INVASION BY NONNATIVE BROOK TROUT IN PANTHER CREEK, IDAHO: ROLES OF HABITAT QUALITY, CONNECTIVITY, AND BIOTIC RESISTANCE

by

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To my wife, Stephanie, and daughter, Rhiannon, for your patience, love, and support.

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ABSTRACT

Theoretical models suggest the invasion of nonnative freshwater species is facilitated through the interaction of three factors: biotic resistance, habitat quality, and connectivity. We measured variables that represented each component to determine which were associated with small (<150 mm) and large (≥150 mm) brook trout occurrence in Panther Creek, a tributary to the Salmon River, Idaho. The abundance of rainbow trout was used as a measure of biotic resistance. Habitat variables included summer and winter temperature, instream cover, and channel size. Lastly, beaver ponds may play an important role in sustaining connected source populations of brook trout; therefore, we measured valley bottom area, which is correlated with the presence of beaver ponds. A composite model, using Akaike's information criterion, for large brook trout included habitat and biotic variables, however, results were inconclusive (odds ratio confidence interval overlapping 1.0) suggesting a more complex association between large brook trout and the variables measured, perhaps due to a more mobile life stage. For small brook trout, winter degree days and maximum summer temperature were the most important model variables and positively associated with presence. For both size classes, rainbow trout abundance showed insufficient evidence to confirm or exclude the importance of biotic resistance to the occurrence of brook trout. The results of this study indicate that habitat, specifically temperature, plays an important role in the occurrence of brook trout; however biotic resistance and connectivity may also play important roles and are worthy of further investigation.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INVASION BY NONNATIVE BROOK TROUT IN PANTHER CREEK, IDAHO: ROLES OF HABITAT QUALITY, CONNECTIVITY, AND BIOTIC RESISTANCE

Introduction

Since the concern regarding invasive species was raised by Elton (1958), increasing attention has been aimed towards understanding processes that influence the establishment and spread of biological invasions (Sakai et al. 2001). Hundreds of plant and animal species have been introduced in aquatic ecosystems in North America (Ricciardi and Rasmussen 1998). In freshwaters, Moyle and Light (1996) suggested a series of empirical rules to explain the invasion process, noting that habitat suitability and biotic resistance are important factors determining to the success of an invading species. Habitat suitability refers to abiotic factors (e.g., temperature, flow, and chemistry) that satisfy a species' physiological needs, whereas biotic resistance results from interactions between an invading species and those in the receiving environment, including competitors, predators, prey, parasites, and pathogens. Moyle and Light (1996) emphasized the importance of habitat suitability over biotic resistance as a key process influencing the success of invasive species. Simply put, they contended that if the environment is suitable for an invasive species, then it should be able to establish, regardless of the biotic community present. In addition to habitat suitability and biotic resistance, connectivity may also be important to the success of invasions (Carlton 1996), because if a species cannot access a suitable site, then invasions are unlikely.

In freshwaters throughout North America, many salmonine fishes have been introduced, particularly for sport fisheries (Rahel 2002; Dunham et al. 2004). In many cases, nonnative salmonines may contribute to declines of native species through competition, predation, hybridization, or transmission of pathogens and parasites (see Fausch et al. in preparation). One introduced salmonine of concern in western North America is brook trout *Salvelinus fontinalis*. Brook trout, native to eastern North America (Fuller et al. 1999), have been intentionally introduced throughout western North America resulting in the widespread establishment and spread of populations in headwater streams and lakes (Bahls 1992; Lee et al. 1997).

Although brook trout are widely established in western North America, invasions have not occurred in every potential suitable habitat, and factors influencing the potential spread of invasions are poorly understood (Dunham et al. 2002). For an invading species to spread, a source population is needed to establish a new population, thereby continuing the invasion cycle (Carlton 1996; Sakai et al. 2001). Therefore, connectivity to source populations could provide an important pathway for the spread of nonnative brook trout. In streams, the direction of brook trout invasion from a source population (i.e., upstream or downstream) can also influence the rate of spread. Downstream-directed movement will allow easier passage through barriers than upstream movement (Adams et al. 2001; Dunham et al. 2002). In a study of nonnative brook trout distribution changes from 1971 to 1996 in central Idaho, Adams et al. (2002) suggested upstream directed invasions occur in pulses during suitable environmental conditions. Similarly, a study in Colorado showed pulsed upstream movement of brook trout from downstream source populations concurrent with high stream flows, and even repopulating a stream where they were previously eradicated (Peterson and Fausch 2003a). The connection between existing populations and potentially new habitats is important and may reduce or stall the spread of invasive brook trout through distance, direction of movement, or barriers (Dunham et al. 2002).

Alluvial valley bottoms (Montgomery and Buffington 1997 and 1998) may be important to fall-spawning charr, such as brook trout. Beaver most often construct dams in lower gradient, alluvial valley bottoms (Suzuki and McComb 1998; Benjamin 2006) providing thermal refugia and rearing habitat for brook trout (Collen and Gibson 2001). However, beaver ponds may be reduced in alluvial valley bottoms by anthropogenic activities (Collen and Gibson 2001). In confined valleys, beaver ponds may be restricted due to physical constraints of the canyon walls (Collen and Gibson 2001). Alluvial valley bottoms also have wider floodplains allowing a greater chance for the development of off-channel habitats controlled by groundwater (Cavallo 1997) which may provide spawning and rearing habitat for brook trout. Furthermore, alluvial valley bottoms may have groundwater and hyporheic influences (Baxter and Hauer 2000) providing warmer temperatures for overwinter egg incubation. Because of all these factors, alluvial valley bottoms may provide source populations of nonnative brook trout.

Nonnative brook trout have been linked to the decline of native species such as federally threatened bull trout *S. confluentus* and cutthroat trout *Oncorhynchus clarkii* in the Rocky Mountains (Rieman et al. 1997; Adams et al. 2000; Dunham et al. 2002). However, it has been suggested that brook trout and the two native species often occur in allopatry because of differences in habitat preference (Paul and Post 2001; Rich et al. 2003; Rieman et al. 2006). Temperature has been shown to be the most strongly linked to the distribution and presence of salmonines (Adams 1999; Dunham et al. 2003a and b), although temperature is often highly correlated with other habitat variables that may be determining factors (Fausch et al. 1994; Nakano et al. 1996; Rahel and Nibbelink 1999). Thus, differences in temperature preferences could explain commonly observed patterns of segregation of bull trout and cutthroat trout in cooler headwaters and brook trout in downstream areas where temperatures are warmer (e.g., Adams 1999; Dunham et al. 1999; Rieman et al. 2006).

Evidence is lacking for the role of biotic resistance in controlling the spread of invasions by nonnative brook trout (Dunham et al. 2002). However, the decline of brook trout in its native range has been shown to be linked to the introduction and spread of nonnative rainbow trout *Oncorhynchus mykiss* (Larson and Moore 1985). In the native range of brook trout, nonnative rainbow trout inhabit the lower sections of streams and brook trout inhabit the headwaters (Cunjak and Green 1983; Larson and Moore 1985; Clark and Rose 1997; but see Strange and Habera 1998). Temperature appears to be the most important habitat variable associated with this segregation (Stoneman and Jones 2000). Given these observations, it seems reasonable to expect that biotic resistance from native rainbow trout may act similarly in western North America to limit invasions by nonnative brook trout. To my knowledge, there are no studies on the potential for rainbow trout to prevent an upstream invasion of brook trout (i.e., act as a biotic barrier to invasion).

The purpose of this study was to identify factors that affect the spread and establishment of nonnative brook trout in an upstream direction. Specifically, I examined how the occurrence of small (< 150 mm) and large (≥ 150 mm) brook trout in Idaho headwater streams corresponds to factors associated with biotic resistance, habitat suitability, and connectivity to potential sources of invasion. My objectives were to 1) document basic habitat characteristics influencing the presence of small and large brook trout (i.e., habitat suitability), 2) determine if a greater abundance of rainbow trout act as a biotic barrier to small and large brook trout (i.e., biotic resistance), and 3) determine if a correlation exists between the presence of alluvial valley bottoms and the presence of brook trout populations in nearby tributary streams (i.e., connectivity). A better understanding of these variables will provide managers with useful information to assess threats posed by current and potential invasions by nonnative brook trout.

Methods

Study Area

Panther Creek, a tributary of the Salmon River, is located in east-central Idaho near the Idaho-Montana border (Figure 1). The main stem of Panther Creek is approximately 69 km in length, and the watershed includes about 644 km of perennial streams (Idaho Department of Environmental Quality 2001) with a catchment area approximately 1,550 km^2. Average annual discharge is 8.5 m^3/s, with high flows between April and June caused by snowmelt. The elevation within the watershed ranges from about 1,000 m at the mouth to over 3,000 m on adjacent peaks. The watershed is characterized by steep slopes and canyons within the Idaho Batholith, an area of granitic bedrock (Platts 1972). Panther Creek and tributaries (including Moyer Creek) are dominated by cobble substrate. Upland vegetation is dominated by lodgepole pine *Pinus contorta* and Douglas fir *Pseudotsuga menziesii*. Riparian vegetation also includes willow *Salix* spp., cottonwood *Populus* spp., and alder *Alnus* spp.

The Panther Creek drainage is primarily used for recreation and cattle grazing. Localized mining operations and timber harvesting, particularly in the Big Deer Creek and Blackbird Creek drainages, and road construction have disturbed the watershed through leaching and increased sediment loads (Idaho Department of Environmental Quality 2001).

The Panther Creek drainage once served as spawning grounds for Chinook salmon *O. tshawytscha* and steelhead trout *O. mykiss* as well as bull trout and westslope cutthroat trout *O. clarkia lewisi*. Chinook runs declined rapidly following the development of Blackbird Mine in 1949 (Platts 1972). According to Idaho Fish and Game records (T. Frew, Idaho Fish and Game, Boise, ID, unpublished data), brook trout were stocked in this system in the mid-1950s in three creeks (Musgrove Creek, Napias Creek, and Panther Creek). My study section contained four salmonine species, bull trout, cutthroat trout, rainbow trout, and brook trout. Other vertebrates found include, shorthead sculpin *Cottus confusus*, tailed frog *Ascaphus montanus*, and spotted frog *Rana luteiventris*.

Study Design and Field Methods

Site selection was based on including representation of the range of variability in predictor variables while ensuring randomness to avoid bias in subjective location of sites. I sampled two stream complexes: Moyer Creek and Upper Panther Creek (Figure 1). Terrain Analysis Using Digital Elevation Models (TauDEM; Tarboton 1997) was used to identify stream segments within these complexes that had a contributing area between 300 and 9,000 ha. Those segments were then numbered and randomly sampled. Within the randomly chosen segments, a distance upstream from the downstream end was randomly determined and used to identify the sample site at which thermographs and sampling was located.

Water Temperature Sampling

I deployed temperature loggers at each sample site following methods described in Dunham et al. (2005). All loggers were deployed before July 1, assuming the maximum water temperature occurred after that date. The loggers used (StowAway Tidbit; Onset Computer Co., Pocassett, MA) recorded temperature in a range of -0.5 to 37 ^{o}C with a precision of 0.2 ^{o}C. Loggers were calibrated before deployment to correct for bias. Temperature was recorded every 30 min for one consecutive year.

Fish Sampling

I sampled presence-absence of fish species during the low flow period (July-September, 2004). Sampling sites were approximately 100 m in length (± 10 m) and were blocked off using 7 mm diameter mesh nets. A four-pass removal procedure using a backpack electrofisher (12B electrofisher, Smith-Root, Vancouver, WA) was used to ensure all fish present were detected (Rosenberger and Dunham 2005). A validation study on the detectablility of brook trout and rainbow trout has been completed before the start of my study (J. B. Dunham unpublished data; Appendix A) and showed that four passes are sufficient. All captured fish were identified to species. Fork length (FL) was measured for salmonines, standard length was measured for sculpins.

Habitat Sampling

After electrofishing, I measured habitat variables within each sample site. Starting at the downstream block net, transects were spaced every 5 m and oriented perpendicular to the active channel. At each transect, I recorded wetted width (m) and depth (m) at one-quarter, one-half, and three-quarters of the wetted width. Undercut banks intersecting transects were measured within each site. To be counted as an undercut bank, the undercut needed to be 10 cm in submerged depth, height, and length, based on the assumption that such a size would provide enough space for a fish to seek cover. Large wood (≥10 cm in diameter and ≥1 m in length) was counted and classified as either within active channel or within bank full channel. Aggregates consisting of four or more pieces of wood meeting the above dimensions were also tallied. Total site length (m), channel slope (measured with a stadia rod and hand level), UTM coordinates (NAD27), and elevation (m) were also measured.

To determine the extent of beaver activity in the study area, the study streams were surveyed from the ground. UTM coordinates (NAD27) and elevations (m) were collected for all beaver dams and ponds in the study area. The maximum width of each pond was measured using a rangefinder (Prostaff Laser 440, Nikon, Shinagawa-ku, Tokyo, 0.46 m accuracy) or tape measure when riparian vegetation was too thick for reliable use of the rangefinder. Location and size data were collected for all beaver ponds where the maximum pond width was at least five times the active channel width directly upstream of the pond. This size criterion was used to exclude new or inactive beaver ponds that probably do not serve as preferred brook trout habitat (see Collen and Gibson 2001; Pollock et al. 2003). Because beaver most often construct dams in lower gradient, wide valley bottoms (Suzuki and McComb 1998), I used alluvial valley bottom area as a surrogate for beaver pond activity. Furthermore, alluvial valley bottoms have the potential to provide off-channel habitat for brook trout (Cavallo 1997). To be considered an alluvial valley bottom, a stream segment needed to consist of a TauDEM segment with a stream magnitude of at least 11, at least 2,000 m of stream length of any magnitude, and at least 150,000 m^2 measured in ArcGIS (version 8.0, ESRI, Redlands, CA). Quantile regression was used to verify that a relationship exists between beaver pond width and the $\log_{10}$ transformation alluvial valley bottom area calculated from ArcGIS. Based on previous literature, I expected more and larger beaver ponds to be in larger valley bottoms while narrower valleys would have fewer and smaller ponds because of the physical constraints of the canyon walls. A modified equation from Moilanen and Nieminen (2002) was used to determine a weighted alluvial valley bottom area (wAVBA) from each valley bottom:

$$\mathrm{wAVBA} = \sum \frac{AVBA_i}{d_{ij}},$$

where AVBA is the area for alluvial valley bottom i and d is the distance from AVBA_i to sample site j (Figure 2).

Analytical Methods

I used the information-theoretic approach for model selection (Burnham and Anderson 2002). I developed candidate a set of *a priori* logistic regression models following suggestions in Burnham and Anderson (2002), which included a global model relating small (< 150 mm FL) and large (≥ 150 mm FL) brook trout occurrence to the biotic, habitat, and connectivity variables mentioned above (Tables 1 and 2). I used a different model for each size class because smaller brook trout were assumed to be sexually immature and less likely to disperse and therefore to occur in areas of spawning, whereas larger brook trout were assumed to be sexually mature and able to move longer distances (Adams 1999). Variables making up the global models and subsequent candidate models included winter temperature, maximum summer temperature, cross sectional area, cover, rainbow trout abundance, and the weighted alluvial valley bottom area. Winter temperature was measured as a modification of degree days to represent egg incubation expressing it as the number of days above 1 ^{o}C between December 1, 2004 and March 31, 2005. The number of days above 1 ^{o}C provides a relative estimate of incubation time in the natural environment (Power 1980; Marten 1992; Curry et al. 2002). Cooler temperatures will prolong incubation providing less time during their first summer that alevins will have to reach a suitable size that will enable them to survival the following winter (Dwyer et al. 1983).

Summer temperature was summarized as the maximum temperature between July 1 and September 30, 2004. Maximum summer temperature correlates strongly with other measures of stream temperature (e.g., median or mean temperatures or the maximum temperature during a particular time period; Dunham et al. 2005). Visual inspection of data sets suggested no anomalies in the temperature output that would be caused by contact of thermograph with direct sunlight or temperatures measured out of the water (Figure 3).

Cover measures included the total number of large woody debris and the total length of undercut banks. Rainbow trout abundance was calculated for rainbow trout with a fork length > 60 mm using the 4-pass removal calibration from Rosenberger and Dunham (2005), in which data was collected in the same area as the present study and under similar environmental conditions.

Based on previous studies, I expected winter and summer temperature and cover to have a positive relationship with the occurrence of both small and large brook trout. Alternatively, cross sectional area and rainbow trout abundance should decrease small and large brook trout occurrence. The connectivity variable, weighted alluvial valley bottom area, should be positively related to small brook trout only, assuming brook trout smaller than 150 mm were less likely to disperse. However, the connectivity variable was not included in the large brook trout models because it was assumed larger brook trout use the alluvial valley bottoms for spawning and overwinter habitat, neither of which occurred during the sampling period.

It is important to note that Panther Creek watershed was the only area with brook trout present, even though brook trout were expected in Moyer Creek (B. Rose, Salmon-Challis National Forest, Salmon, ID, personal communication). The absence of brook trout in Moyer Creek and a comparison of Panther Creek and Moyer Creek was not a component of the study design.

Initial analysis of the small brook trout global model indicated that weighted alluvial valley bottom area was such a powerful explanatory variable that it caused complete separation. When the state of the dependent variable is perfectly predicted by an explanatory variable the result is complete separation, and analysis using logistic regression cannot proceed (Allison 1999). Therefore weighted alluvial valley bottom area was dropped from the small brook trout global model.

Panther Creek had the majority of valley bottoms, except for one in Moyer Creek just upstream of the south fork confluence (Figure 1). Therefore it could be argued that at one scale this study consisted of one watershed with and one without brook trout and one watershed with and one without a substantial quantity of alluvial valley bottoms. Although an ad-hoc analysis, I analyzed the occurrence of small brook trout within the Panther Creek complex only, to counter that argument.

The variables included in the two global models were winter temperature, summer temperature, cross sectional area, cover, and rainbow trout abundance. The Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000) and overdispersion (Pearson χ^2/df; Allison 1999) were examined to verify the fit of both global logistic regression models. Predictors were assessed for evidence of multicollinearity by measuring the variance inflation factor (VIF; Philippi 1994) and by performing separate logistic regressions of the occurrence of small and large brook trout with and without each predictor variable (Hosmer and Lemeshow 2000). Neither method revealed evidence of multicollinearity.

Akaike's information criterion (AIC) with small-sample size adjustment was used to rank the global and candidate models (AIC_c; Burnham and Anderson 2002). Model selection based on AIC_c does not consider one model to be the true model. Instead AIC_c weights each model, including a penalty for inclusion of additional variables, and thereby provides a means for ranking models (Burnham and Anderson 2002). Specifically, Akaike weights are used to assess the relative plausibility of each model. Because more than one model can be plausible, model averaging was done (Burnham and Anderson 2002) using the 1/8 cutoff point (Royall 1997; Thompson and Lee 2002). In other words, models with Akaike weights within 1/8 of the largest weight were averaged based on those weights to create a composite model. In cases where one model was overwhelmingly the single "best" model (at least eight times the AIC_c weight of the next highest weight) averaging was not done.

To provide greater biological relevance to the interpretation of changes in odds ratios, a constant was included in calculating the odds ratio and odds ratio confidence intervals (i.e., $e^{\beta_i * C}$; Hosmer and Lemeshow 2000) of all the variables except for maximum summer temperature. For example, the coefficient for cross-sectional area was multiplied by 0.2 m so that the odds ratio for cross-sectional area would indicate how a change of 0.2 m would affect the odds of finding brook trout at a particular site.

Results

Forty-one segments within the two stream complexes were used in the analysis (Appendix B). Small brook trout were present in 29% of the sites (*n* = 12) and large brook trout in 24% (*n* = 10). Brook trout were present only in the Panther Creek complex, including Cabin Creek and Opal Creek (Figure 1). Rainbow trout were found in 32% of the sites (*n*=13) in both the Moyer and Panther Creek complexes, and were concentrated in the lower elevation main-stem segments, with the exception of four small rainbow trout less than 120 mm in the lower segment of Salt Creek. Small brook trout and rainbow trout occurred together in 15% (*n* = 6) of the sites. Large brook trout occurred with rainbow trout at 10% (*n* = 4) of the sites. Bull trout and cutthroat trout were found in 66% (*n* = 27) and 29% (*n* = 12) of the sites, respectively, with the majority in segments without brook trout, 74% and 50% for bull trout and cutthroat, respectively (Appendix C). Bull trout numerically dominated the sites that had a maximum summer temperature below 11 ^{o}C, whereas rainbow trout numerically dominated the sites above 16 ^{o}C (Figure 4). Brook trout and cutthroat trout were found most commonly at sites with intermediate temperatures (Figure 4).

Before proceeding with the assessment of models to predict occurrence of small brook trout, I first assessed the relationship between alluvial valley bottom area and presence of beaver ponds to justify including the former as a predictor of beaver ponds and other off-channel habitats that may be important for this life stage. The 90% regression quantile indicated a positive relationship between beaver pond size and valley bottom area ($\chi^2 = 15.39$, $P = < 0.001$). Results indicated beaver pond size was greatest in wider valley bottoms, but that beaver pond size declined in narrower valley bottoms. As described in the methods section, the inclusion of weighted alluvial valley bottom area resulted in complete separation of the model, requiring that the variable be dropped from further analysis (Allison 1999).

The global model for small brook trout showed a good fit as indicated by the Hosmer-Lemeshow goodness-of-fit test ($\chi^2 = 4.71$, $df = 8$, $P = 0.79$) and dispersion (Pearson $\chi^2 = 25.70$, $df = 34$, $P = 0.85$). The candidate model that consisted of winter degree days and summer maximum temperature was the best approximating model, and was 2.5 times more plausible than the next best model (Table 1). The composite model contained two variables with conclusive results, winter degree days and summer maximum temperature (Table 3). Both variables had a positive relationship with small brook trout. Odds ratios indicate that an increase of 1 ^{o}C in maximum summer temperature results in an 8% increase in the probability of brook trout being present, and that five additional days above 1 ^{o}C between December 1 and March 31 yield a 1%, increase in the likelihood that small brook trout will be present.

Similar results were seen for the Panther Creek complex only analysis. Cross-sectional area was highly correlated with the other variables and was removed from the models. The composite models for small brook trout within the Panther Creek complex gave similar results to the composite model that included sites from both streams. That is, for small brook trout, the inclusion of weighted alluvial valley bottom area led to complete separation, and maximum summer temperature was positively associated and conclusive (odds ratio = 1.73, confidence interval 1.13 – 2.64). Winter degree days, however, was inconclusive (odds ratio = 1.13, confidence interval 0.96 – 1.34).

The large brook trout global model showed a good fit according to the Hosmer-Lemeshow goodness-of-fit test ($\chi^2 = 6.93$, $df = 8$, $P = 0.54$) and dispersion (Pearson $\chi^2 = 31.09$, $df = 34$, $P = 0.61$). The model consisting of maximum summer temperature and winter degree days was the best approximating model but was only slightly better than the next best model (Table 2). Five other models Akaike weights had at least 1/8 the AIC_C weight of the best approximating model, therefore model averaging was performed to create a composite model (Table 2). None of the variables within the composite model were strongly associated with the presence of brook trout. All had odds ratio confidence intervals that overlap one (Table 3).

Discussion

I investigated the roles of suitable habitat, biotic resistance (Moyle and Light 1996), and connectivity (Dunham et al. 2002) in association with the extent that nonnative brook trout have invaded upstream into a stream network. None of the variables measured could successfully predict the occurrence of large brook trout. However the presence of small brook trout was strongly and positively associated with connectivity to alluvial valley bottoms, which are thought to serve as potential sources for new populations. The presence of small brook trout was also associated with two measures of habitat suitability, maximum summer temperature and winter degree days.

Connectivity

Alluvial valley bottoms may be an important aspect of connectivity of invading brook trout by acting as source populations. I assumed that beaver ponds were important potential sources of nonnative brook trout, as established by previous work (e.g., Gard 1961; Seegrist and Gard 1972). Beaver ponds can also provide important overwinter habitat for brook trout (Chisholm et al. 1987; Cunjak 1996) along with thermal refugia in colder streams (Collen and Gibson 2001). I also considered the importance of off-channel habitats for brook trout (Cavallo 1997), which, like beaver ponds, are more likely to occur in sites with wider valley bottoms and lower channel slopes.

Connectivity in this study was measured as a composite of two factors: the size of the alluvial valley bottoms and the distance from alluvial valley bottoms to sampled sites. My study area indicates that the connectivity of stream reaches to alluvial valley bottoms is important in determining the extent of brook trout invasion. Analysis of this variable with logistic regression resulted in complete separation, which indicates that my measure of connectivity did a near perfect job of explaining whether small brook trout were present (Figure 1 and Figure 5).

Prevalence of alluvial valley bottoms between Panther Creek and Moyer Creek was one of the most obvious differences between these two major stream systems. It is possible that other unmeasured habitat or biotic characteristics vary similarly between these two basins, and it would be necessary to sample a much larger number of watersheds to more fully represent the range of potential variability and minimize confounding factors. However, the result of complete separation in sites with and without small brook trout in the analysis for only the Panther Creek complex strengthens my inference that alluvial valley bottoms may be important in the occurrence of small brook trout and is not a result of other differences between the watersheds. Furthermore, my results agree with other studies that source habitats are important in facilitating the spread of brook trout invasions (Carlton 1996; Adams 1999; Adams et al. 2001).

Habitat Suitability: Water Temperature as a Limiting Factor

Among the variables related to local habitat suitability considered here, maximum summer temperature showed the strongest association with the presence of both small and large brook trout, although the evidence for large brook trout is inconclusive. There are at least two reasons for the failure of local habitat to strongly explain the occurrence of large brook trout; (i) because large brook trout can disperse during unfavorable conditions, my study may have been conducted at an inappropriate spatial scale (ii) I did not consider interactions in the models (see Interactions among Factors section below). However, the improved plausibility of models that included maximum summer temperature lends support to my hypothesis that large brook trout occurrence is more likely in areas within the optimal thermal range for summer growth.

My finding that occurrence of small brook trout was positively associated with warmer summer temperatures, within the range observed, is supported by similar work on brook trout within its native range. For example, brook trout were more likely to be observed at maximum summer temperatures under 20 °C in Ontario, Canada (Barton et al. 1985; Picard et al. 2003), however, in those studies maximum summer temperatures under 12 °C were not observed. Maximum summer temperature in my study area ranged from 8 °C to 19 °C, with both, small and large brook trout, within the range of 11 °C to 19 °C. This pattern of occurrence paralleled optimal temperatures for growth of maturing brook trout found in laboratory studies (12 °C and 19 °C; Hokanson et al. 1973), suggesting that invasion by nonnative brook trout is related to physiological constraints posed by cold temperatures with shorter summer growing season (Adams 1999). If this is true, there are locations within the study area that are potentially vulnerable to invasion (Figure 7). Sites with temperatures under the optimal growth range for brook trout may be less vulnerable to invasion than sites with temperatures within the optimal growth range. For example, sites within Cabin Creek were found to have suitable temperatures to allow upstream spread of nonnative brook trout, whereas others were too cold (e.g., headwaters of Moyer Creek and Mink Creek) or isolated (Opal Creek) to allow invasions to occur (Appendix D).

Results of this work also supported (albeit weakly) the potential importance of colder winter temperatures as a possible factor limiting invasion by brook trout. For fall spawning charrs, colder water temperatures can improve the survival of eggs to hatching (e.g., Hokanson et al. 1973; Humpesch 1985; Marten 1992; Crisp 2000), but freezing and associated mortality of eggs or alevins may also be more likely (Curry et al. 1995; Curry and Noakes 1995; Baxter and McPhail 1999). Longer incubation times associated with colder temperatures also mean that brook trout emerge later in the summer season at smaller sizes, with potential longer-term implications for summer growth and attainment of size or condition needed for overwinter survival (Adams 1999). When winter conditions are very cold, brook trout have been shown to use localized areas of warmer groundwater input for spawning and egg incubation (Curry et al. 1995; Curry and Noakes 1995). Although I did not document groundwater inputs in my study area this could explain the difference in occurrence between the Panther Creek and Moyer Creek complex. For example, Baxter and Hauer (2000) showed bull trout redds were found in greater numbers in wider alluvial valley bottoms which contained more hyporheic flow than confined valley bottoms. The section of Panther Creek in this study was characterized by extensive areas of wider valley bottoms, in contrast to Moyer Creek, where valley bottoms were much more confined (Figure 1). Assuming the confinement of the Moyer Creek sites resulted in limited groundwater inputs or hyporheic influence, this could limit availability of thermally suitable spawning sites and rearing habitat for nonnative brook trout, and a reduced probability of the spread of invasions. Overall, Moyer Creek is represented by cooler maximum summer temperatures and fewer winter degree days than Panther Creek, both of which could potentially limit the establishment of nonnative brook trout in Moyer Creek (Figure 7).

Biotic Resistance

Because rainbow trout have been linked to the decline of brook trout in their native range, I expected rainbow trout to have a similar effect on brook trout in my study area, potentially representing a form of biotic resistance. A weak and negative relationship was seen between rainbow trout and both size classes of brook trout in this study; but the role of biotic resistance is not clear. The lower elevation main-stem segments of Panther Creek and Moyer Creek had high abundance of rainbow trout, whereas brook trout were found in higher numbers only in tributaries of Panther Creek where rainbow trout were not observed. This pattern of segregation is consistent with other studies in the Rocky Mountains (Bozek and Hubert 1992; Adams 1999; Paul and Post 2001). Similar patterns of segregation are also observed within the native range of brook trout, and thought to result from competitive displacement of brook trout by rainbow trout (Power 1980; Cunjak and Green 1983; Larson and Moore 1985; but see Strange and Habera 1998). Finally, while not directly addressed in this study, it is possible that other native species, such as cutthroat trout and bull trout, influence the success of brook trout invasion. For example, cutthroat trout were present in high numbers in upper Cabin Creek, where temperatures were potentially suitable for brook trout, yet brook trout were not observed there (Appendix C).

Potential Effects on Bull Trout

The salmonine fishes present were distributed differently along distinct thermal gradients (Figure 4). Similar patterns have been observed for other ecologically similar species (Fausch et al. 1994; Taniguchi and Nakano 2000) as well as nonnative brook trout and native bull trout, cutthroat trout, and rainbow trout within the Rocky Mountains (Fausch 1989; Magoulick 1994; Dunham et al. 1999; Paul and Post 2001; Gunkel et al. 2002). Behavioral or physiological differences could be controlling the segregation of these species along thermal gradients (Dunham et al. 2002). For example, brook trout become sexually mature earlier than bull trout, increasing propagule pressure and potentially displacing bull trout (Gunkel et al. 2002).

In streams where the two species co-occur, brook trout are typically found in the lower reaches while bull trout dominate the upstream reaches, suggesting that brook trout displace bull trout in an upstream-direction (Paul and Post 2001; Gunkel et al. 2002; Rieman et al. 2006). In Moyer Creek, brook trout were not found. However bull trout were observed throughout the stream network (Appendix C). Whereas in Panther Creek, brook trout were present in the lower elevation sites, bull trout were present in the higher elevation sites, and the two species co-occurred in mid-elevation sites (Appendix C). In Moyer Creek, the numerical dominance of bull trout declined below 80% at approximately 14 ^{o}C whereas in Panther Creek the numerical dominance of bull trout declined below 80% at approximately 11.7 ^{o}C (Figure 6), suggesting that in the presence of brook trout the distribution of bull trout shifts to cooler upstream reaches, indicating that a potential upstream-directed displacement has occurred within Panther Creek.

Interactions among Factors

Because of a small sample size, interactions were not included in the models and their importance could be missing. For example, the interaction between biotic resistance and temperature may contribute to patterns of distribution of salmonine fishes along thermal gradients depending on their competitive ability at certain temperatures (Taniguchi et al. 1998; Taniguchi and Nakano 2000) and may restrict the invasion of nonnative brook trout. The majority of sites where small brook trout were found without rainbow trout were segments where the maximum summer temperature was below 13 ^{o}C, which is below the optimal thermal range for rainbow trout (Cherry et al. 1977; Peterson et al. 1979; Cunjak and Green 1986). Likewise, brook trout were not observed in sites with a maximum summer temperature below 11 ^{o}C where bull trout numerically dominated and may have a competitive advantage (Appendix C). The dominance of bull trout in the cold water segments and rainbow trout in the warm water segments could be preventing the spread of nonnative brook trout in this study area. Another potentially important interaction may be biotic resistance and alluvial valley bottoms. The presence of alluvial valley bottoms may facilitate the coexistence of nonnative brook trout and native species under a variety of habitat conditions. The lack of alluvial valley bottoms in Moyer Creek together with the high abundance of rainbow trout in the lower elevation sites may have prevented the establishment of brook trout within the drainage. In order to account for these interactions and others, removal experiments under natural conditions are recommended (Fausch 1998; Peterson and Fausch 2003b).

Future Research

The inclusion of another field season would have enabled me to sample additional watersheds, resulting in an increase in spatial scale of the study and strengthening of statistical and biological inferences. Additionally, I could have addressed the complete separation that resulted from the inclusion of weighted alluvial valley bottom area. However, an additional field season would have provided little additional strength to my inferences pertaining to temporal variation in stream habitat or the distribution of fish present. Although a small amount of variation is expected in stream habitat from year to year, changes at the scale in this study (i.e. stream reach and watershed) occur on a time scale of decades to hundreds of years (Frissell et al. 1986). Likewise, salmonine fish distribution has been found to be relatively constant from year to year (Gard and Flinter 1974; Meyer et al. 2003; Rieman et al. 2006) and is no different for brook trout in (Strange and Habera 1998) or out (Adams et al. 2002; Dunham et al. 2002) of their native range. Furthermore, the temporal stability of the distribution of the salmonine species in my study area has been well-documented (Corely 1967; Platts et al. 1979; Thurow and Overton 1993; LeJeune et al. 1995).

The patterns seen in this study can be used to guide further studies of brook trout invasion. One obvious study would be to include a larger spatial scale to better understand the role of alluvial valley bottoms. Another study would be to compare streams with and without brook trout, rainbow trout, and combinations of the two, which would provide a clearer picture to the ability of rainbow trout to limit brook trout invasion. Although ethical and legal issues prevent the introduction of brook trout or alteration of habitat, it would be acceptable to conduct manipulative field experiments through the removal of brook trout. Peterson and Fausch (2003b) provide an example to investigate population level effects between nonnative brook trout and cutthroat trout which could be modified to investigate nonnative brook trout and rainbow trout.

The question of whether alluvial valley bottoms facilitate brook trout invasion should also be further examined. One way to do this would be to compare brook trout presence in first to third order streams that differ in presence of alluvial valley bottoms. First a set of streams that are similar in abiotic (elevation, slope, geology, etc) attributes should be identified. These streams should be categorized as to whether or not they are within 1 km of an alluvial valley bottom. The 1 km distance is approximately the maximum distance nonnative brook trout have been found to move (Gowan and Fausch 1996 and 2002; Adams et al. 2002). For the sake of simplicity, streams with only brook trout should be used, and preferably brook trout should be in similar densities before manipulations are performed. Sampling within a stream should begin approximately 500 m upstream to account for wondering individuals. For streams in each alluvial valley bottom distance category, brook trout would then be removed to achieve a variety density. Two-way weirs should also be incorporated to account for immigration and emigration. If alluvial valley bottoms do facilitate brook trout invasions, then the streams within 1 km should show an increase in brook trout populations compared to streams that are greater than 1 km from alluvial valley bottoms.

Conclusion

Results of this study imply that habitat characteristics are important to the occurrence of nonnative brook trout in Rocky Mountain streams, supporting Moyle and

Light's (1996) suggestion that habitat suitability is the major factor influencing the invasion by freshwater fishes. Connectivity appears to play the most important role, whereas the role of biotic resistance was less apparent. Perhaps a different spatial scale may be needed to identify an effect and mechanisms. Furthermore, statistical interactions should be investigated to help determine what contributes and limits the spread and establishment of nonnative brook trout.

At present, native fishes are widely distributed within upper Panther Creek, with the exception of anadromous salmon and steelhead trout, both of which have been impacted primarily by changes to downstream conditions (Platts 1972). Thus, brook trout invasions may not pose a significant threat to native fishes at this time. A major question in this system concerns the future distribution of brook trout. Will populations continue to invade upstream, or do current distributions represent the maximum extent of invasion by brook trout (Adams et al. 2002)? Environmental and biological changes caused by major human or natural disturbances may be important. For example, in 2000, a major wildfire occurred in the lower reaches of Panther Creek, altering habitats substantially. This disturbance occurred outside of the present distribution of brook trout in this watershed, but wildfire in similar systems has been shown to variably influence brook trout invasions (Sestrich 2005). As has been found with brook trout invasions in general (Dunham et al. 2002), the influences of such events were difficult to predict (Sestrich 2005). Given that habitat has a likely influence in terms of limiting the distribution of brook trout, perhaps the best management prescription for long-term health of native fishes in Panther Creek is continued maintenance and restoration of naturally cold water temperatures. Disruption of connectivity through installation of fish movement barriers may also prevent invasion by brook trout, but the importance of connectivity to other native fishes in the system could render this tactic more threatening than the invasion itself (Fausch et al. in preparation).

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Table 1. Candidate logistic regression models for the occurrence of small brook trout in Panther Creek drainage in 2004. Models were ranked by AIC_C weights, with larger AIC_C weights indicating more plausible models. Stemp = maximum summer temperature, wtemp = number of days above 1 ^{o}C between December 1, 2004 and March 31, 2005, cover = total length of undercut banks and total count of large woody debris within the active channel and bankfull channel, CSA = cross sectional area, and rb = rainbow trout abundance >60 mm. The global model included all the variables.

Model	K	AIC_C	ΔAIC_C	AIC_C weight	% of maximum AIC_C weight
Stemp, wtemp	3	39.49	0	0.63	100
Global model	7	41.38	1.89	0.25	38.8
Stemp	2	44.00	4.51	0.07	10.5
Cover, CSA, stemp, wtemp	6	45.46	5.97	0.03	5.1
Stemp, rb	3	46.31	6.82	0.02	3.3
Wtemp	2	51.75	12.26	<0.01	0.2
Wtemp, rb	3	52.40	12.90	<0.01	0.2
Rb	2	53.13	13.64	<0.01	0.1

Table 2. Candidate logistic regression models for the occurrence of large brook trout in Panther Creek drainage in 2004. Models were ranked by AIC_C weights, with larger AIC_C weights indicating more plausible models. Stemp = maximum summer temperature, wtemp = number of days above 1 ^{o}C between December 1, 2004 and March 31, 2005, cover = total length of undercut banks and total count of large woody debris within the active channel and bankfull channel, CSA = cross sectional area, and rb = rainbow trout abundance >60 mm. The global model included all the variables.

Model	K	AIC_C	ΔAIC_C	AIC_C weight	% of maximum AIC_C weight
Stemp, wtemp	3	45.35	0	0.28	100
Global model	7	45.59	0.24	0.25	88.7
Stemp	2	45.96	0.60	0.21	74.0
Stemp, rb	3	47.42	2.07	0.10	35.6
Wtemp	2	48.68	3.33	0.05	19.0
Cover, CSA, stemp, wtemp	6	49.14	3.78	0.04	15.1
Rb	2	49.56	4.21	0.03	12.2
Wtemp, rb	3	50.27	4.92	0.02	8.5

Table 3. Model-averaged results of composite logistic regression model for small and large brook trout occurrence.

Brook trout life stage	Model parameter	Estimated Coefficient	SE	Odds ratio constant	Estimated Odds ratio	95% CI for odds ratio Lower	95% CI for odds ratio Upper
Small	Intercept	-12.027	4.56	--	--	--	--
	LWD	0.006	0.01	5	1.03	0.96	1.12
	Undercut bank	-0.018	0.02	5	0.92	0.72	1.17
	CSA	2.369	2.09	0.2	1.61	0.71	3.64
	Winter temperature	0.045	0.02	5	1.25	1.01	1.56
	Summer temperature	0.671	0.30	1	1.96	1.08	3.55
	RB	-0.014	0.02	5	0.93	0.75	1.17
Large	Intercept	-7.499	4.87	--	--	--	--
	LWD	0.011	0.01	5	1.06	0.954	1.167
	Undercut bank	-0.006	0.01	5	0.97	0.846	1.112
	CSA	2.231	1.92	0.2	1.56	0.736	3.318
	Winter temperature	0.018	0.01	5	1.09	0.964	1.237
	Summer temperature	0.366	0.23	1	1.44	0.913	2.278
	RB	-0.012	0.01	5	0.94	0.837	1.054

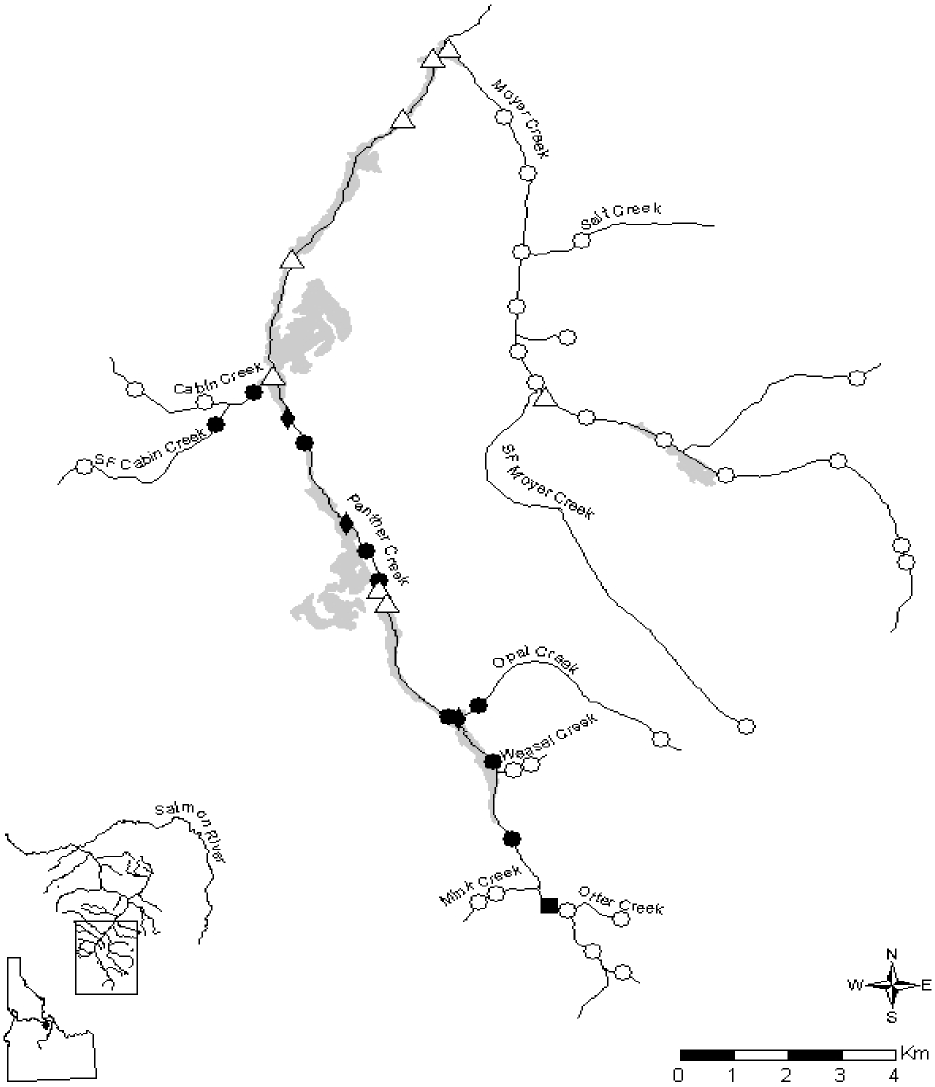

Figure 1. Panther and Moyer Creek watersheds with sampling sites. Black circles represent sites where both small and large brook trout were found, black squares are where only large brook trout were found, and black diamonds are where only small brook trout were found. Open circles represent sites where no brook trout were found. Triangles represent beaver ponds. Gray patches represent valley bottom areas.

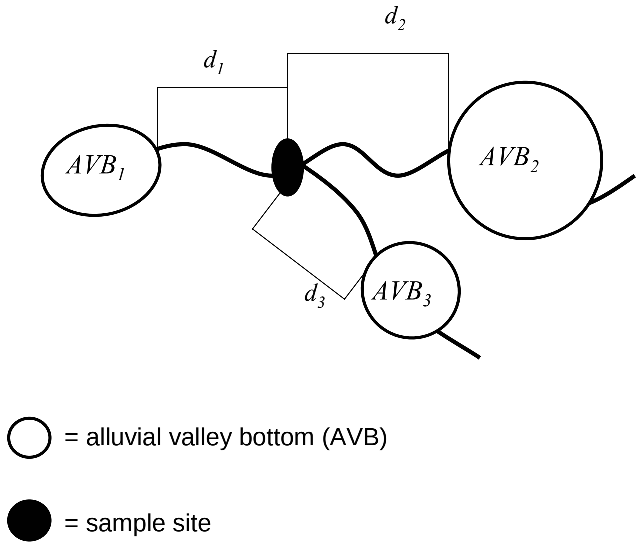

Figure 2. Example of connectivity measurement for weighted alluvial valley bottom area (wAVBA). For each sample site, each alluvial valley bottom area was divided by the distance from the sample site. These quotients were then summed to give an overall connectivity variable, wAVBA.

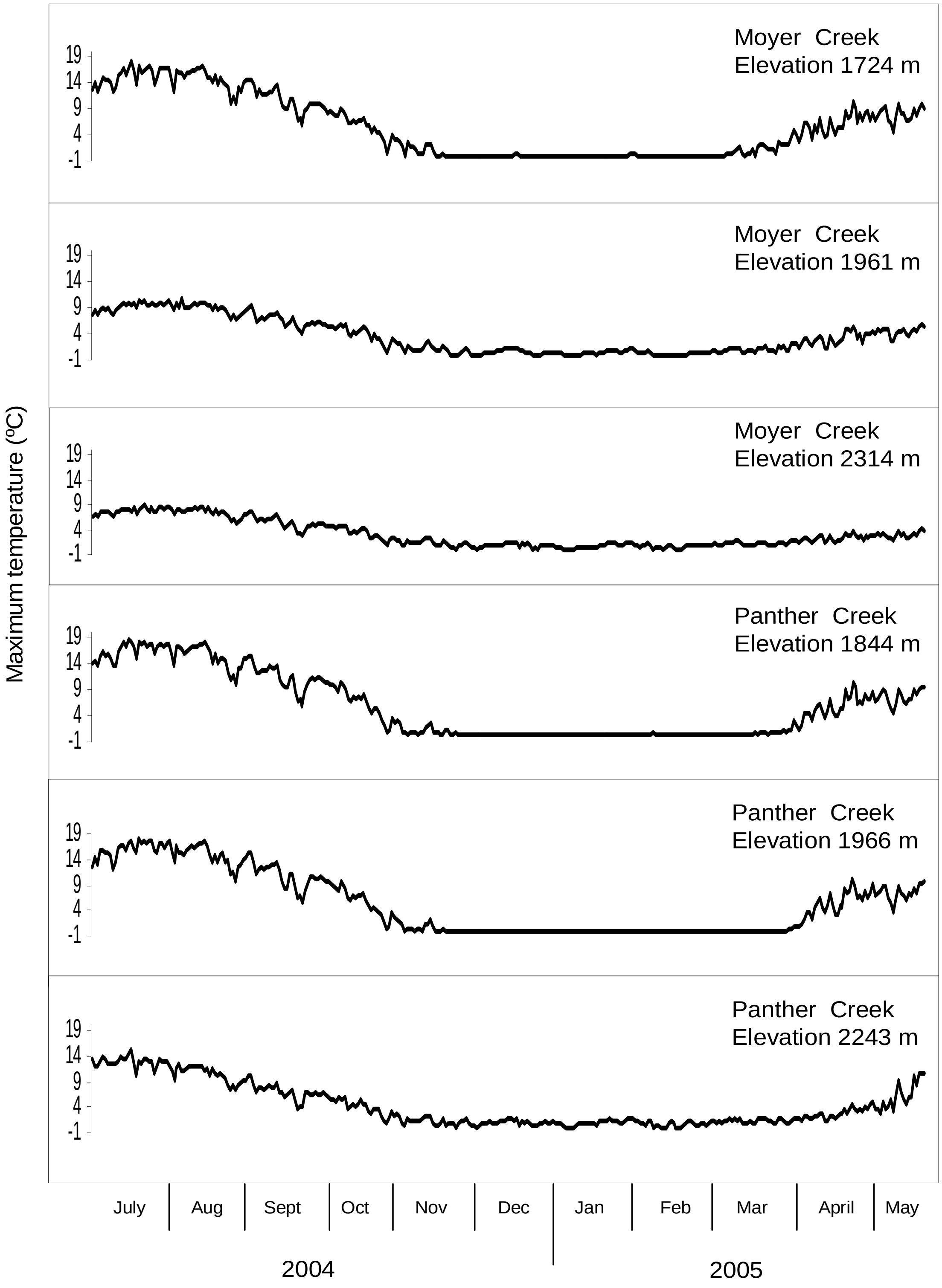

Figure 3. Maximum temperature changes along a longitudinal gradient (lower, middle, and upper reaches) in Moyer Creek and Panther Creek.

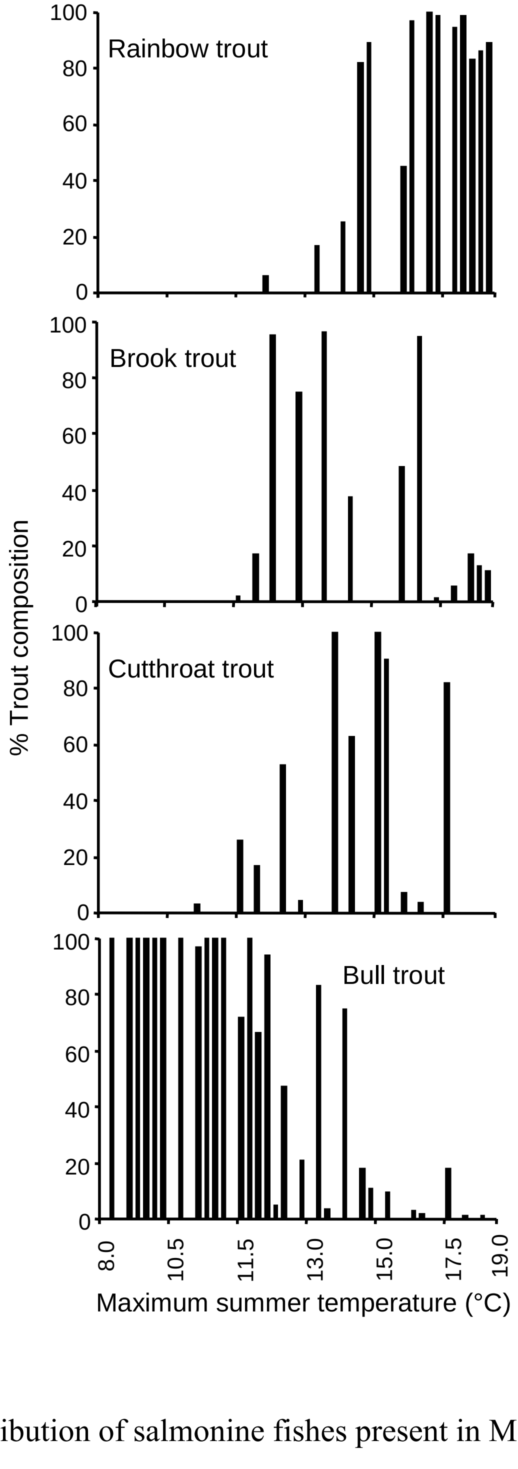

Figure 4. Thermal distribution of salmonine fishes present in Moyer Creek and Panther Creek.

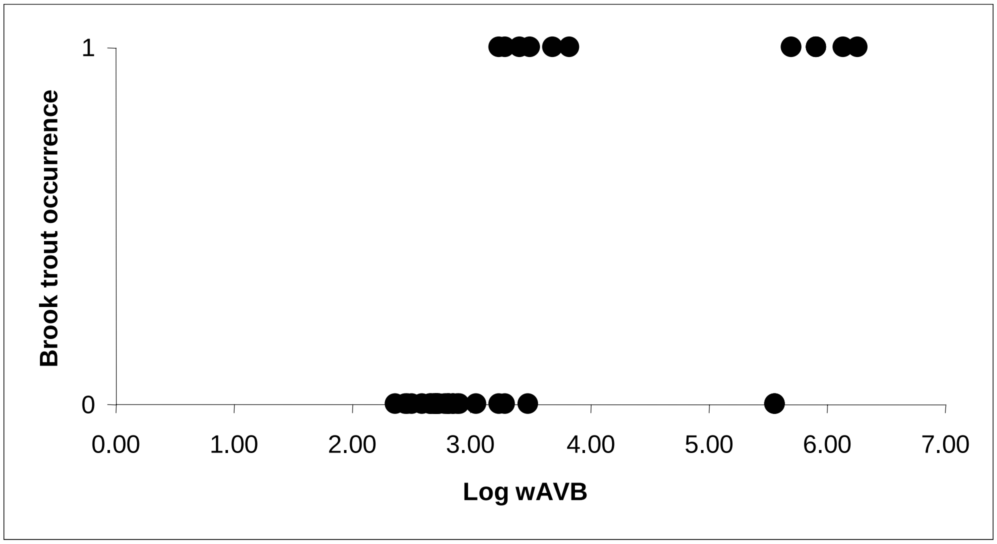

Figure 5. Small brook trout occurrence (1 = present, 0 = absent) in relation to $\log_{10}$ weighted alluvial valley bottom area (wAVBA). Higher wAVBA represent sites where an alluvial valley bottom is relatively close to the sample site.

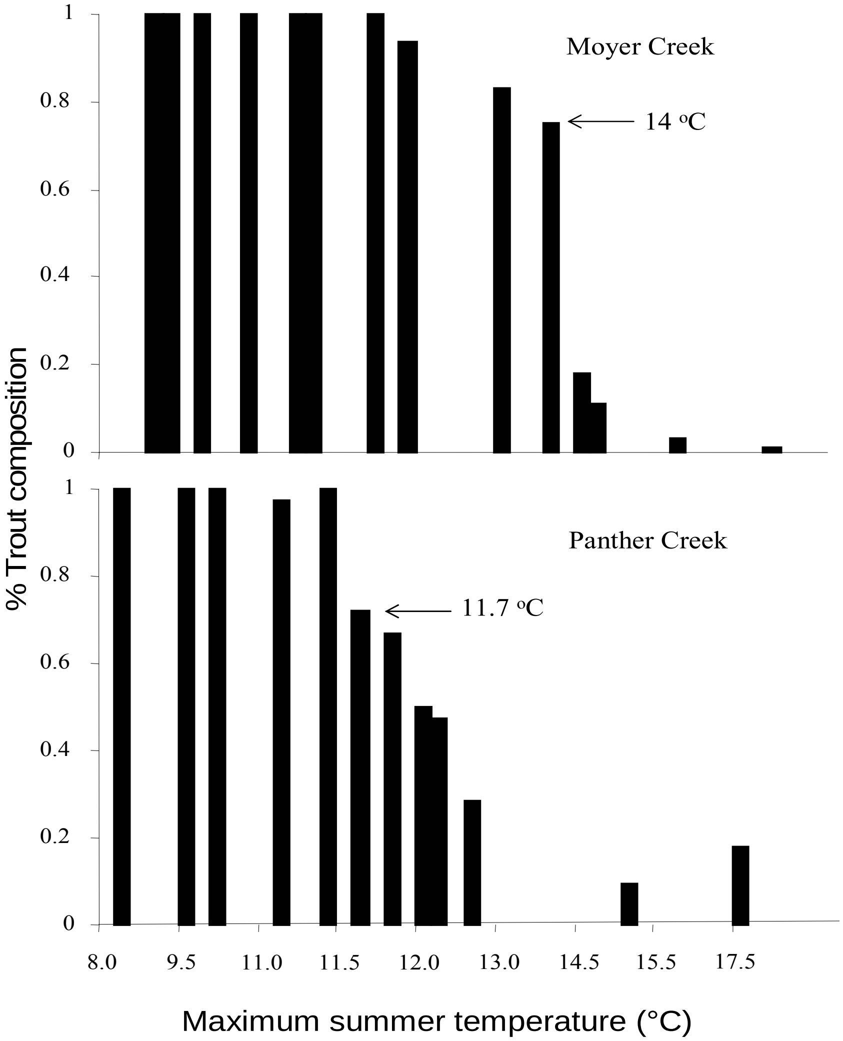

Figure 6. Thermal shift in numerical dominance of bull trout in the presence of brook trout (Panther Creek) compared to a stream where no brook trout were found (Moyer Creek).

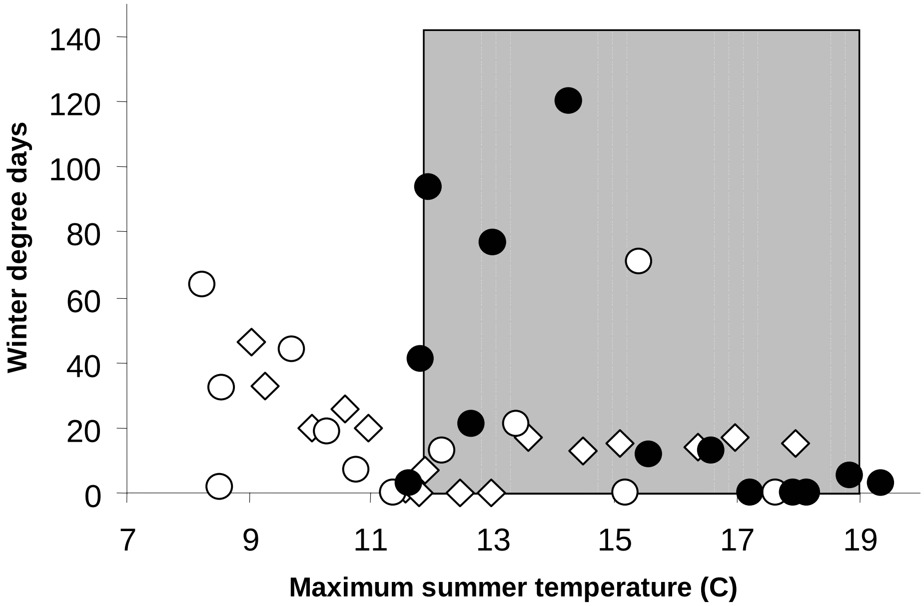

Figure 7. Nonnative brook trout presence (solid symbols) and absence (open symbols) in relation to maximum summer temperature and winter degree days in Panther Creek (circles) and Moyer Creek (diamonds). The gray box represents the optimal growth range for brook trout (11 – 19 °C).

APPENDIX A

Summarized and Raw Data for the Detection of Brook Trout

Table A.1. Detection of marked brook trout (BK) after three passes (pass four results were identical to pass three). For study area and methods see Rosenberger and Dunham (2005). Data from J. B. Dunham (unpublished data).

			# Sites when species was detected			% Detection		
Species	Size	Total # marked sites	Pass 1	Pass 2	Pass 3	Pass 1	Pass 2	Pass 3
Brook trout	<150	11	8	8	11	73	73	100
Brook trout	>150	9	5	7	8	56	78	89

Table A.2. Individual brook trout (BK) capture data in the Boise River and Panther Creek basin; including site location, fork length, whether fish was recaptured (1) or not (0), and what pass recapture occurred (1-4). For study area and methods see Rosenberger and Dunham (2005). Data from J. B. Dunham (unpublished data).

Stream	Basin	Site	UTM Northing	UTM Easting	Species	Length (mm)	Recapture	Pass recaptured
Arnett Cr.	Panther Creek	A	5010273	724008	BK	60	1	1
Arnett Cr.	Panther Creek	A	5010273	724008	BK	61	1	1
Arnett Cr.	Panther Creek	A	5010273	724008	BK	64	1	1
Arnett Cr.	Panther Creek	A	5010273	724008	BK	64	1	1
Arnett Cr.	Panther Creek	A	5010273	724008	BK	132	1	1
Arnett Cr.	Panther Creek	A	5010273	724008	BK	164	1	1
Arnett Cr.	Panther Creek	A	5010273	724008	BK	60	1	3
Arnett Cr.	Panther Creek	A	5010273	724008	BK	62	1	3
Arnett Cr.	Panther Creek	A	5010273	724008	BK	60	1	4
Arnett Cr.	Panther Creek	A	5010273	724008	BK	63	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	64	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	65	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	65	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	66	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	66	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	68	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	103	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	104	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	105	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	108	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	114	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	115	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	139	0	
Arnett Cr.	Panther Creek	A	5010273	724008	BK	157	0	
Arnett Cr.	Panther Creek	B	5010273	722720	BK	60	1	2

Stream	Basin	Site	UTM Northing	UTM Easting	Species	Length (mm)	Recapture	Pass recaptured
Arnett Cr.	Panther Creek	B	5010273	722720	BK	61	1	4
Arnett Cr.	Panther Creek	B	5010273	722720	BK	65	1	1
Arnett Cr.	Panther Creek	B	5010273	722720	BK	103	1	1
Arnett Cr.	Panther Creek	B	5010273	722720	BK	150	1	2
Arnett Cr.	Panther Creek	B	5010273	722720	BK	62	0	
Arnett Cr.	Panther Creek	B	5010273	722720	BK	64	0	
Arnett Cr.	Panther Creek	B	5010273	722720	BK	68	0	
Arnett Cr.	Panther Creek	B	5010273	722720	BK	69	0	
Arnett Cr.	Panther Creek	B	5010273	722720	BK	70	0	
Arnett Cr.	Panther Creek	B	5010273	722720	BK	118	0	
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	64	1	2
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	74	1	4
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	74	1	1
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	117	1	2
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	120	1	2
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	167	1	2
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	211	1	1
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	60	0	
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	60	0	
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	61	0	
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	62	0	
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	105	0	
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	107	0	
Beaver Cr. (Edna)	Boise River	A	4868522	612115	BK	123	0	
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	61	1	1
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	63	1	1
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	66	1	1
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	114	1	1
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	121	1	1
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	130	1	1
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	132	1	1

Stream	Basin	Site	UTM Northing	UTM Easting	Species	Length (mm)	Recapture	Pass recaptured
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	136	1	1
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	150	1	1
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	60	1	2
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	132	1	2
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	70	1	3
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	71	1	3
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	64	1	4
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	64	0	
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	65	0	
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	66	0	
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	69	0	
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	78	0	
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	79	0	
Beaver Cr. (Edna)	Boise River	B	4868737	612066	BK	138	0	
Beaver Cr. (NF)	Boise River	A	4853783	619676	BK	77	1	1
Beaver Cr. (NF)	Boise River	A	4853783	619676	BK	117	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	62	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	62	1	3
EF Smith Cr.	Boise River	A	4824210	620309	BK	62	1	3
EF Smith Cr.	Boise River	A	4824210	620309	BK	63	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	64	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	64	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	64	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	64	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	65	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	66	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	66	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	68	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	68	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	70	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	72	1	2

Stream	Basin	Site	UTM Northing	UTM Easting	Species	Length (mm)	Recapture	Pass recaptured
EF Smith Cr.	Boise River	A	4824210	620309	BK	86	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	91	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	92	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	95	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	95	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	96	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	96	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	96	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	97	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	97	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	98	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	99	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	99	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	100	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	101	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	102	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	103	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	103	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	104	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	104	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	105	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	106	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	106	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	108	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	108	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	109	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	111	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	111	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	112	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	113	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	113	1	1

Stream	Basin	Site	UTM Northing	UTM Easting	Species	Length (mm)	Recapture	Pass recaptured
EF Smith Cr.	Boise River	A	4824210	620309	BK	114	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	114	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	115	1	4
EF Smith Cr.	Boise River	A	4824210	620309	BK	115	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	116	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	119	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	125	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	136	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	136	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	138	1	3
EF Smith Cr.	Boise River	A	4824210	620309	BK	144	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	153	1	2
EF Smith Cr.	Boise River	A	4824210	620309	BK	156	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	160	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	165	1	1
EF Smith Cr.	Boise River	A	4824210	620309	BK	163	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	61	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	61	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	63	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	63	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	63	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	64	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	69	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	69	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	81	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	89	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	101	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	101	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	101	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	103	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	123	0	

Stream	Basin	Site	UTM Northing	UTM Easting	Species	Length (mm)	Recapture	Pass recaptured
EF Smith Cr.	Boise River	A	4824210	620309	BK	128	0	
EF Smith Cr.	Boise River	A	4824210	620309	BK	145	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	61	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	63	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	63	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	68	1	4
EF Smith Cr.	Boise River	B	4824339	619612	BK	83	1	2
EF Smith Cr.	Boise River	B	4824339	619612	BK	83	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	95	1	3
EF Smith Cr.	Boise River	B	4824339	619612	BK	99	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	103	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	104	1	2
EF Smith Cr.	Boise River	B	4824339	619612	BK	104	1	2
EF Smith Cr.	Boise River	B	4824339	619612	BK	106	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	106	1	3
EF Smith Cr.	Boise River	B	4824339	619612	BK	108	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	108	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	108	1	3
EF Smith Cr.	Boise River	B	4824339	619612	BK	109	1	4
EF Smith Cr.	Boise River	B	4824339	619612	BK	113	1	2
EF Smith Cr.	Boise River	B	4824339	619612	BK	115	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	117	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	124	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	124	1	2
EF Smith Cr.	Boise River	B	4824339	619612	BK	124	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	127	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	136	1	2
EF Smith Cr.	Boise River	B	4824339	619612	BK	140	1	2
EF Smith Cr.	Boise River	B	4824339	619612	BK	141	1	2
EF Smith Cr.	Boise River	B	4824339	619612	BK	143	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	149	1	2

Stream	Basin	Site	UTM Northing	UTM Easting	Species	Length (mm)	Recapture	Pass recaptured
EF Smith Cr.	Boise River	B	4824339	619612	BK	172	1	2
EF Smith Cr.	Boise River	B	4824339	619612	BK	176	1	2
EF Smith Cr.	Boise River	B	4824339	619612	BK	184	1	1
EF Smith Cr.	Boise River	B	4824339	619612	BK	60	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	61	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	62	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	64	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	64	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	64	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	64	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	66	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	67	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	83	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	85	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	86	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	89	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	90	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	92	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	93	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	93	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	96	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	98	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	98	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	101	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	102	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	106	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	109	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	110	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	110	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	111	0	

Stream	Basin	Site	UTM Northing	UTM Easting	Species	Length (mm)	Recapture	Pass recaptured
EF Smith Cr.	Boise River	B	4824339	619612	BK	113	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	113	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	114	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	116	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	116	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	116	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	151	0	
EF Smith Cr.	Boise River	B	4824339	619612	BK	154	0	
Panther Cr.	Panther Creek	A	4983730	708670	BK	119	0	
Panther Cr.	Panther Creek	A	4983730	708670	BK	122	0	
Panther Cr.	Panther Creek	A	4983730	708670	BK	141	0	
Panther Cr.	Panther Creek	A	4983730	708670	BK	229	0	
Panther Cr.	Panther Creek	B	4980655	709171	BK	69	1	3
Panther Cr.	Panther Creek	B	4980655	709171	BK	152	1	3
Pikes Fork Cr.	Boise River	A	4869690	615482	BK	107	1	1
Pikes Fork Cr.	Boise River	A	4869690	615482	BK	138	0	
Pikes Fork Cr.	Boise River	A	4869690	615482	BK	199	0	
Pikes Fork Cr.	Boise River	C	4858766	619439	BK	121	1	1
Pikes Fork Cr.	Boise River	C	4858766	619439	BK	85	0	
Pikes Fork Cr.	Boise River	C	4858766	619439	BK	116	0	

APPENDIX B

Location and Characteristics of Study Sites

Stream	Basin	Site	UTM Zone	UTM Northing	UTM Easting	Elevation (m)	Length (m)	Slope (%)
Salt	Moyer	M5	11	4984821	714322	1978	91	9.6
Salt	Moyer	M6	11	4984537	713250	1799	96	11.9
Moyer	Moyer	M9	11	4983362	713153	1815	109	2.5
Unnamed Trib.	Moyer	M12	11	4982808	714116	1979	105	17.2
Moyer	Moyer	M13	11	4982382	713208	1844	100	2.7
Moyer	Moyer	M15	11	4981890	713496	1866	91	2.3
Moyer	Moyer	M17	11	4981106	714437	1907	91	3.0
Moyer	Moyer	M22	11	4980618	715912	1961	88	5.1
Birthday	Moyer	M28	11	4981961	719506	2413	94	4.5
Moyer	Moyer	M31	11	4979881	717071	2042	100	6.0
Moyer	Moyer	M33	11	4980156	719106	2186	105	3.5
Moyer	Moyer	M37	11	4978376	720218	2296	103	3.6
Moyer	Moyer	M38	11	4977954	720366	2314	92	4.2
SF Moyer	Moyer	M50	11	4974662	717470	2438	104	10.0
Moyer	Moyer	M54	11	4987395	712901	1724	97	2.0
Moyer	Moyer	M59	11	4986168	713307	1751	95	2.0
Cabin	Panther	P4	11	4981647	706082	1988	98	3.4
Cabin	Panther	P7	11	4981460	707369	1902	103	3.9
Cabin	Panther	P9	11	4980124	705148	2085	112	3.3
Cabin	Panther	P12	11	4980999	707588	1906	111	5.3
Cabin	Panther	P14	11	4981647	708273	1853	100	1.9
Panther	Panther	P16	11	4981072	708954	1844	97	2.2
Panther	Panther	P17	11	4980576	709233	1867	106	1.7
Panther	Panther	P21	11	4978893	710017	1910	105	2.7
Panther	Panther	P23	11	4978304	710364	1940	90	4.4
Panther	Panther	P24	11	4977699	710616	1966	102	2.0
Panther	Panther	P31	11	4974797	711985	2024	92	2.4
Panther	Panther	P34	11	4973883	712730	2039	101	1.8
Panther	Panther	P37	11	4972325	713040	2104	95	2.5
Panther	Panther	P39	11	4970918	713849	2135	91	2.7
Otter	Panther	P40	11	4970903	714250	2146	104	3.8
Otter	Panther	P42	11	4970506	715166	2203	97	7.1
Panther	Panther	P45	11	4969860	714557	2197	101	3.0
Panther	Panther	P46	11	4969482	715229	2243	101	8.3
Mink	Panther	P50	11	4971205	712801	2207	99	7.0
Mink	Panther	P51	11	4971027	712467	2232	100	6.3
Opal	Panther	P52	11	4974903	712180	2032	79	5.9
Opal	Panther	P53	11	4975118	712505	2066	104	6.5
Opal	Panther	P56	11	4974335	715858	2378	93	7.4
Weasel	Panther	P57	11	4973758	713142	2072	104	5.2
Weasel	Panther	P58	11	4973758	713421	2106	89	7.7

APPENDIX C

Number of Fish Species Captured per Site

SiteID	Brook trout <150 mm	Brook trout >150 mm	Bull trout <150 mm	Bull trout >150 mm	Cutthroat trout <150 mm	Cutthroat trout >150 mm	Rainbow trout <150 mm	Rainbow trout >150 mm	Shorthead sculpin
M5	0	0	0	0	0	0	0	0	0
M6	0	0	59	2	0	0	4	0	0
M9	0	0	1	2	0	0	68	20	189
M12	0	0	0	0	0	0	0	0	0
M13	0	0	5	2	0	0	44	13	203
M15	0	0	12	1	0	0	40	18	164
M17	0	0	26	1	0	0	7	2	47
M22	0	0	47	10	0	0	0	0	0
M28	0	0	0	0	0	0	0	0	0
M31	0	0	39	7	0	0	0	0	0
M33	0	0	20	8	0	0	0	0	0
M37	0	0	11	14	0	0	0	0	0
M38	0	0	23	6	0	0	0	0	0
M50	0	0	33	0	0	0	0	0	0
M54	0	0	1	1	0	0	98	15	240
M59	0	0	0	0	0	0	49	9	231
P4	0	0	0	0	64	2	0	0	0
P7	0	0	0	0	62	4	0	0	26
P9	0	0	18	1	19	2	0	0	0
P12	18	1	0	0	32	0	0	0	0
P14	50	1	1	0	2	0	0	0	209
P16	11	0	1	0	0	0	32	4	193
P17	6	2	0	0	0	0	37	5	135
P21	1	0	0	0	0	0	39	8	102
P23	3	3	0	0	0	0	58	5	52
P24	19	2	0	0	0	0	59	6	170
P31	12	2	0	0	1	1	9	4	90
P34	13	5	4	1	0	1	0	0	257
P37	1	2	7	5	2	1	0	0	227

SiteID	Brook trout <150 mm	Brook trout >150 mm	Bull trout <150 mm	Bull trout >150 mm	Cutthroat trout <150 mm	Cutthroat trout >150 mm	Rainbow trout <150 mm	Rainbow trout >150 mm	Shorthead sculpin
P39	0	1	36	0	9	4	0	0	0
P40	0	0	27	6	1	0	0	0	0
P42	0	0	35	1	0	0	0	0	0
P45	0	0	4	1	19	4	0	0	0
P46	0	0	1	1	18	1	0	0	0
P50	0	0	0	0	0	0	0	0	0
P51	0	0	0	0	0	0	0	0	0
P52	29	0	1	0	0	0	0	0	0
P53	73	3	4	0	0	0	0	0	0
P56	0	0	12	0	0	0	0	0	0
P57	0	0	21	0	0	0	0	0	0
P58	0	0	6	1	0	0	0	0	0

APPENDIX D

Summarized Habitat Data

Site	LWD	Average depth (m)	Average width (m)	CSA (m2)	Total undercut length (m)	Valley bottom	Maximum summer temperature	# day above 1 ^{o}C	Rainbow trout abundance
M5	68	0.05	1.77	0.09	0	457.86	12.98	0	0
M6	14	0.06	1.88	0.11	5.04	523.38	11.89	7	5
M9	4	0.14	3.96	0.56	36.11	495.23	16.36	14	105
M12	6	0.05	1.14	0.05	2.70	450.41	11.58	1	0
M13	16	0.16	5.17	0.83	14.44	491.27	15.08	15	89
M15	5	0.16	5.71	0.94	7.22	510.00	14.47	13	82
M17	7	0.13	3.84	0.50	27.20	698.92	13.58	17	12
M22	19	0.16	3.91	0.63	7.57	360286.87	10.95	20	0
M28	21	0.07	1.59	0.11	16.05	313.01	12.47	0	0
M31	101	0.12	3.36	0.40	18.22	360263.39	10.57	26	0
M33	72	0.12	2.80	0.34	101.14	393.02	10.04	20	0
M37	58	0.11	2.83	0.32	44.89	289.67	9.27	33	0
M38	12	0.09	3.01	0.27	62.71	279.88	9.05	46	0
M50	61	0.09	2.10	0.20	25.73	230.33	11.79	0	0
M54	40	0.14	6.28	0.90	6.83	799.47	17.97	15	239
M59	8	0.15	4.63	0.68	25.03	625.62	16.98	17	80
P4	58	0.07	1.41	0.10	12.13	1104.05	13.39	21	0
P7	29	0.06	1.59	0.10	1.04	1962.98	15.19	0	0
P9	20	0.07	1.01	0.07	19.76	766.52	12.16	13	0
P12	26	0.07	1.51	0.11	10.83	1914.12	14.24	120	0
P14	20	0.08	1.89	0.16	5.87	6878.98	16.59	13	0
P16	12	0.10	4.50	0.44	0.72	1844990.21	18.84	5	51
P17	15	0.31	3.41	1.07	42.18	507203.40	19.35	3	72
P21	1	0.15	3.78	0.55	17.20	1387231.72	17.23	0	53
P23	39	0.14	5.67	0.79	11.95	4849.46	17.91	0	125
P24	24	0.16	5.07	0.83	11.28	3169.46	18.14	0	118
P31	16	0.15	4.38	0.64	5.52	809734.33	15.55	12	20
P34	20	0.10	4.34	0.44	6.86	809621.48	12.64	21	0

Site	LWD	Average depth (m)	Average width (m)	CSA (m2)	Total undercut length (m)	Valley bottom	Maximum summer temperature	# day above 1 C	Rainbow trout abundance
P37	95	0.11	4.14	0.44	8.65	1721.29	11.83	41	0
P39	33	0.09	3.98	0.37	22.84	706.74	11.63	3	0
P40	54	0.08	2.81	0.23	9.05	651.82	10.78	7	0
P42	67	0.07	2.43	0.16	43.70	528.34	9.71	44	0
P45	3	0.08	2.01	0.16	4.34	531.23	17.63	0	0
P46	50	0.04	1.49	0.06	0	475.60	15.41	71	0
P50	16	0.07	1.20	0.08	27.09	658.87	8.58	32	0
P51	35	0.07	1.53	0.11	26.88	607.14	8.23	64	0
P52	3	0.10	1.50	0.14	6.43	809716.59	13.01	77	0
P53	69	0.07	2.76	0.18	5.96	2541.40	11.94	94	0
P56	32	0.08	1.36	0.10	68.67	509.38	8.54	2	0
P57	19	0.05	1.36	0.07	1.85	3001.41	11.38	0	0
P58	47	0.05	1.30	0.06	0	1696.75	10.28	19	0