

Population Dynamics and Management for White Sturgeon in the Sacramento-San Joaquin
River Basin, California

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Shannon E. Blackburn

Major Professor: Michael C. Quist, Ph.D.

Committee Members: Sophie L. Gilbert, Ph.D.; Timothy R. Johnson, Ph.D.

Department Administrator: Lisette P. Waits, Ph.D.

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Authorization to Submit Thesis

This thesis of Shannon E. Blackburn, submitted for the degree of Master of Science with a Major in Natural Resources and titled “Population Dynamics and Management for White Sturgeon in the Sacramento-San Joaquin River Basin, California,” has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor: _____ Date: _____

Michael C. Quist, Ph.D.

Committee members: _____ Date: _____

Sophie L. Gilbert, Ph.D.

_____ Date: _____

Timothy R. Johnson, Ph.D.

Department Administrator: _____ Date: _____

Lisette P. Waits, Ph.D.

Abstract

Recent surveys suggest that the population of White Sturgeon *Acipenser transmontanus* in the Sacramento-San Joaquin River basin (SSJ) is declining. 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 warranted to develop an effective management and conservation plan. The purpose of this research was to establish baseline demographics for White Sturgeon in the SSJ and evaluate possible influences of water management characteristics (i.e., discharge, temperature) on growth. Information from this thesis will provide insight on the population-level responses under different management scenarios. Overall, White Sturgeon in the SSJ experienced higher rates of mortality and growth than other populations. Additionally, growth has increased since the 1980s. Thermal and hydrological variables had little influence on growth of juvenile White Sturgeon, suggesting that annual growth may be affected by other abiotic and biotic factors. 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 continue to decrease. Low levels of exploitation (i.e., < 3%) will be required to prevent growth and recruitment overfishing of White Sturgeon in the SSJ.

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Table of Contents

Authorization to Submit Thesis	ii
Abstract.....	iii
Acknowledgements.....	iv
Table of Contents.....	v
List of Figures.....	vii
List of Tables	ix
Chapter 1: General Introduction	1
Thesis Organization	8
References.....	9
Chapter 2: Population Dynamics and Evaluation of Management Scenarios for White Sturgeon in the Sacramento-San Joaquin River Basin, California.....	16
Abstract.....	16
Introduction.....	17
Methods	21
Study Area	21
Field Sampling and Laboratory Processing	23
Data Analysis.....	24
Results	32
Discussion.....	34
Acknowledgements.....	42
References.....	42
Appendix: Additional Recommendations.....	69
Chapter 3: Effects of Temperature and Discharge on the Growth of Juvenile White Sturgeon in the Sacramento-San Joaquin River Basin, California.....	71
Abstract.....	71
Introduction.....	71
Methods	75
Study area	75
Field Sampling and Laboratory Processing	75
Environmental Data	76

Data Analysis.....	77
Results	79
Discussion.....	80
Acknowledgements.....	85
References.....	86
Chapter 4: General Conclusions	99

List of Figures

Chapter 2

- Figure 2.1** The San Francisco Bay Estuary and the Sacramento-San Joaquin rivers, California 58
- Figure 2.2** 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. 59
- Figure 2.3** 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. 60
- Figure 2.4** 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 standard error. The solid lines represents growth model fit..... 61
- Figure 2.5** 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..... 62
- Figure 2.6** 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..... 63
- Figure 2.7** Population growth rates (λ_G) 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 λ_G of one where a population is considered stable..... 64
- Figure 2.8** Population growth rates (λ_G) 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 λ_G of one where a population is considered stable..... 65
- Figure 2.9** Population growth rates (λ_G) 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 λ_G of one where a population is considered stable..... 66
- Figure 2.10** The effects of changing vital rates on the population growth rate (λ_G) for exploited ($\mu = 13.6\%$, harvest slot length: 102–152 cm fork length) White Sturgeon in the Sacramento-San Joaquin River basin, California. The solid horizontal line represents a λ_G of one where a population is considered stable..... 67

Figure 2.11 Summed elasticity values for exploited ($\mu = 13.6\%$, 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..... 68

Chapter 3

Figure 3.1 Growth increments estimates for ages 1–8 White Sturgeon sampled from various time periods in the Sacramento-San Joaquin River basin, California..... 97

Figure 3.2 Estimated growth coefficients by year for White Sturgeon sampled from various time periods in the Sacramento-San Joaquin River basin, California..... 97

Figure 3.3 Environmental data associated with the Sacramento-San Joaquin River basin and San Francisco Bay Estuary, California, including mean water temperature and discharge during the growing season (01 April–30 September) from 1982–2015..... 98

List of Tables

Chapter 2

Table 2.1 History of fishing regulations for sturgeon in the Sacramento-San Joaquin River Basin, California 56

Table 2.2 Mean vital rates and standard errors used to construct population matrices for the White Sturgeon population in the Sacramento-San Joaquin River basin, California 57

Chapter 3

Table 3.1 Comparison of estimated mean back-calculated lengths at age (cm), samples sizes (n), and standard deviations (SD) for White Sturgeon sampled from various time periods in the Sacramento-San Joaquin River basin, California 95

Table 3.2 von Bertalanffy growth parameters, where L_{∞} is the mean maximum length, K is the growth coefficient, and t_0 is the theoretical age when length is zero, using back-calculated lengths at age with 95% confidence intervals (CI) and mean fork length (FL; cm) and age (years) at time of capture with standard deviations for juvenile (i.e., < age 9) White Sturgeon sampled as various time periods in the Sacramento-San Joaquin River basin, California 95

Table 3.3 Multiple-regression models predicting growth of juvenile White Sturgeon in the Sacramento-San Joaquin River basin, California sampled from various time periods (i.e., 1989–2001; 2014–2016). Explanatory variables include mean annual discharge (Q ; m³/s); the number of the days when discharge was below the 25th percentile ($Q_{.25}$); the number of days when discharge exceeded the 75th percentile ($Q_{.75}$) and mean annual water temperature (Temperature; °C) during the growing season (01 April–30 September). The number of model parameters (K), Akaike’s information criterion corrected for small sample size (AIC_c), AIC_c weight (w_i), and coefficient of determination (R^2) are included 96

Chapter 1: General Introduction

Anthropogenic alterations to aquatic ecosystems has resulted in a widespread loss of biodiversity and the imperilment of many fish species (Ricciardi and Rasmussen 1999; Jelks et al. 2008; Strayer and Dudgeon 2010). In North America, over 700 taxa of fish are listed as vulnerable (230), threatened (190), endangered (280), or presumed extinct (61; Jelks et al. 2008). Evidence suggests that a combination of factors (e.g., water development, pollution, non-native species, overexploitation) have contributed to declines (Nilsson et al. 2005; Jelks et al. 2008; Strayer and Dudgeon 2010; Haxton and Cano 2016). In particular, widespread alterations to the physical, chemical, and biological properties of riverine and estuary systems have played a substantial role in changes to fish abundance and assemblages (Nichols et al. 1986; Moyle and Leidy 1992; Dynesius and Nilsson 1994; Jager et al. 2001; Jelks et al. 2008; Haxton and Cano 2016). Consequently, upper trophic-level fishes that exhibit long life spans, delayed maturation, slow growth, and episodic successful recruitment, such as sturgeon (Acipenseridae), are imperiled (Rieman and Beamesderfer 1990; Birstein et al. 1997; Pikitch et al. 2005; Haxton et al. 2016).

Sturgeon have a Holarctic distribution and inhabit rivers, lakes, estuaries, oceanic environments, and inland seas. Since first evolving approximately 85 million years ago, sturgeon have experienced few morphological changes (Bemis et al. 1997; Haxton and Cano 2016). Over the millennia, sturgeon adapted to large-scale global changes and persisted through mass extinction events (Bemis and Kynard 1997; Haxton and Cano 2016). However, their life history characteristics make them vulnerable to habitat degradation and overexploitation (Boreman 1997; Pikitch et al. 2005). Across much of their distribution, sturgeon have been extirpated or are declining because of the high demand for their valuable

caviar and flesh (Bemis and Findeis 1994; Pikitch et al. 2005). Commercial and recreational overharvest caused the decline of several species beginning in the mid-1800s across North America and Eurasia, and continue to suppress some populations (Birstein 1993; Boreman 1997; Khodorevskaya et al. 1997; Pikitch et al. 2005; Haxton and Cano 2016). Many sturgeon species require immediate conservation action to re-establish population sizes and prevent extirpation (Pikitch et al. 2005; Munro et al. 2007; Hildebrand et al. 2016; Mora et al. 2018). However, an incomplete understanding of sturgeon ecology and population demography has hindered the development of effective conservation and management strategies (Gross et al. 2002; Secor et al. 2002; Heppell 2007; Haxton et al. 2016). For example, considerable effort has been directed towards improving the status of White Sturgeon *Acipenser transmontanus* throughout its distribution, but information regarding behavior, movement, and life history are limited (Chapman et al. 1996; Jager et al. 2001; Schreier et al. 2013; Hildebrand et al. 2016; Jackson et al. 2016).

White Sturgeon are distributed throughout large river basins and estuary systems along the Pacific Coast of North America from British Columbia to California (Hildebrand et al. 2016). Individual fish have been documented in coastal waters near Baja California, Mexico, and as far north as the Aleutian Islands in Alaska (Ruiz-Campos et al. 2011). Several populations are listed as Species at Risk by Canada (i.e., Fraser, Nechako rivers, British Columbia) and endangered under the Endangered Species Act in the United States (i.e., Kootenai River Distinct Population Segment), whereas other populations do not receive federal protection (e.g., Sacramento-San Joaquin River Basin (SSJ), California; lower Columbia River, Washington and Oregon). White Sturgeon are particularly slow to recover from overfishing because of their large-size and delayed maturation (Boreman 1997).

According to Rieman and Beamesderfer (1990), wild, self-sustaining populations cannot withstand exploitation levels greater than 10%. As such, commercial harvest is generally prohibited for White Sturgeon. Recreational angling for White Sturgeon is permitted in the Fraser and Snake rivers as catch-and-release only (Irvine et al. 2007; IDFG 2008). A limited sport harvest is allowed in several reaches of the lower Columbia River and the SSJ. Yet, concerns regarding the population status of White Sturgeon in the SSJ has resulted in progressively restrictive regulations over the last decade (Gingras and DuBois 2013).

In California, White Sturgeon primarily occur in the SSJ and the adjacent San Francisco Bay Estuary (SFE; Schreier et al. 2013). A White Sturgeon population may also occur in the Klamath River in northern California, but encounters are rare and little information exists about its status (Kohlhorst and Cech 2001; Hildebrand et al. 2016). White Sturgeon experienced considerable population decline following Euro-American settlement of California in the mid-1800s (Skinner 1962; Moyle et al. 2011). Urban, agriculture, and mining developments in the 1850s altered or destroyed most of the aquatic and riparian habitat in the SSJ and SFE (Nichols et al. 1986). In the 1870s, commercial fisheries began targeting Pacific salmon *Oncorhynchus* spp. (Skinner 1962). White Sturgeon captured in salmon nets were killed indiscriminately due to the damage they inflicted on the nets. White Sturgeon became commercially important as markets developed for sturgeon eggs and flesh in the 1880s (Skinner 1962; Kohlhorst and Cech 2001). In 1885, the commercial catch for White Sturgeon in the SSJ peaked at 771.1 metric tons (Skinner 1962). By 1901, the catch had declined to 90.1 metric tons and the White Sturgeon commercial fishery was closed (Skinner 1962; Kohlhorst and Cech 2001). Commercial harvest was reopened periodically from 1910 to 1917, but low catch rates suggested that the population had not recovered. In 1917, all

commercial and recreational fishing was prohibited for sturgeon in the SSJ (Skinner 1962). By 1954, the California Department of Fish and Wildlife (CDFW) regarded the White Sturgeon population as recovered and established a recreational fishery (Kohlhorst et al. 1991). From the 1960s through the late-1980s, CDFW estimated low levels of exploitation and considered the population stable (Miller 1972; Kohlhorst 1980; Kohlhorst et al. 1991; Schaffter and Kohlhorst 1999). However, data from recent CDFW surveys of White Sturgeon in the SSJ indicate that the population is declining. For instance, catch per unit effort of adult White Sturgeon in a long-term monitoring study has been at historic lows for almost a decade (DuBois and Danos 2017). Additionally, nearly twenty years of near recruitment failure has been documented with only two moderately strong year-classes detected since 1999 (Gingras and DuBois 2013).

Declining population trends of White Sturgeon in the SSJ are attributed to water development projects, poor habitat quality, invasive species, and harvest (Kohlhorst 1980; Zeug et al. 2014; Linares-Casenave et al. 2015; Jackson et al. 2016). Construction of numerous hydroelectric dams and water diversion plants has fragmented habitat and altered sediment, flow, and thermal regimes, all of which affect habitat for White Sturgeon spawning and early life stage rearing (Jager et al. 2001; IDFG 2008; Fish 2010; Jackson et al. 2016). Successful recruitment is positively correlated with the volume of freshwater discharge through the SFE (Kohlhorst et al. 1991; Fish 2010). Years of high flow are associated with moderate to strong year classes because White Sturgeon benefit from high productivity and habitat availability (Jager et al. 2001; Fish 2010; Jackson et al. 2016). In addition to water development projects, mining, agriculture, irrigation, industrial discharges, urban runoff, and grazing have also been associated with degraded water quality in the SSJ (Skinner 1962;

Nichols et al. 1986; Linares-Casenave et al. 2015; Jackson et al. 2016). White Sturgeon are exposed to a mixture of pollutants and contaminants throughout their long lifespans by direct contact or bioaccumulation through the food chain. As opportunistic benthic feeders, White Sturgeon frequently encounter toxicants including Hg, Se, hydrophobic pollutants, chlorinated pesticides, and chlorinated dioxins. Laboratory studies have demonstrated that several pollutants are toxic to White Sturgeon and may have detrimental effects on their longevity and reproductive capabilities (Feist et al. 2005; Linares-Casenave et al. 2015; Gunderson et al. 2017). Furthermore, non-native species in the SSJ influence the habitat and food resources, as well as increase the risk of predation for White Sturgeon. For instance, the invasive Overbite Clam *Corbula amurensis* is now a major element of the adult White Sturgeon diet (Kogut 2008; Zeug et al. 2014). Overbite Clams contain less nutritional value and energy content than the White Sturgeon's natural prey base (e.g., fish eggs, mussels, *Crangon* spp.) and have been reported passing through fish undigested (Kogut 2008; Zeug et al. 2014). Furthermore, the Overbite Clam has destabilized and changed the trophic web of the SFE. Species such as mysid shrimp, an important prey item for juvenile White Sturgeon, have experienced population declines (Radtke 1966; Feyrer et al. 2003; Bennett et al. 2010).

Another threat to White Sturgeon persistence in the SSJ is overharvest. Although reported annual exploitation of the harvestable demographic has generally been < 10% since the 1950s, historic exploitation rates are now regarded as biased substantially low due to a lack of angler willingness to report catch of tagged fish and the algorithm used to estimate exploitation (DuBois and Gingras 2011; Gingras and DuBois 2014). Furthermore, additional legal and illegal harvest of White Sturgeon has not been fully incorporated when estimating exploitation. For example, data on anglers harvesting White Sturgeon from commercial

passenger fishing vessels (CPFV) are confounded (DuBois and Gingras 2014). Captains of CPFVs are required to keep a log of overall effort and catch, but sturgeon catch prior to 2012 was not identified to species (i.e., Green Sturgeon *A. medirostris* were included).

Furthermore, illegal harvest of White Sturgeon is known to occur throughout the SSJ. The number of illegally harvested fish is unknown but regarded as substantial (M. L. Gingras, CDFW, personal communication). Current sport fishing regulations include a harvest slot limit (102–152 cm fork length) to minimize growth and recruitment overfishing, but are likely not enough protection to prevent population declines.

Habitat alterations and overexploitation negatively affect White Sturgeon and other native fish populations in the SSJ and SFE (Nichols et al. 1986; Moyle and Leidy 1992). In 1992, Congress passed the Central Valley Project Improvement Act (CVPIA) in response to the declining trends in the region's fish populations. The CVPIA mandates that the U.S. Bureau of Reclamation treat fish and wildlife protection, restoration, and mitigation activities with equal priority to irrigation and power generation (USFWS 1995). In addition, the CVPIA also guarantees funds and efforts towards doubling the natural production of anadromous fishes in California's Central Valley waters. For White Sturgeon, the CVPIA has an objective of a sustained increase in the number of age-15 White Sturgeon to 11,000 individuals. This objective, which has yet to be achieved, is referred to as the "doubling goal" since the target number of White Sturgeon in the SSJ is double the estimated average number of fish during the baseline period (i.e., 1967–1991). Monitoring progress towards the doubling goal is difficult. For instance, given that White Sturgeon populations do not exhibit a stable age distribution as recruitment is rarely detectable, selecting a single cohort or age-class to monitor the doubling goal will likely result in failure to demonstrate progress towards the

objective or accurately depict population trajectory (Shirley 1987; Gingras et al. 2013). Additionally, harvest of White Sturgeon reduces the number of age-15 fish in the SSJ. Therefore, using an abundance estimate of age-15 White Sturgeon presents an inaccurate portrayal of progress towards the CVPIA doubling goal.

Continued harvest, degraded environmental conditions, and a decreasing trend in recruitment suggest that the White Sturgeon population in the SSJ will continue to decline. Abundance estimates for adult White Sturgeon in the SSJ have varied from 11,200 (Kohlhorst et al. 1991) to 142,000 (Schaffter and Kohlhorst 1999). A more recent estimate suggested that there are approximately 48,000 White Sturgeon in the SSJ (DuBois and Gingras 2011). As such, protecting White Sturgeon from further reductions in abundance is a focus of CDFW and the U.S. Fish and Wildlife Service. Although the population has been studied since for almost 80 years, information about the population dynamics of White Sturgeon in the SSJ remains incomplete. A paucity of data regarding key population demographics is associated with the depleted and endangered status of many sturgeon populations (Gross et al. 2002; Secor et al. 2002; Pikitch et al. 2005; Munro et al. 2007). Additionally, because information is incomplete regarding the population demographics of White Sturgeon in the SSJ, making inferences on the population level response to management actions (i.e., harvest) is tenuous. Given the knowledge gaps associated with the management of White Sturgeon in the SSJ, this thesis had two main objectives. The first objective was to establish baseline demographic data and use age-structured population models to estimate how White Sturgeon in the SSJ might respond to different management scenarios. The second objective was to evaluate historic White Sturgeon pectoral fin rays for changes in growth over time in the SSJ and possible influences of water management characteristics (i.e., discharge and temperature) on growth.

Thesis Organization

This thesis is composed of four chapters. Chapter two evaluates how the White Sturgeon population in the SSJ is likely to respond to different management actions. Chapter three assesses growth of White Sturgeon in the SSJ over several decades. The final chapter is a general conclusion that synthesizes the results of each chapter as they relate to the management of White Sturgeon in the SSJ and the efficacy of the current recovery goals.

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Chapter 2: Population Dynamics and Evaluation of Management Scenarios for White Sturgeon in the Sacramento-San Joaquin River Basin, California

Shannon E. Blackburn, Marty L. Gingras, Jason DuBois, Zachary J. Jackson, and Michael C. Quist

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 for 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 experienced typically high and unsustainable 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 ($\lambda = 0.97$). 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., $\lambda \geq 1.00$) 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; Jager 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; 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 (DeVore et al. 1995; Jager et

al. 2001; Pikitch et al. 2005; 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 a species of high concern by California Department of Fish and Wildlife (CDFW; Moyle et al. 2015; 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 (Hildebrand et al. 2016). However, results from recent CDFW monitoring studies have provided evidence that the population is declining. As such, protecting White Sturgeon in the SSJ to prevent further declines has become a recent focus of the CDFW and the U.S. Fish and Wildlife Service (USFWS). Concern over the population trajectory for 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, 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 saxatilis* 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 an exploitation of 11.5% by 1988 (Kohlhorst et al. 1991). As a result, several changes to White Sturgeon harvest regulations were implemented (Table 2.1). 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 and has been at historic lows (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 throughout the SSJ and the 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 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 continuous recruitment failure over the last two decades, reevaluation of harvest regulations for White Sturgeon in California is warranted. An excellent approach for evaluating the efficacy of current and future harvest regulations is the use of age-structured population models that 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 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. platyrhynchus* 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; Kohlhorst et al. 1980; 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 California in terms of length and discharge (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 2.1). 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 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 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 2014–2016. 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 to the middle and both ends of the net to help the net drift and to prevent the net from tangling or 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 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 experience 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 analysis

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:

$$L_t = L_\infty \times [1 - e^{-K(t-t_o)}],$$

where L_t (cm) is fork length at time t , L_∞ is the mean maximum length, K is the growth coefficient, and t_o 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 $\geq 99.9\%$ 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. oxyrinchus 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, US\$50, US\$100). Assuming a 100% return rate of the high-reward tags (i.e., US\$150), annual reporting rates (A) were estimated using the equation:

$$A = \frac{R/N}{R'/N'}$$

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

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

where N_r is the corrected number of tags returned for harvested fish, N_0 is the number of available fish tagged, γ is tag retention (i.e., 0.90; Rien et al. 1990), and θ is survival of tagged fish (i.e., $1 - \text{tagging mortality} = 0.99$; Smith et al. 1990). Additionally, because the harvest fishery is structured around specific lengths, we incorporated growth into and out of the harvest slot when calculating 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 ($F = \mu Z/A$) to convert instantaneous fishing mortality (F) to exploitation.

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 ($^{\circ}\text{C}$) from Suisun Bay, California, were used as inputs for equations from Pauly (1980), Hoening (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 (pm_i) were predicted with logistic regression and used as fertility elements in the matrix population models. Fecundity at age (f_i) 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 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 (Hildebrand et al. 2016). 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:

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

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

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

where P_i is the probability of spawning for age-class i , f_i is the fecundity of age-class i , a is the proportion of female offspring, and S_i is the 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 using beta or stretch-beta distributions based on the mean and standard error of their respective vital rates (Morris and Doak 2002; Table 2.2). 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 and 2011 cohort 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 (n_t): $n_{t+1} = An_t$ (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

sampling gear 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 to generate a geometric mean that represented 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). Approximate 95% confidence intervals were generated based on the 5,000 simulations.

The influence of vital rates on λ_G were assessed using sensitivity analyses. Sensitivity analyses are commonly used by managers to quantify the influence of vital rates on population growth and 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 a 20-year period (Morris and Doak 2002). In addition, we conducted an elasticity analysis which represents the proportional contribution of a vital rate to λ_G . Specifically, elasticity analyses predict how λ_G might vary with changes in the survival or fecundity of a specific age-class (Gross et al. 2002). Results from elasticity analyses are used to assist managers in determining which life

stages might make the greatest contributions to λ_G and where additional research may be warranted (Gross et al. 2002; Morris and Doak 2002; Heppell 2007).

Results

During the summer and fall 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 \pm SD; 97.5 cm \pm 27.0) and the majority of fish were between 80 and 90 cm FL (Figure 2.2). Fish varied in age from 3 to 29 years (8.1 years \pm 3.2; Figures 2.3 and 2.4) 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 2.5). 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 ($\mu = 13.6\%$; slot length limit: 102 cm–152 cm FL), the population growth rate was predicted to decline annually by 4.6% ($\lambda_G = 0.95$; 95% CI: 0.89–1.04) over a time period of 20 years assuming a spawning periodicity of 10% (Figure 2.7). With a spawning periodicity of 15%, the White Sturgeon population was predicted to decline at a rate of 2.8% under current harvest conditions ($\lambda_G = 0.97$; 95% CI: 0.91–1.08;

Figure 2.8). 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 and 2011 cohorts would decrease to approximately 3,905 and 2,756 fish respectively over the 20-year projection period. Similar trends for λ were predicted for simulations assuming a 15% spawning periodicity under the current harvest slot length limit over 10-year ($\lambda_G = 0.95$; 95% CI: 0.91–0.99) and 50-year ($\lambda_G = 0.97$; 95% CI: 0.87–1.19) time spans. Additionally, under a spawning periodicity of 25%, the population growth rate of White Sturgeon in the SSJ was predicted to decline at a rate of 1.5 % ($\lambda_G = 0.98$; 95% CI: 0.95–1.18) over 20 years under current harvest conditions (Figure 2.9).

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: 0.93–1.11), 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 $\geq 15\%$. 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 2.7–2.9).

Sensitivity analysis indicated that population growth rate was more sensitive to changes in the mortality rates of age-3 and older White Sturgeon than variations in spawning periodicities (Figure 2.10). For example, increasing mortality by 5.0% resulted in a 3.2%

decrease in λ_G over a 20-year period. Under current conditions, the population growth rate was most influenced by survival (Figure 2.11). Reproductive parameters (i.e., fertility) had the lowest summed elasticity and made the smallest relative contribution to λ . Summed elasticity was greatest (0.57) for sexually mature White Sturgeon (\geq 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 57% change in λ_G , 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 an evaluation of demographics for White Sturgeon in the SSJ with an age-structured population model to better understand population-level responses to perturbations and management actions. The White Sturgeon population in the SSJ exhibited fast growth, had high rates of mortality, experienced variable levels of exploitation, and appears 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 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) 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 represented of the entire population. Nonetheless, these are the best data available for the White Sturgeon population in the SSJ.

Prior studies have documented 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 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). 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. Inaccuracy and imprecision have been identified when using White Sturgeon pectoral fin rays, particularly for fish older than age 20 (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 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 temperature, access to quality habitat, density-dependent interactions (i.e., 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 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 to 24% (upper Columbia River; Beamesderfer et al. 1995) to 37% (lower Columbia River; DeVore et al. 1995). In Lake Winnebago, Wisconsin, Bruch (1999) reported annual mortality rates of 17% for an exploited population of Lake Sturgeon. 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 was 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 small 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 (J. DuBois and M. Harris, 2017 memorandum to M. L. Gingras, CDFW, on pilot sturgeon angler phone survey). Additionally, our estimate probably 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. 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 is expected to 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 (S. E. Blackburn, unpublished). 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 egg-to-age-1 mortality (i.e., S_0) estimates of 99.94–100.00% likely generated typical recruitment rates for White Sturgeon in the SSJ. 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; Pine et al. 2001; Caroffino et al. 2010). 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 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 (IDFG 2008). Reductions in annual mortality in other White Sturgeon populations following closure of fisheries suggest that this is a significant 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 just 350 adults maintains an exploitation of < 2% for Atlantic Sturgeon *A. oxyrinchus oxyrinchus* 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. 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 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, 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 populations 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 population.

Moving forward, managers will be able to model additional scenarios and set appropriate benchmarks for success.

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Table 2.1. History of fishing regulations for sturgeon 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 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	
2006	1 fish	Unlimited	105	164	Harvest of Green Sturgeon prohibited
2007	1 fish	3 fish	105	151	Fishing Report Card required
2013	1 fish	3 fish	102	152	1 single barbless hook; White Sturgeon \geq 173 cm FL may not be removed from the water.

Table 2.2. 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(<i>t</i>)	Value	Error	Source
Fertility elements					
f_t	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	
p_m	Probability of maturity at age t	19	335,355	9,723	Chapman (1989)
		0–9	0.000	N/A	
		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	
p_f	Proportion of offspring that are females	18	0.942	0.142	Chapman et al. (1996)
		19	0.966	0.098	
		20+	1.000	0.200	
		10–19	0.500	N/A	
Transition elements					
S_0	Egg to age 1 survival	0	0.002	0.003	Caroffino et al. (2010)
S_1	Age 1 survival	1	0.250	0.008	Pine et al. (2001)
S_3	Age 2 survival	2	0.840	0.168	Ireland et al. (2002)
S_3 – S_{20+}	Asymptotic survival	3–19	0.946	0.03	This study

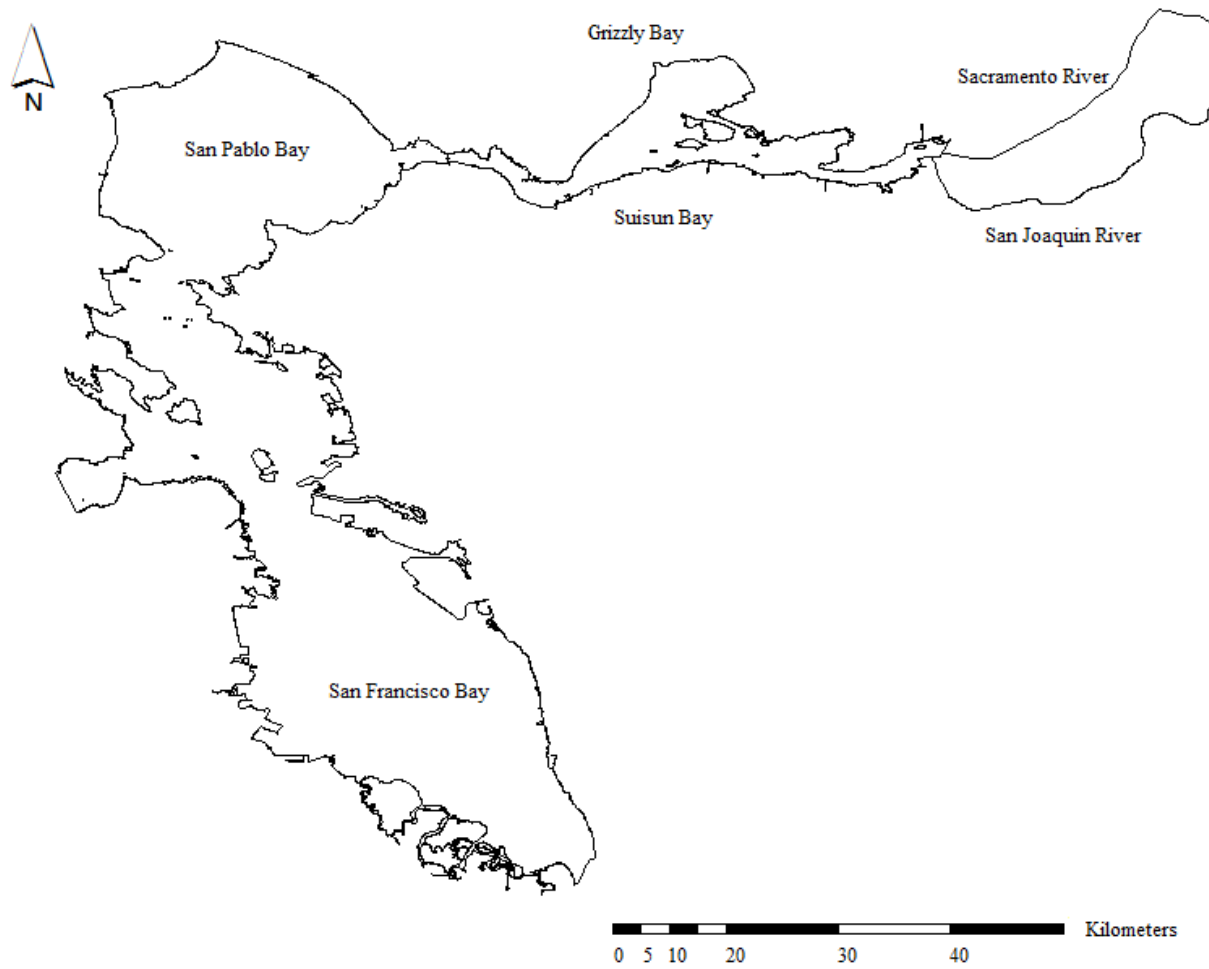


Fig 2.1. The San Francisco Bay Estuary and the Sacramento-San Joaquin rivers, California.

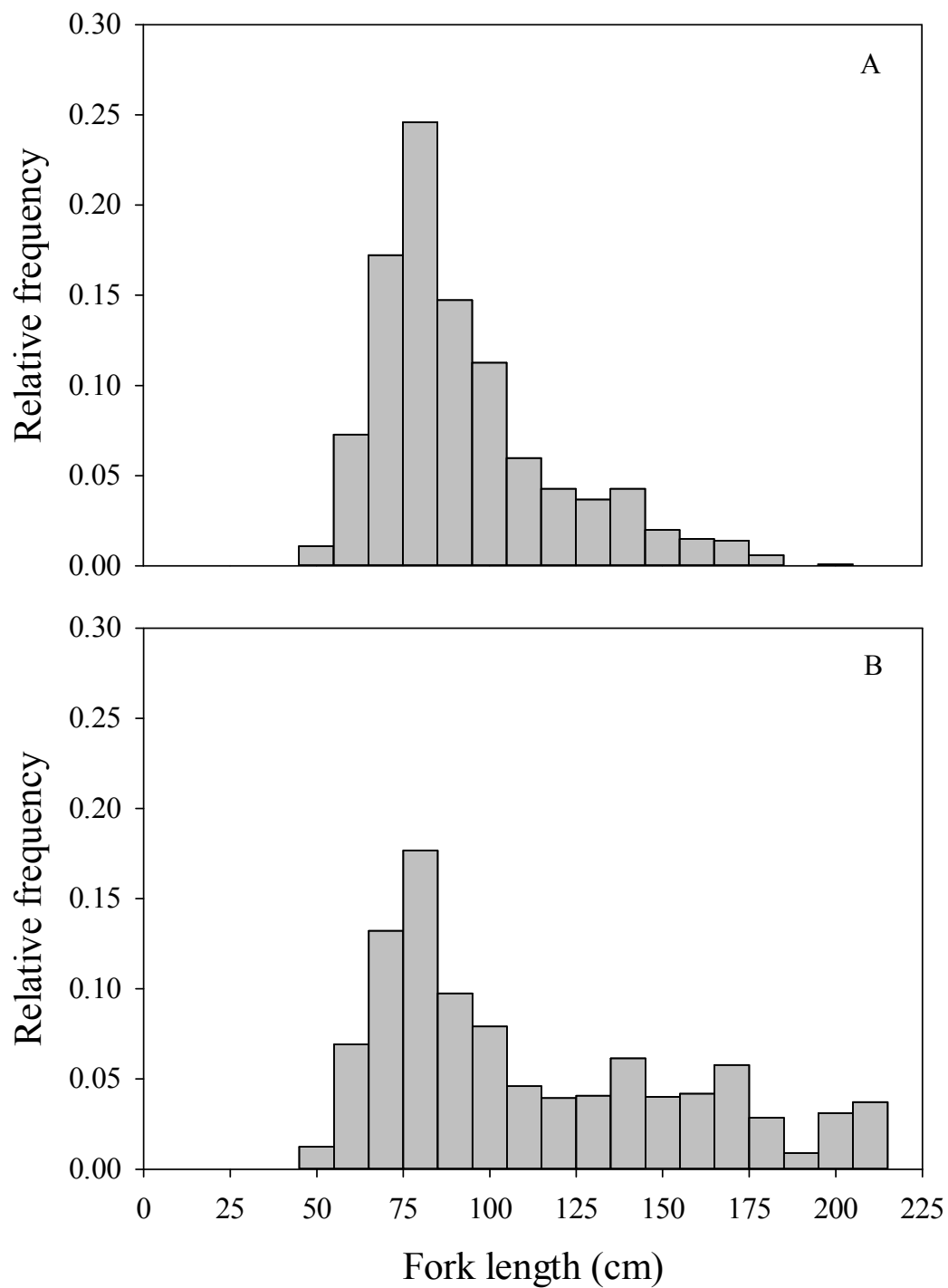


Fig 2.2. Length-frequency distribution of White Sturgeon sampled in Suisun Bay, California during the summer and autumn months of 2014–2016. Data are for fish collected using trammel nets. Data in Panel A are for uncorrected size selectivity and Panel B are corrected for size selectivity.

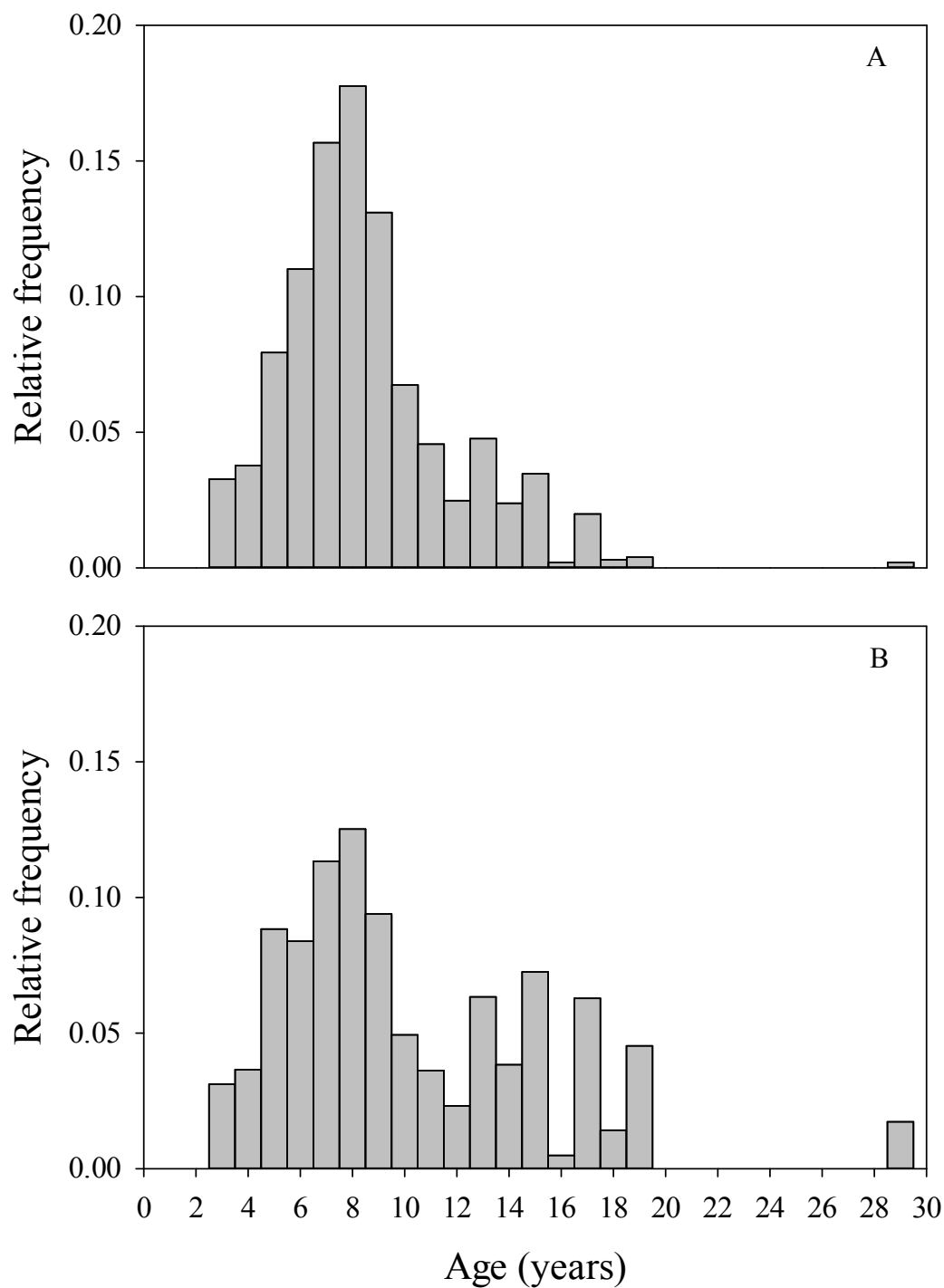


Fig 2.3. Age-frequency distribution of White Sturgeon sampled in Suisun Bay, California during the summer and autumn months of 2014–2016. Data are for fish collected using trammel nets. Data in Panel A are for uncorrected size selectivity and Panel B are corrected for size selectivity.

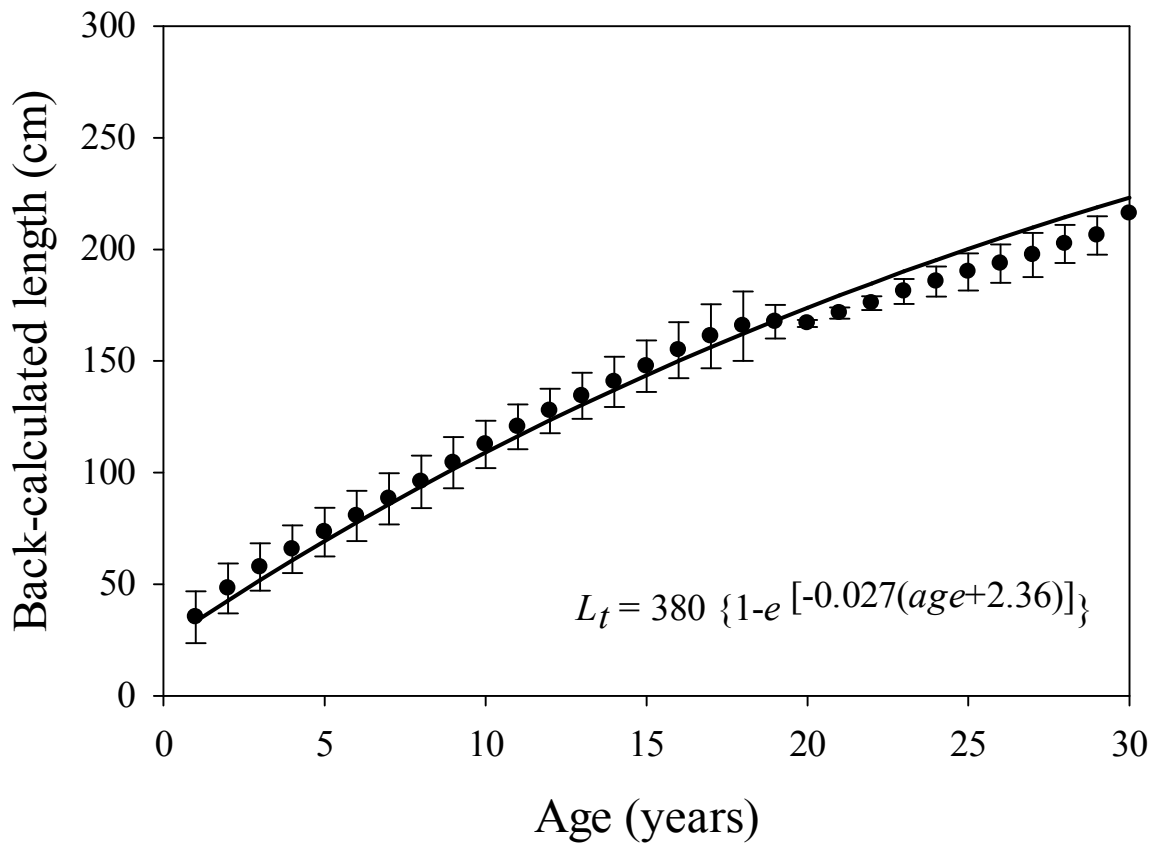


Fig 2.4. Von Bertalanffy growth model for White Sturgeon sampled from August through October 2014–2016 in the Sacramento-San Joaquin River basin, California. The solid circles represent the mean back-calculated length at a given age and the solid lines represents growth model fit.

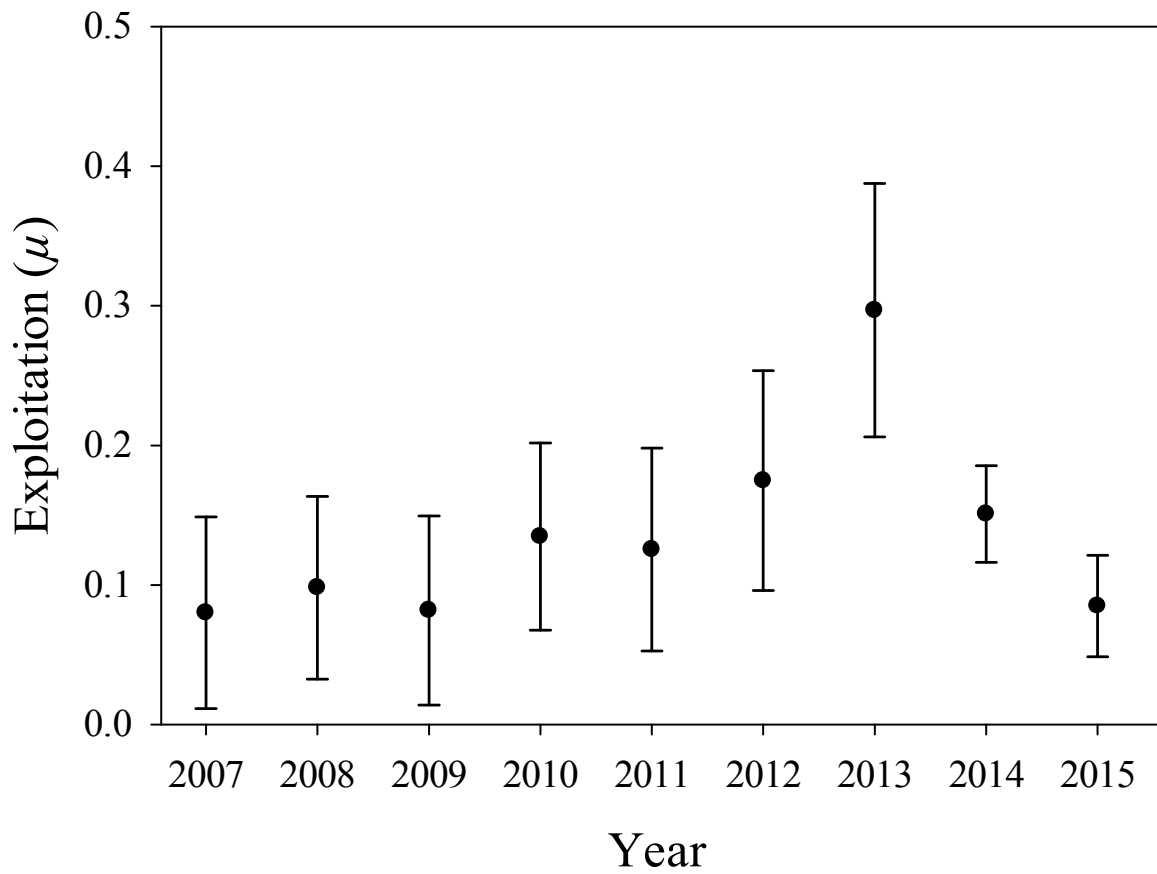


Fig 2.5. Estimates of exploitation (μ) based on adjusted tag return data for White Sturgeon in the Sacramento-San Joaquin River basin (SSJ), California from 2007–2015. Tag return data was adjusted for angler nonreporting, tagging loss, tagging mortality, and growth into and out of the slot length limit.

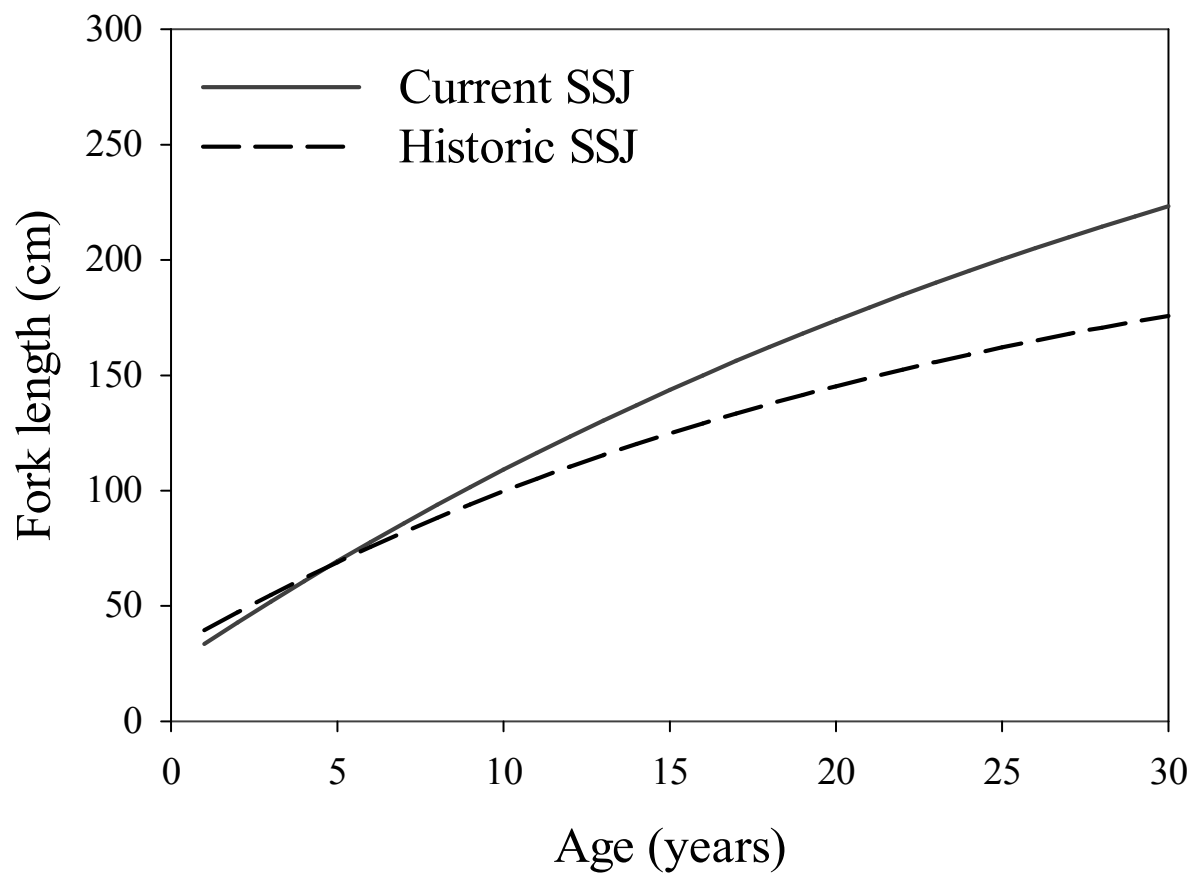


Fig 2.6. Comparison of growth between ages, based on mean back-calculated length at age for White Sturgeon in the Sacramento-San Joaquin River basin (SSJ). Current estimates are from fish sampled using trammel nets from 2014–2016. Historic estimates were sampled with trammel nets and creel surveys from 1973–1976.

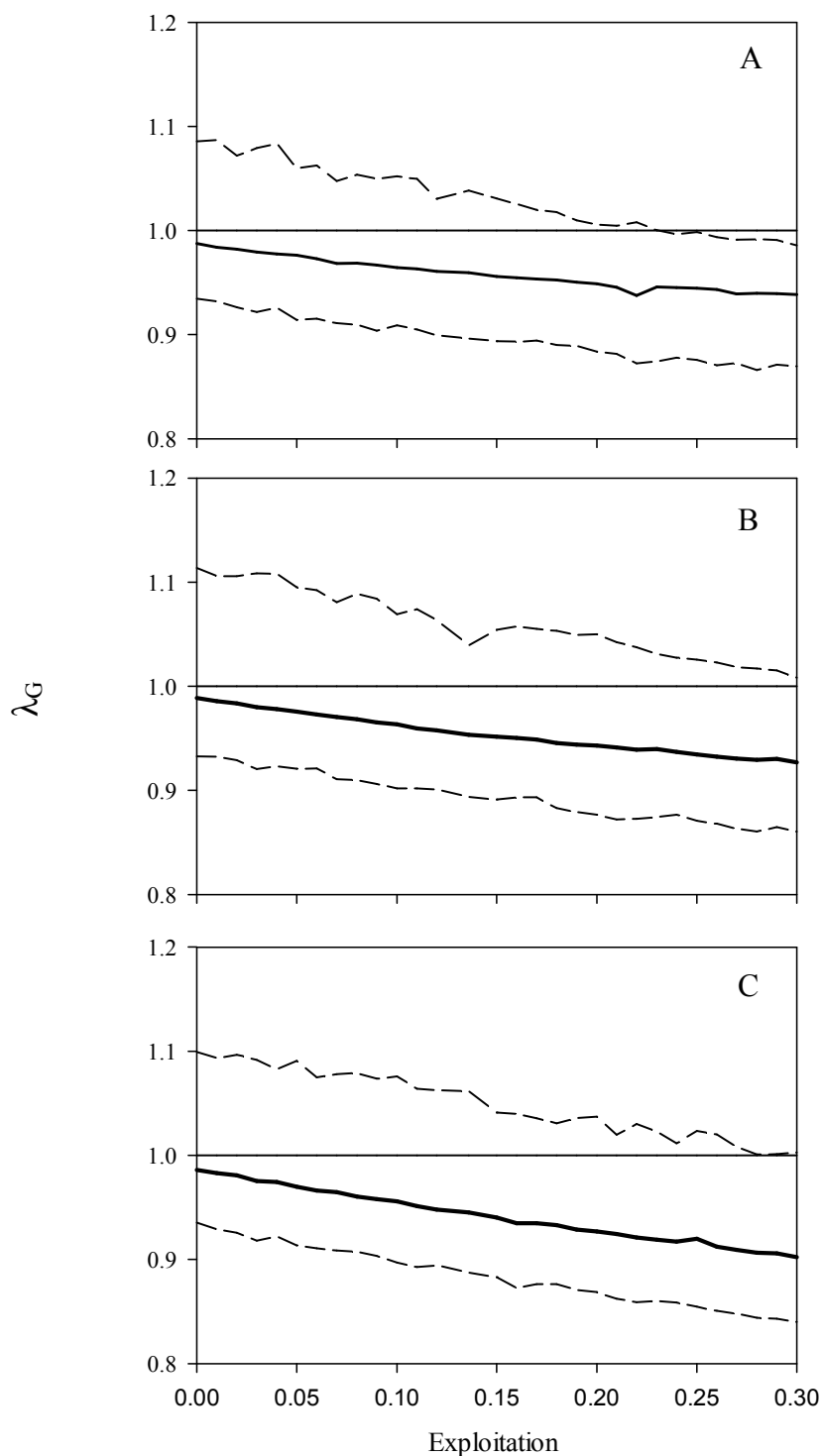


Fig 2.7. Population growth rates (λ_G) over a 20-year time frame for White Sturgeon in Suisun Bay, California assuming 10% of mature females are spawning annually at various levels of exploitation. Panel A represents the smallest slot length limit (77–127 cm FL), panel B the current slot length limit (102 – 152 cm FL), and panel C the largest slot length limit (127–177 cm FL). The solid horizontal line represents a λ_G of one where a population is considered stable.

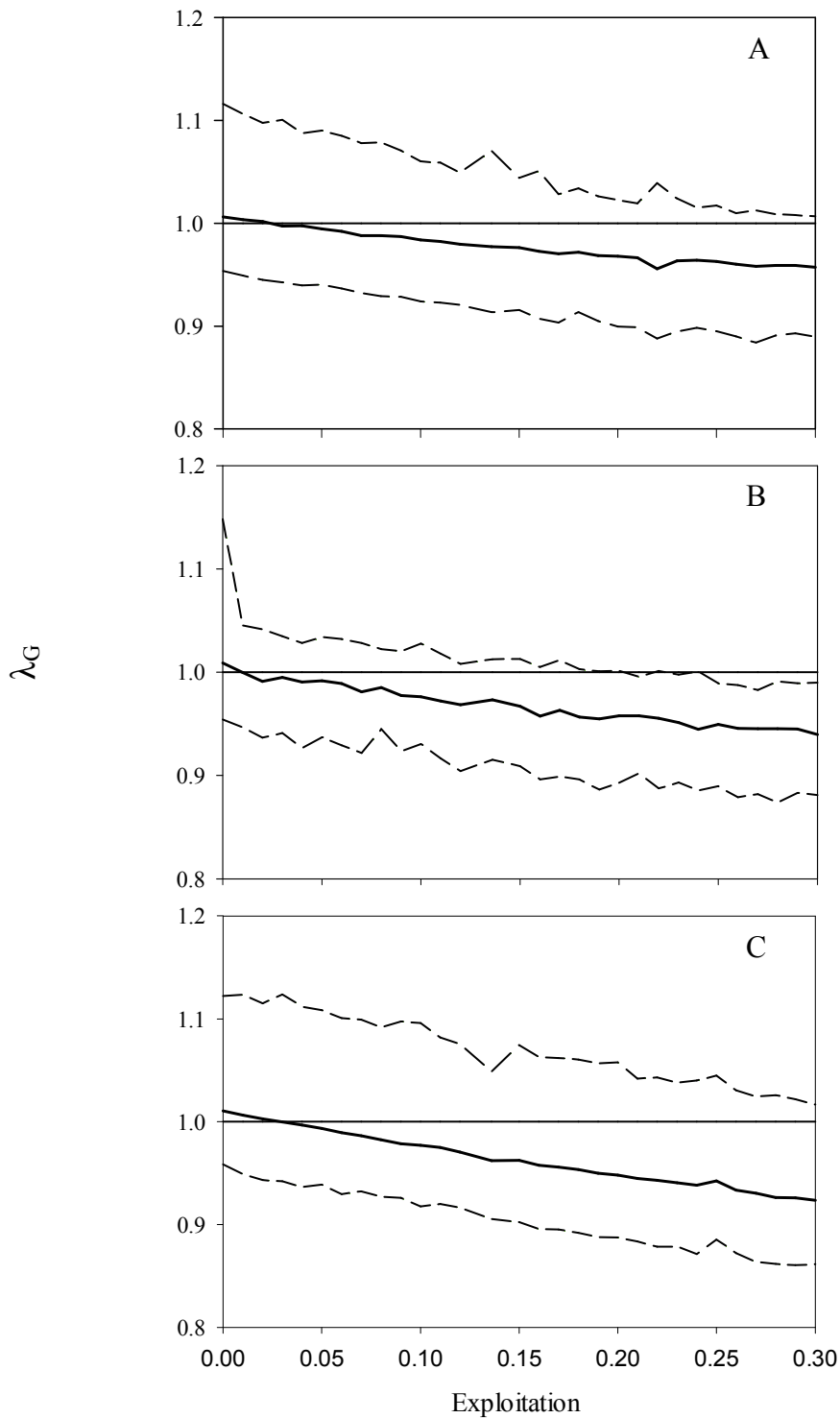


Fig 2.8. Population growth rates (λ_G) over a 20-year time frame for White Sturgeon in Suisun Bay, California assuming 15% of mature females are spawning annually at various levels of exploitation. Panel A represents the smallest slot length limit (77–127 cm FL), panel B the current slot length limit (102 – 152 cm FL), and panel C the largest slot length limit (127–177 cm FL). The solid horizontal line represents a λ_G of one where a population is considered stable.

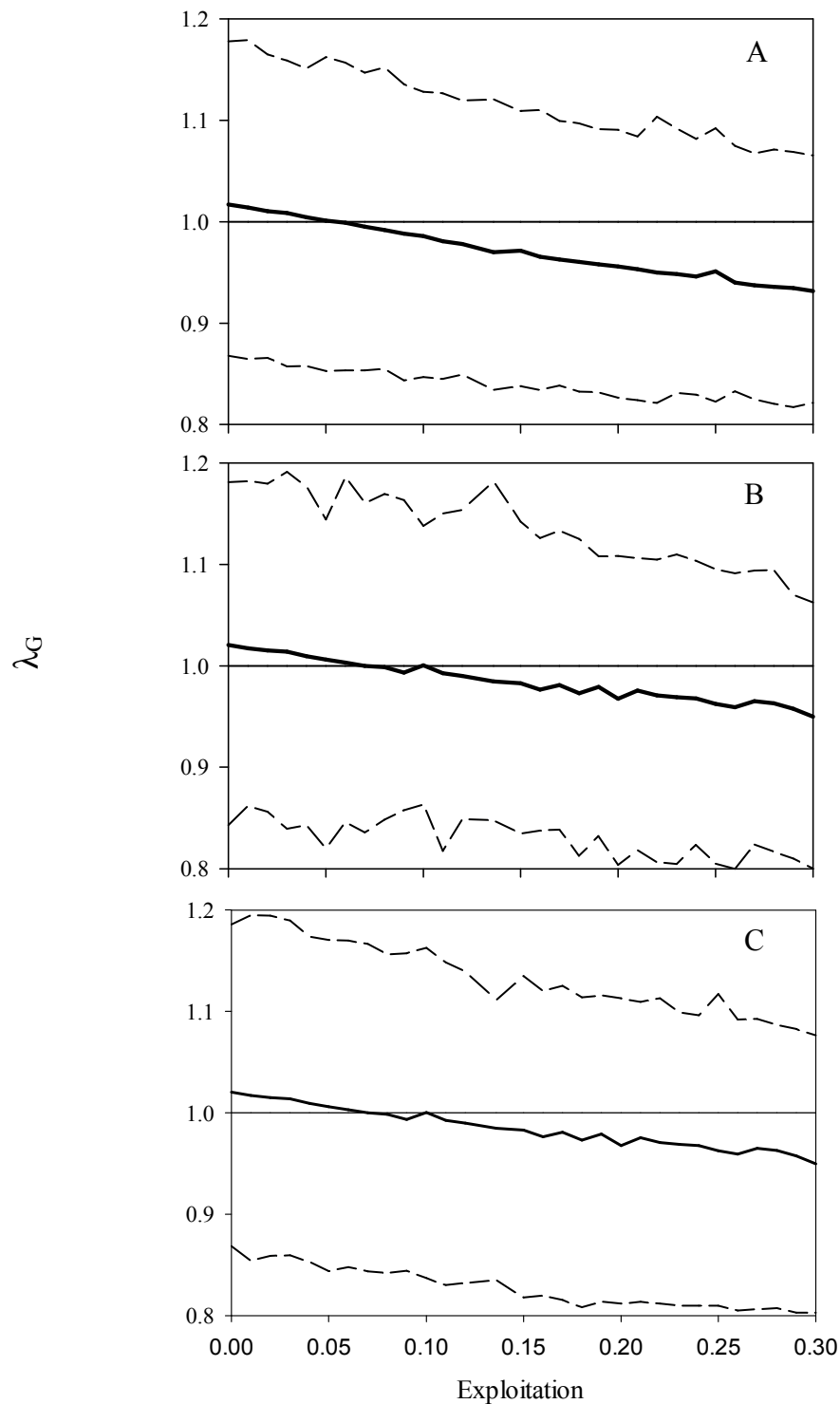


Fig 2.9. Population growth rates (λ_G) over a 20-year time frame for White Sturgeon in Suisun Bay, California assuming 25% of mature females are spawning annually at various levels of exploitation. Panel A represents the smallest slot length limit (77–127 cm FL), panel B the current slot length limit (102 – 152 cm FL), and panel C the largest slot length limit (127–177 cm FL). The solid horizontal line represents a λ_G of one where a population is considered stable.

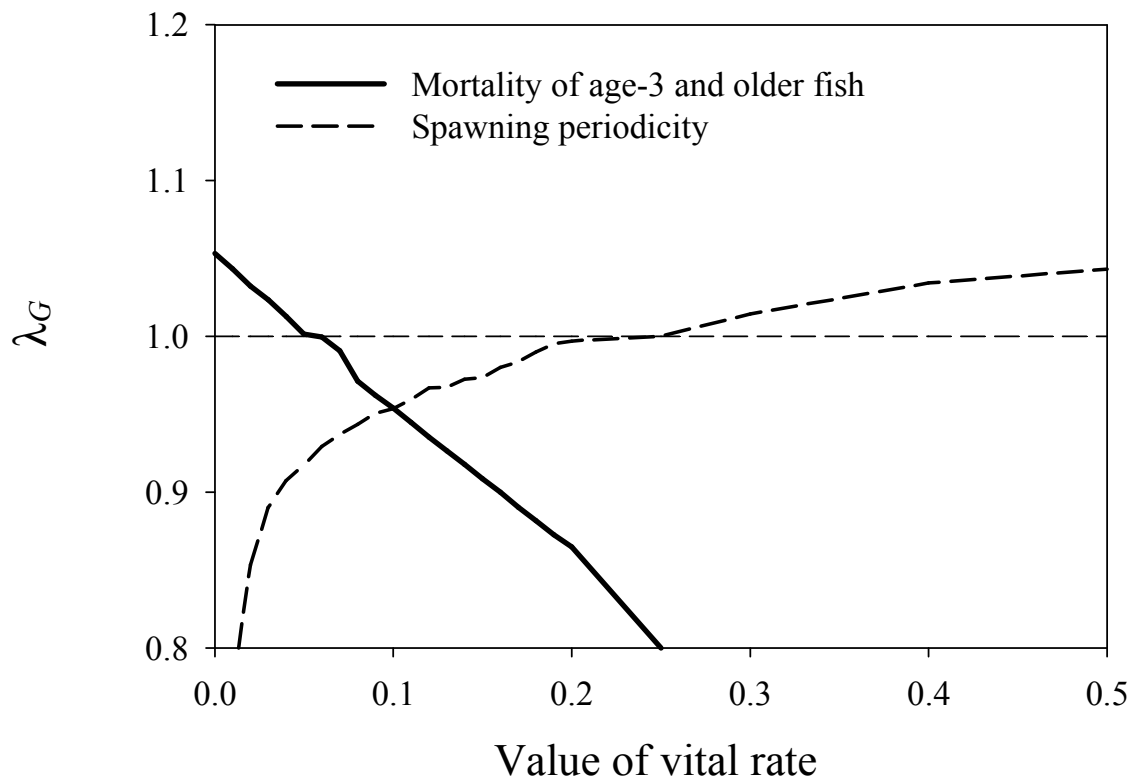


Fig 2.10. The effects of changing vital rates on the population growth rate (λ_G) for exploited ($\mu = 13.6\%$, harvest slot length: 102–152 cm fork length) White Sturgeon in the Sacramento-San Joaquin River basin, California. The solid horizontal line represents a λ_G of one where a population is considered stable.

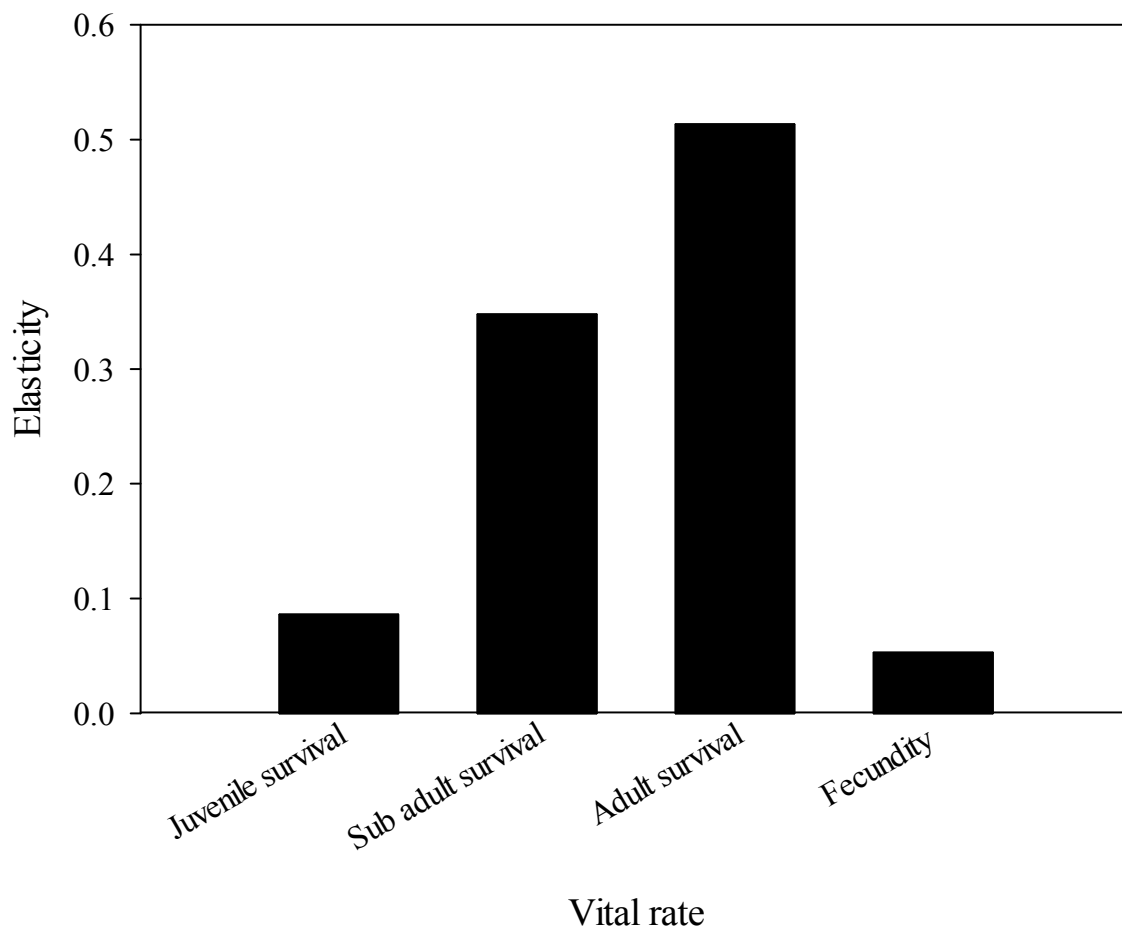


Fig 2.11. Summed elasticity values for exploited ($\mu = 13.6\%$, harvest slot length: 102–152 cm fork length) White Sturgeon vital rates in the Sacramento-San Joaquin River basin, California. Summed juvenile survival is from age 0 through age 2, sub-adult survival is age 3 through age 9, and adult survival consists of age 10 and older White Sturgeon.

APPENDIX

ADDITIONAL RECOMMENDATIONS: MONITORING AND MANAGEMENT

Monitoring

Sub-adult and adult population monitoring

- Sample naturally produced White Sturgeon eggs and larvae to obtain better estimates of egg to age-1 survival rates and recruitment patterns
 - Consider the use of egg mats, trawls, and drift nets in the Sacramento and San Joaquin rivers
- Estimate abundance annually
 - Consider using a robust estimator (e.g., robust Cormack-Jolly-Seber) to estimate abundance and survival
- Establish methods to assess juvenile White Sturgeon abundance in the SSJ
- Expand sampling methods
 - Continue fall trammel net sampling
 - Consider larger mesh sizes or different mesh construction to retain larger individuals
 - Consider repeating studies using baited trot (set) lines (Elliott and Beamesderfer 1990)
- Expand sampling locations
 - Obtain maps of other suspected aggregating areas (e.g., spawning grounds, wintering areas) and associated water quality or benthic maps
 - Possibly divide SSJ/SFE into different sampling regions based on habitat use and movement data
 - Stratified random sampling (e.g., known aggregation areas versus unknown areas)
- Obtain representative sample of sub-adult and adult White Sturgeon with sufficient consistency to describe annual trends that improve understanding of life history characteristics (e.g., growth, survival, age structure) and population characteristics (e.g., relative abundance)
 - Collect ~400 age structures (five pectoral fin rays per 1-cm length bin) every 5 years from the adult survey to evaluate changes in age structure and growth
 - Collect fin rays from fishing derbies for age and growth analysis
 - Collect weight and girth data to evaluate changes in body condition
 - Use passive integrated transponder (PIT) tags
 - Collect tissue samples from caudal fin
- Obtain additional information on reproductive ecology
 - Fecundity, age at maturity, and spawning frequency
- Estimate exploitation annually
 - Account for tagging loss, tagging mortality, angler non-reporting, and growth into and out of harvest slot length

- Conduct tag retention study (repeat study conducted in 1994)

Reward tag program and harvest report cards

- Estimate exploitation annually
 - Direct estimate
 - Compare to survival estimated using mark-recapture methodologies
- Improve response rate of reward tag and harvest report cards
 - Consider implementing penalties for failing to return harvest report card
 - Social media presence to improve visibility of harvest monitoring program

Harvest management

- Establish White Sturgeon management plan that allows rebuilding of the White Sturgeon population while providing harvest opportunities
- Establish guidelines for average harvest limits (e.g., three-year average) that are based on the most current abundance information to ensure that cumulative fishery impacts do not exceed sustainable levels
- Allow emergency actions to be enforced if new information becomes available indicating significant changes in population status
- Consider suspension of White Sturgeon harvest in the SSJ for 5 years to allow 2006 and 2011 cohorts to pass through harvest slot length limit
- Consider closing harvest during spawning months (February–June) in the Sacramento and San Joaquin rivers
- Balance recreational opportunities and harvest between estuary and non-estuary anglers
- Establish adaptive harvest management (e.g., quotas) with mandatory reporting to distribute landings throughout the year to help distribute the catch throughout the SSJ and SFE
 - If these goals are not being met, further modifications (e.g., reduced fishing days-per-week, season closures, reductions in individual annual bag limits, and(or) other harvest regulations) may be warranted

Chapter 3: Effects of Temperature and Discharge on the Growth of Juvenile White Sturgeon in the Sacramento-San Joaquin River Basin, California

Shannon E. Blackburn, Zachary J. Jackson, and Michael C. Quist

Abstract

Extensive water development in estuaries and lotic systems has resulted in many negative ecological effects on native fishes. The San Francisco Bay Delta-Estuary and the adjacent Sacramento-San Joaquin River basin (SSJ) in California is considered one of the most modified aquatic ecosystems in the United States. Accordingly, recent surveys suggest that the population of White Sturgeon *Acipenser transmontanus* in the SSJ is declining. Protecting White Sturgeon from further reductions in abundance has become a focus of state and federal agencies. We evaluated historic and contemporary White Sturgeon pectoral fin rays to assess changes in growth over time in the SSJ and possible influences of thermal and hydrological conditions (i.e., discharge, temperature) on growth. We found that growth of White Sturgeon sampled in 2014–2016 was faster than fish collected during the late-1980s and early 1990s. Incremental growth analysis indicated that growth increments were highest in the first two years of life and in the years 1984, 2013, and 2014. Little variation in growth was explained by the environmental covariates, suggesting that annual growth may be influenced by other abiotic and biotic factors.

Introduction

Estuarine environments are among the most complex and important ecosystems in the world (Nichols et al. 1986; Gunther et al. 1991; Cloern and Jassby 2012). Biologically productive, estuaries provide a unique habitat for species specially adapted to life in brackish

waters (Nichols et al. 1986). Many marine and anadromous organisms, including commercially important fishes (e.g., *Oncorhynchus* spp.) and several sturgeon species depend on an estuarine environment during certain life stages (Cech et al. 1984; Raymond 1989; Mora et al. 2018). Because of the abundance of abiotic and biotic resources, coastal environments have long been a focus of human settlement and activity. As a result, estuaries have been subjected to habitat modifications including the damming and diversion of tributary rivers, modification of shorelines, and degradation of water quality (Nichols et al. 1986; Birstein et al. 1997; Cloern and Jassby 2012). The San Francisco Bay Delta-Estuary (SFE) and the adjacent Sacramento-San Joaquin River basin (SSJ) is considered one of the most modified aquatic ecosystems in the United States (Nichols et al. 1986; Gunther et al. 1991; Moyle et al. 2011; Jackson et al. 2016). Unfortunately, many fish species endemic to the SFE and SSJ have experienced declines in abundance and distribution since the beginning of the 20th century (Skinner 1962; Nichols et al. 1986; Moyle et al. 2011; Kiernan et al. 2012; Romanov et al. 2012), suggesting that alterations to estuarine and lotic environments have negatively influenced native fish populations.

Fishes native to the SFE and the SSJ have evolved to survive in the fluctuating environmental conditions (e.g., attenuating spring-summer flows, high sediment loads, variable salinity) that define the system (Gasish and Resh 1999; Moyle et al. 2011; Romanov et al. 2012). Many fishes of the SSJ synchronize their life cycles with patterns in temperature and discharge. However, dams and water diversions alter thermal, flow, and sediment regimes and disrupt floodplain connectivity (Junk et al. 1989; Dynesius and Nilsson 1994; Jager et al. 2001; Nilsson et al. 2005). Many studies have demonstrated the importance of connectivity between rivers and their associated floodplains for fish growth and abundance (Quist and Guy

1998; Fish 2010; Kiernan et al. 2012). Levees have also modified the SSJ and SFE through channelization and reducing floodplain availability, ultimately threatening fishes adapted to the natural conditions of the SSJ (Jager et al. 2001; Romanov et al. 2012; Jackson et al. 2016). A 2010 assessment of 129 native freshwater fish in California listed 82% of the fish as conservation dependent, including the White Sturgeon *Acipenser transmontanus* (Moyle et al. 2011). Recent estimates of abundance from California's Department of Fish and Wildlife (CDFW) fisheries monitoring program suggest that White Sturgeon in the SSJ are declining and remain well below the only established management objective in California (Central Valley Project Improvement Act 'Doubling Goal' of 11,000 age-15 White Sturgeon; Gingras and DuBois 2013).

White Sturgeon are an important species ecologically and as a sport fish in the SSJ. Numerous studies have been conducted to better understand the ecology of White Sturgeon in the SSJ which have found that they experience relatively fast growth (Kohlhorst et al. 1980; Hildebrand et al. 2016; also see Chapter 2) and highly variable recruitment (Pycha 1956; Shirley 1987; Kohlhorst et al. 1991; Gingras and DuBois 2013). Several studies have found that the age structure of White Sturgeon in the SSJ was generally dominated by young fish with few fish older than age 11 (Kohlhorst et al. 1980; Shirley 1987; Kohlhorst et al. 1991). Length structure of White Sturgeon across years has typically been truncated at a length when fish are first available for harvest. Additionally, Shirley (1987) found that the population exhibits periodic strong year classes that span wide intervals (> 10–15 years) of low recruitment. Since the 1980s, successful annual recruitment of White Sturgeon in the SSJ has decreased (Gingras et al. 2013). Current recruitment is estimated to be at record low levels with only two moderately strong year classes documented in the last 18 years (i.e., 2006,

2011). Annual fluctuations of environmental conditions undoubtedly affect the population dynamics of White Sturgeon in the SSJ. A narrow range of preferred spawning conditions have been observed for water temperature and flows in previous studies, and may influence year-class strength through direct (e.g., age-0 survival) or indirect effects (e.g., growth, spawning cues; Shirley 1987; Kohlhorst et al. 1991; Jager et al. 2001; Fish 2010; Jackson et al. 2016). Recent environmental conditions, such as degraded water quality, heavy metal contaminants, and recent droughts have not been favorable for population growth. Therefore, protecting White Sturgeon from further reductions in abundance has become a focus of the CDFW and the U.S. Fish and Wildlife Service.

Improved understanding of the demographics (e.g., age structure) and dynamics (e.g. somatic growth) of White Sturgeon in the SSJ is warranted for the development of an effective management and conservation plan. In particular, growth is important, as nearly every event in a fish's life is influenced by size (i.e., length, weight; Quist et al. 2012; Kerns and Lombardi-Carlson 2017). Somatic growth of fishes is influenced by effects due to age and the environmental conditions of a given year (Weisberg 1993; Weisberg et al. 2010). As such, growth can provide valuable insight on abiotic perturbations and the availability of resources (Quist and Guy 1998; Quist and Spiegel 2012; Klein et al. 2017; Watkins et al. 2017). The objective of this study was to evaluate historic and contemporary White Sturgeon pectoral fin rays for changes in growth patterns over time in the SSJ and possible influences of environmental conditions (i.e., discharge, temperature) on growth.

Methods

Study area

White Sturgeon in California primarily occur in the SSJ and the SFE. The Sacramento and San Joaquin rivers are the two largest rivers in the SFE. Both rivers flow through California's Central Valley and drain an area of 153,000 km³. Mean annual freshwater runoff into the SFE from the Sacramento and San Joaquin rivers is approximately 34.0 km³, but varies from a low of 7.6 km³ in 1977 to a high of 65.0 km³ in 1983 (Jaffe et al. 2007). Although altered by impoundments, the hydrograph of Sacramento and San Joaquin rivers exhibit fluctuations in discharge common to arid-region rivers (Romanov et al. 2012). Snowmelt runoff generally produces high-flow periods during the spring, whereas summer, autumn, and winter are typically low-flow periods. However, water development projects have decreased the ratio of winter to summer flow by over 70% (Jackson et al. 2016).

Field sampling and laboratory processing

Trends in growth were compared using data from recent and historic CDFW White Sturgeon population surveys. Historic sampling efforts occurred primarily during the summer months (i.e., June–August) from 1989–2001. Several methods (e.g., long lines, gill nets, otter trawls) were used to target sexually immature individuals from the Carquinez Strait to the confluence of the Sacramento and San Joaquin rivers (DuBois et al. 2010). Recent sampling for White Sturgeon took place in Suisun and San Pablo bays during the late summer and early fall (August–October) of 2014–2016 and used trammel nets to collect fish (DuBois and Danos 2017). All captured White Sturgeon were enumerated and measured for either fork length (FL) or total length (TL) to the nearest centimeter. Total length measurements were converted

to FL using the equation provided by Beamesderfer (1993) for White Sturgeon in San Pablo Bay, California. A subsample of fish from all surveys had a section of pectoral fin ray removed for age and growth analyses.

White Sturgeon pectoral fin rays that were not previously cut or mounted onto a slide were prepared for age analysis following methods outlined in Koch et al. (2007). Pectoral fin rays were encapsulated in epoxy and a cross-section was taken from each with a low-speed saw (IsoMet 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. Damaged or unreadable rays were removed from further analyses. Age estimates from cross-sectioned fin rays were obtained 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. The senior author gained ageing experience by estimating ages and measuring growth increments of known-age White Sturgeon from the Kootenai River ($n = 157$) before ageing White Sturgeon fin rays from the SSJ. All fin ray sections were aged by one reader. Each aged fish was assigned a confidence rating from 0–3 following criteria outlined in Spiegel et al. (2010). Fish collected in the winter and early spring (i.e., January–May) were assigned an annulus on the outer edge of the ray.

Environmental data

We focused on temperature and discharge as possible factors explaining growth variability of White Sturgeon in the SSJ. Mean annual water temperature (°C) during the growing season (01 April–30 September) was calculated using data from U.S. Geological Survey gaging stations located throughout the SFE and SSJ from 1982–2015. Because of the

highly migratory behavior exhibited by White Sturgeon, we used the mean water temperature from all the stations ($N = 32$) in the SFE. Daily discharge data (m^3/s) from 1982–2015 were obtained from the California Department of Water Resources estimate of the net Delta outflow index (NDOI). The NDOI is calculated as the daily water outflow at the boundary of the SSJ near Chipps Island using information on river discharge, precipitation, agricultural demand, and water project exports. We estimated mean annual discharge (Q) during the growing season as well as the number of days during the growing season when discharge was lower than the 25th percentile ($Q.25$) and the number of days that exceeded the 75th percentile ($Q.75$; Quist and Spiegel 2012; Klein et al. 2017).

Data analysis

Uncertainty exists regarding the accuracy of age and growth estimates from White Sturgeon pectoral fin rays (Brennan and Cailliet 1989; Rien and Beamesderfer 1994). Although pectoral fin rays are currently the most practical and reliable ageing structure for White Sturgeon, accuracy and imprecision have been identified, particularly for fish older than age 20 (Rien and Beamesderfer 1994; Paragamian and Beamesderfer 2003). Therefore, we only used data from age-8 and younger White Sturgeon for growth comparisons over time. Differences in growth were examined from 1989–1991, 1995–2001, and 2014–2016. White Sturgeon were placed in these groups based on sampling protocols, sample size, and exposure to similar environmental conditions. Using growth increment data, mean back-calculated length at age (MBCL) for individual fish were estimated using the Dahl-Lea method (Quist et al. 2012; Shoup and Micaletz 2017). White Sturgeon growth was described with a von Bertalanffy growth model (VBGM), using back-calculated lengths for ages 1–8:

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

where L_t (cm) is fork length at time t , L_∞ is the theoretical mean maximum length, K is the growth coefficient, and t_0 is the theoretical age when length is zero (von Bertalanffy 1938; Ogle et al. 2017). Confidence intervals for the estimated VBGM parameters were calculated using bootstrapping methods based on the parameter distribution over 1,000 trials (Ogle 2016). Differences in mean back-calculated length at ages were compared between groups using analysis of variance. Statistical analyses were performed in R using the Fish Stock Assessment package (Ogle 2017; R Core team 2018).

A repeated-measures mixed-effects linear model was used to examine the effects of age and year on annual growth increments of White Sturgeon in the SSJ (Weisberg et al. 2010). Age was treated as a fixed effect and year and individual fish were treated as a random effects (Weisberg et al. 2010; Watkins et al. 2017). Repeated measures (i.e., increment measurements) of growth were estimated from individual fish (Weisberg 1993). Annual growth slows substantially as long-lived fish such as White Sturgeon age, making annuli difficult to distinguish and increment measurements prone to error (Weisberg 1993; Watkins et al. 2017). Therefore, we only included “younger” White Sturgeon (i.e., ages 1–8) in our analysis. Additionally, only fish that were assigned a confidence rating of a 2 or 3 were included in the mixed-effects model ($n = 256$). Annual growth coefficients predicted from the mixed-effects model were then used as the response variable in linear models. Linear models were used to evaluate the relationship between growth coefficients, water temperature, and discharge. Eight candidate models were developed for temperature and discharge including a null model and models incorporating only water temperature, mean annual discharge, number of days with low (i.e., $Q_{.25}$) and high ($Q_{.75}$) flows, and additive models that included the

combination of the covariates. An information-theoretic approach corrected for small size (AIC_c) was used to compare candidate models, and the top model was the model that had the lowest AIC_c value (Burnham and Anderson 2002). Additionally, the sum of the Akaike weights (w_i) for all models in which a given predictor variable was present was used as a measure of relative importance. However, AIC_c only ranks models and models may still be a poor indicator of growth; therefore, model fit was also evaluated using the coefficient of determination (R^2).

Results

Overall, 876 White Sturgeon pectoral fin rays were aged from sampling efforts spanning from 1989 to 2016 (1989–1991: $n = 237$; 1995–2001: $n = 265$, 2014–2016: $n = 374$). White Sturgeon collected during 1989–1991 varied in length from 27 to 90 cm FL (mean \pm SD; 66.8 ± 15.6 cm), and in age from 1 to 9 years (4.6 ± 1.9 years). Fish collected during 1995–2001 varied in length from 35 to 112 cm FL (mean \pm SD; 72.3 ± 17.0 cm), and in age from 1 to 12 years (5.0 ± 1.9 years). White Sturgeon sampled during 2014–2016 varied in length from 53 to 217 cm FL (mean \pm SD; $97.5 \text{ cm} \pm 27.0$) and in age from 3 to 29 years ($8.1 \text{ years} \pm 3.2$). Mean back-calculated lengths at age were variable among time periods and White Sturgeon sampled in 1989–1991 grew the slowest (Table 3.1). Fish appeared to be growing faster during the most recent sampling efforts than in the 1980s. Recently sampled (i.e., 2014–2016) White Sturgeon grew on average 7% faster than fish collected from 1989–1991. Fish collected from 1995 to 2001 appeared to be growing faster than sampled fish collected from 2014–2016, but the difference was small ($< 3\%$ average difference). Mean back-calculated lengths at age 8 were significantly different between White Sturgeon sampled

in 1989–1991 and 2014–2016 ($F_{14,210} = 73.5$; $P < 0.001$). Growth model coefficients (i.e., L_{∞} , K , t_0) also appear to be different between sampling years (Table 3.2).

As expected, growth increments were highest during the first two years of life (Figure 3.1). Growth increments were variable among years and highest in 1984, 2013, and 2014 (Figure 3.2). The variations in the thermal and hydrological regime of the SFE and SSJ are summarized in Figure 3.3. Variability in growth was poorly explained by the environmental covariates (Table 3.3). No clear pattern in the direction of influence between independent variables and growth was apparent.

Discussion

Several patterns were observed with regard to growth of White Sturgeon in the SSJ, including fast growth of young fish in recent years and relatively large growth increments in the mid-1980s. Differences in growth between decades could be the result of density-dependent interaction (e.g., increased food availability, decreased interspecific competition). For instance, growth rates of Lake Sturgeon *A. fulvescens* in the Ottawa River, Canada were reported to be more rapid in river reaches that were less densely populated (Haxton and Findlay 2008). In addition, prior studies have demonstrated that prolonged periods of exploitation results in increased growth rates due to reductions in population density (Regier and Loftus 1972; Rieman and Myers 1992; Policansky 1993; Hutchings 2005; Bronte and Sitar 2008). Hutchings (2005) found that two subspecies of Atlantic Cod *Gadus morhua* experienced increased individual growth rates and declines in age-at-maturity following precipitous population declines from three decades of overfishing. White Sturgeon in the SSJ may be experiencing similar changes to their life history. Although there are no current

reliable population estimates for White Sturgeon in the SSJ, results from population modeling and declines in catch per unit effort of adult sturgeon in a CDFW during a long-term monitoring study suggest decreasing abundance (DuBois and Danos 2017, see also Chapter 2). Exploitation for White Sturgeon in the SSJ has increased since the 1980s, from approximately 7% to 14% and is attributable to the population declines (Kohlhorst et al. 1991; M. L. Gingras, CDFW, personal communication, see also Chapter 2).

Prior studies have also found that growth of White Sturgeon in the SSJ has changed over time (Kohlhorst et al. 1980; Brennan and Cailliet 1989). Kohlhorst et al. (1980) suggested that White Sturgeon were growing slower in the mid-1970s than in 1954 (Pycha 1956). Although direct comparisons are difficult due to differences in sampling methods, current growth rates of young White Sturgeon are faster than Kohlhorst et al. (1980) reported. Changes in growth over time may be common as fish respond to changes in their environment and recruitment variability. For instance, the University of California–Davis developed a broodstock program for White Sturgeon in the early 1980s which released hatchery-reared White Sturgeon fingerlings into the SFE as mitigation for the removal of gametes collected from wild fish (PSMFC 2002). However, none of the 500,000+ age-0 White Sturgeon stocked from 1980 to 1988 were tagged and no estimates of survival are available (PSMFC 1992, M. L. Gingras, CDFW, personal communication). Little is known about the fate of the hatchery-released White Sturgeon and their influence on the population demographics of the wild population. The release of many young, fast-growing White Sturgeon may have contributed to the large growth increments between 1984 and 1987. Conversely, a high abundance of juvenile fish may have limited resources (i.e., rearing availability, prey abundance) in the SFE and slowed overall growth of White Sturgeon in the late 1980s and early 1990s. Juvenile

White Sturgeon in the Kootenai River system (KRS), Idaho and British Columbia, experienced density-dependent limitations. As a result of too many released age-0 White Sturgeon, growth of hatchery-reared fish in the KRS is limited (Justice et al. 2009). Thus, the consequences of stocking density on population dynamics remain uncertain and density-dependent interactions should be considered in future management and monitoring strategies for White Sturgeon in the SSJ.

Water temperature may also influence White Sturgeon growth in the SFE.

Temperature is a primary driver of somatic growth (Cech et al. 1984; Mayfield and Cech 2004; Kappenman et al. 2009; Justice 2009). Mayfield and Cech (2004) experimentally evaluated the influence of various water temperatures (i.e., 11°C, 19°C, 24°C) on the metabolism and growth of age-0 and age-1 Green Sturgeon *Acipenser medirostris*. The authors reported that the fish exhibited greatest growth between temperatures of 11 and 15°C and concluded that temperatures exceeding 27°C were lethal. Juvenile White Sturgeon grew fastest at temperatures near 20°C in a laboratory study (Cech et al. 1984), which is close to the temperatures found in the SFE habitat during the growing season. Similarly, juvenile Shovelnose Sturgeon *Scaphirhynchus platyrhynchus* experienced reduced growth rates at temperatures above 24°C (Kappenman et al. 2009). It is likely that temperature also influences the growth of White Sturgeon in the SSJ, but water temperature did not appear to be an important covariate for growth in our model ($R^2 = 0.04$). A lack of variability in water temperature during the growing season may not have been sufficient to find a significant relationship in our study. Additionally, because White Sturgeon often move long distances, our ability to evaluate the influence of water temperature on growth was likely limited (Miller 1972; Hildebrand et al. 2016). Nonetheless, results of other studies suggest that water

temperature is an important mediating factor regarding sturgeon populations and growth (Cech et al. 1984; Paragamian et al. 2005; Kappenman et al. 2009; Porter and Schramm 2018). Given the frequency of long-term droughts and the highly regulated water management practices in California, continued alterations to the thermal regime will likely pose a challenge to the conservation of native fishes, including White Sturgeon.

Streamflow is another environmental factor that may influence the growth of White Sturgeon in the SFE. Productivity of lotic and estuarine systems are dependent on discharge variability and floodplain connectivity (Junk et al. 1989; Jager et al. 2001; Kiernan et al. 2012). River discharge patterns (e.g., duration, timing, quantity) in large systems have been shown to be important predictors of growth in several fish species (Quist and Guy 1998; Kappenman et al. 2009; Quist and Spiegel 2012; Crossman and Hildebrand 2014; Hogberg 2014). Physical changes to riverine environments caused by water development projects have adversely affected many benthic vertebrates, such as sturgeons in several river systems (Parsley et al. 1993; DeVore et al. 1995; Beamesderfer and Farr 1997; Jager et al. 2001; Armstrong and Hightower 2002). In particular, a lack of floodplain availability, reduced spring-flows, and low nutrient loads have been associated with poor White Sturgeon recruitment and growth (Jager et al. 2001; Paragamian and Hansen 2008; Fish 2010). We found that discharge was not a significant explanatory covariate for growth of White Sturgeon in the SSJ. Discharge variability has been demonstrated to be a poor predictor of fish growth in other systems. Growth of Shovelnose Sturgeon in the lower Mississippi River appeared to be minimally influenced by hydrologic conditions, such as flooding events (Porter and Schramm 2018). In river systems dominated by canyons and (or) anthropogenic reductions in main channel-floodplain interactions, the influence of discharge and flooding events on

somatic growth may be lessened. For example, Klein et al. (2017) reported that seasonal flooding did not influence the growth of several catostomid species in three Utah rivers. In the Kootenai River, Watkins et al. (2017) found that discharge was not an important factor influencing growth of Mountain Whitefish *Prosopium williamsoni* and Largescale Suckers *Catostomus macrocheilus*. Similar to the Kootenai River, large water development projects in California have depleted nutrients and eliminated floodplain connections throughout the SSJ and SFE. As such, poor model fit relating growth and discharge characteristics of White Sturgeon in the SSJ was not overly surprising. Although discharge and temperature likely affect fish growth in the SSJ, other disturbances such as heavy metal contaminants (Gunderson et al. 2017) and the presence of non-native species (Zeug et al. 2014) may have an overriding influence on fish growth.

Data limitations likely also constrained our ability to observe a strong influence of environmental covariates on growth. For instance, we removed 38% of the fish from analysis in the mixed-effects model because they had a confidence rating of zero or one. Although removing these individuals likely increased our accuracy and precision with increment measurements, we could have omitted important data from both slow- and fast-growing fish. Slow growth rates have been reported to confound age estimates for White Sturgeon in the Kootenai River as annuli are crowded (Paragamian and Beamesderfer 2003), whereas fish that grow continuously and (or) rapidly have little distinction between annuli (Kowalewski et al. 2012). Furthermore, ageing White Sturgeon using pectoral fin rays occurs with error, even with younger fish (Brennan and Cailliet 1989; Hamel et al. 2016). As such, we might have underestimated both the age and growth of individuals. However, for the juvenile (e.g., sexually immature) White Sturgeon evaluated in our study, it is likely that our age and growth

data are reliable, but any conservation actions based on these results should be applied with caution.

Alterations from historic temperature and discharge regimes are often correlated with decreasing native fish abundances and undoubtedly influence the population dynamics of fishes. Current and future water management projects in the SFE and SSJ will continue to pose a risk to native fishes in California, including White Sturgeon (Nichols et al. 1986; Moyle et al. 2011; Cloern and Jassby 2012; Jackson et al. 2016). Knowledge of the factors that influence population demographics, such as growth, are a key to effectively managing White Sturgeon in the SSJ. Achieving a better understanding of White Sturgeon growth in the SFE and other estuarine and riverine habitats should consider additional environmental variables (e.g., population abundance of White Sturgeon, dissolved oxygen, salinity) that will help in the interpretation of growth differences over time, and evaluation of conservation efforts.

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Table 3.1. Comparison of estimated mean back-calculated lengths at age (cm) for White Sturgeon sampled from different time periods in the Sacramento-San Joaquin River basin, California.

Age	Time period								
	1989–1991			1995–2001			2014–2016		
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD
1	234	28.3	6.1	264	30.9	9.2	222	29.7	6.9
2	230	41.7	5.5	262	44.9	8.3	222	43.3	8.1
3	220	49.7	5.5	232	53.1	8.7	222	52.5	7.5
4	190	56.0	5.8	182	61.1	9.0	199	59.7	7.8
5	130	61.5	6.4	158	68.6	9.2	173	66.5	8.1
6	56	67.0	8.0	104	75.8	9.8	143	72.5	8.3
7	20	72.2	7.9	57	81.3	9.4	105	79.1	8.9
8	9	73.7	8.1	29	88.8	8.4	57	84.5	8.9

Table 3.2. von Bertalanffy growth parameters, where L_{∞} is the mean maximum length, K is the growth coefficient, and t_0 is the theoretical age when length is zero, using back-calculated lengths at age with 95% confidence intervals (CI) and mean fork length (FL; cm) and age (years) at time of capture with standard deviations for juvenile (i.e., < age 9) White Sturgeon sampled as various time periods in the Sacramento-San Joaquin River basin, California.

	Time period		
	1989–1991	1995–2001	2014–2016
L_{inf} (CI 95%)	80.594 (76.373, 86.007)	117.806 (106.488, 137.192)	128.696 (119.286, 141.084)
K (CI 95%)	0.259 (0.220, 0.300)	0.143 (0.108, 0.177)	0.127 (0.107, 0.148)
t_0 (CI 95%)	-0.707 (-0.892, -0.536)	-1.190 (-1.487, -0.952)	-1.245 (-1.448, -1.051)
Mean FL (SD)	63.0 (9.2)	63.0 (9.2)	78.8 (12.8)
Mean age (SD)	5.1 (1.4)	5.8 (2.0)	6.1 (1.7)

Table 3.3. Multiple-regression models predicting growth of juvenile White Sturgeon in the Sacramento-San Joaquin River basin, California sampled from various time periods (i.e., 1989–2001; 2014–2016). Explanatory variables include mean annual discharge (Q ; m³/s); the number of the days when discharge was below the 25th percentile ($Q.25$); the number of days when discharge exceeded the 75th percentile ($Q.75$) and mean annual water temperature (Temperature; °C) during the growing season (01 April–30 September). The number of model parameters (K), Akaike’s information criterion corrected for small sample size (AIC_c), AIC_c weight (w_i), and coefficient of determination (R^2) are included.

Model	K	AIC_c	ΔAIC_c	w_i	R^2
<i>Null</i>	2	-82.85	0.00	0.19	--
<i>Q.75</i>	2	-82.85	0.00	0.19	0.00
<i>Q.25</i>	3	-81.60	0.00	0.19	0.00
<i>Temperature + Q.75</i>	3	-81.60	1.26	0.10	0.04
<i>Temperature + Q.25</i>	3	-81.60	1.26	0.10	0.04
<i>Temperature</i>	3	-81.60	1.26	0.10	0.04
<i>Q</i>	3	-81.60	1.79	0.08	0.02
<i>Temperature + Q</i>	4	-78.98	3.87	0.03	0.05

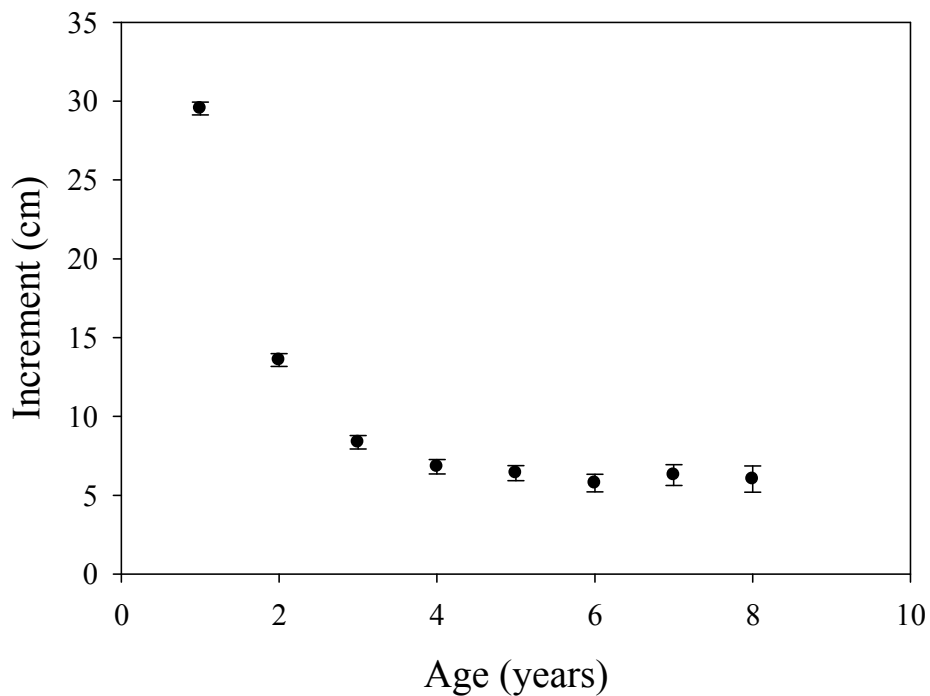


Fig 3.1. Growth increments estimates for ages 1–8 White Sturgeon sampled from various time periods in the Sacramento-San Joaquin River basin, California.

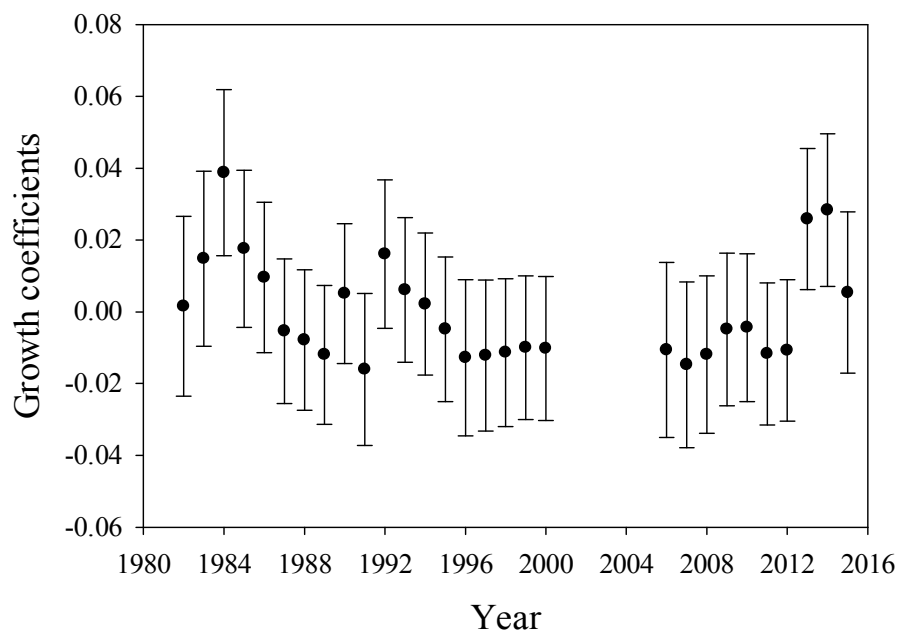


Fig 3.2. Estimated growth coefficients by year for White Sturgeon sampled from various time periods in the Sacramento-San Joaquin River basin, California.

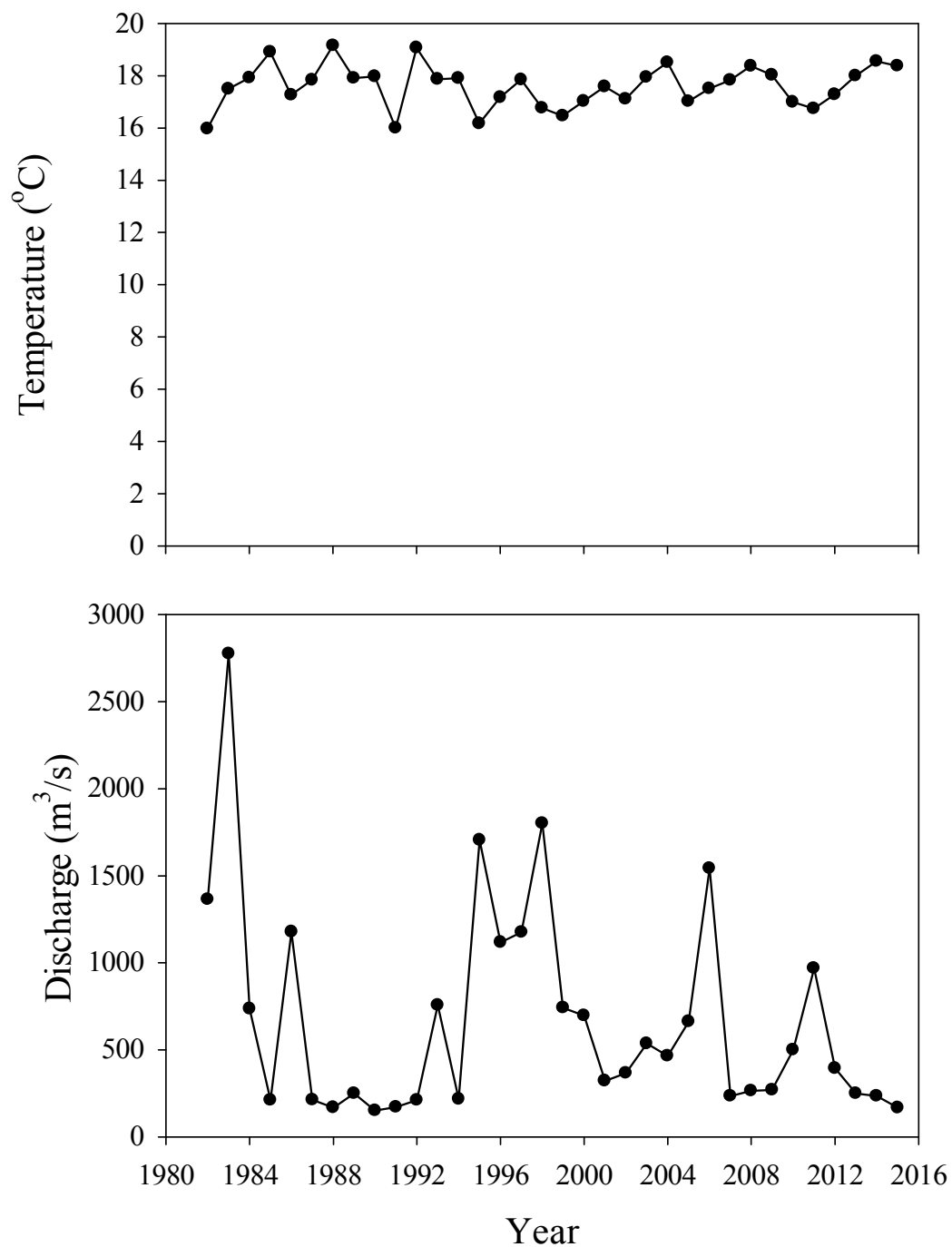


Fig 3.3. Environmental data associated with the Sacramento-San Joaquin River basin and San Francisco Bay Estuary, California, including mean water temperature and discharge during the growing season (1 April–30 September) from 1982–2015.

Chapter 4: General Conclusions

Despite the cultural, commercial, and recreational value of White Sturgeon *Acipenser transmontanus*, knowledge gaps remain regarding key population parameters. Limited dedicated research and monitoring resources have hindered the development of effective management and conservation plans. Consequently, most White Sturgeon populations are declining throughout their distribution. Broadly, this thesis contributed to our knowledge of White Sturgeon ecology and potential population-level responses to anthropogenic effects. The specific goal of this thesis was to establish baseline demographics for the population in Sacramento-San Joaquin River basin (SSJ), California and to address questions related to management decisions. The demographic study coupled with the population modeling assessed several alternative management strategies for the fishery and the feasibility of population recovery. An evaluation of the possible influence of water management characteristics, such as temperature and discharge, had on juvenile growth was also used to address possible management scenarios.

The population evaluation and modeling in chapter two indicated that the White Sturgeon population is declining. Our findings corroborated California Department of Fish and Wildlife (CDFW) results from several recent population monitoring studies. White Sturgeon generally experienced fast initial growth, followed by declining growth rates after age 17. Total annual mortality was higher than other White Sturgeon populations due to unsustainable exploitation. Population modeling suggested that low levels of exploitation (i.e., < 3%) would be required for the population to reach a stable replacement rate. Chapter three sought to evaluate changes in juvenile White Sturgeon growth over several decades and if a relationships existed between water management characteristics and early growth. White

Sturgeon collected from 1995–2016 are growing on average 7% faster than fish sampled in the late 1980s. Although temperature and discharge were not the primary drivers related to White Sturgeon growth in the SSJ in our models, both undoubtedly have an influence on White Sturgeon population dynamics and growth.

Trends in the population dynamics of White Sturgeon in the SSJ demonstrated a definite response to harvest regulations in our models. Given the current situation, harvest of White Sturgeon in California should be managed to mimic natural mortality conditions as much as possible (see Appendix). For example, implementing seasonal closures (i.e., February–May) on spawning grounds could lower overall exploitation and better enable White Sturgeon to take advantage of favorable, episodic recruitment conditions. Other management strategies include defining a harvest quota with mandatory tagging and reporting of harvested fish. Using an exploitation of 2.5% established from the population modeling for an estimated 48,000 adult fish would allow an annual harvest of 1,200 fish. A quota system could potentially aid conservation officers by making it easier to identify illegally harvested fish, especially once the quota has been filled. Additionally, if an annual harvest quota is met, catch-and-release regulations could be implemented in areas that can be closely monitored. By using time-area closures in conjunction with harvest quotas, the White Sturgeon population in the SSJ could be better protected from growth and recruitment overfishing.

Efforts to conserve the White Sturgeon population in the SSJ should remain a high priority for CDFW due to the declining population trends experienced by White Sturgeon and sturgeon worldwide. Our study addressed several data limitations associated with White Sturgeon in the SSJ and provided CDFW with a foundation for future studies. However, further research is warranted. A better understanding of the physical and chemical factors

(e.g., river discharge, salinity) and ecological factors (e.g., invasive species) influencing mortality, growth, reproductive success, and recruitment are critical for the long-term persistence of White Sturgeon in the SSJ and throughout their distribution. In addition to changing and enforcing harvest regulations, CDFW should continue monitoring White Sturgeon recruitment and adult population trends across several generations to establish management and recovery goals for the population.