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Niche Partitioning Among Three Apex Piscivorous Fishes: Evidence of Limited Intraguild Predation

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ABSTRACT

This study aimed to understand the ecological relationship among burbot *Lota lota*, brown trout *Salmo trutta* and lake trout *Salvelinus namaycush*, with a focus on burbot, a species of greatest conservation need in Wyoming. While we hypothesised a reciprocal intraguild predation dynamic, where competition and predation occur between predators based on size or age structure, our findings provided limited support for this hypothesis. Both dietary overlap and trophic position were minimal among burbot, brown trout and lake trout. Instances of reciprocal predation were rare; no predation between burbot and lake trout was observed; and brown trout was the only species consumed by all predators (burbot 0.02 mean proportion by weight; lake trout 0.09 mean proportion by weight). Predation by brown trout on burbot was negligible, contributing only 0.01 to the mean proportion by weight and frequency of occurrence. Additionally, both burbot and brown trout were less piscivorous than expected, with fish comprising 0.36 and 0.17 of their mean proportion by weight in their overall diets, respectively. Overall, our findings suggest that these predators coexist with limited competitive or predatory interactions, likely due to differences in prey selection.

1 | Introduction

Predatory fishes are favoured by anglers and commonly introduced into novel systems due to aggressive feeding behaviours and large body size that support desirable recreational opportunities (Dextrase and Coscarelli 1999). These traits often allow introduced piscivorous fishes to establish and cause negative ecological effects on native species (Moyle and Light 1996a, 1996b). Prey species are often vulnerable and naïve to the introduced predator (Moyle and Light 1996b). For example, the intentional introduction of smallmouth bass (*Micropterus dolomieu*) in the Pacific Northwest for sportfishing (Carey et al. 2011) caused a decrease in native fish populations. Smallmouth bass consumed up to 40% of out-migrating juvenile salmon in the Columbia River Basin (Sanderson et al. 2009) and up to 3% of annual production of Chinook salmon (*Oncorhynchus tshawytscha*) in the lower Yakima River (Fritts and Pearsons 2004).

In addition to decreasing the abundance of native species, introduced apex predators can cause top-down trophic cascade effects by altering food-web complexity (Eby et al. 2006; Tronstad et al. 2010; Ellis et al. 2011). A classic example of a trophic cascade occurred in Yellowstone Lake with the invasion of lake trout (*Salvelinus namaycush*). Lake trout caused a reduction in native Yellowstone cutthroat trout (*Oncorhynchus virginalis bouvieri*), which allowed zooplankton to increase in biomass and led to a

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decrease in phytoplankton biovolume (Tronstad et al. 2010; Koel et al. 2019). The introduction of lake trout altered the number of terrestrial predators that relied on Yellowstone cutthroat trout as a food resource (Koel et al. 2019). Additionally, lake trout within Yellowstone Lake exhibited diet plasticity, switching from Yellowstone cutthroat trout to amphipods when the abundance of Yellowstone cutthroat trout declined (Syslo et al. 2016). The ability of predators to exhibit diet plasticity, alternating prey selection with variation in the abundance of prey species (Syslo et al. 2016; Creel et al. 2018; Robinson et al. 2019; Glassic et al. 2024), allows predators to use either specialised or generalised feeding strategies dependent on prey abundance (Jensen et al. 2008; Syslo et al. 2016; Glassic et al. 2024). Diet plasticity over multiple trophic levels allows predators to maintain fitness and population densities even as preferred prey species decline (McMahon and Bennett 1996; Roseman et al. 2014), which contributes to the success of invasive apex predators (Sinclair et al. 2003; Vejřík et al. 2017).

Direct competition and predation can result when piscivorous fishes are introduced into systems where a native apex piscivorous species already exists (Bacheler et al. 2004; Saylor et al. 2012). Introduced species may displace native apex predators by directly competing for the same limited food source if both species occupy the same ecological niche. For example, invasive lake trout were able to reduce native bull trout (*Salvelinus confluentus*) populations through niche overlap and competition (Donald and Alger 1993). Multiple predators may also interact in an intraguild predation relationship where predation and competition intertwine, leading to scenarios where predatory actions serve to mitigate potential exploitation competition among intraguild predators (Polis 1988). Interactions among intraguild predators become complicated with symmetrical and reciprocal intraguild predation where species can be mutual predators based on length or age (Werner and Gilliam 1984; Taniguchi et al. 2002; van der Hammen et al. 2010; Henkanaththegedara and Stockwell 2014).

The presence of multiple apex predators exhibiting predation causes the food web to become more complex and can result in a decrease in diversity and biomass at higher trophic levels when prey is limited (Wang et al. 2019). This dynamic is particularly relevant in the Torrey Creek drainage in the Wind River basin of Wyoming, where three apex predators interact within a single system. Burbot (*Lota lota*) are the native apex piscivorous fish. Lake trout were first stocked in 1937, and it is assumed that brown trout entered the drainage in the late 1940s or early 1950s (Connell 1977, 1978). It is unknown how brown trout entered the drainage, and if the introduction was intentional. However, all three species are popular sportfish for recreational anglers. In Wyoming, burbot are listed as a species of greatest conservation need with a declining population within the Wind River drainage (Hubert et al. 2008; Wyoming Game and Fish Department 2019). The Torrey Creek drainage represents the south-western extent of the native range of burbot (Glaid et al. 2021). Hypotheses for the declining burbot population in the Wind River drainage included angler harvest, emigration, entrapment in irrigation canals and fluctuations in water levels (Hubert et al. 2008). However, within the Torrey Creek drainage, burbot are at a low risk of overexploitation (Lewandoski et al. 2017), have low emigration rates (Hooley-Underwood et al. 2018), limited instances of entrapment in irrigation canals (Hooley-Underwood et al. 2018) and the Torrey Creek drainage has an unaltered flow regime (Hubert et al. 2008). As a result, the declines in burbot abundance are now hypothesised to be a result of alterations in the food web. Thus, intraguild predation among burbot, brown trout and lake trout in this system may be contributing to the decline in burbot abundance over the past two decades (Hubert et al. 2008).

In this study, we investigate whether burbot, brown trout and lake trout are in a reciprocal intraguild predation relationship where adults of all three species consume juveniles of all three guild species while also competing for the same prey species (Figure 1). Predation on burbot by brown trout was confirmed by the Wyoming Game & Fish Department in the autumn of 2017 in the Torrey Creek drainage (Wyoming Game and Fish Department 2018), and burbot have been observed feeding on juvenile lake trout in Lake Michigan (Van Oosten and Deason 1938; Jacobs et al. 2010). We aim to address how these piscivorous species are interacting in an intraguild predation relationship through the following inquiries: (1) what are the dietary compositions of burbot, brown trout and lake trout; (2) to what extent does dietary overlap occur among burbot, brown trout and lake trout; (3) do burbot, brown trout and lake trout occupy different trophic levels; and (4) does intraguild predation remain constant among seasons when thermal preferences may restrict species to occupy similar habitat?

2 | Materials and Methods

2.1 | Study Site

The Torrey Creek drainage is located in north-western Wyoming and near Dubois, Wyoming, United States (Figure 2) encompassing Torrey Lake, Ring Lake, Trail Lake and Torrey Creek. Of these, Torrey Lake is the largest and most downstream lake (93 ha), Ring Lake is directly upstream (40 ha) and a section of Torrey Creek (0.9 km) connects Ring Lake and Trail Lake (51 ha). The Torrey Creek drainage was created from glacial moraines and is fed by snow melt and glacier melt from the Continental Glacier located in the Wind River Range (Vandeberg and VanLooy 2016). The headwaters of Torrey Creek flow through the Shoshone National Forest before entering the Wyoming Game & Fish Department Whiskey Basin Wildlife Management Area 4.5 km upstream of Trail Lake. Torrey and Ring lakes are largely encircled by private ranches but offer access through public boat ramps. Movement of fish upstream from the Wind River into Torrey Lake, approximately 6 km, is unlikely because a series of steep cascades exist downstream of Torrey Lake (Hubert et al. 2008). We treated the Torrey, Ring and Trail lakes along with Torrey Creek as a single system in all analyses due to movement of tagged fishes being observed.

Native fishes in the Torrey Creek drainage include burbot, mountain whitefish (*Prosopium williamsoni*), Yellowstone cutthroat trout, plains sucker (*Pantosteus jordani*), longnose sucker (*Catostomus catostomus*), white sucker (*Catostomus commersonii*),

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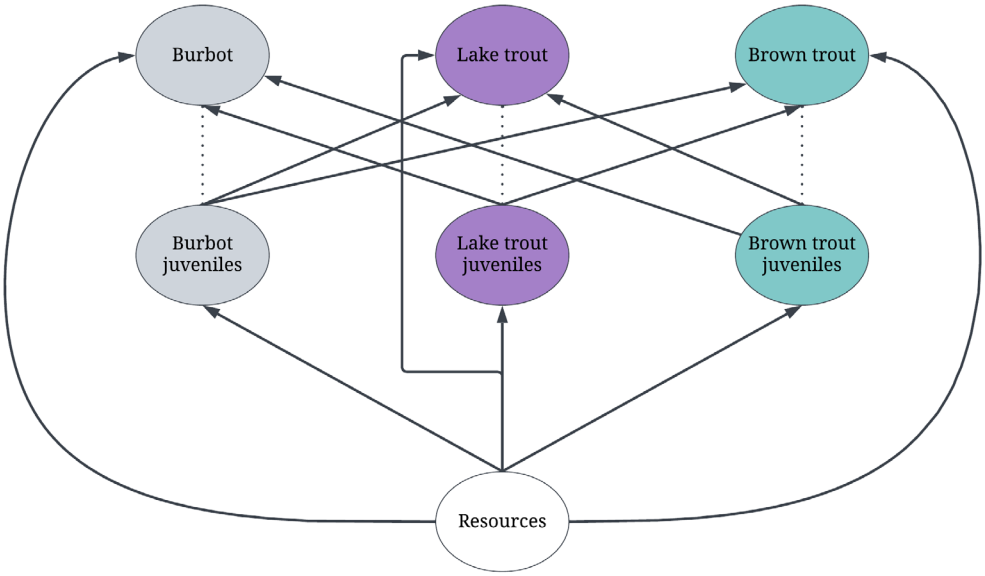


FIGURE 1 | Conceptual model of hypothesised reciprocal intraguild predation with life-history structure occurring within the Torrey Creek drainage, Wyoming, United States, modified from van der Hammen et al. (2010) to include a third predator. In this model, consumers (i.e., burbot, brown trout and lake trout) feed on juveniles of allospecific species while also competing for the same resource. Dotted lines represent growth from juveniles to adult and solid lines represent consumption.

lake chub (*Couesius plumbeus*) and longnose dace (*Rhinichthys cataractae*). Non-native sportfish include brown trout, lake trout and rainbow trout (*Oncorhynchus mykiss*). Rainbow trout are stocked annually in the system as a recreational opportunity by Wyoming Game & Fish Department, with 150,800 total rainbow trout being stocked from 2020 to 2023 (Table S1).

2.2 | Fish Collection

Burbot, brown trout and lake trout were collected from Torrey, Ring and Trail lakes using short duration gill nets and electrofishing. Gill nets were set for a maximum of 3 h but typically for a period less than 2 h and set in all depths within the lakes. The short duration was to reduce mortality and minimise regurgitation of dietary contents (Lester et al. 2009; Garvey and Chipps 2012). Two types of gill nets, an experimental gill net and a standard gill net, were used to collect fish. The experiment gill net was 48.8 m by 1.8 m with eight 6.1-m panels. Mesh size for the panels was 1.91-, 2.54-, 3.18-, 3.8-, 4.45-, 5.08-, 6.72- and 6.35-cm bar mesh. The standard gill net was 61 m by 2.44 m with 4.45-cm bar mesh throughout. Electrofishing was conducted at night using an ETS MBS shocking at 500 V to achieve 2–3 amps. Lake electrofishing surveys primarily targeted nearshore habitats, inlets and outlets with depths less than 4 m. Additional electrofishing was also conducted in deeper areas with dense macrophyte coverage. Backpack, throwable anode and towable cataraft shocking were conducted in Torrey Creek above Trail Lake and in the section that connects Ring and Trail lakes using the same ETS MBS settings as the lakes but conducted during the day. Burbot, brown trout and lake trout were collected by gillnetting annually in spring (late March–May) and autumn (September–November) in 2020, 2021 and 2022. Night electrofishing occurred annually in spring, summer (June–August) and autumn in 2020, 2021 and 2022; and electrofishing in the creek occurred in autumn of 2020 and spring, summer and autumn of 2021. Total length (mm) and weight (g) were measured for all burbot, brown trout and lake trout.

2.3 | Dietary Overlap and Trophic Positioning

Diets were obtained from live fish using a gastric lavage technique (Light et al. 1983; Hakala and Johnson 2004). Using a 12-V 4160 L/h bilge pump, various flexible tubing with outer dimensions varying from 8 to 24 mm (depending on size of oesophageal opening) were attached to a garden hose nozzle to pump water into the oesophagus of the fish. Once the tube was inserted, residential drinking water was pumped into the inverted fish to flush out stomach contents while applying forward pressure externally to the stomach. Discharged contents were strained through a 500-μm sieve and then stored in 70% ethanol. We removed stomachs from incidental mortalities of burbot, brown trout and lake trout for diet collection and stored them in 70% ethanol.

Count, wet mass (g) and dry mass (g) were recorded for all items in the diets. Samples were identified to lowest taxon possible, generally species for fish and family for invertebrates. Fish diet items that were not able to be identified to species were classified as fish parts. Frequency of occurrence O_i, proportion by weight W_i and mean proportion by weight MW_i were calculated for each dietary item for burbot, brown trout <300 mm, brown trout ≥ 300 mm and lake trout using the following equations from Chipps and Garvey (2007):

$$O_i = \frac{J_i}{P},$$

$$W_i = \left(\frac{W_i}{\sum_{i=1}^{Q} W_i} \right),$$

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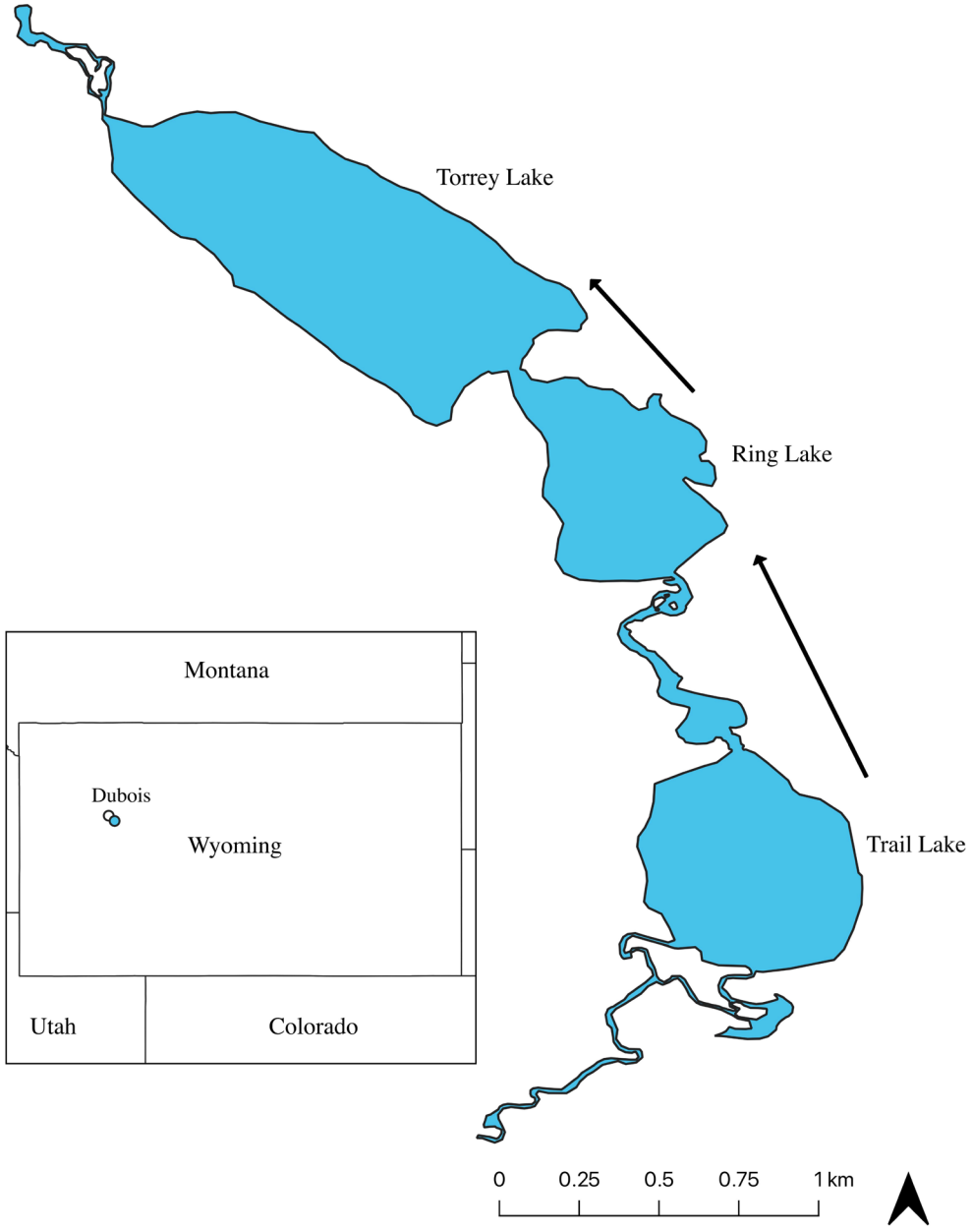


FIGURE 2 | Map of a section of the Torrey Creek drainage near Dubois, Wyoming, United States. The area delineated in the map represents the extent of the sampling locations. Water flows from south to north (indicated by black arrows). The Torrey Creek drainage is marked as a blue dot on the inset map.

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

where J_i is the number of fish containing prey i, P is the number of fish containing food in their stomach, Q is the number of food types and W_i is the weight of prey type i and j is for individual fish. To allow for comparisons, W_i was calculated for individual fish and averaged for each prey type to obtain MW_i (Chipps and Garvey 2007). Frequency of occurrence and mean proportion by weight were selected to inform relative prey importance and used to quantify differences in prey selection among burbot, brown trout <300 mm, brown trout ≥ 300 mm and lake trout. We separated brown trout into two categories (i.e., <300 mm and ≥ 300 mm) because 300 mm has been identified as the point where brown trout become more piscivorous (Næsje et al. 1998; Jensen et al. 2012). Unfortunately, due to small sample sizes for burbot and lake trout, we were unable to separate these species by ontogenetic shifts in diet. To correct for discrepancies in sample size for diet breadth comparison, we bootstrapped, without replacement, the diet samples for brown trout ≥ 300 mm to reduce their number of samples per season to be the average of the samples obtained from the other predator categories (i.e., brown trout <300 mm, burbot and lake trout). This was repeated 500 times per season to obtain an average from the estimates and 95% confidence intervals.

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Diet overlap was analysed using Schoener's index of niche overlap (D; Schoener 1970):

$$D = 1 - 0.5\left(\sum_{i=1}^{n} |p_{ij} - p_{ik}|\right),$$

where p_{ij} is the proportion resource i is of the total resources used by species j and p_{ik} is the proportion of resource i used by species k. The decision to use Schoener's index of niche overlap was made to mitigate bias associated with total weight or count overlap analyses while also being limited in the data regarding the availability of prey resources within the Torrey Creek drainage (Wallace 1981). A D value of 0.6 or higher is considered a noteworthy niche overlap (Wallace 1981).

Stable isotope analyses were performed to estimate trophic position. As fish consume higher trophic level prey, nitrogen isotope ratios increase and carbon isotope ratios are used to identify the source (Minagawa and Wada 1984). The addition of stable isotope analyses helps identify any long-term dietary overlaps among the species when compared to the short-term diet compositions from the stomach content samples. Tissue plugs were collected below the dorsal fin and above the lateral line on burbot, brown trout < 300 mm, brown trout ≥ 300 mm and lake trout with a 4-mm biopsy punch (Biopunch 4; Ted Pella Inc., Redding, CA, USA). Samples were placed in a centrifuge tube and immediately stored on ice in the field and frozen after leaving the field. Tissue plugs were freeze-dried for 18–36 h using a Labconco Freezone 1 (Labconco Corporation, Kansas City, MO, USA) and ground to a powder using a mortar and pestle. The ground samples were analysed by Wyoming Stable Isotope Facility using a Thermo Finnigan Delta Plus XP, Costech 4010 and Carlo Erba 1110 Elemental Analyser, Costech Zero Blank Autosampler, and Finnigan Conflo III interface. Stable isotope ratios were calculated using the procedure outlined in Zanden and Rasmussen (1999) and Hershey et al. (2017). Using the SIBER package (Stable Isotope Bayesian Ellipses, Version 2.1.9) in R (Version 4.2.1; R Core Team (2022), 40% standard ellipses were created for each species to represent the isotopic niche of a group (Jackson et al. 2011). The proportional overlap between ellipses was used to quantify an estimate of niche overlap. Proportional overlaps greater than 60% are ecologically noteworthy, similar to Schoener's index of niche overlap (Guzzo et al. 2013; Pettitt-Wade et al. 2015).

3 | Results

We collected diets from 108 brown trout < 300 mm (total length TL; 89–299 mm; mean 237 mm; SD 39 mm), 372 brown trout ≥ 300 mm (TL; 300–836 mm; mean 462 mm; SD 100 mm), 56 burbot (TL; 164–800 mm; mean 368 mm; SD 172 mm) and 22 lake trout (TL; 356–1021 mm; mean 678 mm; SD 198 mm). Twenty orders and 77 families were identified from the diets (Table S2). Brown trout ≥ 300 mm fed on a wider breadth of taxa across all seasons (number of taxa—spring 68; summer 70; autumn 67) and consumed more unique taxa overall (101) compared to brown trout < 300 mm (number of taxa—spring 28; summer 17; autumn 43; overall 49), burbot (number of taxa—spring 18; summer 15; autumn 26; overall 39) and lake trout (number of taxa—spring 12; autumn 4; overall 14;

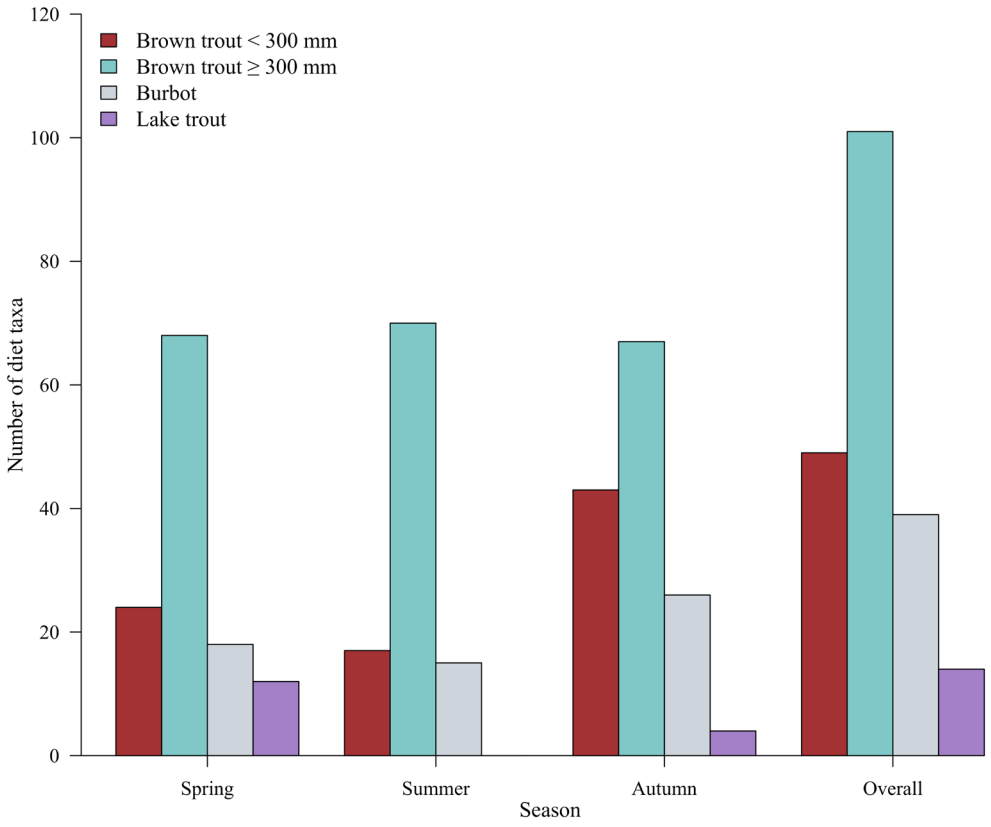


FIGURE 3 | The number of unique taxa found in diet contents of brown trout < 300 mm, brown trout ≥ 300 mm, burbot and lake trout by season within the Torrey Creek drainage, Wyoming, United States, for the years 2020–2022.

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Figure 3). However, when brown trout ≥300 mm had their sample size reduced, diet breadth (number of taxa—spring 33, 26–41 95% CI; summer 31, 23–40 95% CI; autumn 41, 33–48 95% CI) was similar to that of brown trout <300 mm. Brown trout ≥300 mm had the largest breadth of diet taxa consumed in summer, where a single individual had 20 different taxa identified in their diet (Figure 4). Although a single brown trout ≥300 mm had 20 diet taxa, the most abundant number of different diet taxa was one in spring (relative frequency = 0.20), six in summer (relative frequency = 0.17) and one in autumn (relative frequency = 0.20; Figure 4). Brown trout <300 mm followed the same trend with the most abundant number of unique diet taxa occurring in summer (six; relative frequency 0.33), and one for spring (relative frequency 0.21) and autumn (relative frequency 0.24). In contrast, burbot and lake trout had one diet item as the most abundant occurring in individual fish across all seasons (Figure 4).

3.1 | Frequency of Occurrence and Mean Proportion by Weight

Shifts in frequency of occurrence and mean proportion by weight were observed among all species during spring, summer and autumn. Brown trout, burbot and lake trout consumed multiple taxa, and only a limited number of taxa contributed more than 0.1 mean proportion by weight (Figure 5).

3.2 | Brown Trout <300 mm

Daphnia, Chironomidae and Leptoceridae were important prey resources for brown trout <300 mm among all seasons (Figure 5). Leptoceridae were the prominent diet items in spring (64% *O*; 0.21 *MW*) and *Daphnia* were the prominent forage for summer (67% *O*; 0.26 *MW*) and autumn (49% *O*; 0.27 *MW*). Additionally, Gammaridae was seasonally important during spring (36% *O*; 0.09 *MW*) and autumn (49% *O*; 0.19 *MW*) but was noticeably absent in the diets during summer.

3.3 | Brown Trout ≥300 mm

In spring, seven different diet items were present in more than 15% of diets. Gammaridae was the most frequently occurring (42%) and contributed the most to mean proportion by weight (0.12). In summer, brown trout ≥300 mm continued to exhibit a diverse diet, with eight diet categories occurring in more than

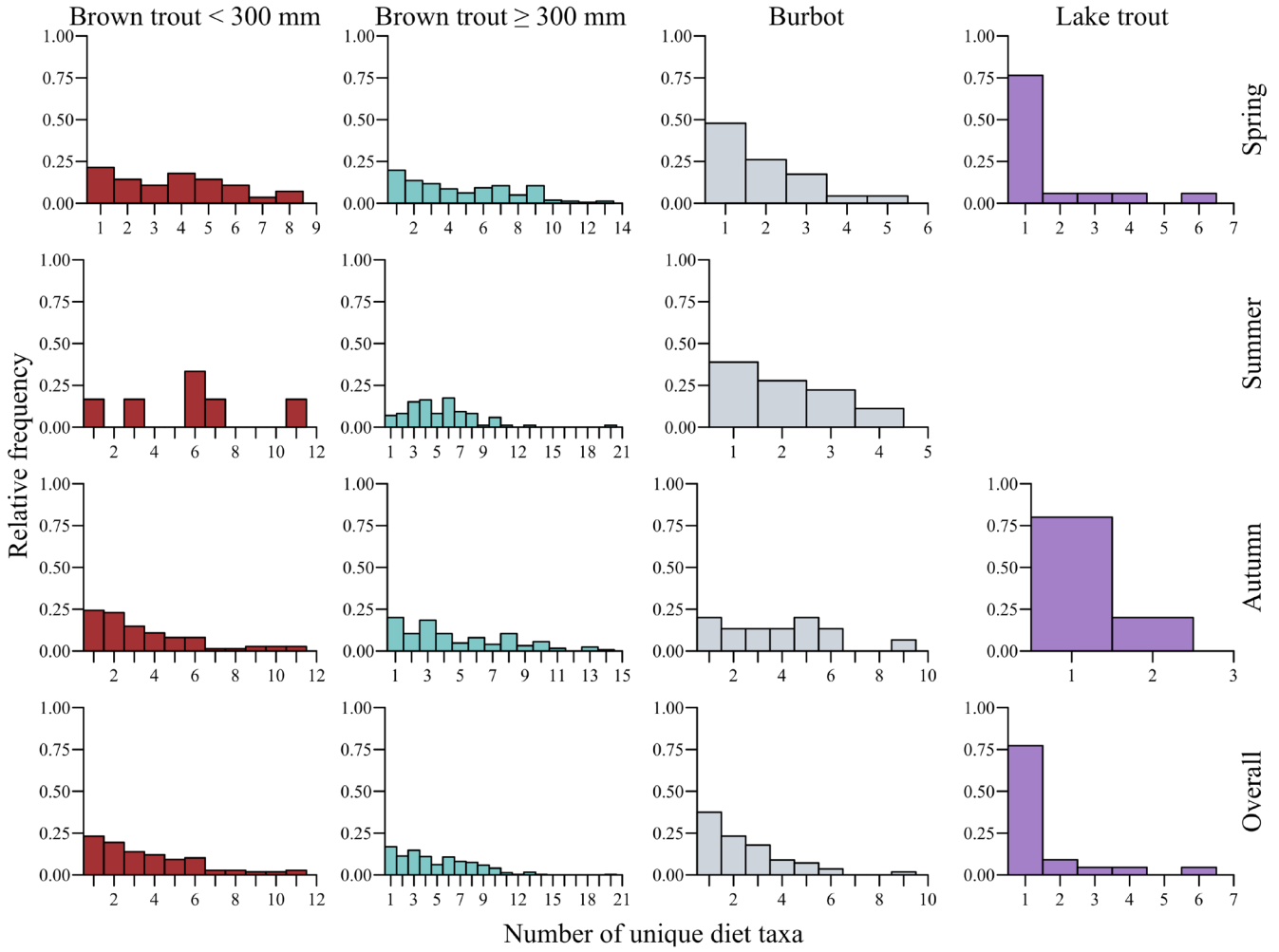


FIGURE 4 | Relative frequency of taxa found in diet contents of individual brown trout <300 mm, brown trout ≥300 mm, burbot and lake trout by season within the Torrey Creek drainage, Wyoming, United States, from 2020 to 2022.

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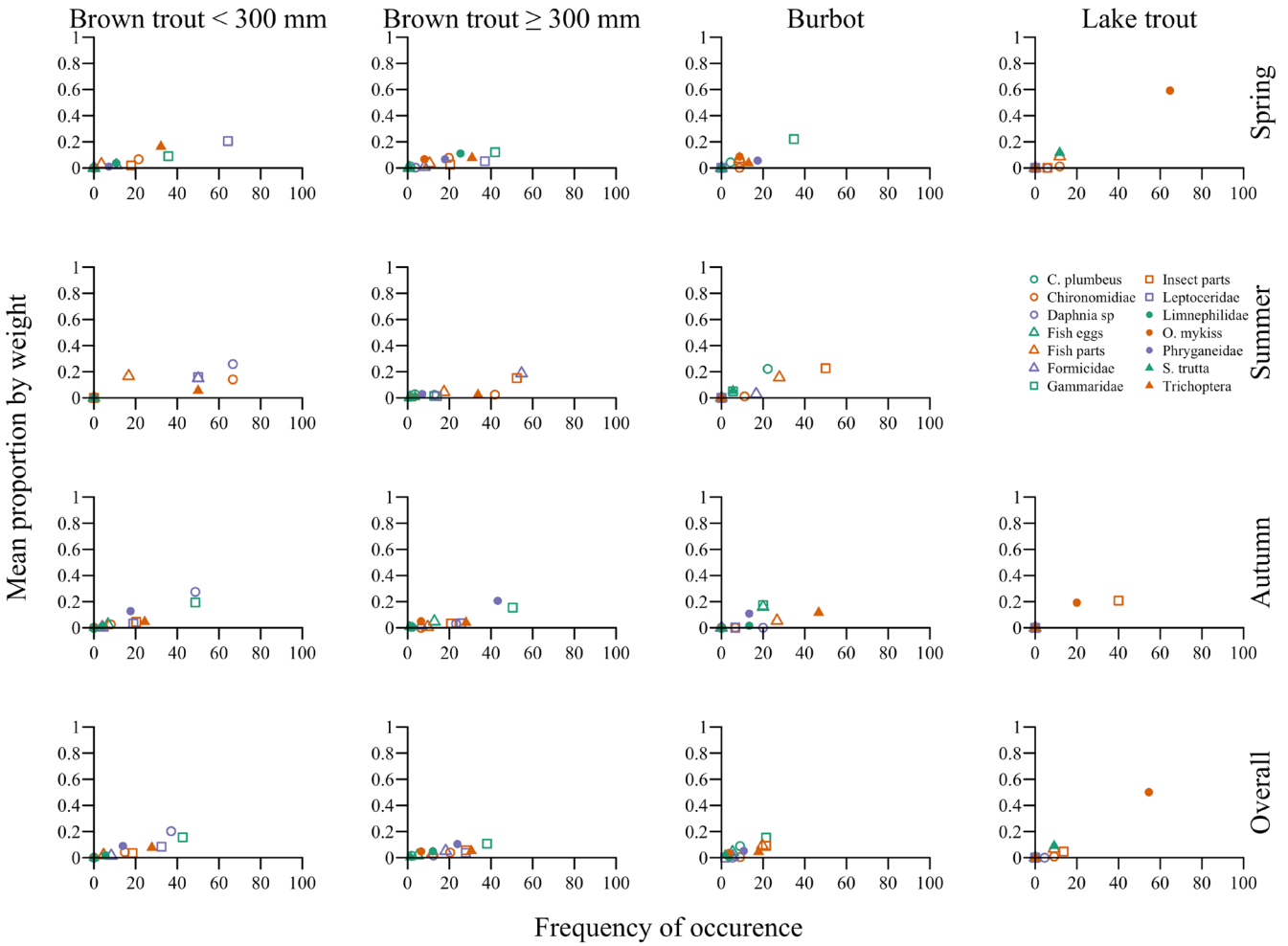


FIGURE 5 | Mean proportion by weight–frequency of occurrence plot for brown trout < 300 mm, brown trout ≥ 300 mm, burbot and lake trout by season and overall. Diet taxa that represented a minimum of 0.1 by mean proportion by weight for any combination of season and species were selected to be displayed resulting in 14 diet taxon categories. Diets were collected from the Torrey Creek drainage, Wyoming, United States, from the years 2020 to 2022.

10% of the diets. Formicidae had the highest frequency of occurrence (55%) and mean proportion by weight (0.19) in summer. Chironomidae followed as the next most frequently occurring diet item (42%), albeit contributing minimally to the mean proportion by weight (0.03). For autumn, Gammaridae occurred in 50% of diets constituting 0.15 mean proportion by weight and Phyrganeidae occurred in 43% of diets and 0.21 mean proportion by weight, thus representing the dominant prey taxa by mean proportion by weight.

3.4 | Burbot

During spring, Gammaridae dominated the dietary composition, accounting for the highest mean proportion by weight (0.22) and frequency of occurrence (35%; Figure 5). In summer, unidentifiable insect parts were the predominant dietary component, occurring in 50% of diets and the highest mean proportion by weight (0.23). Moreover, lake chub (0.22 *MW*; 22% *O*) and unidentifiable fish parts (0.15 *MW*; 28% *O*) constituted notable components compared to other taxa. For autumn, trichopteran parts occurred most frequently (47%) but only represented a 0.12 mean proportion by weight. However, two families of Trichoptera, Phryganeidae and Limnephilidae occurred in 13% of autumn diets each and contributed 0.11 and 0.02 mean percent by weight, respectively. Furthermore, fish eggs were also an important diet item in the autumn, occurring in 20% of diets and representing a 0.16 mean proportion by weight. Despite *Daphnia* being present in 27% of diets and unidentifiable fish parts being present in 20%, they made minimal contributions to the mean proportion by weight, 0.05 and 0.00, respectively.

3.5 | Lake Trout

During spring, lake trout had a concentrated dietary preference in comparison to brown trout and burbot, with rainbow trout constituting a substantial portion of their diet. Specifically, rainbow trout accounted for 0.59 mean proportion by weight and occurred in 65% of lake trout diets (Figure 5). In autumn, lake trout diets were characterised by a near-even split between rainbow trout (0.19) and unidentified insect parts (0.21), representing the largest mean proportions

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TABLE 1 | Mean proportion by weight and frequency of occurrence (in parenthesis) of fish prey consumed by brown trout < 300 mm, brown trout ≥ 300 mm, burbot and lake trout sampled from the Torrey Creek drainage, Wyoming, USA for all seasons combined for years 2020–2022.

	Predator			
Prey	**Brown trout < 300 mm**	**Brown trout ≥ 300 mm**	**Burbot**	**Lake trout**
Brown trout	0.00 (0.00)	0.00 (0.01)	0.02 (0.02)	0.09 (0.09)
Burbot	0.00 (0.00)	0.01 (0.01)	0.03 (0.04)	0.00 (0.00)
Fish parts	0.02 (0.05)	0.03 (0.12)	0.09 (0.20)	0.07 (0.09)
Lake chub	0.00 (0.00)	0.01 (0.02)	0.09 (0.09)	0.00 (0.00)
Longnose dace	0.01 (0.01)	0.02 (0.06)	0.03 (0.04)	0.00 (0.00)
Longnose sucker	0.00 (0.01)	0.03 (0.04)	0.05 (0.05)	0.07 (0.09)
Mountain whitefish	0.00 (0.00)	0.00 (0.01)	0.00 (0.00)	0.00 (0.00)
Rainbow trout	0.00 (0.00)	0.05 (0.06)	0.04 (0.04)	0.50 (0.55)
White sucker	0.00 (0.00)	0.02 (0.03)	0.01 (0.04)	0.09 (0.09)
Total fish prey	0.03 (0.07)	0.17 (0.29)	0.36 (0.48)	0.82 (0.82)

by weight; however, unidentified insect parts occurred more frequently than rainbow trout.

3.6 | Piscivory

Piscivory accounted for 0.82 mean proportion by weight for lake trout for all seasons combined, compared to 0.36 for burbot, 0.17 for brown trout ≥ 300 mm and 0.03 for brown trout < 300 mm (Table 1). Burbot rarely consumed brown trout, with an overall mean proportion by weight and frequency of occurrence of 0.02, and lake trout consumed brown trout infrequently, with an overall mean proportion by weight and frequency of occurrence of 0.09 (Table 1). Brown trout ≥ 300 mm consumed burbot minimally, representing 0.01 overall mean proportion by weight and frequency of occurrence (Table 1). Burbot and brown trout did not consume lake trout, and lake trout did not consume burbot within the Torrey Creek drainage. Cannibalism was documented in brown trout and burbot, albeit minimal. Brown trout cannibalism occurred in 0.01 of brown trout diets, and burbot cannibalism was only observed during spring and occurred in 0.09 of burbot and represented 0.08 of mean proportion by weight.

3.7 | Dietary Overlap and Trophic Positioning

Diet overlap values were less than 0.6 for all seasonal species combinations (Table 2). The highest levels of diet overlap between burbot and both brown trout groups were observed in autumn, with overlap values of 0.44 (Table 2). In contrast, lake trout exhibited a higher degree of diet overlap in spring with all other species combinations compared to autumn, having spring overlap values of 0.13 with brown trout < 300 mm, 0.20 with brown trout ≥ 300 mm and 0.28 with burbot. Notably, intraspecific diet overlap between brown trout < 300 mm and brown trout ≥ 300 mm in spring and autumn had the highest

TABLE 2 | Schoener's Index of Niche Overlap among burbot, brown trout < 300 mm, brown trout ≥ 300 mm and lake trout.

		Species		
Season	**Species**	**Brown trout < 300 mm**	**Brown trout ≥ 300 mm**	**Lake trout**
Spring	Burbot	0.32	0.05	0.28
	Brown trout < 300 mm		0.52	0.13
	Brown trout ≥ 300 mm			0.20
Summer	Burbot	0.20	0.37	
	Brown trout < 300 mm		0.31	
	Brown trout ≥ 300 mm			
Autumn	Burbot	0.44	0.44	0.10
	Brown trout < 300 mm		0.57	0.05
	Brown trout ≥ 300 mm			0.14
Overall	Burbot	0.45	0.55	0.32
	Brown trout < 300 mm		0.60	0.14
	Brown trout ≥ 300 mm			0.26

Note: Niche overlap was calculated from lowest taxonomic identification, species for fishes and family for invertebrates. Fish were collected from the Torrey Creek drainage, Wyoming, USA in 2020–2022. No lake trout were sampled in summer across all years.

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overlap of all seasonal comparisons, and was noteworthy overall with a value of 0.6 (Table 2).

All species were at a similar trophic level in relation to $\delta^{15}N$ from stable isotope signatures. The centre point for 40% Bayesian ellipses of $\delta^{15}N$ varied from 7.8‰ for brown trout < 300 mm to 10.2‰ for lake trout (Figure 6). Based on $\delta^{13}C$, burbot exhibited the most enriched carbon signature at −19.1‰ compared to brown trout < 300 mm (−21.7‰), brown trout ≥ 300 mm (−20.3‰), and lake trout(−22.6‰ Figure 6). Isotopic niche overlap was low for the 40% standard Bayesian ellipses among all pairings (Figure 6). Burbot and brown trout ≥ 300 mm had the highest overlap of 40% ellipses (39%), burbot and lake trout had a 1% overlap and brown trout ≥ 300 mm and lake trout had a 13% overlap. Brown trout < 300 mm shared no overlap with any other species grouping.

4 | Discussion

We predicted burbot, brown trout and lake trout would have been highly piscivorous in the Torrey Creek system; however, there was a low prevalence of fish in the diets of brown trout and burbot. Lake trout exhibited the highest level of piscivory, which was mostly a function of lake trout consuming stocked rainbow trout. Similar increases in piscivory by salmonids have been observed in other systems when stocked fish are available (Hasegawa et al. 2012; Honda et al. 2024); however, it is interesting that lake trout disproportionately took advantage of this increased prey resource compared to brown trout and burbot.

Reciprocal predation of piscivorous fishes (i.e., among brown trout, burbot and lake trout) was minimal except for lake trout predation on brown trout, thus reciprocal intraguild predation is not currently occurring in the Torrey Creek drainage. However, unidentifiable fish parts were observed in 12% of brown trout ≥ 300 mm and 20% of burbot. Thus, some species-specific predation values may have been slightly underestimated. Although lake trout predated on brown trout, the minimal dietary overlap between lake trout and brown trout does not suggest competition is occurring between these species; therefore, the lake trout and brown trout ecological interaction could be described as simple intraguild predation, where only one predator consumes the other (van der Hammen et al. 2010). This was similarly observed in Arctic char (*Salvelinus alpinus*) and brown trout, where intraguild predation was present but had limited evidence of interspecific competition (Persson et al. 2013).

Surprisingly, we did not document any predation occurring between burbot and lake trout within the Torrey Creek drainage. Burbot and lake trout overlap in their native range and demonstrate reciprocal intraguild predation in other systems (Martin 1970; Jacobs et al. 2010; Gorman and Sitar 2013). Our lack of observed predation on lake trout by burbot could be related to the hypothesised limited recruitment of lake trout within the Torrey Creek drainage; however, burbot and lake trout have been documented co-occurring without negative interactions in other systems (Van Oosten and Deason 1938). The frequent stocking of rainbow trout within the Torrey Creek drainage, occurring up to six times per year, could serve as a buffer to protect burbot from lake trout predation. Lake trout took advantage of the repetitively stocked rainbow trout, potentially decreasing the demand for other prey species as stocked fishes are generally naïve to predators (Warner et al. 1968; Hoxmeier and Wahl 2002; Freedman et al. 2012; Becher et al. 2021).

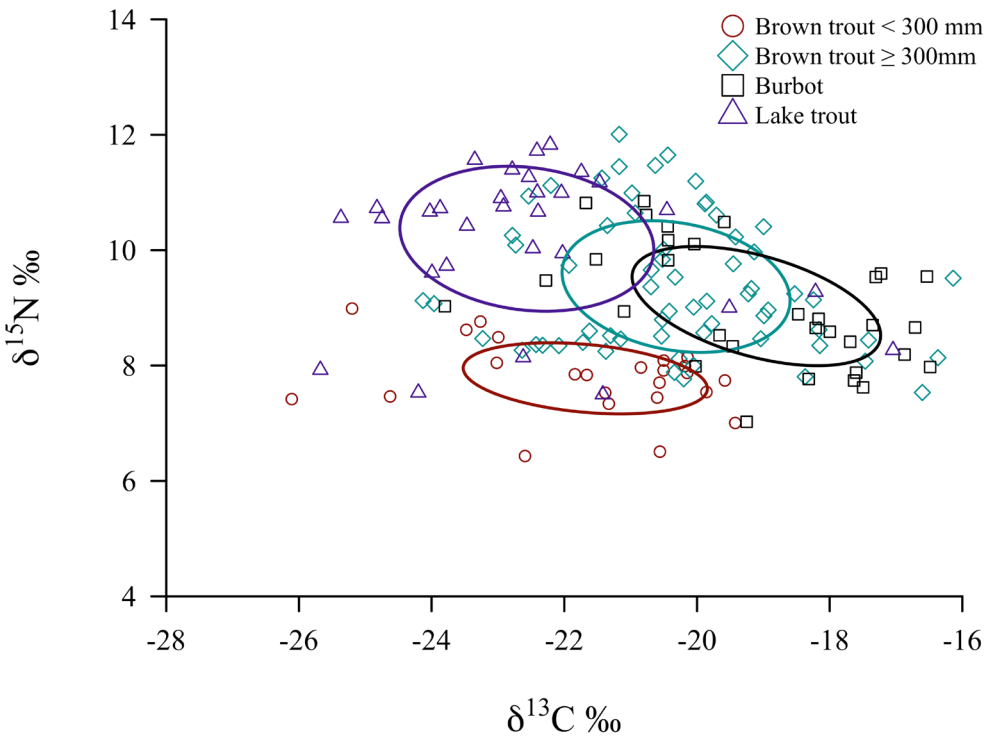


FIGURE 6 | Stable isotope biplot of brown trout < 300 mm, brown trout ≥ 300 mm, burbot and lake trout tissue samples collected from Torrey Creek drainage, Wyoming, United States in 2020 and 2021. Ellipses represent 40% Bayesian standard ellipse areas for stable isotope signatures.

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Cannibalism was documented in brown trout and burbot within the Torrey Creek drainage. Our study revealed that instances of cannibalism among brown trout were relatively infrequent, which is congruent with other research (L'Abée-Lund et al. 1992; Vik et al. 2001; Montori et al. 2006). Conversely, our estimate of the frequency of burbot cannibalism (3%) is lower than reported in the literature where burbot cannibalism varies from 16% to 93% (Jacobs et al. 2010; Knudsen et al. 2010; Gallagher and Dick 2015). Several hypotheses exist for why burbot may cannibalise, including accumulating energy for growth or reproduction (Gallagher and Dick 2015), when competition for shared resources exists (Polis 1988), or lack of refuge (Smith and Reay 1991). However, instances of burbot populations not exhibiting cannibalism have been documented (Fratt et al. 1997; Tolonen et al. 1999; Knudsen et al. 2010).

Diet overlap values among burbot, brown trout and lake trout were minimal by season but increased when compared with all seasons combined, especially for burbot and brown trout ≥ 300 mm. Although burbot in the Torrey Creek drainage consumed less fish than in other systems, we report comparable values of Schoener's index of niche overlap between burbot and lake trout (0.32) to that reported for northern Lake Michigan (0.39; Jacobs et al. 2010). Likely, the separation in diets among burbot, brown trout and lake trout in the Torrey Creek drainage is a response to reduce interspecific competition among these species (Putman and Wratten 1984; Gabler and Amundsen 2010).

Lake trout had the highest trophic position, largely due to their degree of piscivory, as indicated by $\delta^{15}N$. However, they shared a similar trophic level with burbot and brown trout ≥ 300 mm, with a trophic level difference in lakes being represented as a difference of 3.40‰ ± 1.1 in $\delta^{15}N$ (Wada et al. 1991; Zanden and Rasmussen 1999). Notably, some individual brown trout ≥ 300 mm exhibited the higher $\delta^{15}N$ values compared to those of lake trout. This is likely because larger individuals can consume larger prey leading to a more piscivorous diet (Scott and Crossman 1973; Cott et al. 2011). Based on $\delta^{13}C$ values, burbot and lake trout appear to specialise in obtaining their diet from different zones of the lakes (i.e., pelagic and littoral; France 1995). Lake trout had the lowest $\delta^{13}C$ values, indicating a more pelagic origin of carbon, particularly compared to burbot, which had the highest $\delta^{13}C$ values. This is likely due to lake trout predominantly occupying limnetic habitats (Evans 2007; Cott et al. 2011) and feeding on rainbow trout in comparison to burbot consuming larger proportions of macroinvertebrates and fish such as lake chub. Brown trout, both < 300 mm and ≥ 300 mm, had $\delta^{13}C$ values between those of burbot and lake trout, suggesting they feed less exclusively from a single zone. Despite burbot, brown trout ≥ 300 mm and lake trout sharing a similar trophic level, there was no major overlap in isotopic niches according to the stable isotope data. These findings align with the low dietary overlap observed among the species, indicating that both short- and long-term overlaps are likely minimal among these piscivorous predators.

Our results indicate that brown trout or lake trout are not the mechanism for the decline in burbot within the Torrey Creek drainage. However, our finding of limited competition and predation represents ecological interactions among burbot, brown trout and lake trout for the years 2020–2023. Historically, burbot were more abundant in the Torrey Creek drainage, but biologists have been concerned about their decline since the 1990s (Krueger 1997). Survival of age-4 and older burbot was estimated to decrease from 0.60 in 1969–1970 to 0.43 in 1995–1996 (Hubert et al. 2008) and catch rates in fyke nets decreased from 0.22/h to 0.35/h in 1995–1996 to 0.02/h in 2018 (Krueger 1996; Wyoming Game and Fish Department 2019). In 2017, burbot were found in two of six brown trout stomachs sampled (Wyoming Game & Fish Department 2018), suggesting a predatory interaction between the species. It is plausible that brown trout and lake trout predation on burbot in the past has driven the burbot population to such a low abundance that burbot are currently rarely encountered by their intraguild members and thus not frequently consumed. This scenario parallels the situation observed with lake trout and Yellowstone cutthroat trout after lake trout introduction to Yellowstone Lake, where the decline in Yellowstone cutthroat trout populations led to lake trout exhibiting prey plasticity (Syslo et al. 2016; Glassic et al. 2024).

The coexistence dynamics among burbot, brown trout and lake trout within the Torrey Creek drainage are intricately tied to the interplay of competition and predation dynamics among these apex predators. The coexistences hinge on the absence of significant competitive pressures and predation intensity within the ecosystem. The presence of ample resources and productivity in the Torrey Creek system fosters the potential for alternative stable states to emerge among these predators. Particularly, the phenomenon of prey switching, where predators adjust their foraging preferences based on the relative abundance of prey species, plays a pivotal role in sustaining this coexistence framework, especially in regard to an intraguild predation interaction (Holt and Huxel 2007; Nishijima et al. 2014). Intricate ecological interactions, such as those presented here, underscore the complexity of predator–prey relationships and highlight the importance of resource availability in shaping community dynamics within aquatic ecosystems.

Author Contributions

All co-authors developed the conceptual framework and study design; R.W.E., P.C.G., J.W.D., T.E.N., M.A.S. conducted fieldwork; R.W.E. and C.S.G. led the analyses and manuscript preparation with support from all co-authors.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data available upon reasonable request.

References

Bacheler, N. M., J. W. Neal, and R. L. Noble. 2004. "Diet Overlap Between Native Bigmouth Sleepers (*Gobiomorus dormitor*) and Introduced Predatory Fishes in a Puerto Rico Reservoir." *Ecology of Freshwater Fish* 13: 111–118.

Becher, C., S. M. Tyszko, R. D. Zweifel, J. D. Conroy, J. J. Pritt, and S. A. Ludsin. 2021. "Alternative Prey Reduces Largemouth Bass Predation Mortality on Newly Stocked Channel Catfish Fingerlings." *North American Journal of Fisheries Management* 41: 1322–1333.

Carey, M. P., B. L. Sanderson, T. A. Friesen, K. A. Barnas, and J. D. Olden. 2011. "Smallmouth Bass in the Pacific Northwest: A Threat to Native Species; a Benefit for Anglers." *Reviews in Fisheries Science* 19: 305–315.

Chipps, S., and J. Garvey. 2007. "Assessment of Diets and Feeding Patterns." In *Analysis and Interpretation of Freshwater Fisheries Data*, 473–514. USA.

Connell, K. 1977. "Summary of Fisheries Investigations Conducted on Ring Lake." Wyoming Game & Fish Department, Fish Division, Administrative Report. Project 2077-14-7604.

Connell, K. 1978. "Summary of Fisheries Investigations Conducted on Torrey Lake." Wyoming Game & Fish Department, Fish Division, Administrative Report. Project 2076-14-7603.

Cott, P. A., T. A. Johnston, and J. M. Gunn. 2011. "Food Web Position of Burbot Relative to Lake Trout, Northern Pike, and Lake Whiteifsh in Four Sub-Arctic Boreal Lakes." *Applied Ichthyology* 27: 49–56.

Creel, S., W. Matandiko, P. Schuette, et al. 2018. "Changes in African Large Carnivore Diets Over the Past Half-Century Reveal the Loss of Large Prey." *Journal of Applied Ecology* 55: 2908–2916.

Dextrase, A. J., and M. A. Coscarelli. 1999. "Intentional Introductions of Nonindigenous Freshwater Organisms in North America." In *Nonindigenous Freshwater Organisms*, edited by R. Claudi and J. H. Leach, 61–98. Lewis Publishers.

Donald, D. B., and D. J. Alger. 1993. "Geographic Distribution, Species Displacement, and Niche Overlap for Lake Trout and Bull Trout in Mountain Lakes." *Canadian Journal of Zoology* 71: 238–247.

Eby, L. A., W. J. Roach, L. B. Crowder, and J. A. Stanford. 2006. "Effects of Stocking-Up Freshwater Food Webs." *Trends in Ecology & Evolution* 21: 576–584.

Ellis, B. K., J. A. Stanford, D. Goodman, et al. 2011. "Long-Term Effects of a Trophic Cascade in a Large Lake Ecosystem." *Proceedings of the National Academy of Sciences* 108: 1070–1075.

Evans, D. O. 2007. "Effects of Hypoxia on Scope-For-Activity and Power Capacity of Lake Trout (*Salvelinus namaycush*)." *Canadian Journal of Aquatic Sciences* 64: 345–361.

France, R. L. 1995. "Differentiation Between Littoral and Pelagic Food Webs in Lakes Using Stable Carbon Isotopes." *Limnology and Oceanography* 40: 1313–1321.

Fratt, T. W., D. W. Coble, F. Copes, and R. E. Bruesewitz. 1997. "Diet of Burbot in Green Bay and Western Lake Michigan With Comparison to Other Waters." *Journal of Great Lakes Research* 23: 1–10.

Freedman, J. A., R. J. H. Hoxmeier, L. M. Einfalt, R. C. Brooks, and D. H. Wahl. 2012. "Largemouth Bass Predation Effect on Stocked Walleye Survival in Illinois Impoundments." *North American Journal of Fisheries Management* 32: 1039–1045.

Fritts, A. L., and T. N. Pearsons. 2004. "Smallmouth Bass Predation on Hatchery and Wild Salmonids in the Yakima River, Washington." *Transactions of the American Fisheries Society* 133: 880–895.

Gabler, H. M., and P. A. Amundsen. 2010. "Feeding Strategies, Resource Utilization and Potential Mechanisms for Competitive Coexistence of Atlantic Salmon and Alpine Bullhead in a Sub-Arctic River." *Aquatic Ecology* 44: 325–336.

Gallagher, C. P., and T. A. Dick. 2015. "Winter Feeding Ecology and the Importance of Cannibalism in Juvenile and Adult Burbot (*Lota lota*) From the Mackenzie Delta, Canada." *Hydrobiologia* 757: 73–88.

Garvey, J., and S. Chipps. 2012. "Diets and Energy Flow." In *Fisheries Techniques*, edited by A. V. Zale, D. L. Parrish, and T. M. Sutton, 733–780. American Fisheries Society.

Glaid, J., P. C. Gerrity, and C. S. Guy. 2021. "Burbot (*Lota lota*) Exhibit Plasticity in Life-History Traits in a Small Drainage at the Southwestern-Most Extent of the Species' Native Range." *Journal of Applied Ichthyology* 37: 875–884.

Glassic, H. C., D. D. Chagaris, C. S. Guy, et al. 2024. "Yellowstone Cutthroat Trout Recovery in Yellowstone Lake: Complex Interactions Among Invasive Species Suppression, Disease, and Climate Change." *Fisheries* 49: 55–70.

Gorman, O. T., and S. P. Sitar. 2013. "Ups and Downs of Burbot and Their Predator Lake Trout in Lake Superior, 1953–2011." *Transactions of the American Fisheries Society* 142: 1757–1772.

Guzzo, M. M., G. D. Haffner, N. D. Legler, S. A. Rush, and A. T. Fisk. 2013. "Fifty Years Later: Trophic Ecology and Niche Overlap of a Native and Non-Indigenous Fish Species in the Western Basin of Lake Erie." *Biological Invasions* 15: 1695–1711.

Hakala, J. P., and F. D. Johnson. 2004. "Evaluation of a Gastric Lavage Method for Use on Largemouth Bass." *North American Journal of Fisheries Management* 24: 1398–1403.

Hasegawa, K., C. Yamazaki, T. Ohta, and K. Ohkuma. 2012. "Food Habits of Introduced Brown Trout and Native Masu Salmon Are Influenced by Seasonal and Locational Prey Availability." *Fisheries Science* 78: 1163–1171.

Henkanaththegedara, S. M., and C. A. Stockwell. 2014. "Intraguild Predation May Facilitate Coexistence of Native and Non-Native Fish." *Journal of Applied Ecology* 51: 1057–1065.

Hershey, A. E., R. M. Northington, J. C. Finlay, and B. J. Peterson. 2017. "Chapter 23—Stable Isotopes in Stream Food Webs." In *Methods in Stream Ecology*, edited by G. A. Lamberti and F. R. Hauer, 3–20. Academic Press.

Holt, R. D., and G. R. Huxel. 2007. "Alternative Prey and the Dynamics of Intraguild Predation: Theoretical Perspectives." *Ecology* 88: 2706–2712.

Honda, K., K. Hasegawa, M. Ban, Y. Yano, and Y. Ogura. 2024. "Massive Stocking of Chum Salmon (*Oncorhynchus keta*) Fry Fattens Non-Native Brown Trout (*Salmo trutta*) in Hokkaido Japan." *PLoS One* 19: e0307552.

Hooley-Underwood, Z., E. G. Mandeville, P. Gerrity, J. Deromedi, K. Johnson, and A. W. Walters. 2018. "Combining Genetic, Isotopic, and Field Data to Better Describe the Influence of Dams and Diversions on Burbot Movement in the Wind River Drainage, Wyoming." *Transactions of the American Fisheries Society* 147: 606–620.

Hoxmeier, J., and D. Wahl. 2002. *Evaluation of Supplemental Stocking of Largemouth Bass Across Reservoirs: Effects of Predation, Prey Availability, and Natural Recruitment*, 639–647. American Fisheries Society Symposium. American Fisheries Society.

Hubert, W. A., D. Dufek, J. W. Deromedi, K. Johnson, S. Roth, and D. Skates. 2008. "Burbot in the Wind River Drainage of Wyoming: Knowledge of Stocks and Management Issues." In *Burbot: Ecology,*

16000633, 2025, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/eff.70001 by Montana State University Library, Wiley Online Library on [20/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Management, and Culture, edited by V. L. Paragamian and D. H. Bennett, 187–199. American Fisheries Society Symposium 59.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. "Comparing Isotopic Niche Widths Among and Within Communities: SIBER—Stable Isotope Bayesian Ellipses in R." *Journal of Animal Ecology* 80: 595–602.

Jacobs, G. R., C. P. Madenjian, D. B. Bunnell, and J. D. Holuszko. 2010. "Diet of Lake Trout and Burbot in Northern Lake Michigan During Spring: Evidence of Ecological Interaction." *Journal of Great Lakes Research* 36: 312–317.

Jensen, H., K. K. Kahilainen, P.-A. Amundsen, et al. 2008. "Predation by Brown Trout (*Salmo trutta*) Along a Diversifying Prey Community Gradient." *Canadian Journal of Fisheries and Aquatic Sciences* 65: 1831–1841.

Jensen, H., M. Kiljunen, and P.-A. Amundsen. 2012. "Dietary Ontogeny and Niche Shift to Piscivory in Lacustrine Brown Trout *Salmo trutta* Revealed by Stomach Content and Stable Isotope Analyses." *Journal of Fish Biology* 80: 2448–2462.

Knudsen, R., P.-A. Amundsen, and A. Klemetsen. 2010. "Arctic Charr in Sympatry With Burbot: Ecological and Evolutionary Consequences." *Hydrobiologia* 650: 43–54.

Koel, T. M., L. M. Tronstad, J. L. Arnold, et al. 2019. "Predatory Fish Invasion Induces Within and Across Ecosystem Effects in Yellowstone National Park." *Science Advances* 5: 1139.

Krueger, K. L. 1996. *Assessment of Lentic Sport Fisheries for Burbot and Sauger in the Bighorn/Wind River Drainage*. University of Wyoming, Laramie.

Krueger, K. L. 1997. "Assessment of Lentic Burbot Populations in the Big Horn/Wind River Drainage, Wyoming." *Journal of Freshwater Fish* 12: 453–464.

L'Abée-Lund, J. H., A. Langeland, and H. Sægrov. 1992. "Piscivory by Brown Trout *Salmo trutta L.* and Arctic Charr *Salvelinus alpinus* (L.) in Norwegian Lakes." *Journal of Fish Biology* 41: 91–101.

Lester, N. P., P. E. Bailey, and W. A. Hubert. 2009. "Chapter 6: Coldwater Fish in Small Standing Waters." In *Standard Methods for Sampling North American Freshwater Fishes*, edited by S. A. Bonar, W. A. Hubert, and D. W. Willis, 85–96. American Fisheries Society.

Lewandoski, S. A., C. S. Guy, A. V. Zale, et al. 2017. "Empirical Estimation of Recreational Exploitation of Burbot, *Lota lota*, in the Wind River Drainage of Wyoming Using a Multistate Capture–Recapture Model." *Fisheries Management and Ecology* 24: 298–307.

Light, R. W., P. H. Andler, and D. E. Arnold. 1983. "Evaluation of Gastric Lavage for Stomach Analysis." *North American Journal of Fisheries Management* 3: 81–85.

Martin, N. V. 1970. "Long-Term Effects of Diet on the Biology of the Lake Trout and the Fishery in Lake Opeongo, Ontario." *Journal of the Fisheries Research Board of Canada* 27: 125–146.

McMahon, T. E., and D. H. Bennett. 1996. "Walleye and Northern Pike." *Fisheries* 21: 6–13.

Minagawa, M., and E. Wada. 1984. "Stepwise Enrichment of 15N Along Food Chains: Further Evidence and the Relation Between $\delta^{15}N$ and Animal Age." *Geochimica et Cosmochimica Acta* 48: 1135–1140.

Montori, A., J. M. Tierno De Figueroa, and X. Santos. 2006. "The Diet of the Brown Trout *Salmo trutta* (L.) During the Reproductive Period: Size-Related and Sexual Effects." *International Review of Hydrobiology* 91: 438–450.

Moyle, P. B., and T. Light. 1996a. "Fish Invasions in California: Do Abiotic Factors Determine Success?" *Ecology* 77: 1666–1670.

Moyle, P. B., and T. Light. 1996b. "Biological Invasions of Fresh Water: Empirical Rules and Assembly Theory." *Biological Conservation* 78: 149–161.

Næsje, T. F., O. T. Sandlund, and R. Saksgård. 1998. "Selective Predation of Piscivorous Brown Trout (*Salmo trutta* L.) on Polymoprhic Whitefish (*Coregonus lavaretus* L.)." *Ergebnisse der Limnologie* 50: 283–294.

Nishijima, S., G. Takimoto, and T. Miyashita. 2014. "Roles of Alternative Prey for Mesopredators on Trophic Cascades in Intraguild Predation Systems: A Theoretical Perspective." *American Naturalist* 183: 625–637.

Persson, L., P. A. Amundsen, A. M. De Roos, R. Knudsen, R. Primicerio, and A. Klemetsen. 2013. "Density-Dependent Interactions in an Arctic Char—Brown Trout System: Competition, Predation, or Both?" *Canadian Journal of Fisheries and Aquatic Sciences* 70: 610–616.

Pettitt-Wade, H., K. W. Wellband, D. D. Heath, and A. T. Fisk. 2015. "Niche Plasticity in Invasive Fishes in the Great Lakes." *Biological Invasions* 17: 2565–2580.

Polis, G. A. 1988. "Exploitation Competition and the Evolution of Interference, Cannibalism, and Intraguild Predation in Age/Size-Structured Populations." In *Size-Structured Populations*, edited by B. Ebenman and L. Persson, 185–202. Springer.

Putman, R. J., and S. D. Wratten. 1984. "Interspecific Competition and Community Structure." In *Principles of Ecology*, 127–151. Springer Netherlands.

R Core Team. 2022. "R: A Language and Environment for Statistical Computing." R Foundation for Statistical Computing: Vienna, Austria. https://www.R-project.org/.

Robinson, B. W., T. L. Booms, M. J. Bechard, and D. L. Anderson. 2019. "Dietary Plasticity in a Specialist Predator, the Gyrfalcon (*Falco rusticolus*): New Insights Into Diet During Brood Rearing." *Journal of Raptor Research* 53: 115–126.

Roseman, E. F., J. S. Schaeffer, E. Bright, and D. G. Fielder. 2014. "Angler-Caught Piscivore Diets Reflect Fish Community Changes in Lake Huron." *Transactions of the American Fisheries Society* 143: 1419–1433.

Sanderson, B. L., K. A. Barnas, and A. M. W. Rub. 2009. "Nonindigenous Species of the Pacific Northwest: An Overlooked Risk to Endangered Salmon?" *Bioscience* 59: 245–256.

Saylor, R. K., N. W. R. Lapointe, and P. L. Angermeier. 2012. "Diet of Non-Native Northern Snakehead (*Channa argus*) Compared to Three Co-Occurring Predators in the Lower Potomac River, USA." *Ecology of Freshwater Fish* 21: 443–452.

Schoener, T. W. 1970. "Nonsynchronous Spatial Overlap of Lizards in Patchy Habitats." *Ecology* 51: 408–418.

Scott, W. B., and E. J. Crossman. 1973. *Freshwater Fishes of Canada*, 966. Fisheries Research Board of Canada.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. "Patterns of Predation in a Diverse Predator—Prey System." *Nature* 425: 288–290.

Smith, C., and P. Reay. 1991. "Cannibalism in Teleost Fish." *Reviews in Fish Biology and Fisheries* 1: 41–64.

Syslo, J. M., C. S. Guy, and T. M. Koel. 2016. "Feeding Ecology of Native and Nonnative Salmonids During the Expansion of a Nonnative Apex Predator in Yellowstone Lake, Yellowstone National Park." *Transactions of the American Fisheries Society* 145: 476–492.

Taniguchi, Y., K. D. Fausch, and S. Nakano. 2002. "Size-Structured Interactions Between Native and Introduced Species: Can Intraguild Predation Facilitate Invasion by Stream Salmonids?" *Biological Invasions* 4: 223–233.

Tolonen, A., J. Kjellman, and J. Lappalainen. 1999. "Diet Overlap Between Burbot (*Lota lota* (L.)) and Whitefish (*Coregonus lavaretus* (L.)) in a Subarctic Lake." *Annales Zoologici Fennici* 36: 205–214.

Tronstad, L. M., R. O. Hall Jr., T. M. Koel, and K. G. Gerow. 2010. "Introduced Lake Trout Produced a Four-Level Trophic Cascade in Yellowstone Lake." *Transactions of the American Fisheries Society* 139: 1536–1550.

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van der Hammen, T., A. M. de Roos, M. W. Sabelis, and A. Janssen. 2010. "Order of Invasion Affects the Spatial Distribution of a Reciprocal Intraguild Predator." *Oecologia* 163: 79–89.

Van Oosten, J., and H. J. Deason. 1938. "The Food of the Lake Trout (*Cristivomer namaycush namaycush*) and of the Lawyer (*Lota maculosa*) of Lake Michigan." *Transactions of the American Fisheries Society* 67: 155–177.

Vandeberg, G. S., and J. A. VanLooy. 2016. "Continental Glacier Meltwater Contributions to Late Summer Stream Flow and Water Quality in the Northern Wind River Range, Wyoming, USA." *Environmental Earth Sciences* 75: 389.

Vejřík, L., I. Vejříková, P. Blabolil, et al. 2017. "European Catfish (*Silurus glanis*) as a Freshwater Apex Predator Drives Ecosystem via Its Diet Adaptability." *Scientific Reports* 7: 15970.

Vik, J. O., R. Borgstrøm, and Ø. Skaala. 2001. "Cannibalism Governing Mortality of Juvenile Brown Trout, *Salmo trutta*, in a Regulated Stream." *Regulated Rivers: Research & Management* 17: 583–594.

Wada, E., H. Mizutani, and M. Minagawa. 1991. "The Use of Stable Isotopes for Food Web Analysis." *Critical Reviews in Food Science and Nutrition* 30: 361–371.

Wallace, R. K., Jr. 1981. "An Assessment of Diet-Overlap Indexes." *Transactions of the American Fisheries Society* 110: 72–76.

Wang, S., U. Brose, and D. Gravel. 2019. "Intraguild Predation Enhances Biodiversity and Functioning in Complex Food Webs." *Ecology* 100: e02616.

Warner, K., R. P. AuClair, S. E. DeRoche, K. A. Havey, and C. F. Ritzi. 1968. "Fish Predation on Newly Stocked Landlocked Salmon." *Journal of Wildlife Management* 32: 712–717.

Werner, E. E., and J. F. Gilliam. 1984. "The Ontogenetic Niche and Species Interactions in Size-Structured Populations." *Annual Review of Ecology, Evolution, and Systematics* 15: 393–425.

Wyoming Game and Fish Department. 2018. *Annual Progress Report on the 2017 Work Schedule*. Wyoming Game & Fish Department, Fish Division.

Wyoming Game and Fish Department. 2019. *Annual Progress Report on the 2018 Work Schedule*. Wyoming Game & Fish Department, Fish Division.

Zanden, M. J. V., and J. B. Rasmussen. 1999. "Primary Consumer $\delta^{13}C$ and $\delta^{15}N$ and the Trophic Position of Aquatic Consumers." *Ecology* 80: 1395–1404.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

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