	3.75	0.29
BLTR	CR-H	CR-H-1	Mill	153	9	1	0.51
BLTR	CR-H	CR-H-2	Mill	148	13.5	3.5	0.68
BLTR	CR-H	CR-H-3	Mill	158.5	12	1.5	0.67
BLTR	CR-H	CR-H-4	Livingstone	138	14	7	0.78
BLTR	CR-H	CR-H-5	Livingstone	132.5	13.5	8.25	0.71
BKTR	SP-L	SP-L-1	Livingstone	124	3	2	0.67
BKTR	SP-L	SP-L-2	Livingstone	121	14	1.5	0.49

Species	Treatment	Replicate	Population of bull trout competitors	Fork length (mm)	Food capture (number captured)	Per capita aggressive acts (number)	Proportion of time spent in lead position
BKTR	SP-L	SP-L-3	Livingstone	133	8	2.5	0.43
BKTR	SP-L	SP-L-4	Mill	133	1.5	10.5	0.03
BKTR	SP-L	SP-L-5	Livingstone	131	11	7.5	0.68
BKTR	SP-L	SP-L-6	Livingstone	130	9	4	0.77
BKTR	SP-L	SP-L-7	Mill	129	6	6.5	0.37
BKTR	SP-L	SP-L-8	Mill	150.5	3.5	4	0.29
BKTR	SP-L	SP-L-9	Mill	142	0	0	0.69
BKTR	SP-L	SP-L-10	Livingstone	112	0	0	0.56
BKTR	SP-L	SP-L-11	Mill	142	6	5	0.29
BKTR	SP-L	SP-L-12	Mill	153	1.5	0.5	0.03
BKTR	SP-L	SP-L-13	Mill	151	13	3.5	0.35
BLTR	SP-L	SP-L-1	Livingstone	121	17	0	0.33
BLTR	SP-L	SP-L-2	Livingstone	124	6	0.5	0.51
BLTR	SP-L	SP-L-3	Livingstone	129	11	0	0.57
BLTR	SP-L	SP-L-4	Mill	134.5	18.5	4.5	0.97
BLTR	SP-L	SP-L-5	Livingstone	133	9	1	0.32
BLTR	SP-L	SP-L-6	Livingstone	131	11	1.5	0.23
BLTR	SP-L	SP-L-7	Mill	130	13.5	3.5	0.63
BLTR	SP-L	SP-L-8	Mill	152	16	3	0.71
BLTR	SP-L	SP-L-9	Mill	143	19.5	3	0.31
BLTR	SP-L	SP-L-10	Livingstone	113	6	0	0.44
BLTR	SP-L	SP-L-11	Mill	143	14	7.5	0.71
BLTR	SP-L	SP-L-12	Mill	150	18.5	5.5	0.97
BLTR	SP-L	SP-L-13	Mill	148	7	5	0.65

Table A-7: Raw data of night and daytime averaged within-species competitions

Species	Replicate	Fish number	Population of bull trout competitors	Fork length (mm)	Food capture (number captured)	Per capita aggressive acts (number)	Proportion of time spent in lead position
BKTR	BK-1	1	N/A	124	0	0	0.00
BKTR	BK-2	1	N/A	121	8.5	0	0.34
BKTR	BK-3	1	N/A	127	13	26.5	0.82
BKTR	BK-4	1	N/A	126	0	0	0.00
BKTR	BK-5	1	N/A	132.5	4	4	0.94
BKTR	BK-6	1	N/A	129	0	0	0.02
BKTR	BK-7	1	N/A	136	14.5	10	0.96
BKTR	BK-8	1	N/A	136.5	10.5	3	0.98
BKTR	BK-9	1	N/A	150	6.5	0	0.24
BKTR	BK-1	2	N/A	123	14	4	1.00
BKTR	BK-2	2	N/A	119	10.5	0	0.66
BKTR	BK-3	2	N/A	127	2	0	0.18
BKTR	BK-4	2	N/A	127.5	20	16.5	1.00
BKTR	BK-5	2	N/A	132	4.5	0	0.06
BKTR	BK-6	2	N/A	132	18	0	0.98
BKTR	BK-7	2	N/A	136	1.5	0	0.04
BKTR	BK-8	2	N/A	137	9	1.5	0.02
BKTR	BK-9	2	N/A	150.5	10	6.5	0.76
BLTR	BL-1	1	Mill	126	4.5	0	0.47
BLTR	BL-2	1	Mill	120	10	1.5	0.65
BLTR	BL-3	1	Mill	129	5	6.5	0.29
BLTR	BL-4	1	Mill	138	0	0	0.94
BLTR	BL-5	1	Livingstone	120.5	11	0.5	0.90
BLTR	BL-6	1	Livingstone	115	3	0	0.42
BLTR	BL-7	1	Livingstone	123	6	0	0.33
BLTR	BL-8	1	Livingstone	127	3.5	0	0.40
BLTR	BL-9	1	Mill	158	4.5	0	0.84
BLTR	BL-1	2	Mill	126	15	2	0.53
BLTR	BL-2	2	Mill	123	8	2.5	0.35
BLTR	BL-3	2	Mill	132	14	18	0.71
BLTR	BL-4	2	Mill	138	20	0.5	0.06
BLTR	BL-5	2	Livingstone	118	6	0	0.10
BLTR	BL-6	2	Livingstone	115	10.5	0	0.58
BLTR	BL-7	2	Livingstone	125	13.5	0	0.67
BLTR	BL-8	2	Livingstone	126	16.5	0	0.60
BLTR	BL-9	2	Mill	155	15	23.5	0.16

Table A-8: Summary of the number of all fish caught (n) at sampled sites in bull trout spawning and rearing streams of the Oldman River drainage, and the number of those that could be aged successfully (n_a) and had food items in stomachs (n_f).

Stream	Sites	Elevation range (m)	n	n_a	n_f
Carbondale River	3	1412-1554	13	13	12
Lost Creek	3	1433-1489	17	17	14
Mill Creek	3	1375-1474	21	19	20
Whitney Creek	1	1460	3	3	2
Dutch Creek	2	1438-1546	17	15	15
Hidden Creek	1	1660	20	18	20

Table A-9: Back-calculated bull trout size-at-age data from previous literature.

Reference	This study	This study	This study	This study	This study	Oliver 1979	Oliver 1979	Fraley and Shepard 1989	Fraley and Shepard 1989	Fraley and Shepard 1989	Fraley and Shepard 1989	Fraley and Shepard 1989	Bjornn 1961	Bjornn 1961	Underwood et al. 1995	Underwood et al. 1995	Underwood et al. 1995
stream	Carbondale River	Lost Creek	Dutch Creek	Hidden Creek	Mill Creek[1]	Ram creek	Wigwam River	North Fork drainage	Coal Creek	Red Meadow Creek	Trail Creek	Whale Creek	Lower Priest Lake	Upper Priest Lake	Mill Creek, WA	Tucannon River	Wolf Fork
Size age 1 (mm)	75	72	70	59	81	78	64	73	75	64	74	56	71	66	96	66	88
Size age 2 (mm)	119	101	108	95	121	137	114	117	124	113	119	98	114	102	139	105	136
Size age 3 (mm)	155		149	124	164	233	176	155	202	168	158	139	183	155	196	150	192
Size age 4 (mm)						303		228	323	360	228		310	239	241	247	
Elevation	1412-1554	1433-1494	1438-1546	1660	1375-1419	1010	1120	not given	not given	not given	not given	not given	not given	not given	760-890	850-1180	820-1030
Aging structure	otoliths	otoliths	otoliths	otoliths	otoliths	scales	scales	scales	scales	scales	scales	scales	scales	scales	otoliths	otoliths	otoliths
n[2] (age 1,2,3)	13, 5, 1	17, 2	15, 12, 2	18, 18, 12	22, 13, 1	not given	not given	525, 298, 52, 4	145, 62, 23, 14	145, 113, 29, 7	473, 264, 46, 4	52, 34, 6	61*	41*	26, 21, 5, 4	20, 16, 6, 2	20, 5, 1
back-calculation method	fraser-lee	fraser-lee	fraser-lee	fraser-lee	fraser-lee	dahl-lea	dahl-lea	not given	not given	not given	not given	not given	modified fraser-lee	modified fraser-lee	Dahl-lea	Dahl-lea	Dahl-lea

1 Includes three samples from nearby Whitney Creek

2 Fish that were two or three years of age also contributed to sample sizes from previous age classes, since sizes were back-calculated

* Sample sizes for each age class were not given

Figures

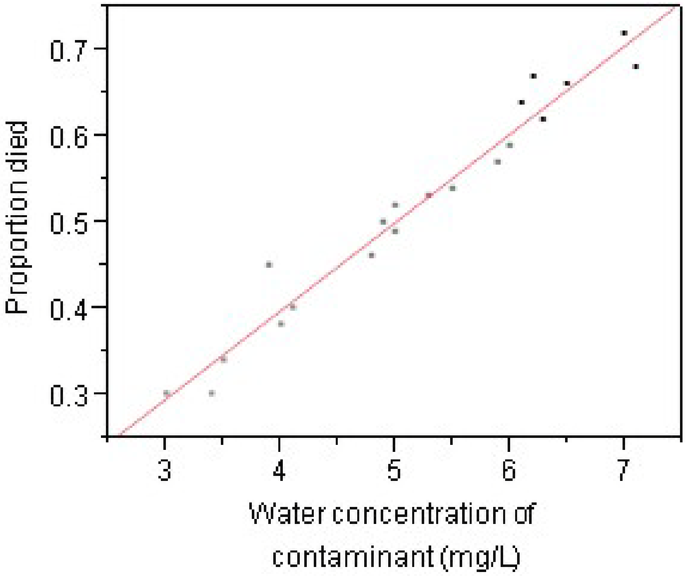


Figure A-1: A hypothetical example where linear regression fits the data (Table A-3) appropriately, as the realistic water concentrations of an environmental contaminant affects the proportion of an organisms' mortality due to predation ($R^2 = 0.96$; $F_{1,19} = 449.2$; $P < 0.001$).

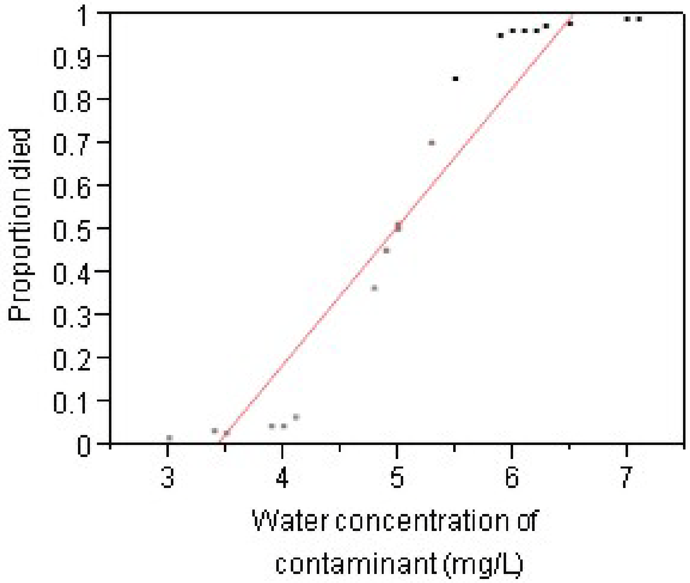


Figure A-2: A hypothetical example where linear regression does not characterize the sigmoidal relationship between water concentrations of an environmental contaminant and proportion of an organisms' mortality due to predation (Table A-4). The overall model fit is sufficient in this case, although not optimal ($R^2 = 0.92$; $F_{1,19} = 209.2$; $P < 0.001$). In addition, the regression equation will provide unsuitable estimates of the proportion died at or close to the boundaries, and will inappropriately predict proportions beyond the boundary limits for extreme water concentration values.

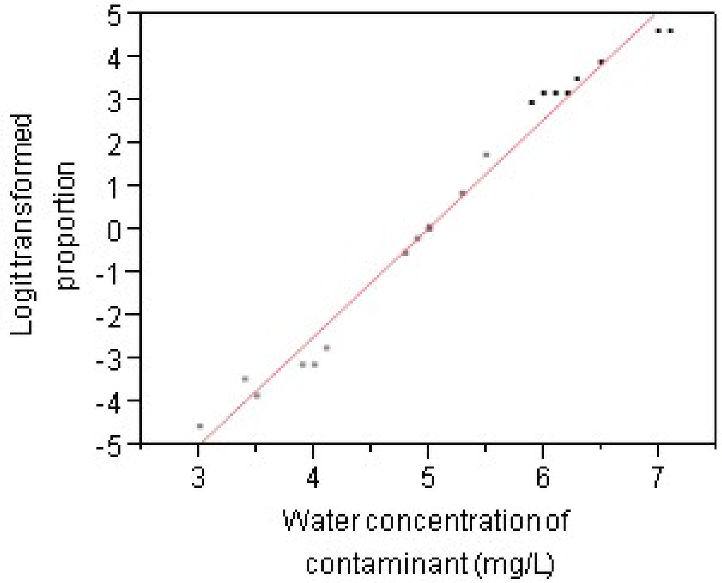


Figure A-3: A hypothetical example where logit-transforming the dependent variable fits the sigmoidal relationship between water concentrations of an environmental contaminant and proportion of an organisms' mortality due to predation (Table A-4). The overall model is optimal in this case (R^2 = 0.98; $F_{1,19}$ = 966.8; $P < 0.001$), providing a better fit than the untransformed dependent variable (Figure A-2).

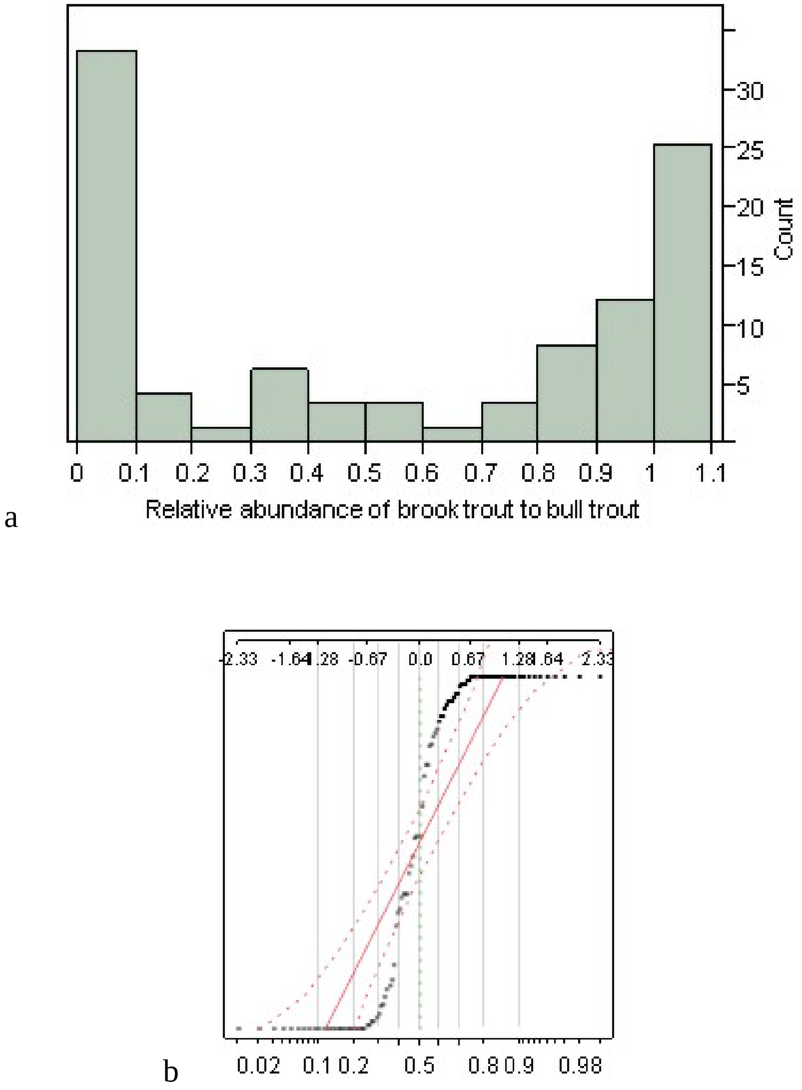


Figure A-4: Sites (n=99) on bull trout streams that contained invasive brook trout tended to have fish communities that were dominated by either brook trout or bull trout (a), resulting in a normal quantile plot of the dependent variable that clearly demonstrates a sigmoidal response, with most data points distributed towards or on the bounds (b).

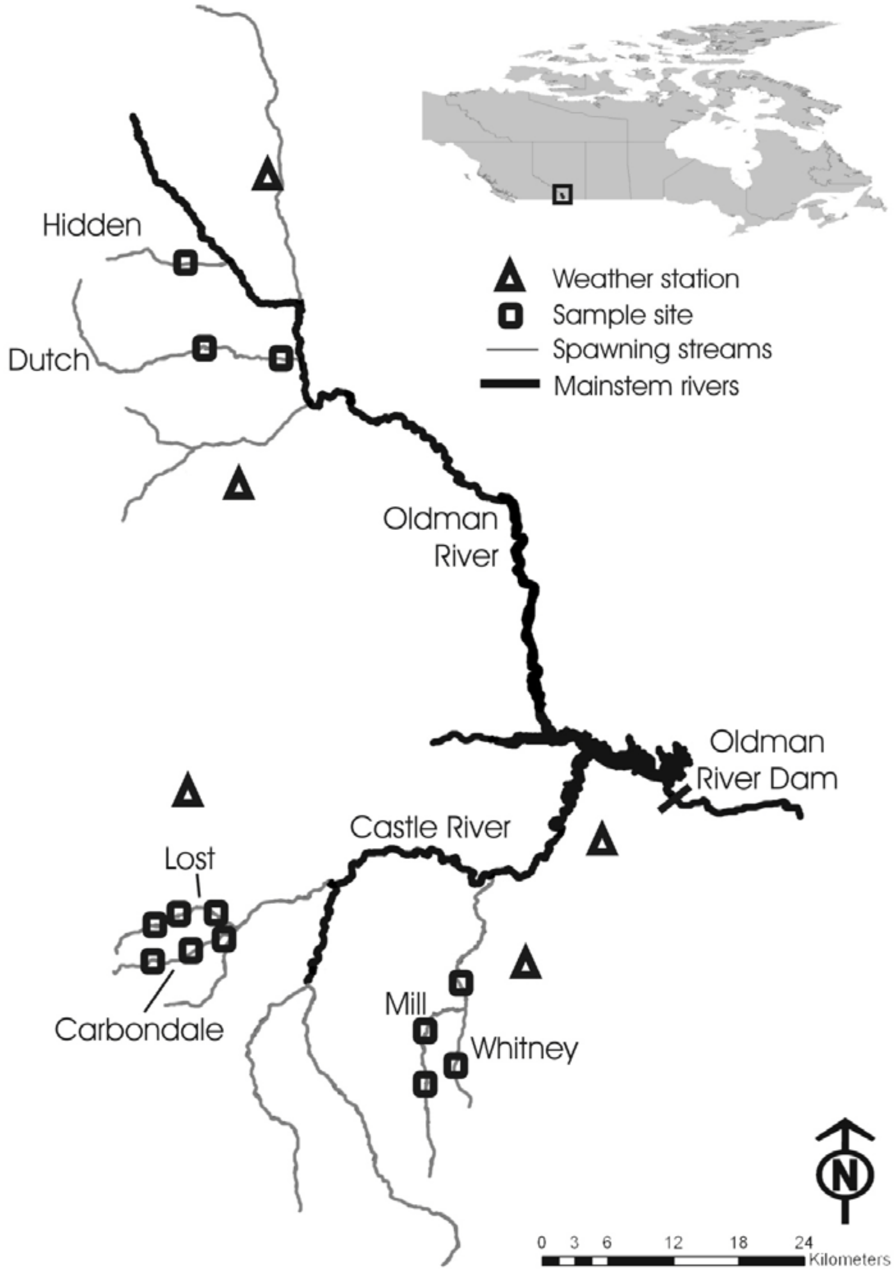


Figure A-5: Study area, displaying sites in which juvenile bull trout were sampled on spawning streams for bull trout in the Oldman River drainage above the Oldman River Dam for aging and diet data. Data were used from nearby weather stations to derive the mean air temperature for each bull trout growing season.

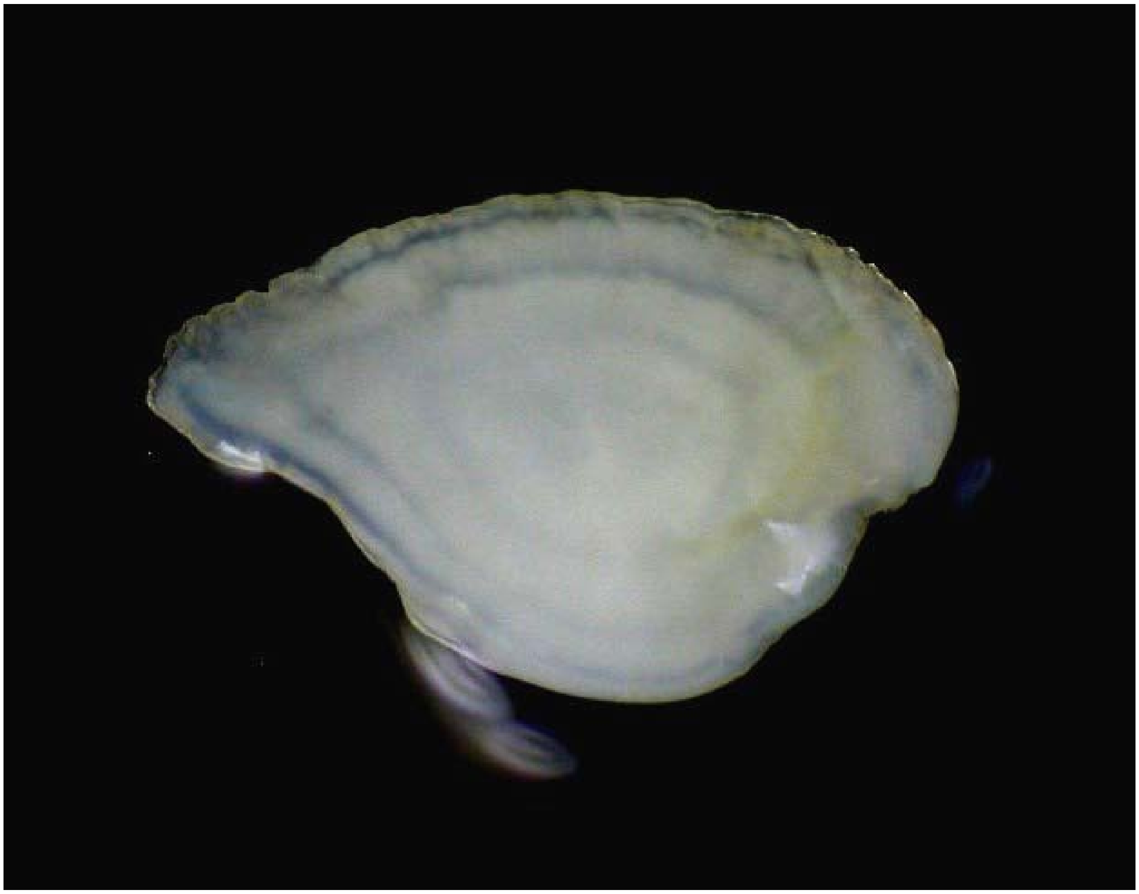


Figure A-6: Photo of an otolith from a 3 year old bull trout. Annuli (dark bands) were used to back-calculate the size-at-age for each fish.

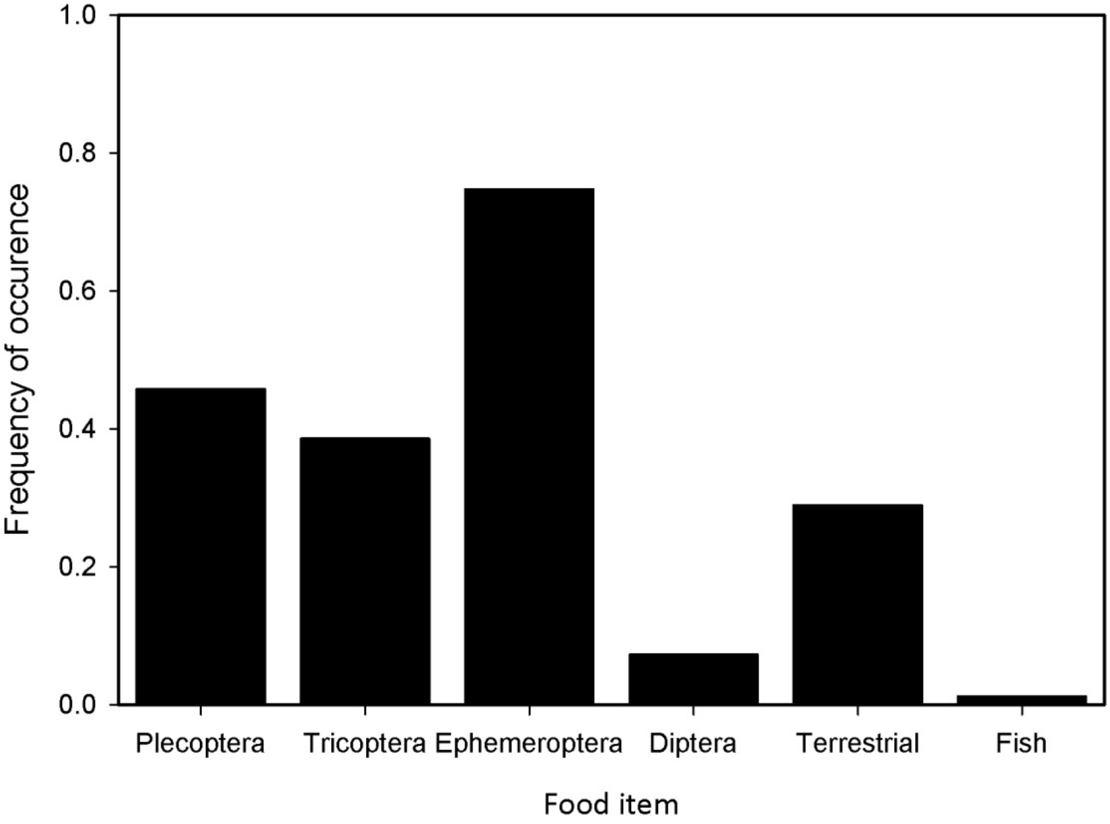
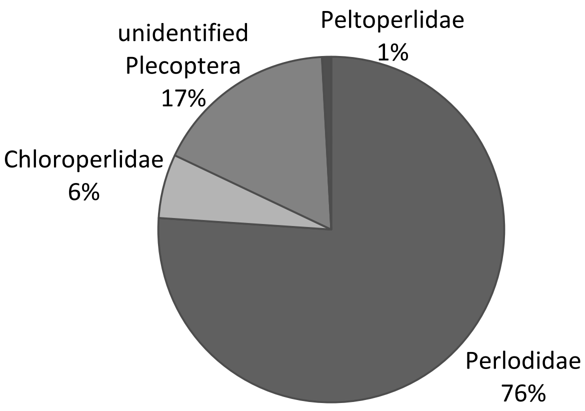
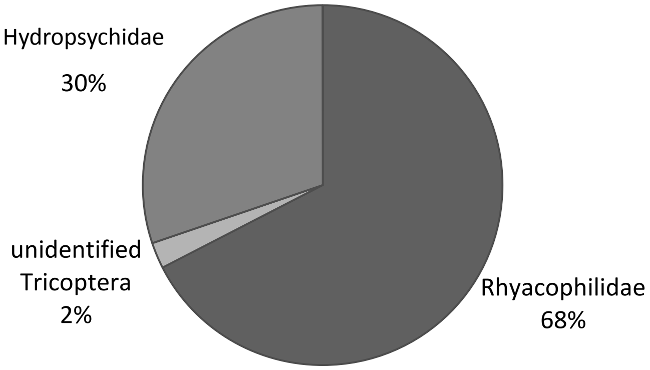


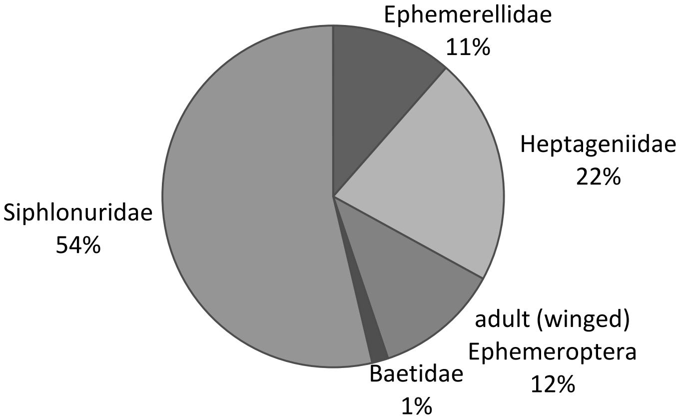
Figure A-7: Frequency of occurrence of major food resources for bull trout that had food in stomachs (*n* = 83).



a.



b.



c.

Figure A-8: Taxonomic composition by number of bull trout diets for each order ([a] Plecoptera [b] Tricoptera and [c] Ephemeroptera) containing multiple insect families.

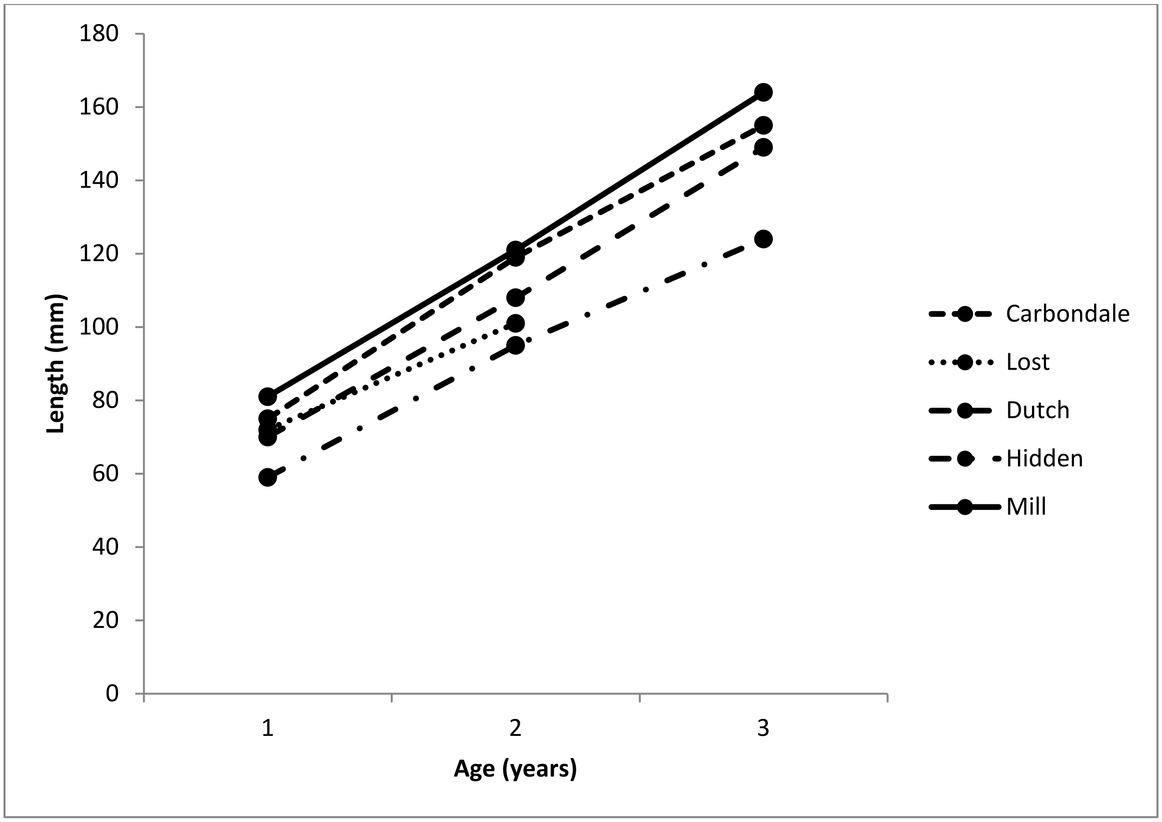


Figure A-9: Bull trout back-calculated mean sizes at each age, for each stream sampled (three fish sampled from Whitney Creek were included in the nearby Mill Creek sample).

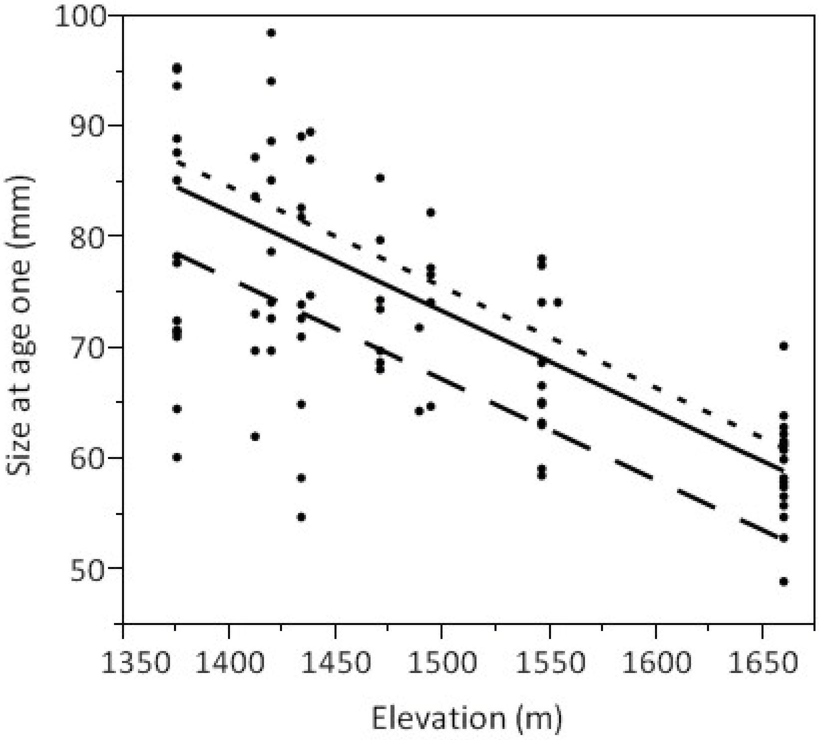


Figure A-10: ANCOVA (R^2=0.50, $F_{3,81}$=26.7, $P < 0.0001$) of back-calculated size at age one for bull trout throughout the elevation gradient of the study area for fish that turned one in 2007 (dotted line), 2008 (solid line) and 2009 (dashed line). Fish that turned one in 2009 were smaller than those in the other two years ($P < 0.05$).

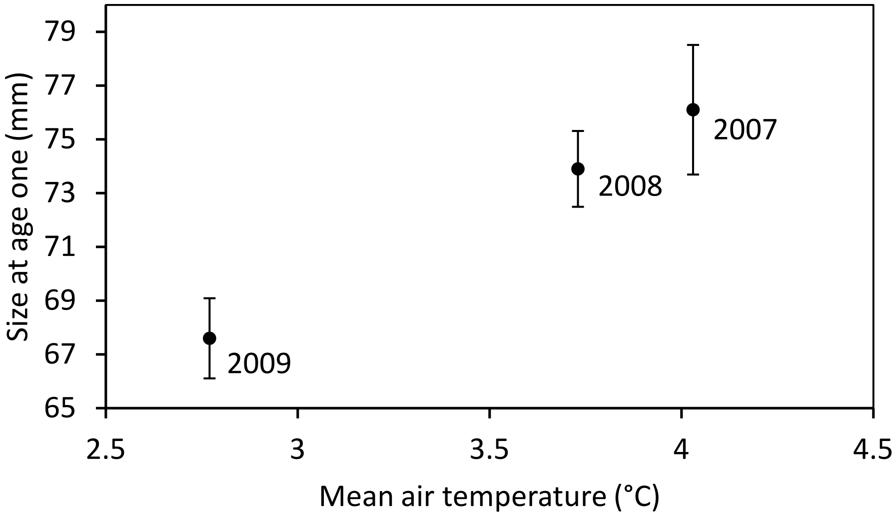


Figure A-11: Model estimated marginal means (+/- SE) for each year that bull trout turned one year of age, plotted with the mean air temperature found throughout the previous years' growing season.