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[Article]

# Carbon Sources for Lake Sturgeon in Lake Winnebago, Wisconsin

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*Abstract.*—Because lake sturgeon *Acipenser fulvescens*, like other sturgeon species, are threatened or endangered in many aquatic ecosystems, it is imperative that we increase our understanding of their role in food webs. Our main objective was to determine the carbon sources for lake sturgeon in Lake Winnebago, Wisconsin, which contains one of the largest populations of lake sturgeon in North America. Gut content analysis revealed that gizzard shad *Dorosoma cepedianum* and *Chironomus plumosus* larvae (56% and 33% by gut content mass, respectively) were the primary prey items for lake sturgeon in the winter. Larger lake sturgeon were more piscivorous than smaller individuals. A mixing model using $\delta^{13}C$ and $\delta^{15}N$ suggests that *Chironomus* contributes 49% and gizzard shad 37% to the carbon assimilated by lake sturgeon. We estimated the carbon half-life in lake sturgeon to be about 0.6–3.0 years based on a model incorporating metabolism and growth. Thus, the stable isotope results integrate over a considerably longer time period than the gut content analysis. Our results provide critical baseline information about the carbon sources for lake sturgeon that can be used to assess how their role in food webs may change after perturbations such as the introduction of exotic species and changes in land use.

Many species of sturgeon (Acipenseridae) are threatened or endangered and population sizes have decreased for several sturgeon species in recent decades (Billard and Lecointre 2001; Pikitch et al. 2005). The reasons for this decline include overfishing, water quality degradation, and the damming of rivers (Beamesderfer and Farr 1997; Pikitch et al. 2005). Given these threats to sturgeon populations, it is imperative that we increase our understanding of the role of sturgeons in food webs and the primary energy sources for them in ecosystems. More complete knowledge of the carbon sources for sturgeons will increase the ability of fisheries scientists and managers to predict how changes in food web structure, caused by perturbations such as increased nutrient loading in lakes (Carpenter et al. 2001), will affect sturgeon populations. Information about the position of sturgeons in food webs also is important for predicting how sturgeon and other fish populations will respond to exotic species (Vander Zanden et al. 1999), which impact many aquatic ecosystems containing sturgeons (e.g., Richman and Lovvorn 2004).

Naturally occurring stable isotopes are frequently used to determine the carbon and nitrogen sources for consumers (Fry 2006). By comparing the ratios of stable isotopes between consumers and potential prey sources, it is possible to estimate the relative contributions of different prey sources to the carbon or nitrogen assimilated by the consumer. Tissues of consumers that turn over quickly, such as the blood, liver, and gonads, are more likely to be in isotopic equilibrium with food sources over short time scales (Perga and Gerdeaux 2005). Tissues with long turnover times, such as bone and muscle, probably integrate diet history over a longer time interval, particularly in relatively slow-growing consumers. The use of tissues with different turnover times offers the potential to track diet history at various time scales, which can be useful for determining how consumers respond to changes in food web structure. When stable isotope approaches are combined with gut content analysis, a more complete picture of the food sources for consumers usually emerges (Bondar et al. 2005; McMahon et al. 2005).

In addition to providing information on the primary prey sources for consumers, stable isotopes (and gut contents) can provide insights into the portions of ecosystems from which consumers obtain their energy. Although several fish species found in lakes rely almost exclusively on pelagic or benthic sources of energy, others rely to varying degrees on sources from both habitat types (Vander Zanden and Vadeboncoeur 2002). Previous diet studies of lake sturgeon *Acipenser*

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TABLE 1.—Physical and chemical characteristics of benthic offshore sampling stations in Lake Winnebago from April to October 2005 (means ± SDs). The sample size is 11 for all variables except chlorophyll *a*, for which it is 3. See Figure 1 for locations of the sampling stations.

| Station | Coordinates | Water depth (m) | Water temperature (°C) | Sediment temperature (°C) | Secchi depth (m) | Chlorophyll *a* ($mg/m^3$) |
|---|---|---|---|---|---|---|
| 1S | N43°55′36″, W88°24′31″ | 5.3 ± 0.1 | 19.1 ± 5.6 | 18.1 ± 5.5 | 1.0 ± 0.6 | 41.3 ± 1.9 |
| 2N | N44°10′20″, W88°21′53″ | 5.4 ± 0.1 | 19.8 ± 6.3 | 18.3 ± 5.4 | 1.3 ± 1.5 | 83.7 ± 11.1 |
| 3W | N44°03′88″, W88°29′55″ | 5.1 ± 0.1 | 19.7 ± 6.2 | 17.7 ± 5.1 | 1.2 ± 0.7 | 45.6 ± 23.2 |
| 4C | N44°03′22″, W88°25′42″ | 6.2 ± 0.2 | 19.5 ± 6.4 | 17.8 ± 5.4 | 1.0 ± 0.6 | 65.6 ± 25.8 |

*fulvescens* suggest that they primarily consume benthic prey as juveniles and adults (Miller 2004; Nilo et al. 2006). However, many of the published studies on sturgeon feeding have only addressed juveniles, which may be more benthivorous than adults (Miller 2004). It is important to understand from which compartments consumers obtain their energy in aquatic ecosystems because disturbances to food webs that affect sturgeons and other fishes are likely to affect one compartment (benthic or pelagic) more than another (Vadeboncoeur et al. 2001).

Trophic position, a continuous measure of the food web position of a consumer relative to primary producers (Post 2002) provides additional insight into where fishes and other consumers obtain their energy. Trophic position is particularly useful because it is an integrative measure of the role of a species in a food web or ecosystem. Obtaining baseline data on trophic position for threatened fish species such as lake sturgeon is important because it establishes a reference point with which future data can be compared to assess whether the role of the species in the food web has changed through time. Changes in trophic position suggest that the amount of basal resources (e.g., primary production) needed to support the population is changing. For example, an increase in trophic position could indicate a shift to piscivory, which, given the constraints on trophic efficiencies (Wetzel 2001), would probably increase the amount of basal resources needed to support the focal population. For threatened groups of fish such as lake sturgeon, a shift in trophic position may have important consequences for population sustainability.

Lake Winnebago in Wisconsin contains one of the largest (if not the largest) populations of lake sturgeon in North America (Bruch 1999), with approximately 37,000 adults (R. M. Bruch, unpublished data). Hundreds to thousands of lake sturgeon are harvested annually during a winter spearing season (Priegel and Wirth 1977; Bruch 1999). The large population size and the large number of individual fish harvested from Lake Winnebago allowed us to conduct one of the most comprehensive diet studies of any sturgeon species performed to date. We used a combination of naturally occurring stable isotopes of carbon and nitrogen and gut content analysis to determine (1) the carbon and nitrogen sources for lake sturgeon in Lake Winnebago, (2) the trophic position of lake sturgeon, and (3) interindividual variation in isotopic signatures and recent feeding history. To estimate the time frame over which stable isotope signatures integrate diet history in lake sturgeon, we estimated carbon turnover in lake sturgeon based on a simple model that incorporates literature estimates of metabolism and growth rates. We are not aware of a previous study that has estimated isotopic turnover for the adult stage of a large, long-lived fish species.

## Methods

*The Lake Winnebago system and lake sturgeon life history*.—Lake Winnebago, which is part of a large eutrophic riverine–lake system, is the largest inland lake in Wisconsin, with a surface area of 55,766 ha and a mean depth of 4.7 m. The bottom is dominated by fine sediments (about 90%), while nearshore and offshore rocky reefs comprise a smaller portion (about 10%). The Secchi depth averages about 1 m, and water column chlorophyll *a* averages 59 $mg/m^3$ (Table 1). Lake sturgeon males and females become sexually mature at 19 and 27 years, respectively (ages at 50% maturity; R.M.B., unpublished data). The somatic growth of lake sturgeon declines as fish increase in age (Probst and Cooper 1955), which can be as great as 82 years (Priegel and Wirth 1977). A regulated winter spearing harvest has occurred in Lake Winnebago since 1932, and the Wisconsin Department of Natural Resources has actively assessed this harvest since the 1940s (Priegel and Wirth 1977; Bruch 1999). A minimum size limit of 91 cm was established in 1997. In addition to lake sturgeon, the fish community in the Lake Winnebago system includes 76 species, of which freshwater drum *Aplodinotus grunniens*, walleye *Sander vitreus*, sauger *Sander canadensis*, yellow perch *Perca flavescens*, white bass *Morone chrysops*, trout-perch *Percopsis omiscomaycus*, gizzard shad *Dorosoma cepedianum*, and emerald shiner *Notropis*

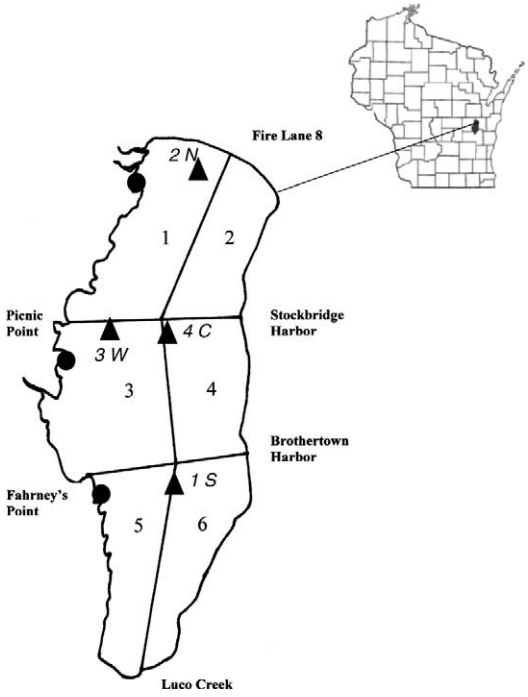


FIGURE 1.—Map of Lake Winnebago indicating the six lake sturgeon spearing zones, four offshore benthic sampling locations (triangles), and three nearshore benthic sampling locations (circles).

*atherinoides* are predominant (Becker 1964; Priegel 1967). The benthic invertebrates in Lake Winnebago include a large population of *Chironomus plumosus* (Hilsenhoff 1966; Koehnke 1997).

*Lake sturgeon sampling*.—Tissue samples for stable isotope analysis and gut contents for identification and stable isotope analysis were collected in February 2006 during the annual spearing harvest on Lake Winnebago. Spearers are required to register all sturgeon at various lakeshore stations, where they report the zone of the lake from which each sturgeon was harvested (Figure 1). The entire alimentary canal was removed from 51 lake sturgeon that came from various locations in Lake Winnebago (Table 2) and kept frozen until analysis of the gut contents. Muscle and blood tissues were collected from 62 and 23 sturgeon, respectively, from throughout Lake Winnebago (Table 2). For 22 sturgeon paired muscle and blood samples were collected. Samples of dorsal–lateral muscle were collected with a cork borer 5 cm ventral from the dorsal midline at the fifth scute posterior to the head. Blood samples were collected from the caudal vein with a 3-mL syringe fitted with a 21G1[1/2] needle. Samples were kept at or below 0°C during transport to the laboratory.

TABLE 2.—Number of lake sturgeon tissue (muscle and blood) samples collected for stable isotope analysis and gut contents collected for prey identification and stable isotope analysis in Lake Winnebago by zone (see Figure 1).

| | Zone | | | | | |
|---|---|---|---|---|---|---|
| Sample type | 1 | 2 | 3 | 4 | 5 | 6 |
| Muscle | 0 | 5 | 7 | 6 | 31 | 13 |
| Blood | 0 | 1 | 0 | 0 | 15 | 7 |
| Gut contents | 1 | 4 | 6 | 6 | 15 | 17 |

*Food source sampling*.—Potential food sources for lake sturgeon were sampled at nearshore and offshore sites for stable isotope analysis. Benthic macroinvertebrates were collected approximately every 2 weeks at four offshore sites (Figure 1; Table 1) with an Ekman grab (23 × 23 cm) from May to October 2005. The four sampling sites had similar water and Secchi depths and water and sediment temperatures but differed up to twofold in chlorophyll *a* (Table 1). The collected sediment was sieved through a 500-μm mesh screen, and invertebrates were immediately transferred to filtered lake water for transport to the laboratory. The majority of the invertebrate biomass in the samples consisted of fourth-instar *Chironomus plumosus* (hereafter, *Chironomus*) larvae. Because of this and the ease of identifying this instar in the field, this was the only *Chironomus* instar sampled for stable isotopes. On average, 10 *Chironomus* larvae were pooled per offshore site. An integrated water column sample (1.25 L) for seston (phytoplankton and, to a lesser extent, zooplankton) was collected at each location using a tube sampler (1.7 cm in diameter, 5.2 m long), samples were placed on ice, and separate aliquots for stable isotope analysis and chlorophyll *a* were vacuum-filtered in the laboratory onto 47-mm Whatman GF/F filters. Benthic macroinvertebrates were collected monthly from July to November at three nearshore locations (Figure 1). Several individuals (typically 5–20) per species per site were pooled for stable isotope analysis. Most invertebrates were collected in 0.3–0.8 m of water from rocks and aquatic vegetation.

Fishes that are known or likely prey for lake sturgeon were collected offshore by trawling on three occasions during summer 2005. On August 8 a large area of Zone 1 was sampled, while Zone 3 was sampled on August 29 and October 4 (Figure 1). The captured fish, most of which were young of the year (age 0), were placed on ice for transport to the laboratory, where samples of lateral muscle were removed with a razor blade for stable isotope analysis. Samples were collected from 8 individuals per species on each sampling date.

During the analysis of gut contents, many prey organisms in the foregut were found to be intact with no signs of digestion. Subsamples of these organisms were processed and analyzed for stable isotopes as described below. Lateral muscle was collected from fish found in guts (typically one prey fish per lake sturgeon), while invertebrate samples consisted of 10 pooled individuals per sturgeon.

*Laboratory processing*.—The samples for stable isotope analysis were dried at 60°C. Lipids were not extracted from the samples. Fish tissues (from both lake sturgeon and forage fishes) and seston were placed in a drying oven within 12 h of sampling. The guts of invertebrates were cleared by placing them in filtered, aerated water from Lake Winnebago, at ambient lake water temperature, for 24 h before drying. Snails were stored at −20°C after gut clearance, and then the soft tissues were separated from the shells and dried as described above. After drying, samples were homogenized with a mortar and pestle (fishes) or fine scissors (invertebrates, seston on filters). Subsamples of dried, homogenized material (~1 mg for animal tissue, ~15 mg samples for seston) were analyzed at the University of California–Davis Stable Isotope Facility with a PDZ Europa ANCA sample combustion unit and a PDZ Europa 20–20 isotope ratio mass spectrometer. Sucrose ($^{13}$C) and ammonium sulfate ($^{15}$N) were used as reference standards. Carbon and nitrogen isotope ratios were expressed in the standard $\delta^{13}$C and $\delta^{15}$N notation relative to Vienna Pee Dee belemnite and atmospheric $N_2$ (Fry 2006).

The contents of the foreguts (anterior to the muscular stomach) of lake sturgeon were analyzed in the laboratory. Small prey items (invertebrates) were collected by sieving bulk gut contents. Pieces of extraneous items (organic detritus) were carefully separated from the invertebrates after sieving. Wet masses of pooled prey items, separated by taxa, were measured to the nearest 0.01 g on an analytical balance.

*Data analysis and modeling*.—A change in $\delta^{13}$C and $\delta^{15}$N across trophic levels, or trophic shift, is commonly observed. We assumed +0.4‰ for $\delta^{13}$C (after Post 2002; McCutchan et al. 2003). Lake sturgeon mainly excrete nitrogen in the form of ammonia across the gill (Medale et al. 1991). Therefore, we assumed a trophic shift of +2.5‰ $\delta^{15}$N between lake sturgeon and their food sources, the average trophic shift for ammonotelic vertebrates in a recent meta-analysis (Vanderklift and Ponsard 2003). This value is lower than the widely used trophic shift value of 3.4‰ for $\delta^{15}$N (Post 2002). We used a three-source, two-element mixing model (Phillips 2001) to estimate the relative contributions of different diet sources to the carbon and nitrogen assimilated by lake sturgeon. The $\delta^{13}$C and $\delta^{15}$N of sturgeon muscle were used in the mixing model because the sample size for muscle was larger than that for blood. We calculated the trophic position for a consumer that obtains nitrogen from three food sources (after Post 2002).

Most studies that have determined the turnover rates of stable isotopes in fishes and other animals have used age-0 or juvenile individuals (Maruyama et al. 2001; Suzuki et al. 2005). For fast-growing fish species or life stages, the growth of new tissue is the predominant component of isotopic turnover (Maruyama et al. 2001; Sakano et al. 2005; MacNeil et al. 2006; McIntyre and Flecker 2006). Metabolism probably plays an increasingly important role in isotopic turnover as growth rates decrease (e.g., in adult fish). We used the following set of equations to determine a half-life for carbon in lake sturgeon:

$$B_t + G_{(t+1)-t} = B_{(t+1)}, \quad B_{(t+1)} + G_{(t+2)-(t+1)} = B_{(t+2)}, \ldots \tag{1}$$

$$C_t - M_{(t+1)-t} = C_{(t+1)}, \quad C_{(t+1)} - M_{(t+2)-(t+1)} = C_{(t+2)}, \ldots \tag{2}$$

$B$ = the total amount of carbon in body mass;
$G$ = the amount of carbon gained due to somatic growth;
$t$ = time;
$C$ = the amount of original carbon remaining since time $t$;
$M$ = the amount of carbon replaced through metabolism.

Each equation proceeds through yearly time steps.

The half-life of the original carbon ($C_t$) is estimated when

$$C_{t_i}/B_{t_i} = 0.50. \tag{3}$$

We estimated carbon half-lives for lake sturgeon with initial wet masses of 10 and 30 kg. The growth rates for lake sturgeon from Lake Winnebago, calculated from data in Probst and Cooper (1955), were 1.10 and 1.09 kg wet mass/year for the 10- and 30-kg size-classes. We assumed that the wet mass : dry mass ratio of lake sturgeon was 4:1 (Beamish et al. 1996) and that carbon was 50% of dry mass. McKinley and Power (1992) determined that the resting mass-specific metabolism of 4–6-kg lake sturgeon was 43 mg $O_2$/kg/h. We adjusted this rate for 10- and 30-kg lake sturgeon (obtaining 36 and 27 mg $O_2$/kg/h, respectively) based on the notion that mass-specific metabolism scales as a quarter-power function of organism mass (Gillooly

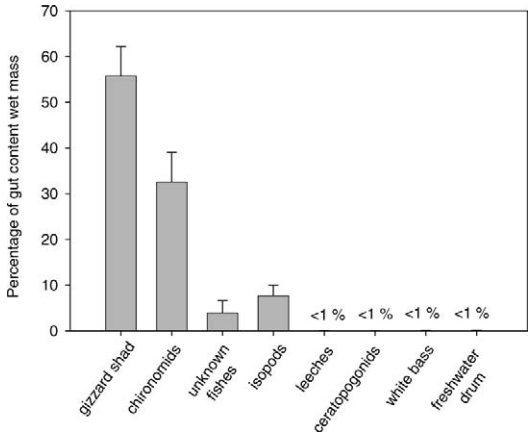


FIGURE 2.—Prey items found in the foreguts of 51 lake sturgeon as percentages (means + SEs) of foregut content wet mass. All fish were age 0. The vast majority of chironomids were fourth-instar *Chironomus plumosus* larvae. All ceratopogonids were larvae.

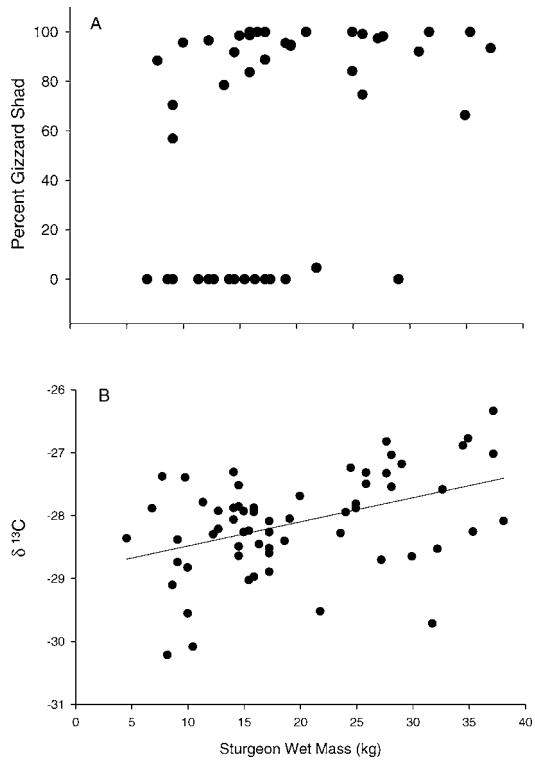


FIGURE 3.—**(A)** Percent gizzard shad in the foreguts of lake sturgeon from Lake Winnebago and **(B)** $\delta^{13}C$ (‰) of lake sturgeon muscle tissue (linear regression: $R^2 = 0.18$, $P < 0.001$).

et al. 2001). We did not adjust the metabolic rates for temperature because McKinley and Power measured sturgeon metabolism at 10°C, similar to the average annual water temperature of 11°C in Lake Winnebago (Wisconsin Department of Natural Resources 2004). In an animal that has recently foraged it is likely that a portion of its oxygen production reflects the metabolism of dietary carbon in addition to body carbon. To account for this, we considered two scenarios when estimating carbon half-lives: (1) all of the metabolized carbon is body carbon and (2) dietary and body carbon contribute to metabolized carbon in a ratio of 3:1. Because the metabolism of new tissue would not cause the original carbon to turn over, we assumed a mass-specific loss of carbon due to metabolism based solely on the original sturgeon mass (at $t$). A respiratory quotient of 0.8 was used to convert $O_2$ consumption to $CO_2$-C production.

One-way analysis of variance (ANOVA) was used to compare the mean isotopic signatures for *Chironomus* ($\delta^{13}C$ and $\delta^{15}N$ separately) among offshore benthic sampling sites. The Tukey honestly significant difference multiple comparison test was used to assess differences between particular sites. Sampling dates were used as replicates ($n = 8$). Sampling dates with missing data from more than one site were not included.

## Results

Age-0 gizzard shad (mean, 55.7%; SE, 6.4) and *Chironomus* larvae (32.5%; 6.5), most of which were fourth instar, made up the majority of the wet mass of lake sturgeon gut contents (Figure 2). The gizzard shad found in lake sturgeon guts ranged from 8 to 15 cm in total length. Isopods and unknown fishes (parts of fish that could not be identified to species) represented 7.7% and 3.9%, respectively, of the gut content wet mass. Leeches (class Hirudinea), ceratopogonid larvae, age-0 white bass, and age-0 freshwater drum were rarely found in the lake sturgeon examined. Individual sturgeon foreguts tended to be dominated by a single prey type. Smaller sturgeon (<23 kg wet mass) tended to contain either gizzard shad or *Chironomus* larvae (Figure 3A), while larger sturgeon mainly contained gizzard shad.

The isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of known and likely prey for lake sturgeon varied both spatially and temporally in Lake Winnebago. *Chironomus* larvae from one of the sampling locations (site 3W; Figure 1) had a more negative $\delta^{13}C$ and a much more negative $\delta^{15}N$ than those from the other three sampling locations (ANOVA: $P \leq 0.001$; Tukey's test: $P \leq 0.003$; Figure 4A, B). The *Chironomus* collected from sturgeon foreguts had $\delta^{13}C$ and $\delta^{15}N$ similar to those of

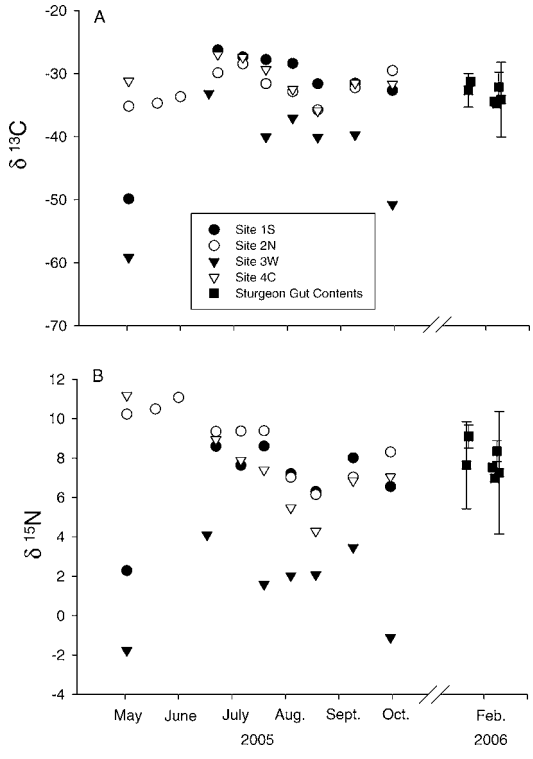


FIGURE 4.—Time series of **(A)** $\delta^{13}C$ (‰) and **(B)** $\delta^{15}N$ (‰) of fourth-instar *Chironomus plumosus* larvae from four offshore sampling locations and lake sturgeon foreguts (means ± SDs) in Lake Winnebago.

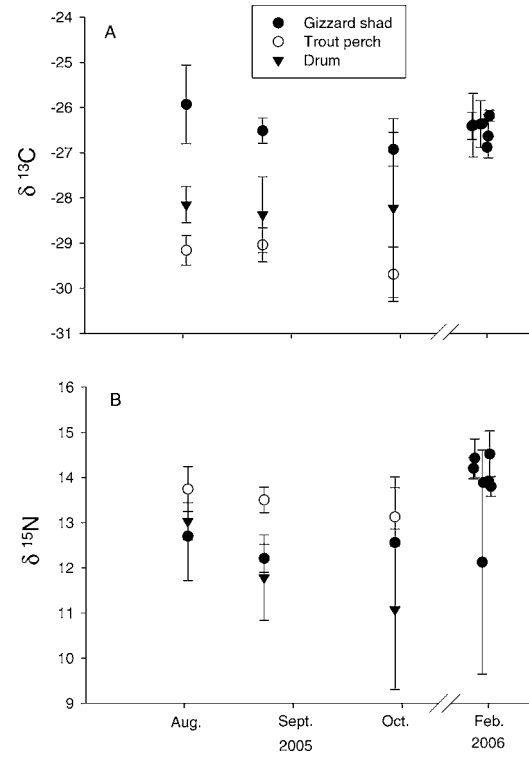


FIGURE 5.—Time series of **(A)** $\delta^{13}C$ (‰) and **(B)** $\delta^{15}N$ (‰) of fishes from trawls (August–October) and lake sturgeon foreguts (February) in Lake Winnebago (means ± SDs). All fish were age 0 except trout-perch. Age-0 white bass (left off of the figure for purposes of clarity) had the following $\delta^{13}C$ and $\delta^{15}N$ means for August, September and October: −26.22, −26.75, and −27.08; and 14.27, 14.84, and 14.30.

*Chironomus* from sediments, particularly at sites 1S, 2N, and 4C (Figure 4A, B). This suggests that the *Chironomus* taken from the sediments at these three sites were isotopically representative of the *Chironomus* consumed by lake sturgeon. The *Chironomus* from site 3W was considered an outlier and was not included in the mixing model used to estimate carbon and nitrogen sources for lake sturgeon or in the estimate of trophic position.

Suspected forage fishes for lake sturgeon differed in $\delta^{13}C$ and $\delta^{15}N$ and tended to be heavier isotopically than *Chironomus* (Figures 5A, B; 6). There was low isotopic variation between the summer and fall sampling dates. Age-0 gizzard shad collected from lake sturgeon in February had similar $\delta^{13}C$ but higher $\delta^{15}N$ than age-0 gizzard shad collected by trawling the previous year (Figure 5A, B). The size range of the gizzard shad collected by trawling (6–16 cm) was similar to that found in sturgeon guts.

A biplot of the $\delta^{13}C$ and $\delta^{15}N$ grand means for various potential food sources revealed substantial isotopic separation, particularly among *Chironomus* larvae, fishes, and nearshore benthic invertebrates (*Asellus* isopods, *Hyalella* amphipods, *Hydropsyche* caddisflies, and *Physa* snails) (Figure 6). The relative positions of the components of the Lake Winnebago food web in the biplot tended to show internal consistency. For example, small fish, which are often planktivorous, had $\delta^{13}C$ values similar to that of seston and $\delta^{15}N$ values about 3–4‰ higher than seston (which are within published estimates of trophic shift). In determining the food sources for lake sturgeon, we considered *Chironomus* larvae, gizzard shad, and isopods as the three end members, based on their prevalence in sturgeon foreguts. We assumed trophic shifts of 0.4‰ for $\delta^{13}C$ and 2.5‰ for $\delta^{15}N$ (see Methods). The isotopic signatures of *Chironomus*, gizzard shad, and isopods, corrected for trophic shift, triangulate the signature of sturgeon muscle tissue (Figure 6). Based on a three-source, two-element mixing model, *Chironomus*, gizzard shad, and isopods contributed 49, 37, and 14%, respectively, to the carbon assimilated by lake sturgeon. For lake sturgeon

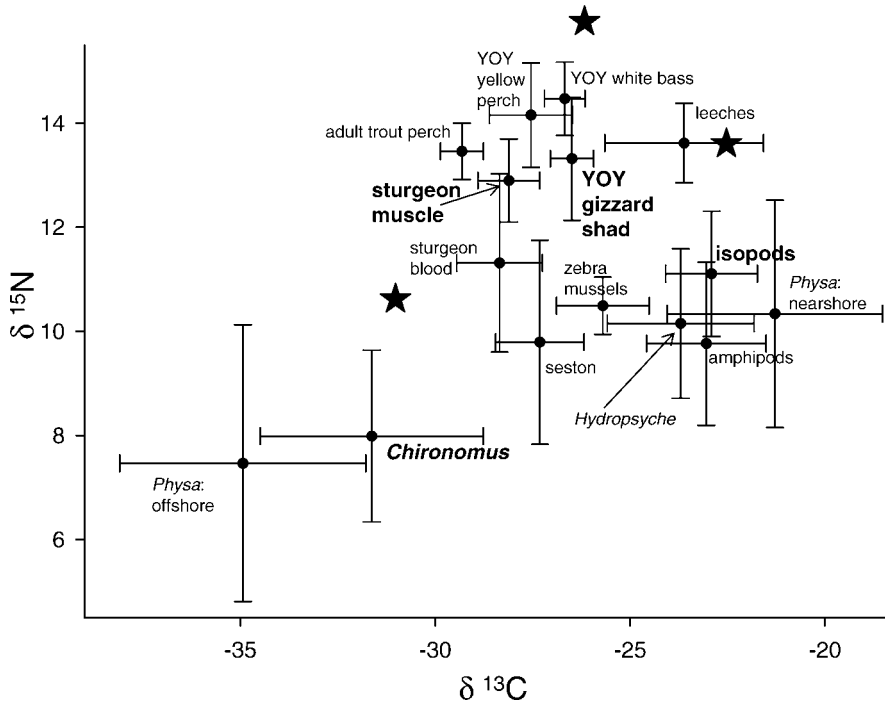


FIGURE 6.—Values of $\delta^{15}N$ and $\delta^{13}C$ (‰) in lake sturgeon muscle and blood, potential prey sources for lake sturgeon, and seston (means ± SDs). The stars indicate the positions of *Chironomus*, age-0 (YOY) gizzard shad, and isopods adjusted for trophic shifts in $\delta^{15}N$ (2.5‰) and $\delta^{13}C$ (0.4‰). Offshore *Physa* were rare overall (only 32 individuals were collected from all sites during the study).

from which we collected paired samples for muscle and blood, muscle was slightly more positive in $\delta^{13}C$ (−27.9 versus −28.3; paired *t*-test: $P = 0.003$). There was a larger difference between sturgeon muscle and blood in $\delta^{15}N$ (12.7 versus 11.3; paired *t*-test: $P < 0.001$). The estimated trophic position of lake sturgeon, based on the contributions from *Chironomus*, gizzard shad, and isopods to the $\delta^{15}N$ of sturgeon muscle, was 3.0.

There was considerable variation among individual lake sturgeon in $\delta^{13}C$ (Figure 3B) and $\delta^{15}N$ (data not shown). The $\delta^{13}C$ of sturgeon muscle tissue was positively correlated with sturgeon wet mass (Figure 3B; $R^2 = 0.18$, $P < 0.001$). This pattern is consistent with the variation in the gut contents of individual lake sturgeon (Figure 3A). Larger sturgeon tend to be heavier isotopically and more piscivorous than smaller sturgeon, and gizzard shad are heavier isotopically than *Chironomus* (Figure 6). Larger lake sturgeon tended to consume larger gizzard shad. There was a positive relationship (linear regression: $r^2 = 0.21$, $P = 0.024$) between the average body size of gizzard shad in sturgeon guts and sturgeon wet mass.

The estimated carbon half-lives for lake sturgeon were 0.6–2.0 years for a 10-kg (initial wet mass) individual and 0.8–3.0 years for a 30-kg fish. The low and high ends of the ranges reflect the two different metabolism scenarios described in the Methods, 0% and 75% contribution of dietary C to overall metabolism. We estimated that 75–94% of the carbon turnover in lake sturgeon was due to metabolism and the remainder to growth.

## Discussion

Most of the previous diet studies on lake sturgeon and other sturgeon species have focused on juveniles (Carlson and Simpson 1987; Kempinger 1996; Brosse et al. 2000; Jackson et al. 2002; Nilo et al. 2006). These studies have found that juvenile sturgeon feed almost exclusively on benthic invertebrates and occasionally zooplankton. Benthic invertebrates are the major component of the diet of various species of adult sturgeons (Probst and Cooper 1955; Miller 2004). We are not aware of another study that has shown lake sturgeon to be piscivorous, although fish consumption is fairly common in some other sturgeon species (e.g., Semakula and Larkin 1968; Gerrity et al. 2006; Wanner et al. 2007). The gut content results and those

TABLE 3.—Percent frequencies of prey items in the stomachs of lake sturgeon from Lake Winnebago. The vast majority of the fish found in 2004 and 2006 were gizzard shad. All data are for adult sturgeon except those of Choudhury et al. (1996), which include both adults and juveniles. The samples for all studies except Choudhury et al. (1996) were taken in winter only.

| Period and prey category | This study | Drecktrah[a] | Choudhury et al. (1996) | | Probst and Cooper (1955) | Schneberger and Woodbury (1944) |
|---|---|---|---|---|---|---|
| | | | Winter | Summer | | |
| Period | 2006 | 2004 | 1992–1993 | | 1954 | 1942 |
| Prey | | | | | | |
| Chironomids | 43 | 6 | 87 | 80 | 87 | 100 |
| Fish | 69 | 64 | 0 | 0 | 2 | 0 |
| Annelids | 12 | 0 | 28 | 4 | 10 | 18 |
| Mollusks | 2 | 4 | 7 | 24 | 2 | 9 |
| Crustaceans | 2 | 2 | 7 | 18 | 1 | 0 |

[a] H. Gene Drecktrah, University of Wisconsin–Oshkosh, unpublished data.

from the mixing models suggest that *Chironomus* and gizzard shad are both important sources of carbon and nitrogen for lake sturgeon in Lake Winnebago, while isopods are less important.

The differences between the gut content results in the winter (when gizzard shad were the most abundant food type) and the mixing model results (in which *Chironomus* were the largest contributor to lake sturgeon carbon) may stem from the fact that gizzard shad are a more ephemeral food resource for lake sturgeon than *Chironomus* larvae. Gizzard shad are at the northern edge of their range in Lake Winnebago (Becker 1983) and regularly experience large die-offs during the winter months. This is when gizzard shad, accumulating on the lake bottom, are probably most available to lake sturgeon and when they are commonly found in sturgeon guts. In the warmer months, the lake sturgeon in Lake Winnebago are probably more reliant on *Chironomus* (Choudhury et al. 1996). Diet studies in Lake Winnebago since the 1940s suggest that chironomids are consistently important prey items for lake sturgeon (Table 3). Collectively, these studies suggest that gizzard shad have only recently become an important carbon source for lake sturgeon in Lake Winnebago. From the 1940s through the early 1990s, gizzard shad and other fishes were rarely found in the guts of lake sturgeon. Gizzard shad were first reported in Lake Winnebago in 1966, but they did not become abundant in trawling samples until 1989 (Priegel 1967; Otis and Staggs 1988; R.M.B., unpublished data). The carbon half-life estimates for lake sturgeon (~0.6–3.0 years) suggest that the $\delta^{13}C$ and $\delta^{15}N$ in muscle tissue are integrating about 1–6 years of diet history. Based on our estimates of C turnover, if lake sturgeon exhibited a fairly recent diet shift to gizzard shad (e.g., in 2003) this change would probably be reflected in the $\delta^{13}C$, and presumably in the $\delta^{15}N$, of lake sturgeon sampled in 2006.

Our results and those from numerous other studies suggest that lake sturgeon heavily exploit the benthic resources in lakes and rivers. This adds to a growing body of evidence demonstrating the importance of benthic animal production for a variety of fish species in lakes (Vander Zanden and Vadeboncoeur 2002; Vander Zanden et al. 2006). Even though the age-0 gizzard shad in Lake Winnebago apparently rely on seston (Figure 6), our observations suggest that they are being consumed by lake sturgeon in benthic habitats during die-offs. Whereas the littoral zone is a particularly important source of carbon for some other species of fish (Vander Zanden and Vadeboncoeur 2002), there was no evidence from the gut content or stable isotope results that lake sturgeon were relying heavily on carbon sources from the littoral zone. Nearshore (littoral) food sources were considerably more positive in $\delta^{13}C$ than lake sturgeon, suggesting that such sources were of minor importance to sturgeon. In addition, the invertebrates typically found in the littoral zones of Lake Winnebago were either not present (e.g., *Hydropsyche* caddisflies and amphipods) or not very abundant (e.g., isopods) in sturgeon guts. The lake sturgeon in Lake Winnebago are probably obtaining most of their carbon and nitrogen from the soft sediments in the profundal zone, where *Chironomus* and gizzard shad (seasonally) are abundant. Owing to their reliance on benthic resources, lake sturgeon are likely to be especially vulnerable to perturbations that affect the benthos, such as invasion by zebra mussels *Dreissena polymorpha* (McCabe et al. 2006).

Our calculated trophic position of lake sturgeon (3.0) in Lake Winnebago suggests that they obtain their energy relatively low in the food web. Estimates of trophic position for a secondary consumer are sensitive to uncertainty in the trophic position of the primary consumers (Post 2002). In calculating the trophic position for lake sturgeon we assumed that *Chironomus*, isopods, and gizzard shad had a trophic position of 2.0. *Chironomus* larvae in the profundal zones of lakes probably consume various types of algae,

including phytoplankton that has settled out of the water column (Hilsenhoff 1966; Johnson 1985). *Chironomus* may also be obtaining energy from bacteria, including methanotrophic bacteria, as suggested by the samples that were depleted in $^{13}C$ (Figure 4A), an indicator of methanotrophy (Grey et al. 2004). We assumed that age-0 gizzard shad fed primarily on phytoplankton in Lake Winnebago based on our observations of high quantities of algae in their stomachs. The difference in $\delta^{15}N$ between age-0 gizzard shad and seston (3.5‰; Figure 6) is also consistent with literature values for $\delta^{15}N$ fractionation (Post 2002). However, we acknowledge that there was high variability in $\delta^{15}N$ among the seston samples (Figure 6). Based on findings in other lentic systems (Yako et al. 1996; Higgins et al. 2006), it is likely that age-0 gizzard shad also consume zooplankton and detritus in Lake Winnebago. Much of the detritus in large, eutrophic lakes such as Lake Winnebago is probably of phytoplankton origin and thus would not necessarily change the trophic position of age-0 gizzard shad. However, if gizzard shad obtain meaningful amounts of energy from zooplankton this would tend to increase their trophic position and that of lake sturgeon.

The difference in $\delta^{15}N$ between lake sturgeon muscle and blood is difficult to interpret. If we assume that the trophic fractionation is similar for blood and muscle and that N turns over more quickly in blood than in muscle (MacNeil et al. 2006), then the lower $\delta^{15}N$ of blood may indicate the recent influence of prey with lighter $\delta^{15}N$, such as *Chironomus*. If the $\delta^{15}N$ and $\delta^{13}C$ of sturgeon blood reflects very recent diet history, we would have expected this blood to me more similar isotopically to gizzard shad, based on the predominance of gizzard shad in sturgeon guts when blood and muscle tissue were sampled. However, the above assumptions may not be valid. Trophic fractionation for $\delta^{15}N$ has been shown to vary among tissues in other fish species (Pinnegar and Polunin 1999; Trueman et al. 2005) and in birds (Hobson and Clark 1992). Although several studies suggest that blood turns over more quickly than muscle in vertebrates (e.g., MacNeil et al. 2006), a recent study suggests that the two tissue types have similar turnover rates (MacAvoy et al. 2001). A laboratory study in which sturgeon are fed controlled diets would be necessary to distinguish the contributions of diet history and trophic fractionation to differential values of $\delta^{15}N$ between sturgeon tissues.

There was considerable interindividual variation in the $\delta^{13}C$ of muscle and the type of prey in the foreguts of lake sturgeon. Taken together, these results suggest that larger sturgeon are heavier in carbon isotopes because they are more piscivorous (and closer to the $\delta^{13}C$ of gizzard shad) than smaller sturgeon. The variation in $\delta^{13}C$ among individual sturgeon may be influenced by factors besides diet, including differences in the turnover of carbon and nitrogen (Matthews and Mazumder 2004) and feeding level (Gaye-Siessegger et al. 2004). It is not clear why larger lake sturgeon tend to be more piscivorous. Possible explanations include differences in energetic requirements and optimal prey choice size among lake sturgeon of different sizes. It is also possible that the difference in diet among sturgeon size-classes is related to differential habitat use.

The gut content analysis and stable isotope results suggest that the lake sturgeon in Lake Winnebago obtain most of their energy from age-0 gizzard shad and *Chironomus* larvae. If we assume that age-0 gizzard shad are primarily consumed while on the lake bottom (dead or dying), it appears that lake sturgeon are highly dependent on benthic food resources, as other studies have suggested. There was striking variation in the diets of individual lake sturgeon. Larger lake sturgeon tended to be more piscivorous than smaller individuals. The causes of this ontogenetic variation and the extent to which the carbon sources for sturgeon vary seasonally are topics that deserve further study. In addition to providing insight about the role of lake sturgeon in lake food webs, our estimates of the carbon sources for lake sturgeon and their trophic position in Lake Winnebago establish a baseline for future comparisons. The changes in carbon sources and trophic position that could accompany the introduction of invasive species or alterations in land use would signal shifts in food web structure that could have major implications for the vitality of this important population.

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