University of Alberta

EFFECTS OF WATER TEMPERATURE ON INTERSPECIFIC COMPETITION BETWEEN JUVENILE BULL TROUT AND BROOK TROUT.

By

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One of the penalties of an ecological education is that one lives alone in a world of wounds. Much of the damage inflicted on land is quite invisible to laymen. An ecologist must either harden his shell and make believe that the consequences of science are none of his business, or he must be the doctor who sees the marks of death in a community that believes itself well and does not want to be told otherwise.

-Aldo Leopold, *A Sand County Almanac*

I am the wiser in respect to all knowledges, and the better qualified for all fortunes, for knowing that there is a minnow in the brook.

-Henry Thoreau, *Journal* 1:109

Dedication

To my family, especially my wife Tracey, for their unflagging support along this journey.

Abstract

Bull trout *Salvelinus confluentus* populations are in decline across the native range. Bull trout distribution and abundance are influenced by a number of factors, including the presence of nonnative brook trout *S. fontinalis*. Where sympatric, bull trout are more likely to persist in higher elevation, cooler streams. To test the hypothesis that competition between these species is independent of water temperature, behavioral observations were made in artificial streams (at 8°C and 15°C) and a natural stream pool (8-17°C). In contrast to brook trout, bull trout increased aggression with water temperature but no concomitant increase in forage rate of aggressive individuals was observed in the artificial streams. In a natural stream, proportionately more bull trout were observed cruising at a given temperature than brook trout but the proportion of foragers did not differ. These observations suggest cold-adapted bull trout may be disadvantaged when competing with brook trout in warmer water.

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Chapter 1: Introduction

Alberta's fin fish fauna consists of 51 native and 8 introduced species, including four introduced salmonids: golden trout *Oncoryunchus aguabonita*, brown trout *Salmo trutta*, Dolly Varden *Salvelinus malma*, and brook trout *Salvelinus fontinalis* (Nelson and Paetz 1992). Most salmonid introductions across North America occurred intentionally to "improve" native fish communities for humans and have had a profound effect on the native fish fauna of the continent (Kruger and May 1991). The naturalization of brook trout beyond its native range in eastern North America throughout the world, particularly in waters from the Rocky Mountains west, has been notably successful (MacCrimmon and Campbell 1969; Kruger and May 1991). This success may have negatively impacted native, ecologically similar species, such as the bull trout *Salvelinus confluentus*.

Nonnative salmonids are biologically very similar to their native counterparts and the potential for common resource requirements and interspecific interactions is strong (Dunham et al. 2002). Interspecific competition is the most commonly cited mechanism explaining the ecological effects of salmonid introductions (Kruger and May 1991). Interspecific competition between salmonids has been studied extensively the last 30 years but the results of many of these studies are equivocal because of poor experimental design that confounds interspecific competitive effects with intraspecific effects (Fausch 1988, 1998; Dunson and Travis 1991). To adequately test both the existence and relative strength of interspecific effects requires a minimum of five experimental treatments including one of each species in allopatry at low- and high-densities to quantify intraspecific competition, and a sympatric treatment to quantify interspecific competition (Dunson and Travis 1991; Fausch 1998). Two broad categories of interspecific competition are recognized, exploitation and interference competition. By definition either type results in a negative effect on the fitness related characteristics of at least one species through either exploitation of a shared resource or interference related to that resource respectively (Fausch 1998). Though abiotic factors delimit a pool of species that could occupy a site, they do not delimit a pool of equally competent species. The outcome of competition between such species will be a result of the interaction between the biotic effects of competition and the species response to abiotic factors (Dunson and Travis 1991). My research was designed to examine the interaction between water temperature, agonisim and foraging behavior, and growth of two species of juvenile salmonid in Alberta: native bull trout and nonnative brook trout. Recent research suggests bull trout may be resistant to brook trout invasion in cool, high-elevation Rocky Mountain streams in Alberta (Paul and Post 2001); my objective was to test the null hypothesis that competition between these species is independent of water temperature.

Results of my research are relevant to fishery scientists and managers alike. Climactic warming is expected to have profound effects on Canadian freshwaters, raising surface water temperatures and accelerating the spread of nonnative, aquatic organisms (Schindler 2001), while a number of current land use practices may lead to the thermal degradation of streams (Poole and Berman 2001). By examining the effects of increased water temperature on interspecific competition between bull trout and brook trout, my research helps identify potential links between watershed and global-scale processes that influence water temperature and species-specific interactions. If conservation of native cold water species such as the bull trout is a priority, these data will be critical to their preservation.

Including the introduction, my thesis is composed of four chapters. Chapter 2 describes the results of an artificial stream experiment where I examined the effects of increasing water temperature on foraging and agonistic behavior, and growth of juvenile bull trout and brook trout. In Chapter 3, I describe bull trout and brook trout distributions, abundance, and foraging behavior in response to environmental variation, particularly in water temperature, in Haven Creek a fourth-order stream in west-central Alberta. In chapter 4, I conclude my thesis with an overview of the significant findings of my research, identify areas where more research is required, and present a general argument for the increased use of behavioral research by land managers.

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Chapter 2: Effects of water temperature on interspecific competition between juvenile bull trout and brook trout in an artificial stream environment.

Introduction

The bull trout *Salvelinus confluentus* is native to northwestern North American and is the only native char to historically occupy all the drainages of Alberta's eastern slopes (Post and Johnston 2002). Bull trout in Alberta exhibit three life history strategies: *stream resident* populations that spawn and rear in tributary streams with no adult migration to other water systems, *fluvial populations* which spawn and rear in tributary streams but adults reside in main stem rivers, and *adfluvial* populations that spawn and rear in tributary streams but adults reside in lakes or reservoirs (Berry 1997; Post and Johnston 2002). Spawning occurs from mid-August to late October (Fraley and Shepard 1989; Post and Johnston 2002) over gravel or cobble substrates in areas of groundwater discharge (Baxter and McPhail 1999). Eggs hatch in early spring and juvenile bull trout from fluvial/adfluvial populations rear in tributary streams for 1-4 years before migrating to rivers and lakes (Post and Johnston 2002). Bull trout in Alberta do not typically reach sexual maturity until their fifth to seventh year (Berry 1997; Post and Johnston 2002).

Populations of bull trout have declined throughout the native range, including Alberta, where the species is designated as "Sensitive" (Post and Johnston 2002). In adjacent waters the bull trout is listed as "Threatened" under the United States Endangered Species Act (Post and Johnston 2002). Habitat degradation, overharvest, and interactions with introduced salmonids such as the brook trout *S. fontinalis* are contributing factors to this range-wide decline (Rieman and McIntyre 1995; Saffel and Scarnecchia 1995; Berry 1997; Swanberg 1997; Watson and Hillman 1997; Post and Johnston 2002).

Native to northeastern North America, brook trout have been widely introduced outside their native range, including Alberta (MacCrimmon and Campbell 1969). Probably first introduced in the early 1900s, brook trout are now distributed throughout most of western Alberta (Nelson and Patez 1992). If brook trout do significantly compete with bull trout the consequences may be considerable as naturalized populations of brook trout occur throughout much of the bull trout's range (MacCrimmon and Campbell 1969), including approximately 40% of the waters along Alberta's east slopes (Nelson and Paetz 1992; Post and Johnston 2002), and where environmental factors are favorable (see Dunham et al. 2002) invasion continues (Adams et al. 2000; Dunham et al. 2002; Kennedy et al. 2003). Brook trout have similar spawning requirements to bull trout but mature rapidly, as early as age one or two (Nelson and Paetz 1992; Dunham et al. 2002). Despite the overlap in distribution and assumed competition, relatively little empirical evidence for interspecific competition between these species is available. Existing research has focused on two mechanisms, hybridization (e.g., Leary et al.1983; Kitano et al. 1994; Leary et al.1993) and competitive interactions for foraging microhabitat (e.g., Nakano et al.1998; Gunckel et al. 2002).

Bull trout are likely to be sensitive to any introduced fish species that occupies a similar niche. Following a study of 34 Rocky Mountain lakes, Donald and Algar (1992) concluded that lake trout *S. namaycush* could displace or exclude bull trout from mountain lakes below 1500 m elevation. A comparable positive correlation between bull trout persistence and elevation has been noted in Rocky Mountain streams (Rieman et al. 1997; Paul and Post 2001; Rich et al. 2003). This trend is thought to reflect superior bull trout performance at lower water temperatures relative to that of competing species. Thus the low water temperatures prevalent at high elevations are hypothesized to enhance the bull trout's ability to resist invasion of brook trout and other nonnatives (Rieman and McIntyre 1995; Saffel and Scarnecchia 1995).

Bull trout are one of the least tolerant of North American salmonids to relatively high water temperature, with an upper incipient lethal temperature (UILT) of 20.9 °C (Selong et al. 2001), considerably lower than the brook trout's UILT of 24.5 °C (McCormick et al. 1972). The bull trout's relatively low thermal optima, and observed restriction to cool, high-elevation streams in many areas of the Rocky Mountains appears to support the elevation refugia hypothesis. This hypothesis implies that native salmonids are resilient to invasion by nonnatives at higher elevations (Paul and Post 2001). The brook trout's ability to ascend steep, headwater streams has been well documented (Gowan and Fausch 1996; Adams et al. 2000) while Paul and Post (2001) found brook trout preferentially moved downstream of stocking locations in Alberta. Based upon these observations, stream gradient and stocking history alone cannot fully explain the brook trout's absence in many bull trout dominated headwater streams in Alberta and elsewhere.

Evidence suggesting these species compete is growing. While stream salmonids satisfy many of the criteria required to demonstrate the existence of interspecific competition in general (Chapman 1966; Fausch 1998), bull trout and brook trout in headwater streams exhibit substantial dietary overlap and little evidence of food partitioning (Gunckel 2000). Both species have been observed to forage mainly on drifting insects in the water column with no significant difference between foraging microhabitat (Gunckel 2000). Bull trout also increased foraging rate and distance and reduced cover use following removal of sympatric brook trout (Nakano et al. 1998). If these species were not competing, it is unlikely that brook trout removal would have had an effect on bull trout foraging behavior (Nakano et al. 1998).

The focus of this study was to test the null hypothesis that the competitive performance of juvenile bull trout and brook trout is independent of water temperature. Juvenile fish were used as competition at this life stage in stream environments is typically intense (Fausch 1998) and likely to effect broader population level relationships. Further, juveniles are likely to be sympatric, given the similar spawning requirements of each species. Finally, previous studies of the thermal requirements, growth, and agonistic behavior of these species have focused on juvenile fish. Specific research objectives were to quantify juvenile bull trout and brook trout agonistic, forage, and growth rates in allopatry and sympatry across a temperature range commonly experienced by fish in the wild and compare research findings to existing literature regarding bull trout distribution, temperature preferences and competitive interactions with nonnative fish species.

Artificial streams were used to test the effect of water temperature on competition between these species. The artificial streams allowed manipulation of water temperature, fish density and species composition while holding other potentially confounding variables (i.e., fish size, light intensity, ration, water velocity etc.) constant. Wild fish were used in the experiment as hatchery rearing has been shown to significantly alter salmonid behavior (Berejikian et al. 1996).

Methods

The experimental design described by Dunson and Travis (1991; Table 2.1) was used to compare intraspecific and interspecific competition of bull trout and brook trout at two temperatures, 8°C and 15°C. The 8°C treatment is within the range of maximum summer temperatures in which bull trout are most common (Hass 2001), juvenile densities are highest (Saffel and Scarnecchia 1995), and juvenile growth occurs (Selong et al. 2001). The 15°C treatment approximates the maximum summer water temperature at which bull trout abundance sharply declines (Saffel and Scarnecchia 1995; Hass 2001; Dunham et al. 2003) but is still within the range of maximum growth (Selong et al. 2001). All other factors being equal, the growth rate of bull trout at 15°C should be greater than that of bull trout at 8°C (Selong et al. 2001). These test temperatures are near the upper and lower limits of water temperature suitable for the growth and survival of juvenile brook trout (McCormick et al. 1972) and include temperatures at which native and naturalized brook trout populations occur (MacCrimmon and Campbell 1969). Individual growth over the experimental period was used to infer competitive performance and the fitness related consequences of competition (Fausch 1998).

Fish Collection

Native bull trout were collected as required from three, third- and fourth-order Albertan streams in the upper North Saskatchewan River drainage basin: Whitegoat Creek (116°29'W, 52°13'N), Elk Creek (115°38'W, 52°3'N), and an unnamed tributary to the North Saskatchewan River (115°25'W, 52°22'N). These populations were identified as being capable of sustaining a limited harvest. Effort was made to collect bull trout from allopatric populations and while bull trout were always the most abundant species encountered, lower numbers of brook trout, brown trout *Salmo trutta*, lake chub *Couesius plumbus*, longnose dace *Rhinichthys cataractae*, mountain whitefish *Prosopium williamsoni*, and rainbow trout *Oncorhynchus mykiss* were also encountered during collections. Brook trout were collected from a nonnative, naturalized population in Vetch Creek (109°4'W, 52°12'N) also located in the North Saskatchewan River basin. Low numbers of brown trout were observed during brook trout collection.

All fish were captured with a Smith-Root (Vancouver, W.A.) Model 12B or 15D backpack electrofisher and dip nets. Electrofishing may negatively affect short-term growth of salmonids (Gatz et al. 1986; Dwyer and White 1995). To reduce fish stress and potential injury, minimum electrofisher settings were maintained given local conditions (200-500 V, 15-60 Hz, 2-6 ms pulse width, 0.18-0.33 output amps) and repeated exposure of individuals was avoided (Gatz et al. 1986; Dalby et al. 1996; Barton and Dwyer 1997). Electrofishing continued until the required numbers of fish of a similar size (~100 mm fork length (FL)) were captured. Fish were transported to the lab in an aerated, 44 L-insulated tub. Brook trout were in transit an average of 0.9 h (range 0.25-2.5 h), bull trout 2.6 hours (1.5-5 h). Water temperature did not rise more than 3°C during transportation.

At the lab fish were anaesthetized using clove oil (25 μL/L; Keene et al. 1998) and randomly assigned an identifying fin clip or combination of two clips from the adipose, upper, and/or lower caudal fins, measured (FL; nearest millimetre), weighed (wet weight; nearest 0.01 g) and placed in an aerated recovery tank. Water in the recovery tank consisted of equal parts water from the collection stream and water from the artificial stream. As relative size of fish may confer a competitive advantage (Sabo and Pauley 1997; Fausch 1998), fish were stratified to minimize size differences between tank mates (Table 2.2) and randomly assigned to an artificial stream and temperature treatment. Once recovered from anaesthesia (~5 min) fish within a treatment were introduced to the artificial stream simultaneously. Water temperature in the artificial streams was adjusted to within 3°C of water temperature in the transportation tub and incrementally adjusted to the treatment temperature over the next two to three days.

Artificial Streams

The experiment was conducted using two 420-L Frigid Units, Inc., Living Streams, Toledo, O.H. artificial streams: 2.1 m long x 0.48 m deep x 0.55 m wide. Water depth was maintained at approximately 0.35 m. Observations were made through a clear plastic window running the length of each artificial stream. Streams were housed indoors near the fish collection streams, southwest of Rocky Mountain House, Alberta, Canada. Well water medicated with non-iodized salt (0.2% solution; Hoffman 1999) was re-circulated through a cooling tower, filter media, and an activated charcoal insert in each stream. Fine mesh screens excluded fish from the cooling tower and filtration areas of each stream, leaving a 0.74 m^2 living area. A single layer of large gravel substrate (20-115 mm measured across greatest axis) was added to each tank. Water temperature was 8.4 ± 0.7°C (mean ± SD) during cold-water treatments and 14.4 ± 1.4°C during warm-water treatments. Ammonia concentration, measured near the end of each replicate, was always below levels considered harmful to salmonids (>0.01 mg/L; Environmental Protection Agency 2002). Water velocity decreased from a maximum of 7 cm/s at the upstream end of the tank to less than 1 cm/s at the downstream end. Artificial light (~35-160 lx measured at the water's surface) was provided by four 34 W Sylvania, Cool White fluorescent bulbs suspended 0.56 m above the tanks on a 12 h dark:12 h light photoperiod. Night observations were made using five Sylvania, S14, 11 W, deep red sign bulbs, which minimize the stimulation of red-sensitive cone photoreceptors found in salmonid eyes and capitalize on the absorbance differences between salmonid and human eyes. This allowed night observations in what the fish perceived as relative darkness (Volpe et al. 2001).

Water depth, velocity, and substrate sizes present in the artificial streams were consistent with those selected by juvenile bull trout in natural streams (Baxter 1997; Bonneau and Scarnecchia 1998; Spangler and Scarnecchia 2001). Between experimental replicates the artificial streams were drained, scrubbed, and rinsed; substrate and filter media were removed, rinsed and returned to the stream, and filter charcoal was replaced.

Each replicate lasted 14 days, including fish collection day. Following a pilot study, fish were fed a ration of 10% body weight per day. Prey consisted of a mix of two parts frozen mosquito larvae *Culicidae* spp., two parts brine shrimp *Artemia* spp., and one part *Daphnia* spp. Food was dispensed using an inverted 2-L plastic jug suspended above each stream at the upstream end of the living area. The jugs were filled with cubed ice and the appropriate ration for a day, topped-up with well water, mixed, and frozen. Dependant on ambient air temperature jugs required approximately 12-36 h to thaw and forage items entered the streams haphazardly over the course of the melting period. Fresh jugs were provided daily. Feeding commenced on day 2 and ended on day 13 to allow for clearing of the gut prior to the end of the experiment on day 14, when fish were euthanized with an overdose of clove oil, measured and weighed.

Three fish were used in low-density treatments (4.1 fish/m^2), six in high-density and mixed-species treatments (8.2 fish/m^2). These densities are higher than bull trout densities reported from wild streams across the species range (0.001-0.01/m^2; Fraley and Shepard 1989; Saffel and Scarnecchia 1995; Thurow and Schill 1996) and Albertan streams specifically (0.0006-0.2/m^2; Paul et al. 2000); but near the upper range of density reported for resident juvenile salmonids in natural streams (Grant and Kramer 1990).

Observations

Alternating day (0800-1200 hours) and night (2000-2300 hours) observations of randomly selected focal fish (Altmann 1974) were made once every 24 hours. During observations observer movements were minimized and dress was standardized to minimize disturbance of the fish. A single observation was made for low-density treatments, two consecutive observations of different fish for high-density and mixed-species treatments. Each observation period lasted 15 minutes; order of observations between streams was randomly determined daily.

During observations, frequency of focal fish agonistic interactions initiated and received (nips, chases, and displays; Noakes 1980), and species targeted in mixed-species treatments were recorded. Foraging frequency and approximate depth within the water column of each forage event (top or bottom half of water column, water surface) of focal fish was noted. Except for the smallest *Daphnia*, forage items were easily observed and a forage event was counted each time an item was ingested by the focal fish, even if subsequently rejected. Multiple rejections of the same forage item by a fish were counted as a single foraging event. At one-minute intervals focal fish activity (moving or stationary) was recorded.

Three replicates of each treatment were completed June-November 2002 and June-October 2003; treatment replicates were interspersed between years. Three bull trout mortalities occurred during the artificial stream experiment when fish jumped out of the stream. To maintain treatment density, replacement fish were added to the stream within 24 hours. Replacement fish were excluded from behavioral observations and growth measurements. No brook trout mortalities occurred during the experiment.

Statistical Analyses

Each two-week treatment in an artificial stream constituted an experimental unit. Observations for each species within a treatment were averaged for each replicate. Interspecific agonisim counts were corrected to account for species asymmetry in mixed-species treatments. Statistical and graphical procedures (Zar 1999) were used to assess the homoscedasticity and normality of data prior to parametric analysis. Count and percentage data were square-root and arcsine-transformed, respectively, when required to meet parametric assumptions (Zar 1999). For ease of interpretation, untransformed results are presented.

Behavioral data were non-independent (behavioral categories were mutually exclusive) so principal components analysis (PCA) was used to condense the information contained in the data set into a new set of combined variables while minimizing information loss (Paukert and Wittig 2002). Principal components were extracted using the Kaiser criterion (i.e., eigenvalue > 1) from the correlation matrix (Kim and Mueller 1978). Resulting principal components were then rotated using the orthogonal varimax method to simplify the factor structure (Kim and Mueller 1978). PCA scores were calculated using the regression method and used as dependent variables in two-way analysis of variance (ANOVA) with temperature, and density as fixed-effects. A multivariate analysis of variance was not necessary as the PCA-derived factors are by definition orthogonal (Kim and Mueller 1978). Species were analyzed separately to contrast differences in their behavioral response to the treatments.

Chi-squared and Fisher's exact tests were used to compare foraging location and the frequency of use of different aggressive behaviours of each species in different density and temperature treatments. To avoid confounding an individual's preferential use of a behavior with that of its species, the number of observation periods in which a behavior was observed rather than the total frequency of use was compared in analyses. In all cases statistical significance was evaluated at $P \leq 0.05$ and statistical tests were two-tailed. Reduced alpha levels ($P = 0.05/n$ where n = number of pairwise comparisons) were used to correct for experiment-wise error rate.

Percentage weight change was used to quantify the per capita effect of intraspecific competition for each species by comparing differences in weight change between high- and low-density treatments. The per capita effect of interspecific competition was defined as the difference in weight between each species in the mixed-species treatment and that species in the low-density treatment at each temperature. A relative measure of weight change was used to account for differences in fish size between replicates. All analyses were performed using SPSS 11.5 (SPSS 2002).

Results

Two hours observation of each low-density replicate and four hours observation of high-density and mixed-species replicates were performed (96 h observation all treatments and replicates combined). Overall both species lost weight (Table 2.3) and no effect of fin clip type on percent growth of bull trout (ANOVA: $F_{5,63} = 0.808$, $P = 0.549$) or brook trout ($F_{5,66} = 1.244$, $P = 0.308$) was observed.

Principal Components Analysis

Bull trout

The three PC's extracted accounted for 79.6% of total variation in the bull trout data set (Table 2.4). Measures of movement and daytime foraging loaded strongly on PC 1. The second PC describes a positive correlation between intraspecific aggression and nighttime foraging. Interspecifc agonisim loads strongest on the third PC.

Percent weight change was factorially complex, being negatively correlated with both nighttime foraging on PC 2 and interspecific agonisim on PC 3.

Brook trout

Three PC's accounting for 76.7% of the variation in the brook trout behavioral data set were extracted by the PCA (Table 2.4). Night activity, positively correlated with growth, loaded strongly on PC 1. Both daytime movement and foraging were positively correlated with the second PC. Interspecific and intraspecific agonisim were both positively correlated with PC 3. Nighttime foraging was factorially complex, being positively correlated with nighttime movement and growth on PC 1 and agonisim on PC 3.

Treatment effects on behavior

Bull trout

Changes in density, temperature or the interaction between the two factors had no effect on movement and daytime foraging behavior of bull trout (PC 1; $P = 0.897$-0.436; Table 2.5). Density ($P = 0.024$) had an effect on intraspecific aggression and nighttime foraging behaviors (PC 2), differing significantly between low- and mixed-species treatments (Tukey's test: $P = 0.019$). Per capita, bull trout lost less weight and experienced more aggressive interactions with conspecifics overall in low-density treatments than when sympatric with brook trout (Table 2.3), while nighttime forage rates were nearly three times as great (Table 2.6). This result is largely a product of the disproportionate increase in intraspecific agonisim and nighttime foraging behavior of bull trout in the low-density treatment at 15°C, reflected in the marginally non-significant interaction between density and temperature ($P = 0.059$). Water temperature ($P < 0.001$) had a highly significant effect on aggression and foraging. Rates of bull trout aggression toward conspecifics at 15°C were approximately 3-26 times as great as rates at 8°C at comparable densities (Table 2.3). Per capita rates of nighttime foraging in warm-water treatments were also between 2-4 times as great as cold water rates (Table 2.6). The significant effect of density ($P = 0.039$) on interspecific aggression and growth (PC 3) reflects the absence of interspecific competitors in low- and high-density treatments and the tendency for bull trout to lose more weight in mixed-species treatments. In contrast to intraspecific aggression, interspecific aggression rates experienced by bull trout did not increase significantly in warmer water ($P = 0.253$) nor was the interaction between temperature and density significant ($P = 0.639$).

Brook trout

There was a non-significant ($P = 0.099$; Table 2.5) trend for brook trout to increase night activity (Table 2.6) and lose less weight (Table 2.3) in low-density treatments. Neither temperature nor the interaction between temperature and density had a significant effect on the behavioral correlates of PC 1 ($P = 0.327$-0.296). Brook trout did not adjust daytime activity (PC 2) in response to changes in density or temperature ($P = 0.970$-0.410) or their interaction ($P = 0.821$). Density, temperature and the interaction term had no significant effect ($P = 0.705$-0.092) on aggression and night foraging rates of brook trout (PC 3) although there was a non-significant trend for brook trout to increase night foraging at 15°C, particularly when sympatric with bull trout (Table 2.6).

Rates of interspecific and intraspecific aggression experienced by bull trout sympatric with brook trout were comparable within temperature treatment (Table 2.3). In contrast, rates of aggressive interaction between brook trout were seven times as great as interspecific interaction rates at 8°C but only twice as great at 15°C. This result was a direct result of brook trout increasing their aggressiveness toward bull trout at 15°C. Rates of brook trout aggression toward bull trout in the mixed-species treatments increased significantly with water temperature (Mann-Whitney *U*-test: $P = 0.046$; Figure 2.1) while rates of bull trout aggression toward brook trout did not differ significantly between water temperatures ($P = 0.376$).

Nature of aggression and foraging behavior

In warm water bull trout increased the proportion of chases ($P = 0.002$) and displays at low density ($P < 0.001$) employed during aggressive encounters. Brook trout did not change the type of aggressive behavior used in response to density or temperature ($P \geq 0.060$). Relative to bull trout, brook trout used more nipping and chasing behaviors in cold water ($P \leq 0.001$) and fewer displays in warm water ($P = 0.001$). Brook trout were also more likely to nip and chase tank mates in high-density treatments than bull trout ($P \leq 0.011$). Bull trout reduced use of display behavior when sympatric with brook trout ($P = 0.012$). Brook trout did not adjust aggressive behavior when sympatric ($P \geq 0.286$).

Density and temperature had no effect on the proportion of bull trout or brook trout foraging events occurring in the top or bottom half of the artificial stream or at the water's surface ($P \geq 0.027$). No significant difference between bull trout and brook trout foraging location was observed at either temperature ($P \geq 0.125$) or any density ($P \geq 0.198$).

When competing among conspecifics the forage rate of individual brook trout was positively correlated with the rate of initiated aggression in warm water treatments ($r = 0.888$; Figure 2.2), a trend not observed in cold water ($r = 0.242$) or for bull trout in either temperature treatment (r: 0.018-0.258). The significance of these relationships was not tested as some individuals shared the same stream environment and were thus non-independent.

A clear winner and loser could frequently be identified in pairs of aggressively interacting brook trout, which typically resulted in a single dominant individual in the stream. The distinction was less evident for bull trout. If brook trout are more effective at dominating conspecifics through aggression, a measure of the relative dispersion of acts of initiated aggression, such as the coefficient of variation ($V =$

SD/mean; Zar 1999), should be greater in treatments involving brook trout (V_{BKTR}) than treatments involving bull trout (V_{BLTR}). Examining the means for each species from allopatric replicates, V_{BKTR} 1.66 ± 0.18 (mean ± SE) was significantly greater than V_{BLTR} 1.16 ± 0.21 (Mann-Whitney *U*-test: $P = 0.028$). This suggests that one or two individual brook trout initiated the majority of aggression in a stream and suppressed tank mates more effectively than individual bull trout.

Competition coefficients

The per capita effect of interspecific competition on percent weight change of bull trout was greater than intraspecific competition at either temperature and greatest overall at 15°C (Table 2.7). In contrast, intraspecific competition between brook trout had a greater per capita effect on weight change than interspecific competition in warm water while coefficients were similar at 8°C. Overall, bull trout competition coefficients were consistently higher than comparable brook trout coefficients. This reflects the significant effect of density on brook trout growth (ANOVA with density and temperature as fixed factors: $F_{1,12} = 23.504$; $P = 0.028$) not observed for bull trout ($F_{1,12} = 0.137$; $P = 0.874$). Brook trout in low-density treatments grew more than those in high-density treatments (Tukey's test: $P = 0.039$). Temperature had no significant effect on growth of bull trout ($F_{1,12} = 4.277$; $P = 0.061$) or brook trout ($F_{1,12} = 2.450$; $P = 0.143$).

Discussion

Condition-specific competition (Dunson and Travis 1991) and more specifically, interspecific competition mediated by water temperature, has been demonstrated for a number of fish species (e.g., Baltz et al. 1982; Reeves et al. 1987; Reese and Harvey 2001), including species of char (e.g., De Staso and Rahel 1994; Taniguchi and Nakano 2000). Water temperature changes with altitude, and temperature-mediated competition is regarded as a major determinant of species distributions along altitudinal gradients (Fausch 1989; Taniguchi and Nakano 2000). Field survey data suggests water temperature is an important mediator of interspecific competition between juvenile bull and brook trout as well. The observed persistence of bull trout in cool, high-elevation streams in regions where brook trout have been introduced (Paul and Post 2001; Rich et al. 2003) may occur in part as a result of the species-specific behavioral responses to decreasing water temperature observed during this study.

Aggression and Foraging

Aggressive behavior is energetically costly for fish (Marchand and Boisclair 1998; Neat et al. 1998) and these costs can be expected to increase with water temperature (Elliot 1976; Tang and Boisclair 1995). With one of the lowest growth optima of the North American salmonids, approximately 1-3°C lower than that of brook trout (Selong et al. 2001), bull trout appear to be disadvantaged when aggressively interacting with brook trout in warm water. Bull trout were observed to significantly increase rates of intraspecific aggression in warm water but the increase did not result in an increase in the forage rate of aggressive individuals, as was observed for brook trout. In mixed-species treatments the per capita rate of intraspecific aggression among bull trout in warm water was six times as great as the cold-water rate, while brook trout rates did not differ significantly. The resulting energetic costs of this aggression for bull trout may have been further increased by their observed switching to proportionately more chasing behavior in warm water. This behavior involves rapid acceleration toward an opponent with frequent turning, which is energetically demanding (Tang and Boisclair 1995) and chases are typically of longer duration than nips or displays (Noakes 1980). Thus, in an environment of relatively high energetic costs, bull trout significantly increased aggression but aggressive individuals failed to secure a corresponding increase in forage.

Increasing aggressiveness with water temperature has been documented for fish species other than bull trout including: redside shiner *Richardsonius balteatus* (Reeves et al. 1987), Sacramento pikeminnow *Ptychocheilus grandis* (Reese and

Harvey 2002), Dolly Varden *S. malma* and white-spotted char *S. leucomaenis* (Taniguchi and Nakano 2000). In contrast, and consistent with the results of this study; little change in rates of brook trout aggression has been observed when water temperature was increased from 8 to 13°C (Cunjak and Green 1986) and reduced aggressiveness of brook trout has been reported as water temperature approaches 20°C (Cunjak and Green 1986; De Staso and Rahel 1994; Magoulick and Wilzbach 1998). Although information is limited, recent research has identified a link between individual metabolic rate, aggressiveness and dominance status of salmonids (Cutts et al. 2001) including Atlantic salmon *Salmo salar* (Cutts et al. 1998), masu salmon *O. masou* (Yamamoto et al. 1998), and Arctic char *S. alpinus* (Cutts et al. 2001). It is possible the increased aggressiveness of some salmonids in warmer water may occur as a result of an increase in metabolic rate with water temperature. Hunger may also bring about an increase in aggression, however the relationship between feeding motivation and metabolic rate can be complex (Cutts et al. 2002). The tendency for bull trout in the artificial streams to increase feeding activity at night is consistent with the general observation that juvenile bull trout increase activity at night (Bonneau et al. 1995; Thurow 1997). This trait has the potential to modify any behavioral response of bull trout associated with increased water temperature in natural streams during the summer where diel temperature fluctuation often results in cooler water temperatures at night (Ward 1985). Examination of the interaction between temperature, aggressiveness, and metabolic rate and how they relate to species-specific thermal preferences and diel activity patterns would be a productive area of future research.

A number of factors probably increased aggression rates observed in the artificial streams relative to rates in a natural environment. An obvious difference is the inability of subordinate individuals to flee aggressive interactions in the artificial stream. Losers of an aggressive encounter were usually unable to sufficiently distance themselves from aggressors and suffered repeated attacks. Relative size of competitors was also closely matched in the artificial streams as larger fish typically dominate smaller ones (Sabo and Pauley 1997; Fausch 1998); thus, the winner of any aggressive interaction was never obvious based on disparity in size alone. Finally, fish were introduced to the artificial streams simultaneously and may have increased aggression in the novel environment with unfamiliar tank mates (Seppä et al. 2001; Cutts et al. 2002). Although conditions in the artificial streams potentially increased rates of agonisim (Sundbaum and Näslund 1998) the frequencies observed include rates reported for free ranging bull trout (Gunckel et al. 2002) and age-0 brook trout (Grant 1990).

Growth

Although individual growth was highly variable and no significant effect of density or temperature on bull trout growth was observed overall, per capita growth of bull trout in cold water exceeded growth in warm water at every density and weight loss was greatest when sympatric with brook trout at 15°C. If these results were strictly a physiological response of bull trout to increased water temperature, fish that gained weight in the warm-water treatments should have consistently gained less weight than those in the cold-water treatments, but this was not the case. Although uncommon, individual bull trout in both temperature treatments gained weight ($n = 14$) and no significant difference in the percent weight gain of fish between temperature treatments was observed (Mann-Whitney U-test: $P = 0.572$). More generally, in a laboratory experiment using age 0-bull trout, feed efficiency (g of growth/g of feed consumed) was found to be similar over an 8-18°C range (Seelong et al. 2001).

In contrast to bull trout, temperature did not have any consistent effect on brook trout growth. In high-density and mixed-species treatments per capita growth was improved in cold water, but growth rates were nearly identical at low-density. Only a doubling of density had a significant effect on brook trout growth. This effect, not observed in bull trout, appears to be a result of the ability of individual brook trout to monopolize forage. Regardless of density, a single aggressive brook trout usually dominated its tank mates, secured the majority of forage and gained weight in each replicate; a common occurrence in small groups of salmonids (Adams et al. 1998;

MacLean et al. 2000). Maximum and minimum percent weight gain of individual brook trout in each replicate did not differ significantly between high- and low-density treatments (Mann-Whitney *U*-test: $P = 0.873$ and 0.200 respectively). Thus the lower mean growth of brook trout in high-density replicates likely reflects a reduction in the effect of the dominant individual's growth on per capita weight change within a replicate. Individual bull trout were rarely observed overtly excluding conspecifics from forage items through aggression.

Though individuals of both species gained mass, most fish lost mass over the course of the experiment, not uncommon in short duration experiments using captive fish (e.g., Fausch and White 1986; Volpe et al. 2001; Gunckel et al. 2002). The relatively high density and uniform habitat of the artificial streams may have led to a reduction in visual isolation between tank mates and increased activity (Sundbaum and Näslund 1998). The amount of forage available to fish was also considerably less than the ten percent of body weight provided. Fish of both species in all treatments were observed capturing drifting items, particularly mosquito larvae, only to reject them shortly thereafter. Once the problem was identified feed composition was not changed to maintain consistency between replicates.

Implications for Interspecific Competition

Although intraspecific agonisim among bull trout increased significantly with water temperature, bull trout did not significantly increase aggressiveness toward brook trout. In contrast, overall rates of brook trout agonisim were unaffected by increasing water temperature but they shifted the focus of their aggression in mixed-species replicates. Intraspecific aggression among brook trout was approximately seven times more frequent than interspecific aggression in cold water, but only twice as frequent in warm water as brook trout significantly increased their aggressive behavior toward bull trout.

The effect of this increased aggressiveness toward bull trout is reflected in each species per capita foraging rates. In cold water, bull trout foraged most often in the mixed-species treatment, approximately three times more frequently than brook trout. In warm water bull trout foraged least often when sympatric, less than half as frequently as brook trout. In contrast to brook trout, aggressive individual bull trout failed to secure more food. The reduced forage rate of bull trout sympatric with brook trout in warm water despite increased aggressiveness, versus the relatively high forage rate in cold-water treatments, suggests that juvenile bull trout may be more proficient as exploitative rather than interference competitors when sympatric with brook trout.

Studies of bull trout behavior performed in natural settings indicate that bull trout may commonly compete through exploitation of shared food resources while brook trout are more successful as interference competitors. In a Montana stream nearly 70% of bull trout sympatric with cutthroat trout *O. clarki lewisi* moved constantly, capturing prey primarily from the streambed, while cutthroat trout held relatively fixed positions in pools (Nakano et al. 1992). Similarly, juvenile bull trout in an Idaho stream were observed to roam slack-water areas and pick prey off the bottom (Bonneau and Scarnecchia 1998). Using a 15-year time series of juvenile bull trout abundance, Paul et al. (2000) found similar slopes regressing finite survival as a function of effective density among one to three-year-old bull trout in Eunice Creek and hypothesized that density-dependant survival was arising through exploitative competition on a limited food resource. If the bull trout were territorial an inequitable partitioning of resources leading to greater growth or survival of dominant individuals would have been expected (Paul et al. 2000). In an instream enclosure study of bull trout and brook trout behavior the mean frequency of interactions in which brook trout dominated bull trout (i.e., gained or maintained feeding territory through aggression; Gunckel et al. 2002) was 26 times the rate at which bull trout displaced brook trout in mixed-species enclosures (Gunckle et al. 2002). Despite the disparity no significant difference between foraging rates was observed and the effects of interspecific and intraspecific competition on bull trout growth were equivalent

(Gunckel et al. 2002). Finally, bull trout significantly increased foraging distance and rate after brook trout removal during a species removal experiment in two Montana stream pools (Nakano et al.1998). Nakano et al. (1998) hypothesized that the increase was most likely a result of the bull trout's release from interference competition with brook trout. Unfortunately the relative strength of interspecific and intraspecific competition could not be measured as fish density decreased as a result of the fish removals (Nakano et al. 1998). In the case of juvenile bull trout, these observations, in conjunction with the findings of this study, bring into question the common assumption that stream salmonids typically defend territories (Grant and Kramer 1990).

Conclusion

Bull trout competed more successfully against brook trout in cold (8°C) than in warm (15°C) water in artificial streams as a result of relatively low rates of aggression and high forage rates. Although individual growth was highly variable and primarily negative, bull trout consistently lost more weight in warm-water treatments and the most when sympatric with brook trout. This probably occurred as a result of the bull trout's tendency to increase aggression in the warm water treatment, which was not matched by a proportional increase in forage rate, and from an increased likelihood of aggressive interaction with brook trout. Competition with brook trout was more costly for bull trout than intraspecific competition at either temperature but the effect of interspecific and intraspecific competition on brook trout growth in cold water was comparable while intraspecific competition had a greater per capita effect on brook trout growth than interspecific competition in warm water.

These results are consistent with the observation that bull trout populations are more resilient to brook trout invasion in higher elevation (i.e., cooler) streams. Fisheries mangers need to consider not only the physiological but also the behavioral consequences of increasing water temperature on native coldwater fish communities. The interaction of factors structuring interspecific competition between these species in nature are undoubtedly much more complex than those manipulated in the artificial environment used for this study. Interactions between other life stages (Fausch 1998), diel or seasonal fluctuations in temperature and invertebrate drift (Nakano et al. 1999), increased habitat complexity (Sundbaum and Näslund 1998), and longer-term fitness consequences (Taniguchi and Nakano 2000) were not considered here and probably further modify the condition-specific behavioral responses observed.

Table 2.1.—Experimental design for testing intraspecific versus interspecific competition of bull trout (BL) and brook trout (BK) at cold (C; 8°C) and warm (W; 15°C) water temperatures and low (LD; 4.1 fish/m^2), high (HD; 8.2 fish/m^2) and mixed-species (MIX) densities, $n = 3$.

	Density of bull trout		
Density of brook trout	0	*n*	2*n*
Cold-water treatment			
0	-	LDC-BL	HDC-BL
n	LDC-BK	MIXC	-
2*n*	HDC-BK	-	-
Warm-water treatment			
0	-	LDW-BL	HDW-BL
n	LDW-BK	MIXW	-
2*n*	HDW-BK	-	-

Table 2.2.—Mean ± SD of maximum difference in fork length and weight of fish (bull trout and brook trout combined) used in artificial stream replicates of three density treatments.

Density	Mean maximum difference	
	Fork Length (mm)	Weight (g)
Low	7.3 ± 7.2	2.8 ± 1.6
High	8.2 ± 3.3	3.9 ± 3.3
Mixed	8.5 ± 3.8	2.7 ± 1.8

Table 2.3.—Mean per capita ± SE percent change in weight, agonisim and forage rates; and percentage of counts spent moving per 15-min period of juvenile bull trout and brook trout in artificial streams at cold and warm water temperatures and three different densities.

	ΔWeight (%)	Intraspecific agonisim	Interspecific agonisim	Forage	% Moving
Bull trout 15°C					
Low	-7.1 ± 2.21	3.19 ± 0.83	-	2.15 ± 1.63	29 ± 7
High	-8.7 ± 1.13	1.42 ± 0.39	-	1.62 ± 0.57	16 ± 3
Mixed	-9.9 ± 2.20	1.99 ± 0.68	1.69 ± 0.74	0.93 ± 0.33	21 ± 7
Bull trout 8°C					
Low	-4.2 ± 1.70	0.12 ± 0.06	-	0.84 ± 0.41	9 ± 4
High	-4.3 ± 1.25	0.39 ± 0.17	-	0.85 ± 0.41	20 ± 5
Mixed	-6.0 ± 2.14	0.33 ± 0.19	0.47 ± 0.25	1.25 ± 0.74	22 ± 7
Brook trout 15°C					
Low	-3.1 ± 2.22	2.84 ± 1.38	-	1.48 ± 0.67	23 ± 10
High	-8.6 ± 1.24	2.39 ± 0.64	-	0.93 ± 0.47	12 ± 3
Mixed	-7.3 ± 2.08	1.97 ± 0.66	1.04 ± 0.34	2.46 ± 0.98	83 ± 7
Brook trout 8°C					
Low	-3.2 ± 2.10	0.67 ± 0.33	-	1.00 ± 0.45	23 ± 6
High	-5.5 ± 1.22	2.38 ± 0.75	-	0.85 ± 0.35	30 ± 5
Mixed	-5.9 ± 1.37	2.24 ± 0.79	0.30 ± 0.12	0.41 ± 0.15	67 ± 11

Table 2.4.—Factor loadings for principal components analyses of observations made of juvenile bull trout and brook trout behavior in artificial streams.

	Principal component		
Bull trout	1	2	3
ΔWeight (%)	0.337	-0.493	-0.688
Intraspecific agonisim	0.010	0.867	0.150
Interspecific agonisim	0.067	-0.065	0.957
Forage day	0.916	-0.185	-0.019
Forage night	0.296	0.706	-0.063
Moving day	0.804	0.380	-0.020
Moving night	0.855	0.226	-0.087
% cumulative variation	34.6	59.2	79.6
Brook trout			
ΔWeight (%)	0.821	-0.311	-0.194
Intraspecific agonisim	0.137	0.092	0.806
Interspecific agonisim	-0.171	0.099	0.724
Forage day	-0.080	0.797	0.323
Forage night	0.664	-0.035	0.632
Moving day	0.072	0.958	-0.084
Moving night	0.844	0.292	0.082
% cumulative variation	27.0	52.0	76.7

Table 2.5.—Results of a two-way ANOVA (factors = density, temperature) of juvenile bull trout and brook trout behavioral PCA scores.

	df	PC 1			PC 2			PC 3		
		SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Bull trout										
Density	2	0.263	0.109	0.897	2.783	5.170	0.024	6.369	4.305	0.039
Temperature	1	0.130	0.108	0.748	9.034	33.565	<0.001	1.065	1.440	0.253
Temperature*density	2	2.144	0.890	0.436	1.953	3.627	0.059	0.689	0.466	0.639
Error	12	14.462			3.230			8.877		
Brook trout										
Density	2	4.512	2.826	0.099	0.079	0.031	0.970	2.027	1.088	0.368
Temperature	1	0.951	1.191	0.296	0.939	0.728	0.410	3.123	3.352	0.092
Temperature*density	2	1.959	1.227	0.327	0.518	0.201	0.821	0.670	0.360	0.705
Error	12	9.579			15.464			11.180		

Table 2.6.—Mean per capita ± SE agonisim and forage rates, and percentage of counts spent moving per 15-min period; of juvenile bull trout and brook trout at cold and warm water temperatures and three different densities during day and night observations.

	Intraspecific agonisim		Interspecific agonisim		Forage		% Moving	
	Day	Night	Day	Night	Day	Night	Day	Night
Bull trout 15°C								
Low	3.21 ± 0.98	2.06 ± 0.81	-	-	0.86 ± 0.37	3.39 ± 2.76	27 ± 6	36 ± 13
High	2.04 ± 0.53	0.97 ± 0.47	-	-	1.24 ± 0.58	1.68 ± 0.76	14 ± 4	19 ± 5
Mixed	2.57 ± 0.77	0.82 ± 0.42	1.36 ± 0.64	2.26 ± 1.65	0.71 ± 0.36	1.05 ± 0.47	18 ± 9	17 ± 5
Bull trout 8°C								
Low	0.06 ± 0.06	0.19 ± 0.13	-	-	0.75 ± 0.62	0.81 ± 0.35	7 ± 4	11 ± 5
High	0.30 ± 0.13	0.46 ± 0.23	-	-	1.12 ± 0.55	0.41 ± 0.20	12 ± 4	25 ± 6
Mixed	0.31 ± 0.25	0.19 ± 0.19	0.39 ± 0.20	0.81 ± 0.48	2.42 ± 1.49	0.50 ± 0.31	18 ± 7	27± 9
Brook trout 15°C								
Low	2.19 ± 1.87	2.04 ± 1.10	-	-	0.61 ± 0.32	1.86 ± 0.86	9 ± 4	28 ± 13
High	2.36 ± 0.73	2.26 ± 0.99	-	-	0.64 ± 0.24	1.43 ± 1.08	10 ± 3	15 ± 5
Mixed	1.32 ± 0.81	2.53 ± 0.84	1.43 ± 0.60	0.69 ± 0.37	1.57 ± 1.11	3.13 ± 1.13	87 ± 6	79 ± 9
Brook trout 8°C								
Low	0.25 ± 0.25	1.38 ± 0.73	-	-	1.33 ± 0.70	0.93 ± 0.66	9 ± 4	50 ± 13
High	3.73 ± 1.58	1.15 ± 0.33	-	-	0.41 ± 0.21	1.19 ± 0.50	25 ± 7	35 ± 7
Mixed	2.07 ± 1.02	2.16 ± 0.74	0.29 ± 0.18	0.38 ± 0.16	0.83 ± 0.33	0.31 ± 0.25	68 ± 15	69 ± 11

Table 2.7.—Coefficients of competition (*a*) of juvenile bull trout and brook trout at cold and warm water temperatures. The greater the absolute value, the greater the difference.

	a_{BLBL}	a_{BLBK}	a_{BKBK}	a_{BKBL}
Cold	-0.1	-1.8	-2.3	-2.7
Warm	-1.6	-2.8	-5.5	-4.2

Note: a_{BLBL} = bull trout intraspecific, a_{BLBK} = bull trout-brook trout interspecific, a_{BKBK} = brook trout intraspecific, a_{BKBL} = brook trout-bull trout interspecific.

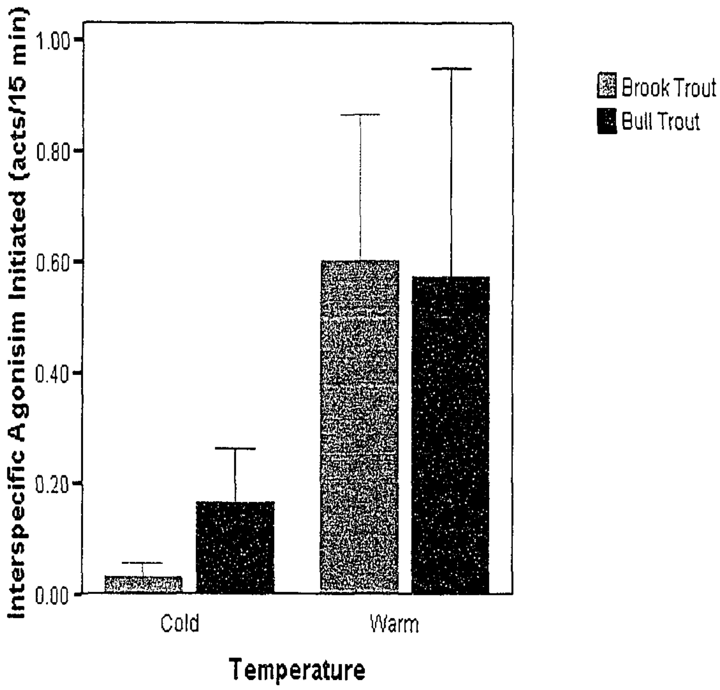

Figure 2.1.—Mean ± SE rate of interspecific agonisim initiated by bull trout and brook trout in mixed-species treatments at cold and warm water temperatures.

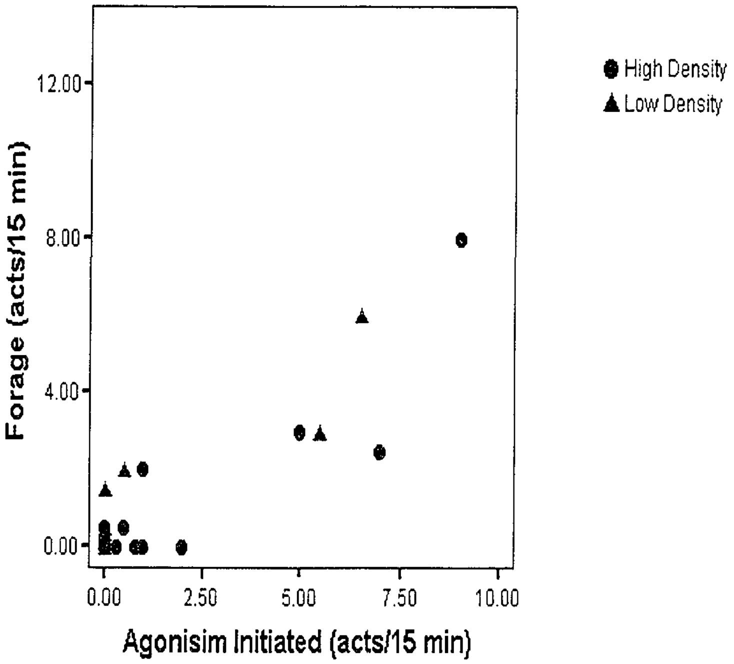

Figure 2.2.—Mean forage rate versus mean rate of initiated aggression of individual brook trout in warm water at high- and low-densities; $r = 0.888$.

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Chapter 3: Environmental factors affecting the distribution, abundance, and behavior of sympatric bull trout and brook trout in Haven Creek, Alberta.

Introduction

The distribution and abundance of bull trout *Salvelinus confluentus* is influenced by a number of physical and biological factors. Factors demonstrated to be important include: stream temperature (Saffel and Scarnecchia 1995; Rieman et al. 1997; Paul and Post 2001; Dunham et al. 2003), elevation (Paul and Post 2001; Rieman et al. 1997), gradient (Rich et al. 2003), width (Rieman and McIntyre 1995; Dunham and Rieman 1999; Rich et al. 2003), abundance of pool (Saffel and Scarnecchia 1995; Watson and Hillman 1997) and woody debris (Watson and Hillman 1997; Rich et al. 2003), road density (Rieman et al. 1997; Dunham and Rieman 1999), isolation from other bull trout populations (Dunham and Rieman 1999; Rich et al. 2003), and the presence of nonnative salmonids (Watson and Hillman 1997; Paul and Post 2001; Rich et al. 2003). Determining the relative importance of these factors is difficult as they often co-vary (Paul and Post 2001; Rieman and McIntyre 1995) and their significance may depend upon the spatial scale at which they are measured (Rieman and McIntryre 1995; Watson and Hillman 1997; Dunham and Rieman 1999).

Presence of nonnative salmonids, including rainbow trout *Oncorhynchus mykiss* (Watson and Hillman 1997; Paul and Post 2001) and brook trout *S. fontinalis* (Watson and Hillman 1997; Paul and Post 2001; Rich et al. 2003) has been negatively associated with bull trout occurrence. Where sympatric with brook trout, bull trout were more likely to occur in higher elevation, cooler streams (Paul and Post 2001; Rich et al. 2003) with more pools and large woody debris (Rich et al. 2003). Although non-significant relationships have been observed in other regions where the two species co-occur, brook trout were typically uncommon and/or occurred at low densities (Dunham and Rieman 1999; Dunham et al. 2003). Considerably more research has been performed on an analogous relationship between distributions of brook trout and native cutthroat trout *O. clarki*, which are longitudinally segregated in many streams of western North America (Fausch 1989; Dunham et al. 2002). The successful invasion of brook trout appears to be influenced by several environmental factors including: temperature, landscape structure, habitat size, stream flow and human influences (Dunham et al. 2002); however, the interaction between factors is complex and research has often generated more questions than answers (Dunham et al. 2002).

This study was designed to examine the interaction between summer distribution and abundance of native bull trout and nonnative brook trout, temperature, and elevation, in a stream containing naturally reproducing populations of both species. Behavior of wild fish was quantified over a range of environmental variation, particularly variation in water temperature, to identify possible links between species-specific behavior and patterns of distribution and abundance. By including key environmental variables known to influence the competitive behavior of salmonids during observations, the relationship of individual behavior to the larger environmental context within which it occurs could be examined. The focus of this research was to test the null hypothesis that the competitive performance of bull trout and brook trout is independent of water temperature. Specific research objectives were to quantify agonisim, activity, and foraging behavior of sympatric bull trout and brook trout in a stream environment during the summer, over a range of environmental variation, particularly in water temperature, and compare research findings to existing literature regarding bull trout distribution, temperature preferences, and competitive interactions with nonnative fish species.

Methods

Study Area

Data were collected in Haven Creek (116°12'W, 52°23'N), a 20 km long, fourth-order tributary to the North Saskatchewan River approximately 90 km west of Rocky

Mountain House Alberta, Canada. Haven Creek was selected on the basis of accessibility and that bull trout and brook trout were known to co-occur in the stream in relatively high numbers. Brook trout and bull trout dominate the fish fauna of Haven Creek (Gardiner et al. 2001; M.R. unpublished data), although brown trout *Salmo trutta*, mountain whitefish *Prosopium williamsoni*, and pearl dace *Margariscus margarita* are occasionally found in lower reaches (Gardiner et al. 2001; Alberta Fish and Wildlife Division files, Rocky Mountain House, Alberta). Brook trout were first introduced to east slope streams in central Alberta in the early 1900s (Rhude and Stelfox 1997) however early records for the Rocky Mountain House area are limited and it is not clear when or how brook trout first colonized Haven Creek. Brook trout were likely first introduced to area waters in the mid-to-late 1940s (S. Herman, Alberta Fish and Wildlife Division, personal communication). Currently brook trout are distributed throughout the Haven Creek drainage (Gardiner et al. 2001). A province-wide zero-bag-limit for bull trout has been in effect since 1995 (Post and Johnston 2002) while a possession limit of two brook trout is allowed (Government of Alberta 2003).

Population Estimates

Population estimates were generated using the removal method (White et al. 1982) at three 300 m study reaches roughly corresponding to the lower, middle and upper main stem of Haven Creek. Reaches were chosen to represent the continuum of elevation, water temperature, and aquatic habitats present within Haven Creek. Estimates were performed during July of 2002 and 2003. At least three passes were performed at each reach with the exception of a single estimate at the upper reach in which two passes were completed as fish numbers were very low. Reaches were blocked at both ends using fine mesh (6 mm) nets anchored to the stream bottom. Fish were captured using a Smith-Root (Vancouver, W.A.) Model 15D backpack electrofisher. Electrofisher settings varied between 200-400 V and 40-60 Hz with a pulse width of 2-6 ms generating 0.18-0.8 output amps, depending upon stream conditions.

Fish were anesthetized using clove oil (Keene et al. 1998), measured to fork length (FL; nearest millimeter), weighed (wet weight; nearest 0.1 g), and fin clipped (single or combination of dorsal, anal, adipose and/or caudal). Age-0 fish (30-40 mm FL) were not sampled although small numbers were collected for identification. Wetted width was measured at 50 m intervals at each reach after the estimate was complete. Onset Stow Away XTI (Pocasset, M.A.) temperature dataloggers were placed at each reach under cover near the thalwag. Dataloggers were deployed July-October in 2002 and June-October in 2003 and recorded maximum temperature at 1.2 h intervals in 2002 and 2 h intervals in 2003. Reach elevations were determined using 1:50 000 topographic maps.

Behavioral Observations

Snorkel observations of fish behavior were performed at an outflow pool of a large (~3 m diameter) culvert where the water level remained relatively stable. The study pool allowed easy access to undisturbed fish and contained habitat similar to that in the smaller, natural pools of Haven Creek.

Pool habitat measurements were made on August 8, 2003 based on a $1m^2$ horizontal grid. Depth and current velocity measurements, measured with a Marsh-McBirney portable velocity meter at the surface and 0.6 times depth, were made at the corner of the grid cells. Discharge and invertebrate drift were estimated each day of observations at a fixed location in a riffle area approximately 30 m upstream of the pool. Discharge was measured using the cross section method (Gallagher and Stevenson 1999). Invertebrate drift was collected using a 500 μm mesh Nitex drift net (20x30 cm opening, 60 cm long) suspended approximately 5 cm off the substrate and extending above the water's surface. Water velocity was measured at the net mouth at the beginning and end of every set and averaged to determine water velocity during the set. The net was set an average of 1.6 h (range 1.4-2.0 h) between 0900 and1700 hours. Drift samples were preserved in 95% EtOH and identified to order or family using taxonomic keys in Bland and Jaques (1978) and Clifford (1991).

Scan samples of fish behavior (Altmann 1974; Martin and Bateson 2001) were performed August 7-September 6 2003. During scan sampling a group of subjects are scanned at regular intervals and the behavior of each individual at that instant is recorded (Martin and Bateson 2001). Water clarity and pool morphology made it impossible to observe the entire pool from any single location so observations were made from one of three fixed locations near the periphery of the pool every observation period. After moving into position a single observer remained motionless for 5 min before beginning observations, five consecutive scans at two-minute intervals were made at each location (single scan took < 30 s to complete). The order of locations from which observations were made was determined randomly every observation period. Observations were performed between 1000 and 1700 hours, observation periods lasted approximately one hour. When multiple observations were made in a single day (maximum of three) a minimum 30 min break between observation periods was observed. A data-logger, placed under cover at the downstream end of the pool, recorded mean water temperature every 36 min in the pool August-September 2003.

During each scan the number and species of fish performing each of three behavioral categories: stationary, foraging or cruising, was recorded. Stationary fish were defined as fish holding station within the water column. Foraging fish exhibited rapid changes in body orientation and directed movement toward forage items. Cruising individuals were defined as fish neither holding station nor foraging. During each observation period all agonistic encounters (nips, chases and displays (Noakes 1980)) were recorded. Species involved in encounters, and if the aggression was mutual or one-sided, was noted. All observations were relayed to a recorder on the bank.

Abundance of bull trout and brook trout in the pool was estimated visually while slowly moving through the pool at the end of each observation period. Foraging and cruising fish were more conspicuous than stationary fish when visibility was low. To estimate this potential source of bias, visibility was estimated by measuring the distance at which a stationary fish was first visible upon approach. The size distribution of each species was estimated weekly by comparing individuals to calibrated rods (1 cm increments) on the substrate throughout the pool. Although no fish were observed moving up through the short riffle section immediately downstream of the pool it is unlikely it acted as a barrier to fish movement during the study. Fish were observed moving from the pool upstream through the culvert.

Statistical Analysis

Population estimates were calculated using the program CAPTURE (White et al. 1982). Estimated fish abundance (when possible), reach length, and mean wetted width were used to calculate fish density (fish/m^2). Effective density, which incorporates the allometry of consumption for differences in fish size (Paul et al. 2000), was used to compare the potential for exploitative competition among reaches (Post et al. 1999). Effective density was calculated as the sum of squared FL (measured in mm)/m^2 (Paul et al. 2000). The proportion of individuals of both species in each of the three behavioral categories was calculated each observation period and entered as dependant variables in stepwise multiple linear regressions (P 0.05 to enter; 0.10 remove). Aggressive interactions were relatively infrequent so counts of aggression initiated by both species were combined for analysis. Independent variables considered for the models included: bull trout and brook trout abundance, visibility, water temperature, stream discharge (m^3/s), and drift rate (number of items$\cdot$m$^{-3}\cdot$s^{-1}). The correlation matrix was examined to identify potential collinearity between independent variables (Zar 1999). Visibility was highly correlated ($P < 0.001$) with brook trout abundance and discharge so it was removed from the models, and the data reanalyzed to evaluate the sensitivity of parameter estimates to the potential effects of collinearity (Zar 1999). To account for error associated with extrapolating daily drift rate from a single measure the reduced data set containing only those observation periods during which drift rate was measured was analyzed. Residual scatterplots and normal probability plots were used to assess normality, linearity, and homoscedasticity of behavioral data; proportion and count data were arcsine- and square-root-transformed respectively (Zar 1999). SPSS 11.5 was used for all statistical analyses (SPSS 2002). Untransformed values are reported for ease of interpretation unless otherwise indicated.

Results

Population Estimates

Over the two years a total of 191 bull trout (62-420 mm FL) and 276 brook trout (44-223 mm FL) were captured at the three reaches (Table 3.1). Effective density of brook trout was 1.5-78 times greater than that of bull trout at all reaches except the uppermost where bull trout effective density was approximately double that of brook trout in 2002. In 2003 no brook trout were captured in the upper reach and bull trout densities were drastically reduced in the upper and middle reaches. Effective density of brook trout remained relatively constant between years at the middle and lower reaches. Comparing fork length frequency histograms, the few bull trout captured in 2003 appear to be the remnants of a strong year-class that dominated the catch in 2002 and then disappeared (Figure 3.1); no comparable trend was observed for brook trout. A single brook trout, clipped in 2002, was recaptured in 2003 at the middle reach. Although age-0 fish were not specifically targeted, age-0 brook trout were observed at every reach except the uppermost on every sampling occasion while no age-0 bull trout were observed.

August mean maximum temperature was negatively correlated with elevation in 2002 ($r = -0.930$) and 2003 ($r = -0.833$) and increased 1.4-2.1°C at all reaches in 2003 (Table 3.2). The number of days in which maximum temperature met or exceeded 15°C, the temperature above which long-term survival of bull trout is unlikely (Seelong et al. 2001), decreased with elevation from approximately 65% of days in

August 2002 in the lower section to 42% and 3% at the middle and upper reaches respectively, and from 84% to 68% and 0% of days in 2003.

Behavioral Observations

Over 12 days, 25 observations were completed, resulting in approximately 18 h of observation over a wide range of environmental variation (Table 3.3). Bull trout density ranged between 0.01-0.06 fish/m^2 and in size from approximately130-170 mm FL. Brook trout density ranged between 0.08-0.29 fish/m^2 and in size between 70-220 mm FL. Overall, discharge decreased over time while water temperature fluctuated daily, with the warmest temperatures occurring during afternoon observations. Visibility and brook trout abundance increased over time. Invertebrate drift was highly variable and dominated by mayfly (*Ephemeroptera* spp.) and diptera larvae early in the study and later by terrestrial insects.

Brook trout typically arranged themselves in a loosely structured group with the largest individuals occupying positions at the head of the pool and smaller individuals positioned downstream or facing into eddy currents near the pool margin. The same individual brook trout (identified by a combination of length and lateral markings) was commonly observed in the same location over a period of several days. Although bull trout would enter the size-structured group they rarely remained in position for more than a few minutes at a time and commonly moved throughout the pool.

A total of 47 aggressive interactions were observed, 9 (19%) initiated by bull trout and 38 (81%) by brook trout. Interactions were infrequent (per capita rate using average abundance; bull trout 0.04 interactions/15 min, brook trout 0.02 interactions/15 min), often confounded by fish size, and included nipping, chasing and display behaviors (Noakes 1980). Aggression initiated by bull trout occurred over a narrower range of temperatures (12.5-15.4°C; mean 13.8°C) than brook trout aggression (9.9-16.6°C; 13.5°C). Thirty percent of all aggressive interactions were interspecific and initiated by each species with nearly equal frequency. It is surprising that the number of aggressive interactions in an observation period increased with bull trout abundance (Table 3.4), reflected in the relatively high proportion of interspecific aggressive interactions observed, given that brook trout outnumbered bull trout approximately 9:1 in the pool on average.

Proportionately more bull trout than brook trout were observed cruising (paired *t*-test: $t = -5.043$; df = 24; $P < 0.001$) but the proportion of fish observed foraging did not differ significantly ($t = 1.929$; df = 24; $P = 0.066$) between species. Thus proportionately more individual brook trout held stationary positions within the pool than bull trout (Figure 3.2). Generally discharge had a significant effect on the behavior of both species; water temperature also had a significant effect on brook trout behavior (Table 3.4). Both species became more active when discharge increased and brook trout foraged and cruised more with increasing water temperature. When visibility was included in the model it replaced brook trout abundance as a significant predictor of the foraging behavior of brook trout. Little difference in the amount of variation explained by either model or a model including both visibility and abundance was observed. Thus it is unclear if reductions in the proportion of brook trout observed foraging were an effect of increased brook trout abundance or a bias resulting from the conspicuousness of brook trout foraging behavior under conditions of reduced visibility. Significant predictors of bull trout behavior did not vary when visibility was included as an independent variable in the regression models. Drift rate did not enter any of the regression models and probably underestimated availability of forage to fish in the pool, as they often fed on newly entered terrestrial insects in slack water around the pool margin.

Discussion

Species Distribution and Abundance

Brook trout occurred at greater effective densities than bull trout at all reaches of Haven Creek except the uppermost. Comparable observations have been made in streams where introduced brook trout are sympatric with native cutthroat trout, potentially a result of lower per capita spatial requirements of brook trout (Dunham et al. 2002). Although elevation and decreasing water temperature were positively associated with bull trout density and negatively with brook trout density in 2002. Bull trout density decreased dramatically in the upper reaches in 2003 while brook trout densities remained comparatively stable at the lower and middle reaches but declined from 0.02 fish/m^2 at the upper reach in 2002 to zero fish in 2003. Clearly, elevation and water temperature alone do not adequately explain the distribution of these species within Haven Creek.

At the upper reach low brook trout recruitment may be limiting their establishment while bull trout persist, albeit in very low numbers. Brook trout captured at the upper reach in 2002 were most likely migratory adults. Mean length of these fish was relatively large (141 mm versus 118 mm and 115 mm at the middle and lower reaches respectively) while the majority of bull trout were probably juveniles (mean FL 84 mm). Adams et al. (2000) found that upstream movements of brook trout through steep channels were dominated by fish greater than135 mm total length and that dispersal of brook trout less than 95 mm was uncommon. Although age-0 fish were not specifically targeted while electrofishing, age-0 brook trout were observed at all reaches except the uppermost both years; however, brook trout pairs on redds were observed immediately upstream of the upper reach in autumn, 2002 (M.R. unpublished data).

Behavioral Observations

Significantly more active than brook trout, bull trout may be disadvantaged when competing with brook trout in warmer water, where their energetic demands are likely greater. Although the proportion of individuals observed foraging did not vary significantly between species, proportionately more individual bull trout than brook trout were observed cruising and fewer remained stationary during observations at any given temperature. Over the course of observations, bull trout moved throughout the pool foraging while the majority of brook trout were observed holding position within the water column. In their study of sympatric Dolly Varden *S. malma* and white-spotted char *S. leucomaenis* in a mountain stream, Nakano et al. (1999) identified two similar modes of foraging: foraging on invertebrate drift from relatively fixed positions, and active searching for benthic prey over large areas of the stream. In contrast to that study, where niche partitioning via shifts in foraging mode with diminishing drift abundance likely enabled coexistence of the two species (Nakano et al. 1999), there is little evidence to suggest bull trout and brook trout spatially partition resources (Gunckel et al. 2002) and both species were observed foraging primarily from invertebrate drift and at the pool's surface. The mobile foraging behavior of bull trout may represent an alternative feeding strategy of subordinate individuals (Adams et al. 1998; MacLean et al. 2000) rather than a species-specific trait per se, however, bull trout were observed successfully displacing brook trout from foraging positions on several occasions. Although both species adjusted their behaviors similarly in response to changes in stream discharge, individual brook trout also increased foraging and cruising behavior with water temperature, probably also increasing the potential for interspecific interaction.

Across the temperature range observations were made, proportionately fewer brook trout remained stationary with increasing water temperature. A comparable relationship between temperature and activity was observed for juvenile brook trout held in pelagic enclosures by Marchand et al. (2003). If bull trout increase aggressiveness with rising water temperature, as observed in artificial streams (Chapter 2) and supported by observations of wild fish during this study (the minimum water temperature at which bull trout initiated aggression was 12°C, observations occurred between 8-17°C), more interspecific conflict is likely to occur. Although brook trout were, on average 9.4 ± 6.4 (± SD) times more abundant than bull trout, 30% of all aggressive interactions were interspecific and the total frequency of aggression observed in the pool was positively associated with bull trout abundance. While rare, aggressive interactions were distributed throughout the study period (21 of 24 observation periods) and appeared to have serious consequences for the fish involved. Individuals of both species were observed violently displacing or being displaced from foraging locations as a result of aggressive interactions. Increased activity linked to behaviors such as foraging and aggression incur higher energetic costs (Marchand and Boisclair 1998; Tucker and Rasmussen 1999; Cutts et al. 2002) that increase with water temperature (Tang and Boisclair 1995). These costs may be disproportionately large for bull trout in warmer water, given their low growth optima relative to brook trout (Seelong et al. 2001), particularly if there is no concomitant increase in forage acquisition as has been observed in artificial streams (Chapter 2).

Conclusion

The summer distributions of bull trout and brook trout in Haven Creek appear to occur as a result of the interaction between species-specific physiological and life history traits and temperature variation, which occurs along an altitudinal gradient within the basin. The relative importance of elevation and water temperature effects on these distributions could not be distinguished however, as the two were strongly correlated. Behavioral observations of wild fish support the conclusion that bull trout sympatric with brook trout are disadvantaged in warmer water. The potential for interspecific encounters increased with water temperature as brook trout increased activity and bull trout appeared to increase aggressiveness in warmer water. Bull trout also cruised more than brook trout to achieve a comparable level of forage irrespective of temperature. When combined, these behavioral responses to increasing water temperature exhibited by the two species have the potential to disadvantage bull trout in warmer waters as the energetic costs associated with these activities are likely more costly for the cold-adapted bull trout.

Human activities that promote the thermal degradation of regional stream environments in North America are pervasive and ongoing and include damming, water withdrawal, channel engineering and vegetation removal (Poole and Berman 2001), and climate warming globally (Schindler 2001). Increasing water temperature is suspected to be particularly detrimental to native, cold water fish species and to promote the spread of nonnative species (Hauer et al. 1997; Schindler 2001). With one of the lowest upper thermal limits of the North American salmonids (Selong et al. 2001), the effects of increased water temperature on bull trout population persistence will be particularly severe. From the results of this study it is clear that land managers must consider not only the immediately apparent acute effects but also the less apparent chronic effects of thermal degradation on native fish stocks when evaluating the consequences of land practices that have the potential to increase stream temperature.

Table 3.1.—Mean ± SD and range of fork lengths, estimated number ± SE, and density of bull trout (BL) and brook trout (BK) at three locations on Haven Creek, July 2002 and 2003.

Location	Year	Species	Mean FL (mm)	FL Range	*N*	Density fish/m^2	Effective density $\sum FL^2/m^2$
Upper	2002	BL	84 ± 30	62-247	129 ± 8.3	0.10	672.9
		BK	141 ± 26	112-195	20 ± 0.3	0.02	312.4
	2003	BL	139 ± 15	118-159	5[a]	0.005	87.3
		BK	-	-	0[a]	0	0
Middle	2002	BL	89 ± 25	69-245	65 ± 2.4	0.05	407.4
		BK	118 ± 35	71-200	56 ± 0.9	0.04	643.7
	2003	BL	125 ± 23	95-154	5[a]	0.004	62.6
		BK	141 ± 33	84-223	42 ± 0.7	0.03	653.7
Lower	2002	BL	112	-	1[a]	0.0006	7.0
		BK	115 ± 30	44-197	75 ± 5.3	0.04	546.5
	2003	BL	229 ± 129	135-420	4[a]	0.002	103.1
		BK	112 ± 26	55-213	102 ± 5.7	0.04	474.9

[a] Insufficient captures for a population estimate.

Table 3.2.—Habitat measurements made at three reaches of Haven Creek during the summer 2002 and 2003. Wetted width and maximum temperature are means ± SD.

Location	Elevation (m)	Year	Month	Wetted width (m)	Maximum temperature (°C)	Days ≥ 15°C
Upper	1392	2002	July	4.4 ± 1.3	NA	NA
			August	NA	8.3 ± 2.2	1
		2003	July	3.7 ± 1.5	8.7 ± 2.4	0
			August	NA	10.2 ± 2.1	0
Middle	1328	2002	July	4.4 ± 0.95	NA	NA
			August	NA	10.6 ± 2.2	13
		2003	July	4.3 ± 1.4	11.4 ± 2.7	7
			August	NA	12.7 ± 2.3	21
Lower	1227	2002	July	6.0 ± 2.2	NA	NA
			August	NA	11.5 ± 3.7	20
		2003	July	8.4 ± 5.8	12.6 ± 3.1	19
			August	NA	12.9 ± 2.9	26

NA = Not available.

Table 3.3.—Mean ± SD and range of habitat measurements made at the Haven Creek observation pool August-September 2003.

	Mean	Minimum	Maximum
Depth (m)	0.68 ± 0.44	0	1.59
Surface velocity (cm/s)	4.2 ± 6.1	0	24.0
Velocity 0.6x depth (cm/s)	2.9 ± 3.7	0	15.0
Width (m)	-	-	11.3
Length (m)	-	-	10.1
Temperature (°C)	11.7 ± 2.1	7.1	17.0
Temperature (°C) during observations	12.8 ± 0.43	8.3	16.6
Visibility (m)	3.6 ± 1.3	1.5	5.0
Discharge (m^3/s)	0.052 ± 0.034	0.030	0.14
Drift rate (number of items$\cdot m^{-3} \cdot s^{-1}$)	0.079 ± 0.063	0.0085	0.19
BL abundance	3 ± 1	1	5
BK abundance	21 ± 5	7	26

Table 3.4.—Linear regression models using stepwise variable selection describing the proportion of stationary, cruising and foraging bull trout and brook trout, and total count of aggressive interactions per observation period (45 min) as a function of discharge (m^3/s), temperature (°C) and bull trout abundance (number of individuals) in a pool of Haven Creek, Alberta, August-September 2003.

Behavior	Species	Model	*R*	*P*
Stationary[a]	BL	51.83-389.18 (Discharge)	0.31	0.004
	BK	95.97-250.74 (Discharge)-2.84 (Temperature)	0.60	<0.001
Cruising[a]	BL	36.68+296.94 (Discharge)	0.25	0.011
	BK	3.90+2.06 (Temperature)+133.74 (Discharge)	0.50	<0.001
Foraging[a]	BL	NS	-	-
	BK	12.22-0.48 (BK Abundance)+1.11 (Temperature)	0.61	<0.001
Aggression[b]	Combined	0.877+0.18 (BL Abundance)	0.24	0.012

[a] Arcsine-transformed.

[b] Square-root-transformed.

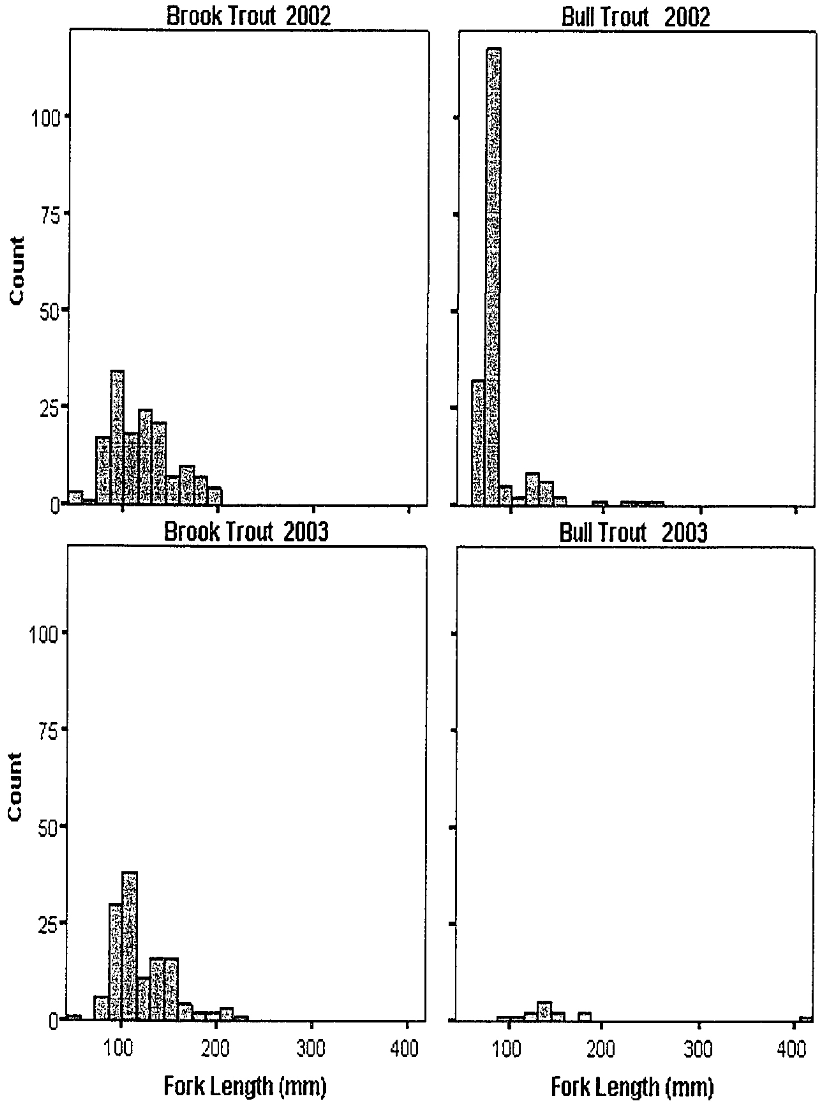

Figure 3.1.—Length-frequency histograms (25 mm size categories) of bull trout and brook trout, combined catch from three reaches in Haven Creek, Alberta, July 2002 and 2003.

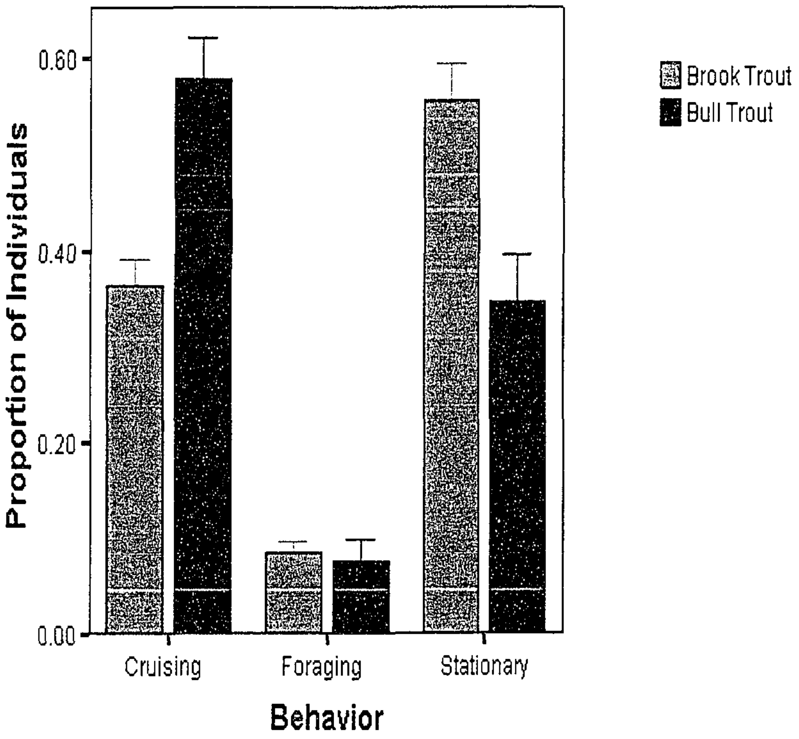

Figure 3.2.—Mean proportion ± SE of individual bull trout and brook trout observed cruising, foraging or stationary during snorkel observation of wild fish in a pool of Haven Creek, Alberta, August-September 2003.

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Chapter 4: Overview/Conclusion

The elevation refugia hypothesis requires that nonnative salmonids are competitively superior to natives at low elevations and that native salmonids be at least equal competitors with nonnatives at higher elevations (Paul and Post 2001). Results of this research clearly demonstrate that a temperature mediated contrast between bull trout and brook trout foraging and aggressive behavior leads to increased fitness (i.e., growth; Fausch 1998) of juvenile brook trout over bull trout in warmer water in an artificial stream. Conversely, the effects of intraspecific and interspecific competition on brook trout fitness were comparable in cold water. Although the interactions were more complex, evidence supporting brook trout competitive superiority over bull trout in warmer water was also observed in a natural stream setting. To the extent that water temperature is negatively correlated with elevation, these observations are consistent with the elevation refugia hypothesis. In Haven Creek, a stream where the species are sympatric, summer water temperature was negatively correlated with elevation over a relatively narrow range in elevation and bull trout abundance was greatest at the highest elevation reach. The observed disappearance of brook trout at this reach and reduction in bull trout density throughout the upper reaches the following summer also suggests no single answer will capture the diversity of circumstances that lead to the observed distributions of these species.

Many of the conclusions drawn over the course of this study are based upon the assumption that the energetic costs associated with increasing activity are greater for bull trout than brook trout near the upper end of the bull trout's zone of thermal tolerance. Although this statement is defensible in general, for these two species specifically it remains largely untested at present. Even if this proves not to be the case and energetic costs are comparable, bull trout are still likely to be negatively impacted when sympatric with brook trout under conditions of increasing water temperature, as warmer water lead to an increased potential for interaction between the two species. For this reason it is important that researchers conducting similar studies in natural environments incorporate the "noise" introduced by environmental variation into their models rather than hope it remains constant over the course of a study (or worse yet ignore it completely). Taken to the extreme the failure to place behavioral observations within the larger environmental context in which they are made has lead to a number of studies (including this one) where observations are made of each species exclusively in areas where they are sympatric without questioning exactly why they occur in sympatry in the first place! An incomplete understanding must surely be the result.

Two apparently contradictory observations regarding bull trout behavior made over the course of this research do not wholly align with current dogma: that juvenile bull trout may be as aggressive or more aggressive than brook trout in warm water, and that bull trout do not necessarily defend territories in a stream environment. The distinctions are of degree rather than absolute and probably reflect the relatively early developmental stage of bull trout behavioral ecology. A number of factors are known to influence territoriality of which, the abundance and spatial predictability of food have been well documented (Maher and Lott 2000). Generally, both the abundance and predictability of macroinvertebrate drift, the primary food resource of stream resident bull trout (Gunckel 2000), is likely to decrease in the relatively stochastic, cooler, environment typical of high-elevation Rocky Mountain streams (Vannote and Sweeney 1980; Death and Winterbourn 1995; Huryn and Wallace 2000), reducing the net benefits of territoriality (Maher and Lott 2000). Thus the apparent switching of juvenile bull trout with decreased water temperature from interference to scramble foraging tactics, not observed for brook trout, should be adaptive in these environments. Conversely conditions that lead to increased predictability or a moderate increase in abundance of food resources (reduced profitability of territoriality is expected when food abundance is high; Maher and Lott 2000) should favour brook trout expansion.

Many of the observations made in this thesis are based upon hypotheses, the subtleties of which are still being worked out for more widely studied species and are practically unmeasured for bull trout. The bull trout's limited distribution, coupled with its relatively recent recognition as a species (Nelson and Paetz 1992), are obvious explanations for this situation but poor excuses. It is essential that ecologists conducting similar behavioral research continually challenge their assumptions or the dominance hierarchies, focal positions, and territorial boundaries studied become self-fulfilling prophecies rather than objective fact. Casting back through the pages of this thesis it soon becomes apparent that this research has generated more questions than answers. Given the preliminary nature of the study this is understandable but hardly desirable. Prima facie, results of behavioral studies such as this may appear only tangentially related to the day-to-day decision-making required of land managers invested with the protection of threatened species, such as the bull trout, and their habitats. This is simply not true. In the current political and economic climate of North America the burden of proof is on the conservationist to prove a particular action *has* a significant impact on the species (habitat, ecosystem etc.) of concern. In many instances environmentally induced behavioral changes may act as an early warning system, enabling detection of sub-lethal stress responses. To use a well worn but powerful analogy: Why wait until the canary's lying dead at the bottom of the cage before evacuating the mine if you can observe it gasping for breath?

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