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Authors
Klimley, A. Peter
Chapman, Eric D.
Cech, Jr., Joseph J.
et al.

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Sturgeon in the Sacramento–San Joaquin Watershed: New Insights to Support Conservation and Management

A. Peter Klimley,[1,2] Eric D. Chapman,[2] Joseph J. Cech, Jr.,[2] Dennis E. Cocherell,[2] Nann A. Fangue,[2] Marty Gingras,[3] Zachary Jackson,[4] Emily A. Miller,[2] Ethan A. Mora,[2] Jamilynn B. Poletto,[2] Andrea M. Schreier,[2] Alicia Seesholtz,[5] Kenneth J. Sulak,[6] Michael J. Thomas,[2] David Woodbury,[7] and Megan T. Wyman[2]

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1 Corresponding author: *apklimley@ucdavis.edu*
2 University of California Davis, Davis CA 95616 USA
3 California Department of Fish and Wildlife, Stockton, CA 95206 USA
4 United States Fish and Wildlife Service, Lodi, 95340 CA
5 California Department of Water Resources
West Sacramento, CA 95691 USA
6 United States Geological Survey, Gainesville, FL 32653 USA
7 National Marine Fisheries Service, Santa Rosa, CA 95404 USA

KEY WORDS

Green sturgeon, *Acipenser medirostris,* white sturgeon, *Acipenser transmontanus,* conservation biology

ABSTRACT

The goal of a day-long symposium on March 3, 2015, *Sturgeon in the Sacramento–San Joaquin Watershed: New Insights to Support Conservation and Management*, was to present new information about the physiology, behavior, and ecology of the green (*Acipenser medirostris*) and white sturgeon (*Acipenser transmontanus*) to help guide enhanced management and conservation efforts within the Sacramento–San Joaquin watershed. This symposium identified current unknowns and highlighted new electronic tracking technologies and physiological techniques to address these knowledge gaps. A number of presentations, each reviewing ongoing research on the two species, was followed by a round-table discussion, in which each of the participants was asked to share recommendations for future research on sturgeon in the watershed. This article presents an in-depth review of the scientific information presented at the symposium with a summary of recommendations for future research.

INTRODUCTION

Green and white sturgeon, two distinct species with very different life history strategies, reside in the Sacramento–San Joaquin River watersheds and pose different conservation and management challenges. Green sturgeon (*Acipenser medirostris*), a more marine species, are currently thought to be comprised of two genetically distinct breeding populations (Israel et al. 2004): a northern distinct population segment (DPS) consisting of fish that spawn in the Rogue River, Oregon (Erickson et al. 2002), and the Klamath River, California (Van Eenennaam et al. 2001), and a southern DPS that spawns in the Sacramento River, California (Heublein et al. 2009) and its tributary, the Feather River (Seesholtz et al. 2015). The southern DPS green sturgeon migrates in the spring to spawn in the Sacramento River and

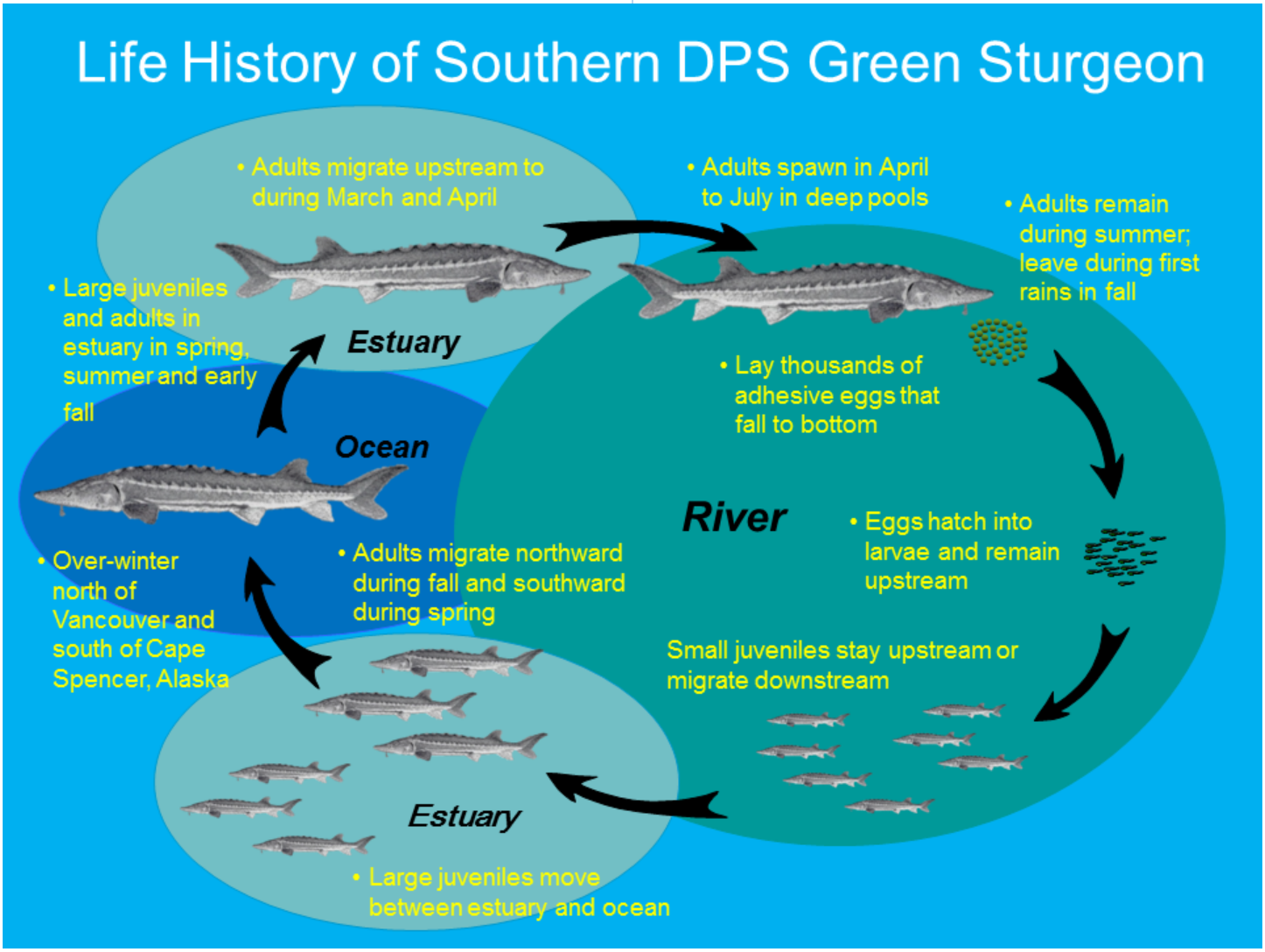

Figure 1 Life history of the southern DPS green sturgeon, *Acipenser medirostris*, within the Sacramento–San Joaquin watershed based on the results of cited studies (see "References" and "Notes"). (Green sturgeon image from Moyle 2002.)

returns to the estuary in the fall, winter, and spring (Figure 1). Adults migrate out through the Golden Gate Bridge at the mouth of San Francisco Bay and travel northward along the continental shelf to the waters off Washington state and Canada before returning to the estuary (Lindley et al. 2008, 2011). By contrast, white sturgeon (*Acipenser transmontanus*) appear to spawn lower in the Sacramento and San Joaquin rivers and remain within the San Francisco Estuary throughout their entire lifespan (Kolhorst 1973; Schaffter 1997; Figure 2). White sturgeon have been shown to form a single population in the Sacramento–San Joaquin watershed based on the similarity in micro-satellite loci (Schreier et al. 2013).

RECENT ADVANCES IN STURGEON BIOLOGY

Biologists actively conducting research or involved in the conservation of the species presented talks on green and white sturgeon during a 1-day symposium on March 3, 2015, *Sturgeon in the Sacramento–San Joaquin Watershed: New Insights to Support Conservation and Management*. The goal of this symposium was to present new information about

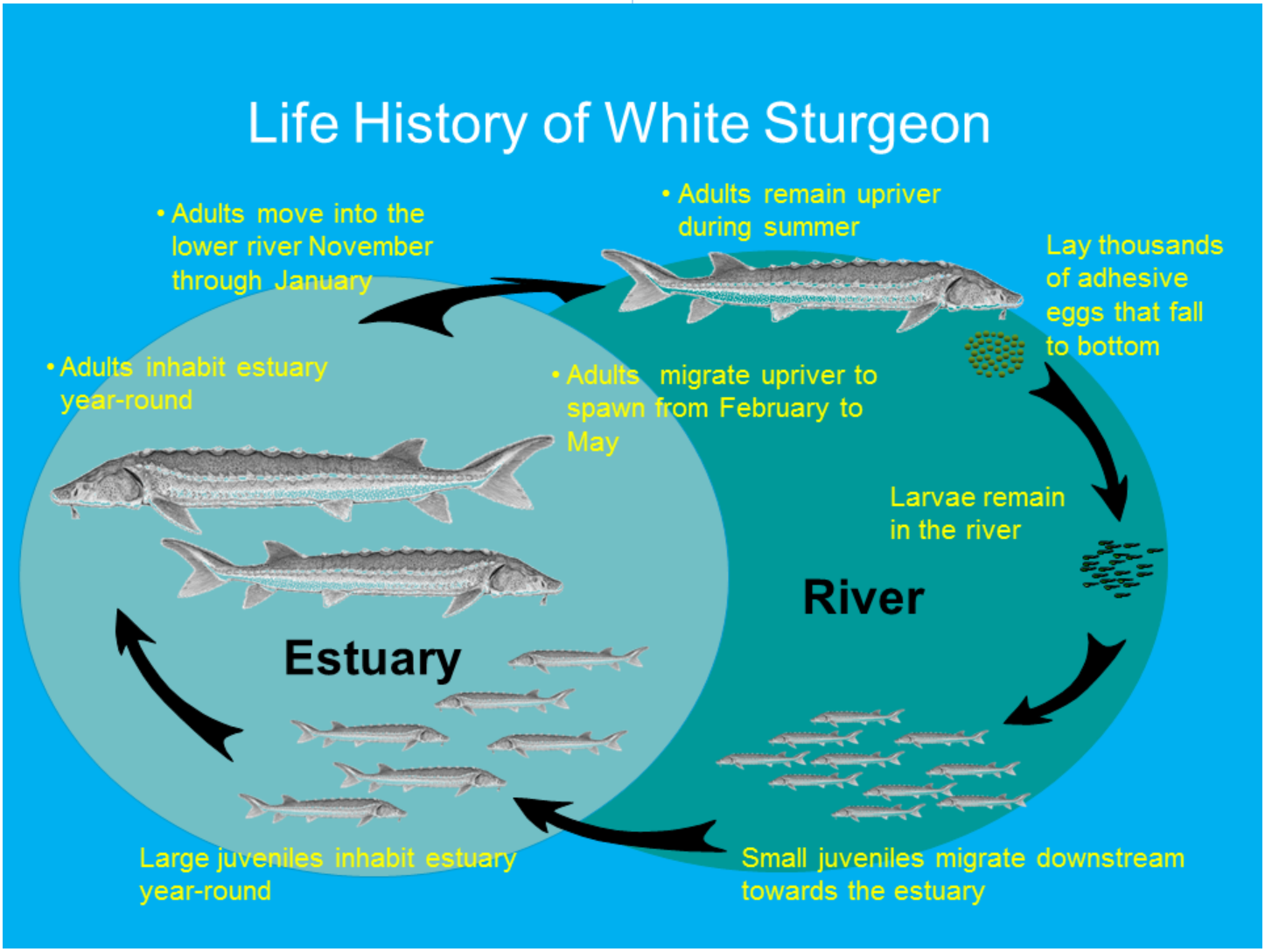

Figure 2 Life history of the white sturgeon, *Acipenser transmontanus*, within the Sacramento–San Joaquin watershed based on the results of cited studies (see "References" and "Notes"). (Green sturgeon image from Moyle 2002.)

the physiology, behavior, and ecology of these two species to help guide enhanced management and conservation efforts within the Sacramento–San Joaquin watershed. This symposium identified current unknowns and highlighted new electronic tracking technologies and physiological techniques to address these knowledge gaps. A number of presentations, reviewing ongoing research on the two species, was followed by a round-table discussion, in which each of the participants was asked to share recommendations for future research on sturgeon in the watershed. The results of the studies described can be presented under four categories: (1) movements and distribution, (2) habitat selection, (3) physiology and behavior, and (4) population biology. The information presented in the talks, and provided in abstracts to A. P. Klimley, will be summarized under these four categories, and at the end of each section, recommendations will be given for future research. The following nomenclature will be used when describing the biology of the various life stages of these two species. We consider as larvae, those sturgeon that possess a yolk-sac. They become juveniles once they begin to feed exogenously. Adulthood is reached once they are sexually mature.

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Movements and Distribution

Electronic tagging studies have been used to describe the movements and distribution of green sturgeon. Individually coded ultrasonic beacons were inserted into the body cavities of adult green sturgeon in San Pablo Bay and the Klamath River, California, and in the Rogue River, Oregon. These multi-year beacons were detected by autonomous tag-detecting receivers moored along the western coast of North America at Monterey Bay, California; Seal Rock, Oregon; Cape Elizabeth and Juan de Fuca, Washington; and the Brooks Peninsula and Queen Charlotte Straits in British Columbia, Canada. Green sturgeon migrated northward over the continental shelf during the fall to the Brooks Peninsula and Queen Charlotte Straits and southward in the spring to Cape Elizabeth (Lindley et al. 2007, 2011). In the spring, the same individuals, carrying coded beacons, were detected by an array of receivers as they moved up 550 river kilometers (rkm) from the mouth of the San Francisco Estuary to the mainstem of the Sacramento River as far upstream as its junction with Cow Creek (Heublein et al. 2009). Before 2009, their upriver migration was blocked by the lowering of the gates of the Red Bluff Diversion Dam (RBDD) on May 15 of each year. Those that arrived at the dam before the gates were lowered could proceed farther upstream to access more spawning grounds; those that arrived afterwards stayed below the gates. Individuals that moved upriver of the gates were able to pass downstream under the gates during late summer and early fall on their migration to the mouth of San Francisco Bay.

The occurrence of green sturgeon was compared over time for three river reaches—one above RBDD and two below it—for sturgeon tagged either in California or Oregon and Washington during three periods (Thomas et al. 2015, unpublished report, see "Notes"). Sturgeon were recorded within the three time-periods: (1) from 2006 to 2008 when the gates were lowered on May 15, (2) from 2009 to 2011 when the gates were lowered on June 15, and (3) from 2012 to 2013 when the dam was no longer present. A general additive mixed model indicated that significantly more sturgeon inhabited the uppermost reach when the gates were non-operational than when they were lowered on May 15th of the year. This provided empirical support that the substitution of a pumping facility for the diversion dam permitted more individuals of the species to access spawning habitat upstream of the dam.

The construction of dams in the Sacramento River and its tributaries has reduced the amount of spawning habitat for green sturgeon. This was determined for the spring months of April through June by identifying river reaches in the mainstem and tributaries that have similar water discharge rates, flow velocities and gradients, and air temperatures to locations within the Klamath and Rogue rivers. Habitats similar to occupied regions in the Rogue and Klamath Rivers were lost above the Keswick Dam on the mainstem of the Sacramento River as well above dams on the Feather, Yuba, American, and San Joaquin rivers (Mora et al. 2009).

Recently, green sturgeon spawning was detected in the Feather River, a major tributary of the Sacramento River. Egg mats were deployed at two lower Feather River sites from April 12 through July 7, 2011, a year characterized by above-average rainfall. Thirteen green sturgeon eggs were collected at one of those sites (Seesholtz et al. 2014). Developmental stages of the eggs ranged from early gastrulation to post-neurulation, which indicated that four independent spawning events occurred between June 12 and 19 after an increase in flow with an optimum temperature of <17.5 °C for egg development (Van Eenennaam et al. 2005). Results suggest that the river reach at Thermalito Afterbay Outlet is important for green sturgeon spawning habitat, and that the lower Feather River can provide a second production area of SDPS green sturgeon.

Shipboard tracking of adults indicated that green sturgeon migrate upstream quickly in the spring to a few upriver pools, such as on the mainstem of the Sacramento River at its confluence with Antelope and Deer creeks (Thomas et al. 2014). After strong rain storms, green sturgeon can stray from the mainstem on to the floodplains and become stranded as the water subsides at locations such as the Tisdale Bypass and Fremont Weir. Coded ultrasonic beacons were placed in the body cavities of 24 stranded green sturgeon that were taken to the mainstem of the Sacramento River and released to ascertain whether

they would continue upstream on their spawning migration. Seventeen continued upstream past Irvine Finch at 412 rkm, the point on the river where the channel turns into pools separated by runs and riffles that are suitable for spawning. Twenty-two of the 24 individuals successfully left the watershed and entered coastal waters. An individual-based model indicated that in the absence of rescue, the current population of green sturgeon in the river would have declined by 33% over 50 years (Thomas et al. 2013).

Much less is known about the movements of juveniles. Six green sturgeon, captured as small juveniles below the RBDD, were grown to a total length (TL) of roughly 30 cm. These fish were released at Santa Clara Shoals during the summers of 2008 and 2010 at 104 rkm in the Central Delta, where individuals were captured by net in the past (Radtke 1966), and tracked by boat in the Delta for 5 days. The juveniles moved within an area of less than 10 km over this period. Individual sturgeon moved during both day and night and their movements were independent of tidal action (e.g., they moved both against and with current direction during most tidal phases; Thomas and Klimley 2015, unpublished report, see "Notes").

Thirty-two juvenile green sturgeon, ranging in fork length (FL) from 30 to 53 cm, with surgically implanted coded beacons were released at Santa Clara Shoals on February 28, 2013. They were captured in a net deployed below the RBDD, transported to the Center for Aquaculture and Aquatic Biology in Davis, California, and grown to a size previously shown to display minimal tag effects (Miller et al. 2014). No differences in growth or critical swimming velocity were found among the three groups of juvenile green sturgeon tested: (1) with dummy transmitters implanted in the peritoneal cavity, (2) sham fish that underwent surgery without tag implantation, and (3) control fish that were handled and anesthetized but did not undergo surgery. Incisions were photographed at the beginning and end of the study to assess inflammation and to score each incision for closure and suture retention. Inflammation declined similarly for tagged and sham fish during the study. The U_{crit}, or critical swimming speed performed in a flow chamber (Brett 1964), was not related to the extent of inflammation or to post-surgery time. All fish showed healing during the 140-day study and 10% of tagged and sham fish showed signs of inflammation by the study's end. These results suggest that current surgical tagging methods do not significantly affect the short-term growth or swimming performance of juvenile green sturgeon.

Upon release, the juvenile green sturgeon exhibited a diversity of movement patterns. Thirty-one of 32 sturgeon were detected for periods ranging from 3 to 290 days over a period of nine and a half months—the battery life of the tags; only one was not detected after release. The amount of time in days, or percentage of all of the days detected, was determined for ten regions of the watershed (Thomas and Klimley, unpublished report, see "Notes"). These regions, in down-river order starting from those farthest upriver, are: (1) East Delta, (2) between East and Central Delta, (3) North Delta, (4) Central Delta, (5) Suisun Bay, (6) Carquinez Strait, (7) San Pablo Bay, (8) Richmond Bridge, (9) San Francisco Bay, and (10) the Golden Gate Bridge (Figure 3). The tagged juvenile green sturgeon resided for the most amount of time within the Delta. Thirty of the 32 tagged individuals were detected in the Central Delta, where they were released. Individuals stayed within this region on average 90.6 days and 44.3% of the time over the nine-and-a-half-month longevity of the tags. The juveniles also stayed within the East Delta and the region between the East and Central Delta (Figure 3). Fourteen individuals spent, on average, 26.7 days and 28% of the time in the former region, and 16 juveniles spent 34.1 days and 31.0% of the time in the latter region. The next most inhabited regions were San Pablo Bay and around the Richmond Bridge, where 15 and 14 individuals, respectively, spent 26.0 and 34.1 days and 12.0% and 13.4% of the time. It is notable that as many as seven individuals were detected by the two cross-bay arrays near the Golden Gate Bridge: juveniles were present in this region for an average of 23.2 days and 9.9% of the total days they were detected in the watershed. Some of these individuals left the bay and moved into the coastal waters. Juvenile green sturgeon exhibited the following six behavioral patterns over the nine-and-a-half-month life of the electronic tags: (1) remained in the Delta, (2) moved into the Carquinez Strait, (3) migrat-

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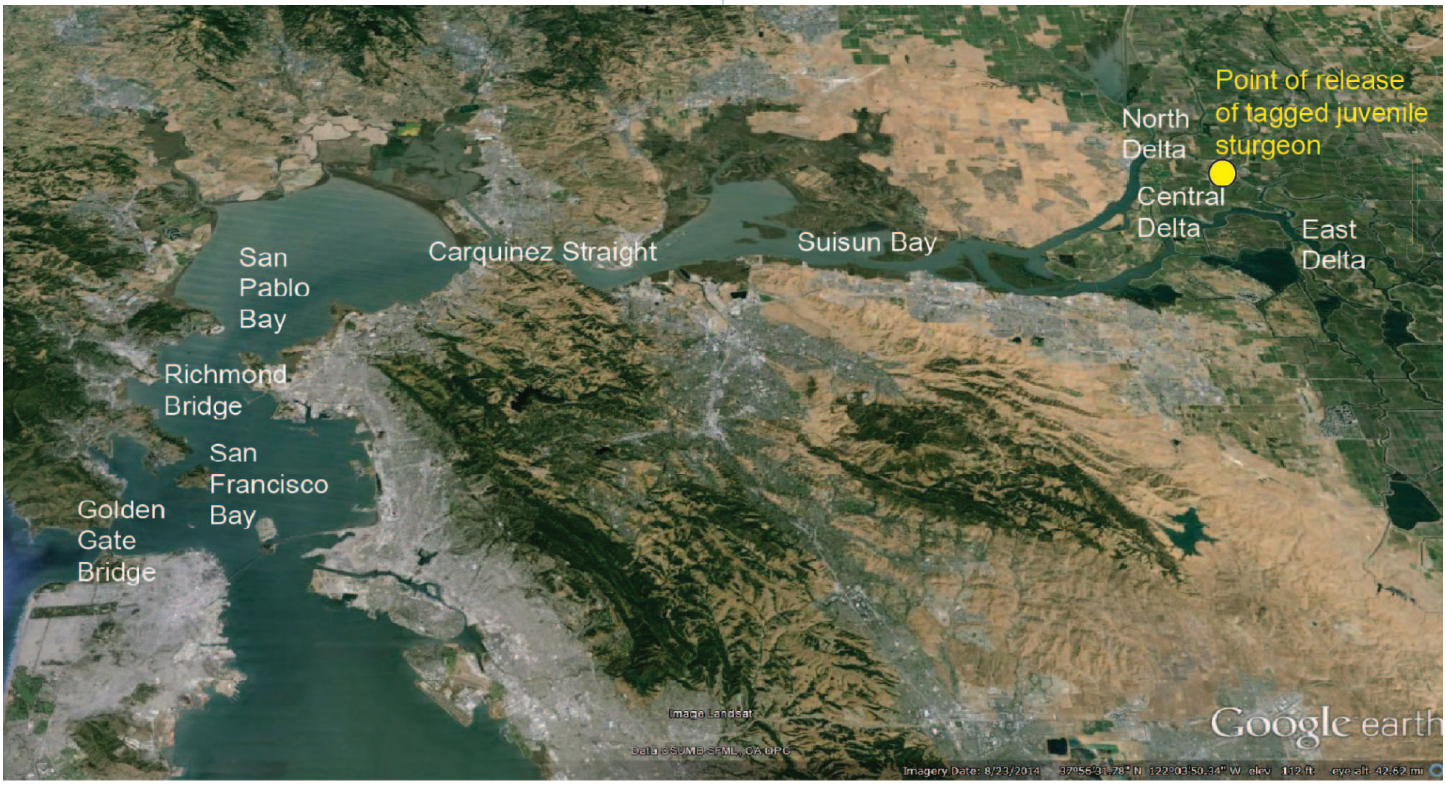

Figure 3 Areas where juvenile green sturgeon were detected over a period of nine months. Juveniles were tagged and released at Santa Clara Shoals (yellow circle). (Source: Google Earth images.)

ed into San Pablo Bay, (4) moved into San Pablo Bay but returned to the Delta, (5) migrated through the estuary and likely left through the mouth of the bay, and (6) left the estuary only to later return.

Unlike green sturgeon, adult and juvenile white sturgeon occupy the Sacramento–San Joaquin watershed year round. Furthermore, mature adults spawn lower in the watershed than the green sturgeon. Our knowledge of the movements of white sturgeon is largely based on a radio-telemetry study carried out in the 1990s (Shaffter 1997). A brief description of this work will provide a context for the more recent studies, which do not use continuous tracking by automobile, boat, or airplane, but depend on the detection of tagged fish at particular sites where autonomous receivers are deployed. Radio transmitters were attached to 59 adult white sturgeon during late winter between Courtland at 56 rkm and Freeport at 74 rkm in the lower Sacramento River. The sturgeon were localized in the river with an antenna attached either to an automobile, boat, or airplane.

In addition, artificial substrate samplers (i.e., egg mats) were deployed at putative spawning sites. The upstream movements of white sturgeon coincided with increases in flow early in March during both years of the study either from to rainfall or melting snow in the Sierra Nevada Mountains. During 1990, two males of 121 and 144 cm total length (TL) moved to 240 rkm, upstream of artificial substrates deployed at 225 rkm on which eggs were collected. The next year, two males of 142 and 147 cm TL moved to 225 and 295 rkm, also either at or above the site where artificial samplers collected sturgeon eggs. Based on the degree of embryological development, the estimated time of spawning occurred between May 6 and 13 after a 40-m^3s^{-1} increase in the flows recorded at 231 rkm at Colusa. The larvae develop into juveniles that apparently migrate downriver towards the rearing grounds in the Delta. Larger juveniles and adults are found in the estuaries during all months, although some over-summer in rivers upstream from the estuary.

It has long been known that white sturgeon spawn in the Sacramento River and pulses of water from the melting snows prompt their in-river movement (*sensu* Schaffter 1997). Although spawning surveys had never been conducted on the San Joaquin River, previous researchers and managers speculated that spawning might occur there in the wettest years (Kohlhorst 1976; Beamesderfer et al. 2004). Recent spawning surveys demonstrated that white sturgeon spawn in the San Joaquin River, the second largest tributary of the San Francisco Estuary (Gruber et al. 2012; Jackson and Van Eenennaam 2013). Potential white sturgeon spawning locations were assessed by deploying artificial substrate samplers during late-winter and spring of 2011–2014 over a 30-km reach of the San Joaquin River beginning near the Stanislaus River confluence and extending upstream. White sturgeon eggs were collected during the 2011 and 2012 sampling seasons. Egg collections, coupled with hydrology data, confirm that white sturgeon spawn in the San Joaquin River in both wet and dry water years as long as there are at least modest increases in streamflow (e.g., 20 to 40 m^3s^{-1}) during the March–May spawning period.

The spatial and temporal differences in the distributions of white and green sturgeon have been determined in a study of niche partitioning (Miller et al. 2013). Coded ultrasonic beacons have been surgically implanted in large juveniles and adults of both species and their seasonal distributions determined based upon their detection by monitors deployed throughout the Sacramento–San Joaquin watershed. Green and white sturgeon were detected within the system throughout the year. Large juveniles of both species were generally found in the estuary.

Adult sturgeon of both species were present year-round in the system even though green sturgeon are highly marine. White sturgeon are resident in the estuary throughout adulthood so patterns of movement were separated into individuals making spawning migrations and those not spawning for each year. Green sturgeon adults in the system are assumed to be making spawning migrations and were generally found at greater river kilometers. White sturgeon spawning adults moved upstream in the winter to spawn in early spring and then moved downstream into the estuary by late spring. Green sturgeon, by comparison, entered the system throughout spring and moved quickly to the upper river to spawn (>411.8 rkm). Green sturgeon were detected throughout the system from September to January as they exited their spawning grounds.

To examine the timing of adult spawning migrations, sturgeon movements were examined by reach. Green and white sturgeon differ in the timing of their migrations in the Sacramento River, most notably with white sturgeon beginning the move out of the estuary and through the delta to the lower river much earlier than green sturgeon. Green sturgeon enter the lower (169 to 239 rkm) and upper river (>239 rkm) to spawn later than white sturgeon. White sturgeon exit the lower Sacramento River and enter the delta (86 to 69 rkm) much earlier than green sturgeon. White sturgeon leave the lower Sacramento River and enter the Delta shortly after spawning while green sturgeon may remain through the summer, fall, or winter. Some white sturgeon remain in the San Joaquin River during the summer (2015 email from Z. Jackson to A.P. Klimley, see "Notes"). The timing of sturgeon movements varied widely within each species, especially for the exit of green sturgeon from spawning grounds. The timing also varied by year, presumably because of inter-annual environmental variation.

Recommendations for Future Study

1. Determine when and where larval and smallest juvenile green sturgeon of a length of from 50 to 200 mm TL rear in the Sacramento River. There is very little information on this life stage after they are last detected in the rotary screw traps near Red Bluff and Glenn Colusa until they reach the Delta. This size–class information is also needed for white sturgeon (Seesholtz).
2. Describe the movements and distribution of juvenile green sturgeon (200 to 500 mm TL) in the lower Sacramento River, Delta, and San Francisco Bay (Klimley).
3. Examine the sex-specific patterns of movement of both green and white sturgeon related to both

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the timing of adult spawning migrations and also non-migratory spatio-temporal differences in distribution. To do this, we need to be able to identify the sex of sturgeon tagged in the future (Miller).

4. Increase the extent of the array of autonomous receivers to identify white sturgeon spawning sites and the favored habitat of resident green and white sturgeon in the San Francisco Estuary. The array has been reduced in spatial extent to minimize the cost of its maintenance. A more dense distribution of the receivers with a greater geographic extent would be needed to answer questions of a fine-scale distribution (Miller).

5. Assess how individual characteristics such as sex, age class, previous experience, or behavior types may influence migration behavior and spawning site preferences. Long-lived, uniquely coded tags provide a wealth of individual data that could be used for this purpose. In relation to this, improving the ability to determine sex in sturgeon based on fin or blood samples would be highly beneficial for this (Wyman).

Habitat Selection

More recently, the following studies have been completed on the favored habitat of juvenile and adult sturgeon. Six juvenile green sturgeon, tracked by boat in the Central Delta, largely swam near the bottom along the steep drop off to the deep channel (Thomas and Klimley, unpublished report, see "Notes"). The individuals were detected in both shallow water (4- to 10-m deep) and within the channel (10- to 25-m deep). Within the estuary, adult green sturgeon tracked by boat spent the majority of their time in shallow waters slowly swimming near the bottom in a non-directional manner, presumably foraging on benthic prey (Kelly et al. 2007). These movements are punctuated by rapid and highly directional movements near the surface either upriver or downriver within the estuary. The adults exhibit negative rheotaxis, swimming in the direction the current flowed during peak flood and ebb tidal stages (Kelly and Klimley 2012).

Empirical measures and modeling have been used to examine the spawning habitat preferences of green sturgeon in the upper Sacramento River (Wyman et al. unpublished report, see "Notes"). Specifically, a 2-dimensional fish-positioning system; habitat measurements of flow, discharge, surface elevation, bathymetry, and substrate; and hydraulic modeling were used to determine suitability curves of depth, flow velocity, and substrate type over two spawning seasons within three sites known to be spawning locations. Each fish position was assigned a depth and a vertically averaged velocity value, based on flow simulations with time-specific discharge levels, and a substrate (sand, cobble, or rock) identified using a DIDSON sonar. Normalized counts of fish positions were used to construct histograms and associated area-weighted suitability curves for each parameter type, both within each site and with all sites and years combined. Time-specific habitat suitability index scores from the three individual habitat parameters—as well as a cumulative habitat suitability score calculated as the geometric mean of the three habitat scores—were graphed in area maps of each site within curvilinear orthogonal grid cells. These maps were animated to show the change in the spatial distribution of scores over the sampling period based on flow simulations of river discharge. The weighted usable area was calculated during the sampling periods for each of the three sites. This index was determined by multiplying the area of each grid cell in each site by its cumulative habitat suitability score at a given discharge then summing these values over the domain of each site. Preliminary results indicate that adult green sturgeon are selecting particular habitat characteristics within the spawning grounds (i.e., preferring moderate flows, deep pools, and gravel bottom) and that the weighted usable area (WUA) in each reach is affected by variation in discharge levels.

Ultrasonic telemetry has been used to determine the frequency and time of exposure for adult green sturgeon at dredged and dredged material placement sites within the San Francisco Bay estuary (Chapman et al. unpublished observations, see "Notes"). Autonomous receivers were deployed for three years within the lower estuary at dredge removal and placement sites

to assess the potential for adverse effects. Green sturgeon were present at the material placement sites during all months of the year but were prevalent during pre- and post-spawn periods. Of the 134 fish detected in the estuary, 81% were detected at one or more dredged or dredged material placement sites. The median estimated exposure times at the dredged material placement sites was 72.5 min at SF-09 near the Carquinez Strait, 141.1 min at SF-10 in San Pablo Bay, and 37.1 min at SF-11 near Alcatraz Island in San Francisco Bay. The median exposure time at the dredged San Pablo Channel was 77.5 min. Nine fish were fitted with depth-sensing transmitters. The majority of detections from these fish were at depths greater than 5 m. These results may be used to inform management decisions that will protect this threatened species at critical times. It brings to light the need for further telemetric and physiological studies on the effects of dredging on benthic fishes, particularly the juvenile life stage.

Recommendations for Future Study

1. Expand the habitat preference analysis to more locations within the upper Sacramento River, including sites which appear to be favorable for sturgeon spawning based on depth profiles, but where sturgeon are not found in great numbers (Wyman).
2. Conduct a cross-system comparison of spawning site preferences by expanding the habitat preference analysis to other systems that are less modified than the Sacramento River, such as the Klamath or Rogue rivers (Wyman).
3. Examine habitat suitability based on historical flow records. It would be worthwhile to know the extent of favorable habitat in the past based on present knowledge of their flow, depth, and bottom type requirements determined from the recent study of habitat suitability (Wyman).
4. Learn more about the physical features and geomorphology of the spawning habitat of white sturgeon (Schreier).
5. Since sturgeon are aggregators, it is important to understand the difference between behavior (i.e., fish are clumped for social reasons rather than lack of habitat) and habitat suitability that drives the density of the species at various holding locations (Seesholtz).
6. Further telemetric and physiological studies need to be conducted on the effects of dredging on benthic fishes, particularly on the juvenile life stage (Chapman).

Physiology and Behavior

Water diversions alter the hydrology of riverine environments and greatly influence the behavior, physiology, and survival of fishes. Many diversions, however, remain unscreened and formal screen criteria specific to sturgeon have not been developed. Furthermore, diversions are typically operated to minimize effects on listed fish such as salmonids and smelt. The California Department of Fish and Wildlife (CDFW) and National Marine Fisheries Service (NMFS) screening criteria are given below:

- *http://www.dfg.ca.gov/fish/Resources/Projects/Engin/Engin_ScreenCriteria.asp*
- *http://www.westcoast.fisheries.noaa.gov/publications/hydropower/fish_screen_criteria_for_pumped_water_intakes.pdf*

To begin to address these knowledge gaps and assess how water diversions in the Central Valley of California affect sturgeon, several laboratory studies were undertaken with larval and juvenile green and white sturgeon. For example, little is known of the swimming capacities of larval sturgeons, though the risk of larval sturgeon entrainment is likely influenced by both the ontogeny of swimming capacity and the interactions of sturgeon with water diversions.

Firstly, the ontogeny and allometry of larval green and white sturgeon swimming capacities was described and compared for fish aged 20 to 60 days post hatch (dph), with total lengths of 3 to 9 cm, which represented the time period associated with larval development into juveniles (Verhille et al. 2014). Absolute critical swimming velocities

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(U_{crit}; cm s^{-1}) as well as relative swimming velocities (U_{crit}; body lengths [BL] s^{-1}) were quantified and related to growth. In both species, absolute U_{crit} increased as size and age increased, though relative U_{crit} decreased as fish grew. Green sturgeon absolute critical swimming velocities were greater than those of white sturgeon throughout the larval life stage. However, white sturgeon growth rates were higher than those of green sturgeon, and white sturgeon eventually were larger than green sturgeon at the end of the larval life stage. These results represented the first assessment of larval swimming capacity in these two species of sturgeon, and this information was integrated with knowledge of sturgeon dispersal and migration timing. Recommendations were then developed for anthropogenic water-diversion facility flow operations for each species during different times of the year, based upon larval sturgeon swimming performance capabilities.

To mitigate for losses of native fishes at water-diversion structures, many are outfitted with a fish-exclusion screen to physically prevent or deter fish from entrainment. How these fish-exclusion screens affect the behavior of migrating juvenile fishes remains largely unknown, especially for sturgeon. To quantify these behavioral responses, individual juvenile green or white sturgeon were placed in a laboratory swimming flume in the presence of standard fish screens at two field-relevant mean water velocities of 20.4 and 37.3 cm s^{-1} (Poletto et al. 2014a). Fish were tested during the day or night and in the presence of possible behavioral deterrents (strobe lights, mechanical near-field vibrations, and a combination of the two). Green sturgeon were much more susceptible to physical interactions with the fish screens, and contacted the screens twice as frequently as white sturgeon, with mean contact rates of 61.2 and 28.3 during a 15-min period. Green sturgeon were also much more likely to become impinged upon screens, and differed in how their behaviors were altered by water velocities and time of day. However, the use of behavioral deterrents such as near-field vibrations and strobe lights did not significantly alter the behavior of either sturgeon species. The species-specific differences in the behavior of sturgeon near fish screens suggest that effective mitigation strategies for these species should be considered separately.

Unscreened agricultural water-diversion pipes that line levees and riverbanks represent a significant threat to fishes, unless individuals exhibit avoidance behavior. Fish can be drawn into (i.e., entrained) into these diversions, and either killed directly by physical damage from water pumps and associated machinery, or indirectly through stranding in the seasonally irrigated canals, ditches, and fields where the water diversions empty. Of the more than 3,300 water diversions located in the Sacramento–San Joaquin watershed, the majority (ca. 98%) are estimated to be unscreened. The number of green sturgeon entrained and killed by unscreened water diversions is unknown. The avoidance behaviors and entrainment susceptibility of juvenile green sturgeon was studied in a large outdoor flume with an open, unscreened water-diversion pipe (Mussen et al. 2014) at different sweeping flow (i.e., main channel velocity) and diversion rates. Overall, fish entrainment was generally high, ranging from 26% to 61% percent of all fish tested in the flume becoming entrained through the pipe. Most fish were entrained at the lowest sweeping flow velocity (15 cm s^{-1}) and highest diversion rate (57 m^3 s^{-1}), likely from a lack of avoidance behavior before they entered inescapable water-inflow conditions. These results were used to estimate the percentage of juvenile green sturgeon entrained after passing (encountering) multiple diversion pipes. A total of up to 52% of juvenile green sturgeon could be entrained after passing within 1.5 m of an active water-diversion pipe three times, underscoring the susceptibility of this species to entrainment and the need for effective management strategies.

To potentially improve mitigation strategies at unscreened water diversions, the efficacy of several methods to reduce green sturgeon entrainment was tested at unscreened water diversions: a strobe light sensory deterrent and two structural pipe modifications, which included a terminal pipe plate and upturned pipe configuration (Poletto et al. 2014b). Juvenile green sturgeon of a mean fork length of 39.4 cm were tested in a large outdoor flume fitted with a 0.46-meter-diameter water-diversion pipe. Under control conditions (an open, unmodified pipe),

an average of 44.0% of fish were entrained through the diversion pipe. Though the presence of the strobe light did not significantly affect fish entrainment rates, the terminal pipe plate and upturned pipe modifications significantly decreased the percentage of fish entrained relative to control conditions. These data suggest that sensory deterrents using visual stimuli are not an effective means to reduce diversion pipe interactions for green sturgeon, but that structural alterations to diversions can successfully reduce entrainment for this species. Building upon this reduction in entrainment rates, three additional structural modifications were tested in the presence of juvenile green sturgeon between 22.7 and 29.2 cm FL. These modifications included the addition of a trash-rack box, a louver box, and a perforated cylinder that sheathed the diversion pipe (Poletto et al. 2015). All three modifications significantly reduced the percentage of fish that were entrained through the pipe from 41.0% entrainment under control conditions (open, unmodified pipe) to as low as only 2.0% for the perforated cylinder. These results are informative for scientists and managers looking to mitigate the effects of water-diversion activities on juvenile green sturgeon, and demonstrate that conservation goals and water-diverter needs can be reconciled through the use of such devices.

Protection of the anadromous green sturgeon may be particularly important during migratory movements, such as during the juvenile outmigration from the upper reaches of freshwater rivers to the more saline estuarine and oceanic rearing environments. These migrations not only expose juveniles to multiple anthropogenic stressors, but also are associated with significant changes in physiology and behavior. For example, Allen et al. (2006) found that juvenile green sturgeon's swimming performance increased as total length increased, before reaching a size of 26.6 cm TL and a mean age of 155 dph, corresponding to when fish are capable of tolerating full-strength saltwater. Beyond this size and age, a negative relationship between swimming performance and age emerged. However, this effect, which may facilitate the downstream migration of seawater-ready juveniles towards the estuary and ocean, is probably a seasonal phenomenon, because older juveniles of 280 dph, of the same seawater-tolerant size, exhibited a positive relationship between total length and swimming performance (Allen et al. 2006). This seawater tolerance in green sturgeon has been shown to be preceded by enzymatic, hormonal, and cell-structural changes associated with survival in hyperosmotic environments (Allen et al. 2011). Studies investigating seawater tolerance and movement in green sturgeon have shown that behavioral preferences for saltwater can develop within 6 to 7 months of age (Poletto et al. 2013), and a trace-element analysis of pectoral fin-ray sections showed that wild, Klamath River adult green sturgeon probably first entered the estuary and ocean at ages 0.5 to 1.5 years old (Allen et al. 2009). Therefore, efforts to increase the number of migrating green sturgeon that successfully reach estuarine and marine environments should focus on juvenile life history stages, and take into account the behavioral and physiological changes that accompany such a migration.

The upstream passage of anadromous fishes, particularly non–salmonid species such as sturgeon, may be impeded or blocked by water-management-related structures, such as dams and weirs in the Sacramento–San Joaquin watershed, California. Many existing passage structures are designed for salmonid species and are known to be ineffective for adult sturgeon passage, probably because of these species' size and benthic cruising behavior. To assist in the design of a sturgeon-compatible fish ladder, the passage performance of wild-caught, adult white sturgeon was tested in a laboratory fish way section (Cocherell et al. 2011). A prototype, mid-section fish way of vertical baffles was designed to dissipate flowing-water kinetic energy as well as to provide guidance for upstream migration of sturgeon in a 24.4-m long flume with a 4% increasing slope. Fish passage performance was measured in this flume under low and high tail water treatments, and the water speeds through the slots between the baffles ranged from 1.7 to 2.1 $m\,s^{-1}$. Successful attraction flows were $>0.45\,m\,s^{-1}$ (Webber et al. 2007), and the maximum adult sturgeon swimming velocities in the flume were 2.57 $m\,s^{-1}$. The percentages of uninjured fish reaching the upstream end of the flume in both the low-and high-tail water treatments, 54% and

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63%, respectively, exceeded the observed 13% of injured fish when tested in the low-tail waters.

Several studies have elucidated aspects of the growth and development of juvenile green sturgeon. Mayfield and Cech (2004) showed that green sturgeon food consumption, growth, and food-conversion efficiency generally increased with temperature increases from 11 °C to 15 °C, but stayed constant between 15 °C and 19 °C. Growth increased and food-conversion efficiency decreased with increased ration size. Oxygen consumption, volitional activity rates, and ventilatory frequency generally increased with temperature increases, though preferred temperature increased and swimming performance decreased with temperature increases from 19 °C to 24 °C (Mayfield and Cech 2004). Further studies have also been conducted to understand how growth and physiological performance is affected by food intake amount in both juvenile green and white sturgeon. Food restriction trials in white sturgeon have been used to develop optimal growth feeding models in juvenile sturgeon, to identify food consumption rates that are necessary for growth to occur, as well as those that promote optimal growth (Lee et al. 2014, 2015b), and to test the effects of altered nutritional status on salinity tolerance (Lee et al. 2015a). These studies have revealed that growth rates are significantly affected by changes in feed rates, and that food-limitation in early life history stages may be a significant stressor. Furthermore, studies looking at multiple stressors in juvenile green sturgeon such as food restriction, increased rearing salinity, and acute salinity exposure have revealed that acute salinity exposure in fish reared at the highest salinity concentrations of 32 ppt and lowest feed rates of 12.5% of optimal resulted in high mortality rates (Haller et al. 2015; Vaz et al. 2015). In light of concerns about ongoing changes to foodwebs in the Sacramento–San Joaquin River watershed, these results underscore the importance of considering how multiple environmental stressors and stimuli may have compounding effects on sturgeon populations already in decline, and highlight our need to further our understanding of their effects.

Recommendations for Future Study

1. Further refine, develop, and test modifications to reduce entrainment of juvenile sturgeon (and other native fishes) into water diversions in ways that can be feasibly implemented without preventing water-diversion activities (Fangue).
2. Develop a mechanistic understanding of what stressors are affecting fish and what is driving declines in particular life history stages (Fangue and Poletto)
3. Assess the risk to juvenile green sturgeon of loss of life from predation. This could be accomplished by laboratory experiments (Poletto).
4. Develop an integrative model that can be used to determine the relative importance of different stressors on green sturgeon in the watershed (Fangue and Poletto).
5. Establish a research broodstock of SDPS green sturgeon so that researchers can conduct experiments using the sturgeon population endemic to the Central Valley watershed. Currently, experiments are being conducted with Northern Distinct Population Segment (NDPS) green sturgeon, and these fish are untested surrogates for SDPS fish. Significant neutral genetic differentiation between the NDPS and SDPS suggests that little gene flow occurs between the populations, and therefore adaptive differences may exist (Israel et al. 2009). Each DPS inhabits a unique ecological region (Klamath Mountain Province vs. California Central Valley; Adams et al. 2007) and may have acquired specific adaptations that allow them to spawn and rear successfully in these different environments. To make the best management decisions for SDPS fish, it is critical to consider if behavioral and/or physiological differences exist between NDPS and SDPS fish (Fangue).

Population Biology

Yearly censuses have been conducted using an acoustical imaging system (DIDSON) of the numbers of green sturgeon inhibiting reaches along the

Sacramento River. The population assessments had three main components: (1) use of a DIDSON to evaluate the presence or absence of green sturgeon at 125 habitat units greater than 5-m deep, (2) estimate the abundance of green sturgeon at each of the habitat units, and (3) combine the five annual estimates of run-size from 2010 through 2014 with an estimate of spawning periodicity to estimate the number of adults in the SDPS.

The study area contained 125 habitat units in the approximately 150-km reach of the Sacramento River between the Highway 32 overcrossing at the southern end and the city of Redding, California at the northern end. First, during June of 2010, 2011, 2012, and 2014, each of these locations was surveyed for the presence or absence of green sturgeon using the methods Mora et al. (2015) describe. Then, during 2010 through 2014, all cumulatively occupied locations were visited during 1 or 2 days to estimate the abundance of green sturgeon. Underwater video camera transects were conducted to estimate the proportion of green to white sturgeon present at each location. Second, the proportion of individuals that had already left the study area before the abundance surveys was determined using detections of individuals carrying coded tags by autonomous receivers.

To estimate the number of adults in the SDPS, the average of the annual run size over a period of 5 years was multiplied by an estimate of mean spawning periodicity of 3.5 years. The average of the 5-year spawning run size was calculated as the mean of the five-point estimates of spawning run size while the variance of this estimate was calculated by dividing the sum of the squared annual variances by the square of the number of estimates. This calculated mean and variance of the 5-year run size was then multiplied by the distribution of spawning periodicities to produce an estimate of the number of adults in the SDPS. The distribution of spawning periodicities was calculated as the interval, in number of years, between spawning migrations of individuals detected in the array of autonomous receivers that were located in the study area.

The presence–absence surveys detected sturgeon in 21 of the 125 habitat units. Sturgeon were detected in all years in only seven habitat units. The results of the presence-absence surveys show that sturgeon repeatedly occupied the same locations in the river during each year of our sampling. The abundance of sturgeon was estimated at each of the habitat units where we detected their presence. The site-by-site abundances were summed to estimate the total number of detected sturgeon in the river during the survey period. Video camera transects revealed that nearly all the identifiable sturgeon were green sturgeon. Only one white sturgeon was detected in 2013, the first after approximately 400 documented sturgeon-camera interactions (Mora 2015, unpublished report, see "Notes").

The analysis of the 111 pooled green sturgeon departure dates from the study area between 2006 and 2014 shows that approximately 13% of the tagged green sturgeon left the study area by June 15. This results in an inflation factor of 1.15 to the in-river abundance estimates. The average run size is then 364 with a variance of 246. If the spawning periodicity is approximated as a normal random variable with a mean of 3.7 and a variance of 0.5, the resulting estimate for the number of adults in the SDPS is 1348 within the 95% confidence interval of ± 524. This preliminary 'pooled data' model was produced to display the status of this investigation specifically for this symposium. A more specific 'annual model,' taking into account annually varying migration patterns has since been developed—and has drastically changed these results.

Nearly 80 years of trend information shows that large variations in white sturgeon recruitment—often five or more consecutive years of negligible recruitment—have been routine (Shirley 1987; CDFW 2014a, unpublished data, see "Notes"). In part from large variations in recruitment, the population has at times been overexploited. Substantial recruitment depends on extremely high Delta outflows during winter and spring (*sensu* CDFW 2015, unpublished data, see "Notes"; Fish 2010). The mechanisms underlying this relationship are the subject of on-going investigations, but are likely some combination of adult attraction to upstream spawning grounds, suitability of spawning substrate, and survival of age–0 fish during the migration downstream to the estuary.

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Managing the white sturgeon population through predictable ebbs in abundance is the key to conservation of the population and the protection of its fishery (2015 email with abstract for talk from M. Gingras to A.P. Klimley, see "Notes"). After a complete closure of commercial and sport fisheries in 1917, a sport fishery was established in 1954 regulated primarily by a minimum size limit and one-fish daily bag limit. Management of the population and fishery was not revised in response to a severe 1964–1974 decline, though it seems the decline prompted some efforts toward hatchery augmentation. Implementation of a first-ever limit on the maximum size of fish legal to harvest was the primary response to a severe 1979–1989 decline. In the midst of an ongoing decline that started in 1998, a series of revisions to the fishing regulations has been implemented. The most important recent revisions to limits on harvest are a first-ever annual bag limit of three fish at 40 to 60 inches FL (101.6 to 152.4 cm FL) (this range includes a mixture of mature and large juvenile females; Chapman et al. 1996) and closure of more than 100 miles of the Sacramento River to sturgeon fishing. Other approaches to regulating the fishery (e.g., a quota) are being assessed. This is because the present and foreseeable fishery has substantial 'excess capacity,' and use of a slot limit has focused that intense fishing effort on a relatively narrow size range of fish. This has resulted in the fishery being volatile (CDFW 2014b, unpublished data, see "Notes") with the population of adults not appreciably increasing in several decades.

Recommendations for Future Study

1. Gain a better understanding of basic juvenile green sturgeon abundance and distribution in the watershed (Mora).
2. Improve institutionalized monitoring of vital rates of green and white sturgeon (Mora).
3. Develop genetic markers that could be used to determine the sex of an individual based on the analysis of a tissue sample (Schreier).
4. Develop an overall management plan for white sturgeon (Gingras and Jackson).
5. Understand what factors drive recruitment of green sturgeon and white sturgeon. An index of the abundance of age–0 white sturgeon in the Sacramento River needs to be developed to complement the index from CDFW's bay study. Furthermore, indices of the abundance of age–0 green sturgeon in the Sacramento River and the San Francisco Estuary are sorely needed. Finally, an estimate is necessary of the annual number of breeders of both species. (Gingras and Schreier).
6. Understand catch-and-release mortality of white sturgeon in the watershed (Gingras).
7. Evaluate current fishing regulations and associated implications for the population trajectory of the white sturgeon (Jackson).
8. Develop a better understanding of the rates of growth, size, and age of maturity, recruitment, and mortality to improve management of the white sturgeon (Jackson).

External Overview

Dr. Kenneth Sulak, whose career has been devoted to studying the biology of the Gulf sturgeon (*Acipenser oxyrinchus desotoi*) in the rivers on the northwestern coast of Florida, was invited to the symposium to describe his work and provide his impressions, as an outsider, about the value of what we have found out and what needs to be learned about the green and white sturgeon in the Sacramento–San Joaquin watershed. The abstract of his talk is given below.

> "The Gulf sturgeon has been a topic of scientific research in Florida since that state instituted a harvest ban in 1984, and particularly since the species was listed as 'Threatened' under ESA in 1992. All seven Gulf Coast natal river populations were fished down to very low levels during unrestricted harvesting from 1895 through 1910. The Suwannee River population is the largest extant population, numbering about 1,500 to 2,500 in the early 1990s, but since recovered to about 7,500 juveniles and adults greater than 1 m TL. The Suwannee River Gulf sturgeon represents a notable success story among depleted sturgeon populations—and may offer productive avenues of research in tracking the trajectory of California

green and white sturgeon populations. Since 1988, 27 years of Suwannee River population research has very substantially increased overall knowledge of the life history, population biology, and conservation biology of the Gulf sturgeon. Research by USGS and colleagues has detailed population size and structure—tracking population increase, effective reproductive population increase, mortality decrease, and increase in successful year–class composition. Research in the river, and also in each of the other six spawning rivers, has additionally addressed spawning site selection, early life history, food habits, foraging patterns, holding area characteristics, migrations, estuarine and coastal foraging habit use, acoustic communication, and why sturgeons jump. Current research focuses upon micro-habitat selection and use patterns via simultaneous application of acoustic telemetry, acoustic Doppler current mapping, side-scan sonar habitat mapping and fish geopositioning, and real-time continuous sampling of water attributes, including dissolved oxygen. The fundamental lesson of Gulf sturgeon recovery in the Suwannee River is that a depressed population will recover naturally (no hatchery supplementation needed) and rapidly, if adult females are protected from harvest, if the river is unimpounded to allow access to spawning grounds, and if other anthropogenic effects (e.g., dredging, sedimentation, gravel mining, channelization) have not eliminated key habitats including deep seasonal holding areas that provide essential resting habitat."

Below are three recommendations aimed at protecting green and white sturgeon based Dr. Sulak's past experience with Gulf sturgeon.

Comments and Recommendations

1. Maintain a healthy population of white sturgeon by eliminating mortality of adult females. Sportfishing harvest of adults should be halted, or fishing at least confined to catch-and-release outside of the spawning season. Having survived the 15- to 20-year period until first spawning, and subsequently only spawning every 5 years, it is essential not to lose the enormous re-population potential of each spawning female. Loss of a single spawning female that will produce several hundred thousand eggs each time she spawns represents the greatest possible anthropogenic effect upon conservation and restoration of the species. No sturgeon harvest should be permitted in tributaries such as the Feather and Yuba, where only a handful of adults appear to be present.
2. Protect and restore critical key habitat in order to conserve and reestablish sturgeon populations. Gravel beds are critical for successful spawning and egg survival. Deep holes are critical as energetic refuges for sturgeon holding in the river.
3. Take a holistic approach to life history and habitat research and monitoring. This should include a robust program of conventional mark–recapture to determine population size, population year–class composition, and mortality rate—in addition to advanced telemetry and habitat mapping methods. This approach should also include continuous monitoring of dissolved oxygen, the most critical environmental factor for oxyphilic sturgeons: they are broadly tolerant of wide ranges in temperature, salinity, and flow that are all much less critical factors for their population success.

CONCLUSIONS

We hope that this description of the most recent work on green and white sturgeon, some of it to be published in greater detail elsewhere, will provide readers with an appreciation of the state–of–the-art in sturgeon studies in the Sacramento–San Joaquin watershed. Under each category, the researchers who conducted these studies have recommended what further research needs to be done to provide managers with what they need to manage the populations of white and green sturgeon in the future.

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Conservation and Management, which served as a basis for this article. Joyce Boulanger of CABA prepared the brochure that identifies the participants and their affiliations, providing their email addresses, the titles of their talks, and an overview of the purpose of the symposium. The speakers would like to thank their agencies for providing the financial support that enabled them to conduct their research and present the results of their studies at this forum. The Yurok Indian Tribe furnished the adult green sturgeon, which provided the progeny used in physiological studies. Finally, the Delta Science Program provided the funding for the senior author and speakers to put together this review of sturgeon biology.

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