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DIETS OF SYMPATRIC LAHONTAN CUTTHROAT TROUT AND NONNATIVE BROOK TROUT: IMPLICATIONS FOR SPECIES INTERACTIONS

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ABSTRACT.—Nonnative brook trout (*Salvelinus fontinalis*) have been implicated in declines of stream-living Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*), a threatened trout endemic to the Lahontan Basin of northeastern California, southeastern Oregon, and northern Nevada. Brook trout may displace Lahontan cutthroat trout through 2 mechanisms: interspecific predation and competition for food. To evaluate the evidence for these alternatives, we examined stomach contents of 30 trout of each species captured in the North Fork Humboldt River, northeastern Nevada, to compare number, size, and taxonomic composition of prey. Taxonomic dietary overlap was high (81.4%) between brook and Lahontan cutthroat trout. Both species were nonselective in their feeding habits. Lahontan cutthroat trout consumed over 2.5 times as many prey on average, but brook trout consumed significantly larger prey. No trout of either species occurred in fish diets. Only a single fish, a Paiute sculpin (*Cottus beldingi*), was found in stomachs, and the majority (>90%) of prey consisted of insect taxa. Size and number of prey consumed were positively related to fish size for Lahontan cutthroat trout, but not for brook trout. These results do not provide compelling evidence to suggest feeding by Lahontan cutthroat trout is limited by presence of large numbers of brook trout in the North Fork Humboldt River. However, fundamental differences in each species' utilization of food in this system indicate that a better understanding of observed differences may help to explain the variable success of brook trout invasions across stream habitats in the Lahontan Basin and their potential effects on Lahontan cutthroat trout.

Key words: Lahontan cutthroat trout, Oncorhynchus clarki henshawi, *diet selection, nonnative species, brook trout,* Salvelinus fontinalis.

Naturalized populations of nonnative salmonid fishes have been implicated in the decline of many native aquatic organisms, including amphibians (Bradford 1989), invertebrates (Polhemus 1993), and fishes (Moyle et al. 1986). Potential mechanisms by which nonnative fishes may interact with native biota include predation, competition, parasite and disease transmission, and hybridization, which may operate directly or indirectly (see Taylor et al. 1984 for a general review). Nonnative salmonids are frequently implicated in declines of native salmonids in the western United States (Allendorf and Leary 1988, Young 1995, Duff 1996). For example, loss of threatened Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) populations in the Lahontan Basin of northeastern California, southeastern Oregon, and northern Nevada has been attributed in part to competition from nonnative salmonids, most notably brook trout (*Salvelinus fontinalis;* Coffin and Cowan 1995). While the decline of Lahontan cutthroat trout appears to coincide with the invasion of brook trout and other nonnative salmonids throughout the Lahontan Basin (Miller and Alcorn 1943), there is very little published evidence describing potential interactions between cutthroat trout and brook trout (see Young 1995), and none for Lahontan cutthroat trout (but see Schroeter 1998).

In this study we addressed 2 possible explanations for negative impacts brook trout may have on Lahontan cutthroat trout populations. First, we examined the evidence for direct predation of juvenile Lahontan cutthroat trout by brook trout. In particular, small young-of-year Lahontan cutthroat trout (average 20–50 mm in length) may be vulnerable to predation by larger conspecifics or by brook trout. Second, we focused on food as a potentially limiting resource that may lead to competition between Lahontan cutthroat trout and brook trout. Stream-living salmonids may compete for a variety of other potentially limiting resources,

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such as space or cover (Chapman 1966, Fausch 1988), but in this study we focused on food limitation. Interspecific competition is a notoriously controversial subject (Fausch 1988 and references therein), and we made no attempt to resolve this issue with regard to all possible interactions between brook trout and Lahontan cutthroat trout. Rather, results of this work were intended to provide descriptive data that may serve as a baseline for more rigorous inquiry as to how and why brook trout may have negative impacts on cutthroat trout populations.

We studied Lahontan cutthroat trout and brook trout in the North Fork Humboldt River, Nevada (Fig. 1), where they have coexisted since the latter were introduced into the system by the early 1900s (Miller and Alcorn 1943, P. Coffin personal communication). In most streams of the Lahontan Basin, these species segregate longitudinally in a typical pattern (Fausch 1989), with cutthroat trout being relatively more abundant in the upstream reaches and brook trout more so in downstream reaches (Fig. 2). Distribution of fishes in the North Fork Humboldt River is rather unusual, however, in that cutthroat and brook trout may be found in the same habitats along a 2- to 4-km reach of stream (Fig. 2, see also Nelson et al. 1992).

Close spatial proximity of individuals in the North Fork Humboldt allowed us to study diets of cutthroat and brook trout that presumably had access to a similar resource supply. We studied diets of both species to determine incidence of predation by brook trout on cutthroat trout and to quantify patterns of diet selection and diet overlap. Our results are compared with those from similar work on other cutthroat subspecies (Griffith 1972, 1974, Bozek et al. 1994) to evaluate the relevance of trophic interactions to the coexistence of brook and Lahontan cutthroat trout.

METHODS

We sampled brook and Lahontan cutthroat trout in the North Fork Humboldt River, Elko County, Nevada (Fig. 1). Sampling was conducted along a 2-km reach of stream at approximately 2100 m elevation. Fish were captured by electrofishing every 4 h for a 36-h period between 20 and 21 August 1995. Equal numbers (n = 30) of brook and Lahontan cutthroat trout were sampled over this period, and individuals of each species were matched for size (fork length) as closely as possible within each of 9 collections to control for the potentially confounding effect of fish size and spatial location (Fausch 1988). We recorded number and size of all trout captured during sampling efforts to provide an estimate of relative size and abundance of each species. Possible size differences between fish in all groups (sampled brook and Lahontan cutthroat trout, unsampled trout) were assessed by analysis of variance. Four hours prior to each fish collection, we placed a 1-mm bar mesh drift net in a riffle just upstream of habitats to be electrofished. Drift net openings were 45 cm^2, with a 1-m tapered net bag length (see Merritt et al. 1984). Nets were placed at the deepest part of the stream in locations that spanned at least 25% of the stream width. The bottom of the net was held flush to the stream bottom by steel rods hammered into the stream substrate. In all cases height of the drift net exceeded water depth, so drift in the entire water column was sampled. Fish and invertebrate sampling proceeded in an upstream direction to avoid disturbance to either. At the end of each 4-h period, we removed drift nets and preserved their contents in 70% ethanol for later sorting, identification, and enumeration. Densities of drifting organisms were quantified following methods described by Smock (1996).

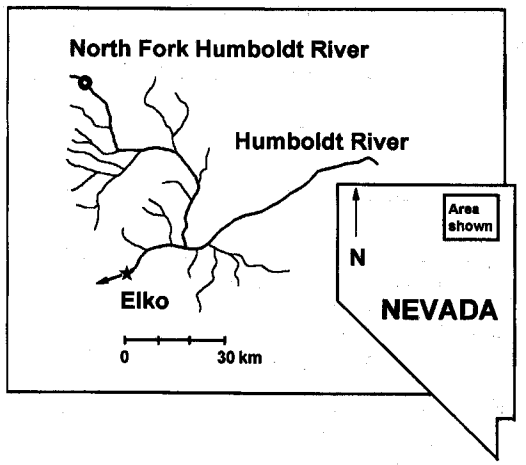

Fig. 1. Map of study site (open circle), North Fork Humboldt River, Elko County, Nevada. Further description of the study area is given by Nelson et al. (1992).

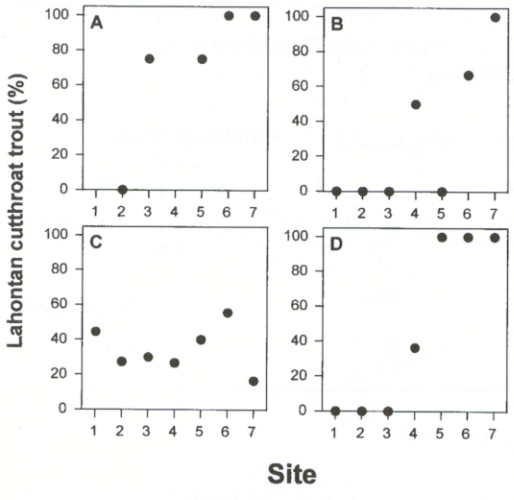

Fig. 2. Scatter plots of Lahontan cutthroat trout density (fish >100 mm), expressed as percentage of total salmonid density (Lahontan cutthroat trout + brook trout). Data are from multiple (3+) pass electrofishing samples at 7 sites in 4 streams in the Humboldt River drainage, 1996 (R.E. Schroeter and J.B. Dunham unpublished data). Sites are 25-m stream reaches spaced 300 m apart and sorted (1 through 7) in a down- to upstream direction. Note there are only 5 data points for stream A because fish were absent from 2 sites. Streams are as follows: (A) South Fork Tierney Creek, (B) North Fork Tierney Creek, (C) North Fork Humboldt River, (D) Abel Creek.

After sampling the invertebrate drift, we captured trout directly downstream (within 30 m) of the drift nets by electrofishing. Stomach contents of trout sampled for diet analysis were collected with a water-filled syringe fitted with a short length of narrow (~3-mm-diameter) surgical tubing. Prior to the study this method was field-tested on live brook trout ($n = 10$) that were later sacrificed to examine any remaining stomach contents. In all cases the method was found to flush 100% of food items in the cardiac stomach. Identification of trout stomach contents and drift net samples was conducted with a dissecting scope equipped with an ocular micrometer. All prey and drift items were identified to order using Merritt and Cummins (1984). Head widths of prey items were measured (to the nearest 0.1 mm) to quantify prey size. We used only maximum head width (excluding movable appendages) because many prey items were partially digested or broken into pieces. This also prevented counting the same individual more than once when total number of consumed prey was determined.

Analyses of diet composition, overlap, and selectivity were conducted on the entire collection of fish (e.g., over the entire 36-h period). No attempts were made to stratify the data by time as sampling within each time period was limited. Fish with empty stomachs were excluded from analyses of diet selection. To evaluate the influence of body size on prey consumption, total number of prey and prey widths were correlated with fish size (fork length) in each species. Taxonomic similarity of all prey in the diets of brook and Lahontan cutthroat trout was estimated by percentage overlap. Percentage overlap between 2 species was estimated as:

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

for $n = 1$ to the total number of resource states (prey orders in this case), where p_{ij} and p_{ik} are proportions of resource i used by species j and k, respectively (Schoener 1970).

Preference for the 5 most abundant prey items (insect orders) was estimated for each individual by the method of Strauss (1979) and calculated as:

$$L = r_i - p_i$$

where r_i is the relative proportion of prey item i in the diet and p_i is the relative proportion of prey item i in the environment. Values of L range between 1 and –1, indicating perfect selection and perfect avoidance of prey, respectively. Because drift rates of prey were very low, we used pooled abundance from the entire sampling period to estimate proportions of prey available in the environment. Statistical differences in prey selection between brook trout and Lahontan cutthroat trout were assessed with Wilcoxon rank sum tests.

RESULTS

Average fork lengths of the 30 Lahontan cutthroat and brook trout sampled for stomach contents were 151 and 158 mm, respectively. Average absolute size difference between paired individuals was 20 mm. Research on other subspecies of cutthroat trout has shown that size differences of this magnitude should have a negligible effect on diet selection (Bozek et al. 1994). Average fork length for an additional 76 brook trout captured during

sampling was 182 mm. Analysis of variance indicated fork lengths differed significantly among these 3 samples ($F_{2,132} = 6.57$, $P = 0.0019$). Mean comparisons (Fisher's protected least significant difference) indicated fork lengths of unsampled brook trout were significantly greater than sampled Lahontan cutthroat trout ($P < 0.01$), but not different from sampled brook trout. As expected, fork lengths of sampled Lahontan cutthroat and brook trout were not significantly different.

If relative rates of capture were a reflection of relative densities of these 2 species, then brook trout outnumbered Lahontan cutthroat trout by over 3.5 to 1 in the section of the North Fork Humboldt River we sampled. This estimate refers only to fish >100 mm in fork length. Smaller fish were present in the study area but were not considered in this study. Capture probabilities were not estimated, but they were probably greater for Lahontan cutthroat trout, since it was the focal species of this study. As a result, the relative number of brook trout may have been underestimated. In any case, our results clearly indicated that brook trout far outnumbered Lahontan cutthroat trout, and that large (>100 mm) brook trout had significantly greater fork lengths.

In the nine 4-h drift net collections, only 221 drift organisms were collected. Drift densities (Smock 1996) were extremely low, ranging between 0.13 and 0.31 drifting organisms per cubic meter. Dipteran insects were the dominant taxonomic group (Table 1) and dominated diel patterns of drift. Size structure of the drift was not quantified. Sizes (maximum head widths) of invertebrates consumed by trout ranged from 1.1 to 5.7 mm, so we were confident the 1-mm-mesh bar drift net captured prey of sizes consumed by sampled trout.

Lahontan cutthroat trout consumed significantly larger numbers of prey items than brook trout (2-tailed Wilcoxon paired-sample test, $P < 0.001$). Individual Lahontan cutthroat trout consumed an average of 28.2 prey, compared to 10.5 for individual brook trout. All 30 Lahontan cutthroat trout had consumed prey, while 4 of 30 brook trout had empty stomachs. Average maximum head widths of prey consumed by brook trout were 1.5 times larger on average than prey consumed by Lahontan cutthroat trout (2.4 versus 1.5 mm, respectively), and this difference was highly significant (2-tailed Wilcoxon paired-sample test, $P < 0.001$). Spearman rank correlations between fish fork length and prey width were significant for Lahontan cutthroat trout ($r_s = 0.53$, $P = 0.003$), but not for brook trout ($r_s = 0.27$, $P = 0.16$). Similarly, number of prey consumed was positively correlated with Lahontan cutthroat trout fork length ($r_s = 0.44$, $P = 0.02$), but not for brook trout ($r_s = 0.16$, $P = 0.39$).

Diet overlap was relatively high (81.4%) between the 2 species. Trichopteran larvae (primarily Ryacophilid larvae) dominated diets of both species, followed by Hymenoptera (Table 1), which, unlike other major prey items, were primarily terrestrial in origin. Overall, both species showed strongest selection for Trichopteran prey, with relatively weak selection ($-0.25 > L < 0.25$) for other prey types. Prey selection did not vary significantly between brook trout and Lahontan cutthroat trout, as indicated by Wilcoxon rank sum tests. We considered selection only for the 5 most abundant taxa, as other taxonomic groups were of minor significance (3.80% of Lahontan cutthroat trout diets and 7.53% of brook trout diets). Fish were rare in trout diets in this study and were represented by a single Paiute sculpin (*Cottus beldingi*) consumed by a Lahontan cutthroat trout. No instances of predation on trout of either species were observed.

DISCUSSION

Results of this study provide several interesting insights into how Lahontan cutthroat trout and nonnative brook trout may interact. It appears that predation and/or cannibalism of young-of-year trout by larger trout may be uncommon. We did not sample stomachs of larger brook trout captured in this study, but our results corroborate numerous anecdotal observations of diets of brook and Lahontan cutthroat trout ($n > 50$ individuals of each species; Dunham personal observation) and results of comparative studies of other cutthroat trout subspecies (*O. c. lewisi*) and brook trout (Griffith 1974).

While direct evidence of predation was lacking, predation may indirectly affect young-of-year trout by altering patterns of habitat use (Dill and Fraser 1984). Large (>200 mm fork length) Lahontan cutthroat and brook trout have been observed to consume other fish on

TABLE 1. Overall percentages of invertebrate prey items found in stomachs of brook trout (BT) and Lahontan cutthroat trout (LCT), and those caught in drift nets. Averaged values of the Strauss linear index of food selection (L) for Lahontan cutthroat trout and brook trout also are shown (standard deviations in parentheses).

	Prey percentages			Strauss' L	
Order	BT	LCT	Drift nets	BT	LCT
Diptera	21.41	16.88	23.64	–0.05 (0.19)	–0.08 (0.17)
Plecoptera	5.43	3.80	5.75	0.002 (0.12)	0.05 (0.16)
Trichoptera	36.42	47.09	13.42	0.23 (0.30)	0.29 (0.28)
Coleoptera	13.74	5.95	10.86	0.00 (0.16)	–0.06 (0.11)
Hymenoptera	15.65	22.47	6.39	0.10 (0.19)	0.11 (0.21)

an intermittent basis, and individuals as small as 150 mm in length will consume adult (≥40 mm) speckled dace (*Rhinichthys osculus*; Dunham personal observation). In this study only a single Paiute sculpin (*Cottus beldingi*) was found in the stomach of a Lahontan cutthroat trout. Thus, large trout may be perceived as potential predators by smaller individuals. During the course of this study, both young-of-year cutthroat trout and brook trout were most obviously abundant in off-channel habitats, a distribution pattern also observed by Moore and Gregory (1988) for coastal cutthroat trout (*O. c. clarki*) in streams.

Piscivory was rare, but trout sampled in this study were found to consume a large number of invertebrate prey items, primarily insects. This was in spite of low observed drift rates. We have no explanation for low drift rates in this study, as there were no obvious disturbances or evidence of extreme habitat degradation at the time. Certainly, fish would be expected to capture more prey since they presumably search the water column for prey items, as opposed to passive capture by drift nets. Furthermore, some fish (see below) may feed on benthic prey in addition to those in the drift.

One of the most striking results of this study was that Lahontan cutthroat trout consumed over 2.5 times more prey items (total) than did brook trout. Similarly, Griffith (1974) observed moderately higher (25%) per-capita consumption rates for cutthroat trout. Brook trout were more likely to have empty stomachs than Lahontan cutthroat trout (13.3% versus 0.0% empty stomachs, respectively). Griffith (1974) sampled age 0 and age 1+ cutthroat and brook trout and found only 2% of stomachs contained no food. The difference in consumption rates between Lahontan cutthroat trout and brook trout cannot be attributed to body size because fish were closely matched for size. Prey selectivity could explain differences in consumption rates, but we found no taxonomic differences in prey selectivity between the 2 species.

Taxonomic diet overlap between brook and Lahontan cutthroat was high, suggesting the potential for food-mediated competitive interactions. Similarly, selectivity did not vary significantly between species, and trout were opportunistic (i.e., nonselective) in their feeding. Different classifications of drift may produce different results with regard to prey selectivity and diet overlap, however. For example, we did not attempt to identify invertebrates below order, nor did we classify invertebrates with regard to a recently published classification of characteristics that may affect their availability to trout (Rader 1997). Furthermore, our focus on drifting organisms may not have accurately characterized potential prey items (sensu Strauss 1979).

Brook trout consumed prey that were larger on average (as indicated by prey head widths), which may have compensated for the large difference in overall consumption rates. Griffith (1972, 1974) found that brook trout exploited both benthic and drifting invertebrates, while cutthroat trout fed more exclusively on drift. This observation was used by Griffith to explain why brook trout may consume larger (benthic) prey items. Differences in gape size could possibly explain why brook trout consumed larger prey, but prey size was not related to fork length (a surrogate of gape size) for brook trout, and research in similar systems suggests gape limitation may not be important (see also Bozek et al. 1994).

Differences in microhabitat selection and interactive segregation between the 2 species also may explain the contrasting consumption rates we observed (see also Griffith 1972, 1974,

DeStaso and Rahel 1994, Schroeter 1998). Within species, social dominance is suggested by the observation that prey size and consumption rate were positively related to fish size (fork length) for Lahontan cutthroat trout, but not for brook trout. Larger Lahontan cutthroat trout may have monopolized higher-quality feeding locations, including higher-velocity microhabitats (sensu Griffith 1972, Fausch 1989) such as riffles, which typically have higher densities of invertebrate prey (Chapman and Bjornn 1969). These habitats may be more energetically profitable in terms of feeding, but less so in terms of swimming costs.

Obviously, consumption rates are only a single factor among many that may determine the net (energetic) profitability of feeding positions in streams (Fausch 1984). For brook trout, relatively high fish densities in the North Fork Humboldt River may have increased intraspecific competition for food and feeding locations, thus lowering per-capita consumption rates. Alternatively, social dominance of cutthroat trout (Griffith 1972, but see DeStaso and Rahel 1994, Schroeter 1998) may have displaced brook trout to less favorable feeding locations.

In summary, we observed a high degree of taxonomic similarity between diets of Lahontan cutthroat trout and brook trout in the North Fork Humboldt River, with no evidence of predation on juvenile trout by either species. Rates of consumption, size of prey consumed, and relationships of these variables to fish size varied dramatically between the 2 species, however. Rates of consumption by both species did not reflect low rates of invertebrate drift we observed, though some brook trout stomachs were found to be empty, suggesting food limitation may have been important (at least for brook trout) at the time of our study.

Results from this short-term look at feeding habits do not provide compelling evidence to suggest feeding by Lahontan cutthroat trout is limited by presence of large numbers of brook trout in the North Fork Humboldt River. There is, however, much evidence to suggest fundamental differences in how Lahontan cutthroat trout and brook trout utilize food, a potentially limiting resource, in this system. Further comparative work on allopatric cutthroat and brook trout populations is needed to see if similar feeding patterns are observed. A better understanding of these differences may help to explain the variable success of brook trout invasions observed across stream habitats in the Lahontan Basin, and their potential effects on Lahontan cutthroat trout

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