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ARTICLE

Spatial and Temporal Distribution of Spawning Events and Habitat Characteristics of Sacramento River Green Sturgeon

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Abstract
Spawning of the Southern Distinct Population Segment of Green Sturgeon *Acipenser medirostris* occurs annually within the Sacramento River in California. Artificial substrate samplers were used to collect Green Sturgeon eggs between 2008 and 2012 and in a reach of the river 94 river kilometers (rkm) long (rkm 426–332). A total of 268 eggs and 5 posthatch larvae were sampled from seven identified spawning sites between April 2 and July 7, primarily from medium gravel substrates. At these sites the mean water column velocities were 0.8 m/s at depths ranging from 0.6 to 11.3 m (6.4 ± 2.3 m, mean ± SD). We noted an average discharge of 314 m^3/s and a median turbidity value of 3.9 NTU during estimated spawning events. Spawning at all sites occurred when average water temperatures were 13.5 ± 1.0°C and during water year types ranging from critically dry to wet. Green Sturgeon eggs averaged 4.11 ± 0.20 mm in diameter (n = 207), were very adhesive, and were between developmental stages 2 (just fertilized) and 44 (posthatch larva). We estimated that eggs were collected from a minimum of 54 different spawning events, based on sample date and location, egg developmental stage at capture, and water temperatures. Green Sturgeon spawning data indicates there is spatial separation from sympatric White Sturgeon *A. transmontanus*, but some temporal overlap exists. The thermally and hydrologically managed Sacramento River with its numerous diversions and competing water demands appears to have an approximate reach of 120 rkm in the 405-km-long river that is favorable for Green Sturgeon spawning in most years. Management decisions need to assess and incorporate the spawning habitat requirements of Green Sturgeon and coordinate this information with that of endangered winter-run Chinook Salmon *Oncorhynchus tshawytscha* while attempting to meet the diverse demands of the limited Sacramento River water resources.

Green Sturgeon *Acipenser medirostris* are considered to be the most widely distributed of the sturgeon family Acipenseridae (Adams et al. 2007) and the most marine-oriented of the sturgeon species (Erickson and Hightower 2007; Lindley et al. 2008). Green Sturgeon collections from the Sacramento River system were genetically separate from populations sampled from the Klamath and Rogue rivers (Israel et al. 2004, 2009) and estimated to have low overall spawner abundance (Israel and May 2010). The Sacramento River in northern California currently hosts the only known recurring spawning population

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of the Southern Distinct Population Segment (SDPS) of Green Sturgeon. However, during a high spring outflow and wet year Green Sturgeon were documented to have spawned in the Feather River, California, (Seesholtz et al. 2015) and may have spawned in the Yuba River (P. Bergman, 2011 memorandum to E. Campbell, Anadromous Fish Restoration Program, on Green Sturgeon observations at Daguerre Point Dam). The SDPS Green Sturgeon was listed as threatened under the U.S. Endangered Species Act (ESA) on June 6, 2006 (BRT 2005; NMFS 2006). The principle risk factor that resulted in the listing of SDPS Green Sturgeon was determined to be the loss of spawning habitat resulting in heightened vulnerability to endangerment of the species due to a concentration of spawning, harvest, and entrainment (Adams et al. 2007). Flow and temperature concerns and overall habitat degradation were also listed as concerns, but lacked river-specific impact information.

Spawning habitat and adult spawning characteristics (e.g., periodicity) were documented for the Northern Distinct Population Segment (NDPS) of Green Sturgeon on the Rogue River (Erickson et al. 2002), and it was determined that adults hold in deep pools or “holes” in the main stem of large turbulent rivers. Eggs are believed to be broadcast-spawned into cobble substrates and settle between interstitial spaces for cover (Moyle 2002). Green Sturgeon eggs are highly adhesive over a localized region of the egg (Van Eenennaam et al. 2008, 2012), but relatively little else has been documented regarding the spawning characteristics of the SDPS Green Sturgeon barring basic evidence of reproduction (Gaines and Martin 2002; Brown 2007; Seesholtz et al. 2015).

Following ESA listing, the U.S. Bureau of Reclamation (USBR) elevated their concern regarding the potential impacts of operating various components of a principal water resource management operation in California, the Central Valley Project, in relation to Green Sturgeon. Specifically, the Red Bluff Diversion Dam (RBDD), a seasonal impoundment in the upper Sacramento River watershed (Figure 1), was indicated to likely jeopardize the existence of the SDPS Green Sturgeon if operations continued unabated (NMFS 2009). Unlike many dams, the RBDD was designed to divert water for agricultural and wildlife refuge needs and functioned under a relatively narrow set of river conditions. The result was the 11 dam gates spanning the Sacramento River could be raised and lowered by mechanical manipulation as water resources were needed, yet had to be raised when river flows exceeded 2,800 m^3/s or the gates were overtopped (USBR 1970).

As noted in Brown (2007), the RBDD forms a complete barrier to adult Green Sturgeon migrants to uppermost river spawning areas. Even though the dam gates were lowered seasonally between May and September in recent decades, the timing of gate lowering oftentimes resulted in large aggregations of sturgeon being observed in the tailrace of the dam between May and July. In 2001, Green Sturgeon spawning areas were coarsely documented through the capture of a single larva 15 river kilometers (rkm) upstream from the RBDD and two eggs immediately downstream (Brown 2007). This realization by the USBR that operations created a barrier to upstream migrants prompted the initiation of a series of studies focused on determining to what extent multiple life history stages of the Sacramento River population may be affected by the operations of the RBDD. From 2008 through 2012, the USBR and the University of California, Davis (UCD) conducted field research primarily on the adult life history phase of SDPS Green Sturgeon. Thomas et al. (2013, 2014), through the acoustic tagging and tracking of adult Green Sturgeon, determined that the timing of the lowering of the RBDD gates occurred at a critical time for mature adults and that access to spawning habitat was denied to a portion of individuals migrating upstream to spawn during optimal temperatures for egg incubation (Van Eenennaam et al. 2005).

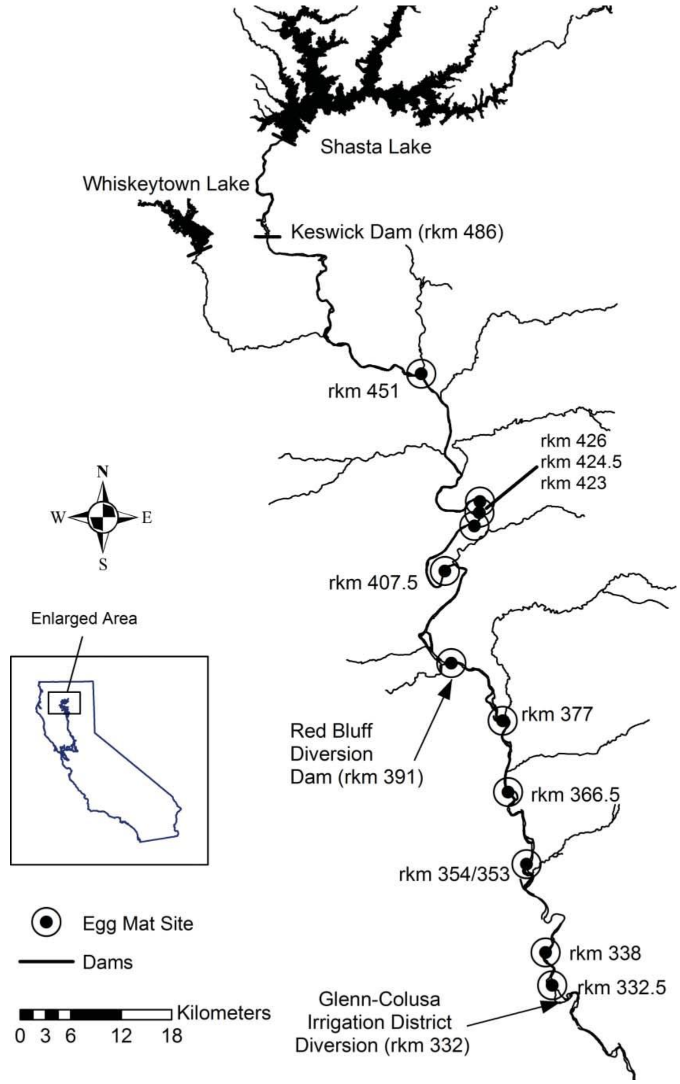

FIGURE 1. Sample sites for Green Sturgeon egg mats on the Sacramento River, California.

The U.S. Fish and Wildlife Service (USFWS) focused efforts on the earliest life history stage through egg deposition surveys. Heath and Walker (1987) noted the importance of sampling eggs and larvae to identify spawning and nursery areas. Knowledge of these areas has been deemed critical to understand the overall abundance of fish populations (Hjort 1914; May 1974; Hempel 1979) and was deemed essential to identify potential impacts of water resource management operations in the upper Sacramento River to the population. Eggs collected on substrate mats have been used to identify spawning areas for a number of North American sturgeon species: Gulf Sturgeon *A. oxyrinchus desotoi* (Sulak and Clugston 1998; Fox et al. 2000), Shortnose Sturgeon *A. brevirostrum* (Cooke and Leack 2004; Duncan et al. 2004), Lake Sturgeon *A. fulvescens* (Caswell et al. 2004; Chiotti et al. 2008), White Sturgeon *A. transmontanus* (Schaffter 1997; Paragamian et al. 2002; Perrin et al. 2003), and to a limited extent, Green Sturgeon (Brown 2007; Seesholtz et al. 2015).

The need for multiple successful spawning populations of Green Sturgeon within the SDPS outside of the main-stem Sacramento River was listed as a primary threat to the SDPS Green Sturgeon (Adams et al. 2007) and is of great concern for those seeking its removal from the ESA list (NMFS 2006). Acquiring knowledge of the primary spawning population's behavior and habitat requirements is a critical first step in recovery efforts for this fish species. The objectives of this study were to document the spatial and temporal distribution of Green Sturgeon spawning events in the Sacramento River through the collection of eggs and describe the physical habitat of egg collection sites during estimated spawning periods.

STUDY SITE

The Sacramento River originates in northern California from the springs of Mt. Eddy near Mt. Shasta (Hallock et al. 1961). It flows south through 600 km of the state, draining slopes of the Coast, Klamath, Cascade, and Sierra Nevada mountain ranges and eventually reaches the Pacific Ocean via the San Francisco Bay. Shasta Dam and its downstream flow-regulating structure, Keswick Dam (Figure 1), have formed a complete barrier to upstream anadromous fish passage since 1944 (Billington et al. 2005). Mora et al. (2009) estimated that Keswick Dam (rkm 485; measured from the confluence with the San Joaquin River at Collinsville) reduced Green Sturgeon access to Sacramento River tributary habitats totaling 39 ± 14 rkm (mean ± SD). The 94-rkm reach between Keswick Dam and RBDD (rkm 391) has been minimally impacted by channel control structures and supports areas of intact riparian vegetation. At and below RBDD, the river has been extensively armored or levied to provide flood control and protect high-value agricultural land from bank erosion. Moreover, a myriad of small water diversions and several large-scale diversion facilities occur along its length as it flows to the Sacramento–San Joaquin Estuary.

Egg sampling was focused within a 132-rkm reach of the Sacramento River from the Deschutes Bridge (rkm 452) to Gianella Bridge (rkm 320), and RBDD is roughly halfway between the two bridges (Figure 1). The study area contained the previously confirmed spawning reach noted in Brown (2007) and was expanded upstream to include potential spawning habitat associated with the presence of adult Green Sturgeon during studies using acoustic telemetry (Heublein et al. 2009; Thomas et al. 2013, 2014) and dual-frequency imaging sonar (DIDSON) (E. Mora, University of California, Davis, personal communication). Additionally, the study area encompassed areas downstream from RBDD known by anglers and researchers (Vogel 2008) to be annual Green Sturgeon holding habitat.

METHODS

Egg collection.—We used artificial substrate mats to determine the location and timing of Green Sturgeon spawning events. Egg mats were constructed using two 89 × 61-cm rectangular sections of furnace filter material secured back to back within a welded steel framework (McCabe and Tracy 1994; Schaffter 1997). Egg mats were held in position by a three-fluke steel anchor attached to the upstream end of each mat with a float attached to the downstream end using 9.5-mm-diameter braided polypropylene rope. Three river mesohabitat types were sampled in 2008 and described as "upstream" (riffle entering the pool), "within pool" (area within and/or flanking the deepest portions of the pool), and "pool tail" (glide exiting the pool extending to pool tail crest). Mats were deployed in the "within pool" mesohabitat (areas flanking deepest portions of pools) in years 2009–2012 based on the results of the 2008 pool mesohabitat comparison study (Poytress et al. 2009). The exact number of egg mats deployed at each site (2–4 pairs) depended upon the physical area of each site and the need to maintain a navigable river channel for public transit and fishing.

Specific locations sampled for Green Sturgeon eggs were selected based upon four data sources: (1) radiotelemetry data from a concurrent study (Thomas et al. 2013, 2014; R. Corwin, USBR, unpublished data), (2) knowledge and experience of local fishing guides and prior egg mat sampling efforts (Brown 2007), (3) side-scan and DIDSON imagery evaluations (E. Mora, University of California, Davis, personal communication), and (4) logistical constraints. The concurrent adult radiotelemetry study (Thomas et al. 2013, 2014) examined movement patterns via mobile and stationary tracking of 43 acoustically tagged adult Green Sturgeon exhibiting spawning behaviors between 2008 and 2012. Sample locations varied annually in an effort to confirm real-time habitat use by adult aggregations. Over the 5 years of the study, we placed egg mats in a total of 11 locations on the Sacramento River at rkm 451, 426, 424.5, 423, 407.5, 391, 377, 366.5, 354–353, 338, and 332.5 (Figure 1). Only rkm 424.5 was sampled in all 5 years of the study.

The sampling period was determined each year by noting the presence of acoustically tagged adults from concurrent (Thomas et al. 2014) and earlier research efforts (Vogel 2008; Heublein et al. 2009) within the presumed spawning reach. Between two and four paired egg mats were set at each site annually for between 1 and 4 months. We attempted to sample egg mats continuously throughout each season, but inevitably egg mats had to be pulled during spring discharge events that occurred between one and five times per year. Egg mats were redeployed within 3 to 7 d after these events.

Egg assessment.—Egg mat sampling consisted of a visual inspection every 72–96 h. Sample effort data were calculated using the date and time individual egg mats were set and retrieved. Egg mats were manually retrieved from the river, placed on a boat in a custom-made egg mat cradle, and initially inspected on both sides by a minimum of two field crew members. Egg mats were then rinsed with river water to remove sediment and coarse debris and reinspected. Rinse water and debris were filtered using a removable 3.2-mm-mesh net inserted below each egg mat within the cradle to capture any displaced eggs. After a second inspection and inspection of the mesh nets, egg mats were redeployed.

Eggs collected from each mat were counted and identified to species in the field whenever possible. All sampled eggs were placed into vials containing 95% ethyl alcohol for species confirmation and further analysis. Eggs were identified as Green Sturgeon by egg color, size, and chorion thickness, as they are larger, of an olive-brown color, and have a thinner chorion compared with those of White Sturgeon (Van Eenennaam et al. 2008). Because most of the eggs were slightly oval shaped, the maximum diameter was measured (±0.001 mm, rounded to 0.01 mm) using a dissecting microscope with camera lucida and a digital image analyzing tablet (Nikon Microplan II). In some cases an accurate diameter could not be measured due to flattened shapes resulting from fixation or breakage during handling, or if the eggs were covered in fungus or algae.

Classification of egg development stage was based on Dettlaff et al. (1993). Eggs that were not viable were either broken during collection and could not be staged, were covered in fungus and/or algae, had mottled or uneven pigmentation with white streaks, or were "unknown." Eggs of unknown stage may have actually been fertilized eggs at a very early stage (1–2 h postfertilization) or relatively fresh unfertilized eggs, since the two are difficult to distinguish from each other (Cooke and Leach 2004). In this study, eggs of unknown stage were considered not viable.

Spawning event estimates.—Methods to estimate spawn date were described in Seesholtz et al. (2015); briefly, the date was back-calculated using an exponential function based on water temperature and rate of embryonic development. The minimum number of females were estimated based on the back-calculated spawn date, the date the egg mats were removed, and the assumption it takes up to 21 h for a female to complete oviposition (Van Eenennaam et al. 2012). We report the data as a minimum number of spawn events, as it is possible that more than one female was spawning in an area at the same time and location during the 72–96-h period between typical egg mat inspections.

Spawning habitat assessment.—Environmental data were collected during both the setting and retrieval of the egg mats. These data were: GPS coordinates recorded at the water surface directly above each egg mat, water turbidity, and river depth at each egg mat location. Hourly water temperature was monitored at or near each site using a Stowaway Tidbit temperature logger maintained by UCD, USBR, or USFWS personnel. Sacramento River hourly flow data for the sites above RBDD were obtained from the U.S. Geological Survey's Bend Bridge gauging station (gauge number 11377100). River flow for the lowermost site was obtained from the California Department of Water Resources' Vina-Woodson Bridge gauging station (http://cdec.water.ca.gov/cgi-progs/queryF?VIn).

Topographic and bathymetric data along with mean water column velocities were collected at six study sites using a survey-grade, real-time kinematic (RTK)-GPS unit (Topcon HiPer+) and an acoustic doppler current profiler (ADCP; RD Instruments Workhorse Rio Grande) in 2013. Data were collected for one physical habitat simulation transect at six sites to simulate the velocities present during the egg mat sampling (USFWS 2013). Egg mat depth and substrates were confirmed using the RTK-GPS, ADCP, and underwater videography (Gard and Ballard 2003). Substrate size was visually classified in nine categories ranging from sand to bedrock using substrate descriptors listed in Gard (2006).

Data analysis.—Catch per unit effort was calculated annually for each site and calculated as total eggs collected divided by total hours sampled and expressed in wetted mat days (wmd; one mat set for 24 h). Egg diameter and physical habitat data are presented as mean ± SD, when applicable, with trends depicted using frequency distributions.

RESULTS

Egg Collections, Assessments, and Estimated Spawning Events

Initiation and duration of egg mat sampling varied annually. Initiation was based on first detection of adults within the putative spawning reach of the river (Thomas et al. 2014), and duration was generally between mid-March and early August of each year. Sampling of the tailrace at RBDD (rkm 391) occurred within a week of gate closure between 2008 and 2011 (Table 1). In 2012, the RBDD gates were not lowered as water diversions were derived from a newly constructed bank-side pumping facility (NMFS 2009). Adult sturgeon were not detected in aggregations in the RBDD tailrace area as fish

TABLE 1. Green Sturgeon egg mat data collected on the Sacramento River between 2008 and 2012: CPUE data in wetted mat days (wmd; one sampler set for 24 h), embryo and larval developmental stages based on Dettlaff et al. (1993), estimated spawning period back-calculated using mean daily water temperatures, and developmental stage. The number of spawn events was based on spawn date, developmental stage, and date egg mats were removed with the assumption it takes up to 21 h to complete oviposition; NA = data not available.

Site	Year	Sample period	Range of collection dates	Eggs or larvae (*n*)	CPUE (eggs/ wmd)	Viable eggs (%)	Mean ± SD egg diameter (mm)	Developmental stage(s)	Estimated spawning period	Estimated spawning events (*n*)
rkm 426	2010	Mar 17–Jul 23	May 10	1	0.003	100	NA	33[a]	May 4	1
	2011	Apr 12–Jul 18	May 27–Jun 20	9	0.031	63	4.25 ± 0.29	21–35[b]	May 24–Jun 14	3
	2012	Apr 5–Jul 10	May 11–14	16	0.088	81	3.91 ± 0.15	3–13	May 10–14	2
rkm 424.5	2008	Apr 22–Aug 1	May 2–Jun 13	12	0.059	67	4.21 ± 0.18	16–30	Apr 30–Jun 10	3
	2009	Mar 30–Jul 30	Apr 2–May 14	9	0.028	67	4.09 ± 0.14	2–19	Apr 2–22	4
	2010	Mar 17–Jul 23	Apr 11–May 27	93	0.298	69	4.10 ± 0.19	3–26	Apr 11–May 21	8
	2011	Apr 12–Jul 18	NA	NA	0.000	NA	NA	NA	NA	NA
	2012	Apr 5–Jul 10	Apr 29–May 23	40	0.111	80	4.08 ± 0.16	3–44[c]	Apr 28–May 19	4
rkm 407.5	2009	Mar 30–Jul 30	May 28–Jun 1	2	0.008	50	4.23 ± 0.00	18	May 26–Jun 1	2
	2010	Mar 17–Jul 23	May 18	1	0.005	0	NA	Crushed	May 18	1
rkm 391	2008	May 28–Jul 18	Jun 20	1	0.006	100	4.42 ± 0.00	13	Jun 19	1
	2009	Jun 26–Jul 31	Jun 29–Jul 1	2	0.014	100	3.89 ± 0.04	23–30	Jun 26–27	1
	2010	Jun 22–Jul 25	NA	NA	0.000	NA	NA	NA	NA	NA
	2011	Jun 26–Jul 29	Jun 29	1	0.008	100	4.60 ± 0.00	21	Jun 26	1
rkm 377	2008	Apr 22–Aug 1	May 9–Jul 7	29	0.151	79	4.08 ± 0.18	3–25	May 8–Jul 4	7
	2009	Mar 31–Jul 31	Apr 24–Jun 23	43	0.127	72	4.14 ± 0.20	2–25	Apr 23–Jun 20	10
	2010	Mar 23–Jul 25	Apr 27–Jun 16	9	0.022	44	4.27 ± 0.15	5–10	Apr 27–Jun 13	3
rkm 366.5	2010	Mar 23–Jul 25	May 11	1	0.002	NA[d]	4.91 ± 0.00	Unknown	May 11	1
rkm 332.5	2011	Apr 12–Jul 15	May 18	1	0.003	100	4.37 ± 0.00	21	May 15	1
	2012	Apr 6–Jul 14	May 27–30	3	0.005	33	4.27 ± 0.00	19	May 25	1

[a]One stage-33 posthatch larva: 13.3 mm TL.
[b]Three stage-35 larvae: two ≈ 13.2 mm TL, one lost in processing.
[c]One stage-44 larvae: 22.5 mm TL.
[d]Unable to verify if just fertilized or unfertilized.

passage was no longer impeded (Brown 2007; Thomas et al. 2014). Egg sampling was therefore not conducted in 2012 at this site.

Between 2008 and 2012, we sampled three to six sites per year for a total of 7,731.8 wmd over a 118.5-rkm reach of the Sacramento River. Annual sampling effort was 1,546.4 ± 380.4 wmd (mean ± SD) and ranged from 1,201.6 to 2,057.4 wmd. We collected between 1 and 93 egg samples per site each year (Table 1) exclusively from the "within pool" mesohabitat. No further effort was expended in the "upstream" or "pool tail" mesohabitats between 2009 and 2012 based on the lack of egg collections from those areas in 2008. Collections were not normally distributed and the median number of eggs collected per site was three per year. Eggs were sampled 53% of the time from the top and 45% from the bottom (facing river substrate side) of the egg mats, sometimes simultaneously, and were found in the rinse water 2% of the time. Eggs were often found well embedded within the furnace filter material. Moreover, the eggs were notably adhesive as most were found to have variable-sized grains of sand and silt adhering to the jelly coat, and those that adhered directly to the steel framework of the mats remained attached even as they were collected under arduous retrieval conditions.

We collected a total of 268 Green Sturgeon eggs and 5 posthatch larvae from 7 of 11 sites sampled (Table 1) over a 93.5-rkm reach between rkm 426 and rkm 332.5 (Figure 1). From 5 years of study the CPUE was 0.041 ± 0.071 sturgeon eggs/wmd with the annual CPUE by site ranging from 0.000 to 0.298 sturgeon eggs/wmd (Table 1). The CPUE varied considerably between years and sites but was generally low (median = 0.008 sturgeon eggs/wmd) as egg collections were sporadic (Figure 2).

Egg samples were collected over the 5 years of sampling between April 2 and July 7 with a median collection date of May 14 (Figure 3). As mentioned previously, 2012 was the first year since 1967 the RBDD gates were not lowered to impound the Sacramento River at Red Bluff during the spring as the new bankside pumping facility was employed. The estimated spawning period in 2012 was 29 d shorter than the average of 58 d determined from sampling years 2008–2011 (range, 39–85 d)

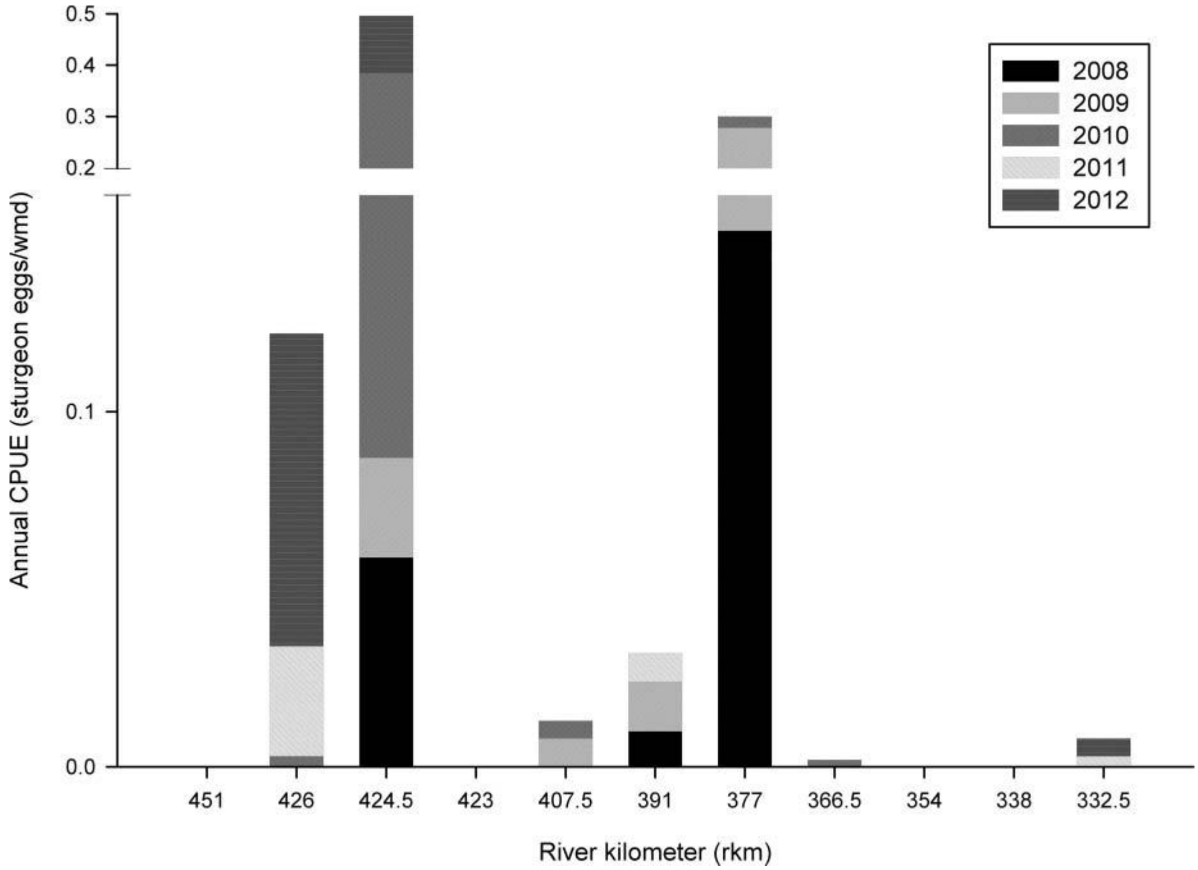

FIGURE 2. Relative abundance of Green Sturgeon eggs collected at sites on the Sacramento River between 2008 and 2012.

when the RBDD was seasonally operated. Although the distribution pattern appeared truncated, no significant statistical difference was detected for the median spawning date between 2012 and the previous 4 years (one-way ANOVA: $F_{4,\ 41}$ = 1.668, $P = 0.176$). Our ability to detect any statistical difference was possibly hindered due to a small sample size and therefore a lack of statistical power (i.e., not collecting eggs from the same sites for several years consecutively over many days). Conversely, the estimated spawning period in 2012 was very similar in duration to that determined in 2010 (Figure 3) and likely indicated variability in species' spawn timing.

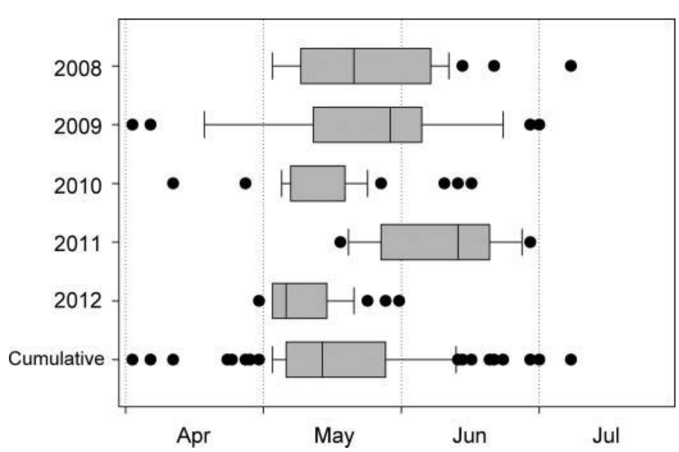

FIGURE 3. Box plots displaying the median and 10th, 25th, 75th, and 90th percentiles with outliers (black dots) of annual Green Sturgeon spawning events (n = egg counts) on the Sacramento River for 2008 (n = 42), 2009 (n = 56), 2010 (n = 105), 2011 (n = 11), 2012 (n = 59), and cumulatively (n = 273).

Of the 268 Green Sturgeon eggs collected, 189 (71%) were viable and they were assessed for developmental stage as described by Dettlaff et al. (1993). The remaining eggs were either crushed, marbled, or fungus-laden, which prevented accurate assessment, and therefore considered nonviable. Embryonic development was between stage 2 (recently oviposited) and stage 44 (posthatch larva). Egg diameter (n = 207) was 4.11 ± 0.20 mm and ranged from 3.42 to 4.91 mm. Posthatch larvae sampled by using egg mats ranged from 13.2 to 22.5 mm TL (median = 13.3 mm, n = 4).

We estimated that eggs were collected from a minimum of 54 different spawning events, based on sample date and location, egg developmental stage at capture, and water temperatures (Table 1). The annual number of estimated spawning events was 11 in 2008 from three sites, 17 from four sites in 2009, 14 from five sites in 2010, 5 from three sites in 2011, and 7 from three sites in 2012.

Spawning Habitat Assessment

Site-specific physical habitat data for all years sampled are presented in Table 2 and results are summarized by attribute hereafter. Between 2008 and 2012, egg mats were placed in water depths ranging from 0.5 to 14.5 m (mean ± SD = 6.0 ± 2.4 m). Water depths for retrieved eggs (Figure 4a) ranged from 0.6 to 11.2 m (mean ± SD = 6.4 ± 2.3 m (Table 2). A rank sum test indicated a significant difference in median egg collection depths between the RBDD tailrace and the other six sites (Mann–Whitney U-test: $U = 1076$, $P < 0.001$).

Eggs were collected on 33 occasions when mean daily water temperatures were decreasing, on 30 occasions as temperatures were increasing, and on one occasion when temperatures were stable for at least 24 h prior to collection. Mean daily water temperatures recorded during the collection events ranged from a minimum of 9.6°C to a maximum of 17.6°C. Averaged over 54 estimated spawning events, the mean (±SD) daily water temperature was 13.5 (±1.0)°C (Table 2).

Eggs were collected on 35 occasions when mean daily discharge was decreasing, on 24 occasions as discharge was increasing, and on five occasions when discharge was stable for at least 24-h prior to collection. Mean daily discharge sampled ranged from a minimum of 141 m^3/s to a maximum of 1,153 m^3/s. During spawning events, the mean daily discharge ranged from 269 to 396 m^3/s (Table 2; overall mean ± SD = 314 ± 57 m^3/s). During spawning events minimum and maximum turbidity values derived from surface grab samples ranged from 0.8 to 187.0 NTU. When averaged by site, the turbidity ranged from 3.4 to 9.7 NTU with an overall turbidity of 4.9 ± 3.5 NTU (median = 3.9; Table 2). Water column velocities at locations where mats collected eggs were 0.8 ± 0.25 m/s (Table 2; Figure 4b) and at locations where eggs were not found velocities were 0.8 ± 0.37 m/s. The median values of mean water column velocities between locations where eggs were and were not collected did not differ significantly (Mann–Whitney U-test: $U = 81225$, $P = 0.960$).

Substrate classes where eggs were found ranged from small gravel to medium cobble, with the exception of one egg sampled on boulder bedrock. Median substrate particle size was calculated to be medium gravel, and the majority of eggs (74%) were sampled within three gravel categories and ranged in size from 2.5 to 76.2 mm (Figure 4c).

DISCUSSION

Sacramento River Green Sturgeon Spawning

The focus of our research was to use egg mats to identify specific spawning sites and their habitat characteristics, and to describe the overall spatial distribution of Green Sturgeon spawning upstream and downstream from the RBDD. Spawning was confirmed each year indicating annual spawning of Green Sturgeon in the Sacramento River was consistent. Only one site was sampled every year (rkm 424.5) and eggs were collected there in 4 of 5 years (Table 1). Spawning could have occurred in 2011, which we may have missed due to incomplete sampling because of high flows early in the sample season or simply the patchiness associated with egg deposition (Caroffino et al. 2010). Acoustic and sonar data indicated limited occupation of this site in 2011 compared with other years, and spawning was confirmed 1.5 rkm upstream at rkm 426 from multiple spawning events where larger aggregations were noted.

Limited financial resources restricted the scope of this study by not allowing us to annually sample each location with increased quantities of mats that could be checked daily. For instance, the site at rkm 377 was the second most productive and eggs were collected in all 3 years sampled, but the site was not sampled in 2011 or 2012 so that effort could be applied in other areas farther downstream. The allocated resources permitted us to verify seven specific spawning sites including what is believed to be the lower river limit of Green Sturgeon spawning in the Sacramento River at rkm 332.5. This is supported by acoustic tag migration data collected by

TABLE 2. Green Sturgeon spawning habitat data collected from egg mat locations. Depth, temperature, discharge, and turbidity data are mean ± SD for each site from estimated spawn date until egg mat sample collection date. Column velocities are mean ± SD from egg collection locations. Substrate class denotes median substrate particle size-class where eggs or posthatch larvae were collected; NA = data not available.

Site	Eggs or larvae (n)	Depth (m)	Temperature (°C)	Discharge (m^3/s)	Turbidity (NTU)	Column velocity (m/s)	Substrate class
rkm 426	26	10.1 ± 1.8	12.9 ± 0.8	396 ± 115	4.3 ± 1.5	0.8 ± 0.4	Gravel/cobble
rkm 424.5	154	6.8 ± 1.8	12.9 ± 1.0	275 ± 52	4.7 ± 5.2	0.6 ± 0.1	Medium gravel
rkm 407.5	3	6.5 ± 2.9	13.9 ± 0.7	269 ± 10	3.8 ± 0.6	0.8 ± 0.2	Small gravel
rkm 391	4	1.2 ± 0.7	14.8 ± 0.9	323 ± 17	3.4 ± 0.8	NA[a]	Small gravel[b]
rkm 377	81	4.6 ± 1.2	14.1 ± 1.2	311 ± 58	3.8 ± 2.4	1.0 ± 0.1	Medium gravel
rkm 366.5	1	6.2 ± 0.0	11.8 ± 0.5	290 ± 0	4.9 ± 0.0	0.3 ± 0.0	Medium/large gravel
rkm 332.5	4	7.3 ± 0.2	14.0 ± 1.8	331 ± 87	9.7 ± 11.0	1.2 ± 0.5	Small gravel

[a]Tailrace of RBDD; no velocity measurements were taken during years of dam operation.
[b]Tailrace of RBDD; substrate class was assessed by direct observation.

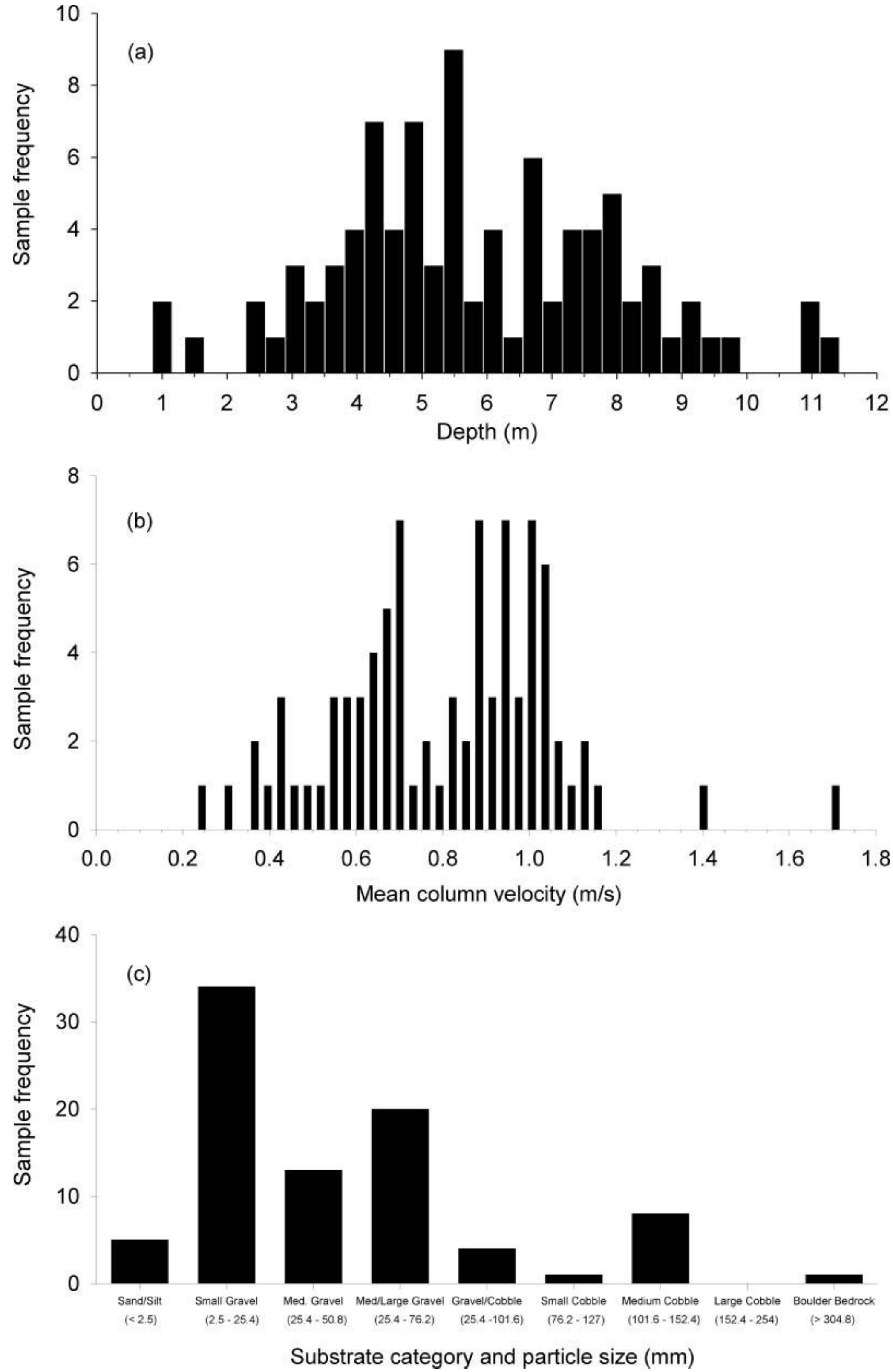

FIGURE 4. Frequency distribution of (**a**) collection depths, (**b**) mean column velocities, and (**c**) observed substrate size-classes Green Sturgeon eggs ($n = 273$) were collected on from the Sacramento River between 2008 and 2012.

USBR and UCD researchers that indicated adults are not holding or spending significant amounts of time below this section of the Sacramento River during pre- or postspawn time periods (Thomas et al. 2013; Corwin, unpublished data). The lower extent of Green Sturgeon spawning could be an effect of spawning habitat limitations, as the substrate of the Sacramento River downstream of rkm 332.5 is largely sand. The lower extent of Green Sturgeon spawning is coincident with the lower extent of spawning of most fall-run Chinook Salmon *Oncorhynchus tshawytscha*. Chinook Salmon also require gravel- to cobble-sized substrates for spawning (Moyle 2002).

Regarding the upper river limit of spawning, Heublein et al. (2009) documented a single acoustically tagged adult male Green Sturgeon near rkm 451 at the end of May in 2005. Occupation of this area is theorized to be associated with flood control releases from Shasta and Keswick dams, which elevated river discharge in excess of 560 m^3/s. Similar flood control releases occurred in the spring of 2011 and flows during the spawning migration (Thomas et al. 2013) exceeded 560 m^3/s for 26 consecutive days in March and April (USGS Water Data Report 2011; http://wdr.water.usgs.gov/wy2011/pdfs/11377100.2011.pdf). The DIDSON surveys at rkm 451 indicated sturgeon were holding for extended time periods and based on timing of habitat use were possibly spawning in 2011 (E. Mora, University of California, Davis, personal communication). However, egg mats were not deployed in this year at rkm 451. In contrast, the 2012 river flows exceeded 560 m^3/s for only 16 h on March 28 and adult fish were not observed at this site during the 2012 DIDSON surveys (E. Mora, University of California, Davis, personal communication), the year we deployed egg mats and recovered no eggs at rkm 451. Future egg sampling during years when adult sturgeon are present will help determine whether this area is used for spawning and if occupation of the area corresponds to periods of high spring flows or when specific adults return back to the system (i.e., exhibit spawning-site fidelity). As a result, we identified rkm 426 as the farthest upstream spawning site and can only hypothesize that rkm 451 is within the range of spawning for SDPS Green Sturgeon in the Sacramento River.

Spatial, Temporal, and Habitat Comparisons between Sympatric Green and White Sturgeon

The results of our 5-year study demonstrate that SDPS Green Sturgeon spawned annually and in at least seven locations over a 94-rkm reach of the Sacramento River. Our data also confirm there is recurring spawning of Green Sturgeon within the same river system as White Sturgeon. Moreover, our data along with concurrent Green Sturgeon adult tracking data (Thomas et al. 2013, 2014) indicate spatial separation of spawning habitat with the Sacramento River White Sturgeon population. In radio-tagging studies of adult White Sturgeon Schaffter (1997) recorded the maximum river ascension of sturgeon during 1990 and 1991 to be rkm 293. Based on movement patterns of acoustically tagged Green Sturgeon adults, Thomas et al. (2014) indicated that the putative spawning grounds appeared to begin at rkm 330, slightly below our most downstream egg sample site at rkm 332.5. No White Sturgeon eggs or larvae were sampled by Kohlhorst (1976) upstream from rkm 233 during a single year of sampling (1973), yet sampling was conducted up to rkm 412 near Bend Bridge.

These limited data, in combination, indicate spatial separation of spawning habitat between species of 37 to 100 rkm. Interestingly, creel survey data collected after the construction of Shasta Dam indicated only White Sturgeon to be present within the lake or a portion of the upper Sacramento River and tributaries (e.g., McCloud, Pit, and Little Sacramento rivers) cut off by the dam (Fisk 1963). Assuming there is a similar timing of adult migration patterns between recent years (Schaffter 1997) and the last time when waters of the Sacramento River allowed fish passage on February 4, 1944 (Flow regulation of the Sacramento River at Shasta Dam commenced on December 30, 1943, but water flowed through a diversion tunnel until February 4, 1944, at which time volitional up- and downstream fish passage ceased [USBR, Volume 8, 1944 Part III of V, Construction of CVP]) (Billington et al. 2005), it may be possible that the cutoff to the upper reaches of the river disproportionately trapped White Sturgeon adults compared with Green Sturgeon. Interestingly, the caption of a photo at the Shasta Dam visitor's center of a sturgeon caught in June 1977 incorrectly describes the fish caught by an angler as a White Sturgeon. Lateral scute counts later indicated the species name was incorrectly assigned on the photo, and to this day anglers still misidentify the sturgeon species. Recreational fishing regulations based on sturgeon species were not implemented in the state of California until 2007 (M. Gingras, California Department of Fish and Wildlife, personal communication), and it appears likely that habitat overlap of the two sturgeon species existed in the unimpounded Sacramento River system.

The annual spawning period has been described for a variety of sturgeon species throughout North America: Atlantic Sturgeon *A. oxyrinchus oxyrinchus* (Smith 1985), Shortnose Sturgeon (Duncan et al. 2004), Gulf Sturgeon (Sulak and Clugston 1998), Lake Sturgeon (Chiotti et al. 2008), White Sturgeon (Parsley et al. 1993; McCabe and Tracy 1994; Paragamian et al. 2002), and Shovelnose Sturgeon *Scaphirhynchus platorynchus* (Tripp et al. 2009). Spawn timing, documented through the capture of eggs and larvae from our research on Green Sturgeon and that of Kohlhorst (1976) and Schaffter (1997) on White Sturgeon indicate there is some temporal overlap of spawning activity between the two species. We estimated spawning to occur as early as April 2 and as late as July 4 (Table 1). Estimated spawn timing for Sacramento River White Sturgeon was estimated to be from February 16 to May 29, with the vast majority (93%) occurring in March and April (Kohlhorst 1976). In the Columbia River system in

Oregon–Washington below Bonneville Dam, McCabe and Tracy (1994) described the period to be from late April to early July of each year, similar to the period we estimated for Green Sturgeon. Our data suggests the majority (10th and 90th percentiles) of spawning for SDPS Green Sturgeon within the Sacramento River occurs between early May and mid-June (Figure 3), similar to that found for NDPS Green Sturgeon in the Klamath River system (mid-April to mid-June: Emmett et al. 1991; April to mid-May: Van Eenennaam et al. 2006). All North American sturgeons spawn predominantly in the spring period, although there is recent evidence of fall spawning by Atlantic Sturgeon (Balazik et al. 2012). We have no evidence to indicate fall spawning in the same reach of the Sacramento River by Green Sturgeon at this time.

The estimated annual spawning period ranged from 29 to 85 d in duration, but this assumes we collected some eggs from the earliest and latest spawn events each year. Because of the limitations to our study in terms of the numbers of mats set, the number of sites monitored, and how often the mats could be checked, we cannot make any definitive conclusions about the length of the spawning season, except that annual variability will occur, depending primarily on water flow, temperature, and timing of the spawning run. The estimated number of spawn events recorded each year is likely very conservative. The fecundity of a female ranges from 59,000 to 242,200 eggs (Van Eenennaam et al. 2006) and yet we recovered only a single egg to document eight separate spawn events (Table 1). Too few egg mats and predation of eggs are likely two of the major factors contributing to the few eggs being recovered. Also, delays between the occurrence of a spawn event and egg mat retrieval will result in egg loss. Caroffino et al. (2010) replaced mats with all Lake Sturgeon eggs still attached after counting, and then 24 h later recovered the mats and recounted the eggs. The egg loss ranged from 20% to 100%. Sulak and Clugston (1998) reported nearly 100% loss of Gulf Sturgeon eggs at 24 h postdeposition. We undoubtedly experienced egg loss with our 3–4-d interval between mat retrievals.

Temperatures at the time we collected Green Sturgeon eggs ranged from 9.8°C to 17.1°C, but showed a tendency to average 13.5°C at all sites over all years (Table 2) and a variety of water year types (critically dry to wet). The wide variation may be explained by temporal and spatial attributes as early spawners in the upper reaches of the river experienced the lowest seasonal temperatures in contrast to late spawners detected in reaches below the RBDD. Schaffter (1997) reported water temperatures for spawning White Sturgeon within the Sacramento River to be between 12°C and 17°C. Perrin et al. (2003) noted water temperatures of 13–19°C (mean = 14.4°C) for White Sturgeon in the Fraser River, British Columbia. They also noted annual increases in temperature in each year of study, in contrast to the temperature-regulated reaches of the upper Sacramento River. We noted increases in temperature in each year only in the lowermost reaches of Green Sturgeon spawning habitat and typically only below major diversions such as the RBDD and Glenn–Colusa Irrigation District water diversions, which remove up to 16% and 28% of Sacramento River flow, respectively (cumulatively up to 44% of water released from Shasta and Keswick dams).

Depths at which Green Sturgeon eggs were collected ranged from 0.6 to 11.3 m (mean ± SD = 6.4 ± 2.3 m; Figure 4a), which was far less than the maximum depths of 24.0–27.0 m Parsley et al. (1993) and McCabe and Tracy (1994) reported, but slightly greater than that of 4.6–5.1 m found by Schaffter (1997) or Perrin et al. (2003) for White Sturgeon. We note the similarity in spawner preference for the deepest areas within the sample reach as Paragamian et al. (2009) noted for Kootenai River White Sturgeon regardless of absolute value. Conversely, the samples collected in the tailrace of RBDD (rkm 391) were, on average, 5.3 m less than any other site with a significantly different median collection depth. Our results indicate that depth may be of secondary importance to other variables including substrate type, water temperature, and complex hydraulics (Thomas et al. 2014) for spawning activity. We hypothesize that the extreme hydraulic turbulence in the RBDD tailrace resulting from water flowing under partially raised dam gates provided cover as a surrogate for depth and was therefore deemed suitable habitat for spawners when coupled with preferred substrates and temperatures.

Green Sturgeon eggs were primarily collected in areas with mean water column velocities of 0.8 m/s over gravel substrates (Figure 4b, c). The range of mean water column velocities varied widely as some eggs were sampled from areas outside of high velocity currents in backwaters (0.3 m/s) and others were sampled in thalweg habitats (1.7 m/s). Mean water column velocities and substrates in areas of successful White Sturgeon spawning in the Columbia River system appeared similar to ours, yet larger substrate materials appear to be a consistent theme (Parsley et al. 1993; Parsley and Beckman 1994). Moyle (2002) indicated Green Sturgeon spawn over larger substrates because these areas have interstitial spaces that result in decreased predation of exposed eggs and enable successful hatching. McAdam (2011) noted the preference of small interstitial spaces within gravel substrates for White Sturgeon yolk sac larvae. Small gravels were a consistent feature present to varying degrees in all locations we sampled eggs. The presence of smaller substrates is likely a vital habitat component resulting in the annual spawning success of the Sacramento River Green Sturgeon population. Addition or enhancement of substrates may also be an important component to consider in areas under consideration for habitat restoration or protection. Mean water column velocities appeared to result in clean gravels in portions of all confirmed spawning sites and reduced the likelihood of egg suffocation by sand (Kock et al. 2006) or decreased hatching success in suboptimal substrates (Parsley and Kofoot 2013). The few locations where we observed spawning over sand and silt substrates could reflect changes in substrate between the time when mats were deployed and when substrate data were collected in 2013, or could reflect spatial errors in the GPS data used to relocate mat positions or simply indicate a variance related to egg drift distance.

Water Resource Management and Competing Needs of ESA-Listed Fish Species

Natural production only occurs with successful spawning (Parsley et al. 2002). Moreover, spawning should only occur when and where survival and growth of progeny are optimal based on environmental conditions (Munro et al. 1990, cited by Parsley et al. 2002). Recovery efforts for several other North American sturgeon species have progressed further than have those for SDPS Green Sturgeon. Chiotti et al. (2008) noted that data regarding the timing and extent of Lake Sturgeon spawning are critical for their rehabilitation efforts. Boley and Heist (2011) noted for Pallid Sturgeon *S. albus* that early life history is probably the single most important limiting factor for recruitment (Bergman et al. 2008), and recovery efforts are limited given a lack of critical knowledge.

In a river system managed for flow and temperature, such as the Sacramento River, which to a certain degree is manipulated for wildlife concerns to primarily benefit juvenile salmonids (Parsley et al. 2002), the annual temporal and spatial distribution of spawners can, in part, be directly influenced by river management operations. The result of manipulation of water resources has been linked to increases or decreases in sturgeon spawning success (Votinov and Kas'yanov 1976; Raspopov et al. 1994; Auer 1996) and has important implications for a threatened fish population; especially a Distinct Population Segment, as defined by the ESA, that appears to have only one recurring spawning population in one regulated river. Water resource management in California is not as simple as the turning of a valve, but is the result of a series of competing demands for stored water resources. These demands, which are estimated to be overallocated by a factor of five (Grantham and Viers 2014), include flood management, energy production, water supply delivery (agricultural and municipal needs), water quality, recreation, and ecosystem support (Lund et al. 2014) for various fish and wildlife needs.

Auer (1996) and Caroffino et al. (2010) found evidence that wide variation in dam discharge created unstable spawning habitat for Lake Sturgeon. The RBDD tailrace is no longer available for spawning, due to the replacement of the dam with a permanent pumping facility (NMFS 2009). Between 2008 and 2011, we found variable effects of the dam and its operations on spawning habitat. Sporadic inputs of sand and small gravels from an ephemeral tributary immediately upstream from the dam's west river margin during storm events deposited easily mobilized sediment disproportionately on the west side of the river below the dam in numerous years. The effect of spring–summer dam operations resulted in the burying of egg mats within 2 d of deployment and limited mat sampling success. We did sample one egg within 24 h of deployment on one occasion in 2008 on the west side, but most attempts to sample the western third of the dam tailrace resulted in equipment failure due to sediment inundation. In contrast, spawning that occurred on the east side likely resulted in less sediment suffocation (Kock et al. 2006), yet predation of eggs by Sacramento Pikeminnow *Ptychocheilus grandis* and Rainbow Trout *O. mykiss* were noted to occur during attempts to capture spawning events on video (J. J. Gruber, unpublished data). The lowered RBDD gates often resulted in concentrations of these species due to suboptimal fish ladders (USFWS 1988). Complementary monitoring efforts in each of the 5 years of egg sampling resulted in the capture of Green Sturgeon larvae indicating successful spawning and hatching occurred to some extent annually at the site, but not uniformly (Poytress et al. 2009, 2014).

Sacramento River water temperature compliance points managed for spawning habitat criteria for endangered winter-run Chinook Salmon (NMFS 2009) typically result in mean daily water temperatures during April through June that are less than or equal to 11°C above rkm 470 in most years. These cooler water temperatures near and upstream from rkm 470 could result in decreased potential habitat by deterring migration of Green Sturgeon spawning adults upstream to the small seasonal barrier created by the flashboard dam of the Anderson–Cottonwood Irrigation District at rkm 480 as well as the terminal anadromous fish barrier created by Keswick Dam at rkm 486 (Figure 1). Laboratory studies have demonstrated some deleterious effects to Green Sturgeon survival as a result of decreased hatch rates and shorter hatchlings at 11°C (Van Eenennaam et al. 2005). If these data can be replicated with a larger number of progenies and lower temperatures verified to be suboptimal, then efforts to maximize utilization of the Sacramento River by Green Sturgeon to spawn in upwards of 70 rkm of potential habitat could be in direct competition with the needs to manage the lower temperature requirements of ESA-listed winter-run Chinook Salmon. The result of this competition may limit the potential to increase the population size of Sacramento River SDPS Green Sturgeon, as population growth often relies on increased survival of the early life stages (Sutton et al. 2003; Vélez-Espino and Koops 2009; Caroffino et al. 2010). Currently, river temperature management primarily for winter-run Chinook Salmon results in an approximately 120-rkm segment, between rkm 451 and rkm 330, where spawning habitat is thermally acceptable during the spring spawning period in most years.

An additional consequence of thermal river regulation specifically for winter-run Chinook Salmon spawning, incubation, and rearing, is a flattening of the upper river thermograph. The result is not only prolonged suitable spawning temperatures in some reaches of the river, but also a likely increase in time for Green Sturgeon embryos and larvae to develop (Van Eenennaam et al. 2005). Longer development time could result in greater losses due to predation or smaller size at emergence resulting in longer migration distance for larvae, which increases the probability of mortality during a vulnerable stage of life as the larvae redistribute from hatching areas (Kynard et al. 2005). These types of effects contribute to recruitment variability (Parsley et al. 2002), which can result in population level effects. Overall, thermal regulation aimed at enhancing the success of endangered winter-run Chinook Salmon spawners likely results in a possible downstream redistribution of Green Sturgeon spawners from their historical spawning grounds or current upstream habitat limits, and may also result in annual temperatures that are optimal in some reach of the river with variable effects on eggs and larvae within and between years.

Mora et al. (2009) modeled the negative effect that dams have on spawning habitat for Green Sturgeon. The Nature Conservancy et al. (2008) also noted the effects of an altered Sacramento River hydrologic regime on a variety of fish and plant species and speculated the effects might extend to Green Sturgeon. We recorded an average discharge of 314 m^3/s and a relatively low median turbidity value of 3.9 NTU during estimated spawning events. The effects of decreased spring outflows and turbidity while water is captured behind Shasta Dam and an increased summer outflow resulting in lower water temperatures and clear water likely alter cues, in most years, for upstream adult migrants in the late winter as well as spawn timing and hatching success in the spring and early summer, respectively. The effects of storage and downstream diversion, in combination, complicate the resultant ecology of the Sacramento River by adding and then subtracting substantial amounts of water exclusively within the spawning habitat we documented. Additionally, a multitude of unscreened diversions in the lower 225 rkm of the river likely negatively affect larval and juvenile habitat and survival (Mussen et al. 2014; Poletto et al. 2014; Verhille et al. 2014).

Knowledge of the physical habitat conditions under which SDPS Green Sturgeon successfully spawn is crucial to assist fishery managers in developing programs for species recovery and population rehabilitation. The information regarding spawning locations, timing, and habitat conditions gained from this study should allow fishery managers to determine with increased accuracy additional locations outside the mainstem Sacramento River where SDPS Green Sturgeon could spawn successfully provided the suite of habitat variables documented exist elsewhere. Prior to this study and during the ESA listing process, these variables were only generally known (BRT 2005). The recent documentation of Green Sturgeon spawning in the Feather River (Seesholtz et al. 2015) and adult presence during the spawning season in the Yuba River (Bergman, memorandum) indicate that multiple areas exist where certain conditions are present to perpetuate the spawning population. Integration of spawn-timing data and habitat characteristics from our studies coupled with habitat information for other rivers where Green Sturgeon are found should be used to determine the best locations for protection, management, and restoration of river systems to assist in the recovery of SDPS Green Sturgeon. Utilization of Sacramento River spawning habitat information and ecologically beneficial thermal and hydrologic management of water project resources, coupled with greater access to suitable spawning habitat, will likely increase population abundance and sustain SDPS Green Sturgeon in the future. Considering the basic needs of Green Sturgeon while balancing the competing beneficial uses of California's water resources may very well prove to be the most difficult step in recovery of the species.

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