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Exploring Crowded Trophic Niche Space in a Novel Reservoir Fish Assemblage: How Many is Too Many?

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Abstract
In highly managed reservoir systems, species interactions within novel fish assemblages can be difficult to predict. In high-elevation Scofield Reservoir in Utah the unintentional introduction of Utah Chub Gila atraria and subsequent population expansion prompted a shift from stocking exclusively Rainbow Trout Oncorhynchus mykiss to include tiger trout (female Brown Trout Salmo trutta × male Brook Trout Salvelinus fontinalis) and Bonneville Cutthroat Trout O. clarkii utah, which composed a novel suite of top predators and potential competitors. We examined the interspecific interactions among Scofield Reservoir piscivores using a multifaceted approach including gut analyses, stable isotopes, and gape limitation. Large Cutthroat Trout consumed 50–100% Utah Chub and tiger trout consumed 45–80%. In contrast, small and large Rainbow Trout consumed primarily invertebrate prey and exhibited significant overlap with small tiger trout, Cutthroat Trout, and Utah Chub. Large Cutthroat Trout and tiger trout occupy a top piscivore trophic niche and are more littoral, while Rainbow Trout occupy an omnivore niche space and are more pelagic. Both Cutthroat and tiger trout varied in niche space with respect to size-class, demonstrating an ontogenetic shift to piscivory at approximately 350 mm TL. Cutthroat Trout and tiger trout are capable of consuming prey up to 50% of their own size, which is larger than predicted based on their theoretical gape limit. Because it appears food resources (Utah Chub) are not limited, and performance metrics are high, competition is unlikely between Cutthroat Trout and tiger trout. In contrast, apparent survival of Rainbow Trout has recently declined significantly, potentially due to shared food resources with Utah Chub or negative behavioral interactions with other members of the community. Collectively, this research aids in understanding biotic interactions within a top-heavy and novel fish community and assists towards developing and implementing suitable management strategies to control nuisance species.

In an era when many aquatic systems and fisheries are man-made, artificial, and highly manipulated, we are continually challenged with understanding the interactions that define food webs and community structure of aquatic systems (Polis and Strong 1996; Terra and Araujo 2011). Fish communities and food web interactions in impounded riverine systems probably differ from those in natural lakes because these communities often include both native stream species that persist in the reservoir and nonnative species intentionally or accidentally introduced (Miranda and DeVries 1996; Matthews et al.)

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Sequential predation is a management tool to control undesired species (Kohler and Courtenay 1986). Using Scofield Reservoir as a model system, our overall goal was to better understand how multiple top predators in a novel food web interact in reservoir systems. Specifically, our study objectives were to (1) explore the food habits, diet overlap, and trophic niche space among the three potential top predators, (2) identify potential for competition, and (3) characterize potential predation and competition linkages. To do this, we used a multifaceted approach including diet analyses, stable isotope analysis, and a gape limitation study including predator morphology and prey body size.

**METHODS**

**Study site.**—Scofield Reservoir is a high elevation (2,322 m) impoundment on the Price River in southeast Utah. The reservoir was created by Scofield Dam in 1926 and is predominantly used for irrigation water storage; recreation and flood control provide additional benefits (U.S. Bureau of Reclamation 2011). The current reservoir has a capacity of 73,600 acre-feet at full pool, mean surface area of 1,139 ha, and a mean depth of 8 m (U.S. Bureau of Reclamation 2009). Scofield Reservoir is classified as eutrophic, with “excessive” total phosphorous enrichment (Utah DEQ 2010), typical of reservoirs, as high loads of organic materials and nutrients correspond to a proportionally large watershed area relative to volume (Wetzel 1990). Blue-green algae predominate the phytoplankton community, indicative of poor water quality. Blooms typically occur in summer, along with thermal stratification, creating hypolimnetic oxygen deficits that historically have led to partial fish kills in some years (Hart and Birdsey 2008).
Scofield Reservoir is managed as a put-grow-and-take sport fishery, and historically, around 600,000 Rainbow Trout (150–250 mm TL) were stocked every year. However, in 2005, in response to the appearance of Utah Chub and fear of a population expansion, the fish stocking program has been adjusted nearly every year since (Hart and Birdsey 2008). Sterile tiger trout and Bonneville Cutthroat Trout have been stocked in the fishery as a potential biological control for the Utah Chub, as well as alternative sport fishes. Utah Division of Wildlife Resources began stocking tiger trout in 2005 and continued to stock an average of 110,000 (about 150 mm TL) each fall since. Additionally, 85,000 Cutthroat Trout were stocked each year beginning in spring of 2007 (200 mm TL). Rainbow Trout were stocked at high numbers in the spring (400,000 fish at 80 mm) and fall (120,000 at 175 mm) from 2005 to 2009, but that effort was later reduced (80,000 at 180 mm TL once yearly). Non-game, native species also present include the Redside Shiner Richardsonius balteatus and Mountain Sucker Catostomus platyrhynchos; however, Utah Chub are by far the predominant nongame fish present in number and biomass (Winters 2014).

Field sampling.—We sampled fishes in spring (April–May), summer (July–August), and autumn (October) of 2012 in Scofield Reservoir. In this type of fixed-station sampling, index sites were selected to be representative of the reservoirs’ longitudinal axis, i.e., from the upper riverine zone to the lower lacustrine zone (McMahon et al. 1996), and maintained consistency with long-term Utah Division of Wildlife Resources annual monitoring (Figure 1). We set horizontal sinking gill nets (24 × 1.8 m with eight monofilament mesh-size panels of 38, 57, 25, 44, 19, 64, 32, and 51 mm) according to standard gill-net methods to capture a representative size distribution of all fish in the reservoir (Beauchamp et al. 2009). We placed two nets at each of eight sample sites in littoral areas perpendicular to shore. Most nets were set approximately 5 m from shore at 3 m deep and ending at 10 m deep; shorelines had consistently steep bathymetry. We set nets before dusk and pulled them at dawn to span two crepuscular periods.

Diet analysis.—We collected Cutthroat Trout, Rainbow Trout, tiger trout, and Utah Chub diets from each gill-net survey. We immediately preserved trout and chub stomachs in 95% ethanol for later analysis. We identified all organisms from stomach contents to the lowest taxonomic level possible (Brooks 1957; Edmonson 1959; Merritt and Cummins 1996) to determine abundance of species and composition. We grouped stomach contents by prey fish (identified to species), zooplankton, organic matter, crayfish, aquatic invertebrates by taxa (Amphipoda, Chironomidae, Coleoptera, Diptera, Ephemeroptera, Hemiptera, Isopoda, Mollusca, and Trichoptera), and terrestrial invertebrates (classified to order). We counted and weighed (blot-dry wet weight to nearest 0.001 g) individual prey fish, and weighed invertebrate prey collectively by taxonomic group. We measured intact prey fish to the nearest millimeter by backbone and standard lengths. We then calculated the contribution of each prey category to the diet of each predator species as the mean proportion by weight (g) for each stomach individually and then averaged across all nonempty stomachs (Chippas and Garvey 2007):

$$MW_i = \frac{1}{N} \sum_{j=1}^{N} \left( \frac{W_{ij}}{Q} \sum_{i=1}^{Q} W_{ij} \right),$$

where $N$ is the total number of fish with nonempty stomachs, $W_{ij}$ is the weight of prey $i$ in the stomach of predator $j$, $Q$ is the total number of prey categories, and $MW_i$ is the mean proportion by weight.

We used Schoener’s index of diet overlap to calculate the percent diet overlap between species:

$$\alpha = 1 - 0.5 \left( \sum_{i=1}^{n} \left| p_{xi} - p_{yi} \right| \right),$$

where $\alpha$ is the degree of overlap, $n$ is the number of food categories, $p_{xi}$ is the proportion of food category $i$ in the diet of species $x$, and $p_{yi}$ is the proportion of food category $i$ in the diet of species $y$ (Schoener 1970). Index values range from 0 to 1, where a value approaching 0 means the species share no prey resources and a value closer to 1 means the species have identical prey utilizations. Values exceeding 0.6 are considered “biologically significant” in terms of overlap in resource use (Wallace 1981). All trout were pooled into small (<350 mm TL) and large (≥350 mm TL) size-classes for each species, and their diet overlap values were calculated for each season of the study period. Utah Chub were pooled into small (<250 mm TL) and large (≥250 mm TL) size-classes. We based size-classes on initial observations of diet differences, sample size limitations (we could not add additional size-classes), and most importantly on the approximate size at which Cutthroat and tiger trout demonstrated a switch to piscivory.

Trophic position analysis.—From all gill-netted trout and chub, we removed a small dorsal muscle tissue sample for isotopic diet analysis. We chose to utilize a representative group of all tissues from October 2011 for analysis, due to the costly nature of isotope preparation and analysis. Fall isotope tissues encompass both the summer and fall growing season, as tissue turnover rates allow for temporal integration of dietary information (Bearhop et al. 2002). We quantified longer-term dietary habits of a subset of Cutthroat Trout ($n = 22$), Rainbow Trout (13), tiger trout (10), and Utah Chub (10) using stable isotope analysis (Vinson and Budy 2011). Specifically, we assessed fish trophic position and dietary carbon source based on the respective $\delta^{13}$N and $\delta^{13}$C signatures of dorsal muscle tissue (e.g., Post 2002). Tissue samples were dried in an oven for 48 h at 70°C, ground to a powder, encapsulated in 8.5 mm
tin capsules, and analyzed at the Washington State University Stable Isotope Core for a mass spectrometry-based determination of isotopic signatures. Signatures are an expressed ratio \(^{15}\text{N} : ^{14}\text{N}\) and \(^{13}\text{C} : ^{12}\text{C}\), as per mille (‰) values relative to ratios of the standard atmospheric \(\text{N}_2\) and Pee Dee Belemnite, respectively.

We then plotted isotopic signature values as coordinates in niche space to determine both resource and habitat use of each species (Newsome et al. 2007). We used the program SIBER (Stable Isotope Bayesian Ellipses in R) to fit standard ellipses based on multivariate normal distributions and maximum likelihood estimators. We then calculated standard ellipse area

FIGURE 1. Map of Scofield Reservoir, Utah, showing the eight locations where fish were sampled in 2011 and 2012, denoted as black circles.
and overlap, corrected for small sample size (Jackson et al. 2011).

Gape limit.—To determine the gape size of predators, which indicates the size of fish prey consumable, we measured several morphometric features of each predator, including total length (mm), and using a digital caliper, measured length of the lower \( L_{LJ} \) and upper \( L_{UJ} \) jaw (0.1 mm). We then calculated gape size \( (G) \) assuming a maximum mouth opening of 60° during food uptake, as per Jensen et al. (2004):

\[
G_{\text{pred}} = [(L_{LJ} \sin 60°)^2 + (L_{UJ} - L_{LJ} \cos 60°)^2]^{0.5},
\]

where \( G_{\text{pred}} \) is the gape size of the predator, \( L_{LJ} \) is length of the lower jaw (mm), and \( L_{UJ} \) is the length of the upper jaw (mm).

Second, we also measured the stretched width (laterally left to right) of the predator’s mouth via a digital caliper (0.1 mm; Truemper and Lauer 2005).

To determine actual sizes of prey consumed by piscivores, we examined diet contents of predators. From fish prey found in diets, when possible, we obtained prey backbone lengths, standard lengths, and total length measurements. Backbone length was measured as the full vertebrae when the fish musculature was digested. To determine the size of prey vulnerable to predators based on their gape, we also measured body depth and total length of prey (i.e., Utah Chub) found in the reservoir, and created a relationship relating body depth to total length: \( BD = 0.27(TL) - 2.81 \), where \( BD \) is the body depth of Utah Chub and \( TL \) is the total length of Utah Chub \( (R^2 = 0.90, n = 40, P < 0.0001) \).

RESULTS

Diet Composition

Food habits varied substantially among trout species and Utah Chub in Scofield Reservoir. We found Utah Chub in the diets of large \((\geq 350 \text{ mm TL})\) Cutthroat Trout \((n = 69 \text{ total}; \text{23}\% \text{ empty})\) throughout every season in 2012 (Figure 2). In the spring, large Cutthroat Trout \((n = 28)\) stomachs contained fish \((56\%)\) and chironomids \((24\%)\). In summer \((n = 12)\), consumption of fish increased \((69\%)\), and by fall \((n = 13)\), 100\% of large Cutthroat Trout diets contained fish. All fish identified in stomach samples were Utah Chub. Small Cutthroat Trout \((n = 75 \text{ total}; \text{13}\% \text{ empty})\) relied more heavily on aquatic invertebrates. In the spring \((n = 22)\) small Cutthroat Trout consumed mostly chironomids \((39\%)\) but also Coleoptera, Diptera, Ephemeroptera, Isopoda, and Mollusca. In the summer \((n = 17)\), we found a variety of items in small Cutthroat Trout diets, including chironomids \((26\%)\), terrestrial invertebrates \((\text{mostly flying ants}; 20\%)\), and crayfish \((18\%)\). Small Cutthroat Trout in the fall \((n = 26)\) shifted to a diet predominated by zooplankton \((54\%)\).

Tiger trout displayed similar food habits to Cutthroat Trout; large tiger trout \((n = 89; \text{36}\% \text{ empty})\) were distinguished by their piscivorous diet, containing a high proportion of Utah Chub that varied by season (Figure 2). In the spring, large tiger trout \((n = 29)\) consumed fish \((46\%)\), crayfish \((22\%)\), and isopods \((10\%)\). In the summer, large tiger trout \((n = 14)\) diet was composed of only fish \((79\%)\) and crayfish \((21\%)\). In the fall \((n = 14)\), large tiger trout diets switched back to include fish \((55\%)\), crayfish \((10\%)\), and chironomids \((15\%)\). Small tiger trout \((n = 44; \text{11}\% \text{ empty})\) consumed large numbers of aquatic invertebrates, in addition to a substantial proportion of crayfish (probably virile crayfish \textit{Orconectes virilis}) throughout all seasons. Small tiger trout in the spring \((n = 5)\) consumed 80\% aquatic invertebrates (including molluscs and chironomids). In the summer, small tiger trout \((n = 16)\) consumed primarily crayfish \((42\%)\), isopods \((16\%)\), and terrestrial invertebrates \((13\%)\), and in the fall \((n = 18)\), their diet was predominantly composed of chironomids \((33\%)\), crayfish \((22\%)\), and zooplankton \((21\%)\).

FIGURE 2. Seasonal diet composition (proportion of diet by wet weight, g) of small (<350 mm TL) and large (≥350 mm TL) Cutthroat Trout, Rainbow Trout, and tiger trout captured in Scofield Reservoir. We did not catch any small tiger trout or large Rainbow Trout in autumn 2011, therefore these columns are blank. All prey in the “fish” category was identified as Utah Chub.
Rainbow Trout diets differed considerably from the trends described above. Diets of small \((n = 69; 3\% \text{ empty})\) and large Rainbow Trout \((n = 15; 13\% \text{ empty})\) were characterized by low proportions of prey fish (Figure 2). Small Rainbow Trout in the spring \((n = 28)\) consumed primarily dipterans \((28\%)\), terrestrial invertebrates, and organic matter. Large Rainbow Trout \((n = 3)\) included crayfish \((33\%)\) in their diet. Similarly, in the summer, small Rainbow Trout \((n = 35)\) continued to consume dipteran \((25\%)\) and organic matter \((22\%)\). Large Rainbow Trout \((n = 8)\) consumed a variety of items, including chironomids, crayfish, terrestrial invertebrates, and organic matter. Noting the relatively small sample size, small Rainbow Trout \((n = 4)\) had a broad diet of crayfish \((25\%)\), zooplankton \((25\%)\), fish \((25\%)\), and terrestrial invertebrates \((25\%)\). We found stomachs of large Rainbow Trout \((n = 2)\) at the same time to have chironomids \((31\%)\) and crayfish.

Utah Chub diets consisted primarily of aquatic invertebrates, organic matter, and zooplankton at both smaller \((n = 55; 45\% \text{ empty})\) and larger \((n = 33; 39\% \text{ empty})\) size-classes. In the spring small Utah Chub \((n = 16)\) diets contained primarily organic matter \((30\%)\), chironomids, and zooplankton. This trend was similar with small Utah Chub in the summer \((n = 10)\), when diets consisted of mostly of zooplankton \((40\%)\) and organic matter \((30\%)\). Large Utah Chub \((n = 13)\) diets in the spring were predominantly dipterans \((58\%)\), switching to a variety of crayfish \((31\%)\), organic matter \((30\%)\), and zooplankton \((20\%)\) in the summer \((n = 5)\). Both small \((n = 4)\) and large Utah Chub \((n = 2)\) relied heavily on zooplankton in the fall \((72-100\%)\).

**Diet Overlap**

Based on Schoener’s index, there was significant diet overlap between small Cutthroat Trout \((\alpha = 0.61)\) and small Rainbow Trout \((\alpha = 0.63)\) with large Utah Chub, probably due to large proportions of chironomids in both fishes diets. Similarly, during the summer season, there was significant diet overlap between small Cutthroat Trout with large Rainbow Trout \((\alpha = 0.68)\) and with small tiger trout \((\alpha = 0.61)\), highlighting a shared reliance on chironomids, isopods, and crayfish. Additionally, there was overlap between small and large Rainbow Trout \((\alpha = 0.62)\) and small and large Utah Chub \((\alpha = 0.70)\). In autumn, we observed significant diet overlap between small Cutthroat Trout and small Utah Chub \((\alpha = 0.68)\) due to a shared reliance on zooplankton, between small tiger trout and large Rainbow Trout \((\alpha = 0.65)\), probably because of similar chironomid and crayfish consumption, and between small and large Utah Chub \((\alpha = 0.72)\).

**Isotopic Signature**

Fish tissues collected for isotopic analyses displayed carbon and nitrogen signatures indicative of their habitat use and feeding position. Tiger trout \((n = 10)\) demonstrated the most enriched carbon isotopic signature, corresponding with their use of more littoral primary carbon sources. Utah Chub \((n = 10)\), however, demonstrated the most negative carbon isotopic signature, reflecting usage of pelagic habitat at all sizes. Utah Chub were significantly more depleted in carbon than tiger trout \((\text{ANOVA: } df = 50, P < 0.001)\), as well as Rainbow Trout \((\text{ANOVA: } df = 50, P = 0.049; n = 13)\). Tiger trout were significantly enriched in carbon compared with Cutthroat Trout \((\text{ANOVA: } df = 50, P = 0.005; n = 22)\). There were no statistical differences between carbon signatures among size-classes \((i.e., \text{ small versus large})\).

Based on \(\delta^{15}N\) results, large Cutthroat Trout hold a position at the top of the food web and higher than all small fish: Cutthroat Trout \((\text{ANOVA: } df = 50, P < 0.001)\), Rainbow Trout \((df = 50, P < 0.001)\), tiger trout \((df = 50, P < 0.001)\), and Utah Chub \((df = 50, P < 0.001)\). Large tiger trout share a similar trophic position to Cutthroat Trout as predators at the top of the food web, having significantly higher nitrogen signatures than small Rainbow Trout \((\text{ANOVA: } df = 50, P = 0.003)\), small tiger trout \((df = 50, P < 0.001)\), and small Utah Chub \((df = 50, P = 0.01)\). The nitrogen signature of large Rainbow Trout is somewhat intermediary, and only significantly higher than small Rainbow Trout \((df = 50, P < 0.001)\).

Based on isotopic signatures, small and large Utah Chub appeared to feed most pelagically. Small Cutthroat Trout fed at nearly the same position as both small and large Utah Chub, a mid-level trophic position. All three trout species varied in niche space with respect to size-class, demonstrating an ontogenetic shift around 350 mm TL, to higher trophic positions \((i.e., \text{ switch to piscivory})\). These results suggest small tiger trout and Rainbow Trout fed in littoral areas, whereas the diet of larger individuals appeared to originate in more pelagic areas. Cutthroat Trout sampled appeared to shift to feeding more in littoral areas as body size increased.

When the isotopic niche of these species is plotted in two-dimensional niche space, large tiger trout demonstrated a very broad niche \((\text{ellipse area [EA] } = 10.4; \text{ Figure 3})\). They consumed food across a wide range of trophic positions, and their isotopic niche space varied with respect to their basal resources. In contrast, large Cutthroat Trout \((\text{EA} = 2.2)\) and large Rainbow Trout \((\text{EA} = 2.7)\) both demonstrated relatively smaller, more focused isotopic niche areas, which overlapped substantially with the tiger trout niche \((78\% \text{ and } 64\%, \text{ respectively})\), and overlapped with each other \((31\% \text{ and } 26\%, \text{ respectively})\). The isotopic niche space of tiger trout only overlapped 17% with both Cutthroat Trout and Rainbow Trout.

Small Rainbow Trout \((\text{EA} = 3.2)\) and small tiger trout \((\text{EA} = 2.8)\) isotopic niche spaces overlapped substantially \((45\% \text{ of the Rainbow Trout niche and } 52\% \text{ of the tiger trout niche})\), indicating they shared similar prey resources at an intermediate trophic position. Small Cutthroat Trout...
appeared to share a similar feeding niche space with all sizes of Utah Chub, 19\% of their niche overlapping with the entirety of the small chub niche.

**Gape Limit**

Cutthroat Trout became piscivorous at approximately 320 mm TL, and consumed Utah Chub near and well above both their estimated horizontal and vertical gape size (Figure 4). Utah Chub found in Cutthroat Trout diets ranged from 80 to 272 mm TL. In several instances, Cutthroat Trout consumed chub greater than 50\% of their body size. In fact, one 425-mm Cutthroat Trout consumed a 272-mm chub (64\% of the trout’s body size). However, on average, Cutthroat Trout consumed prey fish 30\% of their body size. Horizontal gape-width limit was very similar to gape-size limit. Rainbow Trout, however, demonstrated limited piscivory in Scofield Reservoir, and we observed no measurable fish prey in their diets.

![FIGURE 3. Two-dimensional isotopic (δ\^{15}N and δ\^{13}C) niche plots of four fish species from Scofield Reservoir. Top panel depicts large (≥350 mm) Cutthroat Trout, Rainbow Trout, tiger trout, and Utah Chub (≥250 mm); bottom panel depicts small (<350 mm) Cutthroat Trout, Rainbow Trout, tiger trout, and Utah Chub (<250 mm). Dots represent individual isotopic signatures and circles represent Stable Isotope Analysis in R (SIAR)-based isotopic ellipses.](image)

![FIGURE 4. Cutthroat Trout, Rainbow Trout, and tiger trout body length versus length of Utah Chub found in diets of trout in Scofield Reservoir, Utah. Gray circles represent actual sizes of prey found in trout diets. Lines show the calculated gape limit for trout based on two gape measurements. Although Rainbow Trout did consume fish prey, we found no whole measureable fish prey in diets.](image)
DISCUSSION

In our study, we presented new information describing the feeding ecology and potential for interspecific interactions of a novel assemblage of apex predators in a typical western reservoir. Overall, the fish composition in Scofield Reservoir was predominated by the potentially nuisance species, Utah Chub (Ward et al. 2008; Eilers et al. 2011), a species that consumed large quantities of aquatic invertebrates and zooplankton throughout the growing season. We caught consistently low numbers of Rainbow Trout, which consumed few prey fish, and relied substantially on aquatic and terrestrial invertebrates for food resources. Cutthroat Trout and tiger trout were much more abundant (Winters 2014), appeared to share the top trophic position in the food web, and consumed Utah Chub as a large proportion of their diet. Both Cutthroat Trout and tiger trout occasionally consumed Utah Chub at and above theoretical predictions of gape limit, demonstrating they were not food-limited based on gape morphology or prey size. A high degree of diet overlap was demonstrated among all small trout and Utah Chub, indicating the potential for competition.

The potential for competition between top predators was also demonstrated by similar trophic positions among Cutthroat Trout and tiger trout. Interestingly, there was no evidence of intraguild predation by one species on the other, based on isotopes and an absence of identifiable trout in any stomach contents (Polis and Holt 1992; Arim and Marquet 2004). The diets of Cutthroat Trout differed substantially from diets reported from other lentic systems. Within Strawberry Reservoir, Utah, for example, Daphnia were important prey for juvenile Cutthroat Trout and were seasonally important to adult fish; fish were only a minor contributor to adult diet (Baldwin et al. 2000). In our study, zooplankton was important to small Cutthroat Trout only in summer, and adult fish were consistently and strongly piscivorous.

Tiger trout are a relatively new hybrid, one for which there is little empirical information; however, they are thought to represent a voracious predatory trout. Because of their potential to utilize nuisance prey fish, they have been recently added to a large number of stocking programs (Hepworth et al. 2009; Hepworth et al. 2011). We confirmed that perception, given that fish (Utah Chub) were their predominant prey, and Winters (2014) found tiger trout in Scofield Reservoir consumed an extremely large number of Utah Chub across the year. In contrast, tiger trout in eastern Washington appeared to rely substantially on Daphnia and were only intermittently piscivorous (i.e., on Pumpkinseed Lepomis gibbosus and Redside Shiner) and only in the summer months (Miller 2010). Miller postulated that on lakes not dominated by zooplankton, tiger trout had switched to a more benthic diet. While we did observe tiger trout consuming a significant proportion of crayfish, a benthic prey item in this study, fish were still the predominant food source, particularly in summer.

Shared diet among Cutthroat Trout and tiger trout for Utah Chub alone does not necessarily indicate competition for prey resources (Matthews et al. 1982). Rather, resources must be limited and fitness or performance-related factors such as growth, condition, and fecundity must be negatively affected in order for competition to occur. Consequently, since Cutthroat Trout and tiger trout are abundant and caught at large sizes and Utah Chub prey are prolific, there is probably minimal competition between these trout (Winters 2014). However, interspecific competition or predation rates on other organisms may increase if the Utah Chub population collapsed under high predation pressure or if the trout population continued to expand via increases in abundance and survival (Bunnell et al. 2006; Svanyback and Bolnick 2007).

Predator morphology and size, as well as prey size, strongly influence rates of piscivorous predation (Hambright 1991; Fritts and Pearsons 2006). Cutthroat Trout and tiger trout displayed an ontogenetic shift to piscivory around 330-mm TL and consumed prey fish at an average of 30% of their own size, increasing prey size as predator size increased (Juanes et al. 2002). Additionally, the mouth size and morphometry of these top piscivores does not appear to limit prey consumption because both species consumed prey at and above their theoretical gape limits. This ability to consume larger prey may be important to managers attempting to use trout as biological control agents. While some studies suggest the vulnerability of prey larger than predator gape size is reduced to zero (Hambright 1991; Hill et al. 2004), prey can be attacked and then manipulated in such a way as to consume larger than expected sizes (Nilsson and Bronmark 2000).

Predation is also dependent on prey and predator behavior and distribution. Given the high densities of Utah Chub in the reservoir and the relatively small size and simple bathymetry, high spatio-temporal overlap with trout is likely, making foraging for prey fish more favorable. The extremely enriched nitrogen signatures of large Cutthroat Trout and large tiger trout, as well as diet composition consisting of a large proportion of Utah Chub, confirm these predators are piscivorous. As such, they share a top trophic position in the food web, relying heavily on prey fish. Elsewhere, small Cutthroat Trout also consistently consume invertebrates and become increasingly piscivorous as they grow, large adults consuming fish nearly exclusively (Nowak et al. 2004; McIntyre et al. 2006; Heredia 2014).

In contrast to Cutthroat Trout and tiger trout, Rainbow Trout were less piscivorous in Scofield Reservoir. In addition, based on carbon in isotopic signatures (more depleted), Rainbow Trout also occupied a more pelagic habitat than the other trout species, which were more littoral, as has been observed elsewhere (Vander Zanden et al. 1999; Layman et al. 2012). Although our sample size of Rainbow Trout diets was unsurprisingly low, the diet results were corroborated by isotopic signatures and demonstrated a lower trophic position (nitrogen signature). In addition, our results were consistent with some previous studies demonstrating that most strains of Rainbow Trout rely heavily on aquatic invertebrates, zooplankton, or on
only a small percentage of prey fish (Tabor et al. 1996; Baldwin et al. 2000; Haddix and Budy 2005). In contrast, however, there are many studies which depict Rainbow Trout as aggressive piscivores (McDowall 2003; Juncos et al. 2011; Yard et al. 2011). As such, it appears the current suite of top predators in Scofield Reservoir may have indirect effects on Rainbow Trout through exploitative competition or behavioral interactions (Duffy et al. 2007; Sih et al. 2010). The presence of Cutthroat Trout and tiger trout could cause Rainbow Trout to decrease activity, exhibit predator avoidance, or change feeding strategies (Romare and Hansson 2003). Diet overlap between small Rainbow Trout and Utah Chub may also lead to poor fitness, if food is limiting at that trophic level. Accordingly, catch rates of Rainbow Trout throughout our study were low (Winters 2014), implying low survival rates and potentially negative effects from food web interactions.

We observed limited significant isotopic niche overlap between large Rainbow Trout and Utah Chub, contradicting the expectation that Rainbow Trout were performing poorly due to shared food resources with a nuisance species. However, the small sample size of Rainbow Trout may have substantially and unrealistically altered calculations of diet proportions by exaggerating average contributions of diet items. Diets are a short-term snapshot of feeding patterns and subject to stochasticity (Wallace and Ramsey 1983). Nonetheless, Marrin and Erman (1982) also observed minimal diet overlap between Brown Trout and Rainbow Trout with Tui Chub *Siphateles bicolor*, demonstrating these trout and non-game fish partition resources and contradicting the common belief that competition for food resources was the cause for the decrease in trout performance in that system. Although apparent survival of Rainbow Trout, a potential indicator of interaction strength (Keeley 2001), is extremely low in Scofield Reservoir, we may not have captured changes in competitive abilities associated with size and environmental conditions (Hayes 1989).

The trophic positions of small Cutthroat Trout, Rainbow Trout, and tiger trout all shifted to higher nitrogen values at larger sizes, indicating a strong ontogenetic shift in diet (Werner and Gilliam 1984; Grey 2001). Rainbow Trout also shifted to a more negative $\delta^{13}$C value (more pelagic) as they became larger. Interestingly, Vander Zanden et al. (1999) documented a similar carbon shift of Lake Trout *Salvelinus namaycush* in black bass-invaded (*Micropterus*) Canadian lakes, reflecting a diet shift towards zooplankton and reduced dependence on littoral prey fish. This diet shift from the littoral to the pelagic for Rainbow Trout in Scofield Reservoir may indicate Rainbow Trout are altering their trophic niche in response to direct or indirect competition with the relatively newer predators stocked into this system (Correa et al. 2012). Accordingly, their diet and habitat use appear to be limiting their overall performance.

Our dietary findings are particularly relevant given the recent interest in tiger trout and their expanding presence in stocking regimes. Several lines of evidence suggest that tiger trout are performing very well and are not limited by strong food web interactions such as competition or predation. Utah Chub make up at least 30% of the diet of tiger trout seasonally, suggesting encounter rates are high and prey fish are energetically favorable (Wallace 1981). Large tiger trout also have a wide breadth of diet preferences, relying on a diversity of prey. In addition, this hybrid species feeds more littorally than other trout, thus potentially allowing them to minimize competition for food and space (Petchey 2000; Helland et al. 2011). Accordingly, tiger trout hold a top trophic position in the ecosystem, and they are ideal predators to stock into reservoir sport fisheries because they are sterile hybrids and energy normally allocated for gamete production should be diverted into growth (Budy et al. 2012). Finally, for connected water bodies, sterile trout are easier to control over the long-term (Scheerer and Thorgaard 1987), a consideration that has important conservation implications.

In sum, the combination of gut analyses, stable isotopes, and gape limitation studies applied herein provide a more complete understanding of potential limitations due to competitive or predatory interactions among a suite of apex predators in a novel fish community. Competition for food resources between sport and nongame fishes is commonly cited as a reason for decreased trout angling success, and competition is often assumed to exist between desired sport fish and undesired invasive prey species (Marking 1992). Nevertheless, competition does not always occur, and our data suggest two top trout predators in the system are not currently competing, probably because food is not limiting. Both tiger trout and Cutthroat Trout monopolized upon the abundant prey fish, Utah Chub; the growth and survival rates of these predators were high, and there is considerable evidence indicating they are able to control the chub population (Winters 2014). However, reservoirs are dynamic, and for effective management, novel fish communities may need to be monitored carefully because large-scale changes in the food web and annual changes in reservoir volume can alter predator–prey interactions.

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REFERENCES


Utah DEQ (Department of Environmental Quality). 2010. Scofield Reservoir TMDL. Utah Division of Water Quality, Salt Lake City.