

## Experimental Effects of Nonnative Brown Trout on the Individual- and Population-Level Performance of Native Bonneville Cutthroat Trout

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**Abstract.**—In western North America, nonnative trout invasions threaten the persistence of native cutthroat trout *Oncorhynchus clarkii* subsp. through competition, predation, and hybridization. While small-scale individual-level studies on nonnative–native fish interactions have helped elucidate mechanisms of impact, very few investigations have occurred at a scale consistent with that of species replacement. Thus, large-scale population-level studies are needed to understand the effects of nonnative fish as well as to more effectively conserve native fishes in the presence of nonnative fish. For this reason, we conducted an evaluation of the effects of nonnative brown trout *Salmo trutta* on the individual- and population-level performance of native cutthroat trout using a field-experimental approach. We studied local populations of cutthroat trout in the presence and absence of brown trout in long stream reaches and subsequently compared growth, condition, stable-isotope-based measures of dietary habits, movement, and survival between treatment groups. We found clear evidence for reduced cutthroat trout growth owing to the presence of brown trout. Additionally, we observed differences in cutthroat trout dietary habits based on  $\delta^{13}\text{C}$  signatures resulting from our experimental manipulation of brown trout abundance. Finally, brown trout suppressed cutthroat trout movement but had no apparent effect on their survival. Considering previous studies, we concluded that the individual-level effects of brown trout on cutthroat trout are scale invariant. Higher-level impacts (i.e., on movement and survival), in contrast, appear to be more sensitive to the scale at which the investigation is conducted. Overall, our results indicate that brown trout can have strong negative effects on cutthroat trout performance and should therefore be more explicitly considered in native fish conservation plans.

Nonnative species invasions threaten the future of native fish diversity worldwide (Allan and Flecker 1993; Richter et al. 1997; Wilcove et al. 1998). Introduced fishes in particular, have contributed to the demise of many native fishes through predatory impacts, competitive interactions, introgressive hybridization, disease transmission, and other pathways (Witte et al. 1992; Dunham et al. 2002; Weigel et al. 2003; Koel et al. 2005). Nonnative fish invasions may also have indirect consequences for native species encompassing multiple trophic levels or tiers of biological organization (Townsend 2003; Mills et al. 2004); under extreme circumstances, their effects transcend aquatic–terrestrial ecosystem boundaries (Spencer et al. 1991; Baxter et al. 2004). Ultimately, fish introductions can compromise biogeographic barriers and facilitate the homogenization of formerly distinct regional fish assemblages (Rahel 2000).

Throughout western North America, introduced fishes have displaced (Dunham et al. 2002) many populations or entire subspecies of native cutthroat

trout *Oncorhynchus clarkii* subsp. through a variety of mechanisms (Krueger and May 1991; Behnke 1992; Dunham et al. 2002). The effects of nonnative rainbow trout *O. mykiss* (via hybridization; Weigel et al. 2003) and brook trout *Salvelinus fontinalis* (via competition and predation; Griffith 1988; De Staso and Rahel 1994; Novinger 2000) on cutthroat trout have been particularly well documented and occur throughout a broad geographic area. Impacts of these two species are thus regarded as a major impediment to cutthroat trout conservation (Griffith 1988; Allendorf and Leary 1988; Dunham et al. 2002). Consequently, much effort has been directed at eliminating these species from or preventing their access to current or former cutthroat trout habitats (Thompson and Rahel 1996; Novinger and Rahel 2003). In contrast, the impacts of the widely introduced brown trout *Salmo trutta*, which are of Eurasian origin (Fuller et al. 1999), on native cutthroat trout have generally been assumed to be negligible in the context of cutthroat trout conservation (e.g., Quist and Hubert 2004), although this has been rarely studied. Despite this, brown trout are recognized as a threat to native fish diversity elsewhere in the world (Lowe et al. 2000; Townsend 2003) and recent investigations suggest that they may similarly threaten

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Received December 11, 2005; accepted May 24, 2006  
Published online November 2, 2006

cutthroat trout persistence in North America (McHugh and Budy 2005).

Observational and experimental studies on species distributions, abundance patterns, and interactions suggest that the effects of brown trout on native cutthroat trout are considerable. Brown trout and cutthroat trout segregate longitudinally within rivers where they both occur, and across watersheds containing both species their abundances are strongly and negatively correlated (de la Hoz Franco and Budy 2005; Quist and Hubert 2005). These patterns suggest that cutthroat trout displacement has occurred historically (e.g., "the ghost of competition past", Connell 1980). Laboratory and field experiments additionally confirm the potential for negative brown trout effects in a controlled replicated context. For example, Wang and White (1994) documented the strong tendency for behavioral dominance by brown trout over cutthroat trout using observational methods in artificial streams. In addition, a recent field-enclosure experiment confirmed that there are growth and condition consequences to behavioral interactions between these two species (McHugh and Budy 2005). The high degree of overlap in their North American distributions creates widespread opportunity for brown trout to exert a negative impact on cutthroat trout populations; in the Great Basin alone, which is home to several native cutthroat trout subspecies, brown trout are perhaps the most abundant wild salmonid and are found in nearly every major coldwater stream network (Sigler and Sigler 1996).

Despite suggestions that brown trout contribute to the imperiled status of cutthroat trout, additional questions remain that should be considered before the development of a comprehensive brown trout management strategy. First, by confining mobile vertebrates at high densities, a consequence of the inherent tradeoffs of experimental ecology (Underwood 1997), previous studies may have produced interspecific interactions that are not representative of those occurring naturally. Further, it is unknown whether the demonstrated suppression of individual-level cutthroat trout performance (e.g., reduced growth) by brown trout results in a concomitant population-level response (e.g., reduced survival), given the potential relative role of other ecological factors (Taniguchi and Nakano 2000; Peterson and Fausch 2003). This potential for context dependency suggests that results from small-scale experiments may not extrapolate well to explain large scale phenomena (i.e., species replacement; Lodge et al. 1998; Englund and Cooper 2003). To resolve this issue, large-scale population-level investigations on the effects of nonnative species on native fishes are

necessary (Peterson and Fausch 2003; Peterson et al. 2004a).

We present the results of a large-scale experimental study on the effects of brown trout on Bonneville cutthroat trout (*O. clarkii utah*), an imperiled subspecies endemic to the Bonneville Basin of Utah, Wyoming, Idaho, and Nevada. Specifically, we compared individual (growth, condition, dietary habits) and population-level (movement, survival) performance between local populations of cutthroat trout living in the experimental presence and absence of brown trout. We present evidence of the potential for brown trout to suppress the performance and influence the feeding behavior of native cutthroat trout in a largely unconfined setting.

## Methods

### *Study Site Description*

We conducted our experiment at three sites occupying two northern Utah streams (Upper Rock Creek [41°36'32"N, 111°35'12"W], Lower Rock Creek [41°38'06"N, 111°33'39"W], and Curtis Creek [41°36'23"N, 111°32'34"W]). Following a preliminary survey of streams in the region, we selected sites based on the following considerations: (1) local sites needed to contain both brown and cutthroat trout; (2) sites had to represent the spectrum of habitat conditions within which cutthroat trout are currently found in the Bonneville Basin; and (3) sites had to be small enough to facilitate effective backpack electrofishing and accommodate the use of small weirs.

The headwaters of Rock and Curtis creeks originate on the western slope of the Monte Cristo Range of northern Utah; both streams flow westward through narrow canyons toward a wide valley, where they join the Blacksmith Fork River. While Rock and Curtis creeks are separated by less than 5 km, they differ considerably in habitat conditions (Table 1; see Methods: Environmental Variable Measurement for details). The climate of the region is characterized by cold snowy winters and hot dry summers, yielding a hydrograph dominated by a spring-snowmelt flood followed by stable base flow conditions. Cutthroat trout, brown trout, and sculpin *Cottus* spp. comprise the fish fauna of both sites. Rock Creek also contains mountain suckers *Catostomus platyrhynchus*.

### *Experimental Design and Overview*

We designed an experiment to evaluate the effects of brown trout on cutthroat trout performance following a strategy similar to that used in a previous small-scale field experiment (McHugh and Budy 2005). Specifically, we raised cutthroat trout in the presence of high (hereafter referred to as sympatry) and low (hereafter,

TABLE 1.—Site-level (elevation, slope, temperature, and discharge) and reach-level (all others) habitat attributes for reaches used in our study of native Bonneville cutthroat trout in the presence (SYM) or absence (ALLO) of brown trout. See Methods for details on measurement procedures. Abbreviations are as follows: LWD = large woody debris, DSO = median particle size, and EPTD = insect orders Ephemeroptera, Plecoptera, Trichoptera, and Diptera.

Habitat attribute	Curtis Creek		Upper Rock Creek		Lower Rock Creek	
	ALLO	SYM	ALLO	SYM	ALLO	SYM
Elevation (m)		1,758		1,818		1,697
Slope		0.037		0.014		0.023
Mean Temperature (°C)						
Mean		11.1		15.9		16.7
Range		6.6–17.3		8.0–23.5		8.9–24.5
Discharge (m <sup>3</sup> /s)		0.193		0.068		0.068
Reach length (m)	223	261	314	310	390	355
Wetted width (m)	3.9	4.7	2.6	2.8	3.2	3.0
LWD (pieces/km)	313	287	70	39	131	245
% Overhanging vegetation	26	48	31	15	76	50
% Undercut bank	26	33	19	24	29	20
D50 (mm)	64	45	5	34	18	28
% Fines	13	13	50	19	24	23
Pool volume (m <sup>3</sup> )	4.4	5.7	9.2	9.5	5.1	3.6
Pool frequency (number/km)	58	50	61	55	38	68
EPTD density (number/m <sup>2</sup> )	7,641	7,067	4,011	2,900	6,533	4,252
EPTD biomass (mg/m <sup>2</sup> )	778	672	805	558	991	653
Trout density (number/km)	319	484	135	210	100	203

allopatry) relative brown trout densities and subsequently compared growth, condition, diet, movement, and survival between the two groups. In contrast to our earlier study, however, we increased the scale of our investigation by using local populations of trout occupying long reaches (range: 223–390 m; Table 1) as our experimental units. We replicated experimental treatments at three sites (Upper Rock, Lower Rock, and Curtis creeks) to assess summer growth, condition, diet, and movement; we additionally completed a longer-term survival evaluation at our Lower Rock Creek site only.

Before setting up treatments within sites, we isolated two adjacent reaches from each other and the remaining stream using weirs equipped with bidirectional trap boxes. Weirs were constructed out of 6.4-mm black plastic mesh stretched over a PVC frame and secured to the streambed with cable ties and rebar (see Peterson et al. 2004a for a description of trap design). To ensure that weirs served as complete barriers to fish movement, we also buried a 30-cm skirt at the base of each weir. After installing weirs, we established treatments using two-pass electrofishing depletion methods. For each reach within a site, we made two separate electrofishing passes (backpack electrofisher settings: 250–300 V, 30 Hz, 4  $\mu$ s) and netted all trout encountered and retained them in live wells. We were restricted to two electrofishing passes for establishing treatments due to logistical constraints; however, our focus was on creating a substantial difference in species composition between treatments, not on estimating abundance using depletion-based methods.

Captured fish to be used in the experiment were anesthetized with tricaine methanesulfonate (MS-222), weighed, measured (total length [TL]), and tagged (cutthroat trout: PIT tag and T-bar anchor tag; brown trout: T-bar anchor tag only). Upon recovery, we returned only cutthroat trout to allopatric reaches and both species to sympatric reaches. In an attempt to achieve a similar total trout density (i.e., across treatments within sites) and an approximately 1:1 ratio of brown to cutthroat trout (i.e., within sympatric reaches) among fish released at the start of the experiment, we augmented local densities with fish collected immediately upstream or downstream from experimental reaches. We made no conscious manipulations to the size structure of experimental trout populations. Thus, with the exception of species composition, the characteristics of trout populations in study reaches were similar to those present before setting up the experiment.

The experiment commenced in the summer of 2004. We checked and cleaned traps daily for a 72-d summer period and fish were minimally disturbed during this time. In mid-September 2004, the growth, condition, diet, and movement phase of our experiment was completed, and we therefore sampled fish in all reaches using the same two-pass methods described above; fish were weighed, measured, and released at this time. While we initially hoped to extend the experiment through the autumn and winter at all sites for a longer-term survival evaluation, leaf-litter inputs and flooding precluded maintaining weirs as barriers at all but one site (Lower Rock Creek). We therefore terminated the

experiment in Upper Rock and Curtis creeks in September, but extended it through spring 2005 in Lower Rock Creek. To estimate survival and recapture probabilities for cutthroat trout by treatment group in Lower Rock Creek, we additionally sampled fish (i.e., using two-pass depletion methods) at the end of autumn (13 November 2004) and winter (15 March 2005) at this site. Thus, there were two periods in our experiment, each with a slightly different focus: (1) a 2.5-month summer period for which growth, condition, diet, and movement were assessed across three sites; and (2) a 9-month summer-to-spring period for which survival was evaluated at one site only (i.e., the survival component of our study was not replicated).

#### *Environmental Variable Measurement*

In order to describe habitat conditions across study sites and reaches, we measured several physical and biological habitat variables in all sites and reaches (Table 1). Site elevation (m) and slope (m/m) were measured from 7.5-min U.S. Geological Survey (USGS) topographical maps. At each site, water temperature was measured hourly during the summer trial using a single data logger located in the stream between reaches; temperature was summarized based on the mean, minimum, and maximum value. We quantified discharge based on a single base flow measurement made at each site.

In addition, we measured several variables within individual reaches at each site. We measured reach length and wetted width (at 10-m intervals), and we counted all pieces of large woody debris (LWD;  $\geq 1$  m length,  $\geq 10$  cm diameter) within the bankfull channel. We noted the presence or absence of overhanging vegetation and undercut banks at each width cross section (i.e., at 10-m intervals) to estimate the percentage of the reach with these cover features present. We quantified the median particle size (D50) and level of fine-sediment deposition using the pebble-count technique (Wolman 1954). We conducted a separate pebble count on two systematically spaced riffles in each reach. Pool volume was estimated as the product of residual depth (i.e., maximum depth – pool-tail depth) and surface area, averaged across a reach. We also quantified reach-level pool frequency (number/km).

We measured two biotic habitat variables: prey abundance and trout density. We quantified an index of prey abundance based on benthic invertebrate samples (30-cm  $\times$  30-cm Surber sampler) collected within the visual center of three riffles (~25, 50, and 75% upstream from lower end) in each reach. Samples were preserved in 95% ethanol; invertebrates were identified to order and enumerated under a dissecting micro-

scope. We measured up to 30 individuals and estimated biomass based on length-mass regressions (Benke et al. 1999) for each of the insect orders: Ephemeroptera, Plecoptera, Trichoptera, and Diptera (collectively referred to as EPTD). For a given reach, samples were averaged and summarized as density (number/m<sup>2</sup>) and biomass (mg/m<sup>2</sup>). Finally, we estimated trout density (number/km) using a depletion estimator (Zippin 1958) based on the number of brown and cutthroat trout captured in each of two successive electrofishing passes made on the postsummer sampling occasion. While abundance estimates based on two-pass depletions are likely negatively biased, especially in situations with low capture efficiency (Riley and Fausch 1992), our measured values (mean = 0.76, range: 0.60–0.84) were at the high end of those typically observed for salmonids in stream environments (e.g., Riley and Fausch 1992; Peterson et al. 2004b; Rosenberger and Dunham 2005).

#### *Performance Measures*

*Individual-level measures.*—We evaluated the performance of individual cutthroat trout based on instantaneous (specific) growth ( $G = [\log_e W_{\text{final}} - \log_e W_{\text{initial}}]/t] \times 100$ , where  $W$  is weight [g] and  $t$  is time [d]) and pre- and posttrial condition (% relative weight;  $W_r = 100 \cdot W/W_s$ , where  $W$  is observed weight and  $W_s$  is predicted weight based on the standard length–weight relationship [ $W_s = 6.193 \times 10^{-5} \cdot \text{TL}^{2.670}$ ] from McHugh and Budy 2005).

Additionally, we used naturally occurring stable isotopes to evaluate the dietary habits of the sympatric brown trout and allopatric and sympatric cutthroat trout used in our experiment. Specifically, we evaluated the trophic position of individuals and the ultimate source of energy in their diet based on the levels of <sup>15</sup>N and <sup>13</sup>C in their tissue, respectively (Post 2002); in doing this, our goal was to evaluate diet overlap between species and to determine the experimental effects of brown trout removal on cutthroat trout diet. While we do not consider stomach contents in this study, others have considered the relationship between stomach content- and stable isotope-based perspectives on the trophic relationships of species and have observed concordance between approaches (Genner et al. 1999; McGrath 2004; Clarke et al. 2005). In contrast to identifying separation by direct diet analysis (i.e., from stomach contents), organisms may arrive at a similar isotopic signature by consuming different prey in varying proportions (Matthews and Mazumder 2004). Thus, although differences in isotopic signatures can indicate trophic separation, similarities can only suggest diet overlap.

To assess stable isotope composition, we collected dorsal muscle tissue (5-mm biopsy plug) from five similarly sized (150–200 mm TL) sympatric and allopatric cutthroat trout and five sympatric brown trout from each site during the postsummer sampling event (i.e.,  $n = 45$  isotope samples total). We dried tissue for 24–48 h at 60°C, ground it to a powder, and shipped encapsulated samples to the University of California–Davis Stable Isotope Facility for determination of isotopic signatures. Isotope ratios (i.e., heavy : light) were evaluated and expressed as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  per mille (‰) values relative to the ratios of the standards Pee Dee Belemnite and atmospheric  $\text{N}_2$ , respectively.

*Population-level performance measures.*—The population-level response of cutthroat trout to brown trout presence was assessed based on two variables, movement and survival. We computed movement as the proportion of unique recaptures (i.e., total number marked fish recaptured in traps per number of marked fish released initially) made at both upstream and downstream traps during the summer period at all sites. To maintain species composition during the experiment, we did not allow “emigrants” to leave when recaptured (experimental fish were released at the midpoint of their reach of origin), nor did we allow “immigrants” to enter reaches (nonexperimental fish were shuttled around). Thus, our movement variable is a measure of the tendency of a population to emigrate, rather than a true emigration rate.

Finally, we assessed the effect of brown trout on cutthroat trout survival within an unreplicated, experimental context at our Lower Rock Creek site only. To do this, we used a Cormack–Jolly–Seber (CJS) survival modeling approach, which requires a minimum of one release and more than two recapture occasions to provide robust estimates of survival and recapture parameters (Lebreton et al. 1992). Our CJS-survival evaluation is based on a 7 July 2004 release and the three subsequent sampling occasions, spanning a 251-d summer–autumn–winter period. Lastly, because our population was closed to immigration or emigration during the experiment, our estimate is for true survival ( $S$ ) rather than apparent survival ( $\phi$ ; see the subsection on statistical analysis for more CJS details).

### Statistical Analysis

We analyzed individual-level (growth, condition, diet) and population-level (movement, survival) performance measures separately. First, given the hierarchical structure of our individual-level data set (i.e., individuals nested within sites), we compared growth and condition (initial and final) of allopatric and

sympatric cutthroat trout individuals using a multilevel analysis of variance (ANOVA) approach (Wagner et al. 2006). Specifically, we modeled the performance of individuals as a function of treatment group (i.e., allopatry or sympatry, a fixed factor) and site (i.e., Curtis, Lower Rock, or Upper Rock creek, a random blocking factor) effects. We also included initial size (TL, a fixed factor) as a mean-centered covariate in our models, given the known dependence of growth and condition on fish TL. We contrasted stable isotope-based measures of individual diet (i.e.,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  tissue content) between allopatric and sympatric cutthroat trout and sympatric brown trout groups using a similar approach. However, given that we intentionally sampled fish of similar TL for stable isotopes, we did not include a size effect in this analysis; thus, our  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  models included only group and site effects.

We performed growth, condition, and stable isotope contrasts using the MIXED procedure in the Statistical Analysis System 9.1 (SAS Institute 2005). Thus, we fit models and assessed the significance of fixed model effects based on  $F$ -tests (Type-III sums of squares). When the treatment  $\times$  TL effect was significant in either the growth or condition models, we contrasted the least-squares (i.e., model-adjusted) mean response at three different sizes (150, 225, and 300 mm TL; Milliken and Johnson 2000). If the group effect was significant in the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  models, we additionally contrasted mean isotope values between allopatric and sympatric cutthroat trout and sympatric brown trout using Tukey’s honestly significant difference (HSD) post hoc test. We evaluated the proportion of random error due to site-level ( $\sigma_s^2$ ) and individual-level ( $\sigma_e^2$ ) variation based on intraclass correlation coefficients,  $\rho$  [e.g., for site,  $\rho_s = \sigma_s^2 / (\sigma_s^2 + \sigma_e^2)$ ].

At the population level, we evaluated the effect of brown trout on cutthroat trout movement patterns and survival. First, we compared movement between treatment groups using a mixed ANOVA model incorporating both treatment and site (i.e., a random blocking factor) effects. Thus, we evaluated the effect of treatment group membership on movement rates while also accounting for random variation in this response due to differences among sites. As above, we assessed the significance of fixed model effects based on  $F$ -tests performed using the MIXED procedure in SAS. For all hypothesis tests, statistical significance was determined using an  $\alpha$ -level of 0.10.

Finally, we evaluated the effect of brown trout on cutthroat trout survival. However, as discussed above, this parameter was estimated and contrasted at the Lower Rock Creek site only. We evaluated survival effects following the modeling strategy of Lebreton et al. (1992) using Program MARK (White and Burnham

1999) within a corrected Akaike information criterion ( $AIC_c$ )–based model selection framework (Burnham and Anderson 2002). First, we constructed a list of candidate models that reflected biological hypotheses on factors affecting survival. We were primarily interested in evaluating treatment effects (trt) in this context; however, given that survival and recapture probabilities are usually size dependent (Peterson et al. 2004a; Peterson et al. 2004b), we also considered fish size (size, measured as TL in mm) as an individual covariate in our analysis. Owing to limited the number of marked fish ( $n_{\text{allopatry}} = 57$ ;  $n_{\text{sympatry}} = 28$ ) and recapture occasions (i.e., 3), we modeled survival for the entire 9-month time period only and therefore did not assess survival between encounter occasions. Our most fully parameterized (i.e., global) model consisted of treatment group and size effects operating interactively (i.e., trt  $\times$  size).

Following this approach, we first completed a recapture probability analysis, during which we fit five models with a varying recapture structure (i.e., the global and four reduced versions; Appendix) and a constant survival structure (i.e.,  $S[.]$ ). From this, we determined that the best model for recapture probability included treatment and size effects operating additively [i.e.,  $P(\text{trt} + \text{size})$ ]. Using this recapture structure, we fit five different survival models to our data set and ranked them according to  $\Delta AIC_c$  and compared them based on AIC weights,  $w_i$  [ $w_i = e^{-0.5\Delta AIC_{ci}} / \sum e^{-0.5\Delta AIC_{ci}}$ ; Burnham and Anderson 2002] and model evidence ratios (i.e., ratio of the two models'  $w_i$ s). Finally, we extracted maximum likelihood estimates of survival and recapture parameters (and SEs) for treatment groups using either the best model or model averaging, depending on whether or not there was a clear "winner" in our candidate set.

## Results

We installed weirs, measured habitat conditions (Table 1), and established experimental populations in all reaches by 7 July 2004. Habitat conditions varied considerably across the three sites (Table 1). Curtis Creek was larger, colder, steeper, and generally more complex than the two Rock Creek sites. Despite being in the same stream, Upper and Lower Rock creek sites differed considerably. Upper Rock Creek was lower in slope and characterized by a pool–riffle channel, whereas Lower Rock was steeper. Further, though Upper Rock Creek had deeper pools on average, it was depauperate in LWD and overhanging vegetation relative to Lower Rock Creek. Given this variability in habitat conditions across sites, the incorporation of site as a random blocking factor in our analysis was appropriate.

Across the three sites, we marked and released a total of 208 cutthroat trout. In Curtis, Upper Rock, and Lower Rock creeks, respectively, sympatric cutthroat trout averaged  $250 \pm 19$  (mean  $\pm 2$  SEs),  $206 \pm 28$ , and  $195 \pm 17$  mm TL, whereas allopatric cutthroat trout averaged  $243 \pm 13$ ,  $214 \pm 18$ , and  $223 \pm 13$  mm TL at the start of the experiment. Across sites, initial cutthroat trout size did not differ between treatment groups (least-squares adjusted mean value  $\pm 2$  SEs: allopatry,  $227 \pm 23$ ; sympatry,  $217 \pm 24$ ) and sites (ANOVA with treatment and site [block] effects:  $F_{1,204} = 2.31$ ,  $P = 0.1304$ ). Further, initial total length was similar for brown trout and cutthroat trout released in sympatric reaches (least-squares adjusted mean value  $\pm 2$  SEs: allopatry,  $219 \pm 37$ ; sympatry,  $215 \pm 37$ ; ANOVA with species and site [block] effects:  $F_{1,141} = 0.17$ ,  $P = 0.6826$ ).

In this study, we took a large-scale, experimental approach to studying the impacts of brown trout on cutthroat trout. In doing so, we sacrificed some degree of experimental control to keep our experiment relevant to natural conditions. As a result of this sacrifice, our intention to establish and maintain pure allopatric treatments and a substitutive study design was lessened. Thus, our postsummer sampling indicated that we did not remove all brown trout from allopatric treatment reaches during the July set-up phase. However, through our experimental manipulation, we altered species composition toward the sympatric and allopatric treatment goals intended for each reach (Table 2). The relative abundance of brown trout differed significantly between treatments (ANOVA with treatment and site [block] effects:  $F_{1,2} = 30.39$ ,  $P = 0.0314$ ), with brown trout being four times more abundant in sympatric compared with allopatric reaches. Further, ratios of brown to cutthroat trout were considerably reduced in experimental allopatry (mean: 0.4, allopatry; 2.0, sympatry). Finally, total trout density (i.e., both species) was approximately 50% higher in sympatric versus allopatric treatment reaches (ANOVA with treatment and site effects:  $F_{1,2} = 18.49$ ,  $P = 0.0501$ ), rendering our experiment additive (Fausch 1998) in nature. We explored the association between total trout density and performance responses likely to demonstrate density dependence (e.g., growth) based on Pearson correlation coefficients.

### Individual-Level Performance

Individual allopatric cutthroat trout grew significantly more than their sympatric counterparts during the summer period. However, the difference between treatment groups depended on initial size (Tables 3, 4; Figure 1). Specifically, allopatric cutthroat trout individuals grew at a rate nearly double of that of their

TABLE 2.—Attributes of trout populations within experimental reaches, by treatment group, site, and species (BNT = brown trout; CUT = cutthroat trout). Pretreatment (i.e., July set-up phase) and posttreatment (i.e., September recapture event) density values ( $N$  [number/km], with 95% confidence intervals in parentheses) are based on two-pass depletion methods. The term BNT (%) refers to the percentage of total trout density comprised of brown trout.

Treatment group	Site	Pretreatment			Posttreatment		
		BNT ( $N$ )	CUT ( $N$ )	BNT (%)	BNT ( $N$ )	CUT ( $N$ )	BNT (%)
Allopatry	Curtis Creek	73 (49–166)	125 (112–155)	37	45 (45–49)	274 (260–286)	14
	Upper Rock Creek	71 (70–74)	17 (16–23)	81	42 (33–68)	93 (92–96)	31
	Lower Rock Creek	121 (113–137)	41 (41–43)	75	29 (29–32)	71 (67–83)	29
	Mean	88	61	64	39	146	25
Sympatry	Curtis Creek	50 (50–53)	138 (112–170)	27	185 (169–215)	300 (276–337)	38
	Upper Rock Creek	76 (60–120)	31 (28–41)	71	128 (118–147)	82 (82–85)	61
	Lower Rock Creek	157 (146–178)	30 (28–38)	84	149 (126–192)	84 (45–81)	73
	Mean	94	66	61	154	155	57

sympatric counterparts at both small (150 mm) and intermediate (225 mm) sizes, whereas growth was invariant for large individuals (300 mm). By site, growth differences were greatest within Curtis (allopatry,  $0.065 \pm 0.056\%/d$ ; sympatry,  $0.002 \pm 0.059\%/d$ ) and Upper Rock creeks (allopatry,  $0.177 \pm 0.096\%/d$ ; sympatry,  $0.103 \pm 0.071\%/d$ ) but was negligible for Lower Rock Creek (allopatry,  $0.011 \pm 0.041/d$ ; sympatry,  $0.019 \pm 0.055\%/d$ ). Finally, variation among individuals constituted the majority of random error in growth rates; the site effect accounted for greater than 25% of total random error ( $\rho_s = 0.22$ ). Further, the trend in growth across sites was unrelated to variation in total trout density (Pearson  $R = -0.10$ ).

Thus, overall, brown trout were effective at reducing cutthroat trout growth rates.

In contrast to growth, the difference in condition between treatment groups was statistically negligible at both the start and at the end of the experiment (Tables 3 and 4; Figure 2). However, there was a weak trend towards reduced condition ( $\sim 2\%$ ) among sympatric relative to allopatric cutthroat trout at the end of the trial. This difference was driven primarily by Upper Rock Creek fish, where there was a large disparity in condition between treatment groups (allopatry,  $92 \pm 4\%$ ; sympatry,  $84 \pm 6\%$ ). In Curtis and Lower Rock creeks, the difference in condition resulting from brown trout removal was less than 1%. Similar to our growth results, the site-level variance component

TABLE 3.—Mean (SE) values for individual-level (specific growth rate, [ $G$ ]; starting and ending condition, [ $W_{r,Initial}$  and  $W_{r,Final}$ ]) and population-level (emigration or movement [ $E$ ]; survival [ $S$ ]) performance measures of experimental cutthroat trout by treatment and site. Variables  $n_{rel}$  and  $n_{recap}$  are the number of fish released initially and the number recaptured at the end of summer, respectively.

Treatment group	Site	$n_{rel}$	$n_{recap}$	Individual-level measures			Population-level measures	
				$G$ (%/d)	$W_{r,Initial}$ (%)	$W_{r,Final}$ (%)	$E$	$S^a$
Allopatry	Curtis Creek	47	36	0.065 (0.028)	92.2 (1.1)	90.5 (1.2)	0.15	
	Upper Rock Creek	31	19	0.177 (0.048)	95.3 (2.2)	91.7 (2.2)	0.26	
	Lower Rock Creek	57	31	0.011 (0.021)	86.2 (1.0)	84.0 (1.0)	0.16	0.50 (0.07)
Sympatry	Curtis Creek	28	25	0.002 (0.030)	93.3 (1.9)	89.7 (1.4)	0.11	
	Upper Rock Creek	29	25	0.103 (0.036)	91.5 (1.9)	84.3 (3.0)	0.19	
	Lower Rock Creek	16	12	0.019 (0.028)	85.1 (1.7)	83.4 (1.7)	0.03	0.47 (0.07)

<sup>a</sup> Survival was assessed for Lower Rock Creek only; the estimate is based on the period extending from 7 July 2004 to 15 March 2005.

TABLE 4.—Cutthroat trout ANCOVA (growth and initial and final condition) and ANOVA (movement) results. Significant model effects are denoted by bold italics. All models also included a random site (block) effect. The degrees of freedom for the *F*-tests are (1, 142) for growth and final condition, (1, 202) for initial condition, and (1, 2) for movement.

Model	Effects	<i>F</i> -statistic	<i>P</i> -value
Growth	<b><i>Treatment</i></b>	<b>6.76</b>	<b>0.0103</b>
	<b><i>TL</i></b>	<b>68.57</b>	<b>&lt;0.0001</b>
	<b><i>Treatment</i> × <i>TL</i></b>	<b>7.74</b>	<b>0.0061</b>
Initial condition	Treatment	0.04	0.8380
	<b><i>TL</i></b>	<b>97.26</b>	<b>&lt;0.0001</b>
	Treatment × TL	0.02	0.8987
Final condition	Treatment	1.21	0.2723
	<b><i>TL</i></b>	<b>77.1</b>	<b>&lt;0.0001</b>
	Treatment × TL	0.09	0.7678
Movement	<b><i>Treatment</i></b>	<b>12.75</b>	<b>0.0703</b>

accounted for only a minimal amount of random error ( $\rho_s = 0.05$ ) and total trout density effects were negligible (Pearson *R* = 0.21).

Stable-isotope-based analyses of summer dietary habits demonstrated two general patterns of significance to our study objectives. First, based on  $\delta^{15}\text{N}$ , all fish (brown trout and both groups of cutthroat trout) fed at a similar trophic level ( $F_{2,40} = 1.04, P = 0.3639$ ). Sympatric brown and cutthroat trout and allopatric cutthroat trout individuals averaged 9.6, 9.8, and 9.8 ‰  $\delta^{15}\text{N}$ , respectively, across sites. Within sites, the greatest differences observed between groups for  $\delta^{15}\text{N}$  were in Lower Rock Creek (allopatric and sympatric cutthroat trout mean ± 2 SEs, both  $9.6 \pm 0.3\text{‰}$ ; brown trout,  $8.9 \pm 0.3\text{‰}$ ); however, even this difference (0.7 ‰  $\delta^{15}\text{N}$ ) is considerably less than the 3–4 ‰ enrichment that typically occurs between trophic levels. In contrast to growth and condition

results, the random variance due to site effects was substantial ( $\rho_s = 0.55$ ). Second, our comparison of  $^{13}\text{C}$  tissue content between experimental fish groups suggests that a shift in cutthroat trout feeding patterns occurred following the experimental removal of brown trout ( $F_{2,40} = 2.56, P = 0.0902$ ; Figure 3). Specifically,  $\delta^{13}\text{C}$  values were similar for allopatric cutthroat trout and sympatric brown trout (Tukey’s HSD,  $P = 0.7951$ ), whereas sympatric cutthroat trout differed from brown trout ( $P = 0.0834$ ). Thus, although significant overall, this pattern was strongest for Upper and Lower Rock creek fishes. In summary, cutthroat trout and brown trout segregated along a  $\delta^{13}\text{C}$  axis in sympatry (relative to allopatry). Random error in  $\delta^{13}\text{C}$  values was mostly due to variation across sites ( $\rho_s = 0.84$ ).

Population-Level Performance

Across three sites and during nearly 2.5 months, 31 (15% total) unique recaptures were made at two-way fish traps. Based on these data, we observed a significant difference in movement rates between groups, with cutthroat trout moving nearly twice as much in allopatry (least-squares mean: 0.20) compared with sympatry (0.13; Tables 3, 4; Figure 4A) and at a rate unrelated to total trout density (Pearson *R* = -0.36) on average. This disparity was consistent across sites, with movement rates being highest in Upper Rock Creek, lowest in Lower Rock Creek, and intermediate in Curtis Creek. Thus, brown trout clearly suppressed cutthroat trout movement rates.

In contrast to movement, there was no evidence for an effect of brown trout on cutthroat trout survival in Lower Rock Creek (Figure 4B). Our best model, an intercept model containing neither treatment nor size effects [i.e., *S*(.); Table 5], was 2.4 times more likely

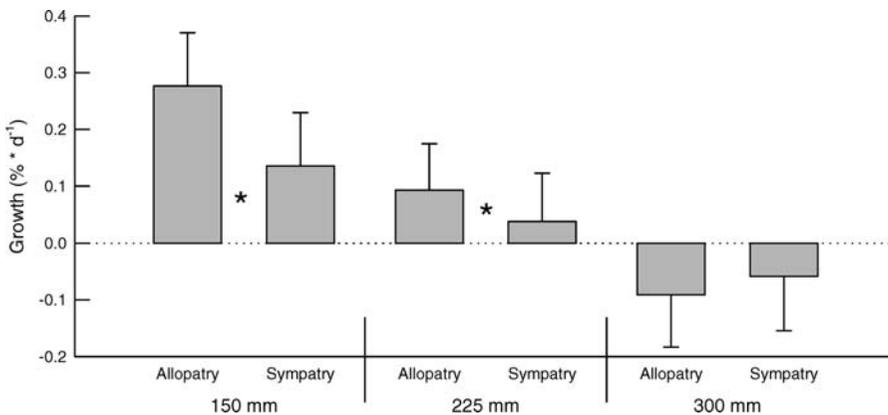


FIGURE 1.—Least-squares mean specific growth rates for small, intermediate, and large cutthroat trout during the summer period in the presence (sympatry) or absence (allopatry) of brown trout. ; asterisks denote significant differences between treatment groups within size classes ( $\alpha = 0.10$ ).

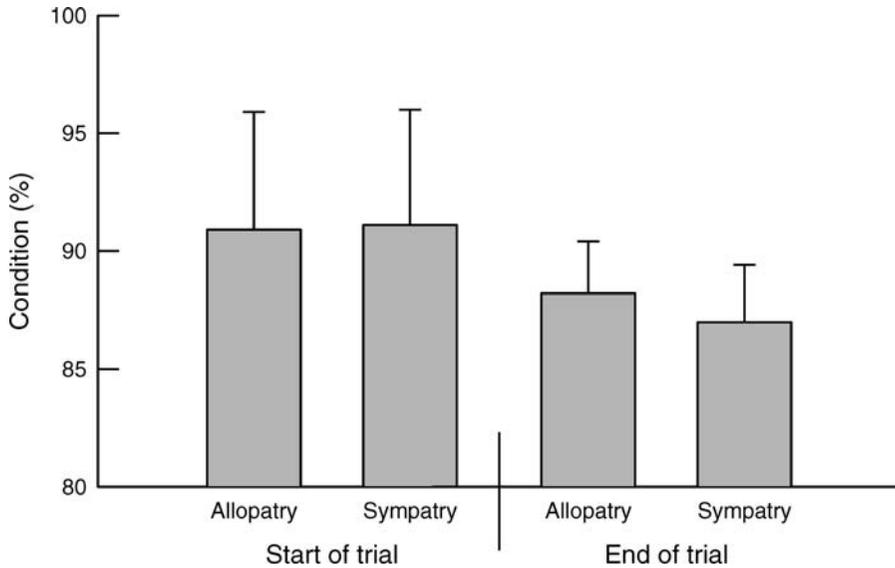


FIGURE 2.—Least-squares mean condition (% relative weight) of cutthroat trout at the start and end of the trial period in the presence (sympatry) or absence (allopatry) of brown trout. Error bars represent 2 SEs.

(based on evidence ratio) than the next best one containing treatment effects [ $S(\text{trt})$ ]. However, in terms of  $\Delta\text{AIC}_c$  there was no unambiguous “winner” among our candidate survival-model set. Thus, we used model averaging to estimate survival and recapture parameters. Model-averaged estimates of cutthroat trout survival were similar and precise for the two treatment groups (allopatric and sympatric maximum likelihood estimates  $\pm 2$  SEs:  $0.50 \pm 0.14$  and  $0.47 \pm 0.14$ ,

respectively), with a modest (3%) improvement in survival in the allopatric reach. In contrast to survival, there was evidence for an effect of brown trout presence on recapture probability (see the subsection on statistical analysis; appendix). Specifically, recapture rates were lower in the case of allopatry than in the case of sympatry (maximum likelihood estimates  $\pm 2$  SEs:  $0.81 \pm 0.10$  and  $0.97 \pm 0.06$ , respectively).

### Discussion

In order to understand, predict, and effectively prevent the impacts of invasive or nonnative species on native organisms, there is a need for experimental research conducted at the appropriate biological and spatial scales (Fausch 1998; Parker et al. 1999; Peterson et al. 2004a). Our study constitutes one of only a few experiments on nonnative–native fish interactions that simultaneously consider a relatively large spatial scale and multiple levels of biological organization. In our field study, we observed individual- and population-level responses among cutthroat trout that were directly attributable to the experimentally manipulated abundance of nonnative brown trout. First, brown trout reduced the growth of individual cutthroat trout. At the population level, cutthroat trout movement was strongly suppressed in sympatry, whereas summer-to-spring survival was minimally affected. Finally, we observed a shift in cutthroat trout dietary habits in response to brown trout presence, based on patterns in  $\delta^{13}\text{C}$  signatures in muscle tissue.

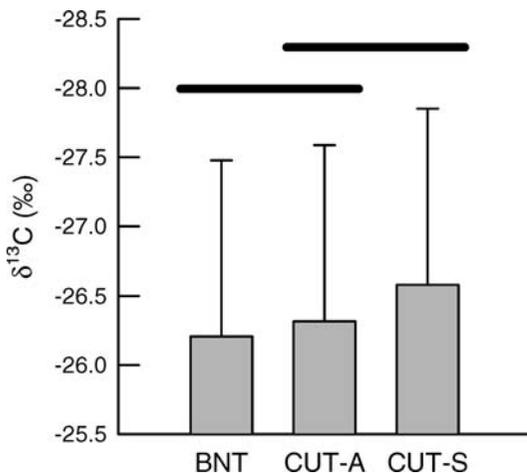


FIGURE 3.—Least-squares mean  $\delta^{13}\text{C}$  values for brown trout (BNT), allopatric cutthroat trout (CUT-A), and sympatric cutthroat trout (CUT-S). Error bars represent 2 SEs; bold horizontal bars denote groupings based on Tukey's honestly significant difference tests.

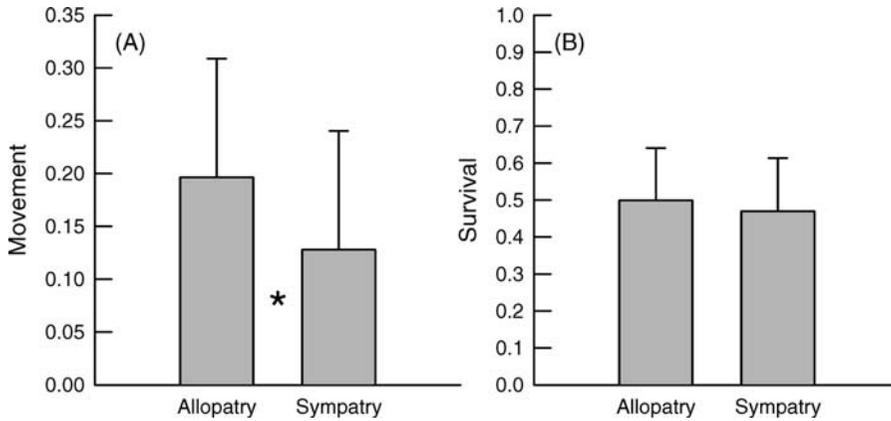


FIGURE 4.—Population-level responses of cutthroat trout in the presence (sympatry) or absence (allopatry) of brown trout. Panel (A) shows least-squares mean movement rates  $\pm$  2 SEs (the asterisk denotes a significant difference between the treatment groups [ $\alpha = 0.10$ ]). Panel (B) shows survival rates  $\pm$  2 SEs for the period 7 July 2004–15 March 2005 for Lower Rock Creek only; survival rates are model-averaged values estimated by Program MARK.

*Individual-Level Effects*

Despite the larger spatiotemporal scale and more natural, less confined setting of our controlled study, the growth and condition effects we observed are consistent with those of experiments conducted at smaller scales. Wang and White (1994) demonstrated that cutthroat trout foraging success was strongly impaired by brown trout. In sympatry, brown trout forced cutthroat trout into positions with limited access to food and ultimately reduced their consumption rates. Additionally, in a short-term (summer only), small-scale (20-m<sup>2</sup> stream enclosures) experiment, McHugh and Budy (2005) found that brown trout presence reduced cutthroat trout condition and growth. The combination of the results from these experiments and the present study suggests that the ability of brown trout to suppress individual-level performance is neither scale dependent nor an artifact of confinement, as has been the case for other studies considering multiple spatial scales (Lodge et al. 1998; Englund and Cooper 2003). Thus, we conclude that cutthroat trout experience growth reductions due to their interactions with brown trout.

Existing information suggests that the negative individual-level impacts of brown trout would translate into a population-level response among cutthroat trout for several reasons. First, at the reproductive level, because maturity may occur at a smaller size under a competitive scenario (e.g., Magnan et al. 2005) and cutthroat trout fecundity is size dependent (Downs et al. 1997; Meyer et al. 2003), brown trout impacts may lead to a reduction in the number of embryos fertilized within a given generation. Second, the period of vulnerability to predation by gape-limited piscivores will be lengthened if cutthroat trout grow more slowly in the presence of brown trout (Persson et al. 1996; Novinger 2000). Given the piscivorous disposition of adult brown trout (Mittelbach and Persson 1998; McIntosh 2000; Museth et al. 2003), this growth detriment may have serious consequences for overall mortality rates. Third, movement rates may increase under a reduced growth scenario (i.e., fish deprived of food may relocate to increase their growth; Railsback et al. 1999; Railsback and Harvey 2002; Hilderbrand and Kershner 2004), and itinerant individuals may expose themselves to hazards they would not experi-

TABLE 5.—Cormack–Jolly–Seber survival (*S*) models evaluated for Lower Rock Creek cutthroat trout. Based on the results of an initial recapture probability model selection analysis (Lebreton et al. 1992), the probability of recapture was modeled as an additive function of treatment group and size [i.e.,  $p(\text{trt} + \text{size})$ ]. Term *K* is the number of estimated parameters; see text for details on  $AIC_c$ ,  $\Delta AIC_c$ , and  $w_i$ .

Model	<i>K</i>	$AIC_c$	$\Delta AIC_c$	$w_i$	Comments
<i>S</i> (.)	4	299.6	0.0	0.50	Survival is invariant.
<i>S</i> (trt)	5	301.3	1.7	0.21	Survival varies by treatment group only.
<i>S</i> (size)	5	301.7	2.1	0.17	Survival varies by size only.
<i>S</i> (trt + size)	6	303.3	3.7	0.08	Survival varies additively by treatment group and size.
<i>S</i> (trt $\times$ size)	7	305.0	5.4	0.03	Survival varies interactively by treatment group and size.

ence otherwise or enter sink habitats (Schrank and Rahel 2004). Finally, by growing less during the summer, cutthroat trout may experience lower overwinter survival, given that lipid reserves at the onset of the winter can determine overwinter survival for temperate fishes (Ludsin and DeVries 1997; Hutchings et al. 1999; Biro et al. 2004). Thus, there are many reasons to anticipate a demographic response by cutthroat trout due to individual-level brown trout effects.

Measured stable isotope values also suggested that cutthroat trout diets varied in response to our experimental manipulation of brown trout abundance. That is, the ultimate source of energy in cutthroat trout diets (i.e.,  $\delta^{13}\text{C}$ ) differed from that of brown trout when these two species lived sympatrically. Allopatric cutthroat trout, in contrast, consumed a diet intermediate between those of their sympatric conspecifics and brown trout. Though  $\delta^{13}\text{C}$  signatures may vary due to changes in prey identity or origin (France 1995; Matthews and Mazumder 2004), either of these possible explanations for the observed pattern constitutes a change in dietary habits. Thus, brown trout may influence cutthroat trout feeding behavior.

The flexible nature of foraging behavior among putative fish competitors has been well studied. Indeed, there are many experimental examples of dietary shifts due to the removal of competitors or predators (e.g., Werner and Hall 1976). Among salmonids specifically, Dolly Varden *Salvelinus malma* can shift their feeding behavior in response to their interactions with both white-spotted char *S. leucomaenis* (Fausch et al. 1997; Nakano et al. 1999) and invasive rainbow trout (Baxter et al. 2004) in Japanese streams. Thus, they readily switch from a predominantly drift-based diet to a benthic-oriented one as food becomes more limiting. Similarly, flexible feeding behavior minimizes interactions between individual Atlantic salmon *S. salar* and brown trout and potentially facilitates the coexistence of dominant and subordinate fish (Harwood et al. 2002). Our isotope-based assessment suggests that cutthroat trout forage differently in response to their interactions with brown trout. However, given the limits to insight that can be gained from stable isotope data (Post 2002; Matthews and Mazumder 2004), this result should be considered further through some combination of stomach content-based diet surveys and behavioral studies.

#### *Population-Level Effects*

Considering previous studies and our individual-level results, the population-level responses that we observed were somewhat surprising. First, while brown trout caused a clear reduction in cutthroat trout

movement rates, results from previous experiments with other salmonids suggest that we should have observed the opposite result. For instance, Nakano (1995) observed that within single pools, sub-dominant masu salmon *Oncorhynchus masou* emigrated more frequently than dominant individuals. Keeley (2001) and Buys (2002) similarly found for steelhead (anadromous rainbow trout) and cutthroat trout, respectively, that emigration rates were elevated among individuals when they experienced intense competition in artificial streams. Assuming that these fine-scale studies are representative of movement patterns on a larger scale, our results are seemingly at odds with existing knowledge.

We believe that the apparent contradiction between our movement results and those from earlier studies is attributable, in part, to a disparity in the spatial scale of inquiry. Specifically, while previous investigators considered the effects of interactions on movement patterns within individual channel units only (i.e., within a single pool; but see Peterson et al. 2004a), fish consider and select habitats for foraging or other activities at multiple and larger scales (Torgerson et al. 1999; Baxter and Hauer 2000; Fausch et al. 2002). In their attempt to maximize growth in a dynamic environment, stream-dwelling salmonids frequently move between sites of varying forage potential, and these shifts not only occur within single pools, but also at the reach scale (Railsback et al. 1999; Gowan and Fausch 2002). Individuals respond quickly to fluctuations in food abundance by relocating to more energetically profitable sites within their reach, thereby demonstrating a high degree of knowledge of larger-scale habitat conditions (Gowan and Fausch 2002). Thus, movement effects documented in single channel units are unlikely to be concordant with those present at larger scales.

The lower movement rates observed among sympatric relative to allopatric cutthroat trout can be further understood in light of individual-based movement and habitat selection theory. Namely, individual fish should depart from their territory only if they are likely to increase their fitness elsewhere (Railsback et al. 1999; Railsback and Harvey 2002). Because despotic brown trout are more aggressive and monopolize the best foraging sites available (Fausch and White 1981; Wang and White 1994), it is unlikely that sympatric cutthroat trout in our study could improve their fitness by relocating. That is, upon finding a suitable foraging territory at the start of our experiment, the best strategy for sympatric cutthroat trout would likely be a sedentary one. In contrast, allopatric cutthroat trout should achieve fitness gains by moving often, given their greater likelihood of displacing conspecifics from

foraging sites (Wang and White 1994). Thus, our results suggest that the effects of nonnative trout on native trout movement documented in previous small-scale studies may have been scale dependent.

In contrast to the clear effect of brown trout on movement, we observed that sympatric and allopatric cutthroat trout survived similarly across a 9-month period. Though survival was slightly higher in allopatry relative to sympatry in Lower Rock Creek, the magnitude of difference ( $\sim 3\%$ ) was minor. Given our initial expectations, the growth, condition, and movement differences observed herein and in other studies, and our initial expectation of reduced cutthroat trout survival due to brown trout presence, this is a noteworthy finding. Based on our individual-level results and the findings of other population-level studies, we believe that the lack of a strong survival effect is potentially an artifact of our study design. Because we relied on the natural population structure for fish present in Lower Rock Creek before the onset of our experiment, the cutthroat trout used were, on average, quite large ( $\sim 200$  mm TL, age-2+; Fleener 1952); the smallest fish present were at least 120 mm long (TL, age-1+). However, in their large-scale study of salmonid interactions, Peterson et al. (2004a) found the strongest demographic response of cutthroat trout to invasive brook trout was among juveniles and potentially due to predation. Similarly, brown trout are known to prey heavily on juvenile salmonids in other systems (Rinne and Alexander 1995; Mayama 1999). Thus, it may simply be that because Lower Rock Creek lacked age-0 individuals, our population structure could have precluded the detection of any survival response.

The second possible cause for the lack of a strong survival effect may be the time scale of the study. Specifically, we had to terminate our survival study at the onset of the spring freshet due to the inability of our weirs to accommodate extreme high flows. Among other salmonids, and particularly brown trout, flooding is a force responsible for causing major fluctuations in population dynamics (Cattaneo et al. 2002; Lobon-Cervia 2004). The high stress and reduced consumption due to prolonged flooding coupled with the growth advantage held by allopatric cutthroat trout may have rendered a survival effect more apparent following the spring-snowmelt flood (e.g., Jensen and Johnsen 1999). However, while there are clear reasons to believe that a survival impact is possible, we must also consider that cutthroat trout survival is unaffected by brown trout or that individuals above a size threshold (e.g., age-2+) can coexist with brown trout. This suggestion is corroborated by the observed phenomenon of apparent coexistence in some streams

(de la Hoz Franco and Budy 2005; Quist and Hubert 2005) and the dynamic stability of other salmonid communities containing brown trout (Strange et al. 1992).

### *Implications*

Our results have important implications for both the conservation of cutthroat trout in the presence of nonnative brown trout and the future of small-scale inquiries on the effects of nonnative species on native fishes. In this paper, we show that individual-level effects of brown trout on cutthroat trout are scale invariant. In contrast, higher-level impacts (e.g., movement and survival) appear to be more affected by scale. Small-scale studies can provide insight into the effect of interactions on some, but not all fitness measures; large-scale studies are particularly necessary to elucidate population-level effects. To completely understand the ecology of nonnative–native fish interactions, multiscale inquiries are necessary.

Our results also extend and support the contention that brown trout contribute to the imperiled status of cutthroat trout and should be regarded as such in conservation plans (Wang and White 1994; McHugh and Budy 2005). This may involve management actions aimed at (1) preventing the expansion of brown trout into unoccupied areas; (2) removing brown trout from streams occupied by high-priority cutthroat trout conservation populations; and (3) increasing the degree of risk-assessment undertaken before stocking brown trout for sport fisheries. Our experimental data may be useful for developing models to aid in prioritizing streams for various brown trout management objectives in order to maximize the conservation benefit for cutthroat trout.

### **Acknowledgments**

We gratefully acknowledge the Quinney Foundation, the U.S. Geological Survey, the Utah Division of Wildlife Resources, and Utah State University (CURI and Water Initiative grants) for funding our study. Logistical oversight was provided by Gary Thiede. The efforts of Lora Tenant, Erin VanDyke, Callie Grover, Wes Pearce, Andy Dean, and several volunteers helped ensure the success of our work. Based on their comments on an earlier draft, Mary Conner, Todd Crowl, Susan Durham, Mike Pfrender, Dan Rosenberg, Jack Schmidt, and members of the Fish Ecology Laboratory helped improve the overall focus and clarity of this manuscript. Finally, we would like to acknowledge Brad Shepard and three anonymous reviewers for their insightful comments on our manuscript.

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### Appendix: Recapture Probability Models

TABLE A.1.—Recapture probability ( $P$ ) models evaluated for Lower Rock Creek cutthroat trout. Based on the recommended model selection analysis of Lebreton et al. (1992), survival ( $S$ ) was held constant for this analysis [i.e.,  $S(\cdot)$ ]. Term  $K$  is the number of estimated parameters, trt stands for treatment; see text for details on  $AIC_c$ ,  $\Delta AIC_c$ , and  $w_i$ .

Model	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$	Comments
$P(\text{trt} + \text{size})$	4	299.6	0.0	0.39	Recapture probability varies additively by treatment group and size.
$P(\text{trt})$	3	299.9	0.3	0.34	Recapture probability varies by treatment group only.
$P(\text{trt} \times \text{size})$	5	302.1	2.5	0.11	Recapture probability varies interactively by treatment group and size.
$P(\cdot)$	2	302.2	2.6	0.11	Recapture probability is invariant.
$P(\text{size})$	3	303.9	4.3	0.05	Recapture probability varies by size only.