Habitat use differences mediate anthropogenic threat exposure in white sturgeon

Running head: Habitat use by white sturgeon

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Data Availability: Raw acoustic telemetry detection data used in this manuscript will be publicly available on the PATH database (<https://fishdb.wfcb.ucdavis.edu>). Analysis code and supporting and derived datasets are available during review at <https://github.com/jonathan-walter/wstelemetrythreats-ms> and will be permanently archived on Zenodo and assigned a DOI upon manuscript acceptance; the Zenodo DOI will be provided in the published version.

Impact Statement: Habitat use by subadult and adult white sturgeon differed by size class, leading to differing levels of exposure to risks associated with recreational fishing and anthropogenic habitat modification.

Abstract

Understanding intraspecific variation in habitat use, particularly of long-lived fishes across multiple life history stages, is core to improved conservation management. Here, we present results from a synthesis of acoustic telemetry data for sub-adult and adult white sturgeon (*Acipenser transmontanus*) from 2010 to 2017 in the San Francisco Estuary and Sacramento River ecosystems. We focused primarily on uncovering spatial patterns of inferred habitat occupancy across life stages, and on linking habitat use to extant anthropogenic threats. We found substantial differences in habitat use across individuals and over time that was related to fish size classes defined relative to the slot limit (102-152 cm) used to regulate recreational fishing. However, differences in habitat use were not explained by fish sex or water year flow conditions. We also estimated indices of overall exposure for two major threats: capture by anglers and habitat modification. Fish of harvestable size were detected less often than others in areas where many are caught. Future monitoring and management of white sturgeon might benefit from examining multiple phases of white sturgeon life history. For example, additional tracking studies could improve our understanding of juvenile habitat use, adult survival rates, patterns of anadromy, and cross-basin habitat utilization.

Key words: *Acipenser transmontanus*, behavior, life stage, occupancy, movement, recreational fishery, water diversions, size class

Introduction

Understanding how patterns of fish habitat use vary within and among populations is essential to conservation and management (Crossin et al. 2017). In fishes, habitat use and movement may differ among individuals of the same population according to life stage, sex, and behavioral types (Hutchings and Gerber 2002; Moyle 2002; Bade et al. 2019; Colborne et al. 2019). As an example of sex-dependent movement, in a population of brook trout (*Salvelinus fontinalis*) on Cape Race, Newfoundland, Canada, males were more likely to disperse and tended to move more than twice as far as females (Hutchings and Gerber 2002). In other examples, distinct movement behavior may be exhibited by groups that do not differ according to characteristics such as age or sex. In the Laurentian Great Lakes, potamodromous and adfluvial lake sturgeon (*Acipenser fulvescens*) exhibited within-population differentiation of movement patterns, with distinct groups occurring in different areas but not differentiated by sex or age (Kessel et al. 2018; Colborne et al. 2019). These behavioral patterns can reflect adaptive functions such as exploiting resources, securing mates, and minimizing competition (Chapman et al., 2012). Differences in habitat use and movement, such as partial migration, may also stabilize populations through a bet-hedging mechanism against local catastrophe, often referred to as the portfolio effect (Secor 1999; Chapman et al. 2012; Gomez et al. 2015; Kessel et al. 2018).

Acoustic telemetry has emerged as a powerful and widely used technology for inferring habitat use and movements of fishes with diverse lifecycles (Donaldson et al. 2014; Hussey et al. 2015). Although telemetry studies have long provided insights for fish ecology and conservation (Crossin et al. 2017), more recent developments such as passive receiver arrays, improvements in transmitter size and longevity, and establishment of cooperative networks of investigators (e.g., GLATOS, the Great Lakes Acoustic Telemetry Observation System, Krueger et al., 2018; OTN,

the Ocean Tracking Network, Iverson et al., 2019) have enabled large-scale, long-term studies across many individuals and across investigating institutions. Leveraging emerging technologies for better long-term tracking of individuals is particularly important for highly mobile, long-lived fishes.

White sturgeon (*Acipenser transmontanus*) is a long-lived, semi-anadromous fish species inhabiting river systems along the Pacific coast of North America (Moyle 2002). In the San Francisco Estuary and Sacramento and San Joaquin River systems of California, white sturgeon support a significant recreational and harvest-oriented fishery. Like other species that take several years to reach sexual maturity (Reynolds et al. 2005; Pinsky et al. 2011), white sturgeon are vulnerable to overfishing, and are listed as a California state 'Species of Special Concern' due to anthropogenic threats including extensive habitat degradation and loss, notably through channel modification, dams, and water diversions (Moyle 2002). Currently, the white sturgeon fishery in California incorporates an annual bag limit (3 fish/angler) and a 102–152 cm (40– 60 in) fork length harvest slot limit. Thus, small fish and large fish are protected from harvest but a substantial portion of the population remains a target of harvesting. Harvest rates are monitored using angler report cards and a fishery-independent stock assessment. A recent analysis estimated that the population growth rate of white sturgeon in the Sacramento and San Joaquin River systems may be below replacement levels and, consequently, the population may be in decline (Blackburn et al. 2019). Moreover, despite consistent monitoring of the fishery, habitat use and movements of white sturgeon in the San Francisco Estuary and Sacramento River system are relatively little studied (but see, e.g., Johnston et al., 2020; Miller et al., 2020), leaving open questions about their ecology, patterns of habitat use, and effective approaches to improving habitat and fishing conditions to reverse declining abundance trends.

This study synthesized eight years of acoustic telemetry records to study patterns of habitat use by sub-adult and adult white sturgeon in the San Francisco Estuary and Sacramento River system. We first asked (1) whether white sturgeon exhibited divergent patterns of habitat use. Finding evidence that white sturgeon differ in habitat use patterns, we next asked (2) whether movement and habitat use patterns were related to fish size, fish sex, and hydrologic conditions. We then asked (3) whether habitat use patterns of groups of white sturgeon were related to river depth preferences. To examine the conservation management implications for these differences, we also asked (4) whether groups of white sturgeon displaying distinct habitat use patterns were differentially exposed to fishing capture and anthropogenic habitat modification. Our results have implications for improved management of white sturgeon in the San Francisco Estuary and Sacramento River ecosystem.

Methods

Study System

The Sacramento River originates in the Klamath Mountains near Mount Shasta and flows through the northern portion of California's Central Valley before joining the San Joaquin River near Antioch, CA. This confluence forms the Sacramento-San Joaquin River Delta, which then flows through Suisun and San Pablo Bays before reaching the San Francisco Bay (Figure 1). In addition to flowing through intensely urbanized and agricultural areas, the system has undergone substantial human modification, including draining of wetlands, levee construction, channel dredging, and water extraction for agricultural and municipal uses (Andrews et al. 2017). Further, the Delta is the heart of California's massive water conveyance system, used to redistribute water across the landscape, in part, to irrigate the country's most productive agricultural region.

Inhabited by many declining populations of native fishes, including white sturgeon, green sturgeon, Delta smelt, and Chinook salmon (Moyle et al. 2011), this system has also been heavily instrumented with acoustic telemetry receivers to facilitate study and management of key species (Singer et al. 2013; Michel et al. 2015; Colborne et al. 2022). Across the range of white sturgeon, many populations are in decline due to overfishing and habitat degradation (Hildebrand et al. 2016), and the extent of state and federal protections varies among regional subpopulations (Schreier et al. 2013; Hildebrand et al. 2016). The Sacramento-San Joaquin population is not currently federally protected, but there is evidence that this population is in decline (Hildebrand et al. 2016; Blackburn et al. 2019).

White sturgeon telemetry data

We used data from three acoustic telemetry studies of white sturgeon contained in the PATH database (<https://fishdb.wfcb.ucdavis.edu>). Capture methods varied depending on original study protocols, while tagging methods remained nearly identical across the three studies. Methods are described in detail in Miller et al. (2020), Johnston et al. (2020) and Thomas et al. (2013). Briefly, large juvenile, subadult, and adult white sturgeon were captured with gill and trammel nets (Miller et al. 2020) in San Pablo Bay, Suisun Bay, and Grizzly Bay; rescued from the concrete channels behind the Tisdale and Fremont weirs, where they had been stranded by receding flood flows (Thomas et al. 2013); or captured in an eight-meter long, three-chambered fyke trap deployed in the Toe Drain of the Yolo Bypass (Johnston et al. 2020). All fish were tagged in the field upon capture and released nearby following the procedure. Each fish was surgically implanted with an acoustic transmitter (V16, V13, or V9; Vemco, Ltd., Halifax NS) while inverted in a V-shaped cradle with continuous water flow across the gills. This tagging

method was shown to have no significant impact on juvenile sturgeon survival, growth, or swimming performance (Miller et al. 2014).

During 2010–2017, >300 acoustic receivers (VR2W-69 kHz, Innovasea Inc., Halifax NS, Canada) were deployed at 94 distinct sites through the collaboration of NOAA Fisheries, US Bureau of Reclamation, US Fish and Wildlife Service, ECORP Consulting, Inc, California Department of Water Resources, and US Geological Survey. In most cases, receivers were not deployed at the same location for the entire 2010–2017 period, so we focused on data from 15 sites in the Bay-Delta and Sacramento River system where at least one receiver was deployed on ≥90% of days from 1 January 2010 to 31 December 2017 (Figure 1). Receivers at two closely spaced sites (200 m) at the upstream intersection of the Sacramento River and Steamboat Slough were combined. All receivers deployed north of the confluence of the Feather and Sacramento rivers (ca. 38.76° latitude) were aggregated into one site denoted “up river.” There were also 8 detection locations on the San Joaquin and Mokelumne Rivers that met our criteria for near-complete deployment during the study period, but these were excluded from further analysis because detections of studied fish, while non-zero at these sites, were proportionally extremely uncommon. Excluding these sites had no substantive impact on our results.

There were 249 sturgeon detected from the 2010 to 2017 water years, and of these 106 were included in this analysis. The California water year runs from October 1 to September 30. Prior to selecting data for analysis, detection records were filtered to remove suspected false detections, which we considered to be those implying movements >15 km/hr. We discarded individuals suspected to have perished or shed the transmitter when their detection records ended with a run of ≥200 detections/day at the same location for ≥30 days. These quantitative criteria were determined from visual inspection of individual fish detection records for records ending on

long runs of repeated detections at the same location, without undetected periods of a day or longer suggestive of a fish moving away from and back toward a location. Because we could not be certain when a fish perished or shed a tag, and because these cases were rare compared to the fairly large number of fish records available, we omitted all detections of these individuals from this analysis. We selected from the remaining fish those that had at least one complete water year in which the fish was detected on 30 different days. Water years were deemed complete if the fish was tagged no later than November 1 of the calendar year the water year began, and if the final detection of that fish was no earlier than September 1 of the calendar year in which the water year ended. There were 257 water years from 106 unique white sturgeon meeting these inclusion criteria. Selected fish were tagged in calendar years 2010 to 2014 in the studies described in Miller et al. (2020) (n = 82), Thomas et al. (2013) (n = 7) and Johnston et al. (2020) (n = 17). Although fish were tagged at different times of year (March through October) and there are seasonal patterns to white sturgeon movement (Miller et al. 2020), these influences were mitigated by analyzing only complete water years for a given fish.

Occupancy analyses

We first examined how frequently white sturgeon were present at different sites and how this may have changed over time. We used telemetry detections to quantify, for each fish-water year combination, the number of fractional days that each fish was detected at each site. By fractional days, we mean that when fish were detected at >1 site on the same day, the fish was considered to have spent $1/n$ days at each unique site, where n is the number of sites where the fish was detected on that day. This approach minimized the effect of fish being detected at multiple receivers in the same site, which could be biased by the number of receivers deployed at

each site and changes therein over time. It also minimizes the effect of fish being detected many times in short succession by the same receiver array, which can occur when fish spend a period of time around the same area. More temporally explicit approaches, such as sequence analysis (Colborne et al. 2019), are poorly suited to this dataset because they require sampling over consistent time periods. To maximize the number of records studied in the present analysis, we used fish whose records spanned different time periods.

We quantified dissimilarity between all pairs of fish-water years in the proportion of days detected at each site and used surrogate- and permutation-based statistical tests to determine whether the observed differences in fish habitat use were greater than expected by chance. Dissimilarity was computed using Hellinger distance (Hellinger 1909). Hellinger distance is defined as $H = \frac{1}{\sqrt{2}}\sqrt{\sum_{i=1}^{k}\left(\sqrt{p_i} - \sqrt{q_i}\right)^2}$, where here p_i and q_i are, respectively, the proportion of detections of fish p and q which occurred at location i in a given water year. Note that p and q may be the same fish in a different water year, different fish in the same water year, or different fish in different water years.

We conducted a surrogate-based statistical test to determine if the occupancy patterns were more dissimilar than expected by chance under a null hypothesis that fish did not differ in their probabilities of being detected at a given site, either across individuals or across water years. We constructed the null model by taking the mean proportional occupancy at each site over all fish-water years and using the mean occupancy profile to simulate a surrogate dataset that preserved the number of fish studied and the number of days each fish was detected in each water year. A surrogate occupancy profile for a given fish in a given water year was generated by randomly assigning a detection to a fish in a location and in a water year, based on the mean proportional occupancy profile constructed previously. Total numbers of detections of each fish

in each water year were kept fixed at the values of the data. This process was repeated to create 1000 complete surrogate datasets. For the empirical dataset and each surrogate dataset, we calculated the total Hellinger dissimilarity among all pairs of two fish-water years and considered divergence in occupancy patterns to statistically differ from the null model of no divergence if the total Hellinger dissimilarity among all pairs of two fish-water years was greater than the 0.95 quantile of that statistic for the surrogates.

To test whether fish size, fish sex, and water year flow conditions statistically explain divergence in occupancy behavior across fish and water years, we used permutational analysis of variance (PERMANOVA; McArdle & Anderson, 2001). PERMANOVA is used to partition dissimilarity matrices among sources of variation in a linear modeling framework and is commonly used in ecology for analyzing differences in community composition (e.g., Hart, Turcotte, & Levine, 2019; Hanna, Raudsepp□Hearne, & Bennett, 2020). We tested whether each predictor explained residual variation in dissimilarity in occupancy behavior while accounting for tagging region and tagging year. Tagging region and tagging year were included to account for studies making different choices about where to tag fish and whether to collect sex data over different years. Only one focal variable (fish size, sex, water year conditions) was tested at a time to avoid partitioning the data into groups with unacceptably low sample sizes.

For the PERMANOVA analyses, we considered three classes of fish size relative to the current slot limit on the white sturgeon recreational fishery in California, which permits only fish between 40 in (102 cm) and 60 in (152 cm) fork length to be kept. Blackburn et al. (2019), analyzing fish from the same region, showed that typical white sturgeon are in the fishery from ages 10 to 15. Using growth curves from Blackburn et al. (2019), we extrapolated length-at-tagging forward in time and classified fish as below slot, in the fishery, or above the slot limit at

each water year. Length at tagging of fish included in this study ranged 84 cm to 192 cm. We observed 24 water years from 18 unique below-slot fish, 114 water years from 60 unique within-slot fish, and 119 water years from 51 unique above-slot fish. Fish sex was considered as male (18 unique fish over 41 fish-water year combinations), female (14 fish, 30 fish-water years), or unknown (74 fish, 186 fish-water years) depending on whether the source study sexed fish. We used water year type designations from the California Division of Water Resources, which categorizes each water year on a 5-point scale: Critically Dry; Dry; Below Normal; Above Normal; Wet. Tagging region was considered either "Bay" (Grizzly Bay, San Pablo Bay, Suisun Bay) or "Sacramento River" (Fremont Weir, Tisdale Bypass, Yolo Bypass). Tagging locations were aggregated to region because of low sample sizes for individual sites.

To interpret how these variables influence habitat occupancy, we categorized fish-water year occupancy records based on the most statistically important variables (i.e., those explaining the most variance in occupancy, which were also those with the lowest *p*-values) and took the mean proportional occupancy by site over groups of those variables.

White sturgeon occupancy by depth

To examine the relationship between habitat use preferences and depth, we estimated the occupancy-weighted mean river depth of areas inhabited by each white sturgeon, where the mean river depth $\overline{D}_i$ associated with fish *i* was calculated as:

$$\overline{D}_i = \sum_j D_j \theta_{i,j}$$

where D_j is the median river depth within 2 km of the detection locations *j*, and $\theta_{i,j}$ is the proportional occupancy of fish *i* at detection location *j*. Depth was determined from Fregoso et al. (2017). We then summarized the $\overline{D}_i$ by groups made using characteristics that explained

differences in habitat use in the analyses above to evaluate whether habitat use groupings may be related to depth. Additionally, we conducted this analysis for the full study area as well as two subdivisions of the study area. The first includes the lowest portions of our study area in the San Francisco, San Pablo, and Suisun bays, and we refer to this as the “Bay” region. The second includes the Delta and upriver portions of the study area, and we refer to it as the “Delta and Sacramento River” region. The division between the two regions is made based on the legal definition of the Sacramento-San Joaquin Delta, and also corresponds to a transition between brackish and freshwater, as well as differences in land-use patterns.

Exposure to fishing and habitat modification

We next evaluated whether any groups, based on characteristics that statistically explained differences in habitat use, experienced differential exposure to fishing capture and to anthropogenic habitat modification. Exposure to fishing capture was quantified using catch report cards and anthropogenic habitat modification was quantified based on the location and volume of water diversions. Fishing involved both removal of individuals (harvesting) from the population, and released individuals that may have poorer outcomes due to sublethal effects of being caught (Campbell et al. 2010). There are numerous possible anthropogenic habitat modifications throughout this system, but we focused on the location and volume of water diversions as an index of habitat modification. Local diversions reduce flows available to fishes, and are associated with other human activities, such as channelization, levee construction, and agriculture, that impact aquatic ecosystems (Herren and Kawasaki 2001; Lehman et al. 2019).

To quantify spatial variation in recreational fishing capture, we analyzed white sturgeon angler report card data collected annually by the California Department of Fish and Wildlife

(CDFW). Fishers catching white sturgeon report the date of their catch, whether it was harvested or released, the length of kept fish, and in which of 29 “fishing regions” the catch occurred. We used these data for 2015 through 2020 to estimate the geographic distribution of catch-and-release and harvest-oriented fishing capture for white sturgeon. Over this period, reporting practices, number of licenses issued, and report card return rates were largely consistent. Although there is uncertainty in fishing capture due to incomplete reporting and poaching, we take these as the best available index of relative differences in fishing capture across habitat zones of interest. We calculated a fishing capture risk index for each fish (C_i) by apportioning region-specific fishing capture to individuals based on their proportional occupancy,

$$C_i = \left(\sum_j \theta_{i,j}\, \gamma_{R_j}\right)/N,$$

where $\theta_{i,j}$ is the telemetry-determined proportional occupancy of fish i at detection location j in fishing region R, γ_{R_j} is the estimated fishing capture in region R where detection location j is located, and N is the total number of white sturgeon captured. To calculate γ_{R_j}, we averaged the reported number of captured sturgeon per region across 2015 to 2020. During 2015-2020, response rates were consistent (29.8% to 33.5%), and we did not attempt to further correct for incomplete reporting because reporting biases are likely but unquantifiable from currently available data. Despite uncertainties over the number of white sturgeon caught, we assert that these data provide valid first-order approximations of the spatial distribution of white sturgeon catch, which was our main objective. We then aggregated by size class to evaluate whether fishing capture risk tended to vary among size classes. We present results considering all caught (harvested + released) fish. Patterns in C_i were similar when considering only harvested fish; however, since some size classes are not exposed to harvest, we focus on results considering both harvested and released fish.

To quantify variation in risk from anthropogenic habitat modification, we analyzed data on the location and volume of water diversions using data from the California electronic Water Rights Information Management System (eWRIMS; https://www.waterboards.ca.gov/waterrights/water_issues/programs/ewrims/). We selected water rights in our study area that had not been cancelled or revoked and used the total amount of water permitted to be diverted under the water right to indicate the magnitude of its potential impact on fish. To calculate the human modification index (M_i), we associated each water right with the nearest detection location within at most 2 km and totaled the volume of water diversions associated with each detection location. We then summed the location-specific water diversion volume, weighted by proportional occupancy of each detection location, for each fish. That is,

$$M_i = \sum_j \left(\theta_{i,j} \sum_{k \in J} V_k \right)$$

where $\theta_{i,j}$ is the telemetry-determined proportional occupancy of fish i at detection location j, V_k is the water right diversion volume of diversion k, and J is the set of diversions k for which detection location j is the nearest detection location. We then aggregated into the three size classes described above to evaluate whether exposure to anthropogenic habitat modification tended to vary with size.

All analyses were conducted in R version 4.0.3 (R Core Team 2021) using the ‘vegan’ (Oksanen et al. 2022), ‘abdiv’ (Bittinger 2020) and ‘stats’ (R Core Team 2021) packages.

Results

Habitat occupancy

Dissimilarity in habitat use of white sturgeon across individuals and water years was much greater than was expected to arise by chance alone: the empirical total dissimilarity in habitat use profiles was greater than all 1000 surrogates.

Fish size class (df = 2, 250; F = 4.18; p < 0.0001), but not fish sex (df = 2, 250; F = 1.57; p = 0.08) or water year flow conditions (df = 3, 249; F = 0.77; p = 0.71) statistically explained differences in habitat use behavior. Fish below the slot limit were detected most frequently in the lowest portions of the Bay-Delta, with a modal detection location in Carquinez Strait (detection location 4, Benicia Bridge), and were detected anywhere upriver of Rio Vista (detection location 7) on fewer than 1% of detections (Figure 1a). Fish within slot size limit for harvesting were detected at a wider range of locations than those below the slot limit, including in areas upriver of the confluence of the Sacramento and Feather rivers (detection location 15; Figure 1b). Fish above the slot limit were more likely than other size classes to be detected in areas upriver of the confluence of the Sacramento and Feather rivers (Figure 1c), which includes known spawning locations (Schaffter 1997). White sturgeon above the slot limit were also observed at the mouth of San Francisco Bay (detection location 1, Golden Gate Bridge) with greater frequency than other size classes, suggesting that large fish more commonly make trips into the Pacific Ocean. White sturgeon were detected at the Golden Gate Bridge in 23 fish-water years; 15 of these were above-slot fish, 8 were within-slot-fish, and none were fish below the slot limit. There was also no significant effect of sex on differences in habitat use behavior when excluding individuals of unknown sex (df = 1, 65; F = 1.15; p = 0.32).

Release region and tagging year had statistically significant effects in all models, showing the importance of controlling for these factors while testing for influence of key variables. Yet, despite the statistically significant effects of size class, release region, and tagging year, these statistical models explained 9% - 22% of differences in total habitat use.

Habitat occupancy by depth

Considering the full study area, as fish size increased across size classes relative to the slot limit, the proportion of detections in shallower portions of the system increased (Figure 2). However, division of the study areas into the “Bay” and “Delta and Sacramento River” regions suggests that larger white sturgeon tend to occupy somewhat deeper parts of the Bay region, but much shallower parts of the Delta and Sacramento River region compared to smaller white sturgeon.

Exposure to fishing and habitat modification

Fish at different size classes experienced differing levels of exposure to fishing capture and harvest. By merging biotelemetry-based habitat use information with angler report card catch data, we showed that fish within the slot limit were less likely than other size classes to be detected in areas where most sturgeon are caught (Figure 3a). By far, most white sturgeon were captured by anglers in Suisun Bay and the lower Sacramento-San Joaquin Delta (Figure 4).

Fish at different size classes were also exposed to variable levels of anthropogenic habitat modification, as estimated using total permitted volume of water diversions (Figure 3b). Below-slot fish were least likely to be detected in areas with high volume water diversions. Note that the fishing capture index and the anthropogenic modification index values are not directly

comparable and are valid only to compare the relative level of the same kind of exposure among size classes.

Discussion

We conducted a synthesis of available acoustic telemetry data on white sturgeon to differentiate patterns of habitat occupancy across size classes in the San Francisco Bay, Sacramento-San Joaquin Delta, and Sacramento River system. Smaller white sturgeon below the slot limit concentrated their occupancy in the upper bays and lowest portions of the delta, which also tended to be the deeper portions of the system. Larger white sturgeon within and above the slot limit were detected increasingly frequently at furthest upriver sites that included known spawning areas, as well as the mouth of the San Francisco estuary, possibly signaling movements into the Pacific Ocean. We combined these data with other relevant data on harvest and habitat modification to improve understanding of sturgeon exposure to broader human impacts. These analyses have implications for conservation management of white sturgeon and demonstrate an approach for synthesis science that leverages available long-term biotelemetry, fishery, and water datasets.

We observed that fish of different size classes tended to be detected in areas of different river depth. Although we are unable to resolve whether depth preferences drive habitat use patterns or instead whether the depth differences we observed are consequences of other habitat preferences that vary by life stage, these findings raise intriguing questions about white sturgeon ecology and conservation. Shallower portions of the bays and lower Delta could be excellent habitat for smaller sturgeon if these areas are rich in resources and have fewer large predators than deeper portions of the bay. Larger sturgeon may have a size refuge from additional predators,

explaining their greater proportional occupancy of deeper portions of the bays, or also use deep channels with strong movement-aiding currents for efficient travel (Kelly and Klimley 2012). Movement of adult white sturgeon to upriver spawning grounds could explain their much greater prevalence in shallower areas of the Delta and Sacramento River. One future consideration for white sturgeon conservation is how habitat preferences intersect with boating traffic, and whether there are adequate deep water refugia for sturgeon to avoid boat strikes. Boat strikes are a documented cause of white sturgeon mortality in this region (Demetras et al. 2020), although the rate and spatial distribution of boat strikes of white sturgeon is currently not well quantified.

Our finding that white sturgeon within the fishery slot limit were detected less frequently in areas where the most white sturgeon are caught, as compared to below- or above-slot fish, has multiple potential explanations. One possibility is that sturgeon are quickly harvested once they reach the slot limit, giving them fewer opportunities to be detected in areas of high fishing pressure than out-of-slot fish. Alternatively, anglers may simply fail to direct their efforts toward areas where within-slot white sturgeon are most prevalent, for example if other factors determine preferences for where to fish. Another possibility is behavioral avoidance. Although, to our knowledge, behavioral avoidance of anglers has not been studied in white sturgeon, other sturgeon species exhibit predator-avoidance behaviors and show signs of experiential learning even at age-0 (Hintz et al. 2013). Other fishes also can use prior experience and adjust behavior to avoid capture by anglers (Louison et al. 2019; Koeck et al. 2020). For behavioral avoidance alone to explain this result, not only must white sturgeon recognize and avoid areas of higher angler pressure, but this response must also be strongest in fish that are within the slot limit. While the former seems plausible, a mechanism making the angler-avoidance response strongest in within-slot white sturgeon is unclear. The hypothesis that habitat use of white sturgeon within

the fishery slot limit reflects behavioral responses to angling could be tested more explicitly in future research.

Our result that habitat use patterns change with sturgeon age complements another recent study of white sturgeon in the San Francisco Estuary and Sacramento-San Joaquin river system, but using very different methods. Sellheim et al. (2022) used fin ray geochemistry to infer age-specific habitat use across a salinity gradient from open ocean to freshwater, with the average salinity inhabited by a fish tending to increase over ages 0 to 10. Fish in this age range are below the slot limit, and below-slot fish, in our study, tended to be found lowest in the system, in areas tending toward higher salinity, compared with larger fish. Note that the youngest fish in our dataset was estimated at 7 years old based on the growth curve presented in Blackburn et al. (2019), which Sellheim et al. (2022) indicate would tend to be using higher-salinity habitats. The discrepancy in ages between these studies also highlights that telemetry data on juvenile white sturgeon are limited, resulting in uncertainty over their habitat use and movements. While studies of other white sturgeon populations have generally found differences among fish in habitat use and movement (Parsley et al. 2008; Nelson and McAdam 2012; Schreier et al. 2013; McLean et al. 2020), direct comparison is challenging because most other studies have been focused on more local spatial scales or have not examined variation across life stages.

Despite our results showing habitat use differences by size class, substantial variability in habitat use behavior was unexplained and could be associated with other factors. Related fish species exhibit habitat use differentiation into groups of individuals with characteristically different occupancy patterns that are not clearly associated with life stage or sex. Migratory populations of native lake sturgeon (*Acipenser fulvescens*) also exhibit spatiotemporally segregated “contingents” with distinct patterns of habitat use in the Laurentian Great Lakes

region, including resident and migrant individuals as well as distinct migration patterns (Kessel et al. 2018; Colborne et al. 2019). For lake sturgeon, habitat use patterns were generally consistent over time, suggesting that sturgeon habitat use groups reflect individuals' intrinsic preferences or specialization, possibly influenced by life history factors. Groups of shortnose sturgeon (*Acipenser brevirostrum*) inhabiting coastal waters and river systems of Maine also exhibit divergent patterns of movement and habitat use (Dionne et al. 2013; Altenritter et al. 2018), and in the same Sacramento River system green sturgeon (*Acipenser medirostris*) exhibit distinctly bimodal early/late downriver migration patterns (Colborne et al. 2022). Sellheim et al. (2022) found evidence for groups of white sturgeon from the same population as this study exhibiting distinct patterns of habitat use with age. Intraspecific variation in habitat occupancy and migration behavior could be a common and linking feature of sturgeon ecology more generally (Miller et al. 2020). Considering the potential bet-hedging effects of divergent behaviors against local catastrophe, this likely has important benefits for population stability, acknowledging also that other life history characteristics that facilitate recovery from disturbance, such as rapid population growth, are not present in sturgeon.

Our findings have important implications for white sturgeon monitoring and management in the San Francisco Estuary and Sacramento River system. Presently, the principal means of monitoring white sturgeon population health in the San Francisco Estuary include a trammel net survey conducted each fall at a single location, a tag-based mark-recapture study limited by low return rates, and the compilation of white sturgeon catch report cards from recreational anglers used in this study. However, our size-specific occupancy analyses suggest that indexing white sturgeon abundance at only a single location is likely to inject bias into abundance index data. For example, we found that above-slot sturgeon (i.e., large fish) utilized upriver habitat

substantially more than within-slot or below-slot fish. Thus, it remains unclear to what extent the current trammel survey indexes abundance of large white sturgeon. And because large females contribute disproportionately to annual recruitment patterns of many species of fishes (Beldade et al. 2012; Saenz-Agudelo et al. 2015), understanding standing stock biomass and abundances of large females is vital to overall sturgeon population sustainability and accurate stock assessment (Bruch 1999). It is implicit in the current slot regulation that there is value to protecting small and large white sturgeon. Yet the extant population monitoring programs may not align with the more complicated habitat use-by-size interactions of sturgeon outlined in this study. Implanting acoustic tags in more small juvenile white sturgeon would improve understanding of their movements, an area of uncertainty in this study due to lack of data. We note that, as is often the case, managers of this system are aware of limitations in their practices, and improvements are limited by operational constraints including financial and personnel resources. But, by leveraging an existing, broadscale, multi-agency acoustic telemetry array (Cordoleani et al. 2021), we can continue to develop new insights, with relatively low additional costs, by continuing to equip white sturgeon with long-lived acoustic transmitters and maintaining an array of acoustic receivers. Continued long-term telemetry studies and monitoring, such as presented here, can provide critical evidence and support toward improving management practices.

In the San Francisco Estuary and Sacramento River system, white sturgeon at different size classes exhibit variable patterns of habitat use. Differentiated patterns of habitat use and movement within populations appear to be a common feature of sturgeon biology across related species (Dionne et al. 2013; Kessel et al. 2018; Altenritter et al. 2018; Colborne et al. 2019, 2022; Sellheim et al. 2022). Further study is needed to resolve the biological underpinnings and

implications for population health and management. Our findings suggest that different size classes of white sturgeon are exposed to different levels of risk from recreational fishing and water diversions, but the extent to which white sturgeon movement behaviors respond to these factors is not yet resolved. Despite these uncertainties, adjusting population monitoring protocols, for example by incorporating additional habitats into annual abundance surveys is likely to benefit management of this species of conservation concern. This study demonstrates the value of synthesis research using long-term tracking studies, particularly for understanding the ecology of organisms such as sturgeon that are long-lived, mobile and use a diversity of habitats across their lifespans.

Acknowledgements

This analysis was supported by California Delta Science Programs grant 18204. This work was also supported by the University of California, Davis Agricultural Experiment Station (grant #2098-H to NAF and grant #2467-H To ALR). Fish tagging was supported by funding and/or in-kind support from the U.S. Army Corps of Engineers and California Department of Fish and Wildlife. The receiver array is maintained through the collaboration of NOAA Fisheries, USBR, USFWS, ECORP, CDWR, and USGS. Colby Hause facilitated angler report card data access from CDFW. We also would like to thank the myriad individuals who tagged sturgeon and maintained receiver arrays, including the Biotelemetry Laboratory at UC Davis, and partners at CDFW, USACE, USBR, NOAA Fisheries, USFWS, CDWR, ECORP, and USGS, whose efforts provided the extensive datasets used for this analysis.

References

Altenritter, M. E., G. B. Zydlewski, M. T. Kinnison, J. D. Zydlewski, and G. S. Wippelhauser. 2018. Understanding the basis of shortnose sturgeon (*Acipenser brevirostrum*) partial migration in the Gulf of Maine. Canadian Journal of Fisheries and Aquatic Sciences 75(3):464–473.

Andrews, S. W., E. S. Gross, and P. H. Hutton. 2017. Modeling salt intrusion in the San Francisco Estuary prior to anthropogenic influence. Continental Shelf Research 146:58–81.

Bade, A. P., T. R. Binder, M. D. Faust, C. S. Vandergoot, T. J. Hartman, R. T. Kraus, C. C. Krueger, and S. A. Ludsin. 2019. Sex-based differences in spawning behavior account for male-biased harvest in Lake Erie walleye (*Sander vitreus*). Canadian Journal of Fisheries and Aquatic Sciences 76(11):2003–2012.

Beldade, R., S. J. Holbrook, R. J. Schmitt, S. Planes, D. Malone, and G. Bernardi. 2012. Larger female fish contribute disproportionately more to self-replenishment. Proceedings of the Royal Society B: Biological Sciences 279(1736):2116–2121.

Bittinger, K. 2020. abdiv: Alpha and Beta Diversity Measures.

Blackburn, S. E., M. L. Gingras, J. DuBois, Z. J. Jackson, and M. C. Quist. 2019. Population Dynamics and Evaluation of Management Scenarios for White Sturgeon in the Sacramento–San Joaquin River Basin. North American Journal of Fisheries Management 39(5):896–912.

Bruch, R. M. 1999. Management of lake sturgeon on the Winnebago System - long term impacts of harvest and regulations on population structure. Journal of Applied Ichthyology 15(4–5):142–152.

Campbell, M. D., R. Patino, J. Tolan, R. Strauss, and S. L. Diamond. 2010. Sublethal effects of catch-and-release fishing: measuring capture stress, fish impairment, and predation risk using a condition index. ICES Journal of Marine Science 67(3):513–521.

Chapman, B. B., K. Hulthén, J. Brodersen, P. A. Nilsson, C. Skov, L.-A. Hansson, and C. Brönmark. 2012. Partial migration in fishes: causes and consequences. Journal of Fish Biology 81(2):456–478.

Colborne, S. F., D. W. Hondorp, C. M. Holbrook, M. R. Lowe, J. C. Boase, J. A. Chiotti, T. C. Wills, E. F. Roseman, and C. C. Krueger. 2019. Sequence analysis and acoustic tracking of individual lake sturgeon identify multiple patterns of river–lake habitat use. Ecosphere 10(12).

Colborne, S. F., L. W. Sheppard, D. R. O'Donnell, D. C. Reuman, J. A. Walter, G. P. Singer, J. T. Kelly, M. J. Thomas, and A. L. Rypel. 2022. Intraspecific variation in migration timing of green sturgeon in the Sacramento River system. Ecosphere.

Cordoleani, F., A. Ammann, C. Vallee, J. Kelly, J. J. Notch, and D. R. O'Donnell. 2021. Summary of Interagency Telemetry Advisory Group Activities - Water Year 2021. Interagency Telemetry Advisory Group.

Crossin, G. T., M. R. Heupel, C. M. Holbrook, N. E. Hussey, S. K. Lowerre-Barbieri, V. M. Nguyen, G. D. Raby, and S. J. Cooke. 2017. Acoustic telemetry and fisheries management. Ecological Applications 27(4):1031–1049.

Demetras, N. J., B. A. Helwig, and A. S. Mchuron. 2020. Reported vessel strike as a source of mortality of White Sturgeon in San Francisco Bay 106(1):7.

Dionne, P. E., G. B. Zydlewski, M. T. Kinnison, J. Zydlewski, and G. S. Wippelhauser. 2013. Reconsidering residency: characterization and conservation implications of complex

migratory patterns of shortnose sturgeon (*Acispenser brevirostrum*). Canadian Journal of Fisheries and Aquatic Sciences 70(1):119–127.

Donaldson, M. R., S. G. Hinch, C. D. Suski, A. T. Fisk, M. R. Heupel, and S. J. Cooke. 2014. Making connections in aquatic ecosystems with acoustic telemetry monitoring. Frontiers in Ecology and the Environment 12(10):565–573.

Fregoso, T. A., R.-F. Wang, E. Alteljevic, and B. E. Jaffe. 2017. San Francisco Bay-Delta bathymetric/topographic digital elevation model (DEM).

Gomez, L., K. W. Larsen, and P. T. Gregory. 2015. Contrasting patterns of migration and habitat use in neighboring rattlesnake populations. Journal of Herpetology 49(3):371–376.

Hanna, D. E. L., C. Raudsepp□Hearne, and E. M. Bennett. 2020. Effects of land use, cover, and protection on stream and riparian ecosystem services and biodiversity. Conservation Biology 34(1):244–255.

Hart, S. P., M. M. Turcotte, and J. M. Levine. 2019. Effects of rapid evolution on species coexistence. Proceedings of the National Academy of Sciences 116(6):2112–2117.

Hellinger, E. 1909. Neue begründung der theorie quadratischer formen von unendlichvielen veränderlichen. Journal für die reine und angewandte Mathematik 136:210–271.

Herren, J. R., and S. S. Kawasaki. 2001. Inventory of Water Diversions in Four Geographic Areas in California's Central Valley:14.

Hildebrand, L. R., A. Drauch Schreier, K. Lepla, S. O. McAdam, J. McLellan, M. J. Parsley, V. L. Paragamian, and S. P. Young. 2016. Status of White Sturgeon (*Acipenser transmontanus* Richardson, 1863) throughout the species range, threats to survival, and prognosis for the future. Journal of Applied Ichthyology 32:261–312.

Hintz, W. D., G. T. Grimes, and J. E. Garvey. 2013. Shovelnose sturgeon exhibit predator avoidance behaviour in the presence of a hungry predator. Journal of Applied Ichthyology 29(1):2–5.

Hussey, N. E., S. T. Kessel, K. Aarestrup, S. J. Cooke, P. D. Cowley, A. T. Fisk, R. G. Harcourt, K. N. Holland, S. J. Iverson, J. F. Kocik, J. E. Mills Flemming, and F. G. Whoriskey. 2015. Aquatic animal telemetry: A panoramic window into the underwater world. Science 348(6240):1255642.

Hutchings, J. A., and L. Gerber. 2002. Sex-biased dispersal in a salmonid fish. Proceedings of the Royal Society B: Biological Sciences 169:2487–2493.

Iverson, S. J., A. T. Fisk, J. Mills Flemming, S. J. Cooke, and F. G. Whoriskey. 2019. The Ocean Tracking Network: Advancing frontiers in aquatic science and management. Canadian Journal of Fisheries and Aquatic Sciences 76(7):1041–1051.

Johnston, M., J. Frantzich, M. B. Espe, P. Goertler, G. Singer, T. Sommer, and A. P. Klimley. 2020. Contrasting the migratory behavior and stranding risk of White Sturgeon and Chinook Salmon in a modified floodplain of California. Environmental Biology of Fishes 103(5):481–493.

Kelly, J. T., and A. P. Klimley. 2012. Relating the swimming movements of green sturgeon to the movement of water currents. Environmental Biology of Fishes 93(2):151–167.

Kessel, S. T., D. W. Hondorp, C. M. Holbrook, J. C. Boase, J. A. Chiotti, M. V. Thomas, T. C. Wills, E. F. Roseman, R. Drouin, and C. C. Krueger. 2018. Divergent migration within lake sturgeon (*Acipenser fulvescens*) populations: Multiple distinct patterns exist across an unrestricted migration corridor. Journal of Animal Ecology 87(1):259–273.

Koeck, B., M. Lovén Wallerius, R. Arlinghaus, and J. I. Johnsson. 2020. Behavioural adjustment of fish to temporal variation in fishing pressure affects catchability: an experiment with angled trout. Canadian Journal of Fisheries and Aquatic Sciences 77(1):188–193.

Krueger, C. C., C. M. Holbrook, T. R. Binder, C. S. Vandergoot, T. A. Hayden, D. W. Hondorp, N. Nate, K. Paige, S. C. Riley, A. T. Fisk, and S. J. Cooke. 2018. Acoustic telemetry observation systems: challenges encountered and overcome in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 75(10):1755–1763.

Lehman, B., M. Gary, N. Demetras, and C. Michel. 2019. Where Predators and Prey Meet: Anthropogenic Contact Points Between Fishes in a Freshwater Estuary. San Francisco Estuary and Watershed Science 17(4):3.

Louison, M. J., C. D. Suski, and J. A. Stein. 2019. Largemouth bass use prior experience, but not information from experienced conspecifics, to avoid capture by anglers. Fisheries Management and Ecology 26(6):600–610.

McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82(1):290–297.

McLean, M. F., M. K. Litvak, E. M. Stoddard, S. J. Cooke, D. A. Patterson, S. G. Hinch, D. W. Welch, and G. T. Crossin. 2020. Linking environmental factors with reflex action mortality predictors, physiological stress, and post-release movement behaviour to evaluate the response of white sturgeon (*Acipenser transmontanus* Richardson, 1836) to catch-and-release angling. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 240:110618.

Michel, C. J., A. J. Ammann, S. T. Lindley, P. T. Sandstrom, E. D. Chapman, M. J. Thomas, G. P. Singer, A. P. Klimley, and R. B. MacFarlane. 2015. Chinook salmon outmigration survival in wet and dry years in California's Sacramento River. Canadian Journal of Fisheries and Aquatic Sciences 72(11):1749–1759.

Miller, E. A., H. E. Froehlich, D. E. Cocherell, M. J. Thomas, J. J. Cech, A. P. Klimley, and N. A. Fangue. 2014. Effects of acoustic tagging on juvenile green sturgeon incision healing, swimming performance, and growth. Environmental Biology of Fishes 97(6):647–658.

Miller, E. A., G. P. Singer, M. L. Peterson, E. D. Chapman, M. E. Johnston, M. J. Thomas, R. D. Battleson, M. Gingras, and A. P. Klimley. 2020. Spatio-temporal distribution of Green Sturgeon (Acipenser medirostris) and White Sturgeon (A. transmontanus) in the San Francisco Estuary and Sacramento River, California. Environmental Biology of Fishes 103(5):577–603.

Moyle, P. B. 2002. Inland fishes of California: Revised and expanded, 2nd edition. University of California Press, Los Angeles and Berkeley, California.

Moyle, P. B., J. V. E. Katz, and R. M. Quiñones. 2011. Rapid decline of California's native inland fishes: A status assessment. Biological Conservation 144(10):2414–2423.

Nelson, R. J., and D. S. O. McAdam. 2012. Historical population structure of White Sturgeon in the Upper Columbia River detected with combined analysis of capture, telemetry and genetics: Population structure of White Sturgeon in the Upper Columbia River. Journal of Applied Ichthyology 28(2):161–167.

Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, P. Solymos, M. H. H. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. D. Caceres, S. Durand, H. B. A. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. O. Hill, L. Lahti, D.

McGlinn, M.-H. Ouellette, E. R. Cunha, T. Smith, A. Stier, C. J. F. T. Braak, and J. Weedon. 2022. vegan: Community Ecology Package.

Parsley, M. J., N. D. Popoff, C. D. Wright, and B. K. van der Leeuw. 2008. Seasonal and Diel Movements of White Sturgeon in the Lower Columbia River. Transactions of the American Fisheries Society 137(4):1007–1017.

Pinsky, M. L., O. P. Jensen, D. Ricard, and S. R. Palumbi. 2011. Unexpected patterns of fisheries collapse in the world's oceans. Proceedings of the National Academy of Sciences 108(20):8317–8322.

R Core Team. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reynolds, J. D., N. K. Dulvy, N. B. Goodwin, and J. A. Hutchings. 2005. Biology of extinction risk in marine fishes. Proceedings of the Royal Society B: Biological Sciences 272(1579):2337–2344.

Saenz-Agudelo, P., G. P. Jones, S. R. Thorrold, and S. Planes. 2015. Mothers matter: contribution to local replenishment is linked to female size, mate replacement and fecundity in a fish metapopulation. Marine Biology 162(1):3–14.

Schaffter, R. G. 1997. White sturgeon spawning migrations and location of spawning habitat in the Sacramento River, California. California Fish and Game 83.

Schreier, A. D., B. Mahardja, and B. May. 2013. Patterns of Population Structure Vary Across the Range of the White Sturgeon. Transactions of the American Fisheries Society 142(5):1273–1286.

Secor, D. H. 1999. Specifying divergent migrations in the concept of stockL the contingent hypothesis. Fisheries Research 43:13–34.

Sellheim, K., M. Willmes, L. S. Lewis, J. Sweeney, J. Merz, and J. A. Hobbs. 2022. Diversity in Habitat Use by White Sturgeon Revealed Using Fin Ray Geochemistry. Frontiers in Marine Science 9:859038.

Singer, G. P., A. R. Hearn, E. D. Chapman, M. L. Peterson, P. E. LaCivita, W. N. Brostoff, A. Bremner, and A. P. Klimley. 2013. Interannual variation of reach specific migratory success for Sacramento River hatchery yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). Environmental Biology of Fishes 96(2–3):363–379.

Thomas, M. J., M. L. Peterson, N. Friedenberg, J. P. Van Eenennaam, J. R. Johnson, J. J. Hoover, and A. P. Klimley. 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(2):287–297.

Figures

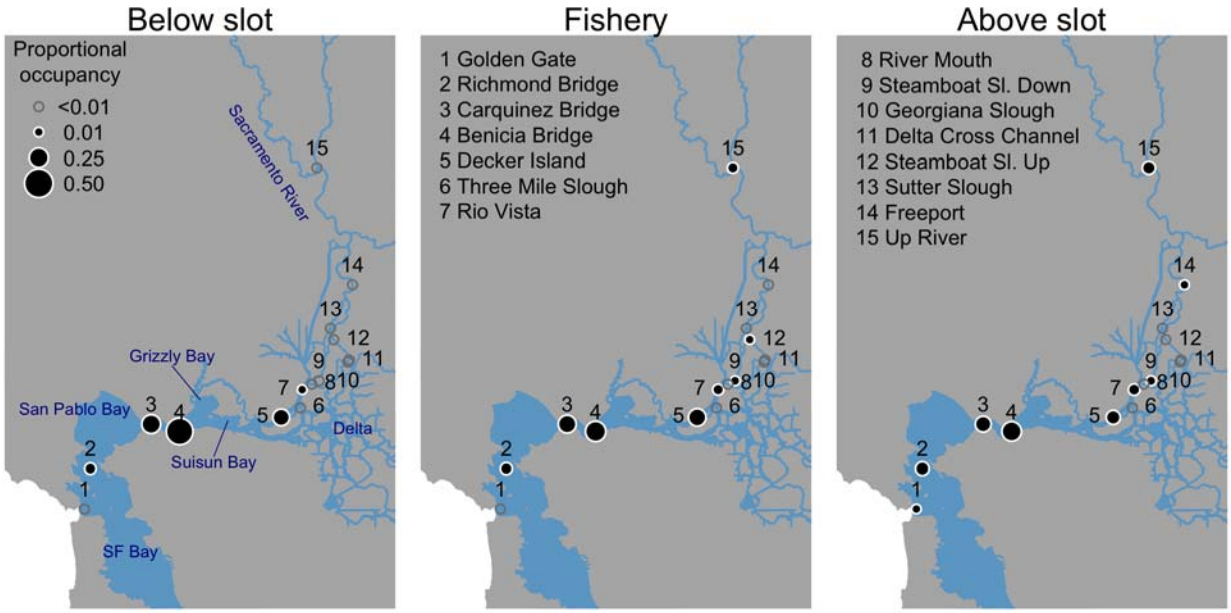

Figure 1. White sturgeon mean proportional occupancy by detection location for below slot limit, fishery (within slot limit), and above slot limit fish.

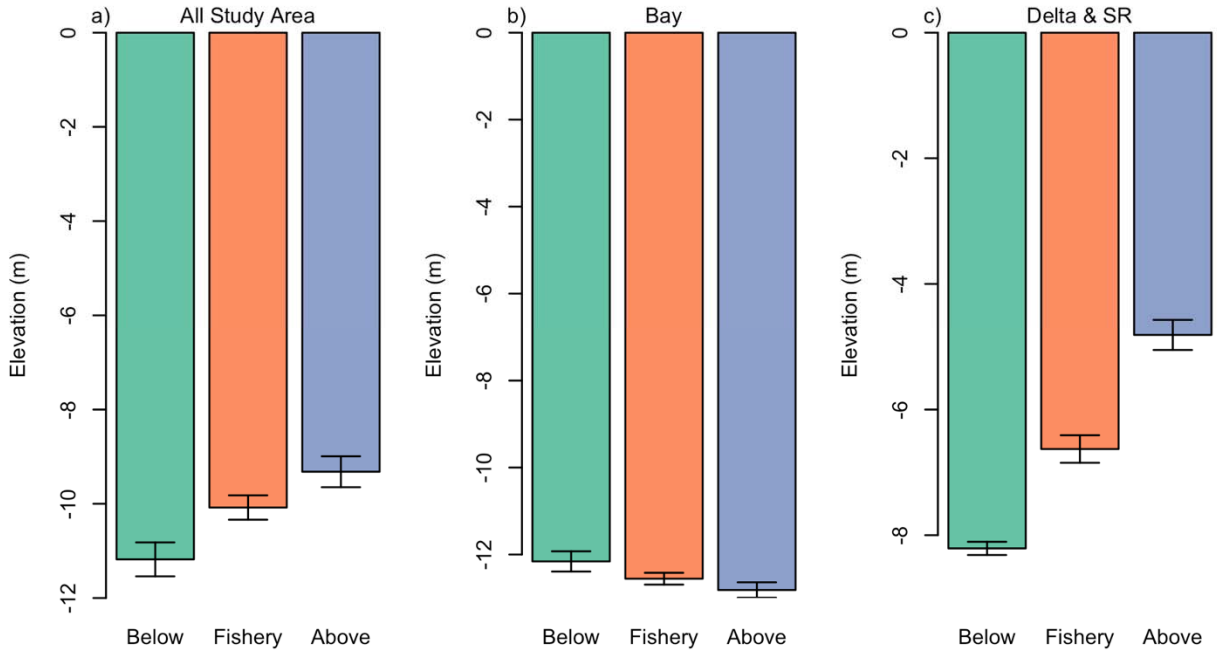

Figure 2. Weighted mean river depth of occupied areas by fish size, considering a) the full study area; b) only the San Francisco, San Pablo, and Suisun bays in the lower portion of the study area; c) only the Delta and Sacramento River (SR) portions of the study area. Error bars indicate one standard error.

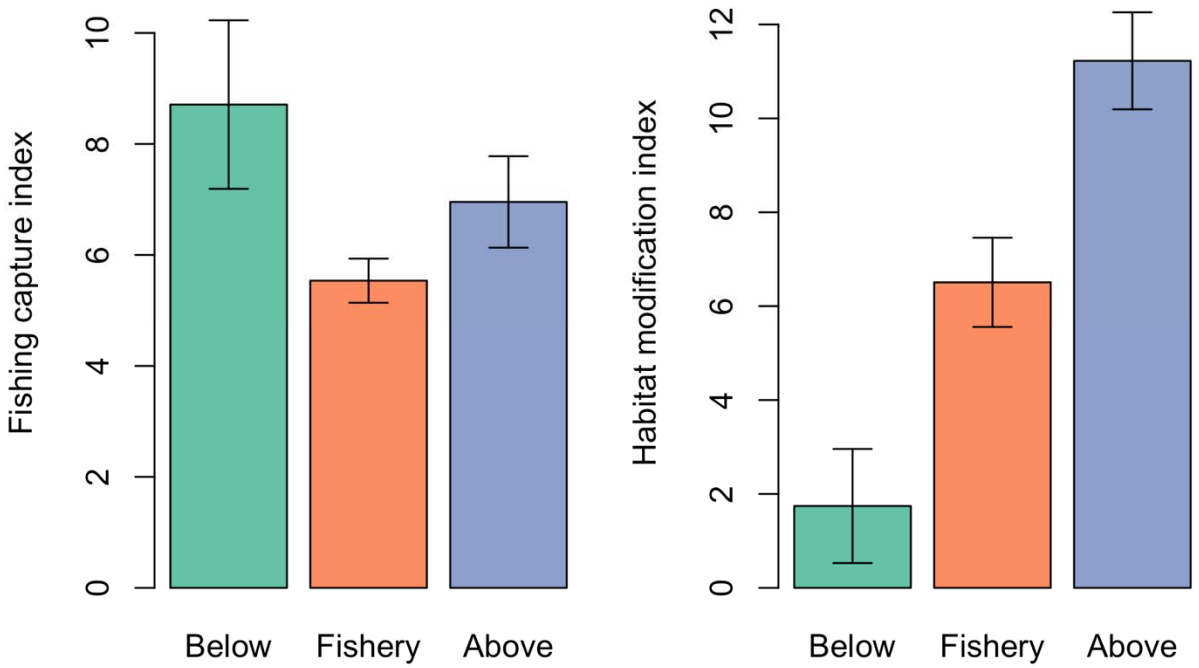

Figure 3. Exposure indices for: a) fishing capture by size class; b) anthropogenic habitat modification by size class. The fishing capture index was computed from self-reported data on the location of caught white sturgeon from 2015 to 2020. Anthropogenic habitat modification is computed based on the estimated volume of water diversions. Error bars indicate one standard error.

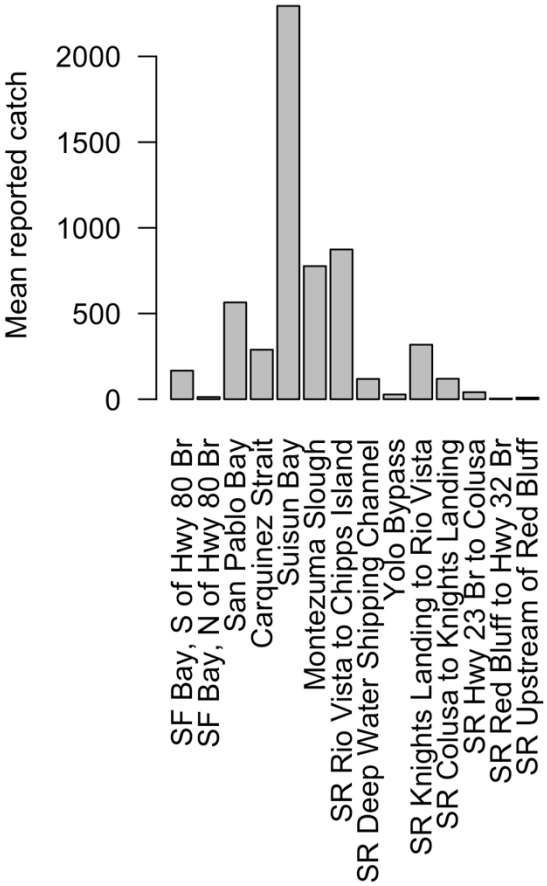

Figure 4. Estimated mean number of white sturgeon caught (harvested + released) by region. Regions are ordered generally, from left to right, from the ocean upstream. Data are from 2015 to 2020.