# Invasion by Nonnative Brook Trout in Panther Creek, Idaho: Roles of Local Habitat Quality, Biotic Resistance, and Connectivity to Source Habitats

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*Abstract.*—Theoretical models and empirical evidence suggest that the invasion of nonnative species in freshwaters is facilitated through the interaction of three factors: habitat quality, biotic resistance, and connectivity. We measured variables that represented each factor to determine which were associated with the occurrence of nonnative brook trout *Salvelinus fontinalis* in Panther Creek, a tributary to the Salmon River, Idaho. Habitat variables included measures of summer and winter temperature, instream cover, and channel size. The abundance of native rainbow trout *Oncorhynchus mykiss* within sampled sites was used as a measure of biotic resistance. We also considered the connectivity of sample sites to unconfined valley bottoms, which were considered habitats that may serve as sources for the spread of established populations of brook trout. We analyzed the occurrence of small (<150-mm [fork length]) and large (≥150-mm) brook trout separately, assuming that the former represents an established invasion while accounting for the higher potential mobility of the latter. The occurrence of small brook trout was strongly associated with the proximity of sites to large, unconstrained valley bottoms, providing evidence that such habitats may serve as sources for the spread of brook trout invasion. Within sites, winter degree-days and maximum summer temperature were positively associated with the occurrence of small brook trout. The occurrence of large brook trout was not related to any of the variables considered, perhaps due to the difficulty of linking site-specific habitat factors to larger and more mobile individuals. The abundance of rainbow trout was not conclusively associated with the occurrence of either small or large brook trout, providing little support for the role of biotic resistance. Overall, our results suggest that source connectivity and local habitat characteristics, but not biotic resistance, influence the establishment and spread of nonnative brook trout populations. Further work is needed to confirm that the patterns observed here are relevant to other localities where brook trout have invaded and to understand the mechanisms contributing to the invasion process.

Since the concern regarding invasive species was raised by Elton (1958), increasing attention has been aimed toward understanding the processes influencing 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 patterns of invasion in freshwaters, noting that habitat suitability and biotic resistance are important components to the success of an invading species. Habitat suitability refers to abiotic resources (e.g., temperature, flow, and chemistry) that satisfy a species' physiological needs, whereas biotic resistance can result 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, if the abiotic environment

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is suitable for an invasive species, then it should be able to establish, regardless of the biotic community present. In addition to the suitability of local sites, connectivity may also be important to the success of invasions (Carlton 1996). 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 (Fuller et al. 1999; 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 (e.g., Crawford 2001; Fausch et al. 2006). 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 the brook trout is widely established in western North America, the relative roles of different factors influencing the establishment and spread of invasions are poorly understood (Dunham et al. 2002). It is possible that invasions may be limited by the suitability of local habitats encountered by brook trout. Among the potential habitat variables that may be important, temperature is most obviously linked to the distribution and presence of native brook trout (Barton et al. 1985; Meisner 1990; Picard et al. 2003), and invasions in western North America may be less likely where temperatures are cooler with shorter growing seasons (Adams 1999), or in unsuitably cold temperatures that limit spawning or egg incubation success in fall and winter (Curry et al. 1995; Curry and Noakes 1995).

Evidence for the influence of biotic resistance on invasions by nonnative brook trout in western North America is lacking (Dunham et al. 2002). However, the decline of brook trout in its native range is 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 rainbow trout may act similarly in western North America to limit invasions by nonnative brook trout (Fausch 1988). To our knowl-edge, there are no studies on the potential for rainbow trout to prevent an invasion of brook trout (i.e., to act as a biotic barrier to invasion).

In addition to habitat suitability and biotic resistance, the connectivity of a potentially invaded site 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, creating new source populations under 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 largely repopulating two stream segments where they were previously eradicated (Peterson and Fausch 2003a; Peterson et al. 2004). The connection between existing populations and new potential 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; Fausch et al. 2006).

Established populations of nonnative brook trout are often associated with unconfined (typically alluvial; Montgomery and Buffington 1997, 1998) valley bottoms that may be important sources for the spread of invasions. For example, American beaver *Castor canadensis* most often construct dams in unconfined valley bottoms (Suzuki and McComb 1998; Benjamin 2006), and constructed ponds can provide thermal refugia and rearing habitat for brook trout (Collen and Gibson 2001). In more confined valleys, beaver ponds may be restricted due to physical constraints of the canyon walls and increased chance of dam failures from high streamflows (Collen and Gibson 2001). Unconfined valley bottoms also have wider flood-plains, allowing additional development of off-channel habitats supplied by groundwater or hyporheic flow (Cavallo 1997), more suitable conditions for winter egg incubation (Baxter and Hauer 2000), and lower probability of flows that scour eggs from redds (Shellberg 2002). Collectively, these conditions may increase the local productivity of brook trout popula-tions and increase the chances they will become sources for the spread of nonnative brook trout populations into adjacent habitats. In landscape ecology, this process has been termed "neighborhood effects" (Dunning et al. 1992), a common influence on

the distribution of fishes in stream networks (Schlosser 1994, 1995). Here we refer to this phenomenon as "source connectivity" based on the assumption that unconfined valley bottoms are sources for brook trout invasion and can lead to the spread of nonnative brook trout.

The purpose of this study was to identify patterns and potential processes related to the establishment and spread of nonnative brook trout in a stream network located in central Idaho. We examined the occurrence of small (<150-mm) and large (≥150-mm) brook trout separately, assuming the former represents an established invasion while accounting for higher potential mobility of the latter. Occurrence is the result of several processes influencing invasion, including arrival, establishment, and potential spread of brook trout in a given stream network (Adams 1999; Dunham et al. 2002). We studied occurrence of brook trout in relation to hypothesized influences of biotic resistance, habitat suitability, and source connectivity. More specifically, our objectives were to (1) document abiotic habitat characteristics (e.g., temperature) influencing the presence of small and large brook trout (habitat suitability), (2) determine whether a greater abundance of rainbow trout act as a biotic barrier to small and large brook trout (biotic resistance), and (3) determine whether an association exists between the presence of unconfined valley bottoms and the presence of brook trout populations in nearby tributary streams (source 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, and the watershed includes 644 km of perennial streams (Idaho Department of Environmental Quality 2001). Average annual discharge is 8.5 m$^3$/s, highest flows generally occurring between April and June due to snowmelt (Idaho Department of Environmental Quality 2001). The Panther Creek drainage once served as spawning grounds for native anadromous salmonines, including Chinook salmon *O. tshawytscha* and steelhead (anadromous rainbow trout) *O. mykiss*, and still supports nonanadromous rainbow trout, bull trout *S. confluentus*, and westslope cutthroat trout *O. clarkii lewisii*. Anadromous populations declined rapidly following the development of Blackbird Mine in 1949 (Platts 1972).

Our study section contained four salmonine species:

bull trout, cutthroat trout, rainbow trout, and nonnative brook trout. According to Idaho Fish and Game records (T. Frew, Idaho Fish and Game, unpublished data), nonnative brook trout were stocked in this system in the mid-1950s in three creeks (Musgrove Creek, Napias Creek, and Panther Creek). Rainbow trout were also stocked in Panther Creek until 1995; however, the time since the last stocking event and lack of fish bearing marks that identify stocked fish (missing adipose fins) suggest the rainbow trout observed in this study were the result of natural reproduction. We could not clearly establish if these fish were ultimately descended from either source (native or stocked fish), but this did not influence our hypothesized effects of biotic interactions. Other stream-living vertebrates found include shorthead sculpin *Cottus confusus*, Rocky Mountain tailed frog *Ascaphus montanus*, and Columbia spotted frog *Rana luteiventris*.

*Study design and field methods.*—Site selection was based on ensuring representation of the range of variability in predictor variables while allowing randomness to avoid bias in the subjective location of sites. We sampled streams draining the headwaters of 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. We selected this range of basin areas to focus our work on streams ranging from approximately 1–10 m (summer low flow width), which most commonly support nonnative brook trout in the region (Rieman et al. 1999). Our sample sites were allocated to individual stream segments defined by TauDEM. A TauDEM stream segment is a portion of a stream bounded on the upstream and downstream end by a tributary junction. The TauDEM stream segments were numbered, and a subset was randomly chosen. 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 were located and fish and habitat sampling were performed.

*Water temperature sampling.*—We deployed one temperature logger at each sample site following methods described in Dunham et al. (2005). All loggers were deployed before July 1, assuming the maximum water temperature is after this date (Dunham et al. 2003). The loggers used (StowAway Tidbit; Onset Computer Co., Pocasset, Massachusetts) recorded temperature in a range of −0.5°C to 37°C with an accuracy of 0.2°C. Loggers were calibrated before deployment to correct for bias. Temperature was recorded every 30 min for one consecutive year (July 1, 2004–June 30, 2005).
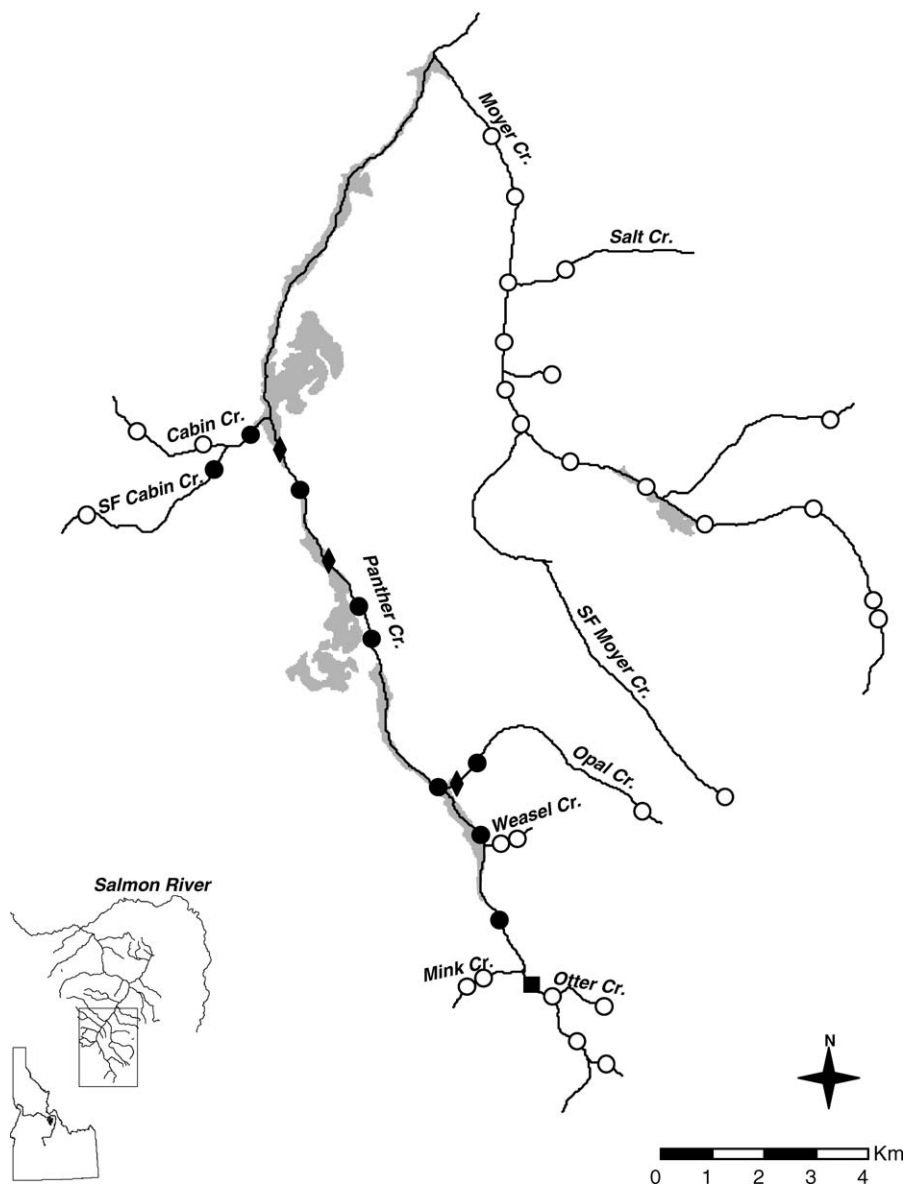
FIGURE 1.—Panther and Moyer Creek watersheds with the sampling sites studied in 2004–2005. Black circles represent sites where both small and large brook trout were found, the black square indicates where only large brook trout were found, and black diamonds indicate where only small brook trout were found. Open circles represent sites where no brook trout were found. Gray patches represent unconfined valley bottoms.

*Fish sampling*.—We sampled fish occurrence during summer low flows (July–September 2004). Sampling sites were approximately 100 m ($\pm$10 m) and blocked at the upstream and downstream ends using mesh nets with a diameter of 6.4 mm (0.25 in). A four-pass removal using a backpack electrofisher (12B electrofisher, Smith-Root, Vancouver, Washington) was used to ensure detection of fish species present (Rosenberger

and Dunham 2005). A validation study on the detectability of brook trout and rainbow trout was completed before the start of our study (Rosenberger and Dunham 2005; Benjamin 2006) to ensure our methods and level of effort ensured very high (>0.85) detectability for all salmonines. All captured salmonine fish were identified to species, and fork length (FL) was measured.

○ = unconfined valley bottom (UVB)
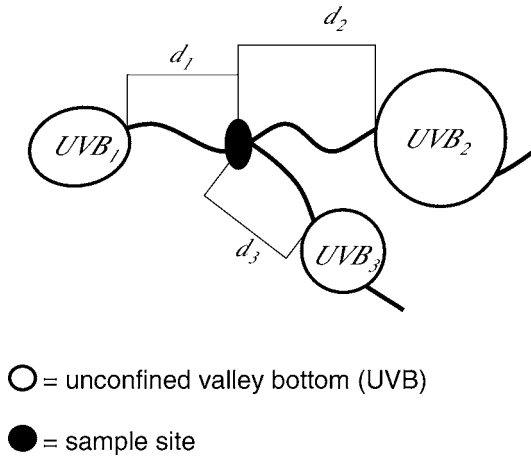
● = sample site

FIGURE 2.—Example of a connectivity measurement for the weighted unconfined valley bottom area. For each sample site, each unconfined valley bottom area (here, $UVB_1$–$UVB_3$) was divided by the distance from the sample site ($d_1$–$d_3$). These quotients were then summed to give an overall connectivity variable (wVBA).

*Habitat sampling.*—After electrofishing, we measured habitat variables within each sampling site. Starting at the downstream block net transects were spaced every 5 m and oriented perpendicular to the active channel. At each transect, we 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 considered, an undercut bank needed to be a minimum of 10 cm in submerged width, height, and length, assuming this would provide enough space for a fish to seek cover. Large wood ($\geq$10 cm in diameter and $\geq$1 m in length) was counted throughout the site and classified as either within the active channel or within the bank-full channel.

To determine the potential source connectivity for each site, we measured unconfined valley bottoms using ArcGIS (version 8.0, ESRI, Redlands, California). To be considered in the analysis, unconfined valley bottoms needed a TauDEM segment with a stream magnitude of at least 11 (i.e., at least 11 first-order streams contributing to the segment); 2,000 m of stream length of any magnitude; and at least 150,000 $m^2$ (D. Nagel, U.S. Forest Service, Rocky Mountain Research Station, personal communication). There are no standard criteria for defining unconfined valley bottoms. We developed our definition based on a visual assessment of the performance of different criteria in relation to areas with which we had strong familiarity. Our use of well-defined criteria based on widely accessible sources of data provides an easily docu-

mented and repeatable approach. A distance-weighted unconfined valley bottom area (wVBA) was estimated for each site location based on the following equation:

$$\text{wVBA} = \sum \frac{\text{VBA}_i}{d_{ij}},$$

where VBA is the area for unconfined valley bottom $i$, and $d$ is the distance from $\text{VBA}_i$ to sample site $j$ (Moilanen and Nieminen 2002; Figure 2).

*Analytical methods.*—We followed the information-theoretic approach for model selection (Burnham and Anderson 2002). First, we developed candidate logistic regression models a priori following suggestions in Burnham and Anderson (2002), which included a global model relating small ($<$150-mm) and large ($\geq$150-mm) brook trout occurrence to the biotic, habitat, and landscape variables mentioned above and candidate models based on these global models (Tables 1, 2). The two different size-classes were used because smaller brook trout were assumed to be sexually immature and to occur in areas of spawning, and larger brook trout were assumed to be sexually mature and able to move longer distances (Riley et al. 1992; Gowan and Fausch 1996; Adams 1999).

Variables making up the global models and subsequent candidate models included winter temperature, maximum summer temperature, mean cross-sectional area, cover, rainbow trout abundance, and the weighted unconfined valley bottom area. Winter temperature was measured as a modification of degree-days to represent egg incubation. It was summarized as the number of days above 1°C between December 1, 2004 and March 31, 2005. Incubation requires approximately 125 d at 2–3°C in a laboratory setting (Power 1980; Marten 1992), although Curry et al. (2002) have shown eggs incubated at less than 1°C for 90 consecutive days still show embryos emerging from the substrate in streams in Newfoundland, Canada. The number of days above 1°C provides a relative estimate of incubation time in the natural environment. The cooler the temperatures during incubation, the less time the alevins will have to reach a suitable size for survival the following winter (Dwyer et al. 1983). Summer temperature was summarized as the maximum temperature between July 1 and September 30, 2004 (Dunham et al. 2005). Maximum summer temperature strongly correlates with similar summary measures of stream temperature (e.g., median or mean temperatures; Dunham et al. 2005). Thus, regardless of the biological implications of acute (e.g., short-term maximum temperatures) or chronic (e.g., seasonal mean temperatures), summary measures are statistically redundant in models such as those used here. Cover included the total pieces of large woody

TABLE 1.—Candidate logistic regression models for the occurrence of small brook trout in the Panther Creek drainage in 2004. Models were ranked by corrected Akaike information criterion ($AIC_c$) weights, larger weights indicating more plausible models. Summer temp = maximum summer temperature; winter temp = number of days above 1°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 the bank-full channel; CSA = cross-sectional area; and rainbow = rainbow trout abundance (>60 mm). The global model included all the variables. Parameter $k$ is the number of parameters, $\Delta AIC_c$ is the difference between the $AIC_c$ score of the model in question and that of the best model.

| Model | $k$ | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ weight | Percent of maximum $AIC_c$ weight |
|---|---|---|---|---|---|
| Summer temp, winter temp | 3 | 39.49 | 0 | 0.63 | 100 |
| Global model | 7 | 41.38 | 1.89 | 0.25 | 38.8 |
| Summer temp | 2 | 44.00 | 4.51 | 0.07 | 10.5 |
| Cover, CSA, summer temp, winter temp | 6 | 45.46 | 5.97 | 0.03 | 5.1 |
| Summer temp, rainbow | 3 | 46.31 | 6.82 | 0.02 | 3.3 |
| Winter temp | 2 | 51.75 | 12.26 | <0.01 | 0.2 |
| Winter temp, rainbow | 3 | 52.40 | 12.90 | <0.01 | 0.2 |

debris and total length of undercut banks. Rainbow trout abundance was calculated for fish greater than 60-mm FL using the four-pass removal model from Rosenberger and Dunham (2005), where data were collected in the Panther Creek drainage under similar conditions. We expected winter and summer temperature and cover to have a positive relationship with the occurrence of both small and large brook trout. Alternatively, mean cross-sectional area and rainbow trout abundance was expected to have a negative relationship with small and large brook trout occurrence (see Dunham et al. 2002). Source connectivity (weighted unconfined valley bottom area, wVBA) was hypothesized to have a positive relationship with small brook trout occurrence only, assuming brook trout smaller than 150 mm were less likely to disperse.

The Hosmer–Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000) and overdispersion (Pearson $\chi^2$/df; Allison 1999) were checked for both global logistic regression models. Predictors were assessed for evidence of multicollinearity by measuring the variance inflation factor (Philippi 1994) and 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 logistic regression models ($AIC_c$; Burnham and Anderson 2002). Model selection based on $AIC_c$ does not consider one model to be the true model; instead it weighs each model, including a penalty for additional variables, and provides a means of ranking of the best approximating models (Burnham and Anderson 2002). This is done by calculating the Akaike weights to assess the relative plausibility of each model. Since more than one model can be plausible, model averaging was done (Burnham and Anderson 2002) using the one-eighth cutoff point (Royall 1997; Thompson and Lee 2002). In other words, models with Akaike weights within one-eighth of the largest weight were averaged based on those weights to form a composite model. In cases where one model showed overwhelming evidence of being the single "best" model (at least eight times the value of the next highest weight), averaging was considered unnecessary.

To provide greater biological relevance to the interpretation of changes in odds ratios, a constant ($C$)

TABLE 2.—Candidate logistic regression models for the occurrence of large brook trout in the Panther Creek drainage in 2004. See Table 1 for additional details.

| Model | $k$ | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ weight | Percent of maximum $AIC_c$ weight |
|---|---|---|---|---|---|
| Summer temp, winter temp | 3 | 45.35 | 0 | 0.28 | 100 |
| Global model | 7 | 45.59 | 0.24 | 0.25 | 88.7 |
| Summer temp | 2 | 45.96 | 0.60 | 0.21 | 74.0 |
| Summer temp, rainbow | 3 | 47.42 | 2.07 | 0.10 | 35.6 |
| Winter temp | 2 | 48.68 | 3.33 | 0.05 | 19.0 |
| Cover, CSA, summer temp, winter temp | 6 | 49.14 | 3.78 | 0.04 | 15.1 |
| Rainbow | 2 | 49.56 | 4.21 | 0.03 | 12.2 |
| Winter temp, rainbow | 3 | 50.27 | 4.92 | 0.02 | 8.5 |

multiplier was included in calculating the odds ratio and odds ratio confidence intervals (i.e., $e^{\beta_i \cdot C}$, where $\beta_i$ is the $i$th logistic regression coefficient; 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.

One potential issue in our study design is spatial dependence of the occurrence of brook trout among sites (i.e., spatial autocorrelation). For several reasons, we did not attempt to explicitly address spatial autocorrelation. First, we explicitly considered variables that captured what we believed to be the most important spatial variables influencing occurrence of brook trout. Second, we had no reason to assume that the simple spatial lags assumed in most models were more realistic than the variables explicitly included in our analyses. Third, we based our inferences on the relative weight of evidence for different models, not absolute probability values, which may be inflated where individual observations do not contribute a true independent degree of freedom, as is assumed in the absence of autocorrelation.

## Results

Forty-one stream segments were used in this analysis. Brook trout were not found to occur within Moyer Creek or its tributaries. Brook trout were present within upper Panther Creek, and tributaries Cabin Creek and Opal Creek. Small brook trout were present in 29% of the sites ($n = 12$) and large brook trout in 24% ($n = 10$) of the sites (Figure 1). Total catch of small brook trout at individual sites ranged from 1 to 73 fish and for large brook trout, 1–5 fish (see Benjamin 2006 for complete list of captured fish with associated independent variables per site). Rainbow trout were found in 32% of the sites ($n = 13$) in both Moyer Creek and Panther Creek and were primarily in the lower elevation main-stem segments, with the exception of four small rainbow trout ($<120$ 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 and rainbow trout occurred together slightly less (10%; $n = 4$). Bull trout and cutthroat trout were also encountered in 66% ($n = 27$) and 29% ($n = 12$) of the sites, respectively, the majority in segments without brook trout (74% and 50% for bull trout and cutthroat trout, respectively).

Initial analysis of the small brook trout global model indicated that source connectivity (wVBA) caused complete separation between presence and absence. When a response variable is perfectly predicted by a predictor variable, the result is complete separation and analysis using logistic regression cannot proceed (Allison 1999). Therefore, weighted unconfined valley bottom area was dropped from the small brook trout global model. The resulting global model for small brook trout showed a good fit according to the Hosmer–Lemeshow goodness-of-fit test ($\chi^2 = 4.71$; df $= 8$; $P = 0.79$) and dispersion (Pearson $\chi^2 = 25.70$; df $= 34$; $P = 0.85$). For small brook trout, the candidate model with both temperature variables, winter degree-days and summer maximum temperature, was the best approximating model, which 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. With an increase of 1°C in maximum summer temperature, there was an 8% increase in the probability of brook trout being present. Similarly, five additional days above 1°C between December 1 and March 31 gave a 1% increase in the likelihood that small brook trout would be present.

Habitat suitability variables may be important in predicting the occurrence of large brook trout. 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 including maximum summer temperature and winter degree-days was the best approximating model but only slightly better than the next-best model (Table 2). Five other models also had large enough Akaike weights that they could not be dismissed, hence model averaging was performed (Table 2). Within this composite model, none of the variables showed conclusive results (odds ratio confidence intervals overlap one; Table 3). The confidence intervals for maximum summer temperature and cross-sectional area were skewed sufficiently to the right to suggest a relationship with large brook trout to be biologically significant (Hosmer and Lemeshow 2000; Alderson 2005).

## Discussion

We investigated the roles of factors representing habitat suitability, biotic resistance (Moyle and Light 1996), and source connectivity (Carlton 1996) in association with the extent of invasion by nonnative brook trout invading in a stream. None of the variables in the averaged model that predicted the occurrence of large brook trout were conclusive. Patterns of occurrence by small brook trout were strongly associated with connectivity to potential source localities (unconfined valley bottoms) and less so with local habitat

TABLE 3.—Model-averaged results of a composite logistic regression model for the occurrence of small and large brook trout. Variables are defined in Table 1; CI = confidence interval.

| Size | Variable | Estimated coefficient | SE | Odds ratio constant | Estimated odds ratio | 95% CI for odds ratio |
|------|----------|----------------------|-----|---------------------|---------------------|----------------------|
| Small | Intercept | −12.027 | 4.56 | | | |
| | Large wood | 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 temp | 0.045 | 0.02 | 5 | 1.25 | 1.01–1.56 |
| | Summer temp | 0.671 | 0.30 | 1 | 1.96 | 1.08–3.55 |
| | Rainbow | −0.014 | 0.02 | 5 | 0.93 | 0.75–1.17 |
| Large | Intercept | −7.499 | 4.87 | | | |
| | Large wood | 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 temp | 0.018 | 0.01 | 5 | 1.09 | 0.964–1.237 |
| | Summer temp | 0.366 | 0.23 | 1 | 1.44 | 0.913–2.278 |
| | Rainbow | −0.012 | 0.01 | 5 | 0.94 | 0.837–1.054 |

suitability, namely maximum summer temperature and winter degree-days. Other variables resulted in inconclusive results, but lack of an effect does not rule out their potential biological importance (Alderson 2005).

### Source Connectivity

Connectivity in this study was measured as a composite of two factors: the size of the unconfined valley bottoms and the distance from unconfined valley bottoms to the sampled sites. We assumed that beaver ponds were important potential sources, as established by previous work (e.g., Gard 1961; Seegrist and Gard 1972). Beaver ponds can also provide important overwinter habitat for small brook trout (Chisholm et al. 1987; Cunjak 1996) along with thermal refugia in colder streams (Collen and Gibson 2001). Beaver ponds were present in every unconfined valley sampled in this work, and there was a positive association between maximum pond size and area of unconfined valley bottom (Benjamin 2006; see also Suzuki and McComb 1998). In addition to beaver ponds, off-channel habitats commonly associated with the presence of brook trout were more likely in sites within unconfined valleys (Cavallo 1997). As we predicted, connectivity to stream reaches with unconfined valley bottoms appeared to be important in determining the extent of brook trout invasion, resulting in complete separation of sites with and without small brook trout. This result is consistent with the hypothesis that habitats associated with unconfined valley bottoms can act to facilitate the spread of invasions by brook trout. Additional confirmatory research would be needed to identify the specific mechanism through which unconfined valley bottoms may act as sources of invasions in nearby locations.

The overall importance of source connectivity and the fact that unconfined valley bottoms were not prevalent in Moyer Creek (Figure 1) prompted some concern about potential confounding between this factor and unknown differences between Moyer and Panther Creek (e.g., "stream effects": Dunham and Vinyard 1997). To address this concern, a separate a posteriori analysis of small brook trout occurrence within Panther Creek only was conducted and revealed similar influences of connectivity (Benjamin 2006). This supported the importance of connectivity to occurrence of small brook trout without the potentially confounding influences of unknown factors affecting occurrence within Moyer Creek. Brook trout have been observed in Moyer Creek in other surveys (B. Roberts, Salmon-Challis National Forest, personal communication) but did not occur within our selected study sites. Thus, brook trout have had several decades of opportunity to invade throughout Moyer Creek, as they have in Panther Creek, yet have not established widespread populations.

### Habitat Suitability: Water Temperature as a Limiting Factor

Among the variables related to local habitat suitability, maximum summer temperature showed the strongest association with the presence of both small and large brook trout, though the evidence for large brook trout is inconclusive. Possible reasons for the inconclusiveness of local habitat for explaining the occurrence of large brook trout include an inappropriate spatial scale for a mobile life stage (i.e., ability to disperse during unfavorable conditions) and lack of interactions considered in the models. However, the improved plausibility of models that contained maximum summer temperature, including the best approximating model, supported our hypothesis that occurrence of large brook trout is more likely in areas within the optimal thermal range for summer growth.
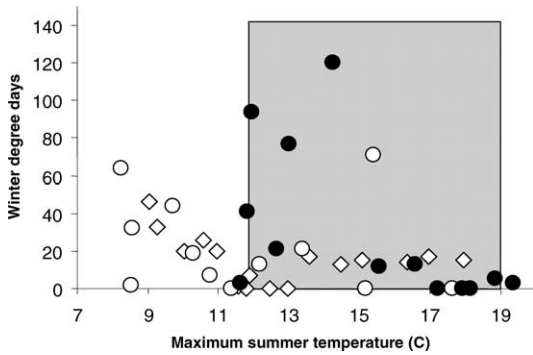
FIGURE 3.—Nonnative brook trout presence (solid circles) and absence (open circles) in relation to maximum summer temperature and winter degree-days in Panther Creek (circles) and Moyer Creek (diamonds). Sites with temperatures below the optimal growth range (12–19°C; Hokanson et al. 1973) for brook trout may be less vulnerable to invasion than sites with temperatures within the optimal growth range. The cooler maximum summer temperatures and lower winter degree-days observed in Moyer Creek may be limiting the establishment of brook trout in these sites.

Our finding that the occurrence of small brook trout was positively associated with warmer summer temperatures within the range observed in our study 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, maximum summer temperatures under 12°C were not observed. Maximum summer temperature in our study area ranged from 8–19°C, and both small and large brook trout occurred within the range of 11–19°C. This pattern of occurrence paralleled the range of optimal temperatures for growth of maturing brook trout found in laboratory studies (12–19°C; Hokanson et al. 1973). This suggests that invasion by nonnative brook trout in Panther Creek may be related to physiological constraints posed by cold temperatures with a shorter summer growing seasons (Adams 1999). If this is true, there are locations within the study area currently without brook trout that are potentially vulnerable to invasion (Figure 3). 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 probably have suitable temperatures to allow upstream spread of nonnative brook trout, whereas others may be too cold (e.g., headwaters of Moyer Creek and Mink Creek) or isolated (Opal Creek) to allow further invasions to occur.

The 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 char *Salvelinus* spp., 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 the associated mortality of eggs or alevins may 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, which, in turn, holds 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 we did not document groundwater inputs in our 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 unconfined 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 unconfined 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 the spread of invasions. Overall, Moyer Creek is represented by cooler maximum summer temperatures and fewer winter degree-days than Panther Creek, potentially limiting the establishment of nonnative brook trout in Moyer Creek (Figure 3).

*Biotic Resistance*

Because rainbow trout have been linked to the decline of brook trout in their native range, we expected rainbow trout to have a similar effect on brook trout in our study area, potentially representing a form of biotic resistance. Consistent with our predictions, a negative relationship was seen between rainbow trout and both size-classes of brook trout in this study, but the effects were not strong and therefore the role of biotic resistance was 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 were 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).

Although we did not have a priori hypotheses of native bull trout or cutthroat trout to resist brook trout invasion, it may be that these native species also play an important role in determining the occurrence of brook trout in our study system or that the net result of interactions among species obscures the potential influences of any individual species. It is also possible that environmentally mediated interactions are important. 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 allow native species to 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°C, 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°C where bull trout numerically dominated and may have a competitive advantage (Benjamin 2006). The dominance of bull trout in the cold water segments and rainbow trout in the warmwater segments could be preventing the spread of nonnative brook trout in this study area (Rieman et al. 2006). Another potentially important interaction may be biotic resistance and unconfined valley bottoms. The presence of unconfined valley bottoms may facilitate the coexistence of nonnative brook trout and native species under a variety of habitat conditions (e.g., Cavallo 1997). The lack of unconfined 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.

## Conclusions

The results of this study imply that source connectivity and habitat characteristics are important to the occurrence of nonnative brook trout in Rocky Mountain streams, supporting Moyle and Light's (1996) and Carlton's (1996) general ideas about factors influencing invasion. The role of biotic resistance was less apparent but may not have been revealed with our study design. No single study or approach can resolve all of the potential complexities that drive invasion of brook trout (Dunham et al. 2002), but insights from studies across more sites or broader spatiotemporal scales may be useful (Fausch et al. 1994) as well as manipulative experiments under natural conditions at scales relevant to specific population processes (Fausch 1998; Peterson and Fausch 2003b). In light of prior work on brook trout invasions, the most novel finding here is the suggestion that context is important, namely the proximity or availability of potential source habitats that may facilitate invasions. This has been demonstrated for downstream invasion of brook trout into streams from established populations in headwater lakes (Adams et al. 2001). Our results suggest less obvious features of the landscape, unconfined valley bottoms, may also play an important role in driving brook trout invasion within stream networks. Though we have been able to predict the present distribution of brook trout and potential factors contributing to invasion, the long-term future of brook trout and native fishes within Panther Creek is not clear.

At present, native fishes within upper Panther Creek are widely distributed, with the exception of anadromous salmon and steelhead trout, which have been impacted primarily by changes to downstream conditions (Platts 1972). Thus, brook trout invasions may not be posing a significant threat to native fishes at this time. A major question in this system, however, concerns the future distribution of brook trout. We studied patterns of occurrence in a single year while acknowledging the dynamics of invasions of brook trout may occur on decadal time scales (Adams et al. 2002). Although a small amount of variation is expected in stream habitat from year to year, changes in fish distributions may be relatively stable (Strange and Habera 1998; Adams et al. 2002; Rieman et al. 2006). Over longer time periods, it is more likely that major changes to habitat that influence invasions could occur (Adams et al. 2001). In this context, 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).

The results of this work may have implications for the management of brook trout and the continued restoration of native fishes in Panther Creek. Given that

threats from brook trout invasion are uncertain and do not appear imminent, direct control may not be the most efficient action (Dunham et al. 2002). Instead, it may be advisable to continue monitoring to track invasions and potential impacts while conducting management to benefit native species. Two of the three factors here could be managed to possibly favor native species. Although we found that unconfined valley bottoms were most important to invasion of brook trout, this habitat feature is not amenable to management action. The weaker potential influences of water temperature and perhaps biotic resistance can be influenced by management. Obvious management actions to address these could include ensuring that natural water temperature regimes are not disrupted through human influences on stream habitats and the restoration of healthy populations of native fishes, including the full complement of migratory life histories (anadromy, long-distance riverine migrations) that existed historically for several native salmonines within Panther Creek. Ultimately, actions and alternatives for managing nonnative trout are embedded within a context of competing threats and opportunities that may not identify a single clear solution to a particular problem (Fausch et al. 2006), and Panther Creek appears to be no exception. Nonetheless, studies such as ours that identify factors influencing invasions on scales that are relevant to management planning (i.e., stream networks; Dunham et al. 2002; Fausch et al. 2002) can help to narrow the range of possibilities.

## Acknowledgments

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