Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

Novel trophic interaction between lake sturgeon (Acipenser fulvescens) and non-native species in an altered food web.

Journal:	*Canadian Journal of Fisheries and Aquatic Sciences*
Manuscript ID	cjfas-2017-0282.R2
Manuscript Type:	Article
Date Submitted by the Author:	12-Mar-2018
Complete List of Authors:	Bruestle, Eric; U.S. Fish & Wildlife Service; SUNY College at Buffalo, Great Lakes Center Karboski, Curtis; U.S. Fish & Wildlife Service Hussey, Anna; University of Windsor, Great Lakes Institute for Environmental Research Fisk, Aaron; University of Windsor, Great Lakes Institute for Environmental Research Mehler, Knut; SUNY College at Buffalo, Great Lakes Center; SUNY College at Buffalo, The Research Foundation of SUNY, Office of Sponsored Programs Pennuto, Christopher; SUNY College at Buffalo, Great Lakes Center; SUNY College at Buffalo, Biology Gorsky, Dimitry; U.S. Fish and Wildlife Service; SUNY College at Buffalo, Great Lakes Center
Is the invited manuscript for consideration in a Special Issue? :	N/A
Keyword:	DIET < General, STABLE ISOTOPES, GASTRIC LAVAGE, NATIVE FRESHWATER FISHES, INVASIVE SPECIES < Organisms

Novel trophic interaction between lake sturgeon (*Acipenser fulvescens*) and non-native species in an altered food web.

Bruestle, Eric L.[1,2], Curtis Karboski[2], Anna Hussey[3], Aaron T. Fisk[3], Knut Mehler[1,4], Christopher Pennuto[1,5], and Dimitry Gorsky[1,2]

1-Great Lakes Center, SUNY Buffalo State, Buffalo, New York 14222, USA

2-U.S. Fish and Wildlife Service, Lower Great Lakes Fish and Wildlife Conservation Office, Basom, New York 14013, USA

3-Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Ontario N9B 3P4, Canada

4-The Research Foundation of the State University of New York, Office of Sponsored Programs, Buffalo State College, Buffalo, New York 14222, USA

5-Biology Department, SUNY Buffalo State, Buffalo, New York 14222, USA

Abstract

Lake sturgeon *Acipenser fulvescens* were once abundantly distributed throughout the Laurentian Great Lakes. However, widespread overharvest and habitat degradation has diminished their numbers. The lower Niagara River contains one of the few remnant lake sturgeon populations in New York State. This study determined the diet of adult lake sturgeon and quantified their trophic position in a non-native species dominated food web. Stomach content analysis assessed recent diet and stable isotope analysis ($\delta^{15}N$ and $\delta^{13}C$) of blood and fin tissue quantified trophic position and carbon source over varying time scales. Two non-native species dominated the diet of lake sturgeon – the amphipod *Echinogammarus ischnus* (62% by number) and round goby *Neogobius melanostomus* (44% by weight). Stable isotopes revealed that round goby was the primary contributor to the long-term (i.e. fin) average diet whereas short-term (i.e. blood) diet was more diverse. In contrast to findings from other systems, adult lake sturgeon in the lower Niagara River were primarily piscivorous, actively targeting live fish prey. The recovery of this population is potentially supported by high availability of energetically-rich, but non-native food resources.

Introduction

Lake sturgeon are large, long-lived, benthic fish whose range-wide abundance has declined precipitously over the past century, resulting in their designation as a species of conservation concern in many U.S. states and Canadian provinces (Peterson et al. 2007). Factors implicated in this decline include overharvest and habitat loss/degradation (Harkness and Dymond 1961; Auer 1999; Pikitch et al. 2005). The scarcity of lake sturgeon across their range hindered early research efforts but the species is receiving increased attention as populations recover (Peterson et al. 2007). However, questions about the basic ecology of the species persist, especially in the realm of diet and trophic position of adult fish, for several reasons. First, lake sturgeon are commonly characterized as generalist benthic feeders, however, their actual diet composition varies greatly from system to system (see Harkness and Dymond 1961; Chiasson et al. 1997; Beamish et al. 1998; Nilo et al. 2006; Guilbard et al. 2007; Stelzer et al. 2008) and thus may not be transferrable among systems. Second, many previous diet studies focused exclusively on juveniles (e.g. Kempinger 1996; Chiasson et al. 1997; Beamish et al. 1998; Nilo et al. 2006) and may not be representative of adult diets due to ontogenetic shifts (Jackson et al. 2002; Stelzer et al. 2008). Finally, the ecosystems and food webs of the Great Lakes have been permanently altered and continue to change in the face of species invasions (Ricciardi 2001; Grigorovich et al. 2003). Just how well lake sturgeon have adapted to these changes and how much their diet has shifted from their historical diet is poorly understood. Therefore, in order to more effectively protect and manage this species it is critical to understand the role of adult lake sturgeon in localized food webs and describe the energy pathways that they utilize.

The establishment of non-native species can have variable and unpredictable consequences on ecosystems (Lodge 1993). In the Great Lakes, the establishment of non-native species like dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) have profoundly altered the flow of energy by rerouting pelagic production to the benthos (Johannsson et al. 2000). This rerouted energy was sequestered in mussel tissue, unavailable to most native fish species, until the arrival of another Ponto-Caspian species, the round goby (*Neogobius melanostomus*). Adult round goby prey on a diversity of benthic invertebrates including dreissenid mussels (Ray and Corkum 1997; Corkum et al. 2004; Brush et al. 2012) and now constitute a new energy pathway for native fish species by facilitating the transfer of energy from the benthos to top predators (Johnson et al. 2005; Dietrich et al. 2006). It is becoming increasingly evident that round goby are a growing proportion of the diets of many piscivorous native fishes including burbot (*Lota lota*) (Madenjian et al. 2011), lake trout (*Salvelinus namaycush*) (Dietrich et al. 2006), smallmouth bass (*Micropterus dolomieu*) (Steinhart et al. 2004), and yellow perch (*Perca flavescens*) (Truemper et al. 2006). There could be considerable benefits, e.g. increased condition (Crane et al. 2015), conferred to native fishes able to take advantage of this mobilized energy which would have otherwise been sequestered in the benthos.

The lower Niagara River (LNR) is home to a recovering, remnant lake sturgeon population. This recovery is occurring in the presence of a benthic community that is dominated by a suite of non-native species including dreissenid mussels, round gobies, and amphipods (*Echinogammarus ischnus*). Greater knowledge of food web structure and the functional role of lake sturgeon in the LNR are crucial to understanding if the recovery is occurring as a result of the altered prey base or in spite of it. Further, a reference trophic position for lake sturgeon and their prey will allow future changes in trophic position or shifts in carbon sourcing to lake sturgeon to be detected. Thus, a more robust understanding of lake sturgeon trophic position will enhance and inform management of the species in the face of environmental perturbations and may help predict its response to future non-native species introductions (Vander Zanden et al. 1999).

Characterizing lake sturgeon feeding ecology in an invaded system will broaden our understanding of the 'typical' lake sturgeon diet established by past studies conducted either in more pristine environments or prior to contemporary species invasions. The objectives of this study were to (1) document the short- and long-term diet history and (2) estimate the trophic position of adult lake sturgeon in the LNR and determine their functional role in this altered ecosystem. To accomplish these objectives we employed stable isotope analysis (SIA) and stomach content analysis (SCA). SIA is a commonly used technique for assessing trophic position and relatively long-term (weeks or months) diet history of organisms (Fry 2006) and can be used to characterize consumer diet at various time scales through the examination of multiple tissue types. Tissues with quick isotopic turnover, like blood, should be more isotopically similar to food resources ingested recently (Perga and Gerdeaux 2005). Fin tissue, with its slower turnover rate (Suring and Wing 2009), should reflect the isotopic composition of the diet over the preceding weeks or months (Perga and Gerdeaux 2005). In contrast, SCA provides a snapshot of the most recent diet, representing material ingested within the last few hours. Using these two techniques concurrently provides a more complete picture of feeding ecology.

Materials and methods

Study Site

The Niagara River is a 58-km connecting channel between Lakes Erie and Ontario that forms a portion of the border between the State of New York and the Province of Ontario (Fig. 1). The river flows northwards from Lake Erie and is divided into an upper and lower portion by Niagara Falls. Below Niagara Falls, the river carves through the narrow Niagara Gorge for 11 km before broadening out at the foot of the Niagara escarpment near Lewiston, NY and continuing another 12 km to Lake Ontario. The river transports considerable sediment into Lake Ontario that settles out and forms the relatively shallow and sandy Niagara Bar. River depth varies from over 50 m in the gorge to less than 5 m on the bar. Several eddies along the river are thought to be important feeding areas for lake sturgeon.

Sample Collection

All lake sturgeon and prey samples were collected from a 10-km section between the Niagara escarpment and the mouth of the river in Lake Ontario from May to September 2014-2015. Lake sturgeon were sampled using a 75-m baited set line anchored at each end, adapted from Thomas and Haas (1999). Gangions with 12/0 circle hooks baited with alewife (*Alosa pseudoharengus*) or rainbow smelt (*Osmerus mordax*) were placed every 3 m along the setline. Lines were set overnight in productive back eddy areas or the Niagara Bar to maximize captures. Collected fish were placed in a sling and anesthetized with a solution of ambient water and tricaine methanesulfonate (MS-222) that was recirculated over the gills and biological data, including total length (TL, mm) and mass (to nearest 0.5 kg) were collected. An induction dose of 200 mg/L buffered MS-222 was used initially, followed by a maintenance dose of 87 mg/L.

Stomach contents were collected from anesthetized fish using gastric lavage methodology adapted from Haley (1998). A modified 7-L garden sprayer attached to 6-mm outer diameter aquarium tubing was used to deliver water. The tube was gently inserted into the pharynx, through the esophagus, and into the stomach. Water was pulsed into the stomach and massaged out causing the fish to regurgitate water and food particles. Regurgitated contents were collected on a 500-μm mesh screen and washed into 500-ml sample bottles. Samples were preserved in 10% buffered formalin until laboratory processing. Stomach contents were identified to family taxonomic level and wet weighed to the nearest 0.01 g.

Stable isotope samples were collected from two points on all collected fish. Fin tissue was clipped from the posterior edge of the pectoral fin proximal to the body, in an area of newest growth and placed into vials and frozen until analysis. Blood samples were collected from the caudal vein with 3 mL unheparinized vacutainer fitted to a 21-gauge sterile needle then immediately centrifuged for five minutes to separate the red blood cells (RBC) from the plasma. Aliquots of RBC and plasma were pipetted into 5 mL microcentrifuge tubes and kept chilled for transport and frozen for storage. Upon completion of sample collection, fish were supplied with recirculated freshwater to recover from anesthesia before being placed in a large holding pen until normal behavior was demonstrated, and then released.

A variety of organisms, informed by their presence in lake sturgeon stomach contents, were collected in 2014 to establish the isotopic structure of the Niagara River food web. Benthic invertebrate species were collected from the same areas of the river as lake sturgeon using a ponar grab (152 x 152 mm). These samples were picked live and separated by taxonomic group. Other invertebrates, such as crayfish (e.g. *Orconectes* spp.) and snails (*Elimia* spp.), were opportunistically collected from acoustic telemetry equipment deployed and retrieved from the river bottom. Preliminary analysis of telemetry data has shown this lake sturgeon population to be seasonally resident, exhibiting a lake-bound out migration in winter. Therefore, localized benthic invertebrate sampling should be spatially representative of prey species available to sturgeon. Round goby were caught using baited minnow traps set overnight and no other fish species were collected in the traps.

Diet quantification

Stomach contents were quantified using the following metrics: mean percent number (%N;

Hyslop 1980), mean percent weight (%W; Hyslop 1980), frequency of occurrence (%O; Hyslop 1980), and prey-specific abundance (%PW; Amundsen et al. 1996). Percent by number and weight were calculated for each stomach and averaged for each prey type. Prey-specific abundance is defined as the proportion by weight that prey *i* constituted among the weight of all prey items in stomachs that contained prey *i*. This metric was used to illustrate lake sturgeon feeding strategy using a technique developed by Costello (1990), then modified by Amundsen et al. (1996), which plots frequency of occurrence against prey-specific abundance.

Isotope sample processing

Digestive tracts of invertebrates were allowed to clear by placing them in filtered river water for 24 h. Then, soft tissue from snails, mussels, and crayfish was removed in preparation for SIA. Individuals of smaller invertebrate taxa (e.g. Oligochaeta, Chironomidae) were pooled together to obtain sufficient mass for SIA. A skinless piece of dorsal-lateral muscle tissue was removed from round goby for analysis. All organisms and lake sturgeon fin tissue was dried at 60° C for 48 h. After drying, individual samples were homogenized with a mortar and pestle and 400-600 µg subsamples were packed into 5 mm x 9 mm tin cups. Red blood cell and plasma samples were freeze dried for 48 h prior to analysis.

Isotopic analyses were conducted at the Chemical Tracers Lab, University of Windsor on a Delta V Advantage IRMS and ConFlo IV gas interface (Thermo Electron Corporation, Waltham, Massachusetts, USA) equipped with a Costech 4010 Elemental Analyzer (Costech, Santa Clarita, California, USA). No tissue samples were lipid extracted or lipid corrected, in the manner proposed by Smith et al. (2015), because mean ± standard deviation C:N ratios were less than 3.5 (3.29 ± 0.15) indicating a low enough proportion of lipids to be inconsequential in analysis (Post et al. 2007). The amounts of carbon and nitrogen stable isotopes relative to a standard in each sample were given using the equation:

$$(1) \qquad \delta R\ (‰) = \left(R_{\text{sample}}/R_{\text{standard}} - 1\right) \times 1000$$

where *R* is the ratio of $^{15}N/^{14}N$ or $^{13}C/^{12}C$. The laboratory standard material was Pee Dee belemnite carbonate for CO_2 and atmospheric nitrogen for N_2 (Fry 2006). Precision, assessed by the standard deviation of replicate analyses of three standards, NIST1577c, internal lab standard (tilapia muscle, *Oreochromis niloticus*) and IVA33802174 Urea (n = 63 for all), measured ≤0.19‰ for $\delta^{15}N$ and ≤0.14‰ for $\delta^{13}C$ for all the standards. Standards were analyzed every 15th sample and, to assess repeatability, every 13th sample was run in triplicate. Accuracy, based on the certified values of USGS 40 (n=44) analyzed throughout runs, showed a difference of 0.01‰ for $\delta^{15}N$ and -0.06‰ for $\delta^{13}C$ from the certified value. Instrumentation accuracy checked throughout the period of time that these samples were analyzed was based on NIST standards 8573 (n = 35) and, 8547 (n = 30) for $\delta^{15}N$ and 8542 and 8573 for $\delta^{13}C$ (n = 39 for both). The mean differences from the certified values were -0.11 and -0.01‰ for $\delta^{15}N$ and 0.06 and -0.06‰ for $\delta^{13}C$, respectively.

When drawing comparisons across ecosystems, the singular $\delta^{15}N$ value of an organism is not enough to estimate trophic position. This is because the basal nitrogen sources that primary producers use vary across systems (Rounick and Winterbourn 1986; Cabana and Rasmussen 1996; Vander Zanden et al. 1999) and therefore differences in $\delta^{15}N$ could either be the result of food web structure or different baselines. To calculate this baseline, Cabana and Rasmussen (1996) and Post (2002) advocated for the use of unionid mussels, relatively large and long-lived primary consumers that integrate temporal isotopic variability from primary producers. In this study, *D. r. bugensis* served as that baseline trophic position of 2.0 against which lake sturgeon fin tissue was compared. Lake sturgeon trophic position was estimated using the equation from

Vander Zanden et al. (1997):

$$\text{(2)} \qquad \text{trophic position} = (\delta^{15}\mathrm{N}_{\mathrm{consumer}} - \delta^{15}\mathrm{N}_{\mathrm{baseline}})/3.0 + 2.0$$

where $\delta^{15}\mathrm{N}_{\mathrm{consumer}}$ is the stable nitrogen isotope signature of an organism, $\delta^{15}\mathrm{N}_{\mathrm{baseline}}$ represents the quagga mussel baseline, 3.0 is the trophic enrichment factor relevant to sturgeon (Vanderklift and Ponsard 2003), and 2.0 is the trophic position of the baseline organism. Lake sturgeon fin tissue was used to calculate trophic position because it has the slowest turnover rate of the sampled tissues and reflects the diet over the longest time period.

Isotopic mixing models are commonly used to estimate the proportional contribution of prey (source) items to the tissues of a consumer. However, there are limitations to mixing models which include: increasing uncertainty with more sources, incorporating variability in isotopic signatures and trophic enrichment factors, and dealing with unidentified dietary sources. Recent Bayesian approaches can provide robust estimates and probable solutions despite these limitations. Therefore, a Bayesian two-element mixing model run by the Stable Isotope Analysis in R (SIAR) (Parnell and Jackson 2013) package was used to estimate the relative carbon and nitrogen contributions of source items to each of the three lake sturgeon tissues (RBC, plasma, and fin tissue). SIAR fits a Bayesian model to the measured isotope values based on a Gaussian likelihood with a dirichlet prior mixture on the mean. Since the model assumes that the stable isotopic values for prey sources are normally distributed, normality was assessed using a Shapiro-Wilk test with a *p* value of <0.05 indicating statistical significance. The mixing model accounts for trophic fractionation of each tissue but the exact fractionation values for the three lake sturgeon tissues have not yet been identified. Therefore, for fin tissue, we used a value of 0.4‰ for δ^{13}C (Post 2002; Stelzer et al. 2008) and 3.0‰ for δ^{15}N, a value deemed appropriate for freshwater ammonotelic stenotherms like lake sturgeon (Vanderklift and Ponsard 2003). For blood components we used 0.24‰ δ^{13}C and 5.17‰ δ^{15}N for red blood cells and 0.06‰ δ^{13}C and 4.39‰ δ^{15}N for plasma, values derived from a controlled feeding study of the catfish species *Pterygoplichthys disjunctivus* (German and Miles 2010).

Results

Sampled lake sturgeon (*n* = 254) had a mean TL ± standard deviation of 142.0 ± 13.7 cm. Stomach contents were obtained from 63 fish, 11% (*n* = 7) of which were empty and excluded from analysis. The prevalence of empty stomachs (11%) was greater in the summer, compared to the spring, as water temperatures and, presumably, digestion rates increased. The wet mass of stomach contents was dominated by two prey items: round goby and amphipods. Round goby had the largest mean (± SE) percent wet mass of diet contents, 44 ± 6.1%, followed by amphipods, 39.9 ± 6.0% (Fig. 2). Amphipods, nearly all of which were non-native *Echinogammarus ischnus,* had the greatest mean ± SE percent by number, 62.4 ± 4.7%; the second most prevalent prey item by number was round goby with 23.1 ± 4.4%. Amphipods were also the most frequently occurring prey item, found in 84% of stomachs. Round goby, chironomids, and crayfish were the next most common items at 64, 41, and 30%, respectively. Other prey items included a variety of benthic invertebrates (e.g. Trichoptera, Isopoda, Ephemeroptera) and fish (e.g. *Notropis* spp., Centrarchidae), which appeared infrequently in stomachs and in inconsequential amounts by numbers or mass. The modified Costello plot showed that these prey groups could be considered rare prey (Fig. 3.). Amphipods were consumed frequently by nearly all lake sturgeon but their prey-specific index of food importance was below 10%. In contrast, round goby were consumed by most individuals (90%) and had the highest prey-specific index of importance (74%). Quagga mussels *D. r. bugensis* were consumed heavily by 9% of individuals.

The bi-plot of δ^{13}C and δ^{15}N for lake sturgeon and their prey items showed distinct separation between organismal groups (Fig. 4). For prey species, filter-feeding *D. r. bugensis* had the most negative δ^{13}C value (mean ± 95% CI), -24.0 ± 0.5, (Table 1), whereas, amphipods had the least negative, -20.1 ± 0.4, suggesting greater consumption of benthic food resources than other organisms. Chironomids and oligochaetes had intermediate δ^{13}C values, -21.7 ± 1.3 and -22.0 ± 0.9 respectively, but with large variance. Primary consumers, such as chironomids and oligochaetes, had δ^{15}N values of 7.7 ± 0.5 and 9.1 ± 0.5, respectively. Crayfish (11.2 ± 0.9) and snails (10.6 ± 0.6) occupied intermediate trophic positions. Round goby had the highest δ^{15}N value, 13.2 ± 0.4, of all prey groups and were isotopically positioned just below lake sturgeon tissues. All three lake sturgeon tissues had higher mean δ^{15}N values than the collected prey, with no overlap in their 95% confidence intervals. Fin tissue had the highest δ^{13}C, -18.9 ± 0.1, not only among the tissues, but also compared to sampled prey items. It also had the highest δ^{15}N, 17.0 ± 0.1, with an estimated trophic position of 4.7. Plasma and RBC had similar nitrogen values, 15.6 ± 0.1 and 15.2 ± 0.2, respectively, but differed in their carbon values, -21.7 ± 0.1 and -20.0 ± 0.1, with plasma being more negative.

Generally, the two-element SIAR mixing model estimated that tissues with faster turnover rates (diet integrated over a shorter time scale) had more variable and diverse prey contributions (Fig. 5). Whereas slower turnover rate tissue (fin tissue) was fully explained by round goby which had a median prey proportion of 98.5%, CI = 96.9-99.4%. Round goby also were an important diet component in the two blood tissues (plasma and RBC) albeit to a lesser degree (RBC: 29.4%, CI = 21.1-36.2%; plasma: 37.0%, CI = 24.8-51.3%). All other prey groups had greater representation in the blood tissues relative to their contributions to fin tissue. Amphipods were estimated to be the largest component of the diet in red blood cells (54.3%, CI = 48.8-

59.2%) along with a sizable crayfish contribution (11.6%, CI = 1.6-24.9). Plasma tissue showed the greatest diversity in dietary composition. Most prey groups were represented in plasma including round goby, snails (35.2%, CI = 5.3-54.9%), and mussels (12.5%, CI = 10.0-30.8%). The distinct isotopic signatures and mixing model results of the three lake sturgeon tissues were indicative of differences between short- and long-term diet composition.

Discussion

Adult lake sturgeon caught in the LNR engaged in piscivory to a degree that is unprecedented for the species. Much of the early diet literature on this species, conducted on juvenile or sub-adult individuals, suggests that lake sturgeon are generalist benthic invertivores (Kempinger 1996; Chiasson et al. 1997; Beamish et al. 1998; Nilo et al. 2006). Recent diet studies of adult fish, document higher levels of fish-derived energy than the early literature indicated. One study, conducted by Stelzer et al. (2008) in Lake Winnebago, Wisconsin, found that dead gizzard shad, on average, comprised 56% of the wet mass of stomach contents and 37% of the carbon assimilated. In this case lake sturgeon were taking advantage of an ephemeral food resource by scavenging gizzard shad remains after a winter die-off (Stelzer et al. 2008). In a second study by Smith et al. (2016) in the Rainy River, Ontario, estimated that approximately 40% of adult lake sturgeon diets were derived from fish eggs and <1% from fish (Smith et al. 2016). However, in both of these studies, lake sturgeon were consuming nonmoving, ephemeral prey items, thus exhibiting opportunistic feeding behavior that is more typical of lake sturgeon. In contrast, in the LNR, lake sturgeon are successfully targeting and capturing live round goby. Perhaps the territorial nature of round gobies (Dubs and Corkum 1996) or their naiveté towards this large benthic predator prevents them from fleeing an approaching lake sturgeon. Regardless of the mechanism, it is clear is that this lake sturgeon population has incorporated this new, abundant round goby food resource.

The establishment and subsequent incorporation of round goby into lake sturgeon diet has altered the lake sturgeon trophic position in the LNR. Jacobs et al. (2017) found that lake sturgeon in the LNR reach a higher trophic position (and $\delta^{15}N$) at a younger age and smaller size than they did prior to the appearance of round goby. Further, it appears that lake sturgeon in this population maintain a higher trophic position compared to other systems. The estimated trophic position, using equation (2) from Vander Zanden et al. (1997), of the LNR population, controlling for baseline $\delta^{15}N$ variation, is 4.8. If we apply the same formula to the Smith et al. (2016) study using their mean $\delta^{15}N$ mussel (1.95) and lake sturgeon (9.70) values, it results in a lake sturgeon trophic position of 4.5. In Lake Winnebago, Stelzer et al. (2008) determined that lake sturgeon occupied a trophic position of 3.0. It is likely that these differences are due, in part, to the incorporation of round goby into the diet.

Non-native dreissenid mussels were a small component of the diet of lake sturgeon in the LNR, appearing infrequently in stomach contents. In fact, 97% of the total mass of dreissenids (*n* = 47) was contained within a single stomach sample. In Oneida Lake, NY, dreissenid mussels are a substantial component of lake sturgeon diets, especially among larger (900 mm TL) fish (Jackson et al. 2002). One major difference between these two systems was that round goby was not present in Oneida Lake at the time of the study. It appears that in the LNR, in the presence of abundant round goby and mussel resources, lake sturgeon are preferentially selecting round goby over dreissenid mussels. This is understandable from an energetic standpoint as round goby have a higher energy content than dreissenid mussels (3.2 kJ/g vs 1.7 kJ/g, respectively; Johnson et al. 2005; Madenjian et al. 2006). It will be interesting to see if the diets of lake sturgeon in Oneida Lake will shift to include round goby as that invader becomes more widely established there.

Stomach contents of LNR lake sturgeon illustrate that this population exhibits both a generalized and specialized feeding strategy. Indeed, the cumulative diets of lake sturgeon from the LNR contained numerous species of invertebrates and fish. However, most of these species were rarely found and sometimes comprised only a few individuals. Instead, the predominant feeding strategy in the spring seems to be more specialized, exemplified by the high frequency of occurrence and high prey-specific index of food importance of round goby. This is indicative of a high level of prey selectivity.

The distinct isotopic signatures of the three lake sturgeon tissues and their resultant mixing model outputs suggest differences between the short- and long-term diet compositions. Various tissues in organisms have different turnover rates and tissues with more rapid turnover rates reflect more recent diet history, while those with slower turnover rates reflect longer-term diet history. There is evidence that blood components turn over faster than fin tissue in fish (Suring and Wing 2009). Given this, the signatures of RBC and plasma reflect a more varied diet that incorporates greater diversity of prey groups, especially amphipods, crayfish, snails, and dreissenid mussels. However, for fin tissue, the mixing model attributes >90% of assimilated energy to round goby. Their caloric content, greater relative size, and abundance could account for this outsized contribution. This indicates that although there is continued use of more typical, historical food resources, the current average diet history of lake sturgeon in the LNR is dominated by round goby.

Characterizing the impacts of a non-native species as either wholly positive or negative is reductive and does not adequately represent the complexity of species introductions. Adult lake sturgeon are clearly incorporation round goby, but whether the net impact of round gobies is beneficial to the lake sturgeon population as a whole is unknown. Round gobies have been shown to compete with native fishes for food and habitat resources (Kornis et al. 2012) and can displace and relegate other benthic species to sub-optimal habitat (Balshine et al. 2005). Such competition could affect juvenile lake sturgeon, which use similar food and habitat resources as round goby. Additionally, round gobies are documented predators of the eggs and larvae of larger fish, including lake sturgeon (Kornis et al. 2012). Whether or not round goby limit lake sturgeon recruitment in the LNR is still an open question and one that requires further study.

In conclusion, stomach content and stable isotope analyses both suggest that non-native round goby are the primary source of energy for adult lake sturgeon in the LNR in the spring. This study establishes the current trophic position for lake sturgeon and their prey items in the LNR and can be used as a point of comparison for future studies. Lastly, this work documents a high degree of piscivory by this lake sturgeon population, suggesting that this species is capable of high, local-resource-dependent diet plasticity. Looking forward, as human-mediated species introductions continue globally, it is important to document and evaluate the interaction between non-native species and native species in order to inform conservation management plans that seek to protect native communities and ecosystems.

Acknowledgements

The authors would like to thank Zy Biesinger, Lyubov Burlakova, Shana DiPalma, and many others for their support in the lab and field. Mention of specific products does not constitute endorsement by the U.S. Government. This study was funded by The Niagara River Greenway Ecological Fund, The Great Lakes Restoration Initiative and The Research Foundation of the State University of New York.

References

Amundsen, P.A., Gabler, H.M., and Staldvik, F. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. Journal of fish biology **48**(4): 607-614.

Auer, N.A. 1999. Population characteristics and movements of lake sturgeon in the Sturgeon River and Lake Superior. Journal of Great Lakes Research **25**(2): 282-293.

Balshine, S., Verma, A., Chant, V., and Theysmeyer, T. 2005. Competitive interactions between round gobies and logperch. Journal of Great Lakes Research **31**(1): 68-77.

Beamish, F.W.H., Noakes, D., L. G., and Rossiter, A. 1998. Feeding ecology of juvenile lake sturgeon, *Acipenser fulvescens*, in northern Ontario. Canadian Field-Naturalist **112**(3): 459-468.

Brush, J.M., Fisk, A.T., Hussey, N.E., and Johnson, T.B. 2012. Spatial and seasonal variability in the diet of round goby (*Neogobius melanostomus*): stable isotopes indicate that stomach contents overestimate the importance of dreissenids. Canadian Journal of Fisheries and Aquatic Sciences **69**: 573-586.

Cabana, G., and Rasmussen, J.B. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Science **93**: 10844-10847.

Chiasson, W.B., Noakes, D.L., and Beamish, F.W.H. 1997. Habitat, benthic prey, and distribution of juvenile lake sturgeon (Acipenser fulvescens) in northern Ontario rivers. Canadian Journal of Fisheries and Aquatic Sciences **54**(12): 2866-2871.

Corkum, L.D., Sapota, M.R., and Skora, K.E. 2004. The round goby, Neogobius melanostomus, a fish invader on both sides of the Atlantic Ocean. Biological invasions **6**(2): 173-181.

Costello, M. 1990. Predator feeding strategy and prey importance: a new graphical analysis. Journal of Fish Biology **36**(2): 261-263.

Crane, D.P., Farrell, J.M., Einhouse, D.W., Lantry, J.R., and Markham, J.L. 2015. Trends in body condition of native piscivores following invasion of Lakes Erie and Ontario by the round goby. Freshwater Biology **60**(1): 111-124.

Dietrich, J.P., Morrison, B.J., and Hoyle, J.A. 2006. Alternative ecological pathways in the eastern Lake Ontario food web—round goby in the diet of lake trout. Journal of Great Lakes Research **32**(2): 395-400.

Dubs, D.O., and Corkum, L.D. 1996. Behavioral interactions between round gobies (Neogobius melanostomus) and mottled sculpins (Cottus bairdi). Journal of Great Lakes Research **22**(4): 838-844.

Fry, B. 2006. Stable isotope ecology. Springer Science & Business Media, New York.

German, D.P., and Miles, R.D. 2010. Stable carbon and nitrogen incorporation in blood and fin tissue of the catfish Pterygoplichthys disjunctivus (Siluriformes, Loricariidae). Environmental Biology of Fishes **89**(2): 117-133.

Grigorovich, I.A., Colautti, R.I., Mills, E.L., Holeck, K., Ballert, A.G., and MacIsaac, H.J. 2003. Ballast-mediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses. Canadian Journal of Fisheries and Aquatic Sciences **60**(6): 740-756.

Guilbard, F., Munro, J., Dumont, P., Hatin, D., and Fortin, R. 2007. Feeding ecology of Atlantic sturgeon and lake sturgeon co-occurring in the St. Lawrence estuarine transition zone, American Fisheries Society, p. 85.

Haley, N. 1998. A gastric lavage technique for characterizing diets of sturgeons. North American Journal of Fisheries Management **18**(4): 978-981.

Harkness, W.J.K., and Dymond, J.R. 1961. The lake sturgeon: the history of its fishery and problems of conservation. Fish & Wildlife Branch, Ontario Department of Lands and Forests.

Jackson, J., VanDeValk, A., Brooking, T., VanKeeken, O., and Rudstam, L. 2002. Growth and feeding dynamics of lake sturgeon, Acipenser fulvescens, in Oneida Lake, New York: results from the first five years of a restoration program. Journal of Applied Ichthyology **18**(4□6): 439-443.

Jacobs, G.R., Bruestle, E.L., Hussey, A., Gorsky, D., and Fisk, A.T. 2017. Invasive species alter ontogenetic shifts in the trophic ecology of Lake Sturgeon (Acipenser fulvescens) in the Niagara River and Lake Ontario. Biological Invasions **19**(5): 1533-1546.

Johannsson, O.E., Dermott, R., Graham, D.M., Dahl, J.A., Millard, E.S., Myles, D.D., and LeBlanc, J. 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of Dreissena spp. with implications for fish production. Journal of Great Lakes Research **26**(1): 31-54.

Johnson, T.B., Bunnell, D.B., and Knight, C.T. 2005. A potential new energy pathway in central Lake Erie: the round goby connection. Journal of Great Lakes Research **31**: 238-251.

Kempinger, J.J. 1996. Habitat, growth, and food of young lake sturgeons in the Lake Winnebago system, Wisconsin. North American Journal of Fisheries Management **16**(1): 102-114.

Kornis, M., Mercado□Silva, N., and Vander Zanden, M. 2012. Twenty years of invasion: a review of round goby Neogobius melanostomus biology, spread and ecological implications. Journal of Fish Biology **80**(2): 235-285.

Lodge, D.M. 1993. Biological invasions: lessons for ecology. Trends in Ecology & Evolution **8**(4): 133-137.

Madenjian, C.P., O'Connor, D.V., Pothoven, S.A., Schneeberger, P.J., Rediske, R.R., O'Keefe, J.P., Bergstedt, R.A., Argyle, R.L., and Brandt, S.B. 2006. Evaluation of a lake whitefish bioenergetics model. Transactions of the American Fisheries Society **135**(1): 61-75.

Madenjian, C.P., Stapanian, M.A., Witzel, L.D., Einhouse, D.W., Pothoven, S.A., and Whitford, H.L. 2011. Evidence for predatory control of the invasive round goby. Biological Invasions **13**(4): 987-1002.

Nilo, P., Tremblay, S., Bolon, A., Dodson, J., Dumont, P., and Fortin, R. 2006. Feeding ecology of juvenile lake sturgeon in the St. Lawrence River system. Transactions of the American Fisheries Society **135**(4): 1044-1055.

Parnell, A., and Jackson, A. 2013. Stable isotope analysis in R [online]. R package version 4.2.Available from https://cran.r-project.org/web/packages/siar/index.html [accessed 31 March 2016.

Perga, M.E., and Gerdeaux, D. 2005. 'Are fish what they eat' all year round? Oecologia **144**(4): 598-606.

Peterson, D.L., Vecsei, P., and Jennings, C.A. 2007. Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Reviews in Fish Biology and Fisheries **17**(1): 59-76.

Pikitch, E.K., Doukakis, P., Lauck, L., Chakrabarty, P., and Erickson, D.L. 2005. Status, trends and management of sturgeon and paddlefish fisheries. Fish and Fisheries **6**(3): 233-265.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology **83**(3): 703-718.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montana, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia **152**(1): 179-189.

Ray, W.J., and Corkum, L.D. 1997. Predation of zebra mussels by round gobies, Neogobius melanostomus. Environmental Biology of Fishes **50**(3): 267-273.

Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an" invasional meltdown" occurring in the Great Lakes? Canadian journal of fisheries and aquatic sciences **58**(12): 2513-2525.

Rounick, J., and Winterbourn, M. 1986. Stable carbon isotopes and carbon flow in ecosystems. BioScience **36**(3): 171-177.

Smith, A., Marty, J., and Power, M. 2015. Non-lethal sampling of lake sturgeon for stable isotope analysis: comparing pectoral fin-clip and dorsal muscle for use in trophic studies. Journal of Great Lakes Research **41**(1): 292-297.

Smith, A., Smokorowski, K., Marty, J., and Power, M. 2016. Stable isotope characterization of Rainy River, Ontario, lake sturgeon diet and trophic position. Journal of Great Lakes Research.

Steinhart, G.B., Stein, R.A., and Marschall, E.A. 2004. High growth rate of young-of-the-year smallmouth bass in Lake Erie: a result of the round goby invasion? Journal of Great Lakes Research **30**(3): 381-389.

Stelzer, R.S., Drecktrah, H.G., Shupryt, M.P., and Bruch, R.M. 2008. Carbon sources for lake sturgeon in Lake Winnebago, Wisconsin. Transactions of the American Fisheries Society **137**(4): 1018-1028.

Suring, E., and Wing, S.R. 2009. Isotopic turnover rate and fractionation in multiple tissues of red rock lobster (Jasus edwardsii) and blue cod (Parapercis colias): consequences for ecological studies. Journal of Experimental Marine Biology and Ecology **370**(1): 56-63.

Thomas, M.V., and Haas, R.C. 1999. Capture of lake sturgeon with setlines in the St. Clair River, Michigan. North American Journal of Fisheries Management **19**(2): 610-612.

Truemper, H.A., Lauer, T.E., McComish, T.S., and Edgell, R.A. 2006. Response of yellow perch diet to a changing forage base in southern Lake Michigan, 1984-2002. Journal of Great Lakes Research **32**(4): 806-816.

Vander Zanden, M.J., Cabana, G., and Rasmussen, J.B. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (delta N-15) and literature dietary data. Canadian Journal of Fisheries and Aquatic Sciences **54**(5): 1142-1158.

Vander Zanden, M.J., Casselman, J.M., and Rasmussen, J.B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature **401**(6752): 464-467.

Vanderklift, M.A., and Ponsard, S. 2003. Sources of variation in consumer-diet delta 15N enrichment: a meta-analysis. Oecologia **136**(2): 169-182.

Table 1.
Mean values ± 95% confidence intervals of $\delta^{13}C$ and $\delta^{15}N$ (‰) of lake sturgeon tissues and prey groups.

Prey groups	*n*	$\delta^{13}C$	$\delta^{15}N$	Trophic Position
Amphipoda	15	-20.1 ± 0.4	8.2 ± 0.2	1.9
Chironomidae	10	-21.7 ± 1.3	7.7 ± 0.5	1.7
Crayfish	5	-20.6 ± 0.7	11.2 ± 0.9	2.9
Lake sturgeon fin	175	-18.9 ± 0.1	17.0 ± 0.1	4.8
Lake sturgeon RBC	130	-20.0 ± 0.1	15.0 ± 0.2	4.1
Lake sturgeon plasma	153	-21.7 ± 0.1	15.6 ± 0.1	4.3
D. r. bugensis	13	-24.0 ± 0.5	8.6 ± 0.2	2.0
Oligochaeta	14	-22.0 ± 0.9	9.1 ± 0.5	2.2
Round goby	6	-20.4 ± 0.5	13.2 ± 0.4	3.5
Snails	13	-22.6 ± 0.8	10.6 ± 0.6	2.7

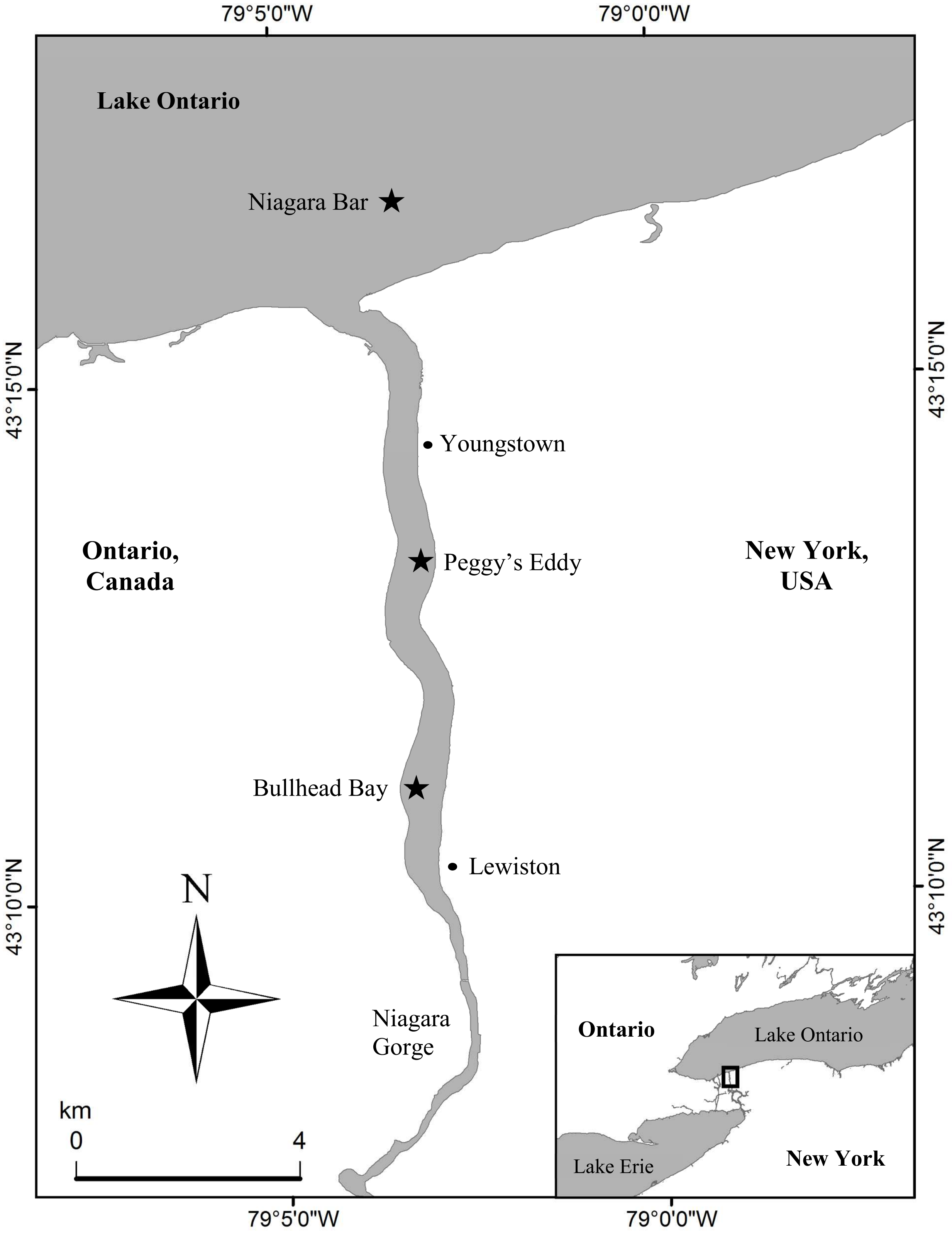
Fig. 1. Study area and fish collection locations (indicated by the stars) on the lower Niagara River, NY, USA.

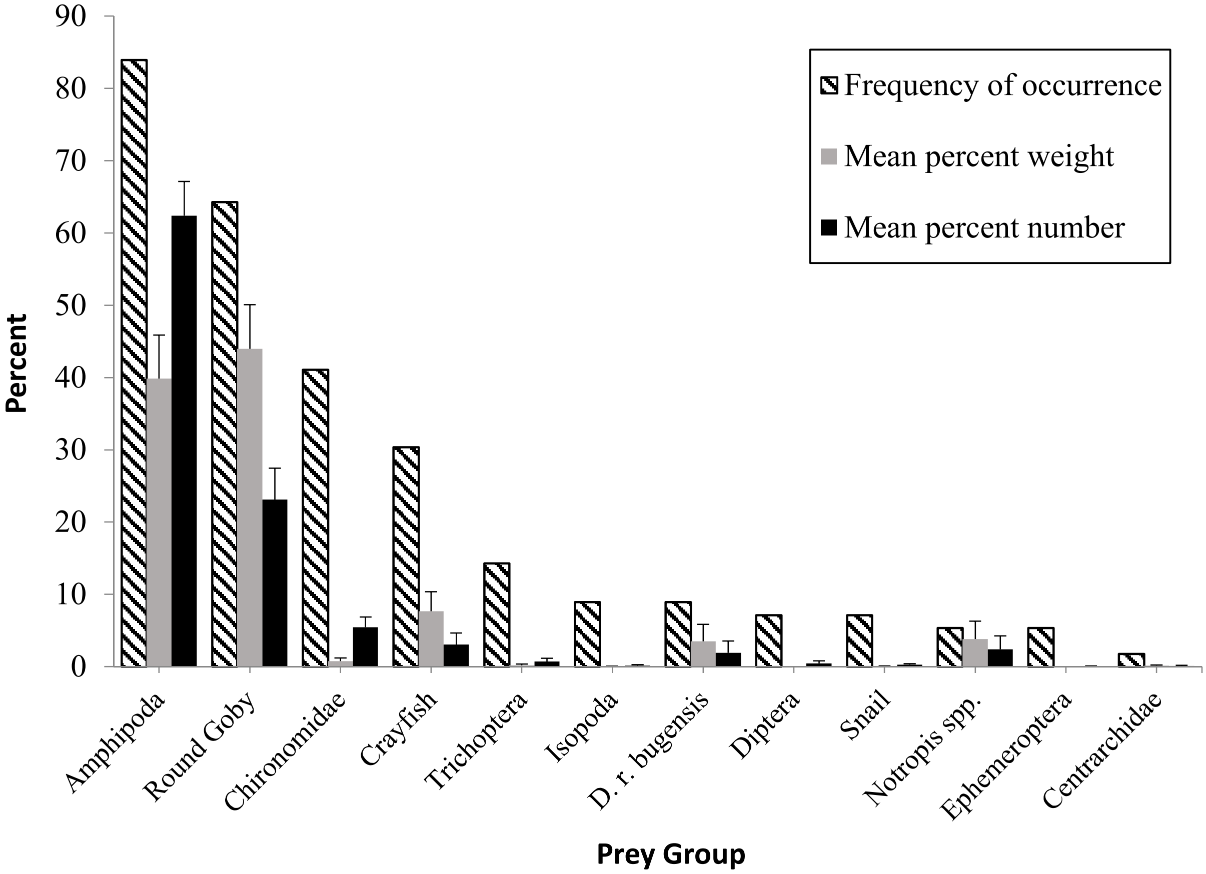
Fig. 2. Percent frequency of occurrence, mean (± SE) percent weight and percent number (calculated for each stomach then averaged for each prey group) of prey items found in the stomachs of adult lake sturgeon (n = 56, excluding empty stomachs) captured from the lower Niagara River, NY.

Fig. 3. Feeding strategy diagram (Costello 1990; Amundsen et al. 1996) of adult lake sturgeon diet plotting prey-specific abundance against frequency of occurrence, where prey-specific abundance is defined as the proportion by weight that prey *i* constitutes of all prey weight in only stomachs that contained that prey *i*. Dominant prey groups occur in the upper right quadrant and rarer prey groups towards the lower left. Prey groups near the origin are: EPH = ephemeroptera, GAS = gastropoda, ISO = isopoda.

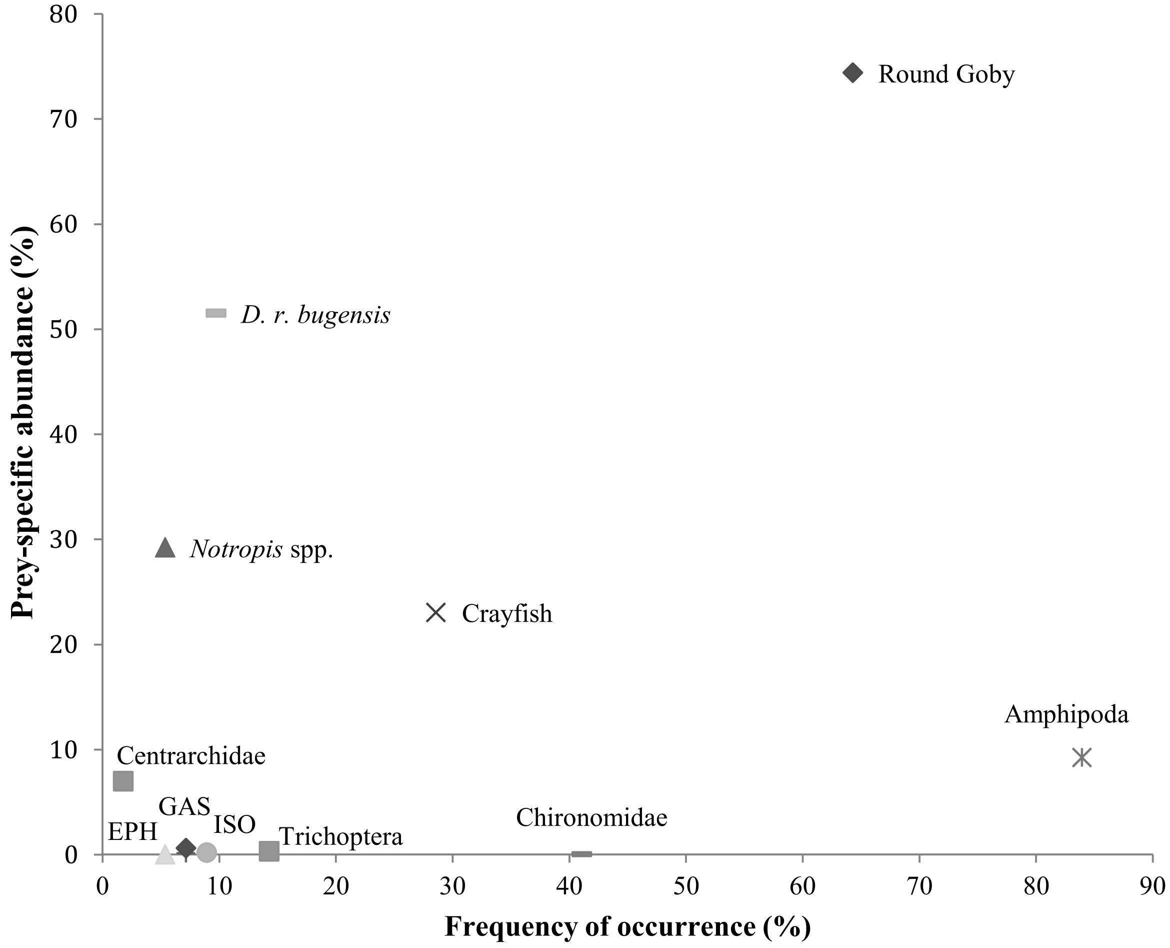
Fig. 4. Mean values and 95% confidence intervals of δ^{15}N and δ^{13}C (‰) in lake sturgeon fin, red blood cell (RBC), plasma tissue, and prey sources. Values are not adjusted for trophic shift.

Fig. 5. SIAR mixing model boxplots of the contributions of different prey items to the diets of adult lake sturgeon reflected in fin, red blood cell, and plasma tissue. The boxplot shading shows credibility intervals at the 95, 75, and 50% levels.

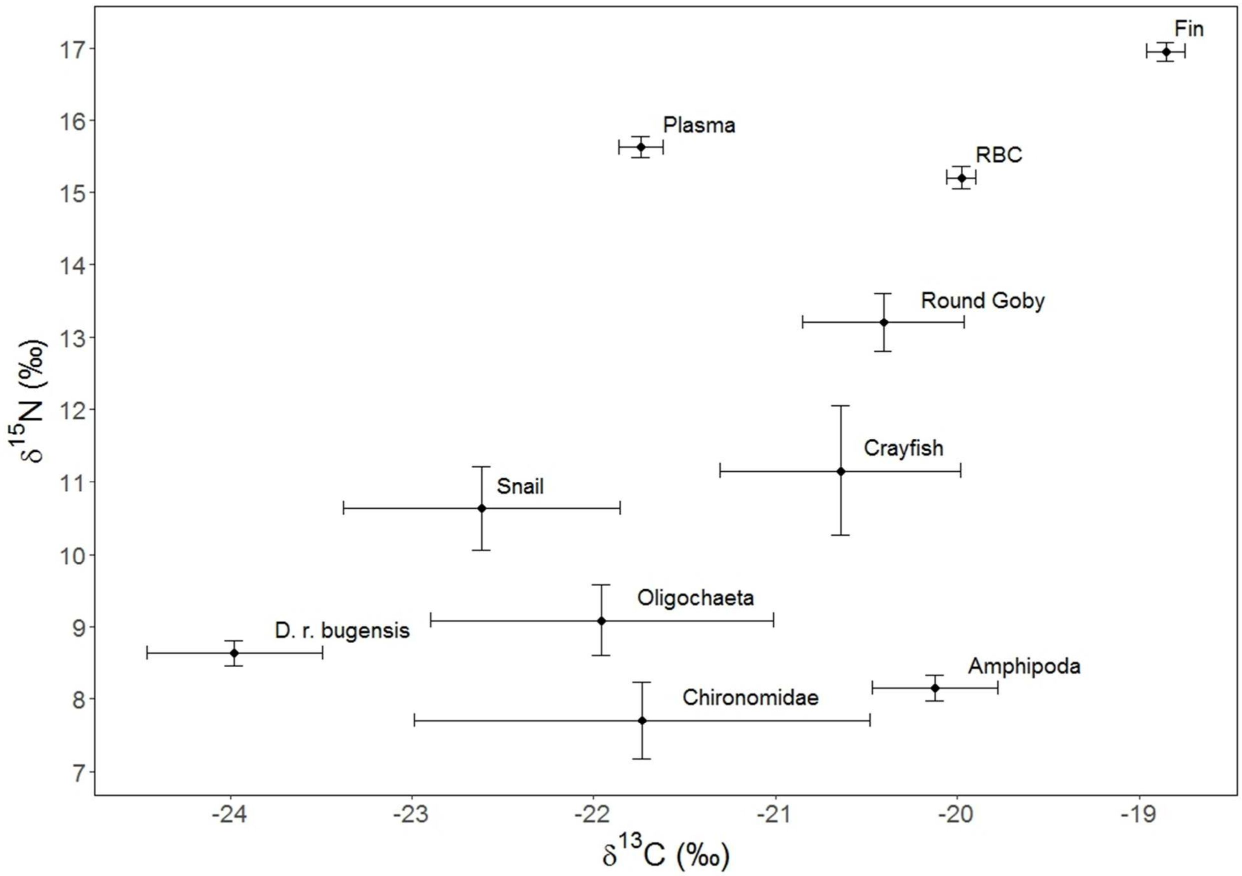

79°5'0"W
79°0'0"W
Lake Ontario
Niagara Bar
43°15'0"N
Youngstown
Ontario, Canada
Peggy's Eddy
New York, USA
Bullhead Bay
Lewiston
43°10'0"N
N
Niagara Gorge
km
0
4
Ontario
Lake Ontario
Lake Erie
New York


Percent
90
80
70
60
50
40
30
20
10
0
▨ Frequency of occurrence
■ Mean percent weight
■ Mean percent number
Amphipoda
Round Goby
Chironomidae
Crayfish
Trichoptera
Isopoda
D. r. bugensis
Diptera
Snail
Notropis spp.
Ephemeroptera
Centrarchidae
Prey Group

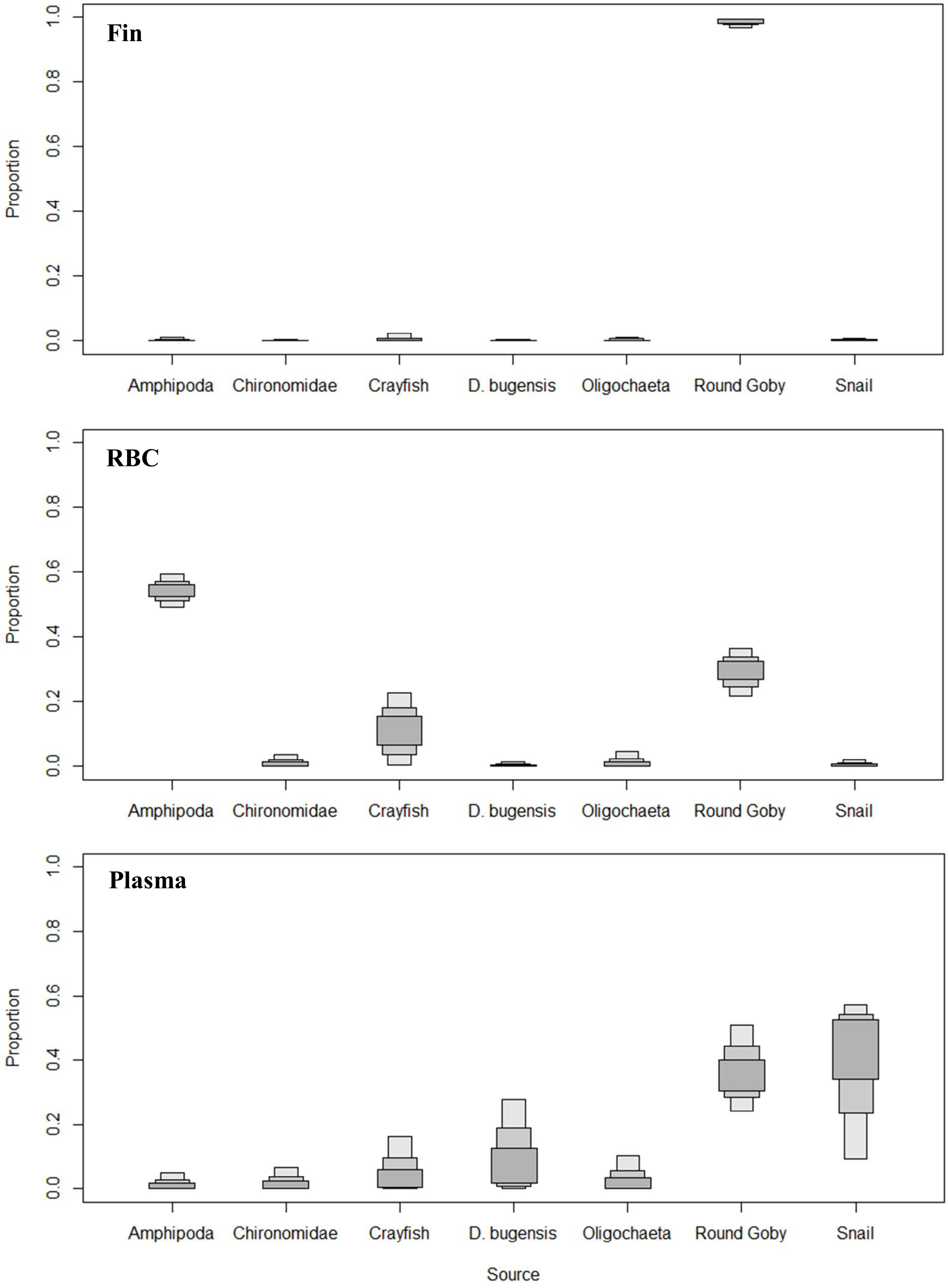
503


80
70
60
50
40
30
20
10
0
Prey-specific abundance (%)
Round Goby
D. r. bugensis
Notropis spp.
Crayfish
Amphipoda
Centrarchidae
GAS
EPH
ISO
Trichoptera
Chironomidae
0
10
20
30
40
50
60
70
80
90
Frequency of occurrence (%)

504


δ^{15}N (‰)
δ^{13}C (‰)
17
16
15
14
13
12
11
10
9
8
7
-24
-23
-22
-21
-20
-19
Fin
Plasma
RBC
Round Goby
Crayfish
Snail
Oligochaeta
D. r. bugensis
Amphipoda
Chironomidae

505


Fin
Proportion
0.0
0.2
0.4
0.6
0.8
1.0
Amphipoda
Chironomidae
Crayfish
D. bugensis
Oligochaeta
Round Goby
Snail
RBC
Proportion
0.0
0.2
0.4
0.6
0.8
1.0
Amphipoda
Chironomidae
Crayfish
D. bugensis
Oligochaeta
Round Goby
Snail
Plasma
Proportion
0.0
0.2
0.4
0.6
0.8
1.0
Amphipoda
Chironomidae
Crayfish
D. bugensis
Oligochaeta
Round Goby
Snail
Source