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A Lake Divided: Regional Shifts in Trophic Niche Structure of Lake Powell Fishes Corresponding to the Invasion of Quagga Mussels

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ABSTRACT

A Lake Divided: Regional Shifts in Trophic Niche Structure of Lake Powell Fishes Corresponding to the Invasion of Quagga Mussels

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Introduced species can become invasive and cause catastrophic alterations to the system they invade. Both zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) have caused significant ecosystem alterations wherever they have invaded. These *Dreissena* species have caused changes in water quality and biodiversity and have disrupted energy pathways which can have cascading effects on other trophic levels. Recently quagga mussels invaded Lake Powell, a reservoir located in the southwestern USA, creating the possibility of a trophic cascade that could alter energy flow in the reservoir and change the trophic niche structure of the fishes in the lake. However, due to Lake Powell's large size, dynamic nature, and complex hydrological structure, the effects of quagga mussels on fish species is uncertain. To determine impacts of quagga mussels on Lake Powell fishes, we quantified trophic niches of five species of sport fish over three years (2017-2019) using stable isotopes of nitrogen, $\delta^{15}N$, and carbon, $\delta^{13}C$. We test the following hypothesis: quagga mussels will cause a shift in trophic niche in more pelagic fishes such that pelagic fishes decrease in trophic position and shift toward use of more littoral energy. In addition, we compare the trophic niche of these species with a previous study on the trophic niche of fish in Lake Powell prior to full colonization of the lake by quagga mussels (2014-2015). In general, fish in the southern region of the lake exhibited a trend of decreasing $\delta^{15}N$ suggesting decreasing trophic position and an enrichment of $\delta^{13}C$ indicating a littoral energy shift in some species. Fish in the northern region of the lake exhibited a slight increase in trophic position and a shift towards pelagic energy across the same time period. These shifts support the hypothesis with pelagic fish experiencing a trophic niche shift, in the direction predicted, but only in the southern region of Lake Powell. Additionally, this shift is not exclusive to pelagic fish, but happened in all five species. Sediment laden input from the Colorado River may offset the impact of quagga mussels in the northern region of the lake resulting in observed regional differences.

Keywords: quagga mussel, Colorado River system, Lake Powell, stable isotopes, trophic niche shift, fisheries, invasive species

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Introduction

When a species is introduced to a novel environment, occasionally it becomes invasive and causes catastrophic alterations that can lead to entire ecosystem restructuring (Knapp, 1996; Dukes & Mooney, 2004). Invasions have led to changes in nitrogen and carbon cycle pathways (Liao et al. 2008; Higgins & Vander Zanden, 2010), altered food webs (Ozersky et al. 2012) and have been a leading cause of extinction of native species (Clavero & García-Berthou, 2005). These effects from species invasions have been prevalent in freshwater systems because these systems are often isolated and evolutionarily naïve making them vulnerable to effects of invasion (Moyle & Light, 1996; Cox & Lima, 2006)

The list of invasive species in freshwater systems is long and their impacts have been felt globally. A few examples of some of the most damaging invaders include, common carp (*Cyprinus carpio*), brown trout (*Salmo trutta*), spiny water flea (*Bythotrephes longimanus*), and New Zealand mud snail (*Potamopyrgus antipodarum*). These species have caused destruction of habitat (Miller & Crowl, 2006; Wahl et al. 2011) and the extirpation and decline of native species (Townsend & Crowl, 1991; Walser et al. 1999; Young et al. 2010; Strecker & Arnott, 2008; Yan et al. 2011). Additionally, some species have altered carbon and nitrogen cycles where they have invaded (Hall et al. 2003; Rakauskas et al. 2018). Two species that have been particularly damaging in freshwater systems are zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*). These two *Dreissena* species have been linked to large-scale community alterations in freshwater systems where they have invaded (Higgins & Vander Zanden, 2010).

When these *Dreissena* species invade lakes and reservoirs, they disrupt energy flow in pelagic and littoral energy pathways (France, 1995; Strayer, 2009; Vander Zanden et al. 2011).

They disrupt these pathways by filtering out phytoplankton and small organic particles, reducing pelagic food bases and depositing the nutrients into the littoral pathway in the form of pseudofeces and feces (Vanderploeg et al. 2000). Additionally, their high filtering capacity leads to increased water clarity which increases the photosynthetic potential of littoral and benthic habitats (Higgens & Vander Zanden, 2010). This nutrient shunt and alteration of water quality redirects energy towards the littoral energy pathway and away from pelagic energy pathway.

This change in energy flow can cause cascading effects throughout food webs. At the basal end of the food web, these *Dreissena* species have on average reduced phytoplankton by 58.5% and zooplankton by 51.3% (Higgins & Vander Zanden, 2010). This reduction at the base of the pelagic energy pathway negatively affects other organisms including benthic detritivores (Watkins et al. 2007), native mollusks (Vanderploeg et al. 2000) and pelagic fish (Strayer et al. 2004, Strayer et al. 2014). In the littoral energy pathway, these *Dreissena* species have increased energy available in littoral and benthic habitats via increased autotrophic activity, expanded macroinvertebrates communities, and increased substrate complexity (Ozersky et al. 2012; Higgins & Vander Zanden, 2010). Clearly, the cascading effects of *Dreissena* species can affect all types of organisms in a lake, but how and to what degree is often difficult to know.

Because invasive *Dreissena* species can cause trophic cascades of energy flow, the measurement of trophic niche becomes a useful way of quantifying these changes in aquatic systems. A common method of quantifying the trophic niche is with the use of stable isotopes of nitrogen, $\delta^{15}N$, and carbon, $\delta^{13}C$ (Bearhop et al. 2004; Vander Zanden et al. 1999). These two isotopes are incorporated through consumption of prey, and breakdown of organic macromolecules and the preferential uptake against the heavier isotopes by the organism into somatic tissue (DeNiro & Epstein,1977; DeNiro & Epstein 1981; Fry, 2006). This differentiation, known as fractionation, reveals energy flow and trophic position, mainly via the variation in isotopic ratios of stable isotopes of carbon and nitrogen (Fry, 2006; Post, 2002). Thus, stable isotope ratios provide a long-term view of an organism's trophic niche and can reveal changes in food web dynamics (France, 1995; Hobson, 1999; Post, 2002; Rossberg et al. 2010).

In 2012, veligers of quagga mussels were first detected in Lake Powell, a large reservoir on the lower Colorado River, on the border of Utah and Arizona in the USA. Over the next five years, quagga mussels migrated up lake fully colonizing the entire system by 2017. A study of trophic niche of fishes in Lake Powell prior to complete colonization of the lake by quagga mussels, showed that quagga mussels occupied a position at the base of the pelagic energy pathway (Verde, 2017), suggesting the possibility of a bottom-up trophic cascade (Higgens & Vander Zanden, 2010). However, Lake Powell is a large and complex reservoir, and it is unclear if a bottom-up trophic cascade might develop and affect fishes uniformly throughout the reservoir.

Lake Powell is a deep-water reservoir on the Colorado River that is long, narrow and confined to cliff walls with intermittent bays and side channels. This topography causes the reservoir to have poor turnover and extensive stratification, leading to temporary anoxic regions and a permanent halocline throughout much of the lake (Gloss et al. 1980). The depth of Lake Powell fluctuates tens of meters among years in response to variation in winter precipitation, agriculture use, evaporation, ground seepage and legal water release requirements in the Colorado River watershed (Gloss et al. 1980; Myers, 2013). This shift in lake level causes a constant fluctuation of available habitat for aquatic organisms. Additionally, the Colorado River inputs heavy sediment loads into the upper regions of the lake which affects nutrient availability and photosynthetic capacity (Gloss et al. 1980). This dynamic nature of the reservoir may ameliorate or influence the effects of quagga mussels on fishes via the predicted trophic cascade (Kennedy, 2007; Nalepa, 2010; Verde, 2017).

To determine the effects of quagga mussels on trophic niches of fish within Lake Powell, we measured changes in trophic niche in five species of fish from 2017 to 2019. We compare patterns of change over these three years and compare current trophic niche values to those measured prior to the full colonization of the lake (Verde, 2017). We used stable isotopes of nitrogen, $\delta^{15}N$, and carbon, $\delta^{13}C$, to characterize trophic niches and to test the following hypothesis; quagga mussels will cause a shift in trophic niche in more pelagic fishes such that pelagic fishes decrease in trophic position and shift toward use of more littoral energy. We test this hypothesis in two distinct regions of Lake Powell to determine if the effects were uniform across this large reservoir.

Methods

Study Site

Lake Powell is located on the Colorado River on the Utah and Arizona border in the southwestern USA, and is one of the largest reservoirs in the nation (Stanford & Ward, 1991). For this study, we divided the reservoir into two regions, the northern region and the southern region from which we sampled fish and algae. We made this division because 1) sediment distribution across the lake is not uniform and most of the sediment settles out in the northern region of the lake (Gloss et al. 1980); 2) there are historical differences in fish abundance between the northern and southern region (Mueller & Horn, 2004); and 3) there are historical differences in trophic niche of some species of fish between the northern and southern regions (Verde, 2017). We realize this division is coarse and does not consider the fine-scale distribution of environmental gradients across the lake. Rather, our goal in this study was to understand large-scale potential effects of quagga mussels on trophic niches of fishes in Lake Powell.

Fish Collection and Preparation

To quantify the changes in trophic niche of fishes in Lake Powell, we focused on five common species of fish: striped bass (*Morone saxatilis*), walleye (*Sander vitreus*), smallmouth bass (*Micropterus dolomieu*), green sunfish (*Lepomis cyanellus*), and bluegill (*Lepomis macrochirus*). These five fish species represent most of the major sports fishes in Lake Powell while also representing the spectrum of energy pathway utilization of fishes within the lake (Verde, 2017). This spectrum from most pelagic to most littoral determined by their $\delta^{13}C$ isotopic ratios is as follows: striped bass, bluegill, walleye, smallmouth bass and green sunfish (Verde, 2017). When we began this project in 2017, we were primarily focusing on bluegill and green sunfish. Beginning in 2018 we expanded the collection to the three other species of fish to account for the full range of energy pathway utilization within Lake Powell. Fish were collected between May and November during all three years of the study (2017 – 2019; Table 1).

We collected fish via angling, gill netting and electroshocking. Additionally, we collected fish carcasses from anglers in both regions of the lake at Wahweap, Antelope and Bullfrog marinas. We recorded standard length, total length, date, and location of capture. For stable isotope analysis, we removed a 5ml portion of epaxial muscle from each fish which was placed in labeled vials and stored at -80˚C until samples were processed.

Baseline Trophic Level Sampling

To ensure the changes seen in trophic niche of fishes were not due to changes in basal trophic levels (i.e. baseline movement), we collected attached algae from both northern and southern regions of the lake for all three years of the study (Post, 2002) to represent the energy fixation baseline (Table 1). We scraped algae from the substrate of the lake and floating structures, placed samples on ice, and then froze them until they were prepared for analysis.

Preparation of Tissue and Isotope Analysis

We prepared animal tissues for stable isotope analysis similar to methods outlined in Fry (2006). We dried tissue samples at 60˚C for 48 hours. We then ground the tissue to a fine powder using mortar and pestle after which we measured a portion weighing 0.6mg to 1.2mg into a 4x6 mm tin capsule.

We prepared algae tissues for stable isotope analysis via the following steps. We first homogenized multiple algae samples from multiple locations. These samples were then dried at 60˚C for 48 hours and then ground to a fine powder. For the years 2018 and 2019 we performed an acid wash to correct for observed $CaCO_3$ influence identified in 2017. This was performed by taking a 10% HCL solution and dripping it into a Polypropylene vial filled with ground algal tissue until CO_2 bubbles ceased forming (Ng et al. 2007). We then re-dried these samples at 60˚C for 48 hours. The mean $\delta^{13}C$ change for the acid washed samples was 5.9‰. After which we used this value to correct 2017 $\delta^{13}C$ algae samples. After 2017 was corrected, it was still observed within the southern region that some algal samples had a carbon influence that could not be removed with this method of correction alone. Since all 2017 samples had been utilized for the isotopic analysis, we could not make any further adjustments. A t-test of $\delta^{15}N$ values indicated no significant change in nitrogen after the acid wash so we made no further adjustment of $\delta^{15}N$ (n=45, df=43, p=.3057). For algae samples, we measured 4mg of tissue into the tin capsules for isotopic analysis to compensate for the differences in nitrogen found between plants and animal tissues.

We sent all samples to Colorado Plateau Stable Isotope Laboratory (CPSIL) located at Northern Arizona University, USA. Samples were processed by the DELTA V Advantage configured through the CONFLO III using the Carlo Erba NC2100 Elemental Analyzer. The following method was used to convert isotope ratio to δ notation as performed by CPSIL. To denote delta notation they used the following equation $\delta^{H}X=[(R_{sample}/R_{standard})-1]*1000$ where the standard used by the laboratory was Pee Dee Belemnite for carbon and air for nitrogen (Post, 2002). Additional standards used include NIST Peach Leaves to measure drift in machine accuracy for both carbon and nitrogen.

Statistical Analysis

We performed an Analysis of Covariance (ANCOVA) using JMP Pro Version 14.2.0 (SAS Institute Inc., Cary, NC, 1989-2019) to determine if there was a change in $\delta^{15}N$ and $\delta^{13}C$ isotopic ratios over the course of the study or among the regions of the lake for all five fish species individually. Our model for analysis contained two main effects, region and year, and we tested the interaction between these two effects. Our continuous covariates were Julian date of capture and standard length of the fish to account for possible variation in isotopic signatures due to catch date within each year and size of fish. For algae an ANOVA was performed with the two main effects of region and year being tested along with their interaction.

For the hypothesis to be supported that quagga mussels are causing pelagic fish to decrease in trophic level and shift towards littoral energy pathways, we would expect to see significant changes in isotopes enrichment, with nitrogen decreasing in enrichment and carbon increasing in enrichment. This would be manifest in the model as the year effect being significant or the year by region interaction being significant. If either of these two effects are significant it would indicate a shift in trophic niche through time. Additionally, if 95%

confidence intervals of our means do not overlap mean values from Verde (2017), that would indicate a significant trophic niche shift compared to previous conditions. Verde (2017) does not report pre-quagga trophic niches for all five species of fish in both regions of Lake Powell, so we can only compare pre-quagga conditions based upon the results available (Figure 2).

Results

Baseline Assessment

Algae had no significant variation in $\delta^{15}N$ over the course of the study while $\delta^{13}C$ showed significant interaction between year and region (Table 2).

Decrease in Trophic Position

Trophic position, as measured by $\delta^{15}N$, decreased significantly in four of the five species of fish in the southern region of the lake, but trophic position increased significantly in three of the five species of fish in the northern region of the lake (Table 3, Figure 2) over the course of the study. Striped bass, the most pelagic species, did not show a significant change in trophic position from year to year in either region of the lake (Table 3). All five species of fish in the northern region are significantly higher in trophic position by 2019 compared to southern region fish (Figure 2).

Energy Shift Towards Littoral Environments

Energy pathway utilization, as measured by $\delta^{13}C$, shifted towards the littoral energy pathway in two of the five species of fish in the southern region of the lake; whereas all five species of fish shifted towards the pelagic energy pathway in the northern region of the lake (Table 3, Figure 2) over the course of the study and compared to prior conditions. All five species of fish are significantly more pelagic in energy pathway use compared to more littoral energy pathway use in the northern region of the lake by the end of the study (Table 3, Figure 2).

Discussion

Our hypothesis was based on the idea that the pelagic energy pathway within Lake Powell would be disrupted and would lead to more pelagic fish decreasing in trophic level and shifting to use littoral energy (Higgens & Vander Zanden 2010; Verde, 2017). This hypothesis was only partially supported in this study. In the southern region of Lake Powell all species showed a decrease in trophic level while only two shifted to use more littoral energy. The most pelagic fish, striped bass, experienced little variation in trophic niche, indicating a surprising resistance to the effects of quagga mussel's observed nutrient shunt. The most striking result, though, was the actual increase in trophic level and shift towards the pelagic energy pathway seen in almost all fish in the northern region of the lake. This is leading to a net effect of quagga mussels facilitating more distinct trophic niches between regions of the lake for fish. Trophic niche shift in the southern region of Lake Powell followed similar patterns seen in other bodies of water including Lake whitefish (*Coregonus clupeaformis*) in Lake Huron, USA, which showed a significant drop in $\delta^{15}N$ and increase in $\delta^{13}C$ enrichment (Rennie et al. 2009) along with lake trout (*Salvelinus namaycush*) in Lake Simcoe, Canada, which exhibited a similar pattern (Langen, 2019). Additionally, baseline variation was stable, supporting that these trophic niche shifts are real, though carbon had significant variation in the southern region. Basal carbon variation in the southern region may be accounted for with high variance, correction methods, and one sample having a significantly different isotopic value than the rest of the samples altering the mean. This study suggesting dynamic systems like Lake Powell after infestation by *Dreissena* species may result in more complex outcomes than predicted. Overall, this may lead to the effect where the large dynamic nature of Lake Powell may ameliorate or alter the effects of quagga mussels on the trophic niches of co-occurring fishes.

Pelagic fish are considered to be a group of organisms most likely to experience a trophic niche shift due to *Dreissena* invasion (Higgens & Vander Zanden 2010). Observations of this have been documented in fish where they change in both growth rates and abundance, (Strayer et al. 2004, Strayer et al. 2014) and they experience shifting isotopic signatures (Rennie et al. 2009; Langen, 2019) in other bodies of water. The two most pelagic fish within Lake Powell, striped bass and bluegill, indicate a niche shift corresponding to the invasion of quagga mussels. For striped bass, the results from this study suggest little change in the means, but when comparing striped bass trophic position and energy pathway utilization from Verde (2017), it appears that there has been a gradual divergence between regions for both trophic level and energy pathway utilization (Figure 2). Additionally, striped bass may be experiencing an increase in niche width as the confidence intervals for $\delta^{15}N$ have expanded considerably from Verde (2017), though sample sizes were near or at the 30 fish mark suggested by other isotope researchers for isotope studies (Syväranta et al. 2013). Why this is the case is unknown. Diet studies of striped bass in Lake Powell indicate highly pelagic food sources with almost a specialization in zooplankton and shad species which account for 40%-70% of their diet (Verde, 2017; Vatland et al. 2008). A widening niche could be explained by the incorporation of other dietary sources to make up for a trophic cascade in the pelagic energy pathway of Lake Powell caused by quagga mussels. For bluegill, regional disparities in $\delta^{15}N$ have been expanding since 2017 with the southern region decreasing in $\delta^{15}N$ enrichment and the northern region increasing in $\delta^{15}N$ enrichment returning to a pre quagga invasion trophic levels (Figure 2). Bluegill are known to be consumers of quagga mussels in other bodies of water (Culver et al. 2019) and have been observed eating quagga mussels in Lake Powell (personal observation). This might help explain a trophic decline in bluegill as quagga mussels are lower trophically than bluegill and their primary food source, zooplankton (Verde, 2017; Werner & Hall, 1988), but does not explain the lack of pelagic energy shift in the southern region.

The two species of fish that reside in the center of the pelagic littoral spectrum, walleye and smallmouth bass, appear to be experiencing strong regional divergence in isotopes (Figure 2). Walleye are known to be negatively affected by the presence of *Dreissena* species since they alter water clarity and habitat leading to possible increased mortality and competition (Lester et al. 2004; Hoyle et al. 2008). It is less clear the effect that quagga mussels have on smallmouth bass, but evidence suggests that they benefit through increased foraging success as water clarity increases due to mussel filtration (Hanley, 2016). The results from this study suggest both walleye and smallmouth bass are being affected in both regions as trophic level is increasing in the northern region and decreasing in the southern region of the lake for both species (Figure 2). This is particularly supported in smallmouth bass as Verde (2017) noted that the differences in $\delta^{15}N$ between regions was non-significant in 2014 and 2015, but by 2019 significant difference between regions in $\delta^{15}N$ has occurred (Figure 2). As noted with pelagic species, energy pathway utilization is diverging for both species suggesting trophic cascades altering carbon flow towards littoral pathways in the southern region for some species.

Littoral fish are known to be affected by *Dreissena* species. Benthic predators that feed on littoral insects were less successful at consuming prey items as *Dreissena* habitat coverage increased (Beekey et al. 2004). Spottail shiners (*Notropis hudsonius*) appear to increase in size after *Dreissena* species invasion suggesting foraging success (Strayer et al. 2014). Unfortunately, little to no research has ever been performed on trophic niche shift of littoral fish using stable isotopes after the invasion of *Dreissena* species, thus making a comparison difficult. Overall, the effect on littoral species is suggested to be positive (Mercer et al. 1999; Higgens & Vander

Zanden, 2010). Green sunfish, the most littoral species in the study appears to be negatively affected in the southern region as trophic position is decreasing but experiencing little to no change in the northern region. Additionally, energy pathways utilization had a dramatic pelagic shift in the northern region from the Verde (2017) study to present day. This can be accounted for by green sunfish consumption of quagga mussels (personal observation) as the mussels invaded the northern region.

Regional Differences

Lake Powell has similar lake structure to other man-made reservoirs and is comprised of a riverine, transition, and a lacustrine region which has effects on nutrient distribution and fish communities (Gloss et al. 1980; Kennedy, 1984). This heterogeneous distribution of nutrients causes fish dispersion across Lake Powell to not be equal with pelagic fish being found at higher concentrations closer to inflows of rivers where nutrients are higher (Mueller & Horn, 2004). This nutrient separation and higher pelagic food source availability between regions could account for the differences seen in carbon enrichment in fish between regions of the lake. This seems to be unlikely as fish like striped bass and smallmouth bass had nearly identical regional carbon isotope ratio in Verde's (2017) sampling but have both experienced a regional trophic niche shift (Figure 2). Because of the $\delta^{13}C$ enrichment values of many fish are becoming regionally differentiated with time, i.e. northern and southern region fish are becoming trophically different, it is more likely that quagga mussels are exacerbating the regional differences of Lake Powell via trophic cascades in both pelagic and littoral energy pathways, but mainly in the southern region.

One other effect that might be causing a regional differentiation in trophic niches in fishes within Lake Powell is sediment input. The Colorado River is known for carrying heavy sediment loads as it enters Lake Powell (Vernieu, 1997). This sediment settles out before it makes it to the lower regions of the lake (Gloss et al. 1980), though plumes of fine particulate matter may extend over 100km down lake during spring runoff in the months of May and June (Naftz et al 2019). Subsequently the upper region of Lake Powell contains higher sediment loads for multiple months out of the year, which vary in concentration and distribution based upon water year and lake level (Naftz et al. 2019). Suspended sediment at concentrations of 100mg/l halts *Dreissena* species ability to filter and respirate effectively (Madon, et al. 1998; Kennedy, 2007). The Colorado River frequently exceeds this threshold even during low flow and always exceeds this at high flows (Van Steeter & Pitlick, 1998). Because of this limiting factor, quagga mussels may experience periods of reduced filtration capacity or even inactivity due to sediment load in the water column in the northern region of the lake providing refuge from their effects for the fish community. This same refuge effect would never occur in the majority of the southern region of Lake Powell due to the distances of major sediment inputs such as the Colorado River and the San Juan River. This would explain the carbon differences seen in the fish in the southern region as they are competing for nutrient availability which is being depleted by quagga mussels, while the northern region organisms appears to be only modestly effected as they have prolonged exposure to high nutrient riche sediment for much of the early spring and into summer months of the year thus allowing for fish to maintain a more stable niche (Stanford and Ward 1991).

Conclusion

Quagga mussels appear to be causing trophic cascades within Lake Powell such that they are effecting most fish's trophic niche in all regions of the lake. The shift in trophic niche for almost all species in the southern region could be a sign of isotopic shifts in lower order organisms in that region or a change in zooplankton structure resulting in niche shift of fishes in the pelagic arm of the southern region of the lake. Overall, Lake Powell may be best described now as a lake divided with quagga mussels appearing to be the catalyst behind this change.

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Table 1: Total fish caught and algae samples processed during the three years of sampling. Species total is the summed total of fish caught per species. Region total is total fish caught per region by species. Standard length (SL) is measured in millimeters.

Species	*Region*	*2017*	*2018*	*2019*	*Region Total*	*Species total*
		N (SL, CI)	*N (SL, CI)*	*N (SL, CI)*		
Striped Bass	North	-	18 (380, ±31.66)	35 (403, ±22.30)	53	107
	South	-	18 (367, ±13.99)	36 (368, ±33.80)	54	
Bluegill	North	61 (105, ±8.93)	50 (136, ±7.34)	32 (153, ±6.38)	143	368
	South	149 (134, ±7.57)	48 (129, ±10.12)	28 (153, ±6.44)	225	
Walleye	North	-	21 (322, ±22.40)	42 (321, ±8.01)	63	101
	South	-	28 (339, ±12.05)	10 (312, ±13.86)	38	
Smallmouth Bass	North	-	28 (197, ±18.93)	44 (194, ±16.54)	72	117
	South	-	19 (227, ±16.77)	26 (220, ±6.44)	45	
Green Sunfish	North	97 (72, ±6.09)	63 (110, ±8.11)	31 (106, ±11.56)	191	250
	South	17 (82, ±14.12)	35 (111, ±11.39)	7 (140, ±18.32)	59	
Algae	North	5	5	4	14	29
	South	5	3	7	15	

Table 2: ANOVA of algae for both nitrogen and carbon.

Species	$\delta^r X$	*Source*	*D.F.*	*sum of squares*	*F-ratio*	*p-value*
Algae	Nitrogen	Year	2	5.42	1.22	0.3128
		Region	1	0.06	0.03	0.8698
		Year*Region	2	3.17	0.72	0.4994
	Carbon	Year	2	23.63	1.85	0.1804
		Region	1	22.5	3.52	0.0735
		Year*Region	2	52.05	4.07	**0.0307**

Table 3: ANCOVA of the effect of year and region on nitrogen and carbon stable isotopes in five species of fish.

Species	*Isotope*	*Source*	*DF*	*Sum of Squares*	*F Ratio*	*Prob > F*
Striped Bass	Nitrogen	Year	1	0.236644	0.1805	0.6718
		Region	1	13.68904	10.4413	**0.0017**
		Length	1	13.89607	10.5992	**0.0015**
		Date	1	0.336877	0.257	0.6133
		Year*Region	1	0.280349	0.2138	0.6448
	Carbon	Year	1	5.884822	13.2493	**0.0004**
		Region	1	15.14158	34.0902	**<.0001**
		Length	1	27.95932	62.9485	**<.0001**
		Date	1	3.234174	7.2815	**0.0082**
		Year*Region	1	3.259952	7.3396	**0.0079**
Bluegill	Nitrogen	Year	2	12.87908	9.6898	**<.0001**
		Region	1	60.22121	90.6174	**<.0001**
		Length	1	2.053916	3.0906	0.0796
		Date	1	21.80957	32.8178	**<.0001**
		Year*Region	2	34.26231	25.778	**<.0001**
	Carbon	Year	2	15.0102	7.1728	**0.0009**
		Region	1	266.498	254.6995	**<.0001**
		Length	1	104.1103	99.5011	**<.0001**
		Date	1	0.31697	0.3029	0.5824
		Year*Region	2	33.70994	16.1088	**<.0001**
Walleye	Nitrogen	Year	1	4.105818	4.9914	0.**0278**
		Region	1	7.408994	9.0071	**0.0034**
		Length	1	0.283847	0.3451	0.5583
		Date	1	0.257399	0.3129	0.5772
		Year*Region	1	8.951164	10.8819	**0.0014**
	Carbon	Year	1	0.461638	1.2636	0.2638
		Region	1	45.23599	123.8161	**<.0001**
		Length	1	21.14471	57.8755	**<.0001**
		Date	1	0.074143	0.2029	0.6534
		Year*Region	1	0.734598	2.0107	0.1595
Smallmouth Bass	Nitrogen	Year	1	3.563121	4.7805	0.**0309**
		Region	1	6.145392	8.2451	**0.0049**
		Length	1	2.265168	3.0391	0.084
		Date	1	3.627867	4.8674	0.**0294**
		Year*Region	1	20.02038	26.8607	**<.0001**
	Carbon	Year	1	0.029676	0.0629	0.8024

		Region	1	38.37705	81.3954	**<.0001**
		Length	1	26.11236	55.3827	**<.0001**
		Date	1	1.64913	3.4977	0.0641
		Year*Region	1	12.19624	25.8675	**<.0001**
Green sunfish	Nitrogen	Year	2	7.739866	5.4225	**0.005**
		Region	1	38.27557	53.6316	**<.0001**
		Length	1	34.66749	48.5759	**<.0001**
		Date	1	0.487296	0.6828	0.4094
		Year*Region	2	6.596859	4.6217	**0.0107**
	Carbon	Year	2	15.77986	5.6433	**0.004**
		Region	1	67.70685	48.4277	**<.0001**
		Length	1	2.232571	1.5969	0.2076
		Date	1	26.53463	18.979	**<.0001**
		Year*Region	2	1.187057	0.4245	0.6546

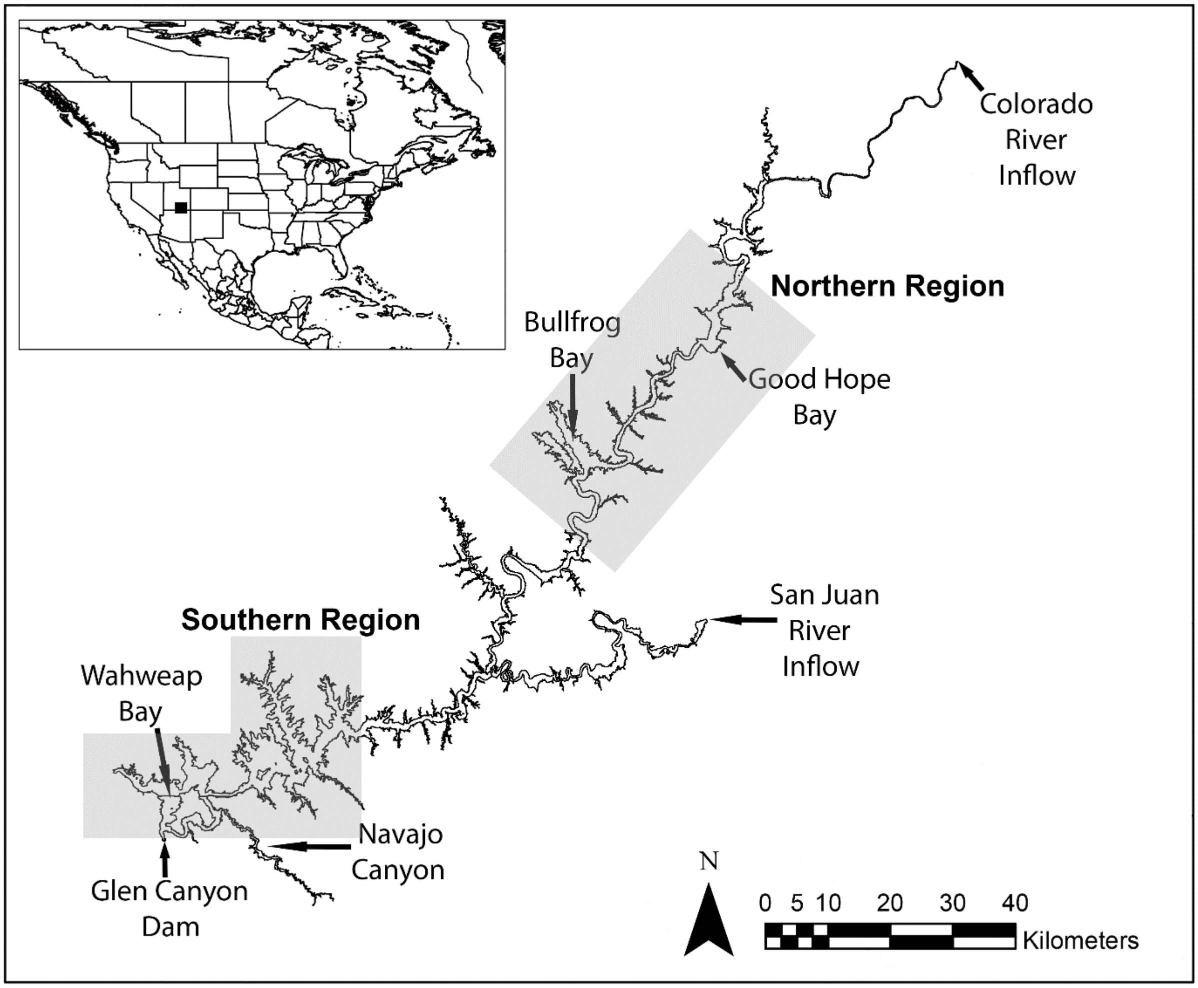

Figure 1: Map of Lake Powell. Highlighted are the northern and southern regions where fish were collected.

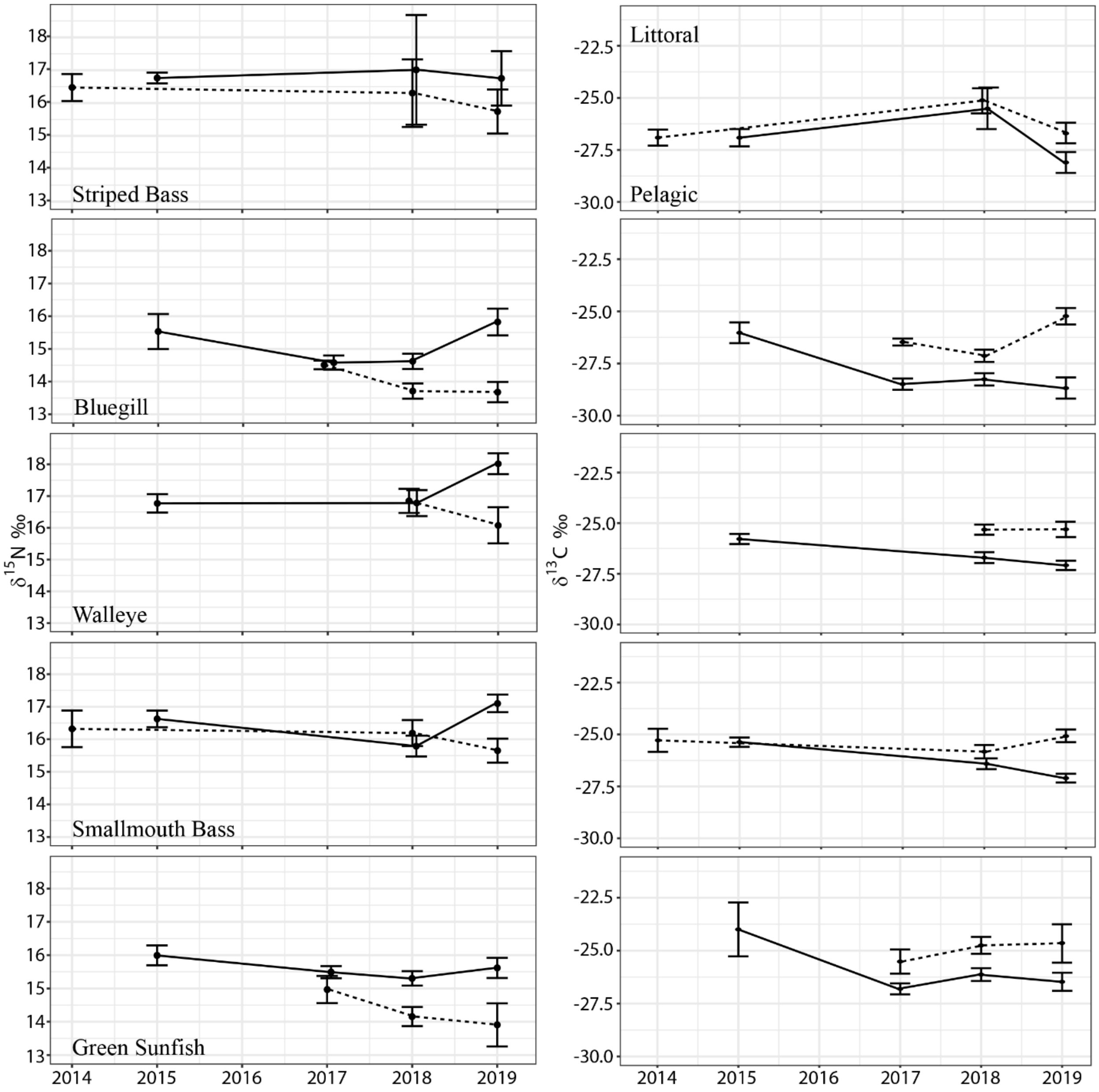

Figure 2: Means with 95% CI for $\delta^{15}N$‰ and $\delta^{13}C$‰ isotope ratios for the five species of fish we analyzed in Lake Powell between 2017 and 2019. Solid lines are fish from the northern region, dashed lines are fish from the southern region. Values from 2014 and 2015 are from Verde (2017).