

Research Article

Transitional Strategies of Juvenile Green Sturgeon from a Riverine to a Brackish Water Environment

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Information on habitat transitions is critical to understand whether efforts to manage the freshwater phase of juvenile green sturgeon (*Acipenser medirostris*) rearing habitats are feasible or beneficial. We implanted microacoustic transmitters in naturally produced age-0 juvenile green sturgeon in the Sacramento River to evaluate residency, general spatial distribution, movement rates, and downstream migration patterns over 300 river kilometers. Furthermore, we investigated whether changes in three environmental variables (discharge, turbidity, and water temperature) were associated with the beginning of movements resulting in the transition from riverine to brackish waters during their outmigration to the Sacramento-San Joaquin Delta Estuary. We captured 183 juvenile green sturgeon by trawl of which 88 were implanted with microacoustic tags. An additional 10 individuals were collected and tagged from the Red Bluff Diversion Dam rotary-screw traps. Linear mixed models showed that individuals caught by trawl had longer upper river residence times, post-tagging, than those caught by trap. Intergate velocity models showed that trap-caught individuals relocated at higher upper river reach velocities than trawl-caught fish, but there were no differences between trap- and trawl-caught fish within the middle or lower reach. Detections showed that juvenile green sturgeon began the downstream transition to brackish water habitat when discharge and turbidity increased. Temperature was not found to significantly influence the initiation of downstream migration. Both continuous and stepped downstream migration patterns were observed in each of the four cohorts, with smaller individuals being more likely to exhibit stepped migration. These data provide information that was previously unknown about the life history of the southern distinct population segment of the North American green sturgeon and can be utilized to assist with water resource management and recovery of this threatened fish species.

1. Introduction

The North American green sturgeon (*Acipenser medirostris*, Ayres 1847) has received increased attention by fishery and water managers in California, USA, since 2006 when the National Marine Fisheries Service (NMFS) published a notification of their listing under the US Endangered Species Act (71 FR 17757; April 2006). Separated from the remnant Eel River population [1–3] on the North Coast within California, the southern distinct population segment (SDPS) of green sturgeon is listed as threatened under the Endangered Species Act (74 FR 52300; October 2009) with the only known recurring spawning population occurring

within the Sacramento River drainage [4]. Since federal listing, significant effort has been applied to address numerous gaps in knowledge about the life history of the SDPS of green sturgeon from egg deposition [5–7], brackish water juvenile habitat use [8, 9], to adult migrations [10–16], spawner locations, behavior, and habitat utilization [17–22] to better manage water resource operations of the Federal Central Valley Project and State Water Project which support California's 50+ billion dollar agricultural economy [23]. Dam construction and water resource management has, in part, resulted in the reduction of potential spawning habitat [24] as well as changes to the natural hydrograph [25] with deleterious effects on recruitment and habitat use by the

species. Recent study efforts focused on the adult life phase of the species have already allowed for evidence-based changes in water project management operations including the removal of the Red Bluff Diversion Dam, a former barrier to spawning habitat within the Sacramento River [6].

Information on age-0 green sturgeon (larvae and juveniles within their first full year of life) within the freshwater environment is comparatively limited and comes primarily from laboratory-based studies [26–29] and energetics modeling [30]. Laboratory studies by Kynard et al. [31] indicated that age-0 green sturgeons show behavior indicative of larval downstream movements at 12–24 days post-hatch (dph) followed by juvenile downstream movements at 110–181 dph. Allen et al. [26] found juveniles become saltwater-tolerant at 106–177 dph with increasing tolerance to salinities of 35‰ once they reach a total length (TL) of 250 mm at 134 dph, on average [32]. Radtke [33] estimated juvenile green sturgeon collected in the brackish water of the Sacramento-San Joaquin Delta Estuary (Delta) were between 6 months and 2 years of age based solely on fish lengths. River conditions, including water temperatures, may play an important role in cueing downstream movement and habitat transition as migration behavior exhibited in a laboratory decreased by 50% when water temperatures dropped below 9.8°C and ceased entirely at 8.1°C [31].

Field collection of incidentally captured exogenous feeding green sturgeon larvae by rotary-screw traps occurs regularly within the Sacramento River [34–36] near Red Bluff, California, as it is located within the spawning grounds [6]. Rotary traps passively sample downstream migrating fish [37] and are typically targeting juvenile Chinook salmon (*Oncorhynchus tshawytscha*) which have been found to be most abundant at depths between 0.6 and 1.2 m below the water surface [38]. Rotary traps may be biased against benthic species capture when the depth of the trap's cone is disproportionately small relative to the depth of the river being sampled. Capture of morphologically developed juvenile sturgeon [39, 40] after 35 dph at Red Bluff has been few and sporadic over 25 years of sampling [34–36], but this could also be a result of size selectivity of rotary traps [35]. By contrast, the use of active gear types that target the benthos, including the benthic trawl, has been very successful in the capture of juvenile white sturgeon (*A. transmontanus*) in the Columbia River [41] and pallid (*Scaphirhynchus albus*) and shovelnose sturgeon (*S. platyrhynchus*) in the Mississippi River [42–44]. More recently, benthic trawls have been successful at capturing juvenile green sturgeon in the Sacramento River with little to no acute, observable impacts on this listed species [45].

Concurrent to the development of best practices for sampling juvenile benthic species, the development of microbatteries and low-cost microacoustic transmitters has helped to identify migration timing, survival, and habitat selection of juvenile fish, including some species of sturgeon [9, 46, 47]. An extensive array of Juvenile Salmon Acoustic Telemetry System (JSATS) receivers [48] exists within California's Central Valley to help understand the timing, movement, distribution, and survival of Chinook salmon

[49–51]. The use of microacoustic transmitters has been successfully tested on young-of-year Siberian sturgeon (*A. baerii*) ranging from 140 to 191 mm TL, resulting in a tag burden of 1.3–2.6% without impacting growth or survival of individuals [52]. Miller et al. [53] observed similar results using juvenile green sturgeon as Ashton et al. did [54] with white sturgeon. The benthic trawling capture technique described by Gruber et al. [45] was effective at capturing individuals of suitable size (>150 mm TL) for being implanted (tagged) with microacoustic transmitters.

The lack of field-based studies investigating the SDPS of green sturgeon's juvenile movements, rearing and foraging habitats, and transition cues from fresh water to brackish and saltwater habitats results in a significant information gap [4] that could potentially be filled by combining benthic trawl sampling and microacoustic telemetry techniques. Temporal and spatial distribution data and information on juvenile green sturgeon habitat transitions are critical to understand how water management techniques may be optimized or habitat restoration activities might be focused and if recovery of the species is achievable [55]. The objectives of this study were to capture naturally produced juvenile green sturgeon in freshwater habitats and implant them with microacoustic transmitters in order to evaluate their rearing time or residency, general spatial distribution, movement rates, and downstream outmigration timing. Furthermore, we investigated whether changes in three environmental variables (discharge, turbidity, and water temperature) influence the initiation of movement resulting in the transition from riverine to the brackish water habitats of the Sacramento River and Delta.

2. Materials and Methods

2.1. Study Area. This study was conducted on the mainstem Sacramento River within a 301 river kilometer (rkm) reach between the town of Red Bluff (rkm 471; measured from the Golden Gate Bridge) and Sacramento (rkm 170) in Northern California, USA (Figure 1). The Sacramento River is the largest river within the Central Valley of California and originates near Mt. Shasta from the springs of Mt. Eddy [56]. It flows south through 600 kilometers (km) of the state draining a combined 68,635 km² from the Coast, Klamath, Cascade, and Sierra Nevada mountain ranges and reaches the Pacific Ocean via San Francisco Bay. Shasta Dam and its associated downstream flow-regulating structure, Keswick Dam (rkm 556), have formed a complete barrier to upstream anadromous fish passage since 1943 [57].

Stream flow in the Sacramento River downstream of Shasta and Keswick Dams is highly managed for flood control, power generation, water delivery for agricultural and municipal uses, and environmental benefits. Water releases throughout the year are highly regulated and do not mimic historic flow patterns since they are elevated in the spring and summer months and then reduced during the fall and winter months to store water within Shasta Lake [25] for Central Valley Project uses. Fall and winter rain events often produce increased runoff from downstream tributaries and provide some variability to the Sacramento River over water

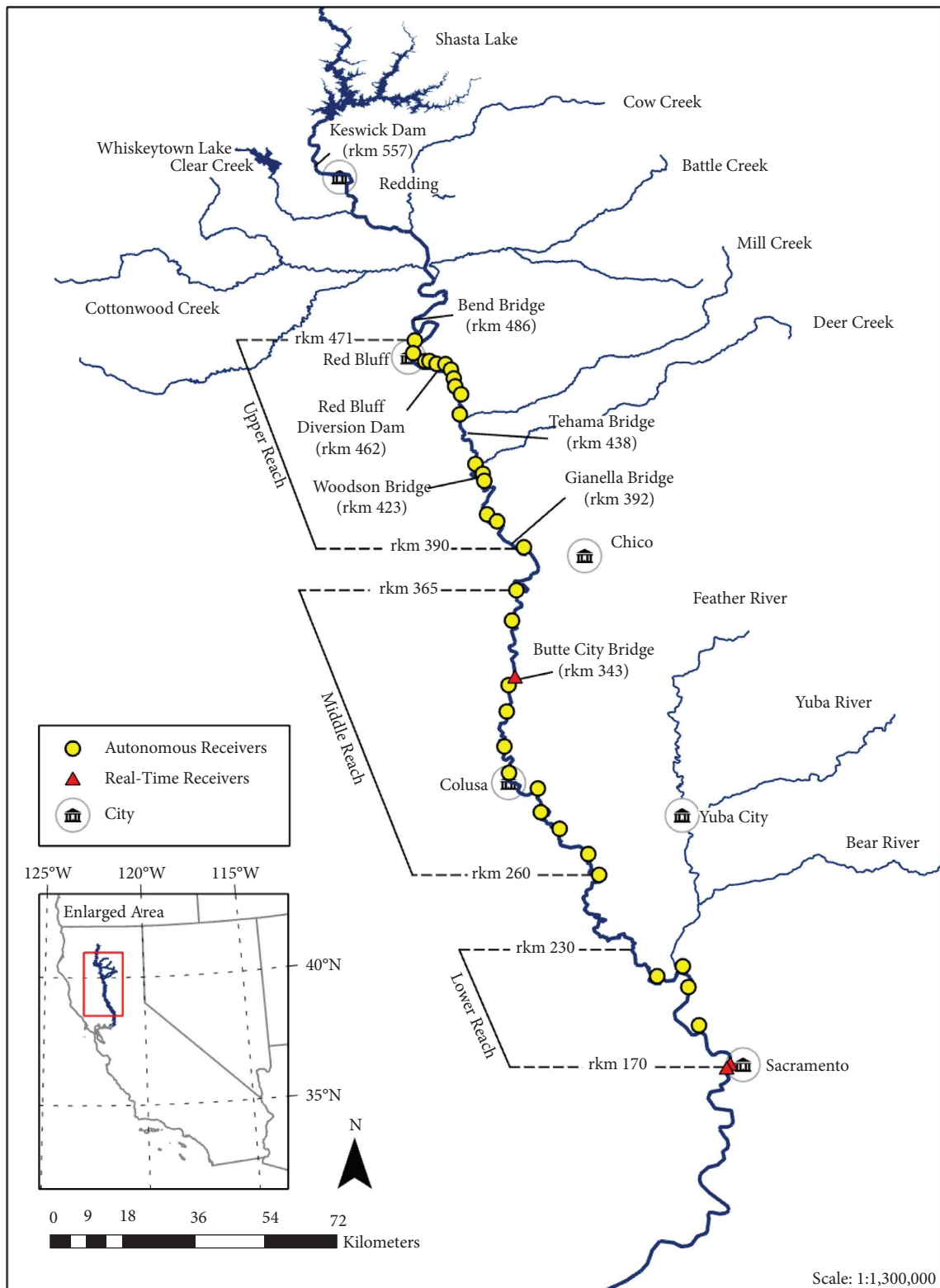


FIGURE 1: Map of the study area. Map depicts Sacramento River reaches and autonomous and real-time acoustic receiver locations used for juvenile green sturgeon outmigration monitoring.

discharged from Shasta Lake and Keswick Dam. The reach between Keswick Dam and the site of the former Red Bluff Diversion Dam (RBDD; rkm 462) supports areas of native

riparian vegetation and largely remains intact. Below RBDD, the Sacramento River becomes increasingly managed for flood control and agricultural benefit with armored levees

and flood bypass channels until it reaches the city of Sacramento with Interstate-80 bridge (rkm 170) being the upstream boundary of the Delta.

2.2. Fish Collection, Tagging, and Acoustic Detections. A benthic trawl net, as described in Gruber et al. [45], was deployed to capture juvenile green sturgeon within the Sacramento River between Red Bluff (rkm 471) and Butte City Bridge (rkm 343; Figure 1) between 2016 and 2019 over a median period of 73 days per year. The 4.9-m benthic trawl net was composed of a 15.9-mm mesh body with a single 3.2-mm mesh cod bag deployed from the bow of a boat and towed downstream while making S-curves through each sample area. The trawl net was towed using 0.95-cm braided floating lines with otter boards used to open the mouth of the net. Otter boards (76.2 cm × 38.1 cm) were constructed of marine-grade plywood reinforced with steel. The trawl net was equipped with a large zipper to remove debris and a chafe skirt to protect the cod end that was tied closed to prevent fish escapement. Tow speeds varied due to river depth and velocity but were generally faster than ambient river velocities, yet slow enough to maintain contact with the river bottom ($\sim 3\text{--}5\text{ rkm}\cdot\text{hr}^{-1}$). Benthic trawl sample sites were selected to facilitate safe vessel transit after dark. Areas with large woody debris, boulder, or bedrock substrates were avoided to reduce the chance of damaging or losing benthic trawl nets. Sampling began each fall predicated on the annual larval green sturgeon emergence timing from the RBDD rotary-screw trap (RST) catch and information from prior years' sampling efforts to target juvenile sturgeons of taggable size [45]. Sampling occurred exclusively during nocturnal hours encompassing periods of peak age-0 sturgeon activity [31, 45, 58]. Season end dates for sample collections were based on real-time acoustic receiver data indicating downstream movements of juvenile sturgeon, while continued trawl sampling was carried out to validate the lack of presence within the upper Sacramento River each year.

All trawl-caught green sturgeon were identified, enumerated, and weighed to the nearest 0.1 gram. Fish were measured for fork length (FL) and total length (TL) to the nearest millimeter (mm). Relative abundance catch rates were defined as catch per unit effort (CPUE) in units of total fish per wetted net hour (WNH). A small number of juvenile green sturgeon captured by the RBDD RST Chinook Monitoring Project (trap-caught) were also used in this study. Rotary trapping methods described by Martin et al. [59] and Poytress et al. [35] were followed.

Trawl- or trap-caught juvenile green sturgeon >150 mm total length that appeared in good physical condition were held for implantation with JSATS acoustic microtransmitters. Juvenile sturgeons were anesthetized to stage four (loss of muscle tone, equilibrium, and spinal reflexes, while maintaining a slow but steady opercular rate) [60] using a 130 mg/L solution of tricaine methanesulfonate (MS-222) buffered with 130 mg/L sodium bicarbonate. Fish were placed either ventral or with left side up in a modified foam block, so that the body of a juvenile sturgeon was cradled in

a v-shaped slot. Ambient temperature, oxygenated river water was continuously pumped over the gills of each fish throughout surgery.

Surgical methods and microacoustic transmitters (tags) varied between years depending on staff experience, fish size, and available tags. Surgery consisted of intracoelomic implantation as described in the study by Thomas et al. [8] or a non-sutured flank incision as described in the study by Liss et al. [61]. Fish >150 mm TL were implanted with an ATS SS300 tag paired with a 337 or 348 battery, or an SS400 tag. Tags operated at 416.7 KHz and were configured to a 10 second ping rate interval (PRI) to achieve a 68, 100, and 111 day lifespan, respectively. Some fish >250 mm were implanted with an experimental Pacific Northwest National Laboratory (PNNL) "Sturgeon tag" configured to a 10 second PRI to achieve an estimated 249 day lifespan [62]. Surgical implantation was completed within 2–4 minutes for each fish. After surgery, fish were transferred to a bucket of aerated river water to fully recover for a minimum of 30 minutes before being released back into the river typically within the detection range of an acoustic receiver nearest their capture location.

To monitor fish movements, tagged juvenile green sturgeon were passively tracked using an autonomous and real-time JSATS acoustic receiver network deployed between Red Bluff (rkm 471) and Sacramento, California (rkm 170; Figure 1). The number, model(s), and initial deployment dates of JSATS receivers that were deployed each year varied. Receivers were manufactured by ATS®, Lotek®, and Teknologic®. The detection range of autonomous receivers is estimated to be between 100 and 200 meters but varied by location based on river depth, bottom type, and water velocity [49, 62, 63]. Paired autonomous receivers were deployed in a gated fashion along the river margins to maximize detection efficiency [64].

Data files from JSATS receivers were postprocessed to remove false positive detections and to produce a final data record that includes only valid detections using a PRI filter described in the study by Deng et al. [46]. Postprocessing filtering was set to two detections within the designated time window ($\text{PRI} * 1.3 * 12 + 1$). Additional false detections were deleted if they resulted in individuals being in two places at one time or resulted in unreasonable travel rates between receiver gates. Individual fish detections were consolidated by fish and receiver gate into detection events that included the first and last time a fish was detected at a gate and the location (rkm) of the gate (see Section 2.3.1).

2.3. Data Analyses. Acoustic telemetry data were analyzed to determine if differences in movement patterns and migration rates differed by the capture method. Environmental conditions were hypothesized to cue the initiation of juvenile fish migration to brackish water habitat and a modeling exercise was performed to quantify the rates of change in flow, turbidity, and water temperature thought to be associated with downstream migrations.

Analyses were based on fish detection data in 3 distinct reaches of the Sacramento River (Figure 1). The upper reach (> rkm 390) contains the area generally defined as green

sturgeon spawning grounds [6, 18]. The middle (rkm 365–260) and lower (rkm 230–170) reaches were divided, roughly in half, using two receiver gates with high detection efficiency over multiple years. River reaches did not overlap to ensure fish were detected leaving and entering the two different reaches and to allow for reach transition event analyses.

2.3.1. Residence Time and Movement Rates. Reach-specific residence time in days (d) was defined as the duration of time beginning with either the release time (upper reach) or the first detection (middle and lower reaches) until the last detection time in each reach. Individual and gate-specific detection events were summarized using each individual's first and last detection at each gate.

To establish notation, fish i detection event j is characterized by a vector $e_{i,j}$ containing the detection event residence time values, the first detection time $t_{i,j,f}$, the last detection time $t_{i,j,l}$, and the gate location in rkm $l_{i,j}$. The event intergate velocity $v_{i,j}$ ($\text{m}\cdot\text{s}^{-1}$) is the change in river location divided by the time between detection events, $v_{i,j} = (l_{i,j+1} - l_{i,j}) / (t_{i,j+1,f} - t_{i,j,l})$. Defined in this way, the start of the relocation velocity is associated with last detection time at an event so that associating relocation velocities with external environmental conditions takes the interpretation of what initiates subsequent (between gate) movement. Reach velocity ($\text{rkm}\cdot\text{d}^{-1}$) was similarly defined but using the first ($e_{i,j1}$) and last ($e_{i,j2}$) event data within a reach, $v_{i,j,\text{reach}} = (l_{i,j2} - l_{i,j1}) / (t_{i,j2,f} - t_{i,j1,l})$. Note that the units of velocity differ based on the spatiotemporal scale of analysis. We used $\text{m}\cdot\text{s}^{-1}$ for the finer scale intergate movement velocities and $\text{rkm}\cdot\text{d}^{-1}$ for the coarser scale river reach movement velocities.

Models for reach residence time ($t_{i,j2,f} - t_{i,j1,l}$), intergate relocation velocity ($v_{i,j}$) and reach velocity ($v_{i,j,\text{reach}}$) were developed using linear mixed models fit in *R* [65] with the lme4 package [66]. The full model for each response variable, generally denoted by $y_{i,j}$, included an interaction between capture type, reach, and their lower order terms, with individual fish as a random intercept. The mean value $\mu_{i,j}$ model is given by:

$$\mu_{i,j} = \beta_0 + \beta_1 \text{reach}_{i,j} + \beta_2 \text{capture type}_{i,j} + \beta_3 \text{reach}_{i,j} * \text{capture type}_{i,j}. \quad (1)$$

Effects were summarized using the emmeans package [67]. Full models were first compared with the corresponding models without fixed effects to assess the importance of modeling individual (random effect) variance, and then, the interaction term was tested using a likelihood ratio test (LRT) with a model without the interaction. Model residual diagnostics computed using the DHARMa package [68] indicated that models of reach residence time or reach velocity needed the response variable transformed to the natural logarithmic scale (i.e., $y_{i,j} = \log(t_{i,j2,f} - t_{i,j1,l})$ for the reach residence time model and $y_{i,j} = \log(v_{i,j,\text{reach}})$ for the reach velocity model).

2.3.2. Environmental Conditions Data. The environmental conditions of interest included river discharge (flow), turbidity, and water temperature that were available hourly from the California Data Exchange Center (CDEC) gauges within the upper Sacramento River (California Data Exchange Center). Upper reach river flow values (converted to $\text{m}^3\cdot\text{s}^{-1}$) used data collected from the Woodson Bridge (VIN; rkm 423) gauge, while upper reach turbidity (NTU) and temperature data (converted to degrees C) were collected from the Red Bluff (RDB; rkm 462) gauge. Missing data of upper reach environmental conditions were linearly interpolated between adjacent nonmissing values prior to use in regression-based analyses of habitat conditions associated with the onset of outmigration (see Section 2.3.3).

2.3.3. Outmigration and Environmental Conditions Analyses. Juvenile green sturgeon movement downstream of the upper Sacramento River 'rearing' reach was analyzed alongside environmental conditions to identify any associations with the initiation of the outmigration process. The spatial distribution of the acoustic receiver array and individual fish detection data did not always allow for identification of the precise moment the outmigration process began (e.g., if a tagged individual held position outside a detection field of any gate prior to beginning the outmigration process). Therefore, we compared environmental conditions between two time intervals leading up to the last time an individual was detected in the upper reach. These were constructed so that the first interval would represent a time period when an individual likely had not yet begun the outmigration process, and the second interval when it had. We also carried out a sensitivity analysis to assess differences based on the choices of time intervals used to make comparisons of environmental conditions immediately prior to and during the initiation of outmigration. By analyzing environmental conditions prior to the last moment in time an individual was detected in the upper reach, the intention was to identify what conditions cause an individual to initiate the outmigration movement behavior.

For each individual i , detected downstream of the upper reach at least once, the last time it was detected in the upper reach, $t_{i,\text{last}}$, was recorded. We compared, using models, how temporal changes in environmental conditions leading up to the beginning of movement were associated with habitat transitioning as follows. First, for each individual, two non-overlapping but adjacent time intervals indexed by j and each of total duration ΔT leading up to $t_{i,\text{last}}$, were delineated. The first interval, defined by $W_{i,j=\text{prior}} = [t_{i,\text{last}} - 2\Delta T, t_{i,\text{last}} - \Delta T)$, was used to capture average environmental conditions "prior to leaving." The second interval immediately followed the first window, defined by $W_{i,j=\text{leaving}} = [t_{i,\text{last}} - \Delta T, t_{i,\text{last}}]$, was used to capture average environmental conditions during the time the individual begins outmigration behavior up to when it leaves the upper reach. Then, environmental data that were generally collected at the hourly interval were averaged within each time interval to construct individual i specific predictor variables $\bar{x}_{i,\text{prior}}$ and $\bar{x}_{i,\text{leaving}}$. The equal size of the windows for summarizing conditions helped make average predictor variables more comparable within and across individuals for

a given choice of ΔT . That is, if $\bar{x}_{i,\text{prior}} = \bar{x}_{i,\text{leaving}}$ then the equality is strictly related to the average conditions being the same in the same amount of time and not the time window being different. Denoting the movement behavior response variable by $b_{i,j} = 0$ for not outmigrating or $b_{i,j} = 1$ for leaving, logistic regression was used to model the effects of average environmental conditions on the probability of beginning outmigration from the upper reach with the probability of outmigration $p_{i,j}$ given by:

$$\text{logit}(p_{i,j}) = \beta_0 + \beta_1 \text{capture type}_i + \beta_2 \text{size}_i + \beta_3 \text{cohort}_i + \beta_4 \bar{x}_{i,j}, \quad (2)$$

where, i denotes the individual, j the window, and terms not related to $\bar{x}_{i,j}$ are included as controls. Models were fit to the $b_{i,j}$ data using the glm function in R [65], diagnostics checked using the DHARMA package [68], and effects analyses summarized using the emmeans package [67].

Model comparisons across choices of ΔT were based on the percent null deviance explained. For different choices of ΔT the response variable has a different technical meaning (i.e., not moving in a different time window), making the use of information-theoretic approaches technically invalid. Despite the different meanings, the actual values of the $b_{i,j}$ do not change, nor does the number of observations. Thus, the saturated and null model likelihoods, and consequently the null model deviance, are the same across all choices of ΔT , making percent null deviance explained comparable across choices of ΔT . Model selections were based on the highest percentage of null deviance explained.

2.3.4. Outmigration Pattern Analysis. Analyses of downstream migration patterns (i.e., outmigration) were conducted with juvenile green sturgeon from the upper reach of the Sacramento River to the upstream boundary of the Sacramento-San Joaquin River Delta. Migration pattern analyses were done for the subset of individuals detected at least once in the middle reach that were subsequently detected in the lower reach.

The downstream migration patterns for all individuals were assessed visually. From this, an individual was labeled as “stepped” if the number of days from the first detection time in the middle reach to its last detection time in the lower reach was greater than 7 days. Migration patterns were labeled as “continuous” if the duration was found to be 7 days or less. The probability of exhibiting either a stepped or continuous downstream migration pattern was modeled as a function of total length (mm) and weight (g) using logistic regression fit using the glm function in R [65], residuals were checked using the DHARMA package [68], and effect analyses were summarized using the emmeans package [67].

3. Results

3.1. Fish Collection, Tagging, and Acoustic Detections. Juvenile green sturgeons were collected by benthic trawl within a 54-rkm reach between rkm 471 and 417. Limited effort was employed downstream of rkm 417 where the river

gradient decreases and channel meander increases resulting in difficulties with sampling these areas at night because of increased in-channel woody debris. Sample effort and CPUE (fish/WNH) varied between years and sample sites, with annual CPUE values ranging between 3.6 and 32.9 fish/WNH (median = 14.0; SD $\pm$ 13.6 fish/WNH). Sampling of five particular trawl sites resulted in 77.6% of the juvenile green sturgeon captured during this four year study, indicating consistent rearing habitat usage between years.

Benthic trawl sampling over four consecutive seasons (2016–2019) collected 183 juvenile green sturgeon with a mean TL of 186 mm (SD $\pm$ 61 mm) and mean weight of 42.5 g (SD $\pm$ 35.4 g). Of those captured, 88 juvenile green sturgeon with a mean TL of 221 mm (SD $\pm$ 44 mm) and mean weight of 59.6 g (SD $\pm$ 33.8 g) were implanted with JSATS microacoustic tags. An additional 10 individuals collected from the RBDD RST site at rkm 462 with a mean TL of 223 (SD $\pm$ 49 mm) and mean weight of 60.2 g (SD $\pm$ 36.0 g) were implanted with microacoustic tags. Implanted sturgeon from both capture types combined ($n = 98$) had a mean TL of 222 mm (SD $\pm$ 44 mm) and a mean weight of 59.7 g (SD $\pm$ 33.8 g). See Table 1 for summary statistics of tag types, mean fish length/weights from combined gear types, and tag burden by year. The maximum tag burden for the various tag types ranged from 0.7% to 1.5%, which is well below the recommended 2% threshold [69, 70]. Surgery time averaged 3.5 minutes and juvenile sturgeon took an average of 8 minutes to fully recover.

Of the 98 individuals implanted with acoustic tags and released back to the river, 3 were never detected by the JSATS acoustic array and 21 were only detected at the release location plus one downstream gate within the array. The remaining 74 individuals were used in the rearing and movement analyses. The elapsed time from release to first detection and subsequent time to last detection of each individual in the upper river reach varied (Figures 2(a)–2(d)) and there was no attempt to restrict analyses to the warranty period of each tag model. Of the 74 individuals whose movements were analyzed, 59 were detected in the middle river reach and 53 were also detected in the lower reach. Age-0 juvenile green sturgeon were detected leaving upper Sacramento River rearing areas within a period of 6 months between late-October and mid-March (Figures 2(e)–2(h)). Individual movement trajectory plots of the 74 individuals used in the rearing and movement analyses can be found in Supplemental Materials, Figure S1.

3.2. Residence and Relocation Velocities. Median upper reach residence time post-tagging was greater for trawl-caught fish (25.3 d; SD $\pm$ 31.9 d) as compared to trap-caught fish (1.2 d; SD $\pm$ 22.2 d). The trap-caught fish had the highest median residence times in the middle reach (10.5 d; SD $\pm$ 17.8 d), while the lower reach fish caught by either gear types had the lowest median residence times (0.9 d; Table 2). The longest residence time of 147.7 days and the highest amount of variability (SD $\pm$ 31.9 d) were detected with fish caught by trawl in the upper reach (Figure 3(a)). Linear mixed models

TABLE 1: Summary statistics of the annual number (N) of juvenile green sturgeon implanted with acoustic tags by tag model with total length in millimeters, weight in grams and estimated tag burden as percentage.

Year	Tag model	N	Mean total length (mm)	Mean weight (g)	Mean tag burden (%)
2016	SS300-337	17	242 (164–301)	70.4 (20.1–119.5)	0.5 (0.3–1.5)
	PNNL	2	296 (280–312)	115.9 (109.6–122.1)	0.6 (0.6–0.7)
2017	SS300-337	10	224 (170–295)	61.3 (28.1–130.5)	0.6 (0.2–1.1)
	SS300-348	18	248 (199–322)	80.4 (37.1–168.9)	0.5 (0.2–0.9)
	SS400	24	178 (152–216)	29.2 (18.5–46.0)	0.8 (0.5–1.1)
	PNNL	3	281 (261–307)	108.5 (90.6–134.8)	0.7 (0.5–0.8)
2018	SS400	9	238 (177–293)	69.5 (28.3–116.8)	0.4 (0.2–0.8)
2019	SS400	15	204 (162–253)	47.3 (19.1–74.8)	0.5 (0.3–1.1)

Ranges are provided in parentheses.

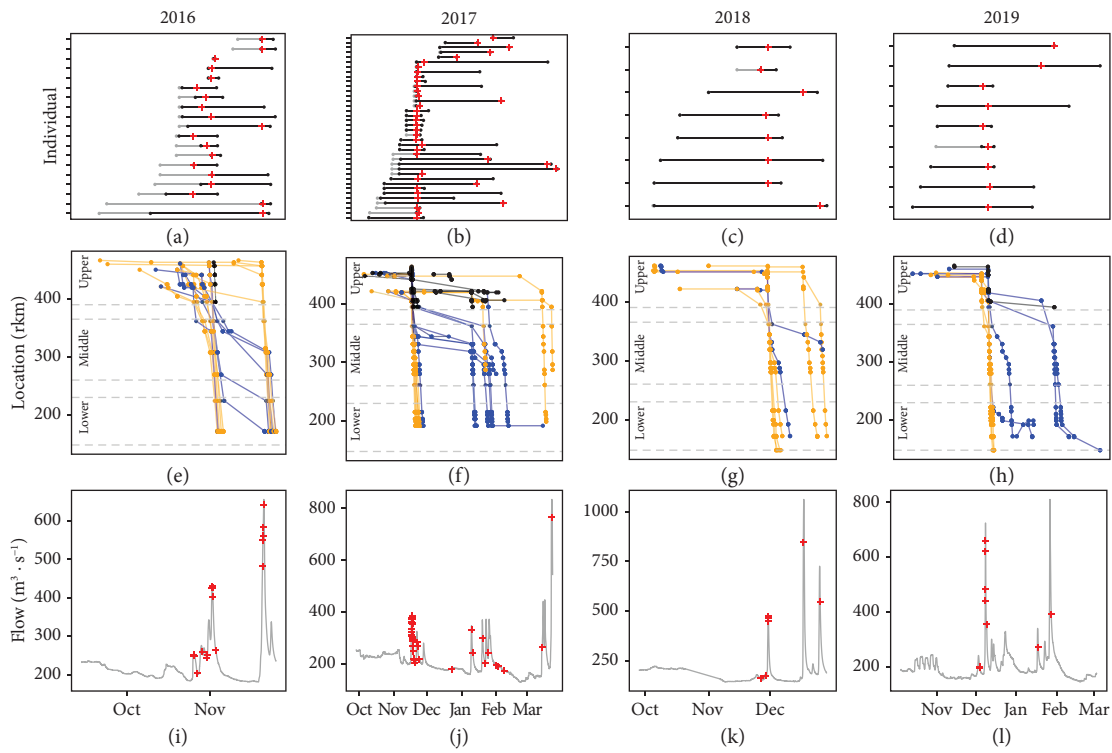


FIGURE 2: Acoustic tag detection plots (top row), fish movement plots (middle row), and Sacramento River flows (bottom row) over the time interval; all individuals were tagged and detected. Vertical panel columns correspond to the birth cohorts (year) shown at the top. Panels (a–d) show acoustic tag detections through time by each individual (unlabeled Y-axis tick marks), with release date (first grey dot), a grey line extending to the first detection time (first black dot), the last detection in the upper river reach (red plus), and the last time an individual was detected (second black dot). Panels (e–h) are waterfall plots of detections and migration patterns exhibited by individuals including continuous (orange lines), stepped (blue lines), and individuals not part of downstream migration pattern analyses (black lines). Panels (i–l) indicate Sacramento River discharge at Woodson gauging station (grey lines) in cubic meters per second ($\text{m}^3 \cdot \text{s}^{-1}$) on the Y-axis and last detection in the upper river reach (red plus) over time in months on the X-axis.

comparing reach residence time indicated a significant interaction of capture type and reach (LRT statistic 128.88, $df=5$, $P<0.01$), indicating that upper reach residence times for trawl-caught fish, post-tagging, were significantly longer than for trap-caught fish. All capture type comparisons with middle or lower reach residence times were not found to be significantly different (Table 2; Figure 3(a)).

A maximum intergate velocity of $2.42 \text{ m} \cdot \text{s}^{-1}$ was estimated from a trap-caught fish within the upper river reach. A greater percentage (38%) of upper reach intergate fish velocity measurements were estimated upstream of rkm 450 for trap-caught fish (due to the static RST sampling location at rkm 462) compared to 12% for trawl-caught fish captured as far as 33 rkm downstream (Figure 1). Maximum intergate velocities of $1.53 \text{ m} \cdot \text{s}^{-1}$ and $1.50 \text{ m} \cdot \text{s}^{-1}$ were estimated within

TABLE 2: Gear type and Sacramento River reach-specific summary statistics of residence time (days), inter-gate velocities in meters per second ($\text{m}\cdot\text{s}^{-1}$) and reach-scale travel velocities in river kilometers per day ($\text{rkm}\cdot\text{d}^{-1}$) for acoustically tagged juvenile green sturgeon sampled between 2016 and 2019.

Reach	Gear	N	Residence time (days)						Inter-gate velocity ($\text{m}\cdot\text{s}^{-1}$)						Reach velocity ($\text{rkm}\cdot\text{d}^{-1}$)					
			Min	Q25	Med	Q75	Max	SD	Min	Q25	Med	Q75	Max	SD	Min	Q25	Med	Q75	Max	SD
Upper	RST	10	0.7	0.9	1.2	5.4	55.8	12.3	22.2	0.01	0.57	1.18	1.43	2.42	1.2	19.9	55.2	79.2	94.4	35.8
	Trawl	64	1.0	10.7	25.3	44.5	147.7	34.5	31.9	0.00	0.17	0.65	1.20	2.09	0.2	0.9	1.8	2.8	23.7	4.5
Mid	RST	8	0.2	2.0	10.5	20.3	52.5	15.1	17.8	0.00	0.25	0.67	0.84	1.41	1.7	4.2	15.3	49.9	94.0	34.4
	Trawl	51	0.0	1.5	2.5	4.9	64.0	7.7	13.9	0.00	0.29	0.65	0.92	1.53	0.0	16.1	32.4	59.5	105.2	28.2
Lower	RST	7	0.5	0.8	0.9	2.2	45.8	7.6	16.9	0.12	0.37	0.74	0.81	1.09	0.5	22.9	28.1	45.3	73.0	23.1
	Trawl	46	0.4	0.7	0.9	1.6	30.2	3.2	6.7	-0.05	0.32	0.67	0.87	1.50	1.7	23.9	41.1	57.4	84.8	22.9

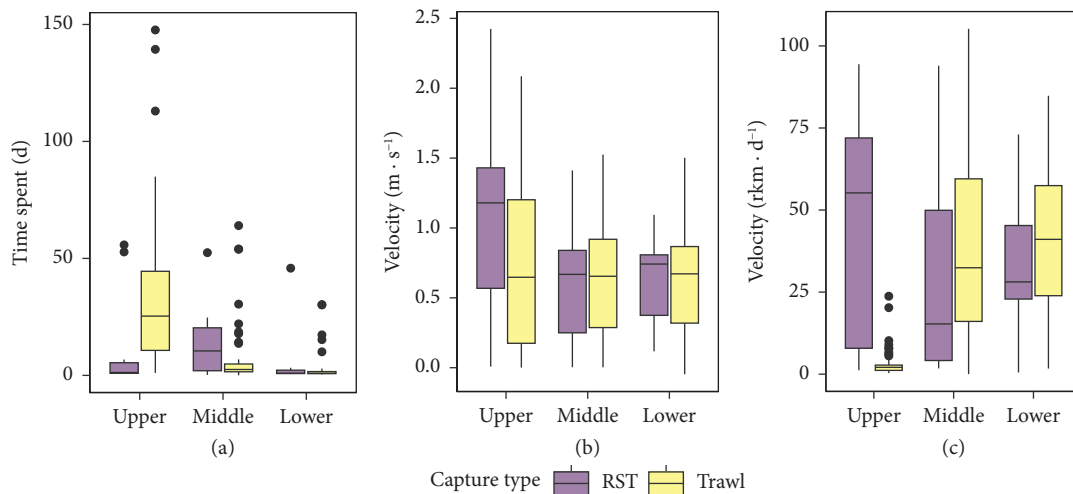


FIGURE 3: Residence time and movement velocity distributions by river reach. Box plots are by capture type and show distributions for (a) residence time in days (d), (b) inter-gate velocity in meters per second ($\text{m} \cdot \text{s}^{-1}$), and (c) reach velocity in river kilometers per day ($\text{rkm} \cdot \text{d}^{-1}$).

the middle and lower river reaches, respectively, from trawl-caught fish (Table 2; Figure 3(b)). Comparisons of intergate velocity models indicated upper reach velocities of trap-caught fish were significantly higher than those of trawl-caught fish (LRT statistic 70.80, $\text{df} = 5$, $P < 0.01$) but not significantly different between trap- and trawl-caught fish within the middle or lower reach.

The median reach velocity rates were the lowest in the upper reach ($2.0 \text{ rkm} \cdot \text{d}^{-1}$; $\text{SD} \pm 21.0$) and increased by more than an order of magnitude for the middle ($32.3 \text{ rkm} \cdot \text{d}^{-1}$; $\text{SD} \pm 28.9$) and lower reaches ($38.2 \text{ rkm} \cdot \text{d}^{-1}$; $\text{SD} \pm 22.8$) of the river. The maximum reach velocity rate for any individual fish occurred within the middle reach and was estimated at $105.2 \text{ rkm} \cdot \text{d}^{-1}$ from a trawl-caught fish (Figure 3(c)). Maximum upper and lower reach velocities were estimated at $94.4 \text{ rkm} \cdot \text{d}^{-1}$ from a trap-caught fish and $84.8 \text{ rkm} \cdot \text{d}^{-1}$ from a trawl-caught fish (Table 2, Figure 3(c)), respectively. Comparisons of overall reach velocity models indicated a significant interaction of capture type and reach (LRT statistic 144.61, $\text{df} = 5$, $P < 0.01$). Upper reach velocities of trap-caught fish were significantly higher than those associated with trawl-caught fish (contrast ratio = 13.67, $\text{SE} = 5.46$, $\text{df} = 190$, $\text{null} = 1$, t -ratio = 6.55, $P < 0.0001$). Reach velocity differences in the upper reach by trap-caught fish provide additional evidence of active migration behavior when compared to the more extensive rearing behavior exhibited by trawl-caught fish, post-tagging.

3.3. Associating Environmental Conditions with Juvenile Movement. Detections over time throughout the entire study area for each individual fish compared with flow showed that juvenile green sturgeon moved downstream with increased flow (Figures 2(i)–2(l); also see Figure S1 in the Supplementary Material for individual migration initiation plots). The 15 different models, each relating one of three environmental

conditions with one of five window size choices to the probability of leaving the upper reach (equation (1)), are summarized in Table 3. Variance inflation factors suggested that while flow and temperature could be included in the same model, flow and turbidity were too correlated to be simultaneously included, so each model used only a single covariate. A window size of two days had the highest percent null deviance explained of the sets of flow and turbidity models. A window size of 10 days had the highest amount of deviance explained amongst the temperature models but in no case was the effect of temperature found to be significant (Table 3). The effects for each model and covariate are shown in Figures 4(a)–4(c) for context. The percent changes in the prior to and leaving averaged environmental values for each window size are shown in Figures 5(a)–5(c), by covariate. The models for flow and turbidity with a two day window had percent change median values of +28% ($\text{SD} \pm 20.4$; Figure 5(a)) and +234% ($\text{SD} \pm 360.4$; Figure 5(b)), respectively. The temperature model with a 10-day window had a percent change median value of -1.9% ($\text{SD} \pm 5.6$; Figure 5(c)).

3.4. Outmigration Patterns: Continuous and Stepped. Both continuous and stepped downstream migration patterns were observed in each of the four cohorts (Table 4 and Figures 2(e)–2(h)). For the 59 individuals detected downstream of the upper reach whose outmigration types were analyzed, the total number of days from the first detection time in the middle reach to the last detection time ranged between 0.77 and 66.64 days. Graphical examination of the detection data through time indicated variability in migration duration between individuals, but a maximum of 7 total days appeared reasonable as a choice to distinguish individuals as exhibiting a continuous versus stepped outmigration pattern. Using this criterion, 22 of the 59

TABLE 3: Summary of logistic regression models (equation (2)) relating average environmental conditions during two windows of time for different choices of interval length (ΔT) to whether or not an individual had begun movement associated with leaving the upper reach.

Covariate	ΔT	Estimate	Std. error	z-value	P-value	Model deviance	% null dev.
Flow	0.5	0.49	0.11	4.40	<0.01	133.29	18.52
	1	1.00	0.18	5.70	<0.01	101.82	37.76
	2	1.95	0.34	5.73	<0.01	82.14	49.78
	3	1.62	0.32	5.13	<0.01	115.27	29.54
	10	0.48	0.28	1.73	0.08	160.14	2.10
Turbidity	0.5	0.04	0.02	2.41	0.02	154.90	4.79
	1	0.19	0.03	5.36	<0.01	118.23	28.89
	2	0.96	0.23	4.15	<0.01	63.11	61.42
	3	0.51	0.10	5.31	<0.01	107.35	33.55
	10	1.02	0.20	5.16	<0.01	116.30	28.58
Temperature	0.5	0.06	0.24	0.27	0.79	163.51	0.04
	1	-0.00	0.24	-0.02	0.99	163.58	<0.01
	2	-0.14	0.23	-0.62	0.54	163.20	0.23
	3	-0.24	0.26	-0.94	0.35	162.69	0.54
	10	-0.63	0.40	-1.59	0.11	160.80	1.70

Results are for the environmental covariate slope parameter (β_4 in equation (2)), the model deviance, and percent null deviance explained (% null dev.).

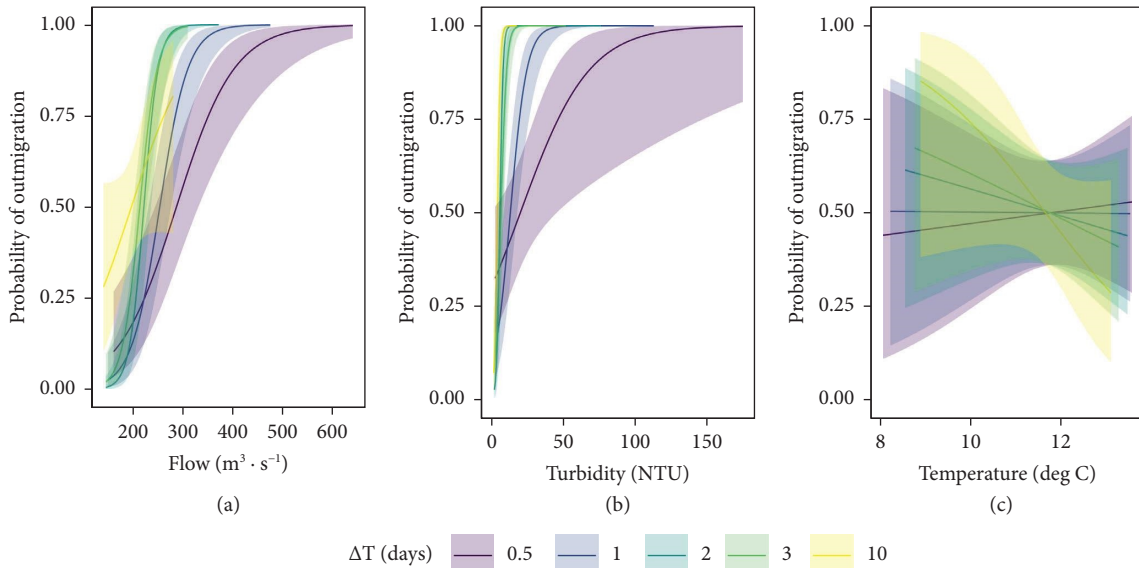


FIGURE 4: Logistic regression model (equation (2)) predictions (lines) and 95% uncertainty intervals (shading) on the probability of beginning outmigration as a function of average environmental conditions ($\bar{x}_{i,j}$ in equation (2)) with panel (a) flow in cubic meters per second ($\text{m}^3 \cdot \text{s}^{-1}$), (b) turbidity in nephelometric turbidity units (NTU), and (c) water temperature in degrees celsius (deg C), for five choices of time prior to and after leaving (ΔT).

individuals (37%) demonstrated a stepped migration pattern and 62% a continuous pattern, irrespective of capture type (Table 4). Stepped migrations or slowed movement patterns were observed primarily within the middle reach. Relatively rapid downstream movement occurred on subsequent flow increases after the original increase associated with leaving the upper reach (Figures 2(e)–2(l)) indicating increased flows are the primary transport mechanism used by juvenile green sturgeon during outmigration events.

A logistic regression model showed that smaller juvenile green sturgeon were more likely to exhibit a stepped downstream migration pattern (slope = -0.013 , SE = 0.0065 , z-value = -1.941 , $P = 0.052$). The substitution of length with weight indicated a similar result (slope = -0.017 , SE = -0.009 , z-value = -1.915 , $P = 0.056$). Mean length and weights of individuals at the time of tagging were nearly identical between capture types and no further estimation of size during migration was made for trawl-caught fish which

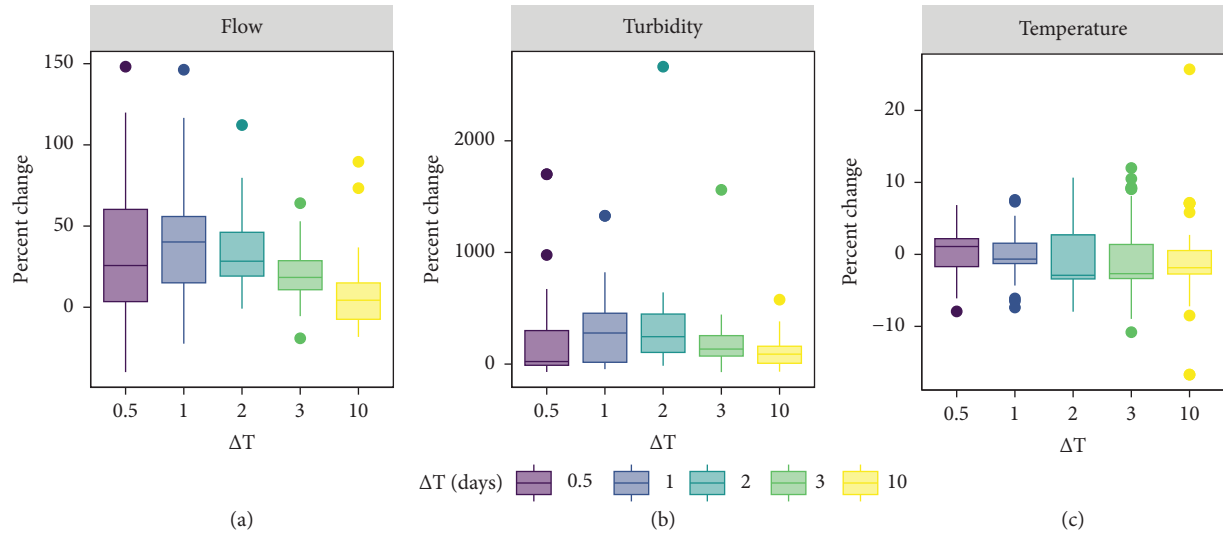


FIGURE 5: Box plots of percent change in the average environmental values from the time window prior to leaving to the time window during the beginning of outmigration, $(\bar{x}_{i,\text{leaving}} - \bar{x}_{i,\text{prior}})/\bar{x}_{i,\text{prior}} * 100$, for 5 choices of time window duration (ΔT). Panels show (a) flow, (b) turbidity, and (c) water temperature. Box plots colors are according to the value of ΔT for ease of comparison with Figure 4.

TABLE 4: Sacramento river juvenile green sturgeon summary of outmigration patterns.

Cohort	Weight (g)	Total length (mm)	Total days	Outmigration type
2016	96	271	19.63	Stepped
2016	110	280	2.40	Continuous
2016	65	239	3.77	Continuous
2016	59	238	4.94	Continuous
2016	90	262	19.57	Stepped
2016	49	221	4.64	Continuous
2016	21	167	2.11	Continuous
2016	55	224	20.68	Stepped
2016	96	287	6.05	Continuous
2016	85	264	3.05	Continuous
2016	120	301	2.80	Continuous
2016	106	282	4.83	Continuous
2016	107	276	5.57	Continuous
2016	74	251	8.16	Stepped
2016	46	216	20.16	Stepped
2016	54	230	20.61	Stepped
2016	54	216	2.81	Continuous
2016	20	164	2.42	Continuous
2017	125	241	1.98	Continuous
2017	42	287	2.29	Continuous
2017	37	199	6.13	Continuous
2017	129	205	1.75	Continuous
2017	169	199	55.69	Stepped
2017	69	302	3.60	Continuous
2017	71	322	4.07	Continuous
2017	119	240	4.74	Continuous
2017	81	241	5.77	Continuous
2017	76	287	5.98	Continuous
2017	109	260	3.24	Continuous
2017	91	246	9.61	Stepped
2017	32	278	4.02	Continuous
2017	22	261	53.83	Stepped
2017	31	159	22.02	Stepped

TABLE 4: Continued.

Cohort	Weight (g)	Total length (mm)	Total days	Outmigration type
2017	20	180	7.13	Stepped
2017	29	165	30.45	Stepped
2017	46	159	66.64	Stepped
2017	37	176	5.96	Continuous
2017	130	173	0.77	Continuous
2017	117	162	5.12	Continuous
2017	88	180	63.83	Stepped
2017	28	216	57.03	Stepped
2017	94	193	2.83	Continuous
2017	44	295	17.03	Stepped
2018	64	293	3.81	Continuous
2018	92	266	5.88	Continuous
2018	21	180	5.82	Continuous
2018	72	266	4.84	Continuous
2018	62	207	2.92	Continuous
2018	34	234	6.32	Continuous
2018	62	177	24.71	Stepped
2018	67	269	10.34	Stepped
2019	75	162	33.34	Stepped
2019	60	234	6.59	Continuous
2019	96	227	3.95	Continuous
2019	110	177	35.19	Stepped
2019	65	231	31.93	Stepped
2019	59	217	3.91	Continuous
2019	90	253	2.53	Continuous
2019	49	231	12.29	Stepped

Summary includes cohort year, capture method, weight in grams (g), total length in millimeters (mm), total number of days from the first detection in the middle reach to the last detection, and outmigration pattern.

results in limitations to the accuracy of these data. Length distributions relative to outmigration pattern were plotted along with the modeled probability of outmigration by length at tagging, indicating larger juveniles had a higher probability of exhibiting a continuous downstream migration pattern (Figure 6).

4. Discussion

4.1. Spatial Delineation of Juvenile Rearing Habitat. This study is the first to investigate juvenile green sturgeon freshwater residency in the Sacramento River. Incidental captures of small numbers of juveniles each year (i.e., 1 to 10) from passive sampling RST's [37] at RBDD prompted this study to pursue active sampling techniques using a benthic trawl [45] as the primary method to collect sufficient numbers of individuals for research on their habitat use and transition movements. Limits to night navigation and exploration of numerous sites coupled with annual variability in juvenile production over 4 years within the 128-rkm green sturgeon spawning reach of the Sacramento River [6, 18] contributed to variable catch rates ranging an order of magnitude between sites and years. The inability to sample the river downstream of rkm 417 potentially limited our understanding of the full extent of rearing habitat. The unsampled portion of the river is assumed to play some role as rearing habitat for juvenile green sturgeon within the Sacramento River, based on the capture of larvae at rkm 390 [58] as well as five juveniles collected during a multiyear

evaluation of 12 unscreened diversions between rkm 254 and rkm 267 [71].

Few trawl-caught juvenile sturgeon were detected immediately after release moving between receiver gates within the upper reach, oftentimes exhibiting lengthy time intervals of residency or continued rearing behavior post-tagging within the upper river. Many tagged individuals spent most of their time in close proximity to their original trawl capture location, as evidenced by telemetry data and the occasional recapture of previously tagged fish within resampled sites. Taken together, these findings indicate that juvenile green sturgeon are consistently using this reach for rearing over many months prior to outmigration and will be the focal area for future research on rearing habitat and relatively fine scale movements using a 2-dimensional acoustic telemetry array. Trap-caught fish exhibited minimal residency, post-tagging, within the upper reach indicating active downstream migration of most individuals sampled by that capture type. Median residence times by either capture type within the middle and lower reaches of the Sacramento River were much less than for trawl-caught fish in the upper river, indicating that these reaches are not used for prolonged periods of time as rearing habitat by juvenile green sturgeon after the initiation of outmigration in the fall or winter. Rearing habitat use by smaller downstream migrants observed in the summer months being entrained by agricultural pumps within these reaches as noted by Vogel [71] should be studied further to determine the importance of these reaches during an earlier

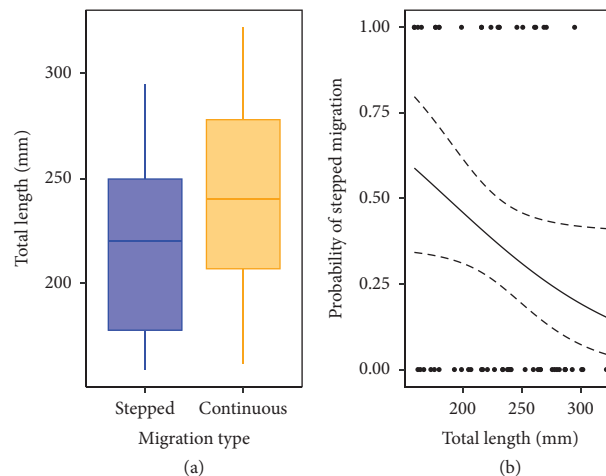


FIGURE 6: Plots of migration patterns and associated fish lengths. Distribution of individual fish lengths grouped according to (a) out-migration pattern and (b) the probability of outmigration as a function of total length; dots are observations, solid line is the model prediction, and dashed lines are 95% confidence intervals.

time period of the year which we could not evaluate with acoustic telemetry due to tagging constraints related to fish size at capture.

4.2. Movement Rates and Attributes. Intergate velocities of trap-caught fish within the upper reach were found to be significantly different than trawl-caught fish. We believe that receiver array locations and the distribution of the receiver gates relative to capture locations partly influenced this result. Few trawl-caught fish were available for analysis upstream of rkm 450 within the highest gradient section of the upper reach in comparison to all trap-caught fish being sampled at rkm 462. Trawl-caught fish had fewer opportunities to be detected moving in the highest gradient sections negatively biasing their intergate velocities within the upper reach. Trawl-caught fish also exhibited a behavioral difference through their lack of intergate detection data immediately following tagging, indicating that rearing continued instead of downstream migration. Trap-caught fish were primarily observed through intergate detections to be actively migrating downstream within the upper reach after tag implantation. Intergate velocities were not significantly different between capture types for the middle or lower river reaches indicating active downstream migration was occurring by all fish detected within these reaches.

Comparing reach velocities, we found trawl-caught juvenile green sturgeon had decreased upper river reach velocities as compared to trap-caught fish. Seven individuals collected and tagged during active rain and storm runoff events by RBDD RST's in 2016 and 2017 exhibited the highest movement rates of all fish within the upper reach (49.3 and $94.4 \text{ rkm}\cdot\text{d}^{-1}$), which were at least two standard deviations above the annual median reach velocities of 5.6 and $2.2 \text{ rkm}\cdot\text{d}^{-1}$, respectively, for trawl-caught fish in those years. These trap-caught fish appeared to be continuing, post-tagging, active downstream migration that was in

progress upon capture. The higher capture rates of the benthic trawl support the use of active sampling methods to collect rearing juvenile green sturgeon which exhibited long residence times and decreased intergate and reach velocities when compared to actively migrating trap-caught fish sampled from the same reach of river. Two additional trap-caught fish that were sampled outside of storm-related events had upper reach migration rates ranked 43 and 45 of the 74 reach velocities analyzed for the upper reach and did not move out of that reach for an additional 48 to 55 days. These individuals were initially detected moving during periods of static river discharge, suggesting they were likely moving passively as a part of nighttime foraging behavior in the vicinity of the RSTs as opposed to actively migrating downstream or transitioning to alternate habitat types.

Reach velocities differed to a much smaller degree in the middle and lower reaches of the Sacramento River when comparing capture types. Median intergate velocities were nearly identical within both reaches regardless of the capture type. Trap-caught fish exhibited slower median reach velocities compared to trawl-caught fish in the middle reach with differences declining in the lower reach. Comparisons between reach and capture type were not found to be statistically significant. Time spent within the middle and lower reaches, with the exception of some outliers in 2017, was not extensive indicating slower migratory behavior as opposed to rearing behavior in these reaches of the Sacramento River. Hassrick et al. [51] observed that Chinook salmon smolts slow down within the middle reach of the Sacramento River in dry water years. In the years that our studies overlapped (2016 and 2017), both juvenile Chinook and green sturgeon passed through this area with minimal stopover times, indicating movement through this river reach is likely influenced by the magnitude of river flows and water velocities in this reach. Michel et al. [72] and Notch et al. [50] also found higher survival of juvenile Chinook when flows through this

reach were on the higher end of the scale of observations in the spring. These data indicate the need to continue analyses or acquire additional data on the habitat conditions of the middle and lower reaches of the Sacramento River, study their influence on fish survival, and determine the quality/quantity of rearing habitat for multiple migratory species in the winter and spring period.

4.3. Cues to Juvenile Outmigration. This work is the first field study documenting the timing and patterns of juvenile SDPS of green sturgeons transitioning from freshwater rearing habitats to brackish water habitats. On average across the four cohorts, 65.5% (range = 36.4–94.5%) of acoustically tagged juvenile green sturgeon were detected at, or downstream of, the boundary of the legal Delta at rkm 170. As demonstrated here, and in many cases with juvenile Chinook salmon, acoustic telemetry can be a powerful technique to study the behavior, movement patterns, or survival of anadromous fishes within river and altered hydrologic systems [46, 73]. The suitability of JSATS technology designed primarily for pelagic fish (i.e., tags and receiver arrays) was uncertain at the beginning of this project when used to study juvenile green sturgeon oriented to the benthos [45] in a potentially acoustically noisy river environment [74] over long distances. The successful detection of juvenile green sturgeon in this study suggests this technology can be usefully applied to study other benthic-oriented juvenile fish in freshwater habitats or for use in additional sturgeon acoustic telemetry-based projects.

In the Central Valley of California, JSATS technology has mainly been used to evaluate Chinook salmon smolt migration and survival in various tributaries and reaches within the Sacramento and San Joaquin River systems and to estimate effects of migration routing through the Delta [50, 72, 75, 76]. Two critical assumptions of survival estimate studies are that all tags are retained within fish and transmitters function throughout the study period [77, 78]. The commercially available JSATS microacoustic tags used during this study had an expected battery life ranging from 68 to 111 days. These tags tend to work well for juvenile salmonid survival estimates of fish raised in a hatchery environment and released as smolts that are physiologically ready to actively migrate downstream. In many cases, the battery life typically exceeds the expected travel time through the area of interest when used on salmonids. Microacoustic JSATS tags were not available to accommodate the extended rearing times exhibited by juvenile green sturgeon sampled in this study. The extended residence times detected primarily by trawl-caught fish coupled with tag life limitations likely would result in a negative bias [79, 80] to survival estimates had we attempted to estimate survival rates to the upstream boundary of the legal Delta. To overcome the limitations to estimating survival we observed, an additional study designed to determine reach-specific survival should be conducted within an appropriate statistical framework [75] using microacoustic tags with prolonged battery life or delayed activation.

Detections during fall and winter storm and runoff events were reduced at several acoustic receiver gate locations resulting in the need to perform reach-scale movement analyses. Modeling efforts to associate environmental conditions with outmigration from the upper reach of the Sacramento River often times had to rely on suboptimal precision of acoustic detections in terms of the exact moment or environmental conditions that outmigration began and is considered a limitation to this study. Imperfect gate-to-gate detections necessitated inference about some detections, especially during elevated outflow events [81] when individuals were not detected by all downstream gates consecutively.

Increased flow and turbidity levels appeared to consistently result in the downstream movement of juvenile green sturgeon, although no single flow or turbidity event resulted in the movement of all available tagged fish at any one time (Figures 2(e)–2(h)). Imperfect detections coupled with a generalized initial location of each tagged fish relative to acoustic receivers during a given runoff event, along with typical swim speeds and distance from the onset of habitat transitioning movements to the lower boundary of the upper reach, all likely contributed to our finding that a 2-day window was the most representative time frame that resulted in outmigration behaviors. A 2-day post-rainfall event interval was observed by Goodman et al. [82] for the large-scale movement (93%) of juvenile Pacific lamprey (*Entosphenus tridentatus*) emigrating downstream in the Sacramento River during fall and winter periods. For juvenile winter Chinook, it was noted that survival increased when downstream migration occurred during increased flow events, yet the movement patterns were more complicated with respect to wet and dry years relative to mean annual flow and intra-annual reach flows [51]. From a management perspective, early season storm events that result in increased median flow rates of +28.4% (interquartile range = 19.2 to 46.2%) and increases in turbidity of +234.6% (interquartile range = 102.0 to 424.6%) over ambient conditions are likely to be associated with the initiation of outmigration of juvenile green sturgeon and, similarly, result in large-scale movements of juvenile salmon and lamprey [35, 82]. These combined data indicate runoff events are highly important for the redistribution and habitat transition of juvenile anadromous fish from one location or habitat type to another. The use of flow and turbidity events by anadromous fish is generally thought to increase survival through increased daytime visual cover and associated reductions in predation and by reducing the energetic demands on juvenile fish that need to migrate long distances. These survival benefits would likely be conferred to juvenile green sturgeon migrating ~300 rkm downstream during increased flow and turbidity events as fish transition to new brackish water rearing habitats in the Delta.

The concept of increasing water diversions as a resource management tool during fall through spring runoff events to provide off-stream water storage for human consumptive uses, water banking, or ground water recharge, has received increased political and financial support in recent years. Diverting water from the first fall and/or winter runoff

events would likely have a profound negative effect on juvenile anadromous fish populations moving downstream within the Sacramento River system during these ecologically important transition events. Off-stream storage and diversions into bypass floodplains should be modeled together and coordinated in practice to balance the potential beneficial effects of additional water resource capture for humans and floodplain inundation for juvenile salmonids [83–86], but should also utilize available real-time juvenile anadromous fish monitoring data to avoid large-scale fish entrainment and mortality of outmigrants.

River water temperature was not strongly associated with juvenile green sturgeon movement up to the 10-day interval we analyzed. This likely indicated that river water temperature does not act directly as a cue or driver of outmigration, but decreased water temperatures could be necessary for successful downstream migration to occur during habitat transition over 100's of river kilometers. Decreasing water temperatures in the fall to winter period are an annual pattern as the number of daylight hours decline with decreasing day length, which was noted by Kynard et al. [31] as an alternate cue for the secondary downstream migration of juveniles in the laboratory. It is likely that through interaction with flow and turbidity increases that decreasing temperature or day length has a synergistic effect on juvenile sturgeon outmigration as they await appropriate conditions to move downstream. Most juvenile green sturgeon outmigrated from the upper Sacramento River at water temperatures between 11 and 12°C (range = 8.1 to 14.9°C). In laboratory observations by Kynard et al. [31], all secondary migration activity ceased at the lowest value of 8.1°C corresponding with the lowest temperature we observed outmigration from the upper reach in the Sacramento River in our study.

4.4. Continuous and Stepped Migration Patterns. Bemis and Kynard [87] described various upstream spawning migrations exhibited by the genus *Acipenser*, but little field-validated information currently exists on the variation in downstream migration patterns of juvenile anadromous or freshwater amphidromous fish of the order Acipenseriformes. Many species of fish, primarily at the adult life stage and including green sturgeon, have been observed making continuous and stepped downstream migration patterns [21, 88]. The results of our study indicated variability in the outmigration patterns of juvenile green sturgeon from the upper reach to the lowest reach of the freshwater portion of the Sacramento River. Additional lower river and Delta migration information is described by Hansen et al. [89]. Despite the documentation of at least two types of downstream migration patterns, all individuals in this study that migrated downstream or were detected completing habitat transition to the Delta did so prior to the completion of their first full year of life. In contrast, sympatric white sturgeon larvae sampled below spawning areas in the Sacramento River near Colusa (rkm 305) drifted downstream in one continuous migration to nursery areas in the river, Delta and Suisun Bay [90, 91]. Zhuang et al. [92] and Huang [93] found

that Chinese sturgeon (*A. sinensis*) in the Yangtze River moved downstream over 2800 rkm at age-0 reaching the ocean near age-1, albeit as a single continuous migration beginning at the larval stage. Fox and Peterson [47] sampled and acoustically tagged juvenile Atlantic sturgeon (*A. oxyrinchus*) downstream of the head of tide and indicated that these fish move downstream as larvae and settle into the estuary as juveniles. From their detection data, estuarine juveniles transitioned to full saltwater in the ocean at age 1 and 2 and were referred to as river-resident and marine-migratory juveniles, respectively. From these investigations, it appears that juvenile acipenserid migrations are highly variable and species-specific, resulting in the need to be cautious when using surrogate species where data are lacking for the species of interest.

Allen and Cech [94] reported 23% mortality of juvenile green sturgeon in full saltwater at 100 dph in laboratory studies. Allen et al. [32] reported full saltwater tolerance of juvenile green sturgeon at 134 dph and ~200 mm FL and 80 g of weight. The fish used in these laboratory studies were reared at a constant 19°C which is higher than temperatures juvenile green sturgeon encountered in the upper Sacramento River within our study. Poletto et al. [28] studied the effects of both temperature and diet, and the interaction of the two was found to be significant as it relates to sturgeon condition factor and assumedly the development of critical organs including the gills, kidneys and gut in preparation for saltwater tolerance [32]. It is difficult to directly compare the static laboratory feed and temperature conditions to those experienced by naturally produced fish in the Sacramento system over 4 different water years. Moreover, length and weight was measured once during the capture and tagging portion of this study. Liss et al. [61] noted implantation of acoustic tags into white sturgeon resulted in reduced growth rates (FL only) for up to 28 days post-implantation. The actual age (in dph), length, weight or condition factor of the juveniles studied here at the onset of their outmigration was unknown for trawl-caught fish but varied widely between individuals from days to months and is a limitation of this study. Furthermore, the spawning groups from which individuals were sampled came from larvae that were detected in RSTs over a period between 42 and 73 days each year [36]. Based on larval emergence timing the outmigrating juvenile green sturgeon studied here are estimated to be between ~180 dph and 270 dph and likely fully saltwater tolerant.

Chinook salmon juveniles in the Sacramento River have been observed making stepped downstream migrations to the brackish water portion of the Delta and have been found to use "stopover" habitats to forage during migration [51]. Currently, the quantity and quality of habitat and forage within the middle and lower reaches at the time of year that we detected short-term residency of sturgeon exhibiting stepped migration patterns are unknown. Green sturgeons have been found to exhibit reduced swimming performance during their juvenile ontogenetic stage when preparing for saltwater entry and at colder (e.g., fall or winter) water temperatures [26, 32]. Juvenile green sturgeon are also thought to be less efficient swimmers who utilize currents to decrease the energetic cost of their movements [12]. The

stepped migrations we observed were not likely a result of caloric deficiency and the need to acquire supplemental energy reserves to continue migration or from lack of physiological development, but potentially insufficient river flows within each year experienced by some juvenile sturgeon during their transition to brackish water habitat. Juveniles who initiate downstream migration during modest flow increase events lacking sufficient magnitude (e.g., $\leq 25^{\text{th}}$ percentile) or duration (e.g., < 2 days) to reach the Delta may simply demonstrate a stepped migration pattern when the flows during the initiation of migration taper off or cease entirely before reaching new habitat types. Additional research of habitat characteristics and the abundance and composition of food resources within the middle and lower reaches of the Sacramento River during the summer (for early migrants) and late fall and winter is recommended to determine how these areas could affect the growth of juvenile green sturgeons rearing in these reaches for days, weeks or months. The potential benefits of having stepped and continuous migration patterns, or simply variation in migration timing and duration as observed by this study, could be to spread the risk of mortality of juvenile migrants over time with varying environmental conditions thus ensuring some fraction of the juvenile population transitions to the next habitat type or life history phase for the continued survival of the species.

5. Conclusions

JSATS technology was used for tracking individual juvenile green sturgeon to determine their freshwater residency and rearing locations, estimate movement velocities on both intergate and reach-scales, and to illicit information about the drivers of their transition between fresh and brackish water habitats. Benthic trawls were able to successfully capture juvenile green sturgeon in the Sacramento River during their residency in rearing areas while rotary traps primarily captured juveniles already undergoing a transitional migration. Migration patterns varied and battery life may have limited tracking the habitat transition movements by some of the study individuals. Often, downstream migrations out of the upper reach of the river were rapid and continuous, with individuals moving hundreds of river kilometers in as little as 2 days. Some juveniles exhibited stepped migration patterns as long as 67 days. River discharge and turbidity over a 2-day window were the most congruent environmental conditions associated with the onset of downstream migrations. Increases in discharge and turbidity of 19 to 46% and 102 to 425%, respectively, were associated with 50% of all migrations out of the upper Sacramento River. Temperature did not appear to have a direct effect on migration initiation. Fish of larger sizes appeared to be more likely to move downstream in a continuous pattern, but precise information on the size at the time of migration initiation was limited as it was based on measurements at capture which occurred days to months before subsequent outmigrations. Fish that moved out of the upper river within the battery life of the JSATS tags were estimated to be between 6 and 9 months of age (180 dph to

270 dph) based on the timing of larval collections, and coincides with saltwater tolerance data collected from laboratory studies of green sturgeon. These data provide information that was previously unknown on the life history of southern distinct population segment of the North American green sturgeon and could be utilized to assist with river and water operations management and recovery of this threatened fish species.

Data Availability

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request. Acoustic telemetry detection data can be downloaded from NOAA Fisheries Southwest Fisheries Science Center's Environmental Research Division Data Access Program, JSATS California Fish Tracking website: https://oceanview.pfeg.noaa.gov/erddap/tabledap/FED_JSATS_detects.html.

Disclosure

The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

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Supplementary Materials

Figure S1: Plots showing individual juvenile green sturgeon detection events spanning the time within the upper reach of the Sacramento River to the first event out of the upper reach. Tag codes with capture type (in parentheses) are used as plot headings. Start times are 7 days prior to the release event (grey x). Event duration is shown by a horizontal line with open and filled circles indicating the start and end times, respectively. The dashed line is at the downstream upper reach boundary location at rkm 390 on the left y -axis. Sacramento River flow from the Vina gauging station (VIN)

is shown by the grey line in cubic meters per second ($\text{m}^3 \cdot \text{s}^{-1}$) on the right y-axis. Dates are relative to each tagged sturgeon in months on the x-axis. (*Supplementary Materials*)

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