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Review

Habitat use of anadromous and amphidromous sturgeons in North America: a systematic review

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Abstract

Sturgeons are among the most endangered fishes in the world. Identifying habitat use characteristics to inform restoration projects is crucial for recovery. However, small sample sizes, inadequate replication of studies, and limited spatial extents complicate our ability to effectively apply the findings of single studies to endangered species conservation across the larger riverscape. We synthesized information from amphidromous and anadromous sturgeons in North America to identify species-specific knowledge gaps and conduct a quantitative comparison of species–habitat relationships. We provided a qualitative summary of substrate use and synthesized estimates of depth and velocity during spawning and non-spawning activity. Generalized patterns among species were identified, such as spawning in fast water on hard substrate and then using slow water with soft substrate areas when not spawning. We noted species-specific variability during spawning that may be attributed to historical maximum length, egg characteristics, and watershed features. This study provides some of the first estimates of habitat use that can be adapted for many populations. Results can contribute to empirically grounded decision-support tools used to prioritize information needs for recovery.

Key words: habitat, anadromous species, endangered species, sturgeon, meta-analysis

Introduction

Threats to biodiversity across the globe are persistent and expanding (Evans et al. 2016). Major contributors to species declines include anthropogenic threats that lead to habitat degradation, such as urban development and climate change (Hulme 2005; Gregory et al. 2013). Loss of habitat has been identified as the single greatest threat to imperiled species globally (Oberdorff et al. 2011) as well as within the United States of America (USA) (Wilcove et al. 1998). Fish species, in particular, have been exposed to drastic modifications to the riverscape such as sediment loading (Kemp et al. 2011), human water use (Gleick 1998), contamination (Niimi 1983), river fragmentation from water development (e.g., dams; van Puijenbroek et al. 2018), and dredging operations (Auster et al. 1996). Anthropogenic pressure on these systems continues to rise and ultimately influences the hydrological and geomorphological state of a river (Sabater and Klement 2010). Changing the structure and function of river systems limits the ecosystem services that they can sustain and leads to river homogenization that restricts biodiversity (Walters et al. 2003; Moyle and Mount 2007; Poff et al. 2007; Petsch 2016; Rolls et al. 2018). Identifying key habitat requirements for protection and restoration becomes increasingly important for the persistence of many species.

Among the most endangered fishes in the world are the sturgeon family, Acipenseridae Bonaparte, 1831 (Birstein 1993). Of the 27 known species of Acipenseriformes worldwide, 26 are currently listed as at risk of extinction (i.e., vulnerable, near threatened, endangered, or critically endangered) by the International Union for Conservation of Nature (IUCN; IUCN 2023). The 27th species, the Chinese paddlefish *Psephurus gladius* von Martens, 1862, is classified as extinct (Qiwei 2022). In North America, there are nine species of sturgeon, and of those, five are either anadromous or amphidromous, meaning they have life history strategies that include the capability of transitioning between marine and freshwater environments. The green sturgeon *Acipenser medirostris*, the Atlantic sturgeon *Acipenser oxyrinchus*, and the Gulf sturgeon *A. oxyrinchus desotoi*, all exhibit anadromous life histories, whereas the white sturgeon *Acipenser transmontanus* and the shortnose sturgeon *Acipenser brevirostrum* are classified as amphidromous. Green sturgeon and white sturgeon are located throughout the Pacific Coast and share many river systems. Shortnose sturgeon and Atlantic sturgeon are distributed throughout the Atlantic coastal region and also share many of the same systems. Gulf sturgeon, a subspecies of the Atlantic sturgeon, can be found throughout the Gulf of Mexico.

Anadromy optimizes recruitment benefits for young through reduced predation and allows adults to use ocean productivity for growth (Waldman et al. 2016). However, transitioning through these different environments makes migratory species increasingly difficult to study and vulnerable to various threats, causing many species to trend towards extirpation (Limburg and Waldman 2009). Habitat degradation has led to the removal of suitable substrates in nursey grounds that are important for protection (e.g., predation, oxygen depletion) and growth during early life stages (De Groot 2002). Fragmentation has limited access to spawning grounds and has led to increased mortality during juvenile outmigration (Rolls and Arthington 2014; Algera et al. 2020). Modifications to hydraulic regimes influence temperatures as well as flow, both of which are important for migration cues and survival (Rolls and Arthington 2014). Restoring habitat connectivity as well as maintaining life history diversity are key characteristics to the resiliency of these fish populations (Waldman et al. 2016). Variation in life history is thought to be important for increasing recruitment success and is likely correlated with environmental heterogeneity and habitat complexity (Schindler et al. 2010; Carlson and Satterthwaite 2011). Homogenizing river conditions might result in only some life stages being supported, creating a bottleneck for specific life history stages (Hickford and Schiel 2011). Connectivity is important not only for access to habitat and migration routes but also for withstanding disturbances in a system (Sedell et al. 1990; Van Looy et al. 2018). Loss of connectivity restricts access to refugia, decreases the potential for re-colonization, and limits functional redundancy post-disturbance (Liu and Wang 2018; Van Looy et al. 2018). Sturgeons are highly vulnerable to these habitat alterations and destructions (e.g., Nakamoto et al. 1995; Farr et al. 2002; Moyle 2002; Secor et al. 2002; Jarić and Gessner 2012). Restoring connectivity alone is not sufficient to combat population declines (e.g., Gessner et al. 2014). Rebuilding populations will require identifying degraded habitat and maintaining complexity for increased survival during various life stages. Therefore, the first step to habitat rehabilitation is identifying the current conditions and parameters associated with sturgeon river and estuary use during various life stages. Many different ways of describing habitat are documented, with one of the simpler definitions being "where an animal lives" (Looijen 1995). Habitat often includes the physical and biological features that are thought to be important to an organism's distribution and abundance (Yapp 1922; Milner et al. 1985; Kearney 2006). Studies that evaluate habitat selection help to identify mechanistic links between the individual and their surroundings and guide decision-making (Kearney 2006). However, many populations currently lack information on where and how sturgeon use their environment, especially during particular life stages.

Systematic reviews have become increasingly important in ecology and are useful for synthesizing information qualitatively and quantitatively to understand ecological processes at multiple scales (Foo et al. 2021). Evaluating the available information qualitatively is beneficial when quantitative data are not available; however, as the number of empirical studies published continues to accumulate, there is a growing need to quantitatively synthesize information (Arnqvist and Wooster 1995). Meta-analysis techniques have become increasingly valuable to increase statistical power, quantify heterogeneity among studies, identify knowledge gaps, and explore large-scale patterns and trends that aid in evidence-based decision-making (Stewart 2010; Lee 2019). The five species of sturgeon listed above all have information related to habitat and life history readily available, but the typical small sample sizes (e.g., sometimes only one or two fish in a study) make it difficult to make broader inferences due to epistemic uncertainty (Regan et al. 2002). In addition, these species all have multiple populations located throughout their distribution, making it difficult to develop place-based estimates of habitat in all locations a species inhabits. As an example, Atlantic sturgeon have 31 rivers along the USA. Atlantic coast that are listed as critical habitat for the species (NOAA 2017). Reproducibility in research is important for gaining strength and combating uncertainty (Nichols et al. 2019; Nichols et al. 2021); however, multiple barriers exist for replicating research on threatened and endangered species (Shaw et al. 2021). Data limitations are common because funding is limited for replicated studies, there is limited access and availability to the species of interest, and small population sizes since they are species at-risk (Ralls et al. 1992; National Research Council 1995; Shaw et al. 2021). By synthesizing studies of habitat use among similar sturgeon species, we can overcome some of the limitations related to these difficult-to-study species and make informed decisions that are grounded in empirical data (Hilton and Richardson 2004).

In this study, we conducted a literature review and synthesis of information on habitat use for North American anadromous and amphidromous sturgeon. The focus of the review was on the depth, velocity, and substrate composition conditions used by sturgeons. These factors are relatively well documented in the literature as informing high use areas by sturgeons in the river (e.g., Phelps et al. 2010; Hildebrand et al. 2016). In addition, these characteristics are often used to predict habitat suitability when integrated with hydraulic models that are commonly used for habitat restoration efforts. Our objectives were to (1) synthesize information on the habitat use of spawning, nonspawning adults, and juveniles in the estuary and river environment for anadromous and amphidromous sturgeon in North America, (2) identify any species-specific knowledge gaps, (3) discuss similarities and differences among habitat use and requirements for each species, and (4) provide a framework to develop robust habitat suitability indices (HSI) to inform broad-scale habitat restoration efforts.

Methods

Data collection

We gathered literature using the Web of Science database; however, to expand the coverage of available information, we also conducted searches using Google Scholar, which has

proven to be a suitable and powerful source for scientific information (Halevi et al. 2017). We restricted our search to studies that observed fish directly and were conducted in a river or estuary environment. In doing so, we omitted articles and reports that reported observations in marine or lake (i.e., Kootenay Lake) environments. Furthermore, we only considered anadromous and amphidromous species in the analysis because of their abilities to use both freshwater and saltwater environments. We conducted the search using each species name "green sturgeon", "white sturgeon", "Atlantic sturgeon", "shortnose sturgeon", OR "Gulf sturgeon", in combination with the habitat characteristics "depth", "velocity", OR "substrate". For example, search terms for green sturgeon were "green sturgeon" AND "depth" OR "green sturgeon" AND "velocity" OR "green sturgeon" AND "substrate". This was repeated for each species. Depth measurements were reported in meters, and velocity was represented using the mean column velocity, measured in meters per second (m s^{-1}). Since velocity measurements at different locations in the water column varied, we maintained equivalent measurement techniques by converting estimates of near bottom velocity or surface velocity to mean column velocity using velocity profiles assuming a trapezoidal channel shape (Wali 2013). When reviewing the literature, we documented characteristics such as the river system, life stage (i.e., egg, larvae, juvenile, subadult, and adult), and activity (i.e., spawning, adult use in the river or estuary, and juvenile use in the river or estuary). Activities were classified based on fish behavior during measurement of the corresponding habitat characteristic. Observed spawning adults or the collection of eggs or larvae were categorized as spawning activities. We classified adult in-river use as adults or subadults using any portion of the river for behaviors other than spawning (i.e., holding, staging, and overwintering). Adults or subadults using the estuary for feeding were described as adult estuary users. We documented juvenile in-river use as juveniles caught before outmigration to the estuary, but also included some instances where juveniles used lower parts of the river for foraging. Finally, we classified juvenile estuary use as juveniles that were observed foraging within the estuary. Citations sorted by species and habitat characteristic for all papers used in this analysis are provided in the supplemental material (Supplementary material A).

We collected information on depth and velocity for each paper by recording the mean, standard deviation, and sample size. If the mean and standard deviation were not provided but data or estimates were presented in figures or tables within the reports, we estimated them by using an online figure reader (Rohatgi 2022) or Bayesian networks in the Netica software (Norsys Software Corp 2020). The latter approach was most commonly used for papers containing frequency tables, which we could discretize, input the corresponding probabilities or proportions, and then calculate the mean and standard deviation. For papers that only reported ranges of values, we estimated the mean and standard deviation using equations recommended by Hozo et al. (2005). Specifically, if the sample size was greater than 29, we used the reported median or midpoint as the mean. Sample sizes that had less than 29 fish; we estimated the mean using:

$$\bar{x} = \frac{a + 2m + b}{4}$$

The minimum of the range is represented by a, the maximum is represented by b, and m is the median. If the median was not given, we used the midpoint of the range.

The standard deviation, θ, for studies with sample sizes less than 15 was calculated as:

$$s^2 = \frac{1}{12}\left(\frac{(a - 2m + b)^2}{4} + (b - a)^2\right)$$
$$\theta = \sqrt{s^2}$$

If sample sizes were between 16 and 70, we estimated standard deviation using:

$$\theta = \text{Range}/4$$

Sample sizes greater than 70 had standard deviation calculated using:

$$\theta = \text{Range}/6$$

We collected descriptive information to gain a better understanding of the types of substrates used by sturgeon and compiled it qualitatively (Supplementary material B, Tables S1–S3). This included recording the primary substrate type, number of fish observed, species, life stage, activity, and river system. Substrate types varied from clay (<0.004 mm) to boulders (>256 mm) (Wentworth 1922). Since hydraulic modeling used to inform riverine habitat restoration efforts often incorporates substrate using broader polygons that usually require binning substrate size classes together, we focused on whether fish were using hard or soft substrate dominated areas during the corresponding activities. We classified soft sediment as sand, silt, and mud (≤2 mm) and hard sediment as granule, pebble, cobble, or boulder (>2 mm) (Wentworth 1922).

Analyses

We used a Bayesian three-level hierarchical meta-analysis (Sutton and Abrams 2001; Higgins et al. 2009; Borenstein et al. 2010) to synthesize estimates of depth and velocity. This method considers the variability within each study as well as the variability among studies, and is represented as:

$$y_i = \beta_{0i} + e_i$$
$$e_i \sim \text{Normal}\left(0,\ \sigma^2\right)$$
$$\beta_{0i} \sim \text{Normal}\left(\mu,\ \tau^2\right)$$
$$\mu \sim \begin{cases} \text{Normal}\,(0, 100)\,, & y = \text{depth} \\ \text{Normal}\,(0, 10)\,, & y = \text{velocity} \end{cases}$$
$$\tau^2 \sim \text{Half Cauchy}\,(0, 0.5)$$

The observed effect size (observed mean from each study) for each study i is given as y_i, the estimated true effect size for each study i is β_{0i}, and e_i is the sampling error within each individual study. e_i is assumed to be normally distributed with

Table 1. Model selection statistics based on differences (Δ) in estimated log pointwise predictive density ($elpd_{loo}$) using the leave-one-out cross-validation information criterion (LOO-IC).

Habitat characteristic	Model	$elpd_{loo}$	SE $elpd_{loo}$	Δelpd	LOO-IC
Depth	Environment	−473.2	29.2	0	946.4
	Environment * life stage	−479.7	29.5	−6.5	959.5
	Environment + life stage	−481.6	30.1	−8.4	963.2
	Life stage	−568.4	74.7	−95.2	1136.8
	Random	−569.1	75.1	−95.9	1138.3
	Fixed	−4397.0	2593.2	−3923.8	8794.0
Velocity	Random	6.3	3.4	0.0	−12.5
	Life stage	5.6	3.3	−0.6	−11.3
	Fixed	2.7	4.9	−3.6	−5.4

Note: Models with larger $elpd_{loo}$ and lower LOO-IC have better predictive fit. Estimates are grouped by the habitat characteristics depth and velocity.

a mean of zero and a standard deviation of σ^2, which is the within study variance for each study i. β_{0i} are assumed to be samples of an effect size that are normally distributed with a mean of the true pooled effect size (μ) and among study variance (τ^2). This three-level structure better represented the variability in the data in comparison to a two-level model ($\tau^2 = 0$) that does not account for among-study heterogeneity. We used leave-one-out cross-validation for model selection by comparing the average differences in the estimated log pointwise predictive density (Table 1; Δelpd ± SE; Gelman et al. 2014; Vehtari et al. 2017). In addition, multiple studies provided numerous effect sizes that would not meet the assumption of independence in a fixed-effect two-level model (i.e., Van den Noortgate et al. 2013). We used uninformative normal priors for the overall effect size (μ) with a mean of 0 and a variance of 100 for depth and a variance of 10 for velocity. Differences in among-study variance τ^2 were accounted for by using a Half-Cauchy prior that places greater weight on estimates with lower variances but still considers those with larger variances (Williams et al. 2018). We reported the mean, standard deviation, and log-based credible intervals (Burnham et al. 1987) for each activity. We then used the combined estimates as an example to create HSI models with frequency distributions in bin sizes of 0.5 m increments for depth and 0.1 m s^{-1} increments for velocity.

Similarities and differences among species during each activity were evaluated by including a predictor variable that separated the data collected for each species. This resulted in a three-level meta-regression model represented by:

$$y_i = \beta_{0i} + \beta_1 x_{1i} + e_i$$

where β_1 is the regression coefficient and x_{1i} is the study-level variable that explains the variation among species. All other aspects and priors described in the previous model remained the same. Sampling bias was best avoided by evaluating each habitat characteristic based on observed activities rather than life stage. For example, estimating spawning habitat using egg mats may yield slightly varied estimates from those based on adult spawner presence. By combining these methods into a single dataset, our data incorporated diverse sampling techniques that contributed to an activity with the same objective and may be more useful for informing management. For each species, we reported the mean, standard deviation, and log-based credible intervals for each activity.

We used the brms package (Bürkner 2017) in program R (R Core Team 2022) to fit and evaluate all models. This package uses Hamiltonian Monte Carlo (HMC) (Neal 2011) methods with a no-U-turn sampler (NUTS) (Hoffman and Gelman 2014) in Stan (Carpenter et al. 2017). Effect sizes were incorporated by combining sample variance (standard deviation) with the corresponding effect size (mean) for each function within the response variable (Bürkner 2017). Each model was run for a minimum of 8000 iterations with a warm-up of 4000 from three chains, resulting in at least 12 000 post warm up draws. We evaluated bulk and tail effective sample sizes to ensure adequate sampling of the posterior distribution and confirmed convergence using the Gelman–Rubin convergence diagnostic ($\widehat{R} \leq 1.01$; Gelman and Rubin 1992).

Results

We found 423 documents related to estimating the depth use of sturgeon. After reviewing them thoroughly, we selected 151 documents that had usable estimates (Fig. 1). In total, 70 documents provided estimates of spawning depth, 25 provided estimates of estuary depth use, and 62 provided estimates of river depth use (Supplementary material B, Figs. S1–S3). LOO-IC model selection results determined that the best grouping structure for non-spawning data was to separate data by river and estuary environments only and not by life stage (Table 1). In addition, the precision of estimates by life stage was evaluated using the 95% credible intervals and determined to be inconclusive based on the nature of the relationship (i.e., whether positive or negative) (95% CRI: −0.59 to 1.36). This was also the case between life stages in the estuary environment (95% CRI: −2.97 to 6.69). All the studied species had more than five available studies providing estimates of depth use during spawning (Table 2). Only two species (Atlantic sturgeon and shortnose sturgeon) had more than five available studies documenting depth use in the estuary, including only one study available for white sturgeon

Fig. 1. Distribution of papers collected in North America that contained estimates of depth (top), velocity (middle), and substrate type (bottom) during a literature review of anadromous and amphidromous sturgeon (ATL, Atlantic sturgeon; GFS, Gulf sturgeon; GS, green sturgeon; SNS, shortnose sturgeon; and WS, white sturgeon) habitat characteristics. The size of a circle represents the number of papers in a single river system. The map uses a geographic coordinate system and the North American Datum of 1983 (NAD 83) projection. Source: Base map from USGS.

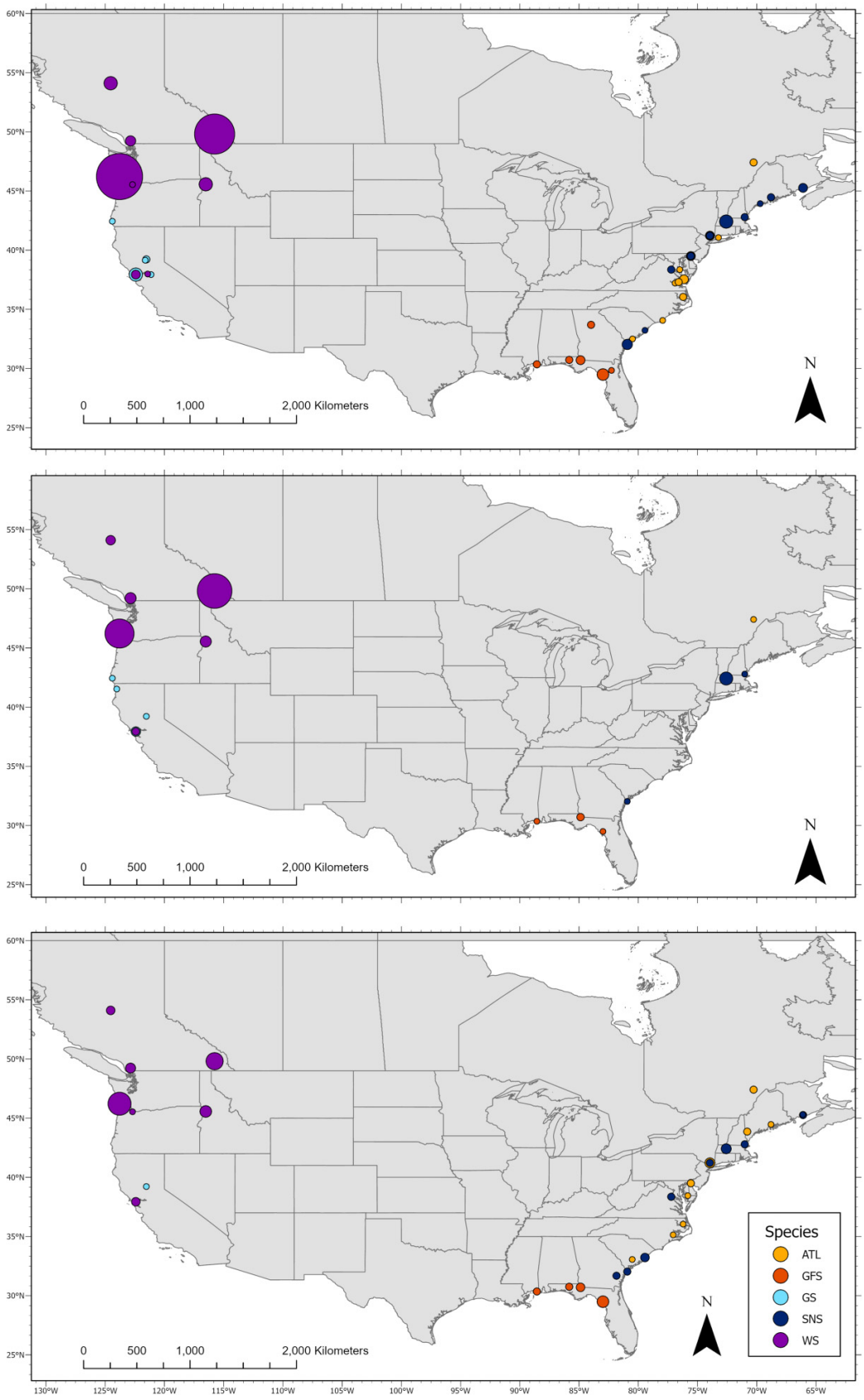


Table 2. Mean and standard deviation (SD) posterior estimates of depth (m) for each species during spawning and non-spawning adult and juvenile river use and estuary use with upper and lower log-based 95% credible intervals.

Activity	Species	*n*	Mean	SD	Lower	Upper
Spawning	Atlantic sturgeon	6	7.79	1.82	4.96	12.24
	Green sturgeon	6	4.94	1.86	2.42	10.07
	Gulf sturgeon	8	3.81	1.56	1.76	8.26
	Shortnose sturgeon	6	5.23	1.72	2.79	9.79
	White sturgeon	45	8.32	0.65	7.14	9.71
	Combined species	70	7.60	4.38	2.66	21.72
Estuary use	Atlantic sturgeon	12	10.24	1.08	8.33	10.24
	Green sturgeon	4	11.55	2.77	7.27	18.35
	Gulf sturgeon	4	2.89	1.74	0.97	8.59
	Shortnose sturgeon	7	6.49	1.09	4.67	9.01
	White sturgeon	1	3.69	3.30	0.82	16.56
	Combined species	25	7.68	3.92	2.30	19.71
River use	Atlantic sturgeon	10	9.25	1.44	6.84	12.52
	Green sturgeon	5	10.12	2.68	6.07	16.87
	Gulf Sturgeon	2	7.15	3.89	2.64	19.39
	Shortnose sturgeon	14	7.73	1.33	5.54	10.80
	White sturgeon	34	13.76	1.13	11.71	16.16
	Combined species	62	10.71	6.09	3.79	30.23

Note: An estimate is given for the combined species and the number of studies corresponding to each estimate is represented by *n*.

Table 3. Mean and standard deviation (SD) with upper and lower log-based 95% credible intervals of the posterior estimates for mean column velocity (m s^{-1}) use for each species during spawning and all non-spawning river use by adults and juveniles.

Activity	Species	*n*	Mean	SD	Lower	Upper
Spawning	Green sturgeon	4	0.76	0.25	0.40	1.44
	Gulf sturgeon	2	0.65	0.35	0.25	1.73
	Shortnose sturgeon	6	0.65	0.21	0.35	1.20
	White sturgeon	35	1.02	0.08	0.87	1.20
	Combined species	47	1.00	0.46	0.42	2.36
River use	Atlantic sturgeon	1	0.44	0.15	0.24	0.83
	Green sturgeon	1	0.57	0.27	0.23	1.39
	Gulf sturgeon	2	0.60	0.18	0.34	1.07
	Shortnose sturgeon	1	0.33	0.14	0.15	0.72
	White sturgeon	12	0.28	0.05	0.19	0.39
	Combined species	17	0.33	0.11	0.18	0.63

Note: A combined species estimate is given for each activity, and the number of studies representing each estimate is given by *n*.

(Table 2). All species, with the exception of Gulf sturgeon, had more than five studies that provided quantitative estimates of non-spawning depth use in the river environment (Table 2).

After conducting our search for documents estimating the velocity use of sturgeon, we found 391 relevant documents. Out of those, we thoroughly reviewed these documents and selected 63 that provided usable estimates (Fig. 1). In total, 47 documents provided estimates of spawning velocities and 17 provided estimates of non-spawning velocities (Supplementary material B, Figs. S4 and S5). We failed to find any documents reporting velocity use by any of the studied species in the estuary environment. The best performing velocity model for non-spawning sturgeon in the river was therefore a random effects model that combined all life stage data (Table 1). Again, the precision of estimates by life stage was evaluated using the 95% credible intervals and determined to be inconclusive (95% CRI: −0.22 to 0.11). We were unable to find any velocity estimates for spawning Atlantic sturgeon, and less than five studies had estimates available for spawning green and Gulf sturgeon (Table 3). White sturgeon comprised the majority of the data, with 35 available estimates (Table 3). Non-spawning estimates were also almost completely comprised of white sturgeon literature. We

found only one or two estimates available for all other species (Table 3).

During our review of literature on substrate use, we compiled and reviewed 546 documents, from which we were able to extract estimates from 90 (Fig. 1). In total, 50 documents provided information on spawning substrate use, 31 included non-spawning adult substrate use, and 24 included juvenile rearing substrate use (Supplementary material B, Tables S1–S3).

Depth

Spawning

We found that white sturgeon and Atlantic sturgeon used deeper spawning areas compared to the other species in this study (Fig. 2). Although Atlantic sturgeon and shortnose sturgeon occupied many of the same river systems, shortnose sturgeon selected for depths that were 1.5 times shallower on average than depths used by Atlantic sturgeon (Fig. 2). White sturgeon and green sturgeon, which are both located on the west coast, also had different spawning depth use. In terms of similarity, the spawning depth use by the green sturgeon was more comparable with that of the shortnose sturgeon, having a 91% posterior overlap (Fig. 2). Finally, Gulf sturgeon used shallower depths than the other species evaluated, with depths approximately 2.2 times shallower than those of white sturgeon (Fig. 2). Collectively, HSI's for spawning North American anadromous and amphidromous sturgeon indicated that the highest probability of depth use (≥0.7) was between 4.0 and 11.0 m deep (Fig. 3).

Non-spawning river use

White sturgeon inhabited deeper areas compared to the other species we evaluated. Green sturgeon were the next closest species in terms of river depth use, but still used areas that were 1.4 times shallower than those used by white sturgeon (Fig. 2). Atlantic sturgeon used depths approximately 1.2 times deeper than those used by shortnose sturgeon. However, there were still overlaps in their depth use, with a 43% overlap in their posterior distributions (Fig. 2). Gulf sturgeon again used shallower depths than the other four species, but this estimate contains great uncertainty due to the limited number of studies available (Table 2). Collectively, HSIs for non-spawning North American anadromous and amphidromous sturgeon in the river indicated that the highest probability of depth use (≥0.7) was between 5.5 and 15.5 m deep (Fig. 3).

Estuary use

The depths used by Atlantic sturgeon were approximately 1.6 times deeper than those used by shortnose sturgeon in the estuary environment. On average, these two species were found in depths 2.9 times deeper than Gulf sturgeon, who again stayed in shallower waters compared to the other species (Fig. 2). Green sturgeon used depths in the estuary that were 1.1 times greater than Atlantic sturgeon; however, much more variability was associated with this estimate (Fig. 2). The only study that reported the depth use of white sturgeon in an estuary found that they used relatively shallow depths, but this estimate had a high level of uncertainty (Table 2). Collectively, HSIs for North American anadromous and amphidromous sturgeon in the estuary environment indicated that the highest probability of depth use (≥0.7) was between 4.0 and 11.0 m deep (Fig. 3).

Velocity

Spawning

Gulf sturgeon, green sturgeon, and shortnose sturgeon all used similar spawning velocities, which were slower in comparison to the estimated spawning velocity of white sturgeon (Fig. 4). On average, the velocities used by spawning white sturgeon were 1.5 times faster than those of the other three species. Collectively, HSIs for North American spawning anadromous and amphidromous sturgeon indicated the highest probability of velocity use (≥0.7) in the river to be between 0.6 and 1.4 m s^{-1} (Fig. 5).

Non-spawning river use

Green sturgeon and Gulf sturgeon used faster velocity areas than the other three species (Fig. 4). Both species used areas approximately 2.1 times faster than those of the white sturgeon (Fig. 4). However, there was a high degree of uncertainty surrounding these estimates due to the limited amount of information available. Velocities used by Atlantic sturgeon and shortnose sturgeon were slightly faster than those used by white sturgeon but much slower than green and Gulf sturgeon (Fig. 4). White sturgeon used slower velocities but had much less uncertainty regarding their use (Fig. 4). Collectively, HSIs for North American non-spawning anadromous and amphidromous sturgeon in the river indicated the highest probability of velocity use (≥0.7) to be between 0.2 and 0.4 m s^{-1} (Fig. 5).

Substrate use

Spawning

The dominant substrate used during spawning, for the most part, consisted of hard substrate (Fig. 6). Green sturgeon were only documented as spawning in areas dominated by clean, hard substrate consisting mostly of cobble and gravel (Fig. 6). A high percentage (74.6%) of Gulf sturgeon also used hard substrate-dominated areas for spawning (Fig. 6). Of the hard substrates used, a majority were using areas dominated by cobble and gravel, as well as larger gravel to boulder substrates. They were not found using any areas dominated by soft substrate, but they were in areas dominated by a mixture of soft and hard substrate that consisted of hard limestone bedrock with clay and fine sediment or coarse sand. Shortnose sturgeon spawning was mostly in areas dominated by hard substrate (60.7%); however, 38.0% of the fish found

Fig. 2. Posterior distributions of depth (m) used by each species of sturgeon (ATL, Atlantic sturgeon; GFS, Gulf sturgeon; GS, green sturgeon; SNS, shortnose sturgeon; and WS, white sturgeon) exhibiting spawning, estuary, and river depth use.

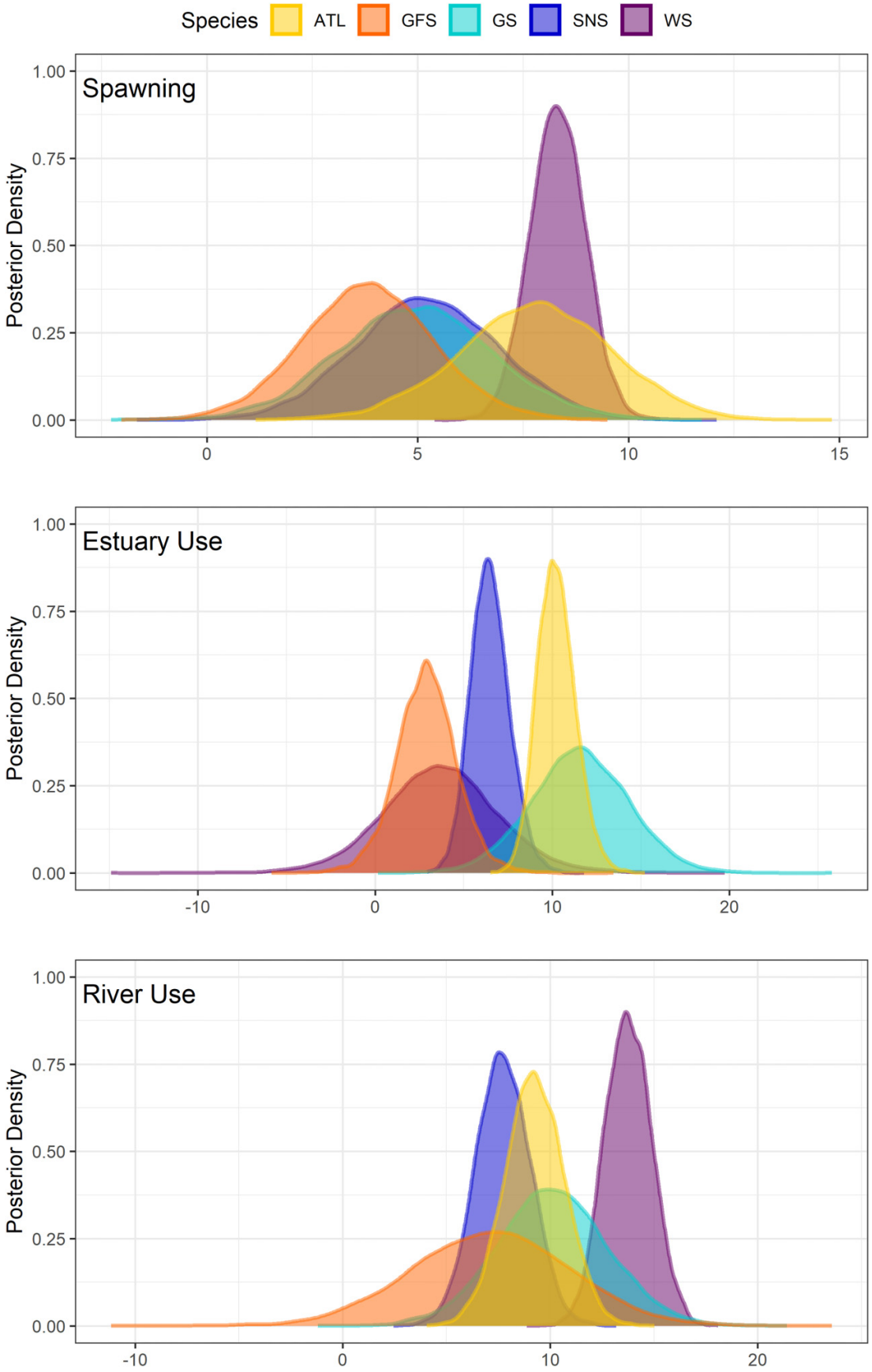
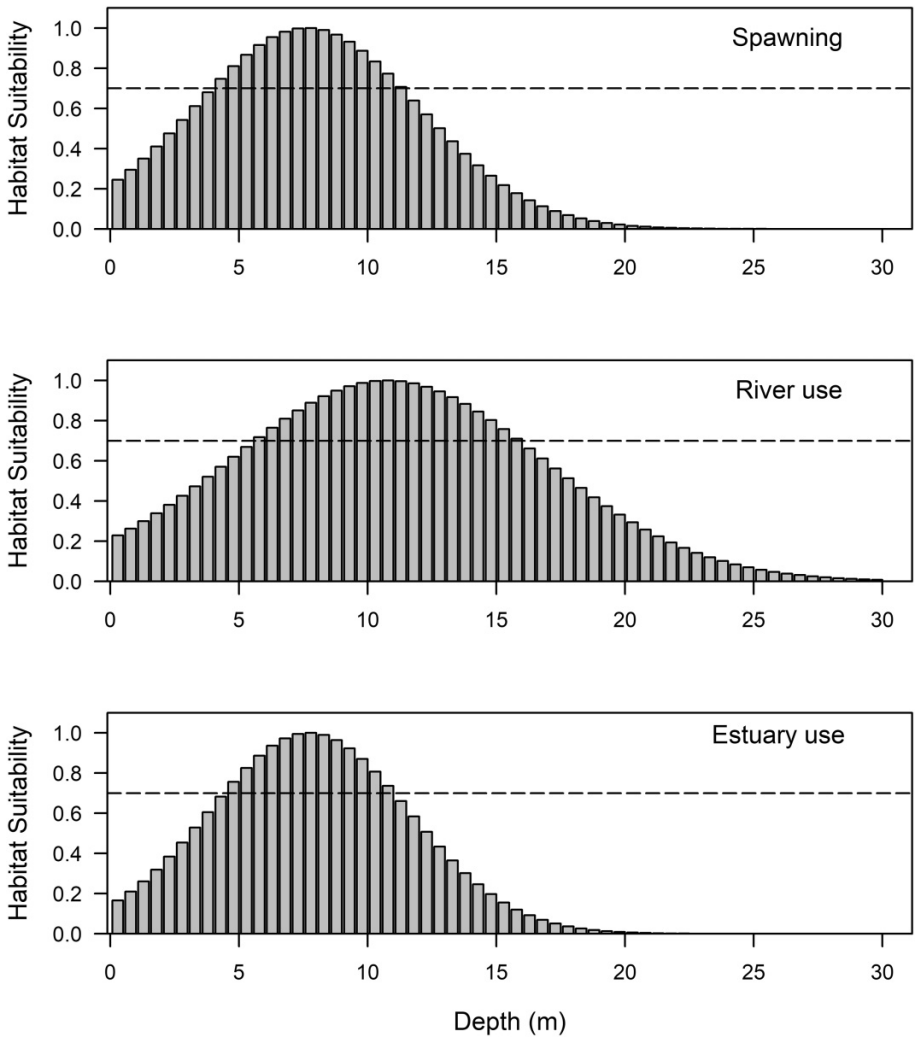


Fig. 3. Habitat suitability indices (HSI) of depth (meters) used by North American anadromous and amphidromous sturgeon during spawning, non-spawning river use, and estuary use. The dashed line represents the probability of use being greater than or equal to 0.7.



during the literature review were documented as spawning in areas dominated by soft substrate, and a small percentage (1.3%) were using areas dominated by a mixture of hard and soft substrate (Fig. 6). A majority of the hard substrate used by shortnose sturgeons was rubble (64–256 mm), boulder, and gravel, whereas the soft substrate consisted of hard-packed clay. White sturgeon spawned in areas dominated by both hard (55.2%) and soft substrate (43.9%), with a small percentage of a mixed-dominated substrate (0.9%) (Fig. 6). The dominant hard substrates used by white sturgeon were cobble and boulder, as well as some areas dominated by gravel. A large percentage of fish used sand as well as other fine sediment combinations such as mud (various combinations of silt, sand, and clay were often referred to as "mud" in the literature), sand, and silt. Lastly, Atlantic sturgeon were a unique case where fine sediment combinations of mud, sand, and silt dominated their spawning substrate use (82.4%; Fig. 6). The small percentage (15.5%) of fish using areas dominated by hard substrate were in areas with bedrock, limestone, boulders, and some gravel. The mixed dominant substrate areas consisted of gravel, sand, and mud. Overall, when all species were combined and evaluated during spawning, a majority of fish (58.0%) used areas dominated by hard substrate, but there were a noticeable number of fish using soft substrate areas (38.4%; Fig. 6).

Non-spawning adults

The dominant substrates used by non-spawning adults were mostly in soft substrate areas (63.8%; Fig. 6). The combined results suggested only a small percentage used areas were dominated by hard substrate (0.3%) and 35.9% were in mixed substrate-dominated areas (Fig. 6). Gulf sturgeon were the only species documented using some areas of dominant hard substrate (3.8%; Fig. 6), which consisted of areas with gravel and some cobble. Areas dominated by mixed substrates used by this species consisted of sand and gravel, and the majority of their used substrate was fine to medium coarse sand with some clay. Atlantic sturgeon adults mostly used areas dominated by mud with some sand and clay use

Fig. 4. Posterior distributions of velocity (m s^{-1}) used by each species of sturgeon (ATL, Atlantic sturgeon; GFS, Gulf sturgeon; GS, green sturgeon; SNS, shortnose sturgeon; and WS, white sturgeon) exhibiting a holding (juvenile and adult) or spawning behavior.

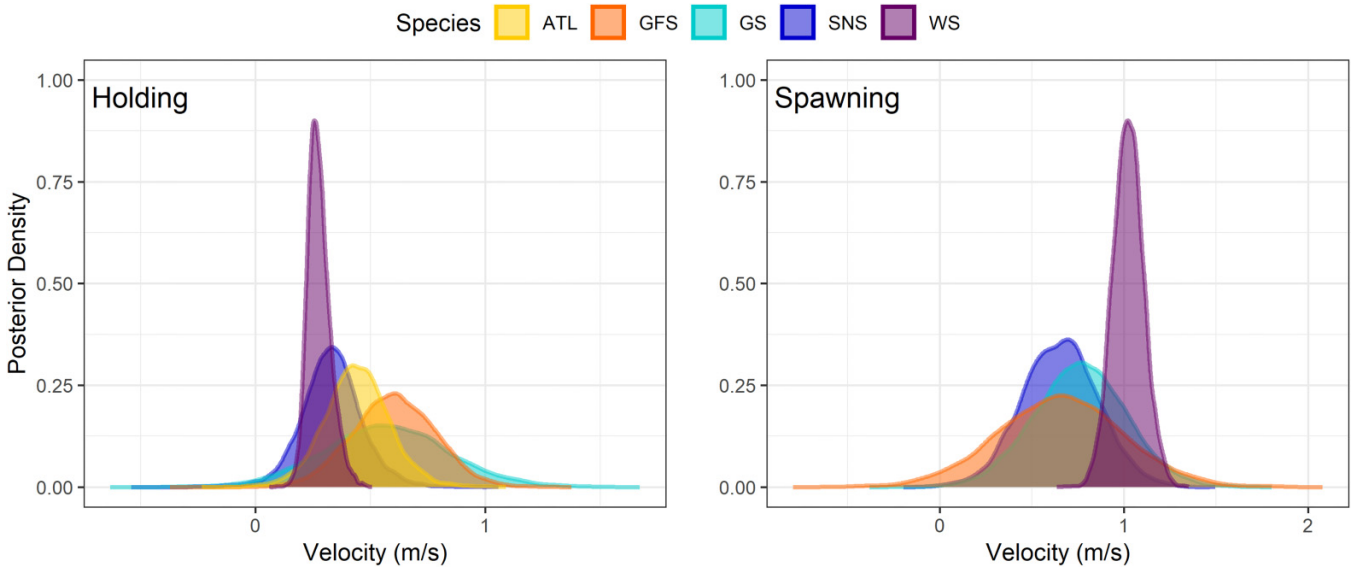
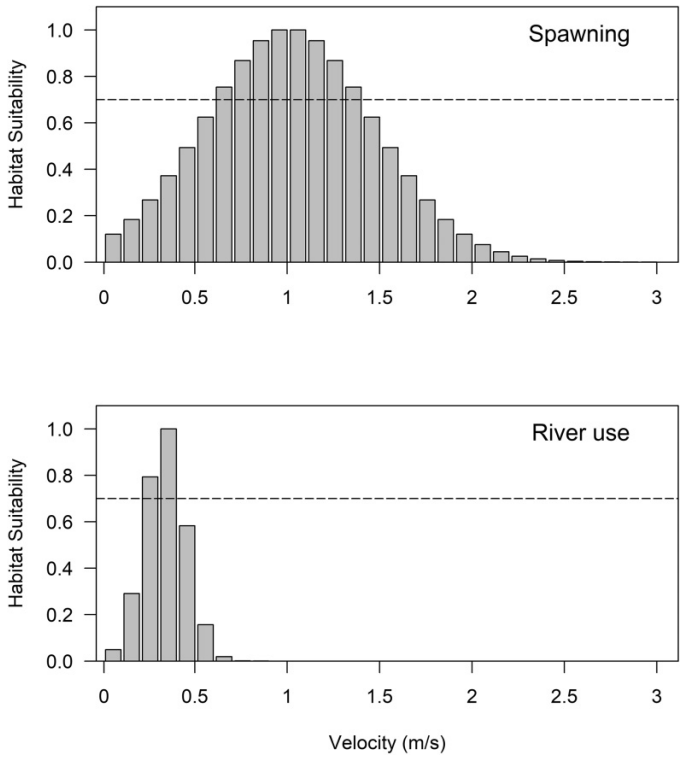


Fig. 5. Habitat suitability indices (HSI) of velocity (m s^{-1}) used by North American anadromous and amphidromous sturgeon during spawning and non-spawning river use. The dashed line represents the probability of use being greater than or equal to 0.7.

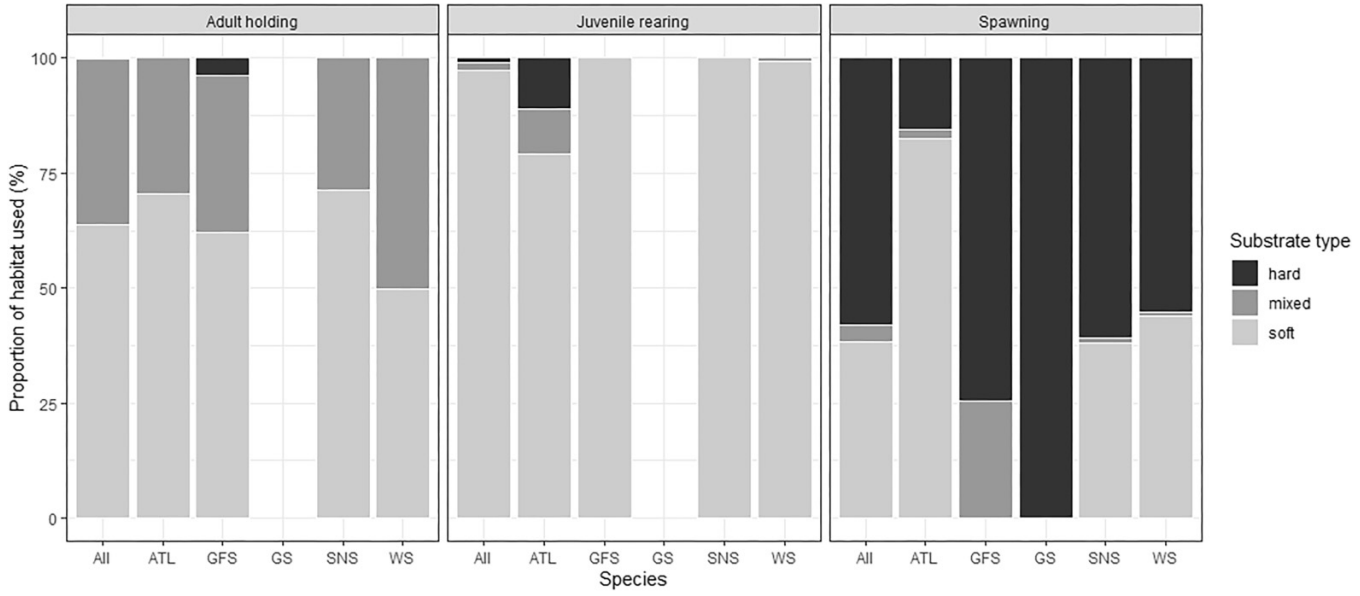


(70.5%; Fig. 6). Mixed substrate-dominated areas contained sand and gravel mixtures as well as some mixed gravel, sand, and mud areas. Shortnose sturgeon were documented as primarily using soft substrate (71.4%; Fig. 6) areas dominated by sand but were also found using mud dominated environments and mixtures of sand and mud substrate. In areas with mixed substrate, shortnose sturgeon were mostly located over a sand and gravel or cobble mix. Lastly, white sturgeon used areas dominated by mud and sand (49.7%), while the rest (50.3%) were using mixed substrates of cobble, silt, and sand (Fig. 6). We found no papers for green sturgeon that directly identified substrate use during adult non-spawning activities in the river.

Juvenile rearing substrate

Juvenile rearing substrate use was dominated by soft substrates (97.3%), and only a small number of fish used areas dominated by hard (1.1%) and mixed (1.7%) substrates (Fig. 6). Gulf sturgeon used sand substrate-dominated areas and shortnose sturgeon used areas with mud and sand with some silt and clay as well. Atlantic sturgeon used areas of soft substrate (79.0%; Fig. 6) consisting of primarily sand and silt mixes with some silt, clay, and mud mixtures. Areas dominated by hard substrate (11.1%) were not thoroughly defined as anything more than "hard substrate" and contained no further specifications on rock or substrate types used (Fig. 6). Mixed substrate-dominated areas (9.8%) consisted of areas mixed with sand and gravel (Fig. 6). White sturgeon juvenile substrate use was primarily areas dominated by sand; sand with some mud and clay; and mixes of clay, sand, and silt (99.1%; Fig. 6). Small percentages of fish used areas dominated by hard (0.03%) and mixed (0.8%) substrates (Fig. 6). These areas consisted of some rubble and gravel with mud; gravel and sand mix; cobble; and silt and cobble mixes. Again, no papers directly identified the number of juvenile green sturgeons using substrate.

Fig. 6. Percentage of sturgeon using primary substrate types for each species of sturgeon during various activities. Atlantic sturgeon (ATL), Gulf sturgeon (GFS), green sturgeon (GS), shortnose sturgeon (SNS), white sturgeon (WS), and combined results for all species (All) are all represented. Substrate types are divided into three major categories: hard substrate (representing cobble, limestone, boulders, and gravel), soft substrate (sand, silt, mud, and clay), and a mixture of hard and soft substrate representing the dominant substrate type. Activities are divided up by spawning, juvenile substrate use, and adult substrate use when not spawning (most of these activities consisted of a holding action).



Discussion

We achieved our objective of synthesizing information on habitat use for anadromous and amphidromous sturgeons in North America. Through the accumulation of evidence across unique studies and systems, we can effectively address the reproducibility and replication of research. Thus, we are able to make results from existing studies more generalizable and quantify the variability observed among populations and studies. Single-study research is important for documenting what we know about a species in a specific system, but without the synthesis of additional information, one study is often insufficient to describe an ecological phenomenon (Nichols et al. 2019, 2021). Synthesizing information incorporates reproducibility across time and space, resulting in a more holistic representation of the true overall effect size, which increases the generalizability and applicability of the results (NASEM 2019; Nichols et al. 2021). Using these techniques, managers experiencing data limitations and regulatory constraints can make informed decisions based on empirical data while still incorporating uncertainty.

During this analysis, we found sturgeon species used a diversity of habitats; however, many of these species shared similar habitat use patterns. For instance, spawning habitat use was similar among species and was likely related to the requirements of egg survival and successful reproduction. Numerous potential benefits exist for spawning in faster water, including the oxygenation of eggs, the removal of fine sediment, disease prevention, and reduced predation (Sulak and Clugston 1998; Forsythe et al. 2013; Parsley and Kofoot 2013). Coarse substrate is often correlated with areas of faster water and is important for recruitment success through reduced egg suffocation mortality and the survival of larvae due to access to crevices for hiding (McAdam et al. 2005; McAdam 2011). Spawning in high-velocity areas without adequate substrate also has its consequences and may result in egg dislodgment and larval drift mortality (McAdam 2011). During non-spawning activities, fish were documented using low-velocity, soft substrate areas likely for the purpose of conserving energy, preventing injury, and prey availability (Sulak and Clugston 1999; Erickson et al. 2002; May and Kieffer 2016). Sturgeon have specific morphological features such as a flattened rostrum and body shape, heterocercal tail, and large pectoral fins for stabilization that are all advantageous for bottom skimming (Wilga and Lauder 1999; Liao and Lauder 2000; Rapp et al. 2011). Previous research has suggested that sturgeon foraging in substrates such as cobble expend more energy swimming and foraging than sturgeon in fine sediment, which can then allocate more energy towards growth (Nguyen and Crocker 2006).

Although general patterns were observed among species, several important differences existed, mostly during spawning. Historically, the maximum lengths of white sturgeon and Atlantic sturgeon were much larger than the other species evaluated, which is one hypothesis as to why these species used deeper areas for spawning. Although what was once considered a typical maximum length is uncommon and unlikely today with declining stocks and declining maximum ages, it is suspected that this may still influence how sturgeon select spawning habitat. Parsley et al. (2008) hypoth-

esized that white sturgeon in the Kootenai River may exhibit site fidelity and return to areas simply because that is where they have always spawned. If this is the case for other populations and species as well, historical documentation of spawning grounds may become increasingly important for restoration projects and management actions (e.g., harvest restrictions). Gulf sturgeon represented an outlier for this maximum length hypothesis. Their use of shallower depths may be influenced more strongly by the river characteristics within which they reside. A majority of the rivers Gulf sturgeon were observed spawning in include the Suwanne, Apalachiocola, Choctawhatchee, and Yellow Rivers, which may not have the depth potential as some of the other rivers used by other species. River characteristics are likely an important function of depth use by many of these species; however, it is important to note that many of these species share river systems and ecoregions and were still identified as using different habitats. Ultimately, the use of different areas within a system is what allows many of these species to coexist. Information concerning habitat avoided (absence data) by sturgeons will be increasingly important to determine whether fish are purposely selecting against habitat or whether it is simply unavailable in a system. Habitat use may change as a function of availability, and it is important to consider those changes when using our findings to inform conservation decision-making, especially in combination with environmental variability (e.g., climate change).

Spawning velocities used by each species may be a function of habitat availability but could also be related to egg characteristics. Being broadcast spawners, all sturgeon species have somewhat adhesive eggs. However, white sturgeon, a species observed using areas of higher velocities, have been specifically noted as having highly adhesive eggs (Siddique et al. 2014). Research that evaluated differences in egg adhesiveness between green sturgeon and white sturgeon described egg chorion in green sturgeon as being approximately half the thickness as white sturgeon (Deng et al. 2002). Egg adhesiveness likely also influences the importance of spawning substrate for each species. As an example, green sturgeon not having as adhesive eggs as white surgeon may add more importance to substrate type. Less adhesive eggs would rely more heavily on becoming trapped in crevices rather than adhering to surfaces to prevent displacement by flow (Dettlaff et al. 1993). This may be why green sturgeons are documented as only spawning in areas dominated by hard substrates (i.e., Brown 2007; Poytress et al. 2015; Wyman et al. 2018). Atlantic sturgeon, shortnose sturgeon, and white sturgeon all used areas with soft substrate during active spawning (i.e., Parsley et al. 1993; Devries 2006;Kazyak et al. 2020). It is unclear if these fish value depth and velocity more when selecting areas to spawn or if this is the only substrate type available. As noted earlier, sturgeon may also choose to spawn in these areas simply because this is where they have always spawned, regardless of changing habitat and environmental conditions. Currently, no known benefits have been identified for fish spawning in soft substrate, and it is a well-documented recruitment issue for these species (Paragamian et al. 2001; McAdam et al. 2005; McAdam 2011, 2015). Specifically, egg suffocation from sand cover and increased predation from lack of cover are both consequences of spawning over soft substrate (Paragamian et al. 2001; Gadomski and Parsley 2004).

An important aspect of meta-analyses and literature reviews is their ability to highlight areas of knowledge gaps. Every species included in this analysis experienced a knowledge gap and benefited from the estimates provided by the other species. During our review, we found no documents that directly observed green sturgeon using substrate as either juveniles or non-spawning adults. We did find descriptive summaries for juveniles that suggest fish use areas with fine substrate for foraging at night and large cobble structures available for hiding during daylight (Kynard et al. 2005; Gruber et al. 2017). We also located descriptive summaries of adults in Washington estuaries using areas dominated by unvegetated fine substrates such as mud, sand, and silt while feeding (Moser et al. 2016, 2017; Stilwater 2018). However, we lacked data that could be incorporated into the framework of this analysis. Another major critical knowledge gap identified was the lack of quantitative estimates available for velocity during Atlantic sturgeon spawning. Expressed throughout the literature is the importance of velocity during spawning for this species (LeBreton et al. 2004); however, techniques to measure velocity can be field-intensive and cost-prohibitive. Lastly, another potentially important knowledge gap identified during this research was the lack of information available during the juvenile life stage. We found no differences between juvenile and adult non-spawning habitat during this analysis, which may be related to a paucity of data and the larger uncertainty estimates associated with juvenile habitat use. It would be valuable to better understand juvenile sturgeon habitat use to determine if adults and juveniles are truly using similar holding and rearing environments.

Modeling habitat availability is often the first step in identifying areas for habitat restoration projects for species of conservation concern. This requires information on habitat use, and preferably habitat use for each unique life stage. None of the sturgeon species evaluated in our study had enough information on their own to address characteristics of habitat use during all life history stages, and it is worth noting that these data gaps are not unique to sturgeon. In such cases, the typical response would be to rely on expert elicitation, assume homogeneity in habitat use across life history stages, or delay action until further studies are conducted. Importantly, delaying action while waiting on the results from additional studies may result in an unnecessary loss of time that at-risk species simply cannot afford. Synthesizing the available literature and conducting a meta-analysis allowed us to provide composite estimates across species and life history stages so that management decision-making can be informed by the best-available, data-driven science when species and life history stage-specific data are lacking. We strongly believe that “collecting more data” is not always the answer to ecological problems, especially when it may be important to consider limiting the disruption and risk of handling threatened or endangered species. Meta-analyses such as ours provide baseline estimates that would be useful to incorporate into the decision-support models that habitat

restoration efforts typically rely on. Although variances are large for some of the estimates and the appropriateness of transferability across species and regions may be questioned, these estimates provide a foundation for decision-support models and the effect of these uncertainties on the decision-making process can (and should) be evaluated through the use of formal sensitivity analyses. Importantly, such an analysis would allow decision-makers to determine whether the uncertainty matters within the context of the decision and whether there is actually a need to work towards decreasing that uncertainty (i.e., further study) to accurately inform management decision-making aimed at achieving specific objectives.

Meta-analyses provide a means to address the issue of data limitations in endangered species management. By synthesizing available information, we gain statistical power and reveal large-scale trends that would have otherwise gone unnoticed through the scope of an individual study (i.e., similarities and differences in spawning depth use among species based on maximum length). As the number of published manuscripts and documents continues to rise and our ability to access the existing literature continues to improve, there is a greater need to synthesize the information available (Arnqvist and Wooster 1995). Reporting effect sizes becomes increasingly important, especially if managers and researchers wish to see their contributions used in efforts such as this. Our review of velocity literature resulted in 391 papers that were downloaded for further review; of those, only 63 reported estimates could be used for this analysis. This meant a 16% inclusion rate, even after putting in extra effort to calculate the mean and standard deviations for those studies that did not report estimates. Many of the papers that were flagged for review used terms such as “slow or high velocity areas” and “deep or shallow areas”. The vagueness of these descriptions can lead to linguistic uncertainty from different interpretations of what is meant by these terms (Reagan et al. 2002). Reporting effect sizes is extremely important for the evaluation of strength and the importance and magnitude of the results. Making effect sizes readily available in reports and publications will improve the quality of meta-analyses and will valuably pass findings on for further use. When estimates or raw data are provided when communicating findings, we open possibilities for synthesis and the leverage of information to be as productive and efficient as possible.

Caveats exist that should be considered in the interpretation of the reported results from this literature review and meta-analysis. Transferability of HSI among various systems is thought to be best supported by the inclusion of absence or non-use data. However, during our literature search, there was not enough information available containing absences that would justify omitting the extent of presence-only data available. HSI developed from presence-only data are well documented as also providing reliable results (Belaud et al. 1989; Moir et al. 2005) and do not contain the unreliability associated with absence data (Cianfrani et al. 2010). Sampling methodology and availability may also influence habitat estimates. For example, many sturgeon species are documented as using deeper habitats during the day and moving to shallower environments at night when they are most active (Parsley et al. 2008). Most sampling, and therefore the estimates provided, were collected during the daytime when it is safe to perform fieldwork and is likely missing important dynamics of habitat use at night. Lastly, there are many other factors besides depth, velocity, and substrate type that contribute to sturgeon habitat use. Aspects such as temperature, cover, food availability, competition, and predation are just as important when defining habitat (Milner et al. 1985; Karr et al. 1986). We chose to evaluate depth, velocity, and substrate type to address the question of “what is sturgeon habitat?” because these habitat descriptors can be and often are integrated with hydraulic modeling to assess current areas of suitable habitat within a river system.

During this literature review and meta-analysis, we were successful in synthesizing estimates of habitat use among North American anadromous and amphidromous species of sturgeon. We noted several similarities among the species and discussed potential differences in habitat use. The estimates we described may provide some river systems with their first ever baseline estimates of habitat for sturgeon. Meta-analytic techniques are becoming increasingly important for the development of empirical estimates to aid in evidence-based decision-making. Without these techniques, we rely on best judgement, expert elicitation, or sometimes a single study that offers little empirical strength for assessing habitat across broader riverscapes. Indeed, our hope is that managers will use the sturgeon habitat estimates we provided herein in conjunction with population and hydrodynamic models to make informed decisions about the prioritization of habitat restoration projects that are frequently based on expert judgement or oversimplified assumptions (i.e., homogenization of habitat use across life history stages). Incorporating all available information (and their associated uncertainties) into a decision-making framework helps managers evaluate the effect of uncertainties and prioritize information needs, given the resolution of data and information needed to properly inform management decisions dependent on the context of the problem. This is increasingly important for endangered species management, where we may need to prioritize some information needs over others, given the often limited resources available to collect new information in a timeframe that meets the needs of managers and the conservation-reliant species they work to recover.

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Data availability

The data were derived from the studies listed in the supplementary material (Supplementary material B). These data are available from the corresponding author upon request.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

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