

Competition between native and introduced salmonid fishes: cutthroat trout have lower growth rate in the presence of cutthroat–rainbow trout hybrids

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Abstract: When nonnative species become established within new communities, competition may play a role in determining the persistence of ecologically similar native species. In western North America, many native cutthroat trout (*Oncorhynchus clarkii*) populations have been replaced by nonnative rainbow trout (*Oncorhynchus mykiss*). Superior competitive ability of rainbow trout and cutthroat–rainbow trout hybrids is often cited for this replacement; however, few studies have tested for mechanisms that might allow introduced rainbow trout to out-compete native trout species. Our previous work found individual-based differences in swimming and foraging ability among cutthroat trout, rainbow trout, and their hybrids. In this study, we tested for the presence and strength of competition between cohorts of cutthroat trout, rainbow trout, and their reciprocal hybrids. We assayed the growth rate of juvenile cutthroat trout in allopatry versus cutthroat trout when sympatric with rainbow trout and each hybrid cross. After controlling for size and density of trout, cutthroat trout cohorts in stream channels that contained hybrid genotypes experienced lower growth than cutthroat trout in allopatry. Averaged across heterospecific treatments, cutthroat trout growth was also lower than that of cutthroat trout cohorts in allopatry. Our study suggests that juvenile cutthroat trout experience a growth disadvantage when competing against cutthroat–rainbow hybrids.

Résumé : Lorsque des espèces non indigènes se sont établies dans de nouvelles communautés, la compétition peut jouer un rôle dans la détermination de la persistance des espèces indigènes à écologie semblable. Dans l'ouest de l'Amérique du Nord, plusieurs populations de la truite fardée (*Oncorhynchus clarkii*) indigène ont été remplacées par la truite arc-en-ciel (*Oncorhynchus mykiss*) non indigène. Pour expliquer cette substitution, on évoque souvent la compétitivité supérieure des truites arc-en-ciel et des hybrides de la truite arc-en-ciel et de la truite fardée; cependant, peu d'études ont cherché à vérifier les mécanismes qui pourraient permettre à la truite arc-en-ciel de gagner la compétition avec les espèces indigènes de truites. Notre recherche antérieure a révélé des différences basées sur l'individu dans la capacité de nage et de recherche de nourriture entre la truite fardée, la truite arc-en-ciel et leurs hybrides. Dans le présent travail, nous cherchons à démontrer la présence et la force de la compétition entre les cohortes de truites fardées, de truites arc-en-ciel et de leurs hybrides réciproques. Nous avons mesuré le taux de croissance de jeunes truites fardées en conditions d'allopatrie ainsi que dans des conditions de sympatrie avec la truite arc-en-ciel et avec chacun des croisements hybrides. Après avoir tenu compte de la taille et de la densité des truites, nous observons que les cohortes de truites fardées dans les cours d'eau contenant des génotypes hybrides ont une croissance plus faible que les truites fardées en conditions d'allopatrie. En moyenne dans toutes les conditions expérimentales hétérospécifiques, la croissance des truites fardées est aussi plus faible que celles des cohortes de truites fardées en conditions d'allopatrie. Notre étude indique que les jeunes truites fardées subissent un désavantage dans leur croissance lorsqu'elles sont en compétition avec des hybrides de la truite fardée et de la truite arc-en-ciel.

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Introduction

The role of competition, predation, and abiotic factors in determining community structure has received much attention from ecologists (Hairston et al. 1960; Strong et al. 1986). In natural communities, ecologically similar species

are thought to coevolve to limit energetically costly competitive interactions (Brown 1971; Simberloff 1981). In contrast, the introduction of nonnative species forces sympatry between taxa that have not coevolved. When such introductions bring together ecologically similar native and nonnative species, competition for resources is likely very strong

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(Fausch 1988; Petren and Case 1996). The pattern of native population declines or extinctions after the introduction of a similar species provides observational support that introduced species experience competitive advantages over native species. Despite large numbers of species introductions followed by native species declines, relatively few studies provide experimental evidence documenting competitive interactions between native and invasive species (Lodge 1993; see reviews by Sakai et al. 2001; Levine et al. 2003).

Introductions of freshwater fish species provide opportunities to study competitive mechanisms occurring between native and nonnative species that may act to shape community structure. Many fish species are propagated in hatcheries and released into waterways to provide sport fisheries and as biological control agents. Aquarium releases and accidental transfer of fish species have also resulted in the establishment of nonnative fish populations. Over 500 nonnative fish species are reported in North America (Fuller et al. 1999), and several are implicated in the extinction of native fish populations. Although predation by nonnative species plays a role in the demise of some native fish species (Crowl et al. 1992), interference competition for limited resources such as food or habitat is probably common between ecologically similar native and nonnative fish species (Fausch 1988). Therefore, as populations of nonnative species become established within ecosystems, differences in interspecific competitive ability may play a large role in determining whether native fish species persist.

In western North America, the dramatic decline of cutthroat trout (*Oncorhynchus clarkii*) populations after the introduction of nonnative trout is of particular concern. Cutthroat trout have experienced drastic declines and extinctions because of habitat alteration and introduced fish species. Rainbow trout (*Oncorhynchus mykiss*) are considered a key reason for the loss of cutthroat trout populations (Young 1995), because cutthroat trout and rainbow trout are phylogenetically and ecologically similar. Cutthroat trout and rainbow trout are considered sister species and readily form fertile hybrid offspring when brought into sympatry (Krueger and May 1991; Behnke 1992). Of the 14 cutthroat trout subspecies endemic to North America, competition and hybridization with rainbow trout have been implicated in the extinction of one subspecies, the Alvord cutthroat trout (*Oncorhynchus clarkii alvordensis*, Bartley and Gall 1991) and designation as species of concern or protection under the US Endangered Species Act for several other subspecies (Allendorf and Leary 1988). Furthermore, the rapid loss of genetically pure cutthroat trout populations has been documented across many cutthroat trout subspecies after the introduction of rainbow trout (Jaeger et al. 2000; Hitt et al. 2003; Weigel et al. 2003), providing observational evidence for competitive exclusion. Although there is a pattern of cutthroat trout declines after rainbow trout introductions, there is little experimental evidence that determines whether cutthroat trout are competitively inferior to rainbow trout and cutthroat-rainbow hybrid trout.

In 2004, we began a series of studies to experimentally investigate potential competitive mechanisms related to swimming and foraging efficiency among native cutthroat trout, rainbow trout, and their hybrids. Salmonid fishes in streams primarily feed on drifting macroinvertebrates (Quinn

2005). Trout and salmon directly compete for feeding territories that provide access to high supplies of macroinvertebrates. Previous work by Seiler and Keeley (2007a, 2007b) indicates that cutthroat trout have lower sustained swimming ability than rainbow trout and hybrids as well as lower foraging success in contests against rainbow trout and hybrids. To assess the fitness implications of these differences, we conducted growth trials in experimental stream channels. We assayed the growth of cutthroat trout in allopatry and when in competition with similar size rainbow trout and first generation hybrid trout. Given our earlier studies and the pattern of declines and extinctions of native cutthroat trout populations after the introduction of rainbow trout (Jaeger et al. 2000; Hitt et al. 2003; Weigel et al. 2003), we hypothesized that cutthroat trout would exhibit lower growth rates when competing against rainbow trout or cutthroat-rainbow hybrids than when in allopatry.

Materials and methods

Collection and rearing of experimental animals

To control for potential environmental effects on the behavior and growth rate of fish in our study, gametes were collected from adult fish to create experimental cohorts and all offspring were reared in a common environment. On 4 April 2006, Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) were collected from a tributary stream of Henrys Lake, Island Park, Idaho, and rainbow trout from the Hayspur Hatchery, Hayspur, Idaho, USA. Eggs or sperm were removed from individual trout and transported to Idaho State University, where we created four genotypes: cutthroat trout, rainbow trout, and reciprocal crosses of first generation hybrids. Maternal cutthroat hybrid trout were created by fertilizing a clutch of cutthroat trout eggs with rainbow trout sperm, and maternal rainbow hybrid trout were created by fertilizing rainbow trout eggs with cutthroat trout sperm. To reduce the chance of using sperm from an infertile male, the sperm from two males were combined and used to fertilize a single clutch of eggs. This protocol was repeated three times per cross using unique fish each time (12 crosses total, three for each genotype). After fertilization, common genotypes were pooled into one incubation basket and suspended in a trough supplied with chilled (13 ± 1 °C) and aerated water.

Over the course of development, dead embryos were removed by hand several times a week. Although we did not quantitatively measure egg survival, cutthroat trout and maternal cutthroat hybrid trout had lower numbers of viable eggs 21 days after fertilization. On 1 May 2006, fertilized eggs were collected from the source populations to supplement the cutthroat trout and maternal cutthroat hybrid crosses. These embryos had been fertilized in a similar manner on 4 April 2006 and incubated at 13 °C (± 1 °C) in Heath trays at the Henrys Lake Fish Hatchery. Approximately 3000 cutthroat trout and maternal cutthroat hybrid trout embryos were transported to Idaho State University and added to their respective incubation basket.

After hatching and development to the stage where all trout had absorbed their yolk sac and begun feeding, approximately 1200 fish from each genotype were transferred to separate compartments of a fiberglass rearing trough (Frigid-

Units Inc., Toledo, Ohio). Each compartment measured 48 cm long \times 55 cm wide \times 40 cm tall. A water chilling unit maintained temperature at 14 °C (\pm 1 °C), and crosses were fed several times daily with standard hatchery feed (Biodry 1000, Bio-Oregon Inc., Warrenton, Oregon).

Experimental procedure

Given the close phylogenetic relationship of cutthroat trout and rainbow trout and the observation of native cutthroat trout population declines after rainbow trout introductions, we were interested in testing for the presence and strength of competition for cutthroat trout in allopatry versus competition with rainbow or hybrid genotypes. Therefore, we used a minimally substitutive experimental design (see Fausch 1998) to measure the competitive effect of rainbow trout, maternal rainbow hybrid trout, or maternal cutthroat hybrid trout on the growth of cutthroat trout. Although the hybrid genotypes are not technically considered separate species from cutthroat trout, we created them to model two possible hybrid genotypes that occur when rainbow trout and cutthroat trout co-occur and use the terms “interspecific” or “heterospecific” when referring to any treatment where cutthroat trout are paired with non-cutthroat trout cohorts.

To simulate an environment where the trout genotypes would compete for food resources as they would in wild populations, we built four identical stream channels by attaching a water pump to a fiberglass trough (240 cm \times 55 cm \times 25 cm). The pump drew water from two outlets on the downstream end and delivered it to a multi-outlet manifold on the upstream end of the channel. We maintained water velocity of each channel at 10 cm \cdot s⁻¹ (\pm 2 cm \cdot s⁻¹) with a valve on the output of the pump and installed polyvinyl chloride (PVC) screens (3 mm diameter holes) located 20 and 15 cm from the downstream and upstream ends, respectively, to prevent fish from entering the pump and to create laminar flow along the length of the channel. We lined the bottom of each channel with a layer of stream gravel (mean size = 31.6 \pm 9.67 mm standard deviation (SD), n = 100) and maintained water depth at 12 cm above the gravel using a standpipe drain. Owing to space and water supply limitations, two stream channels were positioned side by side, and the second set of channels was placed on an 88 cm tall stand above the first set. Chilled and aerated water (14 \pm 1 °C) was gravity fed from a common reservoir to the top channels with overflow from the standpipes draining to the channel below it. Overflow from the bottom set of channels was collected in a common drain, filtered (mechanical, biological, ultraviolet (UV)), and pumped to the header reservoir. An input of fresh dechlorinated water (\sim 3 L \cdot m⁻¹) to the header reservoir assured high water quality throughout the experiment. To provide a consistent photoperiod, a 100 W light was connected to a timer, mounted at 70 cm above the water surface of each channel, and set to a light regime of 13 h light:11 h dark.

On 12 July 2006, we began the experiment by establishing one replicate of fish in four experimental treatments: (i) cohorts of cutthroat trout in allopatry; (ii) cohorts of 1/2 cutthroat trout and 1/2 maternal cutthroat hybrid trout; (iii) cohorts of 1/2 cutthroat trout and 1/2 maternal rainbow

hybrid trout, and (iv) cohorts of 1/2 cutthroat trout and 1/2 rainbow trout (Table 1). Given that relative size affects competitive ability of salmonid fishes (Abbott et al. 1985) as well as many other taxa (see table 9.1 in Archer 1988), fish were haphazardly sampled from each genotype so that fish within stream channels and between treatments were of similar size (mean \pm 9 mm fork length). Individual trout were lightly anesthetized, measured for fork length (\pm 0.5 mm) and wet mass (\pm 0.0001 g) after blotting the fish with a paper towel, and tagged in the snout with a sequential coded wire tag (sCWT, Northwest Marine Technology Inc., Shaw Island, Washington, USA). Juvenile cutthroat trout, rainbow trout, and cutthroat–rainbow trout hybrids have very similar phenotypes; hence, sCWTs allowed us to identify individual trout with minimal stress relative to other tagging methods (i.e., latex injection, fin clips). To equalize the density of trout within troughs while accounting for small size differences between individual trout, each channel was stocked according to the percent habitat saturation model (PHS) of Grant and Kramer (1990). PHS was developed to estimate the maximum density of salmonid fishes in stream environments based on the territory size of individual fish (Grant and Kramer 1990); a PHS of 100% represents a stream where all potential habitat is filled with foraging territories. For cutthroat trout in the allopatry treatment, we measured and tagged enough fish to set the PHS of the stream channel between 108% and 116% (Table 1). For the other treatments, an equal number of cutthroat trout and the competitor genotype was added until reaching PHS between 105% and 117% (Table 1). Trout for all experimental cohorts were allowed to recover from anesthesia in mesh baskets suspended in the rearing trough until the trials began. On the following day, each cohort was introduced to a randomly chosen stream channel. An automated belt feeder (Aquatic Ecosystems, Apopka, Florida, USA) was attached to the upstream end of each channel, and we filled each stream channel's feeder with a ration of food beginning at 0730 each day. We spread hatchery feed across the entire belt feeder to deliver food over a 12 h period and simulate an encounter rate of prey items that fish experience in natural streams (Keeley and Grant 1995). The daily food ration for each channel was based on the size of each fish in the trough at the time of stocking and equal to 100% of the maximum ration predicted by Marschall and Crowder's (1995) model for juvenile salmonid fishes. Expressed as the percentage of body mass for all trout in each stream channel, the daily food ration equaled 4.3% to 4.9% of the wet mass of trout at the start of the experiment. After 7 days, we adjusted the food ration to 75% of the maximum predicted ration (3.2% to 3.7% according to total starting wet weight of trout in each channel) to intensify competition for food resources.

Twenty days after adding cohorts to the channels, all trout were collected, euthanized with an overdose of anesthesia, and individually measured for length (\pm 0.5 mm) and wet mass (\pm 0.0001 g) after blotting with a paper towel. The sCWTs from each fish were retrieved to identify individual fish and allow calculation of change in mass. Between 12 July 2006 and 3 October 2006, we conducted four replicates of the four experimental treatments using new fish from the rearing cohorts for each replicate. Although we did not expect the position of treatment groups within stream channels

Table 1. Size distribution of trout and percent habitat saturation (PHS) within stream channels for each treatment.

| Treatment | Replicate | No. of YCT | No. of hetero-specific trout | Mean fork length (cm \pm 1 SE) | | |
|------------------|-----------|------------|------------------------------|----------------------------------|----------------|-----|
| | | | | YCT | Heterospecific | PHS |
| YCT in allopatry | 1 | 26 | — | 3.92 (0.03) | — | 108 |
| | 2 | 24 | — | 4.03 (0.03) | — | 112 |
| | 3 | 24 | — | 4.05 (0.04) | — | 112 |
| | 4 | 23 | — | 4.16 (0.03) | — | 115 |
| YCT vs. MCH | 1 | 13 | 13 | 3.76 (0.04) | 3.75 (0.05) | 104 |
| | 2 | 12 | 12 | 3.95 (0.05) | 3.92 (0.04) | 109 |
| | 3 | 12 | 12 | 3.95 (0.05) | 3.95 (0.04) | 110 |
| | 4 | 13 | 13 | 3.91 (0.03) | 3.96 (0.04) | 116 |
| YCT vs. MRH | 1 | 12 | 12 | 3.99 (0.04) | 3.98 (0.05) | 113 |
| | 2 | 11 | 11 | 4.11 (0.05) | 4.11 (0.04) | 112 |
| | 3 | 11 | 11 | 4.17 (0.09) | 4.18 (0.08) | 117 |
| | 4 | 10 | 10 | 4.24 (0.08) | 4.28 (0.08) | 112 |
| YCT vs. RBT | 1 | 12 | 12 | 3.94 (0.07) | 3.93 (0.06) | 109 |
| | 2 | 12 | 12 | 4.01 (0.06) | 4.00 (0.05) | 114 |
| | 3 | 12 | 12 | 4.00 (0.05) | 4.00 (0.05) | 114 |
| | 4 | 11 | 11 | 4.16 (0.04) | 4.17 (0.04) | 116 |

Note: YCT, Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*); MCH, maternal cutthroat hybrid trout; MRH, maternal rainbow hybrid trout; RBT, rainbow trout (*Oncorhynchus mykiss*); SE, standard error.

to influence growth of trout between treatments, treatment groups were rotated to each channel over the remaining three replicates.

Statistical analyses

As a measure of the presence and strength of competition, we compared the growth rate of cutthroat trout cohorts among the four treatment levels. By making experimental observations on only cutthroat trout growth, we made an independent observation of competitive interactions between cutthroat trout in allopatry and the cutthroat trout in the other three treatments. Over the course of the experiment, there was no mortality of trout stocked into stream channels; however, some cutthroat trout could not be identified at the end of the experiment because of sCWT loss (13 out of 238 cutthroat trout) and were not included in the analysis of growth. Although our method for stocking each stream channel created similar size distributions within each channel, we could not maintain identical sizes within our rearing cohorts over the course of the experiment. To account for these size differences, we analyzed individual growth as the daily instantaneous growth rate (g) using the following formula:

$$G = \ln(W_f) - \ln(W_i) / (t_2 - t_1)$$

where G is the daily growth rate, W_i is the initial wet mass (g), W_f is the final wet mass (g), and $(t_2 - t_1)$ was equal to 20 days. We compared the growth rate of cutthroat trout between treatments using an analysis of variance (ANOVA) with the mean growth of the entire cohort of cutthroat trout within a stream channel as the unit of observation (16 observations) and a blocking term to account for differences in starting time of the replicates. To determine which treatment levels differed from each other, we used planned a priori contrasts to compare the growth of cutthroat trout co-

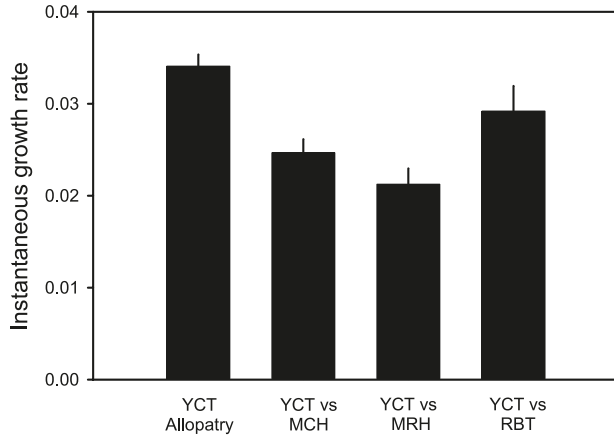
horts in allopatry with the growth of cutthroat trout cohorts in each heterospecific treatment as well as against the growth of cutthroat trout cohorts in all heterospecific treatments combined.

Although the main goal of this study was to test for the presence and strength of competition on cutthroat trout cohorts, we conducted a secondary analysis to investigate the growth rate of individual cutthroat trout in different competitive environments. Within cohorts, the size distribution of cutthroat trout and heterospecific genotypes may influence which cutthroat trout can best compete for profitable foraging locations. If relative size of individual cutthroat trout determines success at capturing food within a cohort of competitors, we expected cutthroat trout that were smaller than the average size trout in a stream channel to experience lower growth rate and larger cutthroat trout to experience higher growth rate. Therefore, we calculated a covariate of relative size by dividing the initial mass of each cutthroat trout by the mean mass of all trout in its stream channel. We then used an analysis of covariance (ANCOVA) to compare the initial relative mass value and growth rate for individual cutthroat trout within each treatment. All statistical tests were performed in SAS 9.1 (SAS Institute Inc. 2003), with significance evaluated at $\alpha = 0.05$.

Results

Over the 20-day trials, we detected large differences in the growth of cutthroat trout cohorts across treatment levels. Cutthroat trout growth rate was different among the four treatments (ANOVA, $F_{[3,12]} = 9.53$, $P = 0.0037$), with the highest growth rate occurring in the allopatric cutthroat trout treatment (Fig. 1). The blocking factor did not account for a significant proportion of the variability in growth rate (ANOVA, $F_{[3,15]} = 1.35$, $P = 0.32$), indicating that timing and initial size of trout cohorts over the course of the experi-

Fig. 1. Growth rate for cutthroat trout cohorts in allopatry and in sympatry with hybrid trout or rainbow trout. Bars represent the mean growth rate (+1 standard error, SE) of cutthroat trout cohorts for four replicates of each treatment. YCT, Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*); MCH, maternal cutthroat hybrid trout; MRH, maternal rainbow hybrid trout; RBT, rainbow trout (*Oncorhynchus mykiss*).



ment was unimportant. When compared according to individual treatments, cutthroat trout growth was lower within the maternal cutthroat hybrid and maternal rainbow hybrid treatments than cutthroat trout growth in allopatry (ANOVA, $F_{[1,7]} = 13.60$ and 25.26 , $P = 0.005$ and <0.001 , respectively). The growth rate of cutthroat trout when rainbow trout were present was lower but not significantly different from cutthroat trout growth in allopatry (ANOVA, $F_{[1,7]} = 3.66$, $P = 0.088$). When compared against all heterospecific treatments combined, cutthroat trout growth in allopatry was higher than cutthroat trout growth in sympatry (ANOVA, $F_{[1,15]} = 18.82$, $P = 0.0019$).

For the analysis of individual cutthroat trout relative size and growth, we detected an effect of the initial relative mass on growth rate ($F_{[1,217]} = 22.3$, $P < 0.0001$), indicating cutthroat trout that were smaller than the average trout within a stream channel grew less than the average cutthroat trout. However, we also detected a treatment effect for individual cutthroat trout growth (ANCOVA, $F_{[3,217]} = 6.85$, $P = 0.0002$), providing further evidence that differences in growth rate exist for cutthroat trout in the presence of heterospecific genotypes. Similarly, a significant interaction between initial relative size and treatment (ANCOVA, $F_{[3,217]} = 5.75$, $P = 0.0008$) indicates that the slope of the regression lines for relative size and growth rate among treatments were different; there is no relationship between initial relative size and growth rate for cutthroat trout in allopatry, while these same relationships for cutthroat trout in channels with maternal cutthroat trout hybrids, maternal rainbow trout hybrids, and rainbow trout have positive slopes significantly different from zero (Fig. 2).

Discussion

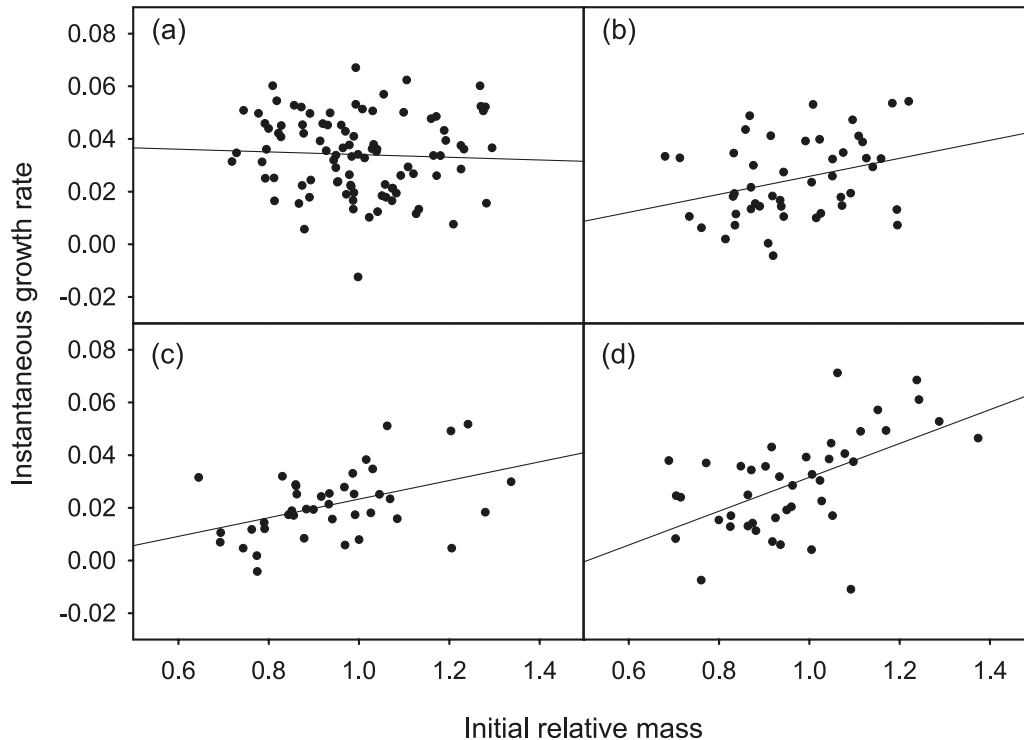
Several recent studies have documented the spread of introduced rainbow trout and cutthroat-rainbow hybrids within cutthroat trout populations (c.f., Hitt et al. 2003; Rubidge and Taylor 2005; Gunnell et al. 2008), bringing attention to

the drastic decline of native cutthroat trout and reinforcing ideas from earlier studies suggesting that rainbow trout genotypes out-compete native cutthroat trout. Our previous studies (Seiler and Keeley 2007a, 2007b) illustrate some of the potential competitive differences among cutthroat trout, rainbow trout, and their first generation hybrids, with cutthroat trout exhibiting lower sustained swimming ability and reduced foraging success when competing against rainbow trout or hybrid genotypes. This study suggests that swimming and foraging differences may have implications for population-level processes; cutthroat trout cohorts in the presence of either hybrid genotype or all heterospecific treatments combined exhibit a lower growth rate than cutthroat trout in allopatry.

Although the growth rate of cutthroat trout cohorts in sympatry with rainbow trout was not significantly lower than growth of cutthroat trout cohorts in allopatry, we believe that this result warrants further research. Given the low feeding rate of cutthroat trout in foraging contests with rainbow trout (Seiler and Keeley 2007b), we expected cutthroat trout growth rate to be lowest in channels with rainbow trout. A possible explanation for higher than expected growth from these cohorts could be that aggression among rainbow trout was higher than aggression among maternal cutthroat trout hybrids and maternal rainbow trout hybrids as suggested by Seiler and Keeley (2007b). If rainbow trout spent a larger proportion of time than either hybrid genotype fighting conspecific genotypes for foraging positions in the stream channels, a greater proportion of food items may have been delivered to cutthroat trout in downstream foraging positions. If we had been able to run our experimental replicates for longer time intervals, we would expect rainbow trout feeding hierarchies to become better established with lower intraspecific aggression; the majority of cutthroat trout, defending downstream positions in the stream channel, would then exhibit a reduction in growth rate.

By collecting data from individual trout within treatments, our study also provides an opportunity to better understand how nonnative species may competitively supplant native species. In salmonid fishes, even small differences in relative size and prior residency can influence the success of acquiring and maintaining a profitable foraging location (Abbott et al. 1985; Cutts et al. 1999; Metcalfe et al. 2003). When comparing growth of individual cutthroat trout within heterospecific competition treatments, we found a positive relationship between initial relative mass and growth rate, indicating that relative size of individual cutthroat trout influenced their ability to acquire food and grow. Cutthroat trout that were smaller than the average trout within these channels fared poorly, while those larger than the average grew as well or better than cutthroat trout in allopatry. These relationships suggest that over the size range within our stream channels, the intensity of competition between cutthroat trout and heterospecific genotypes was only overcome by the largest cutthroat trout. Additionally, in the cohort analysis, we did not detect a difference in growth rate between cutthroat trout in allopatry and cutthroat trout in channels with rainbow trout, despite individual cutthroat trout in channels with rainbow trout exhibiting the same strong relationships between initial mass and growth rate existing for cutthroat trout in channels with hybrid genotypes.

Fig. 2. Relationships between the growth rate and initial relative mass of individual Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) among the four treatments. (a) Cutthroat trout in allopatry. Equation of the line: instantaneous growth rate = $-0.005 \times$ initial relative mass + 0.039 ($r^2 = 0.003$, $n = 94$, $P = 0.64$); (b) cutthroat trout in sympatry with maternal cutthroat hybrid trout. Equation of the line: instantaneous growth rate = $0.034 \times$ initial relative mass $- 0.008$ ($r^2 = 0.097$, $n = 47$, $P = 0.033$); (c) cutthroat trout in sympatry with maternal rainbow hybrid trout. Equation of the line: instantaneous growth rate = $0.035 \times$ initial relative mass $- 0.012$ ($r^2 = 0.20$, $n = 41$, $P = 0.004$); (d) cutthroat trout in sympatry with rainbow trout (*Oncorhynchus mykiss*). Equation of the line: instantaneous growth rate = $0.065 \times$ initial relative mass $- 0.033$ ($r^2 = 0.31$, $n = 43$, $P < 0.0001$).



Similar to findings by Forseth et al. (2003) and Blanchet et al. (2007), our analyses illustrate that individual-level effects of interspecific competition may be concealed at the population level, and thus we recommend that future studies assessing potential competitive influences between native and nonnative species use multiple scales of inference.

Our study is particularly important for understanding the implications of competitive interactions between native and introduced salmonid fishes because the ability of juvenile salmonid fishes to acquire food and grow during a short window of time after hatching is thought to be critical for survival (Elliott 1994). Juvenile trout and salmon that cannot acquire feeding territories in streams either die or are forced to emigrate in search of profitable feeding positions (Elliott 1994; Keeley 2001). Therefore, any competitive disadvantage that young-of-the-year cutthroat trout experience through competition with rainbow trout and cutthroat-rainbow hybrids is likely to have important consequences for the persistence of native cutthroat trout populations. Unlike Keeley (2001), we did not provide a means for competitively inferior fish to emigrate from the streams channels. Given the disparity in mass of cutthroat trout and heterospecific competitors at the end of our experiment, we would expect mortalities of the smaller cutthroat trout to occur if we had extended the experimental treatment beyond 20 days.

In our study, we aimed to test for the effect of competi-

tion on cutthroat trout in the presence of different competitors when trout were of similar size; however, the discrepancy in size and prior residency for rainbow trout, hybrid trout, and cutthroat trout may have important interactions in wild populations. In the South Fork of the Snake River of Idaho and Wyoming, USA, a proportion of wild rainbow trout and cutthroat-rainbow hybrids spawn earlier than the native Yellowstone cutthroat trout (Henderson et al. 2000; De Rito 2004). Young-of-the-year rainbow trout and hybrid trout may therefore emerge earlier and possess a size and prior residency advantage over later emerging Yellowstone cutthroat trout. Validation of the timing of emergence and relative size of young-of-the-year cutthroat trout, rainbow trout, and hybrids upon emergence is possible but would require intensive sampling and genetic analyses because phenotypic differences between these crosses are difficult to identify in the field. However, a long-term survey of trout populations in the South Fork of the Snake River provides evidence consistent with this hypothesis. Despite a reduction in the number of rainbow trout stocked into the South Fork of the Snake River, the proportion of juvenile Yellowstone cutthroat trout has declined, while rainbow trout and hybrids have increased (Schrader and Fredericks 2006). Furthermore, Yellowstone cutthroat trout are approximately 20% smaller in length than rainbow trout and hybrids after their first summer of growth (Schrader and Fredericks 2006), suggesting that timing of emergence, ini-

tial size differences, or prior residency result in large discrepancies in size among these genotypes. These studies in natural populations suggest that the growth rate differences we observed will only be magnified when rainbow trout and cutthroat–rainbow trout hybrids begin with size and residency advantages.

Although our study represents some of the first experimental evidence to indicate that cutthroat trout populations are at a competitive disadvantage to hybrid trout, additional factors thought to influence competitive interactions among stream-dwelling fishes are needed to fully understand how introduced salmonids may interact with native species. For example, we specifically chose hatchery rainbow trout to mimic the common practice of releasing hatchery fish into native trout populations. However, past studies have found that populations of hatchery salmonids tend to have higher levels of aggression than wild populations (reviewed by Weber and Fausch 2003), but genetically-based differences in aggression among populations and the resulting population-level implications have rarely been evaluated. Similarly, the common pattern of cutthroat trout occupying small headwater streams has led some to propose that cutthroat trout are competitively excluded in larger streams with warmer water temperatures (Griffith 1988; Bozek and Hubert 1992). However, surveys of rainbow trout and cutthroat–rainbow hybrid trout within native cutthroat trout populations in the South Fork of the Snake River, Idaho, did not find a strong association between the distribution of rainbow trout and hybridized trout and summer stream temperature or other habitat characteristics (Seiler 2007). Despite the potential importance of these patterns, few studies have demonstrated how differences in competitive ability may translate into population consequences for cutthroat trout, but our study provides a baseline of how cutthroat trout growth rates are affected by competition from rainbow trout and cutthroat–rainbow hybrids.

The evolutionary history of cutthroat trout and rainbow trout may provide additional insight into why rainbow trout and cutthroat–rainbow hybrids are successful when introduced into native cutthroat trout streams. Unlike many terrestrial organisms, fish populations are often isolated from adjacent conspecific and heterospecific populations because of discrete barriers to movement. Yellowstone cutthroat trout, as well as most other cutthroat trout subspecies, evolved in isolation from any other trout species (Gresswell 1995). Because they did not experience competition from other similar salmonid species, cutthroat trout may have evolved as generalists (Griffith 1988). A long history without interspecific competitors may make Yellowstone cutthroat trout particularly susceptible to competition from ecologically similar introduced salmonids (Griffith 1988; Gresswell 1995). In contrast, rainbow trout evolved with a suite of ecologically similar species including Pacific salmon (*Oncorhynchus* sp.) and char (*Salvelinus* sp.; McPhail and Lindsey 1986; Quinn 2005). Hence, repeated stocking of rainbow trout into inland river ecosystems (high propagule pressure; Kolar and Lodge 2001) with relatively simple fish faunas where many cutthroat trout subspecies evolved may promote competitive exclusion of native cutthroat trout.

Several studies in ecosystems where hybridization occurs

between native and introduced species illustrate patterns similar to hybridization between cutthroat trout and rainbow trout. Hybrids between a native and introduced crayfish (*Orconectes* sp.) are dominant over both parental species for limited food resources (Perry et al. 2001), and hybrids between Pecos pupfish (*Cyprinodon pecosensis*) and introduced sheepshead minnow (*Cyprinodon variegatus*) have greater swimming stamina than the native pupfish (Rosenfield et al. 2004). These studies provide examples of hybrid heterosis (Arnold 1997), and accordingly, the lower growth rate of Yellowstone cutthroat trout in treatments with maternal cutthroat trout hybrids and maternal rainbow trout hybrids, coupled with the findings from Seiler and Keeley (2007a, 2007b), provides evidence that juvenile cutthroat–rainbow trout hybrids in the wild probably have advantages over native cutthroat trout. However, hybridization can lead to genomic extinction of native species even when the fitness of hybrids is less than that of parental species by propagating nonnative genes into native populations over time (Huxel 1999; Epifanio and Philipp 2001). Therefore, any fitness advantages that hybrids experience will only serve to hasten the loss of genetically pure native populations. Future studies of ecosystems where hybridization occurs should aim to measure traits correlated with fitness (i.e., growth, survivorship, spawning success) of native species, introduced species, and their hybrids.

Ecologists are making progress at identifying traits common to invasive taxa and ecosystems prone to invasion (Elton 1958; Rejmanek and Richardson 1996; see review by Kolar and Lodge 2001). A stronger quantitative understanding of individual invasions has been called for to achieve the ultimate goal of invasive species ecology: the prediction and prevention of future species invasions (Kolar and Lodge 2001). Similar to studies by Petren and Case (1996) and Holway (1999), our study provides evidence that competition can play an important role in the spread of nonnative species. Additionally, hybridization between cutthroat trout and rainbow trout and the processes described above present special opportunities to study a type of ecological invasion considered to have strong impacts on native species (Rhymer and Simberloff 1996). Further studies that elucidate mechanisms of competition acting between native species and introduced species when hybridization occurs, such as Perry et al. (2001) and Byers and Goldwasser (2001), will add valuable information to the study of invasive species ecology and community ecology in general.

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