ESTIMATING MORTALITY OF LAKE STURGEON IN THE LAKE WINNEBAGO SYSTEM USING TRADITIONAL AGE-BASED APPROACHES AND CAPTURE-RECAPTURE MODELS

By

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ABSTRACT

The lake sturgeon *Acipenser fulvescens* population in the Lake Winnebago System (LWS) supports a culturally and economically important spear fishery. Harvest from the spear fishery is closely monitored and managed by the Wisconsin Department of Natural Resources (WDNR) through use of a safe harvest cap system with a 5% annual exploitation limit reference point. Harvest caps for all males and adult females are based on mark-recapture estimates of population abundance that are adjusted for natural mortality. The current instantaneous natural mortality rate ($M = 0.055$) used to determine harvest caps was estimated using a statistical catch at age (SCAA) model formulated using corrected ages estimated from fin rays. Correction is required because fin ray age estimates are not accurate for older fish. The WDNR marks lake sturgeon captured in annual assessments with passive integrated transponders (PITs). Recapture of fish with PITs during spawning sampling and spearing harvest provides information that can be used to estimate apparent survival and mortality rates using capture-recapture models as an alternative to traditional age-based approaches. Additionally, the WDNR has implanted acoustic transmitters into fish that were detected on receivers located throughout the LWS and its tributaries. The primary objectives of my research were to determine if: 1) total and natural mortality rates are similar among estimation methods that rely on corrected fin ray ages or capture-recapture methods and 2) potential differences in mortality rate estimates would affect safe harvest caps for the spear fishery. Three separate catch curve methods, along with a suite of eleven indirect natural mortality estimators, were used with each age correction method to estimate total mortality for fish handled from 2009 to 2019. Cormack-Jolly-Seber models were created using the encounter histories of fish tagged with PITs from 1999-2020 and for fish with acoustic transmitters detected from 2004 to 2019. Mortality estimates from these models were used to...
simulate harvest caps from 2009 to 2020 for males and females. Estimates of total and natural mortality rates varied among catch curve and capture recapture models (male: $Z = 0.100 - 0.207$, $M = 0.054 - 0.226$; female: $Z = 0.075 - 0.201$, $M = 0.050 - 0.191$). Cormack-Jolly-Seber models, when built separately for both PITs and acoustic telemetry, converged on similar estimates of mortality for each sex and appear to be the most effective way to estimate mortality for lake sturgeon in the LWS. A simulation of harvest caps over an eleven-year period using estimates of $M$ obtained from a suite of age-based and capture-recapture models showed that female harvest could exceed an exploitation rate of 5% in some scenarios. Use of capture-recapture methods for estimating mortality appear to provide the best available approach for describing population dynamics and demographics for the LWS lake sturgeon population.
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INTRODUCTION

Effective conservation and management of fish populations depends on accurate estimation of population dynamics (i.e., growth, mortality, and recruitment; Hildebrand et al. 1999; Schueller and Hayes 2010) because these estimates are used to determine strategies that are implemented to meet management objectives (Yule et al. 2008; Kerns and Lombardi-Carlson 2017). For example, estimates of growth, mortality, and recruitment are routinely used to identify harvest regulations that ensure fishing mortality remains below a specified threshold to increase maximum yield (Miranda 2002; Quist et al. 2004; Kraak et al. 2013) or ensure total mortality does not reduce spawning stock biomass below a specified level (Boreman 1997; Berkeley et al. 2004). Consequently, estimating mortality rates represents a critical component in managing many fisheries around the world (Myers and Worm 2005; Gaichas et al. 2010; Macdonald et al. 2010).

Total mortality rates are often calculated using age frequency distributions that are based on ages estimated from calcified structures (e.g., scales, otoliths, fin rays or spines; Murphy and Crabtree 2001; Paukert and Spurgeon 2017). There are two major sources of error when estimating ages of fish from these structures: process error, associated with the attributes of the structure being examined, and interpretation error, which relates to the process of interpreting age information recorded in the structure (Campana 2001; Henríquez et al. 2016). The accuracy of age estimates is often unknown, especially for older fish (Beamish and McFarlane 1983; Allain and Lorance 2000; Abecasis et al. 2006). One common error associated with this process is the tendency to underestimate ages of older fish using certain structures, such as scales, fin rays or spines once growth slows and annuli are spaced closely (Campana 2001; Sylvester and Berry 2006; Bruch 2008; Harry 2017). Additionally, precision of age estimates for long-lived
fish species is often low (Kocovsky and Carline 2000; Hawkins et al. 2004; Gregg et al. 2006). These issues may lead to incorrect or imprecise estimates of growth, mortality, or recruitment that could direct managers to improper management decisions (Bradford 1991; Reeves 2003; Yule et al. 2008; Koenigs et al. 2013; Tyszko and Pritt 2017).

Catch curve models fit to catch-at-age information obtained from calcified structures are the most common method used to estimate annual mortality rates (Jensen 1985; Dunn et al. 2002; Miranda and Bettoli 2007; Thorson and Prager 2011; Nelson 2019). The two most common methods for estimating mortality via catch curves are through a linear regression procedure or by calculating the Chapman and Robson (1960) estimator (Smith et al. 2012). The instantaneous total mortality rate \( Z \) from a linear regression catch curve is equal to the slope of the descending limb when catch (log \( e \) transformed) is regressed against age (Dunn et al. 2002). Catch curve assumptions are as follows: (1) no trend in recruitment over time, (2) mortality is similar among year-classes or sizes, (3) mortality is constant from year to year, (4) natural and fishing mortality rates are equal among all sizes and ages of recruited individuals, and (5) samples are representative of the sizes and ages in the population (Maceina 2007; Schnute and Haigh 2007). These assumptions may not accurately represent many populations because mortality can change among years and ages due to many factors that may influence survival and exploitation (Allen 1997). Additionally, underestimating ages of older fish included in catch curve models can lead to overestimation of mortality (Koenigs et al. 2013; Bruch et al. 2016).

Understanding relationships among total, natural, and fishing mortality rates can be particularly important when implementing harvest regulations for exploited populations (Pope et al. 2000; Gislason et al. 2010; Zhou et al. 2012). This is especially true for populations that may be highly vulnerable to overfishing due to life history characteristics such as low survival to
adulthood, delayed maturation, and long life spans (Boreman 1997; Denney et al. 2002; Gross et al. 2002; Pikitch et al. 2005). Collapse of the Lake Superior cisco population through overfishing was determined to be the result of an inaccurate understanding of the species life history due to scale-ageing error (Yule et al. 2008). Inaccurate age estimates have also contributed to population declines in many shark species due to continuous overfishing that has caused growing concern for the future of these stocks that may take decades to recover (Stevens et al. 2000; Simpfendorfer and Kyne 2009; Bradley and Gaines 2014; Gallagher et al. 2014). The margin for error in determining safe harvest levels is reduced for long-lived late maturing species and, therefore, obtaining accurate estimates of total, natural, and fishing mortality rates is critical for effective management (Quist et al. 2002; Adams et al. 2007; Jarić et al. 2010).

Fishing mortality rates are often estimated using tag-return studies (Pollock et al. 1991; Hoenig et al. 1998; Pollock et al. 2004). Moreover, an instantaneous natural mortality rate (M) may be calculated if estimates of Z and instantaneous fishing mortality (F) are available because \( M = Z - F \) (Ricker 1975). However, estimates of F are lacking for many fisheries, so various models for estimating M based on theoretical or empirically determined relationships among generalized life history parameters may be applied (Gislason et al. 2010; Maceina and Sammons 2016). Many of these models were created using a combination of various marine and freshwater stocks and rely on age and growth information (Kenchington 2014; Then et al. 2015). These models are generally used in information-limited fisheries but may only provide approximate values of M (Miranda and Bettoli 2007).

Capture-recapture methods (e.g., Cormack-Jolly-Seber models) can also be used to estimate apparent survival rates of a population without relying on calcified structures. These models estimate survival based on encounter histories of unique individuals over time (Pollock et
Identification of individual fish is typically accomplished through various forms of tagging. Use of these models assumes: (1) no tag loss, (2) the survival of each tagged individual is independent of other tagged individuals, (3) survival is not affected by tagging, and (4) that all tags are correctly noted and recorded at each sampling occasion (Pollock et al. 1991; Krebs 2014). However, all these assumptions are really components of one primary assumption: all marked fish have an equal probability of being recaptured or detected within a specific sampling interval.

Lake sturgeon *Acipenser fulvescens* have a unique life history among North American freshwater fish species. Longevity of lake sturgeon may exceed 100 years and individuals estimated to be greater than 50 years old are common in many populations (Pollock et al. 2015; Bruch et al. 2016). Females tend to reach older ages than males (Bruch 1999), with male lake sturgeon first reaching maturity at age 14 and females first reaching maturity at age 21 (males reach full maturity by age 30, females reach full maturity by age 33; Priegel and Wirth 1971; Bruch 2008). Lake sturgeon are iteroparous potamodromous spawners, but often do not spawn every year; females have high fecundity but recruitment to the population is low due to high mortality during early life stages (Peterson et al. 2007; Forsythe 2010). Females typically spawn once every 4-9 years, while males spawn every 1-3 years (Peterson et al. 2007). Spawning individuals have been shown to migrate in response to environmental cues (Bruch and Binkowski 2002; Forsythe et al. 2012a) and can travel over 200 km to reach suitable spawning grounds (Auer 1996a; Bruch and Binkowski 2002). Dam construction and other anthropogenic influences on the riverscape have had long-term effects on adult spawning migrations, larval outmigration, and juvenile riverine habitation throughout their range (Auer 1996b; Fausch et al. 2002; Daugherty et al. 2009).
Lake sturgeon were once abundant in their endemic range that spanned three major watersheds: the Mississippi River, Great Lakes, and Hudson Bay drainage basins (Ferguson and Duckworth 1997). Overharvest, habitat alteration and fragmentation, and water pollution all contributed to dramatic declines in lake sturgeon populations in the last two centuries (Knights et al. 2002; Haxton and Findlay 2008; Bruch et al. 2016). Prior to European settlement, abundance estimates of lake sturgeon exceeded 16 million fish in the Great Lakes watershed and 11 million fish in the Lake Michigan basin alone, however current estimates put the population at less than one percent of the abundance during the pre-settlement period in the 1800s (Harkness and Dymond 1961; Tody 1974; Baldwin et al. 1979; Hay-Chmielewski and Whelan 1997). Many fragmented populations did persist and recovery efforts, including re-introduction programs and habitat improvements, are now relatively common (Ferguson and Duckworth 1997; Bruch et al. 2016; Koenigs et al. 2017).

Lake sturgeon represent one of many individual species where estimating mortality is critical to managing harvest where it occurs. Lake sturgeon are recognized as an endemic species in 19 US states or Canadian provinces, but exploited populations are rare. Two provinces currently support closely monitored commercial harvest fisheries (Ontario and Quebec), eight states and provinces provide recreational fisheries (Alberta, Manitoba, Michigan, Minnesota, Ontario, Quebec, Saskatchewan, and Wisconsin; of which only four, Michigan, Minnesota, Quebec and Wisconsin, allow harvest), and seven states and provinces support tribal or First Nation fisheries and harvests (Alberta, Manitoba, Michigan, Ontario, Quebec, Saskatchewan, and Wisconsin; Bruch et al. 2016). The largest and most well-known lake sturgeon fisheries are the commercial fishery in the St. Lawrence River, Quebec (Mailhot et al., 2011) and the winter spear fishery on the Lake Winnebago System (LWS) in Wisconsin (Probst and Cooper 1955). The lake
sturgeon stock in the St. Lawrence was considered overexploited in 1987 due to high annual mortality, unbalanced age structure, low reproductive potential, and excessive annual yield (Dumont et al. 1987). A new management plan was implemented to help allow the population to recover in 1987, however, catch curves showed mortality remained high over this time (Mailhot and Dumont 1999). An updated management plan was developed in 2000 that further reduced harvest caps and shortened the fishing season, which appears to have been effective in maintaining the current fishery (Maihot et al. 2011).

The LWS supports one of the largest lake sturgeon populations in North America, with an estimated population of over 42,000 adults (Snobl 2017). Lake sturgeon function primarily as a benthivore within the LWS and utilize a large variety of habitats (Bruch and Binkowski 2002). Lake sturgeon in the LWS were originally part of the Great Lakes population, however, following dam construction on the lower Fox River the population was effectively isolated. Genetic assessment of lake sturgeon across the Great Lakes has shown the LWS population to be distinguishable from other Lake Michigan populations (DeHaan et al. 2006; Welsh et al. 2008). Currently, lake sturgeon in the LWS can emigrate to Lake Michigan yet are no longer able to benefit from the immigration of Lake Michigan populations (Holey et. al 2000, Koenigs 2018a).

The lake sturgeon population in the LWS supports a culturally and economically important spear fishery that accounts for the largest recreational harvest of lake sturgeon in North America (Koenigs 2018b). A safe harvest management system was implemented in 1997 to address overharvest issues, and a safe harvest cap system was adopted in 1999 to help improve the sustainability of the fishery (Bruch 2008). Harvest during the spear fishery is closely monitored and managed by the Wisconsin Department of Natural Resources (WDNR) through the harvest cap system where caps serve as a limit reference point designed to maintain annual
exploitation rates that are \( \leq 5\% \) of the mean estimated population over the previous five years (Roughgarden and Smith 1996; Radomski 2003). Since 2009, the total number of lake sturgeon harvested each year has ranged from 566 to 2,158, with a median total annual harvest of 847 fish (\( \pm 415 \) median absolute deviation [MAD]; Table 1). Since 2010, the total safe harvest caps for lake sturgeon each year have ranged from 2,090 to 2,600 total fish, with a median harvest cap of 2,555 fish (Table 1).

Population estimates are based on capture-recapture estimates of population abundance that involve spawning assessments and spear harvest encounters that are adjusted with an estimated natural mortality rate. The current instantaneous natural mortality rate estimate (\( M = 0.055 \)) used for these adjustments was estimated from a statistical catch at age (SCAA) model formulated using corrected age estimates from pectoral fin rays removed from harvested lake sturgeon (Bruch 2008). Pectoral fin ray ages were corrected within this SCAA model using a power function formula provided by Bruch et al. (2009), developed using bomb radiocarbon dating (Worbes and Junk 1989; Olsson 2009) of pectoral fin rays to determine a true age and quantify reader interpretation error (i.e., deviation between estimated age and true age). This method addresses inaccurate age estimates of fin rays for lake sturgeon by providing a single corrected age for each specific fin ray age estimate. However, this age estimation method may not be the best strategy to calculate population vital rates because missing age classes are introduced in the process. Furthermore, there are other age-correction approaches that can be employed (i.e., age correction matrices) to account for the variation in interpretation error (Pauly 1990). The WDNR and the Wisconsin Cooperative Fishery Research Unit have recently assessed different age correction methods, as well as capture-recapture based methods (i.e., Fabens [1965]
formulation of von Bertalanffy model), for estimating age and growth of lake sturgeon without relying on calcified structures (O’Connell 2020).

Capture-recapture based methods could also be used to estimate mortality rates of lake sturgeon in the LWS (Hightower et al. 2001; Keeler et al. 2007; Raabe and Hightower 2014; Hayden et al. 2018). The WDNR has actively marked LWS lake sturgeon captured in annual spawning assessments with unique passive integrated transponders (PITs) since 1999 (Bruch 2008). Additionally, WDNR previously implanted LWS lake sturgeon with acoustic transmitters dating back to 2007 that have been passively detected at fixed receivers located within the Fox, Wolf, Embarrass and Little Wolf rivers (Figure 1). These detections also represent a form of recapture and can be used to estimate survival and mortality using the same suite of models available with physical handling (Hightower et al. 2001; Hayden et al. 2018). Assumptions regarding no tag loss and no tag-induced mortality seem reasonable based on the literature associated with using PITs and acoustic transmitters (Hondorp et al. 2015; Foldvik and Kvingedal 2018), however there may still be a small amount of loss when using PITs (~1% a year; Bruch 2008; Briggs et al. 2019).

When using these two types of capture-recapture data for estimating lake sturgeon survival, models must account for the fact that spawning periodicity will affect detection probabilities associated with both spring spawning surveys (e.g., not all sturgeon are available for capture each year) and detections on fixed acoustic receivers deployed throughout the major spawning tributaries of the LWS. This transition to a potentially unobservable state is known as temporary emigration and may be addressed within the models by: 1) reducing the order of Markovian transition probabilities, 2) imposing a degree of determinism on transition probabilities, 3) removing state specificity of survival probabilities, and 4) and imposing
temporal constancy of parameters (Kendall and Nichols 2002). Currently, the WDNR has not used capture-recapture methods to assess mortality in LWS lake sturgeon.

The WDNR is interested in determining if alternative estimation methods might provide different estimates of mortality rates for lake sturgeon in the LWS and if differences in these estimates could affect management decisions. Consequently, the objectives of my research are to determine if: 1) total and natural mortality rates are similar among estimation methods that rely on ages estimated from calcified structures or capture-recapture of fish tagged with PITs and acoustic tags and 2) potential differences in mortality rates estimated using different methods would affect harvest caps established for the spear fishery.
METHODS

Study area

Lake Winnebago is the largest inland lake in Wisconsin, covering 55,728 ha and is part of the Fox-Wolf watershed, which consists of all tributaries to the Wolf and upper Fox rivers. Water flows from the Wolf and Fox rivers through the three upper river pool lakes of Lake Butte des Morts, Lake Poygan, and Lake Winneconne before reaching Lake Winnebago, and exits through the lower Fox River into Green Bay of Lake Michigan (Figure 1). Lake Winnebago has an average depth of 4.7 m, with a maximum depth of 6.4 m, while the upriver pool lakes have an average depth of 1.8 m, with a maximum depth of 5.4 m, and the connecting Wolf and Fox Rivers contain 200 km and 60 km of spawning and nursery grounds (Davis-Foust 2012; Bruch 2008).

Sampling

Spring spawning assessment

The WDNR conducted annual spawning stock assessments at known spawning sites on the Wolf, Fox, Embarrass, and Little Wolf rivers during spawning migrations that occurred in March, April, and May from 1999 to 2019 (Figure 1). Lake sturgeon were captured from shore using coated nylon dip nets and total length was measured to the nearest 2.5 mm (TL, measured to the longest point of the caudal fin). Sex was determined based on gamete extrusion, and all fish were examined for PITs (125 or 134.2 hHz). Any fish without a PIT was marked by inserting a 12.5 mm tag into the musculature posterior to the skull between the lateral and 1st dorsal scute with a 12-gauge needle and plunger.
Spearing registration and age structure collection

During the spearing season each February, speared lake sturgeon must be registered at an assigned station depending on harvest location. Each registered fish was measured to the nearest 2.5 mm (TL), weighed to the nearest 0.05 kg, and scanned for a PIT. Sex and maturity were determined by visually inspecting gonads through an incision made in the abdomen. Protocols for pectoral fin ray collection varied across seasons, but age structures were generally collected from all fish registered at the upper pool lakes, a random sample of fish registered at each Lake Winnebago station, and all tagged fish harvested during the season. Following removal, fin rays were placed in a coin envelope with a unique identification number and stored in a cabinet dryer at approximately 20-25 °C until dry, following the procedure described by Bruch (2009). Whole pectoral fin ray thin sections were cut using a Buehler™ Isomet low-speed saw to 0.5-mm cross sections, taken immediately distal to the basal propterygium using a Buehler 15HC (102 mm x 0.3mm) diamond-wafering blade (O’Connell 2020).

Variability in descriptive population metrics (e.g., total catch, length) were quantified using the median and the median absolute deviation (MAD; Hampel 1974):

\[
MAD(x) = b \times \{\text{median}(|x_i - \text{median}(x))|\}
\]

where \(x\) = a specific metric, \(b = 1.4826\), which is a constant equal to \(1 / Q(0.75)\) where \(Q(0.75)\) is the 0.75 quantile which assumes the sample population has a normal distribution (Leys et al. 2013). The MAD is a measure of the variability for a univariate sample that is highly robust to outliers and is less influenced by sample size than the standard deviation (Rousseeuw and Croux 1993).
Acoustic telemetry

A subset of 225 male and 168 female lake sturgeon collected in the spring and summer with dip nets, electrofishing and trawls were implanted with acoustic transmitters between 2004-2019 (Table 2). Acoustic transmitters (Vemco® V-16, 10-year battery life, 24 g) were surgically implanted in the body cavity of these individuals (Koenigs et al. 2017) and visual inspection of gonads confirmed sex and maturity status. A total of 35 Vemco® VR100 stationary receivers were deployed at fixed locations throughout the LWS tributary system to track fish movement (Figure 1). Data were downloaded from receivers annually in late June so that post-spawning migrations were complete (Bruch and Binkowski 2002).

Age estimation and correction

Pectoral fin ray thin sections were examined for all available structures collected from speared fish from the years 1999-2019 by a single experienced reader (two readers in total during separate time periods). Thin sections were examined with reflected and transmitted light under a binocular scope at 7-25X magnification to obtain raw age estimates. These raw estimates were then corrected for all fish > age 14 using the power correction formula provided by Bruch (2009):

\[
\text{Power-Corrected Age} = \text{Raw Fin Ray Age}^{1.054796}
\]

where corrected age estimates are rounded to the nearest integer. A third set of age estimates was created using the raw fin ray ages in an age correction matrix (Richards et al. 1992) described by O’Connell (2020). These age-age keys were developed using paired otolith or known age fish and pectoral fin ray estimates. Matrices within this method were created separately for males and females, and all raw fin ray age estimates ≤ age 17 were assigned an age based on the age
distribution of known-age fish, while an otolith age distribution was used to assign ages when raw fin ray age estimates were > 17 (O’Connell 2020).

Age-length keys were created separately for males and females using: 1) raw age estimates, 2) power-corrected age estimates, and 3) matrix-corrected age estimates. Each age-length key consisted of 25 mm length bins with a minimum of 10 fish per length bin (Coggins et al. 2013). If a bin had fewer than 10 individuals, that bin was grouped with the neighboring bin of a smaller size. Somatic growth of adult lake sturgeon was assumed to be minimal from winter spear season to spawning assessments conducted the following spring. Ages were applied to the TL taken at the first encounter of each fish handled during spring spawning assessments from 2009 to 2019 in proportion to the frequency observed in the age-length key for each age estimation method (Isermann and Knight 2005). The largest length bin was treated as all-inclusive in application to any fish with a TL greater than what was included in the age-length key.

Estimating mortality rates

Catch curves

Using ages assigned to fish collected in spring spawning assessments, sex-specific catch curve models were generated separately using pooled age-frequency data from 2009-2019 for each of the three age estimation methods. Pooling age frequencies among years can help mitigate issues associated with recruitment variability that can be problematic when using catch-at-age data from a single year (Miller 1950; Colombo et al. 2007; Miranda and Bettoli 2007). A weighted least-squares regression can minimize heterogenous variance and deflate the importance of older fish when computing the slope of a catch curve by adjusting the fit in
response to higher observed residual values (Slipke and Maceina 2001). A weighted regression
requires two separate calculations, an initial regression using observed data, and a second
regression on the observed data that includes residual information from the first regression to
adjust the slope calculation of the second regression (Ogle 2016). Weighted catch curve
regressions (Maceina and Bettoli 1998; Montgomery et al. 2012) were used to estimate
instantaneous total mortality rates ($Z$) for each sex following the series of steps provided by
Slipke and Maceina (2001) using first an unweighted regression:

$$
\log_e(C_t + 1) = \log_e(C_0) - Bt
$$

(3A)

where $C_t$ is the number of fish observed at age $t$, $C_0$ is the $y$-intercept, and $B$ is the slope of the
unweighted regression. A value of one is added to each $C_t$ so all natural logarithms were positive
and, as a result, any missing age classes were included in the analysis. This regression can also
be described and solved as:

$$
\sum_{i=1}^{n} (\log_e(C_i + 1) - \log_e(C_0) - Bt_i)^2
$$

(3B)

and $n$ is the total number of age classes included. This output was then used to weight each age
included in the analysis by $w_t$ where:

$$
w_t = \tilde{C}_t + 1
$$

(4)

and $\tilde{C}_t$ is the predicted number of fish at age $t$ computed from the unweighted regression with a
value of one added to the weighting term so that all weights were positive and included in the
weighted regression. The weighted regression can be described as:

$$
\sum_{t=1}^{n} w_t (\log_e(C_i + 1) - \log_e(C_0) - Z_t)^2
$$

(5)
where \( Z \) is the slope of the weighted regression. The age of inclusion for the catch curve was considered at the ‘peak,’ or youngest age with the maximum observed catch, and included all age classes, both observed and missing, from the peak to the oldest observed age (Smith et al. 2012).

The Chapman-Robson estimator (1960, Dunn et al. 2002) assumes that the lifespan of an individual follows a geometric distribution, and can be written as:

\[
Z = \log(e^{\left(1 + \frac{T - T_c}{T - T_c}\right)} - \frac{(N-1) \times (N-2)}{N \times [N \times (T - T_c) + 1] \times [N + N \times (T - T_c) - 1]})
\]  

where \( T_c \) is the age of full recruitment, \( \bar{T} \) is the mean age of fish in the sample that are greater than or equal to age \( T_c \), and \( N \) is the sample size of fish greater than or equal to age \( T_c \). The portion of the formula before the subtraction symbol transforms the Chapman-Robson estimate of \( S \) into an estimate of \( Z \) and the remaining portion reduces the bias that is induced by the transform (Smith et al. 2012). An approximate variance estimator for this estimate is:

\[
\frac{[1 - e^{\alpha Z}]^2}{N \times e^{\alpha Z}}.
\]  

Age of inclusion for the Chapman-Robson estimator was the ‘peak plus,’ or one age greater than the ‘peak,’ in order to capture only the descending limb of the relationship that included all observed and missing age classes from the age of inclusion to the oldest observed age class.

Millar (2015) also proposed an estimator for \( Z \) that utilizes a generalized Poisson linear regression model:

\[
\mu_a = e^{\alpha - Z \times a}
\]
where $\mu_a$ is Poisson mean catch at age $a$, $\alpha$ is the intercept and $Z$ is the slope. The model is fit to the catch-at-age via maximum likelihood using a log link function where $\alpha$ and $Z$ are fixed effects, and the $Z$ estimate is the negative of the model slope (Nelson 2019). This model assumes that the model mean is constant, however deviation from the mean scales exponentially with the age. This approach differs from a weighted linear regression by using $\log(e \mu_a)$ rather than $\log(e C_t)$; additionally, all confidence intervals are calculated within the model through the link function before being transformed to the response scale. Age of inclusion for the generalized Poisson linear regression models was the ‘peak plus,’ and included all observed and missing age classes from the age of inclusion to the oldest observed age.

Annual survival rates ($S = e^Z$) and annual mortality rates ($A = 1 - S$) were calculated for each of three sets of ages within each model. Finally, instantaneous natural mortality rates ($M$) were calculated for a range of instantaneous fishing mortality rates ($F$) that spanned from no fishing pressure to roughly double the current LWS limit reference point ($F = 0$ to $0.1$) using the equation $M = Z - F$ (Ricker 1975). All data manipulations, regressions, and visualizations were completed in an R programming environment (R Core Team 2019) using the tidyverse (Wickham 2019) and FSA (Ogle et al. 2019) packages.

**Additional Age-Based Models for Estimating Natural Mortality**

Several methods have been developed that use parameters from the von Bertalanffy model (VBGM; von Bertalanffy 1938) to estimate natural mortality rates in fish populations based on the ecological relationship between growth and mortality (Hilling et al. 2019). Because this suite of models uses age and growth information to indirectly estimate $M$, from this point forward I will refer to these models as indirect estimators. Two different types of VBGM parameters are available for the lake sturgeon population in the LWS: 1) parameters estimated
using traditional VBGM models fit using fin ray age estimates that can be corrected using the previously described methods and 2) parameters obtained using Fabens (1965) parameterization of the VBGM that incorporates observed growth increments obtained from the capture and subsequent recapture of fish. The traditional von Bertalanffy (1938) growth model can be represented as:

\[ L_t = L_\infty (1 - e^{-k(t - t_0)}) \]  

(9)

where \( L_\infty \) is the asymptotic maximum TL of the population, \( k \) is the Brody growth coefficient, and \( t_0 \) is the x-intercept (Ogle and Isermann 2017). This model was applied to fish encountered in the spring using the method to assign ages described earlier. To improve the fit of the VBGM near the intercepts, 4 male and 8 female juvenile lake sturgeon captured during lentic summer trawls in 2018 and 41 young of year lake sturgeon captured during fall lotic spotlighting sampling in 2018 and 2020 were included in the training data. Parameters from the VBGM were used to solve these indirect estimator models:

1) Jensen (1996) model, created by examining the theoretical relationship among life history parameters, where:

\[ M = 1.50 \times k \]  

(10)

2) Cubillos et al. (1999) model, created for estimating natural mortality in a commercial fishery for Chilean Hake *Merluccius gayi*, built off Hoenig’s (1983) regression model but assuming that maximum age can be estimated from \( L_\infty \), where:

\[ M = 4.31 \times \left[ t_0 - \left( \log_e(0.05) / k \right) \right]^{-1.01} \]  

(11)
3) Pauly (1980) model, based on an analysis of 175 unexploited fish stocks, consisting of 84 species from marine and freshwater environments that ranged from polar to tropical waters, where:

\[
\log_{10}(M) = -0.0066 - 0.279 \times \log_{10}(L_\infty) + 0.6543 \times \log_{10}(k) + 0.4634 \times \log_{10}(T)
\]  

(12)

with \(L_\infty\) in cm and \(T\) = mean annual water temperature in °C. Temperature was taken from a USGS stream monitoring station on the Fox River in Appleton, downstream from Lake Winnebago (Gauge 04084445, Latitude: 44°14′53″, Longitude 88°25′23″, coordinate system NAD83). Mean annual temperatures were averaged across all years with complete temperature data between 2009 and 2019.

Instantaneous natural mortality rates were also estimated using several models that incorporate mean asymptotic weight \((W_\infty)\) in g as a predictor variable based on the inverse relationship between mortality and body size. I estimated \(W_\infty\) by calculating weight at \(L_\infty\) using the \(a\) and \(b\) parameters from a \(\log_{10}\)-transformed weight-length regression from harvested lake sturgeon, where \(\log_{10}\)(weight) = \(b + a \times \log_{10}(TL)\), and then used this estimate in the following models:

4) Djabali (1993) model, built by regressing \(M\) against independent variables from Pauly’s (1980) equation for 56 stocks of 24 species of Mediterranean fish species, with temperature being insignificant for the stocks observed in this study, where:

\[
M = 0.8598 \times W_\infty^{-0.0302} \times k^{0.5280}
\]  

(13)

5) Lorenzen (1996) model, built from a pooled equation that found no significant difference among observed lake, riverine, and marine juvenile and adult fish natural mortality and weight relationships, where:
\[ M = 3.00 \times W_\infty^{-0.288} \]  

(14)

6) Peterson and Wroblewski (1984) model, based on the theory that in pelagic marine systems biomass distribution is a function of size and mortality results primarily from predation, where:

\[ M = 1.92 \times W_\infty^{-0.25} \]  

(15)

Additionally, \( M \) was estimated using four models that use age relationships observed in the catch curve samples as predictor variables:

7) Hoenig (1983) model, based on \( Z \) estimates from an analysis of 84 lightly or unexploited fish stocks representing 53 (mostly marine) fish species, where:

\[
\log_e(M) = 1.46 - 1.01 \times \log_e(t_{\text{max}})
\]

(16)

and \( t_{\text{max}} \) = maximum age in the sample in years;

8) Quinn and Deriso (1999) model, built on the inverse relationship between \( M \) and \( t_{\text{max}} \) that rearranged the exponential decline equation to solve for a proportion of the population that reaches \( t_{\text{max}} \), where:

\[
M = -\log_e(P_s) / t_{\text{max}}
\]

(17)

and \( P_s \) = proportion of the population that survives to \( t_{\text{max}} \), recommended by Quinn and Deriso (1999) to be fixed at 0.01 (i.e., assuming only 1% of the population reaches the max age);

9) Chen and Watanabe (1989) model, created using rearranged terms from the VBGM and incorporating life span information to accurately predict observed \( M \) values for seven fish species from the South China Sea, where:

\[
M = 1 / (t_{\text{max}} - t_c) \times \log_e\left\{ \left( e^{k \times t_{\text{max}}} - e^{k \times t_c} \right) / \left( e^{k \times t_c} - e^{k \times t_0} \right) \right\}
\]

(18)
and \( t_c \) = minimum age of the sample included in the catch curve analysis in years;

10) Kenchington (2014) model, created using 13 species from published studies to iteratively solve for \( M \) and assuming the maximum age increases proportionally with the number of fish aged, where:

\[
t_{\text{max}} = \left[ \frac{\log_e(2 \times M \times N_e + 1)}{M} \right] + t_c
\]  

(19)

and \( N_e \) is the effective sample size, or number of aged fish fully represented in the catch curve (i.e., of ‘peak’ age or older);

11) Then (2015) model, created by simulating various \( M \) estimators using a common dataset of 215 species and updating the methods to fit the training data, where:

\[
M = 4.899 \times t_{\text{max}}^{0.916}.
\]  

(20)

The Fabens (1965) parameterization of the von Bertalanffy growth model allows for multiple lengths of the same individual to be modeled and can be expressed as:

\[
L_r = L_\infty - (L_\infty - L_c)e^{kd}
\]  

(21)

where \( L_r \) is the length at recapture, \( L_c \) is the length at first capture, and \( d \) is the time interval between the first and last recapture (Frazer et al. 1990). In the Fabens parameterization \( L_\infty \) is an estimate of maximum length of fish in the population, not the asymptote as in the traditional VBGM, and because of this difference the Fabens parameter estimates were not used in any of the previous models that rely on \( L_\infty \) to estimate \( M \). Furthermore, the Fabens parameterization does not provide an estimate of \( t_0 \) as in the traditional VBGM, however Pauly (1979) proposed a method to determine \( t_0 \) using Fabens (1965) model where:

\[
\log_{10}(-t_0) = -0.3922 - (0.2752 \times \log_{10}(L_\infty)) - (1.038 \times \log_{10}(k)).
\]  

(22)
O’Connell (2020) estimated parameter values for this model using recapture histories for lake sturgeon in the LWS. The parameter values from this work of $k = 0.043$ for males and $k = 0.055$ for females were used to additionally solve for $t_0$ and the Cubillos (2) and Jensen (3) models.

**Capture-Recapture Models**

Encounter histories of lake sturgeon implanted with PITs and detection histories of sturgeon implanted with acoustic transmitters were used to estimate mortality using Cormack-Jolly-Seber (CJS; Cormack 1964; Jolly 1965; Seber 1965) models. Fish may not be encountered in every sampling interval, however, if they are encountered or detected in subsequent sampling intervals, the fish was alive at all previous intervals but was not detected. A CJS model utilizes unique encounter histories to calculate the conditional probability the individual survived and remained in the sample ($\Phi$) and the conditional probability the animal was encountered ($p$).

These capture histories sampled over $T$ occasions of $n$ unique individuals can be represented for an individual $i$ that was first encountered at time $f_i$ as the vector $\{y(i, t)\}^T_{t=f_i}$. Considering the state of an individual, $z(i, t)$, as a Bernoulli random variable describing if individual $i$ is alive ($z(i, t) = 1$) or dead ($z(i, t) = 0$) at time $t$, survival ($\Phi$) can be represented as:

$$z(i, t) | z(i, t-1) \sim \text{Bernoulli}(\Phi_{t-1})$$

(23)

for $t = f_i+1, \ldots, T$ (Royle 2008). Conditional on this state process, encounter observations $y(i, t)$ are independent Bernoulli random variables where:

$$y(i, t) | z(i, t) \sim \text{Bernoulli}(p_t z(i, t))$$

(24)

and $y(i, t)$ is a Bernoulli trial with parameter $p$, given $z(i, t) \neq 0$. 


Encounter history tables were created separately for males and females using PIT tagged fish, where rows represent the capture history of a unique fish and each column represents an annual sampling season (which consists of a winter spear harvest and following spring spawning assessment). A ‘1’ represents an individual that was encountered in each year’s spring spawning assessment, a ‘-1’ represents an individual that was harvested in each season, while a ‘0’ represents an individual not encountered in a spring spawning assessment or harvested. For example, a capture history of ‘1 0 0 1 -1’ would represent a fish that was encountered the first year, not encountered for two following years, encountered during the fourth year and harvested the fifth year.

Encounter history tables for acoustically tagged individuals were created separately for males and females and consisted of a 10-column table that reflected the expected 10-year battery life of an acoustic transmitter. Rows contain encounter histories for a given individual where a ‘1’ represents an individual that was detected on a riverine receiver within a specific year after the date of tagging. A ‘0’ represents a fish not detected on a riverine receiver during a given year, and a ‘-1’ again represents a fish harvested from the spear fishery for any relative year and informs the model that the individual is no longer alive. Models considered fish only for total time while tagged and at large.

Encounter and harvest histories of each uniquely tagged individual in the y matrix were used to inform the z matrix of the known life states. Since the z matrix consists of the latent state of an individual being alive at time t that a CJS model will solve based on the y matrix, computation time can be reduced by informing the z matrix with known true states. A value of ‘1’ was included in each row of the z matrix for all years between the first and last encounter for individuals encountered more than once because an individual must have been alive during all
intermediate sampling periods, while all remaining years in that row were left uninformed. For rows with harvested individuals, informed by a ‘-1’ in the $y$ matrix, a ‘1’ was included in the $z$ matrix from the first encounter until the harvest year, because the individual was encountered alive in that year, and any years remaining in that row of the survey were informed with a ‘0’, effectively informing the model that an individual is no longer alive in any year after being harvested.

If the apparent survival rate estimates from these models are treated as synonymous with estimates of annual survival ($S$) from catch curves, they can be used to calculate estimates of $Z$ ($Z = \log_e(S_A)$). This assumption would be violated if individuals were present but avoid detection or had permanently emigrated from the population, in which case they would still be alive, yet functionally dead within the model. However, the effect of this assumption also applies to estimates determined from catch-at-age-based models. Parameters were held temporally constant to limit the potential influence that spawning periodicity may have on the observation structure (Kendall and Nichols 2002). Kendall and Nichols (2002) also recommended other ways to adjust capture recapture models to improve model precision when dealing with unobservable states, however the CJS models used in this study already have a minimum number of states and would not benefit from the other proposed methods. New ranges of $M$ were calculated for the capture-recapture models using the same range of $F$ (0 to 0.1) used for estimating $M$ with the catch curve estimates of $Z$.

A Bayesian framework allows for effective implementation of state-space models by allowing for the incorporation of prior information (Royle 2008). The underlying mechanism for the process can be expressed by Bayes theorem, where:
\[ p(A \mid B) = \frac{p(B \mid A) p(A)}{p(B)}. \]  

(25)

The theorem is determined by setting two equivalent joint probabilities equal,

\[ p(A \cap B) = p(B \cap A), \]  

(25A)

replacing the joint probabilities with the product of the conditional and marginal probabilities, where:

\[ p(A \cap B) = p(A \mid B) x p(B) \]  

(25B)

and

\[ p(B \cap A) = p(B \mid A) x p(A), \]  

(25C)

substituting these equations into the initial equality, where:

\[ p(A \mid B) x p(B) = p(B \mid A) x p(A), \]  

(25D)

and then dividing both sides by the marginal probability \( p(B) \) so that:

\[ p(A \mid B) = \frac{p(B \mid A) p(A)}{p(B)}. \]  

(25)

In this instance, \( A \) can represent the CJS model and \( B \) the encounter history data. Contrary to frequentist statistics, where a parameter is considered fixed, in Bayesian statistics a parameter is considered random and has its own probability density function (McElreath 2020).

All CJS models were developed separately for males and females in a Bayesian framework using Gibbs Sampling in JAGS 4.3.0 (Plummer 2003) and an R interface (Staton 2020, Yu-Sung Su 2020). Each state space model was run with 3 chains of 500,000 iterations, a burn-in period of 5,000 iterations, and no thinning (Link and Eaton 2012). All models had
uninformed beta priors for $\Phi$ and $p$, with these parameters held temporally constant (Kendall and Nichols 2020), and model convergence was determined by the combination of an acceptable Brooks-Gelman-Rubin diagnostic (Brooks and Gelman 1998) less than 1.1 and by visually inspecting the distribution of each posterior chain.

**Harvest cap simulations**

Ranges of $M$ were used to evaluate potential differences in harvest caps for the lake sturgeon spear fishery during 2010-2020. Annual safe harvest caps are calculated using sex-specific population estimates that utilize a five-year average of Chapman’s (1951) modification of the Peterson method, where:

$$N = \frac{(M+1)(C+1)}{(R+1)} - 1$$  \hspace{1cm} (26)

and $N$ is the population estimate in year $x$, $M$ is the annual count of unique marked fish in the spring of year $x$, $C$ is the number of fish harvested and examined for PITs at check stations during spearing season in year $x + 1$, and $R$ is the number of marked fish in the spear harvest. This estimate is then corrected to account for the removal of the harvested individuals ($C$) from the population:

$$N_{corrected} = N - C.$$  \hspace{1cm} (27)

The total number of fish expected to be available for harvest in year $x + 2$ was calculated as:

$$N_{harvestable} = 0.01025 \times [N_{corrected} \times (e^{-0.055})]$$  \hspace{1cm} (28)

where $0.055 = M$ and 0.01025 is used to adjust for potential PIT loss or missed detection. Five percent of $N_{harvestable}$ was set as the simulated safe harvest cap for each sex.
Using annual sex-specific estimates of $N_{corrected}$ available for 2010-2020 I recalculated the range of $N_{harvestable}$ using the 46 estimates of $M$ that I generated for each sex using the methods described previously. For each catch curve and CJS model, an upper bound ($F = 0.0$), mid-point ($F = 0.05$), and lower bound ($F = 0.1$) were used to evaluate previous annual caps and harvest, while for the additional instantaneous mortality estimator models the upper and lower bounds were determined using the largest and smallest $M$ estimate from the suite of models for each age correction metric, and the mid-point was calculated as the average of the two bounds. All lower bounds of $M$ were limited to a minimum of 0.001 if needed. Difference between the observed harvest cap and each simulated model range were determined using these upper and lower bounds, and model results were determined to be different from the current cap estimation method if the observed cap was located outside of these bounds. Potential overharvest in each year of the simulation was determined if the observed harvest surpassed the lower bound of any of the model results, and the severity of the overharvest was evaluated based on exceedance of the lower bound, mid-point, and upper bound.
RESULTS

Spring spawning assessments

A total of 9,506 males and 2,071 females were handled and tagged with PITs during spring spawning assessments from 2009 to 2019. Over these years, males ranged from 755 mm to 1898 mm (Median: 1440 mm +/- 145 mm MAD), and females ranged from 1165 mm to 2223 mm (Median: 1655 mm +/- 126 mm MAD; Figure 2). From 1999 to 2019, a total of 12,762 males were captured, 9,269 males of those were only captured once, 2,445 males were recaptured once, and 1,048 males were recaptured twice or more. Over that same time, 2,982 females were captured, 2,693 females were only captured once, 261 females were recaptured once, and 28 were recaptured twice or more.

Age estimation and correction

Pectoral fin rays were collected in 1999-2006, 2011-2013, and 2017-2018 from 3191 males, ranging from 915 mm to 1893 mm (Median: 1360 mm +/- 167 mm MAD), and 3691 females, ranging from 853 mm to 2118 mm (Median: 1525 mm +/- 234 mm MAD; Figure 3). Raw fin ray age estimates for males ranged from 7 to 61, and from 9 to 66 for females. Power-corrected age estimates ranged from 7 to 76 for males and from 9 to 83 for females. Matrix-corrected age estimates ranged from 5 to 74 for males and 6 to 78 for females (Figures 4 and 5).

For age-length keys, low sample sizes (<10 fish per 25 mm TL bin) required the merging of the male 900- and 925-mm TL bins together along with grouping any male fish with a TL ≥ 1750 mm TL into a single bin. Female age-length keys required the combination of 850-, 875-, 900-, and 925-mm bins together, while all female fish with a TL ≥ 1925 mm were combined into a
single bin. One male was removed from the spring spawning sample prior to applying the age-length key for being smaller than the minimum male length bin.

*Estimating mortality rates*

**Catch curves**

Age of inclusion and sample sizes used in catch curves varied among age correction methods. Age of inclusion for males ranged from 26 to 39 with associated sample sizes that ranged from 5,207 to 6,430, while the female age of inclusion ranged from 36 to 45 and had sample sizes that ranged from 629 to 1,799 (Table 3). Instantaneous mortality rate estimates varied both between sexes and among catch curve models. Estimates of $Z$ ranged from 0.100 to 0.207 ($M$: 0.001 to 0.107; Table 4) for males and from 0.075 to 0.201 ($M$: 0.001 – 0.101; Figure 6, 7 and 8). Within most of the models, raw age estimates produced the highest $Z$ estimate of the three available age correction methods, however for the male weighted catch curve the matrix corrected ages produced the highest $Z$ estimate.

**Additional Models for Estimating Natural Mortality**

All von Bertalanffy growth models converged (Figure 9) with parameter values varying among age correction methods within each sex (Table 5) for use in the indirect mortality estimation methods. Estimates of $t_0$ using capture-recapture results with Pauly’s method provided estimates of 0.720 for males and 0.954 for females, which were greater than $t_0$ when estimated using ages from calcified structures. A total of 5,733 males and 6,754 females were used to determine sex specific weight length relationships (Figure 10). Average annual water temperatures recorded on the Fox River were 10.72 °C in 2014, 11.39 °C in 2015, 12.12 °C in 2016, and 11.8 °C in 2018. Male estimates of $M$ from the additional indirect estimator models
ranged from 0.068 to 0.226 for raw age estimates, 0.054 to 0.170 for power-corrected age estimates, 0.056 to 0.221 for matrix-corrected age estimates, and 0.059 to 0.065 for capture-recapture parameter estimates. Female indirect estimates of $M$ ranged from 0.063 to 0.191 for raw age estimates, 0.050 to 0.139 for power-corrected age estimates, 0.053 to 0.171 for matrix-corrected age estimates, and 0.075 to 0.083 for capture-recapture estimates (Table 6).

**Capture-Recapture Models**

All Cormack-Jolly-Seber models converged and had a normal distribution (Figure 11, Figure 12). Parameter estimates significantly differed between sexes, with survival estimates of PIT tagged lake sturgeon higher for males ($\Phi = 0.903, 0.900 – 0.907$ 95% Bayesian credible intervals) than for females ($\Phi = 0.856, 0.845 – 0.866$ 95% Bayesian credible intervals), however associated capture probabilities were low for both sexes (male $p = 0.098 [0.095 – 0.100$ 95% Bayesian credible intervals], female $p = 0.064 [0.059 – 0.070$ 95% Bayesian credible intervals]; Table 7). Survival estimates for acoustically tagged fish were similar between sexes and not different than PIT-based estimates based on Bayesian credible intervals (male $\Phi = 0.883 [0.858 – 0.907$ 95% Bayesian credible intervals], female $\Phi = 0.870 [0.841 – 0.896$ 95% Bayesian credible intervals]), however encounter probabilities when using acoustic tags were significantly different and higher than estimates from models created using PITs (male = 0.802 [0.768 – 0.834 95% Bayesian credible intervals], female = 0.689 [0.647 – 0.729 95 % Bayesian credible intervals]).

**Harvest cap Simulation**

The range of potential $M$ values used in harvest cap simulations are shown in Figure 13. For males, the lower bound of the range of $M$ exceeded 0.055 when raw and matrix-corrected
age estimates were used in a weighted linear regression catch curve to estimate Z and subsequently calculate $M$ and when $M$ was estimated using indirect methods. For females, the lower bound of the range of $M$ exceeded 0.055 when: 1) raw age estimates were used in a weighted-linear regression catch curve to estimate $Z$ and subsequently calculate $M$; 2) raw and power-corrected fin ray age estimates were used in the Chapman Robson catch curve model to estimate $Z$ and subsequently calculate $M$; 3) raw fin ray age estimates were used in the generalized Poisson linear regression catch curve to estimate $Z$ and subsequently calculate $M$; and 4) growth model parameters obtained when using raw fin ray age estimates and capture-recapture information were incorporated into indirect estimators of $M$. Annual harvest caps set by WDNR for 2010 to 2020 ranged from 1,000 to 1,250 fish for males and 1,090 to 1,380 fish for females (Table 1). Annual caps from my simulations ranged from a total of 843 to 2,321 fish for males (Table 8) and 942 to 1,457 fish for females (Table 9). Observed male harvest did not exceed the lower bound of any of my simulated harvest cap ranges for any year of the simulation (Figures 14-24). Conversely, observed female harvest exceeded both the lower bound and midpoint of the range for many of my simulated harvest cap ranges for 2010 and 2015 (Figures 14 and 19).
DISCUSSION

Estimates of $A$ from the various direct mortality estimation models used in this study (male: $A = 9.5\% - 18.7\%$; female: $7.2\% - 18.2\%$) were within the range of mortality estimates calculated from direct estimates for lake sturgeon in other systems ($A = 2\% - 25\%$). Baker (1980) estimated the total annual mortality rate for lake sturgeon in Black Lake, Michigan, to be 9.7\% using catch curves, but there was large variation in this estimate due to a limited sample size. The age of inclusion for catch curves in the Baker (1980) study was 25, which was similar to the peak age of 26 for models in my study for males when using raw pectoral fin ray age estimates. However, underestimation of ages when using pectoral fin rays for age estimation would result in overestimates of $Z$ when relying on catch curves to estimate mortality. Subsequent studies of the Black Lake population found lower mortality rates when using capture-recapture models, with $A$ estimates of around 2\% (Pledger et al. 2013). Withers et al. (2019) reported that $A$ estimated for the Eastern Lake Erie lake sturgeon population was 5.4\% when using capture-recapture models but confidence limits around this estimate were 1-44\%. Using capture-recapture models Dieterman et al. (2010) reported that $A$ was nearly constant at 20\% for the lake sturgeon population in the Kettle River, Minnesota, over a 15-year period. Similarly, Mailhot et al. (2011) reported similar estimates of $A$ between 17-25\% for fish aged 14 to 31 in the lower St. Lawrence River where commercial fishing occurs.

Gunderson et al. (2003) recommended a meta-analysis of a variety of models be explored to minimize bias in stock assessments when using indirect natural mortality estimation methods, which is why I incorporated a variety of models in my evaluation. The suite of indirect $M$ estimators I used generally mirror the direct estimation methods that suggest $M$ for the LWS lake sturgeon population may be higher than the rate of 0.055 presently used to set safe harvest caps.
and that males and females have different natural mortality rates. The current estimate of 0.055 was calculated from a SCAA model that was initiated using a single estimate of 0.0715 from Pauly’s (1980) method. Estimates of $M$ using Pauly’s (1980) method in this study were higher for both males and females than what Bruch (2008) previously calculated using Pauly’s method for lake sturgeon in the LWS. One difference between the Bruch (2008) study and this study is that Bruch (2008) used average air temperature (6.4 °C) as a surrogate for water temperatures when calculating Pauly’s $M$, but this study used average water temperatures (11.5 °C) recorded on the lower Fox River which is the outflow for the LWS. Lower Fox River temperature estimates should more accurately reflect the growing environment that lake sturgeon were exposed to during this study.

Estimates of $M$ that relied on weight relationships were typically higher than both the length and age-based estimates, which may be due in part to the pooling of different maturity stages for both sexes when determining the weight-length relationship. The weight measurements used in this study were obtained from individuals harvested in the winter and variation in egg development among females of the same length could influence the weight-length relationship for this sex. Furthermore, $W_\infty$ may have had a different value had it been calculated by directly fitting a curve to the observed weight-at-age relationship, however this specific method was not possible with this survey design. Kenchington’s (2014) estimator, which relies on a combination of age and an effective sample size, provided the highest estimates of $M$ for both males and females, however Then et al. (2014) argued that the estimator’s mathematical derivation is faulty and the underlying geometric model assumptions are unlikely in nature.

My simulations suggest the current estimate of $M$ used to establish harvest caps may allow annual exploitation rates for female lake sturgeon to exceed the 5% annual exploitation
limit reference point. Simulation results varied depending on which approach is used to estimate $M$. The potential for this issue to occur was demonstrated in two years of the simulations, 2010 and 2015, where observed harvest exceeded the lower bound and mid-point for harvest caps estimated from many of the methods I used to estimate $M$. Above average female harvest on Lake Winnebago in these two years contributed to the potential exceedance of a 5% safe harvest limit in these simulations, and the observed female harvest did exceed the cap allocated for Lake Winnebago in 2010 even with the current safe harvest management system closure triggers in place. The true potential for exceeding the 5% exploitation threshold remains unknown because of the uncertainty around these parameter estimates, and further risk assessment simulations would be needed to quantify the probability that exploitation rates might exceed the 5% limit. Additional caution when setting harvest caps may be warranted because female survival during all life stages is crucial for lake sturgeon population maintenance and recovery (Schueller and Hayes 2010) and Haxton et al. (2014) showed that continued exploitation rates greater than 6% were considered unsustainable for Great Lakes sturgeon populations. Additionally, harvest caps are estimated by applying estimates of $M$ to the five-year average population estimates. Hence, any potential errors in annual abundance estimates would result in uncertainty in the harvest cap estimation process, regardless of how $M$ is estimated. Models that incorporated potential variation in both abundance estimates and estimates of $M$ could be developed to assess the risk of exceeding the 5% exploitation limit reference point, but this process would be simpler if the number of methods used to estimate $M$ could be reduced in a logical manner. For example, using raw age estimates obtained from fin rays for estimating mortality rates seems an untenable option given that these ages are likely unreliable for fish older than 14 (Bruch 2009). Similarly, when using a catch-curve based approach for estimating $Z$ and then $M$ where employed, following the
guidance of Smith et al. (2012) to use the Chapman-Robson approach corrected for overdispersion represents a reasonable approach to reducing the number of potential ways to directly estimate $M$.

Capture-recapture studies provide a promising tool for estimating survival and mortality of lake sturgeon in the LWS because inference is not based on the interpretation and subsequent correction of age estimates from calcified structures, which has proven to problematic (O’Connell 2020), nor does it rely on an assumption of no recruitment trends that could be violated in many fish populations. However, spawning periodicity of lake sturgeon could affect encounter probability which is a critical component of capture-recapture models. Adult lake sturgeon may not spawn every year and therefore may not be available for capture in spawning assessments (Bruch and Binkowski 2002, Forsythe et al. 2012b). Encounter probabilities for my PIT-based capture-recapture models (male: $p = 0.098$; female: $p = 0.064$) were lower than estimates reported by Pledger et al. (2013) for male ($p = 0.53$) and female ($p = 0.40$) lake sturgeon in the Black Lake system. However, the smaller Black Lake system does not provide a useful corollary to the LWS in terms of size, number of spawning locations, and numbers of lake sturgeon. My encounter probabilities were below the 0.2 target recommended by Hewitt et al. (2010), which may result in overestimates of survival. Conversely, encounter probabilities for acoustically tagged lake sturgeon were well above the 0.2 baseline, but sample sizes were smaller and survival estimates spanned a larger range than estimates from PIT models. For both tag types, the probability of encountering a tagged fish was lower for females than males. This difference may reflect differences in spawning periodicity and sex-selective bias while sampling adult lake sturgeon during spawning. Survival estimates of LWS lake sturgeon for both tag types were lower than estimates for lake sturgeon in the Black Lake system (Pledger et al. 2013) and in
Eastern Lake Erie (Withers et al. 2019) where harvest is not allowed, which might be expected given the fishery associated with the LWS population. Direct comparison of parameters estimated from the two tagging methods should be approached with some caution because the models include different cumulative time periods (maximum of 10 years for acoustic tags, maximum of 21 years for PITs). Any changes in mortality that have occurred throughout the entire sampling period would more likely be reflected in parameter estimates from the PIT-based models. Both tagging methods did converge on the same survival estimate distribution, with the survival estimate credible intervals for the acoustic tag model completely overlapping with the credible intervals of the PIT tag model estimates for each sex, which indicates survival may have been constant throughout the study. If the subset of tagged fish used in this study is an accurate representation of the lake sturgeon population in the LWS, incorporating these capture-recapture analyses into current harvest management protocols may be an effective and time efficient method for estimating both growth (O’Connell 2020) and survival.

Using ages estimated from pectoral fin rays to inform harvest management decisions for lake sturgeon is fraught with potential pitfalls. Rossiter et al. (1995) expressed concern about accurately quantifying lake sturgeon age estimates from pectoral fin rays due to the increasingly close proximity of annuli as fish get older. To put this in context, the oldest fish encountered by Rossiter et al. (1995) came from a northern Ontario population that was estimated to be 36 years old, which would have been too young to be included in many of the catch curves in this study. Additionally, Bruch et al. (2009) determined that pectoral fin rays begin to underestimate ages after age 14, but the correction method they proposed to address this interpretation error creates erratic patterns in year class strength that complicates the use of linear catch curve estimators. O’Connell (2020) used a pectoral fin ray to otolith correction matrix to address age estimation
errors associated with fin rays, however the sample size used to create this matrix introduces a new set of errors when applied to a large sample. A limited training set of 79 individuals used for the creation of this otolith to pectoral fin ray age correction matrix likely contributed to both a large proportion of missing age classes and some age classes which were overrepresented. Corrections may help lessen the influence of age estimation errors, but correction methods require a robust sample that encompasses the full range of ages in the population. Currently, the power function correction method does not address any reader specific biases, while the matrix correction method has too small of a training set that does not allow for it to scale up effectively for mortality analyses. Furthermore, relying on otolith age estimates as a baseline for correcting fin ray ages for lake sturgeon may not be appropriate. Bruch et al. (2009) verified that otoliths can accurately estimate ages for individuals up to age 52, however many age classes included in the catch curves and growth analyses of this study were older than age 52. Furthermore, O’Connell (2020) found that only 108 otoliths were readable out of the 814 total otoliths sectioned and that variation among readers was large enough when interpreting aging structures that reader specific corrections were warranted. However, if enough structures are collected from known age fish to encompass older ages classes it may be useful to reconsider the use of reader-specific corrections with calcified structures.

My approach for using age-length keys in this study may have introduced error in the age-based growth and mortality models. The age-length key approach assumes that the subsample of fish used to construct the key is representative of the sample that the key is applied to (Ricker 1975). Typically, the subsample of fish used to construct the age-length key is part of a larger sample of fish such that all fish were collected at the same time (Kimura 1977). For my study, I used age estimates obtained from a subsample of mixed mature and immature lake
sturgeon harvested in February and applied the key to samples of spawning fish collected in April and May. I did this so that the catch curves and capture-recapture analyses were created using the same individuals, because all individuals encountered in the spring were tagged while fish encountered during the spear harvest consist of both tagged and untagged individuals. Using immature fish harvested in the winter and applying those younger age estimates to sexually mature fish handled in the spring could potentially influence growth curve estimates near the origin of the graph, however any immature fish would not have been considered based on the age of inclusion in the catch curves used in this study. Modeling done by Coggins et al. (2013) showed that an increase in total sample size when using an age-length key can help mitigate bias and increase precision while also finding negligible benefits in having more than a minimum of 10 replicates per size bin for growth and mortality analyses. The simulations that Coggins et al. (2013) used to inform these recommendations consisted of total sample sizes of 200-1,500 fish and only considered individuals that reached a maximum age of 40 within a limited window of population parameters such as a restricted coefficient of variation for length at age (±10%) and age estimation error (±10%). The total sample size of this study exceeded 1,500 fish but the maximum age exceeded 40 for both males and females, while the assumption that age estimation error is limited to only 10% of any age estimate may not be realistic for lake sturgeon. Given both the longevity of lake sturgeon and the potential for error when estimating ages from calcified structures, this study may have benefited from a greater minimum number of fish per size bin.

Management Implications

At least some of my simulations suggest that current $M$ estimates are currently too low for females and should be updated for future lake sturgeon management decisions. My results,
coupled with those of O’Connell (2020), suggest that relying on ages estimated from calcified structures to guide management of the lake sturgeon population in the LWS is ill advised given the many sources of error that exist. While capture-recapture models have their own potential errors, they would seem to provide a time efficient approach for estimating both mortality and growth (O’Connell 2020) for a species where accurately estimating ages is inherently difficult. Additionally, available age correction methods introduce their own issues to the process of estimating mortality (my study) and growth (O’Connell 2020). Lastly, using ages from calcified structures to determine growth and mortality for lake sturgeon in the LWS is not efficient based on the time required to collect, prepare, and analyze the structures, along with the high potential for process and interpretation error. However, catch curve estimates of $M$ that relied on ages corrected using the power correction method (Bruch et al. 2009) were still similar to the ranges of $M$ when estimated using capture recapture models.

I would recommend that a suite of models be considered annually to estimate $M$ separately for male and female lake sturgeon in the LWS that consists of two catch curves as well as two CJS models. Currently, it would be most effective to create catch curves that rely on ages adjusted using the power correction method (Bruch et al. 2009), however as training sets of structures from known age fish continues to grow it may be beneficial to revisit the matrix correction method in the future. These adjusted catch at age data could then be used to estimate mortality using both a Chapman Robson model and a generalized Poisson linear regression model. Concurrently, mortality could also be estimated using CJS models that rely on PIT recaptures as well as acoustic telemetry. These four separate mortality estimates could then be averaged to limit the influence of any one model on the mortality rate used to determine harvest caps.
If fishery managers adopt this suite of methods to estimate $M$ that rely in part on capture-recapture methods for estimating growth and mortality of lake sturgeon in the LWS, efforts could be made to improve the precision of these estimates. Models built with PIT tags had a low encounter probability in this study, but as PIT array technology improves utilizing these systems in tributaries of the LWS may be a future option to expand encounter opportunities during migratory events. For example, submersible antennas deployed at spawning locations might detect additional fish that were not dip netted during spawning surveys. Models built with acoustic tags are also limited to capturing migratory events, however if additional receivers were deployed in lake environments within the LWS encounter probabilities would likely increase, improving the precision of mortality estimates. I would recommend that the use of PIT and acoustic tags for monitoring lake sturgeon continue within the LWS, and that mortality estimates based on these data be used to generate harvest caps. While most studies use telemetry to describe the movement of fish or wildlife, this approach can additionally provide an effective method for estimating mortality, while combining encounter data from PITs and acoustic tags might provide more precise estimates of lake sturgeon mortality (Withers et al. 2019). Existing information from acoustically tagged lake sturgeon could be supplemented by tagging small numbers (e.g., 10) of lake sturgeon within the LWS each year that would eventually lead to more encounter information and continuous estimates of mortality.
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Table 4: Total mortality (Z), annual mortality (A), and annual survival (S) estimates for male and female lake sturgeon sampled using dip nets in the Lake Winnebago system from 2009-2019. Estimates of each parameter were calculated for three separate catch curve models for each of three separate pectoral fin ray age correction methods, along with the upper 95% confidence interval (UCI) and lower 95% confidence interval (LCI).

Table 5: Parameters of the von Bertalanffy growth model for male and female lake sturgeon encountered in spring samples on the Lake Winnebago system from 2009-2019. Estimates of each parameter were calculated using three separate pectoral fin ray age correction methods, along with the upper 95% confidence interval (UCI) and lower 95% confidence interval (LCI).

Table 6: Parameter estimates of indirect natural mortality (M) models for male and female lake sturgeon encountered during spring sampling on the Lake Winnebago system from 2009-2019 using various growth metrics.

Table 7: Cormack-Jolly-Seber annual apparent survival estimates (Φ̂) and capture probabilities (p̂) with associated 95% Bayesian credible intervals (CI), standard deviation (SD), and sample sizes (n) of adult male and female lake sturgeon in the Lake Winnebago system, Wisconsin, 1999-2019. The physical model used data of PIT-tagged lake sturgeon physically recaptured at spawning grounds, while the passive model used data of acoustic-tagged lake sturgeon passively detected at stationary receivers. Models were informed of harvested individuals.

Table 8: Upper and lower bounds of simulated harvest caps for male lake sturgeon in the combined Lake Winnebago spear fishery based on various M estimate ranges. Catch curve M ranges generated using raw pectoral fin ray age estimates (Raw), power-corrected pectoral fin ray age estimates (PC), and matrix-corrected pectoral fin ray age estimates (MC). Cormack Jolly Seber (CJS) M ranges estimated using encounter history from individuals physically handled with passive integrated

51
transponders (PIT) or passively detected with acoustic transmitters (Telemetry). Indirect estimators determined using growth information calculated from pectoral fin ray age estimates or encounter histories.

Table 9: Upper and lower bounds of simulated harvest caps for female lake sturgeon in the combined Lake Winnebago spear fishery based on various $M$ estimate ranges. Catch curve $M$ ranges generated using raw pectoral fin ray age estimates (Raw), power-corrected pectoral fin ray age estimates (PC), and matrix-corrected pectoral fin ray age estimates (MC). Cormack Jolly Seber (CJS) $M$ ranges estimated using encounter history from individuals physically handled with passive integrated transponders (PIT) or passively detected with acoustic transmitters (Telemetry). Indirect estimators determined using growth information calculated from pectoral fin ray age estimates or encounter histories.
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<td>Harvest Female</td>
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<td>Cap Female</td>
<td>Male</td>
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Table 2. Number of lake sturgeon surgically implanted with 10-year acoustic transmitters in the Lake Winnebago System from 2007-2018.

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<th>Year</th>
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<td>2018</td>
<td>5</td>
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Table 3. Age of inclusion and effective sample size ($N_e$) used in catch curve analyses of male and female lake sturgeon sampled using dip nets in the Lake Winnebago system from 2009-2019. Catch curve models are subdivided into those that either utilize all fish observed from the most abundant age and older (peak) and those that utilize all fish observed from one year older than the most abundant age class and older (peak plus).

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<th>Peak</th>
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<td></td>
<td>Matrix-corrected age estimates</td>
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Table 4. Total mortality (Z), annual mortality (A), and annual survival (S) estimates for male and female lake sturgeon sampled using dip nets in the Lake Winnebago system from 2009-2019. Estimates of each parameter were calculated for three separate catch curve models for each of three separate pectoral fin ray age correction methods, along with the upper 95% confidence interval (UCI) and lower 95% confidence interval (LCI).

<table>
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<tr>
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<td></td>
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Table 5. Parameters of the von Bertalanffy growth model for male and female lake sturgeon encountered in spring samples on the Lake Winnebago system from 2009-2019. Estimates of each parameter were calculated using three separate pectoral fin ray age correction methods, along with the upper 95% confidence interval (UCI) and lower 95% confidence interval (LCI).

<table>
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Table 7. Cormack-Jolly-Seber annual apparent survival estimates ($\hat{\Phi}$) and capture probabilities ($\hat{p}$) with associated 95% Bayesian credible intervals (CI), standard deviation (SD), and sample sizes ($n$) of adult male and female lake sturgeon in the Lake Winnebago system, Wisconsin, 1999-2019. The physical model used data of PIT-tagged lake sturgeon physically recaptured at spawning grounds, while the passive model used data of acoustic-tagged lake sturgeon passively detected at stationary receivers. Models were informed of harvested individuals.

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fin ray age estimates or encounter histories.
Table 9. Upper and lower bounds of simulated harvest caps for female lake sturgeon in the combined Lake Winnebago spear fishery based on various $M$ estimate ranges. Catch curve $M$ ranges generated using raw pectoral fin ray age estimates (Raw), power-corrected pectoral fin ray age estimates (PC), and matrix-corrected pectoral fin ray age estimates (MC). Cormack Jolly Seber (CJS) $M$ ranges estimated using encounter history from individuals physically handled with passive integrated transponders (PIT) or passively detected with acoustic transmitters (Telemetry). Indirect estimators determined using growth information calculated from pectoral  

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Figure 14. Simulated cap ranges for 2010 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.
Figure 15. Simulated cap ranges for 2011 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.
Figure 16. Simulated cap ranges for 2012 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.
Figure 17. Simulated cap ranges for 2013 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.
Figure 18. Simulated cap ranges for 2014 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.
Figure 19. Simulated cap ranges for 2015 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.
Figure 20. Simulated cap ranges for 2016 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.
Figure 21. Simulated cap ranges for 2017 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.
Figure 22. Simulated cap ranges for 2018 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.
Figure 23. Simulated cap ranges for 2019 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.
Figure 24. Simulated cap ranges for 2020 based on instantaneous mortality $M$ ranges from weighted linear regressions (WLR), Chapman Robson (CR), generalized Poisson linear regressions (GPLR), age and growth based indirect estimators (IE), and Cormack Jolly Seber (CJS) models for male and female lake sturgeon in the Lake Winnebago system (LWS). Ranges for WLR, CR, GPLR, and IE models estimated using age estimates from pectoral fin rays using either raw estimates (Raw), power-corrected estimates (PC), matrix-corrected estimates (MC), or growth estimates from multiple encounters of individuals tagged with passive integrated transponders (PIT). Ranges for CJS models estimated from encounter histories of individuals tagged with PITs or detection histories of individuals surgically implanted with acoustic transmitters and detected at acoustic receivers throughout the LWS (Telemetry). Upper and lower bound of the cap range for each model represented as connected points with the midpoint displayed between, while the dashed line represents the observed cap and the dotted line represents the observed winter spear harvest for the season.