

Temperature and Competition between Bull Trout and Brook Trout: A Test of the Elevation Refuge Hypothesis

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Abstract.—We tested the elevation refuge hypothesis that colder temperatures impart a competitive advantage to bull trout *Salvelinus confluentus* and thus account for increased biotic resistance to invasion and displacement by brook trout *S. fontinalis* in headwater streams. Growth, survival, and behavior were compared in allopatry and sympatry at temperatures of 8–20°C in the laboratory. In allopatry, age-0 bull trout and brook trout grew at similar rates at temperatures of 8.0–14.3°C, but brook trout grew significantly faster at higher temperatures. In sympatry, bull trout grew significantly less than brook trout at all test temperatures, with growth differences increasing linearly with increased temperature. Age-1 brook trout had significantly higher feeding and aggression rates than did similar-sized bull trout at 8°C and 16°C. The modeled growth of age-0 bull trout and brook trout based on tributary temperature data from a high-elevation site (mean summer temperature, 10°C) and a low-elevation site (14°C) was similar for both species in allopatry. However, brook trout achieved much greater size than bull trout in sympatry, particularly at the warm site, where the predicted size of brook trout was 21.7 mm (23%) greater in length and 4.9 g (60%) greater in weight. Brook trout therefore had a marked size and growth advantage over bull trout at warm temperatures, but bull trout do not appear to gain a similar advantage over brook trout at low temperatures. Thus, factors in addition to water temperature are relevant to protecting remaining bull trout populations from displacement by brook trout in headwater streams.

A common distribution pattern among many now-rare native potamodromous salmonids is restriction to high-elevation headwaters, with replacement by non-native fishes in lower-elevation reaches (Larson and Moore 1985; Fausch 1989; Paul and Post 2001; de la Hoz Franco and Budy 2005). These population isolates in headwaters often represent the remaining strongholds in what were formerly much more extensive

distribution ranges. Answering the question of why these areas serve as “elevation refuges” (Paul and Post 2001) for native species is vital for the design of effective management actions for protecting remaining isolates as well as promoting range expansion through habitat manipulations and reintroductions.

Several different mechanisms have been proposed to explain why native salmonids appear more resistant to the invasion of nonnatives at higher elevations yet apparently are quite susceptible to invasion at lower elevations (e.g., Griffith 1988; Fausch 1989; Clark and Rose 1997). The distinctive elevational pattern in distribution has led investigators to focus on the idea that some abiotic factor or factors have changed over the length of the stream, resulting in differential

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behavior or physiologic responses affecting competitive interactions and ultimately demographic features of native and nonnative salmonid populations. Gradients in temperature and stream slope are considered the most probable environmental factors that could lead to such condition-specific competition (Fausch 1989; Taniguchi and Nakano 2000).

Most research has focused on the role of temperature, numerous field studies having shown that salmonid distribution is closely associated with elevation and temperature changes within and among drainages (Bozek and Hubert 1992; Fausch et al. 1994; Taniguchi et al. 1998; Dunham and Rieman 1999; Paul and Post 2001; Harig and Fausch 2002; Rieman et al. 2006). Additionally, salmonids exhibit species-specific thermal optima and tolerances (Takami et al. 1997; Selong et al. 2001; Bear et al. 2007), and even small (1–2°C) differences in these parameters may elicit marked differences in species distribution (Fausch et al. 1994).

However, competition experiments conducted with a number of different native and nonnative species pairs have yielded mixed results (see review in McHugh and Budy 2005). Some studies have revealed clear evidence of species dominance changing with temperature—natives dominating at cooler conditions and nonnatives in warmer ones, particularly as temperatures approach lethal levels (Reeves et al. 1987; DeStaso and Rahel 1994; Taniguchi et al. 1998; Reese and Harvey 2002)—whereas others show no reversal of competitive dominance with temperature (Magoulick and Wilzbach 1998a,b; McHugh and Budy 2005). Competition study results can be difficult to interpret because test designs frequently limit the ability to tease apart interspecific from intraspecific differences in behavior and physiology that change over temperature gradients (Dunson and Travis 1991; Fausch 1988, 1998; Volpe et al. 2001; Reese and Harvey 2002). Additionally, most temperature-mediated competition studies have compared species performance over wide temperature differences of 5°C or greater (e.g., DeStaso and Rahel 1994; Magoulick and Wilzbach 1998a; but see Taniguchi et al. 1998 and McHugh and Budy 2005), although species replacement frequently occurs over relatively short distances of several kilometers having only a few degrees of temperature variation and at temperatures well below upper thermal tolerance limits (Larson and Moore 1985; Fausch 1989; Paul and Post 2001; Nelson et al. 2002). This pattern implies that either some mechanism other than temperature is involved in species dominance or that effects of temperature change are more subtle.

Bull trout *Salvelinus confluentus* are likely to be especially sensitive to changes in temperature affecting their biotic resistance to invasion by nonnative

salmonids. The species has among the lowest thermal optima and upper tolerance limits of North American salmonids (Selong et al. 2001), and temperature and elevation are key factors delineating their distributional limits (Saffel and Scarnecchia 1995; Paul and Post 2001; Dunham et al. 2003; Ripley et al. 2005; Rieman et al. 2006). Bull trout are listed as federally threatened over much of its range in the northwestern United States (USFWS 1998) and at risk over parts of its range in Canada (Haas 1998). In many locales, the species is now found primarily in cold, high-elevation tributary streams as headwater residents (e.g., Paul and Post 2001; Rich et al. 2003; Rieman et al. 2006), although their historical range was much more extensive, particularly as fluvial and adfluvial migrants to large rivers and lakes (Fitch 1997).

Nonnative brook trout *S. fontinalis*, rainbow trout *Oncorhynchus mykiss*, and brown trout *Salmo trutta* now occupy much of the lower-elevation tributaries and main-stem rivers formerly occupied by bull trout (Paul and Post 2001; Nelson et al. 2002). Brook trout especially are considered a threat to bull trout through their depressive effect on foraging by bull trout in sympatry (Nakano et al. 1998); dominance over bull trout in aggressive encounters (Gunckel et al. 2002); similar preference for cooler water temperatures (Larson and Moore 1985; Bozek and Hubert 1992); ability to invade and inhabit higher gradient, higher-elevation tributaries (Adams et al. 2000; Gamett 2002; Peterson and Fausch 2003a) where remaining bull trout populations persist; and ability to reproduce with bull trout, creating sterile hybrids (Leary et al. 1993).

Studies of native and nonnative salmonid interactions have generally focused on direct-interference competition, namely, aggressive interactions and access to preferred foraging sites. Relatively few studies have coupled these analyses with concurrent examination of long-term growth and survival, which more directly affect fitness and population-level effects (Taniguchi and Nakano 2000; Peterson and Fausch 2003b). In this study, we experimentally examined the relative role of direct and indirect competition between bull trout and brook trout by comparing growth, survival, behavioral interactions, and energy conversion efficiency of the two species in allopatry and sympatry over a wide range of temperatures in the laboratory. We then applied laboratory results to a growth model to assess the cumulative effects of different temperature regimes on size differences of the two species during their first growing season, as size-structured interactions among age-0 salmonids appear to have the strongest influence on demographic outcomes of nonnative species invasion (Taniguchi et al. 2002; Peterson et al. 2004). We use these data to test the elevation refuge hypothesis (Paul and Post

TABLE 1.—Initial and final lengths, weights, and lipid and protein compositions of bull trout and brook trout in allopatry and sympatry at water temperatures of 8, 12, 16, and 20°C. Values shown are means, with SEs in parentheses. Lipid and protein conversion efficiency is calculated as (grams gained/gram consumed) × 100. Within species, values with the same letter are not significantly different among temperatures. Values that are significantly different between allopatry and sympatry within the same species are indicated by plus signs and those that are significantly different between species at the same temperature by Xs.

Measurement timing and allopatry/sympatry	Temperature (°C)	Length (mm)	Lipids		Protein (%)	Lipid efficiency (%)	Protein efficiency (%)
			g	%			
Bull trout							
Initial		62.2 (0.7)	2.3 (0.1)	3.3	14.4		
Final							
Allopatry	8	80.9 (1.7) z	5.2 (0.2)	4.1 (0.4) z	15.6 (0.1) z	36.8 (7.2) z	41.2 (2.1) z
	12	81.6 (0.7) z	5.3 (0.1)	3.4 (0.1) z	15.6 (0.3) z	23.5 (1.4) y	36.8 (0.6) y
	16	80.2 (1.5) z	5.2 (0.4)	3.5 (0.1) z	15.6 (0.1) z	22.9 (1.2) yX	34.3 (0.8) yX
	20	69.6 (0.7) bX	3.6 (0.1)	3.2 (0.1) z+	14.8 (0.3) z	13.9 (1.1) xX	23.4 (1.0) xX
Sympatry	8	76.5 (1.9) z	4.4 (0.3)	3.4 (0.3) z	15.6 (0.4) z		
	12	79.9 (0.9) z	5.3 (0.2)	3.3 (0.1) z	15.5 (0.3) z		
	16	76.4 (2.8) z	4.5 (0.5)	3.4 (0.2) z	15.4 (0.6) z		
	20	66.9 (0.9) yX	2.9 (0.2)	2.2 (0.2) y+	14.7 (1.3) z		
Brook trout							
Initial		62.3 (0.7)	2.3 (0.1)	4.8	13.4		
Final							
Allopatry	8	79.8 (1.3) z	5.3 (0.5)	4.2 (0.7) z	14.5 (0.2) z	29.0 (10.9) z	39.7 (2.0) z
	12	83.5 (0.7) z+	5.7 (0.1)	4.4 (0.3) z	14.5 (0.2) z	30.3 (5.6) z	36.4 (2.1) z
	16	82.9 (0.8) z	5.7 (0.2)	4.5 (0.2) z	15.0 (0.2) z	32.6 (3.1) zX	40.3 (1.6) zX
	20	79.4 (0.9) zX	5.3 (0.2)	4.0 (0.1) z	14.9 (0.0) z	19.4 (1.0) zX	36.8 (0.7) zX
Sympatry	8	81.3 (0.4) z	5.4 (0.2)	4.8 (0.1) z	14.7 (0.3) z		
	12	89.1 (0.6) y+	7.2 (0.1)	4.8 (0.3) z	14.5 (0.2) z		
	16	87.9 (0.6) y	7.2 (0.1)	4.5 (0.4) z	14.9 (0.3) z		
	20	84.8 (2.4) zX	6.9 (0.8)	4.4 (0.3) z	14.4 (0.7) z		

2001; see also Magoulick and Wilzbach 1998b; McHugh and Budy 2005) that superior behavioral and physiological performance at colder temperatures imparts a competitive and size advantage to bull trout over brook trout and that the reverse occurs at warmer temperatures.

Methods

Survival and growth comparisons.—The bull trout used in experiments were first-generation progeny of a wild broodstock of upper Flathead drainage fish reared at the Creston National Fish Hatchery, Montana. Brook trout were obtained from a wild broodstock maintained in a lake in the upper Flathead River drainage. Eggs were obtained in autumn and transported to the Bozeman Fish Technology Center for rearing separately by species in 8°C spring water until testing. Before testing, fish were held separately in circular tanks with overhead cover and fed with belt feeders rather than by hand to maintain “wild” behavior (normal cover-seeking and fright responses).

Controlled temperature experiments were run using the apparatus and protocol described by Selong et al. (2001). Water from head tanks was supplied to thirty-six 75-L aluminum test tanks measuring 120 × 35 × 25 cm, at a rate of 4 L/min. Rigid foam insulation provided overhead cover over test tanks to simulate undercut bank habitat. Natural light was supplemented

with overhead halogen lights for an approximate 11 h light : 13 h dark photoperiod.

Trials were conducted with fish of age 0 (8 months posthatch) at temperatures of 8, 12, 16, and 20°C. These temperatures represent the range of temperatures typical of trout streams in the Rocky Mountain region of the United States during the growing season (Rieman and Chandler 1999). To separate effects of differing physiological tolerances and of intraspecific competition and interspecific competition (Dunson and Travis 1991; Taniguchi and Nakano 2000), for each of the four test temperatures we compared bull trout and brook trout in allopatry, and both species in sympatry. Three replicate test tanks were randomly chosen for each species × temperature treatment for a total of 36 trials. Fifty fish were randomly selected and added to each tank, 25 fish of each species being added to the tanks with the two species in sympatry. The two species were of equal size at the start of the experiment ($P = 0.35$; Table 1). Equal numbers and sizes of fish were used to minimize potential confounding effects resulting from density and size differences among species in competition experiments (Fausch 1988, 1998; Taniguchi and Nakano 2000). To ensure food limitation and enhance competitive interactions, we fed the fish daily with reduced ration of 66% of satiation for age-0 bull trout (Selong et al. 2001), a level that

approximated food availability common to salmonid streams as inferred from growth rates (Brett et al. 1982; Preall and Ringler 1989).

Fish were held in test tanks for 2 weeks at 8°C before a temperature adjustment of 1.0°C/d to reach the treatment temperature; constant temperatures were then maintained for 60 d. Fish were fed a specially formulated pelleted diet (Selong et al. 2001) daily from 0900 to 1700 hours with an automated belt feeder placed near the head of the test tank to simulate daytime drift. Tanks were cleaned daily; mortalities were removed and weighed and the amount of rations was adjusted accordingly. In all trials, little food remained on tank bottoms after daily feedings. Tank temperatures were measured every 2 h with Onset Stowaway data loggers. Temperatures in test tanks were within $\pm 0.5^\circ\text{C}$ of treatment temperature during the 60-d trials; daily fluctuations were less than 0.2°C .

At the end of the experiment, absolute growth rate (G) was calculated according to the formula $G = (Y_2 - Y_1)/t$, where Y_2 is the final mean weight and Y_1 the initial mean weight of individual fish per tank (adjusted for mortality) and t is the number of days of the experiment (Busacker et al. 1990). Growth-temperature relations for each species and treatment were described by using curvilinear regression (e.g., Lyttikainen and Jobling 1998; Selong et al. 2001). Because we wished to identify point temperatures where growth of the two species diverged, we compared regression lines to determine regions of the species' growth curves that were significantly different. At each 0.1°C point on the growth curves, we calculated the difference in species' growth rate. The associated 95% confidence interval of the paired growth differences was generated using the "g models" routine in the R statistical software (Warnes 2005). The resulting lines were plotted against temperature, and temperatures with significantly different growth rates between species were denoted where the lower 95% confidence line was greater than zero (J. Barber, Montana State University, Department of Statistics, personal communication). To further separate interspecific from intraspecific effects on growth performance, we calculated competition coefficients (Volpe et al. 2001) as the difference in per capita growth between sympatry and allopatry for each species across the test temperature range by using the growth regression equations. Negative competition coefficient values for a species indicate lower growth in sympatry than allopatry, signifying that interspecific competition has a greater effect on performance than intraspecific competition does, whereas positive values indicate the reverse.

Bull trout and brook trout survival in allopatry and sympatry was analyzed with a type I two-way analysis of variance (ANOVA) using species and temperature

as the main effects. A least-significant-difference test was then used to assess differences in species performance within and between each species and temperature treatment. The level of significance for statistical testing was $\alpha \leq 0.05$. Statistical procedures were performed using the Proc GLM procedure in SAS (SAS Institute 2000). All percentage data were arcsine-transformed.

Body composition and conversion efficiency.—Conversion of feed to tissue components (lipid, protein) was also used to compare species performance (Lyytikainen and Jobling 1998). Lipid and protein composition was measured by using standard proximate analysis at the start of the experiment for a random sample of 50 fish of each species and at the end of the study by pooling all fish remaining in each tank. The frozen aggregate sample from each tank was mixed with an equivalent weight of distilled water and ground in a blender. After drying a 2-g subsample for 24 h at 100°C , protein was measured by thermal oxidation (Leco model CN 2000), and lipid by the diethyl ether extraction method (AOAC 1990). Moisture and ash content were also measured but are not reported; moisture and lipid content have a strong inverse correlation (Simpkins et al. 2003) and thus are surrogates for one another, and inorganic ash made up only a small fraction of body constituents ($<2\%$) and varied little in our trials. Lipid and protein conversion efficiency (Dockray et al. 1998) for each species was determined by dividing accumulated protein and lipid (final minus initial body composition) by total consumed (18.5 g of lipid and 51.5 g of protein per 100 g of feed; Selong et al. 2001). Conversion efficiency estimates were limited to allopatry trials because species differences in feed consumption in sympatry could not be measured. Lipid, protein, and conversion efficiency estimates for each species in allopatry and sympatry were compared among temperatures with ANOVA as described above. Analyses of lipid and protein content were confined to within-species comparisons because body composition of bull trout and brook trout differed at the start of the study (Table 1).

Behavioral interactions.—We examined possible underlying mechanisms for the growth differences between bull trout and brook trout by comparing feeding and aggression in allopatry and sympatry. Experiments were conducted at cold (8°C) and warm (16°C) temperatures in glass-sided tanks with dimensions similar to those of the temperature test tanks. Test fish (age 1, 20 months posthatch) were from the same cohort used in growth experiments. Because of their larger size, we used 10 fish per tank (5 of each species in sympatric trials) to match the initial biomass used in the growth study. The test tank was housed behind a

shroud that hid an observer from view. A V-shaped notch was cut into the end of the tank to maintain a water depth of 17.5 cm at a flow rate of 4 L/min. A 5-cm polyvinyl chloride tube glued to the notch provided an exit point for emigrants. Fish emigrating from the tank and entering the exit tube were carried to a screened bucket with a standpipe for capture and enumeration. This system simulated fish emigrating from a pool or run into a shallow riffle (Matter et al. 1989).

Twelve trials were run, with two replicates for each species-temperature combination. The order of the trials was randomly selected for each test temperature. At the start of a trial, fish were randomly selected, measured for length and weight, matched by size, and introduced into the test aquarium. The mean size of test fish was similar across all trials (bull trout: 139 ± 3 mm [mean \pm SE], 25.9 ± 1.5 g; brook trout: 133 ± 3 mm, 24.0 ± 1.5 g). The rear exit of the test tank was screened for 24 h to allow acclimation. Fish were fed daily with pelleted food delivered via a belt feeder from 0800 to 1600 hours at 66% satiation ration. On days 2 and 3, the numbers of feeding and aggressive acts (nipping, lateral displays, or chases) by species were recorded on a tape recorder for 10 min once each day between 1000 and 1200 hours. After behavioral observations were made on day 3, the rear exit screen was removed and the number of emigrants was recorded for 24 h. Differences in feeding and aggression in allopatry and sympatry at the two test temperatures were analyzed by ANOVA, following the methods described above.

Growth model.—On the basis of the daily growth rates from our experiments with age-0 bull trout and brook trout, we simulated the long-term effects of differing thermal regimes by estimating the lengths of bull trout and brook trout at the end of their first growing season under allopatry and sympatry. Water temperatures were obtained from existing thermograph records from a representative bull trout stream, Skalkaho Creek, near Hamilton, Montana, during an average water year. Bull trout occur in moderate to high densities (30 per 100 m) in the upper section above stream kilometer 20 (measured from the mouth), and nonnative brook and brown trout are moderately abundant in the lower section below stream kilometer 15 (50 per 100 m), with a rather short (~ 3 km) zone of sympatry at stream kilometer 12–15 (Nelson et al. 2002). Thermographs were positioned at stream kilometer 1 (elevation, 1,100 m; sampling period: 27 March to 3 October 1996), representing thermal conditions in the nonnative salmonid zone, and at stream kilometer 23 (elevation, 1,397 m; sampling period: 3 July to 21 November 1996), representing thermal conditions in bull trout zone. Temperature–

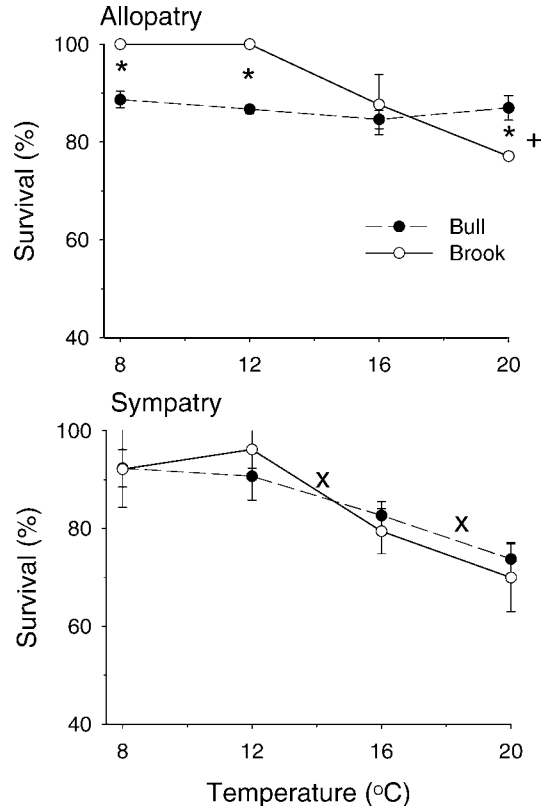


FIGURE 1.—Mean \pm SE survival of age-0 bull trout and brook trout in allopatry and sympatry at test temperatures of 8, 12, 16, and 20°C. Three trials were run for each species \times temperature treatment. Asterisks denote significant ($P < 0.05$) differences in survival between species at a particular test temperature; crosses denote significant differences in survival between test temperatures; and plus signs denote significant differences in survival between allopatry and sympatry within a species.

growth curves (Figure 1) were used to calculate the weight gain per day based on the mean daily temperature. We assumed that age-0 brook trout and bull trout were of equal size (25 mm, 0.12 g) at the time of emergence (May 1; Lentz 1998), and set the growing season as May 1 to November 1—or the period when average daily temperatures were at least 8°C. The final weights of fish were converted to lengths by means of a length-weight (L - W) regression of age-0 fish derived from our laboratory trials (bull trout: $\log_{10} L = 1.684 + 0.3285 \log_{10} W$, $r^2 = 0.99$, $P < 0.001$, $n = 349$; brook trout: $\log_{10} L$ (mm) = $1.689 + 0.3137 \log_{10} W$, $r^2 = 0.99$, $P < 0.001$, $n = 253$). To fill in missing water temperature values at each site (lower site, October 3 to November 1; upper site, April 1 to July 3), we used a predictive relation between mean daily water temper-

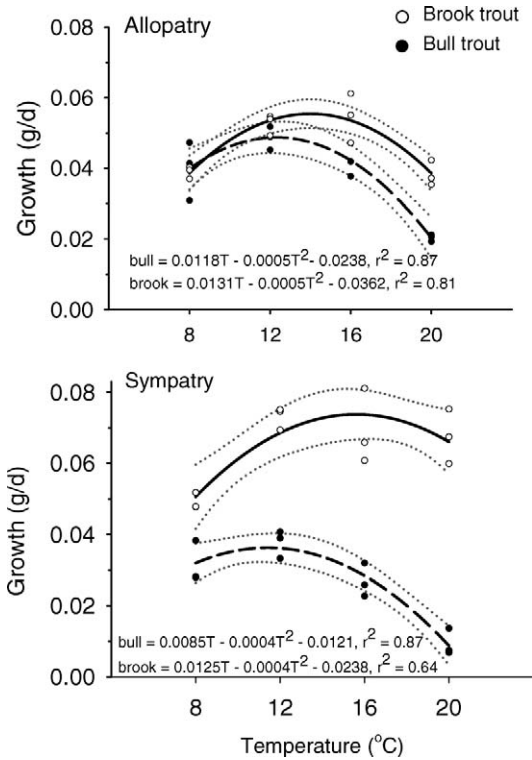


FIGURE 2.—Growth of age-0 bull trout and brook trout in allopatry and sympatry relative to temperature. Three trials were run for each species \times temperature treatment, but only two data points are shown where data overlap. Second-order polynomial regression equations for each growth curve (solid lines) are indicated at the bottom of each panel; T denotes temperature. The dotted lines show the 95% confidence intervals around the regression lines. All regression equations were significant at the 0.05 level.

atures (WT) between the two sites ($WT_{lower} = 3.788 + 1.11 WT_{upper}$, $r^2 = 0.88$, $P < 0.001$, $n = 93$).

Results

Survival and Growth

Survival over our 60-d trials was generally high across all species and temperature combinations (mean, 87%) and neither species had a markedly higher survival advantage at any test temperature (Figure 1). In allopatry, two-way ANOVA revealed significant effects of species ($P < 0.001$), temperature ($P < 0.001$), and a species \times temperature interaction ($P = 0.001$), but differences in survival were generally less than 10%. Bull trout survival was slightly, but significantly lower, than brook trout at 8°C and 12°C, whereas brook trout survival was significantly lower than bull trout at 20°C (77.1% versus 86.9%; $P < 0.05$). In sympatry, only temperature showed a

significant effect on survival ($P = 0.005$), survival decreasing significantly ($P < 0.05$) at 16°C and 20°C. Brook trout showed no difference in survival between allopatry and sympatry at each test temperature ($P = 0.35$ – 0.40). A similar pattern was observed in bull trout, except at 20°C, where survival was significantly lower in sympatry than allopatry (73.7% versus 86.9%, $P = 0.04$).

The growth in weight of bull trout and brook trout in allopatry (Figure 2) was similar in the temperature range 8.0–14.3°C, but brook trout grew significantly faster than bull trout at higher temperatures. Peak growth temperature also differed, growth being highest at 12.3°C for bull trout and 14.0°C for brook trout. Bull trout growth declined sharply at temperatures above 16°C, whereas the decline in brook trout growth at that temperature was much less pronounced. At 20°C, growth of bull trout was approximately half that of brook trout.

The presence of brook trout had a marked depressive effect on the growth of bull trout (Figure 2). Bull trout grew significantly less in sympatry than in allopatry (mean difference, 33%) whereas the opposite was true for brook trout, which averaged 42% more growth in sympatry than in allopatry over the test temperature range of 8–20°C. Growth differences became more prominent at warmer temperatures, increasing from about twofold greater growth in brook trout at 12°C to more than threefold greater growth at temperatures above 16°C. Peak growth temperatures for the two species in sympatry also diverged, shifting downward to 11.4°C for bull trout and upward to 15.6°C for brook trout.

Competition coefficients further revealed that interspecific competition had a greater influence on the growth of bull trout than did intraspecific competition. Competition coefficients for bull trout ranged from -0.008 g/d at 8°C to -0.015 g/d at 20°C, indicating greater growth in allopatry than in sympatry across all temperatures (Figure 3). In contrast, brook trout growth in sympatry was much higher than in allopatry, indicating a stronger intraspecific competitive effect. Competition coefficients for brook trout increased linearly with temperature from $+0.014$ g/d at 8°C to $+0.04$ g/d at 20°C, a nearly threefold increase. For bull trout, competition coefficients showed much less variation with temperature, declining linearly by about 50% from 8°C to 14°C before stabilizing, indicating that the depressive effect of interspecific competition on growth was slightly less at colder temperatures.

Length differences between bull trout and brook trout at the end of the study further illustrated the negative influence of brook trout on bull trout (Table 1). Brook trout and bull trout mean lengths in allopatry were similar at all temperatures except at 20°C, where

mean length of bull trout (69.6 mm) was 10–13 mm shorter than that of brook trout ($P < 0.05$). In sympatry, however, mean length of bull trout was significantly smaller ($P < 0.05$) than that of brook trout at each test temperature, the differences ranging from 5 to 18 mm.

Body Composition and Conversion Efficiency

For bull trout, lipid content varied significantly between allopatry and sympatry ($P = 0.004$) and among temperatures ($P = 0.001$), but the interaction effects were not significant ($P = 0.8$; Table 1). At 20°C, bull trout in sympatry with brook trout had significantly lower lipid content (2.2%), whereas at all other temperatures, lipid content of bull trout in allopatry or sympatry were similar ($P > 0.05$), ranging from 3.4% to 4.1%. There were no significant differences in protein content of bull trout in allopatry versus sympatry ($P = 0.76$), among temperatures ($P = 0.4$), or in the interaction between the two ($P = 1.0$). Brook trout also showed no significant differences in protein content between allopatry and sympatry ($P = 0.7$), among temperatures ($P = 0.5$), or in their interaction ($P = 0.8$); unlike bull trout, they showed no significant differences in lipid content between allopatry and sympatry ($P = 0.2$) or among temperatures ($P = 0.8$).

Lipid and protein conversion efficiencies also differed between bull trout and brook trout. Lipid conversion efficiency for bull trout decreased significantly with temperature ($P = 0.01$), ranging from a high of 36.8% at 8°C to a low of 13.9% at 20°C, a 62% decline. Protein conversion efficiency of bull trout also decreased significantly with temperature ($P < 0.001$), declining from a high of 41.2% at 8°C to 23.4% at 20°C, a 43% decline. In contrast, brook trout showed no significant differences in lipid ($P = 0.6$) or protein ($P = 0.3$) conversion efficiency with temperature. Bull trout had significantly lower lipid and protein conversion efficiencies than did brook trout at both 16°C and 20°C ($P \leq 0.02$).

Behavioral Interactions

In allopatry, bull trout and brook trout fed at similar rates (ANOVA; $P = 0.45$), averaging about 25 bouts per trial for both species, and there was no significant temperature ($P = 0.96$) or species \times temperature interaction ($P = 0.7$) effect on feeding rate (Figure 4). In sympatry, bull trout fed significantly less than in allopatry ($P = 0.01$), averaging about 50% fewer feeding bouts, the difference in feeding between bull trout and brook trout being significant at the warmer temperature (16°C). Brook trout feeding rate showed no difference between allopatry and sympatry ($P = 0.14$).

Bull trout were less aggressive than brook trout in

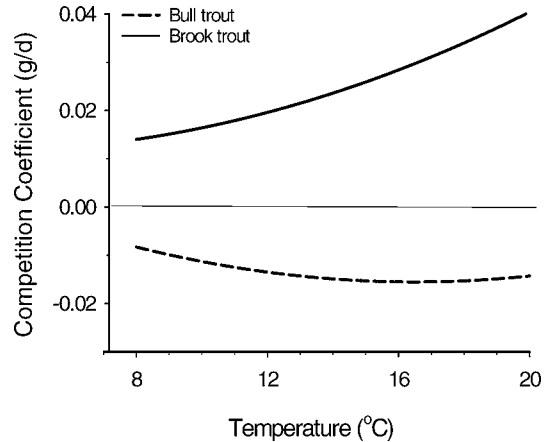


FIGURE 3.—Competition coefficients of bull trout and brook trout relative to temperature as determined by the difference in per capita growth rates in sympatry and allopatry based on the growth curves shown in Figure 2. Negative values indicate lower growth in sympatry than allopatry (interspecific competition > intraspecific competition); positive values indicate the reverse (intraspecific competition > interspecific competition).

allopatry, averaging about half the number of aggressive acts per trial (9.75 versus 19.25; Figure 4), although the differences between species ($P = 0.13$), temperature ($P = 0.13$), and the species \times temperature interaction ($P = 1.0$) were not statistically significant. Aggression differences were much more pronounced in sympatry ($P = 0.002$), where brook trout averaged 25.5 aggressive bouts per trial compared with 4.0 for bull trout. Brook trout in sympatry with bull trout on average initiated 11 aggressive acts per trial towards bull trout compared with only 2 initiated by bull trout towards brook trout. Bull trout were significantly less aggressive than brook trout at both cold and warm temperatures ($P < 0.05$).

Emigration from test tanks during behavior experiments was low in most trials, ranging from 0 to 1 fish per trial (0–10%). Emigration was highest for brook trout in allopatry at 8°C ($40 \pm 10\%$ [mean \pm SE]).

Growth Modeling

Water temperature differed by about 4°C between the upper- and lower-elevation sites on Skalkaho Creek, averaging 10°C in upper Skalkaho Creek and 14°C in lower Skalkaho Creek during summer (1 July–1 September; Figure 5). Upper Skalkaho Creek had a considerably shorter growing season than lower Skalkaho Creek did (74 versus 128 d in which mean daily water temperatures exceeded 8°C). Maximum weekly average temperature (mean of highest 7-d average daily temperatures) was 11.0°C and 15.7°C for

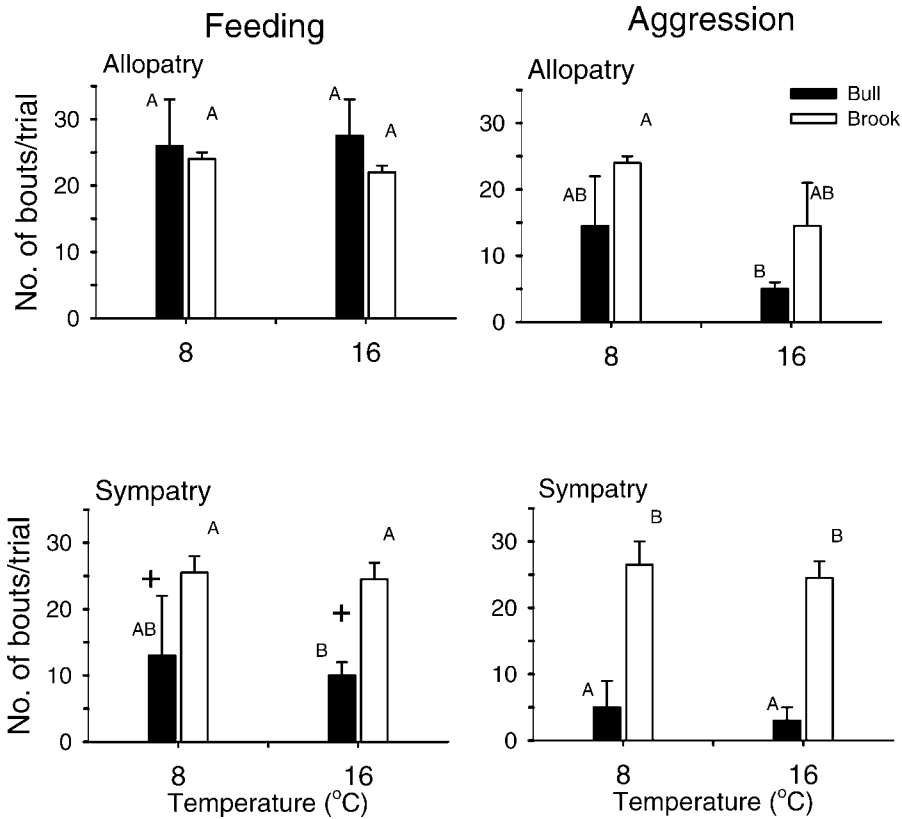


FIGURE 4.—Mean ± SE feeding and aggression rates of age-1 bull trout and brook trout in allopatry and sympatry at test temperatures of 8°C and 16°C. Two trials were run for each species × temperature treatment. Values within each species treatment with the same letters are not significantly different among temperatures. Values that are significantly different ($P < 0.05$) between allopatry and sympatry within the same species are indicated by plus signs.

the upper and lower sites, respectively; maximum temperatures were 13.9°C and 18.2°C.

In allopatry, the size of bull trout and brook trout predicted by the temperature growth model was similar at each site (Figure 6). Modeled length at the end of the first growing season for both species was about 71 mm and 3.3 g in the cooler, upper-elevation site and 83.9–85.1 mm and 5.4–5.9 g in the warmer, lower-elevation site. In sympatry, however, brook trout reached a much greater size than bull trout, particularly at the warm site. At the cold site, the predicted size of bull trout in sympatry with brook trout was 65.2 mm and 2.5 g compared with 78.3 mm and 4.5 g for brook trout, a 13.1 mm (20%) difference in length and 2.0 g (80%) difference in weight. At the warm site, the predicted size of bull trout was 74.2 mm and 3.7 g, compared with 95.9 mm and 8.6 g for brook trout, a 21.7-mm (29%) difference in length and 4.9-g (132%) difference in weight. Modeled growth at the warm site began about a month earlier than at the cold site (June 2 versus July 1) and ended a month later (October 16

versus September 14). At both sites, the predicted sizes of bull trout and brook trout in sympatry diverged rapidly, differences of 5 mm or more occurring within 3 weeks after the estimated date of growth initiation.

Discussion

Our results demonstrated that the presence of brook trout has a marked negative effect on bull trout that is magnified at higher water temperatures. Brook trout exhibited significantly greater growth capacity than bull trout at temperatures greater than 14.3°C and, in sympatry, brook trout growth was significantly higher than bull trout at all temperatures, the growth and size differences increasing with temperature. Brook trout were metabolically more efficient than bull trout at converting dietary lipid and protein to body tissue at warmer temperatures (16–20°C). Brook trout were more aggressive than bull trout, especially at warm temperatures, and the presence of brook trout had a marked depressive effect on bull trout feeding and aggression. Selong et al. (2001) also found that brook

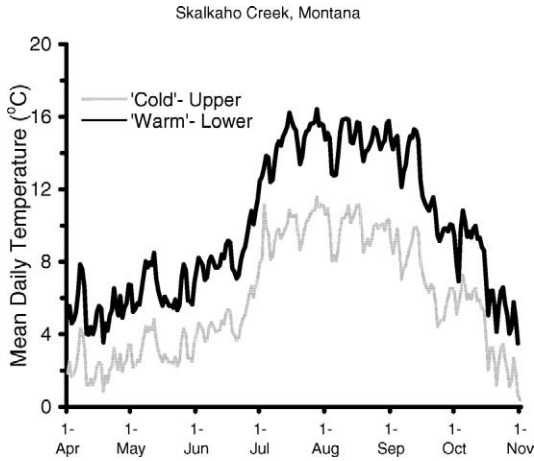


FIGURE 5.—Mean daily water temperatures for Skalkaho Creek, Montana, from April 1 to November 1, 1996, at an upper-elevation site (1,397 m; stream kilometer 23), where bull trout were present and brook trout absent, and at a lower-elevation site (1,100 m; stream kilometer 1), where bull trout were absent and brook trout present.

trout have greater ability to survive short-term and prolonged exposures to temperatures above 20°C than do bull trout. That bull trout are negatively affected by the interacting influence of warm water temperature

and the presence of brook trout is further shown by downstream expansion of bull trout into warmer, lower-elevation reaches of Idaho tributaries, where brook trout are absent (Rieman et al. 2006). Similarly, in lower Skalkaho Creek, where brook trout are present and bull trout absent, we found summer water temperatures were well within the suitable range for growth and survival for juvenile bull trout (Selong et al. 2001), indicating that lower distributional limits for bull trout are not limited by physiological constraints imposed by warm water temperatures. Taken together, the data support the prediction that bull trout populations are more susceptible to invasion and displacement by brook trout at warmer temperatures (Paul and Post 2001; Rieman et al. 2006).

The underlying mechanisms that lead to the loss of bull trout and other native salmonids after brook trout invasion remain uncertain (Dunham et al. 2002; Peterson and Fausch 2003b). We hypothesize that at the start of an invasion, brook trout probably displace bull trout from energetically favored feeding locations (Nakano et al. 1998) and suppress bull trout feeding rates by way of aggressive interference (Gunckel et al. 2002; this study), leading to higher growth and larger size advantage of brook trout over bull trout at the onset of winter, as predicted from our modeling of age-0 growth. Overwinter survival in age-0 salmonids

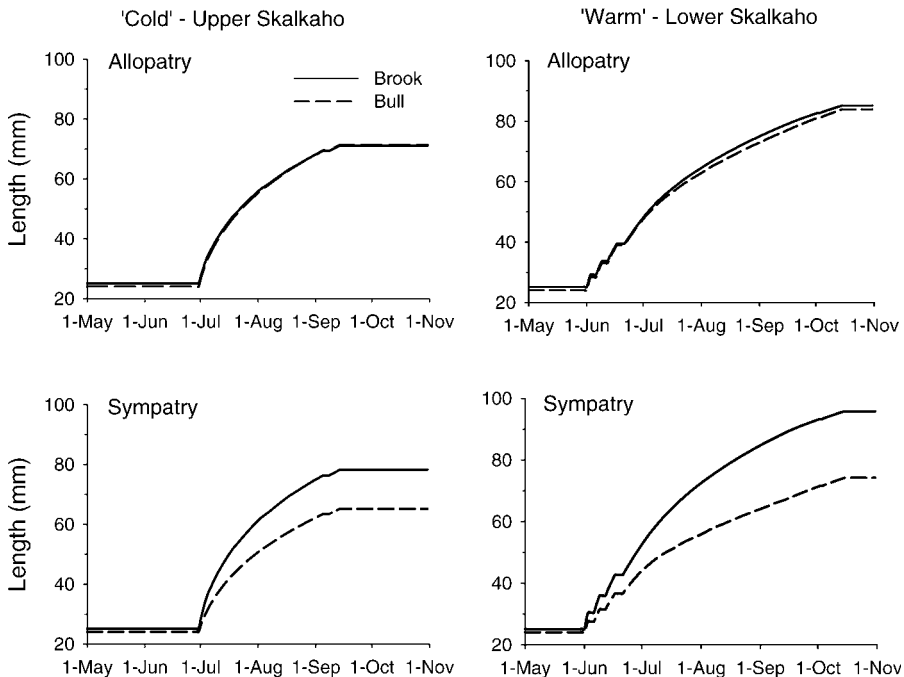


FIGURE 6.—Predicted lengths of age-0 bull trout and brook trout in allopatry and sympatry during the first growing season, based on the growth–temperature curves (Figure 2) and the differing water temperature regimes at high and low elevations (see Figure 5).

is highly dependent on fish size, lipid storage, and winter severity (Gardiner and Geddes 1980; Meyer and Griffith 1997), and the larger size of brook trout at the onset of winter coupled with their greater lipid storage and conversion efficiency at warmer temperatures probably contributes to differential overwinter survival strongly favoring brook trout. Brook trout are likely to have a significant growth and survival advantage at the initial stages of an invasion when they are at low density relative to bull trout, given that growth of brook trout is more strongly affected by intraspecific competition (Figure 2). In turn, the larger size of age-1 brook trout relative to bull trout the following year probably increases their predation on age-0 bull trout (Gregory and Griffith 2000), leading to additional additive mortality of juvenile bull trout and further facilitation of their own invasion (Taniguchi et al. 2002). The cumulative effect of such strong biotic interactions at the individual level over time would cause a recruitment bottleneck for juvenile bull trout (Taniguchi et al. 2002; Peterson et al. 2004). At the population level, higher growth and survival rates for brook trout at warmer temperatures would probably lead to lower age at maturity, faster population growth rates, and higher dispersal, resulting in further suppression of the local bull trout population as well as expansion of the invasion front (Kennedy et al. 2003; Peterson et al. 2004).

In contrast, we found that bull trout did not gain a competitive, size, or survival advantage over brook trout at cold temperature. Both species survived temperatures of 8°C and 12°C at high rates (>85%) over the 60-d test period, in contrast to the marked differences observed in other species pairs, where the high-elevation species had a distinct survival advantage over the low-elevation species at colder temperatures (Taniguchi and Nakano 2000; but see Peterson et al. 2004). Growth modeling and our laboratory results revealed that brook trout would also gain a significant size advantage over bull trout in upper Skalkaho Creek, indicating that the upper distributional limits of brook trout are not limited by growth constraints imposed by colder water temperatures. The lack of a clear behavioral or physiological advantage to bull trout at colder temperatures was unexpected; they are considered to be among the most coldwater-adapted of North American salmonids (Selong et al. 2001) and are typically most abundant where average summer temperatures are less than 10°C (Paul and Post 2001; Gamett 2002; Rieman et al. 2006). The strong negative effects of brook trout on bull trout that we observed at warmer temperatures, but a lack of evidence for competitive reversal favoring bull trout over brook trout at colder temperatures, parallel those observed for other nonnative–native salmonid species pairs, includ-

ing brown trout and Bonneville cutthroat trout *O. clarkii utah* (McHugh and Budy 2005), brook trout and Bonneville cutthroat trout (Buys 2002), and brook trout and greenback cutthroat trout *O. clarkii pleuriticus* (DeStaso and Rahel 1994). Our findings concur with McHugh and Budy's (2005) conclusion, based on their recent review of salmonid competition studies, that temperature-mediated competition alone appears insufficient to account for the segregation of native and nonnative species along elevational gradients.

What, then, accounts for higher elevations serving as a refuge for bull trout from displacement by brook trout? An effect of cold temperature acting on life stages or time periods other than we studied is one possible explanation for the lack of observed competitive advantage for bull trout at cold temperature (McHugh and Budy 2005). We considered the growing season for both species as days when mean temperatures were above 8°C because this was the lower limit used in our growth experiments and because the growth capacity for brook trout and bull trout at temperatures less than 8°C is unknown. However, congeneric Arctic char *Salvelinus alpinus* grow at temperatures as low as 1°C (Brannas and Wiklund 1992) and, in cold headwater streams where water temperatures rarely exceed 10°C (Gamett 2002; Harig and Fausch 2002; Rieman et al. 2006), the majority of the year is below our assumed 8°C growth threshold (e.g., 291 d in upper Skalkaho Creek). Thus, potentially small differences between bull trout and brook trout in growth and food conversion efficiencies at temperatures below what we examined could lead to marked size and survival differences. That bull trout may accrue a growth advantage over brook trout at low temperatures is suggested by the fact that their highest lipid conversion efficiencies occurred at 8°C compared with 12–16°C for brook trout (Table 1). Species differences in growth and lipid storage and food conversion efficiency at low temperature would be expected to become even more divergent at the low ration levels (e.g., Brett et al. 1969) characteristic of low-productivity headwater streams (Sloat et al. 2005). Additionally, the high emigration we observed for brook trout in allopatry at 8°C (40% versus 0–10% in all other trials) suggests that brook trout may show avoidance for low temperatures. Alternatively, cold temperature may be affecting life stages other than the juvenile growth phase. McHugh and Budy (2005) postulated that the low incubation success of brown trout at low temperatures gives cutthroat trout a survival advantage at higher elevations despite the superior competitive advantage of brown trout at the juvenile summer growth life stage. However, environmental constraints occurring at high elevation during the late fall-to-spring period (e.g., low temperatures,

flood disturbance; Fausch et al. 2001) would appear to affect both bull and brook trout equally, given their similar incubation requirements (Curry et al. 1995; Baxter and McPhail 1999) and similar timing of spawning (Kitano et al. 1994), incubation, and emergence (Lentz 1998). Little is known about the relative recruitment success of age-0 bull trout and brook trout in high-elevation streams, where recruitment failures among salmonids appear common (Peterson et al. 2004).

Other abiotic and biotic factors are therefore likely to interact with temperature and competition to influence the displacement of bull trout by brook trout. Bull trout occur most frequently in high-elevation tributaries that have an abundant, neighboring bull trout population in the main stem and high habitat complexity in the form of abundant large woody debris (Rich et al. 2003); in contrast, their abundance is depressed in drainages with high levels of fine sediment, forest harvest, and roads (Ripley et al. 2005). Given the high propensity of brook trout to invade high-gradient reaches where bull trout persist (Adams et al. 2000; Peterson and Fausch 2003a; Peterson et al. 2004), the combination of cold temperature, complex habitat structure, and connectivity to nearby bull trout populations appears vital for protecting remaining bull trout populations from invasion and displacement (see also Dunham and Rieman 1999; Dunham et al. 2003).

Although there was no clear temperature threshold at which competitive dominance shifted between bull trout and brook trout, the performance gain of brook trout over bull trout became more pronounced at temperatures greater than 14°C. This finding concurs with that of field distribution studies, which show that the occurrence of bull trout falls sharply when maximum summer temperature exceeds 14°C (Saffel and Scarnecchia 1995; Rieman and Chandler 1999; Gamett 2002; Dunham et al. 2003). From a management perspective, streams with temperatures above this level will probably be highly susceptible to brook trout invasion and less suitable as potential reintroduction sites. For example, brook trout were present at low density and native westslope cutthroat trout *O. clarkii lewisii* were present at high density in a small Montana stream having an intact riparian forest and maximum daily summer temperature of 12°C; however, a reversal in density was observed in a nearby stream with maximum temperature 1–2°C higher from riparian forest removal and associated habitat change (Shepard 2004). Given the enhanced competitive ability of brook trout over bull trout at warm temperatures, temperature increases are likely to decrease biotic resistance of bull trout populations to brook trout invasion, further contracting the already restricted range of remaining

isolated headwater populations and increasing the risk of local extirpation (Dunham and Rieman 1999). In Idaho streams, the lower distribution limit of bull trout occurs at an average elevation 100–200 m higher when brook trout are present (Rieman et al. 2006). However, this seemingly small elevation difference, corresponding to a thermal difference of about 1.5–3°C (Paul and Post 2001), results in an estimated contraction of bull trout longitudinal distribution by 40% (Rieman et al. 2006). Therefore, protection of existing riparian corridors and restoration of natural temperature regimes by means of riparian restoration and improved flow management are important conservation measures for protecting and expanding fragmented bull trout populations (Ripley et al. 2005).

A unique aspect of our study was the integration of laboratory-derived growth data with field temperature data to model size differences of age-0 fish during the first growing season. Our growth modeling clearly illustrated the potentially large size differences that accrue between species under various temperature regimes. Because dominance among young salmonids is conferred by even small size differences (Fausch and White 1986), the rapid size divergence of age-0 bull trout and brook trout in sympatry in the first few weeks after emergence supports the view that competitive interactions between native and nonnative salmonids at the age-0 stage probably play a key role in native species displacement (Clark and Rose 1997; Shepard et al. 2003; Peterson et al. 2004). The sizes and daily growth rates of these age-0 fish (mean, 0.54 mm/d, range 0.38–0.71) estimated from growth modeling approximated the sizes and growth rates observed by Lentz (1998) for age-0 bull trout and brook trout in Skalkaho Creek and nearby tributaries (mean daily growth rates of 0.5 mm/d during the first growing season), suggesting that our growth models provided reasonable size and growth estimates. Growth modeling holds promise as a useful tool for estimating relative availability of suitable thermal habitat across drainage networks under various thermal conditions (e.g., Sloat et al. 2005), but field validation of laboratory growth estimates are a necessary next step before broader application (Nicola and Almodovar 2004). Our study, like many other competition studies of nonnative and native species, focused on individual-level outcomes of species interactions. Future work should focus on brook trout removal experiments in transition areas downstream of bull trout distribution boundaries, paralleling those conducted with cutthroat trout (Peterson et al. 2004), to assess population-level effects of the hypothesized mechanisms of temperature-mediated interactions identified in this study.

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References

- Adams, S. B., C. A. Frissell, and B. E. Rieman. 2000. Movements of nonnative brook trout in relation to stream channel slope. *Transactions of the American Fisheries Society* 129:623–638.
- AOAC (Association of Official Analytical Chemists). 1990. Official methods of analysis. AOAC, Arlington, Virginia.
- Baxter, J. S., and J. D. McPhail. 1999. The influence of redd site selection, groundwater upwelling, and overwinter incubation temperature on survival of bull trout (*Salvelinus confluentus*) from egg to alevin. *Canadian Journal of Zoology* 77:1233–1239.
- Bear, E. A., T. E. McMahon, and A. V. Zale. 2007. Comparative thermal requirements of westslope cutthroat trout and rainbow trout: implications for species interactions and development of thermal protection standards. *Transactions of the American Fisheries Society* 136:1113–1121.
- Bozek, M. A., and W. A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. *Canadian Journal of Zoology* 70:886–890.
- Brannas, E., and J.-S. Wiklund. 1992. Low temperature growth potential of Arctic charr and rainbow trout. *Nordic Journal of Freshwater Research* 67:77–81.
- Brett, J. R., W. C. Clarke, and J. E. Shelbourn. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile Chinook salmon *Oncorhynchus tshawytscha*. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1127.
- Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada* 26:2362–2394.
- Busacker, G. P., I. R. Adelman, and E. M. Goolish. 1990. Growth. Pages 363–387 in C. B. Schreck and P. B. Moyle, editors. *Methods for fish biology*. American Fisheries Society, Bethesda, Maryland.
- Buys, D. J. 2002. Competition between Bonneville cutthroat trout and brook trout in laboratory and field experiments. Master's thesis. Utah State University, Logan.
- Clark, M. E., and K. A. Rose. 1997. Factors affecting competitive dominance of rainbow trout over brook trout in southern Appalachian streams: implications of an individual-based model. *Transactions of the American Fisheries Society* 126:1–20.
- Curry, F. A., D. L. G. Noakes, and G. E. Morgan. 1995. Groundwater and the emergence of brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:1741–1749.
- de la Hoz Franco, E. A., and P. Budy. 2005. Effects of biotic and abiotic factors on the distribution of trout and salmon along a longitudinal stream gradient. *Environmental Biology of Fishes* 72:379–391.
- DeStaso, J., III, and F. J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. *Transactions of the American Fisheries Society* 123:289–297.
- Dockray, J. J., I. J. Morgan, S. D. Reid, and C. M. Wood. 1998. Responses of juvenile rainbow trout, under food limitation, to chronic low pH and elevated summer temperatures, alone and in combination. *Journal of Fish Biology* 52:62–82.
- Dunham, J. B., S. B. Adams, R. E. Schroeter, and D. C. Novinger. 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. *Reviews in Fish Biology and Fisheries* 12:373–391.
- Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications* 9:642–655.
- Dunham, J. B., B. Rieman, and G. Chandler. 2003. Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. *North American Journal of Fisheries Management* 23:894–904.
- Dunson, W. A., and J. Travis. 1991. The role of abiotic factors in community organization. *American Naturalist* 138:1067–1091.
- Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? *Canadian Journal of Fisheries and Aquatic Sciences* 45:2238–2246.
- Fausch, K. D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? *Physiology and Ecology Japan, Special Volume* 1:303–322.
- Fausch, K. D. 1998. Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. *Canadian Journal of Fisheries and Aquatic Sciences* 55(Supplement 1): 218–231.
- Fausch, K. D., S. Nakano, and K. Ishigaki. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. *Oecologia* 100:1–12.
- Fausch, K. D., Y. Taniguchi, S. Nakano, G. D. Grossman, and C. R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. *Ecological Applications* 11:1438–1455.
- Fausch, K. D., and R. J. White. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in

- a laboratory stream, and implications for Great Lakes tributaries. *Transactions of the American Fisheries Society* 115:363–381.
- Fitch, L. 1997. Bull trout in southwestern Alberta: notes on historical and current distribution. Pages 147–160 in W. C. Mackay, M. K. Brewin, and M. Monita, editors. *Friends of the bull trout conference proceedings*. Trout Unlimited Canada, Calgary, Alberta.
- Gamett, B. L. 2002. The relationship between water temperature and bull trout distribution and abundance. Master's thesis. Utah State University, Logan.
- Gardiner, W. R., and P. Geddes. 1980. The influence of body composition on the survival of juvenile salmon. *Hydrobiologia* 69:67–72.
- Gregory, J. S., and J. S. Griffith. 2000. First-winter survival of caged wild and hatchery cutthroat trout in allopatry and sympatry with brook trout. *Intermountain Journal of Science* 6:217–222.
- Griffith, J. S. 1988. Review of competition between cutthroat trout and other salmonids. Pages 134–140 in *American Fisheries Society, Symposium 4*, Bethesda, Maryland.
- Gunckel, S. L., A. R. Hemmingsen, and J. L. Li. 2002. Effect of bull trout and brook trout interactions on foraging habitat, feeding behavior, and growth. *Transactions of the American Fisheries Society* 131:1119–1130.
- Haas, G. R. 1998. Indigenous fish species potentially at risk in BC, with recommendations and prioritizations for conservation, forestry/resource use, inventory, and research. *British Columbia Ministry of Fisheries Management Report 105*, Vancouver.
- Harig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecological Applications* 12:535–551.
- Kennedy, B. M., D. P. Peterson, and K. D. Fausch. 2003. Different life histories of brook trout populations invading mid-elevation and high-elevation cutthroat trout streams in Colorado. *Western North American Naturalist* 63:215–223.
- Kitano, S., K. Maekawa, S. Nakano, and K. D. Fausch. 1994. Spawning behavior of bull trout in the upper Flathead drainage, Montana, with special reference to hybridization with brook trout. *Transactions of the American Fisheries Society* 123:988–992.
- Larson, G. L., and S. E. Moore. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian mountains. *Transactions of the American Fisheries Society* 114:195–203.
- Leary, R. F., F. W. Allendorf, and S. H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. *Conservation Biology* 7:856–865.
- Lentz, H. S. 1998. Distribution and habitat of recently emerged young-of-the-year trout. Master's thesis. University of Montana, Missoula.
- Lyytikäinen, T., and M. Jobling. 1998. The effects of temperature, temperature shift, and temperature fluctuation on daily feed intake, growth, and proximate composition of underyearling Lake Inari Arctic charr (*Salvelinus alpinus*). *Nordic Journal of Freshwater Research* 74:87–94.
- Magoulick, D. D., and M. A. Wilzbach. 1998a. Effect of temperature and macrohabitat on interspecific aggression, foraging success, and growth of brook trout and rainbow trout pairs in laboratory streams. *Transactions of the American Fisheries Society* 127:708–717.
- Magoulick, D. D., and M. A. Wilzbach. 1998b. Are native brook charr and introduced rainbow trout differentially adapted to upstream and downstream reaches? *Ecology of Freshwater Fish* 7:167–175.
- Matter, W. J., R. W. Mannan, E. W. Bianchi, T. E. McMahon, J. H. Menke, and J. C. Tash. 1989. A laboratory approach for studying emigration. *Ecology* 70:1543–1546.
- McHugh, P., and P. Budy. 2005. An experimental evaluation of competitive and thermal effects on brown trout (*Salmo trutta*) and Bonneville cutthroat trout (*Oncorhynchus clarki utah*) performance along an altitudinal gradient. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2784–2795.
- Meyer, K. A., and J. S. Griffith. 1997. First-winter survival of rainbow trout and brook trout in the Henrys Fork of the Snake River, Idaho. *Canadian Journal of Zoology* 75:59–63.
- Nakano, S., S. Kitano, K. Nakai, and K. D. Fausch. 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. *Environmental Biology of Fishes* 52:345–355.
- Nelson, M. L., T. E. McMahon, and R. F. Thurow. 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. *Environmental Biology of Fishes* 64:321–332.
- Nicola, G. G., and A. Almodovar. 2004. Growth pattern of stream-dwelling brown trout under contrasting thermal conditions. *Transactions of the American Fisheries Society* 133:68–78.
- Paul, A. J., and J. R. Post. 2001. Spatial distribution of native and nonnative salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. *Transactions of the American Fisheries Society* 130:417–430.
- Peterson, D. P., and K. D. Fausch. 2003a. Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Oncorhynchus clarki*) habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1502–1516.
- Peterson, D. P., and K. D. Fausch. 2003b. Testing population-level mechanisms of invasion by a mobile vertebrate: a simple conceptual framework for salmonids in streams. *Biological Invasions* 5:239–259.
- Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of brook trout on native cutthroat trout. *Ecological Applications* 14:754–772.
- Preall, J. R., and N. H. Ringler. 1989. Comparison of actual and potential growth rates of brown trout (*Salmo trutta*) in natural streams based on bioenergetic models. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1067–1076.
- Reese, C. D., and B. C. Harvey. 2002. Temperature-dependent interactions between juvenile steelhead and Sacramento pikeminnow in laboratory streams. *Transactions of the American Fisheries Society* 131:599–606.
- Reeves, G. H., F. H. Everest, and J. D. Hall. 1987. Interactions between reddsider shiner (*Richardsonius balteatus*) and the

- steelhead trout (*Salmo gairdneri*) in western Oregon: the influence of water temperature. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1603–1613.
- Rich, C. F., Jr., T. E. McMahon, B. E. Rieman, and W. L. Thompson. 2003. Local habitat, watershed, and biotic features associated with bull trout occurrence in Montana streams. *Transactions of the American Fisheries Society* 132:1053–1064.
- Rieman, B. E., and G. L. Chandler. 1999. Empirical evaluation of temperature effects on bull trout distribution in the Northwest. Final Report to Environmental Protection Agency, Boise, Idaho.
- Rieman, B. E., J. T. Peterson, and D. L. Myers. 2006. Have brook trout (*Salvelinus fontinalis*) displaced bull trout (*Salvelinus confluentus*) along longitudinal gradients in central Idaho streams? *Canadian Journal of Fisheries and Aquatic Sciences* 63:63–78.
- Ripley, T., G. Scrimgeour, and M. S. Boyce. 2005. Bull trout (*Salvelinus confluentus*) occurrence and abundance influenced by cumulative industrial developments in a Canadian boreal forest watershed. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2431–2442.
- Saffel, P. D., and D. L. Scarnecchia. 1995. Habitat use by juvenile bull trout in belt-series geology watersheds of northern Idaho. *Northwest Science* 69:304–317.
- SAS Institute. 2000. SAS/STAT software, release 8.01. SAS Institute, Cary, North Carolina.
- Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. *Transactions of the American Fisheries Society* 130:1026–1037.
- Shepard, B. B. 2004. Factors that may be influencing nonnative brook trout invasion and their displacement of native westslope cutthroat trout in three adjacent southwestern Montana streams. *North American Journal of Fisheries Management* 24:1088–1100.
- Shepard, B. B., R. Spoon, and L. Nelson. 2003. A native westslope cutthroat trout population responds positively after brook trout removal and habitat restoration. *Intermountain Journal of Science* 8:191–211.
- Simpkins, D. G., W. A. Hubert, C. Martinez del Rio, and D. C. Rule. 2003. Physiological responses of juvenile rainbow trout to fasting and swimming activity: effects on body composition and condition indices. *Transactions of the American Fisheries Society* 132:576–589.
- Sloat, M. R., B. B. Shepard, R. G. White, and S. Carson. 2005. Influence of stream temperature on the spatial distribution of westslope cutthroat trout growth potential within the Madison River basin, Montana. *North American Journal of Fisheries Management* 25:225–237.
- Takami, T., F. Kitano, and S. Nakano. 1997. High water temperature influences on foraging responses and thermal deaths of Dolly Varden *Salvelinus malma* and whitespotted charr *S. leucomaenis* in a laboratory. *Fisheries Science* 63:6–8.
- Taniguchi, Y., K. D. Fausch, and S. Nakano. 2002. Size-structured interactions between native and introduced species: can intraguild predation facilitate invasion by stream salmonids? *Biological Invasions* 4:223–233.
- Taniguchi, Y., and S. Nakano. 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology* 81:2027–2039.
- Taniguchi, Y., F. J. Rahel, D. C. Novinger, and K. G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1894–1901.
- USFWS (U.S. Fish and Wildlife Service). 1998. Endangered and threatened wildlife and plants: determination of threatened status for the Klamath River and Columbia River distinct population segments of trout, Final Rule. *Federal Register* 63:111(10 June 1998):31647–31674.
- Volpe, J. P., B. R. Anholt, and B. W. Gickman. 2001. Competition among juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 58:197–207.
- Warnes, G. R. 2005. G models: R programming tools for model fitting—R statistics software version 2.12.0. Available: www.cran.r-project.org/src/contrib/PACKAGES.html. (July 2006).