**Chapter 2: Population dynamics and evaluation of management scenarios for White Sturgeon in the Sacramento-San Joaquin River basin, California**

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**Abstract**

Recent surveys suggest that the population of White Sturgeon *Acipenser* *transmontanus* in the Sacramento-San Joaquin River basin (SSJ), California is declining. Potential 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 guide management decisions. The purpose of this study was to evaluate the population dynamics for White Sturgeon in the SSJ and use the information to evaluate the population-level response under prospective management scenarios. White Sturgeon in the SSJ exhibit fast growth, high rates of mortality, and experience variable levels of exploitation. Model projections, in conjunction with demographic information, indicated that White Sturgeon in the SSJ are likely overexploited. Under current conditions, the population will likely decrease (λ = 0.972). Population growth of White Sturgeon in the SSJ was most influenced by the survival of sexually mature adults. The models also suggested that the White Sturgeon in the SSJ could reach replacement rate if total annual mortality for age-3 and older fish did not exceed 6%. Low levels of exploitation (i.e., ≥ 2%) would likely be required to maintain a stable population.

**Introduction**

Sturgeon (Acipenseridae) are of conservation concern throughout their distribution (Birstein and Bemis 1997; Pikitch et al. 2005; Jelks et al. 2008; Jager et al. 2016). All sturgeon share life history characteristics (e.g., long-life span, periodic spawning, delayed maturation) that make them vulnerable to anthropogenic disturbances. Most sturgeon species are imperiled due to habitat degradation, altered flow and temperature regimes, and (or) overharvest (Birstein 1993; Beamesderfer and Farr 1997; Boreman 1997; Pikitch et al. 2005; Schreier et al. 2013). In particular, overharvest has been attributed to the decline of sturgeon around the world (Boreman 1997; Hildebrand 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 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; Jager et al. 2016; Hildebrand et al. 2016).

All eight 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 White Sturgeon *A. transmontanus* (Jelks et al. 2008; Haxton et al. 2016). Although White Sturgeon populations are relatively abundant and widespread, alterations to large river habitats (e.g., hydroelectric dam construction) and commercial and sport fisheries have reduced their abundance and distribution (DeVore et al. 1995; Jager et al. 2001; Pikitch et al. 2005; 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 Sacramento-San Joaquin River system (SSJ; California; Hildebrand et al. 2016). In the SSJ, the White Sturgeon population is not listed under the ESA (Schaffter and Kohlhorst 1999; Hildebrand et al. 2016). However, the California Department of Fish and Wildlife (CDFW) and the U.S. Fish and Wildlife Service (USFWS) are concerned that the population is declining.

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 in California (Pycha 1956; Skinner 1962). By 1917, all commercial and recreational fishing was prohibited for White Sturgeon in the SSJ (Skinner 1962). In 1954, the CDFW considered the White Sturgeon population in the SSJ 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 caught as incidental bycatch by Striped Bass *Morone* *saxatillis* 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 exploitation of 11.5% by 1988 (Kolhorst et al. 1991). As a result, several changes to White Sturgeon harvest regulations were implemented (Table 1). For example, the CDFW implemented a harvest slot length limit of 117–183 cm total length (TL) in 1990 to protect mature White Sturgeon. Under current regulations, 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 is still a concern for White Sturgeon in the SSJ (Kolhorst et al. 1991; Gingras and DuBois 2015; Hildebrand et al. 2016). Rieman and Beamesderfer (1990) and Boreman (1997) suggested that most North American sturgeon can only sustain low levels of exploitation (i.e., 5–10%). Additionally, current and historic estimates of exploitation for White Sturgeon may be biased low because information is incomplete regarding illegal harvest, total fishing effort, and the number of anglers.

Recent results from several CDFW monitoring surveys indicate 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, 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 and has been at historic lows (DuBois and Danos 2017). Adding to the concern is a trend of inconsistent recruitment (DuBois and Gingras 2015). Since 1980, the CDFW has been monitoring White Sturgeon recruitment during sample efforts from the San Francisco Bay Study (hereafter termed the “Bay Study”). The Bay Study conducts monthly trawling surveys at fixed sites throughout the SSJ and San Francisco Estuary (SFE) to determine 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 complete recruitment failure during recent droughts (2007–2010; 2012–2016; Shirley 1987; Hildebrand et al. 1999; 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 recruitment failure has the potential to put the population at risk. For instance, partial to complete recruitment failure is largely attributed to the endangered status of White Sturgeon in the Kootenai River (Paragamian and Hansen 2008), as well as Pallid Sturgeon *Scaphirhynchus* *albus* in the Missouri and Mississippi river basins (USFWS 2014).

With declining CPUEs and consistent recruitment failure over the last two decades, reevaluation of harvest regulations for White Sturgeon in California is warranted. An excellent technique for evaluating the efficacy of current and future harvest regulations is by developing age-structured population models that predict population 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 varying 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). 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 (Pycha 1956; Kolhorst et al. 1980; Shirley 1987; Gingras and DuBois 2015; Hildebrand et al. 2016). 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) develop age-structured population models to evaluate population growth rates under 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 terms of length and discharge in California (Jaffe et al. 2007). The Sacramento River flows southwest for 716 km where 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 is 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 shallow tidal marshes with average depths of 5.8 m and 3.7 m, respectively (Jaffe et al. 2007). Both bays are turbid, low-salinity environments with average tidal floods of 0.9–1.3 m. South of San Pablo Bay is the San Francisco Bay.

Before large-scale changes began in the 1850s, 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, urban, 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; Jackson et al. 2016). Water management practices 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, further modifying sturgeon habitat and natural environmental conditions (e.g., floodplain connectivity, temperature, streamflow; Jackson et al. 2016). In addition, water diversions throughout the SSJ and SFE entrain juvenile fishes and reduce water quality (Mussen et al. 2014).

Altered habitat and hydrological conditions are largely attributed to the 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 species of nonnative species have been introduced to the SSJ and SFE (Moyle et al. 2011). Several invasive species, 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). The native fish assemblage of the SSJ and SFE includes 40 species, 17 of which are endemic (Moyle 2002). The six anadromous fishes identified for restoration by the Central Valley Project Improvement Act (CVPIA) are Chinook Salmon *Oncorhynchus tshawtscha*, steelhead *O. mykiss*, Striped Bass, 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 2014–2016. White Sturgeon were sampled with 183-m drifted trammel nets. Nets were composed of four 45.7-m contiguous panels of mesh. The outer wallings were 3.7-m-deep panels with multifilament nylon twine. Each 45.7-m panel had a single inner mesh panel of multistrand monofilament twist gillnet that alternated between 15.2, 17.8, or 20.3-cm stretch mesh. Buoys were attached to the middle and both ends of the net to help the net drift efficiently and to prevent the net from closing 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 evaluated for prior tags (e.g., Carlin disc-dangler reward tags, passive integrated transponder tags), and measured for FL and TL to the nearest centimeter. Additionally, the inner panel mesh size that caught the White Sturgeon was recorded. White Sturgeon measuring 84–204 cm FL were affixed with 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. The leading left pectoral fin ray was removed 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). 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 summarization*

Statistical analyses were performed in 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:

*Lt*= *L*∞ × [1 – e – *K* (*t*–*t*o)],

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 the length and age distributions all White Sturgeon sampled by the 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). The population length-and age-frequency distributions were then estimated by applying the age-length key to the trammel net selected-corrected length frequencies (Erzini et al. 2006; Ng et al. 2016; Paukert and Spurgeon 2017).

Total annual survival for 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 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). 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 tag returns 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, $50, $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 for 2007–2015 as:

where *Nr* is the corrected number of tags returned for harvested fish, *N0* is the number of available fish tagged, is tag retention (i.e., 0.90; Rien et al. 1990), is survival of tagged fish (i.e., 1 – tagging mortality = 0.99; Smith et al. 1990). Additionally, because harvest fisheries are 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. Exploitation was converted to instantaneous fishing mortality (*F*) using the relationship for a Type 2 fishery (*F* = µ*Z*/*A*).

Instantaneous natural mortality (*M*) was obtained by *M* = *Z* – *F* (Ricker 1975). Although we used this value of *M* in the population models, to account for uncertainty we compared our estimate of *M* to the average of four different estimates using meta-analysis estimator equations (Ng et al. 2016; Ogle 2017). 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. As such, 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, 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 and used as fertility elements in the matrix population models. 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, U.C. 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.

*Population modeling*

A female-based Leslie matrix model was used to assess the response of the White Sturgeon population to prospective management actions in the SSJ (Morris and Doak 2002). Analyses were conducted in R using functions from the popbio package (Stubben and Milligan 2007; R Core Team 2018). Data 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 (Hess 1984). As such, an age 20 and older life stage (hereafter 20+) was included in the models so the life span of White Sturgeon was not limited to just 19 years. 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 *S0–S20+*are annual survival rates of White Sturgeon ages 0–20+, and *Ri* is the reproductive rate of age-class *i* estimated by:

*R*i = *P*i × *f*i × *a* × *S*i,

where *P*i 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. Demographic stochasticity was simulated using parametric bootstrapping in which the fate of individuals in each age-class was randomly generated based on the mean and standard error of their respective vital rates (Morris and Doak 2002). We specified 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 (*f*i) 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, harvest length limits, and exploitation levels on the population growth rate (λ). Given the best available data, we assumed that 15% of mature White Sturgeon females spawn in a particular year (Chapman 1989; Chapman et al. 1996); however, the exact interval between spawning events is unknown. As such, 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 different harvest slot length limits, including the current limit as well as two theoretical 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 cohort over a 20-year period. Age specific abundance was estimated by multiplying the Leslie matrix (*A*) by the vector of age-specific abundances at time (*nt*): *n*t+1 = *Ant*.

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 the White Sturgeon population because transient dynamics provide more realistic estimates of population growth over the short-term than using a stable age distribution (Morris and Doak 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 sampling gear so a linear model was used to predict the number of fish in each of these age classes (Caswell 2000). 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 to generate a geometric mean that represents the average population growth rate (λ*G*; Caswell 2001; Morris and Doak 2002). When the population is at equilibrium, λ*G* is equal to one, and growth and decline are represented by an increasing (> 1.0) or decreasing (< 1.0) value of lambda (Horst 1977). Due to stochasticity, approximate 95% confidence intervals were generated based on the 5,000 simulations.

The influence of vital rates on λ*G* were assessed using sensitivity and elasticity analyses. Sensitivity and elasticity analyses are commonly used by managers to prioritize management strategies according to the relative influence of vital rates on population growth (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 vital rates higher and lower by the same proportion (i.e., 1%). Elasticity represents the proportional contribution of vital rate to λ*G*. Results from elasticity analyses are used to assist managers in determining which life stages might make the greatest contributions to population growth and where additional research may be warranted (Gross et al. 2002; Morris and Doak 2002).

**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 (8.14 years ± 3.24; 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 0.207 (95% CI: 0.123–0.291); annual survival was 81.3% (95% CI: 80.1–82.5%). Between 2007 and 2016, 19 US$20 tags, 27 US$50, 45 US$100, and 5 US$150 were reported harvested. After correcting for nonreporting and adjusting for tag loss and mortality, annual exploitation rate varied between 8.0–29.6% with a mean rate 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. The average of *M* using equations from Pauly (1980), Hoenig (1983), and Then et al. (2015) was 0.066. Female White Sturgeon were first mature at age 10. Fifty percent of females White Sturgeon were mature at age 14 (i.e., 148 cm FL) and 90% at age 20 (i.e., 174 cm FL).

Under current harvest conditions (µ = 13.6%; slot length limit: 102 cm–152 cm FL), the population growth rate was predicted to decline by 4.6% (λ*G* = 0.954; 95% CI: 0.893–1.04) over a time period of 20 years assuming a spawning periodicity of 10% (Figure 7). With a spawning periodicity of 15%, the White Sturgeon population was predicted to decline at a rate of 2.8% under current harvest conditions (λ*G* = 0.972; 95% CI: 0.914–1.08; Figure 8). 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 cohort would decrease to approximately 1,076 fish over the 20-year modeling period. Similar trends for *λ* were predicted for simulations assuming a 15% spawning periodicity under the current harvest slot length limit over 10-year (λ*G* = 0.953; 95% CI: 0.907–0.997) and 50-year (λ*G* = 0.965; 95% CI: 0.868–1.19) 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 % (λ*G* = 0.984; 95% CI: 0.948–1.18) over a time period of 20 years under current harvest conditions (Figure 9).

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 λ*G* for White Sturgeon in the SSJ was 0.988 (95% CI: 0.933–1.11), 1.01 (95% CI: 0.952–1.16), and 1.02 (95% CI: 0.968–1.18) for spawning periodicities of 10, 15, and 25%, respectively. To reach the replacement rate, total annual morality 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, changing the harvest slot length limit seemed to have little influence on the overall population growth rate (Figures 7–9).

Under current conditions, the population growth rate was most influenced by survival (Figure 10). Reproductive parameters (i.e., fertility) had the lowest summed elasticity and made the smallest relative contribution to λ. Summed elasticity was greatest (0.565) for sexually mature White Sturgeon (≥ age 10) indicating the population growth rate is most influenced by changes in the survival of adult fish. The elasticity value means that the survival rate of adult White Sturgeon contributes about a 57% change in λ*G*, relative to the other vital rates.

**Discussion**

Although information regarding protection needs and conservation strategies continues to evolve, knowledge of life history, habitat requirements, and the influence of exploitation remain incomplete for White Sturgeon in the SSJ. Therefore, we coupled an evaluation of demographics for White Sturgeon in the SSJ with an age-structured population model to better understand population-level response to perturbations and management actions. The White Sturgeon population in the SSJ exhibit fast growth, high rates of mortality, experienced variable levels of exploitation, and appear to be declining. The size and age structure of the population suggest that White Sturgeon in the SSJ is possibly overexploited. The length-frequency distributions show few White Sturgeon greater than 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 the 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) 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 Calliet 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 represented of the entire population. Nonetheless, these are the best data available for the White Sturgeon population in the SSJ.

Many studies have documented the longevity of White Sturgeon. 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 corroborate 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 which have 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; Hildebrand et al. 2016; Gundersen et al. 2017). In addition, errors in age estimation can confound population dynamics analyses (Hamel et al. 2016; Buckmeier et al. 2017). Although pectoral fin rays are currently the most practical and reliable ageing structure for White Sturgeon (Brennan and Cailliet 1989), uncertainty exists regarding age estimates. Accuracy and imprecision have been identified when using White Sturgeon pectoral fins, particularly for fish older than age 20 (Rien and Beamesderfer 1994; Paragamian and Beamesderfer 2003). However, ageing error might not be 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 1980; Figure 6). Additionally, White Sturgeon in the SSJ appear to exhibit faster growth than all other White Sturgeon populations for what data are available. Using von Bertanlaffy growth models, White Sturgeon in the lower Columbia River were predicted to achieve lengths of 116 cm at 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 access to quality habitat, density-dependent interactions (i.e., competition), and marine-based prey availability. Beamesderer 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 and Nechako rivers, reduced growth of White Sturgeon is likely due to limited food availability as well as an increased distance from estuarine and marine food resources (Ireland et al. 2002; Young 2002). High harvest rates or other factors influencing abundance may also influence the growth of White Sturgeon in the SSJ. Prior studies have demonstrated that growth increases when density decreases (Regier and Loftus 1972; Riemen and Myers 1992; Bronte and Sitar 2008). For example, older age-classes (≥ 2 years) of kokanee *O. nerka* experienced declines in growth with increasing fish density (Riemen and Myers 1992). White Sturgeon in the SSJ may be experiencing a similar density-dependent response in growth.

Estimating mortality for White Sturgeon populations is challenging due to uncertainties in the accuracy of ageing techniques, capture efficiency of sampling gears, and unknown influences of anthropogenic activities (Hildebrand 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% (upper Columbia River; Beamesderfer et al. 1995) to 37% (lower Columbia River; DeVore et al. 1995). In Lake Winnebago, Wisconsin, Burch (1999) reported annual mortality rates of 17% for an exploited population of Lake Sturgeon *Acipenser* *fulvescens*. Additionally, our current estimate of natural mortality in the SSJ (*cm* = 0.056) 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, morality comparisons should be viewed with care because sampling techniques and mortality estimators varied between river systems and studies and all authors reported uncertainty in the mortality rates.

The estimated mean annual exploitation rate (i.e., 13.6%) of White Sturgeon in the SSJ was higher that 5–10% recommended to sustain sturgeon populations (Riemen and Beamesderfer 1990; Beamesderfer and Farr 1997; Boreman 1997). It is likely that our estimates of exploitation are biased low due to poor tag returns. The reason for low tag returns is unknown, but could be due to low catch rates, poor 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 illegal harvested in the SSJ is unquantified, the number is thought to be substantial (M. 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 White Sturgeon population in the SSJ will likely 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. We examined this further by modeling the population growth using the estimates of mortality from the uncorrected age structure. 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 (Pine et al. 2001; Gross et al. 2002; Caroffino et al. 2009). Our egg-to-age-1 mortality estimates of 99.96–100% likely yielded realistic estimates of recruitment. However, 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; Caroffino et al. 2009). 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 (Webb et al. 2002; Gundersen et al. 2017). Unfortunately, the timing of White Sturgeon spawning events are still poorly understood and likely vary among 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 without changes to harvest regulations, White Sturgeon in the SSJ will continue to decline. Although conservation strategies include improving sturgeon spawning habitat (Schafter 1997) and augmenting stream flow to mimic historic regimes (Jackson et al. 2016), reducing fishing mortality is likely the most effective, short-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% could cause a rapid decline in the population. Even modest levels of fishing mortality may negatively affect population size structure and abundance of White Sturgeon (IDFG 2008). Reductions in annual mortality in other White Sturgeon populations following closure of fisheries suggest that this may be a significant conservation strategy. In the Kootenai River, White Sturgeon experienced reductions of 5–10% in mortality rates following closure of harvest (Paragamaian 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). Cochnaur (2001) presented a case of how a catch-and-release fishery improved the age-class structure for a White Sturgeon in the Columbia River. Despite differences in the population dynamics, 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. Additionally, 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 the harvest of large, 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 elasticity analysis and provide additional evidence that White Sturgeon are extremely vulnerable to exploitation. Elasticity analysis can assist managers determine which life stages are in most need of protection (Heppell 2006). 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. 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 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 2006). 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, re-occurring droughts).

Baseline data regarding population demographics are necessary for the effective management and conservation of fishes. 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 help advance understanding of the factors that govern fish population and allow managers to quantitatively assess drivers of population growth and decline. Continued monitoring across several White Sturgeon generations, robust abundance and harvest estimates, and a better understanding of variables affecting recruitment will be essential to refine recovery goals of this populations. Moving forward, managers will be able to model additional scenarios and set appropriate benchmarks for success.

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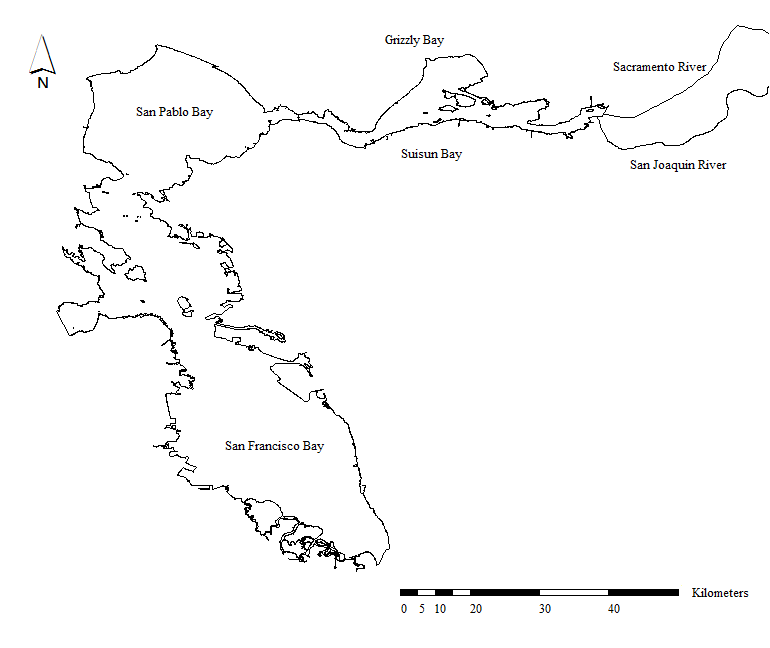


Figure 1. A map depicting Sacramento and San Joaquin rivers as they enter the San Francisco Bay Delta-Estuary, California.



A

B

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.



A

B

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. Comparison of growth between ages, based on mean back-calculated length at age for White Sturgeon in the Sacramento-San Joaquin River basin (SSJ). Current estimates are from fish sampled using trammel nets from 2014–2016. Historic estimates were sampled with trammel nets and creel surveys from 1973–1976.



λG

C

B

A

Figure 7. Figure 8. 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.



A

B

C

λG

Figure 8. 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.



λG

C

B

A

Figure 9. 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 10. 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.

*Table 1. History of recreational White 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 |