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RESEARCH ARTICLE

Food Web Structure Informs Potential Causes of Bimodal Size Structure in a Top Predator

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Abstract:

Background:

Assemblages of fishes in lakes and reservoirs in the western USA are dominated by non-native, large-bodied, piscivorous fishes that lack a shared evolutionary history. Top predators in these crowded systems are often characterized by unstable population dynamics and poor somatic growth rates. One such assemblage is in Fish Lake, located in southern Utah, USA, in which introduced lake trout (*Salvelinus namaycush*, Walbaum) exhibit a bimodal growth pattern. A few lake trout in Fish Lake grow rapidly to large size typical of the species; whereas, most never grow beyond 600 mm total length.

Objective:

To inform competitive interactions in this evolutionarily novel fish assemblage that might cause the low recruitment to large body size in lake trout, we characterized trophic niche (from stable isotope analysis of C and N) of all fishes in the lake.

Methods:

We used a Bayesian mixing model to describe the trophic niche and infer diet of lake trout and their potential prey, and we used Bayesian ellipse analysis to identify potential areas of high competition within the food web. Large lake trout feed mostly on small lake trout and splake (*Salvelinus namaycush*, Walbaum x *Salvelinus fontinalis*, Mitchill) despite availability of abundant yellow perch. (*Perca flavescens*, Mitchill). Small lake trout and splake feed mostly on zooplankton and exhibit substantial overlap of their trophic niche implying competition for food. Yellow perch and Utah chub (*Gila atraria*, Girard; formerly an important food item for lake trout in Fish Lake) exhibit extreme overlap of their trophic niche implying strong competitive interactions.

Results:

Our data suggest that lack of recruitment to large body size in lake trout may result from a reduction in availability of Utah chub resulting from competitive interactions with yellow perch, and increased competition from introduced splake for available prey.

Conclusion:

Management actions that may help ameliorate the poor somatic growth rates of most lake trout include efforts to reduce perch populations or increase vulnerability of perch to predation by lake trout, and removal of splake as a competitor of small lake trout.

Keywords: Stable isotope analysis, Lake trout, *Salvelinus namaycush*, Pelagic forage fish, Splake, Pelagic energy pathway, Food web, Isotopic niche space.

1. INTRODUCTION

Lentic water bodies in the intermountain west are often dominated by a mix of non-native fish species introduced

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from elsewhere in North America and Europe for recreational angling [1 - 3]. Energy flow in these fish assemblages may not facilitate optimal growth and sustainable population size of large predatory fishes because of novel interactions between species with no shared evolutionary history and environmental factors that are different from the species native range [4 - 7]. This problem may be compounded because many aquatic systems have size-structured interactions between species that arise from variation in niche characteristics over ontogeny, in which one species can fill different niches based on its body size or developmental stage [8 - 10]. These complex interactions can result in high competitive overlap and decoupled predator-prey interactions, leading to low energy flow through the food web and highly variable recruitment [11 - 13].

Stable isotope analysis is a useful tool for revealing these complex interactions because it can characterize an organism's trophic niche and resulting food web structure by integrating that organism's diet into two simple but informative variables [14, 15]. Stable isotope ratio of nitrogen ($\delta^{15}N$) is used to estimate the trophic level of an organism because it is enriched from prey item to predator by roughly 3 - 4‰ (parts per thousand) [16 - 18]. The stable isotope ratio of carbon ($\delta^{13}C$) is indicative of the source of carbon fixation (*i.e.*, source of energy) for lake environments [14, 18 - 22]. In a lake ecosystem, the $\delta^{13}C$ is normally used to differentiate between pelagic and littoral carbon sources [23]. Characterization of trophic niches by stable isotope analysis can be used to assess areas of the food web with high levels of competition and energy bottlenecks, and to infer energy flow in the system [24, 25].

Fish Lake is located in central Utah and is a popular sportfish destination supporting about 100,000 angler hours per year [26]. The introduction of sportfish from across North America and non-game fish from elsewhere in Utah has led to the severe decline and likely extirpation of the native fish species-cutthroat trout (*Oncorhynchus clarkii*, Richardson) and mottled sculpin (*Cottus bairdii*, Girard)-resulting in an entirely non-native fish assemblage currently in the lake [27, 28]. Many anglers come to Fish Lake in search of large lake trout which were initially introduced in 1900 [29, 30]. Historically, the lake supported a robust population of lake trout which exhibited a normal size structure with most lake trout measuring between 600 mm to 900 mm. Recently, however, recruitment to large sizes appears to be infrequent, and population studies have revealed the existence of a bimodal size structure in adult lake trout. Most adult lake trout remain below 600 mm in length and have relatively poor body condition, while a few quickly surpass 750 mm and have relatively high body condition [26].

To identify potential causes of low recruitment to large body size in lake trout in Fish Lake, Utah, we analyzed trophic relationships among members of the food web. We characterized trophic niche, from stable isotope analysis of C and N, to infer diet composition and competitive overlap among fishes in this system. We identify two highly competitive relationships that may contribute to a lack of recruitment to large body size of lake trout.

2. METHODS

2.1. Study system

Fish Lake is a natural, graben lake, located in Sevier County, Utah. The lake sits at an elevation of 2695 m, has a surface area of 10 km^2, a mean depth of 16.7 m and a maximum depth of 35.6 m. The native fish have been replaced by a non-native assemblage of fishes including lake trout, splake, rainbow trout (*Oncorhynchus mykiss*, Walbaum), brown trout (*Salmo trutta*, Linnaeus), yellow perch, Utah chub, and Utah sucker (*Catostomus ardens*, Jordan & Gilbert) [28, 30].

2.2. Sample Collection

We sampled splake, rainbow trout, Utah sucker, Utah chub, and yellow perch in May of 2014 from several different locations in the lake using gill nets. We removed a 1 cm^2 tissue sample from the epaxial muscle of each fish and recorded the total length of the fish. We sampled lake trout using gill nets in the fall of 2014 and clipped a 1 cm^2 piece of fin from the pelvic fin. We used a 63 μm plankton tow sampler to collect plankton from the water column and the surface in May 2015 from several locations in the lake and collected plankton from fish stomachs in January 2016. We collected aquatic macroinvertebrates with an Ekman grab sampler in January 2016. We collected algae and aquatic macrophytes near the shore by hand from several locations in May 2015. We kept all samples frozen until lab preparation commenced (Table **1**). Samples were collected at different times and different years based on the susceptibility of fish to sampling and the opportunity to sample macroinvertebrates, zooplankton, and aquatic macrophytes. Turnover rates of isotopes in muscle tissue of large-bodied ectotherms are typically on the order of several months to years, thus the difference in sampling times is unlikely to confound the data [31].

Table 1. Samples sizes, mean lengths (mm) and stable isotope ratios (mean ± CI) of samples collected in Fish Lake, Utah.

Species	Total	Mean Length (Min, Max)	Mean $\delta^{15}N$	Mean $\delta^{13}C$
Lake Trout (Large, over 700 mm)	30	911 (757, 1040)	15.02 ± .25	-22.04 ± .24
Lake Trout (Small, under 700 mm)	39	497 (410, 640)	12.52 ± .26	-25.65 ± .40
Splake	25	356 (188, 425)	12.93 ± .17	-24.51 ± .34
Rainbow Trout	42	283 (170, 404)	11.08 ± .21	-22.71 ± .35
Yellow Perch	25	183 (133, 225)	11.42 ± .29	-20.09 ± .44
Utah Chub	12	236 (132, 300)	11.08 ± .27	-20.32 ± .84
Utah Sucker	25	413 (320, 470)	9.81 ± .43	-20.64 ± 1.46
Zooplankton	13	–	9.00 ± .56	-28.07 ± 1.01
Macroinvertebrates	10	–	5.51 ± 1.07	-17.51 ± 1.35
Macrophytes	5	–	4.76 ± 1.09	-11.79 ± .28
Algae	5	–	4.81 ± .95	-15.94 ± 3.07

2.3. Sample Preparation and Isotopic Analysis

We oven-dried tissue samples at 60°C for 72 hours, then ground the samples into a homogeneous powder with a mortar and pestle and measured 0.6 - 1.2 mg of the powder into small tin capsules and sealed them. We sent the capsules to the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University in Flagstaff, Arizona for stable isotope analysis. The analysis was carried out on a Delta V Advantage Mass Spectrometer (Thermo Electron Corporation, Bremen, Germany) configured through a CONFLO III (Thermo Electron Corporation), using a Carlo Erba NC2100 Elemental Analyzer (Thermo-Quest Italia S.p.A., Milano, Italy). We used delta notation ($\delta^{13}C$ and $\delta^{15}N$) expressed in parts per thousand (‰) for the stable isotope values. The ratio of the stable isotope in the sample is compared to the ratio in international standards (Vienna Pee Dee Belemnite for carbon and atmospheric nitrogen standard for nitrogen) by the following equation: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) – 1] \times 1000$, where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. We calculated the trophic level by using the following equation: Trophic position = $[(\delta^{15}N_{consumer} - \delta^{15}N_{algae})/2.9] + 1$, where $\delta^{15}N_{consumer}$ is the average signature of the organisms in question, $\delta^{15}N_{algae}$ is the average signature for algae, 2.9 is the enrichment factor for one trophic level, and 1 is added to account for the trophic level of the algae [15, 32].

2.4. Fin tissue Isotope Value Correction

As lake trout are relatively rare in Fish Lake, we used non-lethal tissue collection and sampled from the pelvic fin. Pelvic fin tissue may have different isotopic values when compared to muscle tissue [33, 34], so we sampled muscle tissue and fins from 12 small lake trout (under 700 mm) and 3 large lake trout (over 700 mm) to compare the muscle tissue to fin tissue from the same individual. We plotted values of $\delta^{13}C$ and $\delta^{15}N$ for both muscle and fin for all 15 individuals. Values derived from fin tissue were displaced in a common direction from values derived from muscle tissue on the $\delta^{13}C$ by $\delta^{15}N$ plot. We calculated the difference between muscle and fin isotopic signature for each fish and used the mean of those differences as the correction value. For small lake trout, we corrected isotope values by subtracting 1.925 from the fin tissue $\delta^{13}C$ and subtracting 0.373 from the fin tissue $\delta^{15}N$. For large lake trout, we corrected the isotope values of fins by subtracting 3.136 from the fin tissue $\delta^{13}C$ and subtracting 1.315 from the fin tissue $\delta^{15}N$.

2.5. Trophic Niche Analysis

To estimate the diet contribution of food sources to lake trout and splake, we used the Bayesian mixing model Stable Isotope Analysis in R (SIAR) [35]. This model allows the incorporation of uncertainty and variability in both the prey isotopic signatures and trophic enrichment factors. We set the model to run for 500,000 iterations and discarded the first 50,000 iterations. We used standard trophic enrichment values for fish muscle ($\delta^{15}N = 2.9$ SD = 0.32, $\delta^{13}C = 1.3$ SD = 0.30) [32]. To see whether possible food sources could be combined because they showed no statistical difference, we performed ANOVA's followed by Tukey HSD between $\delta^{15}N$ and $\delta^{13}C$ signatures for the different species. Utah chub and yellow perch ($p = 0.999$ for $\delta^{15}N$, $p = 0.963$ for $\delta^{13}C$), and small lake trout and splake ($p = 0.195$ for $\delta^{15}N$, $p = 0.541$ for $\delta^{13}C$) were not significantly different and were combined as possible food sources. Rainbow trout that were smaller than 250 mm and exhibited signs of being in the hatchery were likely stocked from September to November 2013. We grouped these fish separately from other rainbow trout because their muscle tissue would possibly still be influenced by their hatchery diet. Whereas, larger rainbow trout with no signs of being in the hatchery had likely been stocked in the lake over one year prior to sampling [36]. We found no significant difference between the two groups of rainbow trout (p = 0.133 for $\delta^{15}N$, 0.182 for $\delta^{13}C$), so we left them as a single group. For large lake trout, we included Utah chub/yellow perch, rainbow trout, Utah sucker, zooplankton and lake trout (small)/splake as possible food sources. For small lake trout and splake, we included Utah chub/yellow perch, rainbow trout, Utah sucker, and zooplankton as possible food sources.

To calculate the isotopic niche space occupied by certain fish species, we used the program Stable Isotope Bayesian Ellipse in R (SIBER) [37]. This program uses a maximum likelihood function based on the variance and covariance of the stable isotope signatures to construct ellipses that encompass roughly 40% of the data points for each species, which is intended to represent the core niche of that species [38, 39]. We then calculated the overlaps of this core niche area between species including small lake trout, splake, Utah chub, yellow perch and rainbow trout. We used the R statistics package to perform all statistical analyses [40].

3. RESULTS

3.1. Food web structure

Trophic level varied widely among organisms in the food web. Aquatic macrophytes and algae had the lowest nitrogen ($\delta^{15}N$) values placing them as primary producers at trophic level 1. Aquatic macroinvertebrates were also in trophic level 1 but were slightly more enriched in nitrogen ($\delta^{15}N$). Trophic level 2 contained zooplankton and Utah sucker. Trophic level 3 included yellow perch, Utah chub, rainbow trout, small lake trout, and splake. Large lake trout occupied trophic level 4, as expected for an apex predator (Fig. **1**).

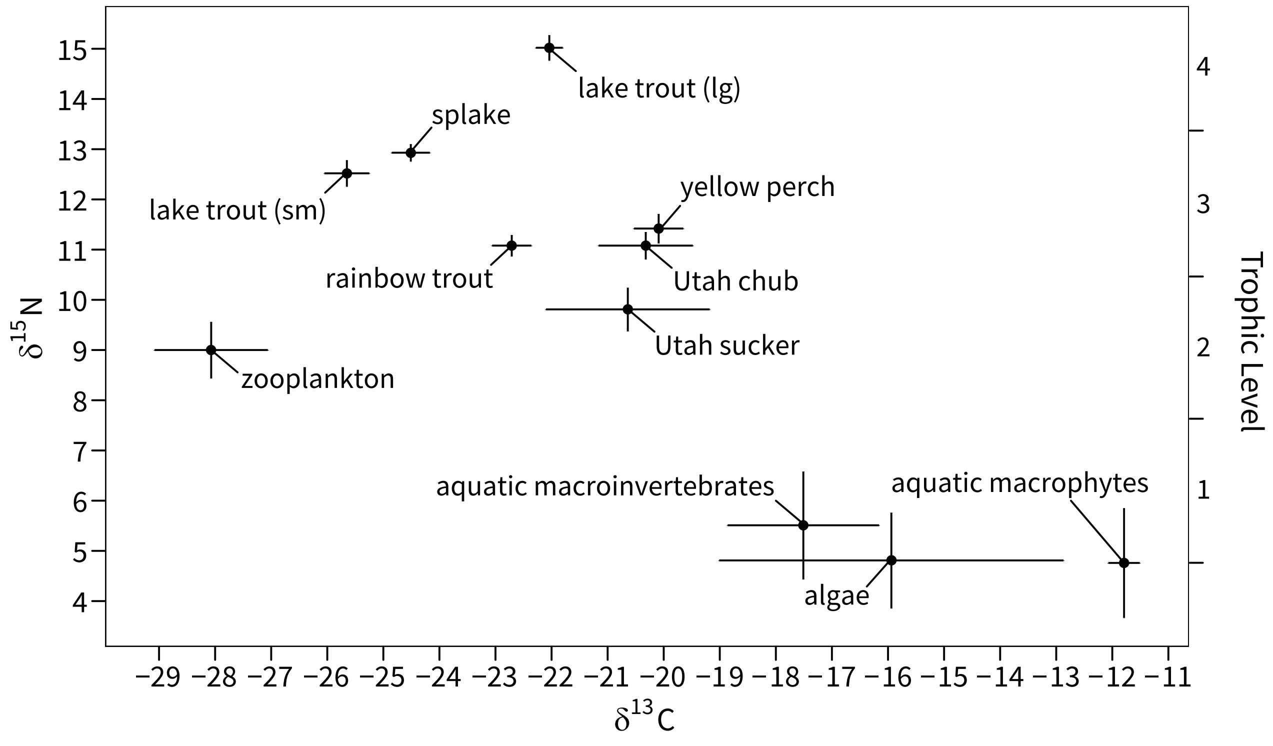

Fig. (1). Bi-plot of average $\delta^{13}C$ and $\delta^{15}N$ signatures of fishes, plankton, aquatic macroinvertebrates, algae, and aquatic macrophytes in Fish Lake, Utah. Error bars represent 95% confidence intervals. Lake trout (lg) = lake trout over 700 mm. Lake trout (sm) = lake trout under 700 mm.

Similar to the trophic level, the carbon ($\delta^{13}C$) level varied widely among the organisms in the food web. Fish Lake exhibited a pelagic and a littoral energy pathway. Aquatic macrophytes were the most littoral, followed by algae and aquatic macroinvertebrates. Zooplankton had the most pelagic signature. Fishes exhibited somewhat intermediate positions between the littoral and pelagic pathways. Small lake trout and splake were less enriched in carbon ($\delta^{13}C$) than other fish, suggesting a higher proportion of pelagic food. Yellow perch, Utah chub and Utah sucker were more enriched in carbon ($\delta^{13}C$) indicating a higher proportion of their food was derived from the littoral energy pathway. Rainbow trout and large lake trout had carbon ($\delta^{13}C$) signatures that were intermediate for the fish (Fig. **1**).

3.2. Trophic Niche Analysis

The diet of small lake trout and splake was dominated by zooplankton, but splake had a slightly higher contribution from rainbow trout. Utah chub, yellow perch, and Utah sucker made up a negligible portion of small lake trout and splake diets. The diet of large lake trout consisted mostly of small lake trout and splake with a smaller proportion of Utah chub or yellow perch. Rainbow trout possibly contribute a small proportion to the large lake trout diet, while Utah sucker and zooplankton contribute little (Fig. **2**).

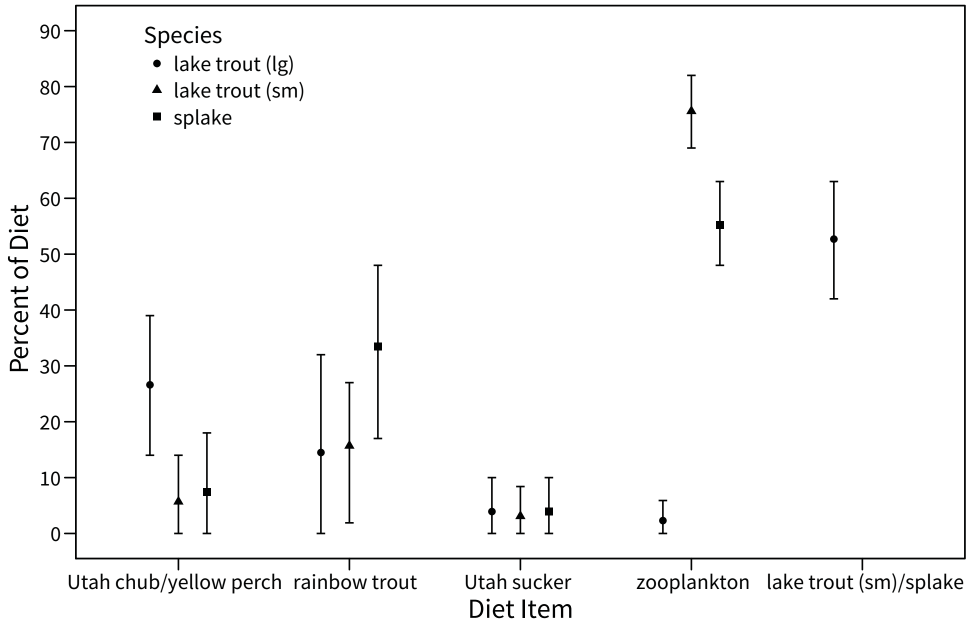

Fig. (2). Diet percentages from SIAR analysis for splake, lake trout (sm) (under 700 mm) and lake trout (lg) (over 700 mm) in Fish Lake, Utah. Error bars represent 95% Bayesian credibility intervals.

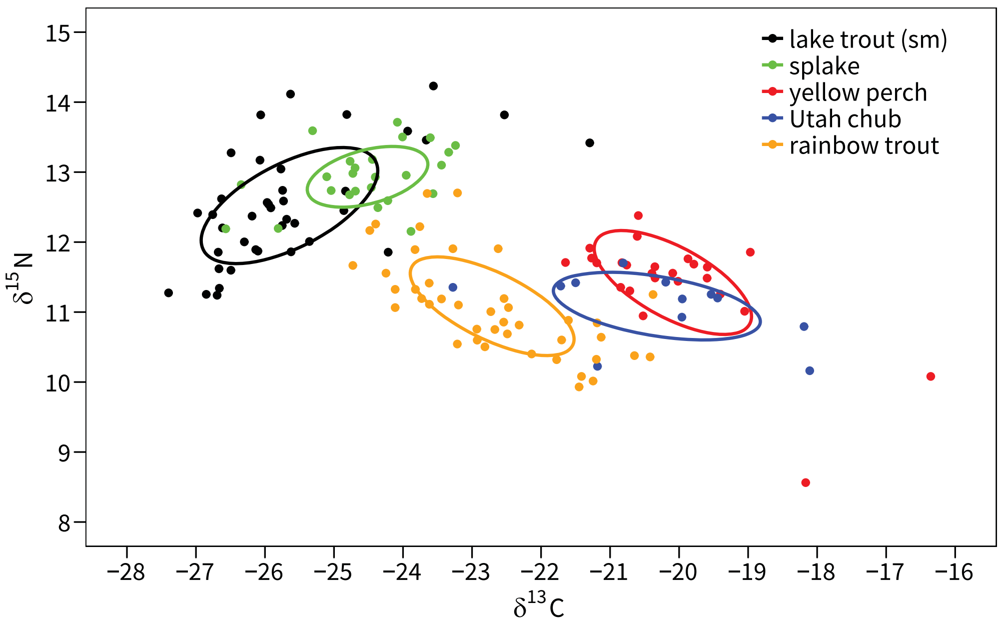

Fig. (3). Bi-plot of isotopic niche ellipses on $\delta^{13}C$ and $\delta^{15}N$ from SIBER analysis for lake trout (sm) (under 700 mm), splake, Utah chub, yellow perch and rainbow trout in Fish Lake, Utah.

The isotopic niche of small lake trout overlapped moderately with splake (22.8%), while the isotopic niche of splake overlapped more substantially with small lake trout (54.9%). The isotopic niche of Utah chub and yellow perch overlapped substantially (53.1% of the Utah chub niche and 50% of the yellow perch niche). Rainbow trout did not significantly overlap with any of the other fish species (Fig. **3**).

4. DISCUSSION

Our isotopic mixing models suggest that the diet of large lake trout consists mostly of splake and small lake trout. This contrasts with stomach analysis data from 2002, which indicated rainbow trout as the primary source of food for lake trout [26]. In other systems, lake trout have changed their diet based on prey availability [41]. Historically, rainbow trout and Utah chub represented 81.2% of the diet of large lake trout, with the percentages of rainbow trout and Utah chub fluctuating based on availability [28, 42]. However, when the Utah chub population was reduced, most likely due to competition with yellow perch, large lake trout apparently began feeding more heavily on rainbow trout [43]. Currently, it appears that lake trout have again changed their diet, from rainbow trout to small lake trout and splake. Splake are typically stocked at a smaller size than rainbow trout, which may make them more accessible to large lake trout [44]. Additionally, cannibalism among apex predators can develop in systems that lack energy flow to higher trophic levels [45, 46]. This change in diet suggests that Fish Lake may lack sufficient open water forage fish to support a large population of large lake trout [47].

The isotopic similarity of yellow perch and Utah chub signatures suggest high competitive overlap. Often in systems with high competitive overlap, one of the competitors is reduced to low numbers [48, 49]. In Fish Lake, Utah chub have been significantly reduced, with the most recent gillnetting surveys showing a decrease from 289 fish caught per net in 1991 to only 13.8 in 2014, while yellow perch are now numerically the most abundant fish in the lake [43, 50]. The high competitive overlap between Utah chub and yellow perch appears to have been exacerbated by the illegal introduction of Eurasian milfoil (*Myriophyllum spicatum*) in the 1970's [43]. Introduction of non-native species often leads to invasion-associated transitions which can rearrange food webs [51 - 53]. Historically, Fish Lake's littoral zone supported a diverse community of aquatic plants that grew up to thirty feet from the shore [54]. The introduction of Eurasian milfoil expanded the available habitat in the littoral zone, likely providing an ideal environment for reproduction and survival of yellow perch [55]. Yellow perch are known to eat the young of year and juveniles of Utah chub, thus intraguild predation likely contributed to the decrease in Utah chub [56 - 58]. The overall effect of this decrease may contribute to the shift from the historic, normally distributed size structure of lake trout to the present bimodal distribution. Any effort to reduce yellow perch, such as encouraging harvest of or mechanical removal, will likely increase Utah chub. In an effort to reduce yellow perch habitat, the Utah Division of Wildlife Resources has introduced a milfoil weevil (*Euhrychiopsis lecontei)* [43].

The isotopic similarity of splake and small lake trout signatures also may suggest high competitive overlap. Our mixing model further supports this, suggesting that these fish have similar diets. Specifically, splake and small lake trout feed on zooplankton, with fish making up a smaller part of their diet. It appears that the abundance of zooplankton may provide sufficient energy to allow both salmonids to coexist at moderately high densities in Fish Lake. Thus, competition for zooplankton may not be a limiting resource, consistent with earlier studies showing that the abundance of zooplankton contributed to the high productivity of Fish Lake [28]. However, competition for limited numbers of forage fish may prevent either species from consistently transitioning to piscivorous diets and attaining larger body size. Our mixing models also infer that splake are more successful than small lake trout at preying on rainbow trout. Thus, the lack of forage fish, compounded with the high competitive overlap with splake, may force small lake trout to feed more exclusively on zooplankton, resulting in lack of growth to large size in most lake trout. As splake are a sterile hybrid, they are entirely controlled by fish stocking. A reduction in stocking would translate to a population decline in splake and could allow small lake trout to better exploit forage fish.

CONCLUSION

The lack of suitable forage fish exacerbated by the competitive dominance of yellow perch over Utah chub, and potential competition between splake and small lake trout, may be responsible for the lack of large-bodied lake trout in Fish Lake. Taking measures to reduce yellow perch, such as promoting harvest, mechanical removal, or mitigation of Eurasian milfoil, may reduce competitive overlap and intraguild predation on Utah chub. This could, in turn, allow the Utah chub population to recover, providing more forage fish for large lake trout [43]. Alternatively, reduction or discontinuance of splake stocking may release small lake trout from competition, allowing more to transition from planktivory to piscivory and thus to attain larger sizes.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Not applicable.

HUMAN AND ANIMAL RIGHTS

Samples were collected under direction of the Utah Division of Wildlife Resources. All sampling was conducted in accordance with the American Fisheries Society Guidelines for the Use of Fishes in Research.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest. This project was funded by the Utah Division of Wildlife Resources and the Department of Biology, Brigham Young University.

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