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FEATURED PAPER

# Estimating the Annual Spawning Run Size and Population Size of the Southern Distinct Population Segment of Green Sturgeon

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*Abstract*

**The Southern Distinct Population Segment of Green Sturgeon *Acipenser medirostris* spawns in the Sacramento River, California, and is listed as a threatened species under the U.S. Endangered Species Act. We estimated the spawning run size and population size in 2010–2015 by using dual-frequency identification sonar (DIDSON) sampling, underwater video camera species identification, and acoustic tag detections. Spawning run size varied from 336 to 1,236 individuals. We estimated the total population size to be 17,548 individuals (95% confidence interval [CI] = 12,614–22,482). The estimated number of adults was 2,106 (95% CI = 1,246–2,966), the estimated number of juveniles was 4,387 (95% CI = 2,595–6,179), and the estimated number of subadults was 11,055 (95% CI = 6,540–**

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**15,571). This study provides the first estimate of Sacramento River Green Sturgeon run size and initiates a time series of abundance that can inform Endangered Species Act recovery processes. Furthermore, these absolute abundance estimates provide a context for evaluating the significance of impacts, such as bycatch in coastal fisheries or entrainment in water diversions, where the number of impacted individuals is known.**

Green Sturgeon *Acipenser medirostris* are anadromous fish that spawn in three major river systems in California and Oregon (NMFS 2006). The species is separated into two distinct population segments (DPSs; Israel et al. 2004), which are managed separately by the National Marine Fisheries Service (NMFS). The Northern DPS (NDPS) consists of individuals that spawn in the Rogue River (southern Oregon) and the Klamath River (northern California); the Southern DPS (SDPS) includes individuals that spawn in the Central Valley of California. The SDPS was designated as a threatened species by NMFS in 2006 (NMFS 2006). The NDPS was designated a species of concern (NMFS 2006), but the concern for NDPS abundance was buffered by the presence of two separate spawning stocks. Loss of spawning habitat is considered a detriment to achieving a sustained population of Green Sturgeon in the Central Valley (Adams et al. 2007).

The amount of historical habitat available to Green Sturgeon varies by population. The NDPS currently has access to 100% of its historically accessible habitat. Spawning by NDPS Green Sturgeon consistently occurs in the main stems of the Rogue and Klamath rivers; however, spawning has also been documented in the Trinity and Salmon rivers, which are tributaries of the Klamath River (Benson et al. 2006). In contrast, the SDPS consists of individuals that spawn almost entirely within a 160-km (100-mi) segment of the Sacramento River below Keswick Dam, which forms a barrier to passage (Adams et al. 2007). In addition, SDPS spawning was documented in the Feather River during June 2011 (Seesholtz et al. 2015), indicating that Green Sturgeon can spawn in major tributaries of the Sacramento River. It is probable that the SDPS historically spawned in portions of the American, Feather, and Yuba rivers that are currently inaccessible due to dams. Today, flow regulation and habitat fragmentation likely constrain their current spawning distribution (Mora et al. 2009).

The NMFS (2006) identified a lack of information describing the total number of individuals in each of the Green Sturgeon populations as a potential risk factor for both populations. At that time, no direct estimates of population abundance existed for either the NDPS or the SDPS, and status designations were prompted by a decline in other indicators of abundance. These indicators included (1) indirect abundance estimates based on the proportion of Green Sturgeon caught with White Sturgeon *A. transmontanus* by the California Department of Fish and Wildlife (CDFW); (2) annual catch in the Yurok tribal Green Sturgeon fishery on the Klamath River; and (3) CPUE estimates from a commercial fishery targeting Columbia River sturgeon. White Sturgeon coexist with Green Sturgeon in the Sacramento River, but White Sturgeon are much more abundant (Moyle 2002). Although there is a body of knowledge about the life history and potential demographic structure of the species (Beamesderfer et al. 2007), DPS-specific estimates of adult abundances, which are necessary to facilitate future status assessments, have yet to be produced. Thus, the objectives of this study were to estimate the number of annually migrating SDPS Green Sturgeon and to estimate the SDPS population size. We also produce estimates of the juvenile and subadult life stages that may be useful for evaluating impacts on those life stages where the number of impacted individuals is known. Estimates of adult abundance will allow the status of SDPS Green Sturgeon to be evaluated relative to recovery criteria.

## METHODS

### Study Site

The Sacramento River is the largest river in California, draining the northern 71,000 km$^2$ of the Central Valley. Our study took place within a 155-km reach between the Anderson–Cottonwood Irrigation District Dam at river kilometer (rkm) 570 and the Highway 32 overcrossing (rkm 415) during June and July of 2010–2015 (Figure 1). We calculated rkm as the distance upstream from the Golden Gate Bridge.

Our sample sites consisted of 125 locations deeper than 5 m as described by Thomas et al. (2014), which were identified based on a mesohabitat survey conducted by the U.S. Bureau of Reclamation beginning in January 2008 and ending in May 2010. In the Rogue River, NDPS Green Sturgeon congregate in locations greater than 5 m deep (Erickson et al. 2002). Thus, in the Thomas et al. (2014) study and in our study, a 5-m depth criterion was chosen to identify potential locations of Green Sturgeon aggregation within the Sacramento River. The U.S. Bureau of Reclamation survey identified 125 discrete habitat units fulfilling this criterion, a portion of which were occupied by Green Sturgeon carrying acoustic tags

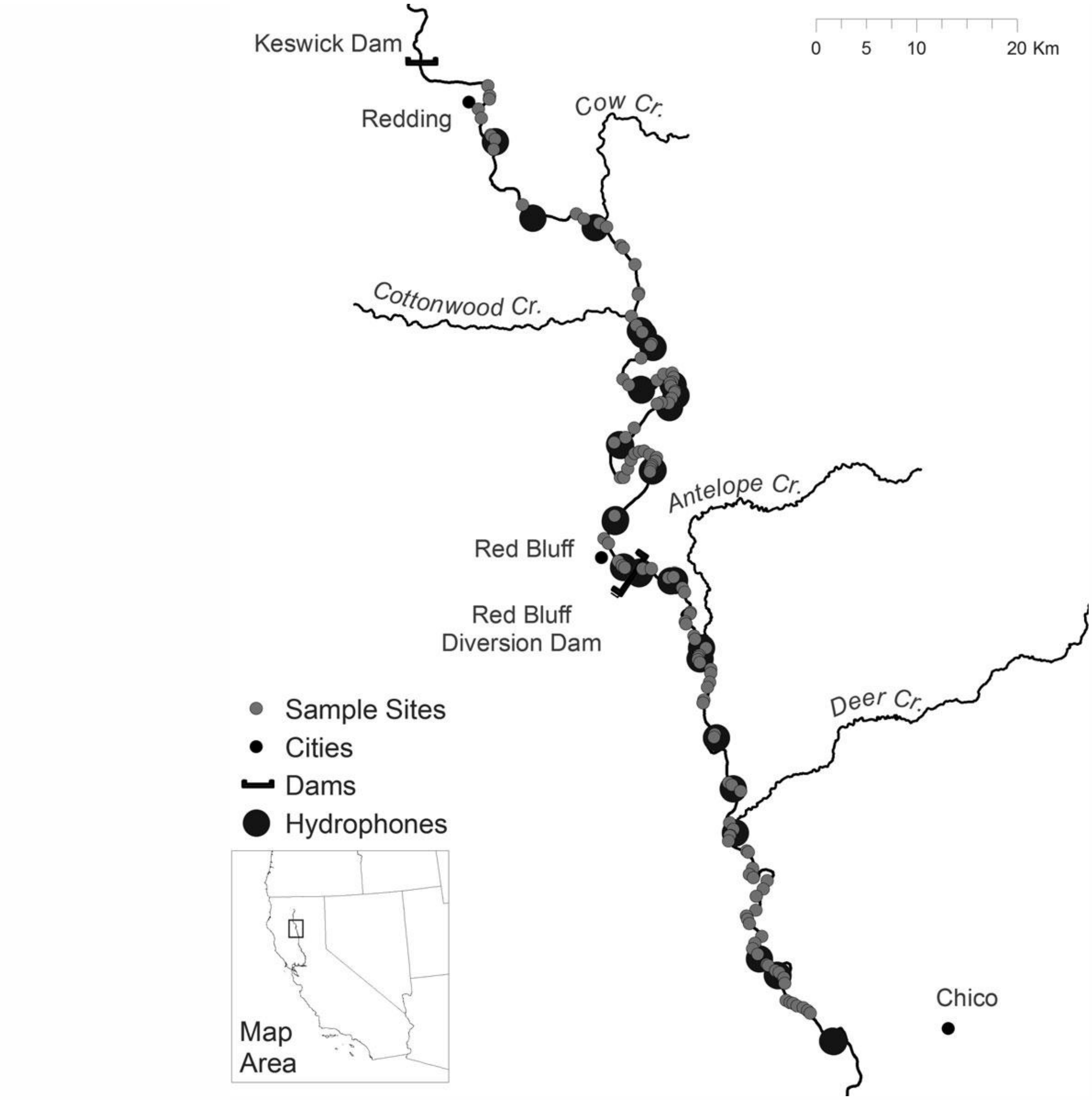

FIGURE 1. Map of the Sacramento River, California, showing the sturgeon sample sites as light-gray dots and tag-detecting monitors as large black dots.

(Thomas et al. 2014). A subset of these surveyed sites was confirmed as spawning locations by Poytress et al. (2013).

## Run Size Estimate

*Estimating abundance with dual-frequency identification sonar.*— We modified the presence–absence and abundance estimation methods described by Mora et al. (2015) to annually estimate the abundance of migrating Green Sturgeon in the Sacramento River. Our modification was that we first censused the sample sites to determine the presence or absence of sturgeon by using dual-frequency identification sonar (DIDSON; Sound Metrics, Belleview, Washington). A DIDSON is an acoustic camera that operates like a medical ultrasound, allowing researchers to see video-like images of ensonified fish, submerged objects, and substrate. The presence–absence surveys were initiated during the first week of June, generally lasted 2 weeks, and were conducted systematically by moving upstream from the downstream-most sample site. We then estimated the abundance of sturgeon at each of the occupied locations over 1–3 d. Depending on the year, the DIDSON surveys were either performed by one or two teams working concurrently. However, video camera sampling (see *Estimating species proportion* below) was always performed by a single team. Our other modification from the methods of Mora et al. (2015) allowed us to account for some of the potential bias inherent in the movement of individual sturgeon during the sample period (see *Estimating migration patterns with telemetry* below).

*Estimating species proportion.*— Both Green Sturgeon and White Sturgeon spawn in the Sacramento River (Kohlhorst 1976). Even though migration studies suggest that their spawning habitats are separated in time and space (Miller 1972; Shaffter 1997; Heublein et al. 2008), we wanted to be sure that the detected sturgeon were the target species, as these two species are indistinguishable in DIDSON images. We used underwater video camera transects to estimate the relative proportions of Green Sturgeon and White Sturgeon at locations of detected sturgeon presence to correct for this potential bias. To gather visual sturgeon detections for species identification (see the Supplement), we towed an underwater video camera (Splash Cam Deep Blue Pro; Ocean Systems, Inc., Everett, Washington) attached to a 10-kg sounding weight at locations where sturgeon densities were high enough to ensure detections (Groves and Garcia 1998). The standard-definition (720-pixel) video feed from the camera was recorded onto DVD (in 2010 and 2011) or digital videotape (2012–2015) for later analysis and was viewed real-time aboard the survey boat to avoid collisions with sturgeon. During 2012–2015, we fitted the towed camera assembly with a high-definition (1,080-pixel) underwater video camera (GoPro Hero2; GoPro, Inc., San Mateo, California) to record a greater field of view and higher image quality compared to the standard-definition images from the Deep Blue Pro. These species proportion surveys occurred during the week after the abundance surveys.

We reviewed the video files, tallied the number of sturgeon detections, and assigned them as Green Sturgeon, White Sturgeon, or undetermined species. Our criteria for identifying sturgeon species are listed in order of decreasing precedence in Table 1 (Moyle 2002).

For each year of the survey, we estimated the proportion of detected sturgeon that were Green Sturgeon as a binomial proportion ($\hat{P}_G$) of the number of sturgeon–camera interactions that were identified as Green Sturgeon ($N_G$) to the number of sturgeon–camera interactions that were identified to species ($N_C$). For each year, we pooled all samples within the study area. A binomial distribution is the distribution of the number of successes resulting from $n$ independent trials, all experiencing the same probability of success $p$. Thus, for each year, we assumed that the proportion of Green Sturgeon ($p$) was uniform within the study area and stable throughout the sample period. Furthermore, we assumed that the results of each trial (each sturgeon–camera interaction [$n$]) were spatially and temporally independent of each other. We calculated $\hat{P}_G$ as

$$\hat{P}_G = \frac{N_G}{N_C}, \tag{1}$$

with variance

$$\hat{V}(\hat{P}_G) = \frac{\hat{P}_G(1 - \hat{P}_G)}{N_C}. \tag{2}$$

TABLE 1. Criteria used to identify sturgeon to species. If none of the criteria was discernable, we categorized the sturgeon as "undetermined species."

| Indicator | Green Sturgeon | White Sturgeon |
|---|---|---|
| Dorsal scutes | 8–11 | 11–14 |
| Lateral scutes | 23–30 | 38–48 |
| Postdorsal scute present | Yes | No |
| Ventral green stripe present | Yes | No |
| Lateral green stripe present | Yes | No |

*Estimating migration patterns with telemetry data.*— Individual Green Sturgeon migrate into and out of the survey area at varying times during each spawning year, so during any given survey, the entire spawning run may not be in the survey area. Mora et al. (2015) described assumptions of our abundance estimation technique that, when violated, will impart bias to the final estimate. They recommended using individual-based information describing migration patterns to correct for these potential sources of bias. To account for the effects of this bias on our abundance estimates, we relied on detections of acoustically tagged Green Sturgeon in the study area. Tagged individuals ($n$ = 288; Heublein et al. 2008; Vogel 2008; Lindley et al. 2011; Thomas et al. 2014) were detected by an array of ultrasonic-tag-detecting hydrophones maintained by the University of California–Davis (UCD) Biotelemetry Laboratory. We utilized these apparent migration patterns to estimate the quantity of two groups of individuals that were not detected during our DIDSON surveys: (1) the proportion of annual migrants that exited the study area prior to our abundance estimate; and (2) the daily average proportion of individuals migrating between units during our study period in June and July of each year. Here, we assume that the mechanisms influencing migration are experienced and acted upon uniformly by all individuals in the study area—that is, $p$ from the binomial distribution example above is the same for all individuals. Furthermore, we assume that each migrant makes the decision to migrate independently of others (i.e., $n$ from the binomial example above). There may be reasons to suspect that migration has a behavioral component and thus may be a contagious dependent process (Lindley et al. 2011); however, we lack the mechanisms to assess how this violation biases our estimate of migration timing.

*Proportion of annual migrants that had exited the study area.*— To estimate the proportion of annual migrants that had exited the study area prior to our abundance estimate, we summarized individual Green Sturgeon detections by week and coded them as either present or having already exited the study site. This was determined for individuals not tagged in the same spawning year as that being summarized, with the exception of 2011, when only two previously tagged fish entered the study area. For 2011, we included the exit dates of 22 individuals that were tagged during that spawning year (Thomas et al. 2014). For all years, the estimate of the proportion of individuals that had exited the study system before our abundance estimate occurred was calculated as a binomial proportion ($\hat{P}_P$) of the number of individuals that had exited the study system by the week of our abundance surveys ($N_S$) to the number of total annual migrants detected on the hydrophone array during that year within the study area ($N_M$),

$$\hat{P}_P = \frac{N_S}{N_M}, \tag{3}$$

with variance

$$\hat{V}(\hat{P}_P) = \frac{\hat{P}_P(1 - \hat{P}_P)}{N_M}. \tag{4}$$

We then utilized the total number of detected sturgeon from the DIDSON transects ($\hat{T}$; from Mora et al. 2015: their equation 5) to estimate the total number of individuals that had exited our study system before our abundance surveys ($\hat{N}_E$) as

$$\hat{N}_E = \left(\frac{\hat{T}}{1 - \hat{P}_P}\right)\hat{P}_P. \tag{5}$$

The variance of $\hat{N}_E$ was calculated using the delta method as in Mora et al. (2015),

$$V(\hat{N}_E) = \left[(\hat{P}_P)^2 \cdot \hat{V}(\hat{T})\right] + \left[(\hat{T})^2 \cdot \hat{V}(\hat{P}_P)\right] + \left[\hat{V}(\hat{P}_P) \cdot \hat{V}(\hat{T})\right]. \tag{6}$$

Equations (5) and (6) result in an annual estimate of the total number of annual migrants that had exited the study area prior to our sampling and the estimated variances of these totals.

*Number of individuals migrating between habitat units.*— To estimate the daily average number of individuals migrating between habitat units in the study area during June and July of each year, we queried the UCD Biotelemetry Laboratory database for Green Sturgeon detections occurring during these months between 0700 and 1900 hours (the daily time period of sampling) and only at hydrophones not located directly in the sample sites. We estimated a daily quantity ($\hat{P}_i$) as a binomial proportion of the number of unique individuals detected and assumed to be migrating between units ($N_D$) to the number present in the study area and not detected during that day and thus assumed to be within the habitat units ($N_M$),

$$\hat{P}_i = \frac{N_D}{N_M}, \tag{7}$$

with variance

$$\hat{V}(\hat{P}_i) = \frac{\hat{P}_i(1 - \hat{P}_i)}{N_M}. \tag{8}$$

To estimate the annual average proportion of individuals that were moving between units during our sample period, we calculated the average ($\bar{P}_I$) of the daily estimates $\hat{P}_i$ as

$$\bar{P}_I = \sum_i^n \frac{\hat{P}_i}{n}, \tag{9}$$

with variance

$$V(\bar{P}_I) = \sum_i^n \frac{\hat{V}(\hat{P}_i)}{n^2}. \tag{10}$$

For each year, we then calculated the total number of individuals that were transiting between sample sites during our abundance surveys ($\hat{N}_T$) as

$$\hat{N}_T = \left(\frac{\hat{T}}{1 - \bar{P}_I}\right)\bar{P}_I. \tag{11}$$

The variance of $\hat{N}_T$ was calculated using the delta method as in Mora et al. (2015),

$$V(\hat{N}_T) = \left[(\bar{P}_I)^2 \cdot \hat{V}(\hat{T})\right] + \left[(\hat{T})^2 \cdot \hat{V}(\bar{P}_I)\right] + \left[\hat{V}(\bar{P}_I) \cdot \hat{V}(\hat{T})\right]. \tag{12}$$

Equations (11) and (12) result in annual estimates of the total number of individuals migrating between units during our annual sample periods and the estimated variances of these totals.

The means and variances of the three estimated annual quantities ($\hat{T}, \hat{N}_E$, and $\hat{N}_T$) were then summed to represent the total number of Green Sturgeon that migrated during each year ($\hat{T}_i$) and the estimated variances ($\hat{V}[\hat{T}_i]$) of those totals.

### Population Estimate

To estimate the number of mature adults in the SDPS, we first had to estimate two quantities: (1) the mean (and variance) of run sizes over a 6-year period; and (2) the distribution of interannual spawning frequencies.

Green Sturgeon are iteroparous, and individuals do not make spawning migrations every year. To estimate the distribution of temporal intervals between spawning migrations from repeat spawners, we again turned to the detection records for acoustically tagged Green Sturgeon. The detection database was queried for all Green Sturgeon performing a spawning migration. Individuals were considered to have completed a spawning migration in a given year if they were detected by a tag-detecting monitor in our study area during that year. We then calculated the interval (in years) between spawning migrations for 41 individuals that had spawned more than once. The identified distribution was used as an estimate of SDPS spawning periodicity. The mean ($\bar{S}_{GS}$) and variance ($V[\bar{S}_{GS}]$) of this distribution were calculated using the standard estimators for a sample mean and variance,

$$\bar{S}_{GS} = \frac{1}{n}\sum_{i}^{n} x_i \tag{13}$$

and

$$V\left(\bar{S}_{GS}\right) = \frac{1}{n-1}\sum_{i}^{n}\left(x_i - \bar{x}\right)^2. \tag{14}$$

We then estimated the average run size of SDPS Green Sturgeon by calculating the 6-year geometric mean of our run size estimates using the following equations. The average run size ($\bar{T}_G$ ) was calculated as

$$\bar{T}_G = \sqrt[6]{\prod\nolimits_i^6 \hat{T}_i}, \tag{15}$$

with variance

$$V(\bar{T}_G) = \sum_{i}^{6} \frac{\hat{V}(\hat{T}_i)}{6^2}. \tag{16}$$

We estimated the total number of adults in the SDPS ($\hat{N}_A$) by multiplying the average run size ($\bar{T}_G$) by the estimated average spawning periodicity ($\bar{S}_{GS}$),

$$\hat{N}_A = \hat{S}_{GS}\bar{T}_G. \tag{17}$$

The variance of $\hat{N}_A$ was calculated using the delta method as in Mora et al. (2015),

$$V\left(\hat{N}_A\right) = \left[\left(\hat{S}_{GS}\right)^2 \hat{V}(\bar{T}_G)\right] + \left[(\bar{T}_G)^2 \hat{V}\left(\hat{S}_{GS}\right)\right] + \left[\hat{V}(\bar{T}_G)\hat{V}\left(\hat{S}_{GS}\right)\right]. \tag{18}$$

Beamesderfer et al. (2007) determined that given multiple assumptions about population characteristics, the SDPS Green Sturgeon population would have an expected life stage distribution of 25% juveniles, 63% subadults, and 12% adults. The juvenile life history stage was defined by Beamesderfer et al. (2007) as "fish during freshwater rearing prior to migration to the ocean (generally one to three years of age and 0–60 cm in length)." They defined adults as "fish larger than the median size and age of female maturation (approximately 165 cm and 20 years of age)." The subadult life history stage refers to individuals between these two age-classes. Combining the proportions provided by Beamesderfer et al. (2007) with our estimate of the number of adults in the SDPS, we estimated the number of individuals in the juvenile and subadult life history classes.

## RESULTS

Abundance sampling occurred over 1–3 d from mid-June to early July each year (Table 2). The number of days required to sample the occupied habitat units varied between years due to the number of cumulatively occupied units and the varying number of sampling teams. During 2010–2012, two crews worked together to sample different units concurrently; however, during 2013–2015, sampling was performed by one crew.

Table 2 displays the estimates of the total number of sturgeon present considering only the DIDSON transect estimate of abundance. As estimates of run size for each year, these values are uncorrected for the bias that was imparted due to species proportion, migration timing, and individual movement between sample sites during our surveys (Mora et al. 2015). We detected an average of 346 sturgeon each year, ranging from 220 sturgeon in 2011 to 526 sturgeon in 2014.

TABLE 2. Dates when the Green Sturgeon abundance estimation surveys occurred and the estimated total number of sturgeon (±95% confidence interval [CI]) resulting from the dual-frequency identification sonar transects, uncorrected for bias due to violations of assumptions.

| Year | Sample dates | $N$ ± 95% CI |
|---|---|---|
| 2010 | Jun 17 | 245 ± 63 |
| 2011 | Jun 16 | 220 ± 41 |
| 2012 | Jun 14, 15 | 329 ± 56 |
| 2013 | Jun 10, 11, 12 | 338 ± 61 |
| 2014 | Jun 30; Jul 1, 2 | 526 ± 64 |
| 2015 | Jun 24, 25, 26 | 423 ± 59 |

TABLE 3. Numbers of Green Sturgeon ($N_{Green}$) and White Sturgeon ($N_{White}$) detected on video camera, the number of unknown sturgeon detected, and the mean and variance of the estimated proportion of Green Sturgeon ($P_{Green}$).

| Year | $N_{Green}$ | $N_{White}$ | Unknown | $P_{Green}$ | Variance |
|---|---|---|---|---|---|
| 2010 | 76 | 0 | 47 | 1.00 | 0.0000 |
| 2011 | 39 | 0 | 40 | 1.00 | 0.0000 |
| 2012 | 50 | 0 | 57 | 1.00 | 0.0000 |
| 2013 | 88 | 2 | 87 | 0.98 | 0.0002 |
| 2014 | 100 | 0 | 64 | 1.00 | 0.0000 |
| 2015 | 37 | 0 | 26 | 1.00 | 0.0000 |

Annual estimates of the proportion of Green Sturgeon in our study area, as calculated from video camera transects, ranged from 0.98 to 1.00 (Table 3). Of the 699 sturgeon that were observed on video, 390 were identifiable to species; of those, only two were White Sturgeon. The two White Sturgeon observations occurred during a single year and were captured on the same day in the same location on the same video camera transect. Classification of a sturgeon as unidentifiable was usually due to (1) a blurred image resulting from the combination of distance and turbidity; or (2) a limited viewing time after the fish was startled and quickly swam away. Otherwise, it was apparent that the majority of sturgeon detected in our study area were Green Sturgeon.

The estimated proportion of annual migrants that had left the study area before our abundance surveys were performed averaged 0.33 and ranged from 0.00 to 0.57 (Table 4). The year 2013 was an outlier, with zero individuals leaving the study area before our abundance surveys. The estimated proportion of Green Sturgeon in transit between sample sites during DIDSON surveys averaged 0.013 and ranged from 0.004 to 0.017 (Table 5).

The estimates of annual run size accounting for the proportion of sturgeon transiting between sites or out of the study area are presented in Table 6. These values represent the total number of adult Green Sturgeon that entered our study area each year. These values do not include the number of migrants that entered tributaries of the Sacramento River, such as those documented by Seesholtz et al. (2015). The average run size was calculated as 571, with a 95% confidence interval (CI) of 529–613.

TABLE 4. Proportion of acoustic-tagged Green Sturgeon that were detected as leaving the study area each year before the initiation of our abundance surveys ($N_{Migrants}$ = number of total annual migrants detected on the hydrophone array within the study area during the specified year; $N_{Exited}$ = number that exited the study area prior to the abundance estimation survey in the specified year).

| Year | $N_{Migrants}$ | $N_{Exited}$ | Proportion not in river | Variance |
|---|---|---|---|---|
| 2010 | 9 | 5 | 0.56 | 0.027 |
| 2011 | 24 | 8 | 0.33 | 0.009 |
| 2012 | 18 | 8 | 0.44 | 0.014 |
| 2013 | 14 | 0 | 0.00 | 0.000 |
| 2014 | 14 | 8 | 0.57 | 0.017 |
| 2015 | 32 | 14 | 0.44 | 0.008 |

TABLE 5. Estimated average daily proportion of tagged Green Sturgeon that migrated between sample sites during June and July in each study year.

| Year | Proportion in transit | Variance |
|---|---|---|
| 2010 | 0.004 | $4.07 \times 10^{-6}$ |
| 2011 | 0.02 | $1.37 \times 10^{-5}$ |
| 2012 | 0.015 | $7.72 \times 10^{-6}$ |
| 2013 | 0.013 | $1.41 \times 10^{-5}$ |
| 2014 | 0.017 | $1.66 \times 10^{-5}$ |
| 2015 | 0.01 | $4.14 \times 10^{-6}$ |

TABLE 6. Estimated number of Green Sturgeon (±95% confidence interval [CI]) that migrated into the study area between 2010 and 2015.

| Year | $N \pm$ 95% CI |
|---|---|
| 2010 | 552 ± 109 |
| 2011 | 334 ± 61 |
| 2012 | 597 ± 98 |
| 2013 | 335 ± 61 |
| 2014 | 1,236 ± 157 |
| 2015 | 756 ± 98 |

Based on the detections of 42 repeat migrations by 41 individuals, a spawning interval of 2–6 years was calculated. The mean spawning periodicity was 3.69 years, with a variance of 0.56 (Figure 2).

We directly estimated the number of adults in the SDPS to be 2,106 (95% CI = 1,246–2,966). Applying the

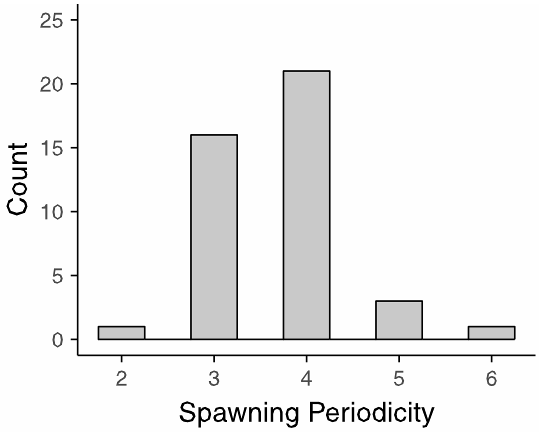

FIGURE 2. Histogram depicting the spawning periodicity (years) of acoustically tagged Green Sturgeon.

life history proportions of Beamesderfer et al. (2007), we estimated there to be 4,387 juveniles (95% CI = 2,595–6,179) and 11,055 subadults (95% CI = 6,540–15,571). This results in a total population estimate of 17,548 SDPS Green Sturgeon, with a 95% CI of 12,614–22,482 individuals.

## DISCUSSION

We estimated that during each year of the study, there were between 1,246 and 2,966 SDPS Green Sturgeon in the reproductive portion of the population. We regard this as a fairly reliable estimate of SDPS Green Sturgeon population size because it overcomes two issues that had hampered earlier estimates: a limited sample region (Israel and May 2010); and estimation of Green Sturgeon abundance based on the ratio of Green Sturgeon to White Sturgeon numbers in a White Sturgeon sampling study (U.S. Fish and Wildlife Service 1995; Adams et al. 2007). Israel and May (2010) used genetic techniques to estimate effective population size ($N_e$) during 2002–2006. Their study sampled out-migrating juveniles at Red Bluff Diversion Dam, potentially omitting the contribution of individuals that were spawned downstream of this location. Estimates of the $N_e$ contributing to their samples ranged from 10 to 28 spawners. These results are unsurprising given two facts. First, $N_e$ is often smaller than the census population size. Second, their sampling occurred during a time when Red Bluff Diversion Dam operated as a temporal barrier to Green Sturgeon spawning, likely reducing the numbers of spawners upstream of this point and thus reducing the number of spawners contributing to their sample (Heublein et al. 2008). The U.S. Fish and Wildlife Service (1995) study estimated the number of adult (>101.6 cm) Green Sturgeon that were present in the Sacramento–San Joaquin Estuary for 8 years throughout the interval between 1967 and 1990. A direct estimate using capture–recapture estimation was not possible, as no recaptures of individuals occurred during sampling in that study. In the U.S. Fish and Wildlife Service (1995) study, the mean number of Green Sturgeon adults was estimated at 983, resulting in a doubling goal of 1,966 individuals. The results of our study suggest that the doubling goal set by the Central Valley Project Improvement Act has been met. If anything, our study likely underestimated the abundance of SDPS Green Sturgeon because it did not include the recently documented spawners in the Feather River, as determined from a collection of 13 eggs identified as originating from Green Sturgeon (Seesholtz et al. 2015). Future population estimates of SDPS Green Sturgeon adults should coordinate DIDSON sampling in the main-stem Sacramento River with concurrent sampling in other Central Valley tributaries.

Our estimates of juvenile, subadult, and total SDPS Green Sturgeon numbers are less reliable than our adult estimates because the former were based on the ratios from Beamesderfer et al.'s (2007) modeling study, which combined data from the NDPS and SDPS. Their estimate of the percentage of juvenile sturgeon is particularly uncertain because so little is known about this life stage. Additionally, their model requires four assumptions that are admittingly rarely met: (1) constant recruitment, (2) population equilibrium, (3) stable size and age structure, and (4) a lack of density dependence (Beamesderfer et al. 2007). However, the present study provides a rough estimate of total abundance that is suitable for assessing the impacts of take, such as that observed in coastal trawl fisheries and at large water diversions.

The demographic recovery criteria, which are under development by NMFS as part of the SDPS Green Sturgeon Recovery Plan, contain quantitative targets of population size used to determine whether significant threats to the recovery of a population have been alleviated. It is clear that further implementation of DIDSON-based surveys for measuring the abundance and distribution of Green Sturgeon during their spawning period will provide information that is crucial to the evaluation of SDPS status. Two of the five draft demographic recovery criteria are based on either abundance (annual run size or total population size) or distribution (successful spawning in at least two rivers within their historical range). Spawning has been recently detected in the Feather River (Seesholtz et al. 2015), and future coordinated DIDSON surveys of the Feather and Sacramento rivers are planned.

This study provides additional evidence that sturgeon present in the study area during June and July are almost entirely Green Sturgeon. The only exception to this was the detection of two White Sturgeon in 2013. Given the findings of Miller (1972) and Shaffter (1997), this pattern was not surprising; however, we had expected a larger proportion of the detected sturgeon to be White Sturgeon based on self-reporting by recreational fishermen to CDFW. Other evidence provides support for Green Sturgeon prevalence. For example, all sturgeon larvae and juveniles that were captured in a screw trap operated at Red Bluff Diversion Dam were identified as Green Sturgeon (Poytress et al. 2014). In addition, initial results of Green Sturgeon and White Sturgeon migration studies conducted by the UCD Biotelemetry Laboratory support our findings (E. Miller, UCD, personal communication).

The high run size estimate from 2014 stands out as an obvious outlier. The sampling for the 2014 estimate occurred roughly 2 weeks later in the spawning season than the other annual estimates. Otherwise, all aspects of the study design in 2014 were the same as those in previous years. For 2014, two components of the estimate of run size were the greatest for any year of our study: the total number of sturgeon detected via DIDSON transects; and the proportion of individuals that had left the study system before our DIDSON sampling began. These two factors clearly combined to inflate the estimate of run size, but we consider their estimated values to be valid because measurements from all years were performed uniformly. It is worth noting that the 2014 and 2015 spawning seasons occurred during a major drought in California, although it is unknown how environmental factors (e.g., reduced flow) influence Green Sturgeon run size and spawning migrations. As our study continues and as our time series expands, we plan to investigate these questions.

Finally, because our model is reliant on individual-based migration information, continued tagging of individuals with long-lasting acoustic tags will be crucial to inform population monitoring efforts into the future. Population monitoring of the Green Sturgeon SDPS is critical for understanding the status of the species. Based on our findings, DIDSON sampling and acoustic tagging appeared to be the most efficient and least invasive methods of tracking SDPS Green Sturgeon status. It would be important to know, for example, whether the greater numbers of adults observed in 2014 represented a reproductive cohort or a response to environmental changes.

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## SUPPORTING INFORMATION

Additional supplemental material may be found online in the supporting information tab for this article.