

Quantifying foraging ecology of two introduced apex predators in Wyoming reservoirs

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Introduction

Predation is one of the most important biological drivers of community and ecosystem structure and function (Carpenter et al. 1987; Hairston, Smith & Slobodkin 1960; Hairston & Hairston 1993). Apex predators occupy the highest trophic position in an ecosystem and are often large, effective hunters with the ability to self-regulate their population (Ritchie & Johnson 2009; Wallach et al. 2015). These predators play a pivotal role in structuring ecosystems by regulating lower trophic levels through top-down control. Trophic cascades initiated by changes in predation rates can alter or entirely restructure food webs through mesopredator release (Polis et al. 2000). For example, zooplankton, a primary consumer, abundance is highly dependent upon the presence or absence of mesopredators which in turn depends on the presence or absence of apex predators. Changes in zooplankton communities following altered food web interactions can restructure primary production of ecosystems (Carpenter et al., 1987; Berthold et al. 2023; Tronstad et al. 2010). Similarly, in terrestrial ecosystems, the introduction of an apex predator like the gray wolf (*Canis lupus*) can increase primary production through mesopredator release (Fortin et al. 2005; Ripple & Beschta 2012). While numerous examples from terrestrial and aquatic ecosystems around the globe highlight the important role of apex predators in structuring food webs (Carpenter et al. 1987; Dulvy, Freckleton & Polunin 2004; Vander Zanden, Casselman & Rasmussen 1999), this remains a highly debated topic in ecology that requires further investigation (Alston et al. 2019).

Predators are generally assumed to be highly mobile adaptive generalists, capable of consuming diverse prey resources to maintain growth and reproduction as prey availability fluctuates while incorporating various levels of opportunistic foraging (Bozek, Baccante & Lester 2011; Chavarie et al. 2016; McMeans et al. 2016; Rooney, McCann & Moore 2008). The capacity of predators to adaptively forage is often context-dependent and driven by environmental and biotic factors, such as habitat availability and the characteristics of the prey community, that can change across predators' ontogenetic shifts (Agrawal et al. 2007). The impact of predation on population growth rates, size structures, and abundances of species throughout the food web is predicted to be stronger in aquatic than terrestrial ecosystems, highlighting the importance of apex predators in aquatic ecosystems, especially lakes (Shurin, Gruner & Hillebrand 2007). Environmental variables driving aquatic food web interactions include, but are not limited to, thermal structure, nutrient availability, and water clarity. Size structure and abundance of predators and their prey are often the most influential biotic variables as gape limitation regulates size-structured interactions in aquatic food webs (Brose et al. 2019; Lester et al. 2004; Persson et al. 1996; Turesson et al. 2007). Prey vulnerability (e.g., sensory capabilities, speed, visibility, and morphology) also structures these interactions (Tronstad et al. 2010) and can change along

environmental gradients. This linkage between the size structure and abundance of predators and prey can become unbalanced, altering ecosystem structure and function and modifying food web architecture.

Consumer foraging strategies, often classified as generalists or specialists, are an important driver of direct and indirect effects of predation on food web architecture (Bolnick et al. 2003; Ceia & Ramos 2015, Stewart et al. 2021). These strategies refer to the type (niche position) and range (niche width) of resources used. Generalist niches are typically large and overlap with other species while specialist niches are small and isolated relative to other species (Chase & Leibold 2003); however, this is dependent on the degree of generalization across time and space (Flaherty & Ben-David 2010). Generalist predators can reduce inter- and intraspecific competition as individuals utilize a broad range of resources, while specialized predators may reduce interspecific competition but experience greater intraspecific competition with conspecifics that compete for the same resources (Schoener 1974). However, classifying predator foraging ecology is more complicated than simply categorizing a population as generalist or specialist. Generalist populations can be comprised of generalist or specialist individuals, widening the population niche through unique foraging strategies (Bolnick et al. 2007). Similarly, specialist populations may specialize on different prey resources, limiting intraspecific competition to a subset of the population (Fry et al. 1999; Svanbäck et al. 2008). Individual foraging strategies are an important component of generalist or specialist populations because populations can be comprised of both generalist and specialist individuals, and the distribution of foraging strategies can shift across environmental conditions and population densities (Fetzer et al. 2015). This intraspecific foraging diversity across individuals can drive the adaptive capacity to respond to environmental changes within and across species via their ability to couple resources, respond to changing resource availability, and ultimately, influence the capacity to maintain communities comprised of apex and intermediate predators.

Stable isotopes are a valuable tool for quantifying predator niche space and foraging ecology, using carbon-13 ($\delta^{13}\text{C}$) to determine individual reliance on basal energy sources and nitrogen-15 ($\delta^{15}\text{N}$) to determine trophic position (Newsome et al. 2007; Post 2002). Aquatic ecosystems provide useful study systems for analyzing foraging ecology through stable isotope analysis as food webs are generally constrained within a defined range of isotopic signatures across habitats and photosynthetic food chains. In aquatic ecosystems, enriched $\delta^{13}\text{C}$ values represent benthic (nearshore) energy pathways while depleted $\delta^{13}\text{C}$ values represent pelagic (offshore) energy pathways. $\delta^{15}\text{N}$ bioaccumulates across trophic levels, so higher concentrations are directly related to higher trophic positions. In this context, isotopic niche refers to the isotopic region encompassed by a species representative of their position in the food web (e.g., Eltonian niche, Elton 1927). Sulfur-34 differs across marine and freshwater gradients and can therefore be used to assess marine subsidies to freshwater ecosystems often in the form of anadromous salmon migrations or the stocking of reservoirs. Stocked salmonids are generally enriched in $\delta^{34}\text{S}$ relative to resident species due to the marine feed they receive in the hatchery (Rosinski et al.

2023). In many western U.S. reservoirs, aquatic apex predators are subsidized annually through high rates of salmonid stocking. Annual stocking efforts essentially turn these reservoirs into large-scale ecosystem experiments where we can assess how foraging behavior shifts across these two apex predators in response to pulses of new resources using sulfur-34 ($\delta^{34}\text{S}$). Quantifying foraging ecology at the individual level through the analysis of muscle and liver tissues that turnover at different rates (months versus weeks) enables assessment of short- and long-term foraging via isotopic signatures over time and the degree of specialization across individuals (Perga & Gerdeaux 2005).

I propose to use stable isotopes from muscle and liver tissues from four Wyoming, USA reservoirs collected across seasons to analyze individual foraging ecology of Lake Trout and Walleye (*Sander vitreus*). Understanding how foraging behavior of these two nonnative, albeit common, predators responds to episodic fluctuations in prey availability in highly modified ecosystems provides unique insights into how foraging ecology can structure food webs and populations and improve predictions for how species and ecosystems respond to environmental change.

Methods

Study Site

Four reservoirs across Wyoming, USA are included in this study (Figure 1): Alcova Reservoir (42.533306, -106.748142), Pathfinder Reservoir (42.433299, -106.910784), Flaming Gorge Reservoir (41.090654, -109.543375), and New Fork Lakes (43.094064, -109.953453). These reservoirs vary in environmental, biological, and morphological characteristics, including elevation, trophic status, size, stocking rates, and water level fluctuations (Table 1). Alcova, Pathfinder, and Flaming Gorge reservoirs were created by impounding river channels, resulting in unique bathymetry in these systems. Flaming Gorge is the largest reservoir in the state of Wyoming, extending 146 kilometers (at full pool) upstream from the dam. It is therefore comprised of diverse habitats, including oligotrophic basins, flooded canyons with vertical walls, and meso-eutrophic river arms. Pathfinder Reservoir features a steep bathymetry that flattens out onto historical floodplains causing drastic changes in habitat availability as water levels fluctuate. Alcova Reservoir is a flooded, steep-sided canyon with stable water levels, and available habitat is dominated by a narrow littoral zone and deep pelagic zone. New Fork Lakes is a natural lake with a dam at the outflow to increase storage capacity. It features two distinct basins separated by a narrow channel. The majority of stocking in these systems occurs either in the spring or fall; Alcova and Pathfinder reservoirs are stocked heavily in October and November as well as in May and June, and Flaming Gorge and New Fork Lakes are stocked heavily from May to July.

Alcova and Pathfinder's food webs contain cool- and cold-water fish communities. Walleye are the apex predator, and lower trophic levels were dominated by stocked salmonids, including Rainbow Trout (*Oncorhynchus mykiss*), Brown Trout (*Salmo trutta*), Bear River Cutthroat Trout

(*Oncorhynchus clarkii utah*), and kokanee salmon (*Oncorhynchus nerka*). Flaming Gorge and New Fork Lakes contain cool- to cold-water fish communities featuring Lake Trout as the apex predator in both systems. New Fork Lakes is also stocked with kokanee salmon and Rainbow Trout, while Flaming Gorge is stocked with kokanee salmon, Rainbow Trout, and Bear River Cutthroat Trout.

Sample Collection

Food web sampling was conducted between 2019-2023 in collaboration with Wyoming Game & Fish Department (WGFD; Roberts 2022; Rosinski 2023; Jaksha 2025). Stable isotope samples collected from these reservoirs targeted key food web compartments and were spatially and temporally representative of all habitats within each system. Stocked salmonid samples were collected directly from WGFD hatcheries immediately prior to stocking. Samples encompassed multiple months, years, and sites for each waterbody (Table 2). The number of paired muscle and liver samples from each waterbody ranged from 43 to 149 individuals (Alcova: n = 142; Pathfinder: n = 149; Flaming Gorge: n = 113; New Fork Lakes: n = 43). All samples were frozen immediately upon capture and transported to the University of Wyoming. At the lab, all fish were identified to species, length and weight measured, and muscle and liver tissues collected for stable isotope analysis. Muscle plugs of dorsal tissue were taken directly anterior to the dorsal fin. Zooplankton samples were collected via vertical tow of a 64 μ m mesh zooplankton net to incorporate any community variability under stratified conditions, and macroinvertebrate samples were collected via benthic grab and from stomach contents. Tissue and baseline samples were placed in centrifuge tubes and either dried in a drying oven at 60°C or freeze dried for 36 hours or until samples were completely dry. Once dried, samples were ground into a powder, and 0.75-0.85 milligrams of material was weighed out and encapsulated. Samples were analyzed at the University of Wyoming Stable Isotope Facility for $\delta^{13}\text{C}$ / $\delta^{15}\text{N}$ / $\delta^{34}\text{S}$ using a Thermo Flash Isolink Elemental Analyzer coupled to a Thermo Delta V IRMS. Standard uncertainty was 0.4‰ for $\delta^{15}\text{N}$, 0.3‰ for $\delta^{13}\text{C}$, and 1.6‰ for $\delta^{34}\text{S}$.

Statistical Analysis

To assess differences in short- versus long-term feeding ecology, I will standardize isotope values across systems to quantify and compare population niche size. To do this, I will convert $\delta^{15}\text{N}$ to trophic position, and $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ to percent stocked salmonid reliance (alpha and beta, respectively) using linear two-source mixing equations specified by Post (2002). Carbon-13 and sulfur-34 baselines will consist of the most enriched and depleted prey items for each isotope. All source isotope means will be corrected with tissue and isotope specific trophic discrimination factors before performing reliance calculations. The two-end member mixing equations used to standardize data assume linear mixing. Lipid corrections will be applied to all carbon-13 values for samples where atomic C:N ratios are greater than 3.5 (Hoffman & Sutton 2010). Following standardization, I will quantify population niche size and overlap in three-dimensional space (alpha, beta, and trophic position) using package ‘nicheROVER’, a Bayesian multidimensional

niche estimator (Lysy, Stasko & Swanson 2023). I will then use muscle tissues to estimate average population niche size and liver tissues to assess short term niche size and overlap with population average muscle niches across seasons. Seasons will be classified as spring (April-June), summer (July-September), fall (October-December), and winter (January-March). Although samples from New Fork Lakes were collected during all seasons, paired muscle and liver samples were only analyzed from the summer and fall seasons. I will also calculate the Euclidean distance between paired muscle and liver tissues to assess temporal changes in individual foraging over time using ANOVA with post-hoc pairwise Tukey HSD tests (Abdi & Williams 2010).

To classify foraging behavior of both populations and individuals, I will use stable isotope mixing models to estimate the relative contribution of prey sources to each consumer. Unique prey sources and informative diet priors will be included for each size class within each population and will be based on gape limitation estimates of Walleye (50% of total length; Mathias & Li 1982) and Lake Trout (40% of total length; Ruzycki, Beauchamp & Yule 2023) and the average length of stocked salmonids. Diet data obtained from stomach content analysis of Walleye and Lake Trout will be used to develop informative priors for mixing models. Prior to running mixing models, overlap between sources used in each model will be assessed using package '*nicheROVER*' in program R to ensure prey sources are sufficiently unique. The relative contribution of each prey source to individual predators will be derived from three end-member ($\delta^{13}\text{C}$ / $\delta^{15}\text{N}$ / $\delta^{34}\text{S}$) Bayesian mixing models run using package '*SIMMR*' in program R (Govan & Parnell 2023; R Core Team 2024). Mixing models will be run using unique trophic discrimination factors for muscle and liver ($\Delta^{13}\text{C}_{\text{muscle}} = 1.7 \pm 0.27$, $\Delta^{15}\text{N}_{\text{muscle}} = 3.7 \pm .44$, and $\Delta^{34}\text{S}_{\text{muscle}} = 1.3 \pm 1.3$, $\Delta^{13}\text{C}_{\text{liver}} = 0.6 \pm 0.47$, $\Delta^{15}\text{N}_{\text{liver}} = 2.8 \pm .48$, and $\Delta^{34}\text{S}_{\text{liver}} = 1.3 \pm 1.3$; Canseco, Niklitschek & Harrod 2022; Raoult et al. 2024).

To assess if temporal differences in estimated diet proportions are present, I plan to use permutational analysis of variance tests (PERMANOVA) on liver signatures across paired months (Anderson 2014). PERMANOVA was chosen since it does not rely on the assumption of multivariate normality, therefore allowing us to identify dissimilarity between multidimensional estimates of prey contribution to a total diet. I will also use Principal Component Analysis (PCA) to identify which prey sources were responsible for the majority of observed variation in diet proportion between months. NMDS, PERMANOVA, and PCA tests will be conducted using the '*vegan*' R package (Oksanen et al. 2007).

Finally, I will calculate specialization and similarity metrics for individual fish using estimated diet proportions from Bayesian mixing model output. Specialization (ϵ) varies between 0 and 1 and represents the Euclidean distance between an individual's estimated dietary proportions and an absolute generalist (equal dietary proportions) or an absolute specialist that consumes only one prey source (Equation 1; Newsome et al. 2012). Here, f represents the diet of a purely generalist consumer, ϕ represents the diet of a purely specialist consumer, and y is the dietary proportion estimates for individual predators. Similarity (s) represents the angular similarity

between an individual's estimated dietary proportions and the population mean dietary proportions where f_1 and f_2 are vectors of dietary proportions. Similarity also varies between 0 and 1 representing exact dissimilarity from or exact similarity to the population mean, respectively (Equation 2; Newsome et al. 2012).

$$\varepsilon = \frac{\sqrt{\sum_{i=1}^n (f_i - y_i)^2}}{\sqrt{\sum_{i=1}^n (\phi_i - y_i)^2}} \quad \text{Equation 1}$$

$$s = \frac{\mathbf{f}_1 \cdot \mathbf{f}_2}{|\mathbf{f}_1| |\mathbf{f}_2|} \quad \text{Equation 2}$$

Expected Results

I hypothesize that Walleye will respond quickly to changes in resource availability and subsequently are generalist populations comprised of generalist individuals while Lake Trout will be less responsive to changing resources and are therefore generalist populations comprised of both generalist and specialist individuals. These foraging differences across species should increase the distance between paired muscle and liver samples for Walleye due to continual shifts in resource use over time compared to consistent resource use in Lake Trout. I expect Walleye will be classified as generalists, utilizing a wide range of resources at both the population and individual level and occupying a narrow isotopic niche as values are averaged across individuals. Alternatively, I predict Lake Trout to be classified as specialists, utilizing a wide range of resources at the population level as individuals specialized on specific prey items and occupying a large isotopic niche driven by increased individual isotopic variation (Flaherty & Ben-David 2010).

Management Implications

Results from this study have the potential to inform reservoir fisheries management on multiple fronts including stocking, sport fish harvest, and nongame fish regulations. While Lake Trout and Walleye are often desirable to anglers, both for consumption and recreation, it's important to remember that they can come with undesired consequences. As these two species continue to spread outside of their current ranges, understanding the differing impacts each species may have on reservoir ecosystems is important for proactive management necessary for maintaining desirable fisheries. This study offers a valuable opportunity to quantify the foraging behavior of these two prominent reservoir species in the same environments they pose the most risk to, providing insight into how reservoir food webs may respond to invasion by either species.

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Tables and Figures

Table 1. Summary of proposed reservoir characteristics including surface area (ha), maximum depth (m), elevation above sea level (m), trophic status (Sillen, Ross & Collins 2023), apex predator, stocked species, and the average stocking rate across species for 2018-2023 in kilograms per hectare. Stocked species abbreviations are: BRC; Bear River Cutthroat trout, BNT; Brown trout, KOE: kokanee salmon, RBT; Rainbow trout, and SRC; Snake River Cutthroat trout. All reservoir morphology data is from the United States Bureau of Reclamation, and stocking data is from the Wyoming Game and Fish Department.

Characteristic	Alcova	Pathfinder	Flaming Gorge	New Fork Lakes
Max Depth (m)	49.4	59.1	132.9	62
Surface Area (ha)	999.6	8907.9	17004.9	390
Elevation (m)	1676.8	1786.0	1841.5	2383.5
Apex Predator	Walleye	Walleye	Lake Trout	Lake Trout
Species Stocked	BRC, KOE, RBT	BRC, KOE, RBT, SRC	BNT, BRC, KOE, RBT	KOE, RBT
Avg. Stocking Rate (2018-2023; kg/ha)	9.56	1.71	2.92	6.09

Table 2. Previously collected sample sizes and sampling information from the four reservoirs included in this study, where sample size is the number of fish for which both muscle and liver tissues were analyzed. Sampling efforts on Flaming Gorge samples were supplemented by Wyoming Game and Fish Department and Utah Division of Wildlife Resources standard gill net surveys, net and mesh dimensions included are for Summer Profundal Index Netting (SPIN) nets. Site numbers exclude locations were collected via angling.

Characteristic	Alcova	Pathfinder	Flaming Gorge	New Fork Lakes
Sample Size	142	149	113	43
Length Range (mm)	248-790	206-828	190-1012	203-917
Sampling Gear	Sinking Gill Net	Sinking Gill Net	SPIN, Angling, Boat Electrofishing, Supplemental Gill Nets	Suspended/ Sinking Gill Nets
Net Size (m)	48.8x1.8	48.8x1.8	64x1.8	48x5.5
Mesh Size (mm)	19, 25, 32, 38, 45, 51, 57, 64	19, 25, 32, 38, 45, 51, 57, 64	57, 64, 70, 76, 89, 102, 114, 127	19, 25, 32, 38, 45, 51, 57, 64
Sampling Duration (start - end)	September 2021 - August 2023	September 2021 - August 2023	June 2019 - May 2020	June 2020 - November 2020
Number of Sites	8	8	77	21

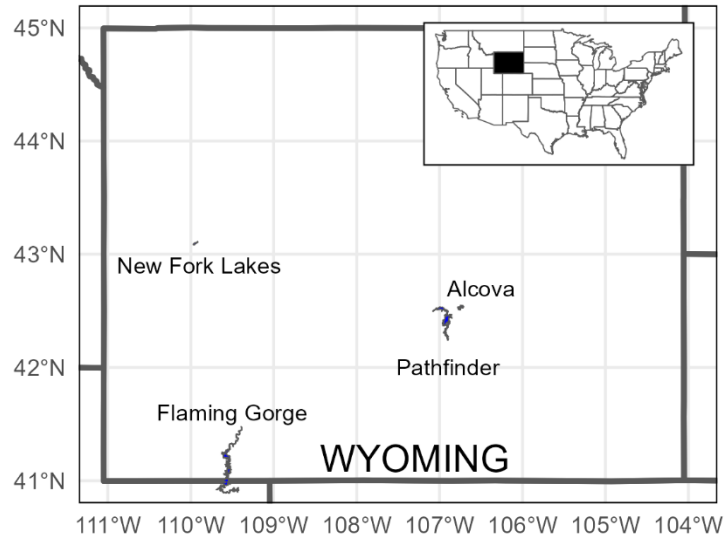


Figure 1. Food web stable isotope samples from four reservoirs across Wyoming, USA were sampled and are proposed to be used in this study: Alcova Reservoir, Pathfinder Reservoir, Flaming Gorge Reservoir, and New Fork Lakes. Alcova and Pathfinder reservoirs feature naturalized populations of Walley (*Sander vitreus*), while New Fork Lakes and Flaming Gorge Reservoir feature naturalized populations of Lake Trout (*Salvelinus namaycush*).