

Final Project Report – Illinois-Indiana Sea Grant

Impacts of Invasive Asian Carps on Native Food Webs

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Summary

1. Bighead Carp and Silver Carp are invasive throughout much of the Mississippi River system, and are threatening to invade the Great Lakes. Despite comprising the majority of the fish biomass in the lower Illinois River, their effects on native species and food webs are not well understood.
2. We used stable isotope analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) to examine the food webs of high and low Asian Carp density sections of the Illinois River, and compared these with historic collections from before the Asian Carp invasion of the late 1990s.
3. We found that fish in the high density lower river fed at lower trophic levels compared to the low density site or historic samples, suggesting that Asian Carps are dominating the food web by consuming the majority of available zooplankton. Carbon isotopes at the low density site were compressed, suggesting that there may be a nutrient bottleneck hindering upstream dispersal of Asian Carp in the Illinois River.
4. Stable isotope signatures of Asian Carp were most similar to Bluegill, Emerald Shiner, and Gizzard Shad, suggesting high trophic overlap with these facultative planktivores that pick zooplankton from the water column. There was less overlap and apparent competition between Asian Carps and filter feeding planktivores Bigmouth Buffalo and Paddlefish.
5. The potential effects on Great Lakes ecosystems if Asian Carps become established are unknown, but could prove catastrophic. Our project shows how Asian Carps impact food webs in the Illinois River, and thus reveals potential effects on food webs in the Great Lakes.

Introduction

Asian carps were imported to the United States in the early 1970s, and became established in the Mississippi River system soon thereafter; by the early 1990s they had become established in the Illinois River (Kolar et al. 2007). Both Bighead Carp, *Hypophthalmichthys nobilis*, and Silver Carp, *H. molitrix*, have been steadily expanding their range throughout the Mississippi River watershed, and towards the Great Lakes. While simulated projection models have been used to estimate their potential effects on the Great Lakes and beyond (e.g., Herborg et al. 2007, Cooke and Hill 2010, Kocovsky et al. 2012), there have been few empirical studies designed to test the assumptions used to create these models. Rather, they have relied on numerous assumptions about the potential impacts of these species.

While it has been shown that Asian carps affect zooplankton communities (Burke et al. 1986, Lu et al. 2002, Cooke et al. 2009, Calkins et al. 2012), most studies of the effects of Asian carps on native species have focused entirely on large planktivorous filter-feeders which, based on gut-content analysis and lower condition, have been shown to have substantial dietary overlap with Asian carps (Irons et al. 2007, Sampson et al. 2009). The impact of Asian carps on the many

planktivorous smaller minnows and juveniles of other species, however, has not been examined, and neither have potential cascading trophic effects on piscivores and benthivores. A decline in zooplankton communities would be expected to have cascading trophic effects throughout the food web, such as reducing the food supply for other planktivores. A decline in zooplankton could also release top-down control on phytoplankton, despite some feeding on phytoplankton by silver carp, and a subsequent decline in benthic productivity as nutrients would be consumed by increased phytoplankton biomass.

We therefore sought to empirically examine direct and indirect effects of Asian carps on native species and food-webs. By defining food-webs in reaches of the Illinois River where Asian carps are already established, we could then compare these “invaded” food-webs with non-invaded food webs. To accomplish this, we used two types of reference sites: historic food webs and contemporary sites near the “invasion-front” (Table 1). By using museum collections to examine historic food webs and comparing these with contemporary “invaded” food-webs from the same geographic locations, we will be able to examine the effects of Asian carps on trophic relationships and nutrient dynamics in these sections of the Illinois River. By examining sites beyond the invasion-front of the Asian carps, we will further gain geographic reference sites which can also be used with historic food-webs to assess changes over time in non-invaded reaches. Crucially for future studies, this will also give us a reference site that can be used to examine food web changes as the invasion-front reaches these sites and as Asian carps become established. Similar to a Before-After-Control-Impact, or BACI study design, this use of both historic and geographic reference sites will allow us to parse out both geographic and temporal changes in food-webs, and to quantify the effects of the Asian carp invasion.

Our objectives were thus to determine the impacts of invasive Asian carps on native fishes and aquatic food webs. We used stable isotope analysis of carbon and nitrogen to compare food-webs in sections of the Illinois River with high and low densities of Asian carps, and compared these to historic food-webs (pre-Asian carp invasion). These data will supplement our ongoing research on Asian carps in the Illinois River, and will help to inform management and conservation decisions in this system. The potentially catastrophic impact of Asian carps in the Great Lakes, and most immediately Lake Michigan, has been the subject of much debate and concern. While environmental variables are different between the Illinois River and Lake Michigan, we expect that Asian carps will have similar impacts on the food webs in both of these systems. For instance, if Asian carp decrease the mean trophic positions of planktivores by over-grazing zooplankton in the Illinois River, we would expect to see similar trends in Lake Michigan food webs. Such effects indeed might be magnified as Lake Michigan has lower nutrient availability than the Illinois River. Several fish species in Lake Michigan are state-listed. For instance, Northern Cisco, *Coregonus artedii*, is a planktivore listed as Threatened by Illinois and as a Species of Special Concern in Indiana, and would be expected to be impacted by competition from Asian carps. By identifying the impacts of Asian carps on planktivores and other trophic groups in the Illinois River, we will have a better understanding of the potential

effects on trophically similar Lake Michigan species, thus allowing us to better inform management decisions regarding the potential invasion of Asian carps into this system.

Methods

Traditional fish sampling and gut-contents analysis provide vital information on food webs and trophic relationships of fish species within rivers. Unless long-term monitoring is done, however, their effective snapshot is limited to that point-in-time. To determine long-term changes in food-webs, we will use stable isotope analysis (SIA) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). Stable isotope analysis relies on the principle of “you are what you eat” and, as such, can be used to trace resource use by fishes and other animals. $\delta^{13}\text{C}$ is the ratio of the stable carbon isotopes ^{13}C to ^{12}C , and varies with different primary producers (such as attached algae and phytoplankton) and across habitats. Generally, ^{13}C depleted values (more negative) are indicative of pelagic basal nutrient sources such as phytoplankton, while enriched ^{13}C signatures (less negative) originate from benthic sources such as periphyton and attached algae. Because $\delta^{13}\text{C}$ is conserved across trophic levels it can reliably be used to trace food source and habitat associations. $\delta^{15}\text{N}$ ($^{15}\text{N}/^{14}\text{N}$) does not vary much among primary producers or habitats, and is thus less efficient at determining habitat associations. However, $\delta^{15}\text{N}$ accumulates in a step-wise fashion at each trophic level (about 3.4 ‰ per trophic level; Vander Zanden and Rasmussen 1999, Vanderklift and Ponsard 2003) and thus indicates “who’s eating who?” When both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are analyzed, we get a comprehensive picture of the food-web: who is eating who, and in what habitat. Because they are conserved in animal tissue, they can provide a medium-to-long-term (days to weeks to months to years) record of diet, depending on the tissue sampled. Stable isotope mixing models and trophic niche models can then be used to estimate dietary overlap among species, and changes in mean stable isotope signatures and trophic dynamics over time.

Contemporary food-webs were sampled as part of our ongoing research on the Illinois River, while historic samples were taken from the fish collection at the Illinois Natural History Survey (Table 1). Ten individuals of each fish species (to compensate for inherent inter-individual variability), and of different size-classes where relevant (e.g., species in which juveniles and adults have different diets), were sampled from contemporary collections for stable isotope analysis (Table 2). Since historic collections will be more limited, we targeted an average of five samples per species from the museum collections. To reconstruct historic food webs, we took tissue samples from preserved fishes at the Illinois Natural History Survey Fish Museum. These fishes ranged from older to more recent pre-invasion collections (approximately 50-10 years ago) taken from sites at which we conducted contemporary sampling. Fish sampled in the study are provided in Table 3.

Table 1: Study Design – Illinois River Sampling Sites.

| | Contemporary Collection | Historic Collection |
|--------------------|----------------------------------------------------|---------------------------------------|
| Lower River | Invaded Site (high Asian Carp abundance) | Historic Reference (No Asian Carp) |
| Upper River | Geographic Reference (low Asian Carp abundance) | Historic Reference (No Asian Carp) |

Table 2: Sampling locations and dates for Illinois River stable isotope survey. River Km refers to the number of kilometers the site is located upstream for the confluence of the Illinois River with the Mississippi River, and Abundance refers to whether the site had a low or high abundance of Asian Carp.

| Site | River Km | Location | Abundance | Dates |
|------------|----------|----------|-----------|------------------------------|
| Morris | 423.2 | Upper | Low | 11 – 13 July 2011 |
| Morris | 423.2 | Upper | Low | 31 August – 2 September 2011 |
| I-55 | 447.4 | Upper | Low | 13 – 15 July 2011 |
| I-55 | 447.4 | Upper | Low | 29 – 31 August 2011 |
| Henry | 305.8 | Lower | High | 23 September 2011 |
| Peoria | 251.1 | Lower | High | 17 August 2011 |
| Havana | 193.1 | Lower | High | 8 – 12 August 2011 |
| Lilly Lake | 133.6 | Lower | High | 25 July 2011 |

Table 3: Common and scientific names, primary diet classification, and status in Illinois for fish sampled in this study.

| Common Name | Scientific Name | Diet | Status |
|-------------------------|-----------------------------------|-------------|------------|
| Bighead Carp | <i>Hypophthalmichthys nobilis</i> | Planktivore | Introduced |
| Silver Carp | <i>H. molitrix</i> | Planktivore | Introduced |
| Asian Carp Hybrid | <i>H. nobilis x molitrix</i> | Planktivore | Introduced |
| Bigmouth Buffalo | <i>Ictiobus cyprinellus</i> | Planktivore | Native |
| Paddlefish | <i>Polyodon spathula</i> | Planktivore | Native |
| Common Carp | <i>Cyprinus carpio</i> | Benthivore | Introduced |
| Grass Carp | <i>Ctenopharyngodon idella</i> | Herbivore | Introduced |
| Bluegill - juvenile | <i>Lepomis macrochirus</i> | Planktivore | Native |
| Bluegill - adult | | Omnivore | Native |
| Largemouth Bass | <i>Micropterus salmoides</i> | Predator | Native |
| Emerald Shiner | <i>Notropis atherinoides</i> | Planktivore | Native |
| Gizzard Shad – juvenile | <i>Dorosoma cepedianum</i> | Planktivore | Native |
| Gizzard Shad - Adult | | Omnivore | Native |

White muscle tissue was used where possible for fish samples, as previous studies have shown it to be less variable than other tissues, with a moderate stable isotope turnover rate on the order of weeks to months. In smaller species and juveniles, samples consisted of whole filets (in which case the individuals must be sacrificed), or of eviscerated or whole specimens. Excised muscle samples were taken from live larger species and individuals. Non-lethal sampling (e.g., fin-clips) was used for some larger and state-listed species; tissue-specific stable isotope correction factors were used to account for any difference in tissue.

All samples were prepared according to standard stable isotope analysis methodology. Each sample was placed into a clean glass vial and thoroughly dried in a drying oven at 60 degrees Celsius (140 Fahrenheit) and then ground to a fine powder using pestle-and-mortar or using a glass stirring rod inside the vial to increase homogeneity and reduce within-sample variability. One mg of this powder was weighed into tin capsules, and samples were sent to the Stable Isotope Facility at University of California at Davis, where were analyzed for ^{13}C and ^{15}N isotopes using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer. Samples from museum collections will be post-hoc transformed to account for preservation and storage in formalin and ethanol (Edwards et al. 2002, Vander Zanden et al. 2003). Circular statistics (Schmidt et al. 2007) were used to quantify changes in stable isotope signatures between upper and lower sites and from historical to contemporary time periods.

Results and Discussion

Due to their ability to resolve food web interactions, we used stable isotope analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) to look at changes in food webs mediated by Asian Carp. In particular, higher ratios of the ^{15}N isotope to the ^{14}N isotope (higher $\delta^{15}\text{N}$) indicate higher trophic level, while lower $\delta^{15}\text{N}$ indicates lower trophic level. Higher ratios of ^{13}C to ^{12}C isotopes (less negative $\delta^{13}\text{C}$) are consistent with benthic nutrients such as attached algae and periphyton, while more negative $\delta^{13}\text{C}$ indicates pelagic carbon sources such as phytoplankton. Changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the upper river (low density of Asian Carp) to the lower river (high density) and from historic to contemporary samples thus show how resource use and trophic levels of the fish community have changed with the Asian Carp invasion.

There were consistent trends in fish stable isotope signatures across sites and through time. Circular statistics showed lower (more negative) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the fish communities from contemporary upper to lower river, but higher $\delta^{15}\text{N}$ in the lower river from historic samples (Figure 1). In the lower river, $\delta^{15}\text{N}$ of the fish community declined from historic to contemporary samples, while in the upper river there was an increase in $\delta^{15}\text{N}$ through time (Figure 1). Thus, our results appear to show declining trophic positions (lower $\delta^{15}\text{N}$) and

increased use of pelagic nutrient sources (more negative $\delta^{13}\text{C}$) of most fish species at the contemporary lower river site relative to the upper river site and lower trophic positions relative to historic samples; these changes may be attributable to Asian Carp invasion.

Bighead Carp from the low density upper river have similar stable isotope values to an historic Bighead Carp from the lower river (captured in 1998), with higher trophic levels than contemporary Bighead Carp from the lower river (Figure 2a). This supports our hypothesis that Bighead Carp may have depressed trophic levels in the lower river by selective consumption of large predatory zooplankton. No silver carp were present in contemporary upper river or historic samples, although at the contemporary lower river site they are depleted in ^{13}C and ^{15}N , consistent with feeding on smaller grazing zooplankton and phytoplankton (Figure 2a).

Bigmouth Buffalo from the contemporary lower river were depleted in ^{15}N than those from all other sites and periods (Figure 2b), suggesting an impact from Asian Carp. Paddlefish from contemporary samples had much lower $\delta^{15}\text{N}$ than from historical samples, although historical Paddlefish also had extremely high signatures (Figure 2b). Common Carp from the contemporary lower river had lower $\delta^{15}\text{N}$ than those from the historical lower river and contemporary upper river (Figure 2c). Common Carp from historical upper river were depleted in both ^{15}N and ^{13}C relative to other sites and time periods; however, this may have been influenced by a single extremely depleted sample. No Grass Carp were caught in the upper river; those from the contemporary lower river were depleted in ^{15}N and ^{13}C relative to a single sample from the historical lower river (Figure 2c).

Both large (>80 mm) and small (<80 mm) Bluegill were depleted in ^{13}C and ^{15}N at the lower contemporary than the upper contemporary sites, while contemporary upper sites were enriched in ^{15}N and the lower sites were depleted in ^{15}N relative to historical samples (Figure 2d). No historical Largemouth Bass were sampled; fish from the lower river were ^{13}C depleted relative to those from the upper river while there were no differences in $\delta^{15}\text{N}$ (Figure 2d). Emerald Shiner from the historic low sample may have unrealistic $\delta^{15}\text{N}$, but appeared to be enriched in ^{15}N over other samples (Figure 2e). Contemporary lower river fish were depleted in ^{13}C relative to other samples. Both large and small contemporary Gizzard Shad were depleted in ^{13}C at lower relative to upper river sites (Figure 2e). Contemporary lower river Gizzard Shad were depleted in ^{15}N relative to historic samples (Figure 2e). Overall, we do not see high trophic niche overlap between the Asian Carps and native filter-feeding planktivores such as Bigmouth Buffalo or Paddlefish; Asian Carp isotopic values are more similar to facultative planktivores/omnivores such as Bluegill and Gizzard Shad, and Emerald Shiner which pick zooplankton from the water column (Figure 3a). The contemporary food web in the lower river comprised a $\delta^{13}\text{C}$ range of 3.90 ‰, calculated using mean species values, indicating a wider range of carbon sources utilized by fishes compared to the upper river where the range was 2.53 ‰ (Figure 3a). This is contrary to our expectations, as we had hypothesized that in the Asian Carp invaded lower river there would be a loss of nutrient pathways due to dominance by Asian Carp.

The contemporary upper river values are consistent with historical food webs in both the upper and lower river, where the $\delta^{13}\text{C}$ ranges were 2.77 ‰ and 2.29 ‰, respectively (Figure 3b). This range is only 1.55 ‰ if we remove the Paddlefish, perhaps suggesting a nutrient bottleneck in the upper Illinois River. Notably, our upper site near Channahon, IL, has been the leading front of the Asian Carp invasion for several years and Asian Carp are present in very low densities relative to the lower river, so there may be an element of food limitation preventing further upstream movement of the invasion front. In the lower river, rather than a loss of carbon sources Asian carp are correlated with expanded use of carbon sources, although the mechanism for this remains unclear.

Nitrogen isotopes showed a range of 4.69 ‰ between the highest and lowest mean consumer $\delta^{15}\text{N}$ values in the contemporary lower food web (Figure 3a). Assuming a mean fractionation of 3.4 $\delta^{15}\text{N}$ per trophic level, this suggests that Grass Carp are feeding at trophic level 2: primary consumer which is consistent with their herbivorous diet, while Largemouth Bass occupy the highest trophic level of about 3.5 indicating an omnivorous predatory diet. The range in $\delta^{15}\text{N}$ in the contemporary upper food web is only 2.97 ‰ (Figure 3b), although this is likely influenced by the lack of true primary consumers in our samples, as it comprises less than one trophic level. The historical upper food webs comprised a range of 4.62 ‰ (Figure 3a), similar to the contemporary lower food web, but higher than the contemporary upper food web. The historical lower food web has a $\delta^{15}\text{N}$ range of 9.62 ‰ (Figure 3b), but this is likely driven by some extraordinarily high and ecologically highly improbable $\delta^{15}\text{N}$ values that would suggest, for instance, gizzard shad feeding at a trophic level of 7 in one sample. Further study will determine whether this is an instance of contaminated samples or high ^{15}N inputs to the environment.

Our data thus show lower $\delta^{15}\text{N}$ indicating that fishes may be feeding at lower trophic levels in the lower section of the Illinois River relative to both upstream and historic references, concordant with the Asian Carp invasion. This may be due to over-predation on large predatory zooplankton, and subsequent increases in small grazing zooplankton such as rotifers. The increase in $\delta^{15}\text{N}$ at the upper river site may be due to increased anthropogenic inputs at this site, while the relative narrowness of $\delta^{13}\text{C}$ sources requires further investigation as to possible cause as well as effect on the Asian Carp invasion. Based on stable isotope signatures, Asian Carp appear to compete more directly with Gizzard Shad, Bluegill, and Emerald Shiner than with native filter feeding planktivores such as Bigmouth Buffalo and Paddlefish. Asian carps may thus alter where and on what competing fish species feed, and by reducing the overall prey base may be able to outcompete native species. We will continue to monitor fish communities in the Illinois River, and in particular the Asian carp invasion-front, in order to prevent their spread into the Great Lakes. The potential effects on Great Lakes ecosystems if Asian Carps become established are unknown, but could prove ecologically and economically catastrophic. Our project shows how Asian Carps impact food webs in the Illinois River, and thus reveals potential effects on food webs in the Great Lakes.

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References

- Burke, J. S., D. R. Bayne, and H. Rea. 1986. Impact of silver and bighead carps on plankton communities of channel catfish ponds. *Aquaculture* **55**:59-68.
- Calkins, H. A., S. J. Tripp, and J. E. Garvey. 2012. Linking silver carp habitat selection to flow and phytoplankton in the Mississippi River. *Biological Invasions* **14**:949-958.
- Cooke, S., W. Hill, and K. Meyer. 2009. Feeding at different plankton densities alters invasive bighead carp (*Hypophthalmichthys nobilis*) growth and zooplankton species composition. *Hydrobiologia* **625**:185-193.
- Cooke, S. L. and W. R. Hill. 2010. Can filter-feeding Asian carp invade the Laurentian Great Lakes? A bioenergetic modelling exercise. *Freshwater Biology* **55**:2138-2152.
- Edwards, M. S., T. F. Turner, and Z. D. Sharp. 2002. Short- and long-term effects of fixation and preservation on stable isotope values ($d^{13}C$, $d^{15}N$, $d^{34}S$) of fluid-preserved museum specimens. *Copeia* **2002**:1106-1112.
- Herborg, L. M., N. E. Mandrak, B. C. Cudmore, and H. J. MacIsaac. 2007. Comparative distribution and invasion risk of snakehead (Channidae) and Asian carp (Cyprinidae) species in North America. *Canadian Journal of Fisheries and Aquatic Sciences* **64**:1723-1735.
- Irons, K. S., G. G. Sass, M. A. McClelland, and J. D. Stafford. 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, USA - Is this evidence for competition and reduced fitness? *Journal of Fish Biology* **71**:258-273.
- Kocovsky, P. M., D. C. Chapman, and J. E. McKenna. 2012. Thermal and hydrologic suitability of Lake Erie and its major tributaries for spawning of Asian carps. *Journal of Great Lakes Research*.
- Kolar, C. S., D. C. Chapman, W. R. Courtenay, C. M. Housel, J. D. Williams, and D. P. Jennings. 2007. Bigheaded carps: a biological synopsis and environmental risk assessment. American Fisheries Society, Bethesda, Maryland.
- Lu, M., P. Xie, H. J. Tang, Z. J. Shao, and L. Q. Xie. 2002. Experimental study of trophic cascade effect of silver carp (*Hypophthalmichthys molitrix*) in a subtropical lake, Lake Donghu: on plankton community and underlying mechanisms of changes of crustacean community. *Hydrobiologia* **487**:19-31.
- Sampson, S. J., J. H. Chick, and M. A. Pegg. 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. *Biological Invasions* **11**:483-496.
- Schmidt, S. N., J. D. Olden, C. T. Solomon, and M. J. Vander Zanden. 2007. Quantitative approaches to the analysis of stable isotope food web data. *Ecology* **88**:2793-2802.
- Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. *Ecosystems* **6**:274-288.
- Vander Zanden, M. J. and J. B. Rasmussen. 1999. Primary consumer delta C-13 and delta N-15 and the trophic position of aquatic consumers. *Ecology* **80**:1395-1404.
- Vanderklift, M. A. and S. Ponsard. 2003. Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. *Oecologia* **136**:169-182.

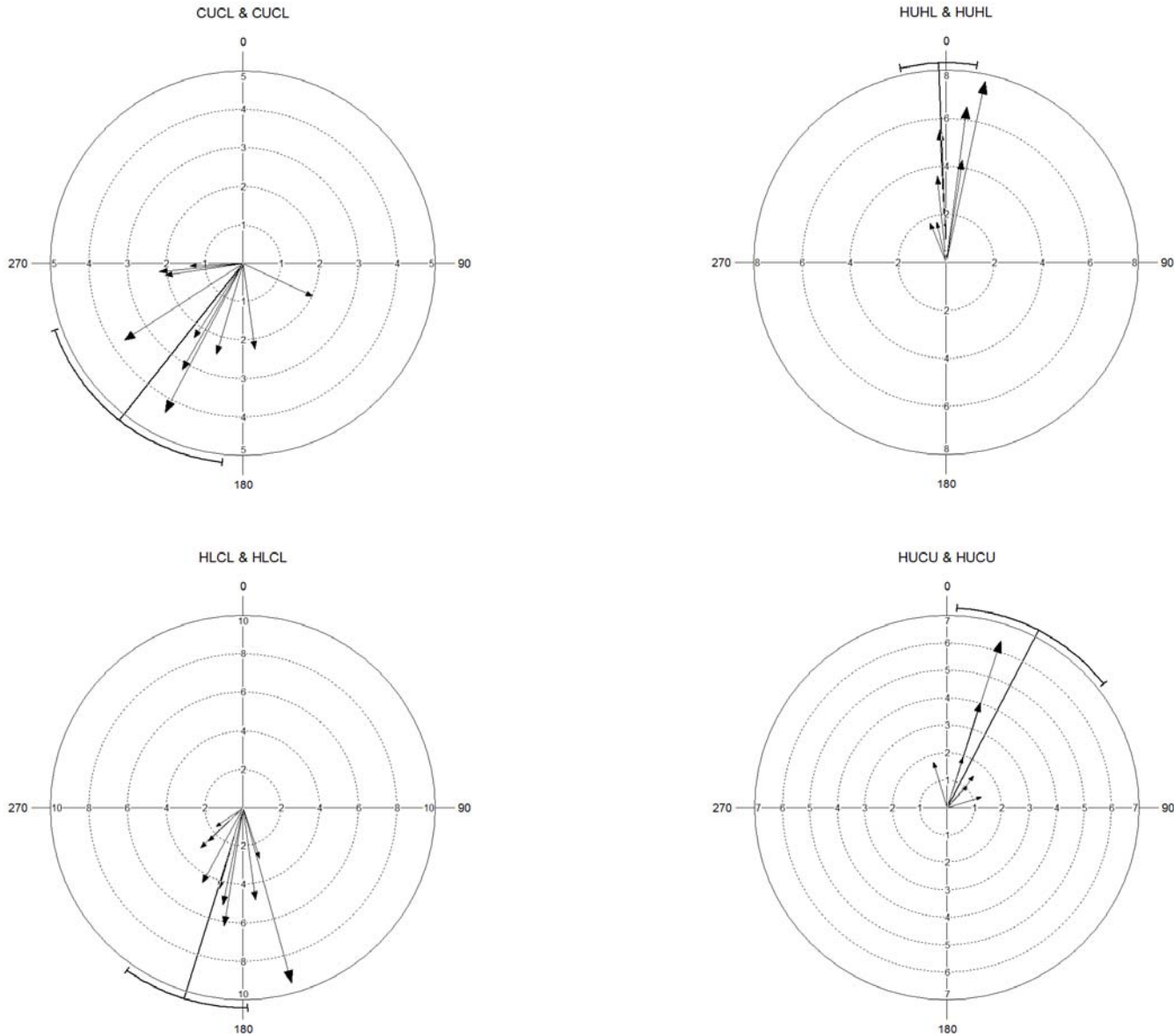


Figure 1: Circular plots of directional food web changes in the Illinois River from Contemporary upper to lower river (CUCL), Historical upper to lower river (HUHL), Historical lower to contemporary lower river (HLCL), and Historical upper to Contemporary upper river (HUCU). Each vector represents a fish species or size-class; the arrows indicate the direction in trophic niche space that the species or size-class moved while the lengths indicate the relative magnitude of directionality from one site or period to the next. Vector directionality towards the top of the plot represent higher $\delta^{15}\text{N}$ (higher trophic position) while the bottom of the graph represents lower $\delta^{15}\text{N}$ (lower trophic position), and to the left and right are depleted and enriched $\delta^{13}\text{C}$ (pelagic and benthic/littoral carbon sources) respectively. The line at the circumference of the plot represents the 95% confidence interval around the mean.

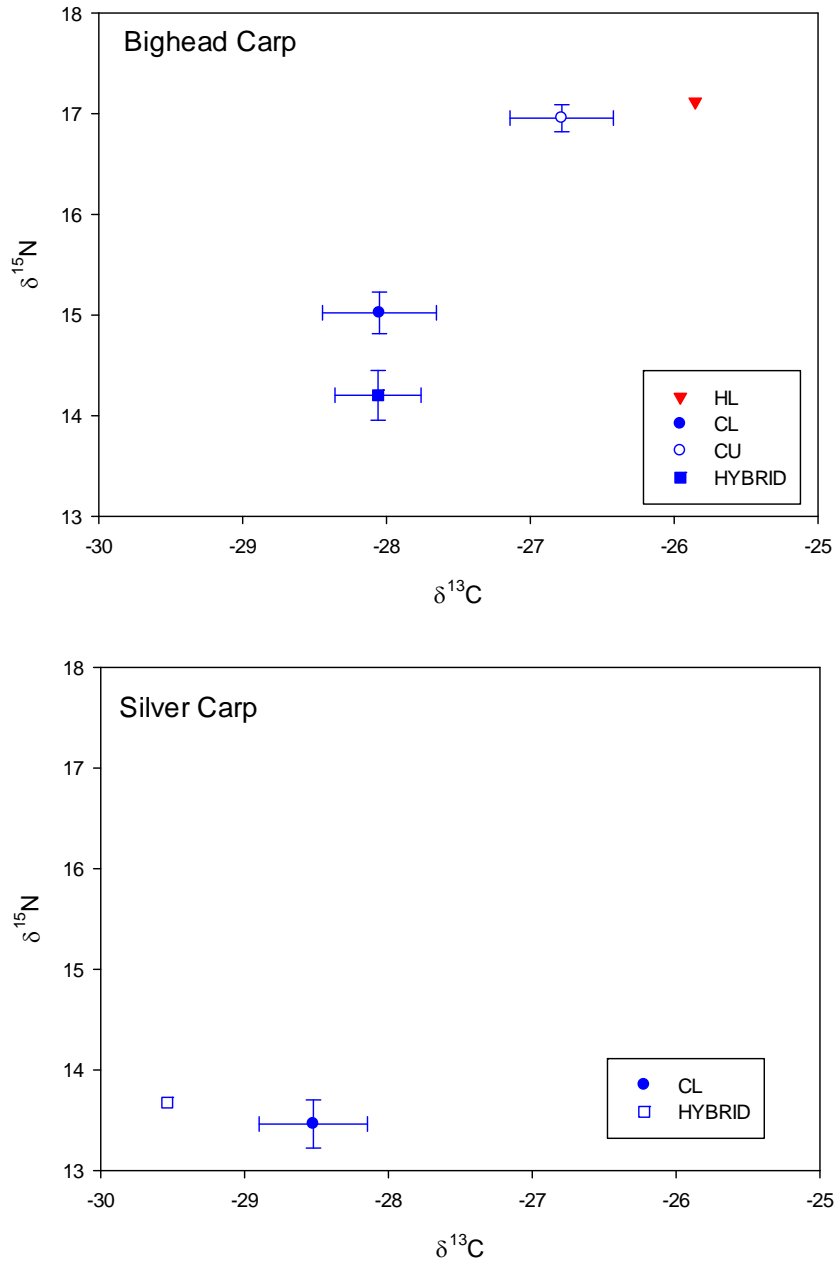


Figure 2a: Stable isotope biplots of Bighead Carp, Silver Carp, and hybrid Asian Carp in the Illinois River. HL: Historical lower river, HU: Historical upper river, CL: Contemporary lower river, CU: Contemporary upper river.

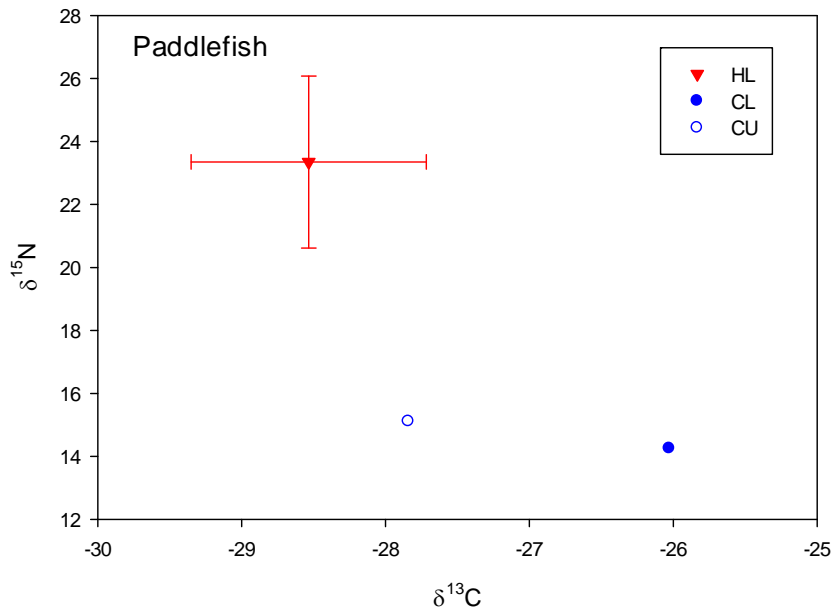
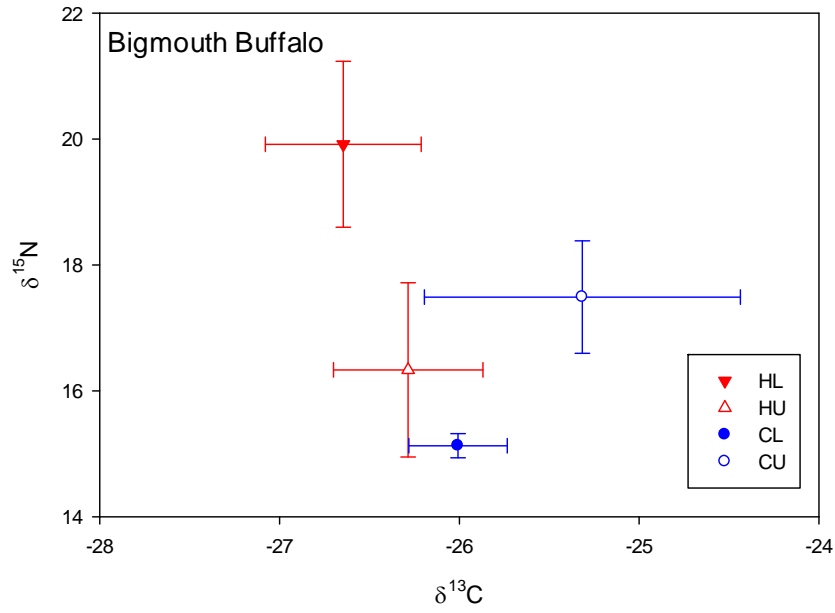


Figure 2b: Stable isotope biplots of Bigmouth buffalo and Paddlefish in the Illinois River. HL: Historical lower river, HU: Historical upper river, CL: Contemporary lower river, CU: Contemporary upper river.

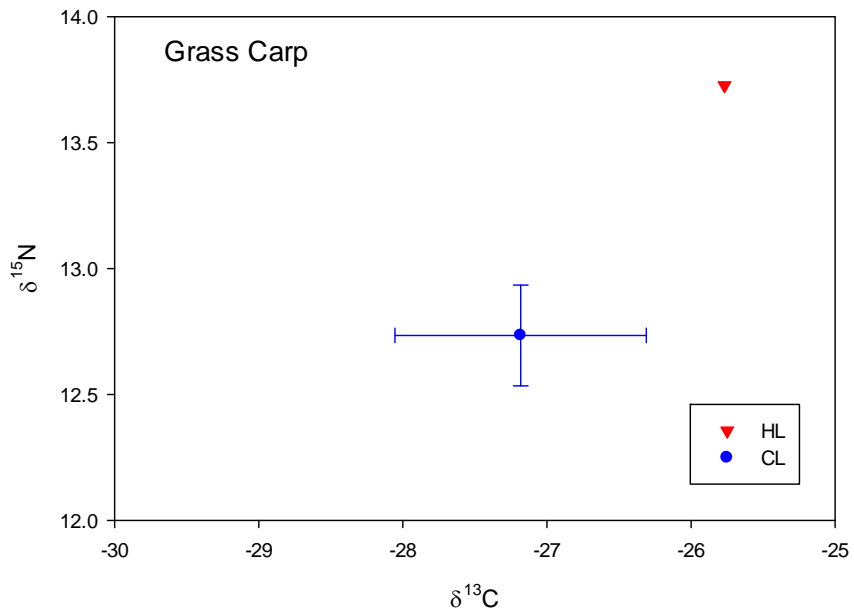
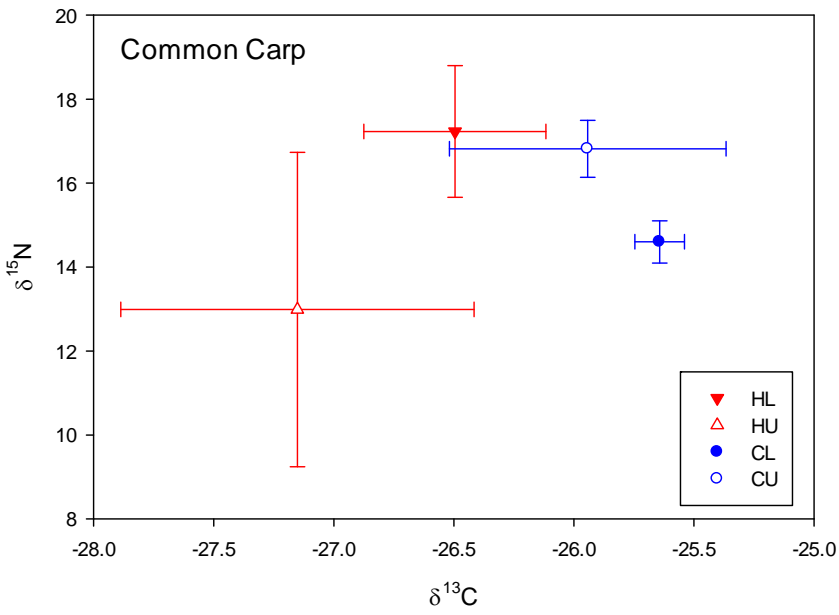


Figure 2c: Stable isotope biplots of Common Carp and Grass Carp in the Illinois River. HL: Historical lower river, HU: Historical upper river, CL: Contemporary lower river, CU: Contemporary upper river.

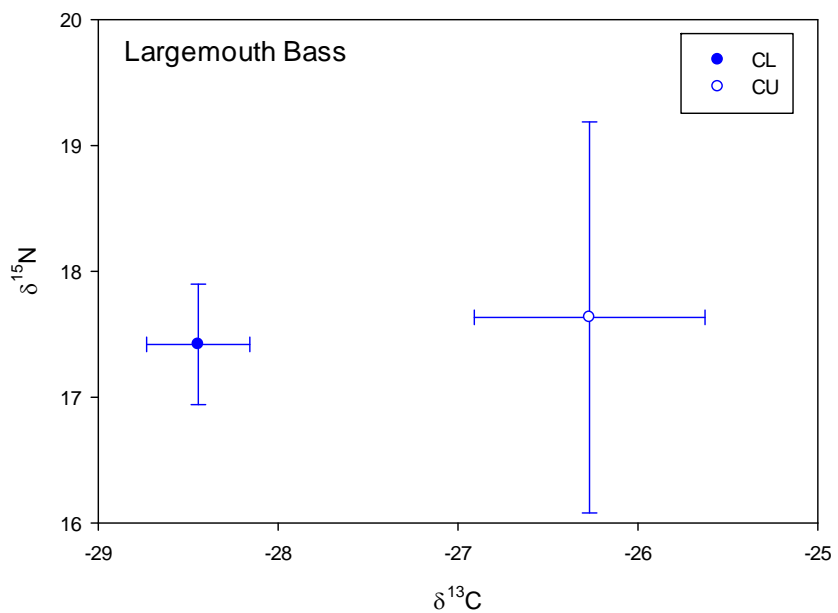
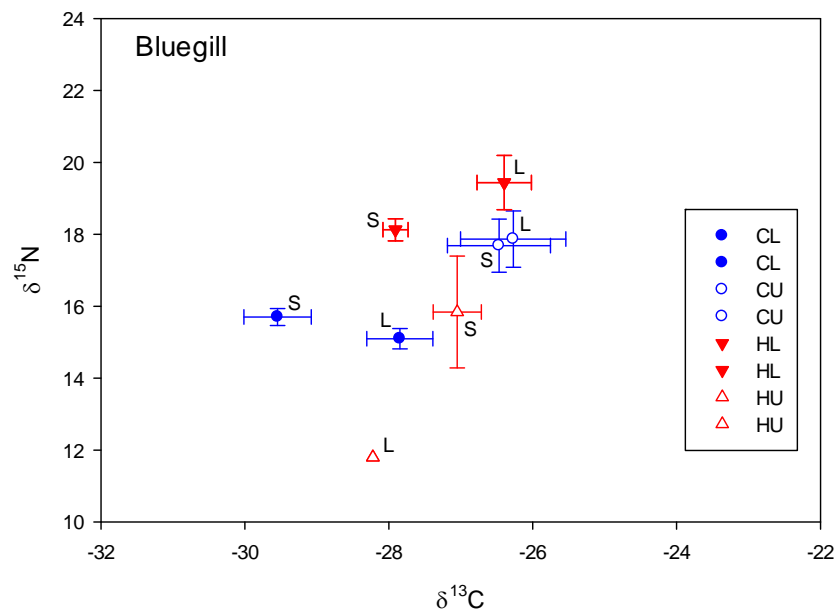


Figure 2d: Stable isotope biplots of Bluegill and Largemouth Bass in the Illinois River. HL: Historical lower river, HU: Historical upper river, CL: Contemporary lower river, CU: Contemporary upper river. L: Large and S: Small Bluegill.

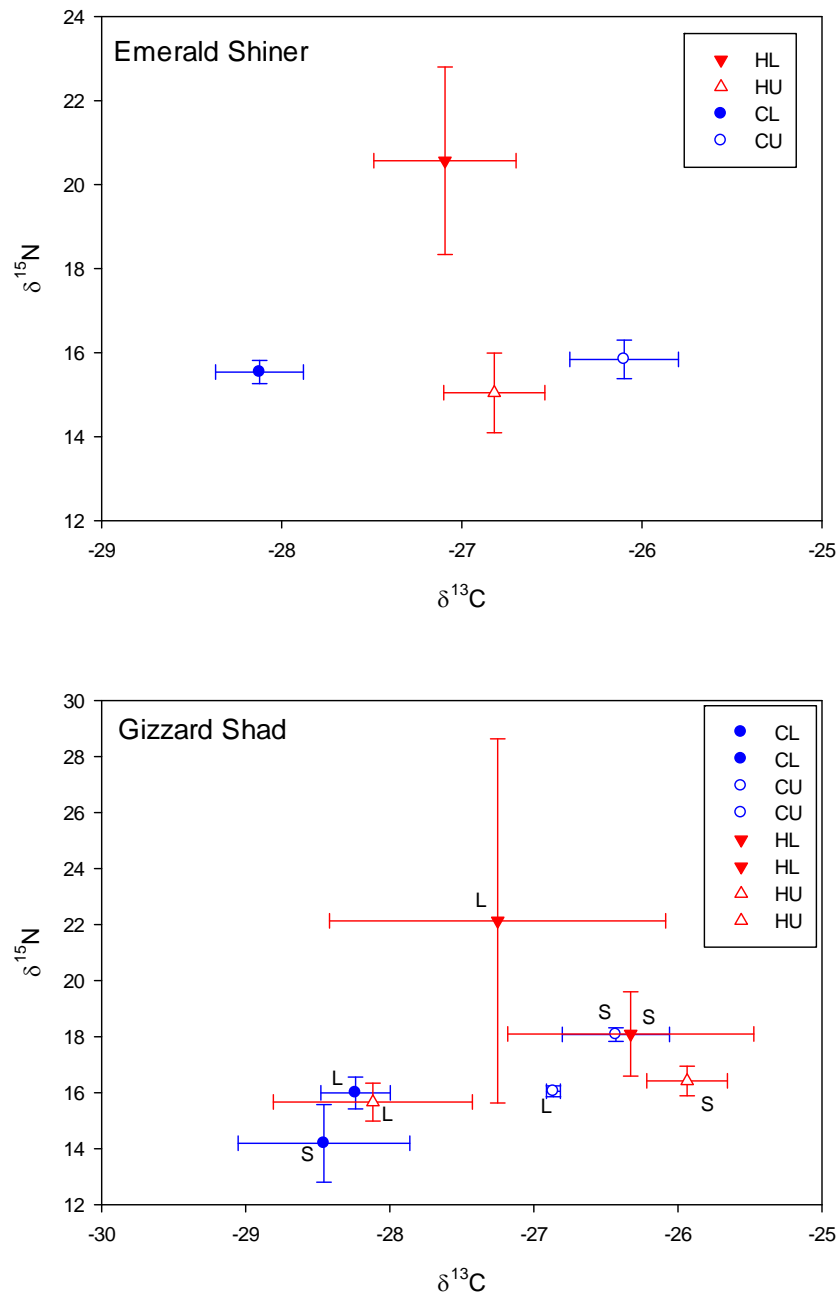


Figure 2e: Stable isotope biplots of Emerald Shiner and Gizzard Shad in the Illinois River. HL: Historical lower river, HU: Historical upper river, CL: Contemporary lower river, CU: Contemporary upper river. L: Large and S: Small Gizzard Shad.

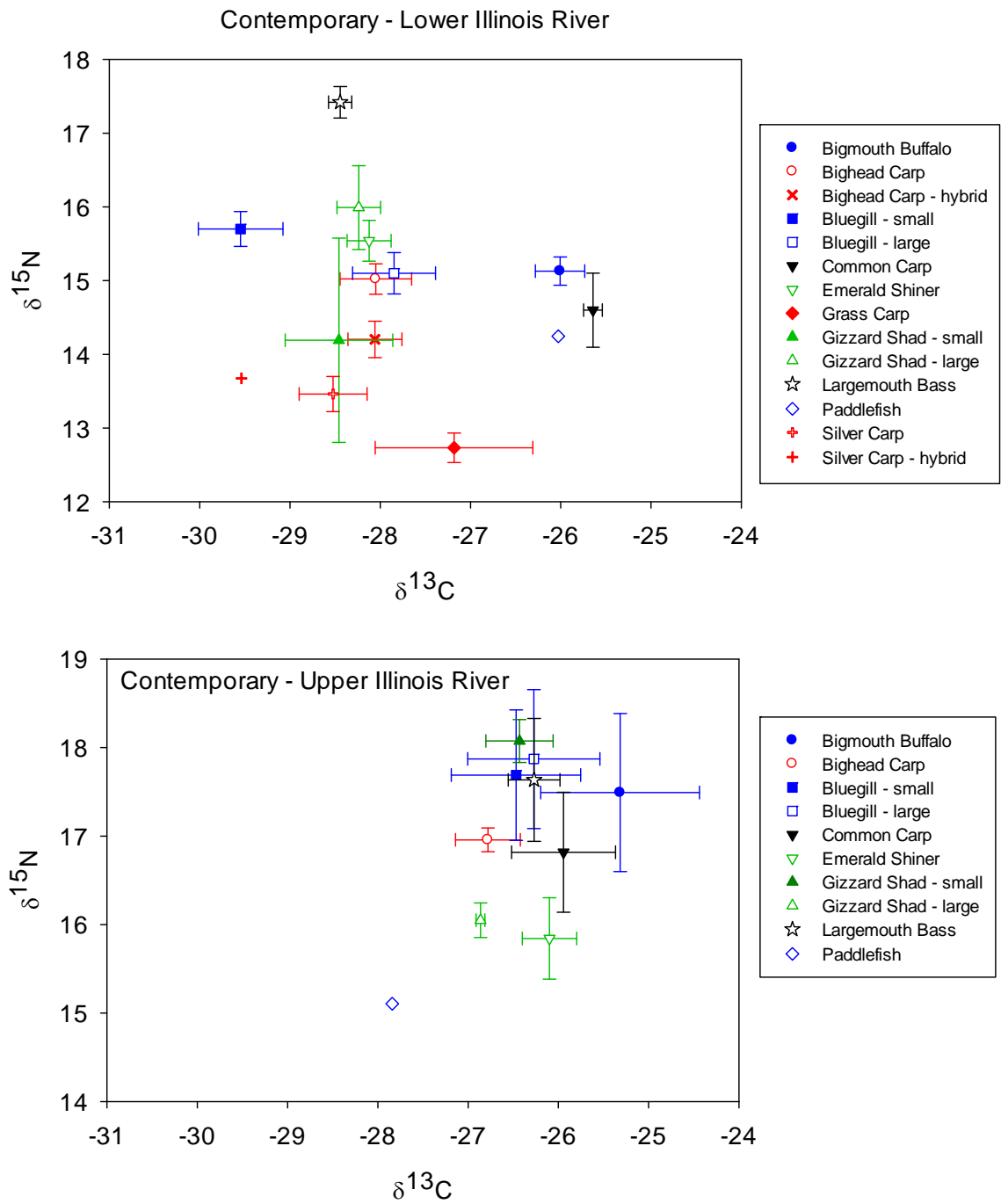


Figure 3a: Contemporary (2011) food webs of the upper (River Kilometers, RKM, 423.2-447.4) and lower (RKM 133.6-305.8) Illinois River delineated using stable isotope biplots of carbon and nitrogen.

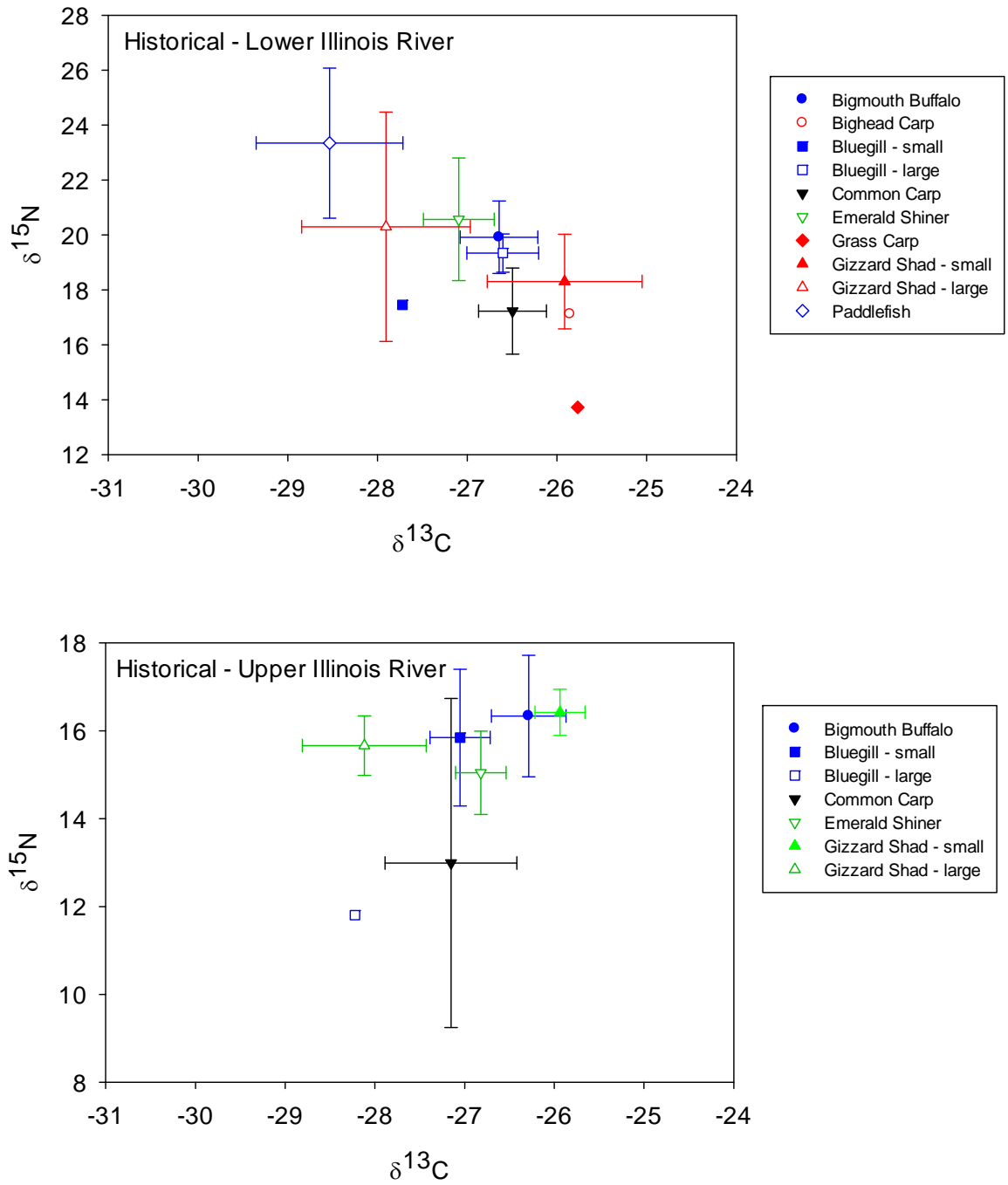


Figure 3b: Historic (1960-2000) food webs of the upper and lower Illinois River delineated using stable isotope biplots of carbon and nitrogen.