Articles

Population status and demographics of Lake Sturgeon in the Bad and White rivers, Wisconsin

Joshua T. Schloesser,* Henry R. Quinlan

U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office, 2800 Lakeshore Drive East, Ashland, Wisconsin 54806

Abstract

Lake Sturgeon *Acipenser fulvescens* rehabilitation efforts in Lake Superior are guided by a rehabilitation plan that sets goals and criteria for a self-sustaining population, including a minimum of 1,500 mature adults, roughly equal sex ratio, and annual exploitation rates < 5%. The Bad and White rivers, Wisconsin host a genetically unique Lake Sturgeon population that is utilized by state-licensed recreational anglers and tribal subsistence fishers. Our objectives were to 1) determine if the Bad River population meets rehabilitation plan targets for a self-sustaining population, 2) assess harvest of Lake Sturgeon by recreational anglers and tribal subsistence fishers for compatibility with rehabilitation goals, 3) determine population trajectory from annual spawning runs, and 4) describe population demographics given the unique physical features of Lake Superior. We sampled Lake Sturgeon in the Bad and White rivers with gill nets over a 17-y period (2001 to 2017). The observed sex ratio in spawning runs was 2.2:1 (male : female), but calculated at 1.6:1 for the entire adult population on the basis of abundance estimates. Weight–length relationships converted to a standardized modified form factor indicated lower condition and possibly lower female fecundity compared with other large North American populations. Annual spawning run size estimates over time indicated that the population trajectory was stable to slightly increasing, and during 2016 was 739 and 241 individuals in the Bad and White rivers, respectively. Total population size (including nonspawners) exceeded 1,500 individuals, which met Lake Superior rehabilitation criteria for a self-sustaining population. Estimates of 1,426 males and 882 females were considered conservative because 472 unknown-sex fish could not be accounted for in return time and abundance models. Spawning return times were 2 or 3 y for males and 4 to 6 y for females, longer than many other populations. Exploitation by recreational anglers and tribal subsistence fishers was 1.3% or lower and met the rehabilitation plan target of < 5%, but we recommend exploitation not exceed 3.1% to maintain a self-sustaining population. These findings help gauge rehabilitation progress in Lake Superior and better describe the demographics of a remnant self-sustaining Lake Sturgeon population in Lake Superior.

Keywords: Bad River; harvest management; Lake Sturgeon; Lake Superior; rehabilitation; spawning return times; spawning run

Received: February 5, 2019; Accepted: August 7, 2019; Published Online Early: August 2019; Published: Month 2019

Citation: Schloesser JT, Quinlan HR. 2019. Population status and demographics of Lake Sturgeon in the Bad and White rivers, Wisconsin. *Journal of Fish and Wildlife Management* 10(2):xx–xx; e1944-687X. [https://doi.org/10.3996/022019-JFWM-005](https://doi.org/10.3996/022019-JFWM-005)

Copyright: All material appearing in the *Journal of Fish and Wildlife Management* is in the public domain and may be reproduced or copied without permission unless specifically noted with the copyright symbol ©. Citation of the source, as given above, is requested.

The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

* Corresponding author: Joshua_Schloesser@fws.gov

Introduction

Rehabilitation of Lake Sturgeon *Acipenser fulvescens* populations in Lake Superior is a long-term effort guided by the Lake Sturgeon Rehabilitation Plan for Lake Superior (Auer 2003, hereafter rehabilitation plan), alongside U.S. State and Canadian Provincial rehabilitation plans (WDNR 2000; Seyler et al. 2011; Hayes and Caroffino 2012; Goldsworthy et al. 2017). Once abundant, population declines are attributed to commercial over-
fishing, construction of dams for hydroelectric power and log drives, and degradation of water quality and habitat from poor land-use practices (Harkness and Dymond 1961; Auer 1996, 2003; Slade and Auer 1997; Schram et al. 1999; Haxton et al. 2014). For these reasons Lake Sturgeon are currently listed as a species of special concern in the states of Wisconsin and Minnesota, and threatened in Michigan and Ontario (MNDNR 2013; WNHP 2016; COSEWIC 2017; MNFI 2018). Long-term rehabilitation efforts are needed in part because of the protracted life-history characteristics of Lake Sturgeon. Lake Sturgeon exhibit slow growth, late age at maturity (12–15 y for males and 18–27 y for females), long life span, and intermittent spawning intervals (Peterson et al. 2007). For full population rehabilitation, efforts in the realm of 60–100 y should be expected, or even longer for a remnant stock to recover naturally (Bruch et al. 2016).

The rehabilitation plan identifies specific goals for restoration, issues limiting recovery with strategies to overcome them, and assessment, research, and management actions to effectively rehabilitate Lake Sturgeon (Auer 2003). The rehabilitation plan recognizes that there is insufficient information on population abundance and demographics to develop workable management strategies. This lack of information is in part due to lengthy monitoring times necessary to fully understand the protracted life-history characteristics of Lake Sturgeon and the sparseness of existing self-sustaining populations. The rehabilitation plan set a target of 1,500 mature spawning individuals that ascend a common tributary for a population to be considered self sustaining (Auer 2003). The rehabilitation plan also recommends that exploitation be limited to < 5% to maintain populations. However, fishery managers can only determine if these targets are being met with knowledge of stock abundance and demographics, which are unknown for most Lake Superior populations.

Lake Sturgeon abundance in Lake Superior was historically lower compared with the other Great Lakes (Hay-Chmielewski and Whelan 1997; Haxton et al. 2014). Most of Lake Superior is inhospitable to Lake Sturgeon, containing cold temperatures, low productivity, and extreme depths that limit suitable habitat to tributaries, nearshore areas, and embayments (Pratt et al. 2014). Several studies (Fortin et al. 1996; Auer 1999; Pratt et al. 2014) implicate the unique physical features of Lake Superior and its habitat restrictions to negatively influence growth, condition, and further delay spawning frequency and age at maturity. Historically, 21 tributaries to Lake Superior (and Lake Nipigon) hosted spawning Lake Sturgeon populations, but presently only 10 tributaries are known to support naturally reproducing populations (Quinlan et al. 2010; Schloesser et al. 2014; Pratt et al. 2016). The Bad and White rivers in Wisconsin support a single remnant population that is considered to be self sustaining on the basis of spawning run estimates (Slade and Auer 1997; Quinlan et al. 2010; Pratt et al. 2016), but total adult abundance has never been quantified. Slade and Rose (1995), Quinlan and Miller (2009), Schloesser and Quinlan (2011), and Schloesser (2013) produced reports on the Bad and White river population, but these analyses were limited in scope because of partial data sets.

Lake Sturgeon in the Bad and White rivers spawn in two areas; at the lower falls of the Bad River and immediately downstream of the White River dam. After spawning, Lake Sturgeon return to Lake Superior where most observations come from nearshore areas (< 15-m water depth) between Chequamegon Bay, Wisconsin and Ontonagon, Michigan, but longer migrations to the St. Louis River in Minnesota and Wisconsin and the Portage Canal in Michigan have been observed (Slade and Auer 1997; U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office, unpublished data). Chequamegon Bay is a large embayment 10 km west of the Bad River mouth that is frequented by Lake Sturgeon because of its soft substrates and thermal refuge from the cold waters of main Lake Superior.

State-licensed recreational anglers harvest Lake Sturgeon in Wisconsin waters of Lake Superior, primarily in Chequamegon Bay. Current recreational fishing regulations for all Wisconsin waters of Lake Superior allow harvest of one sturgeon greater than 127.0 cm (50 in.) per year with a pre purchased tag, no season closures, and mandatory registration of harvested fish. However, the State of Wisconsin is concurrently working through the rule-change process to increase the minimum length limit from 127.0 cm (50 in.) to 152.4 cm (60 in.). Tribal subsistence fishers primarily harvest Lake Sturgeon during the spawning run in the lower Bad and White rivers within the Bad River Reservation, but also occasionally in Wisconsin waters of Lake Superior. There are no size restrictions on tribal subsistence harvest. Managing harvest from both fisheries combined is critical to avoid detrimental impacts from overexploitation.

Great Lakes-wide genetic assessments determined that Bad and White river Lake Sturgeon are genetically similar to each other, but highly differentiated from other spawning populations in Lake Superior and the other Great Lakes (DeHaan et al. 2006; Welsh et al. 2008, 2018; Homola et al. 2010). Given the genetic similarity and physical river connection between the Bad and White rivers, the Lake Sturgeon that use them are considered to be part of the same population and will hereafter be referred to singly as the Bad River population (unless otherwise specified). Genetic differentiation from other Lake Superior populations suggests limited straying of spawning adults, high spawning site fidelity, and natal homing back to the Bad and White rivers (Homola et al. 2010; Welsh et al. 2018). DeHaan et al. (2006) found high genetic diversity within the Bad River population, which is indicative of a remnant population that persisted through the extensive Great Lakes-wide population collapses during the mid-1800s to early 1900s.

Given the unique physical features of Lake Superior, protracted life-history characteristics of Lake Sturgeon, and Bad River population genetic structure, a comprehensive study on the Bad River spawning population is needed to measure rehabilitation progress and population status, and describe population demographics. Our first objective for this study was to determine if the
Bad River population meets rehabilitation plan goals and criteria for a self-sustaining population, including 1) a minimum of 1,500 mature adults, 2) roughly equal sex ratio, and 3) annual exploitation rates < 5%. In addition to measuring annual exploitation, our second objective was to assess harvest of Lake Sturgeon by state-licensed recreational anglers and tribal subsistence fishers in terms of size (total length) and sex using length-based sex proportions to ensure compatibility with rehabilitation plan goals and population sustainability. We also estimated the size of annual spawning runs to determine population trajectory as an indicator of rehabilitation progress. Our last objective was to describe the Bad River population demographics given the unique physical features of Lake Superior and unique genetic structure of this remnant population. We modeled demographic rates of annual survival, adult recruitment, and spawning return times (years between spawning events) by sex, and also evaluated size structure over time and the condition of pre- and postspawn Lake Sturgeon. Few self-sustaining Lake Sturgeon populations exist in Lake Superior or throughout the Great Lakes, making this study important to inform conservation efforts for other depleted populations by providing information on abundance, survival, spawning periodicity, exploitation, sex ratios, and sex-based harvest considerations.

### Study Site

We sampled Lake Sturgeon on the Bad River 12.7 river kilometers (rkm) upstream from the mouth of Lake Superior. Over sampling years, we made only minor adjustments in net placement within the same river bend (< 100 m) because of changing river bathymetry and fallen trees. The largest spawning congregation in the Bad River occurs at the lower falls 35 rkm upstream from Lake Superior, which is a series of low head sandstone ledges that has remained relatively pristine (Figure 1). Throughout Great Lakes tributaries, most Lake Sturgeon spawning migrations extend to the upstream access limit, typically a natural or man-made barrier (Harkness and Dymond 1961). However, in the Bad River, spawning occurs at about half the distance of available upstream access, despite the presence of suitable spawning substrate farther upstream.

The White River empties into the Bad River at rkm 8.6 and we sampled 1.8 rkm upstream from that confluence (Figure 1). Spawning in the White River occurs 49 rkm from Lake Superior and immediately downstream of the White River hydrogenerating station, which has been a run-of-the-river operation from 1907 to present day (Xcel Energy 2019). A natural falls existed at the site of the present-day dam, but it is uncertain whether Lake Sturgeon could or would ascend these falls before construction of the dam and hydrogenerating station. The White River dam may affect Lake Sturgeon spawning, nursery habitat, and reproductive success through altered habitat, flow, and thermal regimes.

### Methods

Fishery crews sampled Lake Sturgeon in the Bad and White rivers over a 17-y period from 2001 to 2017. However, surveys were not conducted during 2005, 2008, 2009, and 2014 because of staff availability or high river flow. Only the White River was surveyed during 2006 and 2007 in conjunction with a logjam study (Quinlan and Miller 2009). Sampling start and end dates varied each year depending on water temperatures and water levels (Table 1). Crews started sampling when river water temperatures reached 8–10°C and removed nets when catch rates declined to only a few (approximately less than five) fish and most were spent or showed signs of having spawned (e.g., concave abdomen, hemorrhaging or scrapes on belly).

Sampling on each river consisted of two gill nets set perpendicular to the current covering the entire river width. Nets used on the Bad River were 61 m long and 2.4 m tall with 25.4 cm stretch multifilament mesh. The same nets were used on the White River, except they were 30.5 m long, as the river is narrower. A 25.4-cm
Table 1. Summary of annual gill-net effort and Lake Sturgeon *Acipenser fulvescens* catch in the Bad and White rivers, Wisconsin. No sampling occurred during 2005, 2008, 2009, or 2014 because of staff availability or high river flow. Gill-net effort was measured in number of net nights, with the exception of five dip-net sampling occasions in 2010 on the Bad River (marked with asterisks).

| Year      | Sampling dates       | Gill-net effort | Sturgeon captured | Unique individuals |
|-----------|----------------------|-----------------|-------------------|-------------------|
|           |                      | Bad R. | White R. | Bad R. | White R. | Bad R. | White R. | Bad R. | White R. |
| 2001      | April 21–May 18      | 22     | 27       | 42     | 21       | 37     | 19       |
| 2002      | May 4–May 18         | 15     | 17       | 65     | 21       | 55     | 19       |
| 2003      | May 1–May 9          | 18     | 18       | 63     | 20       | 53     | 14       |
| 2004      | April 27–May 16      | 37     | 39       | 157    | 67       | 131    | 46       |
| 2006      | April 19–April 26    | -      | 18       | —      | 39       | —      | 33       |
| 2007      | April 24–May 10      | 18     | 26       | —      | 57       | —      | 51       |
| 2010      | April 15–April 30    | 32*    | 32       | 253**  | 116      | 192*** | 86       |
| 2011      | April 21–May 14      | 32     | 36       | 109    | 39       | 99     | 34       |
| 2012      | April 12–May 4       | 46     | 43       | 212    | 62       | 189    | 49       |
| 2013      | May 17–May 19        | 6      | 6        | 14     | 18       | 14     | 18       |
| 2015      | April 27–May 7       | 22     | 22       | 115    | 32       | 99     | 30       |
| 2016      | April 19–May 12      | 38     | 38       | 153    | 65       | 135    | 54       |
| 2017      | May 7–May 12         | 12     | —        | 98     | —        | 96     | —        |

* Does not include five dip-net sampling occasions at the Bad River Lower Falls.
** Does not include 66 captured during dip-net sampling.
*** Does not include 51 unique individuals captured during dip-net sampling.

stretch mesh was used almost exclusively, except for experimental sampling during 2001 where 20.3-cm stretch mesh was used as one of the two nets on both rivers, and in 2010 where 30.5-cm stretch mesh was used as one of the two nets in the Bad River. Crews also used dip nets at the lower falls of the Bad River during 2010 to collect additional fish on the spawning grounds to increase the sample size.

Crews checked gill nets daily and all captured Lake Sturgeon were measured for total and fork length (mm), girth (mm), and weight (kg). Each fish was given a uniquely numbered t-bar anchor tag inserted at the base of the dorsal fin, and a 12-mm-long 125-kHz or 134.2-kHz passive integrated transponder tag inserted at the base of the skull (dorsal posterior on the right side of the head). A biologist assessed maturity stage on each fish and assigned it as being hard (fully developed gonads, having not spawned), ripe (fully developed gametes expelled with light pressure on enlarged abdominal cavity), or spent (having already spawned, with few gametes released and concave/flaccid abdominal cavity). If the fish expelled gametes the biologist assigned it as male or female, or unknown if no gametes were released. During 2016 and 2017, the biologist also used a portable SonoSite Edge ultrasound unit with an HFL38x/13-6 MHz transducer to determine sex according to methods described in Chiotti et al. (2016), including fish that did not freely expel gametes.

We combined the catch from both rivers for all data analyses because genetic analyses indicated that a single population used both rivers (DeHaan et al. 2006; Welsh et al. 2008). We evaluated changes in the population size structure over time using quantile regression of total length over time. Regression lines were modeled at 0.75 and 0.95 quantiles to determine if the upper end of fish length increased over time. A positive regression slope parameter significantly different (P < 0.05) from zero would indicate a population size structure still growing into its full potential and fish have not reached their maximum size.

We calculated length-based sex proportions by 5-cm total length bins over all sampling years to assess harvest management strategies for both state-licensed recreational anglers and tribal subsistence fishers. We fit a logistic regression model to the data to predict sex-specific proportions at total lengths of 114.3 cm (45 in.), 127.0 cm (50 in.), 139.7 cm (55 in.), and 152.4 cm (60 in.). Only Lake Sturgeon with a positive sex determination were used in model development. A bootstrapping procedure was then used to estimate the 95% confidence intervals for the logistic regression model parameters. We also calculated a simple sex ratio of males to females in the spawning run using data only from 2016 and 2017 when most sturgeons’ sex was assigned with high confidence using a combination of observed gametes and an ultrasound unit.

To evaluate condition of pre- and post-spawn Lake Sturgeon, we developed weight–length relationships for each combination of sex and maturity stage (fully developed hard or ripe male [M2], spent male [M3], hard or ripe gravid female [F4], and spent female [F6] [Bruch et al. 2001, 2011]). We only used fish with a definitive sex and maturity stage determination. Maturity stage was an important factor because Lake Sturgeon are at their heaviest just before spawning and lightest immediately after spawning, and both stages were captured in the survey. We fit the weight–length relationship to the standard allometric equation (\(W = aL^b\)), where \(a\) and \(b\) are coefficients determined by a regression of log total length (L; cm) on log weight (W; kg). To compare the weight–length relationships against other North American Lake Sturgeon populations, we calculated a modified form factor (mFF) as described in Bruch et al. (2011).

To estimate the size of annual spawning runs, we used the POPAN formulation of the Jolly–Seber model implemented through Program MARK (Schwarz and
Arnason 1996; White and Burnham 1999), but only for years with adequate sample sizes where model parameters could be estimated with confidence. Lake Sturgeon captured during the dip-net effort in 2010 were excluded from that year’s model data to avoid violating the assumption of equal catchability. We compiled individual capture histories using a series of 1s or 0s at each sampling occasion to indicate whether the fish was captured (1) or not captured (0). The POPAN model estimates apparent survival between sampling occasions ($\Phi$), capture probability ($p$), probability of entry ($P_{\text{ENT}}$) into the study area, and spawning population size ($N$; Schwarz and Arnason 1996). For POPAN models, we interpreted $\Phi$ as the probability of remaining in the study area vulnerable to capture and $1 - \Phi$ was the probability a Lake Sturgeon returned to Lake Superior, out of the effective study area. Likewise, $P_{\text{ENT}}$ was the probability a Lake Sturgeon entered into the effective study area from Lake Superior after the first sampling occasion, and $N$ was interpreted as the size of the annual spawning run. These parameter estimates are within-year estimates only.

We modeled POPAN parameters as constant ($c$), group ($g$; Bad or White), and time ($t$; each sampling occasion) effects. The candidate set of models included all formulations of $\Phi(c, g, t)$, $p(c, g)$, $P_{\text{ENT}}(c, g, t)$, and $N(g)$. A logical biological hypothesis would support $\Phi$ and $P_{\text{ENT}}$ parameters modeled as a function of time ($t$) to represent migratory behavior, but concerns of estimating too many parameters prompted the need to fit simpler constant ($c$) and group ($g$) models. In exploratory analyses there was little support for group by time ($g \times t$) interaction models for $\Phi$ or $P_{\text{ENT}}$ (Schloesser and Quinlan 2011; Schloesser 2013), so they were not run. We assessed goodness of fit using Program RELEASE to test for violations of assumptions; equal survival probability among all animals (test 3) and equal probability of recapture among all animals (test 2). We ranked candidate models using Akaike information criterion corrected for small sample sizes (AICC; Burnham and Anderson 2002). We used model averaging to derive final parameter estimates from all candidate models contributing some weight ($w_i$) of evidence of support for the data. With all the spawning run $N$ estimates over time, we used linear regression to determine spawning population size trajectory for each river.

The life-history characteristic of intermittent spawning presents challenges for estimating total population size that many mark–recapture models cannot properly account for (Pledger et al. 2013). Annually, a portion of adult Lake Sturgeon return to the Bad and White rivers to spawn where they are vulnerable to capture, while at the same time, the remaining adults remain at large in Lake Superior where they are unavailable for capture. We used a model structure developed by Pledger et al. (2013), referred to as a breeding (spawning) return time and abundance model (RETA), which is capable of estimating total population size ($N$) by incorporating estimates for adult recruitment ($b$), survival probability ($\Phi$), capture probability ($p$), and return time probability distribution for spawning ($t$). Pledger et al. (2013) provides a thorough discussion about this model’s development and methodology.

We ran RETA models for males and females separately on the basis of the common understanding that spawning return times differ by sex. To develop the best probability distribution for spawning return time ($t$), we ran a suite of RETA models under varying levels of $M$ (the maximum number of nonsurviving years before returning to spawn or death). For males, $M$ varied from 1 to 4, and females from 3 to 7. Under each level of $M$, we ran a suite of eight RETA models using the Schwarz–Arnason parameterization of the Jolly–Seber model as described in Pledger et al. (2013). The suite of models for males included all formulations of $b(c, t)$, $\Phi(c, t)$, $p(c, t)$, and $t(M1–4)$, and for females all formulations of $b(c, t)$, $\Phi(c, t)$, $p(c, t)$, and $t(M3–7)$. We selected the best-fit model for each sex using Bayes’ information criterion (BIC) to avoid overfitting and select simpler models (Pledger et al. 2013) given our large data set with sparse data in years where little or no sampling occurred. We chose to exclude fish with an unknown sex in RETA models because males and females were expected to have differing spawning return time probabilities and incorrectly assigning the wrong sex would misconstrue $N$ estimates. However, by excluding unknown-sex fish, true total population size is underestimated because those fish are actually part of the population but not factored into the abundance estimates. Therefore, model estimates for $N$ are considered conservative.

Results

Survey effort among years was not consistent, often influenced by river flow levels and water temperature. Survey start and end dates ranged from April 11 to May 19, with means of April 25 and May 10, respectively. Over all survey years, 1,347 Lake Sturgeon were captured in the Bad River and 557 in the White River (Table 1). The heaviest Lake Sturgeon captured was an F4 female weighing 50.5 kg and 176.6 cm total length in the Bad River in 2017. The longest Lake Sturgeon was an F6 female captured after spawning in 2017 that was 183.4 cm total length and weighed 26.5 kg. The longest male Lake Sturgeon was 163.9 cm total length weighing 26.8 kg in the Bad River in 2010.

Mean total length for all males was 132.4 cm and all females was 148.6 cm. Overall mean weight for male sturgeon was 14.3 kg and females was 20.8 kg. Regression at the 0.75 and 0.95 total length quantiles did not significantly differ from zero ($P = 0.93, 0.20$, respectively), indicating that the upper end of Lake Sturgeon total length was not increasing over the study period (Figure 2). There was no evidence of a change in size structure of the spawning population during 2001 to 2017.

The logistic regression model used to predict length-based sex proportions was developed using 613 males and 350 females over all sampling years (Figure 3). Logistic regression model coefficients for the $y$-intercept and regression coefficient were 20.16 and $-0.14$, respectively. On the basis of model predictions, at total
The lengths of 114.3, 127.0, 139.7, and 152.4 cm, the proportion of the spawning population consisting of males was 0.99, 0.92, 0.67, and 0.26, respectively. The use of an ultrasound unit in 2016 and 2017 reduced the number of unknown sex assignments by more than two-thirds, from a mean of 34.5% unknowns between 2001 and 2015 down to 10.7% unknowns. During 2016 and 2017 when most sturgeon had a definitive sex assignment, the ratio of males to females in the spawning run was 2.2:1 in both years.

Weight–length relationships for males and females decreased between pre- and postspawn stages, presumably due to release of gametes during spawning events (Table 2, Figure 4). The mFF for females decreased by 16% and males by 11% after spawning. However, all weight–length models showed an isometric growth form as the 95% confidence intervals for the $b$ parameter included the value of 3.0.

We were able to estimate spawning run size with the POPAN model for sampling years 2002–2004, 2010–2012, and 2015–2016. In other years, the data were not adequate for reliable model performance. For years when the model was run, we found no evidence for lack of model fit in either test 2 or test 3, but these tests also indicated that there was insufficient data to properly assess whether the data fully met model assumptions of equal recapture probability and equal survival probability among all animals. Candidate models that ranked highest tended to be simple models with constant ($c$) or
Table 2. Standard allometric weight–length equation fit to gravid female (F4), spent female (F6), fully developed male (M2), and spent male (M3) Lake Sturgeon Acipenser fulvescens. Sex and maturity stage were determined from Lake Sturgeon captured in gill nets in the Bad and White rivers, Wisconsin during 2001 to 2017 according to Bruch et al. (2001). Parameters $\alpha$ and $\beta$ in the allometric equation ($W = aL^b$) are coefficients determined by a regression of log total length ($L$) on log weight ($W$). The modified form factor (mFF) is a standardized metric to compare weight–length relationships against other North American Lake Sturgeon populations as described in Bruch et al. (2011).

| Sex   | Maturity stage | Sample size | Weight–length equation | mFF |
|-------|----------------|-------------|------------------------|-----|
| Female | F4             | 127         | $W = 0.0021L^{1.24}$  | 6.83|
|        | F6             | 153         | $W = 0.0053L^{2.54}$  | 5.75|
| Male   | M2             | 551         | $W = 0.0081L^{2.94}$  | 6.11|
|        | M3             | 92          | $W = 0.0087L^{2.91}$  | 5.54|

Figure 4. We used weight–length relationships to evaluate the condition of pre- and postspaw Lake Sturgeon Acipenser fulvescens captured in gill nets during the spawning run in the Bad and White rivers, Wisconsin during 2001 to 2017. A biologist assessed maturity stage on each fish according to Bruch et al. (2001). We developed weight–length relationships using weight (kg) and total length (cm) measurements from gravid females (F4, dotted line), spent females (F6, dashed line), fully developed males (M2, dotted and dashed line), and spent males (M3, solid line) and fit to the standard allometric equation ($W = aL^b$). Parameters $\alpha$ and $\beta$ are coefficients determined by a regression of log total length ($L$) on log weight ($W$). Individual females (triangle) and males (circle) were plotted with point markers. We calculated a modified form factor (mFF) from the weight–length relationships by sex and maturity stage to compare condition among other North American populations (Table 2).

that these were poor models for the Bad River population. Models incorporating a time effect for $p$ always ranked higher than constant capture probability models for both males and females, indicating variability in capture probability among annual surveys.

The best-fit male RETA model estimated the superpopulation size at 1,426 (1,219–1,668, 95% CI) total adult males in the Bad River population (Table 5). During the first year of sampling, the number of adult and new male recruits entering the population was 903 individuals (0.63 of the superpopulation). Annual adult male recruitment into the population was constant after the first year at a rate of 33 individuals (0.02 of the superpopulation). Male survival probability was estimated at 1.0, but the model’s failure to produce confidence intervals was an indication that the model did not converge on an adequate estimate. Capture probability averaged 0.15 in years when sampling occurred, but ranged from 0.01 to 0.59. The top-ranked model fit to $\tau(M3)$ estimated return time probabilities for years 1 to 4 at 0.03, 0.47, 0.50, and < 0.01, respectively. Most males exhibit a 2- or 3-y spawning cycle with little support for a 1- (annual) or 4-y cycle.

For the best-fit female RETA model, the estimated superpopulation size was 882 (655–1,187, 95% CI) total adult females in the Bad River population (Table 5). When compared against the male superpopulation size, the estimated ratio of males to females was 1.6:1 for the population as a whole. During the first year of sampling, the number of adult and new female recruits entering
Table 3. POPAN spawning run population models used to determine annual Lake Sturgeon Acipenser fulvescens spawning run size and population trajectory in the Bad and White rivers, Wisconsin during 2002 to 2016. Model parameters include apparent survival (Φ), capture probability (p), probability of entry (PENT), and spawning population size (N), which were modeled as constant (c), group (g), and time (t) effects. The candidate set of models included all formulations for Φ(t, c, g, t), p(t, c, g), PENT(t, c, g, t), and N(t, g). We present the top three best-fit candidate models ranked by Akaike information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002), but we used all candidate models contributing some weight greater than zero in a model-averaging procedure to derive final parameter estimates (Figure 5).

| Year | Model | AICc | ΔAICc | AICc weights | Model likelihood | Number of parameters |
|------|-------|------|-------|--------------|------------------|---------------------|
| 2002 | (Φ(c) p(t) PENT(c) N(g)) | 188.9 | 0.00 | 0.58 | 1.00 | 6 |
|      | (Φ(c) p(t) PENT(g) N(g)) | 190.3 | 1.33 | 0.30 | 0.52 | 7 |
|      | (Φ(c) p(t) PENT(t) N(g)) | 193.8 | 4.83 | 0.05 | 0.09 | 12 |
| 2003 | (Φ(g) p(t) PENT(c) N(g)) | 190.9 | 0.00 | 0.18 | 1.00 | 6 |
|      | (Φ(c) p(t) PENT(c) N(g)) | 191.2 | 0.34 | 0.15 | 0.85 | 12 |
|      | (Φ(c) p(t) PENT(t) N(g)) | 191.6 | 0.71 | 0.13 | 0.70 | 5 |
| 2004 | (Φ(c) p(g) PENT(c) N(g)) | 620.9 | 0.00 | 0.44 | 1.00 | 6 |
|      | (Φ(c) p(g) PENT(t) N(g)) | 622.7 | 1.81 | 0.18 | 0.40 | 7 |
|      | (Φ(g) p(g) PENT(t) N(g)) | 623.1 | 2.13 | 0.15 | 0.34 | 7 |
| 2010 | (Φ(c) p(g) PENT(c) N(g)) | 908.7 | 0.00 | 0.37 | 1.00 | 6 |
|      | (Φ(g) p(g) PENT(c) N(g)) | 909.2 | 0.51 | 0.28 | 0.77 | 7 |
|      | (Φ(g) p(c) PENT(t) N(g)) | 910.6 | 1.88 | 0.14 | 0.39 | 7 |
| 2011 | (Φ(c) p(c) PENT(c) N(g)) | 341.8 | 0.00 | 0.40 | 1.00 | 5 |
|      | (Φ(c) p(c) PENT(t) N(g)) | 343.7 | 1.94 | 0.15 | 0.38 | 6 |
|      | (Φ(c) p(g) PENT(c) N(g)) | 343.9 | 2.15 | 0.14 | 0.34 | 6 |
| 2012 | (Φ(c) p(g) PENT(t) N(g)) | 603.8 | 0.00 | 0.45 | 1.00 | 6 |
|      | (Φ(c) p(g) PENT(g) N(g)) | 605.5 | 1.71 | 0.19 | 0.43 | 7 |
|      | (Φ(g) p(g) PENT(t) N(g)) | 605.6 | 1.81 | 0.18 | 0.41 | 7 |
| 2015 | (Φ(c) p(c) PENT(c) N(g)) | 271.9 | 0.00 | 0.40 | 1.00 | 5 |
|      | (Φ(c) p(g) PENT(c) N(g)) | 273.9 | 1.95 | 0.15 | 0.38 | 6 |
|      | (Φ(c) p(g) PENT(t) N(g)) | 274.0 | 2.13 | 0.14 | 0.34 | 6 |
| 2016 | (Φ(g) p(g) PENT(c) N(g)) | 480.9 | 0.00 | 0.30 | 1.00 | 7 |
|      | (Φ(c) p(c) PENT(g) N(g)) | 481.6 | 0.72 | 0.21 | 0.70 | 6 |
|      | (Φ(c) p(g) PENT(t) N(g)) | 482.9 | 2.04 | 0.11 | 0.36 | 7 |

the population was 254 individuals (0.29 of the superpopulation). Annual adult female recruitment into the population was constant after the first year at a rate of 39 individuals (0.04 entering the superpopulation). Female survival was high, estimated at 0.97 (0.76–0.99, 95% CI) annually. Capture probability was higher for females than males, with a mean of 0.28 in years when sampling occurred, but ranged from 0.0 to 0.99. Return time probabilities for the i(5S) model indicate that most females spawn on a 4- to 6-y cycle, with r4, r5, and r6 being 0.20, 0.66, and 0.10, respectively. A return time probability for r2 was estimated at 0.03 in that model, but was likely the product of a single female recaptured one time the second year after it spawned. There was some evidence for spawning on a 7-y cycle because the second-ranked i(c) Φ(c) p(t) i(5M6) model had a BIC only 0.12 lower than the top model. For this model, the return time probabilities for r4 to r7 were 0.19, 0.63, 0.10, and 0.07, respectively. Superpopulation size was also estimated slightly lower in that model at 863 (644–1,156, 95% CI) females because of the longer return time estimates.

Discussion

We observed only one Lake Sturgeon greater than 50 kg despite the species’ potential to reach weights over 100 kg (Peterson et al. 2007; Bruch et al. 2016). The largest authenticated record in Lake Superior was caught in Batchewana Bay, Ontario in 1922 and weighed 140.6 kg (Harkness and Dymond 1961), demonstrating the enormous growth potential of these fish. During 2001 to 2017, the size structure remained relatively unchanged, an indication that new fish were consistently recruiting into the adult spawning population, but also that maximum size was not increasing. Given slow growth of Lake Sturgeon, a short 17-y time series may not be adequate to detect a significant change in the upper end of the size structure if there was one. When compared with the Sturgeon River, Michigan spawning population, the length distributions, mean total lengths, and mean weights were all very similar (Auer 1999). Sturgeon River Lake Sturgeon had mean total lengths of 134.5 cm and 153.4 cm, and mean weights of 14 kg and 25 kg for males and females, respectively (Auer 1999).

Sex ratios observed in the 2016 and 2017 Bad and White river spawning runs averaged 2.2 males per female. On the Sturgeon River spawning grounds, Auer (1999) found a male-to-female ratio between 1.25:1 and 2.7:1, which encompasses our observations. Smith and Baker (2005) cite other reports of male-to-female ratios for self-sustaining spawning populations ranging from 1:1.06 up to a high of 9:6:1. The male-to-female ratio would expectedly be skewed high during the spawning run because males mature earlier than females, have a shorter spawning frequency, and spend more time on
the spawning grounds over multiple spawning events, leading to a greater likelihood of capture (Harkness and Dymond 1961; Smith and Baker 2005; Bruch et al. 2016). When the sex ratio was calculated from the entire population at large on the basis of male and female RETA spawning run size and population trajectory in the Bad and White rivers, Wisconsin. We ran the models using individual capture histories of Lake Sturgeon captured during spawning-run gill-net surveys in the Bad and White rivers during 2002 to 2016. We present within-year model-averaged POPAN parameter estimates for apparent survival (\(\phi\)), capture probability (\(p\)), probability of entry (\(P_{ENT}\)) into the study area and spawning population size (\(N\)) by river. We modeled POPAN parameters as constant (\(c\)), group (\(g\); Bad or White), and time (\(t\); each sampling occasion) effects and the candidate set of models included all formulations of \(\phi(c, g, t), pl(c, g), P_{ENT}(c, g, t)\), and \(N(g)\). The top-ranked models according to Akaike information criterion corrected for small sample sizes (\(\text{AIC}_c\); Burnham and Anderson 2002) for each year are presented in Table 3. Linear regression through the Bad River population estimate (\(N\)) was not significantly different from zero (\(P = 0.0857\), dashed line), but showed a significant increase for the White River (\(P = 0.0112\), dotted line). We conclude that the Bad River population trajectory is stable to slightly increasing.

<Figure 5. The POPAN formulation of the Jolly–Seber model parameter estimates used to determine annual Lake Sturgeon Acipenser fulvescens spawning run size and population trajectory in the Bad and White rivers, Wisconsin.>
Table 5. Spawning return time and abundance (RETA) model parameter estimates for male and female Lake Sturgeon *Acipenser fulvescens* captured in the Bad and White rivers, Wisconsin during 2001 to 2017. The top-ranked model for both males and females was $\beta(c) \Phi(c) p(t) t(M)$, where $c$ and $t$ represent constant and time effects, respectively, and $M$ the maximum number of nonspawning years. The 95% confidence intervals are presented in parentheses for the $N$ and $\Phi$ parameters. The $\beta$ parameter has a proportion value for sturgeon already present at the start of the study and another for a constant proportion of recruits each year (in parentheses). The time effect in capture probability ranged from 0.0 to 0.59 for males and 0.0 to 0.99 for females, with the mean presented in the table.

| Parameter          | Males | Females |
|--------------------|-------|---------|
| Maximum non-spawning years, $M$ | 3     | 5       |
| Superpopulation, $N$ | 1,426 (1,219–1,688) | 882 (655–1,187) |
| Recruitment, $\beta$ | 0.63 (0.02) | 0.29 (0.04) |
| Survival probability, $\Phi$ | 1.0 (Na-Na) | 0.97 (0.76–0.99) |
| Capture probability, $p$ | mean = 0.15 | mean = 0.28 |
| Return time probabilities |       |         |
| $t_1$ | 0.03 | 0.00  |
| $t_2$ | 0.47 | 0.03  |
| $t_3$ | 0.50 | 0.00  |
| $t_4$ | 0.00 | 0.20  |
| $t_5$ | 0.06 |       |
| $t_6$ |       | 0.10  |

et al. (2011) using a mFF. Most of those mFFs were calculated from unsexed samples during various seasons, providing a mean condition for the overall population, but studies in Lake Winnebago, Wisconsin and Upper Black River, Michigan broke down mFFs by sex and spawning stage, more similar to this study. In Lake Winnebago, the mFF for M2 males was 6.37, F4 females 7.47, and F6 females 5.64. In the Upper Black River, mFF for adult males was 6.98 and adult females 8.84. Bad River mFF for M2 adult males was 6.11 and F4 adult females was 6.83, lower than the other two systems, which means Bad River Lake Sturgeon tend to be less rotund with a thinner body shape. However, F6 females in Lake Winnebago had a mFF of 5.64, which was lower than F6 females in the Bad River at 5.75. The change in weight from a fully ripe F4 female to a spent F6 female was less in the Bad River than in the Winnebago system. We suspect that this may be due to lower fecundity of Bad River females, because weight has been shown to be a good predictor of fecundity (Bruch et al. 2006). It may be plausible that Bad River females develop fewer eggs as a result of lower water temperatures in Lake Superior and suboptimal habitats, but we are unaware of any fecundity studies in Lake Superior to support this hypothesis.

The Bad River population meets the self-sustaining criteria of at least 1,500 mature adults identified in the rehabilitation plan (Auer 2003). Before this study, the Bad River population was considered self sustaining on the basis of spawning run size estimates using the modified Peterson method (Quinlan et al. 2010; Pratt et al. 2016), but total adult population size had never been quantified. Annual spawning run size estimates indicate that the population trajectory is stable to slightly increasing. Most important, there was no evidence of a decreasing population. Harkness and Dymond (1961) recount early reports that Lake Sturgeon were very abundant around the Apostle Islands, Wisconsin, which we suspect was in part due to the Bad River population. For perspective, Hay-Chmielewski and Whelan (1997) estimated historical abundance of Lake Sturgeon in the Great Lakes using commercial catch data. During the year 1885, the population size of Lake Sturgeon over 22.7 kg (50 lbs.) was estimated at 23,000 fish for Lake Superior and 170,000 for adjoining Lake Huron. Haxton et al. (2014) also estimated historical abundance at 44,000 adults in Lake Superior compared with 344,955 adults in Lake Huron. It is unknown what the full potential of the Bad River population was or what the size of this particular spawning population was like, but we likely have not rebounded to those levels yet. The only other self-sustaining population in Lake Superior with an adult population estimate is the Sturgeon River, which was 1,808 individuals on the basis of mark-recapture analysis (Hayes and Caroffino 2012). Some Lake Superior tributaries in Ontario, Canada such as the Batchawana, Black Sturgeon, Goulais, Kaministiquia, Pic, and White rivers meet most rehabilitation criteria, but additional assessments are needed to determine adult abundance (Pratt et al. 2016). One of the limiting factors for obtaining a population estimate using RETA models is the need for long-term data collection (Pledger et al. 2013), in excess of 10 y, and it can be difficult for Lake Superior fishery agencies to commit resources for that duration.

Spawning return times of the Bad River population were longer than many other systems within the Great Lakes region, especially for females. In Black Lake, Michigan the mean spawning interval for males was 2.3 y and females was 3.7 y, but males were also found to return within 1 y of spawning and females as soon as 2 y (Forsythe et al. 2012; Pledger et al. 2013). In four tributaries to Green Bay in western Lake Michigan, acoustically tagged Lake Sturgeon were detected spawning at mean intervals of 1.9 y for males and 3.4 y for females (Donofrio et al. 2018). In the Lake Winnebago system, males generally spawn every other year, with some portion spawning in consecutive years, and females spawn every 3 to 5 y (Bruch et al. 2001; Bruch and Binkowski 2002). More similar to our findings, and rightfully so being a Lake Superior tributary, males in the Sturgeon River spawned at 2- to 4-y intervals and females at 3- to 7-y intervals, but that study did not account for missed detections in those estimates (Auer
parameter in population growth models (Vélez-Espino et al. 2013). High in systems with low human influence (e.g., harvest or dam entrainment), but is also a highly sensitive parameter in population growth models (Vélez-Espino et al. 2006; Vélez-Espino and Koops 2009; Schueller and Hayes 2010). We estimated female total annual survival at 0.97, but suspect the male estimate of 1.0 was too high and likely due to model nonconvergence. If male survival was artificially high, the abundance estimates reported could be overinflated since the model only accumulates more individuals and never removes losses due to mortality. Our survival estimates were similar to the Black Lake population, which also hosts a managed harvest fishery, where survival was estimated at 0.98 for both males and females (Pledger et al. 2013; Borgeson et al. 2016). In Goulais Bay, Lake Superior, Pratt et al. (2014) estimated survival at 0.86 for a mixed-age population that included juveniles. Models run on the Kettle River, Minnesota population for 11–35-y-old sturgeon estimated survival at 0.80, but Dieterman et al. (2010) determined that this population was barely maintaining itself. In the Great Lakes, natural variation in adult survival by sex is expected because males can live to 55 y of age, but females can live to 80–150 y (USFWS 2018).

The rehabilitation plan for Lake Superior recommends a harvest management approach that limits exploitation rates at or near 5% (Auer 2003). Simulation modeling evaluating the sustainability of the Lake Winnebago Lake Sturgeon population found that the current exploitation limit of 4.7% was sustainable, but the actual mean annual exploitation of 3.2% has allowed the population to grow and approach carrying capacity in a relatively short time of 30 y (Bruch 2009). An exploitation rate of approximately 5% is widely accepted because adult recruitment in self-sustaining populations is generally around 4.7 to 5.4% (COSEWIC 2006). However, we estimated annual recruitment of males and females into the adult population at a constant 33 and 39 individuals, which is 0.02 and 0.04 of the sex-specific population estimates, respectively. Harvest of adults (recreational plus tribal subsistence) should not exceed adult recruitment, otherwise the population will start to decline. We believe an exploitation rate of 5% is too high for the Bad River population because adults don’t recruit fast enough to replace all harvested fish at that level (5% of 2,308 adult estimate = 115). We estimate that exploitation should not exceed 3.1% (3.1% of 2,308 adult estimate = 72) or the Bad River population may start to decline.

Recreational harvest by state-licensed anglers in Wisconsin waters (primarily Chequamegon Bay) is monitored through mandatory registration. Between 1991 and 2014, an average of 1.6 Lake Sturgeon were registered annually, but in 2015 and 2016 there were a total of 12 and 16 Lake Sturgeon registered, respectively (Zunker 2016). Genetic analysis of Lake Sturgeon in Chequamegon Bay found that 51.2% had Bad River genetics and the remaining individuals were from populations throughout Lake Superior and northern Lake Huron, indicating a mixed stock consisting of many populations (Welsh 2018). This stock mixing in Chequamegon Bay reduces the exploitation burden solely on the Bad River population by about half and distributes it among other populations in Lake Superior. Lake Sturgeon harvest by tribal subsistence fishers is currently not monitored, but we surmise harvest numbers in the Bad River proper are < 15 fish per year on the basis of interactions with tribal fishers on the water and communication with Bad River Natural Resources Department fishery specialists. Given our modeled abundance estimate of 2,308 individuals and estimated annual harvest of approximately 30 or fewer individuals (assuming all recreational harvest is from the Bad River population), we believe that exploitation during the study period was approximately 1.3% or lower and met the rehabilitation plan target. This low exploitation rate may be a contributing factor to our observation of a stable to increasing spawning run size.

At the present time (July 2019), the State of Wisconsin is working through the rule-change process to increase the minimum length limit from 127.0 cm (50 in.) to 152.4 cm (60 in.). Harvest data through mandatory registration from 2016 (under 127.0 cm minimum length limit) showed that the mean total length of 16 harvested Lake Sturgeon was 136.9 cm (53.9 in.), with a range of 129.5 cm (51.0 in.) to 153.7 cm (60.5 in.; Zunker 2016). Although not directly applicable to the recreational fishery, over our entire study period we only observed 23 males greater in length than the proposed 152.4-cm minimum length limit, which also at that size had a 0.74 probability or greater of being female on the basis of the spawning run size structure. If passed into law, the 152.4-cm minimum length limit for state-licensed recreational anglers in Lake Superior waters should reduce overall harvest numbers, but increase the probability of a harvested fish being female. Continued harvest monitoring of recreational anglers will help determine potential impacts to the Bad River population, as well as other Lake Superior populations that utilize Chequamegon Bay (e.g., St. Louis and Ontonagon rivers; Figure 1).

Total length can be a good indicator of sex for spawning Lake Sturgeon as indicated by the logistic regression model. This relationship can be a useful management tool to minimize harvest of females during the spawning run because as total length increased, the likelihood of a Lake Sturgeon being female also increased. Although there was no evidence of a declining population, harvest of Lake Sturgeon less than 139.7 cm total length (55 in.; 0.67 or greater probability of being male) in the spawning run would help protect females and further enhance the Bad River population. This
length cutoff is only applicable to fish harvested during the spawning run in the Bad and White rivers when immature females are presumed absent and was based on the population’s current size structure, which should be re-evaluated if changes occur over time.

Our results indicate that the Bad and White rivers host a self-sustaining population of Lake Sturgeon that is stable to slightly increasing. Current harvest levels from recreational anglers and tribal subsistence fisheries combined appear to be within rehabilitation goals. However, we recommend that this population continue to be monitored given there are no quotas that limit the total number of fish that can be harvested, which has been a successful management tool used in other systems (Bruch 1999, 2009; Borgeson et al. 2016). Our data indicate that the Bad River population exhibited high annual survival, but longer spawning return times compared with other populations outside of Lake Superior. We suspect overall female fecundity might be lower in Lake Superior because of lower water temperatures and suboptimal habitats. If this is the case, the additive effect of long spawning cycles may reduce the population’s overall reproductive potential and slow recovery should overexploitation occur. These findings help gauge rehabilitation progress and better describe the demographics of a remnant self-sustaining Lake Sturgeon population in Lake Superior.

Supplemental Material

Please note: The Journal of Fish and Wildlife Management is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Table S1. Sampling data of all gill-net and dip-net effort during 2001 to 2017 in the Bad and White rivers, Wisconsin. Included are sample number, gear type, river, start and end date, start and end time, latitude, longitude, gill-net mesh size, start and end water temperature, and river flow.

Table S2. Lake Sturgeon Acipenser fulvescens catch and biological measurement data from all samples in the Bad and White rivers, Wisconsin during 2001 to 2017. Included are sample number, fish number, unique sturgeon number, river, species, total length, fork length, girth, weight, sex, and spawning stage.

Table S3. Tagging data of all Lake Sturgeon Acipenser fulvescens caught in the Bad and White rivers, Wisconsin during 2001 to 2017. Included are sample number, fish number, unique sturgeon number, tag type, tag number, tag color, tag agency, new tag indication, and released alive indication.

Reference S1. Auer NA, editor. 2003. A Lake Sturgeon rehabilitation plan for Lake Superior. Great Lakes Fishery Commission Miscellaneous Publication 2003-02.

Reference S2. Borgeson D, Baker E, Barton N, Caroffino D, Cwalinski T, Donner K, Fessell B, Field M, Garavaglia J, Hanchin P, Holgren M, Jerome C, Martin E, Osga J, Parsons B, Powell J. 2016. Management plan for Lake Sturgeon in Black Lake. Lansing: Michigan Department of Natural Resources.

Reference S3. Bruch R. 2009. Modeling the population dynamics and sustainability of Lake Sturgeon in the Winnebago System, Wisconsin. Doctoral dissertation. Milwaukee: University of Wisconsin.

Reference S4. [COSEWIC] Committee on the Status of Endangered Wildlife in Canada. 2006. COSEWIC assessment and update status report on the Lake Sturgeon Acipenser fulvescens in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada.

Reference S5. [COSEWIC] Committee on the Status of Endangered Wildlife in Canada. 2017. COSEWIC assessment and status report on the Lake Sturgeon Acipenser fulvescens, Western Hudson Bay populations, Saskatchewan-Nelson River populations, Southern Hudson Bay–James Bay populations and Great Lakes-Upper St. Lawrence populations in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada.

Reference S6. Goldsworthy CA, Reeves KA, Blankenheim JE, Peterson NR. 2017. Fisheries management plan for the Minnesota waters of Lake Superior. 3rd edition. Saint Paul: Minnesota Department of Natural Resources. Special Publication 181.

Reference S7. Gorman OT, Brazner JC, Lohse-Hanson C, Pratt TC. 2010. Habitat. Pages 9–13 in Gorman OT, Ebener MP, Vinson MR, editors. The state of Lake Superior. Milwaukee: University of Wisconsin.
Superior in 2005. Ann Arbor, Michigan: Great Lakes Fishery Commission. Special Publication 10-01. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S10 (1.16 MB PDF); also available at http://www.gifc.org/pubs/SpecialPubs/Sp10_1.pdf.

Reference S8. Harkness WJK, Dymond JR. 1961. The Lake Sturgeon: the history of its fishery and problems of conservation. Ontario, Canada: Ontario Department of Lands and Forests. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S11 (7.58 MB PDF); also available at http://files.dnr.state.mn.us/natural_resources/ets/endlist.pdf.

Reference S9. Hay-Chmielewski EM, Whelan GE, editors. 1997. Lake Sturgeon rehabilitation strategy. Lansing: Michigan Department of Natural Resources. Fisheries Division Special Report 62. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S12 (4.7 MB PDF); also available at https://www.michigan.gov/documents/dnr/Sturgeon_Rehabilitation_Strategy_378808_7.pdf.

Reference S10. Hayes DB, Caroffino DC, editors. 2012. Michigan’s Lake Sturgeon rehabilitation strategy. Lansing: Michigan Department of Natural Resources. Fisheries Special Report 62. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S13 (298 KB PDF); also available at http://files.dnr.state.mn.us/natural_resources/ets/endlist.pdf.

Reference S11. [MNDNR] Minnesota Department of Natural Resources. 2013. Minnesota’s list of endangered, threatened, and special concern species. St. Paul, Minnesota. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S14 (812 KB PDF); also available at http://files.dnr.state.mn.us/natural_resources/ets/endlist.pdf.

Reference S12. Pratt TC, Gorman OT, Mattes WP, Myers JT, Quinlan HR, Schreiner DR, Seider MJ, Sitar SP, Yule DL, Yuriesta PM. 2016. The state of Lake Superior in 2011. Ann Arbor, Michigan: Great Lakes Fishery Commission. Special Publication 16-01. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S15 (2.69 MB PDF); also available at http://www.gifc.org/pubs/SpecialPubs/Sp16_01.pdf.

Reference S13. Quinlan H, Miller G. 2009. Influence of multiple log jams on upstream passage of Lake Sturgeon during their spawning run in the White River, Wisconsin. Ashland, Wisconsin: U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S16 (789 KB PDF).

Reference S14. Schloesser J, Quinlan H. 2011. Status of the 2010 Lake Superior Lake Sturgeon spawning population in the Bad and White rivers, Wisconsin. Ashland, Wisconsin: U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office. Technical Report No. 01. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S17 (1.29 MB PDF).

Reference S15. Schloesser JT. 2013. Status of the 2011 and 2012 Lake Sturgeon spawning population in the Bad and White rivers, Wisconsin. Ashland, Wisconsin: U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office. Technical Report No. 04. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S18 (610 KB PDF).

Reference S16. Schloesser JT, Quinlan HR, Pratt TC, Baker EA, Adams JV, Mattes WP, Greenwood S, Chong S, Berglund E, Gardner WM, Lindgren JP, Palverce C, Stevens P, Borkholder BD, Edwards AJ, Mensch G, Isaac EJ, Moore S, Abel C, Wilson T, Ripple P, Ecclestone A. 2014. Lake Superior Lake Sturgeon index survey: 2011 status report. Lake Superior Lake Sturgeon Work Group of the Lake Superior Technical Committee. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S19 (10.79 MB PDF).

Reference S17. Seyler J, Hildebrandl M, Mellow R. 2011. Recovery strategy for Lake Sturgeon (Acipenser fulvescens)—Northwestern Ontario, Great Lakes–Upper St. Lawrence River and Southern Hudson Bay–James Bay populations in Ontario. Ontario Recovery Strategy Series. Report of Golder Associates Ltd. to Ontario Ministry of Natural Resources, Peterborough, Ontario. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S20 (1.06 MB PDF); also available at https://files.ontario.ca/environment-and-energy/species-at-risk/spotprod_086034.pdf.

Reference S18. Slade JW, Auer NA, editors. 1997. Status of Lake Sturgeon in Lake Superior. Prepared by the Lake Superior Lake Sturgeon Subcommittee for the Lake Superior Technical Committee. Ann Arbor, Michigan: Great Lakes Fishery Commission. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S21 (2.46 MB PDF).

Reference S19. Slade JW, Rose JD. 1995. Population characteristics of Bad River Lake Sturgeon. Ashland, Wisconsin: U.S. Fish and Wildlife Service, Ashland Fishery Resources Office. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S22 (1.2 MB PDF).

Reference S20. Welsh, AB. 2018. Source population assignment of Lake Superior Lake Sturgeon, 2011 and 2016 samples. Final Report, Project #F15AC00543, West Virginia University to U.S. Fish and Wildlife Service, Ashland, Wisconsin. Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S23 (239 KB PDF).

Reference S21. [WDNR] Wisconsin Department of Natural Resources. 2000. Wisconsin’s Lake Sturgeon...
management plan. Madison: Wisconsin Department of Natural Resources, Bureau of Fisheries Management and Habitat Protection.

Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S24 (514 KB PDF).

**Reference S22.** [WNHP] Wisconsin Natural Heritage Program. 2016. Wisconsin Natural Heritage working list. Madison: Wisconsin Natural Heritage Program, Bureau of Natural Heritage Conservation.

Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S25 (1.08 MB PDF); also available at https://dnr.wi.gov/topic/NHI/documents/NHIWorkingList.pdf.

**Reference S23.** Zunker C. 2016. Wisconsin’s 2016 Lake Superior creel survey report. Bayfield: Wisconsin Department of Natural Resources.

Found at DOI: https://doi.org/10.3996/022019-JFWM-005.S26 (492 KB PDF).

**Acknowledgments**

The Bad River Band of Lake Superior Chippewa has been an instrumental partner in this study. Ery Soulier, director of the Bad River Natural Resources Department through 2016, supported these surveys and provided staff to assist with fieldwork. We recognize the contributions of Bad River fisheries specialists Joe Dan Rose, Thomas Doolittle, Richard Huber, Tim Wilson, Chris Dean, Angelena Sikora, and Lorrie Salawater, as well as technicians Ed Leoso, Kris Arbuckle, Ed Wiggins, Nick Blanchard, and Josh Johnson. The field efforts of U.S. Fish and Wildlife Service employees Glenn Miller, Tyler Sikora, Jess Zavocet, Eric Vacha, Mike Seider, Sharon Rayford, Evan Boone, Gary Czypinski, and Great Lakes Indian Fish and Wildlife Commission staff William Mattes, Mike Pluscinski, and Julie Nelson were critical to the data collection of this project. Numerous other U.S. Fish and Wildlife Service technicians and volunteers contributed to field efforts over the years. Ed Baker with Michigan Department of Natural Resources provided expertise and help running RETA models. The Great Lakes Restoration Initiative funded this project from 2010 to 2017.

Any use of trade, product, website, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

**References**

Auer NA. 1996. Response of spawning Lake Sturgeon to change in hydroelectric facility operation. Transactions of the American Fisheries Society 125:66–77.

Auer NA. 1999. Population characteristics and movement of Lake Sturgeon in the Sturgeon River and Lake Superior. Journal of Great Lakes Research 25:282–293.

Auer NA, editor. 2003. A Lake Sturgeon rehabilitation plan for Lake Superior. Great Lakes Fishery Commission Miscellaneous Publication 2003-02 (see Supplemental Material, Reference S1).

Borgeson D, Baker E, Barton N, Caroffino D, Cwalinski T, Donner K, Fessell B, Field M, Garavaglia J, Hanchin P, Holtgren M, Jerome C, Martin E, Osja G, Parsons B, Powell J. 2016. Management plan for Lake Sturgeon in Black Lake. Lansing: Michigan Department of Natural Resources (see Supplemental Material, Reference S2).

Bruch RM. 1999. Management of Lake Sturgeon on the Winnebago System—long term impacts of harvest and regulations on population structure. Journal of Applied Ichthyology 15:142–152.

Bruch R. 2009. Modeling the population dynamics and sustainability of Lake Sturgeon in the Winnebago System, Wisconsin. Doctoral dissertation, Milwaukee: University of Wisconsin (see Supplemental Material, Reference S3).

Bruch RM, Binkowski FP. 2002. Spawning behavior of Lake Sturgeon (Acipenser fulvescens). Journal of Applied Ichthyology 18:570–579.

Bruch RM, Dick T, Choudhury A. 2001. A field guide for the identification of stages of gonadal development in Lake Sturgeon, Acipenser fulvescens Rafinesque, with notes on Lake Sturgeon reproductive biology and management implications. WI Department of Natural Resources, Oshkosh and Sturgeon for Tomorrow publication. Appleton, Wisconsin: Graphic Communications Center.

Bruch RM, Haxton TJ, Koenigs R, Welsh A, Kerr SJ. 2016. Status of Lake Sturgeon (Acipenser fulvescens Rafinesque 1817) in North America. Journal of Applied Ichthyology 32:162–190.

Bruch RM, Kamke KK, Haxton T. 2011. Use of a modified form factor to compare condition among North American Lake Sturgeon stocks. Journal of Applied Ichthyology 27:34–40.

Bruch RM, Miller G, Hansen MJ. 2006. Fecundity of Lake Sturgeon (Acipenser fulvescens, Rafinesque) in Lake Winnebago, Wisconsin, USA. Journal of Applied Ichthyology 22:116–118.

Burnham KP, Anderson DR. 2002. Model selection and multimodal inference. 2nd edition. New York: Springer-Verlag.

Chiotti JA, Boase JC, Hondorp DW, Briggs AS. 2016. Assigning sex and reproductive stage to adult Lake Sturgeon using ultrasonography and common morphological measurements. North American Journal of Fisheries Management 36:21–29.

[COSEWIC] Committee on the Status of Endangered Wildlife in Canada. 2006. COSEWIC assessment and update status report on the Lake Sturgeon Acipenser fulvescens in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada. (see Supplemental Material, Reference S4).

[COSEWIC] Committee on the Status of Endangered Wildlife in Canada. 2017. COSEWIC assessment and status report on the Lake Sturgeon Acipenser fulvescens, Western Hudson Bay populations, Saskatchewan-Nelson River populations, Southern Hudson Bay-James Bay populations and Great Lakes-Upper St. Lake Sturgeon, Acipenser fulvescens, in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada. (see Supplemental Material, Reference S5).
Lawrence populations in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada. (see Supplemental Material, Reference S5).

DeHaan PW, Libants SV, Elliott RF, Scribner KT. 2006. Genetic population structure of remnant Lake Sturgeon populations in the upper Great Lakes basin. Transactions of the American Fisheries Society 135:1478–1492.

Dieterman DJ, Frank J, Painovich N, Staples DF. 2010. Lake Sturgeon population status and demography in the Kettle River, Minnesota, 1992–2007. North American Journal of Fisheries Management 30:337–351.

Donofrio MC, Scribner KT, Baker EA, Kanefsky J, Tsehaye I, Elliott RF. 2018. Telemetry and genetic data characterize Lake Sturgeon (Acipenser fulvescens Rafinesque, 1817) breeding ecology and spawning site fidelity in Green Bay rivers of Lake Michigan. Journal of Applied Ichthyology 34:302–313.

Forsythe PS, Crossman JA, Bello NM, Baker EA, Scribner KT. 2012. Individual-based analyses reveal high repeatability in timing and location of reproduction in Lake Sturgeon (Acipenser fulvescens). Canadian Journal of Fisheries and Aquatic Sciences 69:60–72.

Fortin R, Dumont P, Guénette S. 1996. Determinants of growth and body condition of Lake Sturgeon (Acipenser fulvescens). Canadian Journal of Fisheries and Aquatic Sciences 53:1150–1156.

Goldsworthy CA, Reeves KA, Blankenheim JE, Peterson NR. 2017. Fisheries management plan for the Minnesota waters of Lake Superior. 3rd edition. Saint Paul: Minnesota Department of Natural Resources. Special Publication 181 (see Supplemental Material, Reference S6).

Gorman OT, Brazner JC, Lohse-Hanson C, Pratt TC. 2010. Habitat. Pages 9–13 in Gorman OT, Ebener MP, Vinson MR, editors. The state of Lake Superior in 2005. Ann Arbor, Michigan: Great Lakes Fishery Commission. Special Publication 10-01 (see Supplemental Material, Reference S7).

Harkness WJK, Dymond JR. 1961. The Lake Sturgeon: the history of its fishery and problems of conservation. Ontario, Canada: Ontario Department of Lands and Forests (see Supplemental Material, Reference S8).

Haxton T, Whelan G, Bruch R. 2014. Historical biomass and sustainable harvest of Great Lakes Lake Sturgeon (Acipenser fulvescens Rafinesque, 1817). Journal of Applied Ichthyology 30:1371–1378.

Hay-Chmielewski EM, Whelan GE, editors. 1997. Lake Sturgeon rehabilitation strategy. Lansing: Michigan Department of Natural Resources. Fisheries Division Special Report 18 (see Supplemental Material, Reference S9).

Hayes DB, Caroffino DC, editors. 2012. Michigan’s Lake Sturgeon rehabilitation strategy. Lansing: Michigan Department of Natural Resources. Fisheries Special Report 62 (see Supplemental Material, Reference S10).

Homola JJ, Scribner KT, Baker EA, Auer NA. 2010. Genetic assessment of straying rates of wild and hatchery reared Lake Sturgeon (Acipenser fulvescens) in Lake Superior tributaries. Journal of Great Lakes Research 36:798–802.

McDougall CA, Nelson PA, Barth CC. 2018. Extrinsic factors influencing somatic growth of Lake Sturgeon. Transactions of the American Fisheries Society 147:459–479.

[MNFI] Michigan Natural Features Inventory. 2018. Michigan’s special animals. Lansing: Michigan State University Extension, Michigan Natural Features Inventory. Available: https://mnfi.anr.msu.edu/species/animals (December 2018).

[MNDNR] Minnesota Department of Natural Resources. 2013. Minnesota’s list of endangered, threatened, and special concern species. St. Paul, Minnesota (see Supplemental Material, Reference S11).

Peterson DL, Vecsei P, Jennings CA. 2007. Ecology and biology of the Lake Sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Reviews in Fish Biology and Fisheries 17:59–76.

Pledger S, Baker E, Scribner K. 2013. Breeding return times and abundance in capture-recapture models. Biometrics 69:991–1001.

Power M, McKinley RS. 1997. Latitudinal variation in Lake Sturgeon size as related to the thermal opportunity for growth. Transactions of the American Fisheries Society 126:549–558.

Pratt TC, Gardner WM, Pearce J, Greenwood S, Chong SC. 2014. Identification of a robust Lake Sturgeon (Acipenser fulvescens Rafinesque, 1917) population in Goulais Bay, Lake Superior. Journal of Applied Ichthyology 30:1328–1334.

Pratt TC, Gorman OT, Mattes WP, Myers JT, Quinlan HR, Schreiner DR, Seider MJ, Sitar SP, Yule DL, Yurista PM. 2016. The state of Lake Superior in 2011. Ann Arbor, Michigan: Great Lakes Fishery Commission. Special Publication 16-01 (see Supplemental Material, Reference S12).

Quinlan H, Miller G. 2009. Influence of multiple log jams on upstream passage of Lake Sturgeon during their spawning run in the White River, Wisconsin. Ashland, Wisconsin: U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office (see Supplemental Material, Reference S13).

Quinlan HR, Pratt TC, Friday MJ, Schram ST, Seider MJ, Mattes WP. 2010. Inshore fish community: Lake Sturgeon. Pages 19–22 in Gorman OT, Ebener MP, Vinson MR, editors. The state of Lake Superior in 2005. Ann Arbor, Michigan: Great Lakes Fishery Commission. Special Publication 10-01. Available: http://www.glfc.org/pubs/SpecialPubs/Sp10_1.pdf (December 2018).

Schloesser J, Quinlan H. 2011. Status of the 2010 Lake Sturgeon spawning population in the Bad and White rivers, Wisconsin. Ashland, Wisconsin: U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office. Technical Report No. 01 (see Supplemental Material, Reference S14).
Schloesser JT. 2013. Status of the 2011 and 2012 Lake Sturgeon spawning population in the Bad and White rivers, Wisconsin. Ashland, Wisconsin: U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office. Technical Report No. 04 (see Supplemental Material, Reference S15).

Schloesser JT, Quinlan HR, Pratt TC, Baker EA, Adams JV, Mattes WP, Greenwood S, Chong S, Berglund E, Gardner WM, Lindgren JP, Palvera C, Stevens P, Borkholder BD, Edwards AJ, Mensch G, Isaac EJ, Moore S, Abel C, Wilson T, Ripple P, Ecclestone A. 2014. Lake Superior Lake Sturgeon index survey: 2011 status report. Lake Superior Lake Sturgeon Work Group of the Lake Superior Technical Committee. (see Supplemental Material, Reference S16).

Schram ST, Lindgren J, Evrard L. 1999. Reintroduction of Lake Sturgeon in the St. Louis River, Western Lake Superior. North American Journal of Fisheries Management 19:815–823.

Schueller AM, Hayes DB. 2010. Sensitivity of Lake Sturgeon population dynamics and genetics to demographic parameters. Transactions of the American Fisheries Society 139:521–534.

Schwarz CJ, Amason AN. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics 52:860–873.

Seyler J, Hildebrand L, Mellow R. 2011. Recovery strategy for Lake Sturgeon (Acipenser fulvescens)—Northwestern Ontario, Great Lakes–Upper St. Lawrence River and Southern Hudson Bay–James Bay populations in Ontario. Ontario Recovery Strategy Series. Report of Golder Associates Ltd. to Ontario Ministry of Natural Resources, Peterborough, Ontario (see Supplemental Material, Reference S17).

Slade JW, Auer NA, editors. 1997. Status of Lake Sturgeon in Lake Superior. Prepared by the Lake Superior Lake Sturgeon Subcommittee for the Lake Superior Technical Committee. Ann Arbor, Michigan: Great Lakes Fishery Commission (see Supplemental Material, Reference S18).

Slade JW, Rose JD. 1995. Population characteristics of Bad River Lake Sturgeon. Ashland, Wisconsin: U.S. Fish and Wildlife Service, Ashland Fishery Resources Office (see Supplemental Material, Reference S19).

Smith KM, Baker EA. 2005. Characteristics of spawning Lake Sturgeon in the Upper Black River, Michigan. North American Journal of Fisheries Management 25:301–307.

[USFWS] U.S. Fish and Wildlife Service. 2018. Lake Sturgeon biology. Great Lakes Lake Sturgeon Web Site. Available: www.fws.gov/midwest/sturgeon/biology.htm (April 2018).

Vélez-Espino LA, Fox MG, McLaughlin RL. 2006. Characterization of elasticity patterns of North American freshwater fishes. Canadian Journal of Fisheries and Aquatic Sciences 63:2050–2066.

Vélez-Espino LA, Koops MA. 2009. Recovery potential assessment for Lake Sturgeon in Canadian designatable units. North American Journal of Fisheries Management 29:1065–1090.

Welsh A, Hill T, Quinlan H, Robinson C, May B. 2008. Genetic assessment of Lake Sturgeon population structure in the Laurentian Great Lakes. North American Journal of Fisheries Management 28:572–591.

Welsh, AB. 2018. Source population assignment of Lake Superior Lake Sturgeon, 2011 and 2016 samples. Final Report, Project #F15AC00543 West Virginia University to U.S. Fish and Wildlife Service, Ashland, Wisconsin (see Supplemental Material, Reference S20).

Welsh AB, Schumacher L, Quinlan HR. 2018. A reintroduced Lake Sturgeon population comes of age: a genetic evaluation of stocking success in the St. Louis River. Journal of Applied Ichthyology 35:149–159.

White GC, Burnham KP. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

[WDNR] Wisconsin Department of Natural Resources. 2000. Wisconsin’s Lake Sturgeon management plan. Madison: Wisconsin Department of Natural Resources, Bureau of Fisheries Management and Habitat Protection (see Supplemental Material, Reference S21).

[WNHP] Wisconsin Natural Heritage Program. 2016. Wisconsin Natural Heritage working list. Madison: Wisconsin Natural Heritage Program, Bureau of Natural Heritage Conservation (see Supplemental Material, Reference S22).

Xcel Energy. 2019. White River hydro generating station. Available: https://www.xcelenergy.com/energy_portfolio/electricity/power_plants/white_river (July 2019).

Zunker C. 2016. Wisconsin’s 2016 Lake Superior creel survey report. Bayfield: Wisconsin Department of Natural Resources (see Supplemental Material, Reference S23),
Queries for fwma-10-02-21

This manuscript/text has been typeset from the submitted material. Please check this proof carefully to make sure there have been no font conversion errors or inadvertent formatting errors. Allen Press.