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Lake Powell Food Web Structure: Predicting Effects of Quagga Mussel

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A thesis submitted to the faculty of
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Master of Science

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ABSTRACT

Lake Powell Food Web Structure: Predicting Effects of Quagga Mussel

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Food webs in aquatic ecosystems can be dramatically altered by invasive species. Quagga mussels are prevalent invaders that compete with existing species and disrupt nutrient cycling. In 2012, the Quagga Mussel (*Dreissena rostriformus bugensis*) was introduced into Lake Powell and is expected to move throughout the reservoir in the near future. Stable isotope analysis is a powerful tool for characterizing food webs and trophic interactions. To predict the long-term effects of Quagga Mussels, we used stable isotope analysis of primary producers, primary consumers, prey fish species, and predator fish species in Lake Powell to determine food web structure. Quagga Mussel are positioned to disrupt the pelagic arm of the food web by interfering with the link between phytoplankton and herbivorous zooplankton. This will likely have negative impacts on pelagic fish such as striped bass (*Morone saxatilis*) and threadfin shad (*Dorosoma petenense*). Quagga Mussel may also boost benthic productivity in the littoral zone by diverting nutrients from the water column to the benthos. This may have positive impacts on littoral fishes such as largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), bluegill (*Lepomis macrochirus*), and green sunfish (*Lepomis cyanellus*).

Keywords: Lake Powell, quagga mussel, stable isotope analysis

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Introduction

Invasive species are responsible for loss of genetic integrity in species, collapse or disruption of native food webs, and extinction of species (Rhymer and Simberloff 1996, Vander Zanden et al. 2003, Clavero and García-Berthou 2005, Hänfling et al. 2005). Recent invasions have raised concerns about effects on existing food webs, species distributions, and nutrient cycling. Depending on the species that invade, there can be top-down or bottom-up effects. Top-down effects occur when the invading species occupies a high trophic level and alters the food web through predation and trophic cascades (Vander Zanden et al. 1999). Bottom-up effects occur when the invading species occupies a lower trophic level and affects the food web through disruption of resource pathways (Campbell et al. 2009).

Some of the most well-known invaders, with bottom-up effects in aquatic systems, are the Dreissenid mussels - quagga mussel, *Dreissena rostriformus bugensis*, and zebra mussel, *Dreissena polyporpha.* They are successful invaders because of their high reproductive potential and wide tolerance range of freshwater conditions (Nalepa 2010). They cause changes in nutrient cycling and shift the flow of nutrients from the water column to the benthos (Karatayev et al. 1997, Higgins and Vander Zanden 2010, Ozersky et al. 2012). As a result, the trophic position, diet, and abundance of other organisms in the system can shift dramatically, especially at higher trophic levels (Mitchell et al. 1996, Doubek and Lehman 2014).

Quagga and zebra mussels were first found in North America in the late 1980s (Mills et al. 1993, Carlton 2008). The likely transportation vector was ballast water released into the Great Lakes by transoceanic container ships. Further spread was facilitated mainly by the overland movement of recreational watercraft from infested water bodies to non-infested water bodies (Brown and Stepien 2010). This overland movement of recreational watercraft facilitated the invasion of Lake Mead, where the quagga mussel was found in 2007. Soon after, Lake Havasu, Lake Mohave, and several reservoirs in southern California were invaded via the downstream dispersion of the planktonic veliger stage (Nalepa 2010). The colonization of Lake Mead was rapid, with mussels being found in all regions of the reservoir within 2 years (Wittmann et al. 2010). Five years after invasion of Lake Mead (2012), quagga mussel veligers were found in Lake Powell, near Glen Canyon Dam and Wahweap Marina. The following year, adult quagga mussels were reported and reproduction was confirmed. The mussels are expected to spread quickly throughout the reservoir, aided by the upstream movement of adult mussels attached to recreational watercraft. Previous case studies of quagga mussel invasion raise questions about how the mussels will change the structure of the food web in Lake Powell.

Stable isotope ratios of carbon and nitrogen have been used to characterize food webs and trophic niche because they integrate an organism's diet into two simple, but informative variables (Layman et al. 2012). Stable isotope ratios provide a time-integrated measure of an organism's trophic niche for a specific time-window (Post 2002). The stable isotope ratio of nitrogen ($\delta^{15}N$) is used to estimate the trophic level of an organism because it is enriched from prey item to predator by roughly 3-4‰ (parts per thousand; DeNiro and Epstein 1981, Minagawa and Wada 1984, Peterson and Fry 1987). The stable isotope ratio of carbon ($\delta^{13}C$) is indicative of source of carbon fixation (i.e., source of energy) for lake environments (DeNiro and Epstein 1978, Rounick and Winterbourn 1986, Peterson and Fry 1987, France and Peters 1997, Layman et al. 2007). In a lake ecosystem, the $\delta^{13}C$ is normally used to differentiate between pelagic and littoral carbon sources (Layman et al. 2007).

To determine impacts of the recent invasion of quagga mussel in Lake Powell, we used stable isotope data to characterize the food web and as trophic niche indicators for mixing models to determine diet composition for top predators. We used the position of quagga mussels in the food web to infer bottom-up effects on fishes in the reservoir.

Methods

Study system

Lake Powell is a man-made impoundment on the Colorado River located in San Juan, Garfield and Kane Counties in Utah and Coconino County in Arizona. With the completion of Glen Canyon Dam in 1966, the reservoir began filling and reached full pool in 1980. At full pool, the reservoir sits at an elevation of 1127 m and has a surface area of 653 km^2. Lake Powell is meromictic (has layers that do not mix yearly), with a mixolimnion (the layer close to the surface that mixes yearly) that stratifies in the summer and mixes in the winter, while the monimolimnion below the chemocline never mixes with the rest of the reservoir (Lewis Jr 1983, Hueftle and Stevens 2001). The fish assemblage is dominated by a non-native mix of fish introduced from mainly North America, and includes a few native Colorado River fishes in low numbers. Non-native fish in the reservoir include striped bass *(Morone saxatilis*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), walleye (*Sander vitreus*), black crappie (*Pomoxis nigromaculatus*), white crappie (*Pomoxis annularis*), green sunfish (*Lepomis cyanellus*), bluegill (*Lepomis macrochirus*), threadfin shad (*Dorosoma petenense*), gizzard shad (*Dorosoma cepedianum*), channel catfish (*Ictalurus punctatus*), and common carp (*Cyprinus carpio*). Native fish species found mainly in the upper reservoir include razorback sucker (*Xyrauchen texanus*), Colorado pikeminnow (*Ptychocheilus lucius*), flannelmouth sucker (*Catostomus latipinnis*), and bluehead sucker (*Catostomus discobolus*; Mueller et al. 2001).

Sample Collection

We sampled all fish, other than threadfin shad, in the spring of 2014 at Wahweap, spring and summer of 2015 at Bullfrog, and fall of 2015 at Good Hope using angling and gill nets. We removed a 1cm^2 tissue sample from the epaxial muscle of each fish and recorded the total length of the fish. We used a 63µm plankton tow sampler to collect zooplankton from the water column and the surface in summer of 2015 near Bullfrog. We collected aquatic macroinvertebrates and aquatic macrophytes by hand in summer of 2015 near Bullfrog. We collected quagga mussels by hand in January 2016 near Wahweap. We collected threadfin shad by trawl sampling in July of 2016 from Good Hope, Bullfrog and Navajo Canyon. Collection locations are indicated in Figure 1. We kept all samples frozen until lab preparation commenced.

Sample preparation and isotopic analysis

We oven-dried tissue samples at 60°C for 72 hours, then ground the samples into a homogeneous powder with a mortar and pestle and measured 0.6 - 1.2 mg of the powder into small tin capsules and sealed them. Stable isotope analysis was conducted in the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University in Flagstaff, Arizona. The analysis was carried out on a Delta V Advantage Mass Spectrometer (Thermo Electron Corporation, Bremen, Germany) configured through a CONFLO III (Thermo Electron Corporation), using a Carlo Erba NC2100 Elemental Analyzer (Thermo-Quest Italia S.p.A., Milano, Italy). We used delta notation ($\delta^{13}C$ and $\delta^{15}N$) expressed in parts per thousand (‰) for the stable isotope values. The ratio of the stable isotope in the sample is compared to the ratio in international standards (Vienna Pee Dee Belemnite for carbon and atmospheric nitrogen standard for nitrogen) by the following equation: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$, where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Stable isotope signatures within a species

Because some species exhibit ontogenetic niche shifts, we separated samples into two different size classes (<300mm and >300mm total length) for the five large-bodied species – striped bass, largemouth bass, smallmouth bass, walleye, and gizzard shad. We also tested for geographic variation within species by comparing samples of species collected in the upper lake (Bullfrog, Good Hope) to those from the lower lake (Wahweap, Navajo Canyon). We used student's t-tests to test for differences among size classes or geographic locations. Species subgroups that differed significantly between sizes or among geographic areas were represented separately on the food web.

Mixing model analysis

To estimate diet composition of the four top predator species - largemouth bass, smallmouth bass, striped bass and walleye - we used a Bayesian mixing model (Stable Isotope Analysis in R; Parnell et al. 2010). Possible food sources for small size classes of these four species included crappie from the south part of the reservoir, crappie from the north part of the reservoir combined with bluegill, green sunfish, small gizzard shad, macroinvertebrates, zooplankton, threadfin shad from Navajo Canyon, and threadfin shad from Bullfrog and Good Hope. We combined crappie from the north part of the reservoir with bluegill because their isotopic signatures were statistically indistinguishable. Possible food sources for large size classes of top predator species included crappie from the south part of the reservoir, crappie from the north part of the reservoir combined with bluegill, green sunfish, small gizzard shad, macroinvertebrates, zooplankton, threadfin shad from Navajo Canyon and threadfin shad from Bullfrog and Good Hope, small smallmouth bass combined with small largemouth bass and small walleye, and small striped bass. We combined small smallmouth bass, small largemouth bass, and small walleye because their isotopic signatures were similar, although not statistically the same. We set the mixing model to run for 500,000 iterations, and discarded the first 50,000 iterations as burn-in. We used standard trophic fractionation values for fish muscle ($\delta^{15}N$=2.9 SD=0.32, $\delta^{13}C$=1.3 SD=0.30; McCutchan et al. 2003). We used the R statistics package to perform all statistical analyses (R Development Core Team 2016).

Results

Stable isotope signatures within a species

Smallmouth bass and walleye size classes differed in $\delta^{15}N$, but did not differ in $\delta^{13}C$. Largemouth bass and gizzard shad size classes differed in $\delta^{13}C$, but did not differ in $\delta^{15}N$. Striped bass size classes differed in both $\delta^{13}C$ and $\delta^{15}N$. Crappie and threadfin shad from north and south sampling areas differed in both $\delta^{13}C$ and $\delta^{15}N$. These species subgroups were represented separately on the food web.

Food web structure

Trophic structure varied widely between organisms in the food web. Aquatic macrophytes were at the base of the food web (trophic level 0) consistent with their role as primary producers. Macroinvertebrates, quagga mussels, and threadfin shad from Navajo Canyon occupied the first trophic level. Zooplankton occupied the second trophic level indicating that the bulk of the zooplankton samples were composed of secondary consumers rather than primary consumers. Other than threadfin shad from Navajo Canyon, the fish that occupied the lowest trophic level (about 2.3) were gizzard shad, carp, and crappie from Wahweap. The next higher group of fish species on the trophic scale, at 2.8 – 2.9, were green sunfish, bluegill, and crappie and threadfin shad from Bullfrog and Good Hope. The highest trophic levels (3 – 3.3) were occupied by both size classes of walleye, striped bass, largemouth bass, smallmouth bass, and channel catfish (Figure 2).

Lake Powell exhibits a littoral and pelagic energy pathway, and these two pathways converge somewhat at the level of top predators. The base of the littoral energy pathway is occupied by aquatic macrophytes and terrestrial plant detritus (not sampled) and is enriched in $\delta^{13}C$. The base of the pelagic energy pathway is presumably occupied by phytoplankton (not sampled) and is depleted in $\delta^{13}C$. Macroinvertebrates were the most enriched in $\delta^{13}C$, indicative of a littoral source of carbon fixation, whereas quagga mussel and zooplankton were most depleted in $\delta^{13}C$, indicative of a pelagic source of carbon fixation. Fish were positioned somewhat intermediate between the pelagic and littoral energy pathways. Among fishes, small striped bass were most closely aligned with the pelagic energy pathway (depleted in $\delta^{13}C$), followed by channel catfish, threadin shad from Bullfrog and Good Hope, large gizzard shad, common carp, crappie from Wahweap, and large striped bass. On the other hand, green sunfish were most closely aligned with the littoral energy pathway (enriched in $\delta^{13}C$), followed by large largemouth bass, small smallmouth bass, large smallmouth bass, small gizzard shad, small largemouth bass, small walleye, large walleye, crappie from Bullfrog and Good Hope, and bluegill.

Isotopic mixing models

Diets of small size classes of the four top predator species were dominated by threadfin shad from Bullfrog and Good Hope and zooplankton. Zooplankton had the highest diet proportion in small striped bass, and threadfin shad from Bullfrog and Good Hope were the second most important prey item (Figure 4). Zooplankton also dominated the diet of large striped bass, while small striped bass, threadfin shad and crappie from Bullfrog and Good Hope, and bluegill were secondarily important. The estimated diets of large largemouth bass, large smallmouth bass, and large walleye were spread evenly across the sources, with a slightly larger proportion coming from zooplankton (Figure 5).

Discussion

The food web in Lake Powell is similar to many other freshwater lentic ecosystems in that it exhibits littoral and pelagic energy pathways in the food web (Vadeboncoeur et al. 2002). Macroinvertebrates form the base of the littoral energy pathway, and have enriched $\delta^{13}C$ signatures compared to zooplankton in Lake Powell. This is consistent with the observation that littoral sources are enriched in $\delta^{13}C$ when compared to pelagic sources (France 1995). Although the fish assemblage is non-native, most fish species occur in areas of the food web predicted by their trophic niche in their native environment. Consistent with other studies, the fish feeding at the highest levels of the food web do not feed exclusively in either the pelagic or littoral arms of the food web (Vadeboncoeur et al. 2002, Vander Zanden and Vadeboncoeur 2002), but species derive different proportions of their energy from the pelagic or littoral pathways.

Quagga mussel signatures place them at the primary consumer level in the pelagic pathway of the food web and they are positioned to disrupt the pelagic pathway by interfering with the link between phytoplankton and herbivorous zooplankton. High densities of mussels in other systems have been shown to dramatically reduce phytoplankton densities and subsequently zooplankton densities (Garton et al. 2005, Maguire and Grey 2006, Higgins and Vander Zanden 2010, Vanderploeg et al. 2010).

With the disruption of the pelagic energy pathway, species that rely on pelagic food sources, such as zooplankton, will likely be negatively impacted (Kissman et al. 2010). Striped bass and channel catfish have $\delta^{13}C$ signatures that show a high proportion of pelagic food sources and highly enriched $\delta^{15}N$ signatures, which places them as the top predators in the pelagic food web. The signatures of threadfin shad and large gizzard shad place them as pelagic planktivorous fish. Thus, striped bass, channel catfish, threadfin shad, and large gizzard shad will likely decline with widespread mussel invasion. This disruption of the pelagic food web may already be apparent with threadfin shad. Threadfin shad from Navajo Canyon areas are feeding at the primary consumer trophic level, while threadfin shad from Bullfrog and Good Hope are feeding roughly two trophic levels higher as zooplanktivores (Figure 2). The advanced mussel infestation in the southern end of the reservoir appears to have forced the threadfin shad to feed on phytoplankton or detritus.

The level of disruption is likely to vary in different habitats in the reservoir. It will be most pronounced in shallow water at the ends of side canyons where there is a high shoreline to water volume ratio. Quagga mussels will cover most of the available substrate in these areas and will effectively filter the majority of the water. The disruption will be less pronounced in large open water areas of the reservoir where the shoreline to water volume ratio is low because mussels are confined to substrate and water far from shore will be isolated from disruption (Padilla et al. 1996). Shoreline structure will also play a role in determining the effects of mussels. In shoreline areas where vertical cliffs descend below the chemocline, the mussels will shunt nutrients down to the chemocline where they will be effectively lost to the entire food web because no mixing occurs. In shoreline areas with gradual slopes or littoral shelfs, the mussels will divert nutrients from the water column to the oxygenated benthos where it is available to benthic organisms.

Quagga mussels divert nutrients and biomass from the water column to the benthos (Higgins and Vander Zanden 2010, Gergs et al. 2011, Ozersky et al. 2011, Ozersky et al. 2012).

In areas where oxygenated water reaches down to the lake bed during stratification, benthic productivity will be stimulated. The buildup of mussel shells adds habitat complexity that is favored by some benthic invertebrates like amphipods (Stewart et al. 1998, González and Downing 1999). Thus, benthic littoral areas of the reservoir will likely become more productive and have a higher abundance of invertebrates.

The increase in energy, nutrients, and habitat complexity in littoral areas will likely benefit fish that rely heavily on littoral food sources (Strayer et al. 2004). Largemouth bass and smallmouth bass have $\delta^{13}C$ signatures that show a high proportion of littoral food sources. Largemouth and smallmouth bass are the top predators in the littoral arm of the food web. Green sunfish have the most enriched $\delta^{13}C$ signature and likely derive most of their energy from littoral sources. Thus, largemouth bass, smallmouth bass, and green sunfish may increase in abundance in response to widespread quagga mussel invasion.

The effects of quagga mussels on other fish may be difficult to predict. Walleye have intermediate $\delta^{13}C$ and highly enriched $\delta^{15}N$ signatures, and likely feed as a top predator in both littoral and pelagic zones (Vander Zanden and Vadeboncoeur 2002). Crappie and bluegill have similar $\delta^{13}C$ signatures to walleye, but less enriched $\delta^{15}N$ signatures and also likely feed on both littoral and pelagic food sources, although at a lower trophic level than walleye. Because these fish seem to feed in both pelagic and littoral energy pathways, it is difficult to predict the impact that widespread mussel invasion will have on these species. They may be able to take advantage of the influx of nutrients into the littoral zone and avoid the negative effects of reduced energy flow in the pelagic energy pathway. Such a shift would be manifest as a shift in their isotopic signatures and should be detectable via stable isotope analysis after mussel invasion is more advanced (Vander Zanden et al. 1999).

Dreissenid mussels may be a direct source of food for several fish in the reservoir. The planktonic veliger stage ranges from 70 to 300 µm (Ludyanskiy et al. 1993) and will add biomass to the zooplankton in the reservoir. Thus, they may be available to planktivorous fish. Threadfin shad may be able to feed on these and predation by gizzard shad on veligers has been observed in other systems (Mills et al. 1995). The temperature limits for the reproduction of quagga mussel are not well studied (Feng and Papeş 2017), but some studies have shown that quagga mussels are able to reproduce when water temperatures reach between 4^{o} and 9^{o} C (Roe and MacIsaac 1997, Claxton and Mackie 1998). No data on maximum reproductive temperatures is available, but maximum temperature tolerance for quagga mussels is roughly 30^{o} C (Spidle et al. 1995) and reproduction is likely to cease below this temperature. The surface temperature at Lake Powell ranges from 8^{o} to 26^{o} C and the deeper portions of the reservoir remain constant around 8^{o} C (data retrieved from National Park Service https://www.nps.gov/glca/planyourvisit/weather.htm on 4/3/17). Therefore, it is likely that mussel reproduction could occur for most of the year in Lake Powell and may peak in spring and fall when surface water temperatures are more optimal, similar to Lake Mead (Mackie 2010). The addition of veligers to the zooplankton could somewhat counteract reductions in zooplankton due to increased grazing of phytoplankton by adult mussels. Adult mussels will also likely become a food source for fish in the reservoir. Common carp, channel catfish, and bluegill are known predators of dreissenid mussels (Tucker et al. 1996, Molloy et al. 1997, Thorp et al. 1998, Andraso 2005). It is unlikely that predation of veligers or adult mussels will result in population level control of quagga mussels (Thorp et al. 1998, Magoulick and Lewis 2002). Nevertheless, predation of veligers and adult mussels by fish can somewhat mitigate the effects of quagga mussels on the higher trophic levels in Lake Powell by directing nutrients energy back into the pelagic and littoral pathways (Higgins and Vander

Zanden 2010). The magnitude of this mitigation will depend on population sizes and reproductive patterns of quagga mussels and also on utilization rates and population sizes of fish.

Habitat available to quagga mussel will be dictated by a complex interaction of surface level, chemocline depth, and summer stratification. The water level in Lake Powell is influenced by several factors. An annual cycle of snowmelt runoff raises the water level, while releases for power generation and water delivery lower the water level. This fluctuation is normally about 6 meters per year. On a longer time scale, drought cycles reduce the amount of snowmelt runoff while water demand remains constant, resulting in long periods of below average water levels that persist until large snow packs increase runoff. This fluctuation is normally between 15 and 30 meters and occurs roughly every decade and lasts for 3 to 5 years (data retrieved from Bureau of Reclamation https://www.usbr.gov/uc/water/crsp/cs/gcd.html on 4/3/17). Adult quagga mussels are sessile and, once attached, cannot move to more favorable conditions and will be subject to mass mortality events when water levels in Lake Powell drop. When high water levels return, large amounts of substrate are resubmerged and available for recolonization. Chemocline formation is between 20 and 80 m below the surface and is promoted by drought conditions. Only large inflows from the tributary rivers can disrupt the chemocline and freshen the deep water (Hart and Sherman 1996, Hueftle and Stevens 2001). Drought conditions will consequently constrict available habitat for mussels by simultaneously lowering the surface level and forming a chemocline below which inhospitable conditions exist. Conversely, years with large snow packs will increase available habitat by raising the surface level and eroding the chemocline due to increased inflow. Summer stratification may further restrict quagga mussels to shallower water due to anoxia in the hypolimnion directly above the chemocline (Hart and

Sherman 1996). Thus, the amount of habitat in Lake Powell that is available to quagga mussels will likely fluctuate widely and the mussel population is unlikely to reach a stable state.

Conclusion

As quagga mussel becomes widespread in Lake Powell, food web dynamics are likely to shift. Fish that rely on pelagic food sources will likely decline or shift to a higher proportion of littoral food sources. Fish that rely on littoral food sources will likely increase in abundance, while fish that utilize food sources from both zones may shift their diet to a higher proportion of littoral food sources. Due to the complex depth structure of Lake Powell, the effects may be more pronounced in some areas of the reservoir than others.

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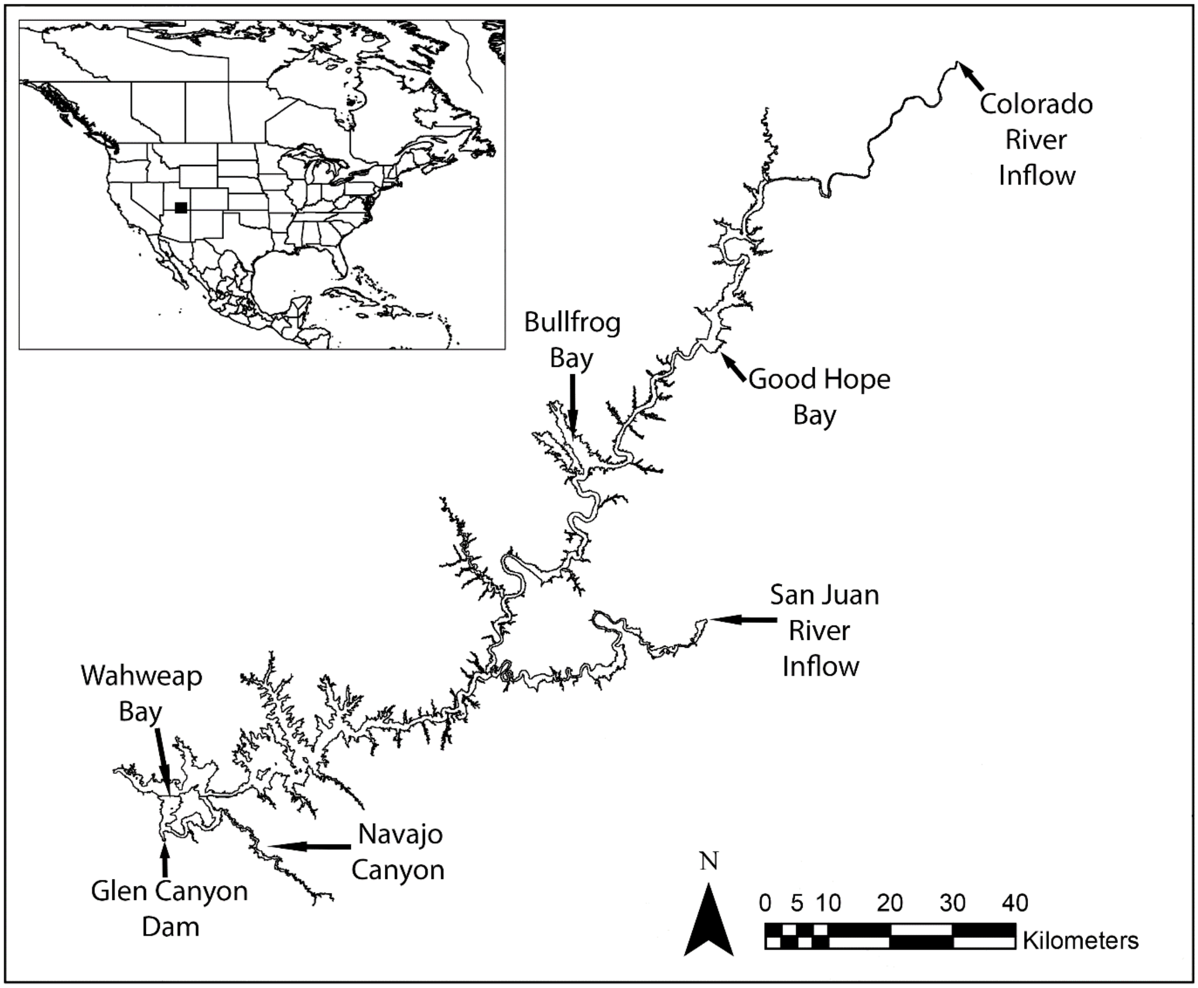

Figure 1. Map of Lake Powell with major inflows, dam, and sampling areas.

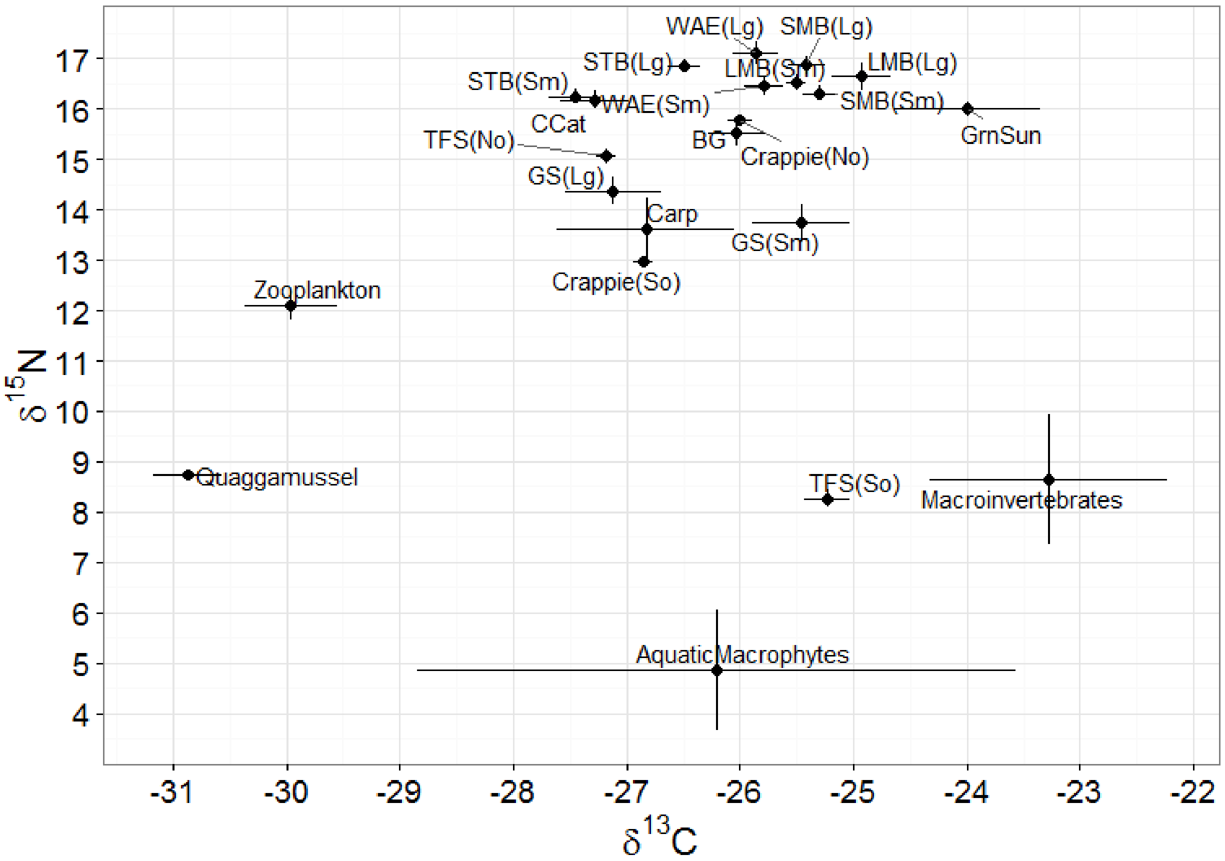

Figure 2. Bi-plot of species mean δ13C and δ15N for the aquatic food web in Lake Powell.

Bi-plot of species mean δ^{13}C and δ^{15}N for the aquatic food web in Lake Powell. Error bars represent 1 standard error. BG = bluegill. Carp = common carp. CCat = channel catfish. Crappie(No) = crappie from Bullfrog and Good Hope. Crappie(So) = crappie from Wahweap. GrnSun = green sunfish. GS(Lg) = gizzard shad over 300mm. GS(Sm) = gizzard shad under 300mm. LMB(Lg) = largemouth bass over 300mm. LMB(Sm) = largemouth bass under 300mm. SMB(Lg) = smallmouth bass over 300mm. SMB(Sm) = smallmouth bass under 300mm. STB(Lg) = striped bass over 300mm. STB(Sm) = striped bass under 300mm. TFS(No) = threadfin shad from Bullfrog and Good Hope. TFS(So) = threadfin shad from Navajo Canyon. WAE(Lg) = walleye over 300mm. WAE(Sm) = walleye under 300mm.

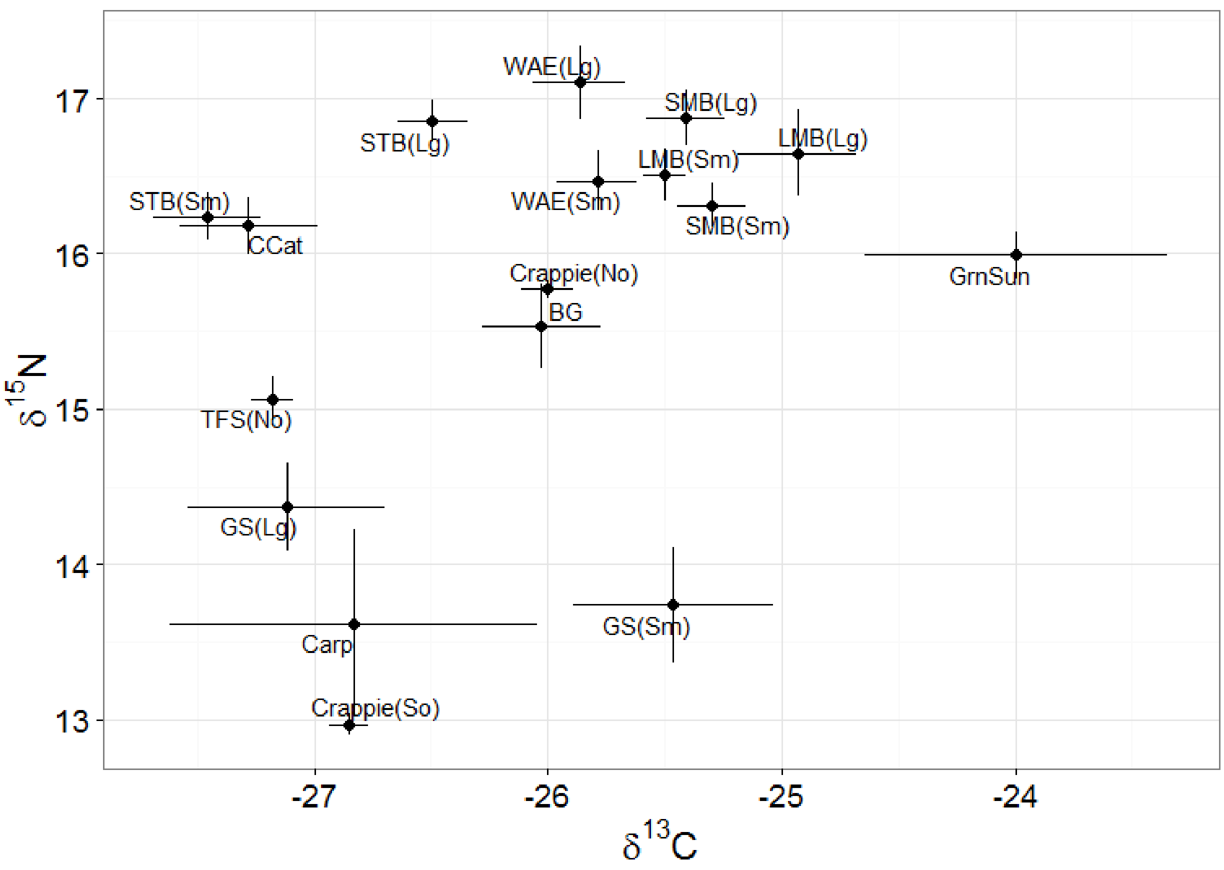

Figure 3. Magnified bi-plot of species mean δ13C and δ15N for the aquatic food web in Lake Powell.

Inset of higher trophic levels of fish from figure 2. Error bars represent 1 standard error. Abbreviations are the same as figure 2.

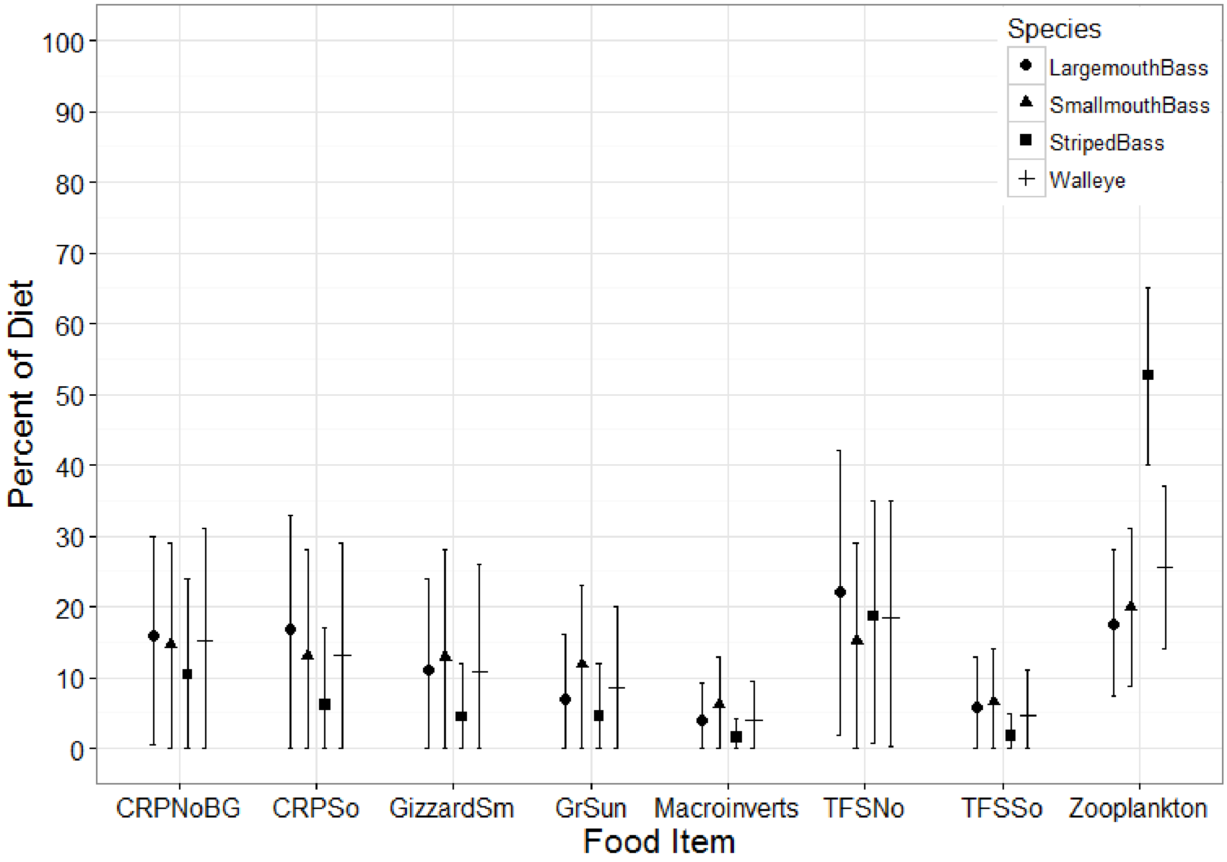

Figure 4. Plot of diet percentage from isotopic mixing models for small size class of largemouth bass, smallmouth bass, striped bass, and walleye.

Error bars represent 95% credibility intervals. CRPNoBG = crappie from Bullfrog and Good Hope combined with bluegill. CRPSo = crappie from Wahweap. GizzardSm = gizzard shad under 300mm. GrSun = green sunfish. Macroinverts = macroinvertebrate species. TFSNo = threadfin shad from Bullfrog and Good Hope. TFSSo = threadfin shad from Navajo Canyon. Zooplankton = Zooplankton.

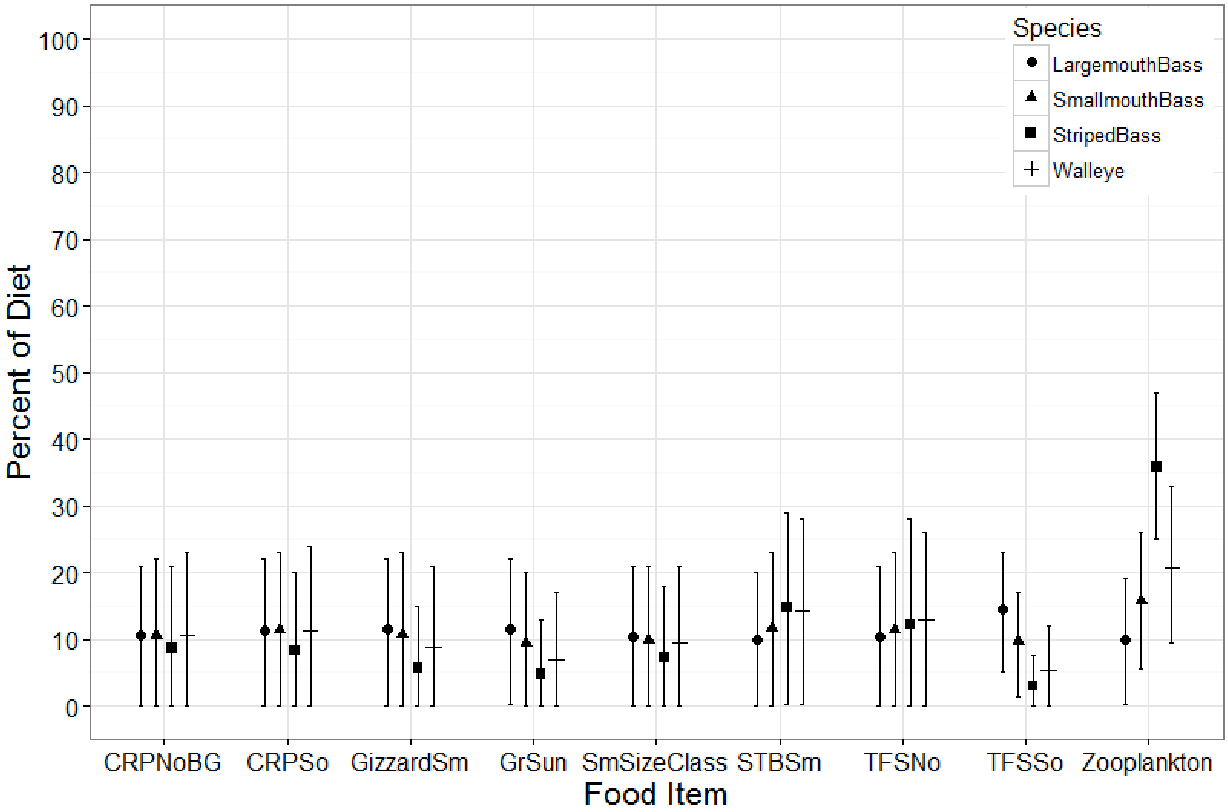

Figure 5. Plot of diet percentage from isotopic mixing models for large size class of largemouth bass, smallmouth bass, striped bass, and walleye.

Error bars represent 95% credibility intervals. CRPNoBG = crappie from Bullfrog and Good Hope combined with bluegill. CRPSo = crappie from Wahweap. GizzardSm = gizzard shad under 300mm. GrSun = green sunfish. SmSizeClass = small size classes of largemouth bass, smallmouth bass, and walleye. STBSm = small size class of striped bass. Macroinverts = macroinvertebrate species. TFSNo = threadfin shad from Bullfrog and Good Hope. TFSSo = threadfin shad from Navajo Canyon. Zooplankton = Zooplankton.