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Effect of Bull Trout and Brook Trout Interactions on Foraging Habitat, Feeding Behavior, and Growth

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Abstract.—Observations of free-ranging sympatric bull trout *Salvelinus confluentus* and nonnative brook trout *S. fontinalis* in two eastern Oregon headwater streams provided little evidence of habitat partitioning. Both species held focal feeding points in similar microhabitats and fed primarily from the water column rather than from the surface or benthos. In an instream experiment, 20 enclosures were assigned one of three treatments: two bull trout, four bull trout, or a mix of two bull trout and two brook trout. In the enclosures, macroinvertebrate drift was restricted and trout densities were elevated, creating an environment of reduced food and habitat resources. Under these conditions, there was no indication of a niche shift by bull trout; feeding behavior and habitat use by bull trout did not differ depending on the presence or absence of brook trout. Brook trout in the mixed-species treatment were the most aggressive, maintained dominance in 75% of the enclosures, and exhibited significantly higher growth than sympatric bull trout. However, the effects of intra- and interspecific interactions on bull trout growth were equivalent. Given the absence of resource partitioning and a niche shift by bull trout in the presence of brook trout (despite obvious interference interactions), we suggest that the displacement of bull trout by brook trout is likely when resources are scarce.

Introduced salmonids are frequently implicated in the declining abundance of native bull trout *Salvelinus confluentus*. Lake trout *S. namaycush* were associated with the extirpation of bull trout from lakes in western Canada and Oregon (Donald and Alger 1993; Buchanan et al. 1997). In California, the introduction of brown trout *Salmo trutta* was related to the extinction of the McCloud River bull trout population (Bond 1992). However, brook trout *Salvelinus fontinalis* may pose the greatest threat to stream-dwelling bull trout populations because they were introduced throughout the range of bull trout (Rieman et al. 1997; Thurow et al. 1997) and are present in many of the same basins (Rieman and McIntyre 1993).

Because bull trout and brook trout spawn in similar microhabitats in the fall (Fraley and Shepard 1989; Kitano et al. 1994), hybridization is probable where the two species co-occur. Female brook trout that mature at 2–3 years may have a reproductive advantage over bull trout, which mature at about 5 years (Leary et al. 1993; Scott and Crossman 1998). The difference in age at maturity could result in a rapid increase of brook trout numbers relative to bull trout, further increasing the probability of hybridization (Leary et al. 1993).

Negative impacts on bull trout from resource competition with brook trout have been suggested (Dambacher et al. 1992; Ratliff and Howell 1992) but not clearly demonstrated. Dambacher et al. (1992) found bull trout and brook trout both preferred pools over riffles and glides, and both species typically maintained positions near the channel margins. Although bull trout and brook trout occupy similar habitats, sympatric salmonid species typically partition habitats on the finer scales of depth, water velocity, cover types, and prey

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location (Griffith 1972; Cunjak and Green 1983; Dolloff and Reeves 1990; Nakano and Furukawa-Tanaka 1994; Nakano and Kaeriyama 1995).

Nakano et al. (1998) demonstrated a shift in bull trout resource use after the removal of brook trout from two pools. In the absence of brook trout, bull trout increased foraging rates and distances, and occupied more exposed feeding positions. The ecological release of bull trout after brook trout removal indicated that brook trout were significant competitors of bull trout, but the relative strength of intra- and interspecific interactions was not determined.

We investigated the relative effect of intra- and interspecific interactions on bull trout feeding behavior by examining microhabitat use, foraging patterns, agonistic interactions, and growth. We assumed that individuals compete for feeding positions (focal points) of varying value as food acquisition sites (Chapman 1966; Fausch and White 1981). Drift-feeding fish minimize the cost of maintaining position by choosing low-velocity focal points but maximize interception of macroinvertebrate drift by feeding in high velocities (Everest and Chapman 1972; Smith and Li 1983; Fausch 1984). Growth, a measure of net energy gain and performance (Werner and Hall 1977), serves as one indicator of competitive success. We used an instream experiment to compare behavior of allopatric bull trout with that of bull trout sympatric with brook trout. The behaviors of free-ranging fish were observed in order to provide context for behaviors of fish in the experiment. Our hypotheses were that in the presence of brook trout, bull trout would (1) feed in less profitable feeding sites, (2) change from drift to benthic foragers, and (3) experience increased agonistic interactions. We also measured growth of fish in the instream experiment and hypothesized that bull trout sympatric with brook trout would exhibit lower growth than allopatric bull trout. Lastly, we expected to see fine-scale microhabitat partitioning and differences in growth between sympatric bull trout and brook trout.

Methods

Study site.—We chose two study sites in eastern Oregon: the Meadow Fork of Big Creek (Malheur River basin; hereafter referred to as Meadow Fork) and the North Powder River (Powder River basin). In both streams, bull trout were allopatric in the upper reaches and sympatric with brook trout in the middle reaches. Pools in the sympatric reaches commonly contained individuals of both species. Approximately 33% of bull trout co-occurred in habitat units with brook trout, and 45% of brook trout co-occurred in units with bull trout. No barriers prevented brook trout movement upstream. Habitat characteristics for all study reaches are described in Table 1.

Study Design

Free-ranging fish.—Bull trout and brook trout were observed in their natural environment in the sympatric and allopatric reaches of Meadow Fork during 1998. Weekly snorkel dives were conducted for 6 weeks, beginning in June. Moving upstream, a diver observed the feeding behavior of 10–20 individuals of each species within each reach. We observed every undisturbed fish that was encountered, regardless of other species present. Over the 6-week period, fish were observed in the entire sympatric reach (2.0 km) and half (2.3 km) of the allopatric reach.

Instream Experiment.—We conducted the instream experiment in the sympatric reaches of the study streams during 1997 and 1998; 20 enclosures were built in pools or slow-water habitats where bull trout were observed (Table 2). Each enclosure was constructed with four to six wood-frame panels (1.2×0.9 m) covered by nylon screen (3.6 cm^2 mesh size). Erosion-proof cloth was attached to the bottom of the panels, which were then secured to the stream bottom with rebar, anchored with rocks, and braced. Sandbags were positioned so as to minimize undercutting. For 13 enclosures, the stream bank served as one side, providing natural cover and a source of terrestrial insects. Each enclosure also contained diverse microhabitats, including slow-water refuge and thalweg flow. Enclosures ranged from 1.8×1.6 m to 2.2×3.2 m, with an average area of 3.6 m^2 and average depth of 0.3 m. The design of enclosures maximized habitat area while providing complete visibility for observations from the outside. To maintain passage of free-ranging fish and avoid failure during high-water events, enclosures never spanned the stream width.

Experimental fish were collected from the sympatric reaches by angling to reduce potential injury and prevent the behavioral aberrations associated with electrofishing (Mesa and Schreck 1989). Each animal was weighed, measured, and uniquely marked with a phototonic dye injected between the caudal fin rays to ensure positive identification. Based on a combination of the minimal additive and minimal substitutive designs (Fausch 1998), each enclosure received one of three treatments:

TABLE 1.—Habitat characteristics and biological attributes of Oregon headwater stream reaches where bull trout–brook trout interactions were studied.

Attribute	Meadow Fork		North Powder	
	Sympatric	Allopatric	Sympatric	Allopatric
Stream order	3rd	2nd	2nd	2nd
Mean elevation (m)	1,719	1,884	1,862	1,945
Length (km)	2.6	4.3	1.0	2.6
Gradient (%)[a]	4.2	6.5	6.1	7.7
Mean width (m)[a]	4.5	3.8		4.0
% of total surface area[a]				
Pools	17	14		10
Rapids	52	38		46
Dominant substrates (%)[a]				
Cobble	45	48		23
Gravel	44	41		24
Sand				22
Daily temperature (°C)[b]				
Mean, 1997	8.7	7.1	10.1	9.7
Range, 1997	6.2–12.6	3.8–11.1	7.2–14.1	6.8–14.1
Mean, 1998	9.5			
Range, 1998	5.8–13.3			
Mean invertebrate drift density/100 m^3, 1997 (SE)[c]	875 (186)	1,334 (723)	1,484 (564)	1,940 (522)
Mean invertebrate benthic density/m^2, 1998 (SE)[d]	5,829 (1,093)	9,266 (226)	2,486 (749)	2,259 (379)
Species present	Bull trout, brook trout, rainbow trout, shorthead sculpin	Bull trout	Bull trout, brook trout	Bull trout

[a] Habitat assessed by the methods of Moore et al. (1997).
[b] Temperature was measured every 30 min during the experiment with electronic loggers.
[c] A 250-μm drift net with a 0.1-m^2 opening was set for 30 min at dawn in the thalweg upstream of three randomly selected pools. Velocity and depth were measured with an electronic flowmeter.
[d] A benthic sample was collected from six pools with a 0.095-m^2 surber sampler equipped with a 250-μm-mesh net. The sample site within each pool was randomly selected.

two bull trout (2Bull), four bull trout (4Bull), or two bull trout and two brook trout (Mix) (Table 2). Assignment of these treatments to enclosures was randomized. Density within enclosures averaged 0.70 fish/m^2 for the 2Bull treatment and 1.19 fish/m^2 for the 4Bull and Mix treatments (Table 3). The mean density of fish in our enclosures exceeded the estimated density of age-1 and older bull trout in pools of 13 eastern Oregon streams (mean = 0.08 fish/m^2, range = 0.005–0.19; Oregon Department of Fish and Wildlife, Aquatic Inventory Project, unpublished data). We selected fish of similar size for each enclosure, thereby minimizing size-structured dominance hierarchies (Table 3). Individuals were introduced to enclosures simultaneously and acclimated for 7 d prior to observations. The behavior of each fish was observed by snorkeling from outside the enclosures one to three times per week for 6 weeks; observations were scheduled to include every hour between 0700 and 1900 hours for each enclosure.

TABLE 2.—Number of replicate treatments in bull trout–brook trout interaction experiments in two Oregon streams, 1997–1998. Treatment designations are as follows: 2 Bull = two bull trout per enclosure, 4 Bull = four bull trout per enclosure, and Mix = two bull trout and two brook trout per enclosure.

Stream	Dates	Treatment		
		2 Bull	4 Bull	Mix
Meadow Fork	4 Jul–18 Aug 1997	2	2	2
North Powder	23 Jul–8 Sep 1997	2	2	2
Meadow Fork	27 Jun–12 Aug 1998		4	4

Macroinvertebrate drift was collected in Meadow Fork during 1998 to compare food availability inside and outside enclosures. For each enclosure, one drift net (250-μm mesh) was set directly upstream, and another was set inside at the upstream end. Distance between the inside and outside drift nets was approximately 1.5 m. Drift was collected inside the enclosures on 3 and 5 August and outside the enclosures on 4 and 6 August between 0450 and 0520 hours. Insects were preserved in 95% ethanol, sorted, dried at 55°C in the laboratory, and weighed.

Observations.—Free-ranging and experimental fish were observed with 5-min focal animal observations (Altmann 1974) during snorkeling. We estimated the size of free-ranging fish by identifying two landmarks at the nose and tail and mea-

TABLE 3.—Size of individual bull trout and brook trout and density in each experimental enclosure constructed in the Meadow Fork and North Powder River, Oregon, 1997–1998. Numbers in bold are for dominant individuals, numbers in italics for fish that replaced escapees. See the caption to Table 2 for an explanation of treatment designations.

Treatment	Enclosure number	Length (mm)		Size range (mm)	Density (fish/m^2)
		Bull trout	Brook trout		
2 Bull	1	**203,** 199		4	0.63
2 Bull	3	176, 172, *169*		7	0.62
2 Bull	16	**204,** 195		9	0.81
2 Bull	18	**164,** 153		11	0.60
4 Bull	5	233, 213, 211, 206		27	1.10
4 Bull	6	169, 163, *162*, **161,** *159*, 157		12	1.09
4 Bull	8	196, 195, 194, **194**		2	0.80
4 Bull	9	209, **204,** 195, 190		19	1.24
4 Bull	12	**253,** 245, 240, 239		14	1.01
4 Bull	14	**190,** 178, 178, 167		23	0.68
4 Bull	15	**183,** 177, 176, 167		16	1.15
4 Bull	20	176, 173, 168, 167		9	1.59
Mix	2	198, 193	195, 195	5	1.26
Mix	4	196, 195	191, **190**	6	1.40
Mix	7	184, 174	**181,** 179	10	0.72
Mix	10	187, 176	**182,** 174	13	0.88
Mix	11	230, 221	**210,** 205	25	1.25
Mix	13	168, 165	174, **165**	9	0.98
Mix	17	186, 176	185, 180	10	1.50
Mix	19	172, 172	162, **155**	17	1.65

suring the distance after observations were completed. Foraging attempts were counted and classified as being directed at the surface, water column, or benthos. Because prey were not always visible, all foraging attempts were counted, regardless of capture success. Interactions between fish were counted and categorized as dominant when the focal fish gained or maintained feeding territory through aggression, or as subordinate when a fish was displaced or lost feeding territory by aggression from another. Individuals that consistently initiated dominant interactions against all other fish in the enclosures, had few subordinate interactions, and regularly occupied focal feeding points at the head of the enclosures were considered to be occupying the highest rank in the dominance hierarchy.

After observations were completed, physical characteristics of the focal feeding points were measured. Focal point location and height were marked with a bobber attached to a fishing weight. Distance from the bobber to the substrate defined the holding depth. The difference between water velocity (measured with a flowmeter) at the focal point and maximum velocity within a 0.6-m radius determined the velocity differential (Fausch and White 1981) and denoted the potential profit of the focal feeding point. We assumed that a greater velocity differential represented greater potential profit. The percentage of feeding territory area with cover was assigned to one of five categories: 0%, 1–25%, 26–50%, 51–75%, or 76–100%. After 6 weeks, fish in the enclosures were weighed, measured, and released.

Statistical Analysis

Free-ranging fish.—Holding depth was divided by water depth to yield a relative position in the water column, with 0% representing the substrate and 100% representing the surface. Differences in feeding and habitat-associated behaviors between allopatric and sympatric bull trout, and between sympatric bull trout and brook trout, were detected with a Mann–Whitney U-test. Nonparametric tests were used because data were nonnormal. Differences in cover use and the proportion of feeding attempts directed at the surface, water column, and benthos were detected with the log-likelihood ratio test (G-test for heterogeneity; Sokal and Rohlf 1981).

Instream experiment.—Because enclosures were the experimental units, observations for each variable were averaged first for individual fish, then for each species within each enclosure. Separate analyses and comparisons were conducted for dominant and subordinate fish in each treatment, and we report only those results that differed from the combined analysis. Differences in bull trout behavior were detected by a three-way general linear model analysis of variance (ANOVA; factors

TABLE 4.—Habitat-associated behavior, feeding behavior, and interactions observed for free-ranging fish in the Meadow Fork and North Powder River. Values are means ± SEs. The behavior of allopatric and sympatric bull trout and of sympatric bull trout and brook trout was compared with the Mann–Whitney *U*-test. Differences in water column use were tested with a log-likelihood ratio test. An asterisk indicates significant differences ($P < 0.05$).

Variable	Allopatric bull trout (n = 114)	Sympatric bull trout (n = 78)	Sympatric brook trout (n= 46)
Habitat-associated behavior			
Percent depth	24.0 ± 1.5	29.6 ± 2.3	24.8 ± 2.2
Velocity (cm/s)	13.1 ± 0.8	13.0 ± 0.9	12.9 ± 1.4
Maximum velocity (cm/s)	37.3 ± 1.8	37.2 ± 2.5	35.7 ± 2.8
Velocity differential (cm/s)	24.2 ± 1.6	24.2 ± 2.4	23.8 ± 2.6
Feeding behavior			
Foraging rate (number/5 min)	18.3 ± 0.8	20.8 ± 1.1*	15.3 ± 1.6
% benthos	3.1 ± 1.0	1.1 ± 0.3	1.4 ± 0.5
% water column	89.5 ± 1.5	86.8 ± 2.3	89.6 ± 3.1
% surface	7.3 ± 1.3	12.1 ± 2.3	4.7 ± 1.3
Interactions			
Dominant interactions (number/5 min)	0.08 ± 0.03	0.18 ± 0.06	0.18 ± 0.06
Subordinate interactions (number/5 min)	0.03 ± 0.02	0.15 ± 0.06	0.02 ± 0.22

= treatment, stream, and year). When significant differences were found, Tukey's honestly significant difference (HSD) test was used for pairwise comparisons. A Kruskal–Wallis test was used in cases of highly skewed distributions. Cover use and feeding location of experimental fish were analyzed in the same manner used for free-ranging fish. Differences between bull trout and brook trout behaviors in the Mix treatment and between macroinvertebrate drift biomass inside and outside of the enclosures were detected with paired *t*-tests. All tests were two-tailed, and significance was determined at *P* values less than or equal to 0.05.

During the experiment, six fish from four enclosures disappeared, and one fish died. Behavior variables were calculated only from data collected when each fish was present, and growth of the remaining individuals represented growth of that species in the enclosure. Two fish escaped within the first 3 weeks of the experiment. Replacement fish were immediately introduced to both enclosures to maintain proper density, but their behavior and growth were not included in the analyses (Table 3).

Results

Free-Ranging Fish

Habitat-associated behaviors.—Physical characteristics of focal feeding positions were similar among allopatric bull trout, sympatric bull trout, and brook trout (Table 4). On average, fish in all groups held positions in the lower third of the water column (Kruskal–Wallis, $P = 0.19$); however, sympatric bull trout held positions in the upper portions of the water column (depth > 30%) slightly more often than allopatric bull trout and brook trout (Figure 1). Average focal point velocity did not differ between allopatric and sympatric bull trout (Mann–Whitney, $P = 0.84$) or between sympatric bull trout and brook trout (Mann–Whitney, $P = 0.63$). Similarly, no differences were detected for maximum velocity or velocity differential between allopatric and sympatric bull trout (Mann–Whitney, $P = 0.76$ and 0.49, respectively) or between sympatric bull trout and brook trout (Mann–Whitney, $P = 0.85$ and 0.92, respectively). Cover use was consistent among fish in all reaches (*G*-test, $P > 0.1$); a majority of the individuals occupied focal points with 25% cover or less (79% of allopatric bull trout, 76% of sympatric bull trout, and 64% of brook trout).

Feeding behaviors.—Sympatric bull trout had significantly greater foraging rates than did brook trout (Mann–Whitney, $P = 0.004$) and allopatric bull trout (Mann–Whitney, $P = 0.03$). All trout fed primarily from the water column and seldom from the benthos or the surface, with no significant difference between reaches (*G*-test, $P > 0.5$) or species (*G*-test, $P > 0.5$) (Table 4).

Interactions.—Sympatric bull trout and brook trout initiated similar rates of dominant interactions. Sympatric bull trout experienced a slightly greater rate of subordinate interactions than allopatric bull trout or brook trout (Table 4); 88% of interactions with brook trout were instigated by the brook trout. However, 87% of interactions between free-ranging fish were confounded by size, such that the dominant fish was the larger of the two individuals.

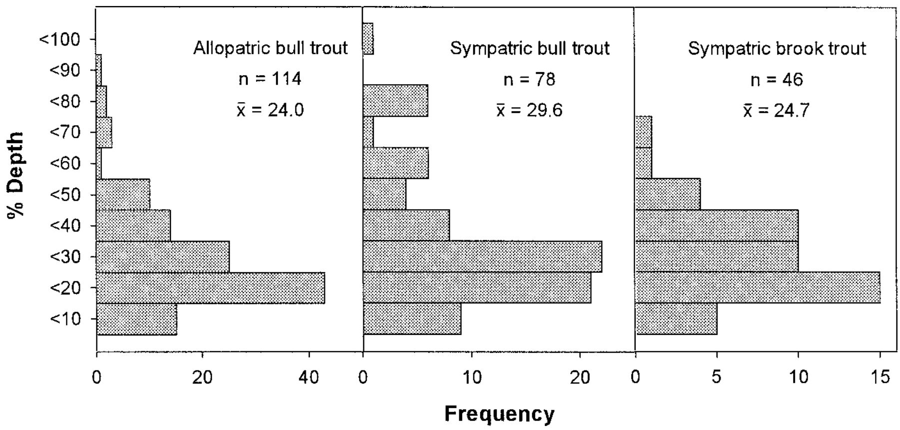

FIGURE 1.—Frequency distribution of depths (% of total depth) of focal feeding points for free-ranging allopatric bull trout, sympatric bull trout, and sympatric brook trout in Meadow Fork, eastern Oregon, in 1998 (0% = stream bottom, 100% = surface).

Instream Experiment

Invertebrate drift.—Invertebrate drift biomass inside enclosures was restricted ($\bar{x}$ = 15 mg) and differed significantly from drift biomass measured outside enclosures ($\bar{x}$ = 29 mg; paired *t*-test, $P <$ 0.001). The mesh deflected a portion of the flow around the enclosure, resulting in reduced flow inside.

Habitat-associated behaviors.—Allopatric and sympatric bull trout occupied similar microhabitats. All bull trout maintained focal feeding positions in the lower third of the water column, though positions of bull trout in the 4Bull treatment were statistically higher in the water column than positions of bull trout in the Mix treatment (Tukey's HSD, $P = 0.018$) (Table 5). Velocity mea-

TABLE 5.—Habitat-associated behavior, feeding behavior, interactions, and growth observed in the instream experiments conducted in the Meadow Fork and North Powder River, Oregon. Values are treatment means + SEs. Behavior of bull trout in all treatments (2 Bull, 4 Bull, and Mix) was compared with three-way general linear model analysis of variance (*F*) or the Kruskal–Wallis test (KW). Groups with differing letters (x or y) within variables were significantly different. Behavior of bull trout and brook trout in the Mix treatment was compared with a paired *t*-test (*t*) or the Mann–Whitney *U*-test (MW). Percent water column use was compared with the *G*-test of heterogeneity (*G*); $P < 0.05$*, $P <$ 0.001**. See caption to Table 2 for an explanation of treatment designations.

	Treatment means				Test statistics	
			Mix			
Variable	2 Bull (*n* = 4)	4 Bull (*n* = 8)	Bull trout (*n* = 8)	Brook trout (*n* = 8)	2 Bull vs. 4 bull vs. bull trout mix	Bull trout mix vs. brook trout mix
Habitat-associated behavior						
Percent depth	16.4 ± 2.3 xy	25.0 ± 2.6 y	17.4 ± 1.1 x	18.7 ± 2.3	*F**	*t*
Velocity (cm/s)	8.1 ± 1.4	9.7 ± 1.8	11.5 ± 1.3	10.3 ± 1.6	*F*	*t*
Maximum velocity (cm/s)	21.4 ± 3.0	26.9 ± 2.7	31.1 ± 3.6	29.3 ± 3.5	*F*	*t*
Velocity differential (cm/s)	13.3 ± 3.9	17.3 ± 2.6	19.6 ± 3.0	18.9 ± 4.0	*F*	*t*
Feeding behavior						
Foraging rate (number/5 min)	5.1 ± 1.5	6.6 ± 1.3	4.6 ± 0.9	5.6 ± 1.1	*F*	*t*
% benthos	4.0 ± 2.5	2.4 ± 0.5	1.0 ± 0.5	1.7 ± 0.6		
% water column	87.8 ± 4.1	84.1 ± 2.7	88.0 ± 3.1	89.1 ± 0.9	*G*[a]	*G*[a]
% surface	8.1 ± 3.2	13.4 ± 2.8	10.9 ± 3.3	9.2 ± 1.0		
Interactions						
Dominant interactions (number/5 min)	0.0 ± 0.0 x	0.09 ± 0.03 y	0.03 ± 0.01 xy	0.33 ± 0.15	KW*	MW*
Subordinate interactions (number/5 min)	0.03 ± 0.03 x	0.16 ± 0.06 xy	0.29 ± 0.08 y	0.04 ± 0.02	*F**	*t**
Growth						
% change in body weight	−7.4 ± 4.1	−12.2 ± 1.5	−13.0 ± 2.8	3.4 ± 3.6	*F*	*t***

[a] One *G*-test of heterogeneity involved % benthos, % water column, and % surface variables.

sures (Table 5) and cover use did not differ among bull trout for any treatment; 78–88% of bull trout maintained a feeding territory with 25% cover or less (*G*-test, $P > 0.1$). Results did not differ when behaviors of dominant individuals were analyzed separately.

Brook trout displayed habitat-associated behaviors similar to those of sympatric bull trout, selecting similar positions and velocities in the water column (Table 5). Cover use also was similar for both groups (*G*-test, $P > 0.1$).

Feeding behaviors.—Mean foraging rates of bull trout were similar among experimental treatments (Table 5). All bull trout fed primarily from the water column and infrequently from the benthos and surface. Likewise, bull trout and brook trout in the Mix treatment had similar foraging rates and commonly fed from the water column (Table 5).

Interactions.—Interaction rates in the enclosures were density-dependent and species-specific. Fewer interactions occurred among bull trout in the low-density treatment (2Bull) than in high-density treatments (4Bull or Mix). Bull trout in the 2Bull treatment had no dominant interactions, significantly below the number observed in the 4Bull treatment (Mann–Whitney, $P = 0.014$) and were displaced significantly less frequently than bull trout in the Mix treatment (Tukey's HSD, $P = 0.041$; Figure 2). Bull trout in the 4Bull and Mix treatments had statistically similar rates of interactions (Figure 2, Table 5); however, in the Mix treatment, bull trout never attained the top position in the dominance hierarchy.

Brook trout held the highest rank in six of the eight Mix treatment enclosures. Fish in the remaining two enclosures did not establish strong social dominance hierarchies. Dominance was expressed through relative location of the focal feeding point within the enclosure and through the rate and type of interactions. The dominant brook trout consistently maintained feeding territories in the front third of the pool. The subordinate fish resided in the rear and were visually isolated from the dominant brook trout. Compared with bull trout, brook trout in the Mix treatment initiated a significantly greater number of dominant interactions (Figure 2a; Table 5); 90% of brook trout interactions involved dominance over bull trout. Brook trout harassed or displaced bull trout at an average rate of 0.26 interactions/5 min, whereas bull trout harassed or displaced brook trout at an average rate of 0.01 interactions/5 min. Rarely did bull trout successfully defend their feeding territory from intruding brook trout or displace brook trout.

Growth.—Fifty-two of the 60 bull trout in the enclosures lost weight over the duration of the experiment. Weight loss is common in captive, experimental fish (Fausch 1984; DeWald and Wilzbach 1992). Bull trout in the 2Bull treatment lost an average of 7% of their initial body weight, which was less than the 12% lost by bull trout in the 4Bull treatment (Tukey's HSD, $P = 0.16$) and the 13% lost by bull trout in the Mix treatment (Tukey's HSD, $P = 0.11$) (Figure 3). Results did not change when the growth of dominant individuals was analyzed separately.

Brook trout in enclosures gained an average of 3% of their initial body weight (Figure 3). In the Mix treatment, the difference between growth of bull trout and that of brook trout was significant (paired *t*-test, $P < 0.001$; Table 5).

Discussion

This study revealed no evidence of a shift in resource use for bull trout in the presence of brook trout. Microhabitat use was consistent among free-ranging bull trout in the allopatric and sympatric reaches. The slight variation we observed in focal point height and surface feeding frequency for bull trout was not sufficient to ameliorate potential competitive interactions or to suggest a niche shift (see Fausch and White [1981] and Nakano et al. [1992] for examples). Despite significantly reduced prey resources and increased fish densities, allopatric and sympatric bull trout in the enclosures also maintained focal points in similar microhabitats. Thus, we accepted our null hypothesis that allopatric bull trout and bull trout sympatric with brook trout exhibit similar feeding and habitat-associated behaviors.

Initially, we hypothesized that bull trout would shift to a benthic foraging mode in the presence of brook trout. Closely related Dolly Varden *Salvelinus malma*, in the presence of white-spotted char *S. leucomaenis*, shifted to a benthic foraging mode when the drift encounter rate fell below a threshold of 15 forays/5 min (Fausch et al. 1997; Nakano et al. 1999). Nakano et al. (1999) suggested that the shift of subordinate fish to a benthic foraging mode might have been due to agonistic interspecific interactions for profitable feeding positions. We did not observe a comparable shift for bull trout dominated by brook trout in the enclosures, although foraging rates were significantly reduced compared to free-ranging fish. However, interaction rates we observed between bull trout and brook trout were an order of magnitude lower than those experienced by Dolly Varden, and may

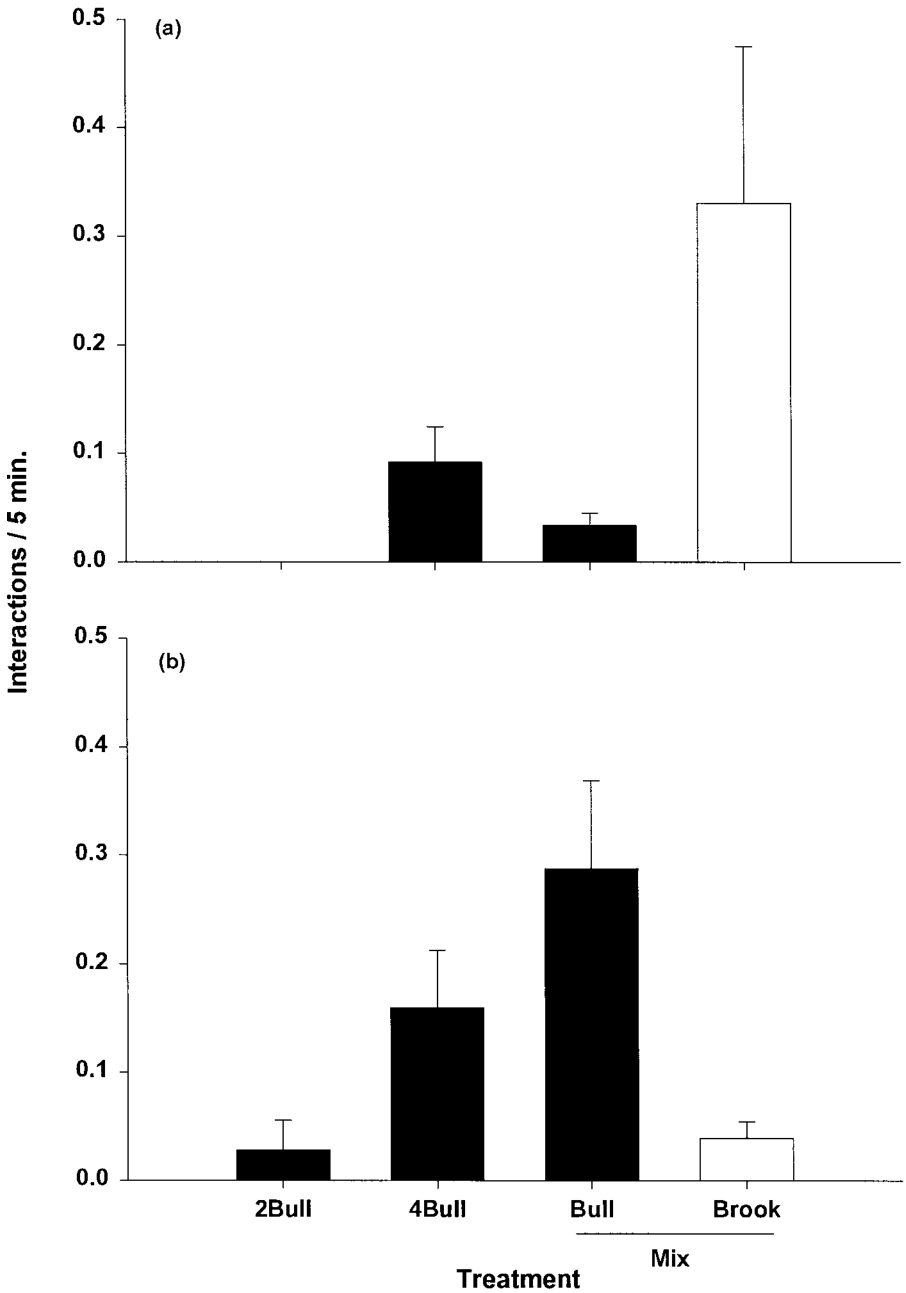

FIGURE 2.— **(a)** Dominant and **(b)** subordinate interactions observed in 5-min intervals among bull and brook trout in experimental enclosures in Meadow Fork and the North Powder River, Oregon, 1997–1998. Treatments were two bull trout (2Bull), four bull trout (4Bull), or two bull trout and two brook trout (Mix) per enclosure. Values are treatment means; whiskers represent 1 SE.

have been too infrequent to elicit a change in foraging mode. Alternatively, the benthic invertebrate community may have been dislodged during the construction of the enclosures, resulting in an inadequate source of prey. However, initial disturbance of invertebrates was unlikely to have prevented a change in bull trout foraging mode because macroinvertebrates began to recolonize the

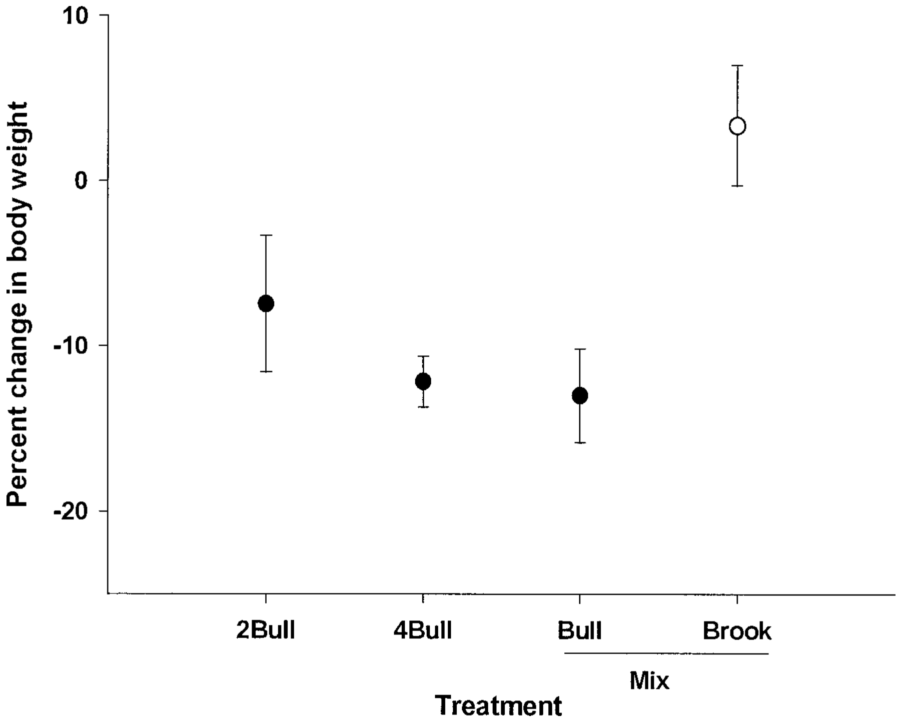

FIGURE 3.—The percentage change in body weight after 6 weeks for bull trout (solid circles) and brook trout (open circle) in experimental enclosures in Meadow Fork and the North Powder River, Oregon, 1997–1998. See the caption to Figure 2 for an explanation of treatment designations. Values are treatment means; whiskers represent 1 SE.

substrate immediately and, based on recolonization rates observed elsewhere, probably resumed average density in 10–30 d (Waters 1964; Townsend and Hildrew 1976). We commonly observed large caddisflies (Limnephilidae) and stoneflies (Perlidae) on the substrate inside the enclosures, indicating that many other common families of smaller-bodied invertebrates were also present.

By controlling for both fish size and density in the enclosures, we detected the relative strength of inter- and intraspecific interactions of bull trout under conditions imposed by the enclosures. Similar growth of bull trout in the 4Bull and Mix treatments demonstrated that the relative interaction strength with brook trout was equivalent to that of intraspecific interactions. These findings expand on those of Nakano et al. (1998), which also indicated potential competition between bull trout and brook trout.

Similarities in sympatric bull trout and brook trout behavior create the potential for competitive interactions. Free-ranging sympatric bull trout and brook trout fed from focal feeding points with similar depth and velocity measures, and primarily captured prey drifting in the water column. In the enclosures, where food and habitat resources were diminished, behavioral similarities persisted. In both cases, we observed more resource sharing than resource partitioning between sympatric bull trout and brook trout.

Shared resource use between bull trout and brook trout is not surprising, given that the species are congeners and that bull trout are native whereas brook trout are introduced. Closely related species that naturally do not exist in sympatry, but that occupy similar environments, have the greatest potential for interference competition (Hearn 1987; Fausch 1988). Naturally sympatric species, such as bull trout and westslope cutthroat trout *Oncorhynchus clarki lewisi* (Pratt 1984; Nakano et al. 1992), are more likely to have evolved mechanisms for partitioning limited resources (DeWald and Wilzbach 1992). In addition, closely related species with similar morphology, such as bull trout and brook trout, typically exploit food and habitat resources in the same manner and overlap in resource use (Werner 1977).

In our instream experiment, brook trout consistently maintained the highest rank in the dominance hierarchy. Brook trout were clearly dominant and aggressive over bull trout of similar size, whereas bull trout never attained the top position in the mixed-species hierarchy. The greater growth of brook trout implies a competitive advantage over bull trout. Confined brook trout gained weight during the experiment, whereas bull trout lost weight. Because measures of velocity for bull trout and brook trout focal feeding points were similar, the net energy expenditures for bull trout and brook trout should have been the same. Greater growth of brook trout may have resulted from the superior ability of brook trout to maintain and defend the most advantageous foraging positions at the head of the pool, where large macroinvertebrates were concentrated in the drift (Furukawa-Tanaka 1992). The best foraging positions were never occupied by bull trout. Alternatively, the difference in growth between the two species may illustrate the greater capacity of brook trout to tolerate confinement, high densities, and stressful conditions (McNicol and Noakes 1984; Schroeter 1998).

If the difference in growth between bull trout and brook trout in the experimental enclosures reflects a similar difference in free-ranging fish, then brook trout likely grow faster than bull trout in streams where the two species co-occur. Because size generally determines dominance and often influences the outcome of interspecific interactions (Fausch 1988, 1998; Fausch and White 1986), we can infer that brook trout of the same year-class as bull trout may eventually attain dominance over bull trout based on size alone.

The growth of an individual cannot be equated to the growth of a population (Fausch 1984). Although this study documents the effects of brook trout on the feeding behavior and growth of individual bull trout, it provides no measure of the effect of brook trout on the demographic parameters of bull trout populations. The aggressive behavior and the reproductive advantage of brook trout, in combination with the potential for hybridization, suggest that brook trout may eventually dominate, outnumber, and genetically alter bull trout (Leary et al. 1993). On the population scale, these factors may force bull trout to emigrate, potentially leading to population decline. In areas where bull trout are restricted to headwater streams, downstream displacement of bull trout may force them to reside in heavily degraded habitat with warmer water temperatures, thus decreasing their chances for survival. Displacement of bull trout upstream into the allopatric reaches may increase bull trout densities, which could negatively affect growth through density-dependent interactions. To fully understand the population-level effects of brook trout on bull trout, a study designed specifically to examine population dynamics of the two species is required.

Our instream experiment identified the aggressive behavior of introduced brook trout and their dominance over bull trout of similar size in two eastern Oregon headwater streams. We saw no evidence of resource partitioning between bull trout and brook trout or a niche shift under experimental conditions. Because of shared resource use, the faster growth and aggressive behavior of brook trout may allow displacement of bull trout in time intervals beyond the scope of our study or when resources are limiting. The impacts of hybridization and the reproductive advantage of brook trout may further magnify the potential for bull trout displacement. Given our understanding of interspecific interactions between bull trout and brook trout, future research should focus on factors mediating possible bull trout displacement under natural conditions and identify the impact of brook trout on the demographic parameters of bull trout populations.

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