NOAA Technical Memorandum NMFS

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Improved Fisheries Management Through Life Stage Monitoring: the Case for the Southern Distinct Population Segment of North American Green Sturgeon and the Sacramento-San Joaquin River White Sturgeon

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Note: The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

Key Words

Green sturgeon, white sturgeon, San Francisco Estuary, monitoring, life history, conceptual models, recovery

Preface

This conceptual model was compiled to support the development of monitoring studies and plans associated with management and recovery of sturgeon species in the San Francisco Estuary (SFE) watershed. Multiple life stages of the southern Distinct Population Segment (sDPS) of North American green sturgeon (*Acipenser medirostris*) and the Sacramento-San Joaquin River white sturgeon (*A. transmontanus*) are endemic to the SFE watershed. Potential increases in consecutive recruitment failures in SFE sturgeon raise concern about the resilience of sDPS green sturgeon and the sustainability of a harvestable white sturgeon stock. Fundamental sturgeon demographic measures are lacking in the existing monitoring and analytical framework. As a result, managers are unable to determine specific causes of poor recruitment, accurately track green sturgeon listing status under the Federal Endangered Species Act, or measure sturgeon population responses to management of water resources and/or harvest regulations. Here, we developed conceptual models for SFE sturgeon and identified 15 monitoring recommendations that would potentially test 41 hypotheses in 7 core areas of sturgeon management. Implementation of these monitoring recommendations would refine our understanding of the key factors influencing SFE sturgeon populations and improve outcomes for California's sturgeon through informed management.

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Executive Summary

Data from life stage monitoring programs form the basis for assessing population status, trends, and recruitment in long-lived fishes. Nearly all elements of sturgeon monitoring in the San Francisco Estuary (SFE) watershed (Figure 1) and subsequent management have required some level of long-term detection or capture of fish at critical life stages (Heublein et al. 2017). However, most information on early life stages of SFE sturgeon involves small datasets collected incidentally by monitoring programs focused on other fishes (Heublein et al. 2017). Studies specifically targeting green sturgeon in the SFE watershed have been implemented recently but in many cases lack long-term support (Heublein et al. 2017).

As a consequence of this monitoring inadequacy, validation of indicators of strong green sturgeon production is limited by a reliance on signals of cohort success observed in adult surveys only. In other words, testing of management actions intended to increase sturgeon spawning success (e.g., adult passage at dams) or understanding population-level effects of presumably poor spawning conditions (e.g., the recent drought) requires a 15-year-plus time interval for cohorts to reach the adult stage. For white sturgeon, measures of recruitment generated from data collected in juvenile and adult surveys have provided managers with a coarse flow-recruitment mechanism for year-class strength (CDFG 1992; Fish 2010). However, the specific life stage where flows influence white sturgeon recruitment remains uncertain. In turn, managers are unable to accurately predict the response of either sturgeon species to actions such as pulse flows, spawning habitat restoration, or harvest regulations.

Here we used monitoring inventories and life history descriptions of southern Distinct Population Segment (sDPS) green sturgeon and SFE (Sacramento-San Joaquin River) white sturgeon from Heublein et al. (2017) to develop conceptual models by species life stage. The conceptual models include 41 combined hypotheses involving factors affecting sturgeon life stage transitions (Table 1; Figures 2 through 8). We then developed 17 monitoring recommendations to potentially test these hypotheses and prioritized 15 recommendations addressing core areas of sturgeon demography and management (Table 1). Monitoring improvements involve all life stages of sturgeon (sturgeon life stages are defined in Heublein et al. [2017]) and are summarized below and in Table 1.

In SFE watershed monitoring, the annual collection of young sturgeon is typically low, and any potential new surveys consistently capturing early life stages will likely require a multi-year development period. Based on this, management of these species requires the continuation or expansion of surveys currently encountering early life stages of sturgeon (Heublein et al. 2017) and additional development of baseline surveys throughout the range of both species. Long-term spawning surveys should be implemented in primary sturgeon spawning areas (Sacramento and San Joaquin rivers), while spawning surveys should be implemented as needed in areas where spawning appears to be episodic (Feather, Bear, and Yuba rivers). Habitat in egg collection locations should be mapped or surveyed to develop suitable spawning habitat criteria and quantify available habitat. Long-term larval surveys should also be implemented in

spawning or larval dispersal areas where surveys are currently lacking (e.g., the middle Sacramento River).

The white sturgeon juvenile year-class index (YCI) provides managers with an early forecast of future adult abundance as well as a linkage between cohort success and spawning and rearing conditions (CDFG 1992; Fish 2010). In turn, recruitment information is critical for multiple aspects of sturgeon management ranging from harvest limits to spawning and rearing habitat suitability guidelines. Hence, a green sturgeon YCI should be developed along with improvements to white sturgeon YCI precision, and this could most likely be accomplished through an increase in sampling effort in existing SFE trawl surveys. Because juvenile green sturgeon are less abundant in the SFE than juvenile white sturgeon, long-term sampling of green sturgeon juveniles (i.e., benthic trawl) should also occur in upper and middle Sacramento River habitats where they appear to be more common.

Catching adult sturgeon of both species is fundamental for mark-recapture and abundance modeling, age and habitat use analyses (tissue analyses), and estimating survival, movement, and spawn timing (telemetry). Trammel net sampling in the California Department of Fish and Wildlife (CDFW) Sturgeon Population Study (hereafter referred to as the Sturgeon Study) is the only monitoring effort in the SFE that consistently catches adult sturgeon of both species. Effort in the Sturgeon Study should be strategically expanded to increase the number of sturgeon (both species) encountered; this could be accomplished with a relatively small increase in effort and would significantly improve our knowledge of fundamental demographic and vital rates in these species. Modeling of fisheries-dependent data (e.g., recovery of disk tags) for both species might improve estimates of angler contact rate and abundance. Methods to increase angler reporting of tagged fish (e.g., external tagging rates, reward values) should be concurrently pursued to improve efficacy of fishery-dependent mark-recapture studies. Abundance modeling of green sturgeon is inherently more complex due to their multi-state movements compared to the mostly local estuarine white sturgeon. A green sturgeon abundance model should be pursued through a multi-state synthesis of collection data (e.g., Sturgeon Study, sampling in Oregon and Washington estuaries, bycatch of the commercial California halibut trawl fishery). All sampling efforts involving large juvenile or adult sturgeon should include tissue collection and implantation of acoustic tags in some individuals given the challenges in encountering these species in routine monitoring efforts.

Detection of green sturgeon implanted with acoustic tags have revolutionized our ability to generate abundance estimates and provide vital information on migration distances and spawn timing and locations (Moser et al. 2016, Klimley et al. 2015). The current run-size estimate model for green sturgeon in the Sacramento River requires acoustic detection of tagged green sturgeon by the Vemco VR2 array in spawning habitat (Mora 2016). A similar run-size survey for white sturgeon would also require acoustic detection of tagged adult white sturgeon in spawning habitat. Acoustic receivers in the SFE and tributaries can detect tags appropriate for both adult (Vemco VR2 array) and small juvenile sturgeon (Juvenile Salmon Acoustic Telemetry System [JSATS] array). Nearshore and non-natal estuarine arrays (Vemco VR2) are primarily

associated with studies of larger fish. Acoustic telemetry (JSATS) should be incorporated into any new juvenile surveys to fill a large data gap in juvenile movement and behavior in both species. Additionally, long-term support should be provided for acoustic receiver arrays (JSATS and Vemco VR2) in spawning rivers and the SFE and for development and maintenance of a publicly accessible tag-detection database.

Estimates of the number of breeding adult sturgeon or annual run-size are a fundamental requirement in evaluating the status of both sturgeon populations and should be included in long-term monitoring efforts. Several technologies and methods can be used to estimate run-size including dual-frequency identification sonar [DIDSON] or side-scan sonar surveys, telemetry-based mark-recapture surveys, and/or genetics. Emerging technologies should be developed and supported for use in generating robust run-size estimates and to ensure monitoring is responsive to evolving technologies. Directed sampling of sturgeon in migration or spawning habitat should also be evaluated as a means to study contaminants and reproduction and verify accuracy of sonar-based abundance estimates.

Existing life stage surveys and subsequent tissue sampling and analyses have greatly improved our understanding of both sturgeon populations (Heublein et al. 2017). Contaminant levels and reproductive condition have been intermittently analyzed in SFE adult sturgeon tissues (Gundersen et al. 2017; Heublein et al. 2017). However, evaluation of contaminants over a longer time-series is necessary to assess the potential response of contaminant levels to varying flow regimes. Analysis of developmental stage of eggs and larvae has generated more precise spawn timing estimates (Poytress et al. 2015; Seesholtz et al. 2015). Analysis of sturgeon age-at-length with pectoral fin ray samples provides a secondary method for estimating recruitment by back-calculating or hindcasting recruitment episodes with sturgeon length records (Shirley 1987). Sturgeon life history may also be recreated through microchemistry analysis of pectoral fin rays (Sellheim et al. 2017). Identification of successful life history strategies may be critical to informing habitat restoration decisions and facilitating more frequent recruitment. Therefore, techniques should be refined to accurately determine age, origin, habitat use, ocean residency, and migration in newly collected and archived pectoral fin rays. Further, these primarily non-lethal efforts should be continued or expanded to include samples from all life stage surveys described above.

Demographic criteria for effective population size are a cornerstone for evaluating Federal Endangered Species Act (ESA) listing status of anadromous fish of the SFE watershed (NMFS 2014). Any new genetic population models and abundance estimates should be used to determine effective population size and verify existing run-size estimates or fishery-dependent abundance measures in both species. Population genetics (i.e., genotyping and parentage) should be refined (along with non-lethal genetic techniques for early life stages) and applied to archived tissues and any new tissues. New life history and genetic information should also be used to understand the contribution of alternative spawning areas or life history strategies to the population and elucidate potential subpopulation structure. Much like the tag detection database

described above, research should be streamlined by supporting a publicly accessible sturgeon genome and microchemistry database.

Some level of modeling and synthesis is necessary to make current and historical data from sturgeon monitoring in the SFE watershed useful to scientists and managers. As described above, multiple opportunities for crossover are available for green and white sturgeon monitoring, modeling, and synthesis. Although an immediate increase in SFE sturgeon monitoring enterprise is critical to manage the species, identification of "surrogacy" in monitoring (e.g., species indices or survey metrics that co-vary) may streamline future monitoring efforts. Thus, a thorough evaluation of surrogacy should be conducted for all existing indexes or life stage abundance measures and included in all future modeling or synthesis efforts.

Table 1. Sturgeon life stage monitoring recommendations with associated core management areas and hypotheses.
Long-term monitoring recommendations are enumerated, directed or short-term monitoring recommendations lack enumeration. Draft sDPS green sturgeon demographic recovery criteria monitoring are identified: 1 = documentation of successful spawning through larval collection (multiple rivers); 2 = trends in juvenile abundance; 3 = subadult and adult census; and 4 = annual run-size and modeled adult census.

Life Stage Transition	Monitoring	Management Area	Hypotheses
Fertilization to hatch	1. Baseline egg surveys throughout spawning range	Tracking recruitment by life stage	H_1 egg and larval abundance and distribution are linked
	2. Mapping of egg collection/ putative spawning habitat	Management targets for habitat attributes- spawning and incubation (*e.g.*, temperature, flow, substrate, depth)	H_2 egg distribution and relative abundance are influenced by temperature in spawning rivers H_3 egg distribution and relative abundance are influenced by streamflow in spawning rivers H_4 incubation habitat availability and quality influences relative embryo abundance and distribution
	3. Regular reproductive condition and contaminants monitoring in spawning adults	Fecundity and survival of eggs and larvae- effects of pre-spawn female reproductive condition	H_5, H_{13} contaminant levels in ovaries influence relative embryo and larval abundance H_{40} elevated water temperature in spawning habitat influences atresia H_{41} contaminant levels in ovaries influences fecundity
	Fish community and predation surveys in incubation and larval/ juvenile rearing habitat	Evaluation of predation	H_6, H_{11}, H_{23} embryo, larval, and juvenile survival is affected by predator community composition in incubation and rearing habitats
Hatch through metamorphosis	4. Baseline larval surveys throughout spawning range[1]	Tracking recruitment by life stage	H_7 larval and juvenile abundance and distribution are linked
	5. Mapping of larval rearing habitat	Management targets for habitat attributes- larval rearing	H_8 relative larval abundance is related to flow in spawning rivers H_9 relative larval abundance is related to temperature in spawning rivers H_{10} larval distribution and relative abundance are related to habitat availability and quality
	6. Benthic invertebrate surveys in larval rearing habitat	Limitations posed by food supply and quality	H_{14} relative larval abundance is influenced by food supply and/or food contaminant levels
	Survey of entrainment at diversions in larval and juvenile rearing habitats	Evaluation of entrainment	H_{12}, H_{22} entrainment in diversions influences larval and juvenile survival

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Complete metamorphosis to ocean migration or 75 centimeters fork length	7. Development and refinement of age-0 and age-1 juvenile surveys and recruitment measures[2] 8. Mapping of juvenile rearing habitat	Tracking recruitment by life stage	H_{15} juvenile and subadult/adult abundance and distribution are linked
		Management targets for habitat attributes- juvenile rearing	H_{16} flows in spawning rivers are positively correlated to age-0 juvenile abundance H_{18} juvenile abundance is influenced by rearing habitat quality H_{21} water quality in juvenile dispersal and rearing habitat influences abundance
	9. Benthic invertebrate surveys in juvenile habitat	Limitations posed by food supply and quality	H_{19} juvenile abundance is influenced by food supply and quality
	10. Acoustic tagging in juvenile surveys and maintenance of riverine and estuarine acoustic receiver arrays for juveniles	Migration and behavior	H_{17} summer and fall flow and temperature in spawning rivers affects freshwater residency and temporal and spatial distribution of age-0 or age-1 juveniles H_{20} juvenile residence duration in the SFE is influenced by summer water temperatures and salinity
Ocean migration and maturity	11. Abundance estimates[3] with modeling and synthesis of multi-year datasets from local and non-natal estuary surveys and fisheries	Tracking recruitment by life stage	H_{24} adult abundance influences run-size and distribution
	12. Additional effort or sampling locations in adult studies for population models and telemetry	Evaluation of fishery management actions	H_{25} harvest is a primary factor influencing subadult and adult abundance
	13. Continued acoustic tag studies and maintenance of riverine, estuarine, and nearshore arrays for adult sturgeon	Migration and behavior	H_{26} water temperature influences timing of estuarine arrival and departure (green sturgeon) H_{27} salinity influences subadult and adult distribution H_{28} habitat quality in the SFE influences spatial distribution and abundance of adults
	14. Study of habitat and forage in estuarine and marine aggregation areas	Limitations posed by food supply and quality	H_{29} marine aggregation sites are related to foraging opportunities and food base (green sturgeon) H_{30} adult abundance is influenced by food supply and/or food contaminant levels
	Pinniped surveys in adult sturgeon feeding and aggregation areas	Evaluation of predation	H_{31} adult sturgeon survival is affected by pinniped abundance and density

Spawning	15. Annual run-size and distribution surveys[4]	Tracking recruitment by life stage	H_{32} egg abundance and distribution are influenced by run-size and distribution
	Mapping of spawning habitat (*Fertilization to hatch #2*)	Management targets for habitat attributes- spawning and migration habitat and restoration (e.g., temperature, flow, substrate, velocity, depth)	H_{34} run-size and spawning distribution is influenced by flows in spawning rivers H_{35} run-size, spawning distribution, and spawning are influenced by water temperature in spawning rivers H_{36} spawning distribution is influenced by spawning habitat availability and quality
	Spawning migration and distribution surveys (*Ocean migration and maturity #13*)	Evaluation of fishery management actions	H_{37} harvest and fishing regulations (*e.g.,* catch and release in spawning habitat) influence run-size and spawning success
		Migration and behavior	H_{33} run-size and distribution are influenced by migration barriers H_{38} post-spawn migration and duration are affected by water temperature in spawning rivers H_{39} post-spawn migration and duration are affected by flow in spawning rivers

Introduction

Green and white sturgeon in the SFE watershed represent the most southerly spawning populations of each species, with spawning occurring primarily in the Sacramento River (Kohlhorst et al. 1991; Poytress et al. 2015). Encounters with juvenile sturgeon in the existing monitoring enterprise are extremely infrequent. This prevents any precise assessment of the inter-annual effects of water management (e.g., reservoir releases, water export) on sturgeon production. Due in part to the rarity of juvenile sturgeon (and presumed poor production) and the loss of habitat in the SFE watershed, sDPS green sturgeon were listed as threatened under the Federal ESA in 2006 (NMFS 2006). Although listing prompted harvest prohibitions for green sturgeon, estimated harvest of white sturgeon in California has remained high (Gingras and DuBois 2013; Gingras and DuBois 2014). There are no long-term monitoring programs that measure demographic recovery criteria[1] for sDPS green sturgeon nor precise harvest rates of white sturgeon. Without improvements to monitoring, effects of fisheries and water management on the persistence of SFE sturgeon will remain unknown. Furthermore, accurate abundance, harvest, and population dynamic rate estimates are necessary to maintain some level of harvest and still reliably protect a population (Fabrizio and Richards 1996).

Fish population dynamics reflect changes in dynamic rate functions (growth, recruitment, and mortality; Ricker 1975). Informed fisheries management requires adequate estimates of these rates to identify appropriate management actions (Quist et al. 2012). Growth information is useful in assessing the health of an individual, the population, and the environment (Birkeland and Dayton 2005; Winemiller 2005; Rowell et al. 2008; Quist et al. 2012). Recruitment variability is the primary driver of population abundance and, if identified early, provides advance notice of future changes in the age structure of the population. Understanding both natural and fishing mortality is important for managing target and non-target commercial and recreational fisheries and actions that affect habitat (e.g., degradation, restoration). Together, these rate functions are used to identify problems in a population (e.g., missing cohorts indicating sporadic recruitment), potential management actions (e.g., reducing mortality of mature adults, managing water), and responses to management actions (e.g., harvest prohibitions; Beamish et al. 2006; Quist et al. 2012).

Recent concern over the significant uncertainty in population abundance estimates, trends, and productivity in both species has resulted in a heightened awareness and need for more focused monitoring of sturgeon and their habitats in the SFE. Accurately coupling periods of poor sturgeon recruitment or life stage survival with specific conditions is necessary to manage and weigh the many competing needs for California's water. Conversely, promptly identifying year-class success (i.e., abundant cohorts) is a key step in adaptive management of sturgeon populations. Year-class success can be linked to environmental conditions, which might then be

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[1] Demographic recovery criteria are used to determine if significant threats to the recovery of a population are alleviated. Draft demographic recovery criteria for sDPS green sturgeon include minimum criteria for effective population size, adult census and annual run-size, documentation of annual spawning in multiple rivers, and indicators of positive trends in juvenile abundance.

reproduced with management or restoration. Thus, appropriate life stage monitoring is necessary for tracking population status, informed resource and fishery management, and supporting resiliency in these long-lived species.

Purpose and Scope

There is increasing awareness that conceptual models can provide a collective framework for researchers and managers to identify key hypotheses and guide research to evaluate the influence of environmental factors and management actions on imperiled species (Wildhaber et al. 2007; Israel and Klimley 2008; Israel et al. 2009; Durand 2015; IEP MAST 2015; Windell et al. 2017). By building on previous efforts for delta smelt (*Hypomesus transpacificus*; IEP MAST 2015), we developed conceptual models for green and white sturgeon to evaluate current hypotheses regarding the influence of environmental factors on sturgeon populations. The framework consists of a hierarchy illustrating the predicted mechanistic pathways that impact the species throughout their life cycle and was used as the foundation for evaluating the impacts of California's recent drought (2012 to 2017) on delta smelt and Sacramento River winter-run Chinook salmon and development of a delta smelt and salmon resiliency strategies (California Natural Resources Agency 2016, 2017).

To develop conceptual models for green and white sturgeon, we gathered information from archival reports, publicly accessible agency databases, and peer-reviewed literature. We then compiled an inventory and evaluation of green and white sturgeon monitoring and research (and associated published and unpublished information; Heublein et al. 2017). With current monitoring inventories, we developed species-level and comparative life history descriptions in Heublein et al. (2017) and expanded upon the previous Israel and Klimley (2008) and Israel et al. (2009) Delta Regional Ecosystem Restoration Implementation Plan (DRERIP) green and white sturgeon life history conceptual models. Differences between our conceptual models and the DRERIP models include an updated delta smelt model structure (IEP MAST 2015) and the addition of recent advances in sturgeon biology.

The conceptual model framework identifies gaps and opportunities in monitoring and connects trends regarding sturgeon responses with environmental conditions and management actions. We apply these conceptual models to 1) provide recommendations for establishing a sturgeon monitoring program that can account for basic management metrics (i.e., abundance and distribution) at each life stage by pertinent geographic region, 2) identify directed studies necessary to begin testing some of the underlying mechanisms hypothesized to link environmental stressors and abundance or identify life stage bottlenecks unique to each region, and 3) link opportunities to generate population-level information with the limited monitoring and analytical resources. Specific life stage monitoring recommendations are described in respective models and mostly involve expansion of existing surveys or implementation of proven techniques. Many hypotheses, sampling techniques, and analytical methods pertain to both sturgeon species. Therefore, green and white sturgeon monitoring and research recommendations are combined throughout this document and, along with a short discussion on emerging sturgeon research and monitoring tools, summarized in the Executive Summary and Table 1.

Organization and Structure

This document is organized by the following sturgeon life stages 1) eggs, 2) larvae, 3) juveniles, 4) subadults and adults, and 5) spawning adults (defined in Heublein et al. 2017). The following standardized geographic regions are also used to promote consistency with other anadromous species models in the SFE and are separated by key monitoring locations or significant changes in geography or ecosystem process (Figure 1):

- **San Francisco Estuary.** The SFE is commonly referred to as the "San Francisco Bay-Delta Estuary" and is a combination of the Sacramento-San Joaquin River Delta[2] (Delta) and the San Francisco Bay[3] (Bay).
- **Middle River.** The Sacramento and San Joaquin rivers (and associated tributaries) upstream of the SFE. The middle Sacramento River also has an upstream boundary at Red Bluff Diversion Dam (RBDD) and includes the Sutter Bypass and upper Yolo Bypass (north of Highway 80).
- **Upper River.** The Sacramento River from RBDD to Keswick Dam.
- **Non-natal Estuaries.** Primarily the Columbia River Estuary, Willapa Bay, Grays Harbor, and Umpqua River Estuary.
- **Ocean.** Marine waters along the North American continental shelf between Baja California and Alaska.

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[2] The Delta is a network of tidal channels and sloughs that extends downstream from the I Street Bridge on the Sacramento River and the confluence of the San Joaquin and Stanislaus rivers to the approximate confluence of the San Joaquin and Sacramento rivers at Chipps Island.

[3]The Bay includes brackish tidal marshes and bays extending from Chipps Island to the Golden Gate Bridge.
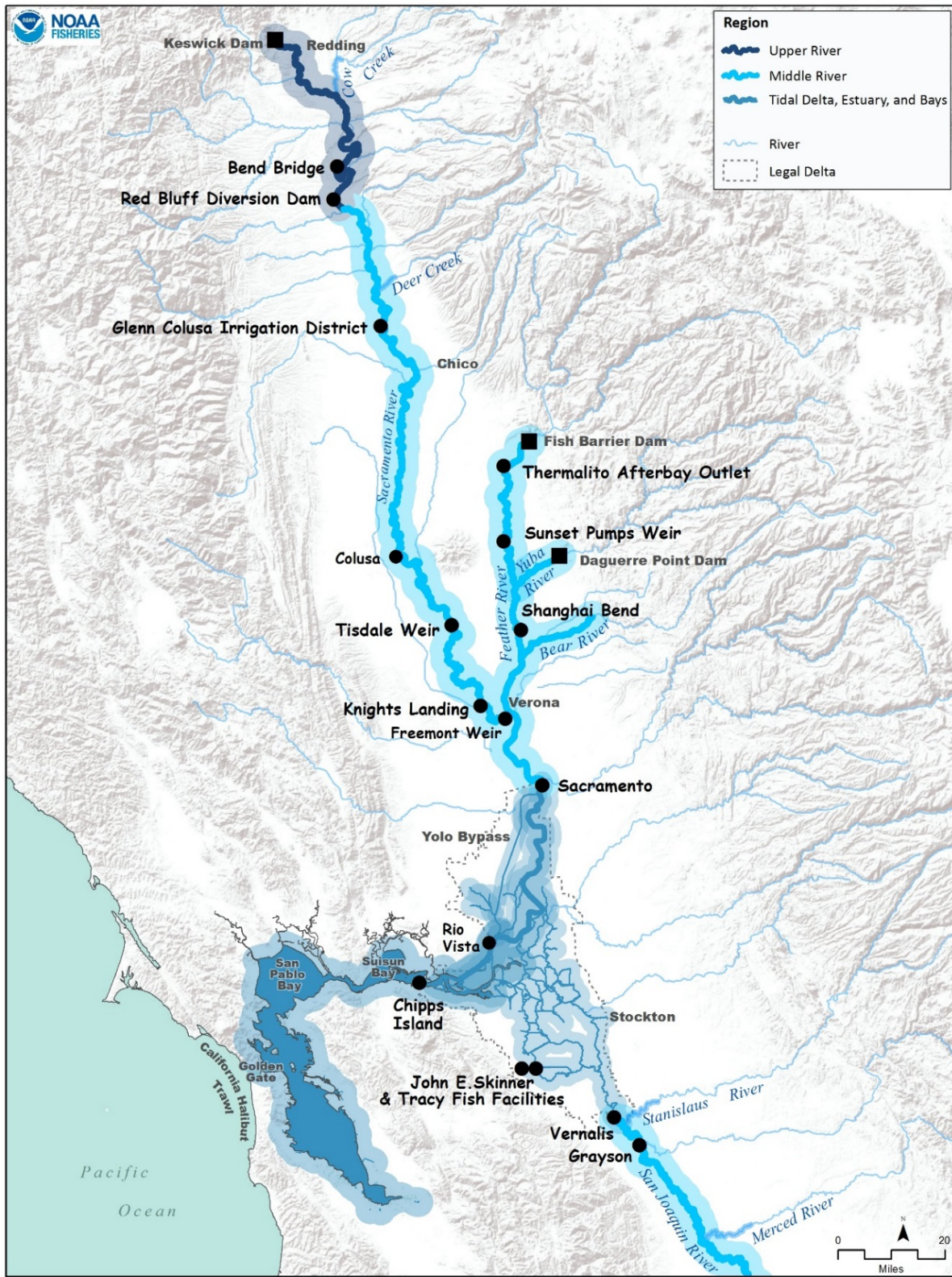
Figure 1. Estuarine and freshwater geographic regions for sturgeon of the SFE watershed.

Processes and Conditions Controlling Sturgeon Life Stage Transitions

Green and white sturgeon in the SFE have similarities in behavior and both partitioned and overlapping habitat (Figures 2 and 3; Heublein et al. 2017). This poses opportunities and challenges in monitoring, analysis, and management. Sturgeon species may not respond similarly to environmental conditions due to differences in distribution or behavior, but many monitoring and analytical techniques apply to both species (Heublein et al. 2017). Thus, green and white sturgeon are combined in the following section. Thorough monitoring inventories and life history descriptions are provided in Heublein et al. (2017) for added detail on monitoring techniques and conditions with species-specific relevance. The figures included in the following section (Figures 2 through 8) are graphical representations of factors affecting sturgeon life stage transitions using five hierarchical tiers, as follows:

- **Tier 1: Landscape Attributes.** Local to system-wide features that change slowly over long periods of time.
- **Tier 2: Environmental Drivers.** Features that occur over broad ranges of temporal and spatial scales and occur within the geographic range of the species; Environmental Drivers are influenced by Landscape Attributes and directly influence Habitat Attributes.
- **Tier 3: Habitat Attributes.** Features that have broad ranges of spatial and temporal scales but directly affect species response (all hypotheses are included in Tier 3).
- **Tier 4: Sturgeon Responses.** Factors associated with the transition to a subsequent life stage (submodel input [previous submodel output], survival, timing and migration, and condition and growth). Sturgeon responses are directly influenced by Habitat Attributes.
- **Tier 5: Life Stage Transition Season.** The period in which the transition between life stages takes place.

Sturgeon conceptual models are organized in life stage submodels. All submodel figures follow a consistent format as illustrated in Figure 4. Submodel figures are not intended to be exhaustive. Rather, they represent important pathways, environmental factors, and hypothesized sturgeon responses while maintaining readability and likelihood of application for a broad range of audiences. Arrows within each submodel figure represent linkages between and within tiers but do not indicate directional interaction (positive or negative) or relative importance of a linkage. In some cases, however, the directional impact and relative importance is identified as a hypothesis. To minimize redundancy, some linkages within tiers (intra-tier) are omitted when also represented as inter-tier linkages: The "Flow" and "Water Temperature" linkage in Tier 3 is omitted because a similar inter-tier linkage is displayed ("Water Operations & Hydrology" [Tier 2] and Water Temperature are linked). Combined intra-tier linkages (e.g., Water Temperature, Flow, and "Incubation Habitat" all influence "Predation Risk") are only included in Tier 3. However, some intra-tier linkages are omitted in Tier 3 (e.g., Water Temperature is not linked to Incubation Habitat) when the indirect connection between two Habitat Attributes is not specifically identified in a hypothesis.

Submodels also include life history and monitoring information (described in detail in Heublein et al. 2017) synthesized into hypothesized life stage responses, management areas or goals, and recommended monitoring improvements (summarized in Table 1). Hypothesis nomenclature (e.g., "H_1") is consistent between Table 1, submodel narratives, and submodel figures. Management actions that may feasibly influence life stage or species responses (e.g., reservoir outflow and temperature, harvest regulations) form the basis for the hypotheses evaluated through the conceptual model framework and subsequent monitoring and research recommendations by life stages (Table 1). Recommended studies that address draft demographic recovery criteria for green sturgeon are also identified in Table 1. Finally, Table 1 includes primarily recommended improvements to life stage surveys. Studies that require data or tissues from these surveys (e.g., tissue analyses, population modeling) are described in the submodels and Executive Summary, but are mostly omitted from Table 1.

Figure 2. Green sturgeon life cycle model.
Sturgeon model figures described in detail in Processes and Conditions Controlling Sturgeon Life Stage Transitions. Green sturgeon illustration by Joseph R. Tomelleri.
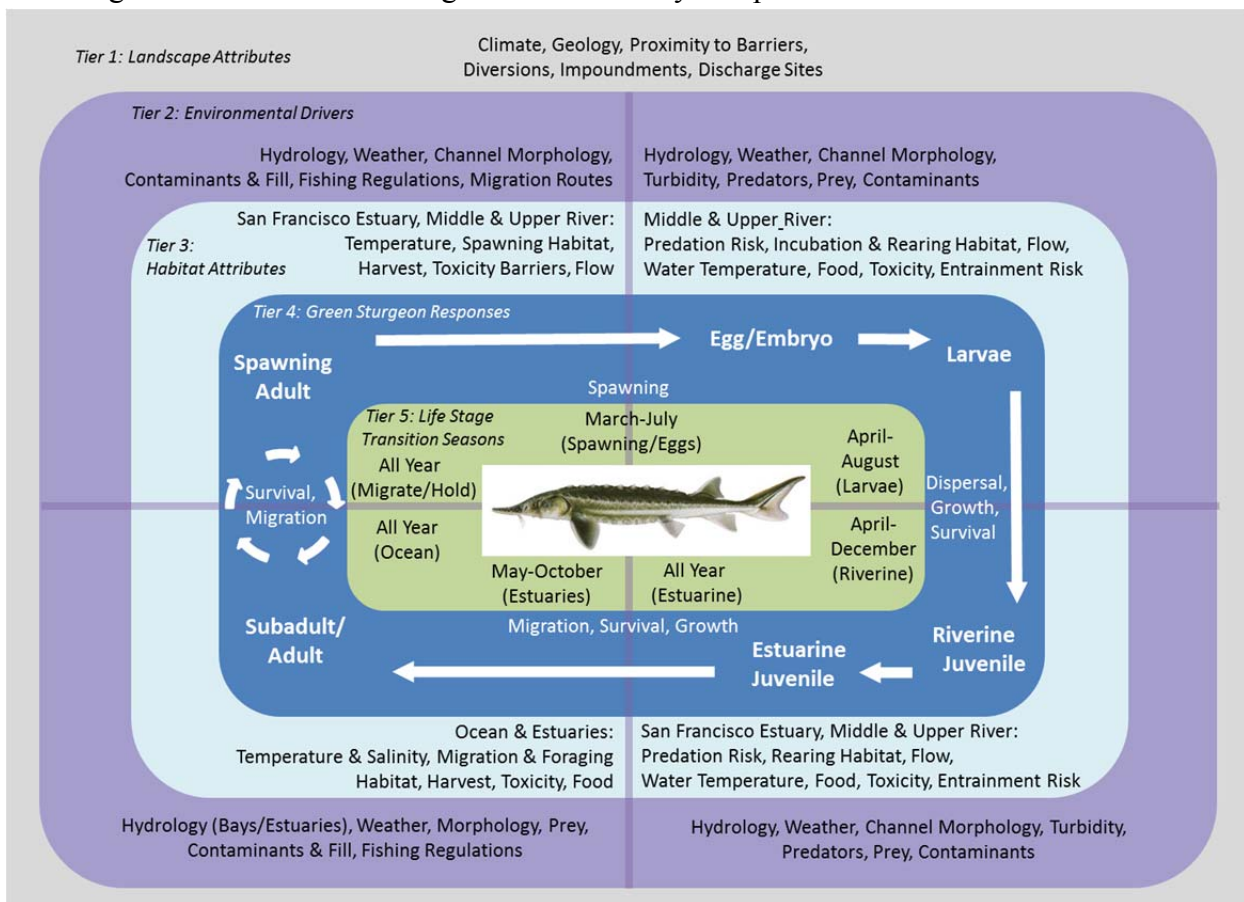
Figure 3. White sturgeon life cycle model.
Sturgeon model figures described in detail below in Processes and Conditions Controlling
Sturgeon Life Stage Transitions. White sturgeon illustration by Joseph R. Tomelleri.
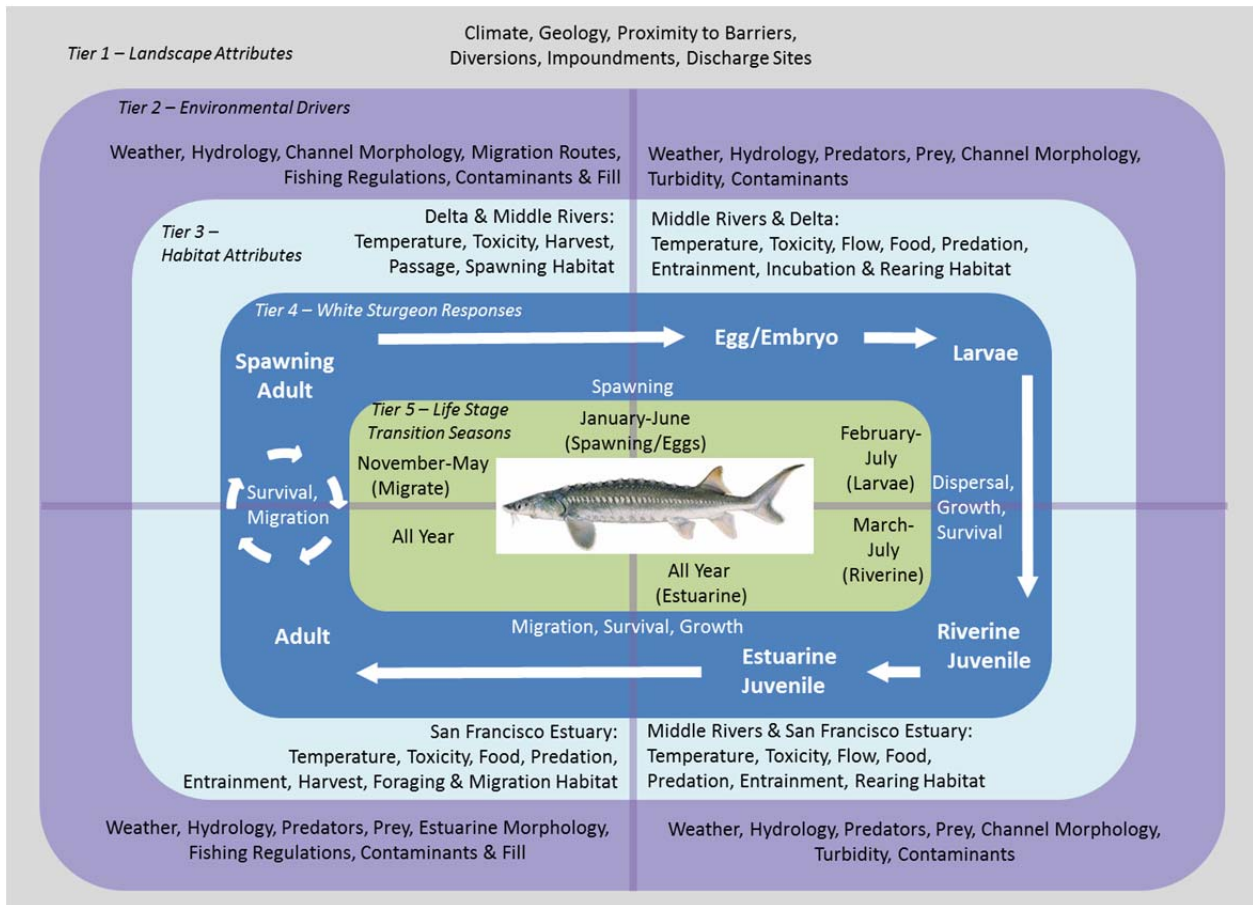
Fertilization to Hatch

Figure 4. Egg submodel.
Green sturgeon egg distribution- Cow Creek to GCID (Sacramento River), Fish Barrier Dam to Shanghai Bend (Feather River). White sturgeon egg distribution- GCID to Verona (Sacramento River), Grayson to Vernalis (San Joaquin River).
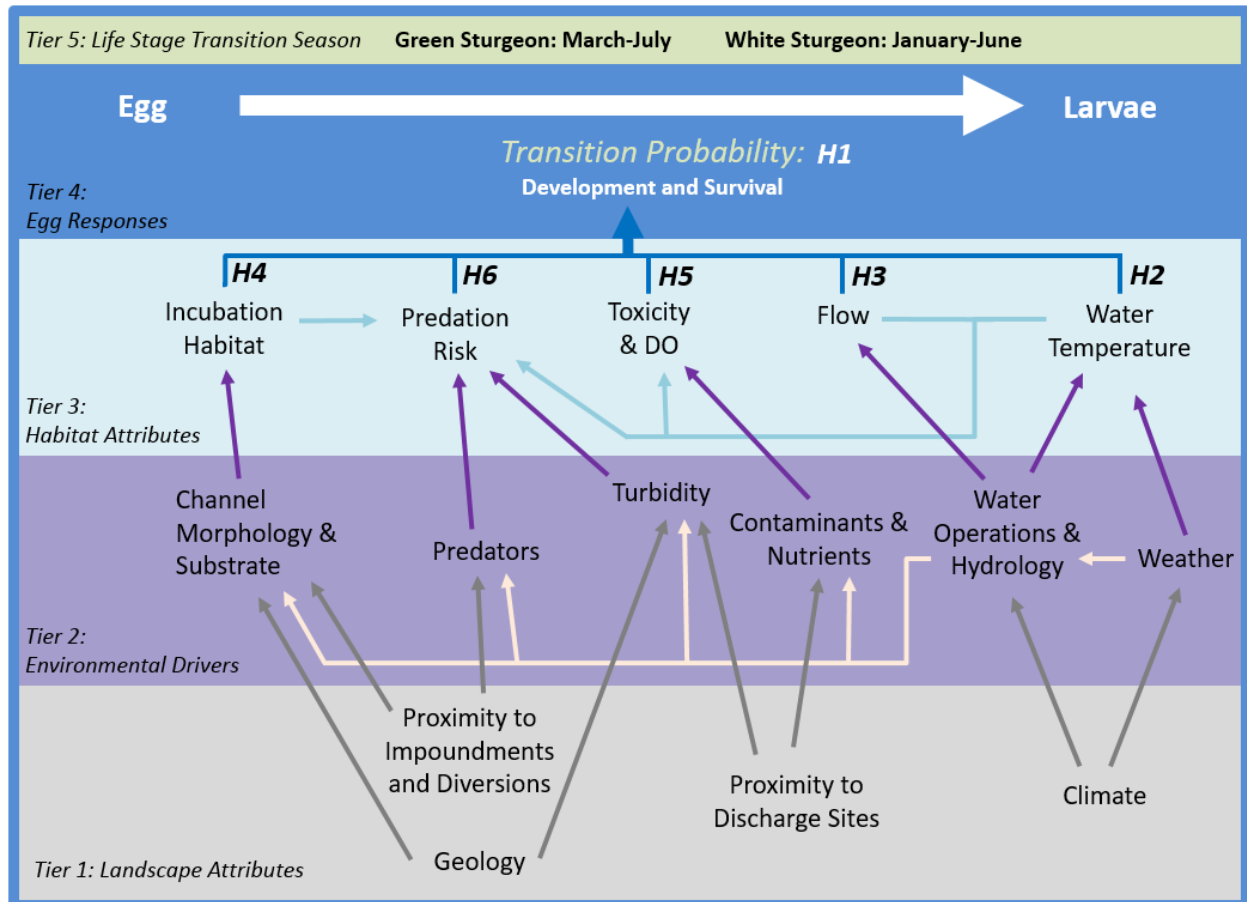
Green sturgeon eggs. There are currently no early indices of green sturgeon cohort abundance or year-class strength. General recruitment patterns in green sturgeon have been identified (Heublein et al. 2017), but the specific early life stage(s) that control episodic recruitment remain uncertain. With some basic monitoring of egg presence and improved larval sampling, managers can infer relationships between egg collection and relative larval abundance. If egg and larval abundance are closely related (Table 1: H_1), then mechanisms for episodic recruitment may occur before fertilization or after metamorphosis. Conversely, if relative egg abundance is unrelated to larval abundance, then mechanisms for recruitment failure or near failure may occur at the egg stage. In addition to informing relative abundance and distribution, parentage analysis of collected eggs and larvae can provide critical information about mating systems and effective population size (Israel and May 2010)—although current sampling efforts and techniques are not likely sufficient for those quantitative analyses. Development of non-

lethal genetic sampling of larvae or small juveniles (e.g., swab) may be one opportunity to increase this sample size.

Managers are interested in understanding the effects of temperature and flow on survival and distribution of spawning adults and early life stages of green sturgeon (Table 1; Heublein et al. 2017). Studying egg distribution and fertilization timing can improve our understanding of inter-annual differences in successful spawning and distribution. Temperature and flow are directly monitored or modeled throughout the Sacramento and Feather rivers (e.g., long-term monitoring stations administered by the California Department of Water Resources [DWR] California Data Exchange Center; specific monitoring or modeling efforts by NMFS and DWR). With annual egg surveys, available temperature and flow data could be compared to egg distribution and relative abundance.

A description of water temperature management in spawning habitat is provided in Heublein et al. (2017). The effects of elevated temperatures in the Feather River and reduced temperatures in the upper Sacramento River on spawning behavior and egg distribution remain unclear. Although it is plausible that inter-annual egg distribution in the Sacramento River is influenced by water temperature management (Table 1: **H$_2$**), attempts to relate spawning and egg distribution in the upper river to temperature are complicated by changes in spawning habitat accessibility. The RBDD gates were permanently opened in 2012 and green sturgeon have had year-round access to the upper river for a relatively short period of time. Our understanding of spawning and incubation in elevated temperatures is also limited by extremely infrequent egg collection on the Feather River, which only occurred in 2011 and 2017 (Seesholtz et al. 2015; M. Manuel, PSMFC, 2017, personal communication, see "Notes"). This suggests that an underlying factor (e.g., attraction flows, adult passage, spawner abundance,) may be influencing spawning on the Feather River.

The effect of individual habitat attributes, such as temperature on incubation, is further complicated by the overarching influence of flow (Figure 4) and the potential positive relationship between high winter and spring flows in spawning rivers and egg distribution and larval abundance (Table 1: **H$_3$**). The highest larval collection on record in the RBDD screw traps and the only larval collection in the Feather River occurred in 2017 when late winter and spring flows were high in larval rearing habitat (W. Poytress, USFWS, 2017a, unpublished data, see "Notes"; M. Manuel, PSMFC, 2017, personal communication, see "Notes"). Sturgeon egg survival has been linked to flow-driven habitat attributes (Figure 4) such as substrate type (McAdam 2011), turbidity (Gadomski and Parsley 2005), and fish community assemblage (Miller and Beckman 1996). Thus, flow may also have an indirect effect on relative egg abundance or distribution through incubation habitat availability and quality (Table 1: **H$_4$**). Monitoring environmental parameters and fish communities where eggs are collected may also improve our understanding of the influence of predation on egg survival (Table 1: **H$_6$**).

White sturgeon eggs. Although juvenile recruitment is currently monitored in white sturgeon, a specific life stage or mechanism for recruitment remains uncertain. In contrast to other sturgeon life stages, egg survival depends on a very specific suite of habitat attributes. Eggs

are relatively intolerant of elevated water temperatures, require particular substrate and water velocity conditions for survival, and are highly vulnerable to predation and contaminants (Hildebrand et al. 1999; McAdam et al. 2005; Paragamian 2012; Parsley and Kofoot 2013). Thus, episodic recruitment may be driven mostly by the rare occurrence of conditions necessary for eggs to transition to larvae.

Monitoring of white sturgeon early life stages in winter and spring may improve our understanding of how annual production in the SFE is affected by egg abundance and survival. Habitat attributes (e.g., water temperature and flow) are currently monitored in relatively few locations throughout the Sacramento and San Joaquin river basins, providing only a coarse map of conditions in egg incubation habitat. Egg monitoring is necessary to assess relationships between the distribution and abundance of drifting eggs relative to attributes of spawning and incubation sites. Because egg mats sample inefficiently, a significant spawning event may be necessary for the collection of a single egg. Similarly, it seems that larvae have only been collected during years that produced strong cohorts. As a result, both egg and larval collection may only occur during high recruitment episodes (Table 1: **H_1**).

In white sturgeon spawning and egg incubation habitat on the Sacramento River, spring water temperatures typically remain within suitable ranges. However, spring water temperatures regularly reach or exceed suitable levels for egg incubation in the San Joaquin River (Heublein et al. 2017), which may become an important factor influencing early life stage abundance if temperatures reach similar levels in incubation and rearing on the Sacramento River (Table 1: **H_2**). Water temperature may also affect embryos through its effect on spawner condition. Monitoring of eggs and other early life stages is required to assess embryo and larval development and condition. These analyses—in combination with annual measures of spawner condition and contaminants in adult tissues—are necessary to understand any link between ovary contaminant levels and embryo abundance (Table 1: **H_5**).

Spring and winter outflow have been identified as major factors influencing white sturgeon year-class strength in the SFE, and outflow influences all those habitat attributes (Shirley 1987; CDFG 1992; Fish 2010). As described above, hydrology of spawning rivers may influence sturgeon egg abundance and distribution (Table 1: **H_3**) through a number of related abiotic (e.g., water temperature, flow, substrate, turbidity) and biotic (e.g., predator community and metabolic rate) incubation-habitat attributes. High flows may also affect predation, spawning habitat availability and quality, and incubation habitat availability and quality for eggs of both species. High flows inundate channel margins and off-channel spawning habitats. Egg survival in those habitats may be higher than survival in channels (e.g., due to lower predator abundance and/or higher quality incubation substrate), such that egg abundance is related to accessibility of higher-quality habitats (Table 1: **H_4**). High flow, reduced temperature, and increased turbidity may indirectly reduce egg predation (Table 1: **H_6**). Monitoring environmental parameters and evaluating predation (e.g., predator stomach DNA) where eggs are collected may improve our understanding of how those factors influence egg survival.

Figure 5. Larvae submodel.

Larval green sturgeon distribution- Cow Creek to Colusa (Sacramento River), Fish Barrier Dam (Feather River) to confluence of Sacramento and Feather rivers at Verona. Larval white sturgeon distribution- GCID (Sacramento River) and Grayson (San Joaquin River) to confluence of Sacramento and San Joaquin rivers at Chipps Island.
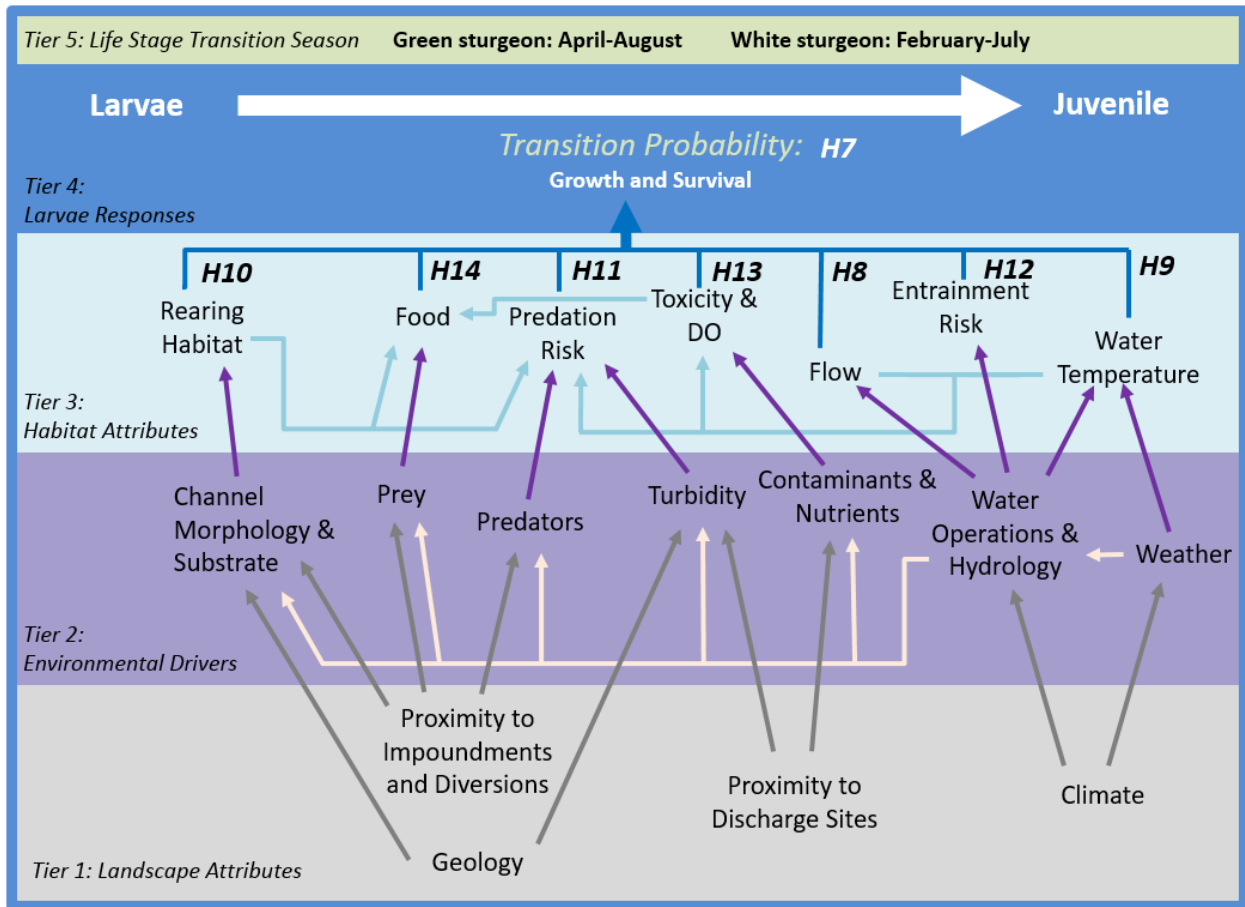
Green sturgeon larvae. Development of long-term studies to assess relative abundance and distribution of early life stages (i.e., egg, larvae, juvenile) is a key management priority for both species (Table 1). As described in the Egg submodels above, linkages between abundance and distribution of early life stages may reveal juvenile recruitment mechanisms and overall drivers for cohort strength. For green sturgeon, agencies now rely on inadequate data in the Sacramento River—primarily bycatch in rotary screw traps used for monitoring of juvenile salmonids—to assess the status of larval green sturgeon. Rotary screw traps should be continuously funded because those data and associated analyses provide some of our only estimates of larval age, growth, temporal spawning distribution, and (coarse) spatial spawning distribution (Heublein et al. 2017). However, rotary screw traps likely selectively capture a

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subgroup of larvae hatching near the sample site rather than a representative sample of the entire spawning population. Thus, some level of larval sampling should occur throughout the estimated spawning range (Table 1).

The CDFW is engaged in efforts to hindcast brood year (or relative annual cohort abundance) using information from juvenile and subadult green sturgeon sampling (Heublein et al. 2017), and it is possible that there is a quantitative relationship between strong year classes and larval abundance (Table 1: **H₇**) at existing sampling sites. In this regard, improvement of larval monitoring may be sufficient for development of a YCI. Any YCI could be compared to various physical habitat attributes (Figure 5, Tier 3) to determine if specific recruitment drivers (i.e., physical, biological, or both) impact the larval life stage. Given that the white sturgeon YCI requires juvenile monitoring through otter trawling in the CDFW San Francisco Bay Study (hereafter referred to as the Bay Study), it is likely that a reliable green sturgeon YCI will also involve increased monitoring of juveniles.

A discussion of water temperature management in larval green sturgeon habitat on the Sacramento River is provided in Heublein et al. (2017). With no current measures of recruitment or cohort strength, the effects of temperature management in the middle and upper Sacramento River on green sturgeon production remain uncertain. Record-high numbers of green sturgeon larvae were collected at RBDD in 2016 and 2017 when water temperatures were below laboratory-based optima for larval growth (Heublein et al. 2017). Based on larval green sturgeon collection patterns in existing surveys and limited indicators of juvenile recruitment success (Heublein et al. 2017), it is unlikely that recruitment failure is caused by reduced water temperatures in the upper ranges of egg and larval rearing habitat. However, this relationship remains anecdotal—specific field-based optima for egg and larval production and ultimately juvenile recruitment are still lacking.

Long-term monitoring of larvae of both species would greatly improve our understanding of the effects of flow and temperature (which in some habitats are closely correlated) on survival and recruitment. Multiple hypotheses have been posed regarding the direct and indirect effects of the managed hydrograph and thermograph on early life stage survival and recruitment of green sturgeon (Table 1). Relative larval and juvenile abundance of green sturgeon has been linked to wet years (Heublein et al. 2017), such that high spring and summer flows may be the primary driver for successful early life stage transitions and episodic recruitment of larvae and juveniles. Thus, it is hypothesized that a positive relationship exists between annual outflow and larval abundance (Table 1: **H₈**). Higher spring and summer flows can be associated with water temperatures that are below optimal or suitable levels measured in laboratory-based studies for larvae of both species (Heublein et al. 2017). Temperature-related factors (e.g., larval metabolic demand) may influence larval survival and abundance such that potential management targets for larvae are below suitable temperatures from laboratory-based studies. Therefore, an increase in larval abundance and distribution in wet years may also be related to water temperature (Table 1: **H₉**).

Flow and temperature in spawning rivers also affect multiple larval habitat attributes (e.g., fish community and composition, food supply, and habitat availability), so general hypotheses regarding flow and temperature may relate to more specific habitat attributes. Issues that affect larger habitat areas (e.g., poor productivity or food supply) may have a measurable effect on larval abundance (Table 1: $\mathbf{H_{10}}$). Although survival of larvae may also be influenced by flow and water temperature through indirect effects on predator community composition, abundance, and metabolic rate (Table 1: $\mathbf{H_{11}}$), it is difficult to quantify. Still, studies addressing those hypotheses (e.g., benthic invertebrate and fish community surveys) may inform management of multiple species and have higher management value in this regard.

Larval green sturgeon are present in areas where substantial water volumes are diverted, and, due to small size and relatively poor swimming performance of larvae, it is almost certain that entrainment effects larval survival (Heublein et al. 2017; Table 1: $\mathbf{H_{12}}$). The RBDD and Glen-Colusa Irrigation District (GCID) facilities include modern fish screens to reduce entrainment of juvenile salmonids, but the effectiveness of screens and facility operations in reducing larval green sturgeon entrainment is poorly understood. Furthermore, many small-scale unscreened diversions are present throughout larval habitat of both species in the mainstem Sacramento River. Periods of extended low flow (e.g., during the recent drought) may reduce the effectiveness of fish protection devices and operational measures intended to reduce entrainment.

White sturgeon larvae. White sturgeon have experienced a preponderance of cohort failures or near-failures over the last decade (DuBois 2017). Measures of abundance and condition of early life stages in winter and spring are necessary to identify the underlying causes of cohort failure or near-failure. With the existing relationship between the juvenile abundance index and cohort strength (Fish 2010), consistent measures of larval abundance may indicate a recruitment bottleneck somewhere between larval and juvenile collection. However, juvenile recruitment measures and intermittent larval collections follow similar patterns such that abundance of the life stages may also be linked (Heublein et al. 2017; Table 1: $\mathbf{H_7}$).

As described in both the Eggs section above, spring and winter outflows are major factors influencing juvenile recruitment and most likely larval survival. Hydrology (e.g., flow, temperature, and turbidity) influences several habitat attributes that may control white sturgeon abundance at the egg, larval, or small juvenile life stages (Table 1: $\mathbf{H_8}$ and $\mathbf{H_9}$). Testing of hydrology-based hypotheses requires coupling larvae with specific habitat attributes and more-refined information on larval distribution and abundance. Water temperature and salinity during winter and spring in the Delta are relatively low and may not limit larval white sturgeon distribution, but by early summer, the temperature of water in the Delta may exceed the optimal range for growth and survival (Heublein et al. 2017). Flow may also influence the abundance of larvae through inundation of channel margin and off-channel areas that include higher quality rearing habitat (Table 1: $\mathbf{H_{10}}$).

As summarized in Heublein et al. (2017) contaminants such as selenium can affect the survival of white sturgeon larvae directly through consumption of contaminated food (Table 1: $\mathbf{H_{14}}$) and indirectly through maternal transfer (Table 1: $\mathbf{H_{13}}$). White sturgeon larvae and spawning

adults forage in heavily contaminated areas, with particularly high concentrations of selenium present in the San Joaquin River.

Complete Metamorphosis to Ocean Migration or 75 Centimeters Fork Length

Figure 6. Juvenile submodel.
Juvenile green sturgeon distribution- Bend Bridge (Sacramento River) and Thermalito Outlet (Feather River) to Golden Gate. Juvenile white sturgeon distribution- GCID (Sacramento River) and Grayson (San Joaquin River) to Golden Gate.
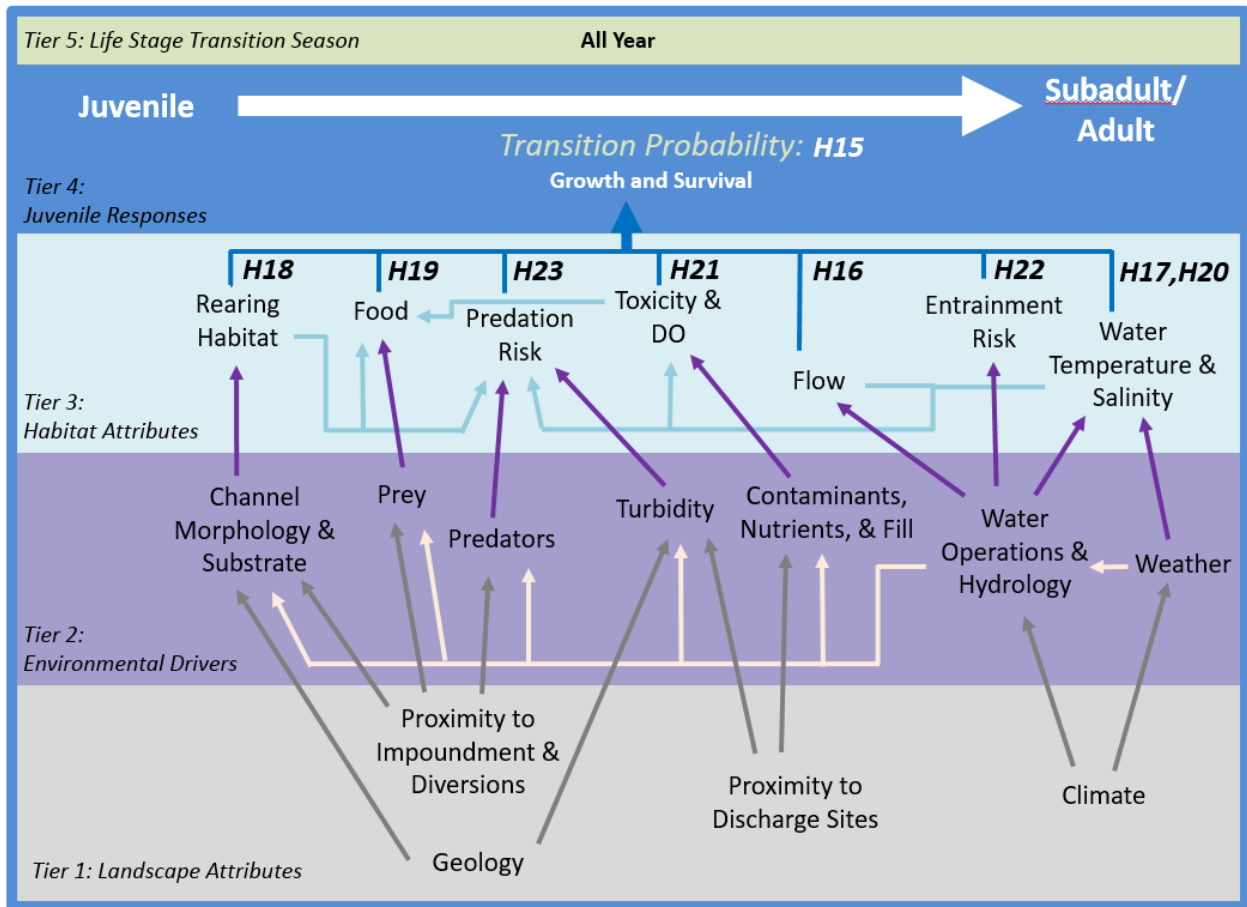
Juvenile green sturgeon. Records of white sturgeon from the Bay Study are used to develop the white sturgeon YCI, and with a long-term increase in effort and quantitative modeling, Bay Study catch data may also provide an opportunity to develop a green sturgeon YCI. The juvenile white sturgeon YCI has high management value as an indicator of successful annual production and predictor of future cohort strength (Heublein et al. 2017). When developing a juvenile green sturgeon YCI, validity of the index—that is, the relationship

between relative abundance of a cohort at the juvenile life stage and later relative abundance of that cohort as subadults and adults—should be verified (Table 1: H_{15}).

Green sturgeon length data (and tissue analyses) from the Sturgeon Study and the CDFW Sturgeon Fishing Report Card program can be used to estimate brood year abundance and validate a potential YCI through ongoing study of age at length. Accurate recruitment or YCI measures are fundamental to identification of mechanisms driving strong year classes and potential year-class failure in green sturgeon. With the recurring anecdotal relationship observed between flows in spawning rivers and egg and larval distribution and abundance (Heublein et al. 2017), it is likely that flow also has some influence on juvenile abundance (Table 1: H_{16}).

The first successful study of juvenile green sturgeon in the Sacramento River occurred in the RBDD area during relatively low flows and high water temperatures in 2015. Based on these limited data, summer and fall flows and water temperatures may also affect freshwater residency (Table 1: H_{16}, H_{17}). Juvenile green sturgeon from this study were tagged with JSATS transmitters in fall 2016 to monitor outmigration behavior (W. Poytress, USFWS, 2017b, unpublished data, see "Notes"). A pilot study is currently underway involving monitoring with the Delta- and Bay-wide array of acoustic tag receivers of a small number juvenile sturgeon captured and tagged in the Delta (M. Thomas et al., UCD Biotelemetry Laboratory and CDFW 2017, report in preparation, see "Notes"). A large data gap would be filled if long-term juvenile monitoring studies specifically targeting distribution and abundance in the both the mainstem Sacramento River and Delta are developed and implemented. Benthic trawling in spawning reaches may also improve YCI measures and allow comparison of environmental drivers and life history diversity.

Juvenile sturgeon habitat attributes (Figure 6) underwent vast transformations in the 20th century. Comparing habitat attributes (e.g., substrate type and food supply in rearing habitat) with demographic data from the potential surveys described above is necessary to understand population dynamics and to develop management strategies for species (Table 1: H_{18}, H_{19}). Because collection of juvenile green sturgeon is so rare, telemetry studies involving the few juveniles encountered annually would greatly improve the understanding of juvenile distribution and behavior, especially in relation to commonly monitored habitat attributes such as temperature and salinity (Table 1: H_{17}, H_{20}). Juvenile telemetry studies would also improve the understanding of habitat preference and utilization, including utilization of the Delta, areas around existing or proposed diversion facility sites, and heavily channelized areas in the middle Sacramento river. As described in Heublein et al. (2017), both juvenile green sturgeon distribution and behavior suggest that entrainment and impingement in diversions affect survival (Table 1: H_{22}). With the exception of pilot studies described in the previous paragraph and telemetry involving laboratory-reared larvae captured at the RBDD (described in Thomas and Klimley 2015), acoustic tagging and tracking of green sturgeon captured sporadically in benthic trawls is currently our only opportunity to directly study juvenile green sturgeon outmigration behavior in the SFE.

Juvenile white sturgeon. The primary emphasis for monitoring of juvenile white sturgeon should be understanding flow-recruitment mechanisms. Juvenile recruitment in all

white sturgeon populations appears to be episodic (Hildebrand et al. 2016); facilitating conditions that increase frequency of recruitment episodes will most likely influence adult abundance (Table 1: **H$_{15}$**).

Addressing uncertainties in recruitment mechanisms currently requires extant recruitment indices (e.g., the YCI from surveys of age-0 juveniles in the Bay Study), additional recruitment indices derived from in-river larval monitoring, and perhaps age-and-growth studies associated with larger fish. A program to collect a substantial number of age-0 fish from the Sacramento River and SFE would improve indices of annual recruitment as well as stock-recruitment relationships. The YCI could also be compared to additional juvenile abundance measures and related habitat attributes (e.g., flow, water temperature, dissolved oxygen) to develop annual mortality estimates and to identify potential recruitment mechanisms (Table 1: **H$_{16}$**, **H$_{17}$**, and **H$_{21}$**). Juvenile monitoring should be carried out by trawling rather than passive sampling (e.g., screw traps) because passive gear has poor sampling efficiency as well as biases that are inherent and difficult to assess.

Channel and tidal marsh modification and contaminated food in rearing habitats may reduce juvenile growth and survival, especially in more estuarine white sturgeon (Table 1: **H$_{18}$**, **H$_{19}$**; Heublein et al. 2017). Through entrainment and impingement—and as a focus for potentially intense predation—fish screens and diversion facilities may also directly affect juvenile white sturgeon survival (Table 1: **H$_{22}$**; Karp and Bridges 2015). Smaller juvenile white sturgeon are eaten by various fish species, and this predation may occur at a level that contributes to year-class failure or near failure (Table 1: **H$_{23}$**; Kohlhorst and Cech 2001; Gadomski and Parsley 2005). As described above, habitat attributes (e.g., streamflow, temperature) influence predator community, abundance, and metabolism along dispersal routes and throughout juvenile rearing areas, such that the flow-recruitment relationship may be connected to predation.

Figure 7. Subadult and adult submodel.
Adult green sturgeon distribution- California, Oregon, and Washington estuaries (May-October), nearshore marine areas (all year). Adult white sturgeon distribution- SFE and infrequent nearshore marine distribution (all year).
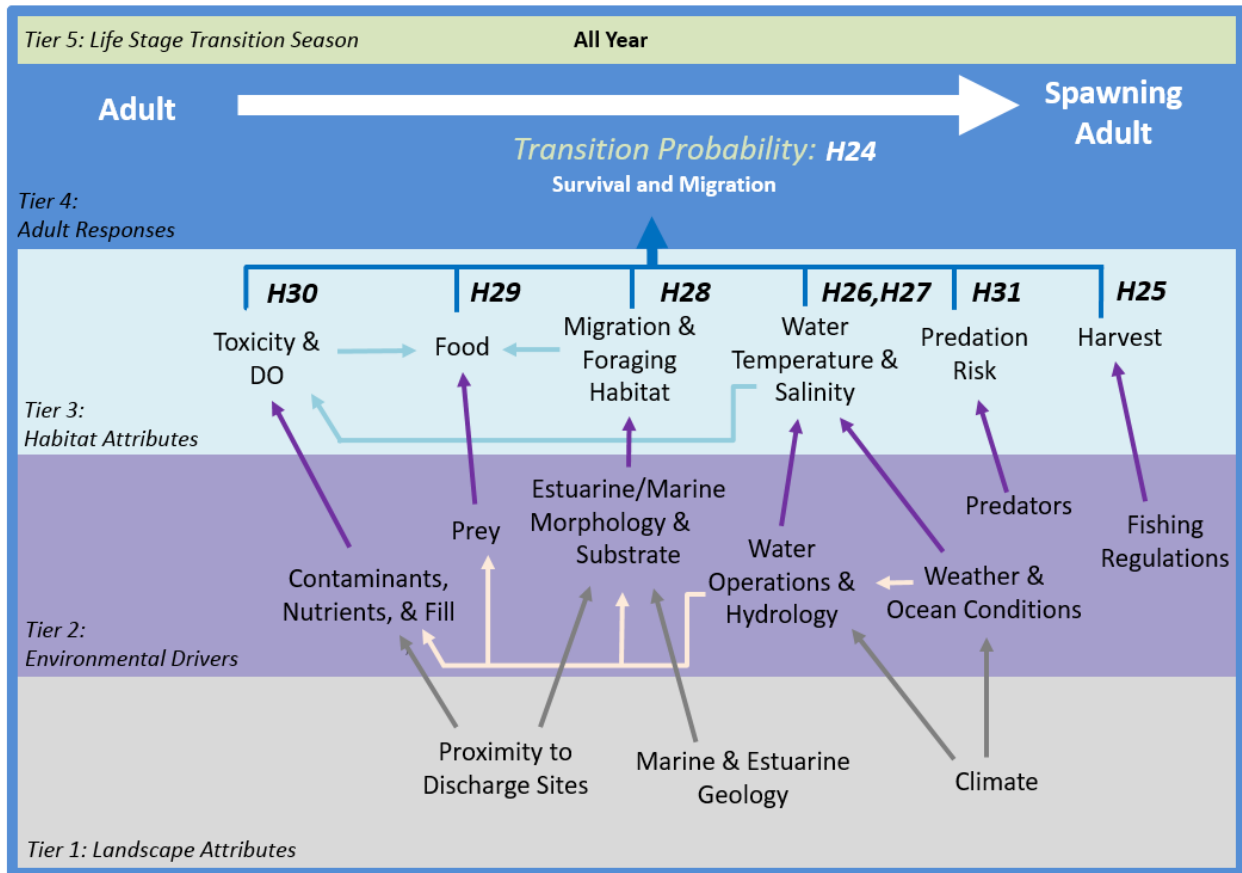
Subadult and adult green sturgeon. Although the annual number of subadult and adult green sturgeon captured in California is typically small, incidental capture in the Sturgeon Study and the California halibut trawl fishery may be large enough in some years to allow a variety of additional study opportunities. Methods should be explored for expanding studies of sturgeon to facilitate routine development of green sturgeon abundance and relative abundance, age-length relationships, and cohort abundance. The Sturgeon Study should routinely apply external tags to green sturgeon as a relatively simple method to estimate fishery bycatch rates. With improved age-length estimates, fishery records (e.g., effort and bycatch observations) could be used for abundance indices or population modeling. In an effort to validate subadult and adult life stage composition or mortality estimates (Table 1: H_{24}), cohort measures with the aforementioned methods could be compared to a potential YCI.

Past records of commercial harvest and estimates of sport harvest should be studied along with current subadult and adult abundance trends. Harvest prohibitions may have had an immediate or delayed impact on subsequent-year adult and subadult abundance and may play a significant role in population recovery (Table 1: $\mathbf{H_{25}}$; Heublein et al. 2017). Furthermore, studying the effect of green sturgeon harvest prohibitions may improve understanding of regulation of other sturgeon fisheries, especially Sacramento-San Joaquin River and Columbia River white sturgeon.

Adverse impacts on sturgeon habitat in estuaries are likely attributable to factors such as reduced freshwater inflow, urban and agricultural runoff, shellfish aquaculture, industrial effluent, shoreline development, and dredging. Nearshore marine habitats might also be impacted by any new implementation and operation of offshore electric generation and hydrokinetic projects (NMFS 2015). Estuarine and nearshore movements of subadults could be better studied through improvement of acoustic array coverage and continued tagging of green sturgeon during sturgeon population studies in California and Washington. For example, our understanding of estuarine habitat requirements and migration patterns could be improved by relating water quality data to movement data (Table 1: $\mathbf{H_{26}}$, $\mathbf{H_{27}}$). Analysis of tissue samples from estuarine studies could also improve the understanding of population dynamics, genetics, and contaminants. It also remains uncertain why green sturgeon aggregate in marine areas or travel so far north, but it is likely related to foraging opportunities (Table 1: $\mathbf{H_{29}}$). Prey base in specific marine aggregation sites should be studied to evaluate fisheries, offshore energy development, and other projected changes in oceanographic conditions that may impact those areas.

Adult white sturgeon. Fishing regulations since the early 1990s—especially the slot limit and annual bag limit—are intended to protect large, mature white and green sturgeon (prior to listing) from harvest and thus provide some resilience to droughts and similar disturbances. Other approaches to regulating the white sturgeon fishery (e.g., a quota) are being assessed because the use of a slot limit has focused intense fishing effort on a relatively narrow size range of fish. This focus may result in depletion of otherwise-strong cohorts before they have the opportunity to spawn or recruit out of the fishery (i.e., exceed the slot size). The present and foreseeable fishery has substantial excess capacity. That is, each Sturgeon Fishing Report Card includes tags for annual harvest of three fish within the slot limit, and the number of tags distributed each year greatly exceeds the estimated number of legal-sized white sturgeon. In the hypothetical scenario that all tags were utilized, large juveniles and mature adults within the slot limit would be harvested at a level that would preclude recruitment to the spawning population. Additional life stage surveys are necessary to understand the effects of harvest on overall white sturgeon production. Although it is almost certain that adult white sturgeon population size and spawning run-size are linked (Table 1: $\mathbf{H_{24}}$), the relationship cannot be verified without additional surveys (i.e., to estimate the annual number of spawners).

Natural mortality in large juvenile and adult white sturgeon is low (Hildebrand et al. 2016), and only the recruitment and harvest are known to substantially influence adult abundance in the SFE (Heublein et al. 2017). With harvest focused on a few strong cohorts, harvest is likely

a primary factor limiting adult abundance (Table 1: H_{25}). Thus, regulation of recreational fishing will continue to be key to management of the adult life stage. Monitoring the fishery should be improved to estimate catch-and-release mortality and to better estimate harvest rates, survival rates, and cohort abundance. Given ongoing declines in white sturgeon abundance, additional insight regarding potential management options is needed. Demographic data (e.g., sex ratio, fecundity, and age structure) derived from improved monitoring are necessary to model responses of the white sturgeon population to changes in harvest management and to identify potential high-value habitat management actions (e.g., habitat restoration and improvement of water quality) that affect adult abundance trends (Table 1: H_{28}).

It is notoriously difficult to capture large numbers of adult fish in scientific sampling efforts before they recruit to the recreational fishery. This issue can be addressed by increasing scientific sampling effort, maximizing the value of data from the recreational fishery, and collecting or analyzing catch data from all pertinent commercial fisheries (e.g., the Bay shrimp trawl fishery; Heublein et al. 2017). Acoustic tagging and increased mark-recapture in the Sturgeon Study could improve estimates of harvest rate, survival, and catch-and-release mortality. To support survival estimates, cohort tracking, and documentation of the effects of management actions, age and growth should be monitored through analysis of fin rays. As one way to collect a large amount of tag-recovery data, the Sturgeon Fishing Report Card should be continued and improved (e.g., to collect lengths of released fish), and actions should be implemented to substantially increase the rate at which Sturgeon Fishing Report Cards are returned to the CDFW.

Factors that affect adult white sturgeon condition and mortality in the SFE probably include consumption of contaminated food and pinniped predation (Figures 6 and 7; Heublein et al. 2017). The impact of food availability (and contaminant levels) on white sturgeon remains unclear. Adult white sturgeon are likely opportunistic consumers, yet more information would be useful for evaluating how foraging patterns are associated with growth or contaminant accumulation (Table 1: H_{30}). Estimates of pinniped predation on white sturgeon in the Bay would allow biologists to understand this potentially high source of mortality (Table 1: H_{31}). Sources of direct, human-caused mortality include dredging in the SFE and entrainment at water diversions. Similar to recent studies involving dredging and green sturgeon (Chapman et al. in review), telemetry could be used to monitor white sturgeon movements around dredge removal and depositions sites. Modeled results could describe risk in relation to locations of dredging, make predictions about potential impacts, and guide monitoring. Entrainment at agricultural sites, power plants, and federal and state Delta pumping facilities is not well documented, and the frequency of entrainment is likely to be site-specific. Israel et al. (2009) reported adult white sturgeon impingement on the trash racks at the John E. Skinner Fish Protection Facility in the south Delta. Improved monitoring and reporting of adult white sturgeon in and near large-scale diversion facilities could provide a more accurate description of the possible impact of entrainment and impingement.

Spawning

Figure 8. Spawning adult submodel.
Green sturgeon migration and spawning distribution- Cow Creek (Sacramento River), Fish Barrier Dam (Feather River), and Daguerre Point Dam (Yuba River) to Golden Gate. White sturgeon migration and spawning distribution- GCID (Sacramento River), Grayson (San Joaquin River), and occasionally other tributaries of the SFE to Chipps Island.
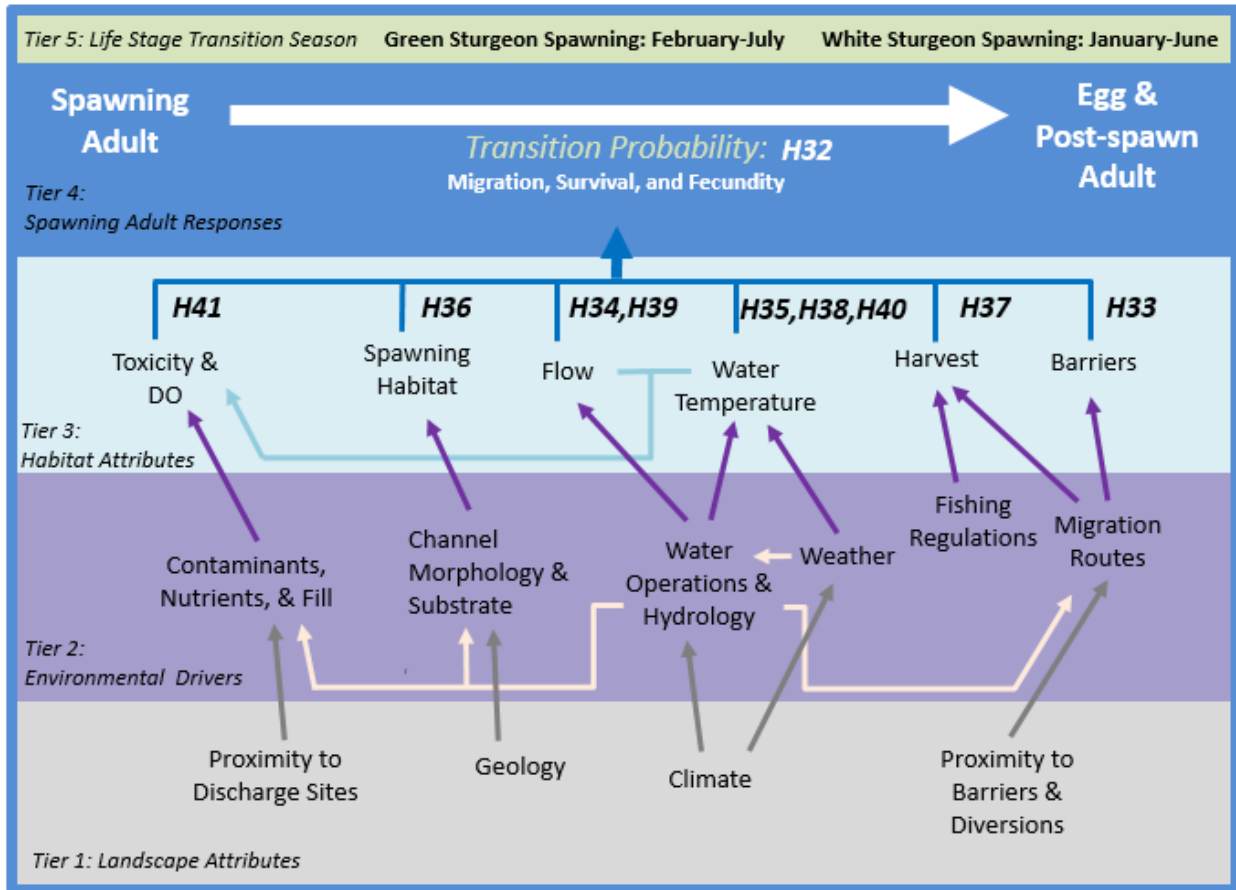
Spawning green sturgeon. Recent acoustic telemetry and DIDSON surveys have established a baseline for annual spawner abundance (run-size) and adult in-river behavior, including pre- and post-spawn migration and holding. Early life stage abundance and run-size are probably linked, but any relationship remains uncertain (Table 1: **H_{32}**).

The number of active acoustic tags in sturgeon is decreasing as tags expire at a greater rate than new tag implantation and acoustic receiver arrays lack long-term support. Long-term monitoring of adult green sturgeon indicators should include both telemetry infrastructure (e.g., database management, analysis, and receiver arrays) and tagging sufficient numbers of individuals to maintain or improve measurements of abundance and survival. This could be achieved in part by implanting acoustic tags in green sturgeon collected in the Sturgeon Study (and/or continued tagging in Oregon and Washington estuaries) and by implementation of a

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long-term program to maintain and improve existing acoustic monitor arrays. Inter-annual spawning-migration data from telemetry studies are also necessary to estimate run-size with DIDSON surveys. Ongoing run-size estimates can be used to quantitatively evaluate the effect of water operations and migration barriers on spawning migration success and distribution (Table 1: **H₃₃**, **H₃₄**, and **H₃₅**).

A hypothetical adult abundance time series has been modeled from recent annual run-size estimates (Mora 2016), but it is likely that far more (greater than10) estimates will be needed to make rigorous estimates of total population abundance. Therefore, run-size and distribution estimates using DIDSON (or a similar imaging method) should be added as an annual long-term monitoring study. Run-size can be used to assess long-term trends in spawner abundance that may be related to harvest regulations, including those that allowed intensive harvest of adult green sturgeon from the spawning and holding area adjacent to the GCID (Table 1: **H₃₇**; Heublein et al. 2017).

Additional information on spatial and temporal spawning habitat and migratory behavior (e.g., fish rescue, migration routing and delays, spawning, or holding areas) is necessary for management of temperature, management of flows, and evaluation of large-scale development and restoration projects in the Sacramento River watershed (Table 1: **H₃₃**, **H₃₄**, **H₃₅**, **H₃₆**, **H₃₈**, and **H₃₉**). To assess the potential benefits of any restoration actions proposed for those habitats, it is imperative that spawning and holding habitat preferences or suitability are established from a synthesis of current data. Mapping of spawning and holding habitat (including surrounding riparian and upland features) should be continued and expanded to improve our understanding of the effects of habitat alteration, restoration, and adult fish passage.

Spawning sturgeon are particularly vulnerable to the effects of water temperature and contaminants as they relate to condition, atresia (egg resorption), and fecundity (Figure 8). Late-season water temperatures in the lower reaches of spawning habitat on the Sacramento River and Feather River may reach levels that cause atresia, affecting fertilization of eggs and survival of embryos (Table 1: **H₄₀**). Habitat segregation and associated bioaccumulation of contaminants through exotic food species suggest that there may be different contaminant signatures between nDPS and sDPS green sturgeon (O. Langness, WDFW, 2016, unpublished data, see "Notes"). If the mixture of heavy metals and organic toxins present in white sturgeon from the SFE (e.g., Gundersen et al. 2017) also occurs in spawning green sturgeon, then green sturgeon condition and fecundity may be adversely impacted, reducing the population size of the next generation (Table 1: **H₄₁**). Based on the potentially high contaminant levels in spawning adults, and the potential effects of any contaminants (and combinations thereof) on fecundity, these factors should be routinely examined.

Spawning white sturgeon. White sturgeon spawning in California is a management concern because of late reproductive maturity, harvest by a substantial recreational fishery, and intermittent periods of successful spawning (Heublein et al. 2017). Key concerns for the spawning life stage include determining the shape of any stock-recruitment relationship, the annual number of breeders (Nb), and spawning habitat quantity, quality, and variability. Without

direct surveys of run-size and eggs, it is uncertain if abundance or distribution of those life stages are linked (Table 1: H_{32}).

As described in the previous submodel, adult white sturgeon abundance is influenced by harvest, but the specific relationship between the adult abundance and run-size is not directly studied. The effect of fishing—harvest as well as catch-and-release—on the annual spawning population (Table 1: H_{37}) could be evaluated with any new data from reports associated with increased reward tagging in the Sturgeon Study and from Sturgeon Fishing Report Cards. Telemetry of reproductively mature adult white sturgeon would provide information on quantity, quality, and variability of spawning habitat (e.g., by water-year type; Table 1: $H_{34}, H_{35}, H_{36},$ and H_{39}). The Sturgeon Study could also provide a consistent source of adult white sturgeon for acoustic telemetry studies. Use of fisheries hydroacoustics (e.g., DIDSON and side scan sonar) could detect adults migrating toward spawning grounds while eliminating the need to capture adults, but data are typically insufficient to generate estimates associated with long-term monitoring such as harvest rate and Nb. Ongoing monitoring of white sturgeon in the vicinity of migration barriers (e.g., DWR Yolo Bypass fyke trap sampling and monitoring at stranding sites; Heublein et al. 2017), along with telemetry methods and DIDSON surveys, should also be used to evaluate potential effects and route selection on run-size and distribution (Table 1: H_{33}).

Results from the tagging studies described above and early life stage monitoring could also be used to inform and evaluate the results of water management actions. Several ongoing regulatory and management processes may increase white sturgeon recruitment by providing necessary hydrologic variability and temperature relief, especially in the San Joaquin River; these include management of flow in the middle Sacramento River, restoration of flow and habitat in the main stem San Joaquin River, and minimum flow requirements mandated by the Federal Energy Regulatory Commission and State Water Resources Control Board. Continuing efforts should be made to refine the relationship between natural hydrologic regimes such as significant streamflow increases (≥ 40 cubic meters per second) during the March to May period and successful white sturgeon spawning (Table 1: H_{34}; Heublein et al. 2017).

Some tissues should be collected from migrating, holding, and spawning adult white sturgeon to determine gonadal development, reproductive stage, age, and hormonal levels. The effects of water temperature and handling on reproductive physiology and atresia could also be assessed in those sampling efforts (Table 1: H_{35}, H_{37}). Long-term monitoring of selenium and trace metal in white sturgeon tissues should be implemented. Existing mechanistic models for selenium should be used to make predictions about how the white sturgeon population is affected by contaminants. Specifically, investigations should be made into the annual relationship between larval abundance, recruitment, and contaminant levels in adults (Table 1: H_{41}). A study of contaminants could use directed sampling or become part of a collaboration with existing studies (e.g., Sturgeon Study).

Blankenship et al. (2017) used genetic analysis of white sturgeon embryo relatedness to estimate the number of spawning adults. A program to genetically analyze a substantial number of age-0 fish from the Sacramento River and estuary would provide an estimate of annual Nb to

inform a stock-recruitment relationship. Effective Nb is also important for fishery managers to consider when developing harvest regulations. Genetic analyses on SFE white sturgeon conducted to date have identified a single population (Schreier et al. 2013). However, available genetic tools may not be adequate for analyzing population structure. With the potential sequencing of the white sturgeon genome, a distinct population in the San Joaquin River could be identified. A finding of that sort would advance efforts to build and maintain SFE white sturgeon population resilience, likely through spawning habitat restoration and managed streamflows in the San Joaquin River and harvest management in both systems. Further, better genetic tools would allow for the coupling of disparate data sources (e.g., telemetry and documented spawning events) to investigate management actions and species responses.

Conclusion

Although compelling life stage and population patterns are apparent, there is a need to improve sturgeon monitoring to a level appropriate for scientifically-based management of these important species. The conceptual models developed here provide recommendations to efficiently fill critical knowledge gaps. Our understanding of sturgeon population dynamics in the SFE is incomplete, but major advancements have occurred over the last 10 years. Thus, we completed this synthesis effort with the understanding that additional syntheses may be necessary to evaluate and refine conceptual models and study recommendations. Further, we recognize that the monitoring recommendations will not result in recovery or increased abundance alone. We suggest that all monitoring recommendations are implemented as complementary surveys until a level of monitoring that accurately tracks population metrics is established. Lower levels of monitoring may be adequate for management if surveys follow similar patterns and can be used interchangeably as surrogate surveys, or if life stages consistently respond to measurable environmental metrics. At that point, we anticipate that drivers of recruitment and mortality will be adequately characterized to allow for identification and implementation of management actions (e.g., water management, habitat restoration, harvest restrictions) that will lead to population recovery or increased abundance.

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