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ARTICLE

Fine-scale habitat selection of green sturgeon (*Acipenser medirostris*) within three spawning locations in the Sacramento River, California

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Abstract: Vast sections of the Sacramento River have been listed as critical habitat by the National Marine Fisheries Service for green sturgeon spawning (*Acipenser medirostris*), yet spawning is known to occur at only a few specific locations. This study reveals the range of physical habitat variables selected by adult green sturgeon during their spawning period. We integrated fine-scale fish positions, physical habitat characteristics, discharge, bathymetry, and simulated velocity and depth using a two-dimensional hydraulic model (FaSTMECH). The objective was to create habitat suitability curves for depth, velocity, and substrate type within three known spawning locations over two years. An overall cumulative habitat suitability score was calculated that averaged the depth, velocity, and substrate scores over all fish, sites, and years. A weighted usable area index was calculated throughout the sampling periods for each of the three sites. Cumulative results indicate that the microhabitat characteristics most preferred by green sturgeon in these three spawning locations were velocities between 1.0 and 1.1 m/s, depths of 8–9 m, and gravel and sand substrate. This study provides guidance for those who may in the future want to increase spawning habitat for green sturgeon within the Sacramento River.

Résumé : De grands tronçons du fleuve Sacramento figurent sur la liste des habitats essentiels du National Marine Fisheries Service des États-Unis pour la reproduction de l'esturgeon vert (*Acipenser medirostris*), bien que la reproduction de ce poisson n'ait été signalée que dans quelques endroits. La présente étude révèle l'éventail de caractéristiques physiques de l'habitat sélectionnées par les esturgeons verts adultes durant la période de reproduction. Nous avons intégré de l'information à échelle fine sur l'emplacement des poissons, les caractéristiques physiques de l'habitat, le débit, la bathymétrie et la vitesse et la profondeur simulées en utilisant un modèle hydraulique bidimensionnel (FaSTMECH). L'objectif consistait à établir des courbes d'adéquation des habitats en fonction de la profondeur, de la vitesse et du type de substrat dans trois sites de reproduction connus sur une période de deux ans. Une note cumulative globale d'adéquation de l'habitat a été calculée qui représente une moyenne des notes pour la profondeur, la vitesse et le substrat pour tous les poissons, sites et années. Un index d'aire utilisable pondérée a été calculé pour toutes les périodes d'échantillonnage pour chacun des trois sites. Les résultats cumulatifs indiquent que les caractéristiques des microhabitats privilégiées par les esturgeons verts dans ces trois sites de reproduction sont des vitesses de l'écoulement de 1,0–1,1 m/s, des profondeurs de 8–9 m et des substrats de gravier et de sable. L'étude fournit de l'information utile aux efforts futurs visant à accroître l'habitat de reproduction des esturgeons verts dans le fleuve Sacramento. [Traduit par la Rédaction]

Introduction

Sturgeon species that inhabit lakes, estuaries, and oceans make upstream migrations in rivers to spawn within the headwaters of rivers. The geomorphology and physical properties of the spawning sites have been well described for the Gulf sturgeon (*Acipenser oxyrinchus*) (Fox et al. 2000), lake sturgeon (*Acipenser fulvescens*) (LaHaye et al. 1992), pallid sturgeon (*Scaphirhynchus albus*) (DeLonay et al. 2007), and white sturgeon (*Acipenser transmontanus*) (Parsley et al. 1993). While coarse-scale descriptions of spawning habitat have been described for the green sturgeon (USFWS 2013; Poytress et al. 2015), no studies have yet described fine-scale habitat selection within these sites. This species is among the most adversely affected species in North America due to inadequate management and restoration capacity and poorly defined habitat criteria (Pikitch et al. 2005).

There are two genetically distinct populations of green sturgeon found along the coast, bays, and rivers of western North America: the northern and southern distinct population segments (nDPS and sDPS, respectively) (Israel et al. 2004). The latter population has been in serious decline primarily due to watershed degradation, water diversions, and dams (Adams et al. 2007; Heublein et al. 2009; Mora et al. 2009), resulting in the listing of sDPS green sturgeon as federally threatened (NMFS 2006). The sDPS population and its recruitment largely rely on spawning habitats found in the main stem of the Sacramento River (Brown 2007; Heublein et al. 2009; Thomas et al. 2014; Poytress et al. 2015), although

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spawning has recently been documented in one of its major tributaries (Seesholtz et al. 2015). Successful management of green sturgeon is highly dependent upon more expansive research (NMFS 2015), particularly on its reproductive ecology given the biologically recent large-scale trend in spawning habitat loss (Adams et al. 2007; Mora et al. 2009).

Currently, vast sections of the Sacramento River have been listed as critical habitat for green sturgeon spawning (NMFS 2009, 2015), yet spawning is known to occur at these and only a few other locations based on egg and larval sampling (USFWS 2013; Poytress et al. 2015). What range of physical habitat variables exists at these confirmed spawning sites? How do green sturgeon utilize the available microhabitat during their spawning period? Do they prefer a particular depth, substrate type, and (or) flow regime? The objective of this study was to address these important questions by modeling habitat selection based on three common descriptors of microhabitat (depth, velocity, and substrate) in combination with fine-scale fish movement data within known spawning aggregation sites in the Sacramento River.

Methodology

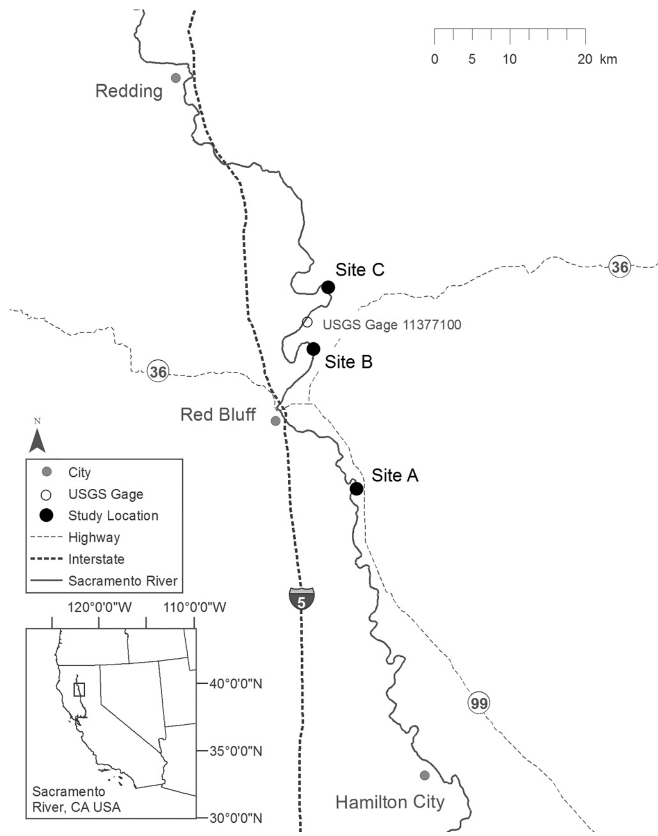
Study sites

Within the main stem of the Sacramento River in northern California, the current putative spawning grounds of sDPS green sturgeon occur from approximately Redding near the Keswick Dam down to near Hamilton City. In general, this diverse riverine habitat exhibits meandering alluvial habitat to constrained bedrock morphology and a mix of agricultural, residential, and natural land uses along the banks. We described green sturgeon habitat selection at three locations as follows: Site A, rkm 377; Site B, rkm 407.5; Site C, rkm 426. These sites were shown to be spawning sites based on net tows and egg mats in other studies (Poytress et al. 2015) (Fig. 1). All study sites are in close proximity to a tributary stream and are characterized by dynamic flows, variable bathymetry extending greater than 5 m deep, and a mixture of substrate types with gravel and cobble predominant amongst scoured areas of boulder and bedrock and areas of sandy deposits. Overall, Sites A and C are relatively similar in substrate and channel bank morphology, whereas Site B has a narrower channel and more complex bedrock formations along the banks. These specific locations were chosen based on previous active telemetry that indicated extended residence of adult green sturgeon at these sites during the spawning season (Thomas et al. 2014). Spawning was confirmed at these sites using egg mat surveys (Poytress et al. 2015).

Acoustic telemetry

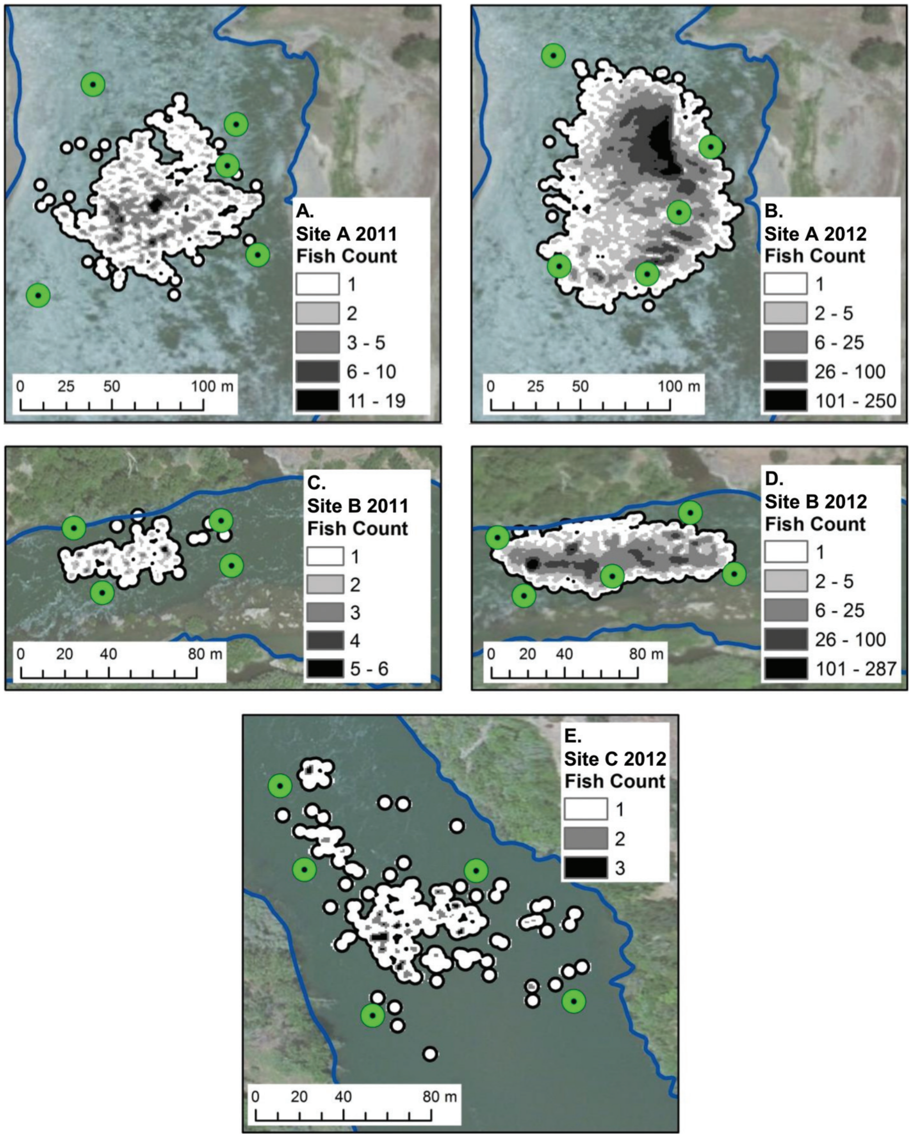
Adult green sturgeon were captured and tagged between 2008 and 2012 in four watersheds. They consisted of the Sacramento River, California, Umpqua River, Oregon, Chehalis River, Washington, and Columbia River, Washington–Oregon (see Matt Pagel, Biotelemetry Laboratory, University of California, Davis, for metadata and sources of tags). During the tagging procedure, a coded ultrasonic transmitter (VEMCO V16-6X) was surgically inserted into the abdominal cavity of each fish (see Thomas et al. 2014 for details on tagging procedure). All surgical procedures performed during tag implantation within the green sturgeon were reviewed and authorized by the University of California, Davis, Animal Care and Use Committee (IACUC) in Protocol 16154. Fish positions were calculated with fine-scale resolution at the three sites on the Sacramento River during the 2011 and 2012 spawning seasons using the VEMCO Positioning System (VPS) (VEMCO Division of AMIRIX Systems, Halifax, Nova Scotia, Canada), an array of underwater acoustic receivers. The receivers making up the VPS were deployed along each bank of the river so that they were able to record positions of sturgeon as they moved throughout these aggregation sites (Thomas et al. 2014; Poytress et al. 2015). At each site, the VPS was composed of four or five hydrophone receivers (VEMCO, VR2Ws with colocated 69 kHz transmitters (“sync tags”) attached to each receiver and a separate 69 kHz transmitter (“reference tag”) (VEMCO V13 and V16) moored in the middle of the receiver locations. These had intervals ranging from 600 to 800 s not to interfere with the coded pulse trains from the transmitters on the sturgeon (Fig. 2). The transmitters on the sturgeon (VEMCO V16) emitted uniquely coded ultrasonic signals at random intervals of mainly 60–90 s, while the receivers recorded the identity of the unique transmitter and the date and time of its detection. The locations of all receivers and transmitters were recorded using a Trimble GeoExplorer XT (Trimble Navigation Limited, Sunnyvale, California) with submeter positioning accuracy.

Fig. 1. Map of the study reach in the upper Sacramento River showing the three sites, rkm 377 (Site A), rkm 407.5 (Site B), and rkm 426 (Site C). Here, the Sacramento River flows from north to south. The common names of the study sites are not given to protect the spawning habitat for the endangered species from poaching.



Tag detections from each receiver were downloaded and subsequently post-processed by VEMCO to derive fish positions with an associated horizontal positioning error (HPE) estimate calculated for each position. HPE is a unitless estimate of error: lower HPE values correspond to smaller scatter of calculated positions (i.e., higher precision) (Smith 2013). Fish positions with HPE >8 m were removed from the data set to increase the accuracy of the fish positions used in subsequent analyses (see Scheel and Bisson 2012; Coates et al. 2013). In general, VPS performance decreased at discharge levels greater than approximately 350–400 m^3/s, as observed through fewer detections, smaller proportions of detections contributing to positions, and reduced positioning efficiency. The mean discharge of water at the United States Geological Survey (USGS) streamgage nearest to the three study sites (gage No. 11377100, above Bend Bridge near Red Bluff) was 390.8 m^3/s during the winter of 2011 and 266.1 m^3/s during the winter of 2012 (U.S. Geological Survey 2014).

Fig. 2. Fish positions (horizontal positioning error ≤ 8) within VEMCO Positioning System (VPS) locations at Site A in (A) 2011 and (B) 2012, Site B in (C) 2011 and (D) 2012 (D), and Site C in (E) 2012. Circular green symbols represent VPS receivers and the thick blue line represents the river's edge. Basemaps from ArcGIS Online World Imagery (sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community). [Colour online.]



Habitat measures

Discharge, bathymetry, and water-surface elevation data were recorded at all three sites on 22–24 May 2013 using an acoustic Doppler current profiler (River Surveyor M9; SonTek, San Diego, California) to develop and calibrate the hydraulic model. The acoustic Doppler current profiler was mounted to an aluminum boat at a fixed transducer depth of 0.2–0.5 m. Position was measured using a co-located global positioning system (GPS) (Trimble R7; real-time kinematic) with centimetre positioning accuracy. At each site, we measured discharge using the acoustic Doppler current profiler by completing three or four cross sections near the top of the reach. Following the discharge measurement, we recorded a longitudinal water-surface elevation. The paired discharge and water-surface elevation profiles were used to calibrate the hydraulic model at each site. The channel bathymetry was measured by completing a perimeter sweep near the water's edge and multiple cross sections through the reach in a zigzag pattern. This pattern resulted in measured cross sections that were separated by less than one channel width apart.

A stage–discharge relationship is required at each site to model flow correctly. The discharges were obtained from the nearest gage to each of the three sites (USGS gage No. 11377100). This gage is approximately 36 and 9 km upstream from Sites A and B, respectively, and 7 km downstream from Site C. In addition, pressure sensors (HOBO; Onset Computer Corporation, Bourne, Massachusetts) were deployed at four locations within each site, three in the channel and one on the closest shore from 8 March to 11 June 2014. The on-land pressure transducers were used to provide an atmospheric pressure correction for the in-channel transducers. The location and datum of each pressure sensor were determined with the GPS. The resulting water-surface elevation at the transducers located at the downstream end of each site was compared to the USGS gage stage data (U.S. Geological Survey 2014). Travel times of approximately −0.5, 1.75, and 3.5 h for Sites A, B, and C, respectively, were determined based on the time-separating peak in the measured stage, recorded in the pressure sensors at each site, with the corresponding peak in measured discharge at the USGS gage of 741.9 m^3/s on 10 March 2014. The shifted discharge was plotted against the measured stage at each location and a third-order polynomial was fit to the data. This functional relationship was used to define the stage–discharge boundary condition at each location. Because of the relatively short travel time between the USGS gage and the three sites, we modeled discharge using the gage's recorded daily discharge values. The simulated discharge at each reach was interpolated within 12 h time steps.

At each site, we used a dual frequency identification sonar (DIDSON) (Sound Metrics Corporation, Lake Forest Park, Washington) to visualize and classify substrate types for inclusion in the selection models. The DIDSON recorded continuous high-quality acoustic images of the channel bottom along with concurrent GPS positions logged by a Trimble GPS on 27–28 June 2013. We made six longitudinal transects at Site A, three at Site B, and five at Site C based on the width of the channel and the complexity of the substrate. The acoustic images of the substrate collected by DIDSON were inspected using Sound Metrics software. Substrate types were categorized into the following size classes based on a modified Wentworth particle size scheme (Wentworth 1922): sand (0.06–2 mm diameter), gravel (3–64 mm diameter), cobble (65–256 mm diameter), and boulder (0.257–3 m diameter), with any boulders larger than 3 m classified as bedrock. Additionally, we characterized large submerged objects (e.g., trees) as snags, although these were only present in Site A. The positions of the substrate points were loaded into ArcGIS 10.1 (ESRI 2012) for conversion into polygon shapefiles. Points of uncertainty were reexamined in situ using an underwater video camera. We also conducted random spot tests to quantify the accuracy of our substrate classification procedure, resulting in the correct match of 80.9% of test points.

Habitat flow model

We used the Flow and Sediment Transport with Morphologic Evolution of Channel Hydrology (FaSTMECH) model (Nelson and McDonald, 1996; Nelson et al. 2016*a*) within the International River Interface Cooperative modeling interface (Nelson et al. 2016*b*) for this study. The model is two-dimensional and flow is assumed to be incompressible, hydrostatic, and quasi-steady. Thus, the simulation of the time-varying discharge hydrograph during the telemetric sampling period is approximated as a piecewise sequence of steady flows. FaSTMECH is quasi-three-dimensional, which means the model solves the vertically averaged equations expressing conservation of mass and momentum and then uses that solution along with similarity vertical structure functions and the streamlines of the vertically averaged flow solution to assign vertical structure along those streamlines. In addition, the model computes secondary flow components associated with channel or streamline curvature perpendicular to those streamlines. The model equations are solved on a curvilinear orthogonal coordinate system (the so-called "channel-fitted" coordinate system). This model has been used and verified extensively on a wide variety of rivers (Lisle et al. 2000; Conaway and Moran 2004; Harrison et al. 2011; Legleiter et al. 2011; Logan et al. 2011; Hafs et al. 2014).

The minimum requirements for the development and calibration of the FaSTMECH model are topography and boundary conditions, typically water-surface elevation at the downstream boundary and discharge at the upstream boundary. The model was developed on an approximately 2 m × 2 m curvilinear orthogonal grid using the measured bathymetric data supplemented with available LiDAR data collected in February and March 2010 (CVFED 2014) to provide bank topography. The model was calibrated using the measured longitudinal profiles of water-surface elevation and the associated measured discharge (357, 413, and 401 m^3/s for Sites A, B, and C, respectively) collected at each of the three sites on 22–24 May 2013.

Following the calibration of the hydraulic model for each site, the flow was simulated during the spawning season in 2011 and 2012. At each site, the flow was simulated between 15 May and 15 July in 2011 and between 16 April and 27 June in 2012. These date ranges span the telemetered fish positions at each site. We simulated flow on a 12 h time step using the stage–discharge relationship developed at each site described previously. The resulting simulations provide time-specific velocity and depth at each node of the computational grid. To facilitate the calculation of the microhabitat metrics, substrate types were also interpolated to the computational grid nodes, although the channel morphology and substrate were assumed to be constant throughout the simulation.

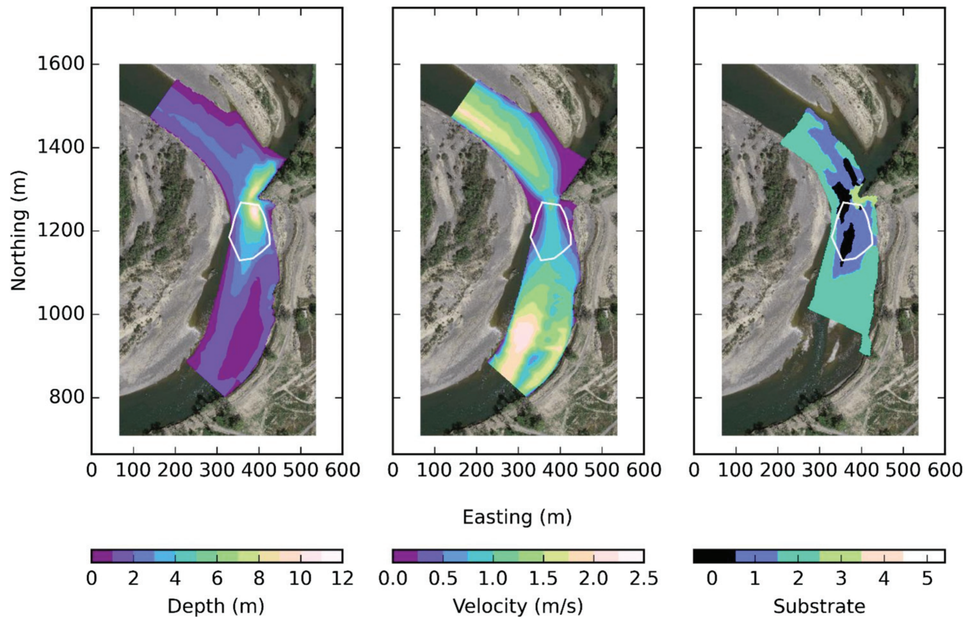
Habitat suitability values

In this section, we describe the procedure to calculate the available and selected physical habitat metrics as determined from the simulated flow within the sampling footprint of the VPS array for each of the three sites. The selected habitat metrics are then converted into habitat suitability values. The simulated flow through the reach is used to (1) determine the available habitat within the footprint of the VPS array and (2) associate each telemetered fish position with a value of depth and velocity as simulated in the hydraulic model and the static measured values of substrate type. The sampled areas corresponded to the spatial extent of fish positions calculated by the arrays of telemetry receivers (Fig. 2). The available habitat values were determined by extracting the simulated depth, velocity, and substrate at each grid node within each VPS sampling area over the duration of the flow simulation period at each 12 h time step. Each telemetered fish position contained a fish identification, a time stamp, and a location in UTM coordinates. A depth, velocity, and substrate type were then assigned to each fish position by interpolating the simulated values at each fish position at the appropriate time step within the simulation. The procedure provides the following: (1) a distribution of depth, velocity, and substrate within the VPS sampling footprint at each simulated time step and (2) a value of depth, velocity, and substrate for each telemetered fish position.

To develop the habitat suitability values, each depth, velocity, and substrate value assigned to a fish location was weighted by the inverse of the areal fraction of that value in the sampled area as follows. For each modeled time step, the fraction of each habitat parameter by area within the sample footprint was determined. For example, if a sampled area contained only two substrate types, sand and gravel, and sand encompassed 70% of the sampled footprint and gravel 30%, then the areal fraction of that substrate value for each fish sample found over sand would be 0.7 and over gravel would be 0.3. The fraction by area for depth and velocity were developed by a parallel method; however, the distribution of these values in the sampling footprint changed at each modeled time step (i.e., every 12 h), as the discharge and downstream stage for the model reach changed with time. The suitability curves were then developed by weighting each sampled value by the inverse of the available fraction. Using the example above, we assigned each fish sample over sand a weight of 1/0.7 or 1.42 and each fish sample over gravel would be assigned a weight of 1/0.3 or 3.33. Weighting by the inverse of the availability of each parameter gives more importance to those patches of substrate that are less available yet still selected.

At each sampled site and year, the number of fish sampled and the number of samples per fish varied. To account for this asymmetry in the number of telemetry samples for each fish, we additionally weighted each habitat suitability value by the inverse of the fraction that each fish contributed to the total numbers of fish observations by site and year. The effect of weighting by the inverse fraction is to equalize the contribution of each fish to the calculated habitat metrics.

Fig. 3. Depth (left), velocity (middle), and substrate (right) at the Site A reach. Depth and velocity values were calculated during the calibration simulation conducted at a measured discharge of 356.55 (E) m^3/s. Substrate values were determined using dual frequency identification sonar (DIDSON) scans (0 = sand, 1 = gravel, 2 = cobble, 3 = boulder, 4 = bedrock, and 5 = snag). The polygon outlined in white depicts the outer boundary of fish locations detected by the VPS in 2011 and 2012. [Colour online.]



Paired distributions of available and the weighted utilized habitat for each site and each year provide insight into habitat selection. We compared the cumulative distributions of the available and selected habitat data using two-sample Kolmogorov–Smirnov (K–S) goodness-of-fit tests to determine if there were significant differences between the utilized and available habitat. Habitat suitability curves were developed for depth, velocity, and substrate by normalizing the selected values by the largest fraction to produce a suitability value between 0 and 1 (0 = least suitable, 1 = most suitable).

Weighted usable area

The physical habitat or "weighted usable area" (WUA, in m^2) at each site was calculated as

$$\text{WUA} = \sum_{1}^{n} \text{CSI} \times a_i \tag{1}$$

where n is the number of nodes in the computational grid, CSI is the composite suitability index value, and a_i is the contributing area for each grid node (Bovee et al. 1998). The composite suitability index value is calculated at each node in the computational grid by converting the simulated habitat metrics to suitability values using the habitat suitability curves and then calculating the geometric mean of these values. The WUA is calculated at each site to assess the quality of the physical habitat as a function of the discharge. The quality as represented by the WUA here is strictly the physical habitat. The WUA in this study was calculated within the entire modeled domain for each reach (approximately 300 m up- and downstream from the VPS). The habitat suitability index values (scaled from 0 to 1) associated with the simulated values of depth and velocity (calculated based on a given discharge), as well as observed substrate type, were plotted in each grid node within the reach surrounding each VPS site/year. For each node, the value of the cumulative habitat suitability was calculated as the geometric mean of the three individual suitability values (i.e., mean of velocity, depth, and substrate suitability indices). The WUA was calculated by multiplying the representative area of each 2 m × 2 m grid node within each reach by its cumulative habitat suitability index value at a given discharge within 12 h and summing these values.

Results

Habitat characteristics

The discharge during the flow simulation period was generally similar in 2011 and 2012 with flows varying between 300 and 425 m^3/s. Figure 3 provides an example of the simulated flow results for depth and vertically averaged velocity at Site A for the calibrated discharge of 357 m^3/s as well as the mapped substrate types. The figure captures the unique characteristics of the physical habitat within the VPS footprint relative to the reach as a whole for a single discharge. Site A has a deep pool (approximately 11.5 m) downstream from a sharp bend in the river. The deep pool is associated with a bedrock spur protruding into the channel constricting and locally accelerating the flow. Adjacent to the accelerating flow are large lateral recirculation eddies along the channel banks downstream from the constriction. The VPS footprint generally covers the downstream extent of the pool and the maximum simulated velocities occur upstream from the VPS footprint.

The simulated depth and vertically averaged velocity values for the grid nodes within the VPS footprint for each study site in each year (termed "available" habitat) over the duration of the simulated flow are summarized in Table 1. In general, the distribution of available habitat is different between sites. We show the distribution only for Site A (Fig. 4). While most depths at Sites A and C were between 2 and 9 m with a steadily decreasing proportion of depths above this level, Site B exhibited a very low relative proportion of depths less than 9 m. A wider distribution of available velocities was noted at Sites A and C, whereas Site B showed very few available velocities at the extreme ends of the scale. The substrates available within the VPS footprints were primarily gravel followed by sand at Site A, gravel followed by cobble at Site C, and bedrock followed by sand at Site B. Overall, the distribution of available depths was similar between 2011 and 2012 in Sites A and B. While the shape of the distribution of available velocities was

Table 1. Fish positions, available habitat, and utilized habitat within VPS footprints.

	Site A		Site B		Site C	All sites
Study year	2011	2012	2011	2012	2012	2011, 2012
Number of fish positions	1241	23458	133	6856	183	31871
Number of individuals	12	26	3	22	3	39
Available habitat						
Depth (m)						
Median	4.45	4.16	10.29	9.75	3.86	4.67
Mean ± SD	4.86±1.95	4.58±1.95	10.03±1.45	9.47±1.42	4.38±2.21	5.56±2.70
Range	0.72–11.64	0.47–11.10	3.70–12.50	3.26–11.46	1.27–11.79	0.47–12.50
Velocity (m/s)						
Median	1.10	0.86	1.03	0.81	0.93	0.93
Mean ± SD	0.99±0.45	0.78±0.40	1.04±0.24	0.80±0.17	0.84±0.35	0.87±0.40
Range	0.001–2.02	0.001–1.63	0.29–1.71	0.21–1.15	0.02–1.68	0.001–2.02
Substrate (% of total)						
Sand	33	33	39.6	39.6	5.3	30.1
Gravel	63	63	3.5	3.5	55.9	37.8
Cobble	3	3	9.9	9.9	38.6	12.9
Boulders	0.5	0.5	1.9	1.9	0.0	1.0
Bedrock	0	0	45.1	45.1	0.2	18.1
Snag	0.5	0.5	0.0	0	0.0	0.1
Utilized habitat						
Depth (m)						
Median	4.57	6.71	11.39	10.40	3.58	7.65
Mean ± SD	4.53±1.13	6.73±1.92	11.28±0.51	10.29±0.75	4.06±1.63	7.41±2.34
Range	0.16–9.38	1.59–10.60	7.44–11.87	4.34–11.37	1.38–9.66	0.16–11.87
Velocity (m/s)						
Median	1.18	1.05	1.25	0.98	0.99	1.02
Mean ± SD	1.09±0.27	1.02±0.19	1.21±0.11	0.97±0.08	0.90±0.26	1.01±0.18
Range	0.06–1.47	0.05–1.43	0.55–1.32	0.24–1.12	0.09–1.41	0.05–1.47
Substrate (% of total)	24.3	15.4	9.5	8.5	24.3	16.4
Sand						
Gravel	48.3	84.3	45.7	20.8	48.3	49.5
Cobble	27.4	0	19.2	36.3	27.4	22.1
Boulders	0	0.3	25.6	11.5	0	7.5
Bedrock	0	0	0	22.9	0	4.5
Snag	0	0	0	0	0	0

similar between the two years at these sites, the distribution was slightly shifted towards higher velocities in 2011.

Fish positions

A total of 31 871 positions from 39 adult green sturgeon were analyzed in this study (Fig. 2), including 21 males, 2 females, and 16 fish of unknown sex. At the time of tagging, fish had an average fork length of 174.03 ± 13.75 cm (mean ± SD, based on data from 36 fish), ranging from 138 to 201 cm, and a girth of 64.15 ± 6.92 cm (mean ± SD, based on data from 36 fish), ranging from 50 to 76 cm. The number of positions per fish ranged from 1 to 4572 (mean ± SD: 1593.55 ± 1198.63). The number of total fish positions per site/year ranged from 133 to 23 458 (Table 1); 50.0% of fish were found in at least one VPS site, 42.7% were found in two sites, and 7.5% were found in all three sites.

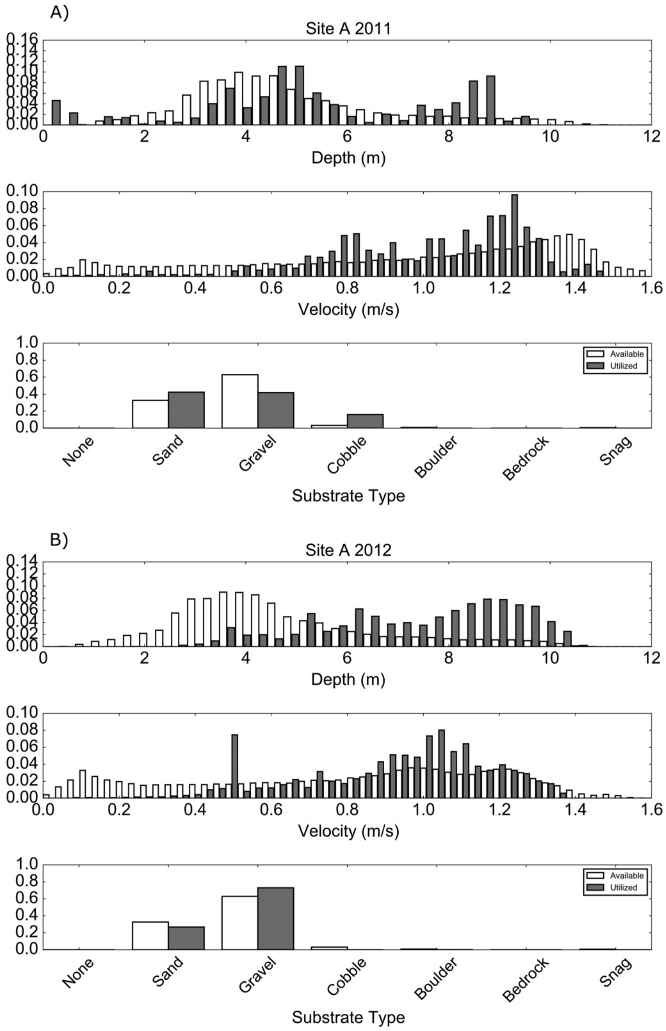
Green sturgeon were positioned at locations with depths between 0.16 and 11.87 m and velocities between 0.05 and 1.47 m/s (Table 1). The mean depth at fish positions within each VPS site ranged from 4.06 ± 1.63 m (Site C, 2012) to 11.28 ± 0.51 m (Site B, 2011), with a collective mean of 7.41 ± 2.34 m across all sites and years. The mean velocity at fish positions within each site ranged from 0.90 ± 0.26 m/s (Site C, 2012) to 1.21 ± 0.11 m/s (Site B, 2011), with a collective mean of 1.01 ± 0.18 m/s across all sites and years. In regards to sturgeon position over substrate type, 30% of all unweighted fish positions occurred over sand, 38% over gravel, 13% over cobble, 1% over boulders, 18% over bedrock, and 0.1% over snags.

Comparisons between available and utilized habitat were conducting using utilization data weighted by areal fraction and by fish counts. At Site A, sturgeon utilized deeper habitats than expected based on availability in both years. In 2011, there was a peak in the distribution of available depths at around 4 m, while sturgeon showed peak usage at around 5 m followed by another peak at around 9 m (Fig. 4A top). There were significantly more shallow depths available within the pool than were occupied by the sturgeon (K–S test, $N = 1242$, $p < 0.01$). During 2012, the distribution of available depths was similar to that during 2011, yet again the sturgeon occupied the deeper depths at the sites ranging from 4 to 10 m with a peak at around 9 m (Fig. 4B top). The difference between depth availability in the pool and that occupied was also significant (K–S test, $N = 23\,459$, $p < 0.01$).

The distribution of velocities present in Site A during 2011 ranged from 0 to 1.6 m/s and was leptokurtotic (skewed to left) with a peak at 1.4 m/s (Fig. 4A, middle). The sturgeon were recorded less often in the slower velocities present from 0.0 to 0.4 m/s but were more often present in the mid-velocities from 0.7 to 1.3 m/s during 2011. These differences between the velocities available and those selected were significant (K–S test, $N = 1242$, $p < 0.01$). Note that fewer sturgeon were present in water flows >1.4 m/s. At Site A, the differences between the velocities present and those selected by the sturgeon were greater during 2012. Whereas the velocities were relatively uniformly distributed from 0.1 to 1.3 m/s, the sturgeon avoided velocities from 0 to 0.4 m/s and selected velocities exceeding those available from 0.9 to 1.3 m/s (Fig. 4B, middle). These differences were also significant (K–S test, $N = 23\,459$, $p < 0.01$).

The sturgeon responded differently relative to substrate at Site A between the two years of the study. During 2011, the sturgeon

Fig. 4. Available and utilized green sturgeon (*Acipenser medirostris*) habitat within the VPS sampling area of Site A for (A) 2011 and (B) 2012. The data are weighted (*y*-axis = fraction of total samples (unitless) according to the number of counts for each fish, thus avoiding one fish having a disproportionate effect on the results of the study).



were present over sandy bottoms slightly more than the availability of this substrate may predict (Fig. 4A, bottom), but during 2012, they were slightly less common over the sandy bottom than expected (Fig. 4B, bottom). During 2011, the sturgeon were over gravel less often than the availability of gravel substrate may suggest. However, they were detected more often over a gravel substrate than expected during 2012. Finally, a greater percentage of the sturgeon positions occurred over cobble than expected based on availability during 2011. In conclusion, at Site A, the sturgeon selected depths ranging from 4 to 10 m and velocities of 0.5–1.3 m/s. The sturgeon were detected more often over gravel and cobble than was expected based on substrate availability.

At Site B, the relative distributions of utilized depths during 2011 and 2012 exceeded those expected (K–S test, 2011: $N = 136$, $p < 0.01$; 2012: $N = 6857$, $p < 0.01$). The sturgeon often occupied waters 10 m or greater in depth. With respect to velocities, the sturgeon also were present more often during the higher velocities in a disproportionate manner to their availability. During 2011, sturgeon were generally present most often in waters 1.1–1.3 m/s but with the highest peak in utilization at 0.8–0.9 m/s. Yet in 2012, they were most present from 0.8 to 1.0 m/s. The frequencies of occupation at the higher velocities were disproportionate to the available velocities (K–S test, 2011: $N = 136$, $p = 0.05$; 2012: $N = 6857$, $p < 0.01$). Fish were positioned most frequently over gravel in 2011 and over cobble in 2012, despite low availability of these substrates.

The relative distribution of utilized depths and velocities at Site C in 2012 was similar to the distribution of available habitat, with a peak in sturgeon positioned at depths of 3 m and velocities of 0.9 m/s. Utilized habitat values indicated that more fish were positioned at greater depths than expected by availability alone (K–S test, $N = 184$, $p < 0.05$), but fish did not appear to be selecting particular velocities (K–S test, $N = 184$, $p = 0.43$), despite a strong usage peak between 1.4 and 1.5 m/s. The sturgeon at Site C were predominantly positioned over cobble and sand at higher levels than expected by availability and over gravel less than expected. Finally, fish also selected sand substrate more often than expected.

Habitat suitability

We determined habitat suitability values by normalizing the weighted depth, velocity, and substrate values associated with fish positions (Fig. 5). Habitat suitability values for depth are shifted towards higher depths at Site B (highest utilization at 10–11 m) (Fig. 5B, top) and Site A (highest utilization at 8–9 m) (Fig. 5A, top) but are similar across most depth bins at Site C (highest utilization at 4 and 6 m) (Fig. 5C, top). Habitat suitability values for velocity are generally right shifted at all sites, with the narrowest range of utilized velocity bins at Site B (highest utilization at 0.9–1.0 m/s) (Fig. 5B, middle) and the widest range at Site C (highest utilization at 0.8–1.0 m/s) (Fig. 5C, middle). The velocity bin with the highest utilization at Site A was 1.0 m/s (Fig. 5A, middle). The highest habitat suitability values for substrate were cobble at Site C (Fig. 5C, bottom), boulder at Site B (with the widest spread in suitability values across substrate types) (Fig. 5B, bottom), and gravel at Site A (Fig. 5A, bottom). When all data were combined, the highest utilization of depth occurred at 8–9 m, for velocity at 1.0 m/s, and for sand and gravel substrate (Fig. 5D, bottom). However, it is important to note that the values in the overall plots of suitability values were heavily influenced by the Site A 2012 data set that produced 73.6% of the total positioned fish (Table 1). The selection of depth, velocity, and substrate over time at Site A during 2012 is illustrated in an animation posted on the Biotelemetry Laboratory website (see http://biotelemetry.ucdavis.edu/images/CJFAS_Wyman_etal_Animation_Site_A_2012.mp4.

Weighted usable area

WUAs were calculated based on discharge rates, associated cumulative habitat suitability indices, and the area of the reach surrounding each VPS array (Table 2). The discharge range of 288.76–670.95 m^3/s during 2011 resulted in a WUA range of 6003–14 303 m^2 at the Site B reach and 5744–10 539 m^2 at the Site A reach. The 2012 discharge range of 217.70–433.14 m^3/s produced a WUA range of 5668–7661 m^2 at the Site C reach, 11 120–14 301 m^2 at the Site B reach, and 8348–10 543 m^2 at the Site A reach.

Animations developed to show habitat suitability and WUA over the measured duration of the spawning season for each site and year are available from the authors. A frame from the Site A 2012 animation depicting habitat suitability and WUA during that year's median discharge rate during the sampling period (308 m^3/s) is shown in Fig. 6. Changes in discharge can affect WUA, as discharge directly impacts both velocity and depth. For example, as discharge increases, some microhabitat areas may become less suitable (e.g., as velocity or depth values rise above preferred levels), while other areas may become more suitable (e.g., areas that were too shallow or slow to be preferable could increase to desirable levels).

Our results show different relationships between discharge and WUA across the different sites and years, but in general, a negative relationship developed when discharge levels rose above ap-

Fig. 5. Histograms of normalized habitat suitability values for depth, velocity, and substrate. Data are presented for (A) Site A with both years combined, (B) Site B with both years combined, (C) Site C, and (D) all sites and years combined. The data are weighted according to the number of counts for each fish, thus avoiding one fish having a disproportionate effect on the results of the study.

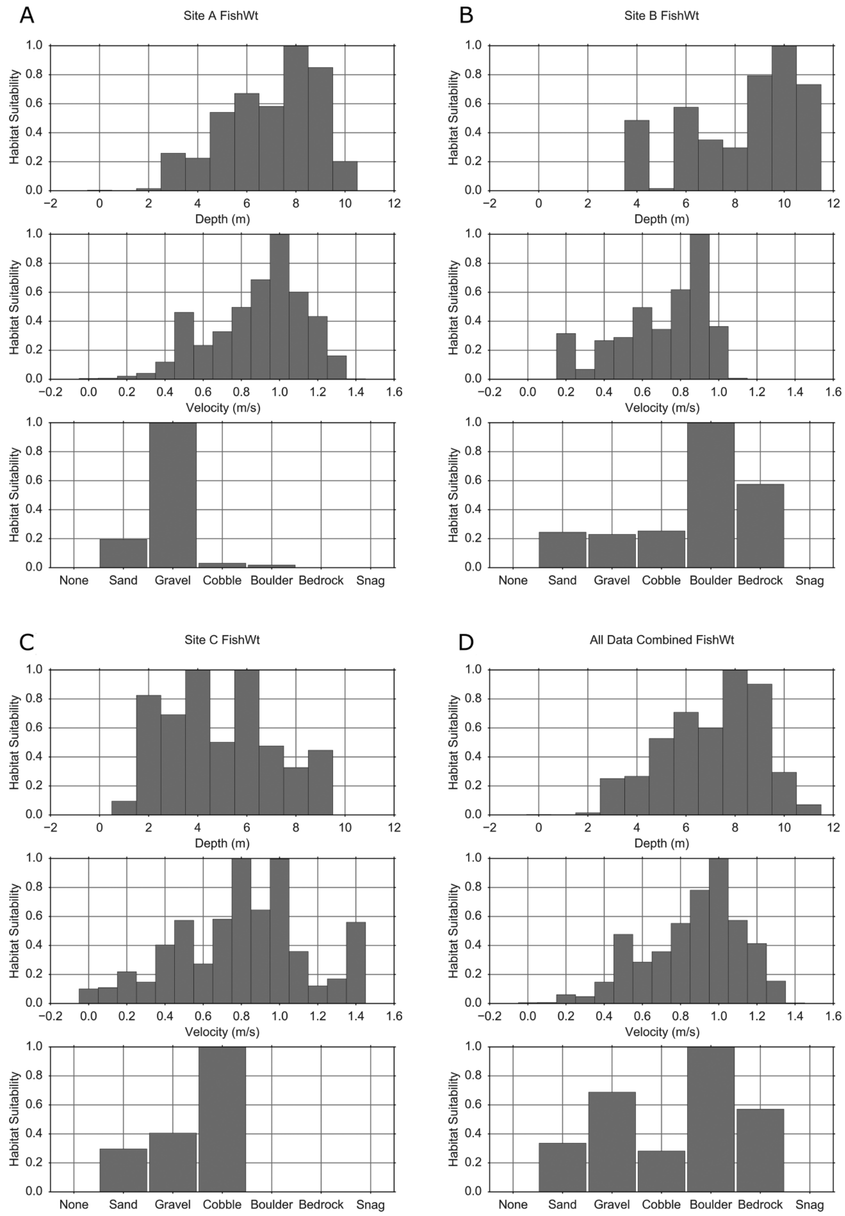


Table 2. Weighted usable area (WUA) in 2011 and 2012 at VEMCO Positioning System locations calculated across the full reach of each study location.

	Site A		Site B		
WUA (m²)	2011	2012	2011	2012	Site C, 2012
Median	9242	10321	13829	13711	7054
Mean ± SD	9043±1012	10178±444	13213±1980	13249±1029	7019±486
Range	5744–10539	8348–10543	6003–14303	11120–14301	5668–7661

proximately 350–400 m^3/s (Fig. 7). This inverse relationship was especially noticeable during the unusually high-flow period experienced in early June 2011. The percentage of habitat with medium or high suitability (as a percentage of total WUA with cumulative suitability scores at medium and above levels, >0.5, or only at high levels, >0.7) was similar between Sites A and C, as was the relationship between discharge and the availability of these habitat suitability levels (Fig. 8). At discharge levels between 240 and 300 m^3/s, the percentage of habitat with at least medium suitability peaked at around 30%–35%, while the percentage of highly suitable habitat peaked at around 8%–10%. Site B had the highest percentage of preferred habitat, with roughly 58% of the reach containing habitat with medium suitability and 27% containing only highly suitable habitat during discharge levels of approximately 350 m^3/s (Fig. 8). In comparison to Site B, Sites A and C showed little variability in the proportion of habitat with medium

Fig. 6. A frame of the animation of habitat suitability at the Site A reach in 2012. (A–C) Simulated depth, simulated velocity, and measured substrate based on a discharge. (D–F) Habitat suitability indices for each of the three habitat parameters at this discharge level on a scale of 0–1 (1 = highest suitability). (G) Cumulative habitat suitability index calculated as the geometric mean of the suitability indices of the three habitat parameters. [Colour online.]

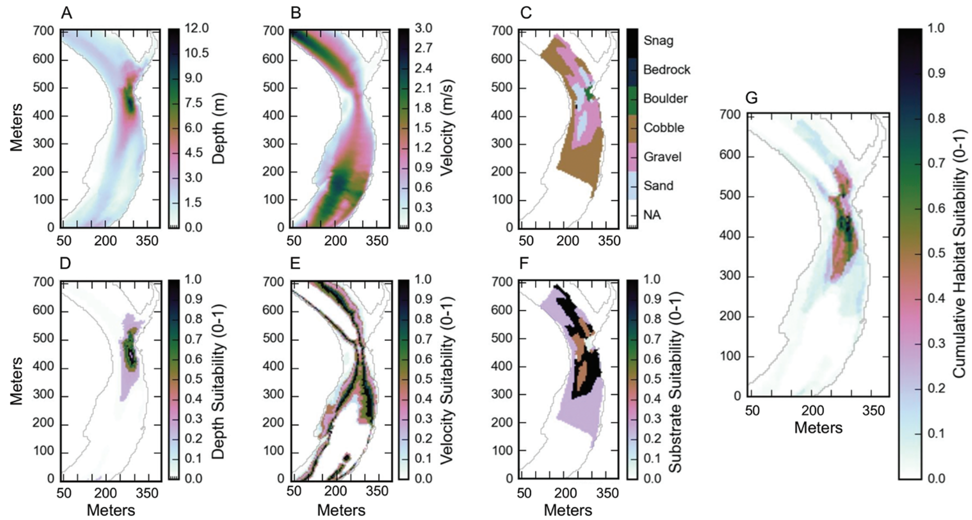
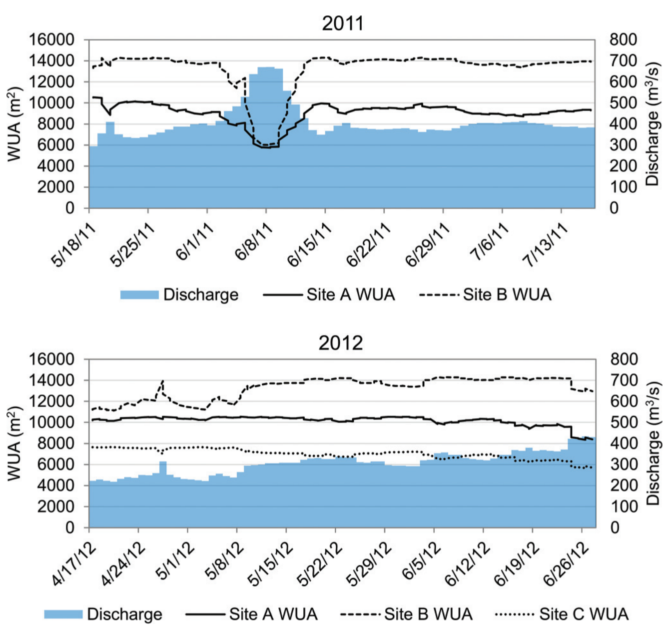


Fig. 7. Weighted usable area (WUA) and discharge over the observed dates in Sites A, B, and C for 2011 (top) and 2012 (bottom). [Colour online.]



or high suitability with changes in discharge. In contrast, Site B displayed sharp increases in overall habitat suitability with increasing discharge up until 350 m^3/s, after which habitat suitability decreased steadily to suitability levels similar to Site A at discharges of 530 m^3/s before falling even lower at higher discharges (Fig. 8).

Discussion

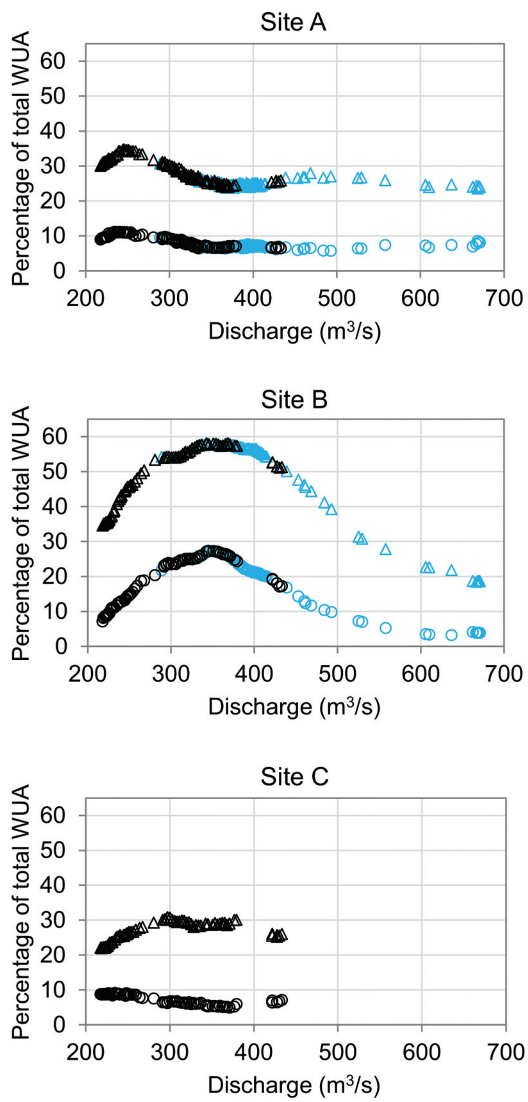
Green sturgeon appear to be selecting particular microhabitats within spawning sites. Habitat suitability values for all three sites combined indicate distinct ranges for the most preferred depth, velocity, and substrate microhabitats. Fish were positioned at depths ranging from 0.16 to 11.87 m, velocities between 0.05 and 1.47 m/s, and a mix of substrate from sand to bedrock. Within these ranges, our findings indicate that the most selected microhabitats included depths between 8 and 9 m, velocities between 1.0 and 1.1 m/s, and gravel and boulder substrate. However, when comparing across sites and between available versus utilized microhabitats within sites, it is evident that green sturgeon displayed more consistent selection for velocities over particular depths or substrates.

Habitat selection

The range of microhabitats over which fish were positioned was similar to the range of microhabitats where green sturgeon eggs were collected in previous studies (USFWS 2013; Poytress et al. 2015), indicating that green sturgeon do spawn over areas containing these microhabitats. The focused use of areas with high depths within our study sites, with highest suitability at 8–9 m, supports previous research that suggested that deep pools were important elements of sturgeon spawning sites. It is possible that there is some density relationship between space available and number of resident spawners. Active tracking telemetry studies showed that adult green sturgeon in the upper Sacramento River spent more time in aggregation sites with deep pools greater than or equal to 5 m during the spawning season (Thomas et al. 2014). Likewise, green sturgeon egg mat surveys in the same region collected eggs most frequently at locations with depths between 5.5 and 5.8 m (USFWS 2013), with an average depth of 6.4 m (Poytress et al. 2015). Adult movement studies of nDPS green sturgeon have also reported utilization of habitats with deep pools during spawning (Erickson et al. 2002; Benson et al. 2007). Tracking and egg mat studies of Atlantic and white sturgeon indicate that they aggregate to spawn similarly in deep water (Parsley and Beckman 1994; Hatin et al. 2002; Paragamian et al. 2002, 2009). Gulf sturgeon spawn over a wide range of depths, 2–6 m (Fox et al. 2000). In contrast, lake sturgeon spawn in shallower water, ranging from 0.1 to 2 m (LaHaye et al. 1992; Auer and Baker 2002; Bruch and Binkowski 2002).

The identified spawning habitats of green sturgeon have been described qualitatively as pools containing high-velocity flows (USFWS 2013; Poytress et al. 2015). While adult green sturgeon in our study were positioned over a wide range of velocities, the most preferred velocities were 1.0–1.1 m/s. These values are slightly higher than the velocities observed at green sturgeon egg collection sites (mean 0.8 m/s: Poytress et al. 2015; most frequently observed at 0.7, 0.88, 0.95, and 1.00 m/s: USFWS 2013). Other species of sturgeon also prefer varying flows for spawning. The veloc-

Fig. 8. Relationship between discharge and the percentage of total WUA (m^2) in each study reach with at least medium (triangles) or only highly (circles) suitable habitat for 2011 (blue symbols) and 2012 (black symbols). [Colour online.]



ities at Atlantic sturgeon spawning sites in the St. Lawrence River varied similarly from 0.25 m/s at the beginning of the ebb tide to 2.2 m/s at its end (Hatin et al. 2002). The lake sturgeon also spawns over a similar range of velocities from 0.5 to 1.3 m/s (Auer 1996; McKinley et al. 1998). The velocities at white sturgeon egg collection sites are slightly higher, between 1.5 and 2.1 m/s in the Columbia River (Parsley and Beckman 1994).

The NMFS (2009) stated that green sturgeon spawning was thought to occur over a wide range of substrate types from hard sand to bedrock, with cobble as the most preferred spawning substrate (Moyle 2002). While egg surveys conducted by Brown (2007) supported the claim that cobble was most associated with the presence of green sturgeon eggs, Poytress et al. (2015) and USFWS (2013) reported that gravel was the dominant substrate type. Our results support the latter study, as gravel was the most preferred substrates within the sample sites (e.g., selective utilization above levels expected based on availability) followed by sand and boulder substrates. In comparison, typical substrates at egg collection sites in rivers regulated by dams ranged from sand (Paragamian et al. 2002) to cobble and boulder (Parsley and Beckman 1994). Lake sturgeon spawn over substrates of coarse gravel or cobble (Auer 1996; McKinley et al. 1998). Atlantic sturgeon spawn over a substrate of rocks and bedrock in the St. Lawrence River (Hatin et al. 2002).

Selective preferences

Preferences for spawning habitats have been reinforced through an increase in fitness benefits associated with spawning in particular microhabitats. Laboratory studies on the characteristics, movements, and survivorship of sturgeon eggs, embryos, and larvae support the assumption that microhabitat choice by adult fish during spawning strongly influences their reproductive success. Green sturgeon eggs are large, dense, and adhesive (Van Eenennaam et al. 2008; Poytress et al. 2015). Their initial adhesive qualities develop at 5–10 s but quickly fade until after fertilization when they become highly adhesive (Van Eenennaam et al. 2012). These properties would facilitate the rapid sinking of eggs in the water column post-oviposition and strong adhesion to substrates after fertilization. Additionally, green sturgeon hatchling embryos are very poor swimmers but prefer cover within interstitial spaces between rocks, as do the more active larvae (Kynard et al. 2005). Specific spawning microhabitat preferences may have evolved if survivorship in these early life stages was influenced by the microhabitat where they were initially deposited (Kynard et al. 2005). These assumptions were supported in white sturgeon. McAdam (2011) provided evidence for substrate selection of pre-exogenous white sturgeon larvae, specifically noting preference for gravel and small cobbles with interstitial spaces for hiding. In the presence of suitable substrate, larvae did not move far from the location where eggs were deposited and larval survival was correlated with the ability of larvae to quickly find those substrates after emergence. In both cases, the initial microhabitat preferences by spawning females for egg deposition would strongly impact larvae survival and thus be subject to selection pressures. While these studies focused on fine-scale benefits derived from suitable substrates, interactions with larger scale flow volume and temperatures are also likely to influence larval survival (Mora 2016).

Our results indicate that adult green sturgeon are selective in their microhabitat use at spawning sites, as the types of microhabitat utilized by the fish did not always reflect the relative distribution of available habitat. The technique of weighting utilized fish counts by the availability of microhabitat bins helps elucidate mismatches between available and utilized microhabitat and points towards potential selective preferences for specific microhabitats. During most surveyed periods and sites, fish seemed to select for deeper locations within the VPS footprint than would be expected by chance given the availability of different depths. This apparent pattern was most strongly illustrated at Site A in 2012 (Fig. 4B, top), which was also the site and year where most fish were positioned. A similar pattern was seen for velocities, as fish appeared to select for higher velocities than expected, except at Site A in 2011 (Fig. 4A, top) and Site C in 2012. Evidence for consistent substrate selection was less apparent. For instance, fish seemed to utilize gravel more often than expected at Site B in both years and Site A in 2012 but less than expected at Site A in 2011 and Site C in 2012.

Interestingly, although fish appeared to prefer deeper and faster microhabitats than expected by chance, patterns suggest that selecting for optimum velocities may be more important than optimum depths. Although higher depths than expected were selected within most sites, the most utilized depth bin varied greatly between sites and years, ranging from 3 m at Site C in 2012 to 11–12 m at Site B in 2011. However, the most preferred velocity bin was similar between all sites and years, ranging from 0.8–0.9 m/s at Site B in 2011 to 1.2–1.3 m/s at Site B and Site A in 2011. Hence, fish may be selecting for depths that produce velocities in a more optimal range, given the discharge conditions at each location. Strong preferences for velocities over depths are not observed in Gulf sturgeon; egg mat surveys reveal that fish spawn over similar velocities and similar depths across years and between sites regardless of river conditions (Flowers et al. 2009).

Changes in river discharge alters the spatial distribution of depth, velocity, and thus substrate composition. As such, the WUA of spawning sites, calculated based on the cumulative suitability index scores for these parameters, also fluctuates in relation to discharge. Alterations to discharge patterns through management decisions, drought, and climate change can therefore have large impacts on the amount and quality of preferred spawning habitat (Gillenwater et al. 2006; Tonina et al. 2011). Decisions that reduce preferred spawning microhabitats are likely to decrease sturgeon reproductive success through reduced survivorship of eggs and larvae, ultimately influencing recruitment and population dynamics within species (Flowers et al. 2009). These relationships highlight the importance of predicting the effects of discharge variation on preferred spawning habitat.

Our results showed that the relationship between discharge and WUA was complex and could vary between sites. In some cases, an increase in discharge led to an increase in WUA, while in others, it led to a decrease or no discernible effect. Sites A and C showed similar responses to discharge in comparison to Site B, most likely due to differences in channel morphology. The two former sites are both characterized by wider channels and gentler bank slopes, while Site B is more channelized with bedrock ledges at the banks. Thomas et al. (2014) documented multiple within-season movements of green sturgeon between spawning and aggregation sites, as did Paragamian et al. (2002) in white sturgeon. It is feasible that these movements could, in part, be driven by the relative increase or decrease in WUA found at each site as a consequence of discharge conditions.

There was a general trend at all sites for discharge and WUA to be inversely related once discharge increased above approximately 350–400 m^3/s (Fig. 7). This was most apparent during the high-water event in 2011 at Sites A and B but was also visible at all sites at the end of the 2012 sampling period. In comparison to Site B, Sites A and C showed little variation with discharge in the percentage of WUA with at least medium suitability or only high suitability (Fig. 8). Site B experienced a steep rise and fall in the proportion of these quality habitats, with the start of this decrease associated with a rise in discharge above approximately 350–400 m^3/s. A similar relationship was reported between discharge and the WUA of highly suitable walleye (*Sander vitreus*) spawning habitat, although the threshold for the start of decreased WUA with increasing discharge occurred at a lower discharge level (Gillenwater et al. 2006). Overall, Site B had the highest percentage of WUA with medium and high suitability. However, the Site A VPS system recorded many more fish positions than the other two sites. This is likely due to the smaller physical area available within the Site B VPS site due to its more channelized and narrow location; positioning efficiency within this location did not differ noticeably from the other locations.

There are two potential explanations for the inverse relationship between discharge and WUA at higher discharge. One interpretation may be that the higher velocities and depths that occur within the VPS array site during higher discharge levels may be less preferable to green sturgeon for spawning habitat. For instance, the velocities may be too high for the sturgeon to effectively hold their positions over or near the spawning grounds. As a result, the fish may move out of the VPS footprint to locations with more preferable velocities or depths at the margins of the river or upstream or downstream. However, low positioning efficiency associated with high discharge rates may also be influencing the relationship between WUA and discharge. At our locations, there was a trend for positioning efficiency to decrease to very low levels when discharge rose above approximately 350 m^3/s. Our overall positioning efficiencies, as well as the relationship between discharge and efficiency, were similar to other studies (see Steel et al. 2014, which includes an assessment of Site A in 2011). Therefore, it is feasible that green sturgeon were present within the VPS sites yet were not effectively positioned due to the environmental noise associated with the higher flow conditions. Additional studies with an expanded VPS array footprint are required to tease apart these competing interpretations. Furthermore, caution should be taken in transferring any conclusions about the WUA–discharge relationship to other systems, as potential differences in habitat suitability criteria may differ between populations or locations (Payne 2003).

A more robust approach is now required that focuses not only on known spawning sites with deep pools but also on alternative sites that may provide preferred spawning grounds under certain discharge conditions or restoration efforts. The potential suitability of tributaries should also be investigated, given the recent spawning evidence from the Feather River (Seesholtz et al. 2015). Indeed, this study highlights the importance of examining microhabitat selection in a variety of conditions. By assessing habitat selection across different sites and years, we were able to better detect patterns in habitat selection, such as the apparent increased importance of velocity microhabitat over depth or substrate. It is important to recognize that habitat site characteristics are derived from complex hydrologic processes that also include variables such as gradient, channel morphology, and the availability of substrates. Given the general assertion that green sturgeon prefer spawning sites with complex hydraulics, future studies should also include a fine-scale examination of vorticity preferences (Wang and Xia 2009). Measuring hydraulic derivatives such as vorticity would provide a more nuanced picture of habitat preferences. Additional monitoring of eggs, larvae, and juveniles may also provide a mechanism for testing if quantity and quality of spawning habitat are in fact a limiting factor to recruitment.

Management implications

Habitat suitability index models have been utilized to examine riverine habitat suitability or selection in relation to resource management (Brown et al. 2000; Vinagre et al. 2006), flow alternations (Zorn et al. 2012), climate change (Tonina et al. 2011), and dam removal/replacement (Gillenwater et al. 2006; Tomsic et al. 2007). We have used this approach to identify the range of available physical habitat variables within three green sturgeon spawning locations in the Sacramento River. As part of the designation of critical habitat for the sDPS green sturgeon, NMFS (2009) stated that suitable spawning sites should include deep pools (≥5 m) with fast, complex flow regimes delivering currents sufficient to impede fungal growth, siltation, and suffocation of eggs. In general, our findings support this characterization and provide important methodologies for precise mapping of selected spawning habitat over a wide range of locations within the putative spawning grounds. It could also be used to more accurately model the effects of management decisions, drought, or climate change on green sturgeon distribution. Indeed, the information from our study could be used in deciding whether to remove weirs on the Feather River to create a secondary spawning area necessary to sustain a robust population of green sturgeon during varying interannual climate changes.

This study provides a framework for evaluating behavioral selection for particular environmental parameters on the microhabitat scale during important life stages within species. By examining habitat selection at this fine scale, we gain a more precise understanding of the mechanisms shaping species behavior and ecology over time. In turn, this information can be used to guide efficacious management decisions regarding a variety of important topics from species recruitment to ecosystem restoration. Indeed, this approach can be used to predict the spawning habitat available for spawning over the 4 year drought between 2012 and 2015 at the three sites.

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References

Adams, P.B., Grimes, C., Hightower, J.E., Lindley, S.T., Moser, M.L., and Parsley, M.J. 2007. Population status of North American green sturgeon, *Acipenser medirostris*. Environ. Biol. Fishes, **79**: 339–356. doi:10.1007/s10641-006-9062-z.

Auer, N.A. 1996. Response of spawning lake sturgeons to change in hydroelectric facility operation. Trans. Am. Fish. Soc. **125**: 66–77. doi:10.1577/1548-8659(1996)125<0066:ROSLST>2.3.CO;2.

Auer, N.A., and Baker, E.A. 2002. Duration and drift of larval lake sturgeon in the Sturgeon River, Michigan. J. Appl. Ichthyol. **18**: 557–564. doi:10.1046/j.1439-0426.2002.00393.x.

Benson, R.L., Turo, S., and McCovey, B.W. 2007. Migration and movement patterns of green sturgeon (*Acipenser medirostris*) in the Klamath and Trinity rivers, California, USA. Environ. Biol. Fishes, **79**: 269–279. doi:10.1007/s10641-006-9023-6.

Bovee, K.D., Lamb, B.L., Bartholow, J.M., Stalnaker, C.B., Taylor, J., and Henriksen, J. 1998. Stream habitat analysis using the instream flow incremental methodology. U.S. Geological Survey, Biological Resources Division, Information and Technology Report USGS/BRD-1998-0004. Available from: https://www.fort.usgs.gov/sites/default/files/products/publications/3910/3910.pdf.

Brown, K. 2007. Evidence of spawning by green sturgeon, *Acipenser medirostris*, in the upper Sacramento River, California. Environ. Biol. Fishes, **79**: 297–303. doi:10.1007/s10641-006-9085-5.

Brown, S.K., Buja, K.R., Jury, S.H., Monaco, M.E., and Banner, A. 2000. Habitat suitability index models for eight fish and invertebrate species in Casco and Sheepscot Bays, Maine. N. Am. J. Fish. Manage. **20**: 408–435. doi:10.1577/1548-8675(2000)020<0408:HSIMFE>2.3.CO;2.

Bruch, R.M., and Binkowski, F.P. 2002. Spawning behaviour of lake sturgeon (*Acipenser fulvescens*). J. Appl. Ichthyol. **18**: 570–579. doi:10.1046/j.1439-0426.2002.00421.x.

Coates, J.H., Hovel, K.A., Butler, J.L., Klimley, A.P., and Morgan, S.G. 2013. Movement and home range of pink abalone *Haliotis corrugata*: implications for restoration and population recovery. Mar. Ecol. Prog. Ser. **486**: 189–201. doi:10.3354/meps10365.

Conaway, J.S., and Moran, E.H. 2004. Development and calibration of a two-dimensional hydrodynamic model of the Tanana River near Tok, Alaska. U.S. Geological Survey Open-File Report 2004–1225. Available from: http://pubs.usgs.gov/of/2004/1225/.

CVFED. 2014. Central Valley Floodplain Evaluation and Delineation (CVFED) Program Lidar: Central Valley. Data available on the World Wide Web (United States Interagency Inventory). Available from: https://coast.noaa.gov/inventory/ [accessed 20 June 2014].

DeLonay, A.J., Papoulias, D.M., Wildhaber, M.L., Annis, M.L., Bryan, J.L., Griffith, S.A., Holan, S.H., and Tillitt, D.E. 2007. Use of behavioral and physiological indicators to evaluate *Scaphirhynchus* sturgeon spawning success. J. Appl. Ichthyol. **23**: 428–435. doi:10.1111/j.1439-0426.2007.00894.x.

Erickson, D.L., North, J.A., Hightower, J.E., Weber, J., and Lauck, L. 2002. Movement and habitat use of green sturgeon *Acipenser medirostris* in the Rogue River, Oregon, USA. J. Appl. Ichthyol. **18**: 565–569. doi:10.1046/j.1439-0426.2002.00403.x.

ESRI. 2012. ArcGIS Desktop: release 10.1. Environmental Systems Research Institute, Redlands, Calif.

Flowers, H.J., Pine, W.E., Dutterer, A.C., Johnson, K.G., Ziewitz, J.W., Allen, M.S., and Parauka, F.M. 2009. Spawning site selection and potential implications of modified flow regimes on viability of Gulf sturgeon populations. Trans. Am. Fish. Soc. **138**: 1266–1284. doi:10.1577/T08-144.1.

Fox, D.A., Hightower, J.E., and Parauka, F.M. 2000. Gulf sturgeon spawning migration and habitat in the Choctawhatchee River system, Alabama–Florida. Trans. Am. Fish. Soc. **129**: 811–826. doi:10.1577/1548-8659(2000)129<0811:GSSMAH>2.3.CO;2.

Gillenwater, D., Granata, T., and Zika, U. 2006. GIS-based modeling of spawning habitat suitability for walleye in the Sandusky River, Ohio, and implications for dam removal and river restoration. Ecol. Eng. **28**: 311–323. doi:10.1016/j.ecoleng.2006.08.003.

Hafs, A.W., Harrison, L.R., Utz, R.M., and Dunne, T. 2014. Quantifying the role of woody debris in providing bioenergetically favorable habitat for juvenile salmon. Ecol. Modell. **285**: 30–38. doi:10.1016/j.ecolmodel.2014.04.015.

Harrison, L.R., Legleiter, C.J., Wydzga, M.A., and Dunne, T. 2011. Channel dynamics and habitat development in a meandering, gravel bed river. Water Resour. Res. **47**: W04513. doi:10.1029/2009WR008926.

Hatin, D., Fortin, R., and Caron, F. 2002. Movement and aggregation areas of adult Atlantic sturgeon (*Acipenser oxyrinchus*) in the St. Lawrence River estuary, Quebec, Canada. J. Appl. Ichthyol. **18**: 586–594. doi:10.1046/j.1439-0426.2002.00395.x.

Heublein, J.C., Kelly, J.T., Crocker, C.E., Klimley, A.P., and Lindley, S.T. 2009. Migration of green sturgeon, *Acipenser medirostris*, in the Sacramento River. Environ. Biol. Fishes, **84**: 245–258. doi:10.1007/s10641-008-9432-9.

Israel, J.A., Cordes, J.F., Blumberg, M.A., and May, B. 2004. Geographic patterns of genetic differentiation among collections of green sturgeon. N. Am. J. Fish. Manage. **24**: 922–931. doi:10.1577/M03-085.1.

Kynard, B., Parker, E., and Parker, T. 2005. Behavior of early life intervals of Klamath River green sturgeon, *Acipenser medirostris*, with a note on body color. Environ. Biol. Fishes, **72**: 85–97. doi:10.1007/s10641-004-6584-0.

LaHaye, M., Branchaud, A., Gendron, M., Verdon, R., and Fortin, R. 1992. Reproduction, early life history, and characteristics of the spawning grounds of the lake sturgeon (*Acipenser fulvescens*) in Des Prairies and L'Assomption rivers, near Montreal, Quebec. Can. J. Zool. **70**(9): 1681–1689. doi:10.1139/z92-234.

Legleiter, C.J., Kyriakidis, P.C., McDonald, R.R., and Nelson, J.M. 2011. Effects of uncertain topographic input data on two-dimensional flow modeling in a gravel-bed river. Water Resour. Res. **47**: W03518. doi:10.1029/2010WR009618.

Lisle, T.E., Nelson, J.M., Pitlick, J., Madej, M.A., and Barkett, B.L. 2000. Variability of bed mobility in natural, gravel-bed channels and adjustments to sediment load at local and reach scales. Water Resour. Res. **26**: 3743–3755. doi:10.1029/2000wr900238.

Logan, B.L., McDonald, R.R., Nelson, J.M., Kinzel, P.J., and Barton, G.J. 2011. Use of multidimensional modeling to evaluate a channel restoration design for the Kootenai River, Idaho. U.S. Geological Survey Scientific Investigations Report 2010-5213.

McAdam, S.O. 2011. Effects of substrate condition on habitat use and survival by white sturgeon (*Acipenser transmontanus*) larvae and potential implications for recruitment. Can. J. Fish. Aquat. Sci. **68**(5): 812–822. doi:10.1139/f2011-021.

McKinley, R.S., Van Der Kraak, G., and Power, G. 1998. Seasonal migration and reproductive patterns in the lake sturgeon, *Acipenser fulvescens*, in the vicinity of hydroelectric stations in northern Ontario. Environ. Biol. Fishes, **51**: 245–256. doi:10.1023/A:1007493028238.

Mora, E.A. 2016. A confluence of sturgeon migration: juvenile survival and adult abundance. Dissertation, University of California, Davis, Calif.

Mora, E.A., Lindley, S.T., Erickson, D.L., and Klimley, A.P. 2009. Do impassable dams and flow regulation constrain the distribution of green sturgeon in the Sacramento River, California? J. Appl. Ichthyol. **25**(s2): 39–47. doi:10.1111/j.1439-0426.2009.01297.x.

Moyle, P.B. 2002. Inland fishes of California. 2nd ed. University of California Press, Berkeley and Los Angeles, Calif.

National Marine Fisheries Service (NMFS). 2006. Endangered and threatened wildlife and plants: threatened status for southern distinct population segment of North American green sturgeon. Fed. Regist. 71:67 (7 April 2006). pp. 17757–17766.

National Marine Fisheries Service (NMFS). 2009. Designation of critical habitat for the threatened southern distinct population segment of North American green sturgeon. Final Biological Report, September 2009.

National Marine Fisheries Service (NMFS). 2015. Southern distinct population segment of the North American green sturgeon (*Acipenser medirostris*). 5-year review: summary and evaluation. NMFS, West Coast Region, Long Beach, Calif.

Nelson, J.M., and McDonald, R.R. 1996. Mechanics and modeling of flow and bed evolution in lateral separation eddies. Glen Canyon Environmental Studies Report. Available from: http://www.gcmrc.gov/library/reports/GCES/Physical/hydrology/Nelson1996.pdf.

Nelson, J.M., McDonald, R.R., Shimizu, Y., Kimura, I., Nabi, M., and Asahi, K. 2016*a*. Modelling flow, sediment transport and morphodynamics in rivers. *In* Tools in fluvial geomorphology. *Edited by* G.M. Kondolf and H. Piégay. John Wiley & Sons, Ltd., Chichester, U.K. doi:10.1002/9781118648551.ch18.

Nelson, J.M., Shimizu, Y., Abe, T., Asahi, K., Gamou, M., Inoue, T., Iwasaki, T., Kakinuma, T., Kawamura, S., Kimura, I., Kyuka, T., McDonald, R.R., Nabi, M., Nakatsugawa, M., Simões, F.R., Takebayashi, H., and Watanabe, Y. 2016*b*. The international river interface cooperative: public domain flow and morphodynamics software for education and applications. Adv. Water Resour. **93**: 62–74. doi:10.1016/j.advwatres.2015.09.017.

Paragamian, V.L., Wakkinen, V.D., and Kruse, G. 2002. Spawning locations and movement of Kootenai River white sturgeon. J. Appl. Ichthyol. **18**: 608–616. doi:10.1046/j.1439-0426.2002.00397.x.

Paragamian, V.L., McDonald, R., Nelson, G.J., and Barton, G. 2009. Kootenai River velocities, depth, and white sturgeon spawning site selection — a mystery unraveled? J. Appl. Ichthyol. **25**: 640–646. doi:10.1111/j.1439-0426.2009.01364.x.

Parsley, M.J., and Beckman, L.G. 1994. White sturgeon spawning and rearing habitat in the lower Columbia River. N. Am. J. Fish. Manage. **14**: 812–827. doi:10.1577/1548-8675(1994)014<0812:WSSARH>2.3.CO;2.

Parsley, M.J., Beckman, L.G., and McCabe, G.T., Jr. 1993. Spawning and rearing habitat use by white sturgeons in the Columbia River downstream from McNary Dam. Trans. Am. Fish. Soc. **122**: 217–227. doi:10.1577/1548-8659(1993)122<0217:SARHUB>2.3.CO;2.

Payne, T.R. 2003. The concept of weighted usable area as relative suitability index. IFIM Users Workshop, 1–5 June 2003, Fort Collins, Colo.

Pikitch, E.K., Doukakis, P., Lauck, L., Chakrabarty, P., and Erickson, D.L. 2005. Status, trends and management of sturgeon and paddlefish fisheries. Fish Fish. **6**: 233–265. doi:10.1111/j.1467-2979.2005.00190.x.

Poytress, W.R., Gruber, J.J., Van Eenennaam, J.P., and Gard, M. 2015. Spatial and temporal distribution of spawning events and habitat characteristics of Sacramento River green sturgeon. Trans. Am. Fish. Soc. **144**: 1129–1142. doi:10.1080/00028487.2015.1069213.

Scheel, D., and Bisson, L. 2012. Movement patterns of giant Pacific octopuses, *Enteroctopus dofleini* (Wülker, 1910). J. Exp. Mar. Biol. Ecol. **416–417**: 21–31. doi:10.1016/j.jembe.2012.02.004.

Seesholtz, A.M., Manuel, M.J., and Van Eenennaam, J.P. 2015. First documented spawning and associated habitat conditions for green sturgeon in the Feather River, California. Environ. Biol. Fishes, **98**: 905–912. doi:10.1007/s10641-014-0325-9.

Smith, F. 2013. Understanding HPE in the VEMCO positioning system (VPS). V1.0. Available from: http://vemco.com/wp-content/uploads/2013/09/understanding-hpe-vps.pdf.

Steel, A.E., Coates, J.H., Hearn, A.R., and Klimley, A.P. 2014. Performance of an ultrasonic telemetry positioning system under varied environmental conditions. Anim. Biotelem. **2**: 15. doi:10.1186/2050-3385-2-15.

Thomas, M.J., Peterson, M.L., Chapman, E.D., Hearn, A.R., Singer, G.P., Battleson, R.D., and Klimley, A.P. 2014. Behavior, movements, and habitat use of adult green sturgeon, *Acipenser medirostris,* in the upper Sacramento River. Environ. Biol. Fishes, **97**: 133–146. doi:10.1007/s10641-013-0132-8.

Tomsic, C.A., Granata, T.C., Murphy, R.P., and Livchak, C.J. 2007. Using a coupled eco-hydrodynamic model to predict habitat for target species following dam removal. Ecol. Eng. **30**: 215–230. doi:10.1016/j.ecoleng.2006.11.006.

Tonina, D., McKean, J., Tang, C., and Goodwin, P. 2011. New Tools for aquatic habitat modeling. *In* Proceedings of the 34th World Congress of the International Association for Hydro-Environment Research and Engineering: 33rd Hydrology and Water Resources Symposium and 10th Conference on Hydraulics in Water Engineering, Brisbane, Australia, Barton, 26 June – 1 July 2011. A.C.T.: Engineers Australia. pp. 3137–3144. Available from: http://search.informit.com.au/documentSummary;dn=360450124413765;res=IELENG.

U.S. Fish and Wildlife Service (USFWS). 2013. Identification of the instream flow requirements for anadromous fish in the streams within the central valley of California and fisheries investigations. Annual Progress Report, Fiscal Year 2013. U.S. Fish and Wildlife Service, Sacramento Fish and Wildlife Office, Sacramento, Calif. Available from: http://www.fws.gov/sacramento/Fisheries/Instream-Flow/fisheries_instream-flow_reports.htm.

U.S. Geological Survey. 2014. National Water Information System data available on the World Wide Web (USGS Water Data for the Nation) Available from: http://waterdata.usgs.gov/nwis/ [accessed 20 June 2014].

Van Eenennaam, J.P., Linares-Casenave, J., Muguet, J.-B., and Doroshov, S.I. 2008. Induced spawning, artificial fertilization, and egg incubation techniques for green sturgeon. N. Am. J. Aquacult. **70**: 434–445. doi:10.1577/A07-073.1.

Van Eenennaam, J.P., Linares-Casenave, J., and Doroshov, S.I. 2012. Tank spawning of first generation domestic green sturgeon. J. Appl. Ichthyol. **28**: 505–511. doi:10.1111/j.1439-0426.2012.02012.x.

Vinagre, C., Fonseca, V., Cabral, H., and Costa, M.J. 2006. Habitat suitability index models for the juvenile soles, *Solea solea* and *Solea senegalensis*, in the Tagus estuary: defining variables for species management. Fish. Res. **82**: 140–149. doi:10.1016/j.fishres.2006.07.011.

Wang, Y., and Xia, Z. 2009. Assessing spawning ground hydraulic suitability for Chinese sturgeon (*Acipenser sinensis*) from horizontal mean vorticity in Yangtze River. Ecol. Model. **220**: 1443–1448. doi:10.1016/j.ecolmodel.2009.03.003.

Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. J. Geol. **30**: 377–392. doi:10.1086/622910.

Zorn, T.G., Seelbach, P.W., and Rutherford, E.S. 2012. A regional-scale habitat suitability model to assess the effects of flow reduction on fish assemblages in Michigan streams. J. Am. Water Resour. Assoc. **48**: 871–895. doi:10.1111/j.1752-1688.2012.00656.x.