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Macroinvertebrate prey availability and food web dynamics of nonnative trout in a Colorado River tributary, Grand Canyon

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Abstract: Nonnative fishes have been linked to the decline of native fishes and may affect aquatic food webs through direct and indirect pathways. These concerns have led to efforts to remove nonnative Brown and Rainbow Trout, which are abundant in tributaries of the Colorado River, to enhance native fish communities. We sampled fish, benthic, and drifting macroinvertebrates in November 2010, January 2011, June 2011, and September 2011 to assess resource availability and to evaluate the effects of nonnative Brown and Rainbow Trout in a tributary of the Colorado River in the Grand Canyon. We evaluated trout diets from stomach samples collected during macroinvertebrate sampling periods, and we estimated annual consumption with bioenergetics models. We used ¹³C and ¹⁵N stable isotopes to examine potential diet overlap between native and nonnative fishes. Contributions to benthic biomass varied among megaloptera (16–35%), trichoptera (19–28%), and ephemeroptera (9–32%), whereas ephemeroptera dominated biomass (44–64%) in drift samples. Ephemeroptera were dominant in diets of small (<150 mm total length [TL]) trout, whereas *Corydalis* and native fish dominated diets of large (>150 mm TL) Brown Trout, and *Corydalis* and algae dominated diets of large Rainbow Trout. Annual resource consumption was 6× higher for large trout than small trout. Stable isotopes suggested diet overlap between native and nonnative fishes. Large nonnative trout occupied the highest trophic positions. Our results suggest that suppression of nonnative trout may have a positive effect on native fishes via reduced predation and resource competition.

Key words: nonnative fish, native fish, tributaries, prey availability, diet analysis, stable isotopes

Declines in diversity and changes in ecosystem function in freshwater habitats throughout the world have been attributed to the widespread distributions and high abundances of nonnative fishes (Schade and Bonar 2005, Gozlan et al. 2010, Cucherousset and Olden 2011). Nonnative salmonids, in particular, are among the most widespread introduced species in freshwater ecosystems and may have adverse and unforeseen effects on aquatic food webs through direct and indirect pathways (Fausch 1988, Flecker and Townsend 1994, Gozlan et al. 2010). Brown Trout (*Salmo trutta*) can decrease insect biomass with subsequent increases in algal standing crops, compete with and prey upon native fishes, and fragment native fish populations (Crowl et al. 1992, Flecker and Townsend 1994). Rainbow trout (*Oncorhynchus mykiss*) can interrupt resource flows

to cause reduced growth, decreased densities, and altered foraging strategies among native fishes (Baxter et al. 2004, 2007). The pervasive effects of nonnative Brown and Rainbow Trout necessitate development of a conceptual understanding of their potential effects on native fish populations in different geographical and ecological contexts around the world.

In the Colorado River Basin of the southwestern USA, nonnative Brown and Rainbow Trout have used niche opportunities arising from long-term environmental changes and have been linked to the decline of native fishes (Minckley 1991, Olden et al. 2006). Predation by Brown and Rainbow Trout in the Little Colorado River, a tributary of the Colorado River in the Grand Canyon, may be a significant source of mortality for native fishes (Marsh and

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Douglas 1997). Yard et al. (2011) corroborated these findings in the Colorado River, Grand Canyon, by documenting that Brown and Rainbow Trout consumed 10,001 and 18,344 native fish, respectively, during a 2-y period. Furthermore, Shannon et al. (2001) found a positive relationship between length and trophic position for Rainbow Trout and native Humpback Chub (*Gila cypha*) in the Colorado River, a result suggesting diet overlap between native and nonnative species and increased piscivory among larger, nonnative fishes. Therefore, efforts to conserve or restore native fish communities may need to account for potential interactions between native and nonnative fishes.

The Colorado River and its tributaries once supported large numbers of endemic native fishes. However, completion of Glen Canyon Dam in 1966 caused profound downstream changes to water temperatures, sediment, and flow regimes (Minckley 1991, Stevens et al. 1997). Subsequent flow regulation in the Colorado River below Glen Canyon Dam has decreased water temperatures and sediment flux, and has altered the aquatic macroinvertebrate fauna often preyed upon by native fishes (Stevens et al. 1997). Disruptions in energy flow and the effects of nonnative fish species mediated by colder water temperatures may contribute to declines of many native fishes in the mainstem Colorado River. At the present time, only 4 self-sustaining populations of native fish, including the federally endangered Humpback Chub (USOFR 1967), the Flannelmouth Sucker (*Catostomus latipinnis*), the Bluehead Sucker (*Catostomus discobolus*), and the Speckled Dace (*Rhinichthys osculus*) exist in the Grand Canyon (Minckley 1991). However, habitat and prey availability in tributaries to the Colorado River in the Grand Canyon are relatively unaltered (Stevens et al. 1997, Oberlin et al. 1999).

Bright Angel Creek, a tributary of the Colorado River in Grand Canyon National Park, is thought to have once supported populations of native fishes. Little is known about the native fish fauna of Bright Angel Creek prior to the introductions and establishment of nonnative Brown (stocked in 1930 and 1934) and Rainbow Trout (stocked from 1923 to 1964) because only anecdotal observations or individual specimens are available (Carothers and Minckley 1981). A dramatic shift in species dominance occurred in Bright Angel Creek between the late 1970s and 1990s when Brown and Rainbow Trout abundance increased and native species abundance declined dramatically (Minckley 1991, Otis 1994). Currently, Speckled Dace and Bluehead Sucker are the only 2 species of native fish that reside annually in Bright Angel Creek (Omana Smith et al. 2012). Moreover, Bright Angel Creek may now be an important spawning site for Brown Trout in Grand Canyon National Park (Speas et al. 2003).

Threats posed by Brown and Rainbow Trout to native fishes in the Colorado River and its tributaries in the Grand Canyon led the National Park Service to reinstate the Bright Angel Creek Trout Reduction project in Octo-

ber 2010 to benefit the federally endangered Humpback Chub and restore native fish communities to Bright Angel Creek to the extent possible (Omana Smith et al. 2012). Nonnative fish species are found in all major tributaries in Grand Canyon National Park (National Park Service, unpublished data), and removal of nonnative fish has been suggested as a way to benefit native species. However, a complete understanding of the stream ecosystem (e.g., resource availability) and interactions between native and nonnative fishes (i.e., diet overlap) in aquatic food webs is needed to maximize the benefits of conservation strategies (Tyus and Saunders 2000). Specifically, an examination of the types of invertebrate prey that are available to and consumed by nonnative fishes in tributaries, such as Bright Angel Creek, may help facilitate conservation strategies and elucidate the effects Brown and Rainbow Trout on native fish communities. Moreover, despite efforts to reduce Brown and Rainbow Trout densities within Bright Angel Creek, no quantitative studies have been done to document the effects of these species in tributaries of the Colorado River within Grand Canyon National Park.

Our primary objectives were to: 1) examine seasonal patterns of benthic and drifting macroinvertebrate biomass and taxon richness, 2) examine seasonal food habits and estimate annual consumption of resources by Brown and Rainbow Trout, and 3) use stable-isotope analyses to examine trophic positions and potential diet overlap between native and nonnative fishes in Bright Angel Creek. We hypothesized the diets of Brown and Rainbow Trout would contain large proportions of native fish and the dominant macroinvertebrate prey taxa, and that ontogenetic shifts would occur among both species. We also hypothesized that diet overlap occurs between native and nonnative fishes in Bright Angel Creek.

METHODS

Study area

The Bright Angel Creek watershed drains ~260 km² of the southern portion of the Kaibab Plateau and originates at Angel Springs, 29.6 km upstream from its confluence with the Colorado River (Oberlin et al. 1999). The study reach had a mean wetted width of 6.4 m and a mean annual discharge of 1.2 m³/s. Stream habitat consists of alternating plunge pools and riffles dominated by cobbles and boulders with a mix of gravel and sand substrata. Seasonal water temperatures range from 2.2 to 21.7°C. Riparian vegetation along the reach consists of horsetail (*Equisetum* sp.), willow (*Salix* sp.), and cottonwood (*Populus* sp.). Four species of fishes (native Speckled Dace and Bluehead Sucker and nonnative Brown Trout and Rainbow Trout) exist in Bright Angel Creek and can travel between the stream and the Colorado River.

Our study site was a 200-m stream reach in Bright Angel Creek ~1 km above the confluence of the Colorado

River near river kilometer 141.6 in Grand Canyon National Park. This portion of the stream is a representative reach in Bright Angel Creek because it has abundant populations of both native and nonnative fish species (Omana Smith et al. 2012). Our study coincided with nonnative trout removal efforts initiated by the National Park Service in October 2010. From October 2010 to February 2011, a weir was placed near the mouth of Bright Angel Creek to prevent Brown and Rainbow Trout from migrating into the creek from the mainstem Colorado River (Omana Smith et al. 2012). Nonnative removal efforts occurred in late October through early November 2010 and in late January through early February 2011. Brown and Rainbow Trout density estimates ranged from 0.03 to 0.04 and 0.02 to 0.04 individuals (ind)/m², respectively, whereas Speckled Dace densities ranged from 0.6 to 1.0 ind/m². Bluehead Sucker captures were too few to facilitate population estimates via depletion analysis. However, mark–recapture analyses indicate that Bluehead Suckers are commonly found in Bright Angel Creek year round (National Park Service, unpublished data). In Bright Angel Creek, Brown and Rainbow Trout have a mean total length of 192 and 161 mm, respectively, whereas the mean total lengths of Speckled Dace and Bluehead Suckers are 76 and 258 mm, respectively (Omana Smith et al. 2012).

Macroinvertebrate prey availability

We sampled benthic and drifting macroinvertebrates in November 2010, January 2010, June 2011, and September 2011 to examine seasonal fluctuations in macroinvertebrate prey availability for fishes. These sampling dates were chosen because they are representative of seasonal changes (e.g., warm vs cold season) in the Grand Canyon and logistical constraints and remoteness of the area prevented further sampling. On each sampling date, we collected benthic macroinvertebrates with a Hess sampler (area: 0.086 m²; mesh: 500 μm) from 12 haphazardly selected locations within the 200-m stream reach. We collected samples by pushing the Hess sampler into the substrata and manually disturbing all enclosed materials until water flowing through sampler net was clear and visual inspection of substrates showed no organic material remained. We transferred benthic samples to a plastic sample bag, preserved them with 10% formalin, and returned them to the laboratory for analysis.

We collected drifting macroinvertebrates on each sampling date by placing 4 drift nets (mouth: 0.14 m²; length: 1.5 m; mesh size: 500 μm) across the width of the stream. The drift sampling locations were at the starting and mid-points (100 m) of the 200-m study reach. We left nets in the water for 24 h and collected samples every ~6 h. Drift nets were only partially submerged and water volume flowing through the nets was calculated using the cross-sectional area of the submerged portion of the net, current velocity, and time in the water. Drift-net clogging can af-

fect the filtering rate, so we obtained mean current velocity by averaging velocity readings taken in both clean and clogged nets (clogged net refers to the state of the net at the end of each 6-h period). We measured current velocity at 60% depth immediately upstream of each drift net with a Marsh–McBirney[®] current meter (Marsh–McBirney, Frederick, Maryland). We stored and preserved drift samples with the same methods as benthic samples.

In the laboratory, we rinsed benthic and drift samples in a 500-μm sieve and removed and identified all macroinvertebrates (genus for aquatic insects, family for terrestrial insects, and order for noninsects) with the aid of keys published by Merritt et al. (2008) and Triplehorn and Johnson (2005). We counted individuals and measured total body length of each specimen to the nearest mm. We estimated biomass for all taxa with taxon-specific length–mass relationships published by Benke et al. (1999) and Sabo et al. (2002). We expressed biomass estimates for benthic samples as mg dry mass (DM)/m² and for drift samples as mg DM/m³. We compared total macroinvertebrate benthic and drift biomass estimates among sampling dates with a 1-way repeated measures analysis of variance (SAS version 9.3; SAS Institute, Cary, North Carolina). We used individual Hess samples (1–6) as a repeated variable for benthic samples and individual drift nets (1–4) as a repeated variable for drift samples.

We estimated turnover from benthic biomass of the dominant aquatic macroinvertebrate prey found in Brown and Rainbow Trout diets (i.e., Ephemeroptera, Megaloptera, and Trichoptera) with published values of annual biomass growth rates (production/biomass [P/B]) from streams with similar annual temperature regimes (Short et al. 1987, Whiting et al. 2011). P/B ratios of 23, 11.9, and 10 were used for ephemeropterans, megalopterans, and trichopterans, respectively. We estimated turnover as the mean aquatic macroinvertebrate biomass of each insect order from the 4 sampling dates multiplied by the respective P/B, and divided by the mean annual consumption of Brown and Rainbow Trout (see methods below).

Diet and stable-isotope analyses

We analyzed the diets of 101 Brown Trout (79–375 mm total length [TL]) and 134 Rainbow Trout (68–490 mm TL) from the 4 sampling dates (November 2010: Brown Trout $n = 10$, Rainbow Trout $n = 11$; January 2011: Brown Trout $n = 47$, Rainbow Trout $n = 49$; June 2011: Brown Trout $n = 18$, Rainbow Trout $n = 36$; September 2011: Brown Trout $n = 26$, Rainbow Trout $n = 38$). One Brown and 2 Rainbow Trout from November 2010 and 3 Brown and 2 Rainbow Trout from January 2011 had empty stomachs. Diet samples in November 2010 and January 2011 were taken from fish collected during the National Park Service nonnative removal efforts, whereas diet samples in June 2011 and September 2011 were taken from fish collected after the

autumn–winter nonnative fish removal effort. We assumed that all Brown and Rainbow Trout collected for our study were representative of the Bright Angel Creek population because they were caught ~1 km above the confluence with the mainstem Colorado River, they were unable to migrate into or out of the stream while the weir was in place, and their stomachs contained macroinvertebrates not commonly found in the Colorado River (ephemeropterans, megaloptera, and trichoptera; Cross et al. 2011). We collected all trout for diet samples, and benthic and drifting invertebrates from the same 200-m reach during the same sampling periods. We collected fish for diet samples 24 to 48 h after macroinvertebrate samples with a Smith–Root LR 20B (400 W; Smith–Root, Vancouver, Washington) backpack electrofishing unit set at 350 V, 30% duty cycle, and an output frequency of 35 Hz. We identified, weighed, and measured TL of all captured trout. We euthanized fish immediately after capture and removed their stomachs. We transferred stomachs to plastic bags and preserved them with 10% formalin for laboratory analysis. We quantified diets of Brown and Rainbow Trout from contents collected from the anterior portion of the stomach to the 1st bend in the digestive tract (Pilger et al. 2010). We identified (species for fish, genus for aquatic insects, family for terrestrial insects, order for noninsects), counted, dried (60°C for 48 h), and weighed contents to the nearest 0.001 g.

We compared diet composition between Brown and Rainbow Trout and among size classes of individual species with nonmetric multidimensional scaling (NMDS) in Primer-E (version 6; Clark and Gorley 2006). Bray–Curtis similarity matrices were generated from \sqrt{x} -transformed DM data for Brown and Rainbow Trout diet items. Individual stomachs were treated as samples, prey taxa were used as variables, and sampling period, species type, and size class (<100, 100–150, 151–200, 201–250, 251–300, >300 mm TL) were used as factors. We used analysis of similarity (ANOSIM) to test for differences between Brown and Rainbow Trout diets among sampling periods and among size classes within each species. The similarity percentages (SIMPER) routine was used to identify the diet items mainly responsible for Bray–Curtis dissimilarities between Brown and Rainbow Trout for each sampling period (Clark and Gorley 2006). We also used logistic regression (SAS; Proc Logistic) to test whether the probability of a trout having a fish in its stomach (piscivory) was related to species (Brown or Rainbow Trout), total length, or sampling month.

We estimated annual individual consumption (g DM) by Brown and Rainbow Trout from bioenergetics simulations for 2 sizes classes (<150 and >150 mm TL) of each species done with the Wisconsin bioenergetics model (Hanson et al. 1997). We used these size classes because diets from the field study showed distinctive diet shifts at 150 mm for both species (see Results). We used parameters published by Dieterman et al. (2004) for Brown Trout and by

Rand (1993) and Railsback and Rose (1999) for Rainbow Trout. We ran the bioenergetics simulations, which were based on an average individual Brown or Rainbow Trout of each size class (<150 and >150 mm TL) and assumed maintenance rations of 0 growth for 314 d, the number of days between our first and last sampling date. We extrapolated individual consumption estimates of Brown and Rainbow Trout using abundance estimates documented in Bright Angel Creek by Omana Smith et al. (2012) to examine population-level estimates of consumption.

We calculated the mean wet mass of Brown and Rainbow Trout in each size class from field measurements and used these values for initial and end masses in bioenergetics simulations. The mean wet masses were 22 g and 165 g for Brown Trout <150 and >150 mm TL, and 19 g and 170 g for Rainbow Trout <150 and >150 mm TL, respectively. We collected daily mean water temperatures (range: 2–21°C) for use in bioenergetics simulations from Bright Angel Creek from November 2010 to November 2011 with HOBO temperature loggers (Onset Corp., Bourne, Massachusetts). Diet proportions were used from stomach contents collected on each sampling date and were summed and categorized as Ephemeroptera, Megaloptera, Trichoptera, other aquatic, terrestrial insects, native fish, and organic matter. Energy densities (J/g DM) for each prey category were obtained from Cummins and Wuycheck (1971).

We also used stable-isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to examine trophic relationships and potential diet overlap between native (Speckled Dace and Bluehead Sucker) and nonnative (Brown and Rainbow Trout) fishes. We obtained pelvic-fin tissue from all trout used for diet analysis and ~5 individuals of each native species (Speckled Dace: 46–118 mm TL; Bluehead Sucker: 170–324 mm TL) on each sampling date. Only 1 Bluehead Sucker was captured in November 2010. We released all native fish alive after tissue collection. We used pelvic-fin tissue instead of white-muscle tissue because fin tissue is a suitable substitute for muscle tissue and is less invasive than white muscle tissue to obtain. Thus, it is more suitable for native species (Sanderson et al. 2009, Jardine et al. 2011).

We collected numerically dominant aquatic macroinvertebrates, Ephemeroptera (Baetidae), Trichoptera (Helicopsychidae, Hydropsychidae, Philopotamidae, Rhyacophilidae), Megaloptera (Corydalidae), and Diptera (Simuliidae) from the stream reach with additional Hess samples (separate from prey-availability samples), identified them in the field, and sorted them into separate containers overnight to allow gut evacuation (Jardine et al. 2005). We used a single composite sample composed of ≥ 5 individuals to represent each group during each sampling period. We preserved all stable-isotope samples in the field with salt, which does not affect C and N isotope values (Arrington and Wine-miller 2002).

In the laboratory, we rinsed isotope samples with distilled–deionized water supplied from a Barnstead water

system (Barnstead Co., Boston, Massachusetts), dried (60°C for 48 h), and homogenized them with a mortar and pestle. We weighed powdered samples and packaged them in 5 × 9-mm pressed-Sn capsules and analyzed them with a Carlo Erba NA 1500 elemental analyzer (Carlo Erba, Milan, Italy) coupled to a Finnigan Delta Plus XL mass spectrometer (Thermo Fisher Scientific Inc., Waltham, Massachusetts) via the ConFlo III interface. Replicate analysis of an acetanilide standard yielded error estimates of 0.1‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Stable-isotope ratios were expressed as parts per thousand (‰) and calculated in the standard notation:

$$\delta X = ([R_{\text{sample}} \times R_{\text{standard}}] - 1) \times 1000 \quad (\text{Eq. 1})$$

where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$.

We calculated means and standard errors of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios for each sampling group (i.e., native and nonnative fish species and numerically dominant macroinvertebrate groups). We inferred trophic relationships between native and nonnative fishes by calculating trophic positions of fishes with the formula:

$$\text{TP}_{\text{fish}} = \left(\frac{[\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{baseline}}]}{3.4} \right) + 2 \quad (\text{Eq. 2})$$

where $\delta^{15}\text{N}_{\text{fish}}$ is the $\delta^{15}\text{N}$ value from the sample fish tissue, $\delta^{15}\text{N}_{\text{baseline}}$ is the baseline macroinvertebrate sample, and 3.4 is the assumed shift between successive trophic levels (Post 2002). We used the combined mean $\delta^{15}\text{N}$ values of 3 macroinvertebrate taxa: *Baetis*, *Simulium*, and *Helicopsyche*, as the baseline macroinvertebrate group because they were abundant on all sampling dates, were found frequently in the diets of nonnative trout, and are likely a source of prey for Bluehead Sucker and Speckled Dace (Muth and Snyder 1995). We used Spearman rank correlation to compare trophic positions of Brown Trout, Rainbow Trout, Bluehead Sucker, and Speckled Dace with TL (mm) to evaluate ontogenetic shifts in diet with increasing length (SAS version 9.3; SAS Institute, Cary, North Carolina).

RESULTS

Macroinvertebrate prey availability

We identified 66 macroinvertebrate taxa from benthic and drift samples combined. Thirty of these taxa were terrestrial forms and were found only in drift samples. Mean total benthic biomass ranged from ~1466 to ~2756 mg DM/m² but did not differ among sampling periods ($F_{3,15} = 2.38$, $p = 0.11$; Table 1). Mean total drift biomass ranged from ~0.23 to ~0.57 mg DM/m³ and did not differ among sampling periods ($F_{3,15} = 2.06$, $p = 0.18$; Table 2). Biomass of aquatic insects dominated benthic samples (94–98%)

across all sampling dates (Table 1). Among aquatic insects, trichopterans were dominant in November 2010 (27%) and January 2011 (27%), whereas ephemeropterans were dominant in June 2011 (32%) and megalopterans in September 2011 (35%). Noninsects contributed <5% to total benthic biomass and were dominated by triclads and oligochaetes (~99%).

Contributions to total drift biomass were similar to benthic samples. Aquatic insects dominated drift samples (85–97%; Table 2). Ephemeropterans (44–64%) dominated drift biomass of aquatic insects across all sampling dates, followed by dipterans in November 2010 (26%), January 2011 (36%), and September 2011 (15%), and trichopterans in June 2011 (25%). Terrestrial insects were common in drift samples on all sampling dates. Dominant contributors included orthopterans, coleopterans, hymenopterans, and lepidopteran larvae (Table 2).

Diet and stable-isotope analyses

Differences between the diets of Brown and Rainbow Trout were evident from the 2-dimensional NMDS plot (Fig. 1) and ANOSIM (Global $R = 0.233$, $p = 0.001$) for all dates combined. Brown and Rainbow Trout diets also differed among sampling dates (November 2010: Global $R = 0.302$, $p = 0.008$; January 2011: Global $R = 0.109$, $p = 0.001$; June 2011: Global $R = 0.476$, $p = 0.001$; September 2011: Global $R = 0.289$, $p = 0.001$).

Diet items differed distinctly between Brown and Rainbow Trout on each sampling date (ANOSIM, November 2010: average dissimilarity = 85.6; January 2011: average dissimilarity = 71.0; June 2011: average dissimilarity = 82.2; September 2011: average dissimilarity = 77.4) (Fig. 2A–D). In November 2010, dissimilarities between diets were attributed mainly to the presence of native fish (16.1% contribution to dissimilarity) and megalopterans (i.e., *Corydalis*; 14.5%) in Brown Trout and organic matter (25.8%) in Rainbow Trout. Dissimilarities between diets in January 2011 were from megalopterans (13.0%) in Brown Trout diets and ephemeropterans (i.e., *Baetis*; 19.6%) and organic matter (18.9%) in Rainbow Trout diets, whereas in June 2011, dissimilarities were from megalopterans (17.3%) in Brown Trout and ephemeropterans (18.6%) and trichopterans (i.e., *Hydropsyche*; 12.7%) in Rainbow Trout. In September 2011, the 2 items contributing most to dissimilarities between Brown and Rainbow Trout diets were megalopterans (26.1%) and organic matter (15.6%), respectively.

The total occurrence of piscivory was higher in Brown (19%) than Rainbow Trout (4%) during the study period. Fish were found only in the stomachs of Brown Trout >188 mm or Rainbow Trout >176 mm. All but 1 fish found in the stomachs of Brown and Rainbow Trout ($n = 25$) were Speckled Dace. One Bluehead Sucker was found in a Brown Trout in January 2011. The probability of pi-

Table 1. Mean (SE) of benthic biomass (mg dry mass/m²) and % contribution of macroinvertebrate taxa in November 2010, January 2011, June 2011, and September 2011. Percent contributions of major groups are % total macroinvertebrate biomass. Percent contribution of each taxon within a group is the % contribution to that group.

Taxon	November 2010			January 2011			June 2011			September 2011		
	mg/m ²	SE	%	mg/m ²	SE	%	mg/m ²	SE	%	mg/m ²	SE	%
Aquatic Insecta	1644.4	232.8	95	2590.5	374.1	94	1691.3	386.8	98	1432.0	329.9	98
Ephemeroptera	147.2	42.4	9	406.5	87.8	16	545.1	143.1	32	220.2	38.5	15
Odonata	97.8	73.9	6	51.2	24.2	2	0.9	0.7	0	7.4	4.3	1
Plecoptera	0.2	0.2	<1	12.2	2.2	<1	0	0	0	0	0	0
Megaloptera	258.8	217.6	16	410.4	310.0	16	494.1	269.2	29	499.5	281.4	35
Trichoptera	445.0	99.0	27	702.1	175.3	27	475.2	149.0	28	265.5	55.3	19
Lepidoptera	297.3	81.1	18	223.5	65.4	9	0.9	0.9	<1	144.5	58.2	10
Coleoptera	156.5	29.2	10	66.6	34.3	6	24.4	5.7	1	133.1	35.2	9
Diptera	241.5	49.8	15	617.9	148.8	24	150.7	40.8	9	161.8	39.6	11
Aquatic Other	76.2	23.1	4	126.9	33.5	5	31.1	11.8	2	30.2	9.9	2
Tricladida	42.0	13.7	55	60.8	23.8	48	3.1	1.1	10	14.1	6.0	47
Oligochaeta	34.0	12.6	45	65.8	22.5	52	28.0	11.0	90	16.1	4.5	53
Ostracoda	0.1	0.1	<1	0.3	0.1	<1	<0.1	<0.1	<1	0.1	<0.1	<1
Hydrachnidia	<0.1	<0.1	<1	<0.1	<0.1	<1	<0.1	<0.1	<1	<0.1	<0.1	<1
Terrestrial Insecta	0.1	0.1	<1	0	0	0	1.1	0.9	<1	1.1	1.0	<1
Hemiptera	0.1	0.1	100	0	0	0	0.9	0.9	84	0.1	0.1	7
Hymenoptera	0	0	0	0	0	0	0.2	0.2	16	1.1	1.1	93
Terrestrial other	5.3	2.6	<1	38.7	16.9	1	3.9	1.7	<1	3.1	2.1	<1
Oligochaeta	5.3	2.6	100	38.7	16.9	100	3.6	1.8	91	3.1	2.1	100
Isopoda	0	0	0	0	0	0	0.4	0.4	9	0	0	0
Total	1726.0	256.6		2756.1	432.5		1727.4	427.4		1466.5	366.5	

scivory for trout varied by species (logistic regression, $\chi^2 = 7.2$, $df = 1$, $p = 0.007$) and TL (logistic regression; $\chi^2 = 12.4$, $df = 1$, $p < 0.001$), but not sampling period (logistic regression; $\chi^2 = 3.5$, $df = 3$, $p = 0.309$). Brown Trout were 4.5× more likely to be piscivorous than Rainbow Trout and increasing TL increased the probability of piscivory for both species.

Contributions to diet biomass differed among size classes of Brown Trout (Global $R = 0.187$, $p = 0.001$) and Rainbow Trout (Global $R = 0.139$, $p = 0.001$) (Appendix S1). Ephemeropterans contributed the most biomass to the diets of Brown Trout <100 mm (42%) and 100–150 mm (67%), whereas megalopterans and native fish contributed the most biomass to the diets of 151–200 mm (66%), 201–250 mm (74%), 251–300 mm (64%), and >300 mm (68%) Brown Trout. Ephemeropterans contributed the most biomass to the diets of Rainbow Trout <100 mm (64%), 100–150 mm (78%), and 151–200 mm (26%). Megalopterans and organic matter (filamentous algae) contributed the most biomass to the diets of 201–250 mm TL (31% and 39%, respectively) and 251–300 mm TL (52% and 17%) Rainbow Trout. Diets of Rainbow Trout in the >300 mm

TL size class were dominated by organic matter (70%) and Acrididae grasshoppers (17%).

Bioenergetics simulations showed differences in annual individual consumption estimates between Brown and Rainbow Trout and between size classes of each species. Total prey consumption was similar between Brown and Rainbow Trout <150 mm TL, but consumption was higher for Rainbow Trout in the >150 mm TL size class (Table 3). Consumption by Brown and Rainbow Trout in the <150 mm TL size class was dominated by ephemeropterans (76% and 39%, respectively) and trichopterans (11% and 22%), whereas consumption by Brown Trout in the >150 mm size class was dominated by megalopterans (44%), trichopterans (20%), and native fish (15%), and consumption by Rainbow Trout was dominated by organic matter (33%; primarily filamentous algae), megalopterans (16%), and terrestrial insects (15%). Consumption of native fish by Rainbow and Brown Trout >150 mm was substantial, and bioenergetics simulations indicated that individual Brown and Rainbow Trout could consume 27.1 and 17 g DM, respectively, of native fish every 314 d (Table 3). Population-level estimates of total prey consumption were similar for Brown and Rainbow

Table 2. Mean (SE) of drift biomass (mg dry mass/m³) and % contribution of macroinvertebrate taxa in November 2010, January 2011, June 2011, and September 2011. Percent contributions of major groups are % total macroinvertebrate biomass. Percentage contribution of each taxon within a group is the % contribution to that group.

Taxon	November 2010			January 2011			June 2011			September 2011		
	mg/m ³	SE	%									
Aquatic Insecta	0.197	0.021	85	0.504	0.114	97	0.513	0.141	90	0.449	0.125	90
Ephemeroptera	0.087	0.018	44	0.288	0.101	57	0.242	0.057	47	0.289	0.093	64
Odonata	0.006	0.001	3	0.003	0.001	<1	0.003	0.002	1	0.004	0.001	1
Plecoptera	<0.001	<0.001	<1	0.006	0.001	1	<0.001	<0.001	<1	0.001	0.001	<1
Hemiptera	<0.001	<0.001	<1	<0.001	<0.001	<1	<0.001	<0.001	<1	<0.001	<0.001	<1
Megaloptera	0.009	0.007	4	0.012	0.011	2	0.036	0.021	7	0.016	0.008	4
Trichoptera	0.028	0.005	14	0.013	0.002	3	0.131	0.067	25	0.051	0.011	11
Lepidoptera	0.013	0.002	7	0.002	<0.001	<1	0.006	0.002	1	0.006	0.001	1
Coleoptera	0.004	0.001	2	0.001	<0.001	<1	0.012	0.004	2	0.016	0.004	4
Diptera	0.050	0.007	26	0.180	0.052	36	0.082	0.021	16	0.067	0.017	15
Aquatic other	<0.001	<0.001	<1	<0.001	<0.001	<1	<0.001	<0.001	<1	0.001	<0.001	<1
Tricladida	<0.001	<0.001	<1	<0.001	<0.001	45	<0.001	<0.001	25	0.001	<0.001	88
Oligochaeta	<0.001	<0.001	10	<0.001	<0.001	41	<0.001	<0.001	71	0	0	0
Ostracoda	<0.001	<0.001	71	<0.001	<0.001	14	<0.001	<0.001	1	<0.001	<0.001	12
Hydrachnidia	<0.001	<0.001	18	<0.001	<0.001	<1	<0.001	<0.001	3	<0.001	<0.001	<1
Terrestrial Insecta	0.030	0.005	13	0.013	0.003	2	0.048	0.012	8	0.046	0.014	9
Orthoptera	0	0	0	0	0	0	0.011	0.007	23	0.016	0.013	34
Hemiptera	0.003	0.001	12	0.001	<0.001	8	0.004	0.002	8	0.003	0.002	7
Coleoptera	0.005	0.001	17	0.002	0.001	12	0.010	0.003	21	0.002	0.001	4
Hymenoptera	0.010	0.002	33	0.003	0.001	22	0.018	0.004	38	0.022	0.003	48
Lepidoptera	0.008	0.004	28	0.006	0.003	47	0.004	0.002	8	0.001	<0.001	2
Diptera	0.003	0.001	10	0.001	0.001	11	0.001	<0.001	2	0.003	0.001	6
Terrestrial Other	0.004	0.001	2	0.003	0.001	<1	0.008	0.003	1	0.004	0.001	1
Pseudoscorpionida	<0.001	<0.001	5	<0.001	<0.001	9	<0.001	<0.001	5	<0.001	<0.001	3
Oligochaeta	0.001	<0.001	22	0.001	<0.001	44	0.001	<0.001	8	<0.001	<0.001	12
Isopoda	0.001	<0.001	19	<0.001	<0.001	5	0.005	0.002	64	<0.001	<0.001	13
Araneae	0.002	0.001	54	0.001	<0.001	42	0.002	0.001	22	0.003	0.001	72
Total	0.232	0.024		0.520	0.114		0.569	0.151		0.500	0.132	

Trout and indicated that the average density of Brown (0.035 ind/m²) and Rainbow (0.03 ind/m²) Trout in this portion of Bright Angel Creek could consume 6035 and 5709 g respectively of prey every 314 d.

Stable-isotope analyses revealed $\delta^{13}\text{C}$ signatures of megalopterans (-26.7 to -25.1‰), dipterans (-28.2 to -24.4‰), and trichopterans (-28.1 to -24.5‰) were most closely aligned with native (Speckled Dace: -25.1 to -23.6‰ ; Bluehead Sucker: -25.2 to -24.3‰) and small (<150 mm TL) nonnative trout (Brown Trout, -27.3 to -23.9‰ ; Rainbow Trout, -26.7 to -24.1‰) during each sampling period, suggesting that these orders are major sources of C in the food web (Fig. 3). Ephemeropterans had the most depleted macroinvertebrate $\delta^{13}\text{C}$ signatures in all sampling periods (-32.3 to -29.1‰). $\delta^{13}\text{C}$ values of small Brown and Rainbow Trout appeared to be centered among the

dominant macroinvertebrate orders (Megaloptera, Diptera, and Trichoptera), but $\delta^{13}\text{C}$ values of large nonnative trout (>150 mm TL) (Brown Trout: -24.3‰ to -22.5‰ ; Rainbow Trout: -24.9‰ to -23.8‰) were more enriched and generally centered among native fish $\delta^{13}\text{C}$ values (Fig. 3A–D).

Trophic positions were positively correlated with TL of Brown Trout ($r = 0.77$, $p < 0.001$; Fig. 4A), Rainbow Trout ($r = 0.51$, $p < 0.001$; Fig. 4B), and Speckled Dace ($r = 0.75$, $p < 0.001$; Fig. 4D), but not Bluehead Sucker ($r = 0.09$, $p = 0.74$; Fig. 4C). The slopes of the regression lines between TL and trophic position differed among species (ANCOVA, $F_{3,182} = 4.40$, $p = 0.005$). Tissue $\delta^{15}\text{N}$ values generally were more enriched for large Brown Trout (9.0–10.4‰) and Rainbow Trout (8.7–10.3‰) than native fishes (Speckled Dace, 7.3–8.3‰; Bluehead Sucker, 6.6–7.4‰)

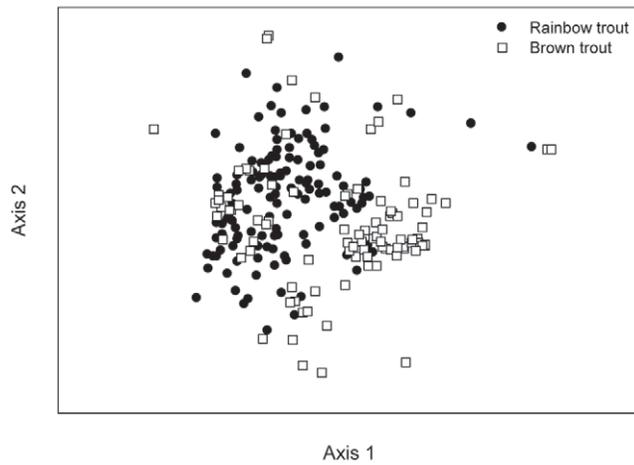


Figure 1. Nonmetric multidimensional scaling plot based on Bray–Curtis similarities of Brown and Rainbow Trout diets for all sampling dates (November 2010, January 2011, June 2011, September 2011) and size classes (<150 and >150 mm total length [TL]) combined.

and small Brown (8.1–8.8%) and Rainbow Trout (8.2–8.9%) during each sampling period, except June 2011, when $\delta^{15}\text{N}$ of small Brown Trout exceeded $\delta^{15}\text{N}$ of large Rainbow Trout (Fig. 3C).

DISCUSSION

Brown and Rainbow Trout consumed a diverse range of prey throughout the study, and ontogenetic shifts in food habits occurred among both species. Salmonids tend to consume larger prey items as they increase in size to maximize the joules consumed per item (Mittelbach and Persson 1998, Nowak et al. 2004). Our results suggest that Brown and Rainbow Trout switch from consuming small (2–10 mm) prey items in the drift (e.g., Ephemeroptera and Diptera) to consuming larger (20–50 mm) benthic macroinvertebrates (e.g., Megaloptera) and native fish once they reach 150 to 250 mm TL. Ephemeropterans (*Baetis*), megalopterans (*Corydalus*), native fish, and organic matter (filamentous algae) were the 4 food types consumed most by Brown and Rainbow Trout throughout the study. How removal efforts may have affected diets of nonnative trout is unclear, but these diet items are consistent with previous data from the Colorado River and other tributaries in the Grand Canyon, which suggest that these diet items are consumed regularly by Brown and Rainbow Trout (Cross et al. 2011, Spurgeon 2012).

Our results suggest megalopterans and native fish contribute substantially to the diets of large (>150 mm TL) Brown and Rainbow Trout. These results agree with those of Spurgeon (2012), who found that Rainbow Trout in a Grand Canyon tributary consumed mostly large predatory macroinvertebrates (i.e., megalopterans [*Corydalus*]) and

native fish as they increased in size, and of Meissner and Muotka (2006) who indicated that Brown Trout are size-selective predators and can strongly affect the largest available prey types. Roell and Orth (1993) found that *Corydalus* were more abundant in the diets of age-2 and -3 rock bass than age-0 and -1 in the New River, West Virginia, indicating a size-selective preference as fish size increases.

Piscivory occurred when trout reached ~175 mm TL and was 4× higher for Brown than Rainbow Trout, a result suggesting that Brown Trout may pose a more direct predatory threat than Rainbow Trout to native fishes. However, both trout species may affect native fishes through predation, particularly trout >150 mm. Estimates from the bioenergetics simulations showed that over a 314-d period, large (>150 mm TL) Brown and Rainbow Trout have the ability to consume 178 and 113 g wet mass of native fish, respectively. Results from the simulations are conservative because they were specified from an average individual Brown and Rainbow Trout, assumed a ration diet of 0 growth, and assumed that diet items found in the stomachs of nonnative trout on the 4 sampling dates were representative of diets throughout the entire 314 d of the study. Extrapolation of these results to a population of

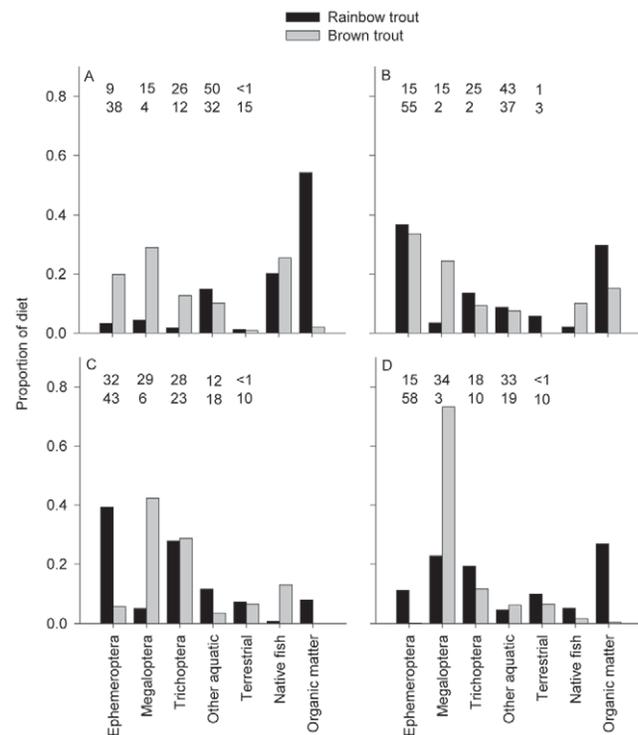


Figure 2. Diets of Brown and Rainbow Trout in November 2010 (A), January 2011 (B), June 2011 (C), and September 2011 (D). All individuals of each species were pooled each month to determine proportion of diet contents by dry mass (g). Numbers above bars refer to % prey items in benthic (top number) and drift (bottom number) samples.

Table 3. Bioenergetics consumption estimates (g DM per individual per 314 days) and energy densities (J/g dry mass) of dominant prey items for Brown Trout and Rainbow Trout size classes (total length [TL], mm). Estimates are based on a 314-d period from November 2010 to September 2011.

Prey type	Brown Trout		Rainbow Trout		Prey energy density
	<150 mm	>150 mm	<150 mm	>150 mm	
Ephemeroptera	29.6	11.9	13.8	21.6	22,882.3
Megaloptera	1.6	80.8	1.6	34.8	21,798.6
Trichoptera	4.1	37.4	7.8	32.2	20,924.8
Other aquatic	3.0	7.1	4.9	10.8	20,188.1
Terrestrial	0	10.7	0.8	32.9	22,138.7
Native fish	0	27.1	0	17.0	27,375.1
Organic matter	0.6	9.6	6.2	75.1	8873.9
Total prey	38.9	184.6	35.1	224.4	

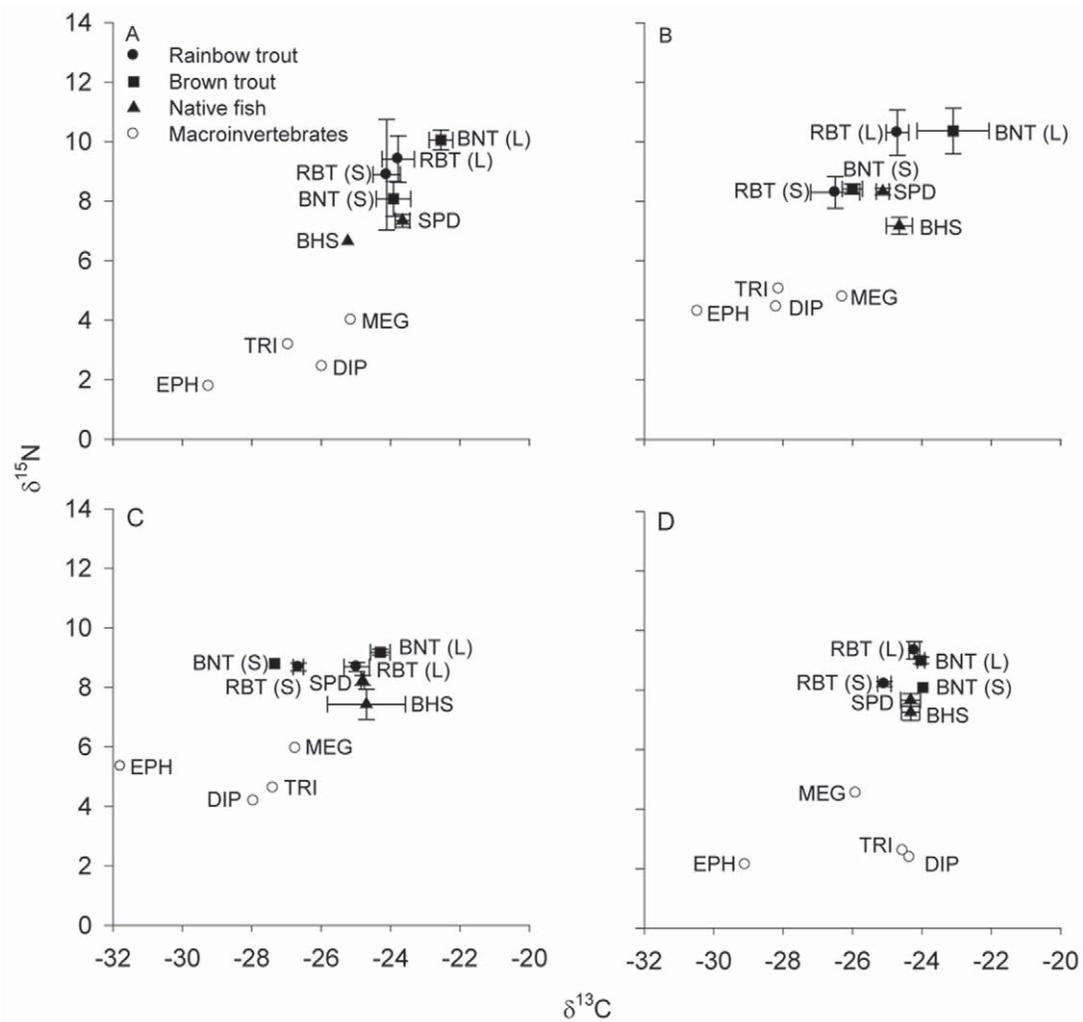


Figure 3. Mean (± 1 SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of numerically dominant macroinvertebrates, native fish, Brown Trout, and Rainbow Trout in November 2010 (A), January 2011 (B), June 2011 (C), and September 2011 (D). EPH = Ephemeroptera, DIP = Diptera, TRI = Trichoptera, MEG = Megaloptera, BHS = Bluehead Sucker, SPD = Speckled Dace, BNT (S) = Brown Trout (<150 mm total length [TL]); BNT (L) = Brown Trout (>150 mm TL), RBT (S) = Rainbow Trout (<150 mm TL), RBT (L) = Rainbow Trout (>150 mm TL).

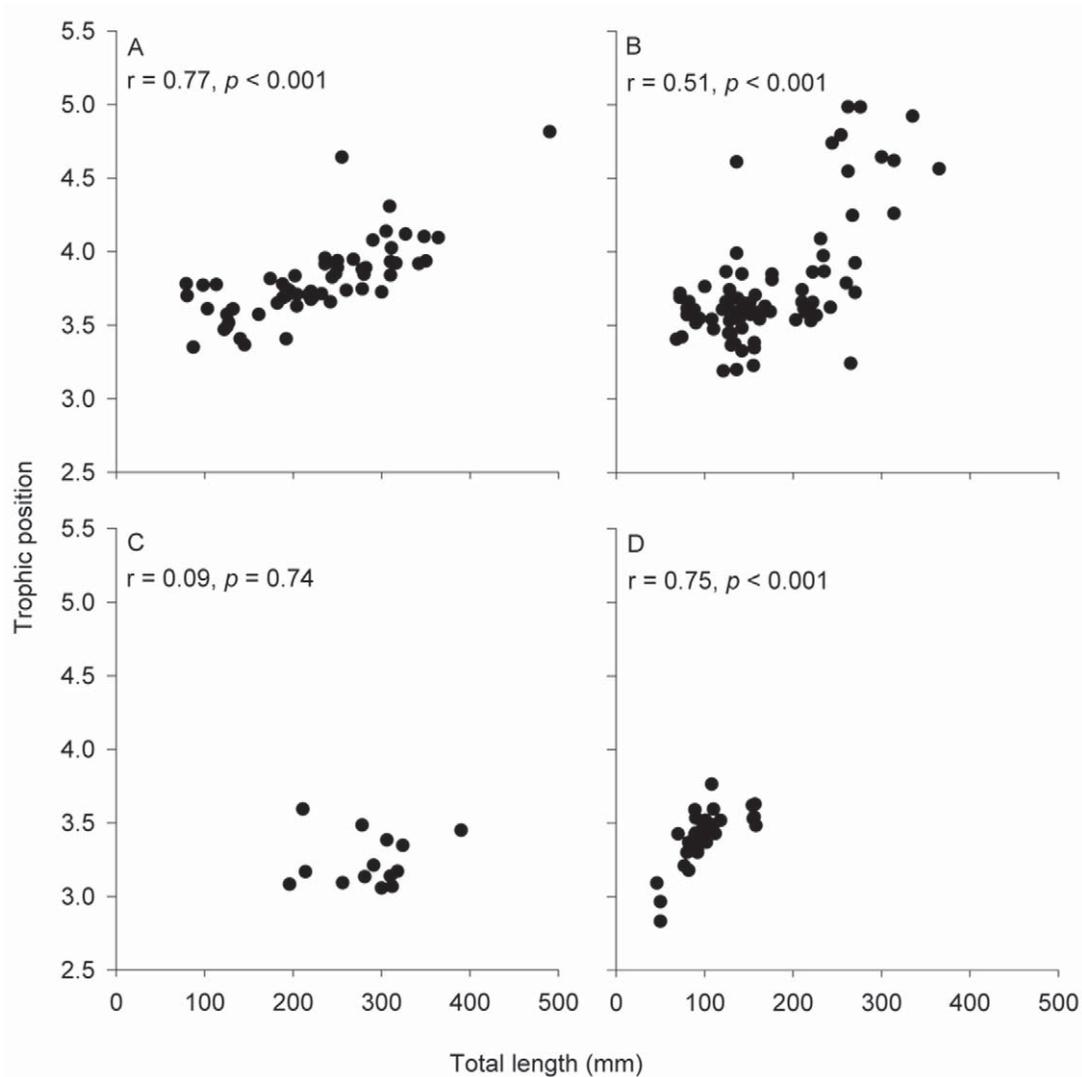


Figure 4. Relationship between Brown Trout (A), Rainbow Trout (B), Bluehead Sucker (C), and Speckled Dace (D) total length (mm) and calculated trophic position.

53 Brown Trout and 44 Rainbow Trout (the average number of trout in a 200-m stream segment of Bright Angel Creek) over a 314-d period yields estimates indicating that these species could consume 718 g and 374 g DM of native fish, respectively, which is equivalent to ~243 Speckled Dace (based on a mean Speckled Dace mass of 4.5 g).

Our results suggest that Bright Angel Creek has higher macroinvertebrate biomass and taxon richness than previously estimated from Bright Angel Creek and the Colorado River in the Grand Canyon (Stevens et al. 1997, Oberlin et al. 1999, Cross et al. 2011). However, our estimates of macroinvertebrate biomass may be limited because we sampled infrequently and we were unable to estimate energy flux between fishes and their prey (e.g., secondary production). Nevertheless, turnover estimates generated from benthic biomass values and annual consumption estimates indicate that high turnover rates among ephemeropterans (5/y),

megalopterans (12/y), and trichopterans (9/y) are needed to meet the energetic demands (i.e., consumption) of nonnative trout. These values correspond to average cohort production intervals of 72, 30, and 42 d for ephemeropterans, megalopterans, and trichopterans, respectively. These estimates indicate that megalopterans and trichopterans may be limited in Bright Angel Creek because of their longer life cycle and dominance in the diets of Brown and Rainbow Trout. Furthermore, Rainbow Trout consumed large proportions of terrestrial insects and organic matter, suggesting that nonnative trout in Bright Angel Creek may be consuming alternative prey items to compensate for limited benthic prey availability. Huryn (1996) showed that Brown Trout required terrestrial macroinvertebrates and >80% of available benthic prey in a New Zealand stream, a result suggesting potentially strong top-down effects in stream food webs with trout.

The combined results of our diet and stable-isotope data suggest that native fishes in tributaries of the Colorado River in Grand Canyon National Park may be affected by nonnative trout through resource competition with smaller drift-feeding fish and predation by larger piscivorous fish. Monthly isotopic values from native and nonnative fishes in Bright Angel Creek were similar and were consistent with our hypothesis that diet overlap exists between native and nonnative species. Stable-isotope analyses complement diet analyses by providing dietary information of species over longer temporal scales and reflect foods that are assimilated by the consumer (Davis et al. 2012). Diet data from nonnative trout in conjunction with isotope data suggest that diets of Rainbow Trout and small (<150 mm) Brown Trout may overlap with native fishes. Diets of Rainbow Trout and small Brown Trout regularly contained filamentous algae and small insects (i.e., Ephemeroptera and Trichoptera). Conversely, our stable-isotope data indicated that $\delta^{13}\text{C}$ signatures of fishes were more enriched than these macroinvertebrate prey items on some of the sampling dates. This result suggests that aquatic macroinvertebrates in Bright Angel Creek may be shifting resource use and consuming ^{13}C -depleted energy sources (e.g., decaying leaf material), or nonnative trout may be obtaining energy from ^{13}C -enriched sources (e.g., filamentous algae; McCutchan et al. 2003, Wellard Kelly et al. 2013). Nevertheless, the primary diet items for Bluehead Sucker and Speckled Dace in the upper Colorado River basin were filamentous algae and small insects (Muth and Snyder 1995), findings that further suggest competition between nonnative trout and native fishes may be occurring in Bright Angel Creek. Our estimates of trophic position suggest that nonnative trout are obtaining resources at a higher trophic level than native fishes, and this difference probably is related to consumption of large predatory macroinvertebrates (e.g., megalopterans) and piscivory. This pattern is consistent with results obtained by Shannon et al. (2001), who showed trophic position of Rainbow Trout in the mainstem Colorado River was correlated with length and indicated an increase in piscivory among larger fish.

Glen Canyon Dam has altered the ecosystem processes of the Colorado River. Food resources have become limited, and native fishes have been extirpated or have suffered population declines (Minckley 1991, Cross et al. 2011, Yard et al. 2011). Our results suggest that unregulated and relatively less impaired tributaries in the Grand Canyon may have diverse and abundant resources compared to the Colorado River. However, nonnative trout are preying upon native fishes and consuming large amounts of macroinvertebrate prey, which may be limiting resources for other consumers. The wide distribution and high abundance of nonnative trout throughout the Colorado River basin may pose a large threat to native fishes, and their management

and control may mitigate their effects (Schade and Bonar 2005). Native Speckled Dace and Bluehead Sucker have persisted with nonnative trout in Bright Angel Creek for >50 y, but little information exists regarding how this coexistence has affected population structure and stream community dynamics (Otis 1994). The coexistence of introduced trout and native fishes in this stream probably occurs because of a combination of differing life histories, alternative diets, and environmental stochasticity (Meffe 1984, Meffe and Minckley 1987). Our results suggest that suppression of larger nonnative trout may have an immediate positive effect on native fishes through reduced predation, and suppression of smaller trout may reduce potential resource competition. Thus, removal efforts may have to be prioritized to maximize conservation efforts and to aid native fish recovery via direct and indirect pathways, including reduced predation and competition.

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