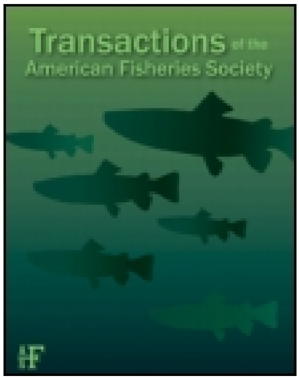

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Differential Interactions of Two Introduced Piscivorous Salmonids with a Native Cyprinid in Lentic Systems: Implications for Conservation of Roundtail Chub

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ARTICLE

Differential Interactions of Two Introduced Piscivorous Salmonids with a Native Cyprinid in Lentic Systems: Implications for Conservation of Roundtail Chub

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Abstract

The effects of multiple nonnative piscivore species on native prey species in lentic systems are poorly understood. We studied the relative predation risks posed by two piscivorous salmonids (brown trout *Salmo trutta* and lake trout *Salvelinus namaycush*) to endemic roundtail chub *Gila robusta* in two lakes within the upper Colorado River basin. Gill nets were set in various habitat types to study habitat use by the three species before and after the onset of summer stratification. Roundtail chub and brown trout were mainly associated with shallow-water habitats, and this association did not change with thermal period. By contrast, lake trout habitat use changed with thermal period as fish moved from shallow areas in the spring to deepwater habitat after stratification. These habitat use patterns indicate that roundtail chub are more susceptible to predation by brown trout than by lake trout because both roundtail chub and brown trout occupy the littoral zone for a prolonged period. Diet data indicated that brown trout consumed littoral fish species (i.e., cyprinids), whereas lake trout primarily consumed opossum shrimp *Mysis* spp. and dipterans (true flies). Brown trout consumed proportionally more fish than did lake trout, began feeding on fish at smaller total lengths, and increased fish consumption during the period of thermal stratification. An important consideration for efforts to conserve lentic roundtail chub populations is the prevention of future introductions of littoral predators.

Introductions of nonnative species have led to declines in native fish faunas around the world (e.g., Witte et al. 1992; Townsend 1996; Ruzycki et al. 2003). The introduction of a single predator may result in declines of native species, as happened with native Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* after lake trout *Salvelinus namaycush* became established in Yellowstone Lake, Wyoming (Ruzycki et al. 2003). However, many systems have been inundated with multiple species that occupy various ecological niches (Olden and Poff 2005; Strayer 2010). Differences in predator morphology, foraging behavior, or habitat use will influence the effects of predators on potential prey (Amundsen et al. 2003; Schmitz 2007). As a result, predators may differentially affect native fishes depending upon the extent of spatial and temporal overlap in habitat use (Kahilainen and Lehtonen 2003; Olden et al. 2006).

Two nonnative piscivores—brown trout *Salmo trutta* and lake trout—were introduced into natural lakes of the upper Colorado River basin during the first half of the 20th century (Figure 1; P. A. Cavalli, Wyoming Game and Fish Department, personal communication). However, the relative potential for predation by either species on endemic roundtail chub *Gila robusta* in these lakes is unknown. Roundtail chub, a species of conservation concern, has experienced declines in both distribution and abundance in lotic systems (Bezzerides and Bestgen 2002); these declines are partly the result of predation by introduced piscivorous fishes (Bestgen and Propst 1989; Ruppert et al. 1993; Barrett and Maughan 1995; Marsh and

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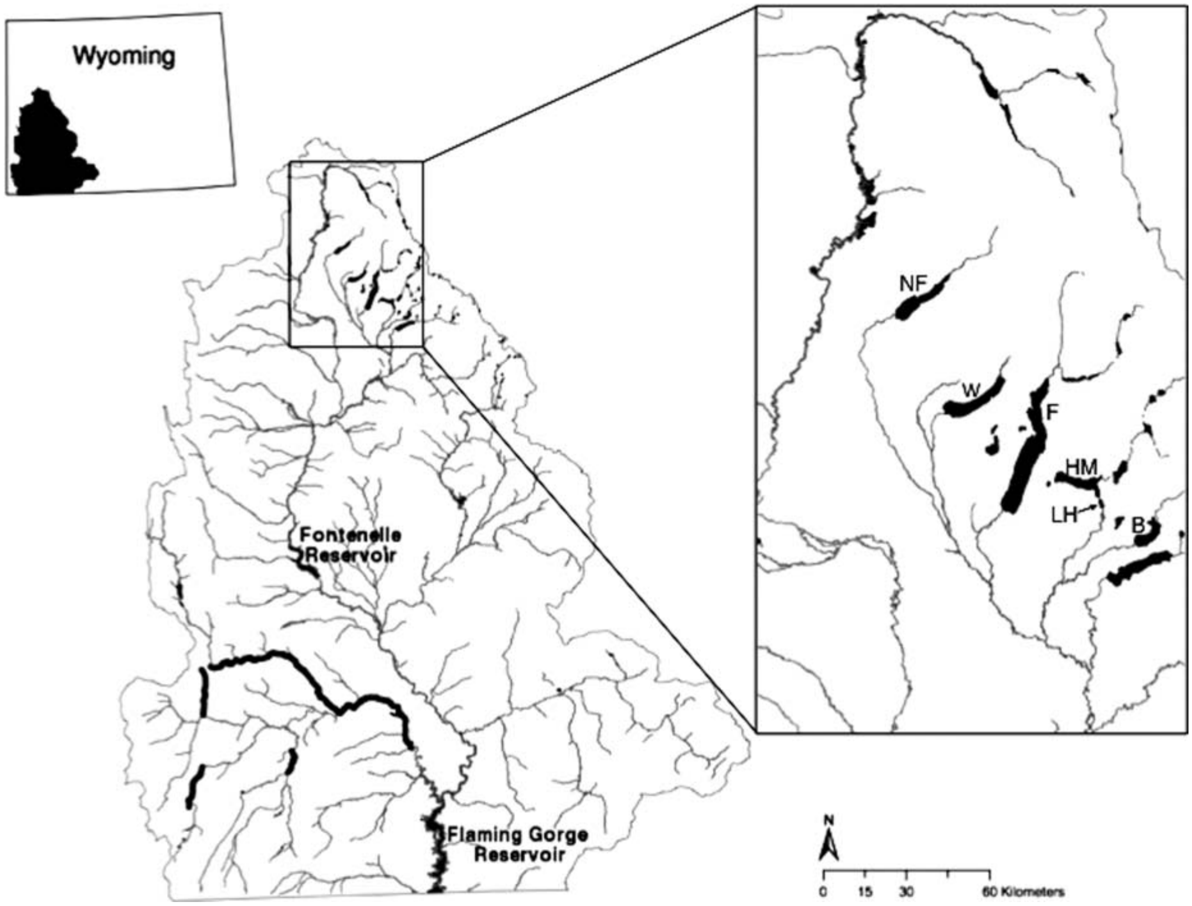

FIGURE 1. Distribution of roundtail chub populations in the upper Green River basin of Wyoming (highlighted stream segments; adapted from Kern et al. 2007); roundtail chub also occur in the following lakes: New Fork (NF), Willow (W), Fremont (F), Halfmoon (HM), Little Halfmoon (LH), and Burnt (B) lakes. Fontenelle and Flaming Gorge reservoirs and their associated dams are movement barriers for roundtail chub.

Douglas 1997). Because of rangewide declines, roundtail chub in natural lakes of the upper Colorado River basin may have important evolutionary value, as they are isolated from other roundtail chub populations and constitute the only such populations found in natural lakes (Binns 1967; Moritz 1994; Laske et al. 2011). Therefore, an understanding of the impacts of introduced predators on roundtail chub in lake systems will benefit the design of species conservation plans.

Due to differences in their habitat use and diets, brown trout and lake trout may have differential impacts on roundtail chub. Brown trout and lake trout are highly piscivorous as adults (Madenjian et al. 1998; Ruzycki et al. 2003; Hyvärinen and Huusko 2006; Jensen et al. 2008). Brown trout feed opportunistically and their diet may vary with size, habitat, and season (Bridcut and Giller 1995); their feeding rate increases as water temperatures rise (Klemetsen et al. 2003). Lake trout are typically confined to areas with cool water temperatures ($<10^{\circ}$C; Ruzycki et al. 2001; Dillon et al. 2003) and are restricted to the hypolimnion during summer months, when surface temperatures increase. However, the distribution of prey rather than thermal preferences may influence the distribution of lake trout (Sellers et al. 1998). Both piscivore species are potential predators of roundtail chub, and determining the extent of habitat overlap among the three species may provide insight into each piscivore's relative probability of predation on roundtail chub.

We examined patterns of habitat use by brown trout, lake trout, and roundtail chub and predation by the two salmonid species on roundtail chub in two glacial lakes of the upper Green River basin, Wyoming. Our objectives were to (1) determine the extent of habitat overlap among brown trout, lake trout, and roundtail chub during periods of thermal mixing and thermal stratification in these natural lakes; and (2) determine whether brown trout or lake trout predation on roundtail chub is a common occurrence in natural lakes and whether thermal stratification alters predation patterns.

METHODS

Study area.—Halfmoon and Little Halfmoon lakes (Sublette County, Wyoming) are in the Pole Creek drainage of the Green River watershed. Halfmoon Lake is located upstream of Little Halfmoon Lake, and a 400-m stream segment connects the two

TABLE 1. Habitats sampled and gill-net configurations used to collect roundtail chub, brown trout, and lake trout in Halfmoon and Little Halfmoon lakes, Wyoming. Gill-net panels were 15.24 m long × 1.8 m deep (habitats: LC = littoral with cover; LNC = littoral with no cover; MB = middepth benthic; SP = surface pelagic; DP = deep pelagic; DB = deep benthic). Habitat types are described in Table 2.

Habitat type(s) sampled	Net configuration	Number of panels	Mesh size(s) (mm)	Total net dimensions (m)
LC, LNC, MB	Single panel	1	19	15.24 × 1.8
	Single panel	1	25	15.24 × 1.8
	Single panel	1	32	15.24 × 1.8
	Single panel	1	38	15.24 × 1.8
	Single panel	1	51	15.24 × 1.8
	Single panel	1	64	15.24 × 1.8
SP, DP	Multipanel	9	19, 25, 32	45.7 × 5.5
	Multipanel	12	32, 38, 51, 64	70.0 × 5.5
DB	Multipanel	3	19, 25, 32	45.7 × 1.8
	Multipanel	3	38, 51, 64	45.7 × 1.8

lakes. Halfmoon Lake has a surface area of 4.3 km^2, a maximum depth of 85 m, and a surface elevation of 2,316 m. The southeast arm of the lake has depths less than 30 m and gently sloping shorelines, whereas the northern and southern shorelines are steeper (Leopold 2000). The substrate over much of the bottom of Halfmoon Lake is unknown, but there are numerous rocky outcrops along the southern and northern shores. Several sandy beaches are present: one in the southern arm near Pole Creek's exit from the lake, another near Pole Creek's entrance to the lake, and one along the western shore. Little Halfmoon Lake has a surface area of 0.24 km^2, a maximum depth of 17 m, and a surface elevation of 2,315 m. The northern half of the lake is less than 2.5 m deep, whereas water is approximately 15 m deep in a narrow area at the southern end of the lake. Substrate is dominated by silt and sand along with isolated patches of dense vegetation in water of less than 4-m depth. The southern shore of Little Halfmoon Lake has large rock and boulder substrates, while the remainder of the shoreline is free of large substrate but is dominated by overhanging riparian vegetation and sandy substrate.

Sampling.—Sampling on Halfmoon and Little Halfmoon lakes was conducted to evaluate habitat use by roundtail chub, brown trout, and lake trout and to obtain data on the stomach contents of brown trout and lake trout. The three species were collected from each lake by using gill nets that were set overnight in various habitats on alternate weeks from June to August 2008 and from May to August 2009 (Table 1). In Halfmoon Lake, six sites of each habitat (Table 2) were sampled (3 sites/year) except surface pelagic habitat (sampled at three sites in 2008 only) and deep benthic habitat (sampled at three sites in 2009 only). In Little Halfmoon Lake, the same three sites for littoral habitat with cover, littoral habitat without cover, and middepth benthic habitat were sampled in both years due to the small size of the lake; in addition, two sites representing surface pelagic habitat were sampled in 2008, and one deep benthic site and one deep pelagic site were sampled in 2009. Gill nets were set every night for 1 week, and mesh sizes were rotated among the sites so that a given mesh size was not set at a site more than once in a week. Additional gillnetting was conducted in Halfmoon Lake during August 2010 to collect brown trout for stomach content analysis.

The same sites in each lake were sampled during two periods: (1) when the lake was thermally mixed and (2) when the lake was thermally stratified. Periods were determined by observing temperature profiles, which were obtained by lowering a temperature probe (Model YSI-550A; Yellow Springs Instruments,

TABLE 2. Descriptions of the habitat types sampled in Halfmoon (HM) and Little Halfmoon (LHM) lakes during 2008 and 2009.

Habitat	Description	Year(s) sampled
Littoral with cover (LC)	Littoral zone: depths less than 6 m; boulders, wood, or macrophytes present	2008, 2009
Littoral with no cover (LNC)	Littoral zone: depths less than 6 m; gravel or sand substrate	2008, 2009
Middepth benthic (MB)	Benthic zone: depths between 9 and 12 m	2008, 2009
Surface pelagic (SP)	Pelagic zone: surface to 6-m depth	2008
Deep pelagic (DP)	Pelagic zone: 6–12-m depth	2008, 2009
Deep benthic (DB)	Benthic zone: depth of 30 m in HM and 15 m in LHM	2009

Yellow Springs, Ohio) from the surface in 1-m increments to identify when and at what depth thermal stratification occurred. Water temperatures were measured to a depth of 12 m in both lakes during 2008; during 2009, temperatures were measured to 30 m in Halfmoon Lake and to the bottom (15 m) in Little Halfmoon Lake.

Brown trout and lake trout were weighed (g) and measured (total length [TL], mm). Gastric lavage (similar to the methods of Hartleb and Moring 1995) was used to extract the stomach contents of live lake trout in 2008–2009 and live brown trout in 2009; after collection of stomach contents, the fish were released. Stomach contents were not collected from live brown trout in 2008. Complete stomachs were removed from all brown trout and lake trout that perished in the gill nets during 2008–2010. Contents were preserved in 95% ethanol or frozen and were later counted and identified; invertebrates were identified to order and fish were identified to species when possible. To aid in fish species identification, reference skeletons of potential prey were used for comparison. Subsamples of the most common invertebrates found in predator stomachs were measured to the nearest 0.1 mm TL with digital calipers. When possible, ingested fish were measured to the nearest millimeter TL.

Data analysis.—Catch per unit effort (CPUE; fish$\cdot$m^{-2} $\cdot$h^{-1}) for roundtail chub, brown trout, and lake trout was summed across the six gill-net mesh sizes for each week of sampling to include all sizes of fish. Mean values of CPUE were then calculated for each year, lake, habitat, and sampling period. Data were natural log transformed and analyzed by using the general linear model function in JMP version 8 (SAS Institute, Inc.) to test the effects of habitat, sampling period, and their interaction on the CPUE of each species. Tukey's honestly significant difference (HSD) tests were used to determine statistical differences among the habitats. Year was included as a random effect in all habitat use models, and the α was set at 0.05.

To determine at what TL brown trout and lake trout became piscivorous, binary logistic regression in JMP version 8 was used to estimate the probability that fish occurred in the diets of brown trout or lake trout given predator TL. Stomachs that contained fish were assigned a value of 1, while stomachs that contained other prey but no fish were assigned a value of 0. Fish with empty stomachs were excluded from this analysis. Percent occurrence of a given prey type in the diet was calculated as the number of predators (brown trout or lake trout) that consumed at least one item of that prey type divided by the total number of fish with prey in their stomachs. Percent occurrence data were used to inform the analysis of wet weight proportions. Any prey that occurred in at least 10% of predator stomachs was included in the analysis of wet weight proportions.

For brown trout and lake trout, mean wet weight proportions of common prey types were calculated by averaging the proportion of each prey type from individual fish stomachs. Fish with empty stomachs were excluded from this analysis. Wet weights of invertebrate prey were estimated by using the length–mass relationships reported by Benke et al. (1999; dry mass), Chipps and Bennett (2000; wet weight), and Sabo et al. (2002; dry mass). Dry mass estimates were multiplied by 4 to convert them to wet weights (Peters 1983). To estimate wet weights of prey fish, we used weight–length relationships that were developed based on (1) fish captured in Halfmoon and Little Halfmoon lakes during the present study and (2) Wyoming Game and Fish Department data. If the TL of an ingested prey fish could not be determined by direct measurement, its length was estimated from equations predicting mean prey length as a function of predator length (lake trout: Ruzycki et al. 2003; brown trout: Jensen et al. 2008). To determine dominance of any particular prey types in the diets, wet weight proportions of prey for brown trout and lake trout collected during the periods of thermal mixing and thermal stratification were analyzed by one-way analysis of variance and multiple comparison tests (Tukey's HSD test). In addition, wet weight proportions of fish prey were compared between brown trout and lake trout to determine whether there were statistical differences in fish consumption.

RESULTS

Thermal Profiles

Halfmoon and Little Halfmoon lakes were thermally stratified by early July; sharp thermocline development was observed in Halfmoon Lake, and relatively weak thermocline development was observed in Little Halfmoon Lake (Figure 2). Overall, Little Halfmoon Lake was warmer than Halfmoon Lake. For example, peak water temperature at 15 m (i.e., the bottom) in Little Halfmoon Lake was 13.9°C, whereas in Halfmoon Lake water temperature at 15 m never exceeded 6.5°C.

Habitat Models

The relative abundance (CPUE) of roundtail chub was greater in Little Halfmoon Lake (0.60 fish$\cdot$m^{-2} $\cdot$h^{-1}) than in Halfmoon Lake (0.27 fish$\cdot$m^{-2} $\cdot$h^{-1}). However, in both lakes, most of the roundtail chub were captured in littoral habitats (Figure 3). Roundtail chub occurred in all habitats within Little Halfmoon Lake but were absent from the deep benthic habitat in Halfmoon Lake. Brown trout relative abundance was similar in both lakes and both sampling periods, and CPUE values did not exceed 0.5 fish$\cdot$m^{-2} $\cdot$h^{-1}. Brown trout occurred in all habitats of Little Halfmoon Lake but were not captured in the deep benthic, deep pelagic, or surface pelagic habitat of Halfmoon Lake. The greatest relative abundance of lake trout was observed in Halfmoon Lake, particularly in the middepth benthic and deep benthic habitats. In all habitats, lake trout CPUE trended higher in the thermal mixing period than in the thermal stratification period, but this difference was not significant for the deep benthic habitat. During the period of thermal mixing, average lake trout CPUE was about six times higher in Halfmoon Lake (0.93 fish$\cdot$m^{-2} $\cdot$h^{-1}) than in Little Halfmoon Lake (0.15 fish$\cdot$m^{-2} $\cdot$h^{-1}). During the period of thermal stratification, average lake trout CPUE was 5.3 times

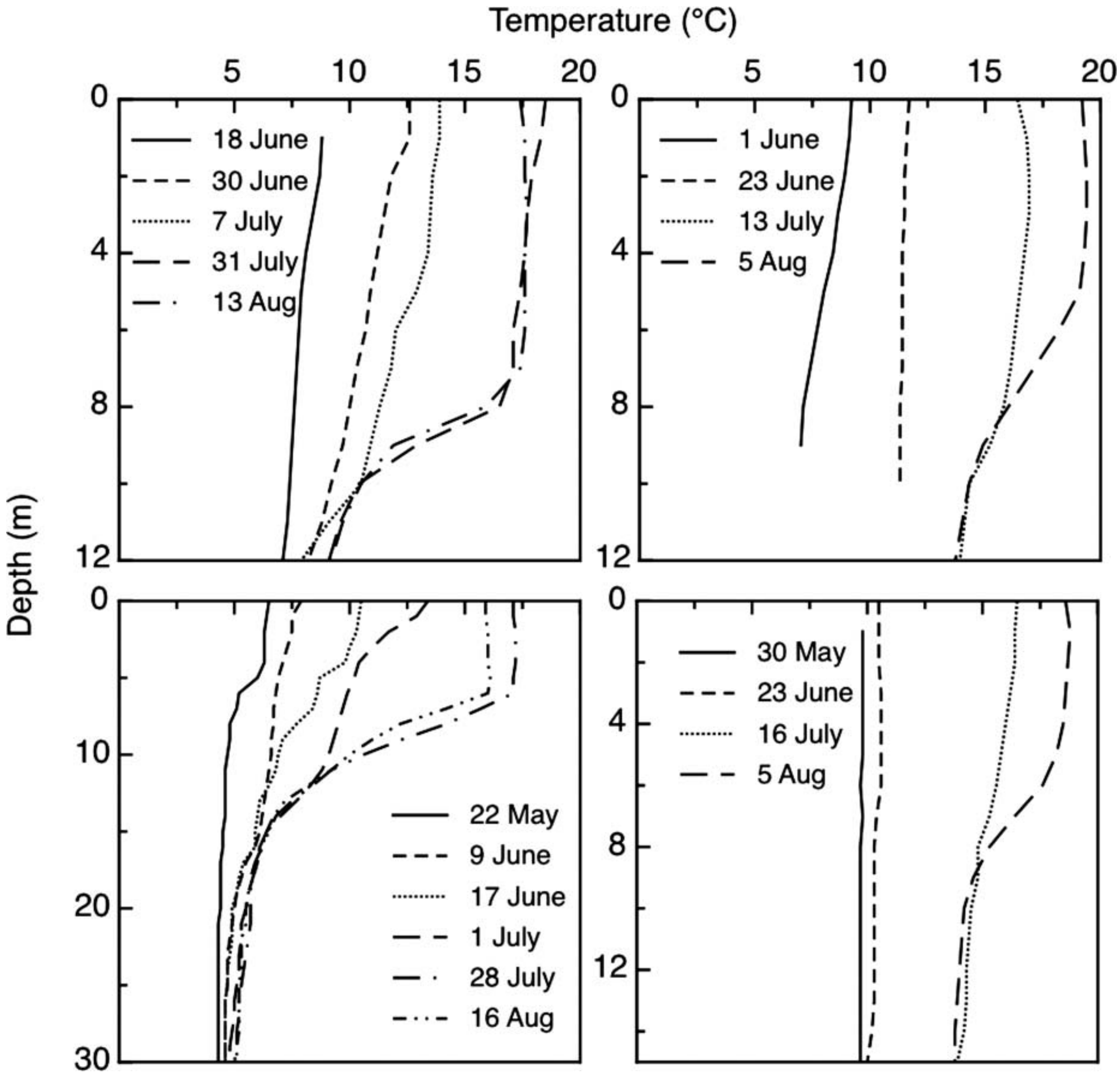

FIGURE 2. Thermal profiles of Halfmoon Lake (left panels) and Little Halfmoon Lake (right panels), Wyoming, in 2008 (upper panels) and 2009 (lower panels). Dates of each thermal profile are shown in the corresponding panel.

higher in Halfmoon Lake (0.32 fish·m^{-2} ·h^{-1}) than in Little Halfmoon Lake (0.06 fish·m^{-2} ·h^{-1}).

Models that examined the effects of sampling period, habitat, and the sampling period × habitat interaction revealed that habitat was the only significant factor related to roundtail chub CPUE and brown trout CPUE in both lakes and to lake trout CPUE in Little Halfmoon Lake (Table 3). All three factors were significantly related to the CPUE for lake trout in Halfmoon Lake, suggesting that lake trout habitat use changed with sampling period.

Tukey's HSD tests comparing CPUE for each habitat type revealed that roundtail chub used littoral habitats more heavily than benthic or pelagic habitats (Figure 3). This was clearly evident in Little Halfmoon Lake, where roundtail chub CPUEs in littoral habitat were significantly greater than those in the other habitats we sampled. In Halfmoon Lake, roundtail chub habitat showed a more graded pattern: CPUE was highest in the littoral sites with cover, intermediate in littoral sites with no cover, and lowest in middepth to deep benthic sites and in surface pelagic sites.

Brown trout in both Halfmoon and Little Halfmoon lakes were concentrated in the littoral and middepth benthic sites, and CPUE did not differ significantly among these habitat types based on Tukey's HSD test (Figure 3). Brown trout were notably absent from the deep benthic, deep pelagic, and surface pelagic habitats.

Two patterns were evident in CPUE data for lake trout in Halfmoon Lake. First, catch rates in all habitat types declined

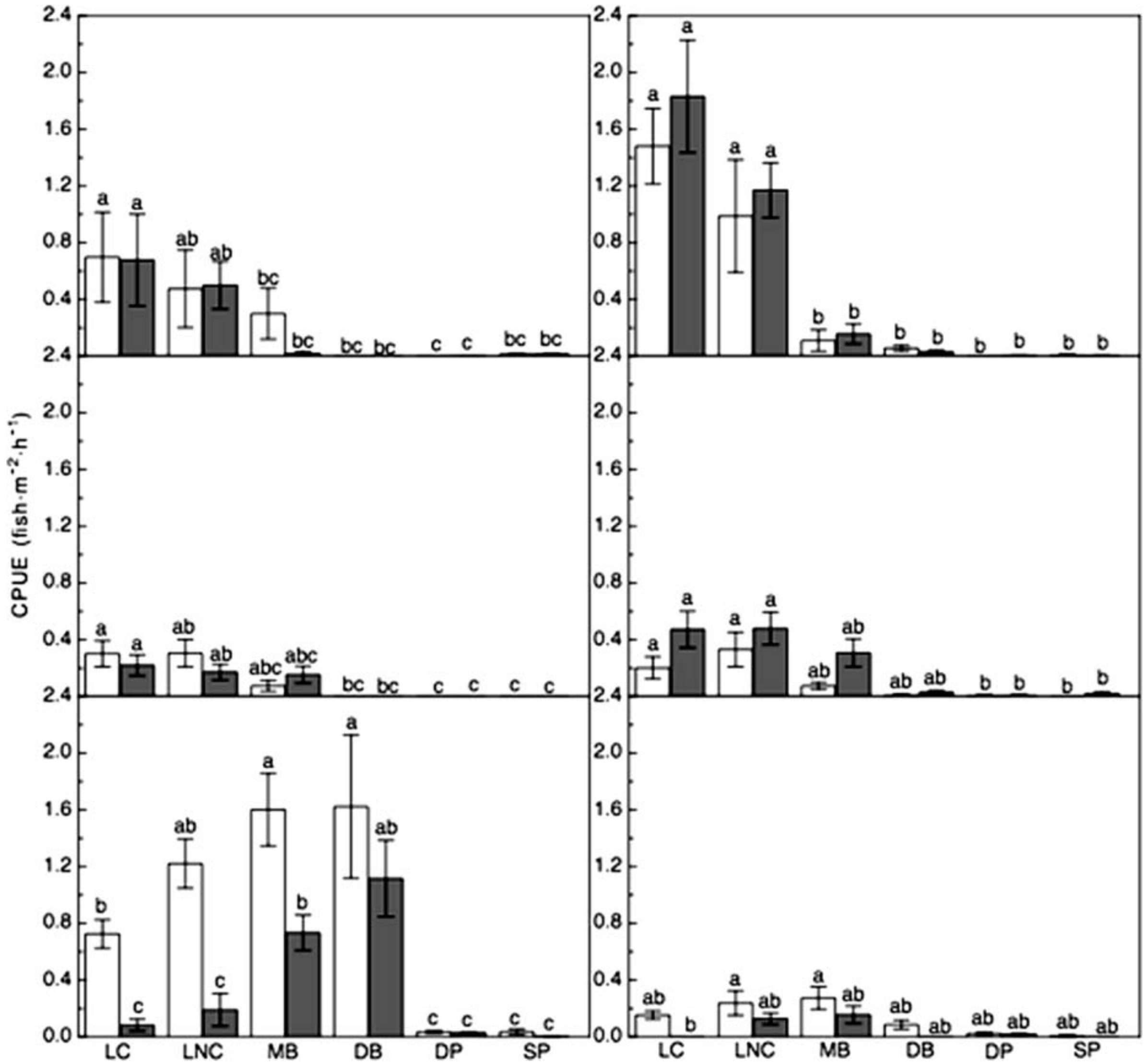

FIGURE 3. Mean ($\pm$ SE) catch per unit effort (CPUE) for roundtail chub (upper panels), brown trout (middle panels), and lake trout (lower panels) in Halfmoon Lake (left panels) and Little Halfmoon Lake (right panels) during the periods of thermal mixing (open bars) and thermal stratification (shaded bars). Habitat types are shown on the *x*-axis (LC = littoral with cover; LNC = littoral with no cover; MB = middepth benthic; DB = deep benthic; DP = deep pelagic; SP = surface pelagic). Within a given panel, bars with the same lowercase letter are not significantly different (Tukey's honestly significant difference test: $P > 0.05$).

after thermal stratification (Figure 3). Lake trout probably retreated to water depths greater than 30 m after stratification and therefore were residing outside of our sampling area. Second, there was a significant sampling period $\times$ habitat type interaction effect on lake trout CPUE. Prior to lake stratification, CPUE was relatively high in the littoral habitats and in some cases was not statistically different from CPUE in the middepth benthic or deep benthic habitat (Figure 3). After thermal stratification, CPUEs in the littoral habitats declined and were significantly lower than CPUEs in the middepth benthic and deep benthic habitats. In Little Halfmoon Lake, the low lake trout CPUE across all habitats and sampling periods made it difficult to detect seasonal shifts in habitat use, although there was a trend for catch rates to decline after the lake became stratified (Figure 3).

Stomach Content Analysis

Empty stomachs occurred in 13% of the brown trout sampled from Halfmoon Lake and 10% of the brown trout sampled from Little Halfmoon Lake. Among lake trout, 10% of those sampled from Halfmoon Lake and 4.5% of those sampled from Little Halfmoon Lake had empty stomachs. Brown trout and lake trout with prey in their stomachs were found to have consumed 17 prey types, including terrestrial and aquatic invertebrates and fishes. Only five prey types occurred in 10% or more of the stomachs sampled: Diptera (true flies), Ephemeroptera

TABLE 3. Results of general linear models relating the catch per unit effort for roundtail chub (RTC), brown trout (BNT), and lake trout (LAT) in Halfmoon (HM) and Little Halfmoon (LHM) lakes to the sampling period (P; i.e., thermal mixing or stratification), habitat type (H; listed in Table 2), and the P × H interaction (asterisks indicate significance).

Lake	Species	R^2	Factor	P-value
HM	RTC	0.40	P	0.860
			H	<0.001*
			P × H	0.9156
	BNT	0.57	P	0.362
			H	<0.001*
			P × H	0.319
	LAT	0.89	P	<0.001*
			H	<0.001*
			P × H	<0.001*
LHM	RTC	0.78	P	0.702
			H	<0.001*
			P × H	0.9958
	BNT	0.48	P	0.356
			H	0.001*
			P × H	0.902
	LAT	0.50	P	0.068
			H	<0.001*
			P × H	0.764

(mayflies) and Trichoptera (caddisflies), fish, opossum shrimp *Mysis* spp., and terrestrial insects.

Binary logistic regression was used to determine the TLs at which brown trout and lake trout became piscivorous and the extent to which they were piscivorous. There was no significant effect of lake on the probability of piscivory for either species, so data from both lakes were combined for analysis. Brown trout piscivory did not increase with increasing TL (chi-square = 1.40, $P = 0.24$), and the proportion of fish consumed remained fairly consistent across all length categories (Figure 4). However, probability of piscivory by lake trout increased significantly with TL (chi-square = 47.15, $P < 0.01$). At smaller TLs, brown trout were more piscivorous than lake trout, but among brown trout and lake trout that were larger than 500 mm TL the proportions of fish consumed were similar.

One-way analysis of variance of prey wet weight proportions revealed no difference among the prey types consumed by brown trout during the thermal mixing period in Halfmoon Lake ($r^2 = 0.07$, $P = 0.47$) or Little Halfmoon Lake ($r^2 = 0.17$, $P = 0.11$). For the thermal stratification period, analyses indicated that the wet weight proportion of fish prey was significantly higher than those of all other prey types consumed by brown trout in Halfmoon Lake ($r^2 = 0.25$, $P < 0.01$) and Little Halfmoon Lake ($r^2 = 0.21$, $P < 0.01$). In Halfmoon Lake during both sampling periods, wet weight proportions of *Mysis* in lake trout stomachs were significantly higher than proportions of other prey types (thermal mixing: $r^2 = 0.27$, $P < 0.01$; thermal stratification: $r^2 = 0.42$, $P < 0.01$); in Little Halfmoon Lake, wet weight proportions of Diptera in lake trout stomachs were significantly higher than those of other prey types (thermal mixing: $r^2 = 0.23$, $P < 0.01$; thermal stratification: $r^2 = 0.38$, $P < 0.01$). Fish were never the dominant prey type for lake trout.

Based on percent occurrence, fish prey were more common in brown trout stomachs than in lake trout stomachs sampled from Halfmoon Lake (Figure 5) and Little Halfmoon Lake (Figure 6) during both periods. Based on wet weight, the proportion of fish in the stomachs of brown trout and lake trout did not differ significantly in Halfmoon Lake (two-tailed t-test test: $P = 0.80$) or in Little Halfmoon Lake (two-tailed t-test test: $P = 0.79$) during the period of thermal mixing. However, wet weight consumption of fish was significantly greater for brown trout than for lake trout during the thermal stratification period in both lakes (one-tailed t-test, Halfmoon Lake: $P <$ 0.01; Little Halfmoon Lake: $P = 0.03$).

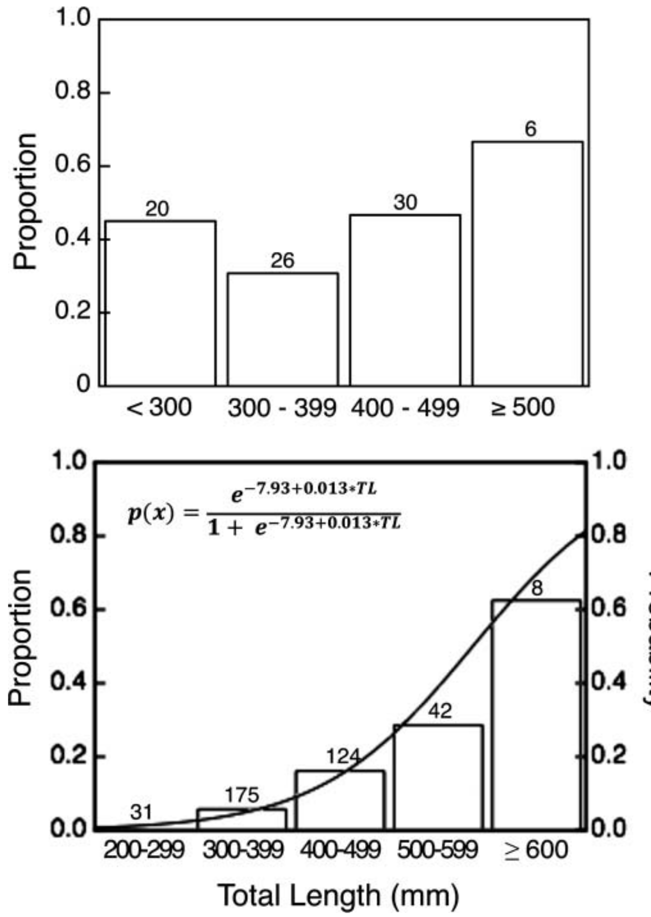

FIGURE 4. Proportions (bars) of brown trout (upper panel) and lake trout (lower panel), by length category, with fish prey in their stomachs (one brown trout in the <300-mm category was less than 200 mm total length [TL]; two brown trout in the ≥500-mm category exceeded 600 mm TL; two lake trout in the ≥600-mm category exceeded 700 mm TL). Sample sizes are shown above the bars. The logistic function relating probability of fish being present in the stomach to lake trout TL is shown by the solid line.

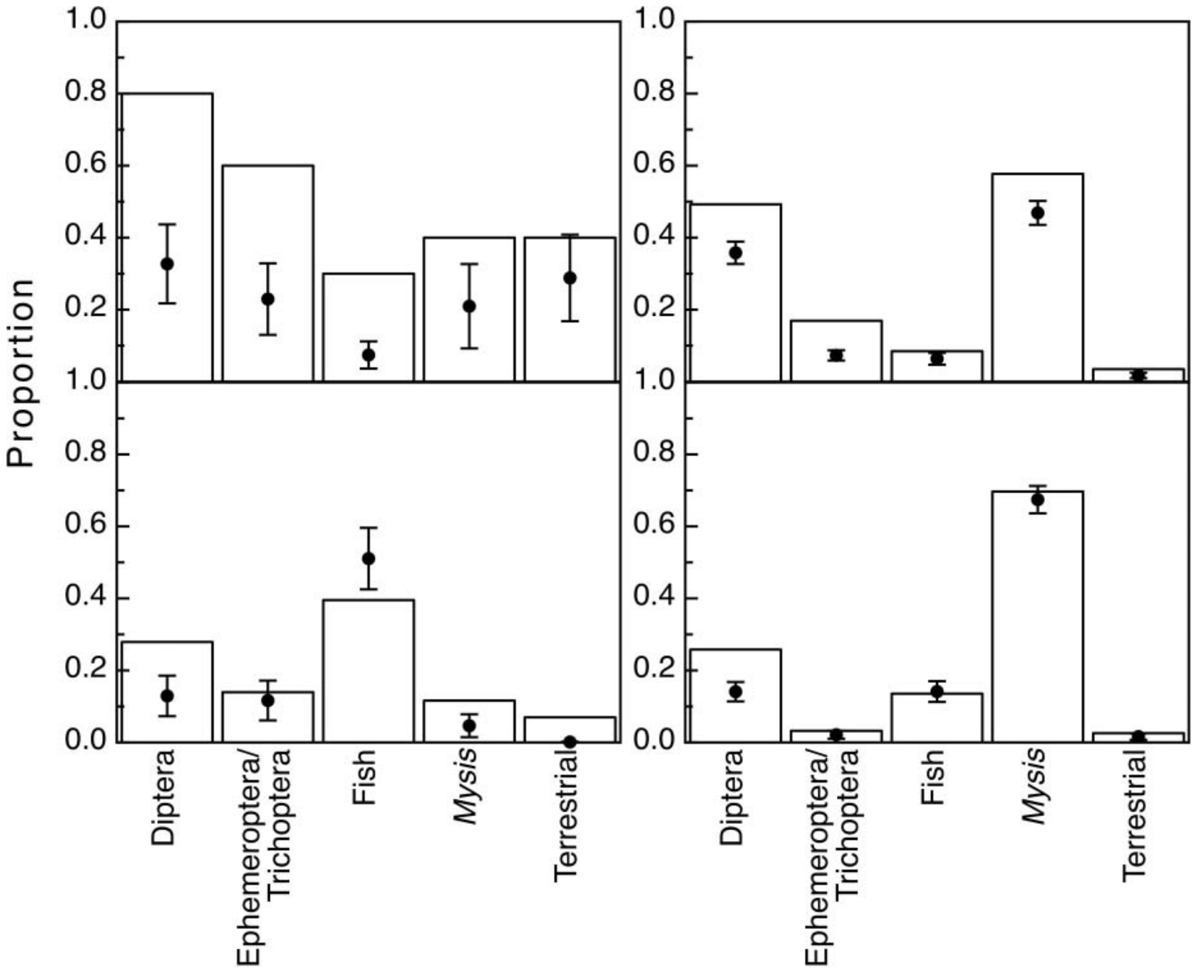

FIGURE 5. Frequency of occurrence (proportion; bars) and mean (± SE) wet weight proportion (circles) of prey items in the stomachs of brown trout (left panels) and lake trout (right panels) during the periods of thermal mixing (upper panels) and thermal stratification (lower panels) in Halfmoon Lake (terrestrial = terrestrial insects). For frequency of occurrence, sample size (n) was 10 brown trout and 201 lake trout during the period of mixing and 43 brown trout and 155 lake trout during stratification. For wet weight proportions, n was 10 brown trout and 169 lake trout during the period of mixing and 34 brown trout and 130 lake trout during stratification.

We examined 422 lake trout and 93 brown trout stomachs; only 3 of the 117 fish remains in the stomachs were positively identified as roundtail chub. Two of the consumed roundtail chub were identified by the presence of a Floy tag found in the stomach of the predator (lake trout in both cases). Prey size at the time of consumption was unknown, but the TL at tagging (summer 2007) was 137 and 178 mm for these two roundtail chub. The third roundtail chub was consumed by a brown trout. Across both lakes, 53% of the identified fish ($n = 43$) consumed by brown trout and 10% of the identified fish ($n = 49$) consumed by lake trout were littoral cyprinids (Figure 7). The probability of consuming a cyprinid was significantly greater for brown trout than for lake trout (Fisher's exact test: $P < 0.01$).

DISCUSSION

The study lakes provided an opportunity to study the overlap of two nonnative salmonid species with an endemic species that is typically thought to live in warm rivers rather than cold lakes. Not only are roundtail chub living in what is considered atypical habitat, but they are also encountering multiple nonnative piscivore species. An individual predator's effects on a prey species may vary with predator morphology, foraging behavior, and habitat use (Schmitz 2007). Shared habitat use among multiple predator species with different morphologies or foraging strategies may result in similar diet compositions and mutual reliance on a principal prey species (Amundsen et al. 2003). However, predator species that occupy different niches have reduced resource overlap and are likely to have varied diets in systems where multiple prey species are available for consumption (Nyström et al. 2001; Kahilainen and Lehtonen 2003; Olden et al. 2006). The latter situation is the case in the study lakes, and our results suggest that the likelihood of predation on roundtail chub is greater for brown trout than for lake trout. Brown trout overlapped with roundtail chub in littoral habitats during

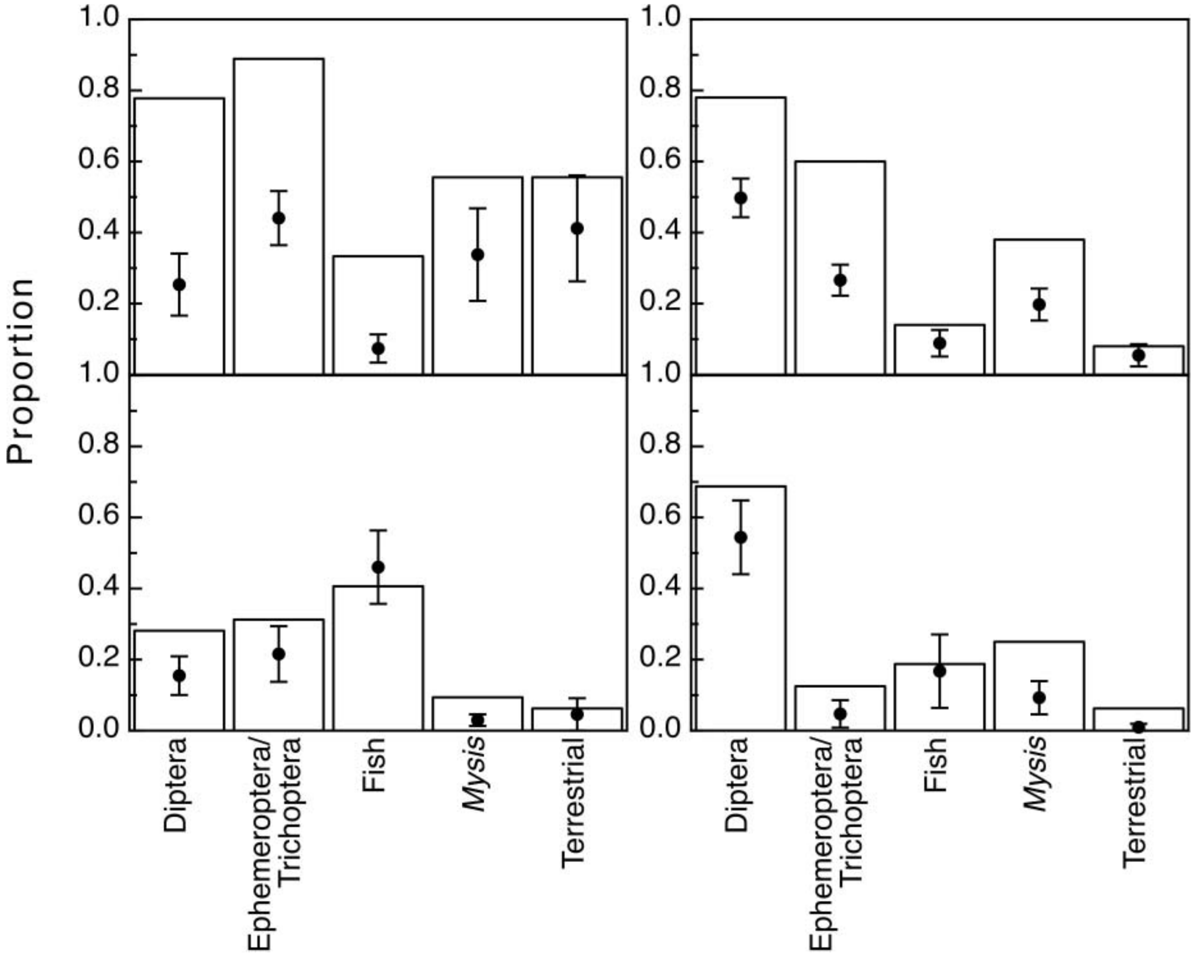

FIGURE 6. Frequency of occurrence (proportion; bars) and mean (± SE) wet weight proportion (circles) of prey items in the stomachs of brown trout (left panels) and lake trout (right panels) during the periods of thermal mixing (upper panels) and thermal stratification (lower panels) in Little Halfmoon Lake (terrestrial = terrestrial insects). For frequency of occurrence, sample size (n) was 9 brown trout and 50 lake trout during the period of mixing and 32 brown trout and 16 lake trout during stratification. For wet weight proportions, n was 9 brown trout and 47 lake trout during the period of mixing and 22 brown trout and 13 lake trout during stratification.

periods of thermal mixing and stratification, whereas lake trout overlap with roundtail chub occurred only during the period of thermal mixing. In addition, stomach content analyses showed that brown trout consumed a greater proportion of littoral fish than did lake trout. Brown trout were also more likely than lake trout to be piscivorous at smaller TLs.

Shared habitat use by native and nonnative fish species can have negative consequences for the native species (McHugh and Budy 2006). In our study lakes, brown trout and roundtail chub overlapped spatially and temporally. By contrast, overlap between lake trout and roundtail chub was limited during the time period we sampled; however, overlap may be higher during autumn through spring. Because brown trout tolerated warmer water temperatures and fed in the littoral zone (Klemetsen et al. 2003; Saksgård and Hesthagen 2004), the probability of encountering and consuming cyprinids (and possibly roundtail chub) during the thermal stratification period was greater for brown trout than for lake trout. This was surprising given that lake trout in other coldwater lakes have been observed to make forays into littoral areas with temperatures as high as 21°C (Sellers et al. 1998), especially if the pelagic prey base is lacking (Vander Zanden and Rasmussen 1996; Morbey et al. 2006). We found no evidence of such forays in our study lakes. After lake stratification, lake trout abundance was reduced in the littoral habitats used by roundtail chub, and lake trout were consuming primarily *Mysis* and dipterans rather than fish.

Compared with brown trout in other systems, the brown trout in Halfmoon and Little Halfmoon lakes appeared to consume larger proportions of fish during summer months. Fish prey occurred in 30% or more of brown trout stomachs, which is greater than the percent occurrence of fish prey (<15%) reported for littoral-feeding brown trout in other lentic systems during summer months (McCarter 1986; Saksgård and Hesthagen 2004). Late-summer diets consumed by brown

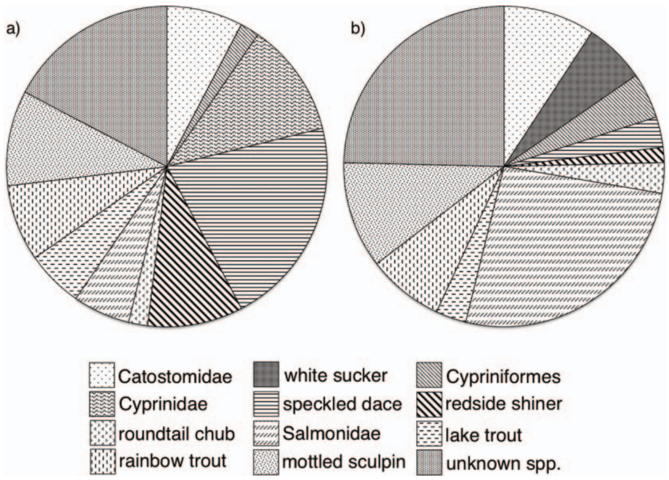

FIGURE 7. Composition of fish prey found in the stomachs of **(a)** brown trout ($n = 52$ fish prey) and **(b)** lake trout ($n = 65$ fish prey) in Halfmoon and Little Halfmoon lakes. Prey were identified to the lowest possible taxonomic group (prey taxa include rainbow trout *Oncorhynchus mykiss*, white sucker *Catostomus commersonii*, speckled dace *Rhinichthys osculus*, mottled sculpin *Cottus bairdii*, and redside shiner *Richardsonius balteatus*).

trout in two Norwegian lakes did not exceed 25% fish prey in terms of wet weight (Gregersen et al. 2006), whereas fish contributed nearly 50% of the prey wet weight in stomach contents of brown trout from Halfmoon and Little Halfmoon lakes. This difference in results may be attributable to shared habitat use by brown trout and prey fishes in the littoral zones of our study lakes (Saksgård and Hesthagen 2004; Olden et al. 2006) and to the increased activity of brown trout in warmer water temperatures (Klemetsen et al. 2003).

Unlike brown trout, which generally preyed upon littoral fish species (Saksgård and Hesthagen 2004), the few fish consumed by lake trout in our study were mainly pelagic and benthic fishes (i.e., salmonids and cottids). Contrary to expectations that lake trout would consume more fish prey during cooler periods of thermal mixing (Yule and Luecke 1993), when habitat overlap among all prey fishes is greatest, the highest proportion of fish consumed by lake trout was observed during the thermal stratification period; even then, the extent of piscivory was low compared with that seen in other systems where lake trout consume pelagic fish. In lakes with a large pelagic fish prey base, lake trout exceeding 400 mm TL have a diet consisting almost entirely of fish (Madenjian et al. 1998; Ruzycki et al. 2001). Halfmoon and Little Halfmoon lakes contain few pelagic prey fishes, and this may explain why lake trout consumed *Mysis* or dipterans along with salmonids, as can occur when *Mysis* are abundant and pelagic prey fishes are not (Stafford et al. 2002).

There is evidence that nonnative predators negatively affect roundtail chub in streams of the Colorado River basin (Bestgen and Propst 1989; Barrett and Maughan 1995; Brouder et al. 2000). The majority of these predators are warmwater fishes (e.g., smallmouth bass *Micropterus dolomieu* and channel catfish *Ictalurus punctatus*) that are found particularly in reservoirs (Bestgen and Propst 1989; Martinez et al. 1994). Roundtail chub declines are commonly observed after reservoir construction (Martinez et al. 1994), but since roundtail chub can live in lentic systems (Laske et al. 2011) their declines in reservoirs may be due in part to the introduction of nonnative piscivorous fishes (Olden and Poff 2005). Smallmouth bass, largemouth bass *Micropterus salmoides*, green sunfish *Lepomis cyanellus*, and channel catfish have all been identified as harmful predators of native fishes, including the roundtail chub (Bestgen and Propst 1989; Marsh and Douglas 1997; Olden and Poff 2005).

Because diet analysis was only conducted during summer months and without population estimates or results of bioenergetics modeling, the full impact of either nonnative predator species on roundtail chub remains unknown. Brown trout may consume fish during winter if prey fish are readily available (McCarter 1986), but brown trout are more active at temperatures above 8°C and consume more prey during warmer months (Klemetsen et al. 2003), so predation on fish would be highest during summer. Lake trout in Flaming Gorge Reservoir consume larger proportions of prey fish during the fall and winter than during the remainder of the year (Yule and Luecke 1993); however, pelagic fishes dominate winter diets, so it is probable that littoral species would escape predation by lake trout. The pelagic fish prey base in Halfmoon and Little Halfmoon lakes consists of rainbow trout and small lake trout; therefore, piscivorous lake trout would consume those species. Lake trout would also continue to consume *Mysis* throughout the fall, winter, and spring because of the availability of this prey type in both benthic and pelagic habitats.

This study has helped to clarify the relationships among two introduced piscivorous salmonids and roundtail chub in natural lakes. Only recently has the ecology of roundtail chub in natural lakes been described (Laske et al. 2011), and knowledge about interactions between the roundtail chub and potential predators will better guide management and conservation of this species.

Roundtail chub have persisted in the presence of nonnative brown trout and lake trout in Halfmoon and Little Halfmoon lakes. The likely explanation for this coexistence has two components: (1) the low spatial overlap between roundtail chub and lake trout because of their different thermal requirements; and (2) the relatively low abundance of brown trout in these lakes as indicated by CPUE data. However, because roundtail chub use littoral habitats, introductions of additional littoral predators or an increase in brown trout numbers could be highly detrimental. Numerous reservoirs in the Colorado River basin have resident populations of nonnative littoral piscivores (e.g., smallmouth bass); although direct consumption by littoral predators has not been quantified, there is clear evidence of declines of native fishes in systems where nonnative littoral predators are present (Martinez et al. 1994; Townsend 1996; MacRae and Jackson 2001). Therefore, an important management consideration for conservation of the roundtail chub and other native cyprinids is the prevention of future introductions of littoral predators.

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