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Lake Sturgeon (*Acipenser fulvescens*) Trophic Position and Movement Patterns in the Lower Niagara River, NY

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Lake sturgeon (*Acipenser fulvescens*) trophic position and movement patterns in the lower Niagara River, NY

by

Eric Bruestle

An Abstract of a Thesis

in

Great Lakes Ecosystem Science

Submitted in Partial Fulfillment

of the Requirements for the Degree of

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College at Buffalo

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ABSTRACT OF THESIS

Lake sturgeon *Acipenser fulvescens* were once widely distributed throughout the Laurentian Great Lakes. However, widespread overharvest and habitat degradation has diminished their numbers. The lower Niagara River, NY contains one of the few remaining recovering populations of lake sturgeon in New York State. The goal of this study was to characterize the trophic position of lake sturgeon in the context of an invasive species dominated food web and to describe their movement patterns and residency within the lower Niagara River. Stomach content analysis and stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope analysis of tissue was used to quantify trophic position. Acoustic telemetry was used to assess movement and residency. Sampled lake sturgeon exhibited a high degree of piscivory not seen in other Great Lakes' populations. Stomach content and stable isotope analysis showed that sturgeon diet primarily consisted of invasive species, particularly the invasive round goby *Neogobius melanostomus*. Stable isotope analysis revealed that long-term average diet was dominantly round goby but short-term diet contained a varied group of benthic macroinvertebrates. Tracked lake sturgeon showed seasonal river residency, with most fish entering in the spring, staying through the summer, and then leaving for Lake Ontario in the winter. Tagged individuals congregated in the highest numbers just outside the mouth of the river in the summer and fall. The findings of this study are valuable to management plans that seek to protect this recovering population.

State University of New York

College at Buffalo

Great Lakes Center, Program in Great Lakes Ecosystem Science

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Lake Sturgeon in the Niagara River

Introduction

Native fish species have declined globally as a consequence of disturbances such as habitat destruction, pollution, and invasive species (Helfman 2007). In the North American Laurentian Great Lakes, native species richness has dropped from 169 to 148 and, of those, 82 species are classified as threatened or endangered (Mandrak and Cudmore 2010). Some threats to native fish biodiversity, like overharvest, respond well to conservation and management actions. However, habitat loss and degradation are more persistent and may worsen with climate change, human population growth, and increased globalization. Managing and conserving native species in the face of anthropogenic development is a daunting challenge and there are few places on Earth that better exemplify the interaction of human society and natural ecosystems better than the Great Lakes.

Some of the most developed areas in the basin lay along a series of large rivers that link the Great Lakes together. Known as connecting channels, these are the St. Mary's River, the St. Clair River, the Detroit River, the Niagara River, and the St. Lawrence River. Unlike other rivers they do not have headwaters or tributaries in the traditional sense, but rather flow from one large lake to the next. All of these rivers suffer from numerous anthropogenic disturbances. Dense human populations draw water for industrial, hydro-electric, municipal, and agricultural uses. They are also impacted by aquatic invasive species that spread through human-mediated introductions, such as ballast water from shipping. Under the Great Lakes Water Quality Agreement, each of the connecting channels along with several other areas were designated Great Lakes Areas of Concern (AOC) with beneficial use impairments (BUI) as a consequence of the degraded habitats and loss of ecological function (IJC 2012). These impairments

compromise the chemical, physical, or biological integrity of the AOC. Each AOC has its own suite of BUIs out of 14 possible BUIs. They cover a wide range of detriments that affect not only fish and wildlife populations, but also human enjoyment of the resource. Recently restoration efforts have been put forth to rehabilitate the ecological integrity of these areas for the purpose of, among other things, restoring fish and wildlife habitat and reviving native fish populations. One reason for this is because large river spawning fish such as, lake whitefish *Coregonus clupeaformis*, walleye *Sander vitreus*, cisco *Coregonus artedi*, and lake sturgeon *Acipenser fulvescens*, have (or had) substantial economic and ecological value. The restoration of native fish populations is one step along the path to delisting Great Lakes connecting channels as areas of concern.

Fishes of commercial or recreational importance are often priority targets for restoration and, historically, few fisheries were as valuable as lake sturgeon. Lake sturgeon are a large, long-lived, benthic species whose abundance has declined drastically since colonial times (Pikitch et al. 2005, Hayes and Caroffino 2012). Prior to European settlement, lake sturgeon populations, estimated to be in the millions, were located in the Mississippi, Hudson Bay and Great Lakes watersheds, making it one of the most widely distributed freshwater fish in North America (Harkness and Dymond 1961, Scott and Crossman 1973, Priegel et al. 1974). However, beginning in the 19th century, overharvest, habitat loss, and declining water quality led to the extirpation or collapse of many of these populations, including in the Great Lakes (Harkness and Dymond 1961, Auer 1999, Pikitch et al. 2005). Today, lake sturgeon are listed as endangered, threatened, or of special concern in seven of the eight Great Lakes states (Léonard et al. 2004). Few remnant populations persist and large populations remain scarce. Despite low abundance,

there are indications that lake sturgeon populations may be recovering thanks to water quality improvements, conservation, and restoration efforts (Wilson and Mckinley 2004).

Like other connecting channels, the Niagara River was home to an abundant lake sturgeon population that supported subsistence, recreational, and commercial fisheries. Early records indicate an annual harvest of 14,000 kg in 1900 had dwindled to 2,100 kg by 1930 (Carlson 1995). A 1928 biological survey of the Erie-Niagara River system conducted by New York State Department of Conservation reported that lake sturgeon were rarely found, fished to a limited extent, and advised a complete fishing ban (Greeley 1928). Downstream of Niagara Falls, incidental catches of lake sturgeon continued through the 1940s and 1950s, indicating that some remnant population persisted (Aug 1992). This was confirmed by Hughes et al. (2005) who found that although population abundance was low, historically speaking, the presence of ripe males and juveniles indicated that spawning and recruitment were still occurring in the river. The most recent population assessment found the population continues to recover and is dominated by a cohort with high somatic growth rates and is nearing reproductive maturity (Biesinger 2014).

The Niagara River was designated an AOC in 1987, with 7 BUIs as a result of its long industrial history (IJC 2012). These include restrictions on fish consumption, fish deformations, degraded benthos, loss of fish habitat, degradation of fish populations, and others (NYSDEC 2012). Owing to its close proximity to Buffalo, NY, the river ranks second among connecting channels in terms of urban and agricultural land use and has the third highest adjacent human population in the Great Lakes (Roseman et al. 2014). There are also two superfund sites, hazardous waste sites, and a whole host of metals and cyanides residing in the bottom sediments

(EPA 2015). Greater knowledge of the requirements of native fish species is needed in order for restoration projects to effectively address BUIs.

This study characterizes movement and feeding ecology of a remnant lake sturgeon population in the lower Niagara River. Recovering lake sturgeon populations present fantastic research opportunities which were previously impossible due to the scarcity of wild fish (Peterson et al. 2007). Known gaps in knowledge about the movement patterns, food preferences, as well as the role of lake sturgeon in food webs can now be addressed with appropriate sample sizes. Migration patterns in the literature are linked to spawning behavior (Auer 1999), but seasonal movements and residency is less well understood. Lake sturgeon likely congregate in locations with a beneficial mix of good habitat characteristics and plentiful food resources and a combination of abiotic factors such as depth, substrate, and flow. By identifying and characterizing these areas, we can gain a deeper understanding of lake sturgeon habitat and dietary requirements to focus protection efforts. This could include protecting certain stretches of river during particular times or protecting benthic energy pathways utilized by lake sturgeon. However, the latter becomes a quandary in invaded ecosystems like the Great Lakes, where such pathways have been usurped by exotic species.

A better understanding of habitat preferences would inform the restoration of degraded habitat and the conservation of critical areas. Additionally, the impact of exotic species introductions or disturbances to the lake sturgeon food base could be quantified with a clearer description of their position in the food web and preferred prey. Given that many threats to lake sturgeon still persist, filling these knowledge gaps is vital for a sustained recovery. This study seeks to address these gaps through the completion of two objectives: (1) document lake

sturgeon diet and trophic position by stomach content and stable isotope analyses and (2) identify residency, movements, and home ranges of lake sturgeon using acoustic telemetry.

Diet and trophic position

This study employed two methods to assess the diet of lake sturgeon: stomach content analysis (SCA) and stable isotope analysis (SIA). These two methods are often used in tandem because they complement each other in several ways. First, whereas SCA provides a snapshot of most recent diet history, material ingested within the last few hours, SIA can estimate diet over longer time-scales depending on the tissues sampled. Second, SIA provides an estimate of the relative contributions of various prey to the diet but needs to be evaluated and verified by the direct observation and identification provided by SCA. Third, SCA through gastric lavage can be constrained by the prevalence of empty stomachs and may not remove every diet item in the stomach. SIA can provide diet information in cases where stomach contents could not be obtained and only takes into account material that is actually assimilated into tissue, not merely ingested. These two techniques characterize separate aspects of diet history and thus, when used concurrently, provide a more complete picture of feeding ecology.

The analysis of ^{13}C and ^{15}N stable isotopes is commonly used in ecological studies to determine the carbon and nitrogen sources of consumers (Fry 2006). The isotopic make-up of tissues is often expressed in delta notation (1), which compares the ratios of isotopes of a sample to a laboratory standard.

$$\delta = \left(\frac{\left[\frac{\#\,\text{atoms}\ rare}{\#\,\text{atoms}\ abundant} \right]_{sample}}{\left[\frac{\#\,\text{atoms}\ rare}{\#\,\text{atoms}\ abundant} \right]_{standard}} - 1 \right) \times 1000 \quad (1)$$

The $\delta^{13}C$ and $\delta^{15}N$ values of a consumer represent the time-integrated contributions of all its food sources. Comparing the ratios of these isotopes in prey items versus consumers can be used

estimate the relative contributions of different prey items to the diet (Fry 2006). Simply put, the $\delta^{13}C$ and $\delta^{15}N$ signature of a consumer is a mixture of all its prey's signatures and thus a reflection of its diet.

Trophic position, a measure of the role a consumer plays in the food web or ecosystem relative to primary producers, can be ascertained through stable isotope analysis (Post 2002). As $\delta^{15}N$ is assimilated into the tissues of a consumer, it becomes enriched in a step-wise manner, known as trophic enrichment factor (TEF), which is informative about its feeding ecology. For nitrogen, this enrichment occurs during metabolism and excretion where the lighter nitrogen isotope, ^{14}N, is lost at a faster rate than ^{15}N, leaving the consumer with a slightly higher $\delta^{15}N$ value relative to its diet (Fry 2006). This regular, step-wise enrichment of ^{15}N between trophic levels is estimated at 2.2-3.2‰ (Minagawa and Wada 1984, Vander Zanden and Rasmussen 2001) and can be used to calculate trophic position. It is important to establish the trophic position of native species as a reference point because ecological perturbations, such as exotic species introductions, can change native food webs, cause shifts in diet, and change the trophic position of consumers, e.g. lowered trophic position corresponding with a shift from piscivory to invertivory (Vander Zanden et al. 1999). Changes in trophic position are less likely to occur in stable, undisturbed ecosystems. Therefore, shifts in the trophic position of threatened species like lake sturgeon could have important implications for population sustainability and recovery.

Compared to nitrogen, $\delta^{13}C$ moves through food chains with little alteration (Rounick and Winterbourn 1986). Often, consumers are enriched an average of 1‰ relative to their diet, perhaps due to the respiration of carbon dioxide that is ^{13}C-depleted compared to the animal's tissues (DeNiro and Epstein 1978). As a result, $\delta^{13}C$ is not used for trophic positioning but rather

identifying which parts of an ecosystem serve as carbon sources, for example, terrestrial or aquatic carbon sources.

The analysis of tissues with different turnover rates allows for the characterization of diet over various time scales based on how quickly food is assimilated into tissue. Tissues with quick turnover, like blood, liver, and gonads, will be isotopically similar to food sources ingested over a short time interval (Perga and Gerdeaux 2005). Within whole blood, the plasma component has a quicker turnover rate than red blood cells (RBC) in fish (German and Miles 2010, Matley et al. 2016). Tissue such as bone, muscle, and fin, reflect the isotopic composition of the diet over a longer time scale. Fin tissue has a slower turnover rate than blood (Suring and Wing 2009) and would reflect the isotopic composition of the diet over a longer time scale (Perga and Gerdeaux 2005). Through the use of different tissues it is possible to track changes in diet and estimate the relative contributions of food sources to a consumer's diet on a seasonal basis.

Movement and habitat use

Acoustic telemetry, the transmission of ultrasonic signals for the purposes of tracking the movements of tagged aquatic animals, is increasingly common in ecological studies (Heupel et al. 2006a, Kessel et al. 2014, Crossin et al. 2017). This technology is suited to organisms that can be fitted with transmitters without significant behavioral alteration. These transmitters output ultrasonic signals that travel through water and are detected by hydrophones (receivers) that log the time, unique ID of the tag, and depending on the tag, depth or temperature sensor information. Receivers can be portable or stationary. Portable receivers are used for actively tracking tagged individuals from a boat and can provide very accurate position estimation. Stationary receivers are deployed in an array configuration that can vary depending on the type

of study. Passive arrays provide less accurate position information, but collect vastly more data, including seasonal patterns, as they can track individuals continuously throughout the year.

To achieve finer-scale position estimates with a passive array, receivers are placed in close proximity so that there is continuous or even overlapping coverage. Positioning error is reduced when tags are detected by more than one receiver simultaneously. In these cases, fish location can be estimated as a center of activity (COA), or the centroid of an area the fish occupied within a period of time. The calculation of COAs is reliant upon the assumption that detection probability is inversely proportional to the distance between tag and receiver, i.e. receivers closest to the tag will have more detections than more distant receivers. Our COA estimates are based upon a method that averages the latitude and longitude of receivers weighted by the number of detections logged within a given time interval (Simpfendorfer et al. 2002). An additional normal distribution weighting scheme was applied, giving greater weight to detections near the center of the time window (Hedger et al. 2008). Using this method it is possible to generate position estimates at a finer scale.

The telemetry portion of this project builds and expands upon previous telemetry work done in the lower Niagara River. Hughes (2002) used acoustic telemetry to actively track lake sturgeon as they moved throughout the river and up to 5 km into Lake Ontario. Starting in 2011, The U.S. Fish & Wildlife Service conducted radio tracking of lake sturgeon to document spawning behaviors. However, it was limited to much larger scales, i.e. sections of the river, lacked the capability to track the vertical movements of tagged fish, and was temporally limited even though some fish were evidently remaining in the river throughout the year. The radio tracking was supplanted by the current project, which seeks to address gaps left unanswered by the previous telemetry studies.

Lake sturgeon populations across the Great Lakes are in different states of recovery. Some populations like those found in Lake Winnebago, the St. Clair River, and the St. Lawrence River are further along in their rehabilitation. The lower Niagara River supports a remnant population that is still in its initial stages of recovery. This means there are many questions about how this population utilizes the habitat and prey resources of this river and if that differs from other populations. Restoration projects should be tailored to address the specific needs and limiting factors present in the ecosystem. Insight into preferred habitat types and areas could direct habitat restoration efforts by identifying areas of high use to serve as models for habitat projects. Tracking lake sturgeon movements will also help locate habitats that are in need of greater protections and the times of year when lake sturgeon are most vulnerable to perturbations. Additionally, identifying the prey base is a step towards determining if and when food resources will limit population growth and the carrying capacity of the system. A robust population of lake sturgeon is ecologically important to the resilience of the lower Niagara River system, especially if they depredate exotic species. Thus, they serve not only as biological control for already established species, but also towards warding off future invaders.

Novel Trophic Interaction Between Lake Sturgeon (*Acipenser fulvescens*) and Invasive Species in an Altered Food Web

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 threatened species in many U.S. states and Canadian provinces (Peterson et al. 2007). Factors implicated in this decline include over harvest, habitat loss/degradation, and poor water quality (Harkness and Dymond 1961, Auer 1999, Pikitch et al. 2005). The scarcity of wild lake sturgeon across their range hindered early research efforts and compromised management but understanding of the species increased as populations have begun to recover (Peterson et al. 2007). Despite our increased knowledge of this species, data gaps still remain with regards to its feeding ecology, as it has been noted that their diet can be quite variable across their range and that diet characteristics from one system may not be transferable to another (Pollock et al. 2015). For this reason, and to more effectively protect and manage this threatened species, it is critical to understand the role of lake sturgeon in localized food webs and to describe the energy pathways they utilize.

Lake sturgeon are often characterized as generalist benthic feeders that consume mostly invertebrates and some fish with a diet that can vary greatly from system to system including within the Great Lakes basin (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). In Lake Winnebago, WI, for instance, Gizzard Shad *Dorosoma cepedianum* represented 55% of the wet mass of lake sturgeon diets (Stelzer et al. 2008) whereas, in Oneida Lake, NY, Jackson et al. (2002) found that amphipods and zebra mussels *Dreissena polymorpha* constituted the largest portion of their diet. Many previous diet studies focused exclusively on juveniles and determined that they feed

primarily on benthic invertebrates and zooplankton (e.g. Kempinger 1996, Chiasson et al. 1997, Beamish et al. 1998, Nilo et al. 2006). However, these findings may not be representative of adult diets as there is some evidence of an ontogenetic shift in lake sturgeon diet with larger individuals tending to be more piscivorous (Stelzer et al. 2008) or feeding more heavily upon invasive zebra mussels (Jackson et al. 2002).

The establishment of invasive species can have variable and unpredictable consequences on native species and ecosystems (Lodge 1993). Invaders can modify ecosystems (e.g. altering physical resources, biogeochemical cycling, energy flow) and food web structure (Baxter et al. 2004) resulting in cascading trophic effects on native biota (Crooks 2002). However, invasive species and their ecological effects are not singularly detrimental but instead more nuanced and multifaceted. These species may fill vacant niches and support food webs by creating alternative energetic pathways that reconnect previously degraded trophic links (Johnson et al. 2005, Dietrich et al. 2006). Greater knowledge of food web structure and the roles of native organisms therein is crucial to understand and foresee the outcomes of species introductions (Vander Zanden et al. 1999).

The Laurentian Great Lakes have an extensive and well-documented history of human-mediated species invasions (Ricciardi 2001, Grigorovich et al. 2003). Perhaps the most notable of which is the invasion by the dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) from the Ponto-Caspian region in the late 1980s (Griffiths et al. 1991). After their establishment, pelagic production was rerouted into *Dreissena* biomass via filtration of particulate organic carbon and sequestered in the benthos, unavailable to all but a few native mussel predators (Johannsson et al. 2000). That is, until the arrival of another Ponto-Caspian species, the round goby (*Neogobius melanostomus*) which feed on a diversity of benthic

invertebrates including amphipods, chironomids, crayfish, mayflies, isopods, fish eggs and larvae, and at larger sizes (>7 cm), dreissenid mussels (Ray and Corkum 1997, Corkum et al. 2004, Brush et al. 2012). The first sighting in the Great Lakes basin was in the St. Clair River in 1990 by Jude et al. (1992) followed by observations in Lakes Huron, Ontario, Erie, and Michigan. Since then, trends in goby abundance varied from lake to lake and from year to year in the Great Lakes. In Lake Ontario, the first reported sighting was near the Welland Canal in 1998 but substantial catches in bottom trawl surveys did not occur until 2003, before peaking in 2008 (Gorman and Weidel 2016). From 2014 to 2015, the years of this study, goby abundance in Lake Ontario increased from 11% to 68% of the peak abundance attained in 2008 (Gorman and Weidel 2016). This underscores that round goby continues to be a firmly established and important part of the Lake Ontario food web.

The invasion of round goby has had varying effects on the native biota of the Great Lakes. Gobies can disrupt benthic food webs by competing with native benthic fish species such as Mottled Sculpin *Cottus bairdi* (Janssen and Jude 2001) and by limiting fish recruitment through egg predation (Steinhart et al. 2004a). Conversely, it is becoming increasingly evident that round goby constitute a growing portion of the diets of many piscivorous native fishes such as Burbot *Lota lota* (Madenjian et al. 2011), Lake Trout *Salvelinus namaycush* (Dietrich et al. 2006), Smallmouth Bass *Micropterus dolomieu* (Steinhart et al. 2004b), and Yellow Perch *Perca flavescens* (Truemper et al. 2006). In this respect, gobies may constitute a new energy pathway for some native fish species by facilitating the transfer of energy from benthos to top predators (Johnson et al. 2005, Dietrich et al. 2006). There could be considerable benefits, e.g. increased body condition (Crane et al. 2015), conferred to native fish species that are able to take advantage of this mobilized energy which would have otherwise been sequestered in the benthos.

It is important to describe the position of lake sturgeon in the lower Niagara River food web because it is key to understanding how this population is influenced by a changing prey base, and how it may respond to future species invasions (Vander Zanden et al. 1999). Also, by establishing current isotopic values for lake sturgeon and their prey, future changes in trophic position or shifts in carbon sourcing in lake sturgeon could be detected, perhaps indicating a response to invasive species establishments or anthropogenic disturbances, or even changes in the health or recovery status of the population. 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 it's response to invasive species introductions (Vander Zanden et al. 1999).

Stable isotope analysis (SIA) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes of tissues is a commonly used technique for assessing feeding ecology and long-term diet history of organisms (Fry 2006). In animals, heavy isotopes of these elements are accumulated (or fractionated) in predictable ways between prey sources and predators, allowing analysis of feeding ecology and feeding location. The fractionation of $\delta^{13}C$ between predators and prey is used to examine habitat use and describe migration patterns whereas, $\delta^{15}N$ has been used to examine diet, feeding ecology, food web ecology and trophic position; most studies assume that $\delta^{15}N$ increases 3.2 ‰ and $\delta^{13}C$ increases 1.0 ‰ between trophic levels (Minagawa and Wada 1984, Vander Zanden and Rasmussen 2001). This step-wise enrichment of elements, the trophic enrichment factor (TEF), is used to calculate trophic level. However, TEFs can vary among species and even individuals based on factors such as diet quality, tissue type, growth, and temperature (Matley et al. 2016). The application of inappropriate TEFs to stable isotope data can have profound impacts on results and interpretations and therefore must be carefully considered. Properly

applied, stable isotope analysis can estimate the relative contributions of prey to the diet of lake sturgeon by comparing the stable nitrogen and carbon isotopic signatures of predator and prey.

Stable isotope analysis can also characterize consumer diet at various time scales through the examination of multiple tissue types. Food is assimilated into tissue not only according to specific TEFs but also at a rate that is dictated by tissue-turnover rate. Tissues with quick isotopic turnover, like blood, liver, and gonads, will be more isotopically similar to food sources ingested more recently (Perga and Gerdeaux 2005). Within whole blood, the plasma component has a quicker turnover rate than red blood cells (RBC) in fish (German and Miles 2010, Matley et al. 2016). Fin tissue has a slower turnover rate than blood (Suring and Wing 2009) and would reflect the isotopic composition of the diet over a longer time scale (Perga and Gerdeaux 2005). Through the analysis of different tissues it is possible to track changes in diet on a seasonal basis.

A complementary method of diet characterization to SIA is stomach content analysis (SCA), providing a snapshot of the most recent diet, representing material ingested within the last few hours. SCA also can provide species specific information on diet, without assumptions of isotope dynamics and informs which prey items should be sampled for SIA. It is recommended that these two techniques be coupled, as they characterize distinct aspects of diet history and thus, when used concurrently, provide a more complete picture of feeding ecology. Through the characterization of lake sturgeon feeding ecology in an invaded system, this study seeks to broaden the concept 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 use SIA and SCA to document (1) the short- and long-term diet history and (2) the trophic position of adult lake sturgeon in the lower Niagara River and determine their role in this altered system.

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 (Figure 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 Niagara 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. 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. An induction dose of 200mg/L buffered MS-222 was used initially, followed by a maintenance dose of 87 mg/L. Biological data, including total length (TL, mm) and mass (to nearest 0.5 kg) were collected.

Collection of stomach contents was performed on 63 anesthetized fish using a gastric lavage

methodology adapted from Haley (1998). Briefly, 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 prior to flushing with water. 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 a 10% buffered formalin solution until laboratory processing. Stomach contents were identified down to family level and wet weighed to the nearest 0.01 g. 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.

Stable isotope samples were collected from two points on all sampled 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 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.

Benthic invertebrate prey species were collected from the same areas of the river as lake sturgeon using a ponar grab (152 x 152 mm) in 2014. 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 off of equipment deployed and retrieved from the river bottom. Round goby were caught using a baited minnow trap set overnight.

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* constitutes among the weight of all prey items in only stomachs that contain prey *i*. This metric is 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 all mean ± standard deviation C:N ratios were <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) $$\delta R\ (‰) = \left(R_{\ sample}/R_{\ standard} - 1\right) \times 1000$$

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 $\delta^{15}N$ value of an organism alone cannot sufficiently calculate trophic position. This is because the basal nitrogen sources that primary producers utilize can vary across systems (Rounick and Winterbourn 1986, Cabana and Rasmussen 1996, Vander Zanden et al. 1999) and therefore differences in $\delta^{15}N$ of an organism could either be the result of food web structure or simply different baselines. To calculate this baseline, Cabana and Rasmussen (1996) and Post (2002) advocated the use of unionid mussels, as they are relatively large and long-lived primary consumer that integrate temporal isotopic

variability in primary producers. In this study, quagga mussels *D. r. bugensis* served as a baseline trophic position of 2.0 against which the trophic position of lake sturgeon fin tissue will be estimated using this formula from Vander Zanden et al. (1997).

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

Where $\delta^{15}\text{N}_{\text{consumer}}$ is the stable nitrogen isotope signature of an organism, $\delta^{15}\text{N}_{\text{baseline}}$ represents the quagga mussel baseline, 3.0 is the trophic enrichment factor relevant to sturgeon (Vanderklift and Ponsard 2003), and 2 is the trophic position of the baseline. Lake sturgeon fin tissue was used to calculate trophic position because it has the slowest turnover rate of the sampled tissues and thus reflects the diet over the longest time period.

Isotopic mixing models are a common tool 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 the 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. SIAR fits a Bayesian model to the measured isotope values based on a Gaussian likelihood with a dirichlet prior mixture on the mean. As the model assumes that the sources are normally distributed, normality was assessed using a Shapiro-Wilk test with a *p* value of less than 0.05 indicating statistical significance. The mixing model accounts for trophic fractionation to 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 $\delta^{15}N$, a value deemed appropriate for freshwater ammonotelic stenotherms like lake sturgeon (Vanderklift and Ponsard 2003). For blood components we used 0.24‰ $\delta^{13}C$ and 5.17‰ $\delta^{15}N$ for red blood cells and 0.06‰ $\delta^{13}C$ and 4.39‰ $\delta^{15}N$ 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 (Figure 2). Stomach contents were obtained from 63 adult fish, 11% (n = 7) of which were empty and excluded from analysis. The prevalence of empty stomachs was greater in the summer as water temperatures and, presumably, digestion rates increased. The wet mass of stomach contents were dominated by two prey items: round goby and amphipods. Round goby had the largest mean (± SE) percent wet mass of diet contents, 43.99 ± 6.09%, followed by amphipods, 39.86 ± 6.03% (Table 1). In terms of prey counts Amphipods, nearly all of which were invasive *Echinogammarus ischnus,* had the greatest mean ± SE percent by number, 62.37 ± 4.74% (Figure 3); the second most prevalent prey item by number was round goby with 23.11 ± 4.36%. 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 shows that these prey groups can be considered rare prey (Figure 4). Amphipods are consumed frequently by nearly all lake sturgeon but their prey-specific index of food importance is below 10%. In contrast, *D. r. bugensis* is consumed heavily by 9% of individuals

and round goby are consumed by most individuals and has the highest prey-specific index of importance (74%).

The bi-plot of $\delta^{13}C$ and $\delta^{15}N$ for lake sturgeon and their prey items showed distinct separation between organismal groups (Figure 5). For prey species, filter-feeding *D. r. bugensis* had the most negative $\delta^{13}C$ value (mean ± 95% CI), -24.0 ± 0.5, (Table 2), whereas, amphipods had the least negative, -20.1 ± 0.4, suggesting greater utilization of benthic food sources than the other organisms. Chironomids and oligochaetes had intermediate $\delta^{13}C$ values, -21.7 ± 1.3 and -22.0 ± 0.9 respectively, but with large variance. Primary consumers, such as chironomids and oligochaetes, had $\delta^{15}N$ 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 positions on the $\delta^{15}N$ scale. Round goby had the highest $\delta^{15}N$ 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 $\delta^{15}N$ values than the collected prey, with no overlap in their 95% confidence intervals (Figure 5). Fin tissue had the highest $\delta^{13}C$, -18.9 ± 0.1, not only among the tissues, but also compared to sampled prey items. It also had the highest $\delta^{15}N$, 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 signatures, -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. In fin tissue, the slowest to turnover, round goby were essentially the only prey group represented with a median prey proportions and 95% credibility interval of 98.5%, CI = 96.9-99.4% (Table 3). In the two blood tissues, gobies continued to be an important dietary component albeit to a lesser degree (RBC: 29.4%, CI = 21.1-36.2%; plasma: 37.0%, CI = 24.8-

51.3%) while other prey groups' representation increased. 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. In addition to gobies, most prey groups were well represented in plasma, particularly snails (35.2%, CI = 5.3-54.9%) and mussels (12.5%, CI = 10.0-30.8%) (Figure 6). The distinct isotopic signatures and mixing model results of the three lake sturgeon tissues were indicative of seasonal diet shifts.

Discussion

Adult lake sturgeon caught in the lower Niagara River engaged in piscivory to a degree that is unprecedented for the species. This is in stark contrast to not only much of the early literature regarding lake sturgeon diet but also, to a lesser degree, the more recent diet studies of this species which document fish consumption. One of the first studies to demonstrate lake sturgeon piscivory, conducted by Stelzer et al. (2008) in Lake Winnebago, Wisconsin, found that Gizzard Shad, on average, comprises 56% of the wet mass of gut contents and 37% of the carbon assimilated. This resulted in an estimated lake sturgeon trophic position of 3.0 and it was concluded that they were taking advantage of the ephemeral winter die-off of Gizzard Shad and consuming the dead fish on the lake bottom (Stelzer et al. 2008). A similar phenomenon occurs in Lake Erie and the Niagara River after especially cold winters (NYSDEC 2013). However, since there was no evidence of gizzard shad consumption in the stomach contents in this study, even from lake sturgeon collected in April, we did not add them into the mixing model as a prey source. A more recent stable isotopic study of lake sturgeon in the Rainy River, Ontario, estimated that 40% of adult diets are derived from fish eggs and the rest from larval invertebrates and crayfish (Smith et al. 2016). If we apply the trophic position formula (2) to the Smith et al.

study (2016) and use 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. Fish eggs and dead gizzard shad are nonmoving prey that could be consumed opportunistically. In contrast, in the lower Niagara River, lake sturgeon are successfully targeting and capturing live round goby via a method we don't yet understand. Perhaps some combination of the territorial nature of round goby (Dubs and Corkum 1996) and their cryptic coloration prevents them from fleeing an approaching lake sturgeon. What is clear is that this lake sturgeon population has adapted to the new, abundant round goby food source and as a result occupies a higher estimated trophic position (4.8) than the previously discussed systems.

Invasive dreissenid mussels were found to be a limited component of the diet of sampled lake sturgeon, appearing infrequently in stomach contents. In fact, 97% of the total mass of dreissenids (n = 47) was contained within a single stomach sample. This is in contrast to lake sturgeon diets in Oneida Lake, New York, where dreissenid mussels are the most frequent prey item for fish 900 mm TL and larger (Jackson et al. 2002). One major difference between these two systems is that round goby had yet to invade Oneida Lake at the time of the study. It appears that in the lower Niagara River, in the presence of abundant goby and mussel resources, lake sturgeon are preferentially selecting round goby over dreissenid mussels. This is understandable from an energetic standpoint as goby have a higher energy content of 3.2 kJ/g (Johnson et al. 2005) than dreissenid mussels 1.7 kJ/g, (Madenjian et al. 2006). In all likelihood, prior to goby establishment, lake sturgeon diets in the lower Niagara River mirrored those in Oneida Lake, and might portend the diets of lake sturgeon in Oneida Lake when round goby becomes widely established there.

Lake sturgeon stomach contents illustrate that the population exhibits both a generalized and

specialized feeding strategy. In the literature, lake sturgeon are characterized as a generalist benthic carnivore with a non-discriminatory feeding behavior (Scott and Crossman 1973, Barth et al. 2013). Indeed, the diet of lake sturgeon from the lower Niagara River 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 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 because it is unlikely that round goby would be consumed incidentally during grazing along the bottom, suggesting that they are targeted specifically.

The distinct isotopic signatures of the three lake sturgeon tissues and their resultant mixing model outputs could indicate temporal diet shifts. Various tissues in organisms have different turnover rates, meaning that the tissue with quick turnover reflect recent diet history and vice versa. There is evidence that blood components turn over faster than fin tissue in fish (Suring and Wing 2009). Within whole blood, plasma turns over faster than RBC in vertebrates (Hobson and Clark 1993, Dalerum and Angerbjorn 2005). Given this, the signatures of RBC and plasma reflect a more varied diet that includes greater utilization of prey groups other than round goby, especially amphipods, crayfish, snails, and dreissenid mussels during the spring and summer months. However, these invertebrate diet items were not consumed in sufficient quantities to appear in the long-term average diet in a meaningful way. This is reflected in fin tissue, which has very little, if any, diet variability other than round goby. This indicates that despite short-term variation in diet, as reflected in the RBC and plasma, the average diet of lake sturgeon over a longer time period is dominantly round goby.

Characterizing the impacts of an invasive species as either wholly positive or negative is

reductive and does not adequately represent the complexity of species introductions. Adult lake sturgeon are clearly relying on round goby, but whether the net impact of gobies is beneficial to the lake sturgeon population as a whole is not settled. Round goby 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 utilize similar food and habitat resources. Additionally, gobies are documented predators of the eggs and larvae of larger fish, including lake sturgeon (Kornis et al. 2012). The use of predator exclusion chambers reduced round goby predation and increased hatch rate of lake sturgeon eggs from <1 to 16% in the lower St. Clair River, MI (Nichols et al. 2003). Whether or not round goby limit lake sturgeon recruitment in the lower Niagara River is still an open question and one that requires further study. However, this study provides clear evidence that round goby has become the most important prey item to adult lake sturgeon in the lower Niagara River. Perhaps the presence of this abundant food source is one factor driving the recovery of this population.

In conclusion, stomach content and stable isotope analyses both suggest that non-native round goby, rather than benthic invertebrates as documented in the literature, are the primary source of energy for adult lake sturgeon in the lower Niagara River. This study establishes the current trophic position for lake sturgeon and their prey items in the lower Niagara River and can be used as a point of comparison for future studies. For instance, had similar research been conducted prior to the establishment of dreissenid mussels and round goby, the effects of those invaders on lake sturgeon could have been quantified. More broadly, this study provides additional evidence of the importance of native predators in increasing biotic resistance to invasion, as shown in other aquatic systems (Baltz and Moyle 1993). However, this resistance is

dependent upon a healthy native predator community. Thus, the decline of lake sturgeon likely contributed to a reduction in biotic resistance and an increased vulnerability to invasion. Looking forward, as human-mediated species introductions continue globally, it is important to document and evaluate the interaction between invasive species and native species in order to inform conservation management plans that seek to protect native communities and ecosystems.

Lake Sturgeon Movement Patterns and Residency in the lower Niagara River

Introduction

Sturgeon species (Acipenseridae) across the globe are imperiled and the prognosis for most species is dire (Birstein et al. 1997). Sturgeons are extremely sensitive to overfishing and require large unobstructed river systems for their spawning migrations (Boreman 1997). They are characterized by their longevity, late sexual maturity, repeated periodic spawning, high individual fecundity, and migratory behavior (Scott and Crossman 1973). These traits were adaptive over the past 100 million years, allowing populations to persist even through several years of unfavorable environmental conditions and maximize reproductive output when conditions improved (Peterson et al. 2007). However, these same traits have made the sturgeons especially vulnerable to modern threats and anthropogenic disturbance (Crouse 1999), as exemplified by the decline of lake sturgeon in the Great Lakes. In order for regulatory agencies to properly protect these species improved basic knowledge is paramount. This includes insight into the behavioral and spatial ecology of sturgeons, gleaned from telemetry of wild fish, to answer questions about migration, residency, and home range size in order to protect sensitive and critical areas such as migration routes and spawning sites (Birstein et al. 1997).

Migratory behaviors in fish are adaptations that take advantage of the many differences among ecosystems, e.g. food availability, predation, physical and chemical characteristics and typically occur during specific times of the year depending on a combination of the physiological state of the fish and external factors such as water flow, temperature, or light (Northcote 1984). Diadromous fish move between ocean and freshwater environments because the benefit of increased food availability outweighs the costs of migration (Gross et al. 1988). There are also migrations taking place in entirely freshwater systems where fish, residing in lacustrine habitats,

migrate to the upper reaches of rivers to spawn. This is the case in the Great Lakes for land-locked salmonid species and lake sturgeon, for example. Migrations are large-scale movements and an instance in which an organism would venture outside of its normal movement extent.

Animals that utilize a discrete area during the course of normal activity possess a home range (Barrows 2011). Home range is defined as the area within which some percentage of activity or time occurs and can simply be the distance between the most upstream and downstream detections of an individual. However, to determine which areas of the home range receive more use it is necessary to calculate a kernel density estimate and utilization distribution from a set of relocation points, e.g. acoustic telemetry detections (Van Winkle 1975). The home range can then be broken down into habitat usage categories during specified time periods (Kernohan 2001). Typically, the area in which a fish has spent 50% of its time is known as the core area and the larger area that encompasses 95% of their activity is the movement extent. The latter percentage excludes sporadic long-range movements or exploratory forays outside of normal activity, like the aforementioned migrations.

Researching the spatial ecology of lake sturgeon is crucial to the recovery of these populations because it promotes the safeguarding of the large river systems and Great Lakes connecting channels they rely on. Unfortunately, connecting channels are centers of human development and global commerce as well as critical habitats for fish populations, especially for large-river spawners like whitefish, cisco, walleye, and lake sturgeon. These fish communities are subjected to artificial water level fluctuations, habitat alterations, dredging and pollution. In order to properly mitigate these impacts managers require better understanding of how these fish populations utilize connecting channel systems.

In continuous lake and river systems, lake sturgeon are thought to spend most of the year in lakes and move to rivers for a few weeks in the spring to spawn (Harkness and Dymond 1961, Scott and Crossman 1973, Priegel et al. 1974). Movement to fast-flowing spawning areas can be far-ranging or more restricted depending on the system (Auer 1999) and is variable among individuals. For instance, sexually mature individuals captured in the North Channel of the St. Clair River were found to exhibit three different migratory behaviors: most fish moved downstream to Lake St. Claire, a few fish went upstream to Lake Huron, and the rest remained in the river for at least a year (Boase et al. 2011). However, lake sturgeon movements are associated with more than just spawning. They will also migrate to find overwintering habitats and will occasionally travel to rivers to feed in the summer (Harkness and Dymond 1961, Scott and Crossman 1973, Priegel et al. 1974). These types of movement behaviors have really been described in only a few systems and expanding that knowledge to other rivers, like the lower Niagara River, would be beneficial.

This study addresses knowledge gaps about the year-round home range, movements, habitats, and depth utilization of lake sturgeon in the lower Niagara River. The specific objectives of the study are to (1) define lake sturgeon temporal use of the river; (2) define seasonal movement and activity spaces; (3) identify areas and depths of high use; and to (4) identify home range size and location. Greater understanding of these components of lake sturgeon ecology in the lower Niagara River is important for the guidance and implementation of restoration or management plans that not only protect areas of the river, but also the species itself.

Methods

Study location

The Niagara River is a connecting channel between Lakes Erie and Ontario and forms a portion of the border between the State of New York and the Province of Ontario. Among the other four connecting channels the Niagara River has the greatest elevation change along its length (99.3 m), owed in large part to the presence of Niagara Falls, which bisects the river into an upper and lower portion (Edwards et al. 1989). Below Niagara Falls, the river carves through a narrow gorge, a stretch characterized by swift water, rapids, and bedrock substrate. Downstream of the gorge the river widens and slows down allowing larger sediment particles to settle out resulting in a predominantly gravel and cobble benthic habitat. Several eddies along the river are areas with a heterogenous mix of gravel sizes, sand, silt, and macrophytes. The river transports considerable finer sediment into Lake Ontario that settles out and forms the relatively shallow and predominantly sandy Niagara Bar. The lower Niagara River is 10.5 km long with a mean water depth of 10 m and maximum depth of 25 m.

Fish collection

Lake sturgeon were captured from the lower Niagara River and Niagara Bar between May and September 2014 - 2015 using baited 75 m set lines with 12/0 circle hooks baited with Alewife *Alosa pseudoharengus* or Rainbow Smelt *Osmerus mordax* placed every 3 m (Thomas and Haas 1999). Up to 8 setlines were deployed for 24 hrs in water depths of approximately 10 m parallel to the flow of the river. Fish were brought from the point of capture to a nearby boathouse for tagging before being released.

Acoustic tagging

Lake sturgeon were placed into a sling and anesthetized with a recirculating solution of ambient water and tricaine methanesulfonate (MS-222). An induction dose of 200mg/L buffered MS-222 was used initially, followed by a maintenance dose of 87 mg/L prior to surgery. Vemco V16-6H transmitters (Vemco Ltd, Halifax, NS, Canada) were surgically implanted into the abdominal cavity of lake sturgeon through a 2-3 cm incision. Ethicon PDS II sterile (Ethicon Inc., Somerville, NJ) synthetic absorbable sutures and needles were used to stitch the muscle and skin layers closed. The area was disinfected with betadine swabs and fish were allowed to come out of anesthesia before being placed back into a holding pen to recover. All tagged fish were in good condition upon capture and release.

The acoustic tags transmitted a unique pulse ID at 69.0 kHz with some tags providing depth information with each transmission. Tags transmissions were randomly spaced between 15 s and 45 s for the first six months of operation and between 60 s and 180 s for the remainder of the study. The change to less frequent transmission extended the battery life of the tags to approximately 10 years. Randomly spaced transmissions reduce signal overlap and collision between tags and increases detection probability.

Acoustic array

Tagged fish were tracked by an array of 39 Vemco VR2W passive acoustic receivers placed throughout the river and its confluence with Lake Ontario (Figure 7). With the exception of lost receivers (<5%), the array was left largely intact year-to-year. The receivers were configured in such a way as to accomplish several objectives. First, receivers were clustered in high catch rate areas in order to capture finer scale movement and location data. Second, a curtain of receivers was placed outside the mouth of the river to detect lake sturgeon movement in and out of the

river. Third, three gates, two pairs of receivers placed in close proximity, served to determine movement directionality. Additionally, a few receivers were tethered to shore in the Niagara Gorge to determine how far upriver lake sturgeon travel. Receivers were retrieved every three months to offload data.

Data analysis

Residency, the proportion of time spent by an individual within the array, is one of the simplest ways of measuring lake sturgeon use of the river. Presence of a tagged fish within the array was defined as at least two detections on any receiver in a single day (a single detection being considered noise). This was used to calculate a residency index: the ratio of the number of days an individual was detected within the array to the number of days monitored (i.e. number of days from tagging to the study end date). Residency index values can range from 1 to 0 with values of 1 indicating total residency within the array and 0 representing complete absence. Residency was examined for each individual across the entire study period as well as on a weekly basis.

The positions of tagged individuals were estimated using a short-term center of activity (COA) algorithm (Simpfendorfer et al. 2002). This method is based on the premise that signal detection probability is inversely proportional to the distance between the receiver and the transmitter and thus, in a given period of time, the receiver that is closest to the transmitter will log the greatest number of detections. The COA position estimate is calculated as the mean location of receiver weighted by the number of receptions over the course of a defined time interval (Simpfendorfer et al. 2002). This weighting scheme also followed a normal distribution—with greater weight given to detections that occur in the middle of the time interval and less to those at the fringes. The length of the time interval must allow for sufficient transmissions/detections without the position of the tag changing too much. We adopted a sliding

window approach where a 15 minute COA was calculated every 3 minutes. This means that individual detections are incorporated into more than one COA calculation but at differing weights.

In linear river systems, position estimates based on river kilometer (rkm) rather than latitude/longitude can be used to characterize fish movements (e.g. Collins et al. 2008, Heupel et al. 2010). Therefore, all COA locations were snapped to the nearest point along the centerline of the river and assigned an rkm value (distance from the Niagara Bar). This river distance metric was used to calculate daily activity and monthly home ranges as the difference between the maximum and minimum rkm for that time period.

Kernel utilization distributions (KUD) are used to define areas in which an animal will occur with some given probability (Worton 1989). Typically, 50% KUDs describe the core areas of animals and 95% KUDs describe movement extent (e.g. Heupel et al. 2006b) and are bivariate (constructed using both X and Y coordinates). However, in river systems, where the shoreline presents a boundary to fish movement, it is advantageous to construct univariate kernel density estimates along the centerline of the river (Vokoun 2003). Using this method, linear kernel densities of tagged fish were created based on river distance for each season. All KUDs were overlaid on the river and a heatmap was constructed in ArcMap 10.3.1 (ESRI, Redlands, CA) based on the level of KUD overlap among individuals.

Results

In total, 60 adult lake sturgeon were captured and tagged, 30 individuals by the end of 2014 and 30 by the end of 2015. Mean total length (± SD) for tagged fish was 1452 ± 148 mm (ranging from 1107 to 1767 mm) and mean weight (± SD) was 23.8 ± 8.9 kg (ranging from 8.5 to 53.5 kg). One fish tagged in 2015 exhibited a movement pattern that indicated it either died or the tag

was dropped and so was removed from further analysis. The monitoring period for individuals, measured from their first detection to the end of the study (March 31, 2016) varied from a minimum of 258 days to a maximum of 673 days. Individuals were detected within the array from 96 to 659 days, with a mean (± SD) of 320 ± 157 days. Maximum consecutive days detected ranged from 20 to 659 days (133 ± 95).

Residency of lake sturgeon across the entirety of the study period ranged from 0.3 to 1.0 with a mean ± SD of 0.67 ± 0.22, indicating that on average fish spent more time in the array than outside of it. The presence plot shows that there is essentially no time of year where sturgeon are absent from the array (Figure 8). However, mean (± 95% CI) weekly residency does change throughout the year with peaks above 0.8 during the summer months dropping down to 0.4 in the winter (Figure 9).

Acoustic tags equipped with pressure sensors logged the current depth of the fish with every transmission. Mean monthly depth calculated use across these fish (n=48) showed slight variation during the course of the year (Figure 10). Fish utilized shallower depths during the summer (11.35 ± 0.42 m) and autumn (11.86 ± 1.49 m). This preference shifts to deeper water during the winter (17.03 ± 2.83 m) and spring (16.02 ± 3.65 m).

Generally, tagged lake sturgeon did not exhibit a high degree of activity or speed of movement. The most frequent daily activity space size was between 1 and 2 km followed by less than 1 km of movement (Figure 11). Days where individuals moved up to 5 km are quite common, but movements greater than 5 km are rare and only include a few instances where individuals moved up to 14 km.

There was also a seasonal effect on mean monthly home range size which ranged from 0.9 – 10 km (Figure 12). In the late spring and early summer, home range sizes are at their

maximum, 7 – 10 km. Then through the summer and autumn home range size shrinks slightly, between 4 and 5 km before reaching its smallest size during the winter at approximately 2 km. This gradual shrinking of the home range size through the year is a repeating pattern among both years' tagged fish.

The linear kernel density estimates illustrate the areas of the river most used by the tagged fish (Figure 13). The 95% kernel, or the movement extent of fish, shows that fish are using the entire length of the river to some degree in all seasons. It is clear, however, that during the summer and autumn, there is a congregation of fish just outside the mouth of the river. The highest concentration of fish (n = 55) occurred on the Niagara Bar in the summer. The 50% kernel, or the area of core usage, is a little more scattered throughout the river but shows a similar pattern. Fish are most concentrated on the Niagara Bar during the summer and autumn, but are still present in some spots of the river as well. Together, these figures show that congregations of fish are smaller in the winter and spring, indicating most of the fish are absent from the array at these times.

Discussion

Monitoring temporal use of the river by lake sturgeon revealed that they are present, to some degree, within the river at all times of the year. However, there is a clear seasonal pattern to residency where the majority of individuals leave the river for the lake each winter. These fish then return to the river in the spring, right around spawning time and remain in the river throughout the summer and fall. All but one fish tagged in 2014 returned to the river the next year. It is unlikely that these fish return solely to spawn, as they are known to spawn only periodically, females once every 4-9 years and males every 1-3 years (Roussow 1957, Fortin et

al. 1996). Importance of lower Niagara River extends beyond spawning habitat, perhaps serving as an important feeding ground.

The daily activity spaces of adult lake sturgeon were quite small, with seasonal averages of less than 2 km per day. There are individual days of extensive movement, up to 14 km. This range of movement is actually larger compared to sturgeon populations of other systems. The mean daily minimum distance sturgeon moved in the Grasse River (Trested et al. 2011) and Rainy River-Lake of the Woods system (Rusak and Mosindy 1997) was less than 1 km for all seasons. In those studies, as in this one, daily movement during the winter was the lowest, indicating that individuals that overwinter in rivers are probably spatially restricted to deeper areas or may be a response to food concentration.

Similarly to daily activity space, monthly home range also had seasonal variation. This is again consistent with findings from the Grasse River, where monthly home ranges were the largest in spring, then falling throughout the rest of the year (Trested et al. 2011). This could have been a result of low-flow conditions that restricted movement or a coping mechanism to reduce thermal stress when water temperatures are at their peak (McKinley et al. 1998). Additionally, home range sizes were nearly identical (11.63 km in spring, 4.32 in summer, 1.93 in fall, and 2.90 in winter) to those in this study, despite the Grasse River being over twice as long. The annual home ranges for lake sturgeon in the Detroit and Kettle Rivers were larger than in the lower Niagara River (>10 km) (Borkholder et al. 2002, Caswell et al. 2004). However, those rivers are twice as long as in this study and so home range as a proportion of the river's length is actually quite similar.

Lake sturgeon in the lower Niagara River mostly utilized depths between 10-20 m. Towards the colder months, the individuals that remain in the river shift to using slightly

deeper habitats, those greater than 15 m deep. This trend occurs in both winter seasons of this study. The river has quite a diversity of depth habitats available. In the Niagara Gorge, there are areas of greater than 30 m deep water. As the river exits the gorge, it becomes slightly shallower but the thalweg is still deeper than 20 m, including an area right at the river mouth that is 25 m deep. There is evidence that in winter sturgeon seek out deep holes in the upper Fox River and Wolf River systems (Bruch and Binkowski 2002). This study suggests that most lake sturgeon overwinter in Lake Ontario proper, but perhaps there are some spots in or near the Niagara River that are deep enough to serve as overwintering habitat and thus retain some individuals through the winter.

The linear home ranges indicate that lake sturgeon tend to aggregate on the Niagara Bar just outside the mouth of the river in the summer and autumn. This area is a relatively calm shallow area with a sandy bottom that may serve as a staging and feeding area between forays into the river. This finding is consistent with other studies that found lake sturgeon were concentrated in transitional areas between high and low flow currents (Knights et al. 2002, Boase et al. 2011). It is thought that the fine sediment that collects in these depositional areas makes them attractive feeding grounds. This area also harbors high round goby densities during this time of the year (Mehler and Pennuto unpublished data), which could explain the congregation of lake sturgeon. Further, there is evidence that round gobies migrate offshore to deeper water during the winter months in the Gulf of Gdansk and Black Sea (Miller 1984, Sapota and Skóra 2005). Thus, winter migration of lake sturgeon out into the lake may not only represent a search for deeper water but also a behavior to follow what has become their primary food source.

Lake sturgeon in the Great Lakes are managed as discrete populations and management plans, often associated with particular rivers. Therefore, it is important to study how each

population utilizes the unique hydrology available to them. This study has provided more information to utilize when managing this species. The results of this study underscore just how important the lower Niagara River continues to be for lake sturgeon in terms of spawning and feeding. It appears that lake sturgeon are seasonal residents of the lower Niagara River and return year-after-year, indicating that there are reasons other than spawning that explain their return. Additionally, knowledge of when and where areas of high use occur will aid in efforts to minimize disturbance to the species. This kind of information is valuable when addressing some of the beneficial use impairments of the Niagara River and other areas of concern. Greater understanding of the movements and habitat usage at all life stages is crucial to the protection and restoration of this species. Future studies should seek to connect movements and residency with habitat types within the river thus providing greater insight into their behavior. Extending these questions to larval and juvenile life stages would also be fruitful. Currently, there is very little known about sturgeon recruitment in the river and an assessment of the habitat use for young of the year and juveniles would be valuable as their habitat requirements are distinct. Knowledge of their movements and habitat use would aid in determining if certain types of habitat are limiting and which types of restoration projects would best promote the recovery of the species.

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TABLES

Table 1. Count (*n*), frequency of occurrence (%O), mean ± SE percent weight (%W), and mean ± SE percent number (%N) of prey items identified in lake sturgeon stomachs (n = 56, excluding empty stomachs).

Prey item	*n*	%O	%W	%N
Amphipoda	6 252	83.93	39.86 ± 6.03	62.37 ± 4.74
Round goby	143	64.29	43.99 ± 6.09	23.11 ± 4.36
Chironomidae	80	41.07	0.75 ± 0.46	5.43 ± 1.45
Crayfish	34	30.36	7.67 ± 2.70	3.04 ± 1.60
Trichoptera	32	14.29	0.20 ± 0.16	0.71 ± 0.44
D. r. bugensis	53	8.93	3.49 ± 2.36	1.92 ± 1.62
Isopoda	10	8.93	0.03 ± 0.02	0.16 ± 0.11
Snails	15	7.14	0.05 ± 0.03	0.25 ± 0.16
Diptera	8	7.14	0.01 ± 0.01	0.44 ± 0.36
Notropis spp.	3	5.36	3.82 ± 2.48	2.41 ± 1.85
Ephemeroptera	3	5.36	0.01 ± 0.01	0.06 ± 0.05
Centrarchidae	1	1.79	0.13 ± 0.12	0.09 ± 0.09

Table 2. 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	8.20 ± 0.2	1.9
Chironomidae	10	-21.7 ± 1.3	7.70 ± 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	8.63 ± 0.2	2.0
Oligochaeta	14	-22.0 ± 0.9	9.00 ± 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

Table 3. SIAR model results showing the median and 95% confidence intervals of dietary contributions of prey items to lake sturgeon fin tissue, red blood cells (RBC), and plasma.

Fin

Taxa	Median	Upper 95% CI	Lower 95% CI
Amphipoda	0.002	0.000	0.012
Chironomidae	0.001	0.000	0.005
Crayfish	0.004	0.000	0.024
D. r. bugensis	0.001	0.000	0.005
Oligochaeta	0.002	0.000	0.010
Round goby	0.986	0.967	0.993
Snails	0.001	0.000	0.008

RBC

Taxa	Median	Upper 95% CI	Lower 95% CI
Amphipoda	0.543	0.490	0.593
Chironomidae	0.012	0.001	0.044
Crayfish	0.115	0.015	0.245
D. r. bugensis	0.004	0.000	0.016
Oligochaeta	0.014	0.001	0.054
Round goby	0.294	0.213	0.361
Snails	0.007	0.000	0.027

Plasma

Taxa	Median	Upper 95% CI	Lower 95% CI
Amphipoda	0.016	0.001	0.059
Chironomidae	0.021	0.001	0.079
Crayfish	0.055	0.003	0.188
D. r. bugensis	0.114	0.008	0.302
Oligochaeta	0.032	0.001	0.119
Round goby	0.363	0.244	0.510
Snails	0.370	0.064	0.551

FIGURES

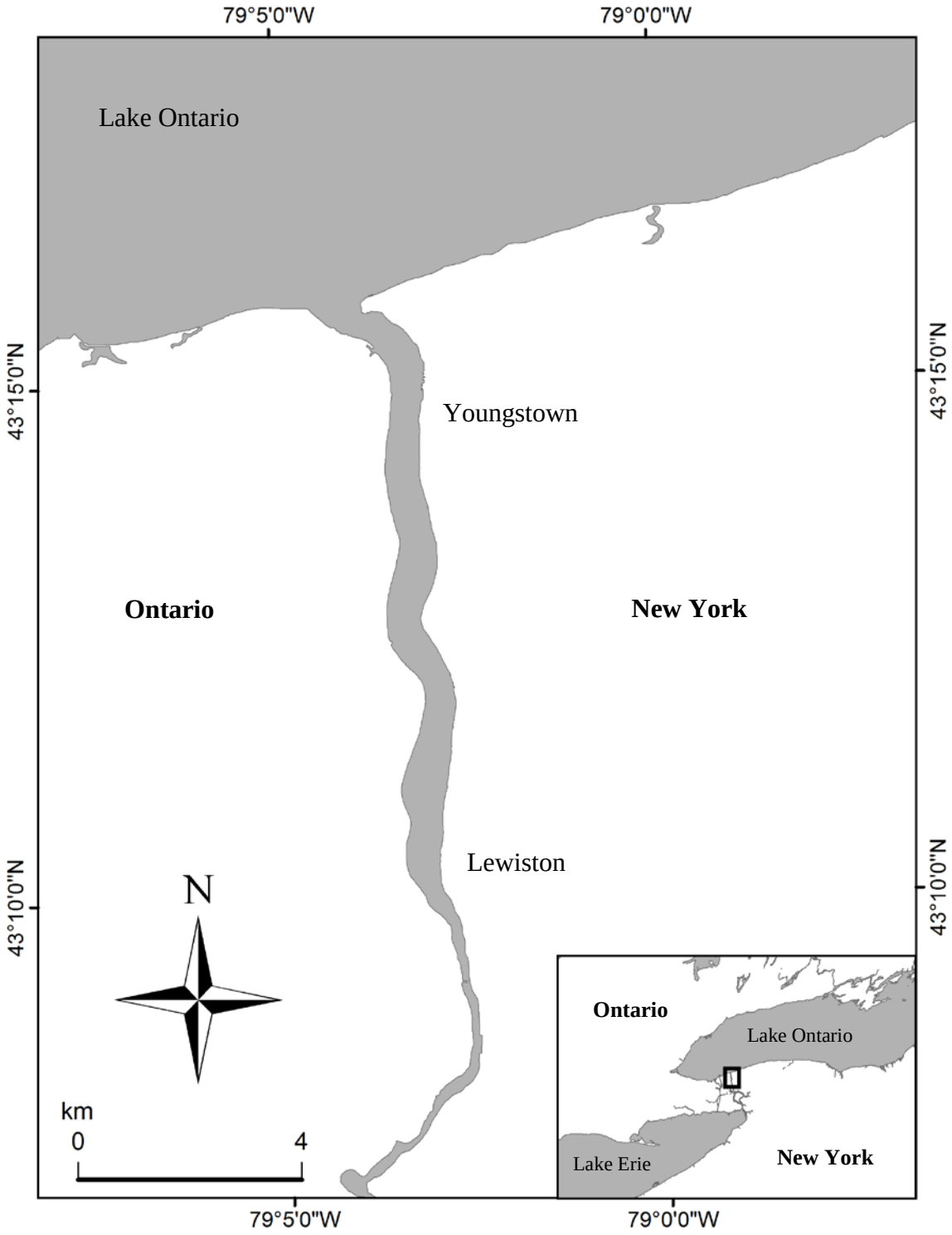


Figure 1. Study area on the lower Niagara River, NY.

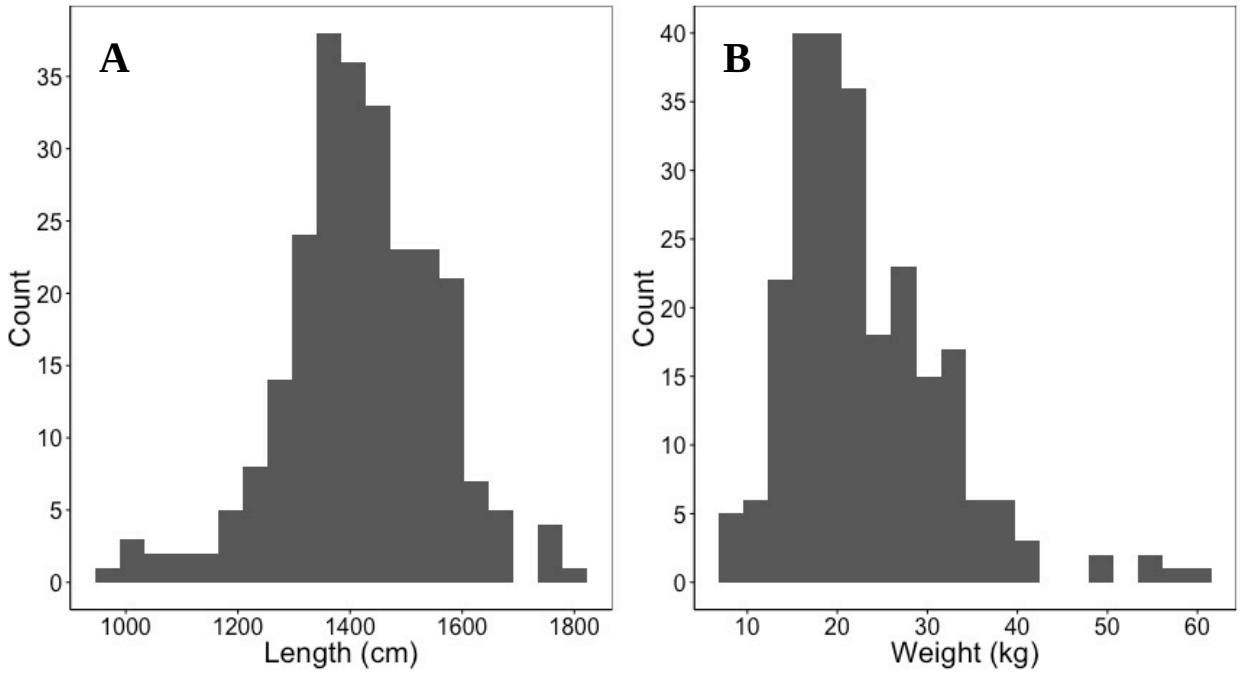


Figure 2. The length (A) and weight (B) frequency distributions of adult lake sturgeon captured from the lower Niagara River, NY.

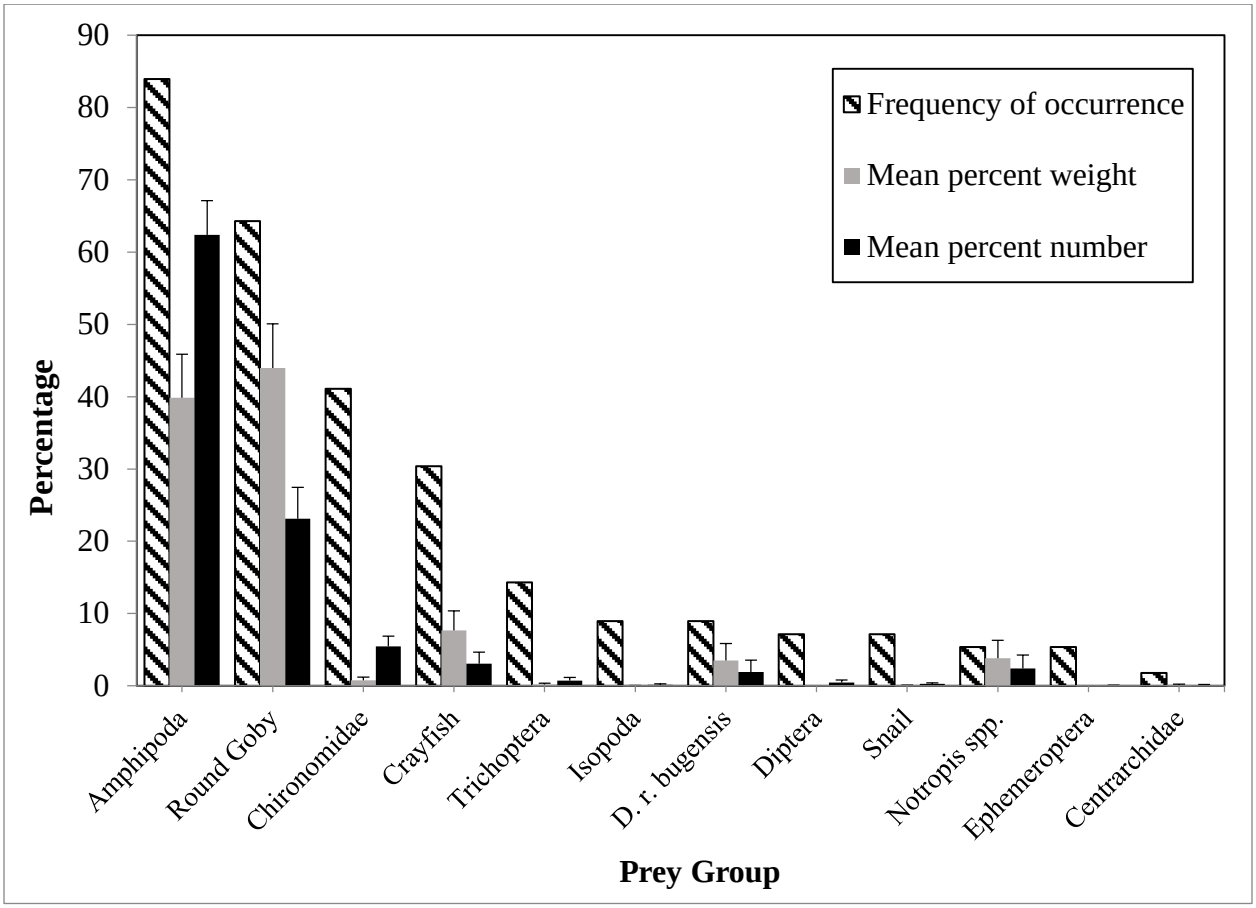


Figure 3. Percent frequency of occurrence, mean (± SE) percent weight and percent number (calculated for each stomach sample then averaged for each prey group) of prey items found in the stomachs of lake sturgeon (n = 56, excluding empty stomachs) captured from the lower Niagara River.

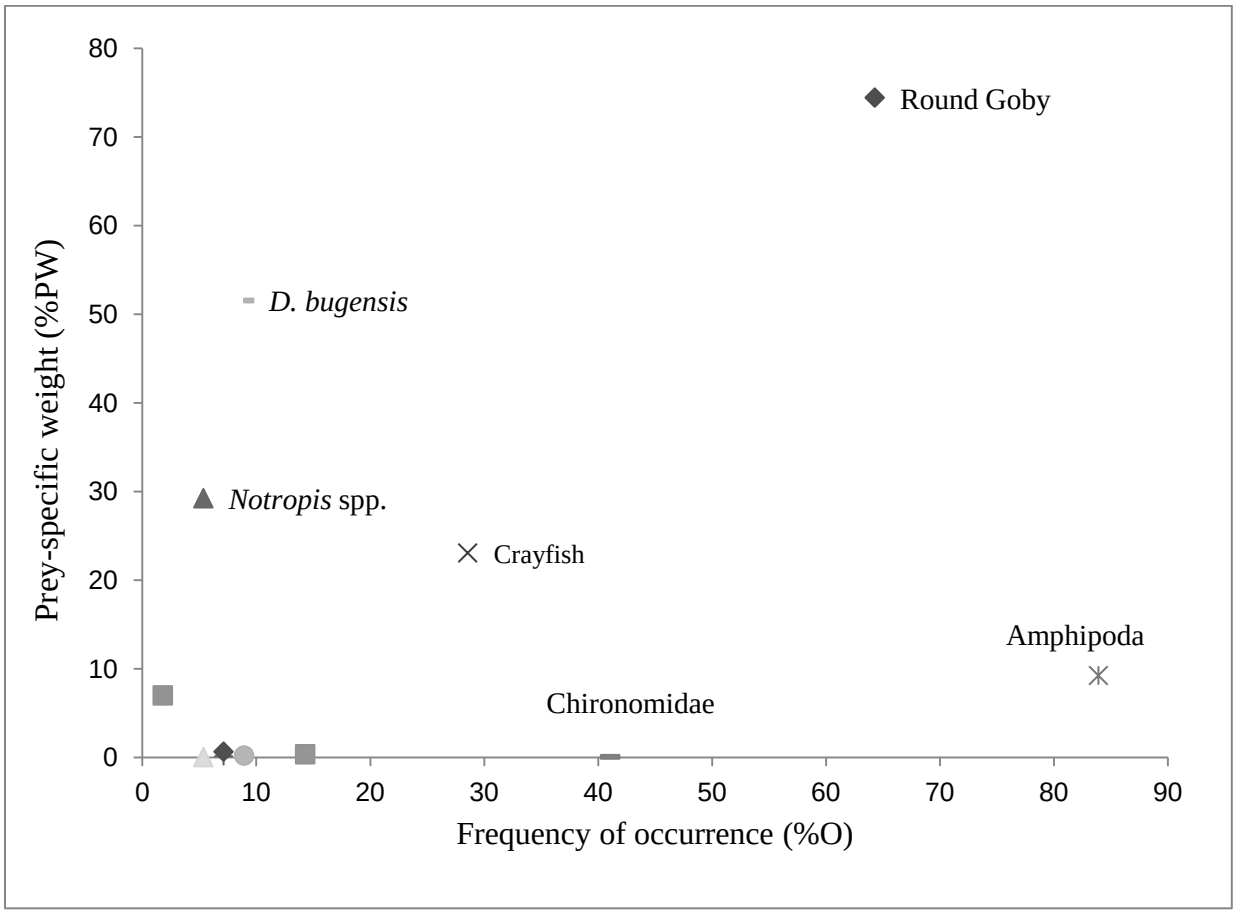


Figure 4. Feeding strategy diagram (Costello 1990; Amundsen et al. 1996) of adult lake sturgeon diet plotting prey-specific abundance against frequency of occurrence, where prey-specific abundance is defined as the proportion by weight that prey *i* constitutes of all prey weight in only stomachs that contained prey *i*. Dominant prey groups occur in the upper right quadrant and rarer prey towards the lower left.

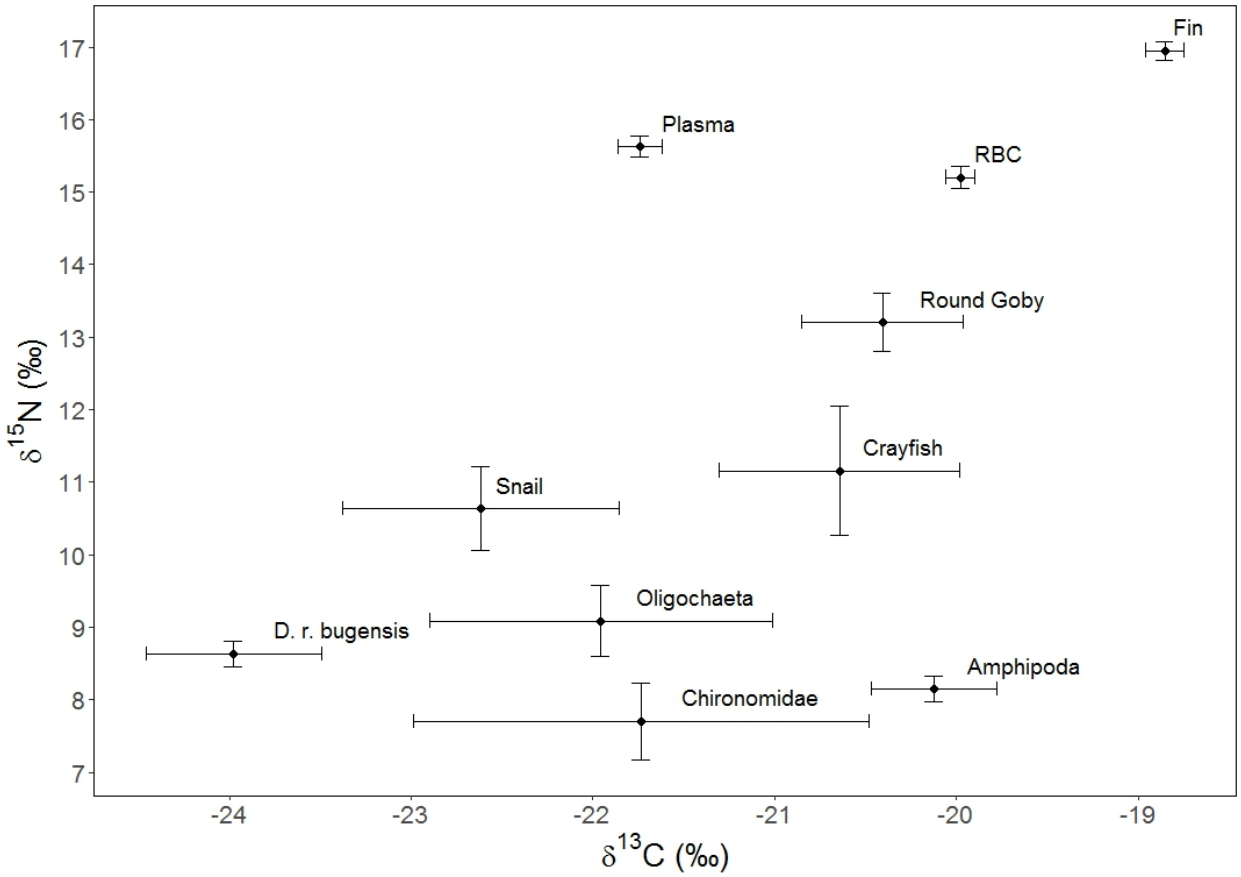


Figure 5. Mean values and 95% confidence intervals of $\delta^{15}N$ and $\delta^{13}C$ (‰) in lake sturgeon fin, red blood cell (RBC), plasma tissue, and prey sources. Values are not adjusted for trophic shift.

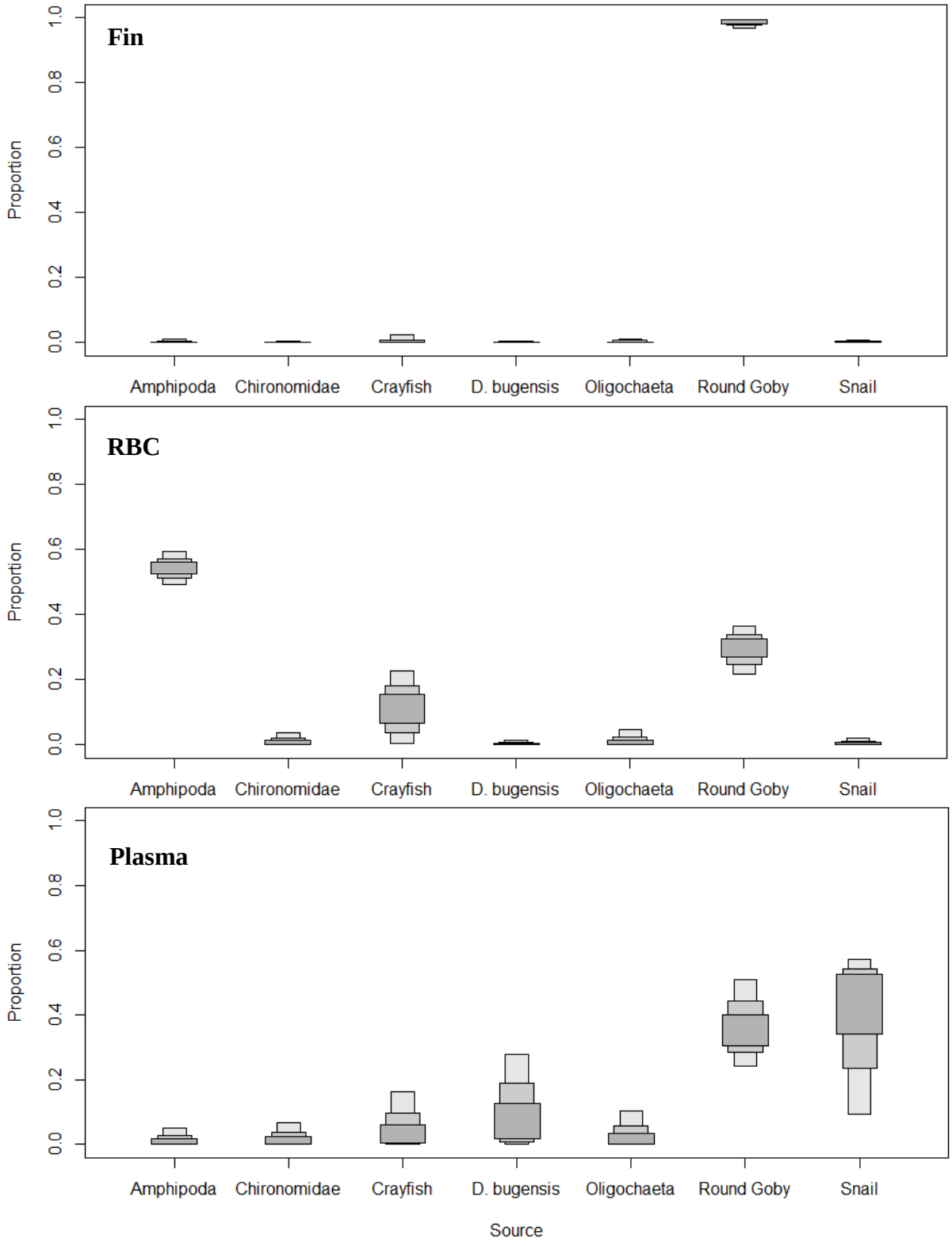


Figure 6. Mixing model results of the contributions of different prey items to the diets of lake sturgeon as reflected in fin, red blood cell (RBC), and plasma tissue. Boxplot shading shows credibility intervals at the 95, 75, and 50 % levels.

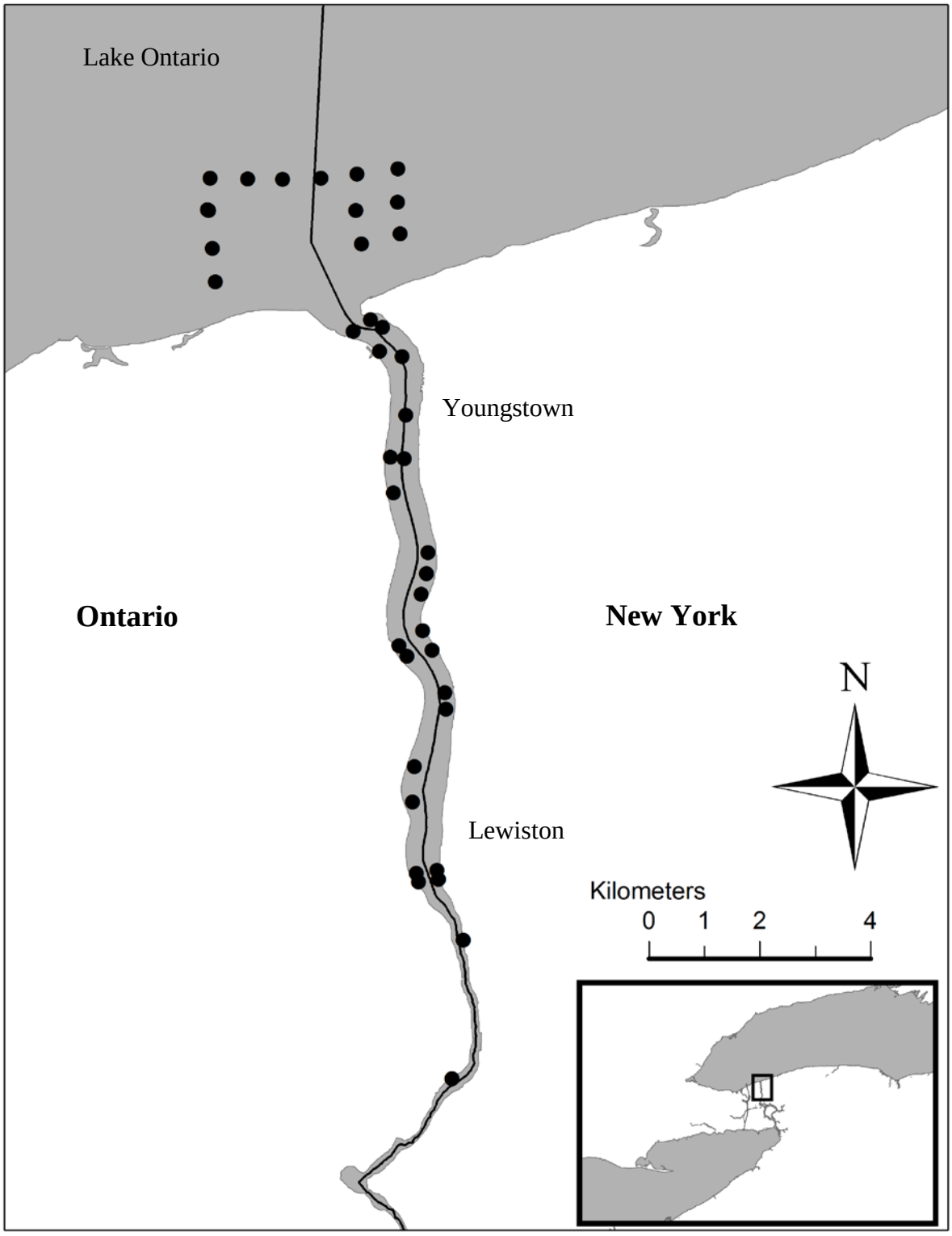


Figure 7. Acoustic receiver positions in the lower Niagara River and Lake Ontario.

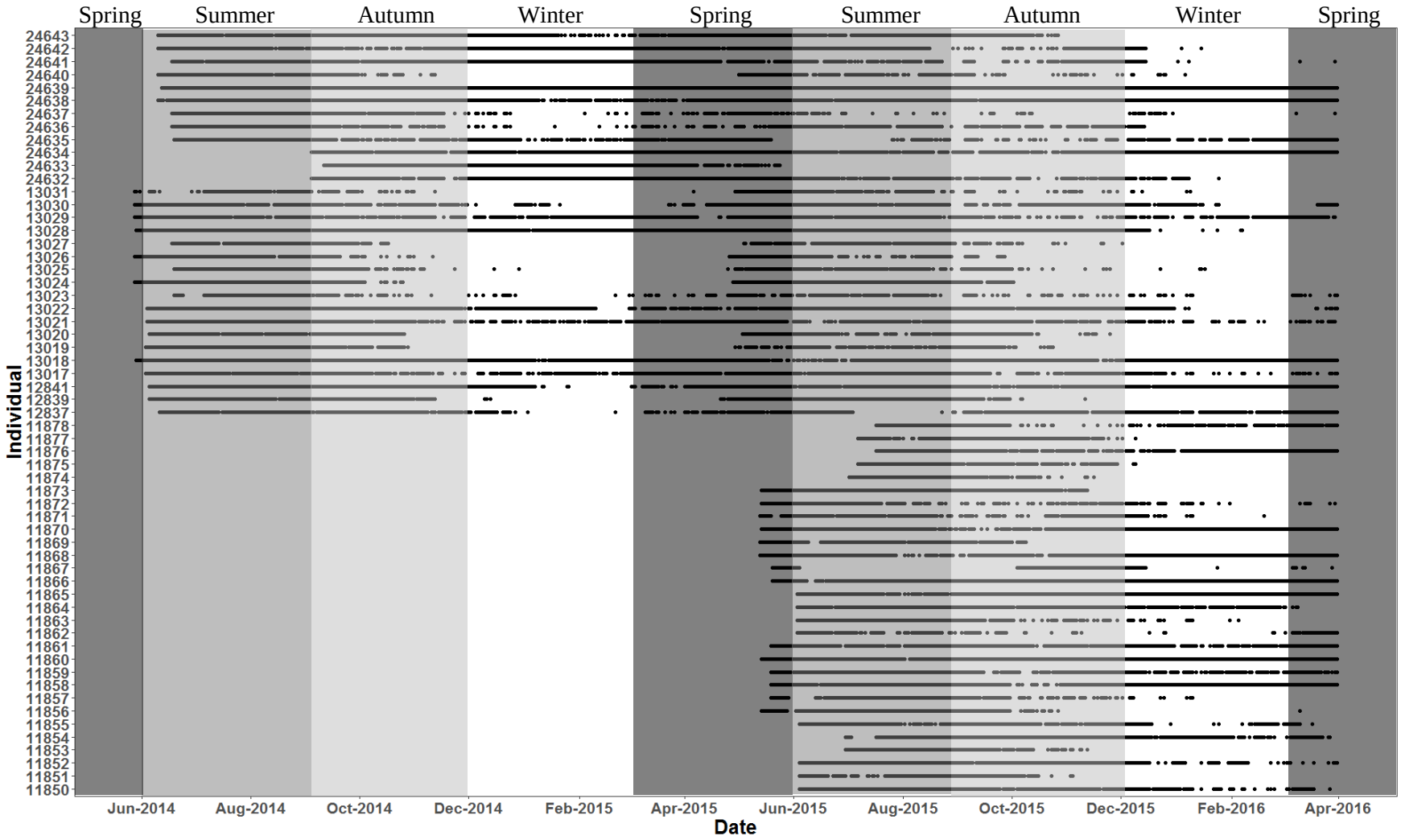


Figure 8. Presence-absence of tagged lake sturgeon monitored in the lower Niagara River during 2014-2016. Each dot represents a day where that individual was detected at least twice in the array. Fish tagged in 2014 occupy the top half of the figure and those tagged in 2015 appear in the bottom half.

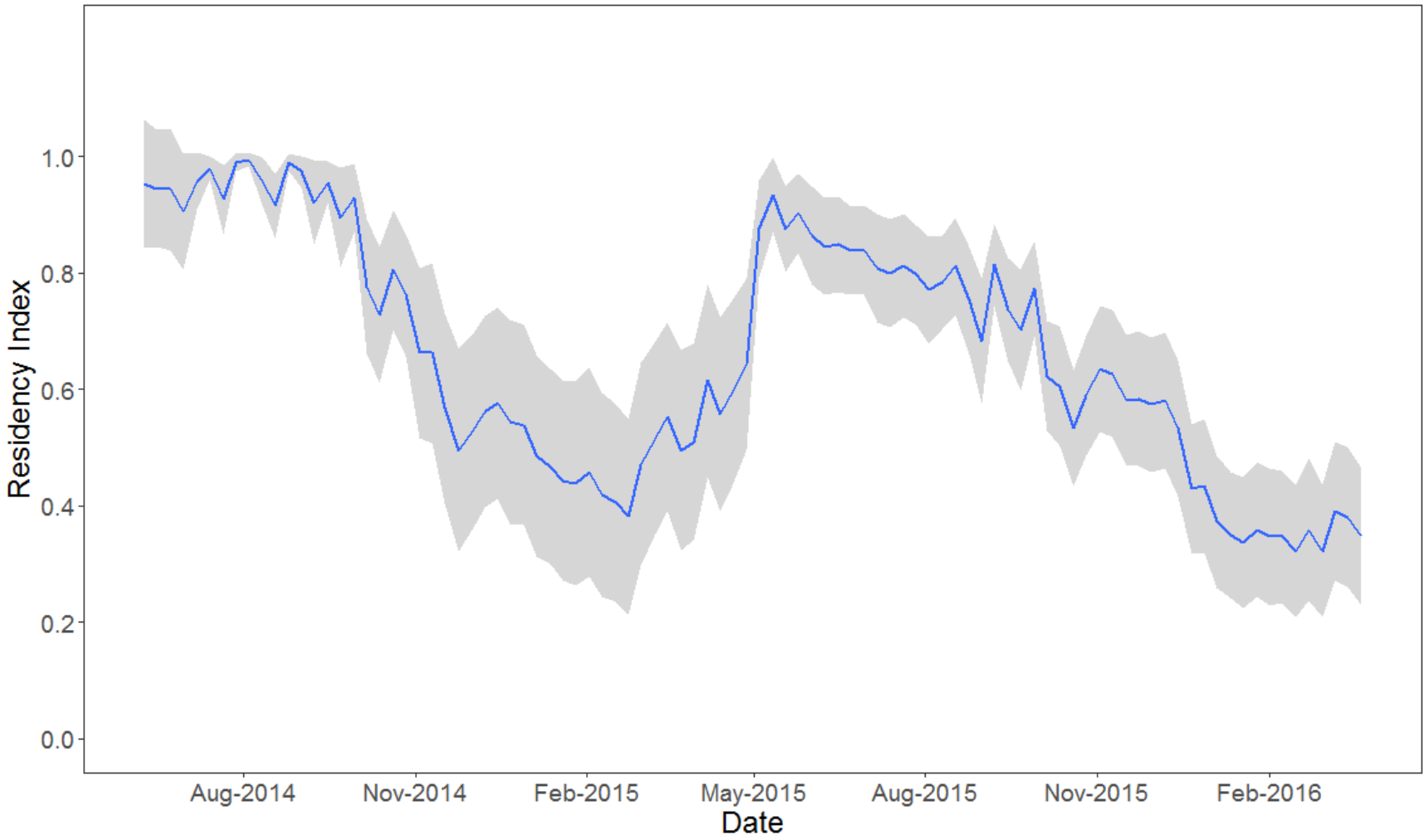


Figure 9. Mean weekly residency index values and 95% confidence intervals for all individuals across the study period.

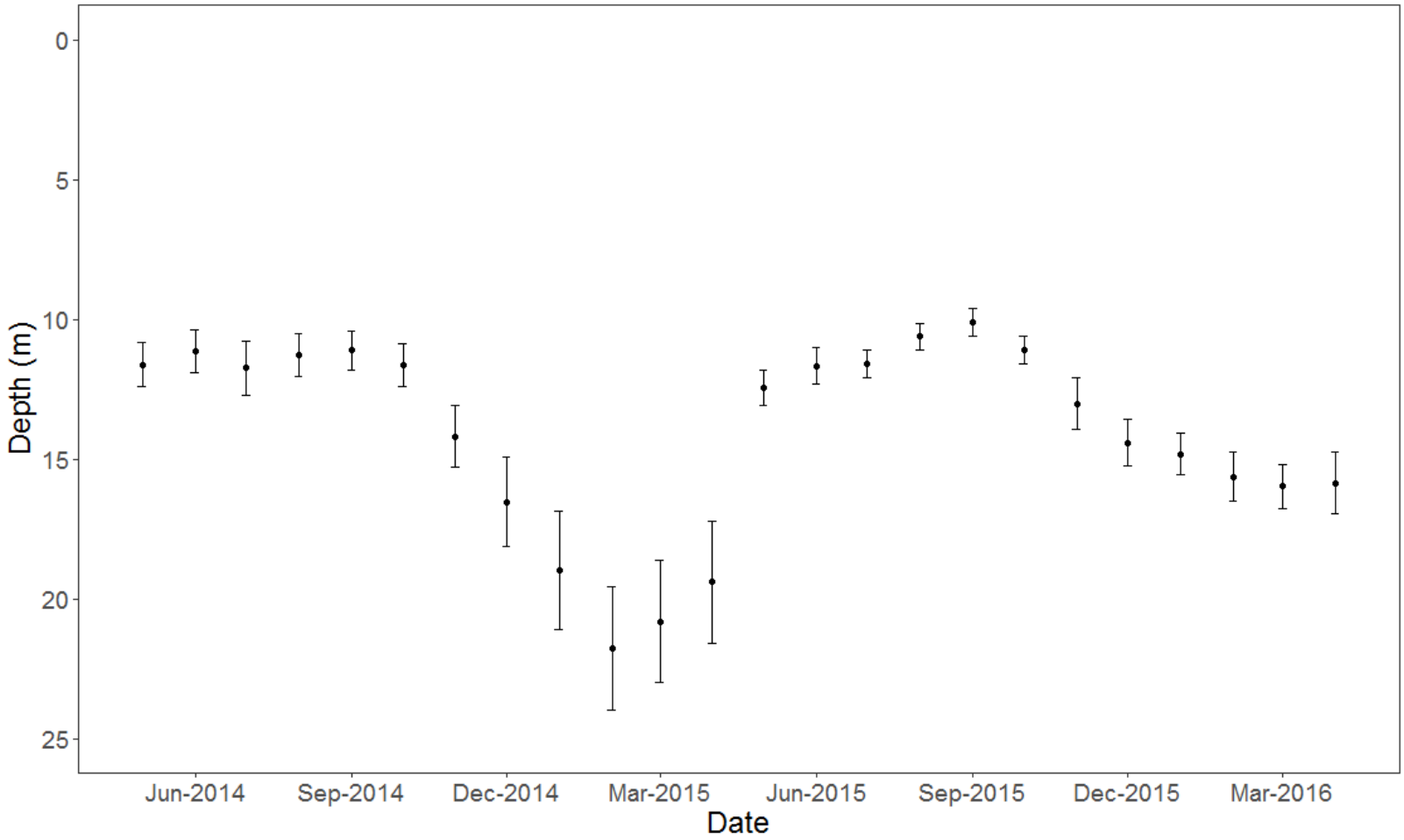


Figure 10. Mean ± SE monthly depth of tracked lake sturgeon.

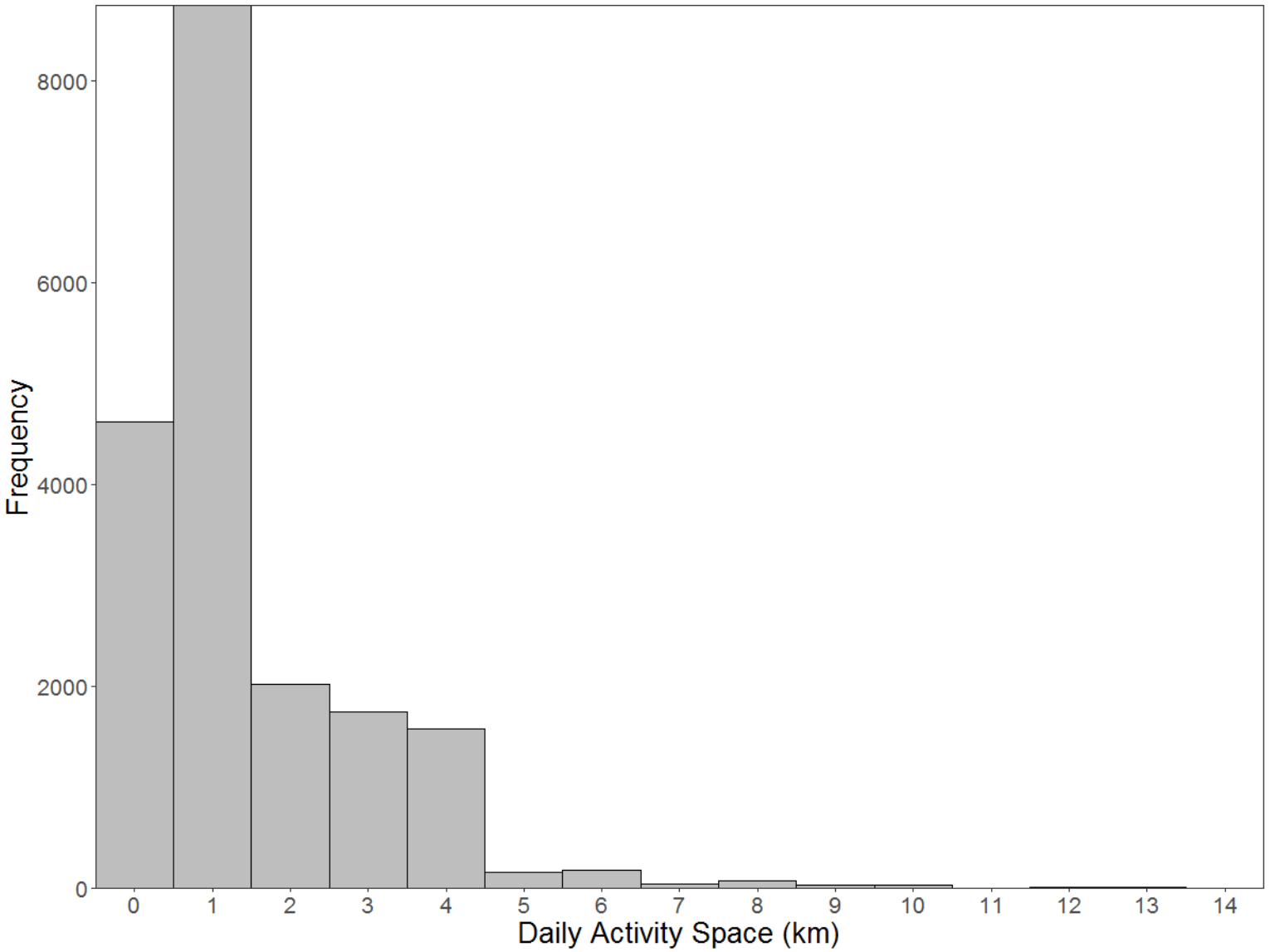


Figure 11. Frequency distribution of lake sturgeon daily activity space (the difference in km between the most upstream and downstream positions in a single day.

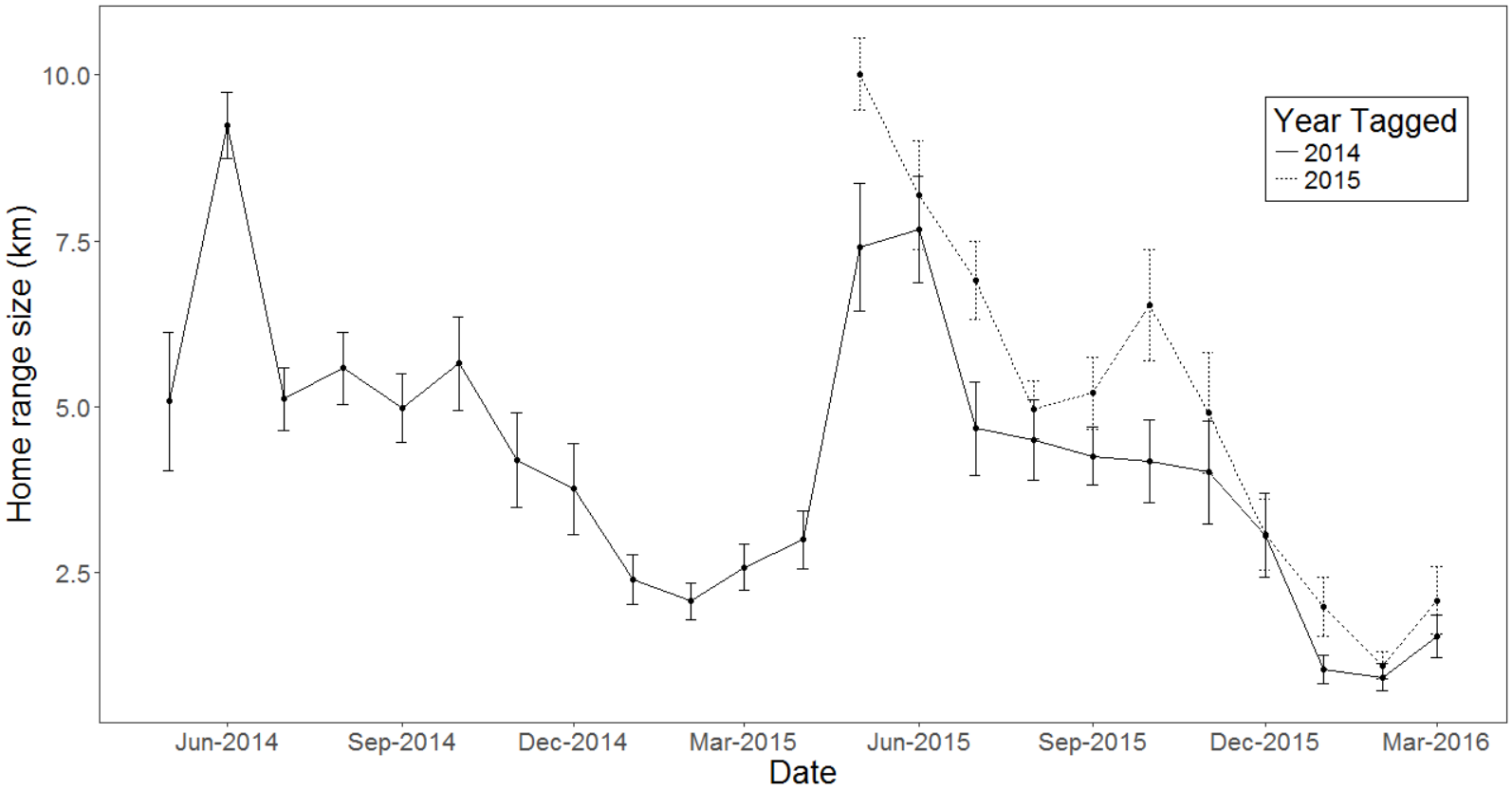
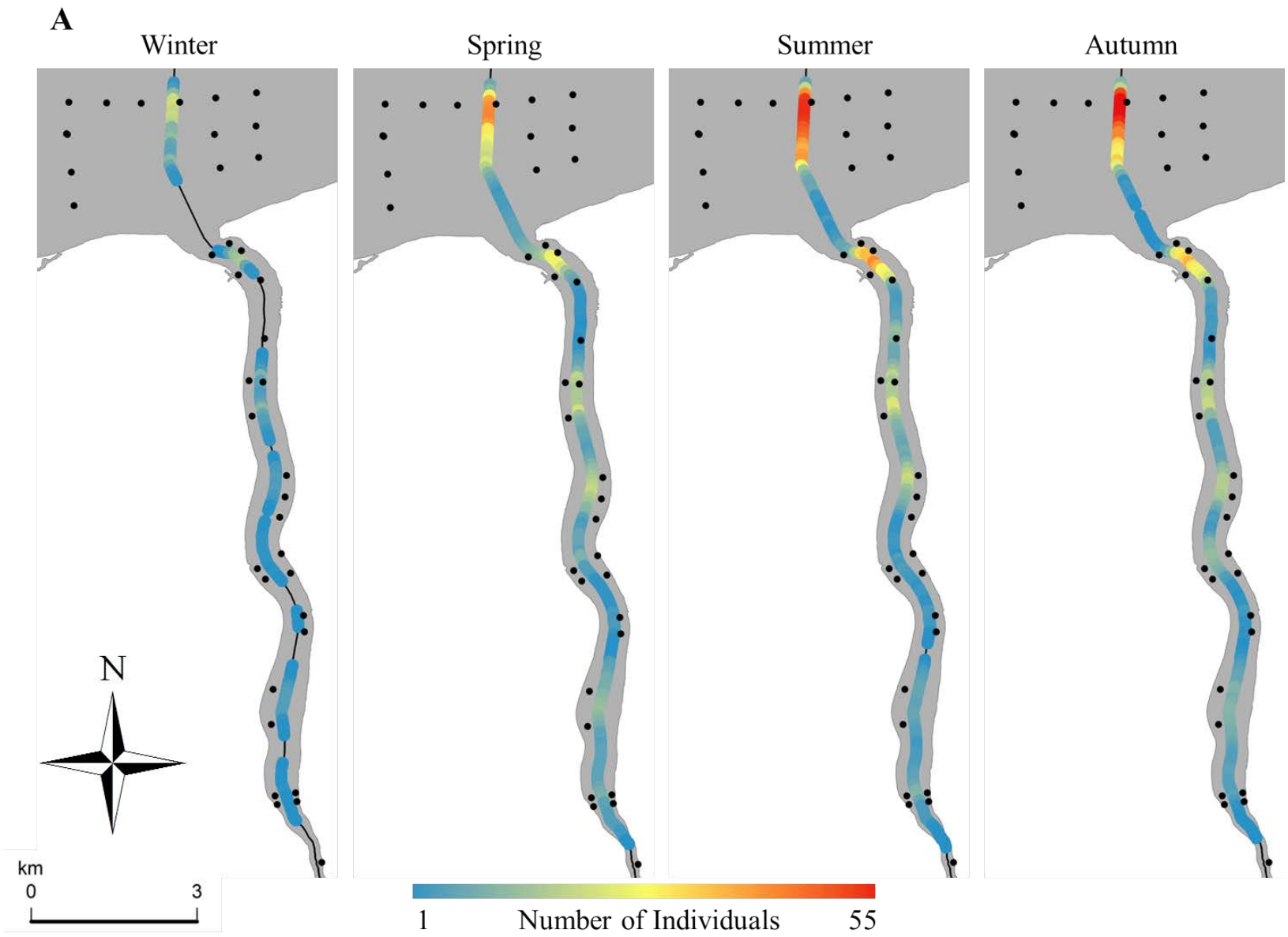


Figure 12. Mean monthly home range size of lake sturgeon tagged in 2014 and 2015.


A
Winter
Spring
Summer
Autumn
N
km
0
3
1
Number of Individuals
55

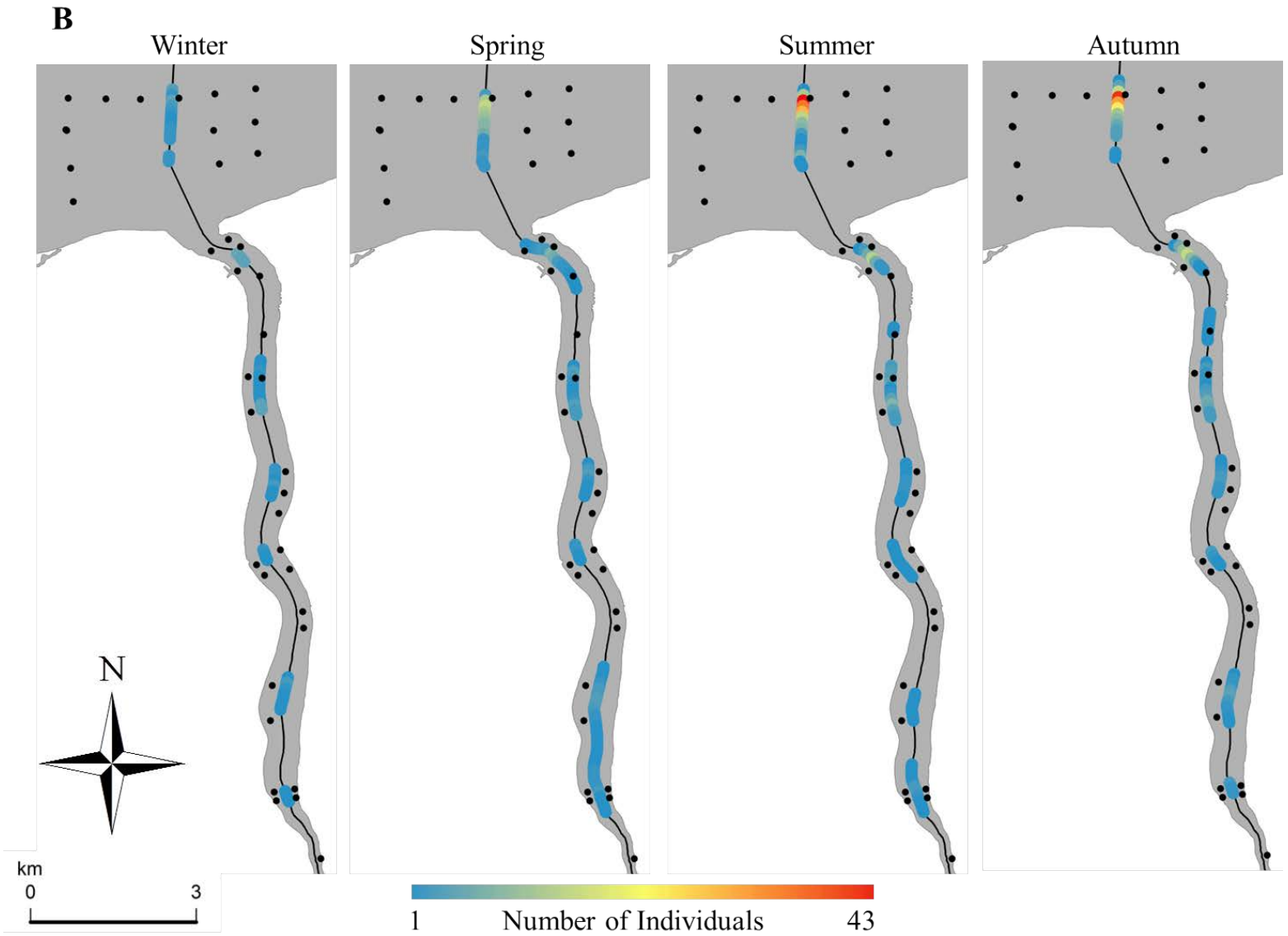


Figure 13. Degrees of overlap within the (A) 95% and (B) 50% linear kernel densities by season. Warmer colors indicate areas used by more tagged individuals.