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Influence of Habitat Type on Food Supply, Selectivity, and Diet Overlap of Bonneville Cutthroat Trout and Nonnative Brook Trout in Beaver Creek, Idaho

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Abstract.—We collected invertebrate drift samples and stomach contents of native Bonneville cutthroat trout *Oncorhynchus clarki utah* and nonnative brook trout *Salvelinus fontinalis* in Beaver Creek, Idaho, during August 1995 to assess food availability and the potential for competition. Regardless of whether samples came from beaver pond or from high-gradient or low-gradient reaches, aquatic Diptera numerically dominated drifting invertebrates by at least fivefold over all other categories captured in 1-h drift samples. Abundances and drift densities of drifting invertebrates were high in the three reach habitat types sampled: beaver pond (3,152 individuals; 18.9 invertebrates/m^3), high-gradient reach (5,216 individuals; 26.5 invertebrates/m^3), and low-gradient reach (4,908 individuals; 17.2 invertebrates/m^3). Cutthroat trout consumed significantly more invertebrates per individual than did brook trout. However, there was no relationship between fish length and consumption. Diets of both brook and cutthroat trout were dominated by Diptera in beaver ponds and terrestrial invertebrates in the high-gradient reach. In the low-gradient reach, Diptera dominated brook trout diets, whereas both Diptera and terrestrial invertebrates dominated diets of cutthroat trout. Both trout species consistently selected terrestrial invertebrates and Trichoptera in all reach types. Diet overlap between brook and cutthroat trout was 92% in beaver ponds, 75% in the high-gradient reach, and 65% in the low-gradient reach. The high degree of diet overlap suggests the possibility of competition between nonnative brook trout and cutthroat trout if food should become limiting, but we found little evidence that food was limiting during late summer in Beaver Creek.

Invertebrates form the vast majority of food items consumed by stream-dwelling trout (Fleener 1951; Griffith 1974; Allan 1978; Hubert and Rhodes 1989; Dunham et al. 2000). Because trout species often show similar feeding behaviors in the same stream (Griffith 1974), there may be a large amount of diet overlap between sympatric species. Although diet overlap should not be an issue when supply exceeds consumption, the potential for competition exists, should food availability become limiting. The presence of seasonal food limitations in some trout populations in winter (Cunjak et al. 1987) and summer (Cada et al. 1987; Ensign et al. 1990) indicates that food can be limiting. When food limitations arise, species having a large amount of diet overlap may compete for food, and the better competitor may eventually replace the inferior species. Replacement may occur over the entire stream or locally in areas where diet overlap is greatest, in cases where habitat may mediate diet overlap.

Circumstantial evidence suggests that nonnative brook trout *Salvelinus fontinalis* can replace native cutthroat trout *Oncorhynchus clarki* in western U.S. streams (Griffith 1988; Varley and Gresswell 1988). Brook trout are native to the eastern USA but have successfully invaded streams inhabited by cutthroat trout in the Intermountain West (Fuller et al. 1999). Brook trout have diets and a feeding strategy similar to those of cutthroat trout (Griffith 1974), which suggests that interspecific competition for food may be a factor in displacement of cutthroat trout. However, little information exists on diets when these species are sympatric, and the results are equivocal. Griffith (1974) re-

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ported high similarity in diets of age-0 brook trout and cutthroat trout; however, similarity decreased in older fish. In contrast, Dunham et al. (2000) found relatively high diet overlap in adults of the two species in Nevada streams. Additional information on feeding behaviors of brook trout and cutthroat trout would be valuable in assessing the potential for interspecific food competition.

In streams where brook trout and cutthroat trout occur together, brook trout tend to predominate in the lower-gradient reaches and beaver ponds, whereas cutthroat trout predominate in higher-gradient reaches (MacPhee 1966; Griffith 1972). If food competition does structure trout distributions, we predict that diet overlap between brook trout and cutthroat trout will be high in beaver pond and low-gradient reaches and low in high-gradient reaches.

In this paper we present information on food availability, consumption, and food selectivity of nonnative brook trout and native Bonneville cutthroat trout *O. c. utah* and assess resource limitation and overlap in resource use, two prerequisites for interspecific food competition. Our first objective is to describe the composition and quantity of the invertebrate drift in Beaver Creek, Idaho. Our second objective is to provide information on diets, consumption levels, and food limitations for nonnative brook trout and native Bonneville cutthroat trout. Our final objective is to use the food availability and consumption information to assess the potential for competition between brook and cutthroat trout.

Methods

Study site description and location.—Beaver Creek originates in southeast Idaho and flows south for approximately 10 km before crossing into northeast Utah, where it joins the Logan River. This first-order stream originates at an elevation of 2,400 m and is sustained by groundwater during summer and autumn after snowmelt. The stream is usually at base flow from mid-July until late winter.

The study area consists of three adjacent reach types: a downstream high-gradient section of step pools flowing through coniferous forest and shrubs; a low-gradient section that meanders through meadows; and beaver ponds constructed with willow *Salix* sp. and aspen *Populus tremuloides* at the upstream end of the study area (Figure 1). Channel slopes in the high gradient are 3–5%, less than 1.5% in the low gradient, and less than 0.5% in beaver ponds, where current velocities are slow (Fallau 1995). Brook trout numerically dominate the beaver ponds, whereas cutthroat trout numerically dominate both high-gradient and low-gradient reaches.

Measurement of food and diet.—We examined taxonomic composition of drifting invertebrates, the extent of diet similarity, and the potential for competition between brook trout and cutthroat trout by a one-time sampling of invertebrate drift and trout stomach contents in late August 1995. In each reach habitat type (beaver ponds, high gradient, and low gradient), we collected three 1-h drift samples (mesh diameter = 225 μm; drift net dimensions = 26 × 45 cm). At the mouth of each drift net, current velocity was measured with a Marsh–McBirney electronic flowmeter; we then multiplied this velocity by the area filtered by each drift net to calculate drift density. All drift samples were taken on the same day and at the same time. Beaver ponds were sampled at the inflow, where current velocities were high enough for adequate drift sampling. Although drift sample contents were identified to family when possible, we grouped the data into orders for comparison with stomach contents data, which could be reliably identified to order only.

On the same day and in the same reaches, we captured trout by electrofishing, anesthetized them with tricaine (MS-222) and collected stomach contents from 26 brook and 81 cutthroat trout by gastric lavage, an effective but nonlethal technique (Meehan and Miller 1978; Light et al. 1983). The trout were distributed as follows: for cutthroat trout, 21 were in beaver ponds, 32 in high-gradient reaches, and 28 in low-gradient reaches; for brook trout, 13 were in beaver ponds, 5 in high-gradient reaches, and 8 in low-gradient reaches. Fish were weighed to the nearest 0.1 g on an electronic balance and their total length was recoded to the nearest millimeter. Invertebrates in the preserved stomach contents were later identified to order where possible and classified as terrestrial or aquatic. Adult invertebrates that emerged from aquatic stages were classified as aquatic. Diet overlap was calculated by taking the minimum percentage of a taxon between the diets of brook and cutthroat trout and summing these percentages for all taxa in the diet as follows:

$$P_{jk} = [\Sigma \text{ (minimum } p_{ij}, p_{ik})]100$$

where p_{ij} and p_{ik} are proportions of prey category i used by species j and k, respectively (Schoener 1970). We determined preferences for the six dom-

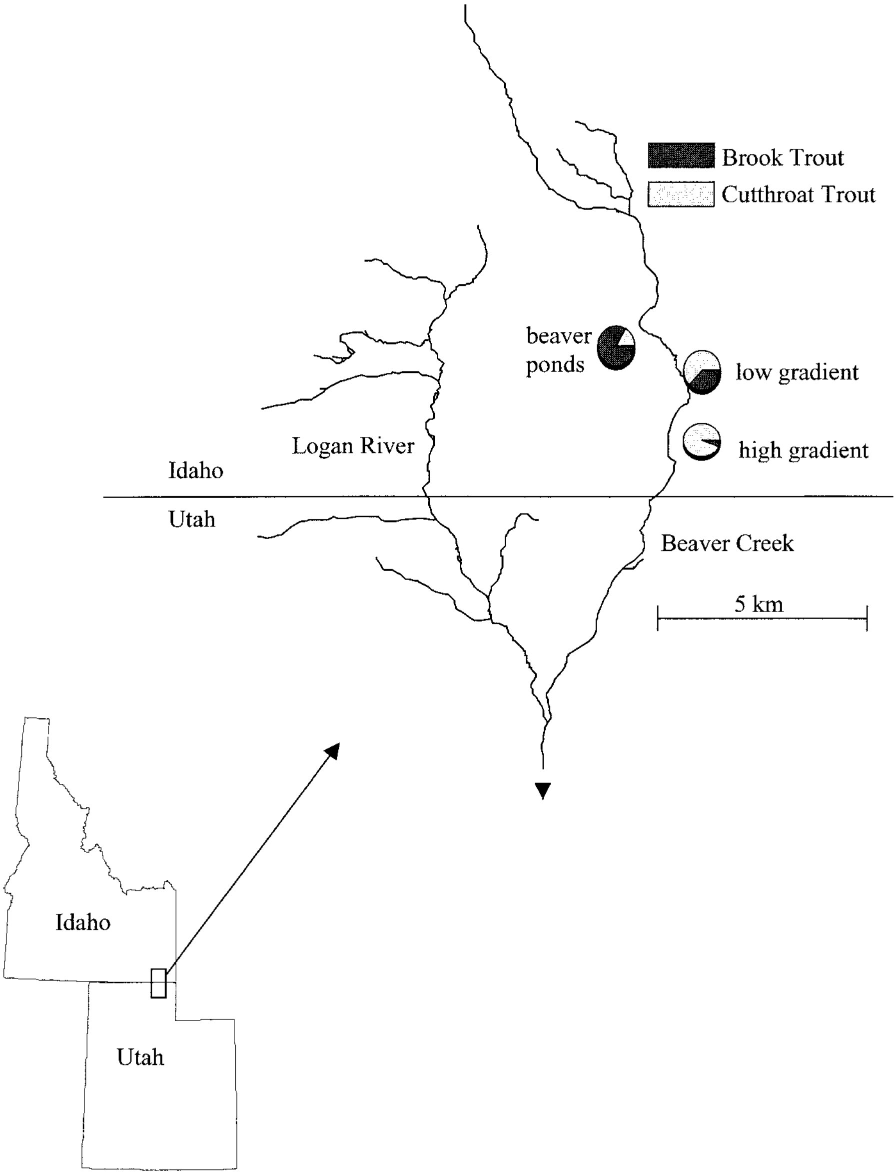

FIGURE 1.—Location of Beaver Creek, Idaho, showing the areas were drift samples and fish were collected and the proportional abundance of brook trout and cutthroat trout in each section.

inant food taxa in trout diets by calculating selectivity according to the linear food selection index (L) of Strauss (1979):

$$L = r_i - p_i,$$

where r_i represents the relative proportion of a prey item i in the diet and p_i is the relative proportion of a prey item i in the stream. The linear food index ranges between -1 (complete avoidance) and $+1$ (strongly selected for).

Overall consumption differences between brook and cutthroat trout were inferred by using analysis of covariance (ANCOVA), comparing between species and reach habitat type with fish length as the covariate. The total numbers of invertebrates consumed was the response variable and was transformed to normality by (1 + a natural log) transformation. Species-specific relationships between consumption and fish length or Fulton's condition factor (Ricker 1975) were tested by using linear

TABLE 1.—Drift density (number of invertebrates/m^3 of flow) and composition of the drift (in total numbers of invertebrates) in a 1-h drift sample in beaver ponds and high-gradient and low-gradient reaches of Beaver Creek.

Variable or characteristic	Beaver Pond	High Gradient	Low Gradient
Drift Density (number/m^3)	18.9	26.5	17.2
Drift composition			
Ephemeroptera	372	524	240
Plecoptera	15	24	36
Trichoptera	24	256	36
Terrestrial	176	592	272
Diptera	2,552	3,704	4,240
Coleoptera	12	116	84
Total	3,152	5,216	4,908

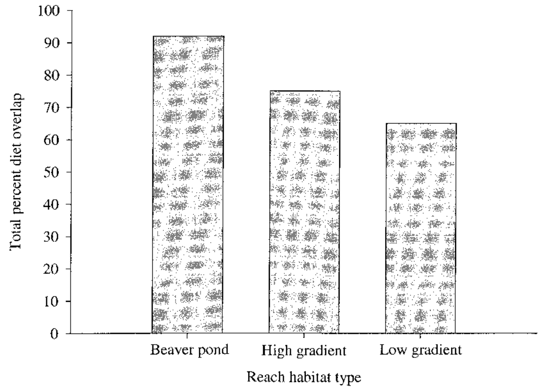

FIGURE 2.—Total percent of overlap (measured as numbers of individuals) in the diets of brook and cutthroat trout in each reach type.

regression. All tests were considered significant at a probability level of 0.05.

Results

Composition of the Invertebrate Drift

The numbers of invertebrates captured in 1-h drift samples were very high, exceeding 4,700 invertebrates in beaver ponds, 8,800 in high-gradient reaches, and 7,400 invertebrates in low-gradient reaches (Table 1). Aquatic Dipterans numerically dominated other invertebrate groups by at least fivefold in all three habitat types and were most abundant in the low-gradient reach (Table 1). Ephemeroptera and terrestrial invertebrates were consistently the next most abundant taxa in all reach types, although both groups were substantially less abundant than Diptera. Ephemeroptera, terrestrial invertebrates, Trichoptera, and Coleoptera achieved their greatest abundances in the high-gradient reach, whereas Plecoptera reached its greatest abundance in the low-gradient reach.

No category of drifting invertebrates collected achieved their greatest abundance in beaver ponds. Drift densities were much greater in the high-gradient reach at 26.4 drifting invertebrates per cubic meter. Although high, drift densities in beaver ponds (18.9 invertebrates/m^3) and in the low-gradient reach (17.2 invertebrates/m^3) were much less than in the high-gradient reach (Table 1).

Food Availability, Consumption, and Diet Overlap

The one-time sample indicated substantial diet overlap between brook and cutthroat trout, but the degree of diet overlap differed among reach types (Figure 2). Diet overlap was greatest in beaver ponds where the two species shared 92% of their diets (Figure 2). In beaver ponds, Diptera dominated the diets of both trout species, accounting for 80% of brook trout diets and more than 85% of cutthroat trout diets (Table 2). However, the low selectivity values for both trout species in beaver ponds indicates that Diptera were consumed at nearly the same proportion as their availability in the drift (Table 2). Terrestrial invertebrates were consumed at slightly greater proportions than their availability in the drift, but accounted for only approximately 10% of the diet in each trout species (Table 2).

Diet overlap between brook trout and cutthroat trout dropped to 75% in the high-gradient reach (Table 2). Terrestrial invertebrates formed the majority of the diets for both species (cutthroat = 57%, brook = 61%) in the high-gradient reach and were preferentially selected relative to their availability in the drift (Table 2). Diptera remained a large percentage of the cutthroat trout diets but were consumed at levels well below their drift availability. In contrast, Diptera were a minor component of brook trout diets in the high-gradient reach, whereas Coleoptera and Trichoptera each formed 14% of brook trout diets (Table 2).

Diet overlap was least (65%) in the low-gradient reach (Table 2). Cutthroat trout diets were nearly equally split between terrestrial invertebrates (49%) and Diptera (46%), selecting for terrestrial invertebrates and against Diptera relative to drift availability (Table 2). In contrast, Diptera represented 65% of brook trout diets in the low-gradient reach, with terrestrial invertebrates (15%) and Trichoptera (12%) also being important (Table 2). Brook trout avoided Diptera and selected terrestrial invertebrates, while consuming Trichoptera at levels similar to drift availability.

Invertebrate consumption differed both among

TABLE 2.—Total numbers of invertebrates consumed, diet composition (% of diet), and food selectivity of brook and cutthroat trout in beaver ponds and high-gradient and low-gradient reaches.

Variable or order	Beaver Pond		High-gradient		Low-gradient	
	Brook trout	Cutthroat trout	Brook trout	Cutthroat trout	Brook trout	Cutthroat trout
Sample size	13	31	5	32	8	28
Consumption						
Ephemeroptera	4	31	1	109	8	52
Plecoptera	0	1	0	14	2	2
Trichoptera	63	24	26	175	22	17
Terrestrial	134	437	107	1,261	30	934
Diptera	957	3,576	15	590	129	881
Coleoptera	20	42	25	18	2	6
Total prey consumed	1,178	4,111	174	2,167	193	1,892
Average prey/fish	90.6	132.6	34.8	67.7	24.1	67.6
Percent diet composition						
Ephemeroptera	0.3	0.8	0.6	5.0	4.1	2.7
Plecoptera	0	0	0	0.6	1.0	0.1
Trichoptera	5.3	0.6	14.9	8.1	11.4	0.9
Terrestrial	11.4	10.6	61.5	58.2	15.5	49.4
Diptera	81.2	87.0	8.6	27.2	66.8	46.6
Coleoptera	1.7	1.0	14.4	0.8	1.0	0.3
Selectivity						
Ephemeroptera	−0.11	−0.10	−0.09	−0.04	0.01	−0.01
Plecoptera	−0.01	−0.01	−0.01	0.01	−0.01	−0.01
Trichoptera	0.09	0.01	0.11	0.04	0.04	0.01
Terrestrial	0.1	0.06	0.48	0.41	0.40	0.38
Diptera	−0.01	0.03	−0.64	−0.41	−0.43	−0.36
Coleoptera	0.02	0.02	0.15	−0.01	−0.01	−0.02

reach habitat types and between trout species. Cutthroat trout consumed significantly more invertebrates per fish than brook trout (ANCOVA; $P = 0.003$) in all three reach habitat types. Consumption was also significantly greater in beaver ponds than in either high- or low-gradient reaches but did not differ between high- and low-gradient reaches (ANCOVA; $P < 0.001$). There was no significant relationship between the numbers of invertebrates consumed and fish length or condition (size range of brook trout, 121–281 mm; of cutthroat trout, 95–266 mm).

To summarize, per capita invertebrate consumption was greatest in beaver ponds, cutthroat trout consistently consumed more invertebrates than did brook trout, and there was no relationship between consumption and fish length or condition. There also was no indication of piscivory in either brook or cutthroat trout we sampled. Both brook trout and cutthroat trout preferentially selected terrestrial invertebrates in all reach types and avoided Diptera in high- and low-gradient reaches despite its prominence in the diet. The high degree of diet overlap between brook and cutthroat trout in beaver ponds suggests the possibility of competition.

Discussion

The nearly complete diet overlap (92%) between nonnative brook trout and native Bonneville cutthroat trout in beaver ponds identifies a potential for food competition in this reach type. In contrast, diet overlap decreased to 75% in the high-gradient reach. These data anecdotally support our prediction of greater diet overlap in reaches numerically dominated by brook trout, given the hypothesis that brook trout are better food competitors. In contrast to our predictions, however, diet overlap was least in the low-gradient reach. However, this prediction was based on trout distributions reported elsewhere (MacPhee 1966; Griffith 1972); predictions intrinsic to Beaver Creek, where cutthroat trout numerically dominate the low-gradient reach, would presumably predict diet overlap to be lower—and it was. Whereas Griffith (1974) found that sympatric brook and cutthroat trout selected against the food items preferred by the other species, we found little evidence of diet partitioning, particularly in beaver ponds. Our study is limited by the small sample sizes of brook trout in both the high-and low-gradient reaches. Greater statistical power with larger sample sizes and replication of reaches could make a stronger case but was not possible in Beaver Creek, given the distributions of both fish and channel features.

Although predictions of diet overlap agree with trout distributions, more evidence is required to conclude that competition for food is actually occurring and is indeed the mechanism for brook trout replacing cutthroat trout in beaver ponds of Beaver Creek. Our data collection was not designed to explicitly test for food competition, and we are inferring process from pattern. Cutthroat trout consumed significantly more invertebrates than brook trout in all reach types. This pattern was also observed in a sympatric population in Nevada (Dunham et al. 2000) but not in northern Idaho (Griffith 1974). If brook trout were so competitively dominant as to readily replace cutthroat trout, we would expect significantly greater consumption of invertebrates by brook trout rather than by cutthroat trout. Perhaps brook trout consumed larger prey items than cutthroat trout, as seen with Lahontan cutthroat trout *O. c. henshawi* being sympatric with brook trout (Dunham et al. 2000), and gained greater energy intake with less effort. We did not measure size of either prey items or drifting invertebrates and do not know whether size selection occurred.

Abundance of drifting invertebrates in Beaver Creek was very high for streams containing cutthroat trout. After accounting for sampling duration, total drift captured in the current study was two orders of magnitude greater than in the North Fork Humboldt River, Nevada (Dunham et al. 2000), one order of magnitude greater than in four northern Idaho steams sampled by Griffith (1974), and at least twice as great as in Cement Creek, Colorado (Allan 1978). Similarly, drift density in the current study ranged from a low of 17.2 organisms/m^3 in the low-gradient reach to a maximum of 26.5 invertebrates/m^3 in the high-gradient reach; in comparison, drift density was 0.13–0.31 invertebrates/m^3 in the North Fork Humboldt River, Nevada (Dunham et al. 2000).

Patterns of invertebrate consumption were similar to those in other trout species (Elliott 1970, 1973; Jenkins et al. 1970; Allan 1978; Hubert and Rhodes 1989). Consumption generally paralleled the availability of an invertebrate group in the drift; as relative availability increased, the percentage of that group in trout diets also increased. However, two notable exceptions became evident. Diptera were avoided by both trout species in both high- and low-gradient reaches, even though they still formed a substantial percentage of trout diets. Perhaps drifting Diptera were too small to be profitable, or possibly more Diptera were drifting than could be consumed and thus were underrepresented in trout diets relative to availability in the drift. Terrestrial invertebrates were preferentially selected in both high- and low-gradient reaches, where they formed a large percentage of trout diets. This pattern is similar to diets of trout elsewhere (Reed and Bear 1966; May et al. 1978; Hubert and Rhodes 1989; Kawaguchi and Nakano 2001), where terrestrial invertebrates may represent more than half of the diet during summer months (Kawaguchi and Nakano 2001). In contrast, cutthroat trout in other studies (Fleener 1951; Griffith 1974; Dunham et al. 2000) show less use of terrestrial invertebrates as food, possibly because of a lack of availability, and partly because of the greater importance to cutthroat trout of Plecoptera, Ephemeroptera, and Trichoptera, which were minor in diets in the current study. We also found no relationship between fish length and consumption for either species, whereas Dunham et al. (2000) found a positive relationship for Lahontan cutthroat trout. These differences demonstrate the large variation in diet among populations of the same species.

Our results demonstrate that diets vary substantially over relatively short spatial scales (less than 2 km) in the same population when channel type changes. Although terrestrial invertebrates were preferred in high- and low-gradient reaches and accounted for a large percentage of trout diets, they made up only a minor portion of both brook and cutthroat trout diets in beaver ponds, where they were consumed at rates only slightly greater than their drift availability. The opposite was true for Diptera. Because of the similar proportions of drifting taxa among reaches, spatial variation in diets appears less related to drift availability and more likely to be intrinsic to the reach. Differential selection of the same food items in different reaches could have a number of causes, including habitat, drift timing, and availability. Nonetheless, spatial variation in food habits is an important factor to consider when examining diets of trout, and extrapolating to unsampled portions of a stream should be done with caution.

Despite little evidence for food competition between brook trout and cutthroat trout in Beaver Creek, high diet overlap could be of concern if similar patterns exist in other streams. Ensuring access to food by acquiring profitable stream positions may take on an important role. In laboratory experiments, similar sized brook trout occupied the most favorable feeding positions in the majority of trials (Buys 2002). If this pattern should hold in food-limited systems, brook trout could more easily replace cutthroat trout.

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