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Authors
Patton, Oliver
Larwood, Veronica
Young, Matthew
et al.

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RESEARCH

Estuarine Habitat Use by White Sturgeon (*Acipenser transmontanus*)

Oliver Patton, Veronica Larwood*[1], Matthew Young,[1] Frederick Feyrer[1]

ABSTRACT

White Sturgeon (*Acipenser transmontanus*), a species of concern in the San Francisco Estuary, is in relatively low abundance because of a variety of factors. The purpose of our study was to identify the estuarine habitat used by White Sturgeon to aid in the conservation and management of the species locally and across its range. We seasonally sampled sub-adult and adult White Sturgeon in the central estuary using setlines across a habitat gradient representative of three primary structural elements: shallow wetland channel (mean sample depth = 2 m), shallow open-water shoal (mean sample depth = 2 m), and deep open-water channel (mean sample depth = 7 m). We found that the shallow open-water shoal and deep open-water channel habitats were consistently occupied by White Sturgeon in spring, summer, and fall across highly variable water quality conditions, whereas the shallow wetland channel habitat was essentially unoccupied. We conclude that sub-adult and adult White Sturgeon inhabit estuaries in at least spring, summer, and fall and that small, shallow wetland channels are relatively unoccupied.

KEY WORDS

White Sturgeon, *Acipenser transmontanus*, Habitat, estuary, wetland, conservation, restoration

INTRODUCTION

Sturgeons are large, long-lived fishes that grow and mature slowly, ranging throughout North America, Europe, and Asia (Birstein 1993; Pikitch et al. 2005). Currently, there are 25 recognized species in four genera (Birstein 1993; Auer 1996; Bemis and Kynard 1997; Billard and Lecointre 2000; Pikitch et al. 2005). Sturgeons have historically been the dominant large fish species in large rivers in the Northern Hemisphere; they are highly valued for consumption of their flesh and roe, and are gaining appreciation as charismatic megafauna (Chapman et al. 1996; Pikitch et al. 2005; He et al. 2018). Collectively, sturgeons are considered one of the most highly imperiled groups of animals, with 85% of species at risk of extinction according to the International Union for Conservation of Nature (IUCN c2020). Over-harvest, various forms of habitat loss

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* Corresponding author: vlarwood@usgs.gov
1 US Geological Survey
California Water Science Center
Sacramento CA, 95819 USA

and degradation, and other anthropogenic disturbances are key factors that stress sturgeon populations worldwide (Birstein 1993).

North America is home to nine species of sturgeon, all of which have some form of protection under the US Endangered Species Act (ESA) (Auer 1996; Haxton et al. 2016). White Sturgeon (*Acipenser transmontanus*) is the largest North American sturgeon and is distributed along the eastern Pacific Ocean from central California to Alaska (Birstein 1993; Jackson et al. 2016), inhabiting rivers, estuaries, and nearshore coastal environments (Pikitch et al. 2005). As a group, White Sturgeon are characterized as amphidromous (Bemis and Kynard 1997) and endemic to Pacific estuaries and coastal rivers of North America (Chapman et al. 1996). Some populations without access to the sea are critically imperiled, such as the land-locked population in the middle Snake River in the Pacific Northwest of the United States (Parks 1978; Hildebreand et al. 2016). The San Francisco Estuary (hereafter the estuary) and its tributaries contain the largest White Sturgeon population in California and the southernmost reproducing population of the species (Chapman et al. 1996; Pikitch et al. 2005; Hildebrand et al. 2016). The estuary White Sturgeon population is considered a species of special management concern by the state of California (Hildebrand et al. 2016; Moyle et al. 2016). The estuary population was nearly extirpated in the late 19th century from commercial harvest, but now supports a recreational fishery (Chadwick 1959; Skinner 1962; Parks 1978; Kohlhorst 1980). However, current harvest levels are unsustainable and, together with the loss of habitat, represent a serious threat to the continued existence of the population (Blackburn et al. 2019).

The estuary White Sturgeon spawn primarily in the Sacramento River with some evidence of limited spawning in other tributaries (Kohlhorst 1976; Schaffter 1997; Jackson et al. 2016). Although adult White Sturgeon use coastal habitats to some degree, juvenile and adult White Sturgeon typically remain in the estuary and lower Sacramento and San Joaquin rivers for rearing and growth (Kohlhorst et al. 1991; Bemis and Kynard 1997). White Sturgeon tend to congregate in deep areas with fine-sediment substrate and are thought to move into shallow subtidal habitats to feed during high tides (Moyle 2002); however, little is known about specific estuarine habitat use. The goal of our study was to evaluate estuarine foraging habitat use by sub-adult and adult White Sturgeon to aid species management and conservation. This information can inform managers about how to prioritize conservation of White Sturgeon across its geographic range, an approach particularly relevant to the estuary where large-scale habitat restoration is planned to benefit native fishes. Actions that are likely to improve habitat in the estuary include restoring wetlands and shallow open water habitat; our objective was to determine how White Sturgeon use these habitats.

METHODS

Study Site and Design

The estuary is located on the Pacific Coast of the United States in central California (Figure 1A). It has an open-water surface area of approximately 1,235 km^2, a mean depth of 4.6 m, and a volume of 5.8×10^9 m^3. The local Mediterranean climate is generally characterized by a warm and dry summer–fall period and a cool and wet winter–spring period. Our study took place in a model wetland system (Ryer Island) located in the central region of the estuary (Figure 1B). The Ryer Island wetland has a surface area of approximately 3.5 km^2 (347 ha) and is one of the few remaining natural wetlands in the estuary. The wetland is flanked by 0.8 km^2 (80 ha) of shallow shoal habitat, which is in turn flanked by 1.6 km^2 (164 ha) of deep channel habitat. The wetland's relatively unaltered state and isolated location within an expansive open-water region of the estuary makes it a natural laboratory to study the functional ecology of wetlands targeted for restoration.

Our study design examined White Sturgeon abundance across a physical habitat gradient characteristic of the three major structural habitats present in the estuary: shallow wetland

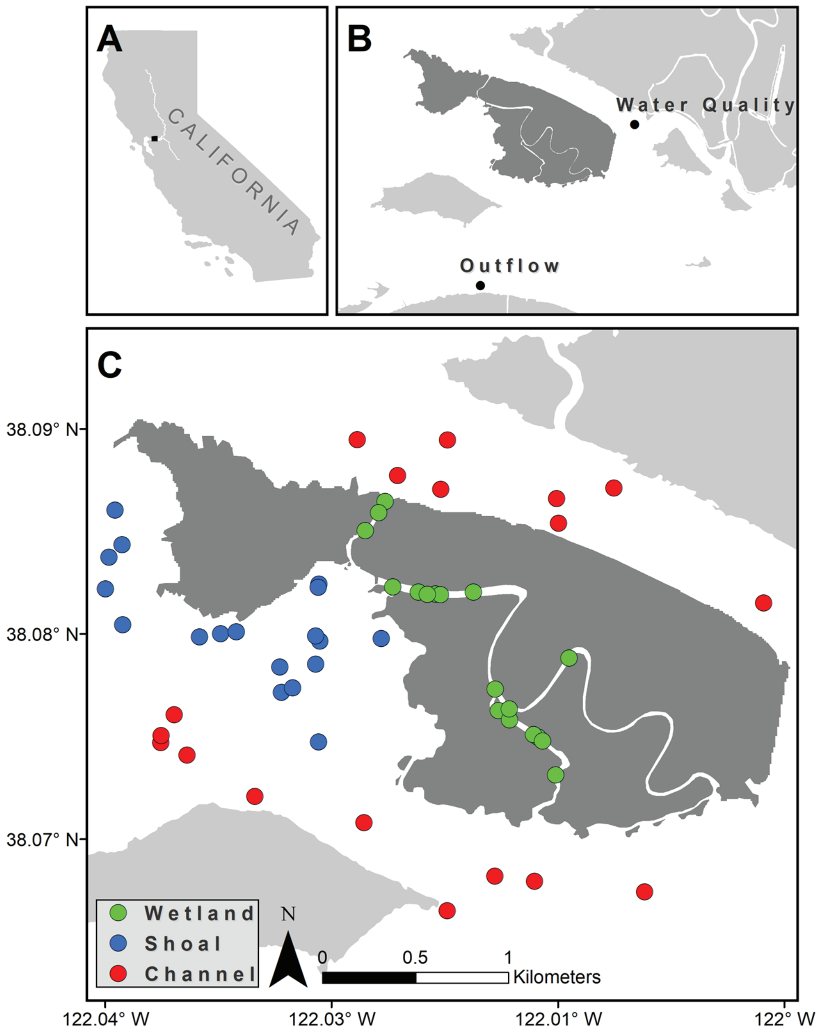

Figure 1 Study area showing the locations of (**A**) the San Francisco Estuary and the Ryer Island wetland in central California, USA, (**B**) California Department of Water Resources' water quality and outflow measurement sites (see Data Availability) relative to Ryer Island (in *dark gray*), and (**C**) each individual setline deployment.

channel, shallow open-water shoal, and deep open-water channel (Atwater et al. 1979; Moyle et al. 2010; Whipple et al. 2012). The deep open-water channel habitat was characterized as a broad, deep (average sample depth = 7 m) non-vegetated channel, which conveys most of the tidal flow volume in the estuary. The shallow open-water shoal habitat was characterized as shallow (average sample depth = 2 m) subtidal habitat that seasonally supports sparsely distributed and variably dense submersed aquatic vegetation (SAV). The dominant SAV species was sago pondweed (*Stuckenia* spp.) (Borgnis and Boyer 2016). The shallow wetland habitat was characterized as shallow (average sample depth = 2 m), small (average width = 6 m) channels within the heavily vegetated tidal marsh. Primary emergent vegetation included common reeds (*Phragmites australis*) and tules (*Scirpus* spp.). The Ryer Island wetland is typical of a historical, natural (i.e., non-leveed) wetland in the estuary in that water inundates the vegetated marsh plain on high tides and then drains into a network of subtidal channels on low tides; wetland sampling took place in the small channels. Substrate in each habitat was not characterized quantitatively but was generally comprised of variable mixtures of mud, sand, and peat.

Data Collection

To collect data over a broad range of environmental conditions, we sampled for White Sturgeon in each habitat from May 2017 through October 2018. We conducted a total of

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six sampling events, one each in May, August, and November 2017 and March, July, and October 2018. During each sampling event, we deployed three individual setlines in each habitat, totaling nine per sampling event. Setlines were generally similar in form to those previously used in White Sturgeon studies in the estuary by the California Department of Fish and Wildlife (Dubois et al. 2010). The setlines were 120 m in length and possessed a total of 18 circle hooks (six each of size 2/0, 4/0, and 6/0) baited with commercially available cut lamprey. Hook gangions were placed approximately 4 m apart, consisted of 1 m of 60-kg test-braided Dacron line, and were attached to the main line with halibut clips (Elliott and Beamesderfer 1990). The main line was composed of 5/16-in tarred, twisted nylon rope and stretched in place by heavy anchors attached to each end. We deployed setlines at midday and retrieved them approximately 24 hrs later; we recorded total hours deployed as sampling effort. In total, 54 setlines with 970 hooks (one setline possessed 16 hooks) were deployed across the six sampling events and were collectively fished for 1,315 hours.

Specific setline deployment sites were determined using satellite imagery and bathymetry to create polygons for each habitat type and random points were generated using the “create random points” tool in geographic information system (GIS) software (ESRI, Redlands, CA). Upon retrieval, we assigned each hook a condition for the presence or absence of White Sturgeon, measured all hooked White Sturgeon for total length (mm), and then released them alive.

Environmental conditions during the study period were characterized from freshwater outflow, water temperature, and specific conductance (a surrogate for salinity) data obtained from the California Department of Water Resources (CDWR). CDWR estimates daily average freshwater outflow through the estuary using a mass–balance calculation, and we calculated daily average values for the water-quality parameters from continuous measurements taken every 15 minutes at a gaging station located within the study site (Figure 1C).

Data Analysis

We used Bayesian generalized linear mixed modeling (GLMM) to examine variability in White Sturgeon counts in relation to each sampled habitat. The overall modeling objective was to elucidate patterns of White Sturgeon abundance across the three habitats. The response variable for our model was counts of White Sturgeon caught in each setline. For modeling purposes, White Sturgeon counts were not structured by size or estimated age of individuals because there was no statistically significant difference in total length of White Sturgeon captured across habitats or sampling events (generalized linear model, p-value ≥ 0.81).

The basic GLMM structure was:

$$[count] \sim \log(Effort(H * h)_i) + \beta_1 Habitat_i + \alpha_{Event_{[k]}}$$

Sampling effort (*Effort*) was included as an offset to standardize counts and was characterized as hours (*H*)*hooks (*h*); hooks was included to account for one setline which had 16 hooks instead of 18. *Habitat* (i.e., wetland, shoal, channel) was included as a categorical variable. Sampling event was included as a random factor variable to allow intercepts to vary across each of the six sampling events. This enabled the model to account for several important factors, including any variation in abundance, water quality conditions, water elevation and tide stage/velocity variables that we could not logistically accommodate in the study design, as well as any other unmeasured factors that could have conceivably influenced catches and varied among the individual sampling events. The sampling event random variable accounted for the effect of water-quality variables on counts.

Modeling was implemented using the “brms” package (Bürkner 2017) in the R statistical computing environment (R Core Team 2019). We used widely applicable information criteria (WAIC) to examine the fit of models, with and without the event variable, constructed with several different distributions suitable for count data: Poisson, zero-inflated Poisson, negative binomial, and zero-inflated negative binomial

(Zuur et al. 2009). We assessed the predictive accuracy of the top models by examining the mean (average error) and the standard error (root mean square error or RMSE) of the difference between the model's predictions and the original data set. The closer average error and RMSE values are to zero the more accurate the predictions. Fixed effects were assigned weakly informative ($\mu = 0$, $\sigma = 10$), normally distributed priors while random effects were assigned weakly informative ($\mu = 0$, $\sigma = 10$) Cauchy-distributed priors. Models were implemented with default values of four chains with 4,000 iterations, proceeded by 1,000 warmup iterations.

Data Availability

Freshwater outflow data were obtained from CDWR and are available at *http://cdec.water.ca.gov/cdecstation2/?sta=DTO*. Water temperature and specific conductance data were obtained from the CDWR and are available at *http://cdec.water.ca.gov/cdecstation2/?sta=RYC.* Original data collected for this study are available in the US Geological Survey's ScienceBase Catalog at *https://doi.org/10.5066/P9087XOC* (Steinke et al. 2019).

RESULTS

Environmental conditions exhibited substantial variability over the study period (Table 1 and Figure 2). Freshwater outflow values ranged from 99 to 3,384 m^3 sec^{-1} (mean = 471, standard deviation = 525). Temperature values ranged from 9 to 24 °C (mean = 17, standard deviation = 4). Specific conductance values ranged from 1 to 22,791 µs cm^{-1} (mean = 8,959, standard deviation = 5,700). For reference, these specific conductance values translate to salinity values of approximately 0 to 16 ppt (mean = 6, standard deviation = 5).

We captured total of 111 White Sturgeon. Of this total, 54 were captured in the deep open-water channel, 56 were captured in the shallow open-water shoal, and one was captured in the shallow wetland. Overall, the number of individuals caught per setline ranged from zero to seven (mean = 2, standard deviation = 2). Total lengths of the individuals captured ranged from 675 to 1,604 mm (mean = 1,111, standard deviation = 186). Bycatch for this study consisted of only 12 individual fishes: ten Striped Bass (*Morone saxatilis*), one Jacksmelt (*Atherinopsis californiensis*), and one White Catfish (*Ameiurus catus*). The overall frequency of retrieving damaged or missing hooks was 2% and the overall frequency of hooks with no bait was 10%.

Modeling results indicated, regardless of statistical sampling distribution, that physical habitat strongly affected White Sturgeon counts (Table 2). Counts of White Sturgeon in the deep open-water channel and the shallow open-water shoal were statistically indistinguishable from each other but were substantially higher than

Table 1 Summary of environmental conditions and White Sturgeon catches across sampling events. Water temperature, specific conductance, and freshwater outflow data were obtained from the California Department of Water Resources (see Methods) and the values in the table are means of the five days preceding and including the sampling date. Sampling hours is the total amount of time the nine setlines were deployed during each sampling event. Total length refers to the mean total length and standard deviation of all sturgeon captured during that sampling event.

Event	Date	Temperature (°C) mean ± SD	Mean specific conductance (µs cm^{-1} ± SD)	Mean freshwater outflow (m^3s^{-1} ± SD	Total sampling hours	Total White Sturgeon captured	Total length (mm) mean ± SD
1	25-May-2017	19 ± 1	261 ± 168	1740 ± 143	213	30	1101 ± 156
2	29-Aug-2017	21 ± 1	7863 ± 2165	330 ± 13	256	25	1105 ± 172
3	29-Nov-2017	15 ± 1	12254 ± 2223	214 ± 27	203	27	1081 ± 198
4	20-Mar-2018	18 ± 1	6958 ± 2403	723 ± 164	217	7	1142 ± 172
5	05-Jul-2018	21 ± 1	13125 ± 2569	159 ± 20	213	9	1033 ± 173
6	10-Oct-2018	21 ± 1	14313 ± 2913	233 ± 96	213	13	1257 ± 217

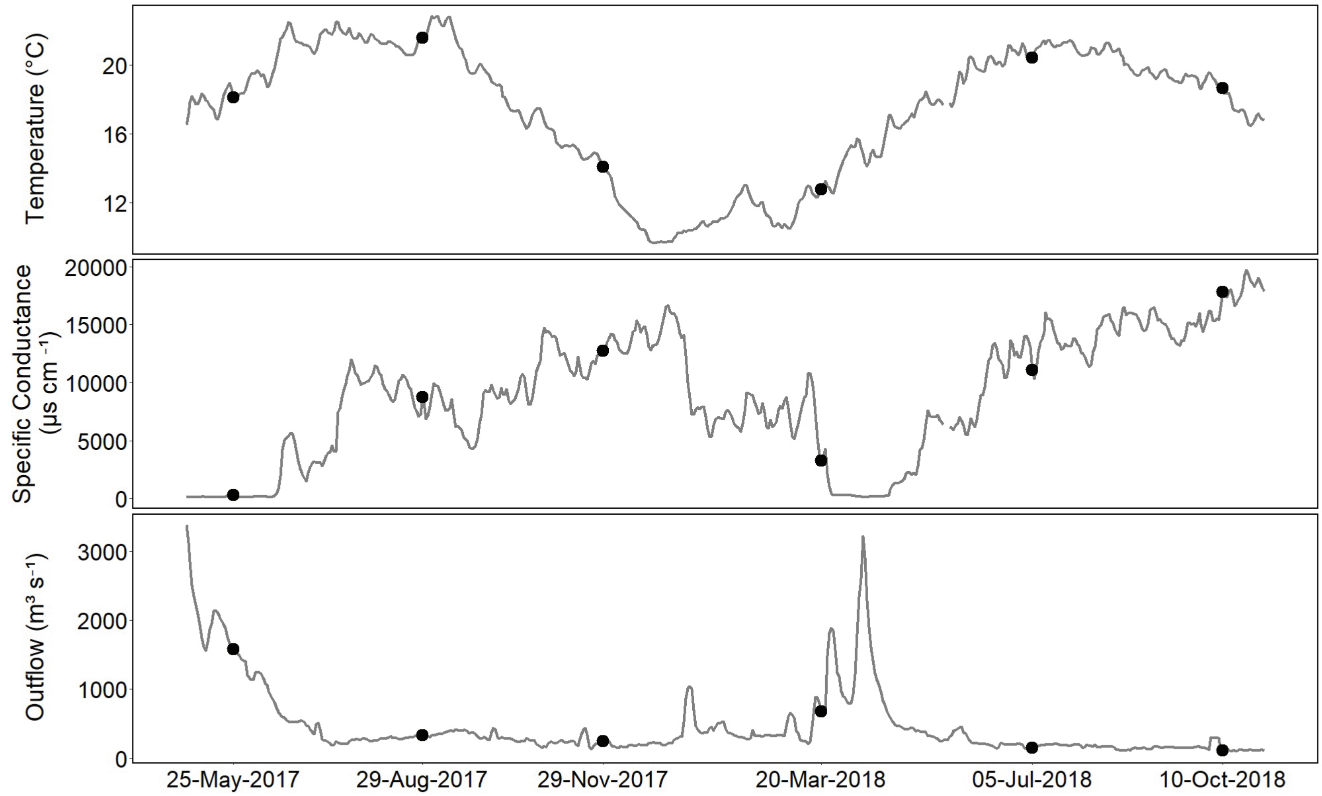

Figure 2 Time series plots of water temperature (°C), specific conductance (µs cm^{-1}), and freshwater outflow (m^3 sec^{-1}) in the study area, from May 2017 to November 2018. *Black points* superimposed on the time series show when the six individual sampling events took place.

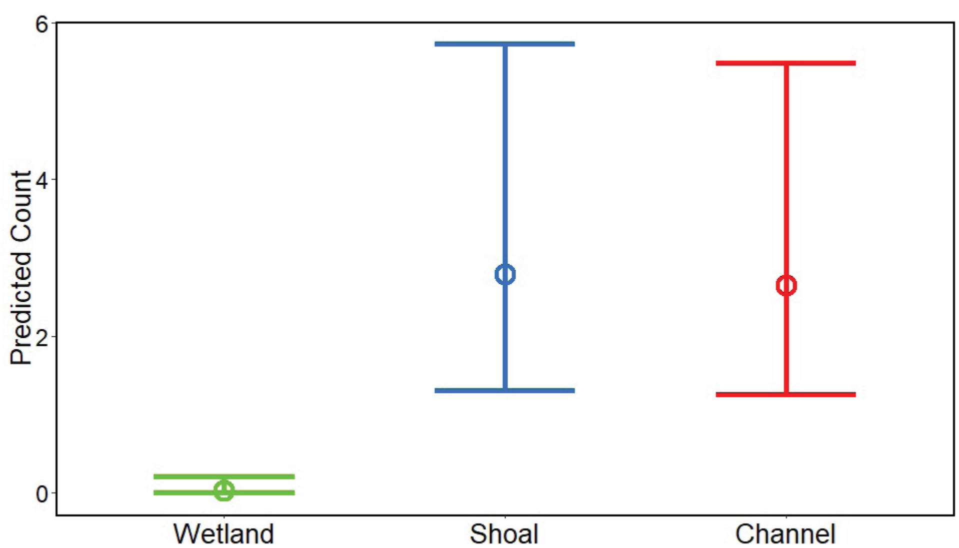

Figure 3. Marginal effects for each habitat type based on the best-fitting model identified in Table 2. Each point signifies the mean expected White Sturgeon count per setline and the whiskers represent the 95% confidence interval for each habitat.

Table 2 Parameter coefficients and 95% credible intervals generated from the best fitting generalized linear mixed models on White Sturgeon counts (see Methods for details). Variables with credible intervals not overlapping zero were deemed significant and highlighted in bold.

Response variable = count, Distribution = Poisson			
	Coefficient ± SE	Lower 95% CI	Upper 95% CI
Intercept	−5.11 ± 0.38	−5.85	−4.38
Wetland (relative to channel)	−4.51 ± 1.28	−7.72	−2.65
Shoal (relative to channel)	0.05 ± 0.19	−0.33	0.42

in the shallow wetland (Figure 2). Regarding the different statistical distributions examined, WAIC values demonstrated that models which included habitat and event fit the data better than models that excluded those parameters, indicating that each distribution generated generally similar results. However, Poisson models had the lowest RMSE (Poisson – 1.44, Zero-inflated Poisson – 1.49; Negative binomial – 1.53, Zero-inflated negative binomial – 1.54) and best fit the data.

DISCUSSION

Our study improves the understanding of White Sturgeon estuarine habitat utilization over a range of environmental conditions in the San Francisco Estuary (estuary). Ryer Island contains three major habitats that White Sturgeon encounter throughout the estuary. This knowledge can help contextualize White Sturgeon habitat use and movement within the estuary, as well as inform resource managers of essential sturgeon habitat when they plan restoration sites.

Of the three habitats at Ryer Island, sub-adult and adult White Sturgeon were relatively abundant in the deep open-water channel and shallow open-water shoal habitats but were largely absent in the wetland habitat. Interestingly, White Sturgeon are found in the larger sloughs of Suisun Marsh, a large, expansive wetland located near Ryer Island (Matern et al. 2002; Moyle et al. 1986). We posit that White Sturgeon did not occupy the wetland habitat at Ryer Island because of its smaller, shallower channels compared to the larger sloughs in Suisun Marsh, which are more comparable in size and depth to the deep open-water channel in this study. In general, the presence or absence of White Sturgeon in wetland habitats may be driven by habitat size and configuration, food and prey availability, and substrate type. We did observe one White Sturgeon within the wetland habitat at Ryer Island. The location of this catch was near the wetland breach, adjacent to shoal habitat. A study on Lake Sturgeon (*Acipenser fulvescens*) has shown that they tend to aggregate near a wetland complex when another suitable habitat is present (Damstra and Galarowicz 2013). It is uncertain if this White Sturgeon was utilizing the wetland habitat for foraging or was baited into the wetland from the shoal habitat.

The physical configuration of the Ryer Island complex provided a unique natural laboratory to test how abundance varies across major structural habitat elements. Limitations of our study included that it was conducted at a single location and that the sampling gear targeted a limited size range of actively feeding fish. While Ryer Island represents a single location, we have no reason to believe that the broad habitat preferences we identified would vary across the estuary. The specific hook sizes and baits used in our study may have contributed to the predominance of sub-adult and adult White Sturgeon observed in the catches. Future research that incorporates a wider selection of hook sizes and baits, or other observational tools such as telemetry, could be conducted to more thoroughly examine habitat usage and movements of all life stages of White Sturgeon. Higher resolution sampling in space and time could potentially increase our understanding of White Sturgeon movement and foraging in the estuary, including evaluating the effects of day vs. night and tidal cycle on White Sturgeon foraging behavior.

Understanding how White Sturgeon, of all life stages, utilize the estuarine environment is an important consideration for habitat restoration projects. Attainable habitat actions include the restoration of shallow inundated habitat, which we have shown to support actively foraging

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sub-adult and adult White Sturgeon within the estuary. Further research on all life stages of White Sturgeon in estuarine habitats would help better inform sturgeon management and the potential role of estuarine habitat restoration.

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