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ARTICLE

Population Dynamics and Evaluation of Management Scenarios for White Sturgeon in the Sacramento–San Joaquin River Basin

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Abstract

Recent surveys suggest a declining population of White Sturgeon *Acipenser transmontanus* in the Sacramento–San Joaquin River basin (SSJ), California. Probable reasons for the decline include overharvest and habitat degradation compounded by poor recruitment during recent droughts. Despite the importance and status of White Sturgeon, knowledge of their population dynamics in the SSJ remains incomplete and additional information is needed to further inform management decisions. The purpose of this study was to evaluate the population dynamics of White Sturgeon in the SSJ and use the information to estimate the population-level response under plausible management scenarios. White Sturgeon in the SSJ exhibited fast growth and high rates of mortality and experienced relatively high levels of exploitation. Under current conditions, the population will likely continue to decrease (population growth rate $\lambda = 0.97$); however, there was considerable uncertainty in estimates of future population growth. Population growth of White Sturgeon in the SSJ was most influenced by the survival of sexually mature adults. The models also suggested that White Sturgeon in the SSJ could reach the replacement rate (i.e., $\lambda \geq 1.00$) if total annual mortality for age-3 and older fish does not exceed 6%. Low levels of exploitation (i.e., <3%) would likely be required to maintain a stable population.

Sturgeons (Acipenseridae) are of conservation concern throughout their distribution (Birstein et al. 1997; Pikitch et al. 2005; Munro et al. 2007; Jelks et al. 2008; Haxton et

al. 2016). All sturgeons share life history characteristics (e.g., long life span, periodic spawning, and delayed maturation) that make them exceptionally vulnerable to

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anthropogenic disturbances. Most sturgeon species are imperiled due to habitat degradation, altered flow and temperature regimes, and overharvest (Beamesderfer and Farr 1997; Bemis and Kynard 1997; Boreman 1997; Pikitch et al. 2005; Schreier et al. 2013; Haxton et al. 2016). In particular, the decline of sturgeon around the world has been attributed to overharvest (Boreman 1997; Pikitch et al. 2005; Haxton et al. 2016). Many sturgeon populations have experienced decades of unregulated exploitation driven by a valuable market for their eggs (i.e., caviar; Boreman 1997; Pala 2005; Pikitch et al. 2005). As a result, several species in Eurasia (e.g., Beluga Sturgeon *Huso huso* and Stellate Sturgeon *Acipenser stellatus*) are listed as critically endangered by the International Union for Conservation of Nature (Birstein et al. 1997; Pikitch et al. 2005). Recent efforts in the USA to conserve sturgeon populations, including bans of imported caviar, strict harvest regulations, increased monitoring efforts, and conservation aquaculture, have yet to improve their overall status (Pala 2005; Pikitch et al. 2005; Haxton et al. 2016; Hildebrand et al. 2016).

All nine sturgeon species that are native to North America are currently listed as endangered, listed as threatened, or considered species of special concern under the Endangered Species Act, including several populations of White Sturgeon *Acipenser transmontanus* (Jelks et al. 2008; Haxton et al. 2016). Although White Sturgeon are relatively abundant and widespread, commercial and recreational fisheries and alterations to large river habitats (e.g., hydroelectric dam construction) have reduced their abundance and distribution (Beamesderfer et al. 1995; DeVore et al. 1995; Jager et al. 2001; Pikitch et al. 2005; Irvine et al. 2007; Hildebrand et al. 2016). The largest populations occur where White Sturgeon still have access to the ocean: in the Fraser River, British Columbia; lower Columbia River, Oregon–Washington; and the Sacramento–San Joaquin River basin (SSJ), California (Schreier et al. 2013; Hildebrand et al. 2016). Currently, the status of White Sturgeon varies across subpopulations (Schreier et al. 2013). For instance, the Kootenai River Distinct Population Segment (Montana, Idaho, and British Columbia) is listed as an endangered species under the Endangered Species Act, whereas the SSJ population of White Sturgeon does not warrant federal protection at this time (Paragamian et al. 2005; Hildebrand et al. 2016). However, results from recent monitoring studies by the California Department of Fish and Wildlife (CDFW) have provided evidence that the population is declining; it is considered a species of high concern by the state of California (Moyle et al. 2015; Hildebrand et al. 2016). As such, preventing further declines of White Sturgeon in the SSJ has become a recent focus of the CDFW and the U.S. Fish and Wildlife Service (USFWS). Concern over the population trajectory of a suite of anadromous species led to passage of

the Central Valley Project Improvement Act (CVPIA) in 1992 and the development of the USFWS Anadromous Fish Restoration Program (AFRP; USFWS 2001). The AFRP was tasked with developing recovery goals, termed “doubling goals,” for five anadromous species (Chinook Salmon *Oncorhynchus tshawytscha*, steelhead *O. mykiss*, American Shad *Alosa sapidissima*, White Sturgeon, and Green Sturgeon *Acipenser medirostris*) and identifying actions to be taken to meet those goals. For White Sturgeon, the CVPIA has an objective of a sustained increase in the number of age-15 White Sturgeon to 11,000 individuals based upon CDFW population estimates from 1956 to 1991; this objective has yet to be achieved (Gingras and DuBois 2013).

White Sturgeon were historically abundant in the SSJ, but altered habitat and hydrological conditions coupled with overexploitation are considered to have caused the declines in SSJ population abundance and distribution (Nichols et al. 1986; Moyle et al. 2011; Hildebrand et al. 2016). Before large-scale changes began in the mid-1800s, the SSJ was characterized as an unregulated tidal marsh that was prone to extensive flooding (Nichols et al. 1986). During the Gold Rush in the 1850s, critical sturgeon habitat was disturbed by mining, urbanization, and agricultural development. Early developments diverted water, desiccated wetlands, channelized small tributaries, and increased salinity across the SSJ (Nichols et al. 1986). Currently, the SSJ serves as the world's largest regulated water storage and transportation system (Nichols et al. 1986; Cloern and Jassby 2012; Jackson et al. 2016). Water management practices in the SSJ and the San Francisco Estuary (SFE), directed primarily for agricultural use, flood control, and power generation, have led to the construction of over 20 dams, 1,600 km of levees, and hundreds of water diversion facilities that further alter natural environmental conditions (e.g., floodplain connectivity, temperature, and streamflow) and sturgeon habitat (Jaffe et al. 2007; Grimaldo et al. 2009; Mussen et al. 2014; Jackson et al. 2016). Water diversion structures throughout the SSJ and SFE entrain fish, including juvenile sturgeon, potentially contributing an additional source of mortality (Grimaldo et al. 2009; Mussen et al. 2014). In addition, more than 250 nonnative species have been introduced into the SSJ and SFE (Moyle et al. 2011). Pinnipeds and several nonnative fishes, such as Striped Bass *Morone saxatilis*, Common Carp *Cyprinus carpio*, and Largemouth Bass *Micropterus salmoides*, have been documented as preying on juvenile White Sturgeon (Miller and Beckman 1996; M. L. Gingras, unpublished data).

Unregulated commercial harvest from the mid-1880s to the early 1900s caused White Sturgeon in the SSJ to decline to near extirpation (Pycha 1956; Skinner 1962). By 1917, commercial and recreational fishing was prohibited for all sturgeon in the SSJ (Skinner 1962). In 1954, the

SSJ White Sturgeon population was thought to be resilient enough to support a recreational fishery (Chadwick 1959). Research conducted during the 1950s to 1980s designated the population as stable with sustainable harvest rates (Chadwick 1959; Kohlhorst 1980). Exploitation (μ) was estimated to vary between 2.0% and 7.3%, with most White Sturgeon caught as incidental bycatch by Striped Bass anglers (Pycha 1956; Miller 1972; Kohlhorst et al. 1991). However, enhanced technology (e.g., fish finders) and an increasing interest in the White Sturgeon sport fishery led to a μ of 11.5% by the late 1980s (Kohlhorst et al. 1991). As a result, several changes to White Sturgeon harvest regulations were implemented. For example, the CDFW designated a harvest slot limit of 117–183 cm TL in 1990 to protect mature White Sturgeon. Regulations continued to change throughout the 1990s and again in 2007 and 2013. Currently, anglers may harvest up to three White Sturgeon per year between 102 and 152 cm FL. Despite increasingly restrictive harvest regulations, the potential for overexploitation of White Sturgeon in the SSJ remains a concern (Kohlhorst et al. 1991; Gingras and DuBois 2014; Hildebrand et al. 2016). Rieman and Beamesderfer (1990) and Beamesderfer and Farr (1997) suggested that most North American sturgeon can only sustain levels of μ around 5%–10%. Additionally, current and historic estimates of μ for White Sturgeon are biased low because information on illegal harvest, total fishing effort, and total number of anglers is incomplete.

Recent results from several CDFW monitoring surveys suggest declining population trends. Since 1967, CDFW has intermittently conducted an adult sturgeon population study that monitors the relative abundance, distribution, exploitation, and growth of sturgeon in the SSJ. Since 2001, the average CPUE (fish per 100 net-fathom hour [NFH], equivalent to a net 100 fathoms [183 m] long fishing for 1 h) of White Sturgeon has been well below the historic average of 2.5 fish/NFH (DuBois and Danos 2017). Adding to the concern is a trend of inconsistent recruitment (Gingras et al. 2013). Since 1980, the CDFW has been monitoring White Sturgeon recruitment during sampling efforts from the San Francisco Bay Study (hereafter termed the “Bay Study”). The Bay Study conducts monthly trawling surveys at fixed sites in the SSJ and the SFE to evaluate the effects of freshwater outflow on the abundance and distribution of fishes in the region (Fish et al. 2012). Catches of age-0 and age-1 White Sturgeon from the Bay Study serve as an index of recruitment. Although successful White Sturgeon recruitment in the SSJ has been documented as highly variable, data from the Bay Study suggest a decreasing trend in White Sturgeon recruitment since the mid-1980s, with undetectable recruitment during recent droughts (2007–2010 and 2012–2016; Shirley 1987; Gingras et al. 2013). Few age-0 and age-1 White Sturgeon have been sampled since 1998, and

only two strong year-classes (2006 and 2011) have been documented in the last 19 years. Continued poor recruitment has the potential to put the population at risk. For instance, the endangered status of White Sturgeon in the Kootenai River (Paragamian and Hansen 2008) and of the Pallid Sturgeon *Scaphirhynchus albus* in the Missouri and Mississippi River basins (USFWS 2014) is largely attributed to prolonged recruitment failure or near failure.

Given the declining CPUEs and frequent recruitment failure or near failure over the last two decades, re-evaluation of harvest regulations for White Sturgeon in California is warranted. An effective approach for evaluating the efficacy of current and future harvest regulations is the use of age-structured population models to predict population-level responses to changes in rate functions (i.e., recruitment, growth, and mortality). For example, Scholten and Bettoli (2005) used age-structured models to estimate the population response of Paddlefish *Polyodon spathula* in the lower Tennessee River to various levels of prospective exploitation and size restrictions. Koch et al. (2009) used population simulations (i.e., yield-per-recruit models) to provide evidence that harvest regulations (e.g., length limits) were inadequate to prevent overfishing of Shovelnose Sturgeon *Scaphirhynchus platyrhynchus* in the Mississippi River. Age-structured models are also useful for identifying the life history stages that are most sensitive to past and future management actions (Horst 1977; Gross et al. 2002; Morris and Doak 2002; Cox et al. 2013; Ng et al. 2016). However, constructing age-structured models requires detailed demographic information on age-specific vital rates (Morris and Doak 2002). Although the White Sturgeon population in the SSJ has been sampled extensively since the 1950s, baseline knowledge of rate functions and population demographics remains incomplete. Therefore, additional information is necessary to guide management decisions. The objectives of this study were to (1) estimate the current population dynamics and demographics of White Sturgeon in the SSJ and (2) evaluate the population-level response to different management alternatives (e.g., bag limits and length restrictions).

METHODS

Study area.—Originating in the Klamath Mountains near Mount Shasta, the Sacramento River is the largest river in California in terms of length and discharge (Jaffe et al. 2007). The Sacramento River flows southwest for 716 km until it meets the San Joaquin River near Antioch, California (Nichols et al. 1986). The San Joaquin River is the second-longest river in California. With headwaters in the central Sierra Nevada, the San Joaquin River travels 531 km through the arid Central Valley before reaching its confluence with the Sacramento River (Nichols et al. 1986). Mean annual freshwater runoff into the SFE from

the SSJ is approximately 34.0 km³ but has varied from a low of 7.6 km³ in 1977 to a high of 65.0 km³ in 1983 (Jaffe et al. 2007). The confluence of the Sacramento and San Joaquin rivers forms the Sacramento–San Joaquin River Delta, which flows into the SFE through Suisun and San Pablo bays (Figure 1). The two bays are shallow, with average depths of 4.6 and 3.7 m, respectively (Jaffe et al. 2007; Cloern and Jassby 2012). Both bays are turbid, low-salinity environments with average tidal floods of 0.9–1.3 m. South of San Pablo Bay is San Francisco Bay.

Field sampling and laboratory processing.—Sampling for White Sturgeon occurred in Suisun and San Pablo bays during August–October 2014–2015 and September–October 2016. White Sturgeon were sampled with drifted 183-m trammel nets. Nets were composed of four 45.7-m contiguous panels of mesh. The outer walls were 3.7-m-deep panels constructed with multifilament nylon twine. Each 45.7-m panel had a single inner mesh panel of multi-strand monofilament twist gill net that alternated among 15.2-, 17.8-, and 20.3-cm stretch mesh. Inflatable buoys were attached in the middle and at both ends of the trammel net to help the net drift and to prevent it from tangling while deployed. Sampling sites in Suisun and San Pablo bays were chosen by the CDFW boat operator based on prior encounters with sturgeon, environmental conditions, and site availability. Trammel nets were drifted perpendicular to the prevailing wind or current in locations with signs of sturgeon aggregations while avoiding known snags. Nets were soaked for approximately 30 min before retrieval with a hydraulic lifter.

Upon net retrieval, captured White Sturgeon were inspected for tags (e.g., Carlin disc-dangler reward tags or PIT tags) and were measured for FL to the nearest

centimeter. Additionally, the inner panel mesh size that caught the White Sturgeon was recorded. White Sturgeon measuring 84–204 cm FL that bore no prior tags had a Carlin disc-dangler reward tag inserted through the musculature proximal to the dorsal fin. Each tag was labeled with a monetary value of US\$20, \$50, \$100, or \$150 and a return address. A section of the anterior left pectoral fin ray proximal to the body wall was taken from five White Sturgeon per 1-cm length-group to estimate fish age (Nguyen et al. 2016).

Pectoral fin rays were mounted in epoxy via the methods outlined by Koch and Quist (2007). A cross section was taken from each encapsulated fin ray with an IsoMet low-speed saw (Buehler, Lake Bluff, Illinois). Two or three sections varying in width from 0.83 to 1.25 mm were cut from the proximal end of the fin ray to ensure that at least one readable section was available for age and growth analyses. Cross-sectioned fin rays were aged using a dissecting scope and transmitted light. Image-Pro Plus software (Media Cybernetics, Rockville, Maryland) was used to measure the distance between annuli. Annuli were enumerated without prior knowledge of fish length. Before aging White Sturgeon fin rays from the SSJ, the senior author gained experience by estimating ages and measuring growth increments of known-age White Sturgeon from the Kootenai River ($n=157$). Furthermore, ages for a subsample of 91 White Sturgeon fin rays from the SSJ were independently estimated by three readers to assess the precision of the age estimates. When a disagreement between age estimates occurred, the readers conferred to produce a consensus age. All remaining fin ray sections were aged by one reader.

Data analysis.—Statistical analyses were performed in R using the Fisheries Stock Assessment package (Ogle

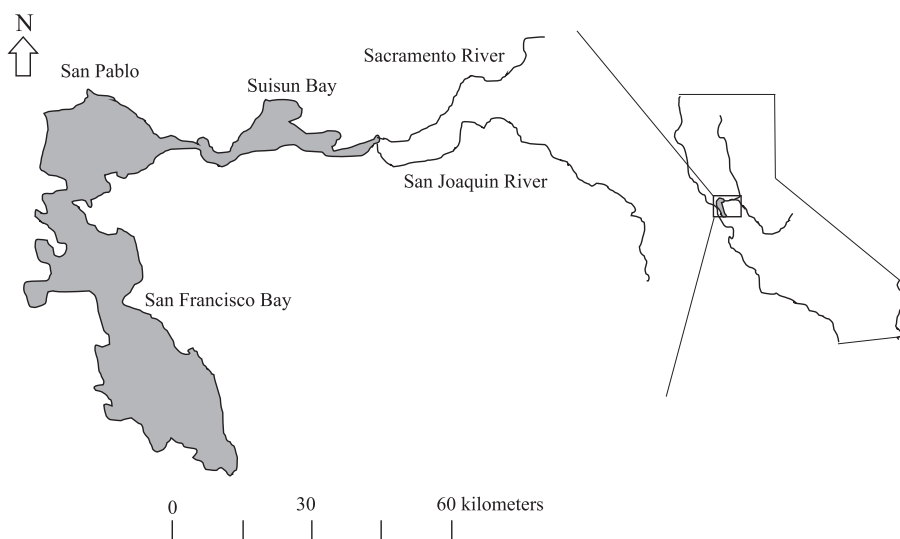


FIGURE 1. Map of the Sacramento and San Joaquin rivers as they enter the San Francisco Bay–Delta Estuary, California.

2017; R Core Team 2018). Mean back-calculated length at age for individual fish was estimated using the Dahl–Lea method (Ricker 1975; Quist et al. 2012). Estimated back-calculated length-at-age data were used to model growth described by the von Bertalanffy growth model for both sexes:

$$L_t = L_\infty \times \left[1 - e^{-k(t-t_0)}\right],$$

where L_t is FL (cm) at time t ; L is the mean maximum length; K is the growth coefficient; and t_0 is the theoretical age when length is zero (von Bertalanffy 1938; Ogle et al. 2017).

An age–length key was used to estimate the age distributions of all White Sturgeon sampled by CDFW from 2014 to 2016 (Quist et al. 2012). However, passive entanglement gears are size selective and produce biased length frequency distributions (Erzini et al. 2006; Hubert et al. 2012; Gabr and Mal 2016). As such, the SELECT (“Share Each Length’s Catch Total”) method was used to estimate the relative retention probabilities for 34 different length-classes (5-cm length-bins) of White Sturgeon from the trammel net catch rates (Millar and Fryer 1999). We adjusted for unequal fishing power among mesh sizes and assessed combinations of five selectivity models (i.e., normal location, normal scale, lognormal, gamma, and bimodal). The model with the lowest mean deviance and residuals was chosen as the top model. Using the top model, the adjusted length distribution was estimated by dividing the catch of each length-class by the estimated overall selectivity for that length-class (Millar 1992; Ng et al. 2016). The population length frequency and age frequency distributions were then estimated by applying the age–length key to the adjusted length frequencies (Erzini et al. 2006; Ng et al. 2016; Paukert and Spurgeon 2017).

Total annual survival (S) and instantaneous mortality rate (Z) of age-3 to age-19 White Sturgeon were estimated for uncorrected catch at age and trammel net selectivity-corrected catch at age using the Chapman–Robson estimator with the peak-plus-one criterion (Chapman and Robson 1960; Smith et al. 2012). Total annual mortality (A) was then estimated using the equation $A = 1 - S$ (Ricker 1975). No direct estimates of age-specific mortality were available for larval or juvenile White Sturgeon in the SSJ, as White Sturgeon of ages 0–2 were absent from our samples. White Sturgeon mortality is assumed to follow a type III survivorship curve, with a mortality rate of at least 99.9% in the larval stage and reaching an asymptotic survival rate by age 3 (Houde 1987; Pine et al. 2001). Mortality estimates for age-0 White Sturgeon were obtained from a study on Lake Sturgeon *Acipenser fulvescens* (Caroffino et al. 2010), those for age-1 White Sturgeon were from a

study on Gulf Sturgeon *Acipenser oxyrinchus desotoi* (Pine et al. 2001), and those for age 2 were from a study on hatchery-origin White Sturgeon in the Kootenai River (Ireland et al. 2002).

Exploitation (μ) of White Sturgeon in the slot length limit was estimated as the fraction of Carlin disc-dangler reward tags reported by anglers divided by the number of tagged fish available for harvest over a 1-year period. The number of tags returned was adjusted for incomplete reporting, tagging mortality, and tag loss (Smith et al. 1990; Rien et al. 1994; Meyer et al. 2012). Research suggests that the angler reporting rate varies by tag value (Pollock et al. 2001; Meyer et al. 2012). Therefore, we used tag return data from the period 2007–2015 to estimate the average reporting rate for each reward tag (i.e., \$20, \$50, or \$100). Assuming a 100% return rate for the high-reward tags (i.e., \$150), annual reporting rates (Λ) were estimated using the equation

$$\Lambda = \frac{R/N}{R'/N'},$$

where R is the number of low-reward tags returned by anglers, N is the total number of low-reward tags used, R' is the number of high-reward tags returned, and N' is the total number of high-reward tags used (Pollock et al. 2001). The number of annual tags returned was then corrected for nonreporting. Annual exploitation from 2007 to 2015 was estimated as

$$\mu = \frac{N_r}{N_0 \times \gamma \times \theta},$$

where N_r is the corrected number of tags returned for harvested fish, N_0 is the number of available fish tagged, γ is tag retention (i.e., 0.90; Rien et al. 1994), and θ is survival of tagged fish (i.e., $1 - \text{tagging mortality} = 0.99$; Smith et al. 1990). Additionally, because the harvest fishery is structured around specific lengths, we incorporated growth into and out of the harvest slot when calculating μ . Based on the von Bertalanffy growth model, White Sturgeon were predicted to recruit to the fishery at 10.2 years of age (102 cm FL) and to remain within the slot limit for 5.2 years (152 cm FL). White Sturgeon that were tagged between the ages of 9.2 and 15.4 years were considered available for harvest (N_0) during the 1-year period after tagging. We used the relationship for a type 2 fishery, where harvest and natural mortality operate at the same time ($F = \mu Z/A$), to convert instantaneous fishing mortality (F) to exploitation (Ricker 1975).

Instantaneous natural mortality (M) was obtained by $M = Z - F$ (Ricker 1975). Although we used this value of M in the population models, inaccurate estimates of M can bias the results of population models (Hamel et al.

2016). Therefore, we compared our estimate of M to the average of four different estimates using meta-analysis estimator equations to help account for uncertainty (Hamel et al. 2016; Ng et al. 2016; Ogle 2016). Parameters from the estimated von Bertalanffy growth model, maximum observed age (i.e., 29 years), and water temperature data ($^{\circ}\text{C}$) from Suisun Bay were used as inputs for equations from Pauly (1980), Hoenig (1983), and Then et al. (2015). Conditional natural mortality (cm ; mortality in the absence of exploitation) was then estimated as $cm = 1 - e^{-M}$ (Ricker 1975).

Data on the reproductive ecology (e.g., mean fecundity at age, age at first maturity, and proportion of females spawning each year) of White Sturgeon are limited. White Sturgeon do not exhibit external sexual dimorphism, thus making reproductive investigations invasive and costly. Therefore, previous research (i.e., Conte et al. 1988; Chapman 1989; DeVore et al. 1995; Chapman et al. 1996) was used to provide information on the reproductive parameters of White Sturgeon in the SSJ. Chapman (1989) examined the gonadal development of 421 wild female White Sturgeon collected from the SSJ; 81 of those females were considered mature. Using these data, age at first maturity and the probability of maturity at age i (pm_i) were predicted with logistic regression. Fecundity at age (f_i) was estimated for age-10 and older White Sturgeon by using the equation developed for White Sturgeon in the lower, unimpounded Columbia River (DeVore et al. 1995). The FL at age i (FL_i ; cm) was used to predict age-specific egg production. We did not use the estimate of fecundity described for White Sturgeon in the SSJ because the equation was based on the number of eggs collected surgically, which is estimated to be 40%–60% less than the number of eggs that would be obtained from natural spawning (J. P. Van Eenennaam, University of California–Davis, personal communication). Additionally, the fecundity equation from Chapman et al. (1996) is based on weight. Weight data were not collected during recent CDFW sampling efforts.

A female-based Leslie matrix model was used to assess the response of the White Sturgeon population in the SSJ to prospective management actions (Horst 1977; Caswell 2001; Morris and Doak 2002). Population modeling analyses were conducted in R using functions from the “popbio” package (Stubben and Milligan 2007; R Core Team 2018). Data for the matrices were only available for SSJ White Sturgeon up to age 19. However, White Sturgeon can live longer than 30 years (Hildebrand et al. 2016). As such, an age-20 and older (age-20+) life stage was included in the models. A postcensus breeding structure was constructed to evaluate the influence of offspring production and complete recruitment failure in a sensitivity–elasticity analysis (Morris and Doak 2002). Projection matrices were in the form

$$A = \begin{bmatrix} R_1 & R_2 & \cdots & \cdots & R_{20+} \\ S_0 & 0 & \cdots & \cdots & 0 \\ 0 & S_1 & & \cdots & \vdots \\ \vdots & \vdots & \ddots & \cdots & \vdots \\ 0 & 0 & \cdots & S_{19} & S_{20+} \end{bmatrix},$$

where S_0 – S_{20+} are annual survival rates for White Sturgeon of ages 0–20+; and R_i is the reproductive rate of age-class i estimated by

$$R_i = P_i \times f_i \times S_i \times a,$$

where P_i is the probability of spawning for age-class i ; f_i is the fecundity of age-class i ; a is the proportion of female offspring; and S_i is the annual survival of age-class i (Morris and Doak 2002). The ratio of female : male offspring was assumed to be 1:1 (Chapman et al. 1996).

A simulation-based approach was used to account for uncertainty and variability in the vital rates (Morris and Doak 2002; Cox et al. 2013). Demographic stochasticity was simulated using parametric bootstrapping in which the fate of individuals in each age-class was randomly generated using beta or stretched-beta distributions based on the mean and SE of their respective vital rates (Morris and Doak 2002; Table 1). We set the variance to be 20% of the mean value if a vital rate was obtained from the literature without a listed SE (Cox et al. 2013; Ng et al. 2016). Age-specific survival rates and probability of spawning were modeled as beta distributions (Morris and Doak 2002). We also incorporated stochastic variation in recruitment by simulating successful age-classes to occur on average once every 8 years based on empirical data from the Bay Study. Fecundity at age (f_i) was generated in each simulation by using a stretched-beta distribution (Morris and Doak 2002). Because White Sturgeon fecundity can vary widely between individuals of the same length, the maximum number of eggs was set to three times the mean number of eggs (DeVore et al. 1995; Chapman et al. 1996).

We modeled various management scenarios to assess the effect of time between spawning events, different harvest slot length limits, and various levels of μ on the population growth rate (λ). Given the best available data, we assumed that 15% of mature White Sturgeon females spawn each year (Chapman 1989; Chapman et al. 1996); however, the exact interval between spawning events is unknown. Therefore, we generated separate modeling results that also included 10% and 25% of sexually mature female White Sturgeon spawning in a given year. We incorporated three harvest slot length limits, including the current limit as well as two prospective limits: smaller (77–127 cm FL) and larger (127–177 cm FL). Exploitation

TABLE 1. Mean vital rates and SEs used to construct population matrices for the White Sturgeon population in the Sacramento–San Joaquin River basin, California.

Symbol	Definition	Age (<i>i</i>)	Value	SE	Source
Fertility elements					
f_i	Fecundity at age <i>i</i>	0–9	0	N/A	DeVore et al. 1995
		10	33,298	11,070	
		11	83,641	8,777	
		12	108,812	7,773	
		13	148,367	6,522	
		14	195,114	5,867	
		15	209,498	5,895	
		16	245,457	6,436	
		17	263,437	6,920	
		18	310,183	8,626	
pm_i	Probability of maturity at age <i>i</i>	0–9	0.000	N/A	Chapman 1989
		10	0.025	0.077	
		11	0.086	0.173	
		12	0.143	0.220	
		13	0.291	0.266	
		14	0.543	0.275	
		15	0.622	0.278	
		16	0.788	0.263	
		17	0.849	0.235	
		18	0.942	0.142	
p_f	Proportion of offspring that are females	10–19	0.500	N/A	Chapman et al. 1996
		20+	1.000	0.200	
Transition elements					
S_0	Egg-to-age-1 survival	0	0.002	0.003	Caroffino et al. 2010
S_1	Age-1 survival	1	0.250	0.008	Pine et al. 2001
S_2	Age-2 survival	2	0.840	0.168	Ireland et al. 2002
S_3 – S_{20+}	Asymptotic survival	3–19	0.946	0.03	This study

was varied from 0.00 to 0.30 in 0.01 increments for each combination of spawning and harvest length limit scenario to evaluate the influence of harvest on λ . Age-specific abundances were estimated by multiplying the Leslie matrix (**A**) by the vector of age-specific abundances at time *t* (**n_t**; Morris and Doak 2002).

Population growth rate was modeled for each combination of scenarios over a period of 10, 20, and 50 years. Additionally, due to the concern over the occurrence of only two strong year-classes since 2000, we estimated the average population size and the age-specific abundance of the 2006 and 2011 cohorts over a 20-year period. We evaluated the transient dynamics of White Sturgeon in the SSJ because White Sturgeon populations rarely exhibit a stable age distribution (Gross et al. 2002). Although the matrix models used are density independent, we used the estimated population abundance (*N*) of 48,000 White Sturgeon as the initial

number of individuals in the models (DuBois and Gingras 2011; Hildebrand et al. 2016). Total population abundance was multiplied by the proportion of individuals in each age-class to acquire starting values for population simulations. Age-1 and age-2 White Sturgeon were not recruited to CDFW trammel nets, so a linear model was used to predict the number of fish in each of these age-classes. The number of age-0 White Sturgeon was estimated by multiplying the number of mature White Sturgeon females spawning in a given year (i.e., 15%) in each age-class by their age-specific fecundity. Each scenario combination was simulated 5,000 times, and a geometric mean of the simulated population growth rates (λ_G) was estimated (Caswell 2001; Morris and Doak 2002). When the population is at equilibrium, λ_G is equal to 1.0, and growth and decline are represented by an increasing (>1.0) or decreasing (<1.0) value of λ (Horst 1977). Approximate 95% confidence intervals (CIs) were

generated based on the 5,000 simulations (Morris and Doak 2002; Cox et al. 2013).

The influence of vital rates on λ_G were assessed using sensitivity analyses. Sensitivity analyses are commonly used to quantify the influence of vital rates on population growth and to prioritize management strategies (Caswell 2001; Morris and Doak 2002). Inaccuracies regarding estimates of mortality and spawning frequency may skew predictions of long-term viability and management decisions (Chapman 1989; Hamel et al. 2016). Therefore, we evaluated the sensitivity of λ_G to perturbations by varying estimates of M and spawning frequencies across a range of plausible values obtained from prior studies. For each value of mortality and spawning periodicity, we recalculated λ_G by constructing a new matrix, with all other vital rates remaining unchanged over the 20-year projection period (Morris and Doak 2002). We also conducted an elasticity analysis representing the proportional contribution of a vital rate to λ_G . Specifically, elasticity analyses predict how λ_G might vary with changes in the survival or fecundity of a specific age-class (Gross et al. 2002). Results from elasticity analyses are used to assist managers in determining which life stages might make the greatest contributions to λ_G and where additional research may be warranted (Gross et al. 2002; Morris and Doak 2002; Heppell 2007).

RESULTS

During the summer and fall of 2014–2016, 1,000 individual White Sturgeon were captured in trammel nets. Sampled White Sturgeon varied from 53 to 217 cm FL (mean \pm SD = 97.5 \pm 27.0 cm), and the majority of fish were between 80 and 90 cm FL (Figure 2). Fish varied in age from 3 to 29 years (8.1 \pm 3.2 years; Figures 2, 3), and nearly 60% of the White Sturgeon were between age 3 and age 9. Only two fish were estimated to be older than age 20. Overall, White Sturgeon grew rapidly until about age 17 (Figure 3). After correcting for trammel net selectivity, peak abundance in the catch occurred at age 8. Total instantaneous mortality for fish of ages 3–19 was 0.21 (95% CI = 0.12–0.29); annual survival was 81.3% (95% CI = 80.1–82.5%). Between 2007 and 2016, 19 \$20 tags, 27 \$50 tags, 45 \$100 tags, and 5 \$150 tags were reported. After correcting for nonreporting and adjusting for tag loss and mortality, annual μ varied between 8.0% and 29.6% from 2007 to 2015, with an overall mean of 13.6% (95% CI = 1.0–26.2%; Figure 4). The estimate of M using these data was 0.056 and was used for the population models. For comparison, the average of M based on the equations from Pauly (1980), Hoenig (1983), and Then et al. (2015) was 0.066.

Under current harvest conditions ($\mu = 13.6\%$; slot length limit = 102–152 cm FL), λ was predicted to decline

annually by 4.6% ($\lambda_G = 0.95$; 95% CI = 0.89–1.04) over a time period of 20 years, assuming a spawning periodicity of 10% (Figure 5). With a spawning periodicity of 15%, the White Sturgeon population was predicted to decline at a rate of 2.8% under current harvest conditions ($\lambda_G = 0.97$; 95% CI = 0.91–1.08; Figure 6). At this rate of decline, the projected total abundance of White Sturgeon in the SSJ in 20 years would decrease to 27,905 fish (95% CI = 8,184–58,569). Specifically, the 2006 and 2011 cohorts would decrease to approximately 3,905 and 2,756 fish, respectively, over the 20-year projection period. Similar trends for λ were predicted for simulations assuming a 15% spawning periodicity under the current harvest slot length limit over 10-year ($\lambda_G = 0.95$; 95% CI = 0.91–0.99) and 50-year ($\lambda_G = 0.97$; 95% CI = 0.87–1.19) time spans. Additionally, under a spawning periodicity of 25%, the λ of White Sturgeon in the SSJ was predicted to decline at a rate of 1.5% ($\lambda_G = 0.98$; 95% CI = 0.95–1.18) over 20 years under current harvest conditions (Figure 7).

Population projections for management scenarios indicated that population increases would be tenable. In general, for all scenarios the mean λ_G approached the replacement rate at near-zero levels (i.e., <3%) of exploitation. In the absence of fishing mortality, the 20-year estimates of λ_G for White Sturgeon in the SSJ were 0.99 (95% CI = 0.93–1.11), 1.01 (95% CI = 0.95–1.16), and 1.02 (95% CI = 0.97–1.18) for spawning periodicities of 10, 15, and 25%, respectively. To reach the replacement rate, A would have to be less than 8% for age-3+ White Sturgeon, assuming a spawning periodicity of at least 15%. Overall, reducing the maximum size of the harvest slot reduced the number of adult age-classes in the catch and increased the population growth slightly. However, overall differences in mean λ between the harvest slot length limits were slight (Figures 5–7).

Sensitivity analysis indicated that λ was more sensitive to changes in the mortality rates of age-3+ White Sturgeon than variation in spawning periodicities. For example, increasing mortality by 5.0% resulted in a 3.2% decrease in λ_G over a 20-year period. Under current conditions, λ was most influenced by adult survival rates (Figure 8). Reproductive parameters (i.e., fertility) had the lowest summed elasticity and made the smallest relative contribution to λ . Summed elasticity was greatest (mean \pm SD = 0.76 \pm 0.13) for sexually mature White Sturgeon (age \geq 10), indicating that λ was most influenced by changes in the survival of adult fish. The elasticity value means that the survival rate of adult White Sturgeon contributed about a 77% change in λ_G relative to the other vital rates.

DISCUSSION

White Sturgeon in the SSJ exhibited fast growth, high rates of mortality, and relatively high levels of

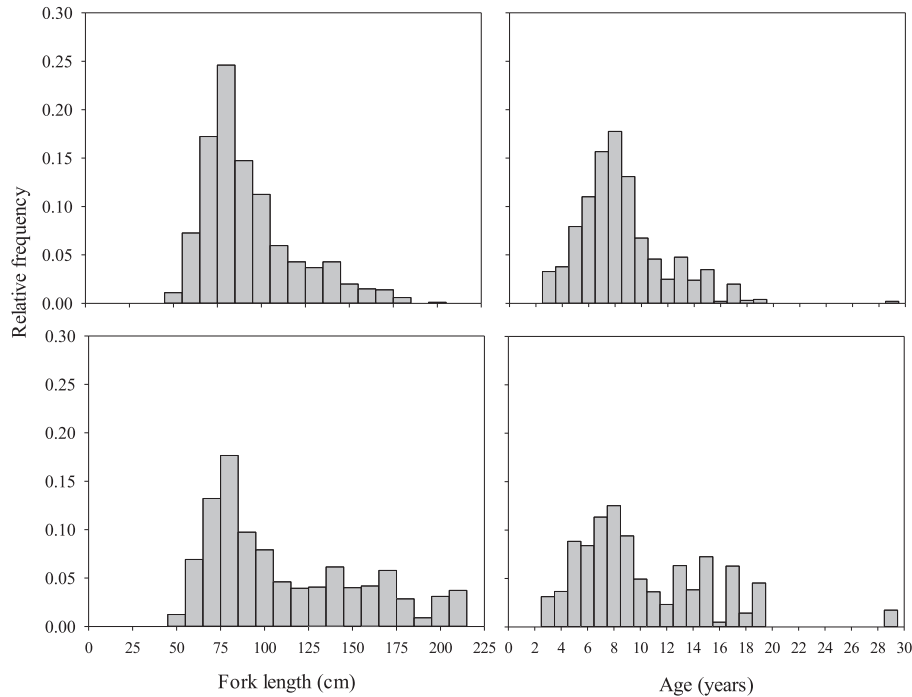


FIGURE 2. Length frequency and age distribution of White Sturgeon sampled in Suisun and San Pablo bays, California, during the summer and autumn months of 2014–2016. Data are for fish that were collected using trammel nets. Top panels are uncorrected for size selectivity, and bottom panels are corrected for size selectivity.

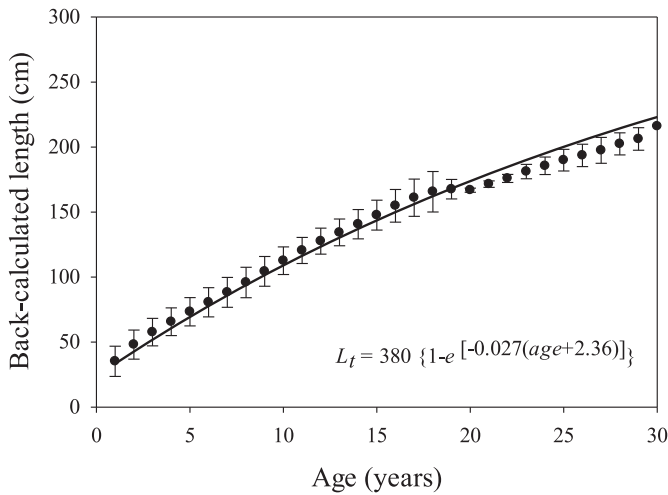


FIGURE 3. von Bertalanffy growth model for White Sturgeon sampled during August–October 2014–2016 in Suisun and San Pablo bays, California. Solid circles represent the mean back-calculated FL at a given age (L_t), error bars represent 95% confidence intervals, and the solid line represents the growth model fit.

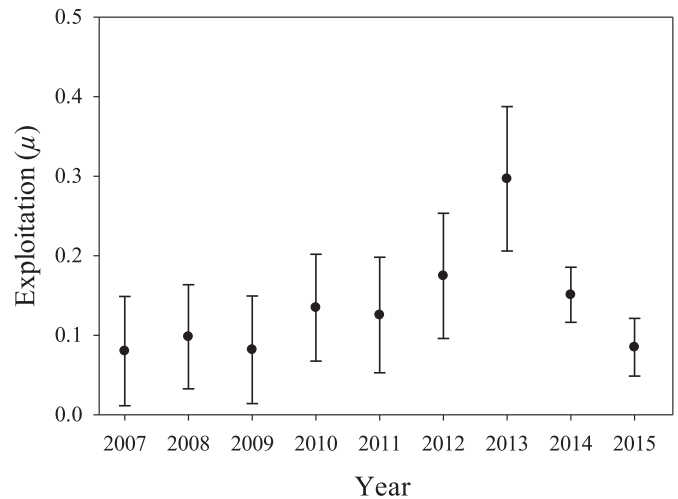


FIGURE 4. Estimates of exploitation (μ) based on adjusted tag return data for White Sturgeon in the Sacramento–San Joaquin River basin, California, from 2007 to 2015. Error bars represent 95% confidence intervals. Tag return data were adjusted for angler nonreporting, tag loss, tagging mortality, and growth into and out of the slot length limit.

exploitation, and the population appeared to be declining. Length frequency distributions show that few White Sturgeon survive the harvest slot (length limit). The current estimated length frequency distribution differed from

frequencies presented in prior studies of White Sturgeon in the SSJ (Kohlhorst et al. 1980; Brennan and Cailliet 1989). The majority of the White Sturgeon sampled in prior studies were between 90 and 160 cm, whereas most

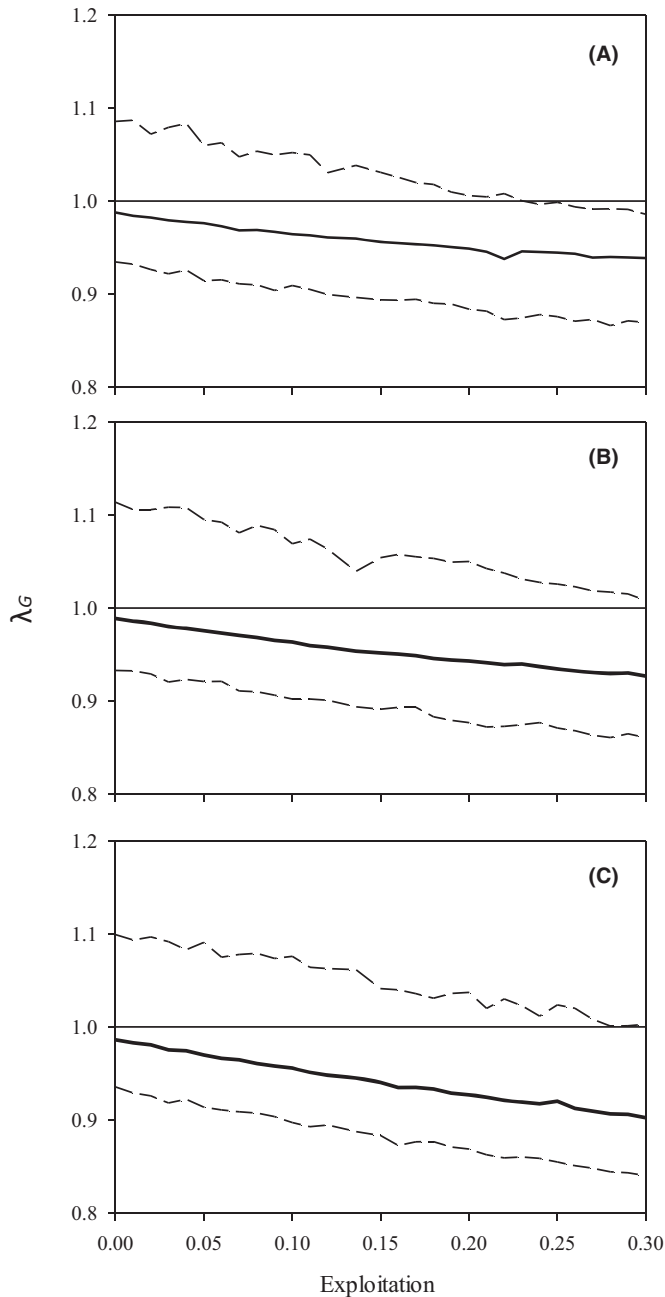


FIGURE 5. Population growth rates (λ_G) simulated over a 20-year time frame for White Sturgeon in the Sacramento–San Joaquin River basin, California, assuming that 10% of mature females are spawning annually at various levels of exploitation under three slot length limits: (A) the smallest limit (77–127 cm FL); (B) the current limit (102–152 cm FL); and (C) the largest limit (127–177 cm FL). The solid line represents the mean value of λ_G , and the dashed lines indicate the 95% confidence interval. The horizontal reference line represents a λ_G value of 1.0, at which a population is considered stable.

of the fish sampled in our study were <90 cm. However, the experimental trammel nets and nonrandom sampling may have contributed to the paucity of large fish and the

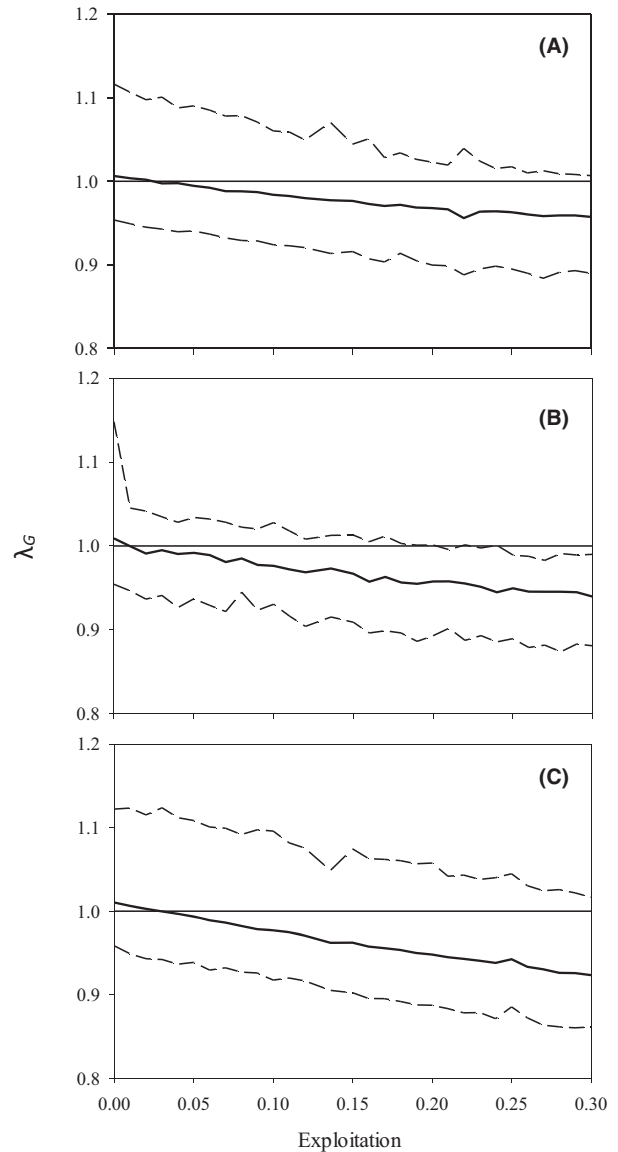


FIGURE 6. Population growth rates (λ_G) simulated over a 20-year time frame for White Sturgeon in the Sacramento–San Joaquin River basin, California, assuming that 15% of mature females are spawning annually at various levels of exploitation under three slot length limits: (A) the smallest limit (77–127 cm FL); (B) the current limit (102–152 cm FL); and (C) the largest limit (127–177 cm FL). The solid line represents the mean value of λ_G , and the dashed lines indicate the 95% confidence interval. The horizontal reference line represents a λ_G value of 1.0, at which a population is considered stable.

skewed size distribution in our study. In particular, the capture efficiency of CDFW trammel nets may be ill-suited for sampling 200-cm FL and larger White Sturgeon. Previous research in the SSJ and in other systems (e.g., lower Columbia River) has used a variety of sampling methods to collect White Sturgeon (e.g., commercial fishing nets, trammel nets, hook and line, and trawls; Kohlhorst et al. 1980; Brennan and Cailliet 1989; DeVore et al.

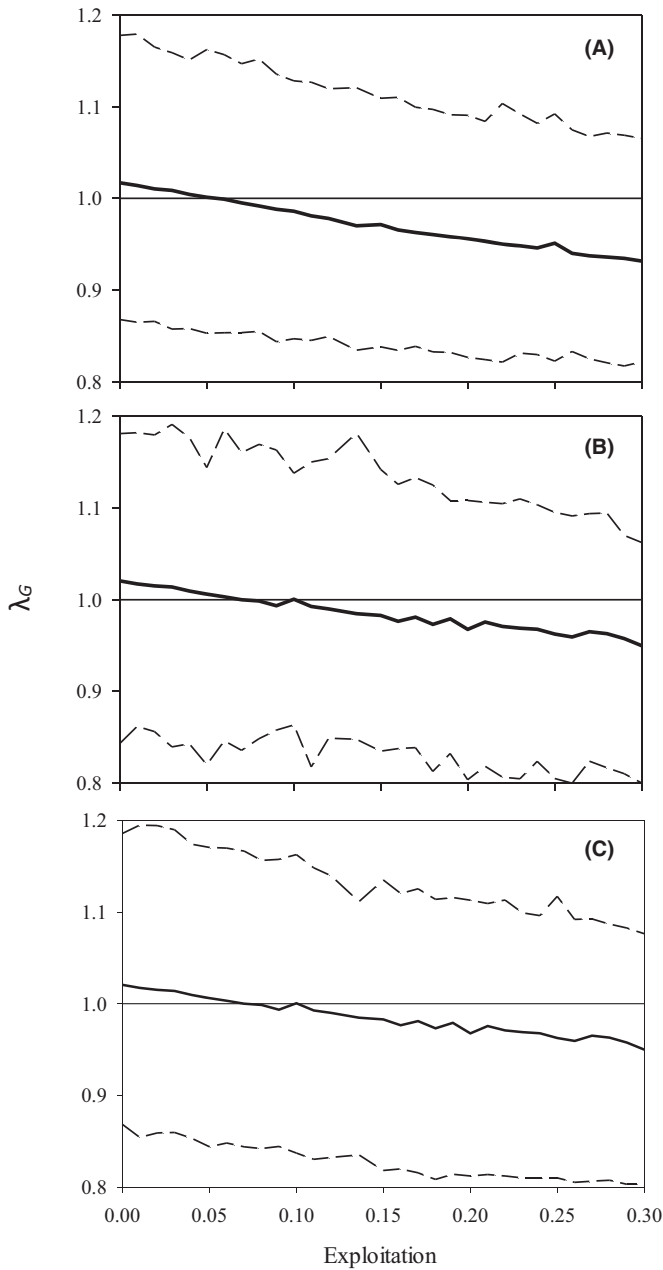


FIGURE 7. Population growth rates (λ_G) simulated over a 20-year time frame for White Sturgeon in the Sacramento–San Joaquin River basin, California, assuming that 25% of mature females are spawning annually at various levels of exploitation under three slot length limits: (A) the smallest limit (77–127 cm FL); (B) the current limit (102–152 cm FL); and (C) the largest limit (127–177 cm FL). The solid line represents the mean value of λ_G , and the dashed lines indicate the 95% confidence interval. The horizontal reference line represents a λ_G value of 1.0, at which a population is considered stable.

1995). As such, catch from nonrandom sampling efforts that occur primarily in Suisun Bay using only trammel nets may not be truly representative of the entire

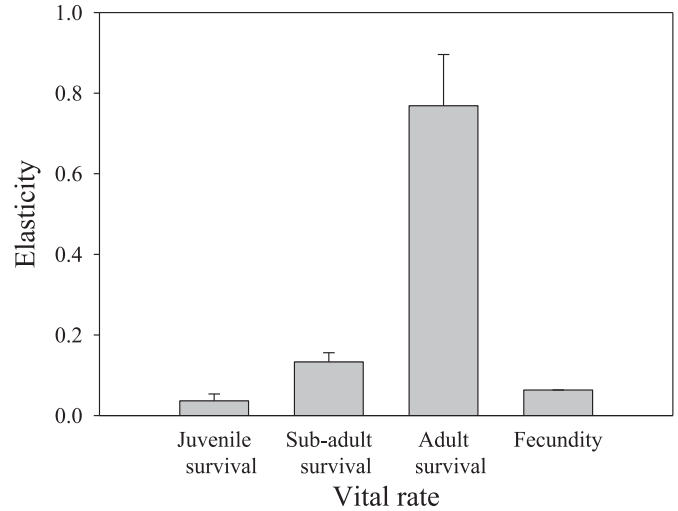


FIGURE 8. Summed elasticity values for vital rates of exploited White Sturgeon (exploitation rate $\mu = 13.6\%$; harvest slot length limit = 102–152 cm FL) in the Sacramento–San Joaquin River basin, California. Summed juvenile survival is for ages 0–2, subadult survival is for ages 3–9, and adult survival is for age 10 and older.

population. Nonetheless, these are the best data available for the SSJ White Sturgeon population.

Prior studies have estimated the longevity of White Sturgeon. For instance, Smith et al. (2002) reported that White Sturgeon can exceed 100 years of age. White Sturgeon as old as 80 years have been observed in the Kootenai River, Idaho (Paragamian and Beamesderfer 2003), and individuals as old as 65 years have been reported from the Columbia River (DeVore et al. 1995). Our data did not match these findings, as the maximum observed age was 29 years. Lower observed maximum ages of White Sturgeon in the SSJ are likely the result of sampling bias and exploitation, each of which has been shown to truncate the age structure of fish populations (Crawford and Allen 2006; Bronte and Sitar 2008; Koch et al. 2009). Anthropogenic disturbances, such as the increasingly challenging environmental conditions (e.g., pollutants and poor water quality) in the SSJ, may also affect the longevity of fish (Feist et al. 2005; Gundersen et al. 2017). In addition, errors in age estimation can confound population dynamics analyses (Rien and Beamesderfer 1994; Hamel et al. 2016). Although pectoral fin rays are currently the most practical and reliable aging structure for White Sturgeon, uncertainty exists regarding age estimates, especially for fish older than age 20 (Brennan and Cailliet 1989; Rien and Beamesderfer 1994; Paragamian and Beamesderfer 2003). However, aging error is unlikely to have been a major issue in our study because the majority of the White Sturgeon were young (age < 10), with only two fish estimated to be over 20 years of age.

Growth analysis indicated that the length at age of White Sturgeon in the SSJ varied widely. However, the general pattern suggests that growth is rapid for larval and juvenile life stages of White Sturgeon and declines at around age 17. Contemporary growth estimates for White Sturgeon in the SSJ were higher than estimates from the period 1973–1976 (Kohlhorst et al. 1980). Additionally, White Sturgeon in the SSJ appear to exhibit faster individual growth than all other White Sturgeon populations for which data are available. Based on von Bertalanffy growth models, White Sturgeon in the lower Columbia River were predicted to achieve a length of 116 cm by age 15 (DeVore et al. 1995), whereas White Sturgeon in the SSJ had a predicted length of 147 cm at age 15. Growth differences are even more pronounced when White Sturgeon in the SSJ are compared with landlocked populations in the northern extent of the species' distribution. White Sturgeon of ages 10–50 in the Kootenai River grow approximately 2.5 cm/year (Paragamian et al. 2005). Over those same ages, White Sturgeon in the SSJ grow nearly twice as fast (i.e., 4.6 cm/year). Differences in growth may be related to temperature, access to quality habitat, density-dependent interactions (e.g., competition), and marine-based prey availability. Beamesderfer et al. (1995) and Van Poorten and McAdam (2010) reported that alterations in hydrology due to dam construction (e.g., limited food resources and habitat availability) may explain differences in White Sturgeon growth. In northern systems like the Kootenai River, reduced growth of White Sturgeon is likely due to limited food availability and long distances from estuarine and marine resources (Ireland et al. 2002; Paragamian et al. 2005). High harvest rates or other factors influencing abundance may also affect the growth of White Sturgeon in the SSJ. Prior studies have demonstrated that growth increases when density decreases (Regier and Loftus 1972; Rieman and Myers 1992; Bronte and Sitar 2008; Haxton and Findlay 2008). For example, older age-classes (age ≥ 2) of kokanee *O. nerka* experienced declines in growth with increasing fish density (Rieman and Myers 1992). Furthermore, in the Ottawa River, Ontario–Quebec, growth rates of Lake Sturgeon were found to be faster in less densely populated sections of the river (Haxton and Findlay 2008). White Sturgeon in the SSJ may be experiencing a similar density-dependent response in growth.

Estimation of mortality for sturgeon populations is challenging due to uncertainties in the accuracy of aging techniques, different capture efficiencies between sampling gears, and difficulty in quantifying influences from anthropogenic activities (Paragamian and Beamesderfer 2003; Koch et al. 2009; Hamel et al. 2016). As such, mortality rates of White Sturgeon exhibit spatial and temporal variability. Our estimate of A after correcting for size selectivity ($A = 18.7\%$) is similar to those reported for

other exploited sturgeon populations. Estimates of A for White Sturgeon in the Columbia River vary from 18–24% (lower river; Beamesderfer et al. 1995) to 37% (unimpounded lower river; DeVore et al. 1995). In Lake Winnebago, Wisconsin, Bruch (1999) reported an A -value of 17% for Lake Sturgeon that were exposed to a limited recreational harvest. Additionally, our current estimate of cm in the SSJ (0.06) is similar to historic estimates ($cm = 0.05$ – 0.10 ; Kohlhorst 1980) and to those for White Sturgeon populations in other water bodies. For instance, cm was estimated at 0.09 in the lower Columbia River (DeVore et al. 1995) and 0.10 for the unexploited population in the Kootenai River (Paragamian et al. 2005). However, mortality comparisons between populations should be evaluated with care because various levels of uncertainty were reported for all of the mortality rates, and sampling techniques and mortality estimators differed between studies.

The estimated mean annual μ (i.e., 13.6%) of White Sturgeon in the SSJ was higher than the 5–10% recommended to sustain sturgeon populations (Rieman and Beamesderfer 1990; Beamesderfer and Farr 1997). It is likely that our estimates of μ are biased low due to a low number of tag returns. The reason for low tag returns is unknown but could be due to low catch rates, inadequate publicity, an unwillingness of anglers to report their catch, or a combination thereof. Additionally, our estimate did not include illegal harvest or fishing mortality due to bycatch in other fisheries. Although the exact number of White Sturgeon that are illegally harvested in the SSJ is unquantified, the number is thought to be substantial (Gingras, unpublished information). Nevertheless, an absolute minimum μ estimate based solely on the proportion of tags returned was 8.0%.

The estimated λ values reported in this study are based on a number of assumptions that may not be reflective of the true status of White Sturgeon in the SSJ. In particular, changes in estimated mortality would substantially influence the population growth rate (Hamel et al. 2016). We examined this further by modeling λ using the estimates of mortality from the uncorrected age structure. Results indicated even lower estimates of mean λ . Additionally, determining the juvenile mortality rates of fishes with type III survivorship curves is difficult (Counihan et al. 1999; Pine et al. 2001; Caroffino et al. 2010). Our variable egg-to-age-1 mortality (i.e., S_0) estimates of 99.94–100% likely portrayed typical recruitment rates for White Sturgeon in the SSJ. Further investigations that address stressors and quantify juvenile mortality rates, particularly during the egg and larval stages, are warranted (Houde 1987; Pine et al. 2001; Gross et al. 2002; Caroffino et al. 2010). Inaccuracies in growth estimates could also influence our results (Hamel et al. 2016). However, when we modeled additional scenarios using both faster and slower growth rates,

the results were similar to or lower than our estimated mean λ . Another assumption that may not be valid is spawning periodicity. For modeling purposes, we used the best available data (Chapman 1989; DeVore et al. 1995; Chapman et al. 1996). However, these studies are approximately 30 years old, and conditions have undoubtedly changed. Numerous contaminants (e.g., Hg, Cu, and Se) exist in the SSJ, and these have been suggested to disrupt and delay spawning activities (Feist et al. 2005; Gundersen et al. 2017). Unfortunately, the timing of White Sturgeon spawning events is still poorly understood and likely varies among years and individuals (Conte et al. 1988; Gross et al. 2002; Hildebrand et al. 2016). Although we modeled a range of spawning periodicities, we may have overestimated the frequency. Additional studies are needed to assess the percentage of females that spawn each year.

Although conservation strategies include improving sturgeon spawning habitat (Schaffter 1997) and augmenting streamflow to mimic historic regimes (Jackson et al. 2016), reducing fishing mortality is likely the most effective, intermediate-term option for increasing the population abundance of White Sturgeon in the SSJ. Specifically, decreasing A to less than 10% for age-10+ White Sturgeon would increase the mean λ to the replacement rate. The predicted pattern in λ indicated that harvesting White Sturgeon at rates exceeding 5% causes a rapid decline in the population. Even modest levels of fishing mortality may negatively affect the population size structure and abundance of White Sturgeon (Boreman 1997; IDFG 2008). Reductions in annual mortality for other White Sturgeon populations after closure of fisheries suggest that this is an important conservation strategy. In the Kootenai River, White Sturgeon experienced 5–10% reductions in mortality rates after harvest closure (Paragamian et al. 2005). In 1971, the implementation of strict catch-and-release regulations for White Sturgeon in the Snake River, Idaho, led to a partial recovery of the population (IDFG 2008). Similar results regarding sensitivity to exploitation have been described for other sturgeon species. For example, Pine et al. (2001) reported a 38% decrease in total mortality of Gulf Sturgeon in the Suwannee River, Florida, 21 years after closure of the commercial fishery. In the Mississippi River system, Koch et al. (2009) suggested that even low levels of harvest could jeopardize the long-term persistence of Shovelnose Sturgeon. Despite the sensitivity to overexploitation, several strictly managed fisheries exist for sturgeon in North America. A harvest quota of 350 adults maintains a μ of <2% for Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* in the Saint John River, New Brunswick (Dadswell et al. 2017). Similarly, the self-sustaining Lake Sturgeon population in Lake Winnebago, Wisconsin, has been attributed to strict and adaptive fishing regulations that maintain μ at or below 5% (Bruch 1999). Promoting a sustainable fishery by

eliminating high harvest rates for mature and highly fecund individuals appears to be an effective conservation strategy for sturgeons.

Efforts that support decreasing the mortality of sexually mature White Sturgeon are further corroborated by results from the sensitivity analyses, which provide additional evidence that White Sturgeon are extremely vulnerable to exploitation. Our models indicated that under current harvest conditions, the survival rates of reproductive adults contribute the most to λ , followed by the survival of subadults. In populations that exhibit nonstable age distributions, such as White Sturgeon in the SSJ, high survival rates of sexually mature adults may be necessary to span lengthy gaps in recruitment (Gross et al. 2002). Elasticity results from our study are similar to those reported by previous researchers. Population simulations of Gulf Sturgeon in the Suwannee River were highly sensitive to changes in adult mortality and illustrated that the survival of sexually mature fish contributed more to λ than did recruitment rates (Pine et al. 2001). Similarly, analysis from an age-structured population model for Green Sturgeon (Heppell 2007) and European Sturgeon *Acipenser sturio* (Jaric and Gessner 2013) showed that λ was highly sensitive to adult mortality. Even small reductions in adult mortality through reduced exploitation may help to offset other challenges experienced by White Sturgeon in the SSJ (e.g., illegal harvest, dams, and droughts).

Baseline data regarding population demographics are essential for the effective management and conservation of fishes (Gross et al. 2002; Cox et al. 2013; Kerns and Lombardi-Carlson 2017). Our study provides insight on the population dynamics and potential population-level responses under various management scenarios for White Sturgeon in the SSJ. The results of this study suggest that population growth was most influenced by the survival of sexually mature adults, and low levels of exploitation are needed to maintain a stable population. Similar to other studies using stochastic age-structured population models, some uncertainty exists in our population projections. Despite limitations, our research can serve as a relative gauge of the population status as well as a foundation for future research and monitoring efforts. Furthermore, age-structured models can help to improve the understanding of factors influencing the rate functions of fish populations and drivers of population change (Gross et al. 2002; Morris and Doak 2002; Ng et al. 2016). Moving forward, managers will be able to model additional scenarios and set appropriate benchmarks for success. Improved monitoring (e.g., expansion of sampling locations and use of multiple sampling gears) across several generations, robust abundance and harvest estimates, and a better understanding of variables affecting recruitment are necessary to refine the recovery goals for White Sturgeon in the SSJ.

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REFERENCES

- Beamesderfer, R. C., and R. A. Farr. 1997. Alternatives for the protection and restoration of sturgeons and their habitat. *Environmental Biology of Fishes* 48:407–417.
- Beamesderfer, R. C., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production of impounded and unimpounded White Sturgeon populations in the lower Columbia River. *Transactions of the American Fisheries Society* 124:857–872.
- Bemis, W. E., and B. Kynard. 1997. Sturgeon rivers: an introduction to acipenseriform biogeography and life history. *Environmental Biology of Fishes* 48:167–183.
- Birstein, V. J., W. E. Bemis, and J. R. Waldman. 1997. The threatened status of acipenseriform species: a summary. *Environmental Biology of Fishes* 48:427–435.
- Boreman, J. 1997. Sensitivity to North American sturgeons and Paddlefish to fishing mortality. *Environmental Biology of Fishes* 48:399–405.
- Brennan, J. S., and G. M. Cailliet. 1989. Comparative age-determination techniques for White Sturgeon in California. *Transactions of the American Fisheries Society* 118:296–310.
- Bronte, C. R., and S. P. Sitar. 2008. Harvest and relative abundance of siscowet Lake Trout in Michigan waters of Lake Superior, 1929–1961. *Transactions of the American Fisheries Society* 137: 916–926.
- Bruch, R. M. 1999. Management of Lake Sturgeon on the Winnebago system—long term impacts of harvest and regulations on the population structure. *Journal of Applied Ichthyology* 15:142–152.
- Caroffino, D. C., T. M. Sutton, R. R. Elliott, and M. C. Donofrio. 2010. Early life stage mortality rates of Lake Sturgeon in the Peshtigo River, Wisconsin. *North American Journal of Fisheries Management* 30:295–304.
- Caswell, H. 2001. *Matrix population models*, 2nd edition. Sinauer, Sunderland, Massachusetts.
- Chadwick, H. K. 1959. California sturgeon tagging studies. *California Fish and Game* 45:297–301.
- Chapman, D. G., and D. S. Robson. 1960. The analysis of a catch curve. *Biometrics* 16:354–368.
- Chapman, F. 1989. Sexual maturation and reproductive parameters of wild and domestic stocks of White Sturgeon, *Acipenser transmontanus*. Doctoral dissertation. University of California, Davis.
- Chapman, F., J. P. Van Eenennaam, and S. Doroshov. 1996. The reproductive condition of White Sturgeon, *Acipenser transmontanus*, in San Francisco Bay, California. *U.S. National Marine Fisheries Service Fishery Bulletin* 94:628–634.
- Cloern, J. E., and A. D. Jassby. 2012. Drivers of change in estuarine-coastal ecosystems: discoveries from four decades of study in San Francisco Bay. *Reviews of Geophysics* 50:1–33.
- Conte, F. S., S. I. Doroshov, P. B. Lutes, and E. M. Strange. 1988. Hatchery manual for the White Sturgeon *Acipenser transmontanus* Richardson with application to other North American Acipenseridae. University of California, Cooperative Extension Publication 3322, Oakland.
- Counihan, T. D., A. I. Miller, and M. J. Parsley. 1999. Indexing the relative abundance of age-0 White Sturgeon in an impoundment of the lower Columbia River from highly skewed trawling data. *North American Journal of Fisheries Management* 19:520–529.
- Cox, B. S., C. S. Guy, W. A. Fredenberg, and L. R. Rosenthal. 2013. Baseline demographics of a non-native Lake Trout population and inferences for suppression from sensitivity–elasticity analyses. *Fisheries Management and Ecology* 20:390–400.
- Crawford, S., and M. S. Allen. 2006. Fishing and natural mortality of Bluegills and Redear Sunfish at Lake Panasoffkee, Florida: implications for size limits. *North American Journal of Fisheries Management* 26:42–51.
- Dadswell, M. J., C. Ceapa, A. D. Spares, N. D. Stewart, R. A. Curry, R. G. Bradford, and M. J. Stokesbury. 2017. Population characteristics of adult Atlantic Sturgeon captured by the commercial fishery in the Saint John River estuary, New Brunswick. *Transactions of the American Fisheries Society* 146:318–330.
- DeVore, J. D., B. W. James, C. A. Tracy, and D. A. Hale. 1995. Dynamics and potential production of White Sturgeon in the Columbia River downstream from Bonneville Dam. *Transactions of the American Fisheries Society* 124:845–856.
- DuBois, J., and A. Danos. 2017. Field season summary for the adult sturgeon population study. California Department of Fish and Wildlife, Stockton.
- DuBois, J., and M. Gingras. 2011. Using harvest rate and harvest to estimate White Sturgeon abundance. IEP (Interagency Ecological Program for the San Francisco Estuary) Newsletter 24:23–26.
- Erzini, K., J. M. S. Goncalves, L. Bentes, D. K. Moutopoulos, J. A. H. C. Soriguer, E. Puente, L. A. Errazkin, and K. I. Stergiou. 2006. Size selectivity of trammel nets in southern European small-scale fisheries. *Fisheries Research* 79:183–201.
- Feist, G. W., M. A. H. Webb, D. T. Gundersen, E. P. Foster, C. B. Schreck, A. G. Maule, and M. S. Fitzpatrick. 2005. Evidence of detrimental effects of environmental contaminants on growth and reproductive physiology of White Sturgeon in impounded areas of the Columbia River. *Environmental Health Perspectives* 113:1675–1682.
- Fish, M. A., J. Messineo, and K. Hieb. 2012. Bay Study fishes annual status and trends report for the San Francisco Estuary. IEP (Interagency Ecological Program for the San Francisco Estuary) Newsletter 24:4–28.
- Gabr, M. H., and A. O. Mal. 2016. Trammel net size-selectivity for *Hippocampus harid* (Forsskal, 1775) and *Lethrinus harak* (Forsskal, 1775) in coral reef fisheries of Jeddah, Saudi Arabia. *Egyptian Journal of Aquatic Research* 42:491–498.
- Gingras, M., and J. DuBois. 2013. Monitoring progress toward a CVPIA recovery objective: estimating White Sturgeon abundance by age. IEP

- (Interagency Ecological Program for the San Francisco Estuary) Newsletter 26:6–9.
- Gingras, M., J. DuBois, and M. A. Fish. 2013. Further investigations into San Francisco Estuary White Sturgeon (*Acipenser transmontanus*) year-class strength. IEP (Interagency Ecological Program for the San Francisco Estuary) Newsletter 26:10–12.
- Gingras, M., and J. DuBois. 2014. Bias in estimated annual harvest rates for White Sturgeon of the San Francisco Estuary. IEP (Interagency Ecological Program for the San Francisco Estuary) Newsletter 27:43–46.
- Grimaldo, L. F., T. Sommer, N. Van Ark, G. Jones, E. Holland, P. B. Moyle, B. Herbold, and P. Smith. 2009. Factors affecting fish entrainment into massive water diversions in a tidal freshwater estuary: can fish losses be managed? North American Journal of Fisheries Management 29:1253–1270.
- Gross, M. R., J. Repka, C. T. Robertson, D. H. Secor, and W. Van Winkle. 2002. Sturgeon conservation: insight from elasticity analysis. Pages 13–30 in W. Van Winkle, P. J. Anders, D. H. Secor, and D. A. Dixon, editors. Biology, management, and protection of North American sturgeon. American Fisheries Society, Symposium 28, Bethesda, Maryland.
- Gundersen, D. T., S. C. Zeug, R. B. Bringolf, J. Merz, Z. J. Jackson, and M. A. H. Webb. 2017. Tissue contaminant burdens in San Francisco Estuary White Sturgeon (*Acipenser transmontanus*): implications for population recovery. Archives of Environmental Contamination and Toxicology 73:5–10.
- Hamel, M. J., J. J. Spurgeon, C. J. Chizinski, K. D. Steffensen, and M. A. Pegg. 2016. Variability in age estimation results in ambiguity and false understanding of population persistence. North American Journal of Fisheries Management 36:541–522.
- Haxton, T. J., and C. S. Findlay. 2008. Variation in Lake Sturgeon (*Acipenser fulvescens*) abundance and growth among river reaches in a large regulated river. Canadian Journal of Fisheries and Aquatic Sciences 65:645–657.
- Haxton, T. J., K. Sulak, and L. R. Hildebrand. 2016. Status of scientific knowledge of North American sturgeon. Journal of Applied Ichthyology 32:5–10.
- Heppell, S. S. 2007. Elasticity analysis of Green Sturgeon life history. Environmental Biology of Fishes 79:357–368.
- Hildebrand, L. R., A. D. Schreier, K. Lepla, S. O. McAdam, J. McLellan, M. J. Parsley, V. L. Paragamian, and S. P. Young. 2016. Status of White Sturgeon (*Acipenser transmontanus* Richardson, 1863) throughout the species range, threats to survival, and prognosis for the future. Journal of Applied Ichthyology 32:261–312.
- Hoenig, J. 1983. Empirical use of longevity data to estimate mortality rates. U.S. National Marine Fisheries Service Fishery Bulletin 82:898–903.
- Horst, J. T. 1977. Use of the Leslie matrix for assessing environmental impact with an example for a fish population. Transactions of the American Fisheries Society 106:253–257.
- Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Pages 17–29 in R. D. Hoyt, editor. 10th annual larval fish conference. American Fisheries Society, Symposium 2, Bethesda, Maryland.
- Hubert, W. A., K. L. Pope, and J. M. Dettmers. 2012. Passive capture techniques. Pages 223–265 in A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.
- IDFG (Idaho Department of Fish and Game). 2008. Management plan for the conservation of Snake River White Sturgeon in Idaho. IDFG, Boise.
- Ireland, S. C., R. C. Beamesderfer, V. L. Paragamian, V. D. Wakkinen, and J. T. Siple. 2002. Success of hatchery-reared juvenile White Sturgeon (*Acipenser transmontanus*) following release in the Kootenai River, Idaho, USA. Journal of Applied Ichthyology 18:642–650.
- Irvine, R., D. Schmidt, and L. R. Hildebrand. 2007. Population status of White Sturgeon in the lower Columbia River within Canada. Transactions of the American Fisheries Society 136:1472–1479.
- Jackson, Z. J., J. J. Gruber, and J. P. Van Eenennaam. 2016. White Sturgeon spawning in the San Joaquin River, California, and effects of water management. Journal of Fish and Wildlife Management 7:171–180.
- Jaffe, B. E., R. E. Smith, and A. C. Foxgrover. 2007. Anthropogenic influence on sedimentation and intertidal mudflat change in San Pablo Bay, California: 1856–1983. Estuarine, Coastal, and Shelf Science 73:175–187.
- Jager, H. I., J. A. Chandler, K. B. Lepla, and W. Van Winkle. 2001. A theoretical study of river fragmentation by dams and its effects on White Sturgeon populations. Environmental Biology of Fishes 60:347–361.
- Jaric, I., and J. Gessner. 2013. A life-stage population model of the European Sturgeon (*Acipenser sturio*) in the Elba River part 1: general model outline and potential applications. Journal of Applied Ichthyology 29:483–493.
- Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. C. Balderas, E. Diaz-Pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P. Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-Soto, E. B. Taylor, and M. L. Warren Jr. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries 33:372–407.
- Kerns, J. A., and L. A. Lombardi-Carlson. 2017. History and importance of age and growth information. Pages 1–8 in M. C. Quist and D. A. Isermann, editors. Age and growth of fishes: principles and techniques. American Fisheries Society, Bethesda, Maryland.
- Koch, J. D., and M. C. Quist. 2007. A technique for preparing fin rays and spines for age and growth analysis. North American Journal of Fisheries Management 27:781–784.
- Koch, J. D., M. C. Quist, C. L. Pierce, K. A. Hansen, and M. J. Steuck. 2009. Effects of commercial harvest on Shovelnose Sturgeon populations in the upper Mississippi River. North American Journal of Fisheries Management 29:84–100.
- Kohlhorst, D. W. 1980. Recent trends in the White Sturgeon population in California's Sacramento–San Joaquin Estuary. California Fish and Game 66:210–219.
- Kohlhorst, D. W., L. W. Botsford, J. S. Brennan, and G. M. Cailliet. 1991. Aspects of the structure and dynamics of an exploited central California population of White Sturgeon (*Acipenser transmontanus*). Pages 277–283 in P. Williot, editor. Acipenser: actes du premier colloque international sur l'esturgeon. Cemagref, Bordeaux, France.
- Kohlhorst, D. W., L. W. Miller, and J. J. Orsi. 1980. Age and growth of White Sturgeon collected in the Sacramento–San Joaquin Estuary, California: 1965–1970 and 1973–1976. California Fish and Game 66:83–95.
- Meyer, K. E., F. S. Elle, J. A. Lamansky, E. R. Mamer, and A. E. Butts. 2012. A reward–recovery study to estimate tagged-fish reporting rates by Idaho anglers. North American Journal of Fisheries Management 32:696–703.
- Morris, F. W., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts.
- Moyle, P. B., J. V. Katz, and R. M. Quinones. 2011. Rapid declines of California's native inland fishes: a status assessment. Biological Conservation 144:2414–2423.
- Moyle, P. B., R. M. Quinones, J. V. Katz, and J. Weaver. 2015. Fish species of special concern in California. California Department of Fish and Wildlife, Sacramento.
- Millar, R. B., and R. J. Fryer. 1999. Estimating size-selection curves of trawls, traps, gillnets, and hooks. Reviews in Fish Biology and Fisheries 9:89–116.
- Miller, A. I., and L. G. Beckman. 1996. First record of predation on White Sturgeon eggs by sympatric fishes. Transactions of the American Fisheries Society 125:338–340.

- Miller, L. W. 1972. White Sturgeon population characteristics in the Sacramento–San Joaquin Estuary as measured by tagging. *California Fish and Game* 58:94–101.
- Miller, R. B. 1992. Estimating the size-selectivity of fishing gear by conditioning on the total catch. *Journal of the American Statistical Association* 87:962–968.
- Munro, J., R. E. Edwards, and A. W. Kahnle. 2007. Synthesis and summary. Pages 1–15 in J. Munro, D. Hatin, J. E. Hightower, K. McKown, K. J. Sulak, A. W. Kahnle, and F. Caron, editors. *Anadromous sturgeons: habitats, threats, and management*. American Fisheries Society, Symposium 56, Bethesda, Maryland.
- Mussen, T. D., D. Cocherell, J. B. Poletto, J. S. Reardon, Z. Hockett, A. Ercan, H. Bandeh, M. Levent Kavvas, J. J. Cech Jr., and N. A. Fangue. 2014. Unscreened water-diversion pipes pose an entrainment risk to threatened Green Sturgeon, *Acipenser medirostris*. *PLoS ONE [online serial]* 9:e86321.
- Ng, E. L., J. P. Fredericks, and M. C. Quist. 2016. Population dynamics and evaluation of alternative management strategies for nonnative Lake Trout in Priest Lake, Idaho. *North American Journal of Fisheries Management* 36:40–54.
- Nguyen, P. L., Z. J. Jackson, and D. L. Peterson. 2016. Comparison of fin ray sampling methods on White Sturgeon *Acipenser transmontanus* growth and swimming performance. *Journal of Fish Biology* 88:655–667.
- Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. The modification of an estuary. *Science* 231:567–573.
- Ogle, D. H. 2016. *Introductory fisheries analyses with R*. CRC Press, Boca Raton, Florida.
- Ogle, D. H. 2017. *FSA: Fisheries Stock Assessment*. R package version 0.8.13.
- Ogle, D. H., T. O. Brenden, and J. L. McCormick. 2017. Growth estimation: growth models and statistical inference. Pages 265–352 in M. C. Quist and D. A. Isermann, editors. *Age and growth of fishes: principles and techniques*. American Fisheries Society, Bethesda, Maryland.
- Pala, C. 2005. Ban on Beluga Sturgeon caviar points to sturgeon's worldwide decline. *Science* 310:37.
- Paragamian, V. L., and M. J. Hansen. 2008. Evaluation of recovery goals for endangered White Sturgeon in the Kootenai River, Idaho. *North American Journal of Fisheries Management* 28:463–470.
- Paragamian, V. L., and R. C. Beamesderfer. 2003. Growth estimates from tagged White Sturgeon suggest that ages from fin rays underestimate true age in the Kootenai River, USA and Canada. *Transactions of the American Fisheries Society* 132:895–903.
- Paragamian, V. L., R. C. Beamesderfer, and S. C. Ireland. 2005. Status, population dynamics, and future prospects of the endangered Kootenai River White Sturgeon population with and without hatchery intervention. *Transactions of the American Fisheries Society* 134:518–532.
- Paukert, C. P., and J. J. Spurgeon. 2017. Age structure. Pages 221–232 in M. C. Quist and D. A. Isermann, editors. *Age and growth of fishes: principles and techniques*. American Fisheries Society, Bethesda, Maryland.
- Pauly, D. 1980. On the interrelationships between natural mortality growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer* 39:175–192.
- Pikitch, E. K., P. Doukakis, L. Lauck, P. Chakrabarty, and D. L. Erickson. 2005. Status, trends, and management of sturgeon and Paddlefish. *Fish and Fisheries* 6:233–265.
- Pine, W. E., M. S. Allen, and V. J. Dreitz. 2001. Population viability of the Gulf of Mexico Sturgeon: inferences from capture–recapture and age-structured models. *Transactions of the American Fisheries Society* 130:1164–1174.
- Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2001. Tag reporting rate estimation: use of high-reward tagging and observers in multiple-component fisheries. *North American Journal of Fisheries Management* 22:727–769.
- Pycha, R. L. 1956. Progress report on White Sturgeon studies. *California Fish and Game* 42:23–35.
- Quist, M. C., M. A. Pegg, and D. R. DeVries. 2012. Age and growth. Pages 677–732 in A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. *Fisheries techniques*, 3rd edition. American Fisheries Society, Bethesda, Maryland.
- R Development Core Team. 2018. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. Available: www.R-project.org. (January 2018).
- Regier, H. A., and K. H. Loftus. 1972. Effects of fisheries exploited on salmonid communities in oligotrophic lakes. *Journal of the Fisheries Research Board of Canada* 29:959–968.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Rieman, B. E., and D. L. Myers. 1992. Influence of fish density and relative productivity on growth of kokanee in ten oligotrophic lakes and reservoirs in Idaho. *Transactions of the American Fisheries Society* 121:178–191.
- Rieman, B. E., and R. C. Beamesderfer. 1990. White Sturgeon in the lower Columbia River: is the stock overexploited? *North American Journal of Fisheries Management* 10:388–396.
- Rien, T. A., and R. C. Beamesderfer. 1994. Accuracy and precision of White Sturgeon age estimates from pectoral fin rays. *Transactions of the American Fisheries Society* 123:255–265.
- Rien, T. A., R. C. Beamesderfer, and C. F. Foster. 1994. Retention, recognition, and effects on survival of several tags and marks on White Sturgeon. *California Department of Fish and Game* 80:161–170.
- Schaffter, R. G. 1997. White Sturgeon spawning and location of spawning habitat in the Sacramento River, California. *California Department of Fish and Game* 83:1–20.
- Scholten, G. D., and P. W. Bettoli. 2005. Population characteristics and assessment of overfishing for an exploited Paddlefish population in the lower Tennessee River. *Transactions of the American Fisheries Society* 134:1285–1298.
- Schreier, A. D., B. Mahardja, and B. May. 2013. Patterns of population structure vary across the range of the White Sturgeon. *Transactions of the American Fisheries Society* 142:1273–1286.
- Shirley, D. E. 1987. Age distribution of White Sturgeon (*Acipenser transmontanus*) in the Sacramento–San Joaquin Bay–Delta. Master's thesis. University of California, Davis.
- Skinner, J. E. 1962. An historical review of the fish and wildlife resources of the San Francisco Bay area. California Department of Fish and Game, Water Project Branch, Report 1, Sacramento.
- Smith, C. T., R. J. Nelson, S. Pollard, E. Rubidge, S. J. McKay, J. Rodzen, B. May, and B. Koop. 2002. Population genetic analysis of White Sturgeon (*Acipenser transmontanus*) in the Fraser River. *Journal of Applied Ichthyology* 18:307–312.
- Smith, M. W., A. Y. Then, C. Wor, G. Ralph, K. H. Pollock, and J. M. Hoenig. 2012. Recommendations for catch-curve analysis. *North American Journal of Fisheries Management* 32:956–967.
- Smith, T. I. J., S. D. Lamprecht, and J. W. Hall. 1990. Evaluation of tagging techniques for Shortnose Sturgeon and Atlantic Sturgeon. Pages 134–141 in N. C. Parker, editor. *International symposium and educational workshop on fish-marking techniques*. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Stubben, C., and B. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software [online serial]* 22(11).
- Then, A. Y., J. M. Hoenig, N. G. Hall, and D. A. Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information from over 200 fish species. *ICES Journal of Marine Science* 72:82–92.

- USFWS (U.S. Fish and Wildlife Service). 2001. Final restoration plan for the Anadromous Fish Restoration Program. USFWS Anadromous Fish Restoration Program, Stockton, California.
- USFWS (U.S. Fish and Wildlife Service). 2014. Revised recovery plan for the Pallid Sturgeon (*Scaphirhynchus albus*). USFWS, Denver.
- Van Poorten, B. T., and S. O. McAdam. 2010. Estimating differences in growth and metabolism in two spatially segregated groups of Columbia River White Sturgeon using a field-based bioenergetics model. *Open Fish Science Journal* 3:132–141.
- von Bertalanffy, L. 1938. A quantitative theory on organic growth. *Human Biology* 10:181–213.