An experimental evaluation of competitive and thermal effects on brown trout (*Salmo trutta*) and Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) performance along an altitudinal gradient

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Abstract: Temperature-mediated competition (i.e., dominance shifts between species depending on temperature) may explain the segregation of salmonid species along altitudinal stream gradients. We evaluated this hypothesis for exotic brown trout (*Salmo trutta*) and native Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) by rearing them in experimental sympatry and allopatry using enclosures constructed at six sites spaced along a 45-km segment of a mountain stream. For both species, we compared condition and growth between allopatric and sympatric treatment groups. We found that brown trout negatively affected cutthroat trout performance, whereas cutthroat trout failed to impart an effect in the reverse direction, regardless of temperature. Thus, we documented asymmetric competition between these species but found little evidence indicating that its outcome was influenced by temperature. Brown trout – cutthroat trout segregation is therefore unlikely to be due to temperature-mediated competition. Instead, brown trout may have displaced cutthroat trout from downstream areas through competition or other mechanisms, while abiotic factors preclude their (brown trout) invasion of upper elevations. Given the magnitude of effect observed in our study, we recommend that brown trout receive greater consideration in cutthroat trout conservation.

Résumé : La compétition reliée à la température, dans laquelle la dominance passe d'une espèce à une autre en fonction de la température, peut probablement expliquer la ségrégation des espèces de salmonidés le long de gradients d'altitude dans les cours d'eau. Nous avons éprouvé cette hypothèse chez des truites brunes (*Salmo trutta*) exotiques et des truites fardées Bonneville (*Oncorhynchus clarkii utah*) indigènes en les élevant ensemble (sympatrie expérimentale) ou séparément (allopatrie) dans des enclos construits à six sites échelonnés sur un segment de 45 km d'un cours d'eau de montagne. Chez les deux espèces, nous avons comparé la condition et la croissance des groupes de poissons élevés dans des conditions de sympatrie et d'allopatrie. La truite brune affecte négativement la performance de la truite fardée, alors que la truite fardée n'arrive pas à avoir d'impact sur la truite brune, quelle que soit la température. Il y a donc une compétition asymétrique entre ces deux espèces, mais il y a peu d'indications que l'issue de la compétition est influencée par la température. La ségrégation entre la truite brune et la truite fardée n'est vraisemblablement pas due à la compétition reliée à la température. Il est possible que la truite brune élimine la truite fardée des zones d'aval par compétition ou par un autre mécanisme, alors que les facteurs abiotiques empêchent l'invasion des altitudes plus élevées par la truite brune. Étant donné l'ampleur des effets observés dans notre étude, nous recommandons de porter plus d'attention à la truite brune dans les travaux de conservation de la truite fardée.

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Introduction

Patterns of fish-species replacement along altitudinal gradients occur commonly in mountain rivers and streams throughout the world (Taniguchi and Nakano 2000). This phenomenon — termed altitudinal species zonation because of the distinct species zones observed along upstream–downstream gradients — occurs in response to factors operating differentially across elevations. Zonation may be due to the response of individual species to the availability of suitable habitat conditions that vary with elevation (e.g., temperature; Vincent and Miller 1969; Rahel and Hubert 1991; Bozek and Hubert 1992). For instance, each species may have a different thermal physiology and thus exhibit a distribution pattern reflecting the spatial arrangement of suitable temperatures within a river network (Magoulick and Wilzbach 1998*a*).

More locally, species-zonation patterns can be the result of an interaction between abiotic and biotic factors (Dunson and Travis 1991; Fausch et al. 1994). For example, temperature-

mediated competition may be the reason why salmonid species segregate along altitudinal gradients (Fausch 1989; Fausch et al. 1994; de la Hoz Franco and Budy 2005). Under this scenario, high-elevation species are hypothesized to be superior competitors at cold temperatures and to exclude low-elevation species from areas dominated by those conditions, while the reverse is thought to be true at low-elevation, warmer sites. In the absence of the competitor(s), each species may be physiologically capable of living at all sites (Taniguchi and Nakano 2000). While there have been several recent experiments designed to evaluate temperature-mediated competition as an explanation for salmonid zonation (see Discussion for a review of these studies), results have been variable (Novinger 2000; De Staso and Rahel 1994).

Because of the threatened and endangered status of many native fishes, it is imperative to understand the influence of temperature-mediated competition on salmonid zonation in streams. Non-native trout invasions are perceived as one of the greatest threats to native salmonid diversity in North America (Dunham et al. 2002; Quist and Hubert 2004). In many watersheds of the western US and Canada, native cutthroat trout (*Oncorhynchus clarkii* subsp.) persist only in headwater reaches, while non-native brook (*Salvelinus fontinalis*) and exotic brown trout (*Salmo trutta*) replace them at lower elevations (Fausch 1989; de la Hoz Franco and Budy 2005). Given the imperiled status of cutthroat trout (Gresswell 1988; Behnke 1992; Young 1995), identifying the causes of zonation in native–non-native trout systems is of considerable importance. Specifically, understanding whether cutthroat trout distributional limits are set by abiotic conditions, competition with exotic species, or an interaction between the two will lead to different strategies when attempting to increase the size and spatial extent of cutthroat trout populations, a goal common to recovery plans (e.g., Lentsch et al. 1997).

In this study, we evaluated the causes of spatial segregation between exotic brown trout and native Bonneville cutthroat trout (*O. c. utah*) in a stream in northern Utah, USA. Native to the ancient Lake Bonneville Basin of the USDA Forest Service Intermountain Region, Bonneville cutthroat trout are only present in a fraction of their historic range and are being considered for US Endangered Species Act protection (Duff 1988; Young 1995; Lentsch et al. 1997). In contrast, brown trout (a species native to Europe and Asia) are widely distributed in the region and abundant in many streams that were historically dominated by cutthroat trout. When they co-occur, brown trout and cutthroat trout segregate along altitudinal gradients (de la Hoz Franco and Budy 2005). To understand this pattern, we experimentally assessed the interacting roles of interspecific competition and water temperature on brown and cutthroat trout performance in a field setting.

Materials and methods

Study site description

We conducted our experiment within a 45-km segment of the Logan River, Utah, USA, a stream that originates in the Bear River Mountain Range of northern Utah and drains into the terminal Great Salt Lake system (Fig. 1). This mountain stream of moderate elevation (study reach range: 1503–2091 m) and gradient (0.015 m·m^{-1}) flows through a broad valley in its upper reaches and a deeply dissected canyon in its lower reaches. The climate of the area is characterized by cold, snowy winters (January air temperature: low, –9 °C; high, 0 °C; mean precipitation 4.0 cm) and hot, dry summers (July air temperature: low, 15 °C; high, 31 °C; mean precipitation 1.6 cm), yielding a hydrograph dominated by a spring-snowmelt flood (554 ft^3·s^{-1}; 1 cubic foot per second = 28.316 dm·s^{-1}) followed by base-flow conditions (~100 ft^3·s^{-1}).

In addition to Bonneville cutthroat trout, the species of primary interest in our study, other native fishes present in the Logan River include mottled sculpin (*Cottus bairdii*) and mountain whitefish (*Prosopium williamsoni*). Introduced species include brown trout, with rainbow (*Oncorhynchus mykiss*) and brook trout also present but in low numbers. Species abundance varies with elevation in the Logan River, producing three fish zones (de la Hoz Franco and Budy 2005): (*i*) a low-elevation zone dominated by brown trout; (*ii*) a high-elevation zone dominated by cutthroat trout; and (*iii*) a mid-elevation transitional area (Fig. 2).

Experimental design

We evaluated the influence of competition and temperature on brown trout – cutthroat trout zonation. An enclosure experiment was set up where these species were reared together (in sympatry) and alone (in allopatry) at six points systematically spaced along the thermal gradient present in the Logan River. The spatial aspect of our design thus incorporated the natural temperature range and the three fish zones of the Logan River, allowing us to simultaneously assess the role of temperature and competitive interactions in zonation. We did this using a substitutive competition experiment (sensu Fausch 1998) within the context of a randomized complete block design. At each site, we constructed three 20-m^2 rectangular enclosures (6.0 m × 3.3 m, long sides parallel to flow) from steel T-posts and 13-mm plastic mesh. Enclosures were arranged within sites so that one side was attached to the riverbank. Also, there was at least 10 m of free-flowing river between enclosures at sites where they were built in an upstream–downstream sequence. We randomly assigned treatments to enclosures within sites. The treatment levels were (*i*) eight cutthroat trout in allopatry, (*ii*) eight brown trout in allopatry, and (*iii*) four brown and four cutthroat trout in sympatry. The density of experimental fish in enclosures (0.40 fish·m^{-2}) reflects the upper limit of densities observed for trout in the Logan River (Budy et al. 2004).

Trout used in the experiment were collected from allopatric locations within the study watershed (brown trout from Right Hand Fork; cutthroat trout from Beaver Creek and the Logan River at Franklin Basin; Fig. 1) using backpack electrofishing methods. Brown trout (mean total length (TL): 180 mm, 95% confidence interval (CI): 175–185 mm) and cutthroat trout (mean TL: 173 mm, 95% CI: 167–178 mm) used in our experiment were of similar starting TL; however, because of the natural size structure present in the Logan River, experimental brown trout were slightly longer than experimental cutthroat trout. Upon collection, we transported all fish to laboratory raceways and held them at 10 °C for an 8-day acclimation period to ensure that all fish had the same recent thermal history prior to exposure to experi-

Fig. 1. Map of the Logan River Drainage in northern Utah, USA. The experimental reach extends from the Idaho border (northern edge of detailed figure) to the lower end of US Forest Service ownership (at the city boundary). Enclosure sites are labeled with shaded symbols and site name. Experimental fish were collected from Right Hand Fork, Beaver Creek, and the mainstem Logan River upstream of the Franklin Basin site.
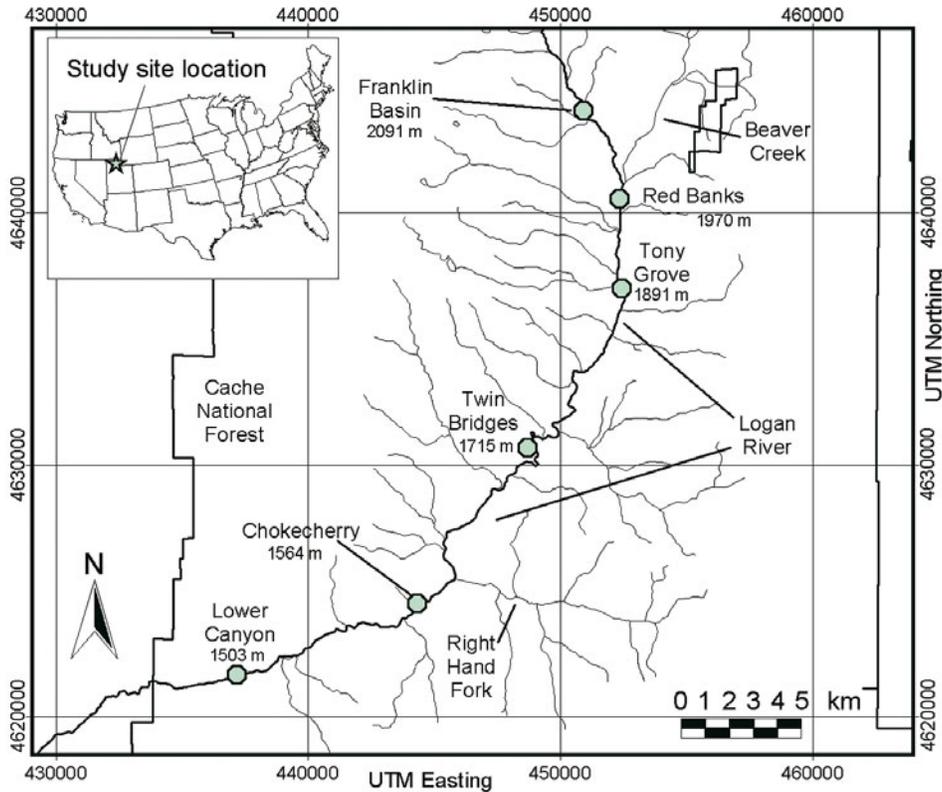

Fig. 2. The brown trout (*Salmo trutta*; shaded symbols) – Bonneville cutthroat trout (*Oncorhynchus clarkii utah*; open symbols) altitudinal species-zonation pattern of Logan River, Utah. Estimates of trout abundance are from Budy et al. (2004) and represent the mean (± range) based on three-pass electrofishing surveys made at five long-term monitoring sites in the summers of 2001–2003.
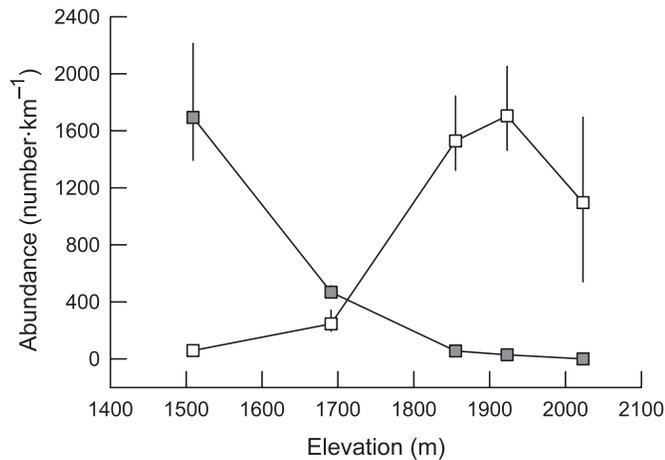
mental temperatures. During this period, fish were starved, weighed, measured, and given a uniquely numbered T-bar anchor tag.

Individual fish were randomly assigned to each site–treatment combination and introduced into enclosures simultaneously on 14 July 2003 to begin a 42-day trial. During this period, fish were assumed to have sufficient prey resources (e.g., terrestrial, benthic, and (or) drifting macroinvertebrates); a pilot study indicated that when enclosure mesh was cleaned of debris, invertebrate drift was unimpeded. We cleaned all enclosures at least once every 48 h during the trial period to provide a regular supply of prey. Other than routine cleaning visits, we allowed fish to interact with minimal disturbance during the experiment. On 25 August 2003, the experiment was concluded, and all fish were collected from enclosures (using electrofishing and underwater collection methods), weighed, and measured. As a rule, we included in our analysis only those enclosures that contained at least five of the eight experimental fish and at least two of each species (for sympatric replicates only). For both species, this resulted in five and six replicates for sympatric and allopatric treatment groups, respectively.

Fish performance

We evaluated the performance response of brown and cutthroat trout to species interactions and abiotic conditions based on two measures. First, we assessed their instantaneous (specific) growth rate, G:

$$(1) \qquad G = [(\ln W_{final} - \ln W_{initial}) \times t^{-1}] \times 100$$

Table 1. Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) and brown trout (*Salmo trutta*) initial total length (TL), release, recapture, and tag retention details by site and treatment.

Site	Treatment	Cutthroat trout TL (mm)	Release (*n*)	Recapture (*n*)	w/tag	Brown trout TL (mm)	Release (*n*)	Recapture (*n*)	w/tag
Lower Canyon	Allopatry	177	8	7	5	185	8	7	7
	Sympatry	176	4	4	4	194	4	4	4
Chokecherry	Allopatry	165	8	7	5	188	8	7	7
	Sympatry	168	4	2	0	179	4	3	3
Twin Bridges	Allopatry	179	8	5	5	181	8	8	6
	Sympatry[a]	169	4	2	2	170	4	1	1
Tony Grove	Allopatry	178	8	7	5	172	8	6	5
	Sympatry	171	4	3	1	166	4	4	4
Red Banks	Allopatry	165	8	7	7	171	8	7	7
	Sympatry	174	4	4	4	170	4	3	3
Franklin Basin	Allopatry	176	8	7	7	187	8	8	8
	Sympatry	177	4	3	3	193	4	4	4

Note: The category "w/tag" denotes the number of fish recaptured that retained their tag. The total density of fish in sympatric enclosures is the sum of brown and cutthroat trout released (i.e., 8).

[a]This enclosure was omitted from our analysis because of fish losses.

where W is mass in grams and t is trial length in days. Owing to high tag loss rates (Table 1) and the disappearance of some fish, however, we were unable to definitively identify every individual on several instances. Thus, we evaluated growth rates using enclosure-averaged start ($W_{initial}$) and end (W_{final}) weights.

In addition to growth, we assessed the condition of individual fish based on the relative weight index, W_r:

$$(2) \qquad W_r = W/W_s \times 100$$

where W is the observed mass (g) of a given fish, and W_s is its predicted mass (g) based on its measured total length (mm) and a standard length–weight relationship for the species. Our standard length–weight relationships were those estimated for wild, Logan River brown and cutthroat trout sampled during annual monitoring activities (brown trout, $W_s = 1.708 \times 10^{-5}$ TL$^{2.905}$; cutthroat trout $W_s = 6.193 \times 10^{-5}$ TL$^{2.670}$; Budy et al. 2004). Pretrial condition values were similar for fish assigned to the two treatment groups for both species (analysis of variance: brown trout, $F_{[1,9]} = 1.5$, $P = 0.256$; cutthroat trout, $F_{[1,9]} = 0.1$, $P = 0.834$), indicating that any differences observed at the end of the trial are due to experimental effects. Finally, although quantifying behavioral performance would have been desirable, preliminary underwater and aerial observations demonstrated that encounter rates were insufficient to warrant such an assessment.

Environmental variable measurement

To evaluate the effects of environmental factors on performance and competitive relationships and to account for cage effects in our analysis, we quantified several habitat characteristics at both the site and enclosure levels. Water temperature, the site-level variable of primary interest in our study, was measured hourly using data loggers. From these data, we computed the daily mean, minimum, and maximum temperature for the 42-day period. We also quantified stream size at the site level using a single, base-flow, discharge measurement made with an electromagnetic flow meter.

In addition to taking site-level environmental measurements, we assessed habitat within individual enclosures. First, we measured the size distribution of streambed particles using a Wolman pebble count (Wolman 1954), which was summarized by the median particle size (D_{50}). To account for fine sediment deposition caused by velocity differences between the inside and outside of enclosures and due to changes in flow across the 42-day period, we estimated the percentage of the enclosed area covered by fines (<10 mm) visually at the beginning and end of the trial. We also estimated the mean depth (cm) and velocity (cm·s^{-1}) based on measurements made at 20 evenly spaced points in a grid spanning each enclosure. Finally, we quantified prey abundance based on the assumption that the area upstream of enclosures was the main source of drifting invertebrates during the experiment. Thus, we collected three benthic invertebrate samples ~2 m upstream of each enclosure using a 0.09-m^2 Surber sampler. Samples were preserved (95% ethanol) and transported to the laboratory, where invertebrates were counted and identified (to Order) using a dissecting microscope. We measured the length of 30 individuals and estimated dry biomass based on length–mass regressions (Benke et al. 1999) for the Orders Ephemeroptera, Plecoptera, Diptera, and Trichoptera; for a given enclosure, we averaged the three samples.

Statistical analysis

Our analysis occurred in two phases. First, we compared the upstream–downstream temperature profile measured during our experiment to literature-based, thermal physiology criteria for each species, without any consideration of trial results. We contrasted minimum, mean, and maximum water temperatures from the six sites with the thermal growth optima of brown trout (13–18 °C; Elliott and Hurley 2000; Ojanguren et al. 2001) and cutthroat trout (13–19 °C; based on the optimum growth temperature – lethal temperature relationship of Jobling (1981) and also on the published thermal physiology data for Bonneville cutthroat trout (Wagner

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et al. 2001; Johnstone and Rahel 2003)). Additionally, we evaluated brown trout growth potential across the six sites using the temperature–growth model of Elliott et al. (1995). This model, based on growth experiments where brown trout were fed maximum ration at several temperatures, predicts growth based on a fish's initial mass ($W_{initial}$ in eq. 1 above), trial duration, mean water temperature, and three parameters. No such model has been developed for Bonneville cutthroat trout (or related subspecies), so we completed this analysis component for brown trout only.

For the second phase of our analysis, we compared the condition and growth of experimental fish separately, between treatment groups, and within species as a function of temperature using analysis of covariance (ANCOVA). Because we were mainly interested in assessing how temperature extremes affect the outcome of competition, we used two temperature metrics (minimum and maximum) in separate analyses. However, based on the potential for site effects due to factors other than temperature (e.g., food availability), we also considered a subset of non-temperature environmental variables (i.e., discharge, end fines, D_{50}, and prey biomass; all uncorrelated with temperature ($|R| < 0.5$) based on an initial screening of Pearson's correlation coefficients). The model structure used was

(3) $\qquad y_{ij} = \mu + \mathrm{trt}_i + \beta_1 X_{1ij} + \beta_{2i} T_{ij} + \varepsilon_{ij}$

where y_{ij} is the performance observed in the jth enclosure within the ith treatment group, μ is an intercept term, trt_i is an effect due to the ith treatment, $\beta_1 X_{1ij}$ is a non-temperature site effect, $\beta_{2i} T_{ij}$ is the treatment-specific effect of temperature (i.e., inclusive of a temperature-by-treatment interaction), and ε_{ij} is the residual error term.

Prior to fitting the final ANCOVA model and evaluating experimental effects, we used a model selection strategy based on Akaike's Information Criterion (AIC$_c$, adjusted for small sample size) (Burnham and Anderson 2002) to identify which environmental variable best accounted for non-temperature site effects (i.e., $\beta_1 X_{1ij}$). We then fit the best model and assessed model-effect significance using F tests (Type III sums of squares). Finally, we compared ANCOVA-adjusted mean performance (condition and growth) between treatment groups in a post hoc context using t tests for both. Post hoc comparisons were completed for both high and low temperature levels when there was a significant treatment–temperature interaction and at average covariate values otherwise. Model-selection analyses were completed using SAS's PROC REG, whereas the final ANCOVA models were completed using PROC GLM (SAS Institute Inc. 2002). Owing to the low replication and high variability of our data set, we assessed significance at $\alpha = 0.10$.

Results

Longitudinal temperature profile

In general, water temperatures measured during the experiment decreased with increasing elevation across the study reach (Table 2). Mean and maximum temperatures increased across the three upper-most sites (Franklin Basin to Tony Grove) and then remained relatively constant in the downstream direction; minimum temperature increased as a nearly linear, inverse function of elevation. The greatest diel

fluctuation (maximum – minimum temperature) was observed at a mid-elevation site (Tony Grove).

Based on published thermal physiology information for brown and cutthroat trout (see Materials and methods), it appears that both species experienced optimum growth temperatures during part of every day at all sites, excluding the uppermost site (Franklin Basin). Using observed mean temperatures and starting weights, the model of Elliott et al. (1995) predicted that brown trout growth rates should be highest at mid-elevation sites (Twin Bridges: 0.766 day^{-1}, and Tony Grove: 0.798 day^{-1}), lowest at high elevation sites (Red Banks: 0.542 day^{-1}, and Franklin Basin: 0.362 day^{-1}), and intermediate at the two lowermost sites (Lower Canyon: 0.656 day^{-1}, and Chokecherry: 0.715 day^{-1}).

Experimental effects of temperature and competition on trout

On average, seven of the eight experimental fish were recaptured in enclosures. Only one replicate (i.e., a site–treatment combination) had to be withheld from analysis (Twin Bridges-sympatric) because of fish losses ($n = 3$ fish remained; Table 1). Documented fish losses were due to predation by birds (P. McHugh, personal observation); however, losses occurred because of unknown causes as well.

Both trout species exhibited positive growth and relatively high condition across the six sites. Thus, there was not a clear trend in performance along the thermal gradient of the study site for either species. Overall, brown and cutthroat trout growth rates averaged 0.904 day^{-1} (range: 0.219–1.604 day^{-1}) and 0.384 day^{-1} (range: 0.039–0.930 day^{-1}), respectively. Brown trout weight was similar to that of non-experimental Logan River fish of the same size, with an overall mean relative weight (condition) of 100.2% (range: 79.7%–119.1%). In contrast, cutthroat trout weighed less than the standard weight equation predicted, attaining a mean condition value of 83.7% (range: 63.5%–106.0%). Brown trout growth and condition were higher in sympatric compared with allopatric enclosures (Figs. 3a and 3b). In contrast, cutthroat trout performance was suppressed in sympatry relative to allopatry (Figs. 3c and 3d).

Our evaluation of the effects of species interactions and abiotic factors on experimental trout performance illustrates three important results. First, site-level differences in non-temperature environmental factors (discharge or prey biomass, selected using AIC$_c$) accounted for a large proportion of variability in trout performance. Second, cutthroat trout presence, water temperature, or their interaction did not have a demonstrable effect on brown trout condition or growth (Table 3; Fig. 3). In fact, post hoc comparisons of ANCOVA-adjusted means indicate that brown trout attained significantly higher condition values in the presence of cutthroat trout (minimum temperature–condition, $t = -4.45$, df = 6, $P = 0.004$; maximum temperature–condition, $t = -3.56$, df = 6, $P = 0.0119$). Brown trout growth differences, though in agreement with the trend in condition between treatment groups, were negligible (see Table 3 for ANCOVA results; post hoc means comparisons: minimum temperature–growth, $t = -0.56$, df = 6, $P = 0.594$; maximum temperature–growth, $t = -0.58$, df = 6, $P = 0.586$). Thus, there was an overall lack of statistical support for a negative competitive effect — temperature mediated or otherwise — of cutthroat trout on brown trout.

Table 2. Site-level and enclosure-level habitat attributes of experimental enclosures.

Site	Treatment	Site-level attributes					Enclosure-level attributes					
		Elevation (m)	Temperature (°C)			Discharge (cfs)	Depth (cm)	Velocity (cm·s⁻¹)	Start fines (%)	End fines (%)	D_{50} (mm)	Prey biomass (mg·m⁻²)
			Mean	Min.	Max.							
Lower Canyon	CUT	1503	13.9	11.8	16.2	32	33	18	6	45	34	5 056
	BNT	—	—	—	—	—	32	32	0	3	90	12 444
	BNT+CUT	—	—	—	—	—	29	25	0	3	60	12 778
Chokecherry	CUT	1564	12.5	10.4	14.8	95	41	16	56	79	12	3 489
	BNT	—	—	—	—	—	34	23	33	74	4	3 178
	BNT+CUT	—	—	—	—	—	33	25	0	43	45	3 800
Twin Bridges	CUT	1715	13.1	10.1	16.0	70	44	17	50	88	4	2 978
	BNT	—	—	—	—	—	33	21	22	73	4	3 600
	BNT+CUT	—	—	—	—	—	28	20	22	45	12	5 033
Tony Grove	CUT	1891	12.9	8.9	17.5	36	26	22	0	45	50	4 367
	BNT	—	—	—	—	—	36	8	22	58	25	2 100
	BNT+CUT	—	—	—	—	—	31	21	11	33	62	3 389
Red Banks	CUT	1970	9.9	6.9	13.8	37	42	32	0	5	112	7 200
	BNT	—	—	—	—	—	30	29	0	30	45	4 722
	BNT+CUT	—	—	—	—	—	34	36	6	5	85	6 756
Franklin Basin	CUT	2091	8.1	6.1	11.2	16	44	22	0	35	95	5 133
	BNT	—	—	—	—	—	27	17	0	28	75	5 833
	BNT+CUT	—	—	—	—	—	26	21	13	42	21	3 889

Note: BNT, brown trout (*Salmo trutta*); CUT, Bonneville cutthroat trout (*Oncorhynchus clarkii utah*); —, value applies to all enclosures at that particular site; cfs, cubic feet per second (1 cubic foot per second = 28.316 dm·s⁻¹); D_{50}, median particle size. See text for measurement and computation details.

Fig. 3. Mean growth and condition (±2 SE) for brown trout (*Salmo trutta*; panels *a* and *b*, shaded bars) and Bonneville cutthroat trout (*Oncorhynchus clarkii utah*; panels *c* and *d*, open bars) raised in sympatry and allopatry. An asterisk denotes a statistically significant difference ($\alpha = 0.10$) between treatment group means adjusted by analysis of covariance.
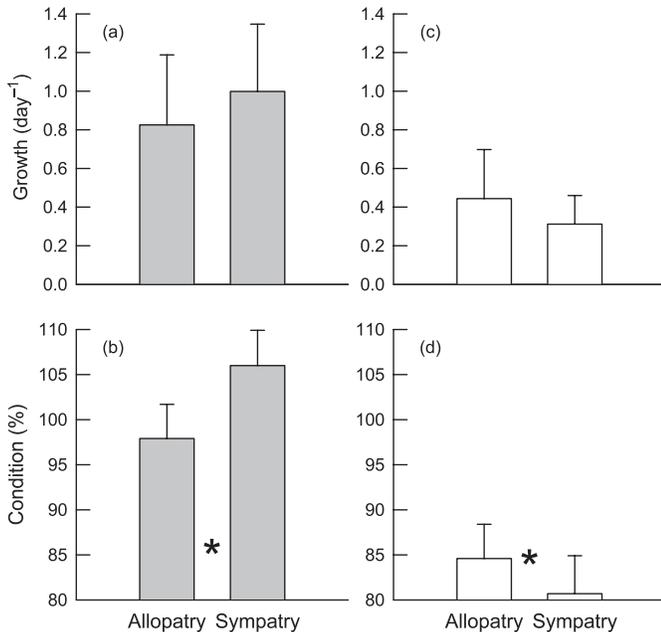
In contrast with our brown trout results, our analysis provided statistical evidence for a negative competitive impact of brown trout on cutthroat trout (Fig. 3). First, treatment and temperature–treatment interaction effects were both significant in the cutthroat trout maximum temperature–condition model (Table 4). Specifically, allopatric cutthroat trout attained a condition value nearly 10% greater than did cutthroat trout reared with brown trout at a maximum temperature of 12 °C (post hoc means comparison: $t = 3.3$, df = 6, $P = 0.016$). Condition was only 2% higher among allopatric relative to sympatric fish at 17 °C ($t = 0.47$, df = 6, $P = 0.655$). In contrast with maximum temperature–condition ANCOVA results, treatment and temperature–treatment interaction effects were not significant in all other models. However, a ANCOVA-adjusted mean comparison based on the minimum temperature–condition model corroborate the maximum temperature–condition findings ($t = 2.41$, df = 6, $P = 0.053$). Finally, although cutthroat trout growth was greater in allopatry relative to sympatry, ANCOVA-adjusted means did not differ significantly between treatment groups for either model ($P > 0.25$).

To summarize, brown trout greatly reduced cutthroat trout performance at all but the warmest of temperatures observed in our experiment. Experimental brown trout performance, in contrast, was generally unaffected by temperature and (or) competition with cutthroat trout.

Discussion

A central tenet of stream ecology is that abiotic conditions and biological communities change predictably along longitudinal (upstream–downstream) gradients (Vannote at al.

1980). This is particularly true for salmonids in stream environments, where species segregate into discrete zones and water temperatures change over relatively short distances (e.g., Vincent and Miller 1969). These systems are thus ideal for assessing the interacting roles of biotic interactions and abiotic factors in determining species distributions. Accordingly, we evaluated the potentially interacting roles of interspecific competition and temperature on the performance of two trout species in an effort to understand the causes of salmonid zonation.

If temperature-mediated competition were the ultimate cause of zonation in our study system, we would expect brown trout to negatively impact cutthroat trout at warm temperatures and cutthroat trout to similarly affect brown trout at cool temperatures. Counter to this prediction, however, brown trout presence reduced cutthroat trout performance at all but the warmest temperatures. Thus, while we present evidence of a negative effect of exotic brown trout on native cutthroat trout, temperature-mediated competition does not satisfactorily explain zonation in our system. Rather, we suggest that altitudinal segregation is due to an abiotic determination of brown trout's upstream limit, coupled with their demonstrated ability to negatively impact cutthroat trout when they co-occur. Specifically, we believe that brown trout have invaded as far upstream as their thermal physiology permits and during this process have displaced cutthroat trout from downstream reaches.

The role of temperature in zonation

Although temperature requirements of Bonneville cutthroat trout have not been fully quantified to date, a simultaneous consideration of their estimated growth optimum (13–19 °C; see Materials and methods for derivation details), the thermal gradient of the Logan River, and experimental fish performance indicates that temperature conditions do not adequately explain their absence from downstream reaches. Even the warmest, low-elevation conditions observed in our study (maximum temperature, 15–18 °C) were well within the derived optimum temperature range. Indeed, some of the highest growth and condition values were documented among allopatric cutthroat trout at our lowermost site. This result is corroborated by a number of recent studies demonstrating that Bonneville cutthroat trout are well adapted to survive and grow at temperatures well in excess of 20 °C (Wagner et al. 1998; Johnstone and Rahel 2003; Schrank et al. 2003). Thus, it is unlikely that warm water temperatures prevent cutthroat trout from occupying low-elevation sites.

Despite the absence of a clear performance–temperature trend for experimental brown trout, existing information suggests that cold temperatures preclude them from high-elevation reaches. First, though altitudinal trends in temperature and predicted growth potential (Elliott et al. 1995) indicate that positive brown trout growth is possible throughout our study river, the lowest predicted rate was for our coldest, highest site (0.361 day^{-1}, Franklin Basin). This site averaged only 8.1 °C (range: 6.1–11.2 °C), whereas brown trout optimum growth occurs between 13 and 18 °C (Elliott and Hurley 2000; Ojanguren et al. 2001). Thus, temperatures at high elevations are less than ideal — though not necessarily unsuitable — for subadult brown trout growth. Abiotic controls on brown

Table 3. Brown trout (*Salmo trutta*) analysis of covariance (ANCOVA) results results by temperature metric (minimum, T_{min}; maximum, T_{max}) and response variable (condition or specific growth rate).

Temperature model	Effect	Condition (% relative weight)			Specific growth rate (day^{-1})		
		R^2	$F_{[1,6]}$	P	R^2	$F_{[1,6]}$	P
Minimum	Treatment	0.89	0.9	0.392	0.45	0.0	0.883
	Site		**16.9**	**0.006**		1.6	0.258
	T_{min}		**12.1**	**0.013**		0.7	0.450
	$T_{min} \times$ Treatment		0.01	0.937		0.1	0.784
Maximum	Treatment	0.80	1.4	0.280	0.42	0.0	0.863
	Site		**8.2**	**0.029**		**3.9**	**0.096**
	T_{max}		0.2	0.716		0.4	0.538
	$T_{max} \times$ Treatment		0.5	0.514		0.0	0.923

Note: Bold F statistics and P values denote effect significant ($\alpha = 0.10$) in ANCOVA models. "Site" is the covariate discharge in both growth models and the minimum temperature–condition model; it is invertebrate biomass for the maximum temperature–growth model.

Table 4. Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) analysis of covariance (ANCOVA) results by temperature metric (minimum, T_{min}; maximum, T_{max}) and response variable (condition or specific growth rate).

Temperature model	Effect	Condition (% relative weight)			Specific growth rate (day^{-1})		
		R^2	$F_{[1,6]}$	P	R^2	$F_{[1,6]}$	P
Minimum	Treatment	0.76	1.7	0.243	0.52	1.4	0.287
	Site		**13.4**	**0.011**		2.1	0.199
	T_{min}		1.4	0.287		0.0	0.928
	$T_{min} \times$ Treatment		0.6	0.470		0.9	0.384
Maximum	Treatment	0.83	**5.8**	**0.054**	0.55	1.6	0.259
	Site		**17.4**	**0.006**		3.6	0.106
	T_{max}		0.8	0.412		0.3	0.610
	$T_{max} \times$ Treatment		**4.1**	**0.090**		1.2	0.319

Note: Bold F statistics and P values denote effect significant ($\alpha = 0.10$) in ANCOVA models. "Site" is the covariate discharge for condition analyses and invertebrate biomass for growth analyses.

trout distribution, however, may more strongly affect other, more sensitive life stages (e.g., embryos; see below).

We hypothesize that ultimately, the limiting effect of cold temperatures on brown trout occurs during a life stage prior to the one used in our experiment. First, it is clear that subadult and adult brown trout can access (Budy et al. 2004) and perform well (Elliott et al. 1995; this study) at sites where their abundance is consistently negligible. If they also occasionally spawn at high-elevation sites, which they presumably do, perhaps temperature conditions are unsuitable for a phase occurring between the egg and subadult stage. Because eggs incubate during extreme winter conditions and are the most temperature-sensitive life stage in the entire brown trout life cycle (Elliott 1994), we posit that the recruitment bottleneck occurs during the embryo stage. While brown trout survival through egg incubation decreases markedly below 4 °C (Ojanguren and Braña 2003), temperatures measured during the period of brown trout incubation (November–March) at upper Logan River reaches are well below this threshold (1–2 °C; Budy et al. 2003). Temperatures measured at sites dominated by brown trout are consis-

tently between 3 and 4 °C. In conclusion, extreme cold incubation conditions may offer the best explanation for the lack of self-sustaining, local populations of brown trout at high elevations of our system as well as in other western North American streams (Vincent and Miller 1969; Rahel and Nibbelink 1999; de la Hoz Franco and Budy 2005).

The role of biotic interactions in zonation

We provide evidence for an asymmetric, negative effect of brown trout presence on cutthroat trout. Allopatric cutthroat trout attained higher condition and growth than did their sympatric counterparts at nearly all sites. Sympatric brown trout, in contrast, performed better than allopatric brown trout everywhere. Our use of a substitutive approach for assessing competition (Fausch 1998) indicates that interspecific competition (with brown trout) is more intense than intraspecific competition for cutthroat trout, while for brown trout the reverse is true. Further, the fact that the condition differential (between treatment groups) for brown trout was consistent (i.e., there was no reversal in competitive ability) at all temperatures suggests a lack of temperature-mediated

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Table 5. Summary of experimental studies on temperature-mediated competition among salmonid species.

Upstream species	Downstream species	Arena (density)	Temperature range	Performance measure(s)	Main result(s)[a]	Reference
Greenback cutthroat trout (*Oncorhynchus clarkii pleuriticus*)	Brook trout (*Salvelinus fontinalis*)	1.8 m × 0.6 m lab stream (5.5 fish·m⁻²)	Constant 10 and 20 °C	Aggressive acts; microhabitat use; frequency of dominance	Brook > cutthroat (all responses) at 20 °C; at 10 °C, brook trout = cutthroat trout in microhabitat use and dominance frequency; there was temperature-mediation of aggression (i.e., brook trout were more aggressive at high temperatures; cutthroat trout were more aggressive at low temperatures)	De Staso and Rahel 1994
Brook trout	Rainbow trout (*Oncorhynchus mykiss*)	1-m² pools and riffles in a lab stream (2 fish·m⁻²)	Constant 13 and 18 °C	Aggressive acts; food acquisition; growth	Brook trout > rainbow trout for all response measures at both 13 and 18 °C	Magoulick and Wilzbach 1998*b*
Greenback cutthroat trout	Brook trout	190-L lab aquaria (12.7 fish·m⁻²)	Diel cycles of 1–8 °C and 9–17 °C	Food acquisition; aggressive acts; microhabitat use	Larger brook trout dominated overall, with greater aggression at 9–17 °C; greenback cutthroat trout never attained an advantage	Novinger 2000
Whitespotted char (*Salvelinus leucomaenis leucomaenis*)	Dolly Varden char (*Salvelinus malma*)	2.8 m × 0.35 m lab stream (51 fish·m⁻²)	Constant 6 and 12 °C	Aggressive acts; foraging frequency; microhabitat use; growth; survival	Whitespotted char generally dominated over Dolly Varden char across temperatures and responses; their effect was diminished at 6 °C, suggesting a mediating role of temperature	Taniguchi and Nakano 2000
Brook trout	Brown trout (*Salmo trutta*)	2 m × 0.6 m lab stream (2.5 fish·m⁻²)	Constant 3, 6, 10, 20, 22, 24, and 26 °C	Food acquisition; aggressive acts	Brook = brown at all temperatures; brook trout had greater mortality than brown trout because of high temperatures	Taniguchi et al. 1998
Bonneville cutthroat trout (*Oncorhynchus clarkii utah*)	Brown trout	20-m² in situ enclosures (0.40 fish·m⁻²)	Ambient cycle range: mean = 8–13 °C; min.–max. = 6.1–17.5 °C; see Table 2	Growth and condition	Brown trout were unaffected by cutthroat trout; cutthroat trout condition was reduced by brown trout at all temperatures, excluding 17.5 °C	This study

[a]"Species 1 > species 2" denotes that species 1 was a more successful competitor than species 2.

competitive resistance to brown trout invasions by cutthroat trout.

While the potential for cutthroat trout displacement from downstream habitats due to brook trout invasions is widely acknowledged (Dunham et al. 2002; Novinger and Rahel 2003; Quist and Hubert 2004), the potential for a similar effect of brown trout is rarely considered. Distributional patterns in the Bonneville Basin (de la Hoz Franco and Budy 2005) indicate that displacement may have occurred, and we provide insight into a possible mechanism. While we did not document the behavioral origin of brown trout impacts in our study, dominance via aggression (i.e., interference competition) is a likely candidate. In a lab study of brown trout – greenback cutthroat trout (*Oncorhynchus clarkii pleuriticus*) interactions, brown trout were more aggressive, attained the best foraging positions, and thereby suppressed cutthroat trout feeding (Wang and White 1994). In other studies, brown trout dominated over masu salmon (*Oncorhynchus masou masou*), whitespotted char (*Salvelinus leucomaenis leucomaenis*), and were unaffected by steelhead trout (*O. mykiss*; Kocik and Taylor 1994; Hasegawa et al. 2004). Brown trout are thus well established as a dominant competitor among salmonids.

In summary, we believe the downstream limit of cutthroat trout is determined by the presence of and their interactions with brown trout. Further, the observation that brown trout performed consistently better with cutthroat trout in our experiment indicates that temperature rather than competitive resistance likely explains the absence of brown trout from high elevations.

Salmonid temperature-mediated competition experiments

Temperature-mediated competition has been proposed as the primary cause of salmonid zonation in rivers and streams throughout the world (Fausch 1989; Fausch et al. 1994; de la Hoz Franco and Budy 2005). In addition to our field experiment, this proposition has been evaluated for several salmonids using a variety of performance responses (Table 5). Encompassing a wide range of temperatures and experimental densities, a simultaneous consideration of these studies illustrates two patterns. First, downstream species are superior competitors in two-species systems (but see Magoulick and Wilzbach 1998*b*); and second, reversals in dominance due to cold temperatures — whereby the upstream species attains superiority — rarely occur (but see De Staso and Rahel 1994).

The lack of a competitive reversal has been attributed to at least one of three causes. First, while competitive effects of downstream species may be dampened under cold conditions, temperatures may not have been sufficiently extreme to induce dominance reversals (Taniguchi et al. 1998; Taniguchi and Nakano 2000). The fact that reversals have not been observed at temperatures as low as 1–3 °C (see Table 5) indicates that this explanation is unlikely. Second, a common thermal physiology for both species might also prevent a competitive reversal (Novinger 2000). Given that thermal tolerance and temperature-related mortality differed among species in at least two studies (see Table 5) suggests that this, too, is an unlikely explanation.

Finally, the lack of a dominance reversal suggests that abiotic factors rather than temperature-mediated competition preclude downstream species from high-elevation reaches. Specifically, downstream species may be unable to avoid starvation (Taniguchi et al. 1998; Taniguchi and Nakano 2000) and (or) complete their entire life cycle (e.g., embryonic phases; De Staso and Rahel 1994; Novinger 2000) under cold conditions, even if juveniles or adults experience positive growth under short-term, experimental conditions. We believe that these are more plausible explanations for why reversals were rarely observed and are deserving of further scientific attention. In summary, our study adds to a growing body of evidence suggesting that salmonid zonation is not the result of condition-specific competition.

Implications for cutthroat trout conservation

The potential for negative effects of brown trout on cutthroat trout and the likely limitation of the present distribution of brown trout by abiotic conditions have important implications for the conservation of cutthroat trout. First, management actions involving the direct removal of brown trout should be considered if increasing the abundance and spatial extent of cutthroat trout is desirable (e.g., Lentsch et al. 1997). Such actions have been aggressively pursued for the conservation of cutthroat trout in the presence of invasive brook trout (Thompson and Rahel 1996; Novinger and Rahel 2003; Peterson et al. 2004), and the demographic benefits (e.g., increased age-0 cutthroat trout survival) are promising (Peterson et al. 2004). Thus, the eradication of exotic brown trout may benefit cutthroat trout where these species co-occur.

While brown trout invasions may have slowed in streams like the Logan River (i.e., they have had ~100 years to invade suitable habitats), this may change under future climatic and land-management scenarios. If temperatures increase, brown trout distributions may shift upstream (Keleher and Rahel 1996) and thus reduce the extent of remaining cutthroat trout populations. Indeed, brown trout distributions have been observed to change rapidly in invaded systems during periods of climate change (e.g., drought; Closs and Lake 1996). While there is little managers can do to affect climate, they can take measures to reduce water temperature changes related to land management (e.g., changes in vegetation, Theurer et al. 1984).

In conclusion, brown trout effects are currently recognized as only a minor threat to cutthroat trout persistence (Quist and Hubert 2004); secondarily to the respective hybridization and displacement impacts of rainbow and brook trout (Dunham et al. 2002; Weigel et al. 2003). However, we suggest that exotic brown trout invasions could have serious consequences for cutthroat trout. Thus, brown trout should be considered more explicitly in cutthroat trout conservation efforts.

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