**Population Dynamics of 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, high rates of mortality, and high levels of exploitation. Model projections, in conjunction with demographic information, indicated that White Sturgeon in the SSJ are likely exploited to an excessive degree. Under current conditions, the population will likely continue to decrease (λ = 0.97). 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 replacement rate (i.e., λ ≥ 1.00) if total annual mortality for age-3 and older fish did not exceed 6%. Low levels of exploitation (i.e., < 3%) would likely be required to maintain a stable population.

**Introduction**

Sturgeon (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 sturgeon share life history characteristics (e.g., long-life span, periodic spawning, delayed maturation) that make them exceptionally vulnerable to anthropogenic disturbances. Most sturgeon species are imperiled due to habitat degradation, altered flow and temperature regimes, and (or) 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, 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*, 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 U.S. to conserve sturgeon populations, including bans of imported caviar, strict harvest regulations, increased monitoring efforts, and conservation aquaculture have yet to improve the overall status (Pala 2005; Pikitch 2005; Haxton et al. 2016; Hildebrand et al. 2016).

All nine sturgeon species native to North America are currently listed as endangered, threatened, or considered a species of special concern under the Endangered Species Act (ESA), including several populations of White Sturgeon *A.* *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 and Washington), and the SSJ (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, British Columbia) is an endangered species under the ESA, whereas the population of White Sturgeon in the Sacramento-San Joaquin River basin (SSJ), California, is not (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 and 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 valuable recreational 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 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, which has yet to be achieved (Gingras and DuBois 2013).

White Sturgeon were historically abundant in the SSJ, but unregulated commercial harvest from the mid-1880s to the early-1900s caused the population 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 White Sturgeon population in the SSJ was thought to be resilient enough to support a recreational fishery (Chadwick 1959). Research conducted during the 1950s–1980s designated the population stable with sustainable harvest rates (Chadwick 1959; Kohlhorst 1980). Exploitation was estimated to vary between 2.0% and 7.3%, with most White Sturgeon harvested incidentally in the Striped Bass *Morone* *saxatillis* fishery (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 an exploitation of 11.5% by the late 1980s (Kohlhorst et al. 1991). As a result, several changes to White Sturgeon harvest regulations were implemented (Table 1). For example, the CDFW designated a harvest slot length limit of 117–183 cm total length (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 102–152 cm fork length (FL). Despite increasingly restrictive harvest regulations, the potential for overexploitation remains a concern for White Sturgeon in the SSJ (Kohlhorst et al. 1991; Gingras and DuBois 2014; Hildebrand et al. 2016). Rieman and Beamesderfer (1990) and Beamesederfer and Farr (1997) suggested that most North American sturgeon can only sustain levels of exploitation around 5–10%. Additionally, current and historic estimates of exploitation for White Sturgeon are biased low because information is incomplete regarding illegal harvest, total fishing effort, and the total number of anglers.

Recent results from several CDFW monitoring surveys suggest declining population trends. Since 1967, CDFW has intermittently conducted an adult sturgeon population study (hereafter termed the “sturgeon study”) that monitors the relative abundance, distribution, exploitation, and growth of sturgeon in the SSJ. Since 2001, the average catch per unit effort (CPUE; fish per 100 net-fathom hour [NFH]) 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 San Francisco Estuary (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; 2012–2016; Shirley 1987; Gingras et al. 2013). Few age-0 and age-1 White Sturgeon have been sampled since 1998, and only two moderately strong year classes (i.e., 2006, 2011) have been documented in the last 18 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 Pallid Sturgeon *Scaphirhynchus* *albus* in the Missouri and Mississippi river basins (USFWS 2014) is largely attributed to prolonged recruitment failure or near-failure.

With declining CPUEs and frequent recruitment failure or near-failure over the last two decades, reevaluation 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, 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 models to provide evidence that harvest regulations (e.g., length limits) were not adequate to prevent overfishing of Shovelnose Sturgeon *S.* *platorynchus* in the Mississippi River. Age-structured models are also useful for identifying the life history stages 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 California’s 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 scenarios (e.g., bag limits, 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 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). Suisun Bay and San Pablo Bay are both shallow with average depths of 4.6 m 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.

Before large-scale changes began in the mid-1800s, the SSJ was characterized as an unregulated tidal marsh 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 SFE directed primarily for agricultural use, flood control, and power generation has led to the construction of over 20 dams, 1,600 km of levees, and hundreds of water-diversion facilities that further augment natural environmental conditions (e.g., floodplain connectivity, temperature, streamflow) and sturgeon habitat (Jaffe et al. 2007; Grimaldo et al. 2009; Mussen et al. 2014; Jackson et al. 2016). In addition, water-diversion structures throughout the SSJ and SFE entrain fishes, including juvenile sturgeon, potentially contributing as an additional source of mortality (Grimaldo et al. 2009; Mussen et al. 2014).

Altered habitat and hydrological conditions are a significant cause of universal declines in abundance and distribution of native fishes in the SFE and SSJ (Skinner 1962; Nichols et al. 1986; Moyle et al. 2011). In addition, more than 250 non-native species have been introduced to the SSJ and SFE (Moyle et al. 2011). Pinnipeds and several non-native fishes, such as Striped Bass, Common Carp *Cyprinus* *carpio*, and Largemouth Bass *Micropterus* *salmoides* have been documented preying on juvenile White Sturgeon (Miller and Beckman 1996; M. L. Gingras, CDFW, unpublished data). The native fish assemblage of the SSJ and SFE includes 40 species, 17 of which are endemic (Moyle et al. 2011). The five anadromous fishes identified for restoration by the CVPIA are Chinook Salmon *Oncorhynchus* *tshawtscha*, steelhead *O. mykiss*, American Shad *Alosa* *sapidissima*, White Sturgeon, and Green Sturgeon *A*. *medirostris*.

*Field sampling and laboratory processing.*—

Sampling for White Sturgeon occurred in Suisun and San Pablo bays from August through October 2014–2015 and in September and October of 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 with multifilament nylon twine. Each 45.7-m panel had a single inner mesh panel of multi-strand monofilament twist gillnet that alternated between 15.2, 17.8, or 20.3-cm stretch mesh. Inflatable buoys were attached in the middle and at both ends of the net to help the net drift and to prevent the net from tangling while deployed. Trammel nets were drifted perpendicular to the prevailing wind or current in locations with signs of sturgeon aggregations while avoiding known snags. Nets soaked for approximately 30 minutes before retrieval with a hydraulic lifter.

Upon net retrieval, captured White Sturgeon were inspected for tags (e.g., Carlin disc-dangler reward tags, passive integrated transponder tags) and measured for FL to the nearest centimeter. Additionally, the inner panel mesh size that caught the White Sturgeon was recorded. White Sturgeon with no prior tags and measured 84–204 cm FL 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, US$50, US$100, or US$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 following methods outlined in Koch and Quist (2007). A cross-section was taken from each encapsulated fin ray with an IsoMet low-speed saw (Beuhler, Lake Bluff, IL). Two or three sections varying in width from 0.83–1.25 mm were cut from the proximal end of the fin ray to ensure 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 (MediaCybernetics, Rockville, MD) was used to measure the distance between annuli. Annuli were enumerated without prior knowledge of fish length. Before ageing White Sturgeon fin rays from the SSJ, the senior author gained experienced by estimating ages and measuring growth increments of known-age White Sturgeon from the Kootenai River (*n* = 157). Furthermore, the ages of 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. All remaining fin ray sections were aged by one reader.

*Data analysis.*—

Statistical analyses were performed in program R using the Fish Stock Assessment package (Ogle 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:

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where *Lt* (cm) is fork length at time *t*, *L∞* is the mean maximum length, *K* is the growth coefficient, and *to* is the theoretical age when length is zero (von Bertalanffy 1938; Ogle et al. 2017).

An age-length key was used to estimate age distributions of all White Sturgeon sampled by CDFW from 2014–2016 (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 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, log normal, gamma, bi-modal). 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-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 of age-3 to age-19 White Sturgeon was estimated for uncorrected and trammel net selectivity-corrected catch-at-age using the Chapman-Robson estimator with peak-plus one criterion (*S*; Chapman and Robson 1960; Smith et al. 2012). No direct estimates of age-specific mortality were available for larval or juvenile White Sturgeon in the SSJ as age-0 through age-2 White Sturgeon were absent from our samples. White Sturgeon mortality is assumed to follow a type-III survivorship curve with ≥ 99.9% mortality rate 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 *A. fulvescens* (Caroffino et al. 2010), age-1 from Gulf Sturgeon *A. oxyrhynchus desotoi* (Pine et al. 2001), and age-2 from 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 angler reporting rate varies by tag value (Pollock et al. 2001; Meyer et al. 2012). Therefore, we used tag return data from 2007–2015 to estimate the average reporting rate for each reward tag (i.e., US$20, US$50, US$100). Assuming a 100% return rate of the high-reward tags (i.e., US$150), annual reporting rates (Λ) were estimated using the equation:

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 was estimated from 2007–2015 as:

where *Nr* is the corrected number of tags returned for harvested fish, *N*0 is the number of fish tagged, γ is tag retention (i.e., 0.90; Rien et al. 1990), and *θ* is survival of tagged fish (i.e., 1 – 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 exploitation rates. Using the von Bertalanffy growth model, White Sturgeon were predicted to recruit to the fishery at 10.2 years of age (102 cm FL) and remain there for 5.2 years (152 cm FL). White Sturgeon that were tagged between the ages of 9.2 to 15.4 years of age were considered available for harvest during the 1-year period after tagging. We used the relationship for a Type 2 fishery (*F* = *µZ*/*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, we compared our estimate of *M* to the average of four different estimates using meta-analysis estimator equations to account for uncertainty (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 (ºC) from Suisun Bay, California, were used as inputs for equations from Pauly (1980), Hoeing (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, proportion of females spawning each year) of White Sturgeon are limited. White Sturgeon do not exhibit external sexual dimorphism 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 which were considered mature. Using these data, age at first maturity and the probability of maturity at age (*pmt*) were predicted with logistic regression. Fecundity at age (*fi*) was estimated for age-10 and older White Sturgeon using the equation developed for White Sturgeon in the lower, unimpounded Columbia River (DeVore et al. 1995). Fork length 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 if eggs were spawned naturally (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 SSJ White Sturgeon population’s response 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 White Sturgeon up to age 19 in the SSJ. However, it is not uncommon for White Sturgeon to live longer than 30 years (Hildebrand et al. 2016). As such, an age-20 and older life stage (hereafter 20+) was included in the models. A post-census 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:

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where *S*0–*S*20+ are annual survival rates of White Sturgeon ages 0–20+, and *R*i is the reproductive rate of age-class *i* estimated by:

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where *Pi* is the probability of spawning for age-class *i*, *fi* is the fecundity of age-class *i*, *a* is the proportion of female offspring, and *Si* is the survival of age class *i* (Morris and Doak 2002). The proportion of female offspring was assumed to be 1:1 (Chapman et al. 1996).

A simulation-based approach was used to account for uncertainty and variability in all 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 stretch-beta distributions based on the mean and standard error of their respective vital rates (Morris and Doak 2002; Table 2). We set the variance to be 20% of the mean value if a vital rate was obtained from the literature without a listed standard error (Cox et al. 2013; Ng et al. 2016). Age-specific survival rates and probability of spawning were modeled as beta distributions with values constrained between 0 and 1 (Morris and Doak 2002). We also incorporated stochastic variation in recruitment by simulating successful age-classes to occur on average once every eight years based on empirical data from the Bay Study. Fecundity at age (*fi*) was generated in each simulation 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 exploitation 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). Finally, we varied exploitation from 0.00 to 0.30 in 0.01 increments to evaluate the influence of harvest on λ. Additionally, we estimated the average population size and the age-specific abundance of the 2006 and 2011 cohorts over a 20-year period. Age-specific abundances were estimated by multiplying the Leslie matrix (***A***) by the vector of age-specific abundances at time (**nt**): **nt+1** = ***A*nt** (Morris and Doak 2002)

Population growth rate was modeled for each combination of scenarios over a period of 10, 20, and 50 years. 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 are density independent, we used an estimated total population abundance (*N*) of 48,000 White Sturgeon as the initial number of individuals used for modeling (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 was estimated to represent the average population growth rate (λG; Caswell 2001; Morris and Doak 2002). When the population is at equilibrium, λG is equal to one, and growth and decline are represented by an increasing (> 1.0) or decreasing (< 1.0) value of lambda (Horst 1977). Approximate 95% confidence intervals 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 which represents the proportional contribution of a vital rate to λ*G*. Specifically, elasticity analyses predict how λG 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 months of 2014–2016, 1,000 individual White Sturgeon were captured in trammel nets. Sampled White Sturgeon varied in length from 53 to 217 cm FL (mean ± SD; 97.5 cm ± 27.0) 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 years ± 3.2; Figures 3 and 4) 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. After correcting for trammel net selectivity, peak abundance in the catch occurred at age 8. Total instantaneous mortality for age-3 through age-19 fish 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 US$20 tags, 27 US$50 tags, 45 US$100 tags, and 5 US$150 tags were reported. After correcting for nonreporting and adjusting for tag loss and mortality, annual exploitation varied between 8.0–29.6% with a mean of 13.6% (95% CI: 1.0%–26.2%; Figure 5). The estimate of *M* using these data was 0.056 and used for the population models. For comparison, the average of *M* using equations from Pauly (1980), Hoenig (1983), and Then et al. (2015) was 0.066.

Under current harvest conditions (*µ* = 13.6%; slot length limit: 102 cm–152 cm FL), the population growth rate was predicted to decline annually by 4.6% (λG = 0.95; 95% CI: 0.89–1.04) over a time period of 20 years assuming a spawning periodicity of 10% (Figure 6). With a spawning periodicity of 15%, the White Sturgeon population was predicted to decline at a rate of 2.8% under current harvest conditions (λG = 0.97; 95% CI: 0.91–1.08; Figure 7). At this rate of decline, the projected total abundance of White Sturgeon in the SSJ in 20 years would decrease to 27,905 White Sturgeon (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 (λG = 0.95; 95% CI: 0.91–0.99) and 50-year (λG = 0.97; 95% CI: 0.87–1.19) time spans. Additionally, under a spawning periodicity of 25%, the population growth rate of White Sturgeon in the SSJ was predicted to decline at a rate of 1.5 % (λG = 0.98; 95% CI: 0.95–1.18) over 20 years under current harvest conditions (Figure 8).

Population projections for management scenarios indicated that population increases would be tenable. In general, for all the scenarios, the mean population growth rate approached replacement rate at near-zero levels of exploitation. In the absence of fishing mortality, the 20-year estimates of λG 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, total annual mortality would have to be less than 6% for age-3 and older White Sturgeon assuming a spawning periodicity of ≥ 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 the mean population growth rate between the harvest slot length limits were slight (Figures 6–8).

Sensitivity analysis indicated that population growth rate was more sensitive to changes in the mortality rates of age-3 and older White Sturgeon than variation in spawning periodicities. For example, increasing mortality by 5.0% resulted in a 3.2% decrease in λG over a 20-year period. Under current conditions, the population growth rate was most influenced by adult survival rates (Figure 9). Reproductive parameters (i.e., fertility) had the lowest summed elasticity and made the smallest relative contribution to λ. Summed elasticity was greatest (mean ± SD; 0.76 cm ± 0.13) for sexually mature White Sturgeon (≥ age 10) indicating that the population growth rate is most influenced by changes in survival of adult fish. The elasticity value means that the survival rate of adult White Sturgeon contributes about a 77% change in λG, relative to the other vital rates.

**Discussion**

Although information regarding effective conservation strategies continues to develop, knowledge of population parameters and the influence of exploitation remain incomplete for White Sturgeon in the SSJ. Therefore, we coupled a demographic assessment of White Sturgeon in the SSJ with age-structured population models to better understand potential population-level responses to perturbations and management actions. The White Sturgeon population in the SSJ exhibited fast growth, high rates of mortality, high levels of exploitation, and appeared to be declining. The size and age structure of the population suggest that the White Sturgeon population in the SSJ is likely overexploited. Length-frequency distributions show few White Sturgeon survive the harvest slot (length limit). The current estimated length-frequency distribution differed from frequencies presented in some prior studies of White Sturgeon in the SSJ (Kohlhorst et al. 1980; Brennan and Cailliet 1989). The majority of the White Sturgeon sampled in those prior studies were between 90 and 160 cm, whereas most of the fish sampled in our study were less than 90 cm. However, the experimental trammel nets and nonrandom sampling may have contributed to the paucity of large fish and skewed size distribution in our study. In particular, the capture efficiency of CDFW trammel nets may be ill-suited for sampling White Sturgeon ≥ 200 cm FL. Previous research in the SSJ and in other systems (e.g., lower Columbia River) have used a variety of sampling methods to collect White Sturgeon (e.g., commercial fishing nets, trammel nets, hook-and-line, trawls; Kohlhorst et al. 1980; Brennan and Cailliet 1989; DeVore et al. 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 population. Nonetheless, these are the best data available for the White Sturgeon population in the SSJ.

Prior studies have estimated the longevity of White Sturgeon. For instance, Smith et al. (2002) reported that White Sturgeon can exceed ages of 100 years. White Sturgeon as old as 80 years have been observed in the Kootenai River, Idaho (Paragamian and Beamesderfer 2003), and 65 years old in the Columbia River (DeVore et al. 1995). Our data did not match these findings as the maximum observed age was 29 years. Lower maximum ages of White Sturgeon in the SSJ is likely the result of sampling bias, anthropogenic disturbances, and (or) 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). Challenging environmental conditions (e.g., pollutants) 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 ageing 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, ageing error is not likely a major issue in our study because the majority of fish were young (< age 10) with only two fish estimated to be over 20 years of age.

Growth analysis indicated that length at age of White Sturgeon in the SSJ varied widely. However, the general pattern suggests that growth of White Sturgeon is rapid for larval and juveniles life stages and declines around age 17. Contemporary growth estimates for White Sturgeon in the SSJ were higher than estimates from 1973–1976 (Kohlhorst et al. 1980). Additionally, White Sturgeon in the SSJ appear to exhibit faster growth than all other White Sturgeon populations for which data are available. Using 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. Age-10 to age-50 White Sturgeon in the Kootenai River grow approximately 2.5 cm per year (Paragamian et al. 2005). Over that same time period, White Sturgeon in the SSJ grow nearly twice as fast (i.e., 4.6 cm per 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, 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 (≥ 2 years) of kokanee *O. nerka* experienced declines in growth with increasing fish density (Rieman and Myers 1992). Furthermore, in the Ottawa River, Canada, 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.

Estimating mortality for sturgeon populations is challenging due to uncertainties in the accuracy of ageing techniques, different capture efficiencies between sampling gears, and unknown influences of 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 total annual mortality after correcting for size selectivity (*A* = 18.7%) is similar to those reported for other exploited sturgeon populations. Estimates of total annual mortality for White Sturgeon in the Columbia River vary from 18 to 24% (lower Columbia River; Beamesderfer et al. 1995) to 37% (unimpounded lower Columbia River; DeVore et al. 1995). In Lake Winnebago, Wisconsin, Bruch (1999) reported annual mortality rates of 17% for Lake Sturgeon exposed to a limited recreational harvest. Additionally, our current estimate of natural mortality in the SSJ (*cm* = 0.06) is similar to historic estimates (0.05–0.10; Kohlhorst 1980) and to White Sturgeon populations in other water bodies. For instance, in the lower Columbia River, *cm* was estimated at 0.09 (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 the mortality rates, and sampling techniques and mortality estimators differed between studies.

The estimated mean annual exploitation rate (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 exploitation 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, and (or) an unwillingness of anglers to report their catch. Additionally, our estimate did not include illegal harvest or fishing mortality due to bycatch in other fisheries. Although the exact number of White Sturgeon illegally harvested in the SSJ is unquantified, the number is thought to be substantial (M. L. Gingras, CDFW, unpublished information). Regardless, an absolute minimum exploitation estimate based solely on the proportion of tags returned was 8.0%, suggesting an exploitation rate that is likely too high to maintain the White Sturgeon population in the SSJ.

Results from population modeling suggest that the abundance of White Sturgeon in the SSJ will decrease under current harvest conditions. However, the estimated population growth rates 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 the population growth using the estimates of mortality from the uncorrected age structure, finding that the results indicated even lower estimates of the mean population growth rate. Additionally, determining 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; Gross et al. 2002; Pine et al. 2001; Caroffino et al. 2010). Inaccuracies in growth estimates could also influence our results (Hamel et al. 2016). Though when we modeled additional scenarios using both faster and slower growth rates, results were similar to or lower than our estimated mean population growth rate. 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, Se) exist in the SSJ which 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 are still poorly understood and likely vary among years and individuals (Conte et al. 1988; Gross et al. 2002; Hildebrand et al. 2016). Although we modeled a range of spawning periodicities, it is likely that we may have overestimated the frequency. Additional studies are needed to assess the percentage of females that spawn each year.

Regardless of uncertainties in the model, population metrics suggest that White Sturgeon in the SSJ will continue to decline without changes to harvest regulations. Although conservation strategies include improving sturgeon spawning habitat (Schaffter 1997) and augmenting stream flow 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 total annual mortality to less than 10% for age-10 and older White Sturgeon would increase the mean population growth rate 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 population size structure and abundance of White Sturgeon (Boreman 1997; IDFG 2008). Reductions in annual mortality in other White Sturgeon populations following closure of fisheries suggest that this is an important conservation strategy. In the Kootenai River, White Sturgeon experienced reductions of 5–10% in mortality rates following closure of harvest (Paragamian et al. 2005). In 1971, the implementation of strict catch-and-release regulations for White Sturgeon in the Snake River, Idaho, led to the 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 the 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 an exploitation of < 2% for Atlantic Sturgeon *A.* *oxyrhynchus* *oxyrhynchus* in the Saint John River, New Brunswick (Dadswell et al. 2017). Similarly, the self-sustaining Lake Sturgeon population in Lake Winnebago, Wisconsin, is attributed to strict and adaptive fishing regulations that maintain exploitation 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 sturgeon.

Efforts that support decreasing the mortality of sexually mature White Sturgeon are further corroborated by results from the sensitivity analyses and provide additional evidence that White Sturgeon are extremely vulnerable to exploitation. Under current harvest conditions, our models indicated that the survival rates of reproductive adults contribute the most to the population growth rate followed by the survival of sub-adults. In populations that exhibit non-stable 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 the population growth rate than did recruitment rates (Pine et al. 2001). Similarly, analysis from an age-structured population model for Green Sturgeon showed that the population growth rate was highly sensitive to adult mortality (Heppell 2007). Even small reductions in adult mortality through reduced exploitation may help offset other challenges that White Sturgeon in the SSJ experience (e.g., illegal harvest, dams, droughts).

Baseline data regarding population demographics are essential for 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 on White Sturgeon in the SSJ. 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 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. Continued monitoring across several generations, robust abundance and harvest estimates, and a better understanding of variables affecting recruitment are necessary to refine recovery goals for White Sturgeon in the SSJ.

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**Figure Captions**

Figure 1. The Sacramento and San Joaquin rivers as they enter the San Francisco Bay Delta-Estuary, California.

Figure 2. Length-frequency distribution of White Sturgeon sampled in Suisun Bay, California during the summer and autumn months of 2014–2016. Data are for fish collected using trammel nets. Data in Panel A are for uncorrected size selectivity and Panel B are corrected for size selectivity.

Figure 3. Age-frequency distribution of White Sturgeon sampled in Suisun Bay, California during the summer and autumn months of 2014–2016. Data are for fish collected using trammel nets. Data in Panel A are for uncorrected size selectivity and Panel B are corrected for size selectivity.

Figure 4. von Bertalanffy growth model for White Sturgeon sampled from August through October 2014–2016 in the Sacramento-San Joaquin River basin, California. The solid circles represent the mean back-calculated length at a given age and the solid line represents growth model fit.

Figure 5. Estimates of exploitation (µ) based on adjusted tag return data for White Sturgeon in the Sacramento-San Joaquin River basin (SSJ), California from 2007–2015. Tag return data was adjusted for angler nonreporting, tagging loss, tagging mortality, and growth into and out of the slot length limit.

Figure 6. Population growth rates (λG) over a 20-year time frame for White Sturgeon in Suisun Bay, California assuming 10% of mature females are spawning annually at various levels of exploitation. Panel A represents the smallest slot length limit (77–127 cm FL), panel B the current slot length limit (102 – 152 cm FL), and panel C the largest slot length limit (127–177 cm FL). The solid horizontal line represents a λG of one where a population is considered stable.

Figure 7. Population growth rates (λG) over a 20-year time frame for White Sturgeon in Suisun Bay, California assuming 15% of mature females are spawning annually at various levels of exploitation. Panel A represents the smallest slot length limit (77–127 cm FL), panel B the current slot length limit (102 – 152 cm FL), and panel C the largest slot length limit (127–177 cm FL). The solid horizontal line represents a λG of one where a population is considered stable.

Figure 8. Population growth rates (λG) over a 20-year time frame for White Sturgeon in Suisun Bay, California assuming 25% of mature females are spawning annually at various levels of exploitation. Panel A represents the smallest slot length limit (77–127 cm FL), panel B the current slot length limit (102 – 152 cm FL), and panel C the largest slot length limit (127–177 cm FL). The solid horizontal line represents a λG of one where a population is considered stable.

Figure 9. Summed elasticity values for exploited (*µ* = 13.6%, harvest slot length: 102–152 cm fork length) White Sturgeon vital rates in the Sacramento-San Joaquin River basin, California. Summed juvenile survival is from age 0 through age 2, sub-adult survival is age 3 through age 9, and adult survival consists of age-10 and older White Sturgeon.

Figure 1.

0

60 kilometers skilometers

30

Sacramento River

San Joaquin River

San Francisco Bay

Suisun Bay

San Pablo Bay

N



B

A

Figure 2.



B

A

Figure 3.



Figure 4.

Figure 5.



C

A

λG

B

Figure 6.



λG

A

B

C

Figure 7.



λG

C

B

A

Figure 8.



Figure 9.

Table 1. History of sturgeon fishing regulations in the Sacramento-San Joaquin River Basin, California.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Year | Daily bag limit | Annual bag limit | Length restrictions (fork length) | | Gear and other restrictions |
| Minimum (cm) | Maximum (cm) |
| Pre-1917 | none | none | none | none |  |
| 1917–1954 | 0 fish | 0 fish | -- | -- | Closed to all White Sturgeon harvest |
| 1954 | 1 fish | Unlimited | 91 | None |  |
| 1956 | 1 fish | Unlimited | 114 | None |  |
| 1963 | 1 fish | Unlimited | 91 | None |  |
| 1990 | 1 fish | Unlimited | 95 | 164 |  |
| 1991 | 1 fish | Unlimited | 100 | 164 |  |
| 1992 | 1 fish | Unlimited | 105 | 164 |  |
| 2007 | 1 fish | 3 fish | 105 | 151 | Fishing Report Card required |
| 2013 | 1 fish | 3 fish | 102 | 152 | 1 single barbless hook; White Sturgeon ≥ 173 cm FL may not be removed from the water. |

Table 2. Mean vital rates and standard errors used to construct population matrices for the White Sturgeon population in the Sacramento-San Joaquin River basin, California.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Symbol** | **Definition** | **Age(*t*)** | **Value** | **Error** | **Source** |
| Fertility elements | | | | | |
| *ft* | Fecundity at age *t* | 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 |  |
|  |  | 19 | 335,355 | 9,723 |  |
| *pm* | Probability of maturity at age *t* |  |  |  |  |
|  |  | 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 |  |
|  |  | 19 | 0.966 | 0.098 |  |
|  |  | 20+ | 1.000 | 0.200 |  |
| *pf* | Proportion of offspring that are females | 10–19 | 0.500 | N/A | Chapman et al. (1996) |
|  |  |  |  |  |  |
| Transition elements | | | | | |
| *S0* | Egg to age 1 survival | 0 | 0.002 | 0.003 | Caroffino et al. (2010) |
| *S1* | Age 1 survival | 1 | 0.250 | 0.008 | Pine et al. (2001) |
| *S3* | Age 2 survival | 2 | 0.840 | 0.168 | Ireland et al. (2002) |
| *S3*–*S20+* | Asymptotic survival | 3–19 | 0.946 | 0.03 | This study |