Status of Lake Sturgeon (Acipenser fulvescens Rafinesque 1817) in North America

By R. M. Bruch¹, T. J. Haxton², R. Koenigs¹, A. Welsh³ and S. J. Kerr²

¹Wisconsin Department of Natural Resources, Oshkosh, WI, USA; ²Ontario Ministry of Natural Resources and Forestry, Peterborough, ON, Canada; ³School of Natural Resources, West Virginia University, Morgantown, WV, USA

Summary
Lake Sturgeon is a potamodromous, fluvial-dependent species from the family Acipenseridae, and one of the largest freshwater fishes within its North American range extending to the Great Lakes, Mississippi River, and Hudson Bay drainages. Like almost all other sturgeon species, Lake Sturgeon populations throughout its range suffered mass declines or extirpation in the late 1800s into the early 1900s, due to extensive overexploitation and habitat loss and alteration. However, Lake Sturgeon are still present in low to high densities throughout their native range due primarily to factors including: the species long life span and resiliency, the remote location of many northern populations, long-term pro-active management programs effectively controlling exploitation, improved habitat and water-quality conditions, and recovery programs that have been in effect since the late 1970s. Recovery programs initiated in the late 1970s are now just beginning to show signs of natural recruitment from populations re-built with stocked fish. Large sustainable recreational Lake Sturgeon fisheries with annual harvests of up to 45 000 kg and a commercial fishery with an annual harvest of up to 80 000 kg still exist and are maintained for Lake Sturgeon due primarily to rigid regulations, harvest controls, enforcement, and user involvement. The prognosis for the species is generally good, although habitat loss and maintaining public interest in the species management and recovery continue to be the greatest threats to local and regional populations. Hydro-power development, especially in the northern part of the species’ range, is especially challenging due to the potential negative impact this type of development can have on a long migrating fish like Lake Sturgeon. Advances in understanding Lake Sturgeon life history, habitat requirements, and distribution within and among water systems has strongly indicated that dams and Lake Sturgeon can co-exist, if the correct planning and necessary mitigative techniques are employed at each site on a case-by-case basis.

Phylogeny
Fossil evidence indicates that sturgeons evolved as a phyletic group approximately 200 million years ago (Bemis et al., 1997). Although Acipenseriformes is generally agreed by taxonomists to be a monophyletic group, the phylogenetic relationships of the genus Acipenser has been questioned with suggestions that the members of the genus do not share a single synapomorphic molecular character indicating possible multiple evolutionary lineages (Birstein et al., 2002). In any event, members of the genus share numerous common morphological features, although LS is the only species in the genus that naturally completes all of its lifecycle in freshwater (i.e. potamodromous).

Distribution and general abundance
LS have one of the widest natural distributions of all freshwater fish in North America (Harkness and Dymond, 1961) and were historically found in the Mississippi, Great Lakes–St.Lawrence River, and Hudson Bay drainages (Fig. 1). Their native range extends from the Hudson Bay southward to the southern border of Arkansas and eastward to the Tennessee River in Alabama, and from the foothills of the Rocky Mountains in Alberta to the estuary of the St. Lawrence River approximately 110 km east of Quebec City (Harkness and Dymond, 1961; Scott and Crossman, 1973).

Historically, LS were considered abundant (Harkness and Dymond, 1961; Tody, 1974). Commercial harvest records from the Great Lakes provide some insight into historical abundance of LS with documented annual harvest of up to one million kg from a single lake (Harkness and Dymond, 1961; Auer, 1999a; OMNR, 2009). Using the commercial

U.S. Copyright Clearance Centre Code Statement: 0175-8659/2016/32S1–162$15.00/0
harvest data for each of the Great Lakes, initial LS biomass was estimated to range from 313,000 kg in Lake Superior to 6,473,000 kg in Lake Erie (Table 1; Haxton et al., 2014a).

However, LS abundance has been greatly reduced in the Great Lakes, and throughout much of their range, (Hubbs and Lagler, 1947) to the extreme low levels where Great Lakes populations are now estimated to be <1% of historical numbers (Hay-Chmielewski and Whelan, 2003). Across their range, LS are currently considered extirpated in four states, endangered in 11 states and provinces, threatened in four states and provinces (considered threatened in only a portion of Ontario), and of special concern in four states and provinces (Table 2). The International Union on the Conservation of Nature (IUCN; www.iucnred-list.org), however, globally lists the status of LS as least concern. The largest LS populations remaining are believed to exist in the St. Lawrence River east of Montreal in Canada (Mailhot et al., 2011), the Lake of Woods/Rainy River population in the United States (Heinrich and Friday, 2014), the Winnebago System in United States (Bruch, 1999), and St. Clair Lake within the Great Lakes (Peterson et al., 2007).

As such, the present range of LS is somewhat retracted from the historical distribution with the species being either absent or sparsely populated in some areas, especially in the far southern and southeastern portions of the range. Several rivers flowing into Hudson Bay represent the last unfragmented habitat (Dynesius and Nilsson, 1994; Nilsson et al., 2005; OMNR, 2009) where LS exist. The remoteness of these populations likely prevented them from the excessive harvests of the late 1800s and early 1900s as fishermen moved inland to tributaries and rivers following population crashes in the Great Lakes (Bemis and Findeis, 1994). Therefore, these populations could be important as they provide the only glimpse into the dynamics of 'pristine' populations.

**Table 1**

<table>
<thead>
<tr>
<th>Waterbody</th>
<th>Estimated historical biomass (1000s kg)</th>
<th>Standard deviation</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Superior</td>
<td>314</td>
<td>99</td>
<td>241</td>
<td>590</td>
</tr>
<tr>
<td>Lake Michigan</td>
<td>3909</td>
<td>1224</td>
<td>3017</td>
<td>7148</td>
</tr>
<tr>
<td>Lake Huron</td>
<td>1929</td>
<td>662</td>
<td>1507</td>
<td>3532</td>
</tr>
<tr>
<td>Lake St. Clair</td>
<td>2054</td>
<td>564</td>
<td>1609</td>
<td>3644</td>
</tr>
<tr>
<td>Lake Erie</td>
<td>6473</td>
<td>2133</td>
<td>5028</td>
<td>11470</td>
</tr>
<tr>
<td>Lake Ontario</td>
<td>1044</td>
<td>321</td>
<td>805</td>
<td>1916</td>
</tr>
</tbody>
</table>

**Population metrics**

**Current abundance**

Populations of LS that currently exist throughout the original range including native as well as new populations that are being restored, have adult abundance levels ranging from dozens of individuals, e.g., many Great Lakes tributaries (Holey et al., 2000) to tens of thousands of individuals, e.g., Winnebago System, WI (Bruch, 1999), Lake of the Woods/Rainy River (Heinrich and Friday, 2014), and lower St. Lawrence River (Dumont et al., 1987) (Fig. 1). The general trend in abundance seems to be positive for LS throughout its range in North America due to increased efforts to improve habitat and water quality, effectively manage or eliminate/minimize exploitation impacts, and improve and/or restore populations through stocking and transfers.
Age and growth

LS, like nearly all other sturgeon species, are known to be slow growing (Harkness, 1923; Schneberger and Woodbury, 1946; Cuerrier and Roussow, 1951; Probst and Cooper, 1954; Prieel and Wirth, 1971; Folz and Meyers, 1983; Rossetter et al., 1995; Bruch, 1999), late maturing (Winemiller and Rose, 1992) periodic life history strategists. While age is one of the most important datum collected on a fish for management purposes, accurate and precise ages are often difficult to collect for most fish species, especially for a long lived cartilaginous fish like LS. Sturgeon have a limited number of bony structures that can be used to estimate age of an individual with counting annual growth increments observed from cross sections of pectoral fin spines being the most commonly applied method. Accuracy of ages estimated from pectoral fin ray spines has been questioned for many years (Brennen and Caillet, 1989; Rien and Beamesderfer, 1994; Paragamian and Beamesderfer, 2003; Bruch et al., 2009). Rossiter et al. (1995) corroborated age estimates for LS by observing that the difference in age estimates derived from pectoral fin spines matched the years at liberty between capture events. However, this is not true validation as the captured fish were not of known-age and the study did not sample fish from the full array of potential ages. Bruch et al. (2009) reported a consistent underestimation error for LS over the age of 14 and developed a correction factor to assign age estimates potentially closer to the true age of the fish for the Winnebago system: True Age = 1.35073 × (Est Age0.9606)

Otoliths have been used and validated for LS (Bruch et al., 2009), but these structures are primarily composed of Vaterite (a thermodynamically unstable polymorph of calcium carbonate; all otoliths are comprised of stable Calcite, metastable Aragonite and/or unstable Vaterite) which make them difficult to work with. Further, fish need to be sacrificed to collect otoliths, which significantly limits their use in management of most LS populations.

The oldest LS age on record was a 94.3 kg (208 lb) fish taken from Lake of Woods, Ontario in 1953 and estimated to be 154 years of age (Online at: http://www.dfo-mpo.gc.ca/species-especes/species-especes/sturgeon6-esturgeon-eng.htm, accessed 10 January 2016). While no one knows for certain whether this fish was actually 154 years old, long term tagging studies have demonstrated that LS can live a very long time and that ages of 150 plus years are not unreasonable. LS biologists will eventually be able to discern the true maximum age of LS given the significant increases in tagging studies, especially studies with low or no-loss tags such as PIT tags in use since the 1990s. Also, almost all populations have been negatively impacted by exploitation and other factors before, during and after the time LS have been scientifically and systematically examined for age (since the 1940s), which would tend to reduce or eliminate the largest and oldest individuals in each population. This phenomenon would result in most LS populations being comprised generally of younger animals, in turn biasing any estimate of maximum age obtained from empirical data. Given the increases in protections and pro-active management that many LS populations in North America now enjoy, along with what we understand as the innate life history of the species, LS may be on track to exhibit their true growth and longevity potential before the year 2100.

Growth in length for LS is considered rapid for the first 10–15 years of life followed by relatively slow growth at the onset of puberty and eventual sexual maturation as energy is directed to gonadal development from somatic growth (Harkness, 1923; Magini, 1960; Scott and Crossman, 1973; Bruch, 2008). Growth in length for both sexes is similar in pre-pubescence, but becomes dimorphic in post-pubescence with females exhibiting faster growth rates and attaining larger sizes as adults (Bruch, 1999, 2008). Estimated length at age data (using corrected age data) for the Winnebago System indicate that both males and females reach 120 cm at age 20 with dimorphic growth resulting in males averaging 168 cm and females 187 cm at age 65 (Fig. 2; Table 3). Growth in LS varies among populations with exclusively lotic populations often exhibiting slower growth (Prieel, 1973) and populations with access to lentic feeding grounds exhibiting faster growth (Bruch, 2008). Growth also varies significantly within populations and within individual fish (Bruch, 2008; Haxton and Findlay, 2008), especially for mature males which typically grow very little following maturation (Bruch, 2008; Heinrich and Friday, 2014). This slow

Table 2

Jurisdictional status of lake sturgeon across states and provinces

<table>
<thead>
<tr>
<th>State/Province</th>
<th>Country</th>
<th>Designation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alabama</td>
<td>United States</td>
<td>Extirpated</td>
</tr>
<tr>
<td>Alberta</td>
<td>Canada</td>
<td>Endangered¹</td>
</tr>
<tr>
<td>Arkansas</td>
<td>United States</td>
<td>Extirpated</td>
</tr>
<tr>
<td>Georgia</td>
<td>United States</td>
<td>Extirpated</td>
</tr>
<tr>
<td>Illinois</td>
<td>United States</td>
<td>Extirpated</td>
</tr>
<tr>
<td>Iowa</td>
<td>United States</td>
<td>Endangered</td>
</tr>
<tr>
<td>Kentucky</td>
<td>United States</td>
<td>Endangered</td>
</tr>
<tr>
<td>Manitoba</td>
<td>Canada</td>
<td>Endangered¹</td>
</tr>
<tr>
<td>Michigan</td>
<td>United States</td>
<td>Threatened</td>
</tr>
<tr>
<td>Minnesota</td>
<td>United States</td>
<td>Special Concern</td>
</tr>
<tr>
<td>Missouri</td>
<td>United States</td>
<td>Endangered</td>
</tr>
<tr>
<td>Nebraska</td>
<td>United States</td>
<td>Threatened</td>
</tr>
<tr>
<td>New York</td>
<td>United States</td>
<td>Threatened</td>
</tr>
<tr>
<td>New Jersey, China</td>
<td>United States</td>
<td>Special Concern</td>
</tr>
<tr>
<td>North Dakota</td>
<td>United States</td>
<td>Unknown</td>
</tr>
<tr>
<td>Ohio</td>
<td>United States</td>
<td>Endangered</td>
</tr>
<tr>
<td>Ontario</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hudson Bay – James Bay population</td>
<td>Canada</td>
<td>Special Concern</td>
</tr>
<tr>
<td>Great Lakes-St. Lawrence population</td>
<td>Northwestern Ontario</td>
<td>Threatened²</td>
</tr>
<tr>
<td>Pennsylvania</td>
<td>United States</td>
<td>Endangered</td>
</tr>
<tr>
<td>Quebec</td>
<td>Canada</td>
<td>At Risk</td>
</tr>
<tr>
<td>Saskatchewan</td>
<td>Canada</td>
<td>Endangered²</td>
</tr>
<tr>
<td>Tennessee</td>
<td>United States</td>
<td>Endangered</td>
</tr>
<tr>
<td>Vermont</td>
<td>United States</td>
<td>Endangered</td>
</tr>
<tr>
<td>West Virginia</td>
<td>United States</td>
<td>Expirited</td>
</tr>
<tr>
<td>Wisconsin</td>
<td>United States</td>
<td>Special Concern</td>
</tr>
</tbody>
</table>

¹Proposed status by Committee on the Status of Endangered Species in Canada.
²Ontario Endangered Species Act.

**References**


to no-growth pattern emphasizes the need to minimize measurement error when measuring sturgeon lengths. Historically spawning and harvested LS on the Winnebago System were measured to the nearest 0.5 inch (1.27 cm) which, given the low mean annual growth increments, resulted in measurement error that could have been avoided had the fish been measured more accurately.

Weight and length

The greatest weight reported for LS was a 180 kg (396 lb) fish captured in the Roseau River, Manitoba (Manitoba Hydro, 2014). A review of recreationally caught LS from states and provinces in the upper Midwest US and Canada show a 122.5 kg angler-caught fish in Saskatchewan in 1962 and a 93.3 kg fish speared in Wisconsin in 2010 (Table 4).

Most LS reported in scientific literature, as well as in angler reports, rarely exceed 50 kg – another possible symptom of past overexploitation of the larger fish in many populations and/or a sign of younger average ages in the stock due to recovery taking place.

The weight–length relationships of LS vary depending upon the sex, maturity, and gonadal condition of the individual fish being sampled. Further, season and location of the population (lentic, lotic, north, south) can strongly influence length–weight relationships. For these reasons, there are dozens of weight–length relationships reported in the literature for LS (e.g. Cuerrier and Roussow, 1951; Probst and Cooper, 1954; Sunde, 1961; Royer et al., 1968; Priegel, 1973; Threader and Brousseau, 1986; Dumont et al., 1987; Nowak and Jessop, 1987; Sandilands, 1987; Fortin et al., 1992; McDonald, 1998; Jackson et al., 2002; Craig et al., 2005; Smith and Baker, 2005; Adams et al., 2006; Bruch, 2008; Lallaman et al., 2008; Bruch et al., 2011).

Weight and length are typically the data most consistently collected by fisheries biologists in field assessments. Given the serious measurement error in determining sturgeon lengths, and the inherent error with estimating age, weight is likely the one metric that can be collected relatively consistently and accurately. The problems with weight data stem from variation in weight at a certain length caused by factors mentioned earlier (i.e., sex, maturity, latitude, location).

Bruch et al. (2011) examined 63 W–L relationships of LS from 43 populations throughout their range and recommended that LS W–L relationships should be developed using data from fish representing different growth stanzas, as well as split by sex and stage of maturity when possible. Further, Bruch et al. (2011) recommended applying a new metric, the Modified Form Factor (mFF), as a quick and simple metric to compare mean condition among sturgeon stocks or between components within a stock. The mFF is represented by the equation:

\[
mFF = \frac{1000}{C^2 (10^{\log_{10}(a/C_0^2)} - b/C_0^3)}
\]

This metric can be used as a tool to evaluate the condition of a LS population, or groups within the population, by comparing their modified form factors to those derived from other LS populations whose weight–length relationships have already been described. Additionally, the condition of LS populations can be compared between regions using a Student's t-test to assess for significance. For example, you could compare two sets of modified form factors calculated from spawning males sampled in Wisconsin to spawning males sampled from Ontario stocks.

Fork length–total length relationship

Fork length to total length relationships were developed for LS from the Winnebago System in Wisconsin based on 388 paired measurements (range: 102–185 cm TL) as

\[
FL = (0.966663 \times TL) - 6.5506
\]

(F. M. Bruch, WDNR, unpubl. data). Comparatively, data collected from 33 paired measurements (range: 32–156 cm TL) from the lower Niagara River, New York, reported a fork length to total length...
relationship as \( FL = (0.96223 \times TL) - 5.85734 \) (Lowie et al., 2000). LS should be measured to the closest mm in total length (in lieu of fork length) in as consistent manner as possible to minimize measurement error and maximize precision.

### Age and size at maturity

The literature reports a wide range of sizes and ages of maturity for LS. Male LS have been reported to first mature at 76 cm (age 19–20) (Dubreuil and Cuerrier, 1950), 83 cm (age 14–15) (Probst, 1954; Cuerrier, 1966), 85–95 cm (ages 18–20) (Magnin, 1966), 102 cm (Bruch, 2008), and 114 cm (ages 14–16) (Priegel and Wirth, 1971). Female LS have been reported to first mature at 84 cm (age 26) (Dubreuil and Cuerrier, 1950), 90–100 cm (age 20–30) (Magnin, 1966), 122 cm (Bruch, 2008), 127 cm (age 22–25) (Probst, 1954; Cuerrier, 1966), and 139 cm (ages 24–26) (Priegel and Wirth, 1971). While variation in reported size at first maturity is not surprising for a slow growing, late maturing, and wide ranging fish like LS, it is likely that some of the spread in size and age at maturity could be attributed to factors such as limited sample sizes within a protracted size range of fish maturing for the first time and ageing error.

Male and female LS from the Winnebago System were found to reach maturity for the first time at 102 cm (age 14) and 122 cm (age 21) (Bruch, 2008), which are smaller sizes and younger ages than previously reported (Priegel and Wirth, 1975). Maturity modeling also revealed that the population of male LS should be measured to the closest mm in total length (in lieu of fork length) in as consistent manner as possible to minimize measurement error and maximize precision.

**Table 4**


<table>
<thead>
<tr>
<th>State/Province</th>
<th>Weight (kg)</th>
<th>Weight (lbs)</th>
<th>TL (cm)</th>
<th>TL (in)</th>
<th>Location</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Michigan</td>
<td>87.5</td>
<td>193</td>
<td>221</td>
<td>87</td>
<td>Mullet Lake</td>
<td>1974</td>
</tr>
<tr>
<td>Minnesota</td>
<td>42.8</td>
<td>94</td>
<td>178</td>
<td>70</td>
<td>Kettle River</td>
<td>1994</td>
</tr>
<tr>
<td>Ontario</td>
<td>76.2</td>
<td>168</td>
<td>175</td>
<td>69</td>
<td>Nottawasga River,</td>
<td>1982</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Georgian Bay</td>
<td></td>
</tr>
<tr>
<td>Saskatchewan</td>
<td>122.5</td>
<td>270</td>
<td></td>
<td></td>
<td>South Saskatchewan River</td>
<td>1962</td>
</tr>
<tr>
<td>Wisconsin (spearing)</td>
<td>96.3</td>
<td>212</td>
<td>214</td>
<td>84</td>
<td>Lake Winnebago</td>
<td>2010</td>
</tr>
</tbody>
</table>

LS fecundity for the Winnebago system: empirical data from spawning assessments, 98 and 122 cm, quite well. In the models suggested by Froese and Binothlan (2000) asymptotic length explained 85% of the variation of length at first maturity in males and 91% in females (based on 467 pairs of \( L_m \) and \( L_s \) encompassing 265 species of fish from 3 classes, 27 orders, and 88 families including 2 species of sturgeon).

The protracted age of first maturity observed for LS of the Winnebago System and the St Lawrence River, Quebec, Canada (Fortin et al., 1992) suggests a life history trait common for the family. A protracted age of first maturity has also been suggested for Shortnose Sturgeon (Acipenser brevisrostrum) (SNS) in the Saint John River estuary, New Brunswick, Canada (Dadswell, 1979), Kaluga (Huaco dauricus) in the Amur River, Russia (Krykhtin, 1986), and Atlantic Sturgeon (Acipenser oxyrinchus oxyrinchus) (AS) in the Hudson River, New York, USA (Van Etenaenam et al., 1996) indicating this life history trait may be common to many of the species within the family Acipenseridae. Literature citations, when reporting size and age of maturity of sturgeon typically provide estimates of size and age of first maturity, but rarely provide the size and age of full recruitment of males and females to the mature stock. The long span of time from earliest to latest maturation of individuals in a sturgeon stock, and relatively old age of 50% maturity provides additional insight into the vulnerability of sturgeon stocks to recruitment overfishing and to why so many stocks have quickly collapsed when subjected to high harvest rates.

**Fecundity**

Fecundity of LS has been reported by Cuerrier (1949 – original data cited in Harkness and Dymond, 1961), Dubreuil and Cuerrier (1950), Harkness and Dymond (1961), Sandilands (1987), and Bruch et al. (2007; Table 5). All of these studies examined a relatively low number of fish, and, except for Bruch et al. (2007), it is unknown whether the authors accounted for ovarian tissue mass or volume, or whether the ovaries examined were in an F4 or ‘black egg’ stage of development (Bruch et al., 2001). Knowledge of fecundity is important not only for increasing the basic understanding of LS life history, but also to allow the use of fecundity as a variable in population dynamic modeling exercises. Bruch et al. (2007) suggested the following models for estimating LS fecundity for the Winnebago system:
Developing functional and useful population models for any fish species requires data to be consistently collected over many years. This may be problematic for sturgeon given their long life span and difficulties encountered when attempting to sample populations. Models characterizing metrics such as age, growth, fecundity, weight-length, and eggs per recruit are fairly straightforward and not as data intensive as models providing long term estimates of mortality and recruitment rates. All of these models (provided they are built with quality data) provide insights into the dynamics of a sturgeon population that are critical for effective management, especially if the population is over many years. This may be problematic for sturgeon as most structures systematically underestimate the age of older fish) that spans a long enough time series.

Population models

Developing functional and useful population models for any fish species requires data to be consistently collected over many years. This may be problematic for sturgeon given their long life span and difficulties encountered when attempting to sample populations. Models characterizing metrics such as age, growth, fecundity, weight-length, and eggs per recruit are fairly straightforward and not as data intensive as models providing long term estimates of mortality and recruitment rates. All of these models (provided they are built with quality data) provide insights into the dynamics of a sturgeon population that are critical for effective management, especially if the population is exploited through recreational, commercial, and/or tribal fisheries.

Population models have been used successfully to better understand the population dynamics and set harvest limits for species such as Yellow Perch (Perca flavescens) (Wiberg et al., 2005), Lake Trout (Salvelinus namaycush) (Linton et al., 2007), and Lake Whitefish (Coregonus clupeaformis) (Ebener et al., 2005), but they have had little application as a tool to better understand or manage sturgeon populations or harvest. At issue of course is first having accurate age data (which is typically very problematic for sturgeon as most structures systematically underestimate the age of older fish) that spans a long enough time series. Pine et al. (2001) estimated a total annual mortality rate of 16% using an age-structured cohort analysis model to examine population growth and mortality trends of the Gulf Sturgeon (Acipenser oxyrinchus desotoi) (GS) over a 10-year period, 1986–95. Haxton et al. (2014a) used a Bayesian approach with a surplus production model to estimate LS abundance and intrinsic rate of increase for the Great Lakes prior to the high exploitation period beginning in the late 1800s. Few other references of age-structured analysis on sturgeon exist in the literature, likely due to the lack of long term catch at age data for sturgeon fisheries, in part because most sturgeon fisheries have been shut down.

Using 60 years of Winnebago LS harvest data, Bruch (2008) developed a statistical catch at age model (SCAA), as well as a series of other models, to estimate various LS population metrics and parameters including: intrinsic rate of population increase, natural mortality rate, length infinity, stock-recruitment parameters, and $F_{0.1}$ yield per recruit. Haxton et al. (2014a) and T. J. Haxton (Ontario Ministry of Natural Resources (OMNR), Peterborough, ON, unpubl. data) also estimated some LS parameters including historic intrinsic rate of population increase for the Great Lakes, and LS growth model parameters and metrics for LS populations across Canada. These parameter estimates are listed in Table 6.

While simulation modeling can be used to predict a sturgeon population’s sustainability and assess extinction risk from alternative management strategies, sufficient long term sturgeon population data are often not available to allow estimation of model parameters with confidence. Thirty years of sturgeon catch data from the lower Danube River in Serbia were used to predict the extinction of the Beluga (Huso huso) in 450 years, and Russian Sturgeon (Acipenser gueldenstaedtii) in 50 years (Lenhardt et al., 2006). Twenty-four years of demographic population assessment data were used to predict the extinction in 30 years of the endangered White Sturgeon (Acipenser transmontanus) (WS) in Kootenai River, Idaho, USA (Paragamian and Beamesderfer, 2004). A long term stochastic trends simulation model for the Winnebago System LS population utilizing 60 years of harvest and population assessment data and parameters from SCAA and stock-recruitment models found that the Winnebago LS population could be maintained at stable levels capable of supporting the annual winter spear fishery at exploitation rates up to the current limit of 4.7%. This was
Table 6
LS population dynamic parameter and metric estimates from Great Lakes region and Canada ($r =$ intrinsic rate of population increase; $M =$ natural mortality rate (age 1 and older); $L_{\infty}$ = length infinity (cm) from von Bertalanffy (vB) model; $K =$ Brody growth coefficient from vB model; YPR $F_{0,1} =$ yield per recruit at a fishing mortality rate 10% of maximum in kg/recruit and a recruit size of 95 cm and age of 12 years and an annual exploitation rate of 3.8%; $u_{\text{max}} =$ sustainable annual exploitation rate). (Haxton p.c. = pers. comm. Haxton, T., Ontario Ministry of Natural Resources, Peterborough, ON)

<table>
<thead>
<tr>
<th>Location, sample type (reference)</th>
<th>Sample type</th>
<th>$r$</th>
<th>$M$</th>
<th>$L_{\infty}$</th>
<th>$K$</th>
<th>YPR $F_{0,1}$</th>
<th>$u_{\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winnebago System unsexed (Bruch, 2008)</td>
<td>Unsexed</td>
<td>0.049–0.138</td>
<td>0.055</td>
<td>2.83</td>
<td>4.7%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winnebago System (Bruch, 2008)</td>
<td>YOY</td>
<td>21.7</td>
<td>16.70</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winnebago System (Bruch, 2008)</td>
<td>Juvenile age 1–12</td>
<td>98.1</td>
<td>0.230</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winnebago System (Bruch, 2008)</td>
<td>Male age 13–69</td>
<td>166.4</td>
<td>0.052</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winnebago System (Bruch, 2008)</td>
<td>Female age 13–96</td>
<td>188.9</td>
<td>0.045</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Great Lakes (Haxton et al., 2014a)</td>
<td>Unsexed</td>
<td>0.079–0.123</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Attawapiskat River (Haxton p.c.)</td>
<td>Unsexed</td>
<td>142.1</td>
<td>0.04</td>
<td></td>
<td>2.0–3.1%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Huron (Haxton p.c.)</td>
<td>Unsexed</td>
<td>163.2</td>
<td>0.09</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Nipissing</td>
<td>Unsexed</td>
<td>165.4</td>
<td>0.08</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ottawa River (Haxton p.c.)</td>
<td>Unsexed</td>
<td>131.9</td>
<td>0.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rainy River (Haxton p.c.)</td>
<td>Unsexed</td>
<td>166.5</td>
<td>0.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winnipeg River (Haxton p.c.)</td>
<td>Unsexed</td>
<td>166.4</td>
<td>0.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Corroborated with a surplus production model estimating sustainable exploitation rates of 4% (2.4–6.1%; Haxton et al., 2014a). Annual exploitation maintained at an average of 3.2%, the average rate from 1997 to 2007, would result in a robust stock of adult females, but at a level 28.3% less than the estimated abundance of the stock with 0% exploitation (Bruch, 2008).

While limited in number, the available sturgeon population simulation models support the common paradigm that sturgeon are very susceptible to overharvest and provides some insight into possible dynamics of stocks exploited at various levels. A modest increase in total annual mortality from 16% to 20% was predicted to cause the GS to decline towards extinction (Pine et al., 2001). Similarly, Shovelnose Sturgeon (Scaphirhynchus platyrhynchus) (SVS) in the Missouri River System were sensitive to even low levels of exploitation (Quist et al., 2002). The simulation model for LS of the Winnebago System predicted a decline in adult stocks to lower and lower levels as exploitation increased from zero. Despite being at lower levels the population appeared to be relatively stable until the number of adult females dropped below 300 and exploitation persisted at 20% or more, after which the model predicted the population was driven to extinction (Bruch, 2008).

Recruitment
Young sturgeon (in the first few years of life) are often difficult to capture in a consistent and reliable manner (Kempinger, 1996; Kennedy et al., 2007; Paragamian and Hansen, 2008), therefore recruitment estimates and stock recruitment models are lacking in the sturgeon literature. Recruitment estimates for sturgeon populations have typically been made through hindcasts of age estimates (Thomas and Haas, 2001; Quist et al., 2002; Woodland and Secor, 2007) or catch rates of first recruits to the fishery (Priegel and Wirth, 1975; Baker, 1980). Accurate recruitment estimates from hindcasts assume that age estimation error is low enough to accurately identify birth years, whereas pectoral fin rays systematically underestimate the age of fish age 14 and older (Bruch et al., 2009). Furthermore, age estimates derived from pectoral fin rays sampled from known-age fish (ages 6–14) from the Winnebago System yielded poor precision between readers, suggesting that age data even on younger fish may not adequately track individual year classes [R. Koenigs, WI Department of Natural Resources (WDNR), Oshkosh, WI, unpubl. data]. While age estimates from other sturgeon species and populations may not exhibit the same error observed for LS from the Winnebago System, the likelihood of significant error is high and therefore needs to be considered when using ageing data to estimate recruitment. Estimating recruitment through catch rate of new recruits into a fishery may also be prone to error if ages assigned are inaccurate.

While the literature offers little quantitative information about LS recruitment, Bruch (2008) estimated the number of LS yearling recruits and 21-year-old female recruits in the Winnebago System from a SCAA model based on age data corrected for age estimation error for the years 1954–2007. The stock–recruitment relationship between adult females and yearling recruits was best defined by a Ricker model:

$$ R_t = 20.07706 \times S \times e^{0.000445 \times S} + \varepsilon, $$

where model parameters $\alpha = 20.07706$, and $\beta = 0.000445$, and $R$ = the number of yearling recruits produced by $S$, the number of adult females in the stock the year prior, and $\varepsilon$ representing stochastic error.

The stock–recruitment relationship between adult females and 21-year-old female recruits was best defined by a Ricker model:

$$ R_t = 2.99395 \times S \times e^{0.000436 \times S} + \varepsilon, $$

where model parameters $\alpha = 2.99395$, and $\beta = 0.000436$, and $R$ = the number of 21-year-old female recruits produced by $S$, the number of adult females in the stock 21 years prior, and $\varepsilon$ representing stochastic error.
Further, Bruch (2008) reported that the yearling/adult estimate from SCAA models was 0.941 (SD 0.974) and that adult stock density heavily influenced yearling/adult estimates (range 0.011–2.597 yearlings per adult). The strength of the inverse S–R relationship was surprising given that LS in the Winnebago System were never observed preying on their young (Stelzer et al., 2008), although LS have been often observed preying on their eggs (Bruch and Binkowski, 2002). Paragamian and Hansen (2008) applied a stochastic density dependent simulation model to estimate that a recruitment level of 0.4 yearlings per adult was needed for recovery of the Kootenai River WS population in Idaho, USA.

If other sturgeon species or populations have recruitment rates as wide-ranging and exhibiting density dependent Ricker stock-recruit patterns similar to those suggested by the Winnebago System LS SCAA model, it, may be difficult to discern these relationships for stocks at low adult densities, or for populations with insufficient data to model recruitment. On the other hand, low density sturgeon populations with a Ricker style stock–recruit relationship should have good potential to produce large numbers of yearling recruits providing adequate spawning and nursery habitats are available and adult abundance has not dipped below a critical threshold. For example, the greatest yearlings/adult production for the Winnebago stock (2.590), was estimated from a point of lowest adult density (7302) in 1968 (Bruch, 2008).

### Mortality

Natural mortality is generally estimated by subtracting an estimate of instantaneous fishing mortality (F) from total instantaneous mortality (Z), which can be estimated as the negative slope of the descending arm of a catch curve (Ricker, 1975). However, catch curves are only as accurate as the age estimates that produced them. Given the potential sturgeon age error issues (Bruch et al., 2009), it is probable that the majority of catch curves previously developed for sturgeon using un-validated age estimates produced inaccurate over-estimates of Z. Instantaneous natural mortality rates (M) of LS populations have been estimated at 0.076 (Black Lake, MI, Baker, 1982), 0.072 (Groundhog and Mattagami Rivers, Ontario, Nowak and Jessop, 1987), 0.12–0.20 (St. Lawrence River, Quebec, Dumont et al., 1987), and 0.055 (Bruch, 2008). Bruch (2008) used corrected age data incorporated into a SCAA model to estimate instantaneous natural mortality (M) of 0.055, and a conditional natural mortality rates (n) for age 1 and older LS of 5.4%. Pauly’s (1980) equation applied to the same Winnebago LS data estimated instantaneous and conditional natural mortality to be 0.0715 and 6.9% (Bruch, 2008). Pauley’s equation (Pauly, 1980), has also been used to produce estimates of M of 0.049–0.70 for WS in the lower Columbia River, Oregon and Washington, USA (Beamesderfer et al., 1995), and 0.04 for Beluga in the southern Caspian Sea, Iran (Taghavi, 2001).

Estimates of M of other sturgeon species derived from catch curves include 0.020 for SNS in the Hudson River, New York, USA (Woodland, 2005), 0.108–0.138 for SNS in the St. John River Estuary, New Brunswick, Canada, 0.07 for Pallid Sturgeon (Scaphirhynchus albus) (PS) in the Mississippi River, USA (Killgore et al., 2007), 0.10 for WS in the lower Columbia River, Oregon and Washington, USA (DeVore et al., 1995), and 0.092 for WS in the Kootenai River, British Columbia, Canada, and Montana and Idaho, USA (Paragamian et al., 2005).

Taghavi (2001) also used a model suggested by Richter and Efano (1976) using age of 50% maturity to estimate M:

\[
M = \frac{(1.521/150\%_{\text{Mat}}^{0.72}) - 0.155}{\text{Ln}Z - 1.46 - 1.01 \times \text{Ln}t_{\text{max}}},
\]

where: \(t_{50\%_{\text{Mat}}}\) = age of 50% maturity, which provided estimates of M for male and female Beluga of 0.05 (\(t_{50\%_{\text{Mat}}} = 16\)) and 0.03 (\(t_{50\%_{\text{Mat}}} = 18\)). Bruch (2008) applied the \(t_{50\%_{\text{Mat}}}\) formula to male and female maturity data (19 and 27) from Winnebago System LS to derive estimates of M of 0.028 and –0.013 (a negative M for females).

Finally, Kennedy and Sutton (2007) used a model suggested by Hoenig (1983) relating total instantaneous mortality to fish maximum age:

\[
\text{Ln}Z = 1.46 - 1.01 \times \text{Ln}t_{\text{max}},
\]

to estimate an M of 0.115 for SVS in the upper Wabash River, Indiana, USA. Applying this model to LS demographics from the Winnebago System, Bruch (2008) estimated M’s of 0.035 for males and 0.001 for females (given empirical estimates of F and \(t_{\text{max}}\) for males and females of 0.024, 70, and 0.040, 100).

While it is well understood that pectoral fin rays, and other aging structures underestimate that age of older fish (Bruch et al., 2009), underestimating the age of older fish leads to overestimates of Z and consequently M, if F is accurately estimated. Despite the potential error from use of un-validated age data, and the potential shortcomings of generic mortality models, nearly all of the estimates of natural mortality for the various sturgeon species listed above are low and within a range that would be expected for slow-growing, late maturing, and long-lived animals exhibiting a k-selected or periodic (Winemiller and Rose, 1992) life history strategy.

Obviously the generic formulas for estimating M have important utility in the absence of other data for a particular fish stock, but their utility is somewhat limited, and until independent estimates of M are developed for various species and stocks, it is probably prudent to be careful about application of M estimates from these formulas, especially for species with intrinsically low M’s. The SCAA model estimate of 0.055 for Winnebago LS (Bruch, 2008) was developed using unsexed catch at age data. Given the differences in life history and dimorphic growth patterns exhibited by males and females (Bruch, 2008), it is reasonable to suspect that male and female LS may experience different natural mortality rates. An additional attribute of M more difficult to evaluate is its variability. Catch curve analysis could potentially provide some insight into M’s variability, but the error inherent in sturgeon age data may mask our ability to confidently determine the potentially narrow range of natural variation in M.
Lake Sturgeon are potamodromous and fluvial-dependent (Bemis and Kynard, 1997; Randall, 2008). However, they are known to tolerate brackish waters such as in the lower St. Lawrence River and in James and Hudson Bays (LeBreton and Beamish, 1998). Habitat requirements for LS vary seasonally and ontogenetically (Table 7). In rivers, LS spawning habitat is generally found in fast flowing areas of relatively shallow, well-oxygenated waters which are often below natural rapids, a dam, or an impassable barrier. Although LS are thought of as being philopatric, which has contributed to population structuring within large lakes (DeHaan et al., 2006; Welsh et al., 2008; Homola et al., 2010; Kerr, 2011), the species is also known for ‘wandering’ from home waters to take up residence and even join spawning groups in waters hundreds of kilometers away from home (R.M. Bruch, WDNR, Oshkosh, WI, unpbl. data; M. Donofrio, WDNR, Peshtigo, WI, pers. comm.; Heinrich and Friday, 2014). Spawning generally occurs in water depths 0.1–6.0 m (LaHaye et al., 1992; Lane et al., 1996; Threader et al., 1998; Bruch and Binkowski, 2002; Wilson and McKinley, 2004; Chiotti et al., 2008), however, LS may spawn in deeper (up to 12 m) areas with adequate flows and substrate (Manny and Kennedy, 2002). Spawning flows are highly variable among populations but are generally between 0.34 and 2.0 m s\(^{-1}\) (Threader et al., 1998; Billard and Lecointre, 2001; Caswell et al., 2004; Johnson et al., 2006; Peterson et al., 2007; Chiotti et al., 2008). Spawning does not appear to consistently occur in areas with flows exceeding 2 m s\(^{-1}\) (LaHaye and Fortin, 1990) or <0.5 m s\(^{-1}\) (R.M. Bruch, WDNR, Oshkosh, WI, unpbl. data). In lakes, LS have also been observed spawning on rocky wave-exposed shoreline or areas having strong wind and/or stream driven currents (Nevin, 1919; Galarowicz, 2003). Spawning areas are generally comprised of coarse (>2.1 mm) substrate (Peterson et al., 2007; Daugherty et al., 2008), with a preference to cobble and boulders (Threader et al., 1998) or coarse substrate interspersed with boulders and large rocks (LaHaye et al., 1992; Lane et al., 1996; Desloges et al., 2004). The availability of suitable spawning substrate is believed to be critical for reproductive success (Bemis and Kynard, 1997).

Habitat requirements of YOY and juvenile LS remains one of the largest information gaps pertaining to LS biology. LS YOY and juveniles generally select sandy areas devoid of vegetation (Kempinger, 1996; Peake, 1999; Benson et al., 2006).

<table>
<thead>
<tr>
<th>Life stage</th>
<th>Habitat characteristics</th>
<th>Preferred (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spawning</td>
<td>Water depth (m)</td>
<td>0.5–3.0 (0.3–10.0) Staging areas 2.0–10.0 m deep</td>
</tr>
<tr>
<td></td>
<td>Water velocity (m s(^{-1}))</td>
<td>0.5–2.0 (0.1–2.5)</td>
</tr>
<tr>
<td></td>
<td>Substrate</td>
<td>Coarse cobble, rubble and boulders.</td>
</tr>
<tr>
<td></td>
<td>Water temperature (°C)</td>
<td>12.0–16.0 (10.0–21.0)</td>
</tr>
<tr>
<td>Young-of-Year</td>
<td>Water depth (m)</td>
<td>Relatively shallow (2–5 m)</td>
</tr>
<tr>
<td></td>
<td>Water velocity (m s(^{-1}))</td>
<td>Reduced (&lt;1–2 cm s(^{-1})) but detectable current</td>
</tr>
<tr>
<td></td>
<td>Substrate</td>
<td>Fine substrates (sand and silt) devoid of vegetation</td>
</tr>
<tr>
<td></td>
<td>Water temperature (°C)</td>
<td>14.0–17.0</td>
</tr>
<tr>
<td>Subadult</td>
<td>Water depth (m)</td>
<td>5.0–10.0 (2.0–60.0)</td>
</tr>
<tr>
<td></td>
<td>Water velocity (cm s(^{-1}))</td>
<td>Detectable to moderate (25.0–50.0) current preferred (10.0–75.0)</td>
</tr>
<tr>
<td></td>
<td>Substrate</td>
<td>Clean sand, gravel, or clay substrates</td>
</tr>
<tr>
<td></td>
<td>Water temperature (°C)</td>
<td>&lt; 20.0</td>
</tr>
<tr>
<td>Adult</td>
<td>Water depth (m)</td>
<td>Relatively shallow (3.0–5.0) areas Overwinter pools 6.0–11.0 in depth</td>
</tr>
<tr>
<td></td>
<td>Water velocity (cm s(^{-1}))</td>
<td>&lt; 70.0 (0.0–80.0)</td>
</tr>
<tr>
<td></td>
<td>Substrate</td>
<td>Flat areas having silt, sand or clay substrate</td>
</tr>
<tr>
<td></td>
<td>Water temperature (°C)</td>
<td>&lt; 20.0</td>
</tr>
</tbody>
</table>

Table 7
General habitat requirements of lake sturgeon by life stage (from Kerr et al., 2011)
Juvenile LS have also been observed in areas of sand and pea gravel immediately below woody debris (Holtgren and Auer, 2004) and organic substrate types (Smith and King, 2005b). Although YOY LS generally have been observed to select shallow areas <2 m (Benson et al., 2005), more specifically, 0.2–0.55 m deep (Ecologistics Limited, 1987; Friday, 2006) or <0.75 m deep (Kempinger, 1996), YOY have also been observed to utilize deeper offshore habitat at mean depths of 9 m (Smith and King, 2005b). YOY and juvenile LS are typically observed in water velocities <0.3 m s⁻¹ (Friday, 2006) to <0.6 m s⁻¹ (Benson et al., 2005).

Field studies indicate that LS appear to spend most of their first summer in the lower stretches of spawning rivers and adjacent bays (Auer and Baker, 2002; Baker, 2006; Daugherty et al., 2008), with some age-0 LS leaving their natal river as water temperatures decline (Caroffino et al., 2009) and as gravid adults move upriver to winter pre-spawn staging areas (R.M. Bruch, WDNR, Oshkosh, WI, unpubl. data). Yearling LS are often found in bays or near a river mouth (Harkness and Dymond, 1961). Subadults [individuals >80 cm TL, <115 cm TL, and approximately age 15 (Haxton et al., 2008)] are believed to occupy different habitat types than adult LS. They are often found in deeper offshore waters of lakes (Smith and King, 2005b). Overall, early life stages of LS select habitats providing an abundance of food along with protection from predators (Randall, 2008).

Juvenile LS, the stage from YOY (i.e., yearlings) to the onset of maturity including subadults, demonstrate high site fidelity and displays localized movement (Haxton, 2003; Lord, 2007). Juveniles (subadults) generally select deeper water depths than adults (Holtgren and Auer, 2004; Smith and King, 2005b) and are generally found in water depths 3–8 m (Harkness and Dymond, 1961; Threader et al., 1998; Nilø et al., 2006), but rarely in depths >14 m (Threader et al., 1998). Holtgren and Auer (2004), however, captured juveniles from depths 4–17 m, often in depths >10 m, whereas Smith and King (2005b) captured juvenile LS from depths of 5.4–13.4 m. In large, deep rivers, juveniles were selective to 12–18 m (Lord, 2007; Haxton, 2011), and purportedly seek deeper sections of rivers (Smith and King, 2005b; Barth et al., 2009). Habitat preference is perceived to be largely determined by food abundance (Chiasson et al., 1997; Beamish et al., 1998) however, food availability is not necessarily always the primary factor (Nilø et al., 2006). Sandy habitat is preferred (Mosindy and Rusak, 1991; Lane et al., 1996; Chiasson et al., 1997; Benson et al., 2005; McCabe et al., 2006; Nilø et al., 2006), but juveniles will also select gravel (Smith and King, 2005b; McCabe et al., 2006; Lord, 2007), clay (LaHaye, 1982; Chiasson et al., 1997), and organic substrates (Smith and King, 2005b; McCabe et al., 2006). Flow velocities of 0.4–0.75 m s⁻¹ (Threader et al., 1998) or 0.25–0.5 m s⁻¹ (Nilø, 1996) are preferred. Juveniles have rarely been found in velocities exceeding 0.7 m s⁻¹ (Billard and Lecointre, 2001).

Adult LS are bottom dwellers, prefer moderately turbid waters, and often frequent productive lake shoals and river deltas (Cech and Doroshov, 2004). They have been mostly observed residing in shallow water, preferring depths 3–9 m (Houston, 1987; Knights et al., 2002; Smith, 2003; Wilson and McKinley, 2004), but have been caught as deeps as 43 m (Harkness and Dymond, 1961; Scott and Crossman, 1973). Habitat selectivity is highly variable among LS adult populations and is dependent on habitat available in the waterbody (Haxton et al., 2008). Silt, or mixture of silt/sand is preferred substrate (Haugen, 1969; Morse et al., 1997; Threader et al., 1998; Knights et al., 2002), however, LS have also been reported to select for organic (Hay-Chmielewski, 1987; Morse et al., 1997; Nilø et al., 2006), clay (Chiasson et al., 1997), sand, gravel and rubble substrates (Seyler, 1997). Adult LS are rarely found among aquatic vegetation (Baker, 2006).

Lake Sturgeon have been found to select and congregate in pools for overwintering (Harkness and Dymond, 1961; Kerr, 2011). These sites are generally 6–11 m in depth (McKinley et al., 1998; Threader et al., 1998) but rarely deeper than 10 m in Lake of the Woods (Rusak and Mosindy, 1997).

Food habits
Lake Sturgeon have historically been thought to be generalist opportunistic benthic feeders that preyed primarily on the most available and abundant benthic macroinvertebrates in the specific system the LS population happened to be residing in. Typical prey items historically reported included various species of Ephemeroptera, Diptera, Mollusca, and Decapoda with fish present as an occasional and almost accidental ingestion (Bajkov, 1930; Schneberger and Woodbury, 1946; Probst and Cooper, 1954; Harkness and Dymond, 1961; Magnin and Harper, 1970; Priegel and Wirth, 1971; Magnin, 1977). Diet studies on LS since the early 1990s have confirmed the importance of benthic macroinvertebrates in the LS diet throughout its range, but have also revealed that the species will consume large quantities of fish, plankton, and their own eggs in some situations and/or life history stages. Choudhury and Dick (1993) characterized the gastrointestinal parasite assemblage of LS in the Winnebago System, Wisconsin. They found no fish in the samples they examined at that time, but found significant seasonal variation in prey selection by adults residing in Lake Winnebago, including substantial quantities of Cladocera, primarily Daphnia and Leptodora spp., in summer samples. Stelzer et al. (2008) reported a significant shift in the diet of adult LS in the Winnebago System between the early 1990s and the mid 2000s from strictly invertebrates to a mix of invertebrates and fish. Using stable isotope analysis Stelzer et al. (2008) showed that by the mid-2000s LS in the Winnebago System were acquiring 37% of their carbon from fish, exclusively Gizzard Shad (Dorosoma cepedianum) during the winter months when the shad experience an annual die-off and litter the bottom of the lake making them easy prey for foraging LS. Smith et al. (2016) also found that LS in the Rainy River System, Ontario also obtain a large portion of their energy from fish in their diet. Bruch and Binkowski (2002) reported observing LS, especially males, ingesting LS eggs on LS spawning sites in the Wolf River, Wisconsin in between spawning bouts with ovulating females or after spawning was completed at a site.
The results reported by Choudhury and Dick (1993), Stelzer et al. (2008), and Smith et al. (2016) reinforce the early conclusion that LS are indeed opportunistic feeders that will also feed pelagically for plankton and eat large quantities of fish if they are readily available. Recent work has shown that LS will also adapt quite readily to new prey items that come upon the scene. Gizzard Shad were rare in the Winnebago System prior to the early 1990s but became quite common and very abundant in the System in some years by the mid to late 1990s (R. Koenigs, WI DNR, Oshkosh, WI, pers. comm.). After zebra mussels (*Dreissena polymorpha*) became established and abundant in Oneida Lake, New York, LS began to utilize them as prey becoming the dominant prey item in fish >900 mm (de Lafontaine and Costan, 2002). Interesting though is the insignificant amount and occurrence of zebra mussels found in the diet of LS in the Winnebago System after the mussels became established and extremely abundant in those waters (Stelzer et al., 2008; R. Koenigs, WDNR, Oshkosh, WI, pers. comm.). These findings reaffirm other recent observations by Nilo et al. (2006) and Smith et al. (2016) that the species, while opportunistic, will be somewhat selective when choosing their prey, especially seasonally.

In summary, LS can be categorized as generalist opportunistic feeders, that also exhibit some seasonal prey selectivity as well as planktonic and piscivorous feeding behavior, including active feeding on their own eggs laid at spawning sites.

### Ontogenetic migrations

LS are potamodromous, migrating strictly within freshwater (Scholl, 1986; Kempinger, 1988; Rusak and Mosindy, 1997; Auer, 1999a,b; Knights et al., 2002). Due to their extensive migrations to feed and spawn, LS require watersheds having diverse and unobstructed habitat (Beamersdfer and Farr, 1997; Earle, 2002). Although Auer (1996a) suggested that a barrier-free distance of at least 250–300 km of lake/river range should be maintained to support self-sustaining LS populations, numerous populations in fragmented river systems maintain viable populations in sections of river as short as 45 km (Scholl, 1986; WDNR, 2000; Barth et al., 2011).

Changes in water temperature, water level and flows all provide environmental cues to LS (Auer and Baker, 2002; Bruch and Binkowski, 2002; Wishingrad et al., 2014). Natural flow regimes are important and sudden changes in river flow can initiate movements. Generally, LS have the tendency to move upstream during periods of increased discharge and drop back downstream when flows are decreasing (Borkholder et al., 2002). Similar seasonal movements are noted in spring and autumn (Kampa et al., 2014).

Lake Sturgeon will migrate upstream past seemingly ideal spawning areas to spawn at sites further upstream (Harkness and Dymond, 1961; Bruch and Binkowski, 2002), and will consistently spawn at the base of dams (Kempinger, 1988; LaHaye et al., 1992; Auer, 1996a,b, 1999b; D’Amours et al., 2001; Bruch and Binkowski, 2002; Haxton, 2003). Prolonged swimming speeds have been found to be 45–75 cm s\(^{-1}\) with burst speeds in the range of 75–85 cm s\(^{-1}\) (Hoover et al., 2005). Migrations to spawning areas can occur either in the autumn or the spring (Bemis and Kynard, 1997). Staging areas in close proximity (<3 km) to spawning sites are important regardless of the timing of pre-spawn migrations (Daugherty et al., 2008).

Lake Sturgeon seemingly possess homing tendencies which enables them to return to their natal river or watershed (Boiko, 1993; Bemis and Kynard, 1997; Bruch and Binkowski, 2002; Baker, 2006; DeHaan et al., 2006; Welsh et al., 2008). However, spawning site fidelity of LS may be relatively weak on systems with numerous spawning sites (R.M. Bruch, Koenigs, K., WDNR, Oshkosh, WI, unpubl. data). LS from the Winnebago System have been observed utilizing different sites, as well as different rivers, from one spawning year to the next. Furthermore, males spawned at two or more sites in up to two different rivers within the same year (R.M. Bruch, Koenigs, K., WDNR, Oshkosh, WI, unpubl. data). The spawning migration behavior and site utilization of adults observed in the Winnebago System suggest that other LS populations exhibiting strong site fidelity may be doing so because suitable spawning habitat is limited on a consistent basis from year to year. Following spawning, adults generally return to feeding areas (Bemis and Kynard, 1997; Rusak and Mosindy, 1997; Thuemler, 1997; Bruch and Binkowski, 2002; Adams et al., 2006).

Following egg deposition at the spawning site, extensive egg predation may occur by LS, especially males, and other fish such as Catostomidae and Cyprinidae species, as well as by crayfish (Bruch and Binkowski, 2002). Paradoxically, the movement and feeding by predators actually cleans the substrate, which likely provides greater opportunity for water flow and circulation through the interstitial spaces where eggs are incubating below the substrate surface (Bruch and Binkowski, 2002). Mortality rates from eggs to YOY, and from larva to YOY on the Peshtigo River in Wisconsin, were estimated to be 99.9%, and 90.5–98.3% respectively (Carofino et al., 2010).

Yolk-sac larvae emerge about 11–19 da post peak spawn (LaHaye et al., 1992; Smith, 2003; Smith and King, 2005a). Peak drift occurs nocturnally between 2100 and 0200 hours (Kempinger, 1988; D’Amours et al., 2001; Smith, 2003) and generally drift downstream with currents dispersing as it dissipates. Duration of drift varies but has the potential of extending up to 40 da (Auer and Baker, 2002) which may be up to 40–50 km from their natal site within the first month (Dick et al., 2006).

Outside of spawning migrations, LS can sometimes be rather sedentary (Fortin et al., 1993; Haxton, 2003; Barth et al., 2011). Most LS move within their home range of 12–14 km (Peterson et al., 2007; Kampa et al., 2014) and display site fidelity despite the potential to move extensively (Borkholder et al., 2002; Knights et al., 2002; Haxton, 2003; Barth et al., 2011; Gerig et al., 2011; McDougall et al., 2013), although extensive movement has been observed to occur (Knights et al., 2002; Shaw et al., 2013; Wishingrad et al., 2014). Differences in minimum distance moved is typically not detectable among sexes or among seasons, however putatively reproductively ‘ready’ females travelled greater distances than non-reproductive females (Shaw et al., 2013).
Juvenile movement can be quite restricted within a regulated river with the majority of fish remaining within 1.5 km of their capture site (Barth et al., 2011). In Portage Lake, Michigan, Holtgren and Auer (2004) found that diurnal movements of juvenile and subadult LS were related to light intensity, moving into shallow water at night and back to deep water during the day. Age-0 LS have also been observed being more active at night (Benson et al., 2005). Adult movement is generally greater than subadult and juveniles (Trested et al., 2011; McDougall et al., 2013) and it appears that the latter life stages may be limited by flows and natural constrictions within some rivers (McDougall et al., 2013).

Juvenile (Altenritter et al., 2013) and adult LS (McKinley et al., 1998; Threader et al., 1998; Wishingrad et al., 2014) often move to deep pools or a lake environment supporting relatively low water velocities during winters. There is evidence of fidelity to overwinter habitats (Auer, 1996a,b; Knights et al., 2002; Wishingrad et al., 2014) but not consistently (Rusak and Mosindy, 1997). During this time, they have often been found in aggregations and to display sedentary behaviour (Rusak and Mosindy, 1997; Kerr et al., 2011; Shaw et al., 2013). It has not been demonstrated how important these overwintering areas are for LS survival, but winter habitat selection may be a behavioural response to highly dynamic lotic systems.

Reproduction and spawning

Spawning behavior

Lake Sturgeon spawn in late spring/early summer, depending on location, at temperatures between 9 and 18°C (Harkness, 1923; Scott and Crossman, 1973; Bruch and Binkowski, 2002; Nicols et al., 2003; Heinrich and Friday, 2014), and often exhibit a protracted period in which two or more spawning peaks occur in the same season. Typically, the same males participate in all of the peaks even if they are spread out over a month or longer (Auer and Baker, 2002; Bruch and Binkowski, 2002; Nicols et al., 2003). Bruch and Binkowski (2002) made extensive field observations of spawning LS in the Wolf and upper Fox Rivers in Wisconsin over a 20-year period and succinctly summarized LS spawning behavior:

Lake sturgeon display an intricate set of sexual behavior responses to water temperature during their spawning period. When water temperatures rise to 6.6–16.0°C, sturgeon begin exhibiting a porpoising behavior in the vicinity of the spawning grounds. As the water continues to warm, this behavior increases in intensity and continues until slightly past the peak of spawning activity. In the range of 8.8–16.0°C, males move onto the spawning grounds and begin cruising, apparently searching for signs of ovulating females. Individual females will move onto a site at water temperatures of 8.8–19.1°C, with the maximum number of females and heaviest spawning activity on a site occurring generally within 11.5–16.0°C. Lake sturgeon were observed spawning both during the day and night at wide temperature ranges, 8.8–21.1°C. Whereas males arrive first at the spawning site, females ultimately determine the duration of spawning through the timing and intensity of their use of that site. During the spawning act, activity also keys off the females, with the males responding to cues from the female to participate in 2–4 s spawning bouts during which a relatively small number of eggs (estimated 947–1444 eggs per bout) are released by the female into a cloud of sperm (estimated 200–800 billion sperm) from two to eight males. The males beat the abdomen of the female with their tails and caudal peduncles while ejaculating. While ejaculating, males emit a dull, thunderous vibrating sound which attracts other males to the area. The female initiates a spawning bout at approximately 1.5 min intervals and will continue oviposition for 8–12 h, even if the water temperature decreases or increases outside the optimal range (11.5–16.0°C). Spawning typically occurs for 2–4 days on each site, depending on the number of females utilizing the site. At cessation of the spawning season, Wolf River sturgeon quickly move back into the main river channel. While water temperature is a key environmental signal affecting the onset and duration of the spawning period, the rate of water temperature increases prior to spawning appears to influence the actual temperature at which spawning begins. Sturgeon exhibit complex polygamous mating behavior whereby several males may fertilize the eggs of a single female, and each male may participate in spawning with several females while on the spawning grounds. The breeding system is both polyandrous and polygynous, thereby maximizing the opportunities for mating with numerous individuals and subsequently maximizing the genetic diversity of the offspring.

Bruch and Binkowski (2002) also reported observing a phenomenon with LS spawning behavior in the Winnebago System known as the ‘2nd’ and ‘3rd spawning runs’, which has also been observed in other LS populations (Online at: http://www.sturgeonfortomorrow.org/research-2003-sum.php, accessed 1 May 2016; [P. Talmadge, MN Dept. of Natural Resources (MDNR), Baudette, MN, pers. comm.]). Based on over 20 years of observations and water temperature data before and during the LS spawning seasons on the Winnebago System LS were observed to sustain a second and sometimes a third separate subsequent period of spawning activity in the Wolf and Upper Fox Rivers in some but not every year. The phenomenon was typically observed in years when spring water temperatures slowly rose to a point to induce initial LS spawning activity, but then quickly dropped due to a cold front and/or snowfall. Initial spawning activity would continue until females that had begun ovulating and spawning were finished, but activity would not sustain as females that had not initiated spawning prior to the temperature drop would hold-off and wait until the water temperature would rise again with the next warm weather system. In these situations, the water temperatures needed to re-induce spawning activity were typically at a point that was higher than the temperatures were when initial spawning ended. Also, based on assessments made of LS captured during the
‘1st’, ‘2nd’ and ‘3rd’ runs on the Wolf River, the 1st run typically was always found to be the most robust with the largest number of females spawning, while the 2nd and, when occurring, 3rd runs were found to be comprised a small number of females that apparently spawned at higher temperatures, and large numbers of males that had remained in the river waiting to spawn with the females that had yet to ovulate. The period of time between 1st and 2nd runs was observed to be as much as 3–4 weeks in some years on the Wolf River, with males observed and captured during spawning in the 1st run, also observed spawning and captured during the 2nd and even 3rd runs, even if the subsequent spawning periods occurred weeks after the 1st (Bruch and Binkowski, 2002; R. Koenigs and R. Bruch, WDNR, Oshkosh, WI, unpubl. data; D. Folz, WDNR, Oshkosh, WI, pers. comm.).

### Sound production during spawning

Lake Sturgeon have been found to make sounds associated with spawning. Bocast et al. (2014) recorded low fundamental frequency (5–8 Hz) drumming, rumble, and hydrodynamic sounds of male and female LS on the Wolf and Embarrass River Systems in Wisconsin during observed active LS spawning. Male LS were recorded making a distinctive drumming sound while ejaculating around the ovulating female during egg expulsion, also observed by Bruch and Binkowski (2002), which could break the surface of the water occasionally and propagate harmonics in the terrestrial atmosphere, creating the drumming sound known by local Native Americans as ‘sturgeon thunder’. Bocast et al., 2014 further reported that females appeared to make a low frequency rumble or growling sound just prior to egg expulsion. All of the sounds recorded by Bocast et al. (2014) coalesce into a distinctive acoustic signature of lake sturgeon spawning activity. Knowledge of this signature and the equipment needed to capture the sounds could be used to document LS spawning activity which would be especially useful in systems where spawning can not be observed due to water depth and/or turbidity, or on systems where documentation of first spawning of restored populations is desired.

### External biology/functional morphology

Peterson et al. (2007) published a very comprehensive summary of external morphology of LS which has been reproduced as part of this paper:

The physical appearance of lake sturgeon [Fig. 3]) is similar to that of most other Acipenser species; and like all other members of the genus, they are easily recognized by several primitive morphological features that distinguish them from other North American fishes. Perhaps the most noticeable of these is the scaleless body, which is protected by five lateral rows of bony plates or scutes. The heavy-set body is spindle shaped, the greatest body depth occurring slightly anterior to the midsection. The origin of the anal fin is located posterior to that of the dorsal, its tip rarely extending beyond the caudal fulcrate plate. Other morphological features that distinguish lake sturgeon from other North American freshwater fishes include a heavily armoured skull, a spiral valve intestine, and a cellular swim bladder that retains some of the lung-like characteristics of early actinopterygians (Harkness and Dymond, 1961).

Basic morphology of the lake sturgeon is similar to that of other Acipenserids. The elongated body in cross-section is pentagonal in young juvenile specimens but becomes progressively more rounded with age (Scott and Crossman, 1973). Dorsal, lateral, and ventral scute counts are typically 9–17, 29–42, and 7–12, respectively. Dorsal fin rays number 35–45; anal fin rays 25–30 (Vladykov and Greeley, 1963; Scott and Crossman, 1973). The slightly upturned rostrum is disproportionately large in juveniles, often exceeding post-orbital distance in juveniles <50 cm; however, this proportion is gradually reversed with age (Vladykov and Greeley, 1963). The large, transverse mouth typically measures approximately 66–93% of the interorbital width (Vladykov and Greeley, 1963). The top lip is continuous; the bottom lip interrupted [Fig. 4]. Mouth shape and size in proportion to head width is most similar to that of shortnose sturgeon (A. brevirostrum) (Vladykov and Greeley, 1963; Hochleitner and Vecsei, 2004). As in the elasmobranches, the sturgeon jaw is detached from the skull, allowing the mouth to project downward during feeding (Vecsei and Peterson, 2004). Lake sturgeon barbels are situated closer to the tip of the snout than to the origin of the mouth—an important diagnostic character distinguishing the species from acipenserids. Gill rakers are short and typically number 25–40 (Vladykov and Greeley, 1963). The thick-walled, gizzard-like stomach is connected to a spiral-valve intestine, a primitive alimentary arrangement shared by many Acipenserids adapted to a diet of benthic crustaceans and molluscs (Harkness and Dymond, 1961).

Body armouring is extensive on juveniles but becomes progressively reduced with age (Priegel and Wirth, 1971; Scott and Crossman, 1973; Vecsei and Peterson, 2004). In juveniles <100 cm, the laterodorsal and lateroventral scutes are typically progressively reduced with age, 50–80 cm, posterior to the first anal fin ray, and 80–100 cm, between the anal fin rays 1–2 or 2–3, respectively (Scott and Crossman, 1973; Vecsei and Peterson, 2004). Several other scutes are also noticed, such as the praecaudal, preanal, and postanal scutes as well as the lateral and ventral scutes. Additionally, the lateral and caudal fins are covered with small, hard scutes that are usually present on the body of an adult sturgeon (Vecsei and Peterson, 2004).
surfaces are protected by a layer of tightly-spaced denticles evenly distributed between the five principal rows of scutes. Sharp, apical hooks are particularly prominent on the scutes of juveniles, but these gradually disappear with age until the scutes themselves are almost completely resorbed later in adulthood. In contrast, most anadromous sturgeons retain ossified scutes that continue to grow throughout their entire lifecycle. Hence, the process of scute resorption in adult lake sturgeon probably illustrates an important trade-off in the functional morphology of body armouring within the genus. In freshwater environments devoid of sharks and other large biting predators, the protective advantage of body armour diminishes with increasing body size, yet the energetic costs of overcoming frictional drag caused by the rough armoured surfaces increases exponentially. By adulthood, lake sturgeon have simply outgrown all potential aquatic predators and hence, their need for body armouring.

The skull of all acipenserids, including the LS, is heavily armoured by a series of contiguous bony plates that are most apparent in juveniles and sub-adults [Fig. 5]. Variation and complexity in the ossification of the Acipenser skull roof has been noted by several researchers (e.g. Jollie, 1980); however, only the skull structure of shortnose sturgeon has been well studied (Hilton and Bemis, 1999). Although the LS skull is comparatively less variable, Jollie (1980) noted considerable intraspecific and ontogenetic variation.

Peterson et al. (2007) go on to say:

“...In lake sturgeon the postdorsal plates are typically seen as 1–2 unpaired elements (Vladykov and Greeley, 1963; Peterson et al., 2003); however, the second predorsal may appear as a paired element in some individuals. The relatively large preanal plates always occur in single file and number 1–2 (Vecsei and Peterson, 2004). These ossifications may be considered definitive in all cases except on very old individuals where they may be completely resorbed.

Body coloration of lake sturgeon is variable among stocks but is typically dark brown or dark gray dorsally with a similar but slightly lighter coloration on the lateral surfaces. The ventrum is typically white or cream-colored. Some individuals have gray or black pigmentation on the underside of the head, particularly on the lips and barbels (Harkness and Dymond, 1961). Rarely, adults may exhibit white or milky blotches or spots on the lateral body surfaces. The dorsal and lateral scutes are typically the same color as the surrounding skin, although rare specimens may have slightly lighter lateral scutes or dark pigmentation on the lateral surfaces of the ventral scutes.

Although lake sturgeon exhibit considerable morphological ontogeny, the changes in color pattern from early juvenile to adulthood are among the most pronounced (Vladykov and Greeley, 1963; Priegel and Wirth, 1971; Peterson et al., 2003). In juveniles <30 cm, two large black saddles typically are present across the gray or brown dorsum and sides [Fig. 6]. Black speckling on the upper surfaces of the body also is common, often producing a ‘peppered’ appearance on the juveniles. Scutes and other dermal ossifications of juveniles are usually of the same color as the surrounding skin, but lateral scutes may sometimes be lighter (as in the adults). In 2–4 year-old
juveniles (>60 cm) the large saddle marks are lacking but the black speckling may persist into early adulthood."

**Internal biology**

Sturgeon are unique, described as living fossils dating back to the Lower Jurassic some 200 million years ago (Bemis and Kynard, 1997; Bemis et al., 1997; Pikitch et al., 2005) that have changed very little morphologically (Choudhury and Dick, 1998a). The digestive system within North American sturgeon are very similar (Buddington and Christofferson, 1985), however, as a group they have unique features internally. LS possess a large, cellular swim bladder that retains some of the lung-like characteristics of early actinopterygians (Harkness and Dymond, 1961; Singer et al., 1990 Peterson et al., 2007). The inside layer of the swimbladder contains isinglass, a gelatinous material that historically was sought for use in glue (Prince, 1905), used as a clarifying agent for beer and wines, and used in the preparation of jellies (Holzkamm and McCarthy, 1988).

The alimentary channel consists of the esophagus, stomach, pyloric stomach, upper intestine and spiral valve intestine (Kempinger, 1996) The pyloric stomach is a thick walled, gizzard like stomach (i.e., pyloric caecum) used to grind prey (Nilo et al., 2006; Peterson et al., 2007) and is connected to the spiral valve which is considered a primitive arrangement (Harkness and Dymond, 1961; Peterson et al., 2007).

Male and female gonads in reproductively ready LS represent a significant portion of the peritoneum. Gametes are released into the peritoneal cavity, collected by the Meulien ducts and transported to the urogenital pore.

Lake Sturgeon blood serum displays similar osmotic and ionic composition to other North American freshwater sturgeon species. Juvenile LS do not appear capable of homeostasis above 15°C nor are they tolerant to environments exceeding 25°C. However, greater tolerance to elevated salinities was noted with increased size (LeBreton and Beamish, 1998). Lake Sturgeon use nonesterified fatty acids (NEFAs) for the mobilization of plasma lipids for energy metabolism and selectively mobilize different NEFAs depending on the season (McKinley et al., 1993).

**Parasites and diseases**

Lake Sturgeon have been examined for disease and parasites extensively in Wisconsin, as the annual spear harvest on the Winnebago System provides the opportunity to collect the
tissue samples needed for disease testing and parasite necropsies (WDNR, unpubl. data). Additionally, samples have been collected in Manitoba through cooperation with First Nation domestic and commercial sturgeon fishermen (Choudhury and Dick, 1993).

Lake Sturgeon harvested from the Winnebago System have been tested for WS Irido-like virus (WSIV), Large-mouth Bass Virus (LMBV), Infectious Hematopoietic Necrosis (IHN), Infectious Pancreatic Necrosis (IPNV), Viral Hemorrhagic Septicemia (VHSV), Oncohynchus Masou Virus (OMV), Channel Catfish Virus (CCV), Renibacterium salmoninarum (Rsal), Yersinia ruckeri (Yruc), Aeromonas salmonicida (Asal), Myxobolus cerebralis (Mcer), and Bothriocephalus acheilognathi (Bach). Through 2012 sampling, all results have been negative except for positive hits of Rsal bacterium initially in 2002, and Yruc bacterium initially in 2011 (R. Koenigs, WDNR, Oshkosh, WI, unpubl. data.)

Lake Sturgeon have been challenged with VHSV in laboratory experiments conducted at Michigan State University to determine if the species was susceptible to and/or a carrier of the virus. Dr. Mohamed Faisal, DVM & Professor Aquatic Animal Medicine at Michigan State University reported study results on LS from his lab in a letter dated 28 September 2010 to Gary Whelan, Fish Production Manager of the Michigan Department of Natural Resources: “Lake sturgeon was found to be totally refractory to VHSV-IVb to the extent that when the virus was injected, it could not be re-isolated or even detected by nested RT-PCR or quantitative PCR. The reason for this resistance to the virus deserves further investigation and is probably due to the lack of a receptor compatible with VHSV glycoproteins.” As a result, LS are not listed as a VHS susceptible fish species.

Dr. Anindo Choudhury, St. Norbert College, DePere, WI, has extensively examined LS for parasites in both US and Canada. To date he has documented more than 20 different new species of nematode (Spinitectus acipernseri 1998b; Choudhury et al., 1996), including descriptions of the eggs of sturgeon and paddlefish; the parasite has been isolated or even detected by nested RT-PCR or quantitative PCR. The reason for this resistance to the virus deserves further investigation and is probably due to the lack of a receptor compatible with VHSV glycoproteins.” As a result, LS are not listed as a VHS susceptible fish species.

Mitochondrial DNA (mtDNA) has been used to identify phylogenetic relationships among sturgeon species. LS were identified as a sister group to the SNS (Krieger et al., 2000; Ludwig et al., 2001), confirming previous genetic studies documenting that relationship (Artayukhin, 1995; Brown et al., 1996). On a broader scale, LS are part of the Atlantic clade, which includes SNS and several European species (Ludwig et al., 2001). LS are not known to naturally hybridize with any other sturgeon species.

Genetic relationships to other sturgeon species

Much debate has surrounded the determination of ploidy level in LS. Initially, LS were thought to be octoploid through karyotype analysis (Blacklidge and Bidwell, 1993). However, subsequent karyotype characterization determined that LS were most likely tetraploid (Fontana et al., 2004), which has been further confirmed by the number of alleles observed at microsatellite loci (Ludwig et al., 2001) and inheritance studies using microsatellites (Ptyatskowitz et al., 2001; McQuown et al., 2002; Welsh and May, 2006). Microsatellite studies have demonstrated that the LS genome appears to be a mixture of tetrasomic and disomic loci, with 79% of the loci as tetrasomic and 21% of the loci as disomic (Welsh et al., 2003). Triploidy also appears to be relatively common in LS, indicating that the mechanisms of polyploidization may be a current evolutionary force acting on the LS genome (Blacklidge and Bidwell, 1993; Welsh and May, 2006). It has been hypothesized that the LS genome is evolving to the diploid state through a functional reduction in ploidy level (Ludwig et al., 2001). The extra chromosomal copies may not be functional variants, but may instead represent non-functional pseudogenes. The maintenance of multiple variants may reflect a slow rate of concerted evolution throughout the LS genome, reducing the rate of homogenization among chromosomal copies (Krieger and Fuerst, 2004).

Status of Lake Sturgeon in North America
Population genetics

Genetic variation throughout the LS range has been assessed. Initially, it was thought that LS had low genetic variation. Early studies using mtDNA found only two haplotypes, with the majority of the sturgeon in the Great Lakes/St. Lawrence River having a single haplotype and LS in the Hudson Bay system having both haplotypes (Ferguson and Duckworth, 1997). Subsequent studies using a larger, more variable portion of the mtDNA have revealed significant mtDNA variation, with 22 haplotypes being identified in 11 populations in the Great Lakes (DeHaan et al., 2006).

The subsequent use of microsatellites has facilitated finer-scale delineation of LS population structure. The deepest level of genetic divergence is observed between LS in the Hudson Bay and Great Lakes systems (Welsh et al., 2008; McDermid et al., 2011). It has been hypothesized that this divergence may be due post-glacial colonization from different glacial refugia, with populations from northwestern Ontario and Lake Superior possibly having ancestry from the Missourian refugium and populations from the St. Lawrence River system originating from the Mississippian refugium (McDermid et al., 2011).

Within the Great Lakes basin, most populations have significant genetic differences, indicating the likelihood of natal fidelity (McQuown et al., 2003; DeHaan et al., 2006; Welsh et al., 2008). The highest levels of genetic differentiation within the Great Lakes were observed in Lake Superior and may be a result of natural migration barriers due to the geography of the lake (Welsh et al., 2008). There is genetic evidence for potential natural recolonization in the Great Lakes. Lake Sturgeon in the St. Clair River are genetically indistinguishable from LS in the Lower Niagara River, suggesting the possibility of population reestablishment at a location where sturgeon were thought to be extirpated (Welsh et al., 2008). Despite many populations in the Great Lakes having substantially reduced population sizes, remnant populations have appeared to retain relatively high levels of genetic diversity. No correlation between genetic diversity and population size has been observed (DeHaan et al., 2006).

Within the Hudson Bay system, population differences have been observed between river systems (McDermid et al., 2011). However, unlike the Great Lakes drainage, LS in the Hudson Bay system are primarily river residents, with multiple spawning groups existing in a single waterway. Genetic differences were not observed among spawning groups in connected waterbodies (e.g., southern and main stems of the Saskatchewan River; McDermid et al., 2011), despite the presence of potential natural barriers to upstream movement within a river system (Welsh and McLeod, 2010). Populations in the Hudson Bay system generally have lower genetic diversity relative to populations in the Great Lakes (Welsh et al., 2008; McDermid et al., 2011). However, as in the Great Lakes, levels of genetic diversity are not correlated to population abundance (McDermid et al., 2011).

Few natural populations of LS remain in the Mississippi River system. Those that do are genetically distinct from both the Great Lakes and Hudson Bay systems (Drauch et al., 2008). The White River population in Indiana is the last LS population in the Ohio River drainage. It has slightly lower genetic diversity than other LS populations, but the population does retain some unique genetic variants, indicating its potentially distinct evolutionary trajectory relative to other LS populations (Drauch et al., 2008). In the northern part of the Mississippi River system, the LS population in the east fork of the Chippewa River is more genetically similar to LS populations in the Great Lakes than to the White River population in the Ohio River (Drauch et al., 2008). However, although genetically distinct, the east fork of the Chippewa River in the northern portion of the Mississippi River is more closely related to Great Lakes populations than the population remaining in the Ohio River basin, with a low 3.5% straying rate (Homola et al., 2010). In Lake Michigan, high rates of straying were observed (average = 10%); these rates were asymmetrical and had high variance across populations (Homola et al., 2012). Despite these high rates of straying, significant genetic differentiation was observed among spawning populations, indicating these movements do not always result in successful reproduction (Homola et al., 2012). Assignment of individuals to their most likely spawning population has also provided data on which populations are being impacted by harvest (e.g., Bott et al., 2009) and which populations are colonizing restored habitat (Marranca et al., 2015).

As new genomic approaches become more accessible for non-model organisms like LS, genetic markers from throughout the genome will provide greater resolution for detecting population differences and for identifying adaptive variation. Lake Sturgeon can exhibit high individual repeatability regarding spawning time (i.e., early and late spawners) and breeding area within a spawning site (Forsthe et al., 2012). Therefore, genetic differences likely exist among these groups, but the current suite of microsatellite loci do not have sufficient power to detect these differences.

Fisheries and impacts

There are 19 US states and Canadian provinces that recognize LS as a native species (Fig. 1). Two currently have commercial harvest fisheries, eight have recreational fisheries (four of which allow harvest while the others are catch and release only), and six have Tribal or First Nation fisheries and harvests (Table 8). The largest and most well-known LS fisheries are the commercial fishery in the St. Lawrence River in Quebec (annual harvest of about 80 000 kg) (Mailhot et al., 2011); the winter spear fishery on the Winnibago System in Wisconsin (annual harvest of 45 000 kg (~1000 LS) during the 2014 and 2015 seasons; R. Koenigs, WDNR, Oshkosh, WI, unpubl. data) and the recreational hook and line fishery on Lake of the Woods between Minnesota and Ontario (annual harvest of about 4500 kg; 350 LS) (P. Talmage, MDNR, Baudette, MN, unpubl. data). These fisheries have all been intensively managed over time to produce sustainable harvests.
Table 8

Lake sturgeon commercial (Comm), recreational (Recr), and Tribal/1st Nations (Tribal) fisheries, and harvest estimates by state and province, USA and Canada

<table>
<thead>
<tr>
<th>State/Province</th>
<th>Comm. harvest</th>
<th>Recr. fishery</th>
<th>Recr. harvest</th>
<th>Tribal harvest</th>
<th>Recent harvest estimates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alabama</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Alberta</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td>Georgia</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Illinois</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Indiana</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Iowa</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Kentucky</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Manitoba</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td>Michigan</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Anglers on Lake St. Clair reported harvesting 4 legal LS (3% of estimated catch of legal lake sturgeon) in 2007. Tribal fishermen are allowed to take 1–2 incidentally caught LS home for domestic use per year. Registered harvest of 356 LS in 2015 (~8825 lbs)</td>
</tr>
<tr>
<td>Minnesota</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Missouri</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>New York</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Ohio</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Ontario</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>There are First Nation harvests and commercial licenses, but there is no means to keep track on numbers harvested. Estimates of 450–680 kg annual 1st Nation subsistence harvest from Lake of the Woods. Recreational fisheries were closed in 2008 with two exceptions (FMZ 1 and 8 although no harvest allowed) 80 000 kg annual commercial harvest Harvest records before the closure were never obtained. Spear harvest of 2158 LS (44 000 kg) during 2015 season. Hook and line harvest in 2014 of 37 LS statewide.</td>
</tr>
<tr>
<td>Pennsylvania</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Quebec</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td>Saskatchewan</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td>Tennessee</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Wisconsin</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
</tr>
</tbody>
</table>


Major anthropogenic habitat impacts

Nearly all sturgeon species are considered at risk due to the combination of overexploitation and habitat degradation (Birstein et al., 1997; Pikitch et al., 2005). Activities including pulp and paper mill effluent, raw sewage discharges and other toxic effluents have all contributed to water pollution and impaired water quality for LS (Mosindy and Russak, 1991; Dumas et al., 2003; OMNR, 2009; Heinrich and Friday, 2014). Further, environmental degradation in the form of sediment pollution, damming of rivers, destruction of spawning habitat, deterioration of water quality, and siltation occurred throughout the range of LS distribution (Billard and Lecointre, 2001; Pikitch et al., 2005; Aadland, 2015). Lake Sturgeon are also known to be sensitive to the lampricide TFM (Johnson et al., 1999).

For the most part, LS overexploitation is now controlled with stringent regulations (Rochard et al., 1990) supported by consistent and comprehensive monitoring (Dumont et al., 1987; Bruch, 1999). Therefore, habitat alteration/degradation is now considered to be the greatest remaining threat to LS populations. A study of the different anthropogenic stressors affecting LS in a large regulated river concluded that regardless of historical practices, water power management (i.e., presence and operation of hydroelectric facilities) was now
the factor impeding population recovery the most (Haxton and Findlay, 2009). Similarly, the variation in LS abundance across Ontario was primarily explained by the presence of hydroelectric generating stations (Haxton et al., 2014b). In comparison, LS populations are recovering and/or sustaining viable fisheries in other parts of the LS range despite waterways being fragmented by dams for over 100 year (Scholl, 1986; WDNR, 2000). These observations suggest that dams and sturgeon can co-exist if the correct planning and mitigative techniques are employed (Haxton et al., 2014b; Aadland, 2015).

Dams are often designed and managed to reduce flow variability in the rivers downstream (i.e., provide water when required and reduce peak flows to control flooding) by increasing water level fluctuations in upstream reservoirs (Baxter and Glaude, 1980; Nilsson and Berggren, 2000). As a result, many rivers with the aforementioned regulation strategy have been transformed into a series of storage reservoirs and run-of-the-river impoundments (Nilsson and Berggren, 2000) changing characteristics of the system from lotic to lentic (Nilsson and Berggren, 2000; Friedl and Wuest, 2002). Lake Sturgeon populations can sustain themselves quite well with additional lentic areas on systems created by hydro dams providing adequate spawning and nursery areas are still available in the lotic areas (Barth et al., 2009, 2011).

Lake Sturgeon are migratory with large distances often separating spawning, nursing and overwintering habitats (Harkness and Dymond, 1961; Houston, 1987; Beamesderfer and Farr, 1997; Ferguson and Duckworth, 1997; Baker and Borgeson, 1999; Williot et al., 2002). Dams may form barriers eliminating the upstream movement of fish and fragmenting populations. However, sturgeon can persist in fragmented systems providing adequate habitat is present to the meet the life history requirement (Beamesderfer et al., 1995). Therefore, it is critical for sturgeon management and recovery programs to identify the habitat available in all sections of the river (between dams) and set population objectives that will assist in determining where habitat needs to be developed and/or re-connected. This process can also be used to decide where and how to move LS past dams to meet objectives.

Anadromous species may be unable to migrate for spawning or nursing purposes if insufficient water is passed through the dam to provide adequate habitat downstream for LS populations to successfully complete critical life history requirements (Geen, 1974; Rochard et al., 1990; Liu and Yu, 1992; Mirza and Ericksen, 1996; Cada, 1998; Gehrke et al., 1999; Dudgeon, 2000; Nilsson and Berggren, 2000; Williot et al., 2002). In these cases, flow regimes need to be negotiated and implemented that address upon LS management and/or recovery objectives and balance the need for alternative uses of water with the needs of the LS population.

Dams alter habitat and flood natural rapids that may have been traditionally used for spawning (Zhong and Power, 1996; Nilsson and Berggren, 2000; Aadland, 2015). As mentioned earlier, LS spawn in shallow, fast-moving waters; areas that are usually sites for dam construction because they are generally areas of greatest hydraulic head. Typically, LS will concentrate below these dams and attempt to spawn on the remaining natural substrate or on substrate that was placed on the river bed through the dam construction process. Regulated flows that disrupt normal spawning patterns (Fernandez-Pasquier, 1999) and diurnal fluctuations in flows that de-water spawning areas leaving their eggs exposed to desiccation (Il'ina and Gordeyev, 1972; Gaboury and Patlalas, 1984; Humphries and Lake, 2000) need to be mitigated to ensure adequate flows are maintained through the spawning, incubation, and larval swim-up periods for LS.

Drastic and rapid changes in flows or water levels may affect downstream passage of many individuals and cause entrainment or entrapment in less than ideal conditions (Geen, 1974; Cada, 1998; Pringle et al., 2000). Entrainment may artificially increase mortality of spawning fish, which ultimately could impact future spawning stocks (especially species with traditionally low adult mortality). The migratory nature of LS makes them prone to entrainment (McKinley et al., 1998; McDougall et al., 2013, 2014). In northern Ontario, LS have been entrained during the operation of Adam’s Creek sluice gates and became stranded in pools downstream during de-watering (Seyler et al., 1996; Sheehan, 1997). The remotely controlled sluice gates are operated to pass water down a diversion during excessive flow and has a discharge capacity of 4970 m$^3$ s$^{-1}$ (Sheehan, 2001). Lake Sturgeon from upstream reaches (Little Long Headpond) have been entrained during their post spawning migration, and while many LS were observed to sustain extensive injuries, tagging projects suggested that not all injuries were fatal. A relocation project moving LS stranded in pools back into Little Long Headpond has been implemented until such times that entrainment can be prevented (Seyler et al., 1996; Sheehan, 2001). During the period from 1990 to 2000, approximately 3500 LS were relocated representing approximately 14% of the population (Sheehan, 2001). Entrainment at this location is still an issue since 472 and 226 LS required relocation in 2007 and 2008 respectively (Barbour, D. OMNR, Kapuskasing, ON, pers. comm.). The numbers relocated does not account or reflect the LS that died during stranding or washed downstream from the high flows.

If appropriate measures are not taken (i.e. effective trash rack spacing on turbine inflow bays), entrainment through hydro-electric stations can result in turbine mortality of sub-adult and adult LS. Several LS carcasses with obvious blade strikes were located immediately downstream of a hydro-electric facility during an American Eel (Anguilla rostrata) turbine mortality study (Bendig, A. OMNR, Kemptville, ON, pers. comm.). However, young sturgeon can survive entrainment quite well, especially if it occurs through the sluicegates at the facilities (McDougall et al., 2014). Fingering and yearling size LS were shown to have exceptionally high survival (>90%) passing through turbines in a recent experiment conducted on the Wolf River in Wisconsin (R. Koenigs, WDNR, Oshkosh, WI, unpubl. data).

Dredging is a major problem in many of the Great Lakes connecting waters and in large rivers (Beamesderfer and Farr, 1997; Auer, 2003). Dredging activities can remove spawning habitat and underwater cover required by LS (e.g.,
Casswell et al., 2004; Nilø et al., 2006) or depauperate LS prey through deposition of material on nursery areas (Gerig et al., 2011). Dredging can also increase turbidity, reduce light penetration and decrease levels of dissolved oxygen. Due to their relatively poor swimming abilities and benthic orientation, juvenile sturgeon can also be entrained during dredging activities (Veshchev, 1981; Boysen and Hoover, 2009).

Other stochastic natural impacts
Lake Sturgeon, along with other sturgeon species, have evolved very efficient and effective life history strategies for dealing with the inherent stochasticity of natural systems. Animals that are short-lived, small-sized and early-maturing have been classified as $r$-strategists ($r$, the intrinsic rate of population increase), whereas animals like sturgeon that are long-lived, large-sized, very fecund, and late-maturing are $K$-strategists ($K$, the carrying capacity of a species in a particular population) also known as periodic strategists (Pianka, 1970; Winemiller and Rose, 1992).

Natural appearing cycles in abundance of animals are commonly observed with various species of animals (Zimmerman et al., 2008), but these cycles are often exacerbated or exaggerated by human exploitation or human caused habitat alterations. Stock recruitment dynamics, other population factors, and naturally cycling environmental factors will affect the cycling of abundance as well. LS, even as periodic life history strategists, would not necessarily be immune to being impacted by natural stochastic factors which ultimately could cause local or regional populations to cycle.

Bruch’s (2008) stochastic simulation modeling results suggest LS may experience natural cycling of abundance in the Winnebago System. With a Ricker stock–recruit relationship (the best fit S-R model for the Winnebago data) and an annual conditional natural mortality rate of 5.4%, adult females were predicted to naturally cycle from high abundance to low abundance every 28 years. Further, the average level of abundance over the long-term was dependent upon the level of exploitation. The model indicated that recruitment was increasing in the early 2000s, but that the adult stock was moving towards the next low point predicted to occur around the year 2034, which was then followed by a high point of abundance in approximately 2062. Model outputs suggested cycling of abundance to be consistent over the 500 years that were simulated.

Emerging impacts, threats and risks
Likely the greatest emerging threat to LS throughout their range, aside from the renewal of overexploitation, any further loss of habitat, an outbreak of a new detrimental disease or parasite, and/or some other unforeseen natural or man-made disaster, would be the loss of interest on the part of the public and politicians. This interest is key to the financial support needed to fund management, recovery, research, and habitat programs and LS programs would be set back 50 or more years without this interest. Maintaining this support is challenging given the long term nature of sturgeon recovery and the relatively high costs for sturgeon aquaculture, monitoring, research, and habitat development. While maintaining public interest in sturgeon programs is key to maintaining financial and political support for programs, keys to maintaining public interest are pro-active meaningful public involvement programs that engage and interest people in LS. Interest that, where possible, can be spurred by the hope of participating someday in recreational fisheries for restored LS populations, even if the fisheries are non-harvest catch and release only. The fishing licenses sold in Wisconsin, Michigan, and Minnesota are exemplary examples that a licence system can produce revenues that can go a long way to keeping LS management and recovery programs in business for many, many years. Engaging the public from the ground-up in the development of recovered LS populations and fisheries that will ultimately be created builds public ownership in the program and helps ensure long term program funding.

Population recovery actions
Lake Sturgeon restoration efforts through stocking and habitat improvements have been ongoing in several jurisdictions since the early 1980s. Pioneering efforts to artificially propagate lake sturgeon can be traced back as early as 1919 in Ontario (Harkness and Dymond, 1961; Kerr, 2006), however were unsuccessful as effective methods were not honed until the late 1970s (Czeskleba et al., 1985; Smith and Hobden, 2011). LS habitat development, specifically spawning habitat, has been occurring unintentionally and intentionally for over 50 year.

The placement of riprap in LS river systems to stabilize river banks and beds, and as part of the process of dam construction and maintenance has created many new areas for LS to spawn in areas on rivers where in many cases LS had previously never spawned (K. Koenigs, WDNR, Oshkosh, WI, unpubl. Data, 2000; Bruch and Binkowski, 2002). Lake sturgeon favoured a spawning site constructed downstream of the Carillon Dam on the Ottawa River for American Shad (Alosa sapidissima) (Rochard et al., 1990). The success of the man-made LS spawning sites created through riprap projects inspired other even larger scale successful spawning rehabilitation sites such as those built in Des Prairies River (Quebec Canada) (Dumont et al., 2011) and on the Detroit River system in Michigan (Roseman et al., 2011).

Successful population re-establishment through stocking has been documented in numerous watersheds with successful natural reproduction from stocked fish occurring in the Mississippi River, Missouri (Moore, T., Missouri Department of Conservation, Hannibal, MO, pers. comm.), and in St. Louis River, Wisconsin/Minnesota (Margenau, T., WDNR, Bayfield, WI, pers. comm.). While most LS restoration efforts have relied primarily on stocking and habitat management or development, which requires 35–40 year of effort to show initial success of natural reproduction, a recent effort to restore a LS population in Wisconsin without stocking or habitat alterations has resulted in successful natural reproduction of a newly created spawning stock within 1 year of initial work. A capture and
transfer program initiated on the Wolf River in fall 2011 aimed to restore LS spawning activity to two upstream sections of the river where spawning had been absent for 50–100 years, while also establishing a local resident LS population. Both objectives were achieved within the first few years, with spawning activity observed in the first year, following fish transfer and progeny from the transferred adults captured following observed spawning of the transferred fish in the 2nd year. Fish were captured and transferred from downstream sections of the river where a natural population exists to a section of the river above two dams that have prevented movement of spawning fish into this section of river since the early 1900s. Aquatic invasive species issues on the river currently prevent volitional movement of fish upriver which complicates efforts for considering the installation of fish passage at the two dams bypassed by capture and transfer operations (Koenigs, R., WNDR, Oshkosh, WI, unpubl. data).

Recovery monitoring and timeline predictions

Based on results cited above from restoration efforts in Missouri Wisconsin, and Wisconsin/Minnesota boundary waters, LS recovery appears to be very achievable and assessable. Time and patience (in addition to consistent funding) are of course essential elements in any recovery program, especially in programs that are attempting to rebuild sturgeon stocks from scratch through stocking or from low remnant levels through natural recovery. A substantial time element is also required for recovery being pursued through adult capture and transfer, but with LS a time savings of 30–35 years may be enjoyed using this method if an adequate donor population is available. Overall based on the 35+ years of experience and initial findings from these recovery efforts a recovery timeline (starting with remnant stock of 0–200 adults) could potentially consist of:

If using stocking of fingerlings or yearlings as the primary recovery tool:

1. 1st 30–50 years – stocking annually to rebuild adult spawning stock; sources have been from local hatcheries and from streamside rearing units; “head starting” or raising captured wild larvae in a hatchery for a time before release to minimize mortality has also been used on some recovery waters (Peterson et al., 2007); all fish stocked should be permanently marked (PIT tag or other effective permanent mark); target adult densities should be estimated and stocking calibrated over time once tag returns and abundance estimates of stocked year classes in assessments provide an indication of survival/mortality rates; tag return rates of young fish that can be accurately aged will provide measure of any natural recruitment occurring during rebuilding period. Habitat improvements (if needed) should be made where possible during this period anticipating ultimate use by new sturgeon stock.
2. 2nd 30–50 years – no stocking; focus on assessment of stocked (and existing natural) fish for distribution, densities, growth, mortality, natural recruitment.

If using ‘Capture and Transfer’ of adults as the primary recovery tool:

1. 1st 10 years– set long term density and distribution goals for new population being created by transferred fish; capture and transfer optimum minimum of 100 adults (30 gravid females and 70 gravid males optimum) per year; monitor post transfer behavior, movement, spawning activity (telemeter released fish during first 3 years of transfers – track long term; PIT tag all released fish), and spawning success. Habitat improvements (if needed) should be made where possible during this period anticipating ultimate use by new sturgeon stock.
2. 2nd 10 years – calibrate capture and transfer numbers and final transfer timeline based on distribution, density, spawning and larval assessments of fish transferred in previous 10 years.

If using natural recovery of remnant stock assuming some (100–200) remnant adults remain within the target recovery area:

1. 1st 50–100 years – monitor densities (relative or absolute), and spawning activity/success of remnant stock. Improve habitat where needed and possible.
2. 2nd 50 years – initiate stocking or adult capture and transfer if no signs of natural recovery are evident. If some recovery signs are evident, continue to monitor.

Research needs – priority data gaps

1. Document success or failure of ongoing long-term LS recovery methods and efforts.
2. Develop/Update the best management practices for conservation genetics, gamete collection strategies, rearing strategies, and stocking strategies.
3. Determine distribution, habitat selectivity, and movement of juvenile and subadult LS, as well as the variability in this behavior across the wide range of waters inhabited by LS in North America
4. Implement genomic approaches to studying and conserving genetic diversity in an effort to better manage for adaptive genetic variation
5. Determine on a case by case basis when and where fish passage is needed for LS on fragmented systems and develop technology and/or methods to facilitate/ensure upstream and downstream movement of LS at targeted dams and hydroelectric facilities.
6. Evaluate fish passage facilities for effectiveness to guide design, and optimize efficiencies of future facilities.
7. Document effectiveness of current strategies and methods designed to create or enhance LS habitat as well as mitigate negative impacts of various anthropogenic activities on sturgeon habitat.

Current prognosis for species

Lake Sturgeon is one of two Acipenseriformes listed as ‘least concern’ by IUCN’s Redlist (http://www.iucnredlist.org/)
with the other of the 24 species listed with some kind of status be it ‘threatened’, ‘critically endangered’ etc. in the wild. As detailed in the ‘Distribution and general abundance’ section, many robust populations remain. In addition, the status of LS population is unknown in many northern Ontario and Quebec waterbodies. Lake Sturgeon, as with other Acipenseriformes, are gaining notoriety. Attention has been refocused on this species. Therefore, greater efforts have been concentrated at determining science needs and recovery efforts (Peterson et al., 2007). However, the current demand for renewable energy and subsequent development of many northern rivers for hydro-electric purposes will add pressure to these remote, pristine populations. Some robust populations, for example the Winnebago Lake system in Wisconsin and St. Lawrence River in Quebec are excellent models that show, through aggressive and pro-active management, that populations can be maintained at a high levels and can be sustainably harvested through commercial or recreational fisheries (Dumont et al., 1987; Bruch, 1999; Mailhot et al., 2011).

Overall, LS populations today enjoy much greater protection from over-exploitation and have greater opportunities for recovery and sustainability throughout their range than they have experienced for more than a century. A combination of factors including; increased attention over the last 30–40 years by state and provincial governments to effectively manage harvest and conduct proper assessments, increased public awareness of LS and their extreme vulnerability to overexploitation, improvements in assessment techniques, improvement in LS propagation techniques and stocking strategies, exponential expansion of population studies and research, increasing awareness and efforts to improve habitat and water quality, and the formation of the North American Sturgeon and Paddlefish and World Sturgeon Conservation Societies have all contributed to greater protection and recovery potential. While these are all positive steps that collectively should allow many LS populations to continue or start down the road to recovery, there are still waters and populations that may not be getting the attention needed to allow their recovery to occur. Generally, though, things are better now than they were 30 years ago for LS across the landscape of North America and, for the most part, things are moving in a positive direction.

Acknowledgements

We would like to acknowledge Drs. Doug Peterson, Paul Vecsei, and Cecil Jennings, as well as the publisher Springer, for their generous permission to reproduce an excerpt and four figures on general morphology of Lake Sturgeon from their review paper Peterson, D. L.; Vecsei, P.; Jennings, C., 2007: Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Rev. Fish Biol. Fisher. 17, 59–76. We also would like to acknowledge the very helpful contributions made by Dr. Anindo Choudhury to the ‘Diseases and parasites’ section of the manuscript.

References


Status of Lake Sturgeon in North America


Friday, M. J., 2006: The migratory and reproductive response of spawning lake sturgeon to controlled ﬂows over Kakabeka Falls on the Kaministiquia River, ON. 2006. Ontario ministry of Natural Resources Upper Great Lakes Management Unit, Lake Superior QUIK report 06.02. Rosslyn, ON, Canada, 13 pp.


Froese, R.; Binohlan, C., 2000: Empirical relationships to estimate asymptotic length, length at ﬁrst maturity, and length at maximum yield per recruit in ﬁshes, with a simple method to evaluate length frequency data. J. Fish Biol. 56, 758–773.

Froese, R.; Binohlan, C., 2000: Empirical relationships to estimate asymptotic length, length at ﬁrst maturity, and length at maximum yield per recruit in ﬁshes, with a simple method to evaluate length frequency data. J. Fish Biol. 56, 758–773.


LaHaye, M.; Fortin, R., 1990: Caractérisation de l'habitat de fraie et de l'habitat des juvéniles de l'esturgeon jaune (Acipenser fulvescens) dans la région de Montréal. Département des sciences biologiques, Université du Québec à Montréal, Canada, 81 pp. + app.


Mailhot, Y.; Dumont, P.; Vauchon, N., 2011: Management of the Lake Sturgeon Acipenser fulvescens population in the lower St. Lawrence River (Québec, Canada) from the 1910s to the present. J. Appl. Ichthyol. 27(2), 405–410.

Manitoba, 2012: Manitoba Conservation and Water Stewardship Branch. (Online at: http://fw.ky.gov/Fish/Pages/Lake-Sturgeon.aspx)


McDougall, C. A.; Anderson, W. G.; Peake, S. J., 2014: Downstream passage of lake sturgeon through a hydroelectric...
generating station: route determination, survival, and fine-scale movement. N. Am. J. Fish. Manage. 34, 546–558. 


Nilo, P., 1996: Year class strength, habitat, and feeding of juvenile lake sturgeon (Acipenser fulvescens) in the St. Lawrence system. MSc Thesis. University of Quebec, Montreál, QC. 


Randall, R. G., 2008: Narrative description and quantification of the habitat requirements of lake sturgeon (Acipenser fulvescens) in the Great Lakes and upper St. Lawrence River. Research Document, Department of Fisheries and Oceans, Burlington, ON, Canada, 16 pp. 


Author’s address: Ronald M. Bruch, Wisconsin Department of Natural Resources (retired), 818 Hennessy St., Oshkosh, Wisconsin, USA.
E-mail: ronaldmbruch@gmail.com