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Publisher: Taylor & Francis

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North American Journal of Fisheries Management

Publication details, including instructions for authors and subscription information:
<http://www.tandfonline.com/loi/ujfm20>

Stranding of Spawning Run Green Sturgeon in the Sacramento River: Post-Rescue Movements and Potential Population-Level Effects

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To cite this article: Michael J. Thomas, Matthew L. Peterson, Nick Friedenberg, Joel P. Van Eenennaam, Joseph R. Johnson, Jan Jeffrey Hoover & A. Peter Klimley (2013): Stranding of Spawning Run Green Sturgeon in the Sacramento River: Post-Rescue Movements and Potential Population-Level Effects, North American Journal of Fisheries Management, 33:2, 287-297

To link to this article: <http://dx.doi.org/10.1080/02755947.2012.758201>

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ARTICLE

Stranding of Spawning Run Green Sturgeon in the Sacramento River: Post-Rescue Movements and Potential Population-Level Effects

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Abstract

The lower portion of the Sacramento River, California, has been highly engineered to protect low-lying surrounding communities from annual flood events. While engineered floodplains have provided adequate protection for the surrounding communities, there remain unintended consequences to migratory fish that become stranded during high flow events. In April 2011, we rescued 24 threatened Green Sturgeon *Acipenser medirostris* that were stranded in two flood diversions along the Sacramento River. We tagged these 24 Green Sturgeon with acoustic tags and analyzed their survival and migration success to their spawning grounds. Additionally, we provided a population viability analysis to show the potential impacts of stranding and the benefits of conducting rescues at the population level. We found that 17 of these 24 individuals continued their upstream migration to the spawning grounds. Modeling suggests that recurrent stranding of a similar magnitude without rescue could affect the long-term viability of Green Sturgeon

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Received May 4, 2012; accepted December 6, 2012

in the Sacramento River. Population viability analyses of rescue predicted a 7% decrease below the population baseline model over 50 years as opposed to 33% without rescue. Despite the mitigated impact to the population with rescue, fish passage improvements should be considered as a long-term goal for preventing population risks at flood control diversions.

Over the past century, the environments of many fishes have been highly altered to meet overwhelming anthropogenic needs. The construction of dams and flood control structures has direct and indirect consequences to fish populations. With respect to intensely studied and managed species such as salmonids, effects from environmental changes have been identified and appropriate management actions have been implemented for many populations. In contrast, species of sturgeon (*Acipenseridae*) are generally understudied, resulting in relatively little information with which to manage the species. Green Sturgeon *Acipenser medirostris* in particular were historically understudied, and despite a recent surge in publications (see Jarić and Gessner 2012), there remains a considerable void in our understanding of their basic biology.

The hydrology of the Sacramento River and Sacramento–San Joaquin Delta, California, has been highly altered through the construction of dams, levees, and water diversions. Large engineered floodplains have been constructed to divert floodwaters away from major urban areas during sustained periods of rainfall and snowmelt. Flooding of the two biggest diversions, Sutter Bypass and Yolo Bypass, are controlled by a concrete feature commonly referred to as a weir. During high water events in the main-stem Sacramento River, water is either released via gate operation or enters the bypass by spilling. The Fremont Weir located at river kilometer (RKM, measured from Golden Gate Bridge) 226 runs east and west at the northernmost point of Yolo Bypass (Figure 1). Flooding of Yolo Bypass is controlled by the operation of a flood gate when flows are below bank-full levels or by overtopping. To the north of Yolo Bypass is Tisdale Weir (RKM 286.0). Tisdale Weir runs north and south, parallel to the Sacramento River, and controls inundation only when the main stem is below spill stage (Figure 1). Tisdale Weir is inundated when flows of the Sacramento River exceed $595 \text{ m}^3/\text{s}$ and the Fremont Weir is inundated when flows increase above $200 \text{ m}^3/\text{s}$ (Feyrer et al. 2006). The flood recurrence interval in the Yolo Bypass averages every 2 years (Sommer et al. 2005). In most years, flooding of the Yolo Bypass occurs during the months of January through March.

Sturgeon species are vulnerable to water diversions during floods (USFWS 2009) principally due to their comparatively low swimming endurance in high water velocities and to their substrate appression behavior (Boysen and Hoover 2009; Hoover et al. 2011). For imperiled species, field monitoring is critical for effective rescue efforts, quantifying “take,” and evaluating long-term impacts of floods and artificial river structures on the conservation status of individual populations.

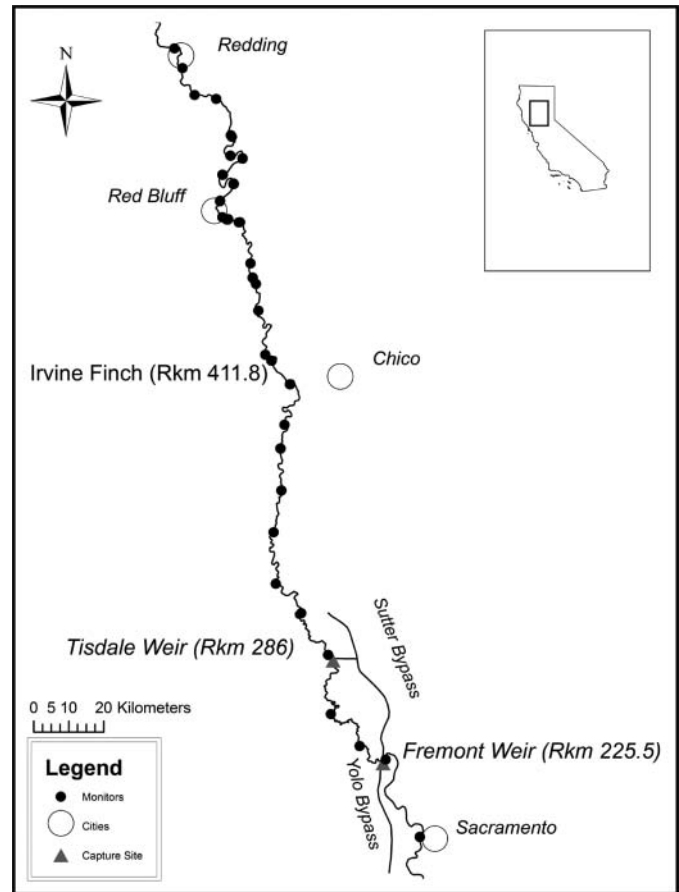


FIGURE 1. Study area of Green Sturgeon rescue sites in the Sacramento River, California, showing river channel, monitor locations, and major cities.

The Sacramento River Green Sturgeon, known as the southern Distinct Population Segment (DPS), is federally listed as threatened. The southern DPS Green Sturgeon is an anadromous migratory species found throughout the bay and inlets of the Pacific Northwest as adults and subadults. Genetic analyses of spawning populations show signs of significant genetic isolation between Green Sturgeon found in the northern rivers compared with those found in the Sacramento River (Israel et al. 2004). Two similar northern spawning populations were identified in the Klamath and Rogue rivers and because of their genetic similarity were classified as the northern DPS. Alternatively, the Sacramento River population was identified as genetically different to those individuals from the Klamath and Rogue rivers, and was therefore classified as a separate population segment.

There is currently no consensus on the abundance of southern DPS Green Sturgeon. However, those estimates, which have been provided in the literature or reports, are on the order of thousands rather than tens of thousands. Currently our best sense of population trajectory is based upon entrainment rates from the state and federal water export facilities located in the southern Sacramento–San Joaquin Delta and from incidental catch from the White Sturgeon *A. transmontanus* monitoring program in San Pablo Bay. In either case estimates from these two programs are either inherently exaggerated or biased and offer managers little concrete evidence as to the true population trajectory (see Adams et al. 2007).

Managers have already identified potential passage-related features that present potential population-level risk including the Fremont Weir (NMFS 2006). Potential risk from stranding in flood diversions was unknown until numerous Green Sturgeon were rescued from two diversions during the spring spawning migrations in 2011.

Despite a mandate to preserve the Sacramento River population of Green Sturgeon, resource agencies have failed to adequately monitor several flood control structures that have been previously identified as potential barriers to fish migration (NMFS 2006). Sturgeon have previously been stranded at Fremont Weir during high flood events. Informal sturgeon rescues were performed at Fremont Weir in 2001, 2003, and 2004 (Zoltan Matica, California Department of Water Resources, West Sacramento, personal communication). In 2006, a sturgeon rescue was conducted by the California Department of Fish and Game at Fremont Weir (California Department of Fish and Game, unpublished data). Neither numbers nor species were recorded for the years of 2001–2004; however, 26 unidentified sturgeon were removed from Fremont Weir in 2006.

Spawning migrations of Green Sturgeon typically occur during the months of March through June (Benson et al. 2007; Erickson and Webb 2007; Heublein et al. 2009). Spawning of Green Sturgeon in the Sacramento River has been documented from RKM 423.9 near Glenn–Colusa Irrigation District (GCID) pumping facility to the confluence of Inks Creek at RKM 516.0 (Brown 2007; Poytress et al. 2009, 2010, 2011, 2012).

During March and April 2011, Tisdale and Fremont weirs were flooded for approximately 26 and 24 d, respectively (California Department of Water Resources, California Data Exchange Center [CDEC], unpublished data). Personnel from the California Department of Fish and Game identified numerous stranded sturgeon on 11 April 2011 once water levels had receded. While it was unknown if any of the sturgeon stranded were Green Sturgeon during the first sightings on 11 April 2011, rescue operations were organized on 12 and 13 April 2011 to remove all fish stranded. During rescue operations both White Sturgeon and Green Sturgeon were found stranded at each of the two diversions.

To our knowledge, the movements of Green Sturgeon have yet to be described after releases from such an impediment. Furthermore, the potential for population-level effects of stranding

through increased mortality and forgone reproduction has not been explored for this population segment. The major features of the southern DPS—small estimated population size (e.g., Israel and May 2010), late maturity, episodic spawning, and a long-lived adult stage—all contribute not only to its overall vulnerability but also to the possible impact of any threat targeting reproductive adults (Heppell 2007). Therefore, the objectives of this study were to (1) describe the reproductive condition of Green Sturgeon individuals and poststranding movements using acoustic tags, (2) assess postrescue survival while in the river system, (3) determine which factors, if any, influenced movement rates and arrival of Green Sturgeon at the spawning grounds, and (4) assess the population level impacts of stranding and benefits of rescue activities for Green Sturgeon listed under the U.S. Endangered Species Act.

METHODS

Capture and tagging.—In total, 25 Green Sturgeon were located within the two stranding sites. Sturgeon were captured using block nets at four separate sites at Fremont Weir and one at Tisdale Weir (Figure 1). Upon capture, 23 Green Sturgeon were found to be in “good” condition, based on the absences of lacerations and abrasions from the concrete weir. One individual was considered to be in “poor” condition due to excessive abrasions and the presence of a spear tip near the back of the head. One gravid female was found dead at the time of rescue and was presumed to be a victim of poaching activities the night before. All 24 living Green Sturgeon were removed from the concrete channel behind each weir, turned upside down, and placed in a hooded cloth stretcher. Gills were ventilated by pumping water into the hood to maintain a continuous flow of fresh water. Fork length (FL) and total length (TL) (± 0.5 cm) were measured with a retractable tape measure prior to surgery. Differences in lengths between males and females were tested at a later date using a Student’s *t*-test implemented with JMP version 4 software (SAS Institute, Cary, North Carolina). Water temperatures during the rescue at Fremont Weir ranged from 14.2°C to 16.6°C. No water temperatures were taken during the rescue at Tisdale Weir. Average daily air temperatures during the days of rescue were 11.3°C, with a high of 18.8°C and a low of 4.4°C.

A uniquely coded beacon (V16-6L, VEMCO) with a frequency of 69 kHz, a 75-s delay, and battery life of 3,650 d was implanted within the peritoneum of each Green Sturgeon (see Heublein et al. 2009 for surgical procedure). Prior to insertion of the telemetry tag, the gonads were examined to determine sex and stage of maturity. For all males, except one that was releasing milt at capture, a small section of the testis was collected for histological processing as described in Webb and Erickson (2007). From each female approximately 15 eggs were collected for measurement of size and calculation of the polarization index (PI) using the methods described by Van Eenennaam et al. (2001, 2006). Surgery times ranged from 3 to 5 min, and total handling times averaged 10 min. Upon completion each

sturgeon was transported approximately 0.1 km by foot or truck and released into the Sacramento River.

The eggs were examined to determine the reproductive state of mature females. Egg length and width ($n = 11$ females) were measured using a dark-field dissecting microscope equipped with a camera lucida, an image-analyzing tablet, and a micro-computer interface (± 0.001 mm). The eggs were then bisected with a razor blade along the animal-vegetal axis, and the distance of the germinal vesicle from the inner border of the egg chorion and egg diameter were measured and used to calculate PI, a morphologic criterion of egg ripeness (Dettlaff et al. 1993; Chapman and Van Eenennaam 2007). Histological slides were examined under a compound scope and the germ cells scored for stage of development using the developmental stages described in Webb and Erickson (2007).

Monitoring movements.—An array of 47 stationary acoustic monitors (VR2 and VR2W, VEMCO) and a mobile tracking receiver (VR100, VEMCO) were used to describe postrescue movements and survival of tagged Green Sturgeon (Figure 1). The lowermost-confirmed Green Sturgeon spawning site (GCID Hole) is located at RKM 424.0. Spawning was confirmed by egg collection at RKM 424.0 in 2010, by ongoing monitoring of egg mats conducted by U.S. Fish and Wildlife Service (Poytress et al. 2011). Due to considerations of detectability we selected the Irvine Finch monitor location (RKM 411.8) as our endpoint for determining migration success. A Green Sturgeon detected at or above this location was judged to have reached the spawning grounds. A Green Sturgeon detected below the Fremont Weir (RKM 225.5) was judged to have left the river system. Survival was defined by a successful summer or winter out-migration past RKM 225.5. Detection probabilities of monitors between Fremont Weir and the GCID monitor (RKM 225.5–424.0) were calculated using methods similar to Melnychuk et al. (2007). Despite only moderate detection probabilities (by individual monitors; mean \pm SD probability of detection, 0.71 ± 0.15), overall likelihood of detection was high due to the extensive monitor array. Thus, we had high confidence in our ability to determine survival and movements. Detections of tagged sturgeon were filtered to obtain the first and last detections at any particular monitoring site and movement rates and residence times between monitors were calculated using the last detection at monitor i and the first detection at monitor $i + 1$. Records at certain monitors were pooled due to overlap in detection ranges.

A generalized linear model (GLM; binary logistic regression) was used to identify which, if any, explanatory variables were associated with migratory success (defined as reaching the spawning grounds at RKM 411.8) and a series of potential explanatory variables (Stauffer 2008). Explanatory variables used in the modeling included length, sex, surgery time, reach-specific migration rates, and reach-specific residence times. Sixteen candidate models (in two groupings: [1] all Green Sturgeon included, $n = 24$, and [2] Green Sturgeon from Fremont Weir, $n = 12$) using combinations of the explanatory variables were

evaluated using Akaike's information criterion (AIC; Stauffer 2008).

Population viability analysis.—In the absence of consensus on whether there is an upward or downward trend in the Sacramento River Green Sturgeon population, we constructed a baseline model in which the expected size of the population was neither growing nor declining. Modifications to the trendless baseline model were then used to assess the marginal contribution to ecological risk (Ginzburg et al. 1982) attending specific scenarios of stranding and rescue. To be conservative, all rates were assumed to be density independent (Ginzburg et al. 1990).

Projections of population growth were governed by a matrix of transition rates describing the survival, development, and reproduction during distinct stages of the life history of Green Sturgeon. Parameter values were compiled from previous studies (Beamesderfer et al. 2007; Heppell 2007) and Green Sturgeon records of detections from monitors in the Sacramento River. The life history of Green Sturgeon was divided into five stages: juveniles (ages 1–4), marine juveniles (ages 5–10), subadults (ages 11–15), young adults (ages 16–25), and adults (age 26+). No maximum age was imposed. Life history parameters and justifications for choosing them are given in Table 1.

The baseline model was implemented as a stochastic Monte Carlo simulation using RAMAS Metapop 5.0 software (Akçakaya and Root 2007). The Metapop software simulates population growth in a variable environment by sampling distributions of vital rates defined by user-provided means and standard deviations; the same means are used in all replicate simulations. Mean transition rates and fecundities are given in Table 2. Deterministic analysis of the stage-based model provided the expected stable stage structure indicated in Table 3. Asymptotic elasticity analysis (Caswell 2001) performed by the Metapop software provided a measure of the sensitivity of population growth rate to proportional changes in elements of the stage matrix. Only fecundity and adult survival yielded unambiguous elasticity; other entries jointly represented probabilities of survival and rates of development. Without information on environmental stochasticity, we assumed 5% annual variability of mortality and 10% annual variability of fecundity. Annual variation was lognormal. Under these conditions, the average population size declined by an average of fewer than six individuals over 50 years. The model tracked only females under the assumption of a 1:1 sex ratio. All model projections used the same means and standard deviations for transition rates for 10,000 replicated 50-year projections. All simulations started with the population at its stable stage distribution.

The single recorded observation of stranding of Green Sturgeon at the Fremont and Tisdale weirs provides only an anecdotal understanding of the frequency and magnitude of such events. We used a set of assumptions, described in the following paragraphs, that link stranding with hydrological data to inform a population projection model. Within this set of assumptions, we used uncertainty regarding a subset of parameters to develop

TABLE 1. Underlying parameters used to calculate survival and fecundity of Green Sturgeon in the Sacramento River under baseline (no entrainment) conditions.

Parameter name	Symbol for model	Value for model	Duration (year)	Proportion transitioning in duration	Justification
Survival	<i>S</i>	0.93			Beamesderfer et al. (2007)
Transition to marine juvenile	<i>Mm</i>	0.54	3	0.9	Transition rates chosen for appropriate residence time in stage according to Heppell (2007).
Transition to subadult	<i>Ms</i>	0.11	6	0.5	
Transition to young adult	<i>My</i>	0.13	5	0.5	
Transition to adult	<i>Ma</i>	0.07	10	0.5	
Mature young adults	<i>Xy</i>	0.29			Stage average based on linear interpretation of Heppell (2007).
Mature adults	<i>Xa</i>	0.93			
Eggs young adult	<i>eggy</i>	11,383			Egg production based on Beamesderfer et al. (2007) using stage average weighted by sexual maturity (females only).
Eggs adult	<i>egga</i>	73,465			
Egg to age-1 survival	<i>s0</i>	0.00002			First year survival and spawning success chosen to balance births and deaths in base model.
Spawning success	<i>spwn</i>	0.80			
Reproduction frequency	<i>P</i>	0.30			Telemetry data for Sacramento River.

objectively optimistic and pessimistic assessments of the impact of stranding on Green Sturgeon population dynamics.

We defined floods of concern as river stages that exceeded the Fremont Weir’s controlling elevation of 10.2 m by at least 0.3 m during the upstream migratory period from February through May. This criterion was chosen arbitrarily to help select flood events in which appreciable volumes of water entered the diversions. We assumed that inundation at Fremont was a good indicator of overall stranding risk and did not use weir-specific estimates of stranding. Data from 1984 to 2011 at the Fremont

gauge station (Figure 2) indicated a 0.43 annual probability of a flood of concern occurring and lasting at least 1 d. Sustained periods of dry and wet years were implemented as conditional flood probabilities. In the gauge data record, years with a flood were followed by flood years with a probability of 0.64, whereas years without floods were followed by floods with a probability of 0.31. While we included this autocorrelation in simulations, it was not statistically significant ($\chi^2 = 2.8$, $df = 25.26$, $P > 0.09$) and had a negligible effect on results compared with additional simulations using the uniform flood probability of 0.43. Flood durations were measured in days. The 2011 inundation of Fremont Weir was a flood of concern for 23 d. The average duration of floods of concern over the Fremont gauge record was 28.25 d (SD = 17.34).

TABLE 2. Transition and fecundity rates used in the stage-based model of Green Sturgeon in the Sacramento River. Formula parameters and their values are defined in Table 1. The asymptotic population growth rate is 1.0000.

Total rates	Formula	Value
Juvenile survival	$s \cdot (1 - Mm)$	0.432
Juvenile to marine	$s \cdot Mm$	0.498
Marine survival	$s \cdot (1 - Ms)$	0.829
Marine to subadult	$s \cdot Ms$	0.101
Subadult survival	$s \cdot (1 - My)$	0.810
Sub- to young adult	$s \cdot My$	0.120
Young adult survival	$s \cdot (1 - Ma)$	0.868
Young adult to adult	$s \cdot Ma$	0.062
Adult survival	s	0.930
Fecundity young adult	$eggy \cdot s0 \cdot spwn \cdot p$	0.060
Fecundity adult	$egga \cdot s0 \cdot spwn \cdot p$	0.388

TABLE 3. Stable stage distribution and abundance of Green Sturgeon in the southern Distinct Population Segment under baseline conditions assuming an average of 200 male and female spawners per year.

Stage	Proportion	Fraction mature	Female spawners	Total Females	Total females
Juvenile	0.123	0		214	
Marine	0.359	0		625	
Subadult	0.191	0		333	
Young adult	0.173	0.29	26	301	
Adult	0.154	0.93	74	268	1,741

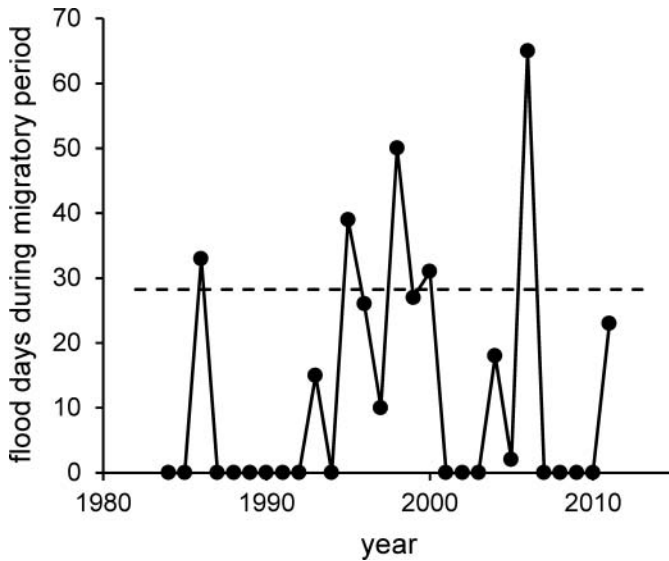


FIGURE 2. The duration (in days) of floods of concern during the Green Sturgeon migratory period at Fremont Weir for the period 1984–2011. The dashed horizontal line indicates the average flood duration of 28.25 d (excluding years without floods). Floods of concern were defined as river stages that exceeded the weir's controlling elevation by 0.3 m for at least 1 d during the migratory period, February through May.

To project possible demographic consequences of stranding, we needed to establish a population size for Green Sturgeon in the Sacramento River. Population size estimates vary widely. For instance, Israel and May (2010) estimated that 5–14 females contribute to juvenile production every year, translating to a range of 90–252 young adult and adult females according to the parameters in Table 3. Moyle (2002) gave a range of 70–800 female adults. Here, we used results of a river survey that estimated 220 total upstream migrants in 2010 (Ethan Mora, University of California, Davis, unpublished data). We conservatively assumed this observation represented an above-average year and assumed the average spawning run was 200 adults. With a 1:1 sex ratio, stable stage distribution, and an annual spawning probability of 0.3, the number of spawners corresponded to 569 young adult and adult females and a total female population size of 1,741 (Table 3).

The stranding rate used in the population model was developed using the total number of Green Sturgeon ($n = 25$) found stranded at Tisdale and Fremont weirs during 2011. We assumed that all individuals stranded were found and treated stranding as a system-wide risk rather than a site-specific rate. To estimate the proportion of migrants at risk of stranding during the 2011 flood, we developed a daily probability of migration during floods of concern. First, we used 2009–2011 records of tag detections in the array of monitors to find monthly probabilities of migration among tagged Green Sturgeon in the Sacramento River (M. J. Thomas, unpublished data). We then converted these to daily probabilities by dividing by the number of days in each month. Then we summed the daily probability of migration over the course of each flood of concern on record in the Fremont gauge data. Finally, we regressed these accumulated migration probabilities against flood length with an intercept constrained to zero. The resulting daily probability of migration during floods of concern was 0.0123 ($r^2 = 0.98$, $F_{1, 27} = 2,746$, $P < 0.0001$). We assumed all migrants were at risk of stranding without respect to position in the river. Assuming 200 total migrants per year, the expected number of migrants during the 23 d of the 2011 flood was 56.6, with a Poisson 97.5% confidence interval (CI) of 41–76. This led to an estimated 0.44 per capita rate of stranding with a joint 95% CI of 0.216–0.780 (including uncertainty about both the number of migrants and the true probability of stranding). Applied to the average flood duration of 28.25 d, the per capita stranding rate yielded an expected stranding of 15.4 females with a 95% CI of 7.3–27.1 in years with floods, assuming a 1:1 sex ratio. It is important to note that similar stranding levels would result from any method that assumes stranding risk is proportional to the duration of floods. The translation of stranding levels into effects on adult survival and fecundity is most apparent for the fecundity multiplier, assuming the population is at the stable stage distribution, and rescued individuals survive stranding with 90% probability and spawn with 50% probability (Table 4).

To model the effect of the 2011 event in isolation, we ran replicated stochastic simulations starting with a single stranding event averaging 16 females (4.16 young adults and 11.84 adults). Vital rate multipliers under 2011 stranding levels were 0.986 for young adult survival, 0.956 for adult survival, and 0.840

TABLE 4. Mean and 95% CI around the impact of entrainment and rescue on Green Sturgeon demographic rates.

Parameter	Lower estimate		Mean		Upper estimate	
	No rescue	Rescue	No rescue	Rescue	No rescue	Rescue
Females stranded		7.3		15.4		27.1
Proportion of young adults		0.006		0.011		0.023
Proportion of adults		0.020		0.035		0.075
Proportion of spawners		0.073		0.154		0.271
Young adult survival multiplier	0.994	0.999	0.989	0.999	0.977	0.998
Adult survival multiplier	0.980	0.998	0.965	0.997	0.925	0.993
Fecundity multiplier	0.927	0.964	0.846	0.923	0.729	0.865

TABLE 5. Biological information for tagged Green Sturgeon ($n = 24$) at the Fremont (12 April 2011) and Tisdale (14 April 2011) weirs. M = male, F = female.

Tag identification	Location / site	FL / TL (cm)	Sex	Maturation status	Polar index
GS1	Fremont / 1	182 / 200	M	Mature	
GS2	Fremont / 1	144 / 161	M	Mature	
GS3	Fremont / 1	183 / 202	F	Eggs	0.048
GS4 ^a	Fremont / 2	175 / 190.5	M	Mature	
GS5 ^b	Fremont / 2	156 / 175	F	Eggs	0.038
GS6	Fremont / 2	188 / 207	F	Eggs	0.056
GS7	Fremont / 2	164 / 179	M	Mature	
GS8	Fremont / 2	173 / 158.5	M	Mature	
GS9 ^b	Fremont / 3	207 / 219	F	Eggs	0.067
GS10	Fremont / 3	163 / 177	M	Mature	
GS11	Fremont / 3	193 / 213	F	Eggs	0.066
GS12	Fremont / 3	166 / 185	F	Eggs	0.054
GS13	Fremont / 3	150 / 167	M	Mature	
GS14	Tisdale / 1	199 / 213	F	Eggs	0.072
GS15	Tisdale / 1	150 / 165	M	Mature	
GS16	Tisdale / 1	202 / 215	F	Eggs	0.056
GS17	Tisdale / 1	190 / 201	F	Eggs	0.040
GS18	Tisdale / 1	185 / 201	M	Mature	
GS19 ^b	Tisdale / 1	171 / 184.5	F	Eggs	0.031
GS20	Tisdale / 1	182 / 195	F	Eggs	0.036
GS21	Tisdale / 1	183 / 200	M	Mature	
GS22	Tisdale / 1	160 / 174	M	Mature	
GS23	Tisdale / 1	174 / 182	M	Mature	
GS24	Tisdale / 1	163 / 177	M	Mature	

^aGS4 not included in movement analyses.

^bEggs in early stages of atresia.

for fecundity. Vital rate multipliers with rescue were 0.999 for young adult survival, 0.996 for adult survival, and 0.920 for fecundity.

RESULTS

Reproductive State and Movements of Rescued Sturgeon

Ultimately, 56 White Sturgeon and Green Sturgeon were captured and moved from behind the two weirs and returned to the main-stem Sacramento River. In total, 11 female and 13 male Green Sturgeon were rescued from Fremont and Tisdale weirs. Males were significantly smaller than the females (Student's t -test: $P < 0.05$). Males were 179.4 ± 14.8 cm TL (mean \pm SD) and females were 200.5 ± 13.8 cm. All Green Sturgeon were determined to be mature adults on their spawning migration (Table 5). Through examination of histological sections from the testis, we verified that all testicular cysts contained differentiated spermatozoa (stage 5; Webb and Erickson 2007), and one individual (GS4), although injured from a poaching attempt, was spermiating upon capture. Rescued females were in the late stages of final maturation with large, oval-shaped, olive-brown-colored eggs that averaged 4.27 ± 0.13 mm in length and 3.75 ± 0.05 mm in width. The mean polarization index

of females was 0.051 ± 0.014 , indicating spawning readiness (Table 5). However, three females had eggs showing early signs of atresia, a form of degradation manifested by softening and marbling of the egg chorion.

Movement records showed a combined 71% migration success (reached RKM 411.8) for both males and females from the Fremont and Tisdale rescue sites. Site-specific success was variable depending on sex and location. Migration success from the Fremont Weir was three of six (50%) for females and five of six (83%) for males. Success to the spawning ground was higher for females stranded at Tisdale Weir with four of five (80%) reaching the spawning grounds. Males stranded at the Tisdale Weir had the same migratory success as those stranded at the Fremont Weir (five of six, 83%). Counting females only, 7 of 11 (64%) rescued female Green Sturgeon reached the spawning grounds, a rate higher than the 50% we used in our population models for spawning success. Individuals exhibited two different periodicities of occupation of the spawning grounds, either spending weeks on the spawning grounds before out-migrating in early summer or overwintering and out-migrating in early winter (Figure 3).

A total of 16 candidate models were examined, and were made up of eight candidate models that included all Green

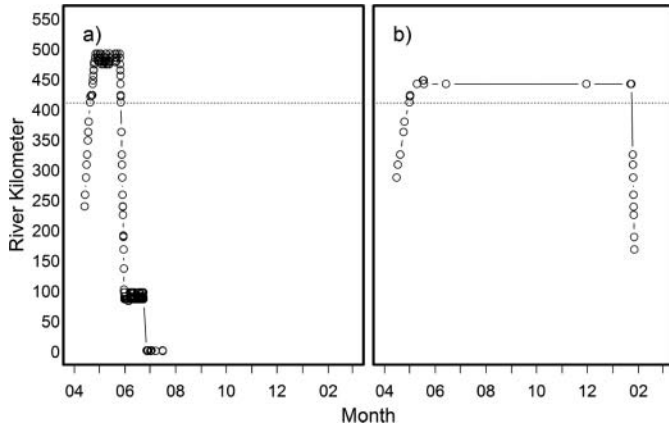


FIGURE 3. River kilometer plots for two individual Green Sturgeon, (a) GS13 and (b) GS17. Note period of out-migration for GS13 occurred in late May compared with the out-migration of GS17, which did not occur until late January.

Sturgeon (Table 6) and eight that included only those rescued at Fremont Weir (Table 7). Of the models that included all 24 Green Sturgeon, no strong candidate model was observed among the eight candidate models when evaluated by AIC values and associated model likelihoods. In fact, the null model had the lowest AIC value and the strongest model likelihood (Table 6). Similarly, of the models that only included Green Sturgeon rescued at Fremont Weir, the null model was ranked as the second-best model (Table 7). Interestingly, the top model included water temperature at the time of rescue, but the model did not provide vast improvement in AIC values compared with other potential models. Upon examination of this model, a slightly negative, but insignificant, relationship was observed ($P = 0.140$).

All but two individuals successfully out-migrated; male GS4, an individual that had a spear tip removed from its head, and male GS1 that was repeatedly tracked throughout the spawning grounds and was not detected after 16 June 2011. Assuming these two individuals died, the observed survival rate of rescued Green Sturgeon was 91.7% compared with the 90% used in our population models.

Population Viability Analysis

Model projections over 50 years indicated that chronic stranding in flood control structures could have biologically significant impacts on the viability of the Sacramento River Green Sturgeon population (Figure 4). The estimated mean frequency and severity of stranding events reduced expected final adult female abundance by 33% compared with baseline conditions (Figure 4), from an average baseline population of 563 individuals to an average impacted population of 378 individuals after 50 years. As indicated by the lighter-weight series in Figure 4, individual replicates in each scenario led to higher or lower final abundance. In addition to this uncertainty, caused by environmental variability, there is uncertainty about the entrainment rate that stems from our lack of knowledge. Using high and low estimates of entrainment (Table 4), minimum abundance during the 50-year projections ranged from 246 to 435 adult females (15–52% below the baseline expected minimum of 513). The range of population projections stemming from uncertainty in the entrainment rate led to increases in the risk of 20% decline greater than five times the baseline level. Under baseline conditions, longer simulations yielded a median time to 20% decline of 200 years; the probability of 20% decline in 50 years was 0.12 (Figure 5). With stranding, the median time to 20% decline was 13–39 years and the probability in 50 years was 0.68–1.0 (Figure 5).

Simulations suggested that monitoring and rescue operations could greatly reduce the impact of stranding on population viability. Rescue with the estimated mean frequency and severity of stranding events resulted in a final female adult abundance 7% below baseline (to 524 individuals, Figure 4). Expected minimum adult abundance over 50 years was 466–502 (2–9% below baseline). Uncertainty about the entrainment rate resulted in a range of population projections that included a slight to moderately elevated 20% decline risk after rescue (Figure 5). Rescue resulted in median times to 20% decline of 58–108 years; the probability of 20% decline in 50 years was 0.19–0.45. Hence, rescue increased the time to 20% decline by a factor of 2.8–4.0 compared with the stranding scenario and decreased the 50-year risk of decline by 55–72%.

TABLE 6. Summary of binary logistic regression models ranked on Akaike's information criterion (AIC) and AIC weights to explain migratory success (success defined as reaching RKM 411.8) among individual Green Sturgeon ($n = 24$) rescued during spring 2012.

Model name	AIC score	Parameters	Number of parameters	Model likelihood	AIC weights	Δ AIC
Null	30.975	None	1	1.000	0.202	
2	31.503	Total length	2	0.768	0.156	0.528
8	31.682	Group	2	0.702	0.142	0.707
5	32.466	Sex	2	0.474	0.096	1.491
3	32.683	Estimated weight	2	0.426	0.086	1.708
6	32.732	Surgery time	2	0.415	0.084	1.757
30	33.239	Surgery time, total length	3	0.322	0.065	2.265

TABLE 7. Summary of binary logistic regression models ranked on Akaike's information criterion (AIC) and AIC weights to explain migratory success (success defined as reaching RKM 411.8) among individual Green Sturgeon ($n = 12$) rescued from Fremont Weir during Spring 2012.

Model name	AIC score	Parameters	Number of parameters	Model likelihood	AIC weights	Δ AIC
1	18.825	Water temperature	2	1.000	0.184	
Null	19.320	None	1	0.781	0.144	0.495
10	19.768	Residence time (Knights Landing to China Bend)	2	0.624	0.115	0.943
25	19.865	Water temperature, sex	3	0.595	0.109	1.040
9	19.929	Migration rate (Knights Landing to China Bend)	2	0.576	0.106	1.104
12	19.951	Residence time (China Bend to Tisdale Weir)	2	0.570	0.105	1.125
11	20.016	Migration rate (China Bend to Tisdale Weir)	2	0.551	0.101	1.191
27	20.797	Water temperature, surgery time	3	0.373	0.069	1.972
26	20.822	Water temperature, total length	3	0.369	0.068	1.996

If the stranding event of 2011 was an isolated event, it posed only a small risk to the population; rescue completely offset the 50-year impact. One-time stranding decreased the expected minimum abundance of young adults and adults from 513 to 501 over 50 years and increased the probability of 20% decline from 0.10 to 0.17. When rescue was included in the simulations, both minimum abundance and decline risk returned to baseline levels.

Elasticity analysis of the baseline model provided a general overview of the sensitivity of population growth rate to proportional changes in elements of the stage matrix. Elasticity of adult survival was 0.35 compared with 0.026 for adult fecundity and 0.0046 for young adult fecundity.

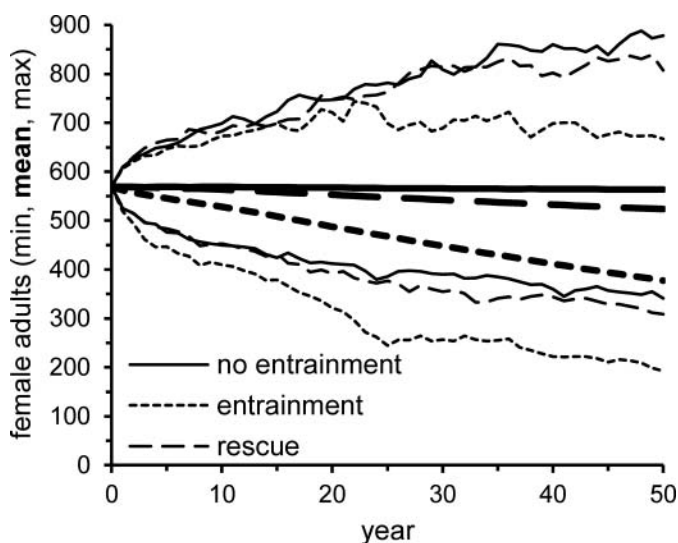


FIGURE 4. Projected adult female Green Sturgeon abundance in the Sacramento River population under estimated mean stranding rates with and without rescue. Both models assume that the expected population trajectory was flat in the absence of stranding. Bold curves depict means of 10,000 replicates. Lighter series indicate minimum and maximum projected abundance in each year.

DISCUSSION

Our analysis of Green Sturgeon population viability in the Sacramento River suggests that stranding could have a biologically significant impact if it is a recurring event. Furthermore, it appears that monitoring and rescue will substantially reduce, though not completely offset, that impact. While our analysis indicated that the single event observed in 2011 was, by itself, a small risk to population viability, it has since emerged that similar events have occurred at least four times over the last decade (California Department of Fish and Game, unpublished data; Zoltan Manteca, California Department of Water Resources, West Sacramento, personal communication).

The projected impact of stranding on the southern DPS can be attributed primarily to increased adult mortality rather than

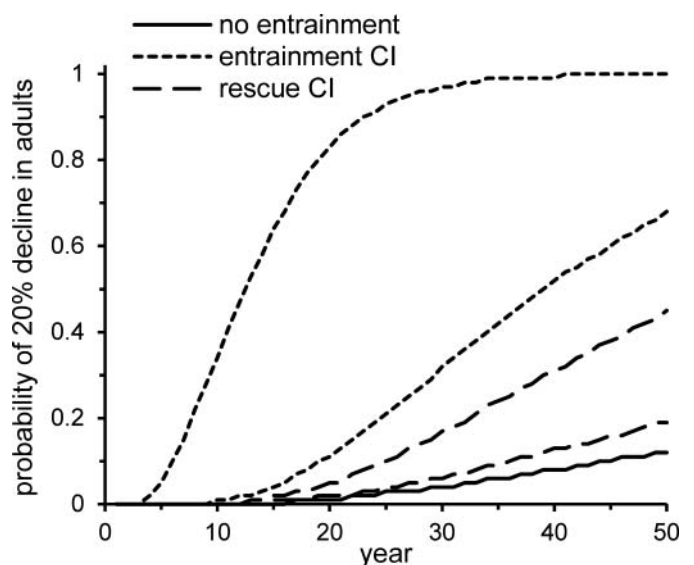


FIGURE 5. The effect of stranding and rescue on the probability of a 20% decline in adult Green Sturgeon abundance over 50 years. The solid curve represents background risk in the absence of stranding. Remaining curves describe the 95% CI developed around model assumptions, as described in the Methods.

episodic reductions in fecundity. In long-lived species with delayed reproductive maturity, including sturgeon, population growth rate is most sensitive to adult survival (Heppell 2007). Analysis of our baseline stage matrix demonstrated that population growth rate was more than an order of magnitude more sensitive to changes in adult survival than to proportional changes in fecundity. Rescued adults, if they survive, may return to the estuary rather than continuing their spawning migration, a phenomenon referred to as “dropback.” However, 1 year of foregone spawning only slightly lessens lifetime reproductive output. It is worth noting that the same holds true for short-term research activities that may lead to “dropback.” If handling fish provides greater understanding of population size and migration behavior, the gains in management efficacy easily exceed the maximum possible negative biological impact so long as adult survival is not reduced.

We made several consequential assumptions when modeling stranding and rescue. First, we assumed that searches behind diversion structures located all stranded individuals. Second, we assumed that stranding frequency is a simple function of flood frequency at a single weir. Third, we assumed the magnitude of stranding is proportional to flood duration. Finally, we used a density-independent model of population growth.

The assumption of 100% search efficiency has a two-fold effect on our results. First, it minimizes our estimate of the per capita stranding probability. Second, undetected fish would not be rescued, diminishing the degree to which rescue efforts would offset the impact of stranding.

The assumption that stranding occurs no more or less frequently than inundations at Fremont Weir that exceed the controlling elevation by 0.3 m during the migratory season greatly limits both the complexity of the model and the range of results it can project. Obviously, the model overestimates the impact of stranding if the stranding event of 2011 was in reality a rare occurrence. It is less obvious how a site-specific consideration of the six flood-control structures on the Sacramento River would affect projections. Gauge data near Tisdale Weir indicate that it is inundated more often than Fremont Weir and that the duration of inundation is generally longer. All else being equal, a model using the site-specific information on stranding and inundation at Fremont and Tisdale weirs would predict more frequent stranding events.

In addition to reducing the impact of stranding, monitoring would result in a better understanding of its frequency, magnitude, and causes. Our assumption that the magnitude of stranding is proportional to the duration of inundation limited the range of impact projected by the model. There is a chance that stranding is better predicted by other metrics, such as the volume of water diverted, or by a multivariate suite of factors. Simulation of the stranding event of 2011 in isolation, in which we not only assumed a low frequency of stranding but were also freed of the need to make a duration–magnitude assumption, indicated a slightly elevated 50-year probability of decline. Though this result bolsters the conclusion that stranding is probably a biologically meaningful burden on the population viability of Green

Sturgeon in the southern DPS, it makes clear that the uncertainty regarding that burden is larger than the interval represented in our chronic stranding scenarios. A monitoring program would provide data critical to reducing that uncertainty.

In the interest of being conservative with respect to population viability, we assumed Green Sturgeon population growth was density independent. This factor, in contrast to the three aforementioned assumptions, could overestimate effects of stranding. If we allowed the parameters contributing to fecundity (sexual maturation, spawning interval, spawning success, egg production, or survival from egg to age 1) to increase with decreasing abundance, then the Green Sturgeon population would exhibit some level of compensatory growth and therefore a smaller long-term response to stranding (Ginzburg et al. 1990). It is interesting to note that the use of a density-dependent population growth model would also be likely to make projections sensitive to the temporal autocorrelation of stranding events (Jonzén et al. 2002).

Future Green Sturgeon monitoring during stranding should attempt to detail the condition of fish at the time of rescue through blood collection and hormone testing. It should be noted that even prior to early ovarian atresia, observed at the histological level, plasma testosterone and estradiol-17 β levels decrease dramatically in female sturgeon when stressed by elevated temperatures (Talbot et al. 2011). Therefore, eggs may appear perfectly normal in the field or after histological processing and examination, but in actuality the female has stopped steroid production and will not spawn. Eggs of females that did not reach the spawning grounds may have already been atresic due to stranding stresses. While results from the GLM did not find any strong candidate models or variables to explain migratory success, there were many environmental and physiological variables, including plasma testosterone and estradiol-17 β levels, that could have been measured during the 2011 rescue efforts. Furthermore, our definition of success (a fish made it to the spawning grounds) does not necessarily mean that a fish was successful in passing on its genetic material. Future research should be carried out to determine the relative genetic contributions of rescued Green Sturgeon to any larvae captured in ongoing juvenile Green Sturgeon monitoring.

To minimize the impacts of flood control diversions to either Green Sturgeon or White Sturgeon we believe there needs to be more formal monitoring at Tisdale and Fremont weirs and additional flood control diversions not evaluated in this study. Such monitoring should not only identify presence of sturgeon species within these structures but include a timely rescue response.

This study illustrates both the risks and the successes in managing for stranding in two flood diversions. We show that removal of sturgeon from such diversions can allow a majority of individuals to both survive and continue natural migratory behavior with low to moderate population level effect. However, rescue efforts should only be considered as a short-term management strategy to reduce population-level risks of stranding. Ultimately, major modifications to flood control structures

will be necessary to prevent stranding risks of sturgeon species during their spawning migration.

ACKNOWLEDGMENTS

We are grateful to the many staff members and volunteers of the California Department of Fish and Game for their exhaustive efforts to capture and return sturgeon back to the river. Without the foresight of agency personnel to include a telemetry component to the rescue, this study would not have been possible. Tagging support was provided by Brian Mahardja and Emily Miller from University of California, Davis, and Robert Chase from the U.S. Bureau of Reclamation. Funding for population modeling was provided by the U.S. Army Corps of Engineers, Sacramento District. Permission to publish was provided by the Chief of Engineers.

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