

# Have brook trout (*Salvelinus fontinalis*) displaced bull trout (*Salvelinus confluentus*) along longitudinal gradients in central Idaho streams?

Bruce E. Rieman, James T. Peterson, and Deborah L. Myers

**Abstract:** Invasions of non-native brook trout (*Salvelinus fontinalis*) have the potential for upstream displacement or elimination of bull trout (*Salvelinus confluentus*) and other native species already threatened by habitat loss. We summarized the distribution and number of bull trout in samples from 12 streams with and without brook trout in central Idaho and used hierarchical regression analysis to consider whether brook trout have displaced bull trout along gradients of temperature and elevation. Brook trout generally were observed in higher numbers downstream of bull trout. Brook trout presence, number, and both temperature and elevation were important variables explaining the observed distributions and number of bull trout among streams. Our analyses support the hypothesis that brook trout have displaced bull trout, but results were highly variable and stream dependent. Although brook trout appeared to have displaced bull trout to higher elevations or colder temperatures, there was no clear influence on overall number of bull trout. Brook trout probably do influence bull trout populations and facilitate if not cause local extinctions, but threats probably vary strongly with environmental conditions. Bull trout in smaller streams could be more vulnerable than those in larger streams.

**Résumé :** Les invasions d'ombles de fontaine (*Salvelinus fontinalis*) non indigènes peuvent potentiellement déplacer vers l'amont ou éliminer les ombles à tête plate (*Salvelinus confluentus*) ou d'autres espèces indigènes déjà menacées par les pertes d'habitat. Nous avons compilé la répartition et l'abondance des ombles à tête plate dans des échantillons provenant de 12 cours d'eau avec ou sans ombles de fontaine dans le centre de l'Idaho; nous avons utilisé l'analyse de régression hiérarchique afin de voir si l'omble de fontaine a déplacé l'omble à tête plate le long de gradients de température et d'altitude. L'omble de fontaine se retrouve et s'observe généralement en plus grand nombre en aval de l'omble à tête plate. La présence et le nombre d'ombles de fontaine, ainsi que la température et l'altitude, sont des variables explicatives des répartitions observées et des nombres d'ombles à tête plate dans ces cours d'eau. Nos analyses appuient l'hypothèse qui veut que l'omble de fontaine déplace l'omble à tête plate, mais les résultats sont très variables et ils changent d'un cours d'eau à un autre. Bien que l'omble de fontaine semble avoir déplacé l'omble à tête plate vers les altitudes plus élevées ou les températures plus froides, il n'y a pas d'influence claire sur les nombres totaux d'ombles à tête plate. L'omble de fontaine influence vraisemblablement les populations d'ombles à tête plate et facilite, sans nécessairement les causer, des extinctions locales; le danger varie cependant fortement d'après les conditions du milieu. Il se peut que les ombles à tête plate des plus petits cours d'eau soient plus menacés que ceux des cours d'eau plus grands.

[Traduit par la Rédaction]

## Introduction

Distributions of ecologically similar fishes within individual rivers or streams are sometimes complementary (e.g., Quist et al. 2004). Two native chars (*Salvelinus leucomanis*, *Salvelinus malma*) found in Japan, for example, are distributed differently along distinctive altitudinal or thermal gradients (Fausch et al. 1994; Nakano et al. 1996; Taniguchi and

Nakano 2000). Although distributions may overlap, one species (*S. leucomanis*) predictably occurs in allopatry in warmer downstream water, with the other (*S. malma*) upstream in colder water. Similar patterns have been observed with an introduced char, brook trout, and either native cutthroat trout (*Oncorhynchus clarkii*) (Fausch 1989; Dunham et al. 1999, 2002a) or bull trout (Paul and Post 2001; Gunckel et al. 2002) in the western US and Canada. Brook

Received 17 December 2004. Accepted 30 July 2005. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 6 December 2005.  
J18466

**B.E. Rieman.**<sup>1</sup> USDA Forest Service, Rocky Mountain Research Station, Boise Aquatic Sciences Laboratory, 316 E. Myrtle, Boise, ID 83702, USA.

**J.T. Peterson.** US Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit, Warnell School of Forest Resources, University of Georgia, Athens, GA 30602, USA.

**D.L. Myers.** 8870 Purple Sage Road, Middleton, ID 83644, USA.

<sup>1</sup>Corresponding author (e-mail: [brieman@fs.fed.us](mailto:brieman@fs.fed.us)).

trout are typically found downstream of, and overlapping with, the native forms unless they are introduced to a headwater lake that essentially reverses the thermal gradient and direction of invasion from that in streams without lakes (Adams et al. 2001).

Maintenance of distinctive distributions may result from important differences in behavior and physiological responses controlling individual species habitat use and (or) their interactions along thermal gradients (Fausch 1989; Taniguchi et al. 1998; Dunham et al. 2002a). For native species that have coexisted within individual watersheds for thousands of years, selective segregation could minimize overlap. In the case of introduced and native species such as brook trout and cutthroat or bull trout, direct interaction could be more likely and could have important implications for conservation management (Dunham et al. 2002a).

Some believe that brook trout (and other introduced species) are one of the primary causes of decline in cutthroat trout (Young 1995; and see Dunham et al. 2002a for a review) and bull trout (Rieman and McIntyre 1993; Rieman et al. 1997) throughout the range of the latter two species. Anecdotal evidence of a widespread loss of native species precipitated by brook trout seems strong. Brook trout now occur in most of the US Geological Survey 5th code (~15 000 ha) watersheds of the interior Columbia River basin (Lee et al. 1997). Managers throughout the region have experimented with brook trout removal and installation of in-stream barriers in hopes of stemming the invasion (Kruse et al. 2001; Dunham et al. 2002a; Novinger and Rahel 2003).

The empirical evidence is less clear. Leary et al. (1993) demonstrated a progressive shift in numerical dominance from bull trout to brook trout at sampling sites in the zone of sympatry in Lolo Creek, Montana, but a population-level effect could not be discerned. Others have found evidence of direct interaction between brook trout and native species (Peterson et al. 2004a; Gunckel et al. 2002), but the results are variable (Dunham et al. 1999; Rich et al. 2003) and some invasions appeared to be stalled (Adams et al. 2002). From our own work (B.E. Rieman, unpublished data) and that of others, it appears that co-occurrence of brook trout and native salmonids within individual streams may be common (Adams 1994, 1999; Dambacher and Jones 1994). Although co-occurrence does not imply indefinite coexistence, it does suggest elimination of native forms is not inevitable throughout the range of streams accessible to brook trout (Dunham et al. 2002a).

Taniguchi and Nakano (2000), Fausch et al. (1994), and others have shown that the interactions of species may be strongly conditioned by temperature, which produces predictable patterns of occurrence along thermal gradients. The nature of those interactions, however, may be complex (Fausch 1989; Fausch et al. 1994), producing variation in patterns across distinctive environments. A full understanding of the processes and complexity involved will undoubtedly require carefully designed, manipulative experiments (e.g., Taniguchi and Nakano 2000; Peterson and Fausch 2003; Peterson et al. 2004a). A better documentation of patterns that exist in current distributions, however, can provide important clues about the generality and scale of interactions between species not possible with typical manipulative ex-

periments focused on habitat-unit or even stream-reach scales. If a strong interaction and displacement are important, we anticipate that elevation or thermal distribution limits of a native species will differ in the presence or absence of the introduced form.

In this work, we focused on patterns of occurrence of bull trout and their co-occurrence with brook trout. Bull trout is a species of particular concern in the northwestern United States (Rieman et al. 1997) and is currently listed as a threatened species under the US Endangered Species Act. The natural distribution of bull trout includes much of the northwestern US and Canada (Haas and McPhail 1991). Bull trout may express a variety of life history patterns, but in general, juveniles rear in natal or nearby streams for at least 1–3 years. Subsequently, some fish may migrate to a downstream river or lake and return to the natal stream to spawn for the first time at 5–7 years of age (Rieman and McIntyre 1993). Other resident fish may remain in the natal streams throughout life (Rieman and McIntyre 1993). Both life histories appear to be common throughout the range. In central Idaho, migratory fish may be found virtually anywhere in the large river systems they inhabit, but spawning adults and juvenile fish, as well as residents of all ages, occur almost exclusively in higher elevation, colder, headwater streams (Dunham and Rieman 1999; Dunham et al. 2003). Selong et al. (2001) have shown that temperatures associated with optimum growth efficiency of bull trout are lower than those for other salmonids of the region, including brook trout.

Brook trout have been widely established by introduction and subsequent invasion throughout the region beginning before 1900; they are now one of the most widely distributed species within the interior Columbia River basin (Lee et al. 1997). There has been relatively little work describing the life history of brook trout in the region, but they can mature much earlier (2–3 years of age; Adams 1999; Kennedy et al. 2003) than bull trout. Brook trout have been associated with low gradient streams and commonly have been found inhabiting lower elevations of streams occupied by other native salmonids (Adams 1999; Dunham et al. 1999; Paul and Post 2001). Adams (1999) demonstrated that stream gradient and swimming ability did not limit upstream distributions, but declining growth associated with reduced temperature could produce a demographic constraint to an upstream invasion. Nakano et al. (1998) and Gunckel et al. (2002) demonstrated that competition may be important between brook trout and bull trout, and Adams (1994) provided some evidence that an upstream displacement of the lower limit of bull trout distribution may occur in the presence of brook trout. Hybridization between brook trout and bull trout also has been widely documented where the two species overlap (Markle 1992; Leary et al. 1993; Kanda 1998). It appears that hybrids may be sterile or experience low survival (Leary et al. 1993; Kanda 1998). If brook trout mature earlier or occur at higher densities than bull trout, they could ultimately displace bull trout through a reproductive advantage (Leary et al. 1993).

Even if brook trout do not entirely displace bull trout, they could push the populations into more and more restricted distributions in headwater streams. Because smaller and more isolated bull trout populations are vulnerable to local extinction through other causes (Dunham and Rieman 1999),

even incomplete upstream displacement by brook trout could seriously threaten remnant bull trout populations.

To consider whether brook trout have had an important effect in streams of central Idaho, we used regression analysis to describe the occurrence and number of bull trout along elevation and thermal gradients in streams with and without brook trout. We hypothesized that bull trout would occur in strong association with either temperature or elevation, but that distribution and density would be altered in the presence of, or at higher densities of, brook trout. Conceivably, brook trout might simply replace (rather than displace) bull trout as bull trout distributions or numbers contract because of other causes such as habitat degradation. If that were the case, we would anticipate no consistent brook trout effect in the analysis. We predicted that if brook trout do displace bull trout, brook trout would either be associated with (i) a reduction in overall density or probability of occurrence of bull trout evidenced by a negative effect in the analysis or (ii) upstream displacement of fish, evidenced as an interaction effect (i.e., the relationship with temperature or elevation would change with brook trout).

## Materials and methods

### Study streams

Bull trout and brook trout occur in tributary streams of several of the larger river basins in south central Idaho. We selected streams that spanned the elevation range encompassing the lower limits of bull trout distributions observed in other work (Dunham and Rieman 1999) that were small enough to sample effectively by snorkeling and backpack electrofisher and that had no headwater lakes that might support a downstream rather than upstream invasion of brook trout. We chose streams known from recent sampling to support both brook trout and bull trout or bull trout alone. Other species that occurred at least occasionally included rainbow trout (*Oncorhynchus mykiss*), sculpin (*Cottus* spp.), and Chinook salmon (*Oncorhynchus tshawytscha*), all native forms. Because we could not find enough streams fitting our criteria within a single river basin, we selected streams distributed across three neighboring river basins (Fig. 1). All streams were located in mountainous terrain and predominantly forested watersheds. All streams were located in geologies of igneous and metamorphic origin with low conductance (<120  $\mu$ S). Average annual precipitation across sites has been ~40 cm, predominantly as snow. Study streams were small (mean width 3.8–9.2 m at summer low flow), cold (summer mean temperatures <12.4 °C), and supported modest amounts of large woody debris (~1–6 pieces·100 m<sup>-2</sup>) (Table 1). Observed densities of small bull trout among streams and sites varied by more than an order of magnitude; observed brook trout densities were more consistent where brook trout occurred (Table 1).

### Field sampling

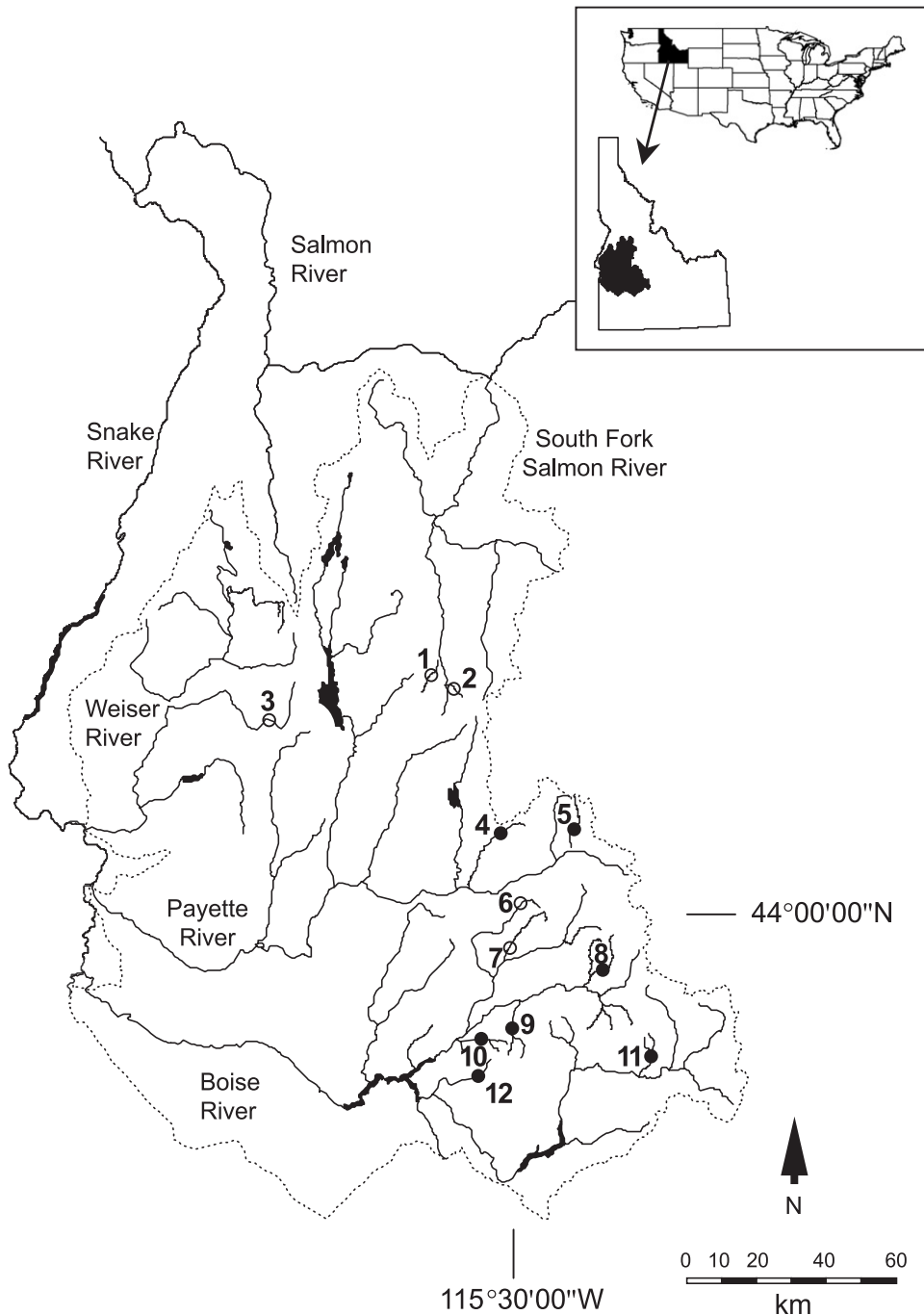
Our general approach was to distribute sampling sites throughout each study stream over the elevation ranges bounding the lower limits of the bull trout distribution. Sampling in 1996 was conducted as a pilot study to identify the general bounds of the species distributions and to insure that both species were either present or absent in the proposed

study streams as anticipated. We sampled 14 streams in 1996. In 1997, we dropped two streams from further consideration: one because of recent disruptive land use and the other because of logistical constraints. In 12 streams (five bull and brook trout; seven bull trout only) included in our final analysis, we sampled 11–31 sites above and below the anticipated lower bound of the bull trout distribution in each stream. We distributed sample sites to insure longitudinal representation, but access to some stream reaches was not possible. The number and distribution of sites ultimately sampled in each stream was a function of both systematic and logistic constraints. Sampling was conducted in late summer when streams were at or near base flow to minimize changes in channel characteristics and maximize sampling effectiveness.

Our sampling encompassed a minimum of 12 m of stream at each site. The distance sampled was varied to ensure that at least two pools (believed to be preferred habitat for bull trout) were included in each site; length of all sites averaged about 36 m. In 1996, we used snorkeling or electrofishing to sample fish at each site. Snorkeling was conducted during the day following the procedures established by Thurow (1994). In 1997, sampling was conducted exclusively by electrofishing following the procedures outlined by Rieman and McIntyre (1995). We used electrofishing for the final collection methods because detection efficiencies for daytime snorkeling are generally lower than those for electrofishing (Peterson et al. 2002) and because snorkelers were not confident in their discrimination between brook trout and bull trout that were not encountered at close range. The two species have similar coloration and markings and may be confused at a distance. We classified the two species based on presence (brook trout or hybrid) or absence (bull trout) of pigmentation in the dorsal fin and vermiculations on the back. Discrimination of the two species “in hand” can be highly accurate, although hybrids may be problematic (Adams 1994). To verify our classifications, we collected fin tissues from all putative bull trout, brook trout, or hybrids sampled in the field and submitted a blind sample for genetic analysis as described by Spruell et al. (2001) for confirmation. Field classification was accurate for species (i.e., no fish visually classified as bull trout were really brook trout and vice versa; Table 2), although hybrids were less clear. We limited our analysis to fish classified either as bull trout or brook trout and excluded hybrids from our analysis.

Total length was recorded for every fish sampled. We summarized numbers of bull trout observed as a density with the total number of bull trout smaller than 150 mm divided by area sampled. We summarized the number of all brook trout in a similar fashion. We limited our analysis to small bull trout because they are most closely associated with the elevation and thermal gradients that appear to define the extent of suitable natal environments or patches (Dunham and Rieman 1999; Dunham et al. 2002b). We also assumed that small fish are more likely to interact directly with brook trout or to represent the outcome of any past interaction between adults. We did not correct our samples for incomplete or variable detection probabilities of either species, so there is the possibility of some bias in our estimates relative to the true number of fish present in each sample site. However, preliminary studies indicated that electrofishing capture effi-

**Fig. 1.** Study streams located in central Idaho, USA: (1) Trail Creek, (2) Lodgepole Creek, (3) Little Weiser River, (4) Clear Creek, (5) Canyon Creek, (6) Crooked River, (7) Bear River, (8) Queens River, (9) Roaring River, (10) Sheep Creek, (11) Skeleton Creek, (12) Rattlesnake Creek. Open and solid circles represent streams with brook trout (*Salvelinus fontinalis*) present and absent, respectively. The dotted line outlines watershed boundaries depicted by the inset.



ciencies were similar and averaged 14.6% and 16.3% for brook trout and bull trout, respectively (J.T. Peterson, unpublished data).

At each site, we recorded the elevation and two channel characteristics, mean wetted width and density of large wood, that have been commonly associated with the distribution or number of bull trout (Dambacher and Jones 1997; Dunham and Rieman 1999; Rich et al. 2003). Elevation was recorded from standard topographic maps. Wetted width was measured at the top, bottom, and approximate midpoint of

each sample site and averaged. All large wood (>10 cm diameter; >3 m length) within or above the wetted channel was counted and summarized as total pieces divided by area sampled.

Thermographs were installed in each stream at three to seven sites. One thermograph was placed near the highest and lowest sample sites, and others were distributed between those two. Temperatures were recorded at 4 h intervals and summarized to a single mean for the period between 15 July and 31 August, an interval roughly symmetric about the



**Table 1.** The number of sampling sites ( $N$ ), mean, and standard error (in parenthesis) of selected characteristics for the 12 study streams in central Idaho.

Stream	$N$	Elevation (m)	Average stream temperature ( $^{\circ}\text{C}$ )	Mean wetted width (m)	Wood density (no.·100 $\text{m}^{-2}$ )	Small <sup>a</sup> bull trout ( <i>Salvelinus confluentus</i> ) density (no.·100 $\text{m}^{-2}$ )	Brook trout ( <i>Salvelinus fontinalis</i> ) density (no.·100 $\text{m}^{-2}$ )
Bear River	12	1562 (210)	10.85 (0.22)	6.41 (0.39)	1.49 (0.36)	0.36 (0.23)	0.50 (0.17)
Canyon Creek	14	1829 (380)	8.85 (0.03)	5.73 (0.67)	2.30 (0.76)	2.77 (0.60)	0
Clear Creek	30	1943 (150)	7.97 (0.11)	5.32 (0.30)	2.99 (0.25)	0.44 (0.12)	0
Crooked River	20	1813 (420)	9.28 (0.40)	6.61 (0.51)	1.44 (0.28)	0.73 (0.31)	0.40 (0.19)
Lodgepole Creek	16	1715 (150)	9.04 (0.16)	3.78 (0.22)	5.70 (1.00)	2.10 (0.53)	0.51 (0.28)
Little Weiser River	19	1577 (420)	11.41 (0.23)	5.34 (0.33)	0.91 (0.19)	0.54 (0.25)	0.16 (0.09)
Queens River	17	1699 (220)	9.55 (0.09)	9.16 (0.52)	1.51 (0.28)	0.17 (0.12)	0
Roaring River	15	1544 (340)	11.09 (0.26)	7.66 (0.24)	1.62 (0.56)	0.28 (0.14)	0
Rattlesnake Creek	20	1507 (340)	12.35 (0.33)	4.63 (0.15)	5.43 (1.03)	0.61 (0.25)	0
Sheep Creek	18	1507 (210)	11.60 (0.20)	5.49 (0.25)	2.22 (0.66)	0.13 (0.09)	0
Skeleton Creek	19	1892 (460)	9.49 (0.22)	4.95 (0.30)	4.53 (0.97)	1.55 (0.53)	0
Trail Creek	13	1678 (270)	10.21 (0.20)	5.34 (0.72)	5.10 (1.19)	1.16 (0.43)	0.18 (0.13)

<sup>a</sup><150 mm.

**Table 2.** Cross classification of brook trout (*Salvelinus fontinalis*), bull trout (*Salvelinus confluentus*), and brook trout  $\times$  bull trout hybrids identified by visual observation in the field and by genetic analysis to detect pure and hybrid fish.

Field class (visual)	True class (genetic)		
	Bull trout	Brook trout	Hybrid
Bull trout	33	0	2
Brook trout	0	17	3
Hybrid	1	0	25

warmest period in these streams. We estimated the mean temperature for each sample site by linear interpolation.

### Statistical analysis

We were primarily interested in the association of bull trout density and occurrence along gradients of temperature and elevation with varied occurrence and density of brook trout. We included wood density and mean stream width as “nuisance” variables in the analysis because they have also been associated with the density and detection of bull trout in streams and could confound the analysis if not accounted for in the models (Peterson et al. 2004b).

We conducted analyses with both estimated temperature and elevation for each sample site. Elevation is strongly correlated with temperature in these data, and we assumed that the influence of temperature was the primary mechanism explaining any patterns that emerged in association with either variable. Because we estimated temperature through interpolation, an error was introduced into the independent variable. Temperature estimates were not possible for sites outside the thermograph distribution, and thermograph failures also reduced the number of observations, so the analyses with temperature were more limited than those based on elevation. We contrasted the associations of temperature and elevation to provide the best model to evaluate brook trout effects, but we did not consider temperature or elevation simultaneously in any of the candidate models, with exception of the global model.

We considered both density and occurrence (presence–absence) of bull trout observed in our samples in separate analyses. Density may provide more information, but patterns of occurrence for locally rare or low-density species like bull trout may carry almost as much information (Royle and Nichols 2003) and often can be collected with lower cost. Absence also carries a different implication than low numbers from a conservation perspective (i.e., local extirpation vs. decline). We wanted to contrast the analyses to consider their consistency and the utility of alternative sampling approaches in future work.

We summarized data graphically to display general patterns along elevational gradients in streams with and without brook trout. We were concerned that observations within streams could be spatially autocorrelated, which would preclude the use of traditional regression techniques (Sokal and Rohlf 1995). Thus, we initially fit a global (i.e., all predictors) linear and logistic regression model of bull trout density and presence, respectively. An analysis of variance of the residuals from each global model indicated significant spatial autocorrelation for linear ( $F = 5.510$ ;  $df = 11, 198$ ;  $P < 0.001$ ) and logistic ( $F = 2.891$ ;  $df = 11, 198$ ;  $P = 0.002$ ) regression models. To account for the spatial autocorrelation, we examined relationships among sample site characteristics (Table 1) with hierarchical models. Hierarchical models differ from more familiar regression techniques in that autocorrelation among sample sites within streams, defined as lower level units (sample sites) within upper level units (streams), is incorporated by including random effects for lower level intercepts and slopes (Snijders and Bosker 1999). For our study, random effects are estimates of the variability of the effect of site-specific (lower level unit) characteristics on bull trout density and presence among streams (upper level units). For example, a stream temperature random effect estimates the extent to which the relationship between stream temperature and bull trout presence (i.e., the regression slope) varies from stream to stream. Fixed effects are estimates of the average effect of site-specific characteristics across streams and the effect of stream-level characteristics (e.g., mean brook trout density; Table 1) on bull trout density and presence.

**Table 3.** Biological interpretation of predictors used in candidate models relating the local and watershed-level factors influencing bull trout (*Salvelinus confluentus*) density and presence.

Predictor variables	Biological interpretation (hypothesis)
Elevation	Longitudinal position and local climate effects; potential surrogate for stream temperature
Mean temperature	Mean summer water temperature influencing behavior and physiology
Mean width, wood density	Channel characteristics influencing cover and the amount and capacity of local habitats
Mean brook trout ( <i>Salvelinus fontinalis</i> ) density	Direct interaction influencing density or occurrence through aggression, competition, or predation throughout the stream
Elevation × mean brook trout density	Direct interaction influencing bull trout density or occurrence through aggression, competition, or predation mediated by elevation
Mean temperature × mean brook trout density	Direct interaction influencing density or occurrence through aggression, competition, or predation mediated by temperature gradients

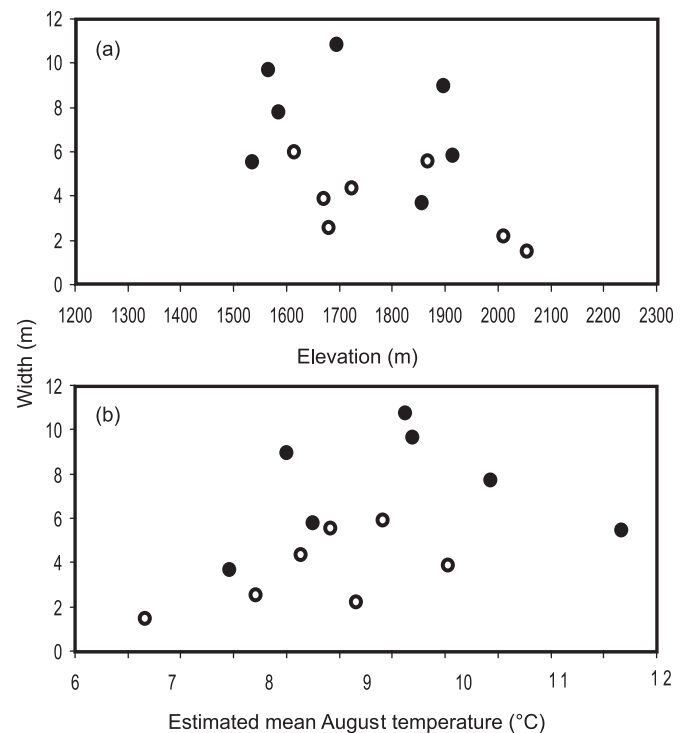
Prior to model selection, we evaluated goodness-of-fit for each candidate model by examining (i) normal probability plots of the lower (site) level residuals and (ii) plots of the empirical Bayes residuals by their corresponding  $\chi^2$  scores with  $Q - 1$  degrees of freedom, where  $Q$  is the number of upper (stream) level effects included in the candidate model (Bryk and Raudenbush 1992).

We used the information-theoretic approach, described by Burnham and Anderson (2002), to evaluate the relative plausibility of models relating sample site and stream characteristics to bull trout density and occurrence. For each response, we constructed a global model with all predictors (Table 3). From the global model, we constructed a subset of 15 candidate models. Six were based on temperature and six on elevation. Our primary hypotheses of interest reflected the influence of brook trout on the distribution or density of bull trout, so we first contrasted models with and without brook trout effects. A model with a brook trout interaction (brook trout × elevation; brook trout × temperature) always included the main effect (brook trout and elevation or temperature). We also contrasted models that systematically excluded temperature, elevation, and width and wood density to determine whether these variables were actually useful in explaining variability among sites and streams as anticipated. As explained above, width and wood density were not evaluated independently.

To assess the relative fit of each candidate model, we calculated Akaike's Information Criterion (AIC; Akaike 1973) with the small-sample bias adjustment (AIC<sub>c</sub>; Hurvich and Tsai 1989). AIC is an entropy-based measure used to compare candidate models for the same data (Burnham and Anderson 2002), with the best-fitting model having the lowest AIC<sub>c</sub>. The number of parameters used to estimate AIC<sub>c</sub> included the fixed effects, random effects, and random effect covariances when two or more random effects were included in the candidate model (Burnham and Anderson 2002). The relative plausibility of each candidate model (i.e., hypothesis) was assessed by calculating Akaike weights as described in Burnham and Anderson (2002). These weights can range from 0 to 1, with the most plausible candidate model having the highest weight.

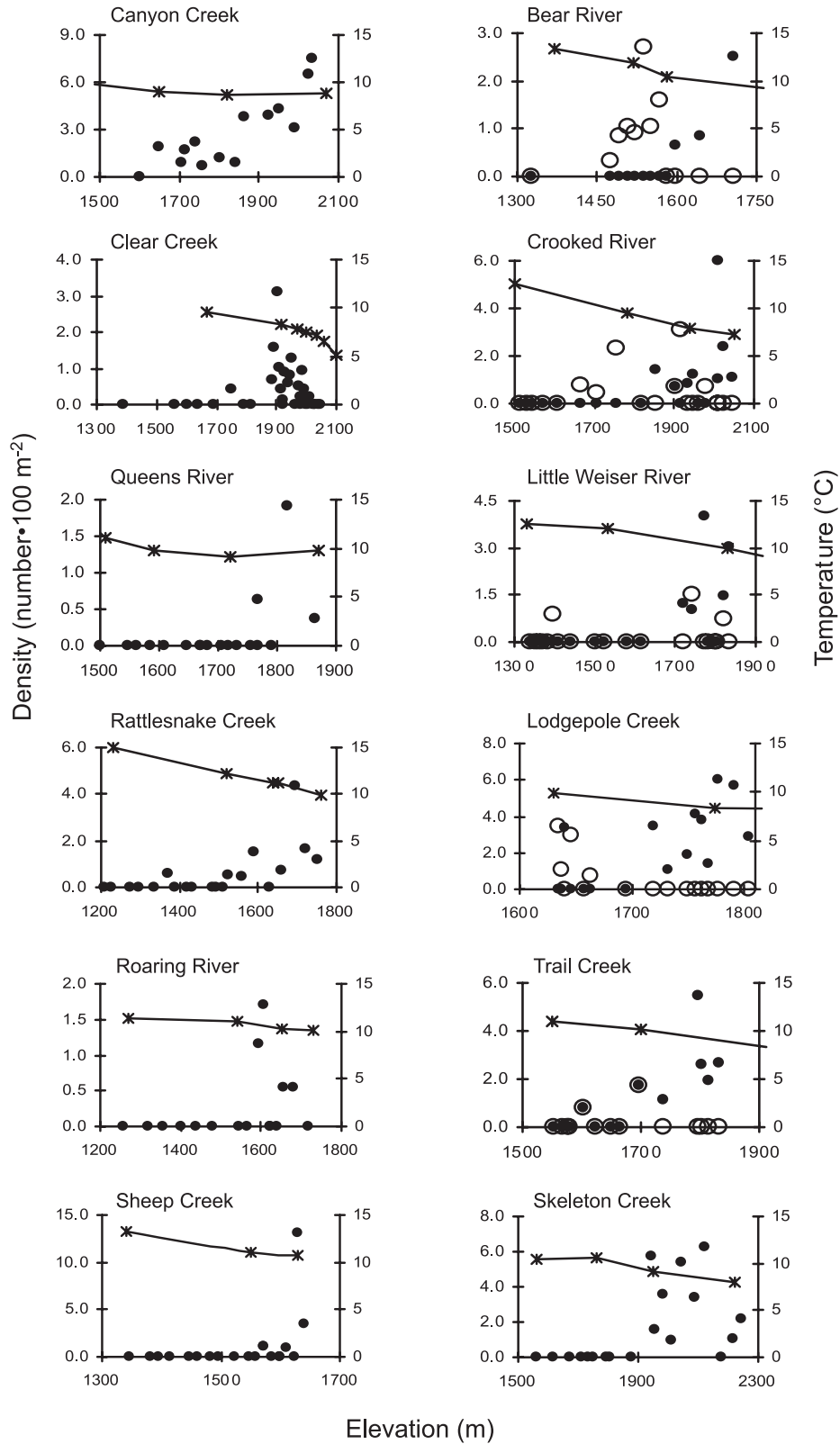
Model averaging, as a means of incorporating model selection uncertainty into parameter estimates, is not appropri-

**Fig. 2.** Stream width and (a) elevation or (b) estimated mean August temperature associated with the lowest observations of bull trout (*Salvelinus confluentus*) in 14 study streams with brook trout (*Salvelinus fontinalis*) present (open circles) or absent (solid circles) sampled by snorkeling and electrofishing in 1996.



ate for models consisting of fixed and random effects (K. Burnham, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA, personal communication). Therefore, instead of basing our inferences and predictions on a single best model, we report estimates of fixed and random effects for our confidence set of hierarchical linear and logistic models, as determined by the Akaike weights. A confidence set of models is analogous to a confidence interval for a parameter estimate and is a useful means of assessing model selection uncertainty (Burnham and Anderson 2002). Because the ratio of Akaike

**Fig. 3.** Observed densities of bull trout (*Salvelinus confluentus*) (solid circles) and brook trout (*Salvelinus fontinalis*) (open circles) and estimated mean August temperature (\*) by elevation in 12 study streams sampled by electrofishing 1997.



**Table 4.** Predictor variables, number of parameters ( $K$ ), log-likelihood ( $\text{Log}L$ ), Akaike's Information Criterion with the small-sample bias adjustment ( $\text{AIC}_c$ ),  $\Delta\text{AIC}_c$ , and Akaike weights ( $w_i$ ) for the set of candidate models ( $i$ ) for predicting bull trout (*Salvelinus confluentus*) density.

Candidate model	$K$	$\text{Log}L$	$\text{AIC}_c$	$\Delta\text{AIC}_c$	$w_i$
Elevation, mean brook trout ( <i>Salvelinus fontinalis</i> ) density, elevation $\times$ mean brook trout density	8	-119.14	255.00	0.00	0.648
Elevation	6	-122.22	256.86	1.86	0.256
Elevation, mean brook trout density	7	-122.17	258.89	3.89	0.093
Elevation, mean width, wood density, mean brook trout density, elevation $\times$ mean brook trout density	17	-115.17	267.55	12.55	0.001
Elevation, mean width, wood density	15	-117.93	268.34	13.34	0.001
Mean temperature, mean width, wood density	15	-118.69	269.87	14.87	0.000
Elevation, mean width, wood density, mean brook trout density	16	-117.74	270.32	15.32	0.000
Mean temperature, mean width, wood density, mean brook trout density	16	-118.39	271.61	16.61	0.000
Mean temperature, mean width, wood density, mean brook trout density, mean temperature $\times$ mean brook trout density	17	-117.65	272.51	17.51	0.000
Mean temperature	6	-131.71	275.84	20.84	0.000
Mean temperature, mean brook trout density, mean temperature $\times$ mean brook trout density	8	-130.29	277.31	22.31	0.000
Mean temperature, mean brook trout density	7	-131.44	277.44	22.44	0.000
Mean temperature, elevation, mean width, wood density, mean brook trout density, mean temperature $\times$ mean brook trout density, elevation $\times$ mean brook trout density	24	-113.24	281.00	26.00	0.000
Mean width, wood density, mean brook trout density	11	-142.03	307.39	52.39	0.000
Mean brook trout density	4	-168.78	345.77	90.76	0.000

**Note:** Akaike weights are interpreted as relative plausibility of candidate models.

weights for two candidate models can be used to assess the degree of evidence for one model over another (Anderson et al. 2000), the confidence set of models included only those candidate models with Akaike weights that were within 10% of the largest weight (Thompson and Lee 2000), which is similar to the general rule of thumb (i.e., 1/8 or 12%) suggested by Royall (1997) for evaluating strength of evidence.

To allow for ease of interpretation of the relative magnitude of fixed and random effects, we plotted empirical Bayes (shrinkage) estimates (Snijders and Bosker 1999) of the relationship between site-level characteristics and bull trout density and presence for each stream using models within the confidence set. The precision of each fixed and random effect was estimated by computing 90% confidence intervals based on a  $t$  statistic with  $n - 1$  degrees of freedom (Littell et al. 1996). The relative importance of individual predictor variables was estimated as the sum of Akaike weights for candidate models in which each predictor occurred (Burnham and Anderson 2002).

## Results

In 1996, our lowest observations of bull trout ranged from about 1500 to 2000 m elevation (Fig. 2) in the streams we sampled. Mean temperatures ranged from 6.7 to 11.7 °C. The lowest observations and warmest temperatures associated with our observations of bull trout were in streams without brook trout. The streams with brook trout and bull trout tended to be narrower than the streams with bull trout alone.

In 1997, we observed bull trout more frequently in upper than in lower reaches sampled in each stream. When brook trout were present in a stream, we generally observed them

in higher densities in the lower reaches we sampled (Fig. 3). Temperatures generally declined with elevation across streams, although the slope varied and in some cases temperature changed little or even increased slightly between a downstream and upstream thermograph.

## Statistical analyses

### Bull trout density

An examination of the normal probability plot of lower-level residuals from all candidate linear models relating site-specific characteristics and mean brook trout density to bull trout density indicated that the residuals departed from expected (i.e., the plots were curvilinear rather than linear). To normalize these data, we natural log transformed the data and refit the candidate models. An examination of normal probability plots of lower-level residuals and the  $\chi^2$  plots of the empirical Bayes residuals from each candidate model fit with the transformed data indicated that all of the models fit adequately.

The most plausible model of bull trout density contained elevation, mean brook trout density, and an elevation by mean brook trout density interaction and was 2.5 times more likely than the next best approximating model, which contained elevation alone (Table 4). The confidence set of models included these two and a third model that included elevation and mean brook trout density.

Elevation was positively related to small bull trout density across models (Table 5), but the relationship was highly variable among streams. The elevation random effect from the elevation-only model suggested that the influence of elevation (i.e., the parameter estimate) varied by more than 73% ( $\sqrt{3.148/2.420}$ ) among streams (Table 5). The smaller



**Table 5.** Estimates (standard error in parentheses) of fixed and random effects for confidence set of hierarchical linear models of bull trout (*Salvelinus confluentus*) density.

Parameter estimate	Estimate	90% confidence interval	
		Lower	Upper
<b>Elevation, mean brook trout (<i>Salvelinus fontinalis</i>) density, elevation × mean brook trout density</b>			
Fixed effect			
Intercept	-2.172 (0.847)	-3.561	-0.783
Elevation	1.510 (0.536)	0.631	2.388
Mean brook trout density	-10.472 (3.928)	-16.913	-4.031
Elevation × mean brook trout density	0.649 (0.246)	2.447	10.530
Random effect			
Intercept	4.228 (1.091)	2.439	6.016
Elevation	1.737 (0.691)	0.604	2.871
Residual	0.158		
<b>Elevation</b>			
Fixed effect			
Intercept	-3.653 (0.910)	-5.145	-2.161
Elevation	2.420 (0.565)	1.493	3.347
Random effect			
Intercept	8.046 (0.656)	6.971	9.122
Elevation	3.148 (0.417)	2.464	3.832
Residual	0.159		
<b>Elevation, mean brook trout density</b>			
Fixed effect			
Intercept	-3.614 (0.899)	-5.089	-2.139
Elevation	2.409 (0.561)	1.488	3.329
Mean brook trout density	-0.119 (0.275)	-0.571	0.332
Random effect			
Intercept	7.823 (1.905)	4.699	10.947
Elevation	3.098 (0.614)	2.091	4.106
Residual	0.159		

**Note:** Random effect estimate is a variance component.

elevation random effect in the model containing the elevation by mean brook trout density interaction (1.737) compared with the elevation random effect in the model without brook trout (3.148), suggested that 45% of this variation was attributed to mean brook trout density. Nonetheless, the remaining variation among streams was relatively high (Fig. 4a). The relationship between mean brook trout density and bull trout density was negative. The parameter estimate for mean brook trout density in the model without the elevation × brook trout interaction, however, was relatively small and imprecise, whereas the estimate was much larger and relatively precise for the model with the interaction.

Model predictions based on the model containing elevation, mean brook trout density, and their interaction (Table 5) indicated that bull trout density increased with elevation across a range of brook trout densities (Fig. 4b). At lower elevation sites (<1.5 km), our model predicted that bull trout were only present (i.e., density >0) when brook trout were absent in the stream. However, at higher elevation sites (>1.7 km), bull trout density was predicted to be greater in streams with relatively high brook trout densities.

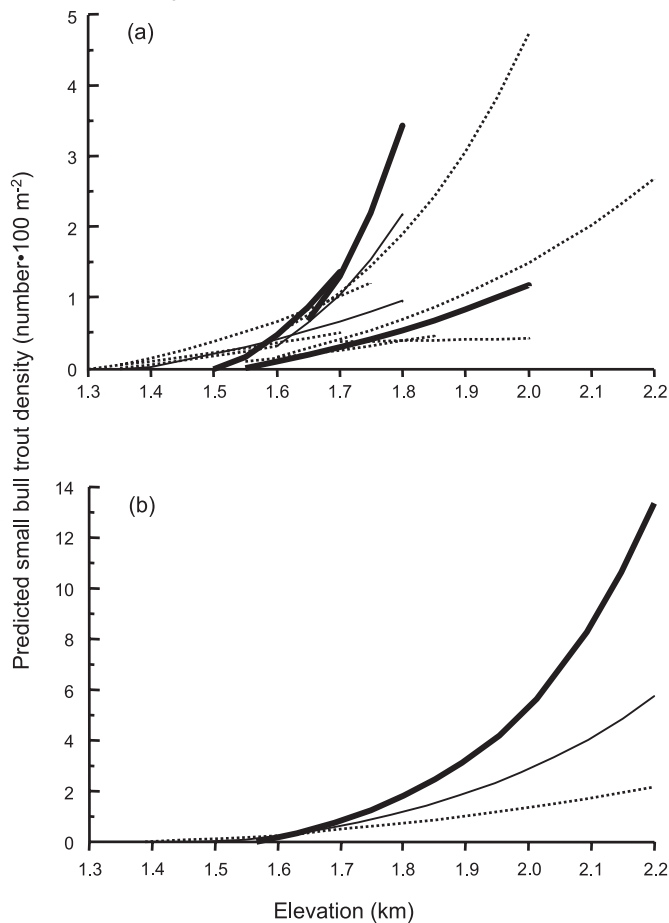
#### **Bull trout presence**

The most plausible logit model of bull trout presence contained mean temperature, mean brook trout density, and a

temperature by brook trout density interaction, but was only 1.06 times more likely than the next best approximating model that contained elevation only (Table 6). The confidence set of models included these two models and four others that contained either (i) temperature, mean brook trout density, and their interaction or (ii) elevation, mean brook trout density, and their interaction.

The confidence set of models indicated that bull trout presence was negatively and positively related to temperature and elevation, respectively. However, the temperature random effect in the temperature-only model suggested that the influence of temperature on bull trout presence varied as much as 54% among streams, whereas elevation varied as much as 40% among streams in the elevation-only model (Table 7). The smaller random effects in models containing the temperature by mean brook trout density and elevation by mean brook trout density interactions compared with models without interactions suggested that 24% and 51% of the variation in temperature and elevation effects, respectively, was attributed to mean brook trout density (Table 7). The remaining variation among streams, however, was relatively high when the brook trout density interaction was included in both the temperature and elevation models (Figs. 5a and 5b, respectively). Bull trout presence was positively and negatively related to brook trout density among

**Fig. 4.** Empirical Bayes estimates of the relationship between elevation and juvenile bull trout (*Salvelinus confluentus*) density for each of 12 study streams (a) and the average relationship between elevation and juvenile bull trout density for three levels of brook trout (*Salvelinus fontinalis*) density (b). Thin broken lines indicate no brook trout in the stream, and thin and heavy solid lines indicate streams with brook trout densities less than and greater than  $0.4 \cdot 100 \text{ m}^{-2}$ , respectively. Stream-specific relationships in (a) are only plotted for the sampled range of elevations. The average relationship in (b) is based on the best-fitting hierarchical model of juvenile bull trout abundance.



models in the confidence set (Table 7), and parameter estimates were relatively imprecise (Table 7).

Model predictions based on the hierarchical logit model containing temperature, mean brook trout density, and their interaction indicated that the probability of bull trout presence increased with decreasing temperature across a range of brook trout densities (Fig. 6a). At temperatures  $>9^\circ\text{C}$ , the model suggested that the probability of bull trout presence was highest when brook trout were absent in the stream, but at colder temperatures ( $<9^\circ\text{C}$ ) the probability of bull trout presence was highest in streams with high brook trout density ( $\geq 0.4 \cdot 100 \text{ m}^{-2}$ ). In contrast, model predictions of bull trout presence based on the model containing elevation, mean brook trout density, and their interaction indicated the probability of presence increased with elevation across a range of brook trout densities (Fig. 6b). At relatively low elevations ( $<1600 \text{ m}$ ), the probability of presence was highest

when brook trout were absent, whereas at high elevations the probability was highest when brook trout were abundant.

### Contrasting models

For the linear models of bull trout density, the Akaike importance weights for elevation, mean brook trout density, and their interaction were more than 100 times greater than those of temperature, mean width, wood density, and the temperature by mean brook trout density interaction, which indicated that there was stronger evidence for the models with elevation (Table 8). In contrast, in the models of bull trout presence, importance weights for elevation and temperature were similar, indicating there was insufficient data to discern which was the more important predictor (Table 8). The brook trout effects were also more ambiguous in this group of models, suggesting the loss of information associated with the use of bull trout occurrence rather than density may be important.

### Discussion

Samples of bull trout and brook trout exhibited the anticipated longitudinal patterns in density and occurrence. These patterns were generally consistent with other observations of complementary distributions of two or more ecologically similar salmonids occurring in mountain streams. Either temperature or elevation was the single most important variable explaining the distribution of bull trout. Brook trout were more abundant downstream of bull trout, and a brook trout effect was apparent in our models. Our results support the hypothesis that brook trout displace bull trout, although the results were highly variable, stream dependent, and uncertain at the scale of the entire population. Our results are also consistent with the hypothesis that a thermal gradient may influence both the patterns of occurrence of each species as well as their interactions.

A brook trout effect was included in the most plausible models in our analyses, although our results did not suggest the effect was dramatic or easily generalized. Brook trout density and interactions with elevation or estimated temperature were consistently important variables, but random effects (e.g., stream-level effects) were large, and predicted responses varied among streams. The coefficients associated with brook trout density also changed sign or varied in weight and precision among the most plausible models for either bull trout density or presence. The inclusion of the interaction terms helped clarify the response. Brook trout were associated with reduced density or probability of occurrence of bull trout at lower elevations or warmer temperatures, but also with higher bull trout density and probability of occurrence at higher elevations or colder temperatures. Higher probability of occurrence could be due to higher overall density because detection is a function of density and capture efficiency (Bayley and Peterson 2001). So on average, brook trout did appear to have displaced bull trout upstream, but they were not associated with a strong negative change in overall bull trout density or occurrence. Variable associations between bull trout and brook trout suggest that some (unknown) watershed-level factor(s) may influence overall fish production, while the distribution within a watershed is influenced by brook trout. The unknown factor(s) may be re-

**Table 6.** Predictor variables, number of parameters ( $K$ ), log-likelihood ( $\text{Log}L$ ), Akaike's Information Criterion with the small-sample bias adjustment ( $\text{AIC}_c$ ),  $\Delta\text{AIC}_c$ , and Akaike weights ( $w_i$ ) for the set of candidate models ( $i$ ) for predicting bull trout (*Salvelinus confluentus*) presence.

Candidate model	$K$	$\text{Log}L$	$\text{AIC}_c$	$\Delta\text{AIC}_c$	$w_i$
Mean temperature, mean brook trout ( <i>Salvelinus fontinalis</i> ) density, mean temperature $\times$ mean brook trout density	8	-280.99	578.70	0.00	0.284
Elevation	6	-283.20	578.82	0.12	0.267
Elevation, mean brook trout density, elevation $\times$ mean brook trout density	8	-281.70	580.11	1.41	0.140
Mean temperature	6	-283.89	580.19	1.49	0.135
Elevation, mean brook trout density	7	-283.19	580.94	2.24	0.092
Mean temperature, mean brook trout density	7	-283.31	581.18	2.48	0.082
Elevation, mean width, wood density, mean brook trout density, elevation $\times$ mean brook trout density	17	-279.17	595.54	16.83	0.000
Elevation, mean width, wood density	15	-281.78	596.04	17.34	0.000
Elevation, mean width, wood density, mean brook trout density	16	-281.19	597.22	18.52	0.000
Mean brook trout density	4	-296.83	601.86	23.16	0.000
Mean width, wood density, mean brook trout density	11	-291.17	605.68	26.98	0.000
Mean temperature, mean width, wood density, mean brook trout density, mean temperature $\times$ mean brook trout density	17	-284.35	605.91	27.21	0.000
Mean temperature, elevation, mean width, wood density, mean brook trout density, elevation $\times$ mean brook trout density, mean temperature $\times$ mean brook trout density	24	-277.17	608.87	30.17	0.000
Mean temperature, mean width, wood density	15	-289.50	611.48	32.78	0.000
Mean temperature, mean width, wood density, mean brook trout density	16	-297.27	629.37	50.67	0.000

**Note:** Akaike weights are interpreted as relative plausibility of candidate models.

lated to geology, soil productivity (e.g., Thompson and Lee 2000), or large-scale habitat features that were not included in our models.

The biological significance of displacement at the stream or local population level is not apparent in our data. We did not conduct complete population estimates, but the lack of an obvious change in densities suggests that brook trout have not had a dramatic influence on the absolute size of the bull trout populations in these streams. They may, however, constrain the area or size of the habitat that might be occupied by bull trout. Gunckel et al. (2002) demonstrated resource competition between brook trout and bull trout and concluded that brook trout are likely to displace bull trout when resources are scarce. They predicted that displaced bull trout would either be lost from the stream or be forced upstream into higher densities where intraspecific competition might reduce growth across the population. Our results suggest that the upstream displacement is likely, but they do not point to population-level effects.

Such an effect may still be important. Restriction of bull trout to a smaller area and a subsequent reduction in growth might reduce the resilience of a population and increase vulnerability to extirpation associated with environmental variation or catastrophic events. A reduction in available area might also reduce the extent and variability or complexity of habitats available to bull trout and thus restrict the number or extent of internal refugia available to populations experiencing extreme disturbances (e.g., fires and floods; Rieman and Clayton 1997; Dunham and Rieman 1999). Dunham and Rieman (1999) demonstrated a strong association between persistence of local bull trout populations and the size of local habitat patches. Habitat patches were defined as the watershed area above the point where temperatures become low enough to consistently support bull trout spawning and juve-

nile rearing. Morita and Yamamoto (2002) demonstrated a similar pattern for whitespotted char (*Salvelinus leucomaenis*) isolated in small streams by erosion control dams. In each case, local extinctions might be explained by a variety of genetic or demographic processes that follow from restriction in population size or from the demographic response suggested above. In either case, a population that is less resilient is more prone to either deterministic extinction or stochastic variation near the extinction threshold.

The magnitude of constraint in patch size implied by our data is not obvious, but some simple calculations provide perspective. Based on the most plausible models, it appears that the average displacement of the lower limit in bull trout distributions might be on the order of 100–200 m in elevation. The relative significance of that displacement will depend largely on the length of stream and channel gradients above that point. For example, in a stream with a mean gradient of 5% that initially had 10 km of habitat available for bull trout, an upstream displacement 200 m in elevation would represent a loss of 4 km (40%) of available stream; the loss would be greater in area if the stream becomes narrower upstream. In relative terms, the loss would be proportionally greater in smaller patches or with lower stream gradients and less in larger patches or with higher gradients. Such losses could equate to substantial increases in the extinction risk in patches that were already small, but might be insignificant for those that were large (Dunham and Rieman 1999).

Rich et al. (2003) provided evidence that brook trout and bull trout were more likely to coexist in larger streams, whereas brook trout may have eliminated bull trout in smaller streams. Brook trout also appear more likely to use small streams than large ones (Rich 1996), while bull trout appear less likely to persist in smaller streams (Rieman and

**Table 7.** Estimates (standard error in parentheses) of fixed and random effects from best-fitting candidate hierarchical logistic regression models of bull trout (*Salvelinus confluentus*) presence.

Parameter estimate	Estimate	90% confidence interval	
		Lower	Upper
<b>Mean temperature, mean brook trout (<i>Salvelinus fontinalis</i>) density, mean temperature × mean brook trout density</b>			
Fixed effect			
Intercept	10.506 (3.775)	4.315	16.696
Mean temperature	-1.043 (0.364)	-1.640	-0.446
Mean brook trout density	28.946 (17.077)	0.940	56.952
Mean temperature × mean brook trout density	-3.109 (1.767)	-6.006	-0.211
Random effect			
Intercept	53.354 (8.623)	39.212	67.496
Mean temperature	0.466 (0.075)	0.343	0.590
<b>Elevation</b>			
Fixed effect			
Intercept	-21.313 (3.937)	-27.770	-14.856
Elevation	12.455 (2.380)	8.552	16.358
Random effect			
Intercept	63.295 (31.807)	11.132	115.458
Elevation	24.897 (11.473)	6.081	43.714
<b>Elevation, mean brook trout density, elevation × mean brook trout density</b>			
Fixed effect			
Intercept	-16.136 (3.907)	-22.544	-9.727
Elevation	9.369 (2.446)	5.357	13.380
Mean brook trout density	-45.039 (21.867)	-80.901	-9.178
Elevation × mean brook trout density	26.754 (13.317)	4.915	48.594
Random effect			
Intercept	21.967 (14.330)	0.000	45.469
Elevation	12.165 (8.450)	0.000	26.023
<b>Mean temperature</b>			
Fixed effect			
Intercept	14.162 (3.262)	8.812	19.511
Mean temperature	-1.440 (0.326)	-1.975	-0.904
Random effect			
Intercept	61.316 (12.828)	40.279	82.353
Mean temperature	0.610 (0.165)	0.339	0.881
<b>Elevation, mean brook trout density</b>			
Fixed effect			
Intercept	-21.475 (3.988)	-28.015	-14.936
Elevation	12.658 (2.429)	8.675	16.642
Mean brook trout density	-1.051 (2.030)	-4.380	2.279
Random effect			
Intercept	64.350 (29.58)	15.842	112.857
Elevation	26.224 (8.32)	12.586	39.861
<b>Mean temperature, mean brook trout density</b>			
Fixed effect			
Intercept	14.624 (3.442)	8.979	20.269
Mean temperature	-1.452 (0.337)	-2.004	-0.900
Mean brook trout density	-1.985 (1.923)	-5.138	1.168
Random effect			
Intercept	70.910 (13.72)	48.416	93.404
Mean temperature	0.670 (0.14)	0.445	0.895

**Note:** Random effect estimate is a variance component.



**Table 8.** Akaike importance weights for parameters from candidate models of bull trout (*Salvelinus confluentus*) density and presence.

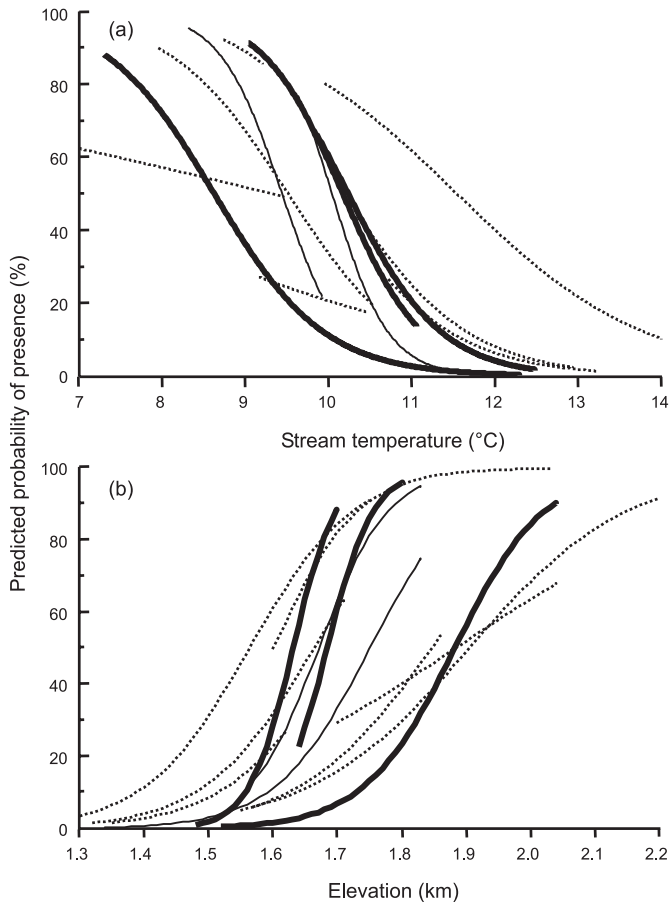
Model parameter <sup>a</sup>	No. of candidate models	Importance weights	
		Small <sup>b</sup> bull trout density	Bull trout presence
Elevation	7	0.999	0.500
Mean temperature	7	0.001	0.500
Mean width	8	0.003	0.000
Wood density	8	0.003	0.000
Mean brook trout ( <i>Salvelinus fontinalis</i> ) density	11	0.743	0.598
Elevation × mean brook trout density	3	0.649	0.140
Mean temperature × mean brook trout density	3	0.000	0.284

**Note:** Importance weights were estimated as the sum of Akaike weights from individual candidate models containing the parameter.

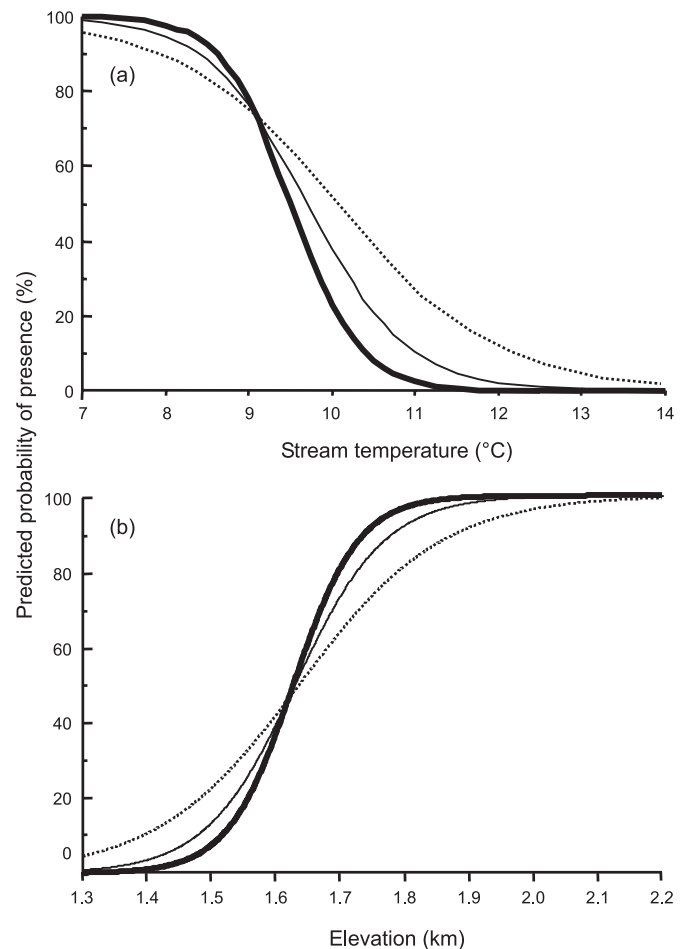
<sup>a</sup>The intercept was included in all candidate models; hence, the importance weight equals one.

<sup>b</sup><150 mm.

**Fig. 5.** Empirical Bayes estimates of the relationship between temperature (a) and elevation (b) and the probability of bull trout (*Salvelinus confluentus*) presence for each of 12 study streams. Thin broken lines indicate no brook trout (*Salvelinus fontinalis*) in the stream, and thin and heavy solid lines indicate streams with brook trout densities less than and greater than 0.4·100 m<sup>-2</sup>, respectively. Stream-specific lines are only plotted for the sampled range of temperatures.



**Fig. 6.** The average relationship between temperature (a) and elevation (b) and the probability of bull trout (*Salvelinus confluentus*) presence for three levels of mean brook trout (*Salvelinus fontinalis*) density. Thin broken lines indicate no brook trout in the stream, and thin and heavy solid lines indicate streams with brook trout densities less than and greater than 0.4·100 m<sup>-2</sup>, respectively. Predictions were based on best-fitting hierarchical models of bull trout presence.



McIntyre 1995; Dunham and Rieman 1999). It may be that brook trout hold some ecological advantage in small streams. Because small streams are associated with small patches (Rieman and McIntyre 1995), it might also be that any interaction and upstream displacement of bull trout by brook trout ultimately holds greater consequences in terms of patch-level extinction processes in small streams than in large ones.

Our results add to evidence that introduced brook trout can displace native salmonids, including bull trout. Invasion could influence the persistence of populations even if displacement is incomplete, but the population-level consequences of these effects remain an important question. In some systems, local extinctions of native species have followed the establishment of brook trout (M. Enk, US Forest Service, 1101 15th Street North, Great Falls, MT 59405, USA, personal communication), while the species coexist in others. In our streams, we found evidence that brook trout have had an effect, but these bull trout populations have obviously persisted with modest numbers of individuals. Because we nonrandomly selected study streams where we knew bull trout occurred, our observations may not represent the future for all populations threatened by brook trout invasion. It may be that the displacement predicted from our models is a measure of a “debt of extinction” yet to be paid (Hanski 1996) or of the resistance of bull trout on the brook trout invasion front.

Brook trout probably do displace bull trout and may well catalyze if not directly cause local extinctions. Obviously, from a native species-conservation perspective, further introductions of brook trout or management that favors their expansion into the range of native species (e.g., the stocking or maintenance of populations in headwater lakes; Adams et al. 2001) is imprudent. Despite the obvious threats, however, our work and other studies (see Dunham et al. 2002a for a review) indicate the influence of brook trout at both a habitat scale and stream or population scales is highly variable. The complete elimination of bull trout or other species is not a foregone conclusion. Brook trout have not invaded all of the habitats accessible to them (Adams et al. 2002) or eliminated native species in many places where they co-occur (Dunham and Rieman 1999; Rich et al. 2003). Longer-term studies also indicate that some populations of native salmonids can persist in the face of invasions and habitat loss (Strange and Habera 1998; Meyer et al. 2003).

Continued efforts to understand the population and landscape-level patterns of brook trout invasion, species displacement, and subsequent local extinctions could prove critical to management that must prioritize limited conservation resources or controversial control measures. Manipulative experiments will be important to understand the underlying mechanisms in any detail. However, broadly replicated studies and newer statistical methods examining the patterns of distribution within streams distributed over large regions could add substantially to knowledge of where threats exist. Our results suggest that even simple occurrence data (as opposed to density) can be useful for detecting important patterns; although some information is lost, the potential to sample extensively could help clarify this issue.

## Acknowledgements

D. Horan, K. Gillogly, P. Hanna, J. McGlathery, S. Adams, and A. Rosenberger provided important help with data collection, summary, and supporting literature. P. Spruell conducted the genetic analysis of potential hybrids. J. Dunham, D. Isaak, W. Thompson, K. Fausch, and two anonymous reviewers provided comments that improved the manuscript. This work was supported by USDA Forest Service, Rocky Mountain Research Station and US Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit.

## References

- Adams, S.B. 1994. Bull trout distribution and habitat use in the Weiser River drainage, Idaho. M.S. thesis, University of Idaho, Moscow, Idaho.
- Adams, S.B. 1999. Mechanisms limiting a vertebrate invasion: brook trout in mountain streams of the northwestern U.S.A. Ph.D. thesis, University of Montana, Missoula, Mont.
- Adams, S.B., Frissell, C.A., and Rieman, B.E. 2001. Geography of invasion in mountain streams: consequences of headwater lake fish introductions. *Ecosystems*, **4**(4): 296–307.
- Adams, S.B., Frissell, C.A., and Rieman, B.E. 2002. Changes in distribution of nonnative brook trout in an Idaho drainage over two decades. *Trans. Am. Fish. Soc.* **131**: 561–568.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. *In* Second International Symposium on Information Theory. *Edited by* B.N. Petrov and F. Csaki. Akademiai Kiado, Budapest, Hungary. pp. 267–281.
- Anderson, D.R., Burnham, K.P., and Thompson, W.L. 2000. Model hypothesis and testing: problems, prevalence, and an alternative. *J. Wildl. Manag.* **64**: 912–923.
- Bayley, P.B., and Peterson, J.T. 2001. Species presence for zero observations: an approach and an application to estimate probability of occurrence of fish species and species richness. *Trans. Am. Fish. Soc.* **130**: 620–633.
- Bryk, A.S., and Raudenbush, S.W. 1992. Hierarchical linear models: applications and data analysis methods. Sage, Thousand Oaks, Calif.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- Dambacher, J.M., and Jones, K. 1997. Stream habitat of juvenile bull trout populations in Oregon and benchmarks for habitat quality. *In* Friends of the Bull Trout Conference Proceedings, Calgary, Alberta, 5–7 May 1994. *Edited by* W.C. MacKay, M.K. Brewin, and M. Monita. Bull Trout Task Force (Alberta), Trout Unlimited Canada, Calgary. pp. 353–360.
- Dunham, J.B., and Rieman, B.E. 1999. Metapopulation structure of bull trout: influences of habitat size, isolation, and human disturbance. *Ecol. Appl.* **9**: 642–655.
- Dunham, J.B., Peacock, M.M., Rieman, B.E., Schroeter, R.E., and Vinyard, G.L. 1999. Local and geographic variability in the distribution of stream living Lahontan cutthroat trout. *Trans. Am. Fish. Soc.* **128**: 875–889.
- Dunham, J.B., Adams, S.B., Schroeter, R.E., and Novinger, D.C. 2002a. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. *Rev. Fish Biol. Fish.* **12**: 373–391.

- Dunham, J.B., Rieman, B.E., and Peterson, J.T. 2002b. Patch-based models to predict species occurrence: lessons from salmonid fishes in streams. *In* Predicting species occurrences: issues of scale and accuracy. *Edited by* J.M. Scott, P.J. Heglund, M. Morrison, M. Raphael, J. Haufler, and B. Wall. Island Press, Covelo, Calif. pp. 327–334.
- Dunham, J.B., Rieman, B.E., and Chandler, G.L. 2003. Influences of temperature and environmental variables on the distribution of bull trout at the southern margin of its range. *N. Am. J. Fish. Manag.* **23**: 894–904.
- Fausch, K.D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook char and other salmonids in streams? *Physiol. Ecol. Jpn. Spec.* **1**: 303–322.
- Fausch, K.D., Nakano, S., and Ishigaki, K. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. *Oecologia*, **100**: 1–12.
- Gunckel, S.L., Hemmingsen, A.R., and Li, J.L. 2002. Effect of bull trout and brook trout interactions on foraging habitat, feeding behavior, and growth. *Trans. Am. Fish. Soc.* **131**(6): 1119–1130.
- Haas, G.R., and McPhail, J.D. 1991. Systematics and distribution of Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*) in North America. *Can. J. Fish. Aquat. Sci.* **48**: 2191–2211.
- Hanski, I.A. 1996. Metapopulation dynamics: from concepts and observations to predictive models. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* I.A. Hanski and M.E. Gilpin. Academic Press, New York. pp. 69–71.
- Hurvich, C.M., and Tsai, C. 1989. Regression and time series model selection in small samples. *Biometrika*, **76**: 297–307.
- Kanda, N. 1998. Genetics and conservation of bull trout: comparison of population genetic structure among different genetic markers and hybridization with brook trout. Ph.D. thesis, University of Montana, Missoula, Mont.
- Kennedy, B.M., Peterson, D.P., and Fausch, K.D. 2003. Different life histories of brook trout populations invading mid-elevation and high-elevation cutthroat trout streams in Colorado. *West. N. Am. Nat.* **63**(2): 215–223.
- Kruse, C.G., Hubert, W.A., and Rahel, F.J. 2001. An assessment of headwater isolation as a conservation strategy for cutthroat trout in the Absaroka Mountains of Wyoming. *Northwest Sci.* **75**: 1–11.
- Leary, R.F., Allendorf, F.W., and Forbes, S.H. 1993. Conservation genetics of bull trout in the Columbia and Klamath river drainages. *Conserv. Biol.* **7**(4): 856–865.
- Lee, D., Sedell, J., Rieman, B., Thurow, R., and Williams, J. 1997. Assessment of the condition of aquatic ecosystems in the Interior Columbia River Basin. Chapter 4. *In* An assessment of ecosystem components in the Interior Columbia Basin. Vol. III. *Edited by* T.M. Quigley and S.J. Arbelbide. US Dep. Agric. For. Serv. Pac. Northw. Res. Stn. PNW-GTR-405.
- Littell, R.C., Milliken, G.A., Stroup, W.W., and Wolfinger, R.D. 1996. SAS system for mixed models. SAS Institute Inc., Cary, NC.
- Markle, D.F. 1992. Evidence of bull trout × brook trout hybrids in Oregon. *In* Proceedings of the Gearhart Mountain Bull Trout Workshop, 1989. *Edited by* P.J. Howell and D.V. Buchanan. Oregon Chapter of the American Fisheries Society, Corvallis, Oreg. pp. 58–67.
- Meyer, K.A., Schill, D.J., Elle, S., and Schrader, W.C. 2003. A long-term comparison of Yellowstone cutthroat trout abundance and size structure in their historical range in Idaho. *N. Am. J. Fish. Manag.* **23**: 149–162.
- Morita, K., and Yamamoto, S. 2002. Effect of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conserv. Biol.* **16**(5): 1318–1323.
- Nakano, S., Kitano, F., and Maekawa, K. 1996. Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming. *Freshw. Biol.* **36**: 711–722.
- Nakano, S., Kitano, S., Nakai, K., and Fausch, K.D. 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, *S. confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. *Environ. Biol. Fishes*, **52**: 345–355.
- Novinger, D.C., and Rahel, F.J. 2003. Isolating cutthroat trout upstream of artificial barriers in small headwater streams: effective long-term conservation strategy. *Conserv. Biol.* **17**(3): 772–781.
- Paul, A.J., and Post, J.R. 2001. Spatial distribution of native and non-native salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. *Trans. Am. Fish. Soc.* **130**(3): 417–430.
- Peterson, D.P., and Fausch, K.D. 2003. Testing population-level mechanisms of invasion by a mobile vertebrate: a simple conceptual framework for salmonids in streams. *Biol. Invas.* **5**: 239–259.
- Peterson, J.T., Dunham, J., Howell, P., Thurow, R., and Bonar, S. 2002. Protocol for detecting bull trout presence. Western Division American Fisheries Society, Bethesda, Md. Available from [http://www.wdafs.org/committees/bull\\_trout/bull\\_trout\\_committee.htm](http://www.wdafs.org/committees/bull_trout/bull_trout_committee.htm) [accessed 11 November 2005].
- Peterson, D.P., Fausch, K.D., and White, G.C. 2004a. Population ecology of an invader: effects of brook trout on native cutthroat trout. *Ecol. Appl.* **14**(3): 754–772.
- Peterson, J.T., Thurow, R.F., and Guzevich, J.W. 2004b. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. *Trans. Am. Fish. Soc.* **133**: 462–475.
- Quist, M.C., Hubert, W.A., and Isaak, D.J. 2004. Factors affecting allopatric and sympatric occurrence of two sculpin species across a Rocky Mountain watershed. *Copeia*, 2004: 617–623.
- Rich, C.F. 1996. Influence of abiotic and biotic factors on occurrence of resident bull trout in fragmented habitats, western Montana. M.S. thesis, Montana State University, Bozeman, Mont.
- Rich, C., McMahon, T., Rieman, B., and Thompson, W. 2003. Influence of local habitat, watershed, and biotic features on bull trout occurrence in Montana streams. *Trans. Am. Fish. Soc.* **132**: 1053–1064.
- Rieman, B.E., and Clayton, J. 1997. Fire and fish: issues of forest health and conservation of native fishes. *Fisheries*, **22**(11): 6–15.
- Rieman, B.E., and McIntyre, J.D. 1993. Demographic and habitat requirements for conservation of bull trout. US Dep. Agric. For. Serv. Gen. Tech. Rep. INT-302.
- Rieman, B.E., and McIntyre, J.D. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Trans. Am. Fish. Soc.* **124**: 285–296.
- Rieman, B.E., Lee, D.C., and Thurow, R.F. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath basins. *N. Am. J. Fish. Manag.* **17**: 1111–1125.
- Royall, R.M. 1997. Statistical evidence: a likelihood paradigm. Chapman and Hall, New York.
- Royle, J.A., and Nichols, J.D. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology*, **84**: 777–790.

- Selong, J.H., McMahon, T.E., Zale, A.V., and Barrows, F.T. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. *Trans. Am. Fish. Soc.* **130**(6): 1026–1037.
- Snijders, T., and Bosker, R. 1999. *Multilevel analysis: an introduction to basic and advanced multilevel modeling*. Sage, Thousand Oaks, Calif.
- Sokal, R.R., and Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. Freeman, New York.
- Spruell, P., Bartron, M.L., Kanda, N., and Allendorf, F.W. 2001. Detection of hybrids between bull trout (*Salvelinus confluentus*) and brook trout (*Salvelinus fontinalis*) using PCR primers complementary to interspersed nuclear elements. *Copeia*, 2001: 1093–1099.
- Strange, R.J., and Habera, J.W. 1998. No net loss of brook trout distribution in areas of sympatry with rainbow trout in Tennessee streams. *Trans. Am. Fish. Soc.* **127**: 434–440.
- Taniguchi, Y., and Nakano, S. 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology*, **8**: 2027–2039.
- Taniguchi, Y., Rahel, F.J., Novinger, D.C., and Gerow, K.G. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Can. J. Fish. Aquat. Sci.* **55**: 1894–1901.
- Thompson, W.L., and Lee, D.C. 2000. Modeling relationships between landscape-level attributes and snorkel counts of chinook salmon and steelhead parr in Idaho. *Can. J. Fish. Aquat. Sci.* **57**: 1834–1842.
- Thurrow, R.F. 1994. Underwater methods for study of salmonids in the Intermountain West. US Dep. Agric. For. Serv. Gen. Tech. Rep. INT-GTR-307.
- Young, M.K. (Editor). 1995. Synthesis of management and research considerations. *In* Conservation assessment for inland cutthroat trout. US Dep. Agric. For. Serv. Rocky Mt. For. Range Exp. Stn. Gen. Tech. Rep. RM-256. pp. 55–61.