

Tracking Lake Trout Diet and Trophic Interactions in Blue Mesa Reservoir Using Stomach Contents and Stable Isotopes

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Introduction

Blue Mesa Reservoir, Colorado, the largest reservoir in the state at over 3,700 ha, has been considered one of the state's premier destination fisheries. Blue Mesa Reservoir is the uppermost of three reservoirs within the Aspinall Unit of the Colorado River Storage Project, and is contained within the Curecanti National Recreation Area. Non-wildlife related activities are co-managed through an agreement between the National Park Service (NPS) and the Bureau of Reclamation (NPS 1997). The fishery in Blue Mesa Reservoir is managed by Colorado Parks and Wildlife (CPW), and has exhibited some of the fastest growth rates on the continent for lake trout *Salvelinus namaycush* (Martinez et al. 2009). An abundant supply of kokanee salmon *Oncorhynchus nerka* forage led to four consecutive state record size lake trout being taken from the system, beginning with a 17 kg fish in 1998. Two records were obtained in 2003, and the latest at 22.8 kg was captured in 2007. Very high growth has also been observed in the kokanee salmon population due to abundant zooplankton and relatively warm water of Blue Mesa Reservoir (Johnson and Martinez 2000, Hardiman et al. 2004). Current CPW creel data show that the primary species of interest in Blue Mesa reservoir is kokanee salmon, with 45% of anglers traveling to the location to specifically target the species (Dan Brauch, CPW, unpublished data). The kokanee salmon fishery has been valued at more than \$5 million per year to the local economy (Johnson et al. 2009). Lake trout are only targeted specifically by 7-8% of the anglers surveyed. As with other reservoirs and lakes in the west, lake trout were introduced

into this system (albeit accidentally through unintentional stocking). After the initial event, lake trout continued to be intermittently stocked in Blue Mesa Reservoir until 1993 when naturally occurring reproduction was first observed. Gill net catch per unit effort showed a shift in population size structure indicative of increased recruitment, even though the slot limit was removed and bag limit increased to eight fish per day in 1996. Relative weight of larger individuals ($> 1,000$ mm TL) has decreased in recent years from > 154 in 2000 to 108 in 2009, suggesting a substantial decrease in forage availability for lake trout.

Sonar and creel surveys have shown a significant decrease in kokanee salmon abundance (Dan Brauch, CPW, unpublished data). Annual sonar surveys have estimated that pelagic fish (mostly kokanee) abundance has decreased 90% from $>1,000,000$ in 2002 to $<100,000$ in 2009. Similarly, creel survey data show a decrease in angler harvest from 130,000 kokanee in 2002 to $<20,000$ in 2009. This decline in the kokanee population occurred despite efforts to boost population abundance through increased stocking of fry from 1.4 million in 1994 to 3.3 million in 2009. Partly because Blue Mesa Reservoir has supplied up to 90% of the state's hatchery supply of kokanee eggs, in turn used to stock 26 other water throughout Colorado, the current state of the kokanee population has caused tremendous concern for both CPW and NPS. In 2009 the CPW decided to undertake a lake trout removal program in an attempt to save the kokanee population from extirpation.

Another concern was an illicit introduction of yellow perch *Perca flavescens*, which had become prevalent in the creel in 2000. It was not known how this newcomer to Blue Mesa Reservoir would fit into the existing food web and possible implications that could arise in combination with the expanding lake trout population. Previous stable isotope research by Johnson et al. (2002), when used in conjunction with earlier direct diet analysis by Johnson and

Martinez (2000), gives a baseline to the trophic interactions within Blue Mesa Reservoir. This follow up study will determine what shifts have taken place in the food web of the reservoir since the lake trout expansion, resulting decline of kokanee salmon abundance, and illegal introduction of yellow perch. The sustainability of Blue Mesa Reservoir as a premier destination fishery and kokanee salmon egg supplier to the State of Colorado is at serious risk.

Methods

Diet Composition

Diet composition was determined by following a standard operating procedure developed by Dr. Brett Johnson (CSU Fisheries Ecology Laboratory). In the field, a shallow incision was made from the vent to the isthmus and the stomach from the esophagus to pyloric sphincter was removed and placed in a muslin bag. The stomachs (n = 845) were then stored in 10% formalin solution to fix contents and halt further digestion. In the lab, diet items were identified to lowest taxonomic level possible given the state of digestion. Percent composition as well as number of prey items was then quantified. If prey fish total length could not be measured, then a standard equation specific to the species was used to transform backbone length to total length. The equation had the form:

$$TL = a * BBL + b$$

where TL is total length of the prey item in mm and BBL is backbone length in mm. Both coefficients a and b are species specific and were determined with on hand samples using linear regression techniques. The exception is yellow perch, where the coefficients were obtained from Knight et al. (1984). Current diet was compared to those collected from previous research to determine if a shift in prey composition has occurred due to a change in availability of prey species.

Stable Isotopes

Aside from diet composition, stable isotopes are another method of tracking trophic interactions in food web structures (Peterson and Fry 1987, Johnson et al. 2002). A naturally occurring stable heavy isotope of carbon (^{13}C) is indicative of the primary carbon source, whether it originates from terrestrial, littoral, or pelagic areas. Change in carbon isotope ($\delta^{13}\text{C}$) when compared other organisms from the same system will give an indication of what diet primarily consists of, as ratios will be similar when trophic levels are compared (Fry 2006). A heavy isotope of nitrogen (^{15}N) can indicate trophic position within a system, and an increase in the proportion of nitrogen ($\delta^{15}\text{N}$) compared between species indicates a higher trophic level.

A 1 cm³ muscle plug was collected during CPW gill net sampling (spring) and removal (fall) seasons from lake trout, kokanee salmon, brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, white sucker *Catostomus commersonii*, longnose sucker *Catostomus catostomus*, and yellow perch. Epaxial muscle tissue with skin removed was taken from between the dorsal fin and lateral line, then each sample placed into a separate bag and stored frozen. All invertebrates collected were left whole and frozen in separate bags by species.

In the lab, samples (n = 300) were dried at 60°C for 48-72 hours then ground to a fine powder with a mortar and pestle. Each sample was placed into a tin cup and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyzer. Isotopic signatures were then expressed as δ values, in parts per thousand (‰) differences from C and N standards:

$$\delta_{\text{sample}} = [(R_{\text{sample}} / R_{\text{standard}} - 1)] \times 1000$$

where R is the isotopic ratio ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) of the sample or standard (Fry 2006).

Standards used were Atmospheric Air for $\delta^{15}\text{N}$ and Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$.

Lipids are known to be depleted in ^{13}C when compared to muscle tissues, and lipid content can vary greatly between individual fish within a species as well as when comparing species. To avoid potential bias from differing lipid concentrations between samples and species, mathematical corrections for lipid content from Post et al. (2007) were applied to $\delta^{13}\text{C}$ values from the 2010 samples. The equation used was:

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{measured}} - 3.32 + 0.99 * \text{C:N}$$

where C:N is the ratio $\delta^{13}\text{C} / \delta^{15}\text{N}$.

Once δ values were determined, a mixing model was applied to find the proportion of prey species being consumed:

$$p_1 = (\delta_{\text{sample}} - \delta_{\text{source2}}) / (\delta_{\text{source1}} - \delta_{\text{source2}})$$

$$p_2 = 1 - p_1$$

where δ_{source1} and δ_{source2} are the isotopic signatures of the prey, δ_{sample} is the predator signature, and p_1 and p_2 are the proportions of each prey item. The fractionation rate of $\delta^{15}\text{N}$ is about 3.5 per trophic level, and an increase in $\delta^{15}\text{N}$ is representative of a predator-prey interaction.

Similarly, $\delta^{13}\text{C}$ is fractionated at a rate of 1-1.5 per trophic level. Plots of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicate likely predators and prey.

Lake trout were divided into three size classes due to distinct growth stanzas arising from trophic ontogeny (Figure 1). The smallest size class was <426 mm TL and corresponds to the size threshold above which piscivory begins in many systems, the middle size was 426-600 mm TL, and largest was >600 mm TL. Diet and isotope data were compared to previous research (Johnson et al. 2002) to determine if a change in trophic interactions occurred due to changes in lake trout and kokanee abundance.

Results

Diet Composition

There were 25,461 prey items identified out of 622 non-empty stomachs analyzed, the most numerous of which were *Daphnia* spp. (19,070; Table 1). *Daphnia* spp. were only found in brown trout, rainbow trout, and lake trout under 600 mm TL and were most numerous (10,435) in lake trout from 426-600 mm TL. All kokanee salmon stomachs (n = 25) analyzed were empty, but it was assumed that the species primarily consumes *Daphnia* spp. as well due to previous research completed on Blue Mesa Reservoir (Johnson and Martinez 2000). Terrestrial insects, consisting mainly of Formicidae (ants) with an occasional Dipteran were found in brown trout ranging in size from 250-296 mm TL, but were not found in any other predator. Aquatic insects were found in all predators but yellow perch, the majority of which were Chironomid larvae and pupae (38.9% and 43.6 %, respectively) with 17.5% consisting of Ephemeroptera and Culicidae larvae. Crayfish *Orconectes* spp. were observed in all predatory fish but rainbow trout and were most commonly observed (59.3%) in yellow perch stomachs. The only other diet item found in yellow perch was a single unidentifiable fish. Crayfish were also found in 37.6% of the mid-sized lake trout, and in brown trout (33.9%) ranging in size from 275-558 mm TL.

Yellow perch were the most numerous prey fish species found in stomachs, and comprised of 85% of the fish in brown trout stomachs, 55% of fish found in lake trout <426 mm TL, 75.6 % of fish in mid-sized lake trout, and 25.8% in the largest lake trout size class over 600 mm TL. The most common fish item found in lake trout >600 mm TL was rainbow trout, and made up 54.2% of fish species found. The highest proportion of kokanee salmon was in lake trout <426 mm TL at 15%, followed by 5.8% in the 426-600 mm size class, then 4.2% in lake trout >600 mm TL. A small amount of kokanee salmon were also observed in brown trout

stomachs, and made up 3.8% of the prey fish total. A slight amount of cannibalism was discovered in the two larger lake trout size classes. Three were in stomachs of lake trout >600 mm TL and one in a 465 mm fish. Only one catostomid was found out of 787 prey fish in stomachs, a 105 mm TL white sucker in a 471 mm lake trout.

Stable Isotopes

Carbon signature was strongly related to length of lake trout and showed distinct enrichment with length from 300 to 600 mm TL, and then became depleted as fish length increased above 600 mm (Figure 2). Carbon signature was also related to total length in rainbow trout with the highest concentration of ^{13}C in the smallest fish, until about 290 mm then became depleted (Figure 3). Brown trout showed a change in carbon signature as well, but it occurred in the opposite direction. The smallest brown trout were most depleted, and they became enriched starting at 400 mm TL (Figure 4). Neither yellow perch nor kokanee salmon showed any relationship when comparing $\delta^{13}\text{C}$ as a function of total length, suggesting a consistent diet among all sizes of these fishes.

Nitrogen signature also showed a relationship to total length in lake trout, but a much more subtle increase as length increased (Figure 5). Rainbow trout nitrogen signature had a similar trend as its carbon signature. No change in trophic position was apparent until the fish grew beyond 300 mm total length (Figure 6). Again, brown trout showed an enriching trend in $\delta^{15}\text{N}$ values beginning at about 10 with the smallest fish and ending at a value of about 13.5 for the largest (Figure 7). As with $\delta^{13}\text{C}$, neither yellow perch nor kokanee salmon showed any relationship when comparing $\delta^{15}\text{N}$ as a function of total length.

A comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the prominent predator and prey species is shown in Figure 8.. Kokanee salmon had the lowest carbon signature of all species analyzed and

a slightly elevated nitrogen signature as compared to the majority of prey items in Blue Mesa Reservoir. All size classes of lake trout had more enriched $\delta^{15}\text{N}$ values than all other species except for the largest yellow perch (>160 mm TL), which was equal to the largest lake trout. Brown trout >426 mm TL had elevated values of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ when compared to smaller brown trout and rainbow trout. Crayfish had a lower nitrogen value than all fish, and zooplankton had the most depleted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

When comparing fish $\delta^{13}\text{C}$ values between 2000 and 2010, a distinct shift in carbon signatures was discovered in all but rainbow trout (Figure 9). The greatest shift was found in the two smallest size classes of lake trout, at -2.7 for those under 426 mm and -3.3 for lake trout 426-600 mm (Table 2). Lake trout >600 mm were depleted by 0.7. Kokanee salmon showed the third largest difference between years, and were at -33.9 in 2010 compared to -32.4 in 2000. Rainbow trout were the only more enriched species, going from -26.6 to -24.1. Despite these shifts, the relative position among species remained about the same in 2000 and 2010, suggesting either a change in carbon signature at the base of the food web between 2000 and 2010, or the shift may be an artifact of samples processed at different laboratories in the two periods.

Nitrogen signature also showed an increase in all fish species except for rainbow trout (Figure 9). The greatest difference was in the smallest lake trout (<426 mm), going from 13.1 to 13.9, and the difference between years decreased with an increase in lake trout size (Table 2). Mid-sized lake trout had an increase of 0.6 while larger lake trout increased by 0.4. Kokanee salmon showed an increase of 0.3, up from 11.7. The only species exhibiting a decrease in $\delta^{15}\text{N}$ value was the rainbow trout, going from 10.8 to 10.5. Again, the relative position among species remained about the same in 2000 and 2010, suggesting either a change in nitrogen signature at the base of the food web between 2000 and 2010, or the shift may be an artifact of samples

processed at different laboratories in the two periods. We are awaiting additional analyses of samples from 2000 to address this question.

Discussion

There have been some slight shifts when comparing current stomach content analyses with those done in 2000 for lake trout of all sizes. Although previous research on Blue Mesa Reservoir showed catostomids as 10% of the prey items in large (>600 mm) and about 5% in intermediate sized lake trout, current analyses had only found one catostomid in an intermediate sized lake trout indicating a large decline in consumption (Johnson and Martinez 2000, Johnson and Koski 2005). Catostomids were therefore not included in the mixing model.

Since introduction, yellow perch constitute a much greater proportion of prey items. Previous work only observed yellow perch in one instance in 2001, and were <5% of the diet in lake trout 442-827 mm TL (Johnson and Koski 2005). Today yellow perch are found in all predatory fish species but their own, and make up the greatest proportion (by number) of fish prey items in all but the largest lake trout. In stomach content analysis of the largest lake trout, rainbow trout (n = 65) were more than twice as frequently found as yellow perch (n = 31) whereas only five kokanee salmon were identified. This is contrary to the stable isotope findings as an increase in consumption of kokanee salmon was indicated across all size classes of lake trout (Table 3).

Using the mixing model, the proportion of kokanee salmon in the diets has gone up since previous work by Johnson et al. (2002). Intermediate sized lake trout had the greatest increase in consumption of kokanee salmon going from 6.9% to 53.4%. Lake trout >600 mm TL had the smallest increase, but still constitute a very significant proportion of the diet at 87%. Lake trout <426 mm also had an increase in kokanee proportion, and went from 60.3% to 75.8%. The

assumption that lake trout are consuming much more kokanee salmon depends on the significantly depleted carbon signature of kokanee compared to all other fish species. Lake trout are only slightly enriched from the kokanee, and all other fish species are more enriched than they are.

Caution is warranted when interpreting differences between the mixing model and stomach content analyses, as temporal scales can vary significantly between the two methods (Johnson et al. 2002). Stomach contents allow a brief snapshot of what the organism consumed just before capture, likely the previous 24 hours. On the other hand, stable isotopes are incorporated into the muscle tissues being analyzed and turn over time is much longer than digestion. This means isotope data reflect a broader time scale of consumption patterns than does stomach analysis.

Two more caveats are important to interpreting the diet. The rainbow trout stocking regime in Blue Mesa Reservoir changed in 2010, going from sub-catchable (≈ 150 mm TL) to catchable (≈ 250 mm TL) size fish. Thus, most rainbow trout were not vulnerable to predation by lake trout < 600 mm TL in 2010. Also, the mean size of rainbow in the stomachs was 184mm TL compared to 84 mm TL for kokanee salmon and 71 mm TL for yellow perch. Thus, diet composition on a mass basis will differ from that based on a frequency of occurrence; those analyses are ongoing.

We believe lake trout consume yellow perch primarily in fall-spring when there is no thermal segregation of lake trout and perch (preferred temperature of lake trout = 10°C and of yellow perch = 24°C , Hanson et al. 1997). These temperature differentials result in an effective thermal barrier to lake trout in summer, and this segregation was observed in Blue Mesa Reservoir during the summer 2011 Summer Profundal Index Netting sampling. This seasonal

pattern in spatial overlap could explain the conflicting results from diet and isotope analyses. It may be that during the summer, when lake trout consumption rates are likely highest due to the warmer temperatures, lake trout consume primarily salmonids, most of which are kokanee. Thus, kokanee may indeed be the most important prey for lake trout, as reflected in the stable isotope data.

We conclude that, given our analysis of trophic relationships at Blue Mesa Reservoir, that lake trout continue to pose a significant threat to the kokanee population and fishery. Because of the importance of kokanee to fishing and visitation at the CNRA, and the dependence of the state's hatchery system on the Blue Mesa Reservoir kokanee egg take, Colorado Parks and Wildlife should consider increasing efforts to remove lake trout and reduce predation pressure on kokanee salmon to sustain sport fishing at Blue Mesa Reservoir and other coldwater reservoirs across the state.

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Table 1. Frequency of occurrence of 13 prey types in stomach content analysis of 845 fish captured in Blue Mesa Reservoir during spring and fall sampling of 2010. There were 622 stomach found with contents and 223 empty. The predator species analyzed were brown trout *Salmo trutta* (LOC), yellow perch *Perca flavescens* (YPE), kokanee salmon *Oncorhynchus nerka* (KOK), rainbow trout *Oncorhynchus mykiss* (RBT), and three sizes of lake trout *Salvelinus namaycush* (small MAC_S <426 mm TL, medium MAC_M 426-600 mm TL, and large MAC_L >600 mm TL). All KOK stomachs were found to be empty. Invertebrate prey species found were *Daphnia* (DAPH), terrestrial invertebrates (primarily ants; TINV), aquatic invertebrates (primarily mayflies; AINV), chironomid larvae and pupae (CHL and CHP, respectively), and crayfish (CFI). Some contents could only be identified to family *Salmonidae* (SAL) and other fish samples were unidentifiable (UFI) due to state of digestion.

Predator spp.	n	Prey spp.												
		DAPH	TINV	AINV	CHL	CHP	CFI	KOK	LOC	MAC	RBT	YPE	SAL	UFI
LOC	224	208	345	665	291	453	184	6			9	136	3	6
RBT	7	1112			3							1		1
YPE	27						28							1
KOK	24													
MAC _S (<426 mm)	78	10435		66	131	616	32	3				11	1	5
MAC _M (426-600 mm)	351	7315		108	1437	1011	225	28	1	1	45	366	5	38
MAC _L (>600 mm)	133					5	4	5	2	3	65	31	7	7

Table 2. A comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between 2000 and 2010 in Blue Mesa Reservoir, Colorado for both predator and prey fish species. The species analyzed were yellow perch *Perca flavescens* (YPE), kokanee salmon *Oncorhynchus nerka* (KOK), rainbow trout *Oncorhynchus mykiss* (RBT), longnose sucker *Catostomus catostomus* (LGS), white sucker *Catostomus commersonii* (WHS), and three sizes of lake trout *Salvelinus namaycush* (MAC_S <426 mm TL, MAC_M 426-600 mm TL, and MAC_L >600 mm TL). Yellow perch were not prevalent in Blue Mesa during the 2000 study, thus no comparison could be made.

Species	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
	2000	2010	Change	2000	2010	Change
YPE	--	-28.6	NA	--	13.0	NA
KOK	-32.4	-33.9	-1.5	11.7	12.0	0.3
RBT	-26.6	-24.1	2.5	10.8	10.5	-0.3
LGS	-28.7	-29.6	-0.9	10.2	10.7	0.5
WHS	-27.9	-28.1	-0.2	10.1	10.2	0.1
MAC _S (<426 mm)	-30.1	-32.8	-2.7	13.1	13.9	0.8
MAC _M (426-600 mm)	-27.0	-30.3	-3.3	13.3	13.9	0.6
MAC _L (>600 mm)	-31.2	-31.9	-0.7	14.1	14.5	0.4

Table 3. Diet composition (percent) of three size classes of lake trout *Salvelinus namaycush* (MAC) from Blue Mesa Reservoir during 2000 and 2010, as estimated by a mixing model and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$. The two prey species shown here are kokanee salmon *Oncorhynchus nerka* (KOK) and rainbow trout *Oncorhynchus mykiss* (RBT).

MAC size (TL)	2000		2010	
	KOK	RBT	KOK	RBT
MAC _S (<426 mm)	60.3	39.7	75.8	24.2
MAC _M (426-600 mm)	6.9	93.1	53.4	46.6
MAC _L (>600 mm)	79.3	20.7	87.0	13.0

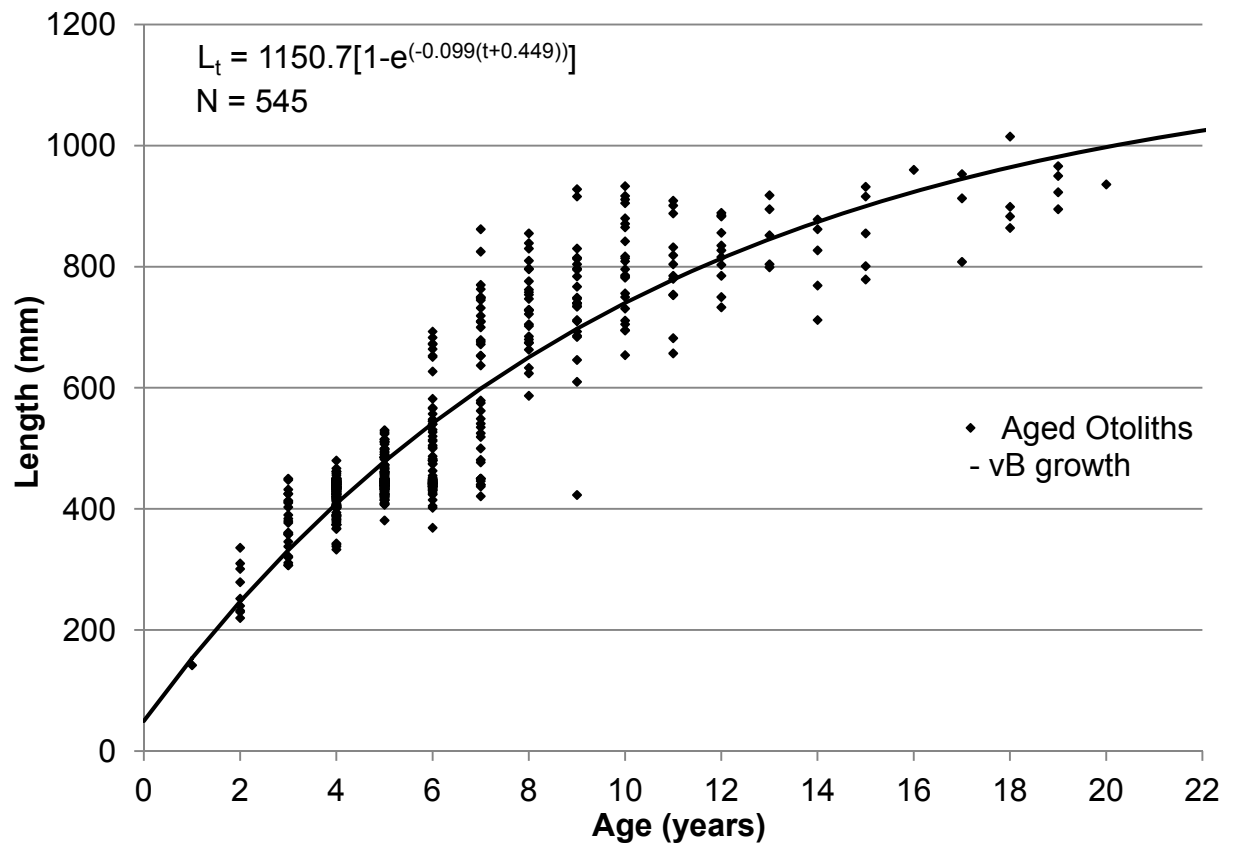


Figure 1. Aged otoliths from Blue Mesa Reservoir lake trout *Salvelinus namaycush* collected in 2010 (William Pate, CSU, unpublished data), and the resulting von Bertalanffy (vB) growth function $L_t = L_\infty[1 - e^{(-K(t-t_0))}]$ where L_t = length (mm) at time t , L_∞ = theoretical maximum length, K = growth coefficient, t_0 = theoretical time where length is zero. Two distinct growth stanzas occur due to trophic ontogeny of the lake trout, and were observed below 600 mm and above 600 mm.

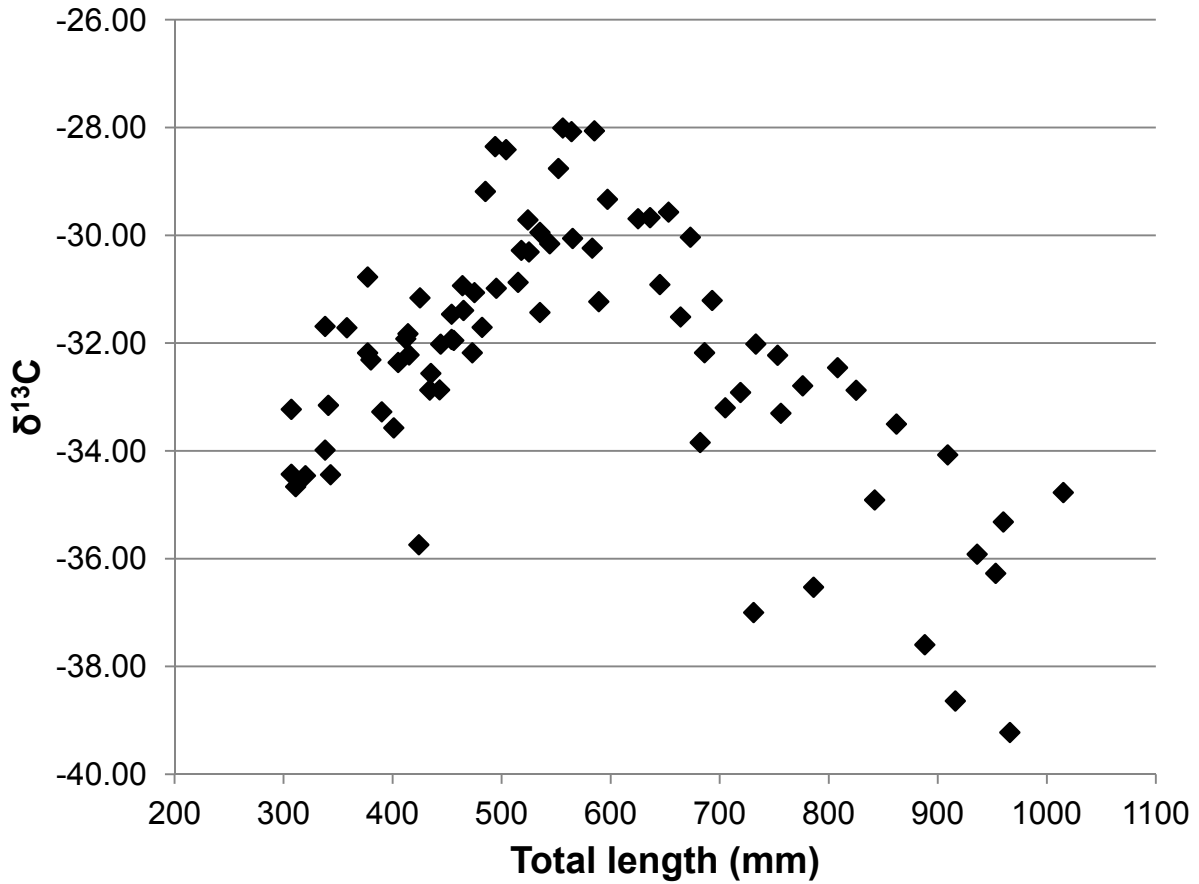


Figure 2. Lipid normalized carbon signature related to total length (mm) for 82 lake trout *Salvelinus namaycush* in Blue Mesa Reservoir, Colorado in 2010. Carbon signature becomes significantly enriched from 300 to 600 mm, and then decreases rapidly indicating a large ontogenetic shift.

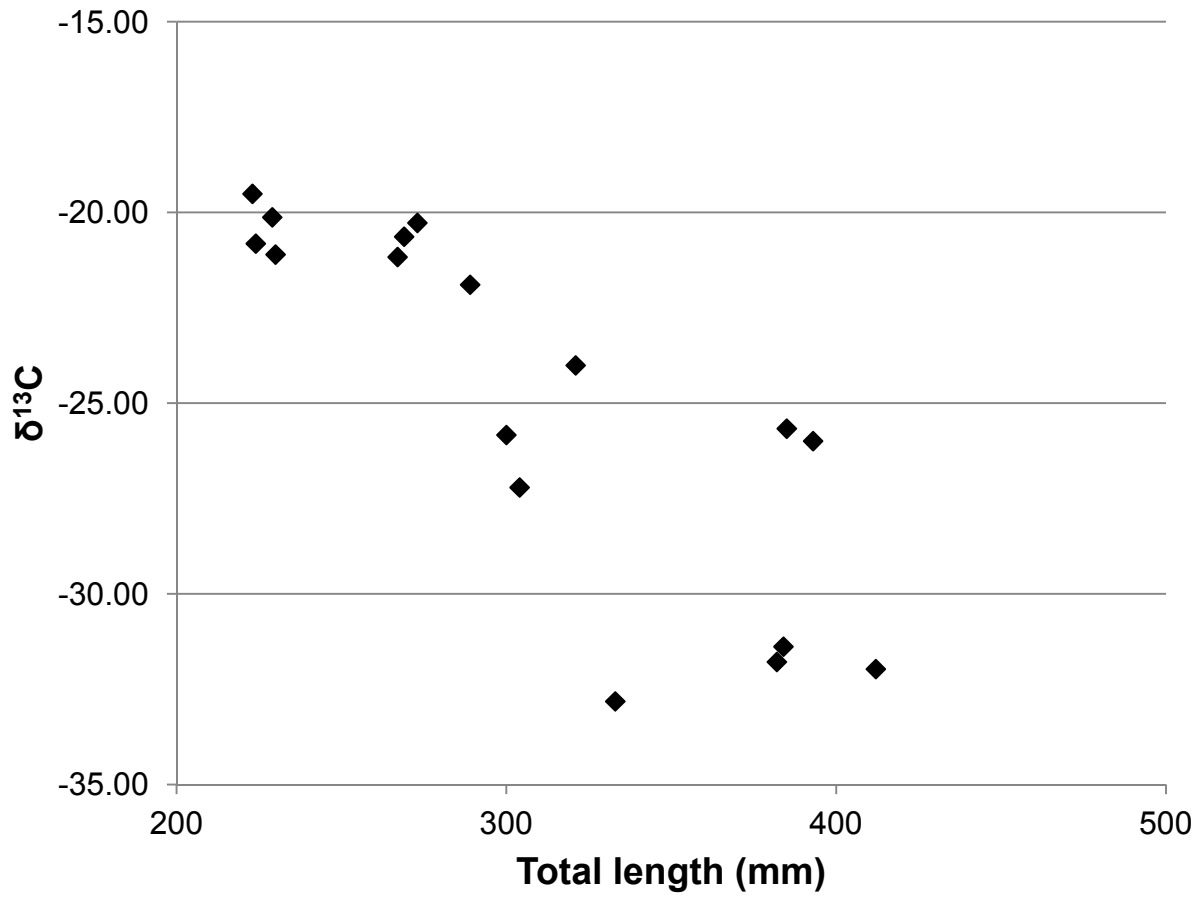


Figure 3. Lipid normalized carbon signature related to total length (mm) for 17 rainbow trout *Oncorhynchus mykiss* in Blue Mesa Reservoir, Colorado in 2010. Carbon signature decreases with duration of residence in the reservoir, with $^{13}C \approx -20$ being the hatchery signature present at the time of stocking.

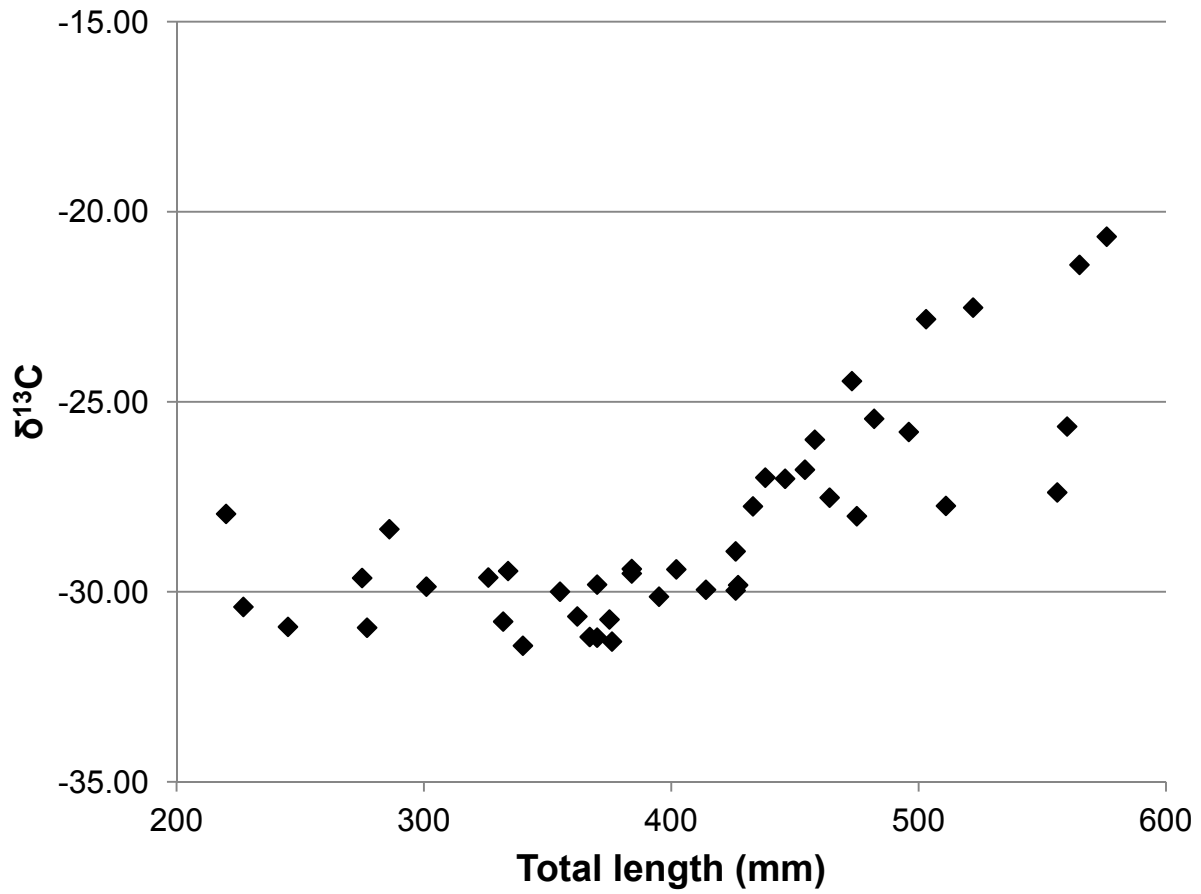


Figure 4. Lipid normalized carbon signature related to total length (mm) for 44 brown trout *Salmo trutta* in Blue Mesa Reservoir, Colorado in 2010. Carbon signature becomes enriched after the fish grows to more than 420 mm TL.

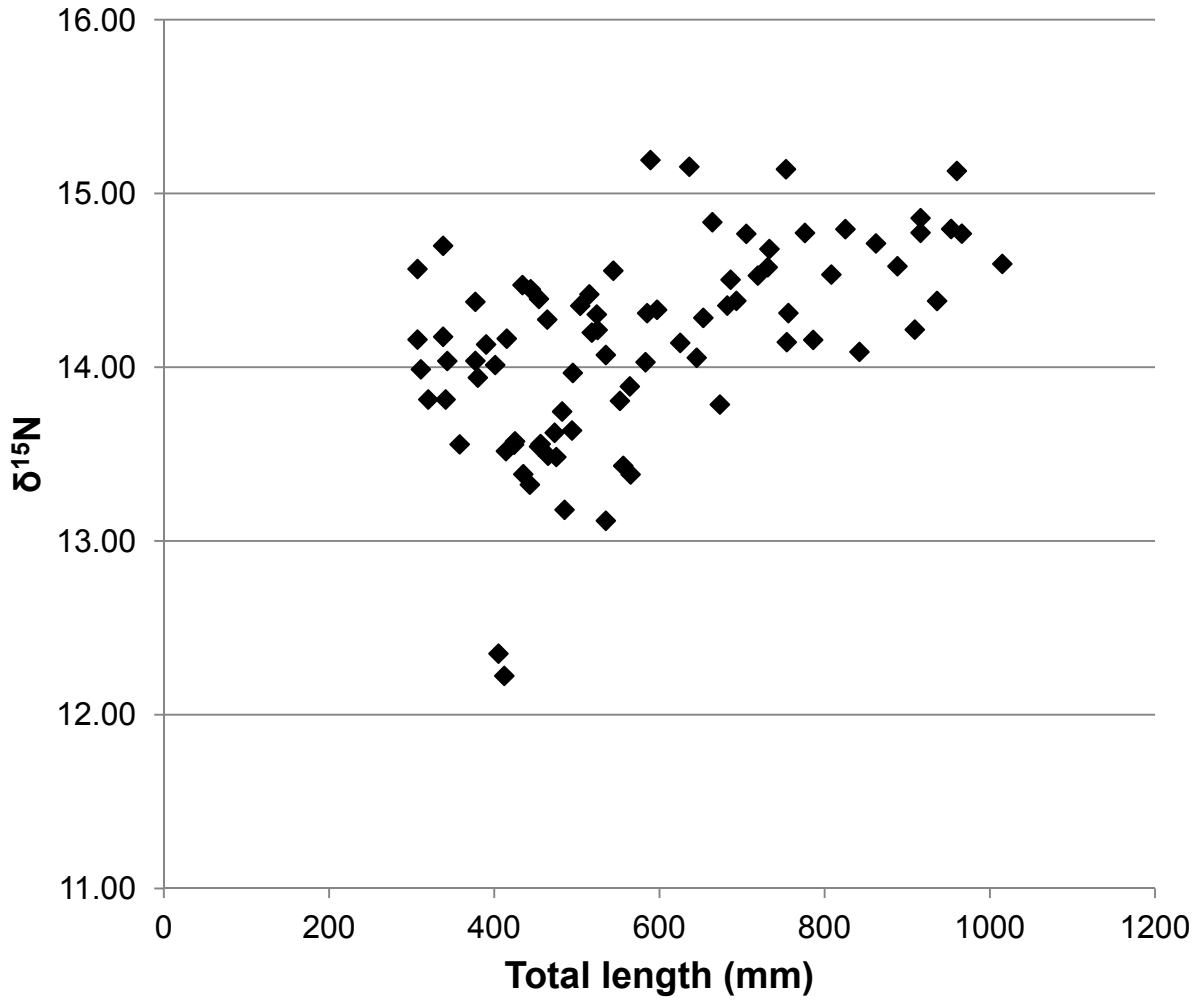


Figure 5. Nitrogen signature related to total length (mm) for 82 lake trout *Salvelinus namaycush* in Blue Mesa Reservoir, Colorado in 2010. There is a slow trend in increasing $\delta^{15}\text{N}$ as total length increases, indicating a slow rise in trophic position.

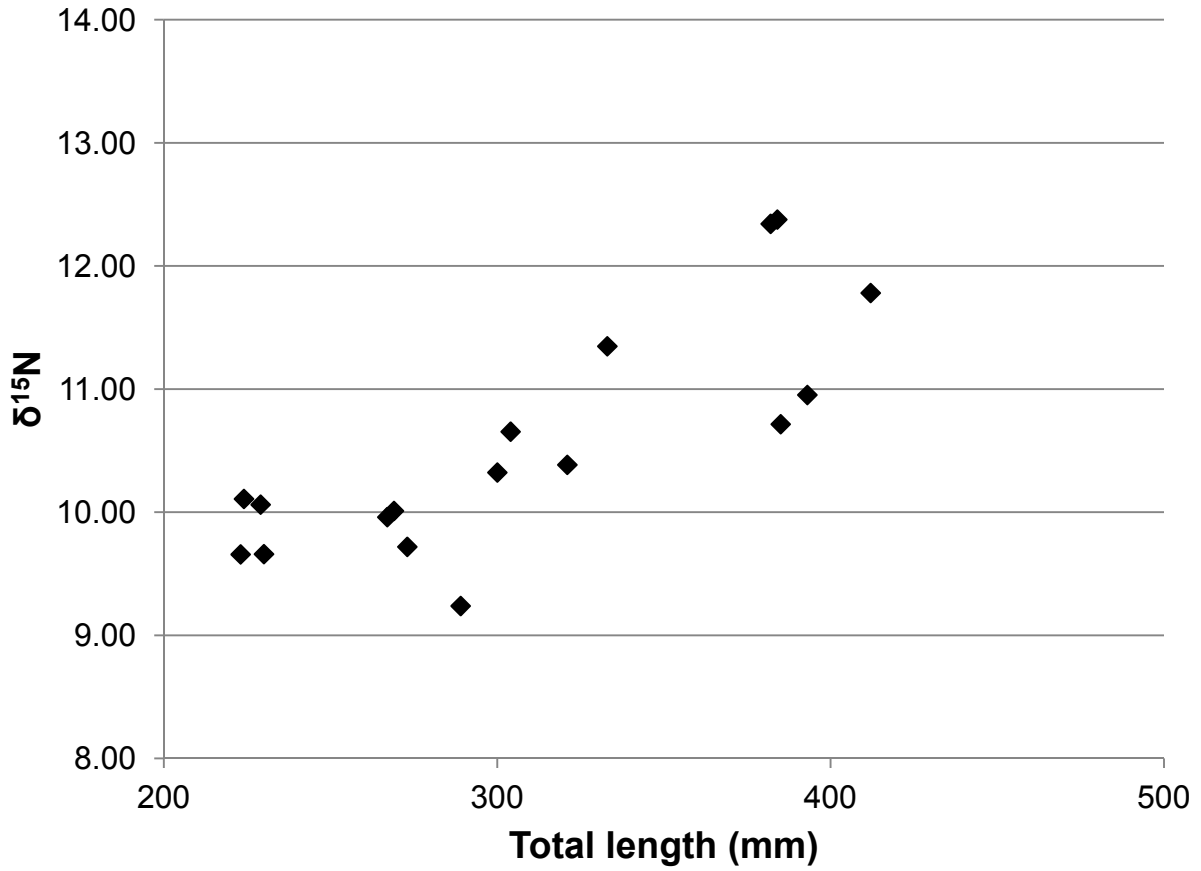


Figure 6. Nitrogen signature related to total length (mm) for 17 rainbow trout *Oncorhynchus mykiss* in Blue Mesa Reservoir, Colorado in 2010. Nitrogen signature becomes quickly enriched when the fish grows beyond 300 mm total length (approximate size at stocking).

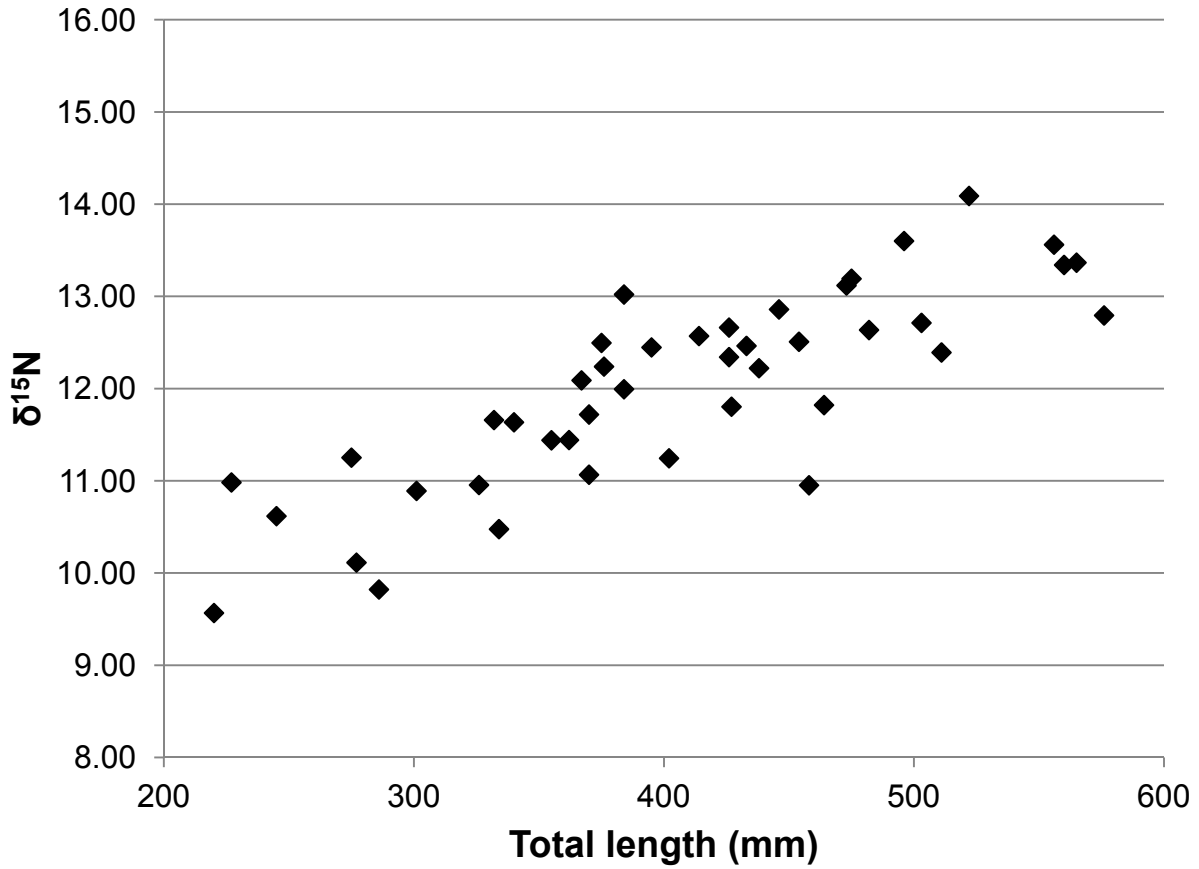


Figure 7. Nitrogen signature related to total length (mm) for 44 brown trout *Salmo trutta* in Blue Mesa Reservoir, Colorado in 2010. There is a slow trend in increasing $\delta^{15}\text{N}$ as total length increases, indicating a rise in trophic position.

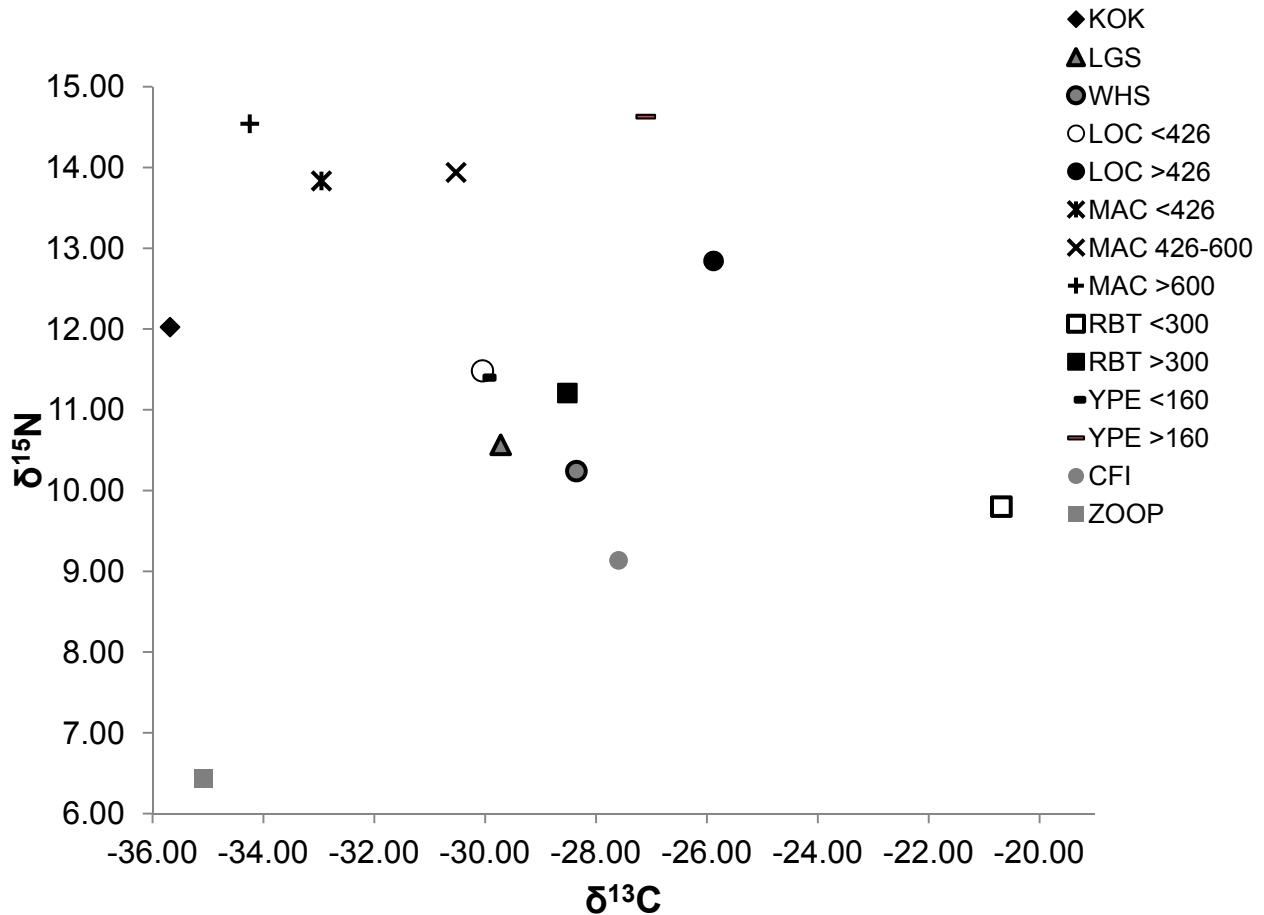


Figure 8. Stable isotope analysis of prominent predator and prey species (n = 300) found in Blue Mesa Reservoir, Colorado in 2010. The fish species analyzed were kokanee salmon *Oncorhynchus nerka* (KOK), rainbow trout *Oncorhynchus mykiss* (RBT), longnose sucker *Catostomus catostomus* (LGS), white sucker *Catostomus commersonii* (WHS), two sizes of brown trout *Salmo trutta* (<426 mm TL and >426 mm TL), two sizes of yellow perch *Perca flavescens* (<160 mm TL and >160 mm TL), three sizes of lake trout *Salvelinus namaycush* (MAC <426 mm TL, MAC 426-600 mm TL, and MAC >600 mm TL). Invertebrates analyzed were crayfish *Orconectes* spp. and zooplankton (mainly *Daphnia* spp.).

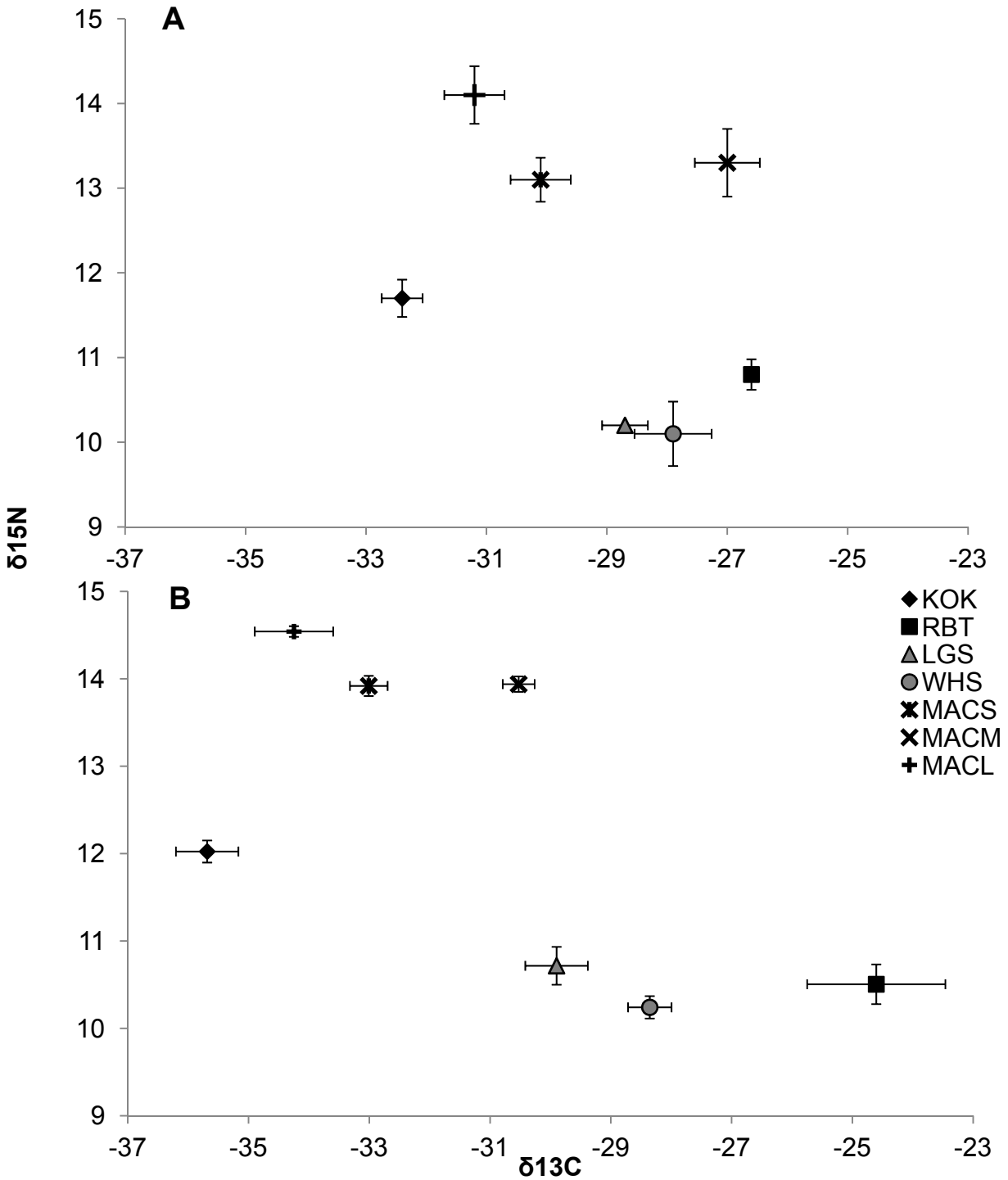


Figure 9. A comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between 2000 (A) and 2010 (B) in Blue Mesa Reservoir, Colorado for both predator and prey fish species. The species analyzed were kokanee salmon *Oncorhynchus nerka* (KOK), rainbow trout *Oncorhynchus mykiss* (RBT), longnose sucker *Catostomus catostomus* (LGS), white sucker *Catostomus commersonii* (WHS), and three sizes of lake trout *Salvelinus namaycush* (MAC_S <426 mm TL, MAC_M 426-600 mm TL, and MAC_L >600 mm TL). Error bars represent ± 1 SE.