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Competitive Interactions Between a Native and Exotic Trout Species in High Mountain Streams

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COMPETITIVE INTERACTIONS BETWEEN A NATIVE AND EXOTIC TROUT SPECIES IN HIGH MOUNTAIN STREAMS

by

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ABSTRACT

Competitive Interactions Between a Native and Exotic Trout Species in High Mountain Streams

by

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Populations of the introduced brook trout, *Salvelinus fontinalis*, have recently become more widespread and abundant in western North American streams, possibly at the expense of native Colorado River cutthroat trout, *Oncorhynchus clarki pleuriticus*. We examined the intensity and potential mechanism of competition between these species.

Feeding experiments in laboratory stream channels showed that cutthroat trout feeding efficiency decreases in the presence of brook trout. Decreased feeding efficiency appeared to be due to interference, as cutthroat trout were inactive in the presence of brook trout. Evidence for interference competition in the feeding experiments was also given by the fact that brook trout feeding efficiency was lower than the feeding efficiency of cutthroat trout. The decreased feeding efficiency of cutthroat trout in the presence of brook trout was due to decreased attack rates by cutthroat trout, and was not due to attacks and consumption of the food items by brook trout.

A field enclosure experiment, in which riffle-pool sections of a stream were isolated by fencing, was performed to determine if the presence of brook trout had a negative effect on the growth, fat content, and diet of cutthroat trout. Cutthroat trout fat levels were significantly lower in the presence of brook trout. The growth of cutthroat trout was not significantly different in the presence and absence of brook trout, but there was a trend for lower growth of cutthroat trout in the presence of brook trout. Diet choices and total biomass of prey consumed by cutthroat trout in the field experiment and in a survey of three streams were not affected by the presence of brook trout.

The observed decreased feeding efficiency of cutthroat trout in the presence of brook trout may be the mechanism responsible for significantly decreased fat levels during the relatively short, summer growing season and may result in reduced population sizes due to high overwinter mortality and delayed sexual maturity.

(52 pages)

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Heather M. Thomas

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INTRODUCTION

The importance of competition has been a controversial issue in ecology for several decades (Wiens 1977, Schoener 1982, 1983, Connell 1983), with much of the evidence considered to be circumstantial (Pianka 1981). Interspecific competition has not been considered to be an important mechanism regulating herbivorous insect communities (Strong 1983). Interspecific competition also has been considered unimportant in systems with a variable environment or in systems where predation is strong (Wiens 1977, Schoener 1982). However, interspecific competition has been found to be an important mechanism structuring rocky intertidal communities (Menge and Sutherland 1976, Underwood 1978), freshwater lakes (Lynch 1978, Werner and Hall 1976, 1977, Brown 1982, see Schoener 1983 and Connell 1983 for reviews), and various terrestrial plant and animal systems (Werner 1977, Price 1978, Dunham 1980, see Schoener 1983 and Connell 1983 for reviews).

Competition occurs when two or more organisms prevent one another from obtaining resources (Pianka 1981). Two forms of competition can occur, interference (direct) competition and exploitation (indirect) competition. Interference competition occurs when one individual denies another individual access to resources by fighting, poisoning, or intimidating to improve its competitive position (Levine 1976, Schoener 1983). Exploitation competition occurs when individuals consume the same limiting resources and one individual, by consuming those resources first, prevents another individual benefits gained by those resources (Schoener 1983). Interspecific competition can result in one species exhibiting niche shifts in sympatry (Pianka 1981) or expansion of a species range of habitat or resource use in the absence of a competitor (Diamond 1975). Species that have not evolved together may also have greater ecological overlap in food type and microhabitat use because there has been no opportunity for natural selection to produce differences in resource use (Schoener 1983, Fausch 1988). Greater ecological overlap in food type and microhabitat use may then lead to a higher tendency to compete. Inland cutthroat trout, *Oncorhynchus clarki*, that evolved with few or no other fish species, particularly other salmonid species, may have a higher tendency to compete with introduced species.

Many introduced salmonids have been thought to interact negatively with native fish species (Fausch 1988, Crowl et al. 1992). However, most studies of interspecific competition between salmonids have not been based on well defined experiments that identify competitive mechanisms (Hearn 1987, Fausch 1988). Indeed, many field studies of interspecific competition between salmonids and other exotic fish species have simply compared spatial distributions and diet composition of allopatric and sympatric populations (Nilsson 1963, Nyman 1970, Andrusak and Northcote 1971, Griffith 1974, Nilsson and Northcote 1981, Glova 1987, Tremblay and Magnan 1991, Glova et al. 1992, McIntosh et al. 1992). Many of these studies concluded that interactive segregation occurs among sympatric populations, in which niche shifts by one or both species results in reduced overlap of resources (Andrusak and Northcote 1971, Fausch 1988). Experimental manipulations in the field and in simulated laboratory streams have been used to examine interactions between salmonids as well (Schutz and Northcote 1972, Fausch and White 1981, 1986, Cunjak and Green 1984, 1986, DeWald and Wilzbach 1992, DeStaso and Rahel 1994), but many of these studies were not designed to reveal competitive mechanisms.

Recent introductions of brook trout, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, in the last 100 years throughout western North American streams have been linked to the decline of several subspecies of cutthroat trout (Moyle and Vondracek 1985, Gerstung 1988, Griffith 1988). Brook trout were stocked in many of the small, high mountain streams of the Colorado River basin and may have altered fish communities in these streams (Binns 1977). These stocking programs appear to have resulted in increasing numbers of brook trout and decreasing numbers of cutthroat trout in at least some streams (Binns 1977). Colorado River cutthroat trout, *Oncorhynchus clarki pleuriticus*, is considered a rare subspecies and its decline is probably due to several factors including habitat loss, as well as the introduction of nonnative salmonids (Martinez 1988). In this study, we investigated potential competitive interactions between Colorado River cutthroat trout and brook trout. Interspecific competition between cutthroat trout and brook trout should be high in the summer when food and space are limiting (Griffith 1988).

The first objective of this study was to determine if brook trout affected the diet of cutthroat trout in the field. The second objective was to determine if brook trout affected the feeding efficiency and behavior of cutthroat trout in a laboratory setting. The final objective was to determine if brook trout affected cutthroat trout under natural conditions in a manner consistent with laboratory behavioral observations. In a field enclosure experiment, we measured growth, lipid deposition, and diets of cutthroat trout, which are known to affect fish survival.

STUDY SITE

The field survey was conducted in Gilbert Creek, Little Gilbert Creek, and Steel Creek. All three streams are small, first- and second-order streams located in the Uinta Mountains Wyoming-Utah, USA. The fish assemblage in Gilbert Creek and the lower portion of Little Gilbert Creek consisted of cutthroat trout, brook trout, and mottled sculpin, *Cottus bairdi*. The fish assemblage in Steel Creek and the upper portion of Little Gilbert Creek consisted of cutthroat trout and mottled sculpin. Brook trout were introduced between 1940 and 1950. The main substrate in the study areas was gravel-cobble with some boulders. Gilbert Creek has an average baseflow width of 3 m and Steel Creek and Little Gilbert Creek have an average baseflow width of 1.5 m. Summer temperatures in the study areas can range from 7 to 21°C during a 24-h period. The riparian vegetation was moderately dense and mostly consisted of willow, *Salix* spp., with an occasional lodgepole pine (*Pinus contorta*).

METHODS

Diet Survey

Cutthroat trout diets and diel feeding patterns were assessed in streams with and without brook trout. Diets of cutthroat trout were used to determine (1) if the types of prey consumed and the time of day (dawn, midday, or dusk) prey are consumed by allopatric cutthroat trout differed from those sympatric with brook trout and (2) if the total biomass of prey consumed by allopatric cutthroat trout differed from cutthroat trout sympatric with brook trout.

There were three streams sampled for this survey, Gilbert Creek and the lower reach of Little Gilbert Creek, which contained sympatric populations, and Steel Creek and the upper reach of Little Gilbert Creek, which contained allopatric populations. A dawn (0600-0800), midday (1500-1700), and dusk (2100-2300) sample was taken for each stream once during the summer of 1993. Gilbert Creek was sampled on 11-12 July, Little Gilbert Creek was sampled on 21-22 August, and Steel Creek was sampled on 1-2 September. Ten cutthroat trout were electrofished from the stream during each sampling time, and fish were weighed to the nearest 0.01 g and measured to the nearest 0.1 mm. Cutthroat trout ranged in sizes from 7.0 cm to

23.0 cm. Stomach contents of the fish were evacuated with a modified syringe that forced water into the digestive tract, resulting in regurgitation. Diets were preserved in 95% ethanol. To relate fish diets to food availability, drift samples were taken during each sampling time. Two drift nets (0.46 m x 0.25 m) were set in riffle areas that were not disturbed by electrofishing approximately 6 to 8 h before each sampling time. Drift nets were pulled from the stream at the beginning of each sampling time and preserved in 95% alcohol. Diets and drift samples were later identified, counted, and measured in the laboratory. Diets and drift were converted to biomass using regression equations relating prey length to prey mass (Rogers et al. 1976, Smock 1980, and C. Hawkins *unpublished data*). To determine if cutthroat trout sympatric with brook trout differed in prey use from allopatric cutthroat trout, biomass of prey in the diets and drift were converted to Chesson's Alpha (Chesson 1978). Chesson's Alpha is defined as:

$$\alpha_i = (r_i/p_i)/\sum r_i/p_i$$

where r_i is the proportion of items of food type i in the consumer's diet and p_i is the proportion of items of food type i in the environment. A two-way ANOVA comparing fish treatment (allopatric and sympatric cutthroat trout) and time of day (dawn, midday, and dusk) was used to analyze

Chesson's Alpha for each of the prey categories (Ephemeroptera, Trichoptera, Diptera larvae, other aquatics, and terrestrials). A two-way ANOVA was also used to determine if the total biomass of prey consumed differed between the allopatric and sympatric populations of cutthroat trout and time of day. The total biomass was log transformed to normalize the data. The significance level for all analyses reported was set *a priori* at 0.10 due to low replication.

Laboratory Feeding Experiment

We performed a laboratory experiment in artificial stream channels during the fall of 1993. We designed the experiment to determine (1) if cutthroat trout feeding efficiency changed when brook trout were present and (2) if interference or exploitation was the most probable mechanism for observed effects.

Feeding experiments were conducted in flowing, oval stream channels. The stream tanks were divided into two sections (3.25 m x 0.61 m, depth = 0.5 m) with average velocities of 0.93 ± 0.015 m/s (± 1 SD) (FIG. 1). Black plastic curtains were placed on both the inside and outside of the stream tanks to prevent interference from outside light and activity. Viewing windows were cut in the plastic so that an individual could observe feeding

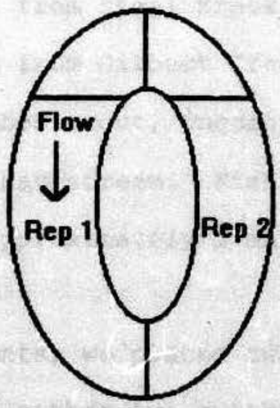

FIG. 1. Experimental stream channels.

interactions by looking down on the fish while minimally disturbing the fish. Six concrete bricks (0.2 m x 0.1 m) were placed into each section to allow cover and resting areas for the fish. A plastic feeding tube was placed at the upstream end of each section and could be reached from inside the tank. Temperatures ranged from 13-1 °C and simulated daytime summer temperatures in Uinta mountain streams, from which the experimental fish were derived. A 12-h dark/12 h-light photoperiod (set by timers) was used during experiments. In addition, red lighting was used during 1730-1830 to simulate evening lighting conditions. Fish used in the experiment were collected by electrofishing streams located in the Uinta Mountains. Brook trout were collected from Gilbert Creek; cutthroat trout were collected from Steel Creek, Utah. Cutthroat trout were not taken from Gilbert Creek because they have hybridized with rainbow trout, *Oncorhynchus mykiss* (Bischoff 1995) in that stream. Fish were held in flowing circular tanks for approximately 1 mo before experiments began.

In the experiments, we placed two fish of similar length in each tank, either two cutthroat trout or one cutthroat trout and one brook trout. Each treatment was replicated five times. Fish length ranged from 82 to 159 mm, with no more than a ± 10 mm difference between pairs. One cutthroat trout in the cutthroat-only treatment was fin clipped so that individual fish could be identified. There was a 2-d acclimation period before the feeding trials were started to insure the fish were familiar with the experimental tank and stream flow, and also to control the feeding history of the fish. Fish were fed twice a day during this 2-d period (1000 and 1800). Feeding trials began on the morning of the third day at 1000. Experiments lasted for 3 d, with both morning and evening feeding events (1000 and 1800) recorded for each day. Feeding trials began when a single piece of freeze-dried krill was placed in the feeding tube, which was then washed through the tube and into the water. To determine if cutthroat trout were surface or midwater feeders, krill were released from either the surface of the water column or the middle of the water column. Ten pieces of krill were randomly released one at a time from either the top of the water to simulate surface prey or from the middle of the water column to simulate drifting prey. Another piece of food was introduced either after consumption of the previous food item or after the previous food item traveled the distance of the stream section. A feeding trial was terminated if both fish did not respond to 20 pieces of food. Trout were given additional food at the end of each feeding trial so that starvation did not occur. Individual encounters, attacks, and captures were recorded for each fish for every food item, as well as the fish's position in the water column (middle/bottom).

Results from the feeding experiments were interpreted in terms of encounter rate (no. encounters/no. food items released), attack rate (no. attacks/no. encounters), and capture rate (no. captures/no. attacks). Because the concept of predation can be thought of as a cycle of sequential events (encounter → pursuit → attack → capture), the total probability of a successful predation event or the probability of ingestion of a prey item can be defined by no. captures/no. food items released (O'Brien 1979). A modified version of O'Brien's equation (1979) was used. O'Brien's equation for a predation cycle is defined as:

$$P_I = P_L \times P_P \times P_A \times P_C$$

where P_I = the probability of ingestion of the food item, P_L = the probability of location of the prey, P_P = the probability of pursuit, P_A = the probability of attack, and P_C = the probability of capture. Three of the four components (location = encounter, attack, and capture) of O'Brien's equation were used because pursuit and attack were not measured independently during the experiment. Due to low statistical power (see Table 1), the alpha level was set *a priori* at 0.10 for all statistical analyses. Because a focal fish was not chosen prior to the feeding experiments, the probabilities of feeding efficiency for the cutthroat trout-only treatment were calculated by taking an average of the two fish. A one-way ANOVA did not show any significant differences in probabilities between the two fish in the cutthroat trout-only treatment. A two-way repeated-measures ANOVA was used to determine differences in feeding efficiencies for fish treatment (cutthroat trout only and cutthroat trout + brook trout) and for food item location (surface of mid-water). Repeated measures were taken on each fish within day (morning and evening observations) for 3 d. A chi-square test was used to compare water column position (middle/bottom) of cutthroat trout in the presence and

TABLE 1. Power analyses for laboratory feeding experiment.

Feeding Efficiency	Two-Way Repeated Measures ANOVA
Encounter Rate	0.10
Attack Rate	0.13
Capture Rate	0.10
Total Probability	0.12

absence of brook trout.

Enclosure Experiment

General methods.--A field experiment was performed in Gilbert Creek in the summer of 1994 to determine if interspecific competition between cutthroat trout and brook trout affected cutthroat trout growth rates, lipid levels, and diets in a natural setting. Six riffle-pool sequences were sectioned off with plastic fencing (mesh size = 1.0 mm) with at least 12 m between experimental sections (see Table 2 for habitat descriptions). Fences were constructed on 28 June-10 July and extended 1 m into each bank (fences ~ 1 m above water surface). Fences were reinforced with three fence posts and were buried 0.15 m into the sediment to prevent fish movement into and out of the manipulated areas. Each section was electrofished for 3 d to remove all fish from each section before experiments were started. In addition, stream sections between each of the experimental units were electrofished and all fish were moved downstream of the lowest experimental section.

TABLE 2. Habitat descriptions of manipulated stream sections in Gilbert Creek. Means ± 1 SD and ranges for each habitat variable are given below.

Habitat Description	Average	Range
Riffle Length	7.1 ± 1.03 m	5.3 - 9.1 m
Riffle Width	3.4 ± 0.65 m	2.1 - 4.0 m
Pool Length	2.8 ± 0.41 m	2.1 - 3.3 m
Pool Width	3.0 ± 0.55 m	1.8 - 3.6 m
Area	30.8 ± 4.83 m^2	23.7 - 37.3 m^2
Length Between Sections	38.8 ± 23.01 m	12.7 - 86.0 m

Treatments consisted of cutthroat trout only and cutthroat trout + brook trout (n = 3 replicates) and were randomly assigned to the six experimental sections. Trout were stocked on 12 July at a density of 0.5 fish/m^2. This density was the average density for all trout species found in Gilbert Creek during the summer of 1992 (P. Cavalli, *personal communication*). Cutthroat trout used in the experiment (96-133 mm total length; average = 116.42 ± 1.06 mm) were obtained from nearby Steel Creek and brook trout (95-135 mm; average = 115.46 ± 1.25 mm) were taken from Gilbert Creek. Fish were individually marked with visual implant tags, so that individual growth, lipid levels, and diets could be monitored throughout the experiment. Trout were measured to the nearest 0.1 mm and weighed to the nearest 0.01 g before being stocked into the sections.

Individual trout lengths, weights, and diets were sampled on 12 August (30 d after initiation of experiment) by backpack electrofishing Diets were preserved in 95% ethanol. Prey items were later identified, counted, and measured in the laboratory. To relate fish diets to food availability, drift samples were taken within 1 wk of fish sampling. Drift nets were placed in the interface between the riffle-pool habitat because most trout were observed in the pool habitat (*personal observation*). Drift nets were set in place 1 h before darkness and drift was sampled for approximately 2 h. Drift samples were preserved in 95% ethanol and drifting prey were counted and measured in the laboratory.

Experiments ended on 12 September. Trout were electrofished from the experimental sections and fish lengths and weights were recorded as before. Trout were sacrificed in the field with MS-222 and frozen in liquid nitrogen. Gut contents were later removed in the laboratory for identification, enumeration, and measurement. A drift sample was taken as described above

1 or 2 d prior to the end of the experiment.

Growth Rates.--Growth rates of cutthroat trout were used to determine if brook trout affected cutthroat trout in the field. Growth rate was calculated as a change in weight ($weight_{final} - weight_{initial}$). A one-way ANOVA was used to determine any significant differences in growth rates between the fish treatment. One of the cutthroat trout-only replicates had to be thrown out for all analyses (growth rates, lipids, and diets) because a very large brook trout (223 mm total length) was electrofished out of the section on 12 August.

Lipid Levels.--For lipid analysis, fish were dried at 60°C for 24 h and weighed to the nearest 0.01 g. Fat was then extracted with petroleum ether using a modification of the procedure described by Bligh and Dyer (1959). The percent fat of the whole fish was determined by dividing total fat grams by the dry weight of the fish (in grams).

Diets.--Diets of cutthroat trout were used to determine if cutthroat trout showed a shift in prey preference when brook trout were present. Diets taken on 12 August and drift sampled 21-23 August were converted to biomass using regression equations (as described previously). Cutthroat trout diets from the last day of the experiment were not analyzed due to inadequate preservation. To determine if cutthroat trout differed in prey preference when brook trout were present, biomass in the diets and drift were compared using Chesson's Alpha (Chesson 1978). One-way ANOVAs were used to analyze Chesson's Alpha for each of the prey categories (Ephemeroptera, Trichoptera, Diptera larvae, other aquatics, and terrestrials) between the treatments. Total biomass was analyzed with a one-way ANOVA. Total biomass was transformed as described previously.

RESULTS

Diet Survey

Cutthroat trout sympatric with brook trout did not differ in prey use or in the time when the prey were consumed when compared to allopatric cutthroat trout. No significant differences in prey use of cutthroat trout were found among fish treatment, time of day, or the interaction for any of the prey groups ($P > 0.10$, Appendix A). There was also no significant difference in the total biomass of prey consumed among the fish treatment, time of day, or the interaction ($P > 0.10$, Appendix B).

Laboratory Feeding Experiment

Encounter and capture rates as well as the total probability of a successful predation event of cutthroat trout were not significantly different among treatments, food positions, or the interaction of the two factors when analyzed as a two-way repeated-measures ANOVA (Table 3, Table 4, and Table 5). Attack rate, however, was significantly different for both treatment and food position, but not for the interaction (Table 3, Table 4, and Table 5). Cutthroat trout attacked significantly more food items per food items encountered (0.49 ± 0.044 [mean ± SE]) in the absence of brook trout than in the presence of brook trout (0.34 ± 0.051). Cutthroat trout also

TABLE 3. Means and standard errors of feeding efficiency shown for each of the treatment levels for the laboratory feeding experiment.

Source	Treatment	Mean(SE)
Encounter Rate	Cutthroat Only	0.07(0.009)
	Cutthroat + Brook Trout	0.07(0.009)
	Surface Food	0.07(0.009)
	Midwater Food	0.08(0.009)
Attack Rate	Cutthroat Only	0.49(0.044)
	Cutthroat + Brook Trout	0.35(0.051)
	Surface Food	0.26(0.050)
	Midwater Food	0.57(0.045)
Capture Rate	Cutthroat Only	0.88(0.035)
	Cutthroat + Brook Trout	0.83(0.048)
	Surface Food	0.82(0.049)
	Midwater Food	0.90(0.033)
Total Probability	Cutthroat Only	0.04(0.011)
	Cutthroat + Brook Trout	0.04(0.011)
	Surface Food	0.02(0.011)
	Midwater Food	0.05(0.011)

TABLE 4. Means and standard errors of feeding efficiency shown for each interaction of the treatment levels for the laboratory feeding experiment.

Source	Treatment	Mean(SE)
Encounter Rate	Cutt*Surface	0.08(0.012)
	Cutt*Midwater	0.07(0.012)
	Cutt+Brook*Surface	0.06(0.013)
	Cutt+Brook*Midwater	0.09(0.013)
Attack Rate	Cutt*Surface	0.30(0.063)
	Cutt*Midwater	0.67(0.061)
	Cutt+Brook*Surface	0.22(0.077)
	Cutt+Brock*Midwater	0.48(0.065)
Capture Rate	Cutt*Surface	0.81(0.052)
	Cutt*Midwater	0.96(0.046)
	Cutt+Brook*Surface	0.82(0.082)
	Cutt+Brook*Midwater	0.85(0.049)
Total Probability	Cutt*Surface	0.04(0.016)
	Cutt*Midwater	0.04(0.016)
	Cutt+Brook*Surface	0.01(0.016)
	Cutt+Brook*Midwater	0.06(0.016)

TABLE 5. Results from laboratory feeding experiment of cutthroat trout in the presence and absence of brook trout. Fish Treatment (cutthroat trout only/cutthroat + brook trout) and food position (surface/midwater) were the factors used in the analysis.

Feeding Efficiency	Source of Variation	df	F	P
Encounter	Fish Treatment	1,110	0.02	0.88
	Food Position	1,110	0.35	0.56
	Fish*Food	1,110	2.27	0.13
Attack	Fish Treatment	1,95	4.51	0.04
	Food Position	1,95	22.25	0.00
	Fish*Food	1,95	0.66	0.42
Capture	Fish Treatment	1,73	0.72	0.40
	Food Position	1,73	2.17	0.14
	Fish*Food	1,73	0.88	0.35
Total Probability	Fish Treatment	1,110	0.00	0.96
	Food Position	1,110	3.37	0.07
	Fish*Food	1,110	2.20	0.14

attacked significantly more food items that were released from the middle of the water column (0.57 ± 0.044 [mean ± SE]) than food items released from the surface (0.26 ± 0.050).

Results from a chi-square analysis suggest that there were no significant differences in the frequency of location of cutthroat trout (middle or bottom of the tank) between the two treatments ($\chi^2 = 0.173$, df = 1, $P > 0.10$).

Enclosure Experiment

Growth Rates.--Growth rate was not significantly different between treatments ($F = 1.48$, df = 1,3, $P = 0.3110$); however, there was a trend of higher growth rates for the cutthroat trout-only treatment (4.07 ± 0.953 g [mean ± SE]) than for the cutthroat trout with brook trout (2.58 ± 0.777 g).

Lipid Levels.--Lipid levels of cutthroat trout were significantly higher in the absence of brook trout ($t = 2.4495$, df = 3, $P = 0.0917$, 0.18 ± 0.001 [mean ± SE]) than in the presence of brook trout (0.15 ± 0.009).

Diets.--Cutthroat trout did not differ in preferences for prey items when brook trout were present. No significant differences in diet electivity by cutthroat trout were found between treatments for any of the prey groups ($P > 0.10$, FIG. 2, Appendix C). The total biomass of prey consumed also did not differ between the treatments (P > 0.10, Appendix D).

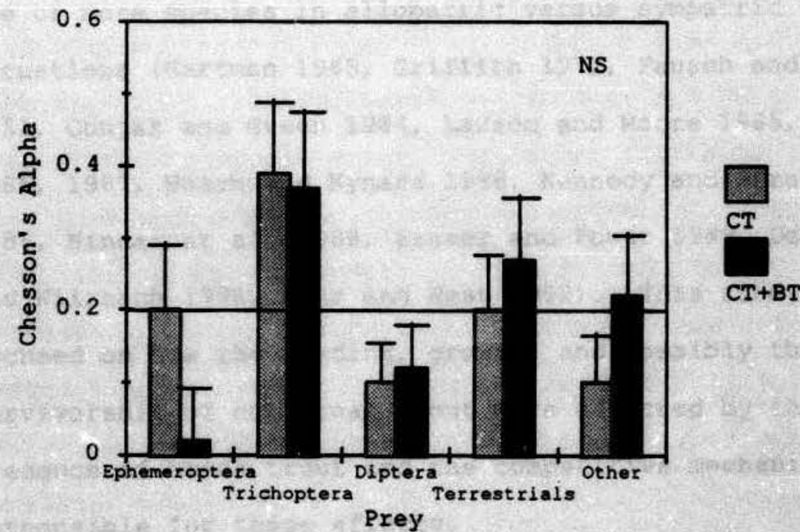

FIG. 2. Electivity indices of cutthroat trout with and without brook trout. Solid line indicates neutral selectivity of prey. Means and standard errors are shown.

DISCUSSION

Most investigations of competitive interactions between salmonids have focused on microhabitat shifts of one or more species in allopatric versus sympatric situations (Hartman 1965, Griffith 1972, Fausch and White 1981, Cunjak and Green 1984, Larson and Moore 1985, Glova 1986, 1987, Hearn and Kynard 1986, Kennedy and Strange 1986, Hindar et al. 1988, Fraser and Power 1989, DeWald and Wilzbach 1992, Lohr and West 1992). This study focused on how the feeding, growth, and possibly the survivorship of cutthroat trout were affected by the presence of brook trout and the competitive mechanism responsible for those effects.

Results from the laboratory experiment suggest that the feeding efficiency of cutthroat trout declined in the presence of brook trout. The decline in feeding efficiency was in the form of decreased attack rates of cutthroat trout when brook trout were present. Attack rates and the total probability of a successful predation event were found to be significantly lower for surface prey than for midwater prey. This result might be explained by trout preferring to feed on drift rather than surface food items or perhaps the fish felt more vulnerable to aggressive attacks by the other fish when food was released as surface prey. It should be noted that the decrease in feeding efficiency of cutthroat was not due to the fact that brook trout attacked and consumed most food items (average feeding efficiency of brook trout, encounter = 0.02 ± 0.003, attack = 0.44 ± 0.064, capture = 0.73 ± 0.070, total probability = 0.02 ± 0.019), resulting in prey depletion, but rather cutthroat trout were less aggressive in the presence of brook trout, resulting in fewer attempts to attack food items. While aggressive attacks of one fish on another were never frequent enough to quantify during feeding trials, almost all aggressive acts noted were from brook trout on cutthroat trout.

Other studies have shown decreased feeding efficiency of native salmonids in the presence of exotic competitors. DeWald and Wilzbach (1992) found that prey capture rates of native brook trout declined in the presence of brown trout. Their finding of decreased prey capture rates was due to a behavioral shift of brook trout in the presence of brown trout. In this study, cutthroat trout almost always remained inactive and were typically positioned behind brook trout. However, when a cutthroat trout was paired with another cutthroat trout, both fish actively fed and moved throughout the experiment. The change in behavior of cutthroat trout in the presence of brook trout probably resulted in a decreased feeding efficiency. This behavioral shift could be the reason growth rates and lipid levels of cutthroat trout declined in the presence of brook trout in the field experiment. Dominant trout have previously been shown to grow faster and more efficiently and have higher lipid levels (Li and Brocksen 1977). In a study looking at intraspecific competition of rainbow trout for space, Li and Brocksen (1977) showed that dominant trout had an average fat content of 15%, whereas subordinate trout only had an average of 10% fat. Rose (1986) showed a decrease in the growth rate of subyearling brook trout after the emergence of rainbow trout. However, Rose (1986) did not have an allopatric control for comparison with sympatric rainbow trout. Although the above studies have shown how negative interactions reduce growth rates of salmonids in the field and in the laboratory, not all interactions between salmonids have resulted in negative results. In a study with brown trout, Kocik and Taylor (1994) found that interactions with steelhead did not have any negative effects on the growth or survival of brown trout.

The field enclosure study showed that the presence of brook trout resulted in significantly decreased fat levels and slightly lower growth rates of cutthroat trout in their natural environment. The nonsignificant result of growth rates may be misleading, however, because the power for the analysis was only 0.12. It was also discovered that one of the cutthroat trout + brook trout replicates differed greatly from the other two replicates (growth rate means for replicate 1 = 1.84 g, replicate 2 = 1.76 g, and replicate 3 = 4.13 g). It is suspected that higher temperature in replicate 3, due to less overhanging riparian vegetation, is the reason for this outlier. Decreased growth and fat levels could have negative effects on the overwinter survivorship of cutthroat trout. Overwinter survivorship has been shown to be higher for larger fish than for smaller fish and is probably the result of higher levels of energy storage (Smith and Griffith 1994). Cunjak and Power (1987) showed that despite continued feeding in the winter, the condition factors of brook trout and brown trout decreased significantly in the early winter and remained low until the onset of spring. They suggested that the decreased condition factors were the result of an early-winter depletion of lipid reserves. Any decrease in the accumulation of lipid reserves prior to the onset of winter may contribute to the inability of cutthroat trout to survive long, cold winters.

Lower growth rates and fat levels may also have negative effects on the reproductive output of cutthroat trout. Because cutthroat trout in the Uinta mountains may have a relatively short, summer growing season, decreased growth rates may prevent cutthroat trout from reaching sexual maturity as early as they could if brook trout were not present. Because lipid reserves are important for the reproductive energy budget in fish (Meffe and Snelson 1993), cutthroat trout may not have adequate energy reserves for springtime reproduction, especially if those reserves are spent trying to survive a long winter.

The decreased fat levels of cutthroat trout observed in the field are most likely the result of interference competition. Diets taken from the field experiment and from the previous summer did not show any differences in prey use of cutthroat trout in the presence of brook trout. If exploitative competition were important, one might expect to see a difference in the types or amounts of prey consumed, or a difference in the time at which prey were consumed by cutthroat trout in the presence of brook trout. Griffith (1974) showed that subyearling and older cutthroat trout differed little in food preferences, independent of whether they lived allopatrically or sympatrically with brook trout. Interference competition is the most likely mechanism responsible for negative interactions between the two salmonids because there were no differences in prey use or differences in the amount of prey consumed in the field and because laboratory experiments implied a behavioral shift in cutthroat trout when brook trout were present. We caution, however, that diets and food availability could only be analyzed for one day in the stream survey and in the field enclosure experiment, because we did not want to stress the fish by sampling more often and because the diets from the end of the experiment were not preserved properly.

This research focused on interactions between 2+ age fish. It is not known if the interactions seen in this study also occur in other life-stages such as reproducing adults and subyearling cutthroat trout, but effects on subyearling cutthroat trout may be especially severe. Subyearling brook trout have been shown to maintain a 20-mm size advantage over cutthroat trout of the same year-class (Griffith 1972), because brook trout fry emerge in the spring and cutthroat trout fry do not emerge until late summer. The size advantage of subyearling brook trout may produce pronounced negative interactions with subyearling cutthroat trout and, thus, may increase the possibility of higher overwinter mortality and delayed sexual maturity.

Interactions between cutthroat trout and brook trout may also be altered by temperature and gradient in the stream. Brook trout have been found to be more aggressive and consume more food than cutthroat trout at high temperatures of 20°C; however, no differences between the two species were found at 10°C (DeStaso and Rahel 1994). In contrast, Cunjak and Green (1986) found that brook trout were dominate over rainbow trout at both 8 and 13°C, but neither species showed a competitive advantage at 19°C. Gradient has also been suggested to affect the distribution of salmonids in streams. Fausch (1989) noted that cutthroat trout find refuge from brook trout upstream reaches of streams where physical conditions may be unsuitable for the introduced brook trout.

This study provides evidence for how an introduced species can affect the behavior, growth, and lipid levels of a native species. Because growth and lipid accumulation are important to fish survival, cutthroat trout overwinter survivorship and reproduction may be in jeopardy if brook trout are present. Puckett and Dill (1985) have suggested that for animals in which rapid growth is linked to survival and fitness, a net energy maximizing foraging strategy should be favored (Puckett and Dill 1985). Cutthroat trout in the Uinta mountains may not have efficient foraging strategies when brook trout are present. If so, interference competition with brook trout may be an important mechanism contributing to the decline of Colorado River cutthroat trout.

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APPENDICES

Appendix A

Results of two-way ANOVA tests for Chesson's Alpha for diet survey.

Prey	Source of Variation	df	MS	F	P-Value
Ephemeroptera	Fish Treatment	1	2.06	2.68	0.15
	Time	2	0.07	0.09	0.91
	Fish*Time	2	0.89	1.16	0.38
Trichoptera	Fish Treatment	1	0.32	0.24	0.64
	Time	2	0.73	0.56	0.60
	Fish*Time	2	1.13	0.86	0.48
Diptera	Fish Treatment	1	0.19	0.07	0.79
	Time	2	0.78	0.30	0.75
	Fish*Time	2	0.68	0.27	0.77
Terrestrials	Fish Treatment	1	0.32	0.24	0.64
	Time	2	0.73	0.56	0.60
	Fish*Time	2	1.13	0.86	0.48
Other	Fish Treatment	1	11.18	2.63	0.16
	Time	2	0.85	0.20	0.82
	Fish*Time	2	0.09	0.02	0.98

Appendix B

Results from two-way ANOVA for the total biomass of prey consumed by cutthroat trout for diet survey.

Source of Variation	df	MS	F	P-Value
Fish Treatment	1	0.07	0.04	0.84
Time	2	0.35	0.22	0.81
Fish*Time	2	0.13	0.08	0.92

Appendix C

Results from one-way ANOVA's for Chesson's Alpha for field enclosure experiment.

Prey	Source of Variation	df	MS	F	P-Value
Ephemeroptera	Fish Treatment	1	6.37	0.12	0.75
Trichoptera	Fish Treatment	1	0.28	1.85	0.27
Diptera	Fish Treatment	1	12.94	0.48	0.54
Terrestrials	Fish Treatment	1	3.36	0.20	0.68
Other	Fish Treatment	1	4.81	0.24	0.66