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Research Article

Incorporating ecological heterogeneity and intraspecific variation differentiates complex interactions between apex predators and stocked fish

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Abstract

Ecological heterogeneity and intraspecific variation can impact energy flow from the base of the food web to top predators. We evaluated the effect of intraspecific variation on estimates of lake trout (*Salvelinus namaycush*) consumption of stocked kokanee (lacustrine sockeye salmon, *Oncorhynchus nerka*) in a 390 ha oligotrophic lake with two distinct basins. Lake trout stomach content analyses, stable isotope niche space, and catch rates indicated high intraspecific variation in resource use across habitats and basins. Intraspecific variation and ecological heterogeneity were incorporated into two bioenergetics modeling approaches: one lake-wide model, and one partitioned model that accounted for differences in lake trout diet composition and population size across habitats. The ecologically partitioned model highlighted that lake trout consumption was primarily in the epilimnion of one basin, while the lake-wide, unpartitioned model performed similarly but failed to provide ecological context for where that consumption occurred. Incorporating ecological heterogeneity and intraspecific variation into bioenergetic models can more accurately represent top predators foraging patterns across habitats and inform management actions to mitigate impacts to stocked fish.

Key words: trophic relationships, bioenergetic, ecological heterogeneity, lake trout

Introduction

Accounting for ecological heterogeneity is necessary to accurately understand relationships between environmental conditions and species interactions. Ecological heterogeneity exists across spatial and temporal scales and at all trophic levels. In aquatic ecosystems, heterogeneity across spatial scales may arise from differences in underlying abiotic and biotic conditions such as water clarity, carbon cycling, or habitat complexity (Fragoso et al. 2008; Loken et al. 2019; Opdal et al. 2019). Across temporal scales, factors like seasonality, climate change, or migration may induce heterogeneity (Polovina 1996; Xu et al. 2010). Often, spatial and temporal sources of heterogeneity interact to form complex mosaics of environmental conditions. These conditions can impact all trophic levels, from primary producers to top predators, often manifesting as changes in species abundance, diversity, distribution, or behavior (Antón-Pardo et al. 2016; Bunnell et al. 2021). Given the effect of ecosystem heterogeneity on spatial and temporal food web dynamics, accounting for this underlying variability is critical to understanding trophic structure and energy pathways supporting production at higher trophic levels.

In many aquatic systems, apex piscivorous fishes are highly mobile and able to integrate production across multiple energy pathways (Vander Zanden and Vadeboncoeur 2002). Ecosystem heterogeneity can modify the productivity of different energy pathways and impact the ability of fish to access production across habitats. For example, in lakes with distinct benthic and pelagic energy pathways, many apex piscivorous fishes may only have access to all pathways during times of the year when the lake is unstratified (Guzzo et al. 2017). However, use of these pathways may be mediated by a variety of ecological conditions, including temperature, lake bathymetry, and water clarity (Dolson et al. 2009; Guzzo et al. 2017; Nakayama et al. 2018). By foraging across different energy pathways, apex predators are often resilient to environmental perturbation and able to maintain stable populations despite changes at lower trophic levels (McMeans et al. 2016).

Heterogeneity also exists within populations, as individual organisms often differ in their behavior, resource use, and capacity to adapt to ecosystem change. In some cases, populations able to access prey across multiple pathways are not comprised of generalists, but rather individual specialists that use a subset of the total population niche. The large, generalist niche space of these species is not the result of high individual plasticity, but rather high rates of individual specialization and intraspecific variation in resource use (Bolnick et al. 2007; Smith et al. 2011). Efforts to quantify population-level dynamics need to account for this heterogeneity, as individuals may not respond symmetrically to ecological change (Fetzer et al. 2015). When intraspecific niche variation is high, describing the population niche space requires an understanding of the extent of individual specialization, how this affects individual plasticity, and whether individuals within the population will respond synchronously or asynchronously to perturbations.

Bioenergetics models are commonly used in fisheries research to estimate fish growth and consumption by linking estimates of environmental temperature and population size, diet, and growth rates to describe predator foraging dynamics and quantify the effect of predator consumption on prey (Kitchell et al. 1977; Hansen et al. 1993; Deslauriers et al. 2017). Over the past two decades, researchers have increasingly advocated for greater incorporation of ecological heterogeneity into bioenergetics models. Boisclair (2001) advocated for a spatially explicit approach to modeling aquatic ecosystems like puzzles, with each piece having flexible biotic and abiotic attributes. Bioenergetics modeling efforts are beginning to address this need by evaluating the effects of changing temperature and primary productivity on consumption estimates (Budy et al. 2011; DeWeber et al. 2022) and constructing multiple bioenergetics models for different habitats and geographic areas (Fetzer et al. 2016; Madenjian et al. 2018; Hamza et al. 2021). Increasingly, these efforts are demonstrating the need to incorporate ecological heterogeneity to accurately model predator–prey dynamics; however, more research is needed to groundtruth whether modeling outputs match observed ecological dynamics.

In this study, our objectives were to (1) assess whether the apex predator, lake trout (*Salvelinus namaycush*), exhibits intraspecific variation across three ecologically distinct habitats in a small oligotrophic lake with two unique basins, and (2) quantify the effect of incorporating ecological variation on bioenergetics model-derived estimates of lake trout consumption of stocked kokanee (lacustrine sockeye salmon, *Oncorhynchus nerka*). To assess intraspecific variation, lake trout short- and long-term foraging (stomach and stable isotopes, respectively) were compared across three habitats; the upper basin pelagic, lower basin pelagic, and lower basin benthic. The upper and lower basins differ in stocking practices and environmental conditions, and we hypothesized that these sources of heterogeneity would affect lake trout foraging and drive differences in kokanee consumption across habitats. To estimate the effect of bioenergetics model complexity on kokanee consumption estimates, we compared two bioenergetics models; one that accounts for intraspecific variation resulting from ecological heterogeneity, and one that does not. Model outputs were compared to known stocking rates, estimates of angler harvest, and observed kokanee spawning weir returns to validate each approach and identify more directed management actions.

Methods

Study site

New Fork Lakes is an hourglass-shaped lake located in northern Sublette County, Wyoming, USA (Fig. 1; elevation 2383 m). New Fork Lakes is part of the Wyoming Finger Lakes, a district of deep, ice-scour piedmont lakes, located along the western slope of the Wind River Mountains. New Fork Lakes was formed by a series of terminal moraines that created distinct upper and lower basins connected by a narrow channel. A dam was constructed in 1934 that raised water levels approximately 5 m and further connected the two basins. The upper basin has a surface area of approximately 150 ha and is characterized by steep sides and a maximum depth of 62 m. The lower basin has a surface area of approximately 240 ha and a maximum depth of 43 m. The two basins have similar temperature regimes but vary greatly in water clarity due to fine sediment washing into the upper basin from the New Fork River following a forest fire in 2008 and subsequent landslides in the watershed (Table 1).

The fish community of New Fork Lakes is composed of a small number of native species and introduced sportfish. Native fish include mountain whitefish (*Prosopium williamsoni*) and mottled sculpin (*Cottus bairdii*), which both appear to exist at low densities. Nonnative lake chub (*Couesius plumbeus*), redside shiner (*Richardsonius balteatus*), and speckled dace (*Rhinichthys osculus*) are also present. The most numerous species observed during this study were nonnative sportfish introduced by the Wyoming Game and Fish Department (WGFD) to develop the New Fork Lakes fishery; lake trout, kokanee, and rainbow trout (*Oncorhynchus mykiss*) were the most numerous, and brook trout (*Salvelinus fontinalis*) were observed at low densities. Lake trout were first stocked in 1938, with additional stocking events in the early 1940s. Since the population was established, it has been maintained solely by natural reproduction. Kokanee have been stocked annually since 1976. Kokanee are stocked at the New Fork River inlet in the upper basin at total lengths of approximately 94 mm. Rainbow trout were first stocked in 1937 and have been stocked nearly annually since 1942. Rainbow trout are stocked at the boat ramp in the lower basin of New Fork Lakes at a total length of approximately 222 mm. Brook trout have not been stocked since 1985. Lake trout are the apex predator in New Fork Lakes across basins; however, prey fish communities differ across basins and are likely driven by differences in stocking practices (rainbow trout in lower basin, kokanee in upper basin) and water clarity impacts on the availability of benthic and pelagic energy pathways (Table 1).

Field collections

We sampled New Fork Lakes every 3–4 weeks during the open water period, from June to November, in 2020 and 2021. During each sampling event, pelagic and profundal habitats were sampled with suspended and benthic gill nets, respectively. In 2020, suspended nets were 48 m long by 5.5 m deep, and consisted of eight, 6 m long panels with square mesh ranging from 19 to 64 mm (19, 25, 32, 38, 45, 51, 57, and 64 mm). In 2021, three additional small-mesh pan-

Fig. 1. Bathymetric map of New Fork Lakes, with inset map showing location in Sublette County, Wyoming (orange dot). Depth is shown in 6 m delineations. The upper basin (right) is joined to the lower basin (left) by “the Narrows”. The New Fork River flows into the upper basin and water then moves through the Narrows and into the lower basin.

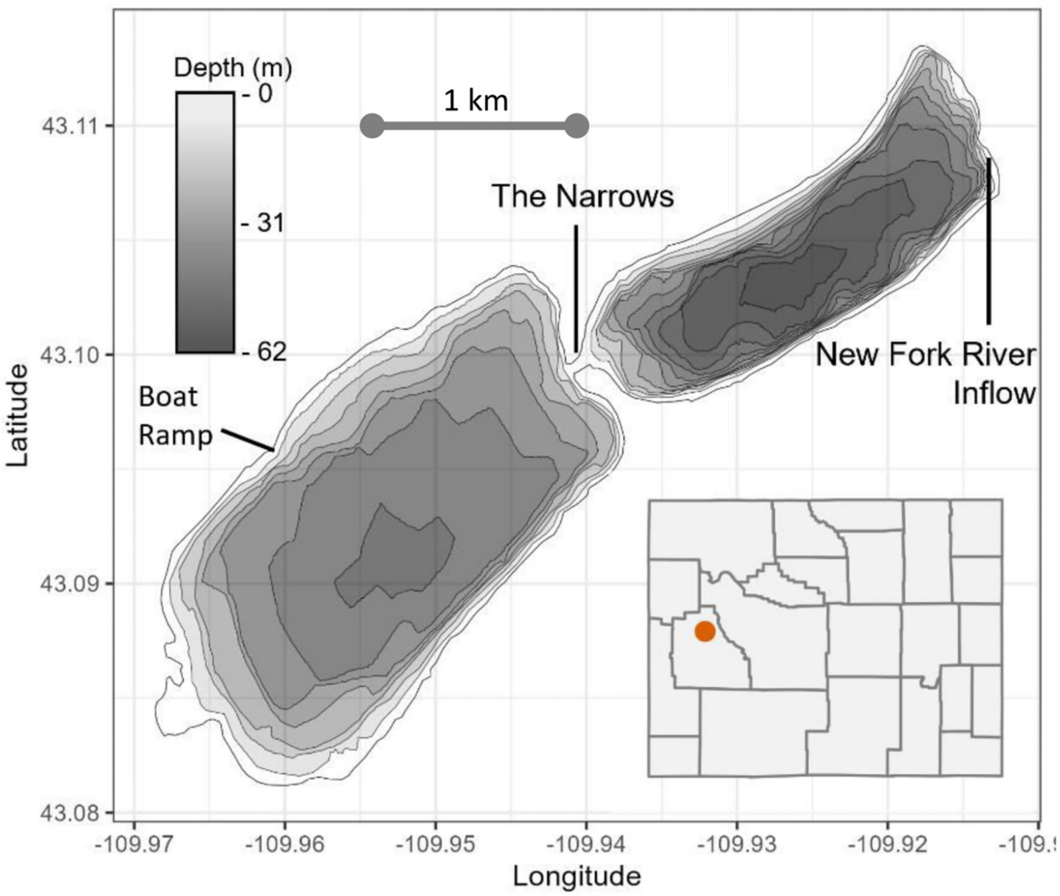


Table 1. Summary of environmental measurements during the sampling period and stocking history for the upper and lower basins of New Fork Lakes.

Measurement	Upper basin	Lower basin
2021 surface temp (°C)		
Minimum	6.6	7.1
Maximum	21.0	21.7
2021 hypolimnion temp (°C)		
Minimum	4.9	5.5
Maximum	8.4	9.8
2020 secchi depth (m)		
August	1.5	9.6
October	4.6	10.4
November	5.6	11.3
5 year mean fish stocked (*N*; kg)		
Rainbow trout	0	15 623; 1966
Kokanee	38 813; 209	0

els were added to these nets (6 m long, 5.5 m deep, and square mesh measurements were 10, 13, and 16 mm). Benthic nets were 73.2 m long by 1.8 m deep, and consisted of six 12.2 m long panels, with square mesh ranging from 25 to 51 mm (25, 29, 32, 38, 45, and 51 mm). All panels were made of thin monofilament (diameter ranging from 0.20 to 0.33 mm).

For each sampling event, we set nets overnight, and soak times ranged from 11 to 25 h (mean 17.1 h, median 17.3 h). Each night in the upper basin we set three suspended nets, fished at the surface, 6.1 m, and 12.2 m, and one benthic net. These net depths roughly corresponded to above, at, and below the thermocline during the stratified period and are based on the design of long-term WGFD surveys at New Fork Lakes. In the lower basin, we set two suspended nets, fished at the surface and 6.1 m, and two benthic nets each night. Net locations were chosen randomly. Sets differed between the two basins based on available habitat and gill net catch data from previous netting events in this system. Upon net retrieval, fish were identified to species and the mesh size they were caught in and net depth were recorded. All live fish were euthanized with a lethal dose of MS-222 or blunt trauma to the head followed by exsanguination, depending on the severity of weather conditions. All harvested fish were immediately placed on ice and transported to a freezer on the same day. The WGFD conducted sampling in 2020 and all fish collected were donated to the University of Wyoming. The WGFD and University of Wyoming researchers conducted sampling in 2021.

In addition to fish sampling, we collected a range of abiotic and biotic data during 2020 and 2021. During each sampling event in 2020, we measured temperature profiles in each basin using a YSI ProDSS with a temperature probe (Yellow Springs Instruments, Yellow Springs, OH). In 2021, temperature data were collected continuously during the open water period via HOBO Pendant temperature sensors (model MX2201, https://www.onsetcomp.com). We moored temperature monitoring buoys in each basin of New Fork Lakes in 2021 and water temperature was measured hourly at the surface, 10 m, and 20 m below surface. We measured water clarity via secchi depth on three sampling dates in 2020. During each sampling event in 2020 and 2021, we collected a vertical zooplankton tow (0.5 m diameter net with 153-micron mesh and weighted cod-end) in each basin. Tows were typically collected in late morning, and during sunny conditions when possible. For each tow, the zooplankton net was lowered to 30 m deep and raised back to the surface at a rate of 1 $m{\cdot}s^{-1}$. Zooplankton samples were placed in a Whirl-Pak and frozen.

Laboratory processing

We thawed fish and measured their total length and weight, and determined their sex. For all lake trout and a subset of other fish species (e.g., rainbow trout, kokanee, mountain whitefish), we removed gastrointestinal tracts from the esophagus to the pyloric caeca, collected muscle samples, and removed sagittal otoliths. Muscle samples were collected from immediately anterior to the dorsal fin. We froze all samples upon collection.

We weighed stomach contents from nonempty stomachs in aggregate for each fish. We then sorted contents to the lowest possible taxonomic level. Fish were sorted to species when possible. If fish were too digested, we sorted them to the greatest specificity possible (e.g., unidentified salmonid, unidentified fish). Zooplankton were classified as either *Daphnia* spp. or Copepoda. Terrestrial insects were identified to order (e.g., Coleoptera, Hymenoptera, and Diptera). Chironomidae prey were identified to life stage (e.g., larvae vs. pupae). Other aquatic macroinvertebrates were identified to a practical taxonomic level (e.g., Amphipoda). All nonzooplankton prey were counted. For large zooplankton quantities, we used volumetric subsampling to estimate the total number of individuals. For all prey types, we measured a maximum of 10 individuals of each prey type using an ocular micrometer. Vertebrate prey items were also weighed to the nearest centigram.

To convert stomach content data to estimates of percent biomass, we converted invertebrate lengths to dry weights using published length–weight regressions and converted to wet weights using published dry–wet weight relationships (see Rosinski et al. 2020 for more details and equations). We summed the weight of each prey type by individual fish to get a total weight of each prey item in the gut. We then calculated percent biomass by dividing the total weight of the prey item by the total weight of the stomach contents and multiplying by 100. Percent biomass of each prey type was calculated for each individual lake trout and then averaged across size and habitat groups (Garvey and Chipps 2012). We assigned unidentified fish and unidentified salmonid percentages to prey categories by randomly drawing from a species distribution created using the observed percentages of identified fish/salmonid in the stomachs. We calculated frequency of occurrence for stomachs containing prey by dividing the number of fish that had a particular prey item by the total number of fish and multiplying by 100.

Previous studies show that small lake trout are invertivorous and then transition to a more piscivorous diets at larger lengths (e.g., Vinson et al. 2021). Results of stomach content analyses determined consumption of kokanee was rare for lake trout <400 mm and only comprised a very small portion of the total biomass. Kokanee began reliably appearing in stomach contents of lake trout >400 mm. This 400 mm length cutoff was applied to future stomach content overlap, stable isotope, and bioenergetics analyses.

Muscle samples from 76 lake trout were dried in a 70 °C drying oven until desiccated (approximately 48 h). Dried muscle tissue was ground with a mortar and pestle into a fine powder and 0.75–1.00 mg was encapsulated in a tin capsule for stable isotope analysis. Samples were submitted to the University of Wyoming Stable Isotope Facility (http://www.uwyo.edu/sif/). The samples were analyzed with a Thermo Flash Isolink Elemental Analyzer coupled to a Thermo Delta V Isotope Ratio Mass Spectrometer. Stable isotope ratios, δ^{13}C, δ^{15}N, and δ^{34}S, are reported in parts per mil (‰) with respect to Vienna Pee Dee Belemnite, Air-N2, and Vienna Cañon Diablo troilite, respectively.

We estimated lake trout age for a length-stratified, random subset of all fish collected. We mounted otoliths from 169 lake trout in resin and cut a thin cross section (0.63 mm) transversely through the nucleus with a low-speed IsoMet Low-Speed Precision Cutter (Buehler Corp, Lake Bluff, IL). We mounted this cross section on a glass microscope slide using Shandon Mount and polished the exposed side with 800–1200 grit sandpaper. We photographed otoliths with an Olympus SZX7 microscope mounted with a DP23 camera. Mineral oil was used on top of the otolith during microscopy to enhance the appearance of annuli. We analyzed images using the R package RFishBC (Ogle 2022) to determine age and measure the distance from the core to each annulus. Age assignments for each otolith were based on the consensus age from two independent readers. If a consensus could not be reached, we omitted the otolith from further analyses.

Partitioning lake trout bioenergetic inputs

To inform spatial partitioning of key inputs to the bioenergetic models, we quantified intraspecific variation in lake trout diets and stable isotope values between fish caught in each of four habitats: upper basin pelagic, upper basin benthic, lower basin pelagic, and lower basin benthic. Pelagic lake trout were those caught in suspended gill nets, and benthic fish were caught in benthic gill nets.

We used Schoener's proportional similarity index to evaluate differences in diets between habitats (eq. 1; Schoener 1968). We limited analyses to prey categories that occurred in >3% of lake trout stomachs, which included kokanee, mottled sculpin, rainbow trout, chironomid pupae, chironomid larvae, and *Daphnia*).

$$\alpha_{xy} = 1 - 0.5\left(\sum_{i=1}^{n} |p_{x_i} - p_{y_i}|\right) \tag{1}$$

where α_{xy} is the proportional diet similarity between predators x and y, p_{x_i} is the proportion of prey item i in the stomach of predator x, and p_{y_i} is the proportion of prey item i in the stomach of predator y.

Stomach content analysis provides a short-term evaluation of diets (i.e., hours to days). The addition of stable isotope analysis of lake trout liver and muscle samples provides a longer term evaluation of individual specialization and diet overlap (e.g., the elements integrated into lake trout tissues over months). Before analysis, we lipid corrected lake trout stable isotope δ^{13}C values using a mathematical correction based on the observed C:N ratio (McConnaughey and McRoy 1979). We assessed individual specialization by comparing stable isotope values of liver and muscle tissues collected from the same lake trout. Liver and muscle stable isotope values falling near the 1:1 line suggest a high degree of specialization across intermediate- to long-time scales. However, stable isotope values away from the 1:1 line suggest lake trout are generalist and regularly feed across isotopic space over time. We then evaluated overlap in lake trout muscle stable isotope values across habitats using the R package nicheROVER (Lysy et al. 2021) for lake trout larger than 400 mm (cutoff for piscivory). This package was used to create Bayesian 95% niche regions for each habitat and to calculate overlap probabilities among niches using all three stable isotopes. We aimed to use this analysis to understand if dietary differences persist over longer timeframes than are evaluated using stomach contents.

Lake trout growth rates and age structure

We fit a length-at-age model to the von Bertalanffy growth equation in the R package FSA (eq. 2; Ogle et al. 2023) to quantify lakewide lake trout growth rates and develop a age-length key to assign ages to unaged fish based on their length.

$$L = L_\infty\left[1 - e^{-K(T-t_0)}\right] \tag{2}$$

where L is length, L_∞ is the maximum mean length of the population, K is the Brody growth coefficient, T is the age, and t_0 is the age when fish mean length is zero. Note that t_0 is an artifact of allowing the model to fit the adult growth pattern and does not have true biological interpretation (e.g., t_0 can be negative or positive; Beverton and Holt 1957; Ogle et al. 2017).

Bioenergetics modeling

To assess how incorporation of environmental heterogeneity and intraspecific variation influenced performance, we constructed bioenergetics models using two approaches. We built an unpartitioned model using inputs derived from lake-wide estimates, and a partitioned one using inputs derived from habitat and (or) basin-specific values. Bioenergetics models were built in the R package FB4 (Fisheries Bioenergetics 4.0; Deslauriers et al. 2017) using the built-in lake trout parameterization (Stewart et al. 1983) and fit using estimates of temperature, prey and predator energy densities, diet proportions, and observed lake trout growth rates. Lake trout predator energy density was based on published values (Johnson et al. 2017*b*). We calculated prey energy densities from dry weights for kokanee and rainbow trout using equations published in Johnson et al. (2017*b*). All other prey energy densities we obtained from the literature (Table A1). We used temperature, diet compositions, and growth rates measured for New Fork Lakes in this study.

We ran all bioenergetic simulations from 1 May to 15 November (ice-off period) based on the assumption that growth under the ice is limited and only makes a small contribution to total annual growth (Guzzo et al. 2017). We divided diet compositions into three functional seasons: spring (1 May to 10 July), summer (11 July to 30 September), and fall (1 October to 15 November). The spring and summer periods were separated based on timing of kokanee stocking (10–15 July), while the summer to fall cutoff was based on the approximate timing of fall lake turnover. Data were not available to run winter simulations, and despite evidence that lake trout are actively feeding during winter, winter water temperatures approach 0 °C and are well below the thermal optimum for lake trout growth. Further, the few studies documenting lake trout winter foraging indicate high reliance on littoral prey (Vinson et al. 2021). Therefore, we assume growth and pelagic kokanee consumption during winter contribute minimally to annual estimates. We only ran bioenergetic models for lake trout >400 mm, as stomach content analyses indicated negligible piscivory below this threshold (see the "Results" section).

Consumption rate from bioenergetics models was expressed as grams of kokanee consumed daily for lake trout of each age. We converted kokanee consumption (g) for each lake trout age class to a numerical estimate of kokanee consumption (n) using the observed weights at stocking and observed growth within the system. We limited our analyses to consumption of newly stocked kokanee because analyses of stomach contents suggest consumption of large kokanee is very rare (mean length of kokanee prey = 96 mm, median = 84 mm, and range 54–206 mm). Because kokanee are stocked at the beginning of the summer season, individuals consumed in the spring season were converted using the average weight of age-1 fish captured during spring gill net surveys (e.g., those stocked in summer the previous year), while kokanee consumed in the summer and fall were converted using the average weight of age-0 fish on that date. We completed this growth conversion using data from field-sampled kokanee by creating a linear regression of days since stocking versus average kokanee weight to estimate the weight of kokanee on each day of the model simulation. This methodology may overlook some consumption of larger kokanee not evidenced in our stomach content analyses; however, the absence of kokanee >206 mm in the stomach contents suggests that these fish likely comprise a very small proportion of the kokanee eaten in this system.

We modeled consumption of kokanee beginning at age-6 (mean age that lake trout exceed 400 mm based on von Bertalanffy lengths-at-age model) to age-29 (growth to age-30). We selected this upper age cutoff because very few lake trout were estimated to be older than 29 (five fish total), their ages tended to be skewed based on poor von Bertalanffy model fit at very large sizes, and the annual increase in number of kokanee consumed per individual was low past age-29. We grouped these five individuals with the age-29 year class to account for their presence.

For both bioenergetic modeling approaches, we calculated age-specific consumption estimates and scaled them up to a population-level estimate based on estimates of lake trout densities in the literature and the observed age-structure in New Fork Lakes. We estimated population size using the average lake trout density in systems with nonnative populations (6.5 fish/ha; Hansen et al. 2021). These analyses produced an estimated population size of 2551 lake trout, with 1102 of those fish being >400 mm. To account for the high degree of uncertainty in this population estimate, we explored a range of possible lake trout population sizes by modifying the population estimate by ±20%. This range produced similar population estimates to other systems in the Rocky Mountain region with attributes similar to New Fork Lakes and with similar sampling gear selectivity (e.g., Johnson and Martinez 2000; Cox 2010). Across population estimates, we used the observed age-structure to partition the population into abundance for each age-class based on proportion of the total catch.

Bioenergetics modeling—unpartitioned bioenergetic model

We calculated lake trout length-at-age estimates from the von Bertalanffy growth equation fit to all aged lake trout from New Fork Lakes. We converted these lengths to weight-at-age with a natural log transformed length–weight regression (Fig. A1) to calculate average weights for each year of life.

The temperatures for the unpartitioned bioenergetics model were an average across the 10 and 20 m temperature sensors in both basins. The diet proportions we used were stomach content biomass averages for all lake trout >400 mm, separated by each of the functional seasons.

To scale consumption-by-age values to the estimated lake trout population size, we used the whole-lake von Bertalanffy growth function to calculate age from lengths for all lake trout captured. We then calculated the proportion of lake trout of each age and multiplied the proportion by the total lake trout population estimate, yielding the number of lake trout of each age. We then multiplied the bioenergetics model estimate of annual kokanee consumption for an individual fish of each age by these age-partitioned population estimates and summed outputs to reach a total population consumption value.

Bioenergetics modeling—partitioned bioenergetic model

Our comparisons of stomach contents and liver and muscle stable isotopes values across lake trout caught in the upper basin pelagic habitat, lower basin pelagic habitat, and lower basin benthic habitat indicate that fish in each of these groups foraged differently from the other groups and these differences were maintained across relative long time scales (see the "Results" section). This finding led us to conduct bioenergetics modeling for each of these habitats separately using an ecologically partitioned bioenergetics approach. We omitted the upper basin benthic net from these analyses because of exceedingly low catch-per-unit-effort (CPUE; number caught per net hour) of lake trout >400 mm, resulting in insufficient sample sizes and the assumption that such low CPUE is indicative that this habitat has a minimal contribution to kokanee consumption. Modeling for these partitioned groups followed the same general methods as the whole-lake model described above, but with data inputs representing each group, as described below.

Percent biomass for each prey type was calculated following the protocol described above but calculated separately for each habitat group. As with the unpartitioned model, we calculated lake trout length-at-age estimates from the von Bertalanffy growth equation fit to all aged lake trout from New Fork Lakes. We converted these lengths to weight-at-age with a natural log transformed length–weight regression (Fig. A1) to calculate average weights for each year of life.

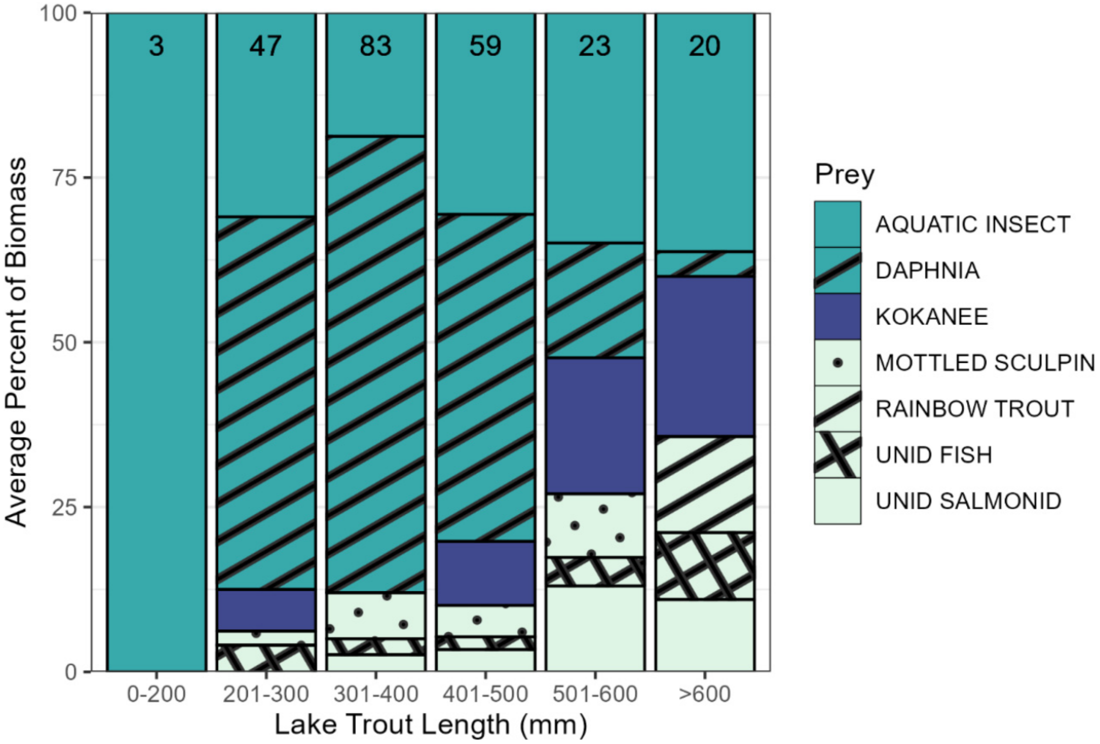
To model pelagic lake trout caught in suspended (pelagic) gill nets, we used temperatures from the 10 m sensor. Although some lake trout were caught in surface waters, these fish likely reside in the metalimnion or hypolimnion and were caught during foraging forays into the epilimnion, resulting in a minimal effect on metabolic rate during these brief experiences of warmer temperatures (Sellers et al. 1998; Morbey et al. 2006; Marsden et al. 2021). The 10 m upper basin temperature sensor stopped working on 29 September; however, by this point in the season the 10 m and surface temperatures had converged following turnover. We substituted surface temperatures for the missing data in October and November. To model lake trout caught in benthic nets we used temperatures from the 20 m sensor.

We partitioned the whole-lake population estimate among the three habitats by applying the proportion of our total CPUE that came from each habitat. We then partitioned the number of fish in each habitat among the estimated age distribution using the same methods described above but integrating the sampling gear-specific von Bertalanffy growth functions.

Bioenergetics modeling—model comparisons

We compared the consumption estimates from unpartitioned and partitioned bioenergetics models to stocking rates of kokanee and measured sources of kokanee mortality in New Fork Lakes. Stocking rates were available from the WGFD. We derived estimates of kokanee mortality from two sources: the measured returns of spawning adult kokanee and estimated angler harvest. The WGFD collects spawning adult kokanee annually at a weir on the New Fork River and uses these fish as a source of broodstock for the state's hatchery system. The New Fork River is thought to be the only spawning location for kokanee in New Fork Lakes, so spawning returns give a good estimate of kokanee survival and, when paired with stocking numbers, total mor-

Fig. 2. Average percent biomass of stomach contents for all lake trout caught in New Fork Lakes. Numbers at the top of each bar represent sample size. Aquatic insects were primarily Chironomidae larvae and pupae. UNID (unidentified) fish and salmonid categories were later partitioned among corresponding identified fish/salmonid prey (i.e., unidentified salmonids partitioned among identified salmonids in that length bin according to their proportions, unidentified fish partitioned among all identified fish species).



tality. Additionally, in 2021, the WGFD conducted a creel survey to estimate angler harvest of kokanee. These surveys were completed following WYOCREEL (version 1.63) standard sampling protocols, with surveys completed from May to September (Yule et al. 2000). WGFD analyzed the resulting data to produce a total kokanee harvest estimate for the months represented by the sampling period. Informal creel surveys were conducted opportunistically during the 2021 ice season, but no kokanee harvest by ice anglers was observed.

Results

Lake trout intraspecific variation

We caught 320 lake trout ranging from 91 to 917 mm total length (Fig. A2). Gastrointestinal tracts from 307 lake trout were thawed and dissected, and stomachs without contents or containing minimal unidentifiable material were recorded as empty (n = 65, 21%). Stomach content analysis revealed an ontogenetic transition from primarily invertivory (*Daphnia* and aquatic insects) to omnivory (continuation of *Daphnia* and aquatic insects, with increasing amounts of kokanee, mottled sculpin, and rainbow trout) as lake trout grew (Fig. 2). Kokanee began reliably appearing in the stomachs of lake trout >400 mm and supported limiting bioenergetic analyses to lake trout >400 mm. There was a small amount of kokanee consumption in the 201–300 mm length bin (6%); however, no kokanee were observed in the diets of lake trout 301–400 mm despite large sample sizes (Fig. 2). We excluded lake trout >400 mm caught in upper basin benthic nets from future analyses because catch rates were very low (4% of lake-wide average CPUE (lake trout >400 mm/30 m net-h): 0.14 fish/net-h in upper basin benthic, 0.59 fish/net-h in upper and lower suspended, and 2.13 fish/net-h in lower basin benthic nets). Low catch rates limited our ability to characterize diet diversity in the upper basin benthic habitat, and overall, we assume this habitat makes a negligible contribution to lake-wide consumption estimates.

The average percent biomass of prey in lake trout stomach contents varied between the upper and lower basins of New Fork Lakes and between benthic versus suspended nets (Table 2). *Daphnia* and aquatic insects were the dominant diet items in the lower basin benthic nets. Aquatic insects and *Daphnia* were the dominant prey items in spring and fall in lower basin suspended nets, while fish (kokanee and rainbow trout) composed a larger portion of percent biomass in summer. Kokanee and aquatic insects were the dominant diet items in the upper basin suspended nets (Table 2), though spring diets were potentially biased by a low sample size.

Schoener's proportional dietary similarity index for lake trout >400 mm was 0.45 between the lower basin suspended and benthic nets, 0.60 between the lower and upper basin

Table 2. Sample size (n) and average stomach content percent biomass for nonempty lake trout >400 mm, partitioned by net and season.

Net	n	Chironomidae	*Daphnia*	Kokanee	Mottled sculpin	Rainbow trout
Upper basin suspended						
Spring	1	100.0	0.0	0.0	0.0	0.0
Summer	12	16.7	0.0	74.9	8.5	0.0
Fall	9	22.2	11.1	66.7	0.0	0.0
Lower basin suspended						
Spring	17	70.6	5.9	23.5	0.0	0.0
Summer	5	5.0	15.1	37.6	0.0	42.3
Fall	3	0.0	66.7	0.0	0.0	33.3
Lower basin benthic						
Spring	9	78.1	0.0	8.5	2.6	10.8
Summer	32	25.1	71.8	0.0	3.1	0.0
Fall	10	10.4	63.0	0.0	26.2	0.0
All nets combined						
Spring	27	74.2	3.7	15.6	1.1	5.4
Summer	49	20.1	46.5	25.7	4.9	2.7
Fall	22	12.7	38.7	27.1	12.8	8.3

Note: Prey categories listed are those that occurred in at least 3% of all nonempty lake trout stomachs. Chironomidae include larval and pupal stages.

suspended nets, and 0.34 between lower basin benthic and upper basin suspended nets. Similarity values >0.60 suggest biologically significant overlap (Schoener 1968), indicating dissimilar diets across the three habitats in New Fork Lakes. Observed dietary differences were also supported over longer timeframes by stable isotope analysis. Individual lake trout feeding ecology was specialized in isotopic space across intermediate- and long-time scales, as liver and muscle stable isotope values from individual lake trout were consistently near the 1:1 line for carbon and sulfur stable isotopes or generally matched expected differences in fractionation rate between liver and muscle for nitrogen (Figs. 3 and A3). Additionally, if lake trout were not maintaining intraspecific variation across longer time scales, we would expect stable isotope niche overlap probabilities near 100%. Probability of overlap from lake trout muscle stable isotope values across the three habitats ranged from 56% to 85% (Fig. A4). Individuals caught in lower basin suspended nets had a broad isotopic niche, resulting in high probability that lower basin benthic and upper basin suspended net fish would be found within it (overlap probability of approximately 85% for each; Fig. A4). Conversely, the upper basin suspended net fish had the smallest niche area, driven by a more limited range in δ^{13}C values that were more depleted than the other two habitats (Fig. 4). This constrained niche area led to lower probabilities that lower basin benthic and suspended fish would be found within this niche (62% and 55%, respectively; Fig. A4).

After reconciling ages between two readers, ages from 150 lake trout remained for analysis (89% of all lake trout otoliths analyzed). Lake trout ages ranged from 2 to 31 years. The Brody growth coefficient was 0.073, and the maximum mean length for the population was 950.7 mm (Fig. 5).

The significant differences in diets and stable isotope values across the upper basin pelagic, lower basin pelagic, and lower basin benthic habitats supported development of an ecologically partitioned bioenergetics model that evaluated these three habitat/basin groups independently.

Bioenergetic modeling

The population age distribution was right-skewed (Fig. 6) with a median age of 8 years. Lake trout reached 400 mm (the length at which they started to become piscivorous) at age 6, so we conducted modeling for lake trout age 6 to age 29. The bioenergetics output in grams of kokanee consumed was converted to number of individuals using the linear regression of average kokanee weight versus days since stocked: kokanee weight (g) $= 6.09 + 0.131 \times$ days since stocked (p-value < 0.01, $R^2 = 0.99$).

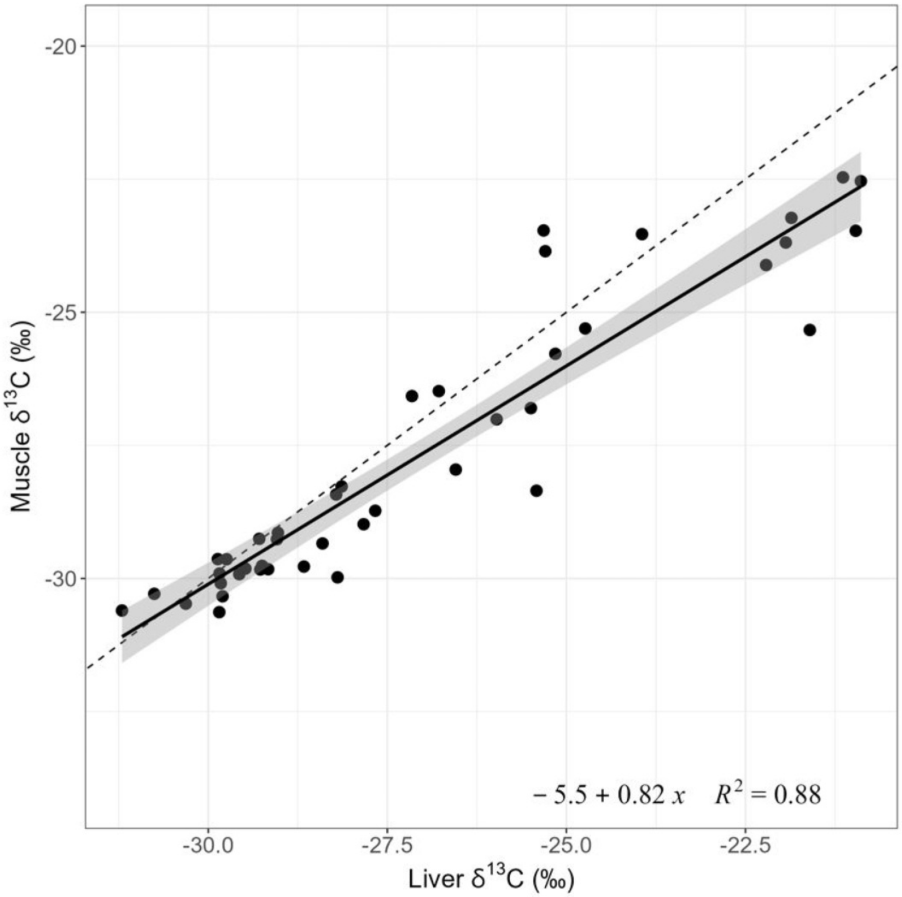
Bioenergetics modeling—unpartitioned model results

In the unpartitioned model, individual kokanee consumption steadily increased with lake trout age and ranged from 19 kokanee/year for age-6 fish, to 65 kokanee/year for age-29 fish (Fig. 7). This model resulted in a total kokanee consumption estimate of 35 018 fish. Because 50% of the population was estimated to be age-8 or younger, scaled consumption estimates were largely based on many lake trout eating relatively low numbers of kokanee. Lake trout ages 6–8 ate 13 180 kokanee, representing 38% of all estimated kokanee consumed (Fig. 8).

Bioenergetics modeling—partitioned model results

By applying the relative proportion of our CPUE in each habitat to the whole-lake lake trout population size estimate, we estimated 609 lake trout in the lower basin benthic, 219 in lower basin pelagic, and 274 in the upper basin pelagic habitats. In the lower basin benthic net, individual kokanee consumption was near-zero for all age classes; the highest

Fig. 3. Relationship between liver and a muscle δ^{13}C values collected from individual fish. 1:1 line indicated with dashed line.



consumption was for age-29 fish, estimated to eat two kokanee/year. Consumption by lower basin suspended net fish was intermediate, ranging from 13 kokanee/year for age-6 fish to 47 kokanee/year for age-29 fish. The highest consumption per individual lake trout was by fish in upper basin suspended nets, with age-6 fish eating 45 kokanee/year and age-29 fish eating 153 kokanee/year (Fig. 7). After scaling individual consumption estimates to the whole lake trout population, lake trout in upper basin suspended, lower basin suspended, and lower basin benthic nets accounted for 73%, 25%, and 2% of kokanee consumption, respectively. Upper basin suspended net fish aged 6–11 ate 12 195 kokanee annually, representing over half of kokanee consumption by lake trout in this habitat, and 42% of total kokanee consumption estimated in the partitioned model (Fig. 8). Though larger fish eat more kokanee per individual, their relatively low abundance prevents them from disproportionately affecting total kokanee consumption.

Comparison of bioenergetics models

The ecologically partitioned model estimated total annual kokanee consumption to be 29 248 individuals, compared to 35 018 individuals estimated by the unpartitioned model, a difference of approximately 17% (Fig. 8). Scaling population size by ±20% resulted in a kokanee consumption range of 23 399–35 098 fish for the partitioned model and 28 015–42 022 fish for the unpartitioned model (Fig. 8).

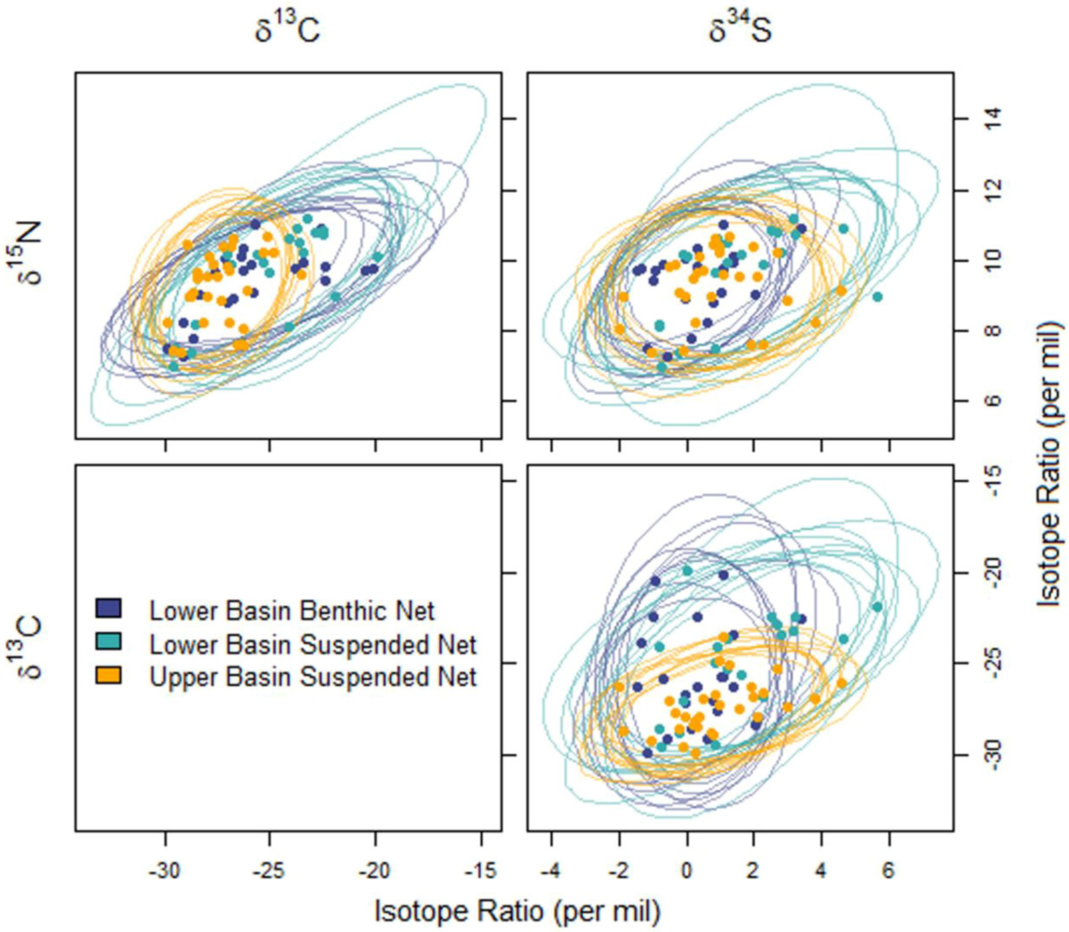
From 2017– to 2021, the WGFD stocked an average of 38 813 kokanee into the upper basin each year and had an average of 1294 mature individuals return to the New Fork River (the only known spawning location in the system) to spawn. Additionally, creel surveys in 2021 led to an estimate that approximately 83 kokanee are caught by anglers annually. It is reasonable to assume all these fish die, either because of harvest or delayed mortality. Coupled with the spawning return data, we estimate an average cohort mortality of 37 436 kokanee. Using the bioenergetics model estimates of consumption, if we assume relatively similar consumption numbers across years and stable stocking rates, the estimate from the partitioned model accounts for 78% of a kokanee cohort's mortality, while the estimate from the unpartitioned model accounts for 94% of annual kokanee mortality. However, the unpartitioned model provides no information on what habitat this mortality is occurring in.

Discussion

Lake trout life history across habitats

Persistent ecological differences across basins and habitats in New Fork Lakes manifested in feeding ecology differences of the apex predator, lake trout. In the upper basin, littoral habitat is limited due to steep bathymetry, and sus-

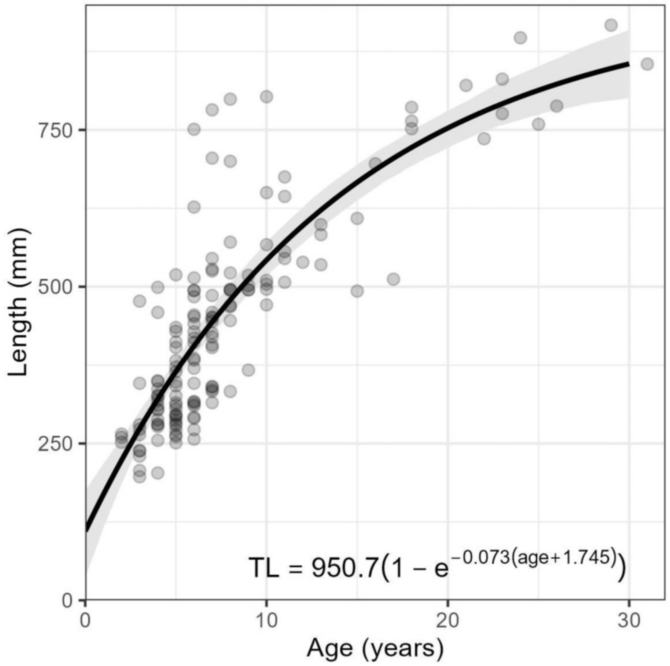
Fig. 4. Isotopic values (points) and projected niche space (ellipses) for lake trout in each of the three main habitats in New Fork Lakes. Ellipses are drawn to encompass a 95% niche region, with 10 random niche regions generated by Bayesian analysis using R program nicheROVER.



pended sediment causing shading and likely limiting benthic productivity (Vadeboncoeur et al. 2008; Blain et al. 2021). In this basin, we observed high biomass of pelagic prey in stomach contents, and a constrained niche space with lower δ^{13}C relative to the lower basin habitats. δ^{13}C varies on a nearshore to offshore gradient in many lakes (France 1995), and the lower values observed in the upper basin are consistent with high reliance on offshore, pelagic energy pathways. This is also consistent with catch data that indicate few lake trout reside in the upper basin benthic habitat, a likely outcome of limited pelagic and benthic productivity to support profundal consumer production. Conversely, the lower basin has shallower maximum depth and more gradual bathymetry resulting in more littoral habitat. The lower basin also had higher light penetration, higher lake trout density in the benthic habitat, and a broader isotopic niche space, reflecting reliance on pelagic, benthic, and profundal energy pathways in that basin. While upper basin lake trout appear reliant on pelagic energy, including that of stocked kokanee, lower basin lake trout have a greater diversity of energy pathways to exploit, lessening the relative importance of kokanee. Ecological heterogeneity driven by bathymetry, water clarity, and stocking practices led to differences in the foraging ecology of the apex predator in this system.

Stomach content analyses indicated low to moderate dietary overlap between fish caught in each habitat, with the greatest differences emerging from comparisons of fish in benthic and suspended nets. Comparisons of stable isotope values from paired liver and muscle samples collected from individual lake trout suggest fish are utilizing similar isotopic niche space across intermediate to long time scales and may be linked to a high degree of habitat fidelity. Differences between basins were also consistent with stable isotope niche estimates that showed upper basin suspended net lake trout were more exclusively reliant on pelagic energy sources than lower basin lake trout. Interestingly, stable isotope results indicate a relatively high degree of habitat fidelity in New Fork Lakes. Muscle tissues reflect prey use over approximately 6–12 months (Skinner et al. 2017), so if individual lake trout were using all three habitats across the course of a year, we would expect to see higher overlap in stable isotope niche areas. Though catch rates demonstrate the ability of fish to move between basins (e.g., catching kokanee in the lower basin), the differences in isotopic niche space and presence of niche overlap probability values as low as 55% between

Fig. 5. Von Bertalanffy growth curve for total length (TL) of all lake trout in New Fork Lakes. After reconciling ages, 150 lake trout ages remained for analysis.



the two basins suggest persistent differences across habitats indicative of habitat fidelity.

We explored the possibility of applying different growth rates to lake trout caught in benthic versus pelagic nets, as it seemed reasonable to believe that growth and activity rates may differ as a result of different diets. Lake trout caught in pelagic nets had higher proportions of fish in their diets than those caught in benthic nets, and the higher energy density of fish compared to invertebrates can lead to increased growth rates (Chavarie et al. 2015; Johnson et al. 2017*a*). Additionally, activity rates likely vary between lake trout foraging on fish versus invertebrates and across basins and could also contribute to different growth rates (e.g., Rennie et al. 2011). While some growth rate differences were observed between benthic- and pelagic-caught lake trout, these differences were minimal and had only minor effects on bioenergetic model outcomes. Because it is difficult to know lifetime habitat fidelity for very old lake trout, we applied lake-wide growth models for all fish.

Implications for predator–prey interactions

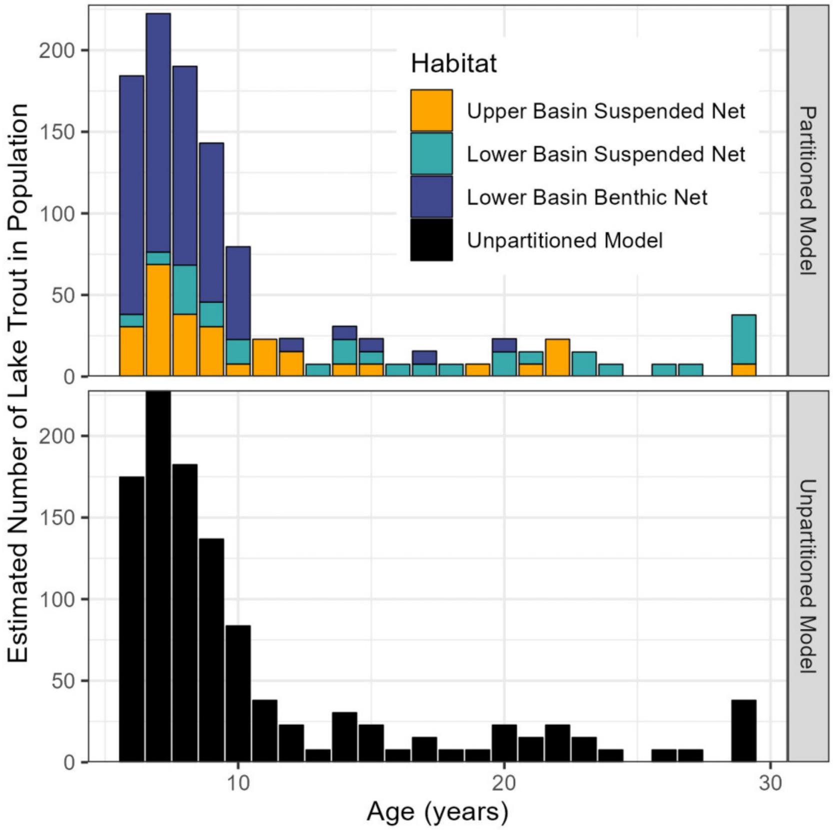
Intraspecific variability across habitats influenced habitat-specific species interactions and the subsequent impacts of lake trout predation on prey populations. In the partitioned model, 73% of kokanee consumption occurred in the upper basin pelagic habitat, despite that habitat accounting for only 25% of the lake trout population >400 mm. Kokanee stocking and the lack of benthic energy pathways in this basin result in high habitat overlap between lake trout and kokanee, promoting higher rates of predation. Apex predator consumption of recently stocked fishes has been documented in many species and systems (e.g., Martinez et al. 2009; Grausgruber and Weber 2021), and lake trout have clearly capitalized on this prey source in New Fork Lakes. In other systems in the western United States, stocking has been documented to promote imbalances between predator and prey densities (Johnson and Martinez 2000). At a minimum, stocking practices in New Fork Lakes subsidize otherwise low production in this oligotrophic system.

Despite larger population sizes, lower basin lake trout had a much smaller impact on lake-wide kokanee consumption than upper basin lake trout. Kokanee consumption in the lower basin was highest in spring and summer, likely reflecting consumption of the previous year's stocked fish that passed through the Narrows to the lower basin during the unstratified, spring-runoff period. Connectivity between basins is highest in spring and we hypothesize this drives a pulse of kokanee movement to the lower basin. During summer and fall, thermal stratification and low water levels, respectively, reduce or eliminate movement of fish between basins. Thermal stratification has been documented to reduce movement of lake trout between basins in other systems (Gallagher et al. 2022), and we expect similar behaviors are exhibited in New Fork Lakes.

Both the partitioned and unpartitioned models produced total kokanee consumption estimates that were below the biologically feasible limit (total annual kokanee mortality as determined by kokanee stocking rates, creel data, and spawning return numbers; 78% and 94% of estimated annual mortality for the partitioned and unpartitioned models, respectively). However, the partitioned model provided greater ecological context for how kokanee consumption is occurring in New Fork Lakes. With the partitioned model approach, we could ascertain that kokanee consumption is highly variable across habitats and highest in the upper basin. This finding is critical to management of the system and could direct future management actions aimed at increasing kokanee survival. New Fork Lakes is managed as a multispecies fishery, with lake trout and kokanee as two target species. Specifically, managers can target management on removal of lake trout in the upper basin, which could alleviate kokanee predation and continue to provide lake trout angling opportunities in the lower basin. While the unpartitioned model may have produced a biologically feasible kokanee consumption estimate, it fails to provide a nuanced understanding of the lake's ecology to guide management actions.

There is some uncertainty in our results, stemming from two primary sources. First, total population consumption estimates are based on an estimated population size derived from the literature. While this is an imperfect method, there is no reason to suspect the New Fork Lakes population is outside of the range estimated, and our results suggest ecologically partitioning bioenergetics models mattered more in total consumption outcomes than population size. A focused effort to calculate lake trout population size in New Fork Lakes would provide more certainty to our results but could have negative impacts on the population size as a mark-recapture study would require many fish to be collected using gillnets set in water over 30 m, possibly leading to de-

Fig. 6. Estimated abundance of lake trout of each age from the partitioned and unpartitioned modeling approaches. Abundances are based on an estimated population size of 1102 lake trout >400 mm. In the partitioned model, the population estimate was split across habitats with 609 lake trout in lower basin benthic, 219 in lower basin pelagic, and 274 in upper basin pelagic habitats.

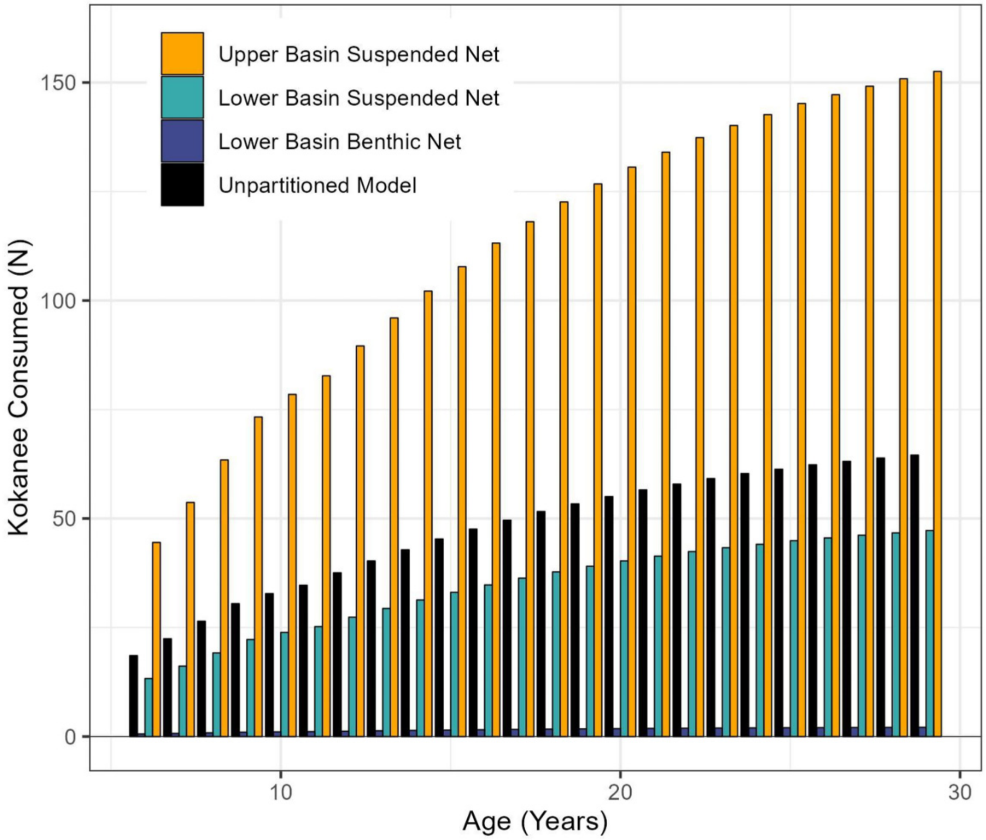


layed mortality of tagged individuals. Second, we had low stomach content sample sizes for lake trout >400 mm for two habitat-season groups (upper basin pelagic spring and lower basin pelagic fall). We had aimed to develop larger sample sizes, but the combination of low catch rates and a small lake trout population resulted in a tradeoff between achieving higher sample sizes and excessively reducing the lake trout population. Given the approximate population estimate used, we estimate our research could have harvested up to 10% of the lake trout population susceptible to our sampling gears, and additional mortality was not desirable. The typical solution to this would be to conduct nonlethal sampling (e.g., gastric lavage); however, in this deep, oligotrophic system, we encountered two factors that limited this possibility. First, CPUE was extremely low in all nets used, so short net sets were unlikely to return sufficient sample sizes. Second, benthic nets were set at a range of depths (12–58 m in upper basin, 12–40 m in lower basin), and many lake trout caught in deeper depths were dead upon retrieval or showed signs of barotrauma, decreasing their odds of survival if released. While larger sample sizes were desirable, we had to operate within the bounds of what was logistically feasible and minimize the impacts of our research to the ecosystem. While these two limitations should be considered, the importance of ecologically partitioning the bioenergetics models to accurately describe consumption dynamics remains clear.

Relevance to other systems and species

Across systems, the relative importance of intraspecific niche partitioning and environmental conditions on consumption estimates likely depends on a few factors. First, species characteristics like trophic position and individual/population plasticity are important drivers of niche partitioning. Lake trout are well-documented to have individual foraging variation, with studies demonstrating individual specialization across habitats, time, and prey abundance (Chavarie et al. 2015, 2021; Vinson et al. 2021). Comparatively, some other apex predators display more synchronous foraging, where prey may change over time, but all individuals tend to exploit prey resources similarly (i.e., a generalist population comprised of generalist individuals; Fetzer et al. 2016). Consideration of the ability of an individual to move flexibly between energy pathways, and the prevalence of this behavior within a population, will inform the degree of intraspecific niche partitioning observed. For example, unpublished data from lake trout eye lens stable isotope analysis suggest a high degree of lifetime foraging variation among

Fig. 7. Bioenergetic model estimates for the number of kokanee eaten annually by an individual lake trout at each age. Colors represent the four bioenergetics modeling scenarios: three representing each of the partitioned ecological groups, and one representing the unpartitioned, whole-lake modeling approach. These individual lake trout consumption estimates were then scaled by population size and age-structure to estimate total consumption of kokanee by the whole lake trout population.

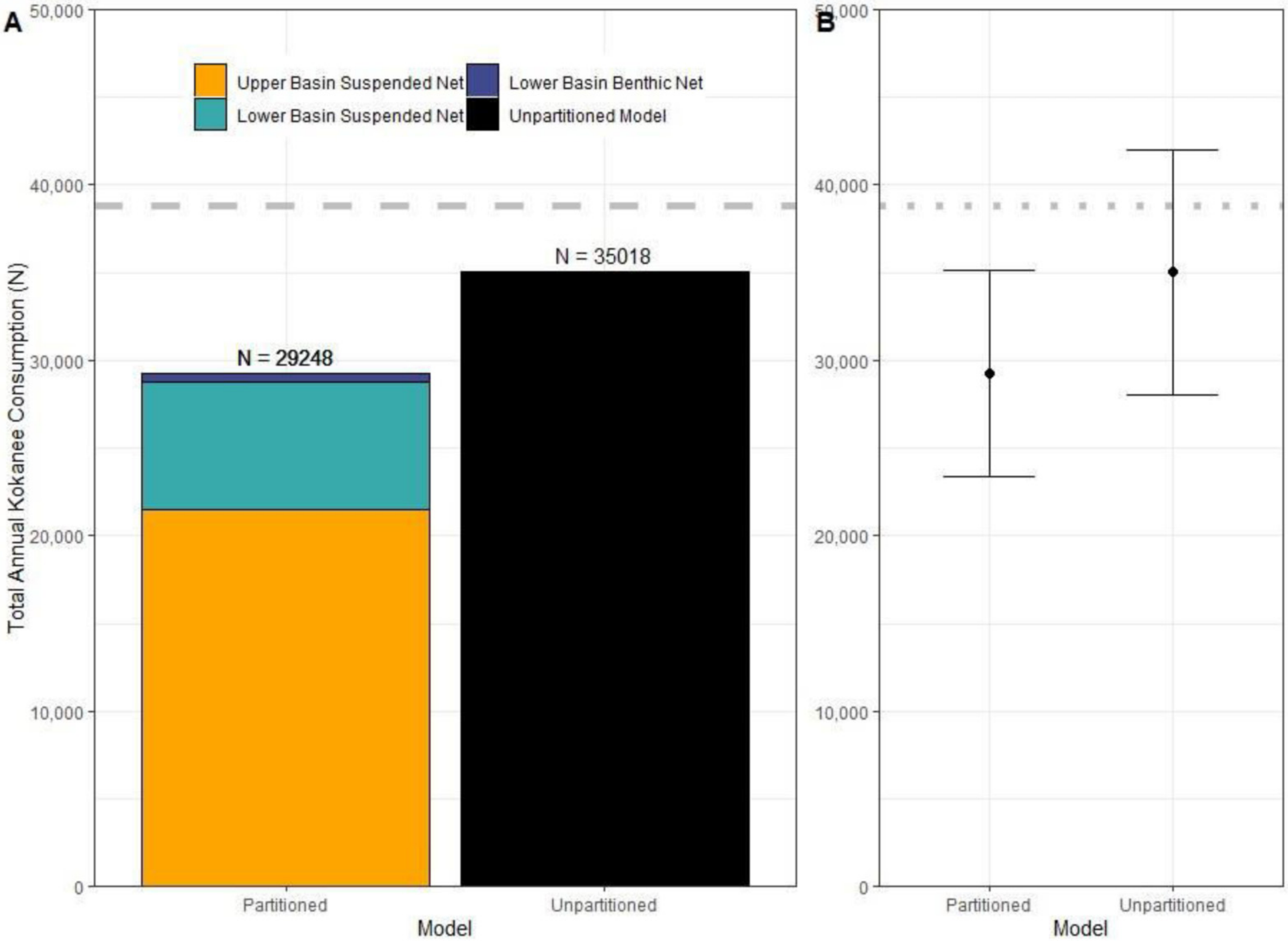


and between individuals that may help further explain difference in growth rates among individuals (Rosinski, unpublished, 2024). Coupled with data from this study, these results suggest New Fork Lakes lake trout form a generalist population, likely comprised of specialist and generalist individuals. Future research should apply stable isotope analyses of lake trout eye lenses to determine the distribution of feeding strategies in the population more directly and evaluate the impact of feeding strategy on important outcomes like growth rates.

The degree of environmental heterogeneity within a system could also be considered. While environmental heterogeneity in New Fork Lakes is clearly defined because of its two distinct basins, most lake ecosystems contain a mix of distinct and continuous habitats based on temperature, light regimes, and nearshore to offshore gradients, which likely impact the behavior of fish and resulting prey consumption. For example, in a large, shallow lake, walleye (*Sander vitreus*) consumption of yellow perch (*Perca flavescens*) varied between nearshore and offshore habitats (Fetzer et al. 2016). Though large, the relatively simple bathymetry of this lake might suggest low levels of heterogeneity; however, these results similarly indicate a need to incorporate ecological heterogeneity to understand apex predator foraging dynamics.

While we do not believe lake trout in New Fork Lakes have diverged to the extent of forming distinct populations or ecotypes, the intraspecific variation displayed by New Fork Lakes lake trout is consistent with the diverse life history strategies documented across the distribution of lake trout (Muir et al. 2016; Chavarie et al. 2021). These diverse strategies allow lake trout to persist in a range of habitats and fluctuations in prey variability and require researchers to incorporate ecological heterogeneity to develop a clearer understanding of this apex fish predator. Many apex predators vary prey selection to capitalize on changes in prey composition and availability (Galarowicz et al. 2006; Vinson et al. 2021) across environmental gradients like depth and distance from shore (Dryer et al. 1965; Olson et al. 1988); however, bioenergetics models often use diet averages across vast extents to represent consumption. In this study, comparing kokanee consumption estimates of the partitioned and unpartitioned models highlights that accounting for ecological heterogeneity can have a large impact on our understanding of apex predator foraging. Namely, as habitat heterogeneity increases, increased model partitioning may more accurately describe species interactions across different ecological contexts. Trophic ecology studies rely on an ability to track the flow of energy through ecosystems, and partitioning models based on important sources of heterogeneity is a critical step

Fig. 8. Population-scaled bioenergetics estimates for the total number of kokanee consumed by lake trout annually in New Fork Lakes. Panel A shows the breakdown of consumption for the partitioned and unpartitioned models using the standard population size estimate, with total annual consumption noted at the top of each bar. The error bars in panel B show consumption estimates when the population size estimate is scaled up and down by 20%. The horizontal dashed lines represent the 5-year mean number of kokanee stocked annually.



to do this effectively. By understanding this complexity, fisheries biologists and managers can assess the feasibility of different management actions and focus limited resources to achieve desired outcomes (e.g., suppress upper basin pelagic lake trout to improve kokanee survival; Rosinski 2023).

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

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Appendix A

Table A1. Prey energy densities used for bioenergetics modeling.

Prey item	Prey energy density used (J/g)	Calculated value (J/g; mean + St. Dev)	Source
Chironomid	4090	–	Johnson et al. (2015)
Daphnia	1190	–	Luecke and Brandt (1993)
Kokanee	−6551.1 + (475.1 ∗ DM)	7371.4 + 1149.2	Johnson et al. (2017*b*)
Mottled sculpin	−530.85 + (230.85 ∗ DM)	4670.9 (approx.)	Hondorp et al. (2005); Ruetz et al. (2009)
Rainbow trout	−2886.6 + (348.9 ∗ DM)	6947.4 + 1355.2	Johnson et al. (2017*b*)

Note: Kokanee and rainbow trout energy densities were calculated by conducting wet weight to dry weight laboratory studies, then using dry weight percentage (DM) to energy density conversions. All other prey energy densities were determined from published literature values. Mottled sculpin energy densities are approximate and based on available data from other sculpin species, as published data on this species are limited.

Fig. A1. Length–weight relationship for all Lake Trout collected from New Fork Lakes in 2020 and 2021. The equation of the regression line was used to convert mean lengths-at-age to weights.

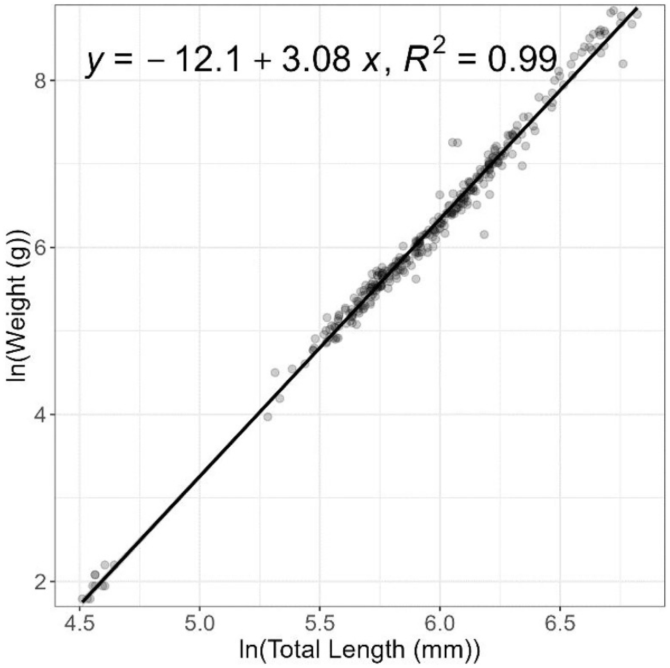

Fig. A2. Length-frequency distribution for all Lake Trout caught in New Fork Lakes, separated by gear. More Lake Trout were caught in benthic nets than suspended nets, and size distributions varied between the two gears, though both gears caught a wide range of Lake Trout sizes.

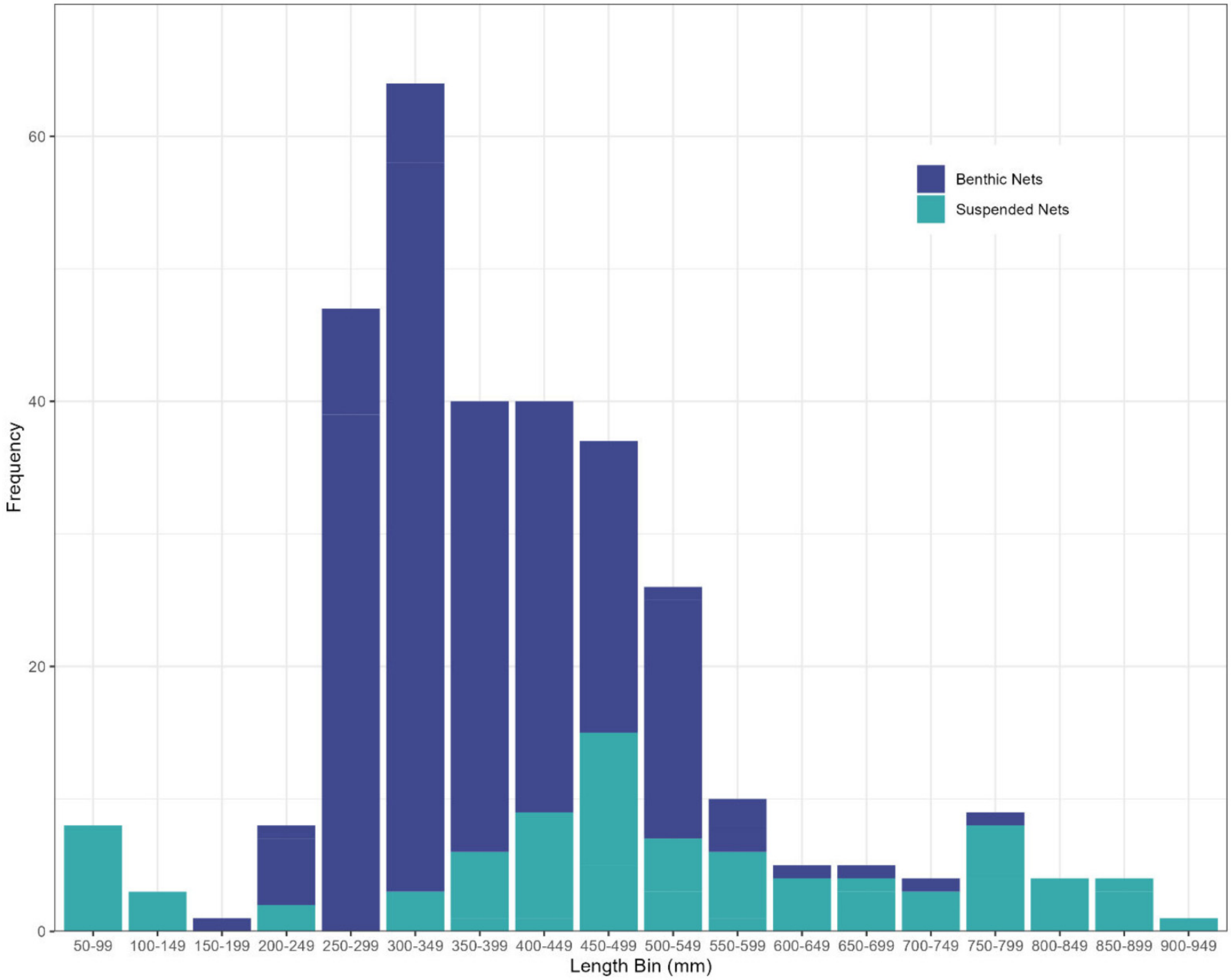

Fig. A3. Relationship between liver and a muscle ^{15}N and δ^{34}S values collected from individual fish. 1:1 line indicated with solid line.

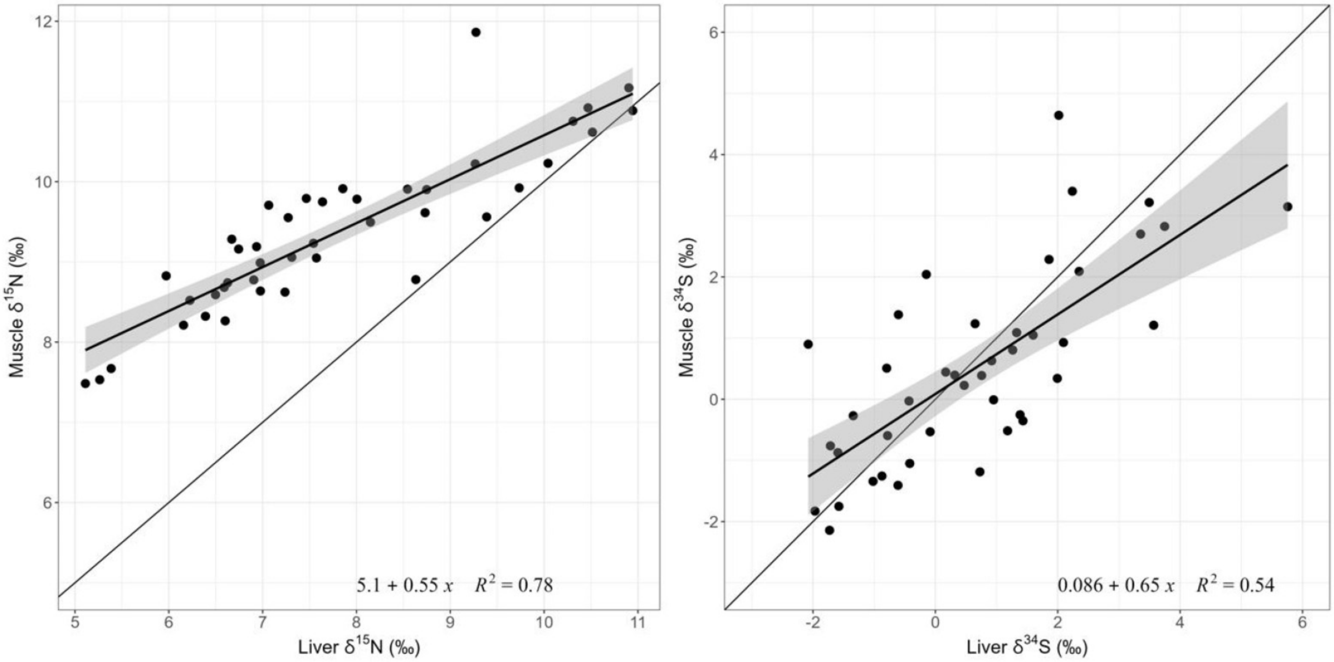

Fig. A4. Niche overlap between lake trout in each of the three main habitats in New Fork Lakes, calculated using muscle δ^{13}C, δ^{15}N, and δ^{34}S stable isotope values. Overlap is presented as the probability that a fish from the habitat listed in the row is found in the niche of the habitat listed in the column, as denoted by the top left box. Overlap probabilities are lowest for lower basin fish being found in the niche space of the upper basin.