

# Trophic relationships of nonnative brown trout, *Salmo trutta*, and native Bonneville cutthroat trout, *Oncorhynchus clarkii utah*, in a northern Utah, USA river

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**Abstract** Nonnative trout invasions have caused the widespread decline of cutthroat trout populations in western North America. In contrast to other nonnative salmonids, the role of nonnative brown trout in native cutthroat trout decline is poorly understood. Specifically, the level of ecological similarity that occurs between these species and the importance of other trophic mechanisms (e.g., predation) in their interactions are key uncertainties. We evaluated the trophic relationships of brown trout and cutthroat trout in a northern Utah river using a combination of diet and stable isotope analyses. We compared the dietary habits of these two species using multiple and complementary measures. Based on both stomach contents and  $\delta^{13}\text{C}$  signatures, we found that these species consumed a similar and opportunistic diet (i.e., they were nonselective in their foraging patterns). However, at most sizes, brown trout ingested larger prey—including fishes—and occupied a higher relative trophic position (i.e.,  $\delta^{15}\text{N}$ ) than cutthroat trout. Overall, these results demonstrate a high degree of dietary similarity and therefore strengthen earlier conclusions

regarding interspecific competition between these two species. Our study, when considered alongside the work of others, suggests there is potential for predatory interactions between these species (i.e., brown trout preying on small cutthroat trout). We believe that future research on brown trout–cutthroat trout interactions should consider predatory effects in greater detail.

**Keywords** Nonnative species · Cutthroat trout · Brown trout · Competition · Predation

## Introduction

Nonnative-fish introductions and/or invasions constitute one of the greatest threats to the future abundance of Earth's piscine fauna (Richter et al. 1997; Wilcove et al. 1998). In western North America in particular, introduced salmonids have displaced (sensu Dunham et al. 2002) regionally endemic cutthroat trout subspecies, *Oncorhynchus clarkii* subsp., from both riverine and lacustrine habitats (Quist and Hubert 2004; Koel et al. 2005). Rainbow trout, *Oncorhynchus mykiss*, brook trout, *Salvelinus fontinalis*, and lake trout, *Salvelinus namaycush*, have all contributed to cutthroat trout decline through hybridization, competition, and/or predation (Griffith 1988; Ruzycki et al. 2003; Weigel et al. 2003). Given these impacts and the sensitive status of cutthroat

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trout throughout their native range (Young 1995), aggressive management strategies based on combinations of nonnative species removal (e.g., using mechanical methods) and conservation by isolation (e.g., using barriers) have been employed in situations where nonnative salmonids are a threat (Novinger and Rahel 2003; Koel et al. 2005).

In contrast to other salmonids, only recently have the potential impacts of brown trout, *Salmo trutta*, an introduced fish of Eurasian origin (Fuller et al. 1999), been considered within the context of cutthroat trout conservation. This lagged interest in the role of brown trout in cutthroat trout decline has occurred despite their widespread watershed-level co-occurrence and complementary distributional patterns (de la Hoz Franco and Budy 2005; Quist and Hubert 2005). Recent competition experiments demonstrate that brown trout can attain dominance via aggression (Wang and White 1994) and ultimately suppress cutthroat trout growth, condition, and movement in a controlled setting (McHugh and Budy 2005, 2006). While these results provide considerable insight into the mechanism of competition for cutthroat trout displacement, the level of ecological similarity that exists between wild sympatric brown and cutthroat trout remains unknown. Further, despite the documented effects of brown trout as a top predator (e.g., Museth et al. 2003) capable of causing native-fish declines elsewhere (e.g., Townsend and Crowl 1991), the role of predation on cutthroat trout by brown trout as a mechanism for cutthroat trout displacement has not been considered to date. Given the incomplete nature of knowledge on brown trout–cutthroat trout trophic interactions and the precarious state of cutthroat trout, there is a need for detailed studies that directly assess the extent of dietary overlap and potential for predatory interactions between these two species.

The goal of our research was to quantify and compare attributes of their dietary habits using a survey-study approach. Our primary objectives were to: (1) evaluate the extent of dietary overlap and similarity in prey selection that occurs between these species, as a validation of ecological similarity implied by prior competition experiments; and (2) assess the potential role of

piscivory in brown trout–cutthroat trout interactions. To do this, we measured the dietary habits of both species using a combination of stomach content and stable isotope analyses. Specifically, we quantified and compared diet composition (prey identity and size,  $\delta^{13}\text{C}$  isotope signatures), prey selection, and relative trophic position (i.e.,  $\delta^{15}\text{N}$ ) using fish sampled from a northern Utah river where these species locally coexist. By providing evidence of ecological similarity and demonstrating that a potential exists for piscivorous interactions between these species, our study provides detailed information of direct relevance to native cutthroat trout conservation efforts.

## Materials and methods

### Study site description

We conducted our study on the trophic relationships of brown and cutthroat trout in a mid-elevation (1,691 m) reach of the Logan River in northern Utah, U.S.A. (UTM Zone 12, 449678 E, 4630377 N). We chose this particular reach based on earlier electrofishing surveys which indicated that both brown and cutthroat trout of all age classes exist within it at moderate abundances (2001–2003 density range, 649–787 trout  $\text{km}^{-1}$ ) in similar proportions. Additionally, this site was chosen because it is part of a larger effort toward understanding factors influencing the dynamics of Bonneville cutthroat trout populations in northern Utah (Budy et al. [in press](#)).

Our study reach (Twin Bridges) which occurs within a narrow canyon of Paleozoic carbonate rocks, is moderately steep (0.015 m/m), contains primarily gravel-to-cobble-sized substrate, and flows at approximately  $3.2 \text{ m}^3 \text{ s}^{-1}$  during the summer period (May–September). The daily average water temperature of this section of the Logan River is  $13^\circ\text{C}$  (range  $10$ – $16^\circ\text{C}$ ) during the summer (Budy et al. 2004). In addition to brown and cutthroat trout, the most recent electrofishing records for this site indicate that both mountain whitefish, *Prosopium williamsoni*, and mottled sculpin, *Cottus bairdi*, are present. For a more detailed description of the physical and biological

characteristics of this site, see de la Hoz Franco and Budy (2005) and McHugh and Budy (2005).

### Fish collection

We collected 64 fish during annual population monitoring activities in late July 2003 ( $n = 12$  brown and 13 cutthroat trout) and 2004 ( $n = 25$  brown and 14 cutthroat trout) using a canoe-mounted electrofishing unit. Upon collection, fish were euthanized with a lethal dose of MS-222, weighed and measured (total length, TL), and held on ice. Stomachs were extracted from fish, punctured, and preserved in 10% formalin or 90% ethanol within 4 h of capture and stored for later dissection and analysis of contents.

### Stomach-content description

To determine the similarity in dietary habits and the extent of piscivory for brown and cutthroat trout, we examined the contents of all stomachs collected. Under a dissecting microscope, we classified to the lowest practical taxonomic level (typically order), counted, and weighed (blot-dried and grouped) all items found within individual trout stomachs. Contents were classified as Ephemeroptera, Trichoptera, Plecoptera, Diptera, Hemiptera, Coleoptera, Annelida, terrestrial insects, fish, vegetation (i.e., seed or leaf matter), or unidentified organic matter.

We summarized diet composition at the whole-sample level based on the percent of all stomachs containing individuals of a given prey category,  $i$  (i.e., percent occurrence, %  $O_i$ ); individual fish dietary patterns were summarized using percent abundance by number (%  $N_i$ ) and weight (%  $W_i$ ) of the same categories. As a composite measure of %  $O$ , %  $N$ , and %  $W$ , we also computed the index of relative importance (% IRI) for each prey category  $i$ , where %  $IRI_i = [\% O_i(\% N_i + \% W_i)] / (\sum \% IRI_i)$  (Cortés 1997). We described the similarity of trout stomach contents using the percent dietary overlap index (% overlap =  $\Sigma[\text{minimum}(P_{ij}, P_{ik})]$ , where  $P_{ij}$  and  $P_{ik}$  are the mean %  $N$  (or %  $W$ ) of prey item  $i$  in the stomach of species  $j$  and  $k$ , respectively; Schoener 1970). In addition to prey identity measures of stomach contents, we evaluated the size composi-

tion of organisms found in diets. To do this, we measured the body length of all intact and identifiable items using an ocular micrometer and subsequently calculated mean prey size, weighted by %  $N_i$  for each category, for each fish.

We summarized and included in our analysis only information on identified, nonvegetation stomach contents. Observations with >25% (by mass) of unidentifiable contents were excluded from our final dataset.

### Prey-selection behavior

To contrast prey selection between species, we quantified the abundance and composition of aquatic invertebrates in our study reach. Prior to electrofishing in 2003, we collected benthic invertebrate samples ( $n = 4$ ) from riffles using a 0.09-m<sup>2</sup> Surber sampler. We also sampled drifting invertebrates using 0.10-m diameter nets fished mid-channel for 30 min at dusk (21:00;  $n = 7$ ). Upon collection, we preserved samples in 70% ethanol and stored them for later processing. Under a dissecting microscope, we identified and counted all invertebrates in samples and summarized them in terms of taxonomic composition (i.e., %  $N$ ) and total density (no. m<sup>-2</sup> for benthic samples; no. m<sup>-3</sup> for drift samples). We excluded meiofauna (predominantly *Hydracarina* arachnids in drift samples) and gastropods (benthic samples only) from our summary and subsequent analysis, because of their low abundance in the environment and absence from trout stomachs. Further, we could only process a single drift sample (i.e.,  $n = 1$  processed drift sample) due to logistical reasons (sample desiccation).

We quantified prey selection for the most common prey items for each individual trout using Strauss's linear electivity index,  $L$  ( $L_i = r_i - p_i$ , where  $r_i$  and  $p_i$  are the proportional abundances of prey item  $i$  in the diet and in the environment, respectively; Strauss 1979).  $L$  ranges from  $-1$  to  $+1$ , with negative values indicating avoidance, positive values indicating preference, and neutral use occurring in the range  $-0.25 < L < 0.25$ . To identify tendencies toward a particular feeding mode (i.e., drift feeding versus benthic feeding), we completed a separate analysis of prey-selection patterns relative to drift and benthic invertebrate

samples and considered these results within the context of published information on drift behavior (Rader 1997).

While our use of invertebrate data assumes that 2003 community conditions approximate those existing in both 2003 and 2004, several lines of evidence suggest that this is a reasonable expectation. First, many studies illustrate that invertebrate communities are stable across time periods ranging from a few years (e.g., Robinson et al. 2000) to a few decades (e.g., Woodward et al. 2002). This is especially true when extreme flows are lacking (Milner et al. 2006) and community composition is assessed at coarser taxonomic (i.e., family and above) scales (Metzeling et al. 2002). With only a minor snowmelt flood occurring between 2003 and 2004 (i.e., at  $16.2 \text{ m}^3 \text{ s}^{-1}$ , it was the 11th smallest in a >100-year record), environmental conditions were stable at our site during the period in question.<sup>1</sup> Further, an independent time series from a site 10-km downstream from our own (M. Vinson, Utah State University, unpublished data) demonstrates that elsewhere in the Logan River drainage invertebrate communities varied little between 2003 and 2004. The combination of these observations indicates that the 2003 data are generally representative of relative prey abundance in both years.

#### Stable isotope analysis

As a complement to our snapshot perspective of trout trophic relationships based on stomach contents, we also quantified longer-term dietary habits of a subset of brown ( $n = 9$ ) and cutthroat trout ( $n = 10$ ) using stable isotope analysis. Specifically, we assessed the trophic position (i.e., as a surrogate for predation potential) and dietary carbon source (i.e., similarity in diet) based on the respective  $^{15}\text{N}$  and  $^{13}\text{C}$  muscle-tissue content for individuals of each species (Vander Zanden et al. 1997; Post 2002). We dried 5-mm dorsal muscle-tissue plugs for 24–48 h at  $60^\circ\text{C}$ , ground them to powder, encapsulated them in standard-weight tin capsules, and shipped them to the University of

California-Davis Stable Isotope Facility for a mass-spectrometry analysis of isotopic signatures. Isotopic ratios ( $^{13}\text{C}:^{12}\text{C}$  and  $^{15}\text{N}:^{14}\text{N}$ ) were estimated and are expressed as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , per mil (‰) values relative to the ratios of the standards Pee Dee Belemnite and atmospheric nitrogen, respectively.

#### Statistical analysis

We contrasted brown trout and cutthroat trout dietary habits and prey-selection patterns using a combination of univariate and multivariate statistical techniques. With respect to whole-sample diet descriptors first, we contrasted prey occurrence (% *O*) and relative prey importance (% IRI) between trout species using Fisher's exact test (i.e., on a taxon-by-taxon basis) and a  $\chi^2$  test, respectively. Regarding individual fish, we analyzed differences based on the numerical (% *N*) and gravimetric abundance of prey (% *W*) in diets in greater detail using multivariate statistical techniques. First, to identify clusters of individuals with similar diets and to understand the taxonomic basis of any dietary separation, we performed an ordination on both % *N* and % *W* datasets (untransformed) using nonmetric multidimensional scaling (NMDS) with a Bray–Curtis (Sorenson) distance matrix ( $n = 400$  iterations, 40 runs with real data, 50 with randomized data; stability level = 0.00001). We tested for a species difference in % *N*- and % *W*-based diet composition by comparing pair-wise Bray–Curtis distances between individuals using the multiresponse permutation procedure (MRPP), a nonparametric randomization test. Finally, using *t*-tests, we tested for a difference in prey-selection behavior (i.e., Strauss's *L*) between species for the four most common prey taxa.

To account for effects of fish size on diet (e.g., changes in gape limits), we contrasted prey size and stable isotope tissue content ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , separately) between species using analysis of covariance (ANCOVA). We determined the structure of all ANCOVA models using the procedure of Milliken and Johnson (2000). Thus, our most fully parameterized ANCOVA models (i.e., for  $\delta^{15}\text{N}$  and prey-size responses) included *species*, *size* (mean-centered TL), and *species*  $\times$  *size*

<sup>1</sup> <http://water.usgs.gov>, gauge number 10109000

interaction effects; our  $\delta^{13}\text{C}$  model included *species* and *size* effects only. All tests for species differences were based on post hoc contrasts of least-squares estimated means and standard errors (SE); if the *species*  $\times$  *size* interaction effect was significant in the fitted model, we contrasted the response for the mean size (213 mm TL) and at  $\pm 1$  standard deviation (i.e., 67 mm).

We performed our analysis using the Statistical Analysis System (SAS) version 9.1 (*t*-test and ANCOVA analyses; SAS Institute 2005) and PC-Ord (NMDS and MRPP analyses; McCune and Grace 2002). In order to detect ecologically meaningful patterns in a modest and variable dataset and minimize a type-I error rate, we assessed statistical significance using an a priori  $\alpha$ -level of 0.10 (note, we also present raw *P*-values).

**Results**

In total, we collected 64 trout (*n* = 29 cutthroat and 35 brown trout) for stomach content and stable isotope analysis over a 2-year period. Although both species spanned a similar range of sizes (TL) and size was invariant between years within species (two-way analysis of variance, with *species*, *year*, and interaction effects; *year*:  $F_{1,60} = 0.85$ ,  $P = 0.3605$ ), the cutthroat trout included in our analysis were significantly larger than the brown trout ( $F_{1,60} = 4.86$ ,  $P = 0.0314$ ) on average. Mean cutthroat trout TL was 230 mm (range 104–322 mm), whereas brown

trout TL was 192 mm (range 121–389 mm). We performed stomach-content analysis on all 64 trout and stable isotope analysis on a subset of 19 (*n* = 10 cutthroat and 9 brown trout). Of the 64 stomachs examined, one was empty (a cutthroat trout) and four others (*n* = 2 brown and 2 cutthroat trout) contained a considerable portion of unidentified matter (i.e., >25% by weight). Thus, our full analysis was based on 59 fish for stomach-content analysis and 19 fish for stable isotope analysis, with all fish being pooled across years to maximize statistical power. Note that although we do not present them here, we also performed year-specific analyses. Year-specific results generally matched those obtained using the pooled dataset (i.e., year effects were not significant,  $P \gg 0.25$ , when incorporated into ANCOVAs; overlap and electivity patterns were similar between years).

Stomach-content analysis

With the exception of Hemiptera for brown trout, members of all nine prey taxa occurred in the stomachs of both species (% *O*; Table 1). However, the majority (~90%, by weight and count) of individual trout diets were dominated by four taxa: Ephemeroptera, Plecoptera, Trichoptera, and Diptera. Of these groups, trichopterans were the most important prey for both species, based on % IRI. Our comparison of brown and cutthroat trout stomach contents illustrates that although a strong degree of dietary similarity

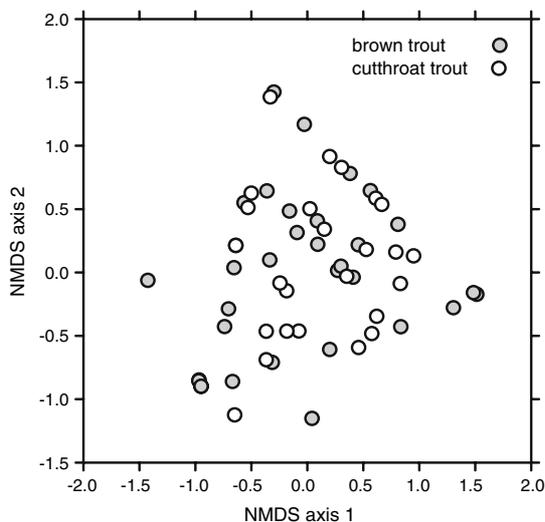
**Table 1** Taxonomic composition of brown and cutthroat trout stomach contents

Prey category	Brown trout ( <i>n</i> = 34)				Cutthroat trout ( <i>n</i> = 25)			
	% <i>O</i>	% <i>N</i>	% <i>W</i>	% IRI	% <i>O</i>	% <i>N</i>	% <i>W</i>	% IRI
Ephemeroptera	61.8	27.0 ± 9.7	22.2 ± 11.2	24.8	84.0	29.4 ± 10.2	19.1 ± 9.5	26.8
Trichoptera	82.4	36.9 ± 12.0	35.4 ± 12.8	48.5	88.0	27.0 ± 9.4	36.1 ± 12.8	36.5
Plecoptera	29.4	6.0 ± 4.5	13.1 ± 9.1	4.6	60.0	5.6 ± 3.0	17.6 ± 8.9	9.1
Diptera	64.7	24.3 ± 9.4	13.5 ± 8.4	19.9	80.0	31.4 ± 9.7	14.8 ± 7.0	24.3
Hemiptera	0.0	0.0 ± 0.0	0.0 ± 0.0	0.0	12.0	0.7 ± 0.9	0.7 ± 1.2	0.1
Coleoptera	8.8	0.6 ± 0.8	0.4 ± 0.5	0.1	4.0	0.1 ± 0.1	0.1 ± 0.2	0.0
Annelida	8.8	0.5 ± 0.6	2.9 ± 4.4	0.2	8.0	1.0 ± 1.6	1.0 ± 1.4	0.1
Terrestrials	11.8	2.6 ± 2.8	3.3 ± 4.7	0.6	40.0	4.5 ± 3.8	6.7 ± 7.6	3.0
Fish	14.7	2.0 ± 2.2	9.1 ± 9.2	1.3	4.0	0.5 ± 1.0	4.0 ± 7.9	0.1

Values are means ± 2 SE for the overall frequency of occurrence (presence/absence) in all stomachs (% *O*), the average abundance per stomach, by count (% *N*), and the average abundance, per stomach, by weight (% *W*). ‘% IRI’ corresponds to the % index of relative importance (see text for computational details)

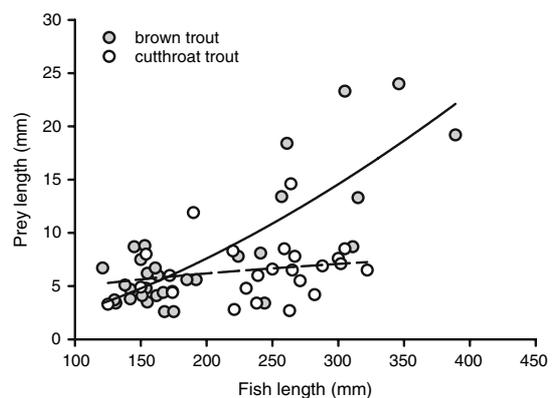
existed between species, there were also subtle differences in what fish had recently consumed.

With respect to dietary similarity, the overall importance of the different prey items (i.e., % IRI) did not differ between species ( $\chi^2 = 6.31$ ,  $df = 5$ ,  $P = 0.277$ ; Table 1), and the results from the analysis of individual-level % *N* and % *W* patterns corroborate these findings. The MRPP comparison indicated an overall lack of difference between species (% *N*:  $T = -0.236$ ,  $P = 0.308$ ; % *W*:  $T = 0.111$ ,  $P = 0.454$ ). The NMDS ordination, which accounted for 87% of % *N*-based diet variation in just two axes, provides a visualization of this result (Fig. 1). Correlations between NMDS axes and % *N* values for particular taxa suggest that overall diet variation is due mostly to differing numbers of ephemeropterans (axis-2 Pearson correlation coefficient, hereafter,  $R = 0.918$ ), trichopterans (axis-1  $R = -0.725$ , axis-2  $R = -0.708$ ), and dipterans (axis-1  $R = 0.915$ ) in stomachs. The % *W* NMDS ordination produced a similar result ( $R^2 = 0.67$  in two axes); however, in contrast to % *N*, both fish (axis-1  $R = -0.690$ ) and plecopteran prey (axis-1  $R = 0.724$ ) contributed measurably to the total amount of diet variation explained. Finally, percent diet overlap was high between species, at 87.5 and 89.5% for estimates based on % *N* and % *W*, respectively.



**Fig. 1** NMDS ordination plot of brown (gray circles) and cutthroat trout (white circles) % *N* diet composition. See Sect. 'Results' for correlations between NMDS axes and prey taxonomic groupings and for the proportion of variance explained for in two axes

Despite these similarities, we also found evidence for differences in the stomach contents of brown and cutthroat trout. There were significant differences between species for the population-wide occurrence (% *O*) of some prey taxa in diets (Table 1). Specifically, there was a higher occurrence of ephemeropteran ( $P = 0.083$ ), plecopteran ( $P = 0.032$ ), hemipteran ( $P = 0.071$ ), and terrestrial prey ( $P = 0.015$ ) in cutthroat trout relative to brown trout stomachs. In addition, the size of items ingested differed between species, but this difference depended on fish size [ANCOVA of  $\log_e(\text{prey size})$ : *species*,  $F_{1,52} = 4.90$ ,  $P = 0.0313$ ;  $\log_e(\text{size})$ ,  $F_{1,52} = 17.81$ ,  $P < 0.0001$ ; *species*  $\times$  *size*,  $F_{1,52} = 5.53$ ,  $P = 0.0225$ ; Fig. 2]. While prey size increased as a function of fish TL for brown trout ( $H_0: \beta_1 = 0$ ,  $t = 2.35$ ,  $P = 0.0225$ ), cutthroat trout ate similarly sized prey across sizes ( $H_0: \beta_1 = 0$ ,  $t = 1.13$ ,  $P = 0.2632$ ); thus, at a small TL (i.e., mean - 1 SD, or 146 mm), both trout consumed prey of similar size (least-squares means contrast,  $P = 0.7442$ ), whereas at an average (i.e., 213 mm TL) and large TL (i.e., mean + 1 SD, or 280) brown trout ate significantly larger prey ( $P = 0.0594$  and 0.0011, respectively) than did cutthroat trout. This pattern, however, was likely driven by the greater proportion of brown trout (15%) relative to large cutthroat trout (4%) that consumed fish, all of which were mottled sculpin (Table 1).



**Fig. 2** Plot of mean prey body length as a function of fish TL for brown trout (gray circles, solid line) and cutthroat trout (white circles, dashed line). Best-fit lines represent power functions resulting from  $\log_e(\text{fish size}) - \log_e(\text{prey size})$  regressions

### Prey-selection behavior

Based on our invertebrate samples, ephemeropteran mayflies (predominantly *Baetis*) and dipterans (predominantly chironomids) dominated (>90% of total sample) the drift, whereas trichopterans and dipterans dominated the benthos (Table 2). Both drifting and benthic invertebrate densities were relatively high, at 9 individuals  $m^{-3}$  and 4,687 individuals  $m^{-2}$  (range 2,822–6,411 individuals  $m^{-2}$ ), respectively. Our evaluation of stomach contents relative to the availability of invertebrates in the environment illustrates two important results. First, brown and cutthroat trout exhibited similar selection patterns (*t*-tests contrasting Strauss's *L* between species,  $P \gg 0.20$  for all taxa for benthos and drift). Second, electivity values suggested weak (i.e.,  $-0.25 < L < 0.25$ ) selection for some taxa. However, there was a moderate preference for drifting trichopterans (brown trout mean  $\pm 2$  SE,  $0.36 \pm 0.10$ ; cutthroat trout,  $0.26 \pm 0.12$ ) and benthic ephemeropterans (brown trout,  $0.25 \pm 0.10$ ; cutthroat trout,  $0.27 \pm 0.11$ ), and avoidance of benthic dipterans (brown trout,  $-0.38 \pm 0.09$ ; cutthroat trout,  $-0.30 \pm 0.10$ ; Fig. 3).

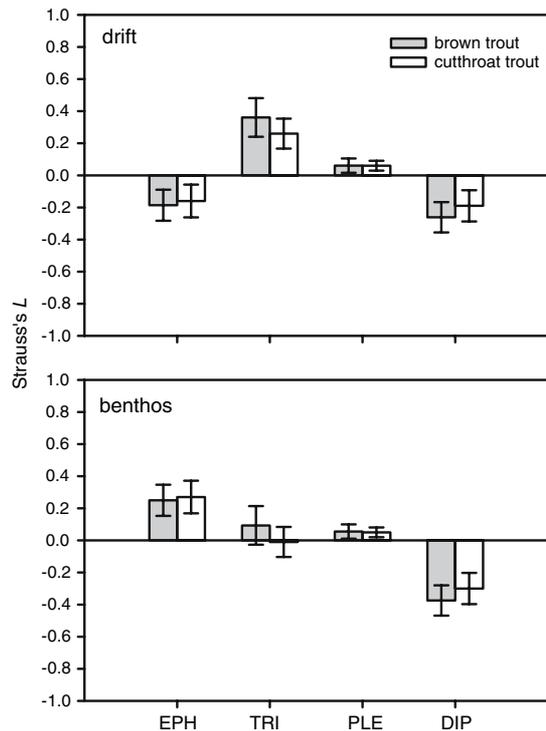
### Stable isotope analysis

To complement our stomach-content analysis, we evaluated dietary patterns on a longer-term basis using stable isotopes. With respect to the ultimate

**Table 2** Relative abundance of prey taxa in the environment

Prey category	Drift (%)	Benthos (%)
Ephemeroptera	45.7	2.1 $\pm$ 2.0
Trichoptera	0.8	27.6 $\pm$ 29.1
Plecoptera	0.0	0.5 $\pm$ 0.6
Diptera	50.4	61.7 $\pm$ 28.5
Hemiptera	0.0	0.0 $\pm$ 0.0
Coleoptera	1.6	5.2 $\pm$ 4.4
Annelida	0.0	2.9 $\pm$ 1.9
Terrestrials	1.6	NA
Fish	NA	NA

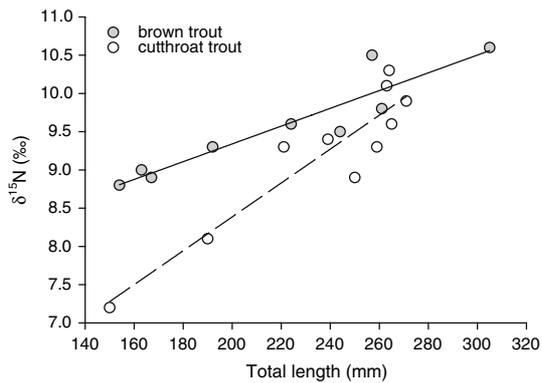
Values represent percent of total invertebrate abundance (by count) in drift ( $n = 1$ ; see Sect. 'Materials and methods' for details) or benthic invertebrate samples ( $n = 4$ ). Benthos values are means  $\pm 2$  SE. 'NA' is not available due to the lack of that taxon's representation in samples



**Fig. 3** Mean electivity values (Strauss's *L*,  $\pm 2$  SE) for brown trout (gray bars) and cutthroat trout (white bars) stomach contents for the prey categories Ephemeroptera (EPH), Trichoptera (TRI), Plecoptera (PLE), and Diptera (DIP), relative to drift (upper panel) and benthic (lower panel) invertebrate samples

carbon source in their diets, our ANCOVA-based comparison of  $\delta^{13}C$  signatures indicated a lack of statistically significant dietary separation between species (ANCOVA of  $\delta^{13}C$ : *species*,  $F_{1,16} = 1.78$ ,  $P = 0.2010$ ; *size*,  $F_{1,16} = 3.60$ ,  $P = 0.0758$ ). Based on the trend in  $\delta^{13}C$  means (least-squares) across species, brown trout ( $-28.0\text{‰}$ ) were slightly more ( $-0.6\text{‰}$ ) enriched in  $^{13}C$  than cutthroat trout ( $-28.6\text{‰}$ ).

In contrast to  $\delta^{13}C$  results, our analysis of  $\delta^{15}N$  demonstrates an interactive effect of size and species on the trophic position of individuals (ANCOVA of  $\delta^{15}N$ : *species*,  $F_{2,15} = 5,824.30$ ,  $P \leq 0.0001$ ; *size*,  $F_{1,15} = 86.57$ ,  $P < 0.0001$ ; *species*  $\times$  *size*,  $F_{1,15} = 8.67$ ,  $P = 0.0100$ ). While  $^{15}N$ : $^{14}N$  ratios increased steadily with increasing TL for both species, brown trout were more enriched in  $^{15}N$  than cutthroat trout at small (mean - 1 SD, 146 mm) and intermediate (mean,



**Fig. 4** Plot of  $\delta^{15}\text{N}$  (‰) as a function of body length for brown trout (gray squares, solid line) and cutthroat trout (white squares, dashed line)

213 mm TL) sizes (least-squares means contrast,  $P = 0.0005$  and  $0.0003$ , respectively), but not at a large (mean + 1 SD, 280 mm) size ( $P = 0.7359$ ; Fig. 4). At 1.6 and 1.2‰, respectively, the magnitude of difference observed between species at small and intermediate size classes, however, was less than what is typically considered a full trophic level difference (i.e., ~3.4‰).

To summarize our results overall, our analysis of stomach contents, prey-selection patterns, and  $^{13}\text{C}$  tissue content demonstrates that the average brown trout and cutthroat trout consume a diet of similar composition and origin. However, we also found evidence for dietary differences based on patterns of prey occurrence (i.e., % *O*), prey-size differences, and  $\delta^{15}\text{N}$  signatures.

## Discussion

Quantifying patterns of prey resource use is a fundamental step in the process of identifying behavioral mechanisms responsible for the displacement of native fishes by nonnative, invasive species. By studying the dietary habits of nonnative fishes living sympatrically with native fishes, we can gain substantial insight into the relative roles of competitive and/or predatory interactions in native-fish decline (Dunham et al. 2000; Ruzycski et al. 2003). Whereas multiple investigators have assessed the trophic relationships of cutthroat trout and brook trout through diet studies (Griffith 1974; Dunham et al. 2000;

Hilderbrand and Kershner 2004; McGrath 2004), little research has been conducted in this area for cutthroat trout living sympatrically with brown trout.

In our study, we used a complementary approach whereby we measured dietary similarity and trophic position based on a combination of both stomach content and stable isotope analyses (Beaudoin et al. 1999; McGrath 2004). We found that on average these two species foraged similarly and nonselectively, with both trout consuming the same taxa in proportion to their availability in the environment. Further, this overlap in stomach contents was corroborated by time-integrated isotope-based measures of diet (i.e.,  $\delta^{13}\text{C}$ ). Despite these similarities, our analysis also shows that brown trout and cutthroat trout differed in terms of their overall prey use (i.e., % *O*) and prey-size selection patterns, as well as in their relative trophic positions. Based on their higher  $\delta^{15}\text{N}$  tissue content and consumption of larger prey (including fish), brown trout operated on a somewhat higher trophic level than cutthroat trout. By foraging almost exclusively as an insectivore, cutthroat trout tended to consume a diet containing more terrestrial insects and ephemeropterans than that of brown trout. In the following discussion, we consider the significance of these findings, highlight their relevance to previous studies, and offer suggestions for future research.

### Trophic relationships and the potential for interspecific interactions

Although a demonstration of dietary overlap alone does not constitute a formal test of competition between fish species (see Fausch 1988, 1998 for reviews), ecological similarity—in the form of dietary or other resource needs—is necessary for competition to occur under the classical definition (Birch 1957). Whereas we present evidence of extensive overlap (i.e., 88%) in dietary niche dimensions herein, others provide experimental evidence of competition between these species (Wang and White 1994; McHugh and Budy 2005, 2006). Wang and White (1994), through a set of behavioral experiments, showed that brown trout effectively monopolize the most profitable foraging sites when living sympatrically with cutthroat

trout. Additionally, the results from two separate field experiments illustrate that the behavioral interactions documented by Wang and White (1994) have growth and condition consequences for cutthroat trout (McHugh and Budy 2005, 2006). Thus, the diet analysis we present here provides a formal validation of dietary similarity assumed by earlier investigators and therefore may strengthen our understanding of interspecific competition as a mechanism by which brown trout can impact cutthroat trout.

Despite this evidence for overlap and interspecific competition, we collected fish for the present study at a site where these species have co-occurred in recent years, albeit at a somewhat reduced level (Budy et al. *in press*). Thus, it seems necessary to consider the potential effects of subtle dietary differences on the outcome of nonnative-fish invasions. To summarize the differences we observed first, dipterans and terrestrial insects were more important (i.e., % IRI) to cutthroat trout than brown trout, whereas trichopterans and to a lesser extent fish were more important to brown trout. Considering this result in the context of published drift propensities for these invertebrates (Rader 1997), our findings are consistent with previous suggestions that brown trout have an affinity toward an epibenthic foraging mode (Bachman 1984; Kreivi et al. 1999; Kara and Alp 2005) whereas cutthroat trout are drift- and surface-obligate feeders (Griffith 1974). Given that shifts toward benthivory form the basis of interactive segregation and coexistence among multiple salmonid species elsewhere (Fausch et al. 1997; Nakano et al. 1999; Baxter et al. 2004), the potential ecological importance of these subtle dietary differences could be great. Also of possible importance, however, is the differing disposition of these two species toward preying on larger organisms, including fishes.

While piscivory as a mechanism for the impact of brown trout on cutthroat trout has not been explicitly considered elsewhere, our results suggest that predator–prey interactions may apply in this context. Prey-size consumption patterns,  $\delta^{15}\text{N}$  differences, and ultimately the higher occurrence of fish prey in their diets all point toward brown trout occupying a higher trophic level than cutthroat trout across a considerable size range.

Thus, although we do not demonstrate direct predation on cutthroat trout here, three separate and complementary measures relating to piscivory potential imply that predation by brown trout on cutthroat trout is possible.

Though we cannot conclude that brown trout predation is a major factor in cutthroat trout decline based on our results alone, the ability of this nonnative fish to structure native-fish populations and whole-stream communities through predation is widely recognized in other systems (McIntosh 2000; Townsend 2003). At 130–160 mm TL, brown trout typically exhibit an ontogenetic diet shift by switching from a diet consisting solely of insects toward one that includes both insects and fishes (Mittelbach and Persson 1998; Mayama 1999; Museth et al. 2003). Across systems, seasons, and sizes, nearly 10% of their energy budget can be due to piscivory (Mittelbach and Persson 1998), a value in agreement with the 9% average (by weight) we observed here. However, brown trout are also flexible foragers and can increase their predation rates further in response to seasonally available forage-fish resources (L'Abée-Lund et al. 2002). For example, nearly half (45%) of the diet of stream-dwelling brown trout consisted of masu salmon, *Oncorhynchus masou*, fry during the period following fry emergence in a Japanese river (Mayama 1999), and at consumption rates of an even lesser magnitude, brown trout can effectively regulate the abundance of their fish prey on an annual basis (Museth et al. 2003). Thus, predation by brown trout has the potential to be of significant consequence to sympatric-living cutthroat trout populations. As such, a diet-sampling scheme more synchronous with the availability of newly emerged cutthroat trout fry could be revealing.

Relationship to brook trout–cutthroat trout diet studies

In response to the widespread nature of nonnative brook trout invasions as a threat to cutthroat trout populations in North America (Dunham et al. 2002; Quist and Hubert 2004), several authors have studied the dietary relationships of these species with objectives and methods similar

to our own (Dunham et al. 2000; Hilderbrand and Kershner 2004; McGrath 2004). Given that brown trout and brook trout invasion patterns differ on a large scale (e.g., Fausch 1989), we believe that there is insight to be gained by contrasting our results with these earlier studies.

With respect to common findings, the extensive diet overlap we observed is consistent with the level of ecological similarity documented previously between brook trout and cutthroat trout by Dunham et al. (2000) and Hilderbrand and Kershner (2004). The magnitude of diet overlap found in these studies, approaching 80–90% (based on the same index), is comparable to what we found for brown trout and cutthroat trout. Further, the lack of separation along a  $\delta^{13}\text{C}$  axis corresponds well with McGrath's (2004) comparison of stable isotope tissue content for brook trout and cutthroat trout in Colorado. The opportunistic feeding patterns (i.e., neutral selection) we document also concur with prior brook trout–cutthroat trout electivity analyses (Dunham et al. 2000; Hilderbrand and Kershner 2004). Thus, there is generality to the conclusion of ecological similarity and a high potential for interspecific competition between both introduced brook and brown trout and native cutthroat trout.

However, our study also suggests that a distinction should be made regarding these two introduced species and their subsequent effects on native cutthroat trout. This difference lies in the tendency toward piscivory by brown trout described above. Despite the fact that brook trout are not gape limited with respect to small (i.e., age-0) cutthroat trout and that predation has been observed in an experimental context (Novinger 2000), none of the diet studies in question present strong field evidence suggesting that brook trout act as significant piscivores in invaded habitats. This conclusion is based on both stomach content- (Dunham et al. 2000; Hilderbrand and Kershner 2004; McGrath 2004) and stable isotope-based analyses (McGrath 2004) of trophic relationships. Ultimately, we suggest that this differing propensity toward piscivory may be important in determining the consequences of brook trout relative to brown trout invasions for cutthroat trout.

## Limitations and strengths of our approach

Our study has several important strengths and limitations. Foremost among strengths, we used a combined stomach content–stable isotope analysis approach to glean information about the trophic relationships of sympatric-living brown and cutthroat trout. These two methods provide different, but complementary pieces of information (Beaudoin et al. 1999). Stomach-content analysis provides insight into the taxonomic identity of what individuals consumed most recently (Cortés 1997); stable isotopes provide a more time-integrated measure of average foraging habits (reviewed in Post 2002). Because we used both techniques, we can be more confident in our conclusions regarding dietary similarity and trophic linkages. This strength is particularly germane, given the limitations of stable isotope analysis when used as a method by itself (Overman and Parrish 2001; Matthews and Mazumder 2004; Trueman et al. 2005).

Despite its strengths, we also acknowledge two potential shortcomings of our study. First, our sample sizes—both for fishes and drifting invertebrates—were small relative to recommended sample sizes for these organisms (e.g., Allen and Russek 1985) and spanned a narrow seasonal range. For fish, we were limited primarily by the sensitive status of cutthroat trout at our study site. We suggest, however, that this limitation is of minor importance given the strong agreement between stomach content and stable isotope results and the fact that the selection patterns we observed concurred with those documented under similar conditions (e.g., Hilderbrand and Kershner 2004). Second, we cannot be certain that the results from our stomach-content analysis would not have differed if we had used a finer level of taxonomic resolution in our efforts or sampled in different seasons. Given the partially degraded state of insects in sampled stomachs, however, this fine-resolution identification would not have been consistently possible.

## Implications and suggested future research

Our work has important implications for understanding interactions between native and

introduced salmonids, as well as for future research in this area. Our results strengthen earlier notions on the ecological similarity of brown trout and cutthroat trout but also provide evidence of subtle differences in foraging—differences which could be influential in determining where and when they will coexist. Perhaps of greater significance, our findings when taken in combination with a review of the literature, suggest that predation may have a considerable role in the cutthroat trout displacement process.

In closing, our survey provides a context for suggesting future research on trophic interactions between brown trout and cutthroat trout. We believe that detailed behavioral assays—both on a survey and experimental basis—are needed to fully integrate our knowledge on competition between these species. Such studies could allow for a formal quantification of foraging mode differences between species as well as interspecific aggression. Finally, we feel that the role of piscivory in brown trout–cutthroat trout interactions should be considered in greater detail through a combination of additional diet surveys and modeling. For example, one could quantify fish diets on a seasonal basis, particularly emphasizing the time period encompassing cutthroat trout fry emergence, and subsequently model annual consumption and its demographic effect using bioenergetics and population models (e.g., Cartwright et al. 1998; Ruzycski et al. 2003).

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