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Reach specific use of spawning habitat by adult green sturgeon (*Acipenser medirostris*) under different operation schedules at Red Bluff Diversion Dam

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Summary

Mature green sturgeon, *Acipenser medirostris*, enter rivers along the western coast of North America in late winter to late spring and migrate upriver to spawning sites. After spawning, they may leave the river or spend the summer and autumn holding in deep pools before departing from the river with the onset of winter rains. Evidence exists that the seasonal Red Bluff Diversion Dam (RBDD) was an obstacle to the upriver migration of green sturgeon in the Sacramento River in Central California. We compared the migratory movements of green sturgeon under three different dam operation schedules, including post-decommissioning, to assess the impact of this management action. The proportion of green sturgeon carrying acoustic transmitters that moved above the RBDD was higher when the gates were closed on June 15, one month later than the historical closure date of May 15, and increased again after the dam was decommissioned. The application of statistical analyses (generalized linear and additive mixed models) to the detection records of green sturgeon highlighted an improvement in connectivity after dam decommissioning. The data also indicate that interannual variation in river condition is an important driver of sturgeon presence on the spawning grounds.

1 | INTRODUCTION

Green sturgeon, *Acipenser medirostris*, are only known to spawn in three river systems along the western coast of North America. Genetic evidence indicates two distinct populations exist: the southern population of fish that spawn in the Sacramento River watershed, and the northern population of fish that spawn in the Rogue and Klamath rivers (Israel, Cordes, Blumberg, & May, 2004). The southern population is protected as a threatened distinct population segment (DPS) under the U. S. Endangered Species Act (NOAA Federal Register, April 2006). Freshwater habitat loss and degradation, due to dams, temperature alterations, and habitat simplification, was deemed an important factor in the population decline (Adams et al., 2007). Mature green sturgeon enter rivers in late winter to late spring and migrate upriver to spawning sites (Benson, Turo, & McCovey, 2007; Erickson & Webb, 2007; Heublein, Kelly, Crocker, & Klimley, 2009). The peak spawning season for southern DPS in the Sacramento River occurs between early May and mid-June, with favorable spawning habitat occurring along approximately 120 river kilometers (rkm) of the mainstem (Poytress, Gruber, Van Eenennaam, & Gard, 2015). After spawning, adults may leave freshwater or spend the summer and autumn residing in deep pools before departing from the river with the onset of winter rains (Benson et al., 2007; Erickson, North, Hightower, Weber, & Lauck, 2007; Heublein et al., 2009).

In the Sacramento River, the Red Bluff Diversion Dam (RBDD) has been an obstacle to the spawning migrations of green sturgeon (Heublein et al., 2009). This gate-operated diversion dam is located in the mainstem of the river at rkm 479 (measured from the Golden Gate Bridge) and was completed in 1964 to supply water to irrigation canals. The gates were closed seasonally between 15 May and approximately 14 September each year until 2009, when gates were closed a month later on 15 June to reduce impacts on migratory movements of fishes, especially green sturgeon. When gates were closed the only opportunities for sturgeon to pass the dam were through a fish ladder designed for salmonids (Mahmoud & Garcia, 2000) or through a narrow gap (≤0.5 m) between the flood gates and the river bottom. Green sturgeon were never observed swimming up the fish ladder, and the rapid acceleration of water through the narrow passage between the gates and river bottom is likely to have impeded up-river movement (Brown, 2007). Beginning in 2012 the dam was decommissioned when a pumping plant was completed to divert water to the irrigation canals.

Through the collection of green sturgeon eggs and juveniles, as well as passive and active telemetry monitoring of adults, spawning sites have been identified both upstream and downstream of the RBDD (Brown, 2007; Heublein et al., 2009; Poytress et al., 2015; Thomas et al., 2014). Manual tracking of tagged green sturgeon showed that during the spawning season some individuals exhibit frequent movements over tens of kilometers between suitable spawning habitats (Thomas et al., 2014), similar to behaviors observed in other closely related sturgeon species (Paragamian, Wakkinen, & Kruse, 2002). Thus, in addition to blocking access to upstream spawning habitat for late-migrating adult green sturgeon, the diversion dam posed a barrier to natural movements between suitable spawning sites, effectively fragmenting the spawning population.

It is important to note that all sturgeon species in the United States have experienced range contraction, resulting in a 22% reduction in historical range across all species (Jager et al., 2016). While green sturgeon fall on the lower end of absolute habitat loss (~15%, Jager et al., 2016) the associated biological impact can still be significant. The fragmentation of southern DPS green sturgeon habitat resulting from the presence of the RBDD, occurs at a crucial location (within the spawning reach) and at a crucial time (within the spawning season). While the population effects associated with such a disturbance is not clearly understood, they could be assumed to be significant.

Effective management of migratory species, such as green sturgeon, depends upon reliable information on the seasonal movements of individuals (Nelson et al., 2013). Acoustic telemetry techniques are a suitable means to gather these data, through the use of either automated detection stations or manual tracking. The migratory movements of adult green sturgeon in the Sacramento River were recorded with automated stations both below and above the RBDD, to assess the improvement in connectivity resulting from changes in operation of the RBDD. We compare the probabilities of adult sturgeon presence in three segments of the spawning reach under the three dam operations schedules (closure May 15, closure June 15, and no closure). Understanding the individual and population level effects of management actions throughout the range of green sturgeon in the Sacramento River is necessary for assessing the risks to the southern DPS.

2 | MATERIALS AND METHODS

2.1 | Automated monitoring

Since 2002, coded acoustic tags have been surgically implanted in close to 350 adult green sturgeon along the western coast of North America (data in SQL database administered by Biotelemetry Laboratory, University of California, Davis; Table 1). All tags were made by Vemco (Bedford, Nova Scotia, Canada), and implanted in wild caught sturgeon using appropriate field-based surgical techniques. Equipment, capture, and surgery methods varied by research program (Table S1) and details about specific studies can be found in Moser and Lindley (2007), Kelly, Klimley, and Crocker (2007), Heublein et al. (2009), and Thomas et al. (2013, 2014). In brief, sturgeon were generally captured by trammel net in the estuary or the river, and carefully brought to either a boat or the shore for surgery. A Vemco coded transmitter (V-16, variable programming, variable tag life, Table S1) was implanted into the peritoneal cavity through a 2–4 cm incision made between the third and fourth scute, approximately 1–2 cm off the ventral line. The incision site was closed with interrupted sutures. Post-surgical fish were released in the location of capture. We assume that tagged individuals were representative of the greater population, and that tag effects were minor or short-lived and did not meaningfully affect the behavior of the sturgeon. All individuals captured and

TABLE 1 Tagging history of green sturgeon used in this analysis. Total tags are tabulated as of December 31 of a given year (in the SQL database maintained by the Biotelemetry Laboratory), assuming tags lasted ten years (with exception for 3-year tag duration if implanted 2004–2006). Study reach was upstream of the rkm 412 (Hwy 32 Bridge)

Year	Tagged (CA)	Tagged (OR/WA)	Total tags[a]	Number (%) detected in study reach	Date of dam closure
2003	0	1	1	–	May 15
2004	2	2	5	–	May 15
2005	12	4	21	–	May 15
2006	28	0	49	–	May 15
2007	0	0	45	7 (16)	May 15
2008	10	0	39	14 (37)	May 15
2009	29	0	40	38 (97)	June 15
2010	19	0	59	28 (48)	June 15
2011	29	8	96	25 (26)	June 15
2012	13	1	110	27 (25)	No Closure
2013	0	0	109	13 (12)	No Closure

[a]2004–2006 assumed tag-life of 3 years; after 2007 assumed tag-life of 10 years.

tagged through UC Davis were handled under approval from the university's Institutional Animal Care and Use Committee.

After release, those individuals which migrated up the Sacramento River were detected by Vemco VR2 or VR2W automated receivers placed throughout the river (Figure 1; Table S2). Receivers were deployed on cabled moorings attached to shore. The moorings consisted of 30–40 lbs of weight and deployment distances were 15–30 m from shore. A vertical cable, approximately 1.5 m in length was attached to the weighted mooring and floated with a standard 12.7 × 30.5 cm PVC crab float attached at the end of the cable. The acoustic receivers were mounted to the vertical cable approximately 0.5 m above the weights. A detection probability analysis was conducted on the collected data to evaluate our assumption that tagged fish had equal probabilities of detection throughout the spawning reach. Detections recorded by these receivers between 2007 and 2013 were analyzed to describe movement past the dam site and quantify annual changes in distribution throughout the spawning reaches of the river.

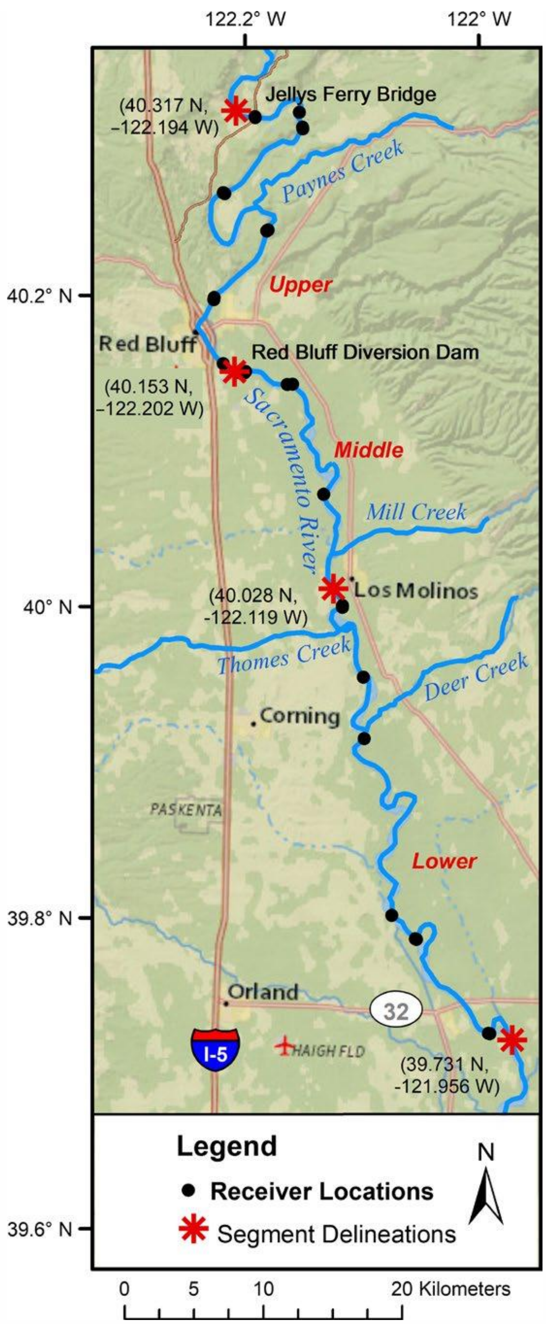

FIGURE 1 Map of the Sacramento River, CA, showing the segmentation of the green sturgeon spawning reach into the upper, middle, and lower segments used for modeling. The Red Bluff Diversion Dam is located at the delineation between the middle and upper segments. Autonomous receivers are indicated in the deployment locations of 2008

2.2 | Statistical analysis

Detections at automated receivers were used to quantify how many adult green sturgeon accessed spawning habitat above and below the RBDD site under each dam operation schedule, and to estimate when individuals transited past the dam site. We classified the spawning reach into three segments: a lower segment (49 rkm in length) from just below the Hwy 32 bridge near Hamilton City, California (rkm 410) to Los Molinos, California, a middle segment (20 rkm in length) from Los Molinos, California to the RBDD, and an upper segment (39 rkm in length) from RBDD to Jellys Ferry Road Bridge. The spawning reach was divided into three segments in order to identify separate reaches above and below RBDD, as well as a lower reach that included known aggregation sites (Poytress et al., 2015). Specific locations of reach delineations were selected to ensure that throughout the study each segment had between four and eight receiver stations across the entire study period to detect the presence of tagged green sturgeon (Figure 1). Detection probabilities were evaluated using Cormack-Jolly-Seber equations to ensure there was no systematic bias in detection across reaches and years (Appendix S1).

We used two approaches to evaluate green sturgeon movement on the spawning grounds. First, we used a generalized linear mixed model (GLMM) to evaluate differences in the proportion of tagged individuals passing RBDD under different dam operation schedules. Each individual that arrived in the spawning reach (upstream of rkm 410) from 2007 to 2012 was assigned a "terminal segment", defined as the segment containing the most upstream detection. We then constructed a binomial GLMM with a logit link, using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) in the R environment (R Core Team, 2016). The binomial response was positive if the terminal reach of a spawning migration was above RBDD. An identifier of individual sturgeon was specified as a random effect to control for non-independence of multiple spawning runs by the same individual. Detection year was not included in this model due to its collinearity with the dam operation schedule, but the effect of detection year was evaluated in a separate model. The significance of dam operation schedule and detection year as independent predictors of dam site passage were compared using Akaike's information criterion (AIC) to quantify improvement over the null model equivalent.

Our second analysis assessed temporal changes in distribution of adult green sturgeon throughout the spawning reach of the Sacramento River. To standardize detections across the year, we selected one detection per week for each individual fish, choosing the last detection recorded in each seven-day window. This detection was assigned to one of the three previously defined spawning reach segments. Due to the nature of the passive detection array, while a fish remained at a point between receivers its exact location could not be recorded. Thus, if an individual was not detected over a period of three or fewer weeks, but the prior and subsequent detections were in the same spawning reach segment, the individual was assumed to have remained within that segment during the intervening time period. Additionally, mobile surveys were conducted by boat in two years (2011 and 2012) between Redding, CA and the Hwy 32 bridge. Surveys lasted three days, and were repeated 10 times (2011) or 11 times (2012) each season between April and October. These results were used to confirm locations of individuals holding between receiver stations, and were integrated into the detection record to augment gaps between detections at stationary receivers.

A detection history was constructed for each fish indicating weekly movement into the spawning reach, holding behavior, transit among segments of the spawning reach, and downstream movement out of the spawning reach. When fish were tagged within the spawning reach this movement history was only constructed for weeks after capture. If a fish did not complete its downstream migration into the estuary before the end of the calendar year, all detections after December 31 were removed from the analysis so to not confound upstream movements of other individuals in the following late-winter or spring. From these detection histories we developed a binomial generalized additive mixed model (GAMM) for each reach to describe the probability that a given fish was present in that reach during each week of the year. Models had a logit link function and thin plate spline smoothers, with a smoother for the week of the year as the primary explanatory variable (Zuur, Leno, Walker, Saveliev, & Smith, 2009). We also considered the dam operation schedule, the interaction of the week of the year and the dam operation schedule, and the detection year as possible additional explanatory variables (Table 2). For each reach, the resulting suite of potential models were evaluated using Akaike's information criterion, corrected for small sample sizes (AICc; Wood, 2006) to select the most appropriate combination of fixed explanatory effects. Detections from all years were combined to increase the power of the analysis, while the identifier for individual fish was used as a random effect within the model to control for non-independence of multiple spawning runs by the same individual. In the model selection process, we also examined the explanatory power of a binary variable to indicate if a fish was tagged in the spawning reaches.

A conservative estimate of model fit for the final GAMMs was obtained using the approach suggested by Gilman, Chaloupka, Wiedoff, and Willson (2014) because traditional measures of fit are not available for GAMM analyses. We first calculated the percent deviance explained (a measure of goodness-of-fit) of an equivalent generalized additive model (GAM) which contained the smoothed and fixed effects but no random effects. When the AICc for a GAMM was higher than the AICc of its corresponding GAM, this indicated that incorporating

TABLE 2 Model structure and AICc values for generalized additive mixed models (GAMMs). Models were used to assessing the influence of dam operation schedule (seasonal gates put into operation on May 15, June 15, or not operated) on the location of adult green sturgeon in the spawning reaches of the Sacramento River, CA. All models also included the individual tag identifier as a random effect. AICc values were used to compare model structures within each reach, while the deviance explained by a corresponding generalized additive model (GAM; no mixed effects) was used to compare model fit across reaches. The deviance explained by each corresponding GAM provides a conservative estimate of the model fit for models with mixed effects, as current statistical research does not support a means of directly assessing goodness-of-fit for GAMMs

Model	Model structure	AICc	ΔAICc	Weight	GAM: Deviance explained (%)
Upper reach	s(period) × operation schedule	995.3	0.0	0.999	27.9
	s(period) + operation schedule	1009.7	14.4	0.001	24.6
	s(period) + detection year	1011.1	15.8	0.000	27.1
	s(period)	1012.3	17.0	0.000	23.6
	Null	1552.2	556.9	0.000	0.0
Middle reach	s(period) + detection year	1325.5	0.0	0.976	15.9
	s(period) + operation schedule	1333.1	7.6	0.021	13.6
	s(period)	1337.6	12.1	0.002	13.1
	s(period) × operation schedule	1351.7	26.2	0.000	14.3
	Null	1471.9	146.4	0.000	0.0
Lower reach	s(period) + detection year	2223.0	0.0	0.999	14.8
	s(period) + operation schedule	2237.7	14.7	0.001	11.8
	s(period) × operation schedule	2246.8	23.8	0.000	15.3
	s(period)	2270.8	47.8	0.000	11.5
	Null	2480.4	257.4	0.000	0.0

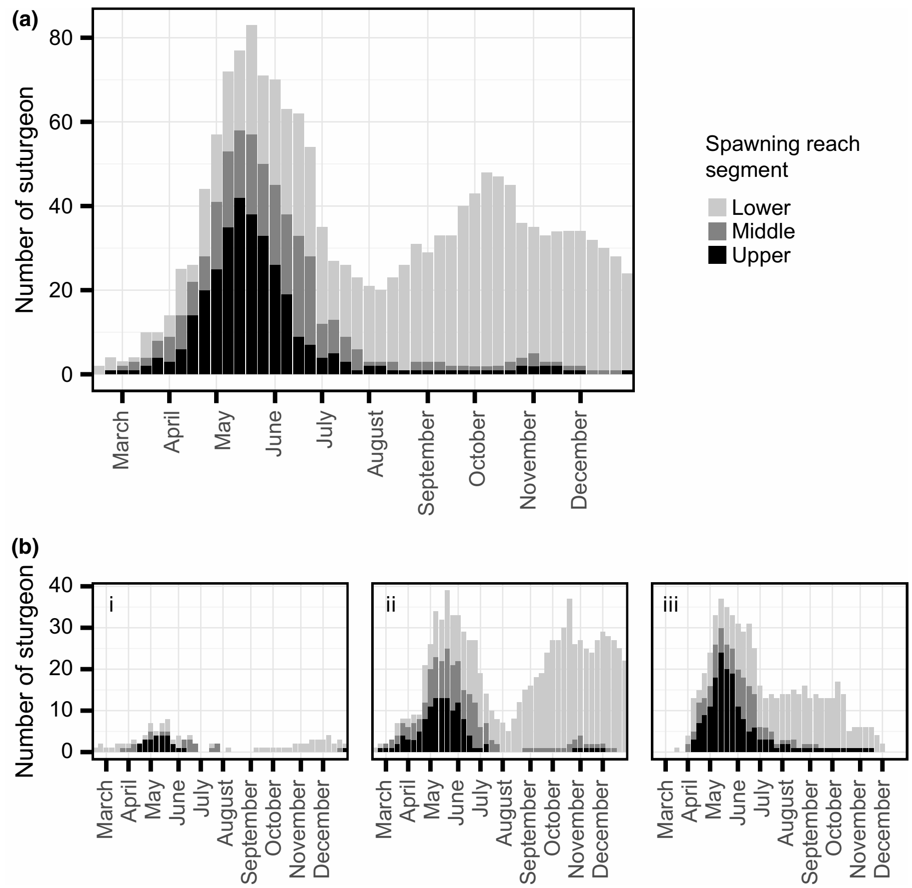

FIGURE 2 Annual variation in green sturgeon presence within spawning reaches of the Sacramento River. Detections of 127 green sturgeon with implanted acoustic transmitters were recorded by autonomous receivers. In each week, detections were assigned to segments of the spawning reach below the RBDD (lower and middle) and above the RBDD (upper). The number of detections in each week of the year were combined across all seven years (a), and were grouped according to dam operation schedule (b), with operation of the seasonal gates beginning on May 15 during 2007–2008 (i), on June 15 during 2009–2011 (ii), and not being operated during 2012–2013 (iii). Note the increase in tagged sturgeon present in the system after 2009

mixed effects improved the model, and therefore the GAMM explained at least as much deviance as the equivalent GAM. Thus the deviance explained by the GAM serves as a conservative estimate of the fit of the corresponding GAMM (Gilman et al., 2014).

3 | RESULTS

We recorded the presence of 127 green sturgeon in the spawning reach of the Sacramento River (i.e. above rkm 410), during 152 distinct spawning runs between 2007 and 2013. The detection probability analysis indicated that there was no systematic bias in detection across dam operation schedules (Figure S1). During each phase of dam operations a different number of tagged fish were present in the spawning reach (Table 1). However, across years the detection records indicate a single peak in the abundance of individuals recorded on a weekly basis above the RBDD during the period from early May to the middle of June, indicating the likely peak spawning period (Figure 2). Many of these individuals did not exit the watershed immediately after spawning, but remained in the lower reach from July through December and into the following year.

When the lowering of the gates of the Red Bluff Diversion Dam was delayed from the 15th of May (annual closure date in 2007 and 2008) to the 15th of June (annual closure date from 2009 to 2011) a greater number of tagged green sturgeon migrated into the reach above the dam. Prior to dam-reoperation (2007–2008) there were 4 tagged green sturgeon that moved above RBDD, out of 21 total tagged sturgeon detected above rkm 410 (19.0%). After the gate closure was delayed by one month (during 2009–2011), there were 32 tagged green sturgeon that moved above RBDD, out of 91 total sturgeon detected above rkm 410 (35.2%). Only 23 of these 32 fish (72%) moved above RBDD before May 15. An additional nine (28%) moved above the RBDD between May 15th and June 15th during the month-long delay in dam closure. The study years after dam operation ceased (2012–2013) saw 29 tagged green sturgeon move above RBDD, out of 40 total sturgeon detected above rkm 410 (72.5%). However, these two years experienced earlier arrivals at the RBDD site, with only one of 29 fish passing the site after May 15th. The overall enhanced movement into the upper reach is apparent from examining the proportion of tagged fish migrating above the dam versus those that remained below in each year of the study (Figure 3).

The GLMM analysis used to assess the correlation between dam operation schedule and passage above the RBDD site indicated that there were significant differences between operation schedules. We compared a null model with the terminal segment as the binomial response variable and only one random explanatory effect of individual identifier (AIC = 211.5), with a second model including dam operation schedule as a fixed effect as well as a random effect of individual identifier. Inclusion of dam operation schedule improved the model (AIC = 193.3; ΔAIC = −18.2) supporting the conclusion that dam operation schedule was a significant predictor of the terminal segment achieved during these individual migrations. Tukey HSD post-hoc

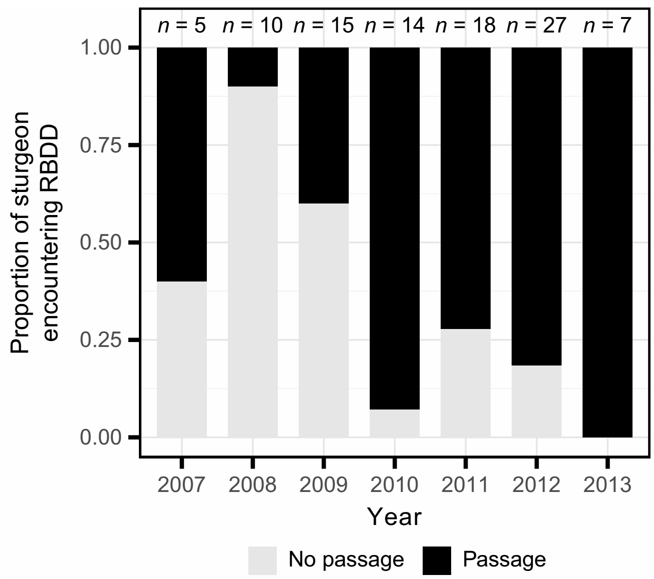

FIGURE 3 Passage above Red Bluff Diversion Dam (RBDD) site during the seven years of study, shown as proportion of sturgeon that entered the middle spawning segment (20 km reach downstream of dam site). The total number of tagged sturgeon detected in either of the middle or upper spawning segments in any given year are indicated above the bars. Seasonal dam operation schedule varied during the study, with closure beginning on May 15 during 2007–2008, on June 15 during 2009–2011, and no closure during 2012–2013

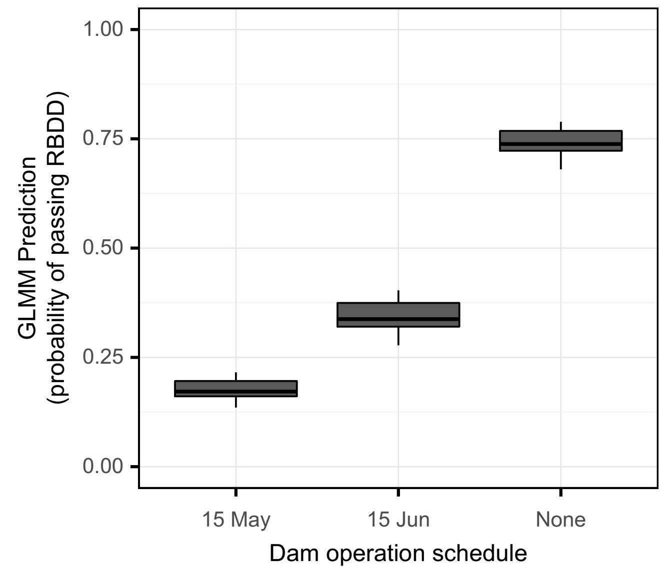

FIGURE 4 Predictions from the generalized linear mixed model (GLMM) of the probability of an adult green sturgeon passing above the Red Bluff diversion dam site under a given dam operation schedule. The dam gates were either closed on May 15th (2007 and 2008), on June 15th (2009 to 2011), or not closed at all (2012 and 2013). Tukey post-hoc tests indicated that the predicted passage probabilities were significantly different when the dam gates were not closed versus when they were closed on May 15th ($p = .004$) or on June 15th ($p = .003$). Predictions are shown as boxplots to encompass variation explained by the random effect of individual included in the model

comparisons ("multcomp" package; Hothorn, Bretz, & Westfall, 2008) indicate that there was a statistically significant difference in upstream passage when the dam was not operated at all versus when it was closed on May 15th ($p = .004$) or on June 15th ($p = .003$). This can be visualized in the model predictions of the probability that a tagged individual would move above RBDD under each dam operation schedule (Figure 4). However, a secondary model constructed using the year of detection in place of the dam operation schedule had stronger support (AIC = 182.8; ΔAIC = −28.7), suggesting that interannual variation in environmental conditions may be confounded with the effects of dam operation for predicting green sturgeon presence in at least some of the spawning reach segments.

The GAMM analyses detected strong effects of the week of the year for all segment-specific models ($p < .001$). The models supported the pattern seen in the tag detections, identifying late May and early June as the period when the upper reach of the Sacramento River is most likely to be used by individual sturgeon (Figure 5). The models also indicated that adults are likely to be present for a longer period of time in the middle reach (April through July) while there is a high probability throughout the fall of detecting an adult sturgeon in the lower reach.

GAMM analyses also indicated the dam operations had a measurable impact on within-year variation in habitat use. Based on AICc (Wood, 2006), inclusion of the dam operation schedule (as either an additive or an interacting effect) improved model fit for all reaches. In the upper reach, inclusion of the dam operation schedule as an interaction with week of the year resulted in the most heavily weighted model (weight = 0.999; Table 2). In contrast, the most heavily weighted model for the middle and lower reaches included an additive effect of detection year (middle reach: weight = 0.976, lower reach: weight = 0.999). The second-best model for both the middle and lower reaches included an additive effect of the dam operation schedule (middle reach: weight = 0.021, lower reach: weight = 0.001). An additional random effect was also assessed which indicated whether a fish entered the spawning reach with a tag or was tagged within the spawning reaches, but this effect removed from the final analysis because it provided no significant improvement to the model (evaluated using AICc, Zuur et al., 2009). Visualizing predictions from the top weighted models that included dam operation shows that when the dam was no longer operated, the probability of sturgeon presence in the upper reach increased substantially (Figure 5b), while the probability of sturgeon presence in the middle reach decreased (Figure 5a). Additionally, the models show a long holding period in the lower reach from July through September (Figure S2).

4 | DISCUSSION

The completion of the Red Bluff Diversion Dam (RBDD) in 1964 fragmented the spawning habitat available to green sturgeon in the Sacramento River. Suitable habitat appears to exist both above and below the dam site (Wyman et al., 2017), yet access to the upper spawning grounds was prevented when dam gates were seasonally closed. Additionally, adults of this species have been observed to

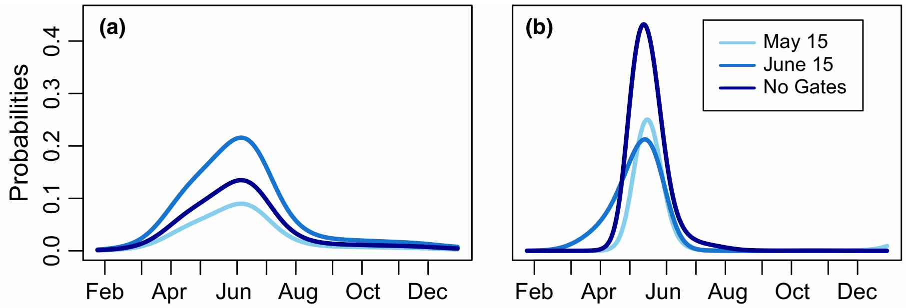

FIGURE 5 Predictions from generalized additive mixed models showing probabilities of green sturgeon presence in the spawning reaches, dependent upon operation schedule of the gates on the Red Bluff Diversion Dam. Data were collected from 127 acoustically tagged adult green sturgeon. The impact of dam operation was less pronounced in the middle segment downstream of the dam site (a) while it was more pronounced in the upper segment upstream of the dam site (b). Predicted probabilities are displayed for three gate operation schedules for each spawning segment: gates in place on May 15th (2007 and 2008), gates in place on June 15th (2009 to 2011), and no gates in place (2012 and 2013). Predictions come from the best model (based on AICc) constructed independently for each segment of the spawning reach, constrained to include dam operation schedule. In the middle reach, this model included week of the year and dam operation schedule, while in the upper reach this model included an interaction between week of the year and dam operation schedule. Corresponding predictions for the lower reach can be found in Appendix S1.

move among several suitable spawning sites during a season (Thomas et al., 2014). Reduction of the access to, and connectivity between, viable spawning areas may have negatively impacted the genetic diversity of the population. In small populations, such as the southern DPS of green sturgeon, even the loss of reproduction from a few individuals can have significant long-term implications for the population's demographic and genetic resilience (Thomas et al., 2014). Thus the reoperation and decommissioning of the RBDD had the potential to positively impact this threatened sturgeon population.

The telemetered movements of green sturgeon presented here highlight an upstream movement of the population during spring and a downstream movement of the population during the summer, with some individuals remaining within lower areas of the river during the fall and winter. This is consistent with information about green sturgeon of the Northern DPS (Benson et al., 2007; Erickson et al., 2007), and smaller scale telemetry information available for the Southern DPS (Heublein et al., 2009). Further, these data show that when gate closure was delayed until June 15th, additional individuals were able to move upstream past the RBDD site. The statistical models indicated that more adult sturgeon were expected to transit past the dam site and to be present in the uppermost segment of the spawning habitat (above RBDD) after the dam was decommissioned. Additionally, seven of the telemetered individuals who encountered RBDD after its operation schedule was shifted one month later were observed to move past the dam site on multiple occasions. Therefore we can conclude that the delay in dam gate closure and the ultimate decommissioning of the dam has enhanced movement into the upper spawning reaches and connectivity among spawning sites.

It is important to note that this analysis also indicates a significant role of interannual variation in environmental conditions. AICc comparisons of the GLMMs indicated that the year of the spawning migration was a better predictor of passage at the dam site than dam operation schedule. The GAMM analysis also indicated that the probability of a fish being present in the two segments of the spawning reach below RBDD was predicted better by a GAMM model which included the year of the spawning migration rather than the dam operation schedule. This finding is consistent with the hypothesis that dam operations are important in fostering connectivity to upstream spawning grounds, while environmental variation should be the predominant driver of sturgeon presence below the dam site. This may explain the reduced model fit for these lower reaches, as there are almost certainly additional factors beyond dam operation that influences the overall migratory behavior. The timing of spawning migrations is often influenced by cues such as water temperature or flow variation (Benson et al., 2007; Erickson et al., 2007; Erickson & Webb, 2007; Fernandes, Zydlewski, Zydlewski, Wippelhauser, & Kinnison, 2010). These factors vary with annual precipitation, snow pack, and upstream dam management, and thus are encompassed in detection year in the model. Future work should focus on evaluating the specific environmental conditions associated with abundance and timing of the green sturgeon spawning migration.

Finally, these data indicate that the lower spawning grounds may provide important habitat during the post-spawn period in the fall, as adult sturgeon are most likely to be found in the lower reach from August through December. This suggests there may be different habitat features in this reach that are attractive for post-spawn recovery, prior to migration back to the ocean. Because green sturgeon is an iteroparous species, long-term conservation of this population would benefit from protection or restoration of habitat used by post-spawn adults as well as habitat used for spawning. Future work should assess the spatial and temporal extent of riverine habitat use in the fall and winter, and should identify characteristics of high-quality post-spawn habitats.

The construction of dams on the mainstem and tributaries of the Sacramento River has reduced the spawning habitat available to green sturgeon. We presented empirical observations with statistical support that showed the delay in RBDD gate-closure and ultimate decommissioning successfully enhanced access to suitable spawning habitat above the dam. We also note that there may be important effects of inter-annual environmental variation in migration timing and habitat use. We expect that increased connectivity will foster increased spawning success, greater genetic diversity, and ultimately a more robust population of southern DPS green sturgeon.

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REFERENCES

Adams, P. B., Grimes, C., Hightower, J. E., Lindley, S. T., Moser, M. L., & Parsley, M. J. (2007). Population status of North American green sturgeon, *Acipenser medirostris*. *Environmental Biology of Fishes*, *79*, 339–356. https://doi.org/10.1007/s10641-006-9062-z

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Benson, R. L., Turo, S., & McCovey, B. W. Jr (2007). Migration and movement patterns of green sturgeon (*Acipenser medirostris*) in the Klamath and Trinity rivers, California, USA. *Environmental Biology of Fishes*, *79*, 269–279. https://doi.org/10.1007/s10641-006-9023-6

Brown, K. (2007). Evidence of spawning by green sturgeon, *Acipenser medirostris*, in the upper Sacramento River, California. *Environmental Biology of Fishes*, *79*, 297–303. https://doi.org/10.1007/s10641-006-9085-5

Erickson, D. L., North, J. A., Hightower, J. E., Weber, J., & Lauck, L. (2007). Movement and habitat use of green sturgeon *Acipenser medirostris* in the Rogue River, Oregon, USA. *Journal of Applied Ichthyology*, *18*, 565–569. https://doi.org/10.1046/j.1439-0426.2002.00403.x

Erickson, D. L., & Webb, M. A. H. (2007). Spawning periodicity, spawning migration, and size at maturity of green sturgeon, *Acipenser medirostris*, in the Rogue River, Oregon. *Environmental Biology of Fishes*, *79*, 255–268. https://doi.org/10.1007/s10641-006-9072-x

Fernandes, S. J., Zydlewski, G. B., Zydlewski, J. D., Wippelhauser, G. S., & Kinnison, M. T. (2010). Seasonal distribution and movements of Shortnose sturgeon and Atlantic sturgeon in the Penobscot River Estuary, Maine. *Transactions of the American Fisheries Society*, *139*, 1436–1449. https://doi.org/10.1577/T09-122.1

Gilman, E., Chaloupka, M., Wiedoff, B., & Willson, J. (2014). Mitigating seabird bycatch dyring hauling by pelagic longline vessels. *PLoS ONE*, *9*, e84499. https://doi.org/10.1371/journal.pone.0084499

Heublein, J., Kelly, J. T., Crocker, C. E., & Klimley, A. P. (2009). Migration of green sturgeon in Sacramento River. *Environmental Biology of Fishes*, *84*, 245–258. https://doi.org/10.1007/s10641-008-9432-9

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*, 346–363. https://doi.org/10.1002/bimj.200810425

Israel, J. A., Cordes, J. F., Blumberg, M. A., & May, B. (2004). Geographic patterns of genetic differentiation among collections of green sturgeon. *North American Journal of Fisheries Management*, *24*, 922–931. https://doi.org/10.1577/M03-085.1

Jager, H. I., Parsley, M. J., Cech, J. J., McLaughlin, R. L., Forsythe, P. S., Elliott, R. F., & Pracheil, B. M. (2016). Reconnecting fragmented sturgeon populations in North American rivers. *Fisheries*, *41*, 140–148. https://doi.org/10.1080/03632415.2015.1132705

Kelly, J. T., Klimley, A. P., & Crocker, C. E. (2007). Movements of green sturgeon, *Acipenser medirostris*, in the San Francisco Bay estuary, California. *Environmental Biology of Fishes*, *79*, 281–295. https://doi.org/10.1007/s10641-006-0036-y

Mahmoud, M. R., & Garcia, L. A. (2000). Comparison of different multicriteria evaluation methods for the Red Bluff diversion dam. *Environmental Modelling and Software*, *15*, 471–478. https://doi.org/10.1016/S1364-8152(00)00025-6

Moser, M. L., & Lindley, S. T. (2007). Use of Washington estuaries by subadult and adult green sturgeon. *Environmental Biology of Fishes*, *79*, 243–253. https://doi.org/10.1007/s10641-006-9028-1

Nelson, T. C., Doukakis, P., Lindley, S. T., Schreier, A. D., Hightower, J. E., Hildebrand, L. R., … Webb, M. A. H. (2013). Research tools to investigate movements, migrations, and life history of sturgeons (Acipenseridae), with an emphasis on marine-oriented populations. *PLoS ONE*, *8*, e71552. https://doi.org/10.1371/journal.pone.0071552

Paragamian, V. L., Wakkinen, V. D., & Kruse, G. (2002). Spawning locations and movement of Kootenai River white sturgeon. *Journal of Applied Ichthyology*, *18*, 608–616. https://doi.org/10.1046/j.1439-0426.2002.00397.x

Poytress, W. R., Gruber, J. J., Van Eenennaam, J. P., & Gard, M. (2015). Spatial and temporal distribution of spawning events and habitat characteristics of Sacramento River green sturgeon. *Transactions of the American Fisheries Society*, *144*, 1129–1142. https://doi.org/10.1080/00028487.2015.1069213

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Thomas, M. J., Peterson, M. L., Chapman, E. D., Hearn, A. R., Singer, G. P., Battleson, R. D., & Klimley, A. P. (2014). Behavior, movements, habitat use of adult green sturgeon, *Acipenser medirostris*, in the upper Sacramento River. *Environmental Biology of Fishes*, *97*, 133–146. https://doi.org/10.1007/s10641-013-0132-8

Thomas, M. J., Peterson, M. L., Friedenberg, N., Van Eenennaam, J. P., Johnson, J. R., Hoover, J. J., & Klimley, A. P. (2013). Stranding of spawning run green sturgeon in the Sacramento River: Post-rescue movements and potential population-level effects. *North American Journal of Fisheries Management*, *33*, 287–297. https://doi.org/10.1080/02755947.2012.758201

Wood, S. (2006). *Generalized additive models: An introduction with R*. Boca Raton, FL: CRC Press.

Wyman, M. T., Thomas, M. J., McDonald, R. R., Hearn, A. R., Battleson, R. D., Chapman, E. D., … Klimley, A. P. (2017). Fine-scale habitat selection of green sturgeon (*Acipenser medirostris*) within three spawning locations in the Sacramento River, California. *Canadian Journal of Fisheries and Aquatic Sciences*. https://doi.org/10.1139/cjfas-2017-0072

Zuur, A., Leno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in ecology*. New York, NY: Springer. https://doi.org/10.1007/978-0-387-87458-6

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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