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Behavior, movements, and habitat use of adult green sturgeon, *Acipenser medirostris*, in the upper Sacramento River

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Abstract We conducted the first continuous shipboard tracking of southern Distinct Population Segment green sturgeon, *Acipenser medirostris*, in the Sacramento River. Tracking of adult green sturgeon occurred between river kilometer (rkm) 434.8 and 511.6, a section of the putative spawning grounds located near Red Bluff, California. The recorded positions of acoustically tagged green sturgeon were analyzed using First Passage Time analysis to determine differences in habitat use between suitable and non-suitable habitats. Classification and Regression Tree modeling was used to determine explanatory inputs attributable to above average habitat use. Green sturgeon exhibited above average habitat use at five sites, identified as potential spawning aggregate sites. Three types of movements (holding, milling, and directed) could be categorized from tracks. Lastly, we show that green sturgeon while on the spawning grounds exhibit a high degree of mobility throughout the spawning grounds, often making large movements between specific habitat units. Our study illustrates how the application of shipboard tracking can be useful for describing movement, behavior and habitat utilization at a spatial scale not achieved by stationary acoustic monitors.

Keywords Acoustic telemetry · First passage times · Habitat utilization · Site fidelity · *Acipenser medirostris* · Sacramento River

Introduction

Green sturgeon, *Acipenser medirostris*, is one of two sturgeon species found in the Sacramento/San Joaquin drainage. The green sturgeon is a long lived, highly fecund, anadromous species (Moyle 2002). Although little is known about the early life history of green sturgeon it is believed that juvenile green sturgeon migrate downstream at approximately age one (Moyle 2002). Juvenile green sturgeon may spend between 1 and 4 years rearing in the lower reaches of their natal rivers, deltas, and estuaries before entering the ocean (Moyle 2002). Sub-adults may then spend between 6 and 10 years migrating along the continental shelf of the western Pacific between the Bering Sea and Ensenada, Mexico, before returning to their natal river to spawn (Moyle 2002; Erickson and Hightower 2007; Lindley et al. 2008). The green sturgeon is a late maturing species. Males and females

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mature at slightly different rates, though maturation typically occurs between age 13 and 27 years. The earliest reported age of maturity for males and females in Klamath River green sturgeon was 14 and 16 years respectively (Van Eenennaam et al. 2006) and spawning migrations may occur every two to four (Moyle 2002; Erickson and Webb 2007). Recent genetic work on green sturgeon has shown a strong delineation of allele frequencies from northern and southern Distinct Population Segments (DPS) green sturgeon, suggesting that at least for the southern DPS, spawning is limited to natal rivers (Israel et al. 2004). There are currently only three known spawning population along the west coast. Spawning populations to the north in the Klamath River, California and Rogue River, Oregon are classified as the northern DPS due to genetic similarities between these two populations. The green sturgeon population from the Sacramento River watershed is classified as the southern DPS (NMFS 2009).

Adult green sturgeon typically arrive in the Sacramento River between the months of March and June (Heublein et al. 2009; M. Thomas unpubl. data). Green sturgeon, from the Klamath River, has been shown to be in the late stages of final maturation at the time of river entry. Therefore, mature green sturgeon which have entered the river are capable of spawning at any point (Van Eenennaam et al. 2006). There is currently no description of green sturgeon spawning behavior. However, it is commonly thought that most North American sturgeon species exhibit similar spawning behaviors as those described for lake sturgeon (see Bruch and Binkowski 2002) where spawning timing and location appear to revolve around the female. Male white sturgeon, *Acipenser transmontanus*, a congener of green sturgeon have been shown to move onto the spawning grounds early with females following behind by several weeks (Paragamian and Kruse 2001). Females may exhibit multiple spawning bouts each lasting several minutes in which multiple males may fertilize eggs. The green sturgeon is a broadcast spawner. Eggs have a sticky coating which adheres to substrate as they settle out of the water column (Dettlaff et al. 1993; Van Eenennaam et al. 2012). The polygamous mating behavior of green sturgeon may continue for several days until females have completed spawning. Males are polygynous, spawning with multiple females during the spawning season, and will thus continue seeking out additional females throughout the spawning season. In the case of lake sturgeon males have been found to move about the spawning grounds continually searching for females with which to spawn (Bruch and Binkowski 2002).

Telemetry studies of adult green sturgeon have been conducted in the Rogue, Klamath, and Sacramento River using stationary receiver arrays (Erickson et al. 2002; Benson et al. 2007; Heublein et al. 2009). Results from these course grain studies showed adult green sturgeon exhibited similar migratory patterns such as spawning run timing, in river residency, and outmigration timing. Similar methods have been used to identify spawning aggregation sites of Atlantic sturgeon (*A. oxyrinchus*; Hatin et al. 2002) and of Kootenai River white sturgeon (*A. transmontanus*; Paragamian et al. 2002). White sturgeon were similarly shown to move between aggregation sites multiple times (Paragamian et al. 2002), a behavior believed to be associated with males searching out ovulating females.

Within the Sacramento/San Joaquin River drainage there has been no historic documentation of spawning in the Feather, Yuba and/or San Joaquin Rivers (Beamesderfer et al. 2007). However, recent monitoring of the Feather River confirmed the presence of green sturgeon eggs in 2011 (Alicia Seesholtz, California Department of Water Resources, West Sacramento, personal communication). It is still unclear rather spawning in the Feather River occurs on an annual basis or rather it is limited to years of high flow as was seen in 2011. With respect to the management of the species, the Sacramento River is considered the primary reach where most if not all of the effective population originates. Concern over the isolation of southern DPS green sturgeon to the Sacramento River was identified as one of the potential extinction risks to the population during the ESA listing process (NMFS 2006).

The Sacramento River has sustained a considerable amount of habitat loss and degradation, yet much of the habitat above rkm 400 (Fig. 1) is in relatively good condition when compared to the Feather, Yuba, or San Joaquin Rivers. Nonetheless, there are many threats which have been identified as potential stressors to southern DPS green sturgeon within the Sacramento River. Some of the threats identified in Adams et al. (2007) include impassable barriers, adult migration barriers, insufficient flows, increased temperatures, juvenile entrainment, exotic species, poaching, pesticides, and heavy metals. Many of these same threats were identified in in the ESA listing of the Sacramento River green sturgeon in 2006 (NMFS 2006).

Fish passage and habitat improvements in major tributaries to the Sacramento River are likely to be crucial recommendations of recovery planning. However,

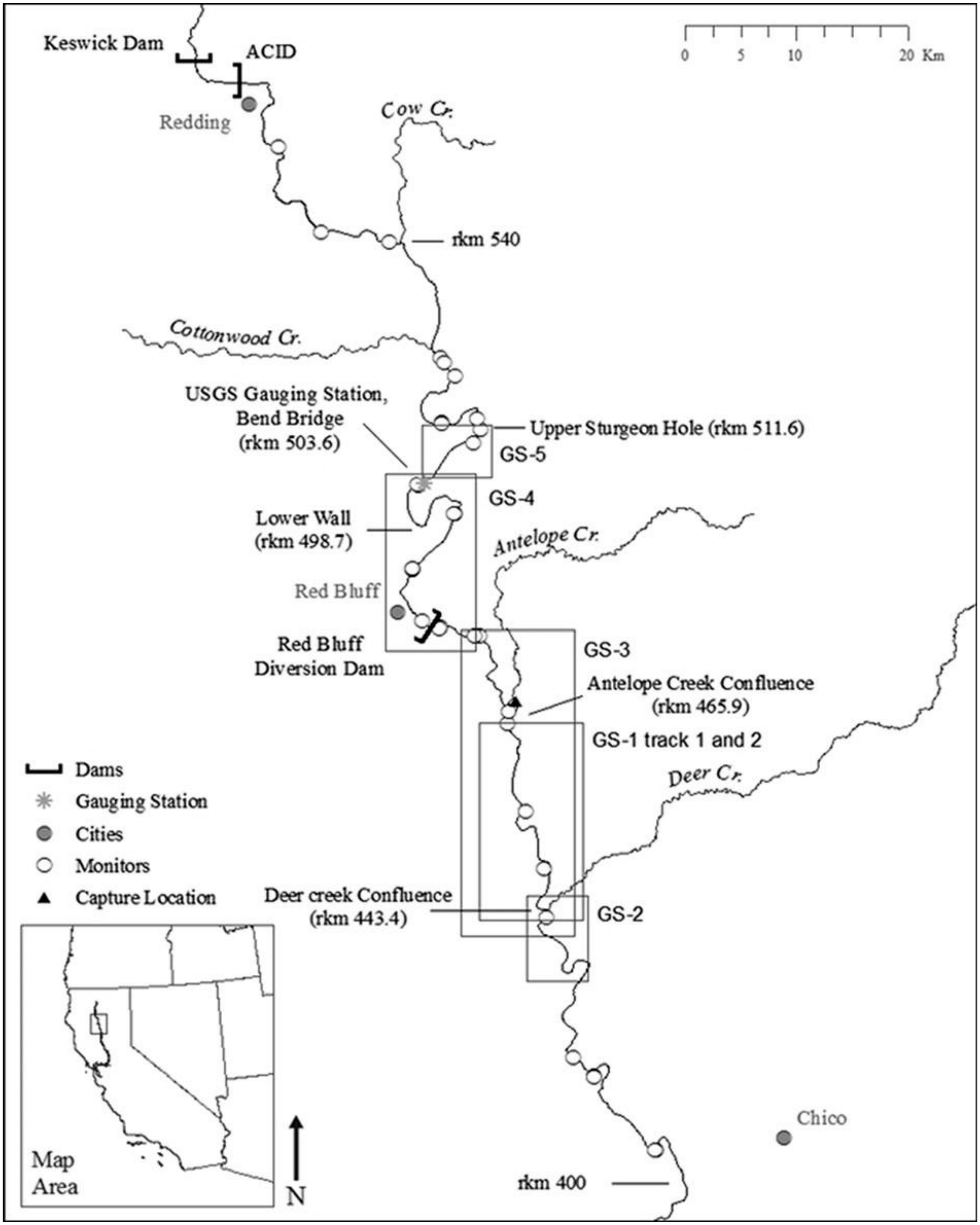

Fig. 1 The study area including locations of tracks (shown in boxes with fish identification numbers), capture location, gauging stations, dams, and stationary acoustic monitors

limited information on behavior, habitat use, and aggregation site fidelity of adult green sturgeon in the upper Sacramento River currently exists.

To address the lack of basic biological information available on southern DPS green sturgeon we conducted a telemetric study during spring 2008 and 2010 with three objectives: (1) describe the behavior and movements between habitat units on the putative spawning grounds, (2) identify potential aggregate sites, and (3) identify site fidelity and habitat use to potential or known aggregate locations.

Materials and methods

Study area

The Sacramento River is the largest river in California, with a watershed area of about 70 000 km2. Major tributaries include the Pit, McCloud, Feather, Yuba, American and San Joaquin rivers. Brown (2007) described the reach of the Sacramento River from Keswick Dam to Colusa as the “upper” reach. The upper reach consists of pool-riffle-run types of habitats with increased leveed bank protection with increased distance downstream. Tracks were conducted from river kilometer (rkm) (rkm measured from the Golden Gate Bridge) 434.4 to rkm 511.7 (Fig. 1). The putative spawning grounds begins below the lowest track at a habitat unit located at rkm 424. To date the habitat unit at rkm 424 is the lowest unit where eggs have been sampled to confirm spawning (Poytress et al. 2012). The uppermost reaches of the historic spawning grounds are currently blocked by Shasta and Keswick Dam (Fig. 1). Below Keswick are two seasonal barriers used for agricultural irrigation needs. Located at rkm 569 in Redding California, is the Anderson-Cottonwood Irrigation District (ACID) dam (Fig. 1). The ACID dam is a low head dam which operates between April and October. The ACID dam currently only provides fish passage for salmonids during the periods when the dam is operated. Red Bluff Diversion Dam (RBDD) is the second of the seasonally operated dams located at rkm 479 (Fig. 1). The RBDD is a gate-operated diversion used to move water to the adjacent irrigation canal. Gates of RBDD historically went down on May 15 until 2009, and began going down on June 15 in 2010. Beginning in 2012 the operation of RBDD was suspended. Water diversion at this site is now achieved by pumping water directly from the river. Unlike RBDD the new pumping facility presents no physical barrier to adult sturgeon passage. During period of gate operations, there was no upstream passage for green sturgeon.

Capture, tagging and tracking procedures

We captured green sturgeon in both years of sampling using monofilament gill nets. Gill nets were between 5 and 27 m in length, 2–5 m in depth, and mesh sizes ranged from 15 to 23 cm. Fishing efforts were primarily focused at Antelope Creek hole at rkm 465.9, a previously identified aggregation site (USFWS 2009, 2010, 2011; R. Corwin, United States Bureau of Reclamation [USBR], pers. comm.) (Fig. 1). Sampling at additional locations was performed on multiple occasions though was abandoned due to the inefficiency of the nets in these higher gradient locations. Surface water temperatures during the 2008 sampling season routinely reached 16 °C late in the day. Individuals captured at the elevated temperatures, exhibited erythema, an indication of stress. Daily capture activities were suspended when river temperatures exceeded 16 °C in an effort to reduce any additional stress to the fish. During 2010, water temperatures did not exceed 16 °C during fishing activities.

Upon capture, fish were rotated ventral side up in a sling while a pump circulated water into the canvas hood that their head was placed in. A 20 mm incision was made approximately 1 cm off the mid-ventral line, between the third and fourth ventral scute. A continuous depth- and temperature-sensing ultrasonic transmitter (VEMCO, V16TP-4H) and a 69 kHz coded pinger (VEMCO, V16-6 L) was inserted into the coelomic cavity of each sturgeon (see Heublein et al. 2009 for surgical methods). Both transmitters had a diameter of 16 mm; the former was 98 mm long, weighed 36 g in air, with tag life of 97 days; the latter was 71 mm long, weighed 25 g in air, and tag life of 3650 days (random delay of 60 s to 90 s). Gonads were visually inspected to determine sex and maturation (Van Eenennaam et al. 2001; Van Eenennaam et al. 2006). Incisions were closed using PDSII absorbable sutures (size #0 or 1, CP2 cutting needle) with three to four interrupted stitches. After completion of the surgery, sturgeon were reoriented and held upright until they swam away under their own volition.

A 6.7 m inboard jet boat equipped with a directional hydrophone and ultrasonic receiver (VR100, VEMCO, Halifax, Nova Scotia, Canada) was used for tracking. An integrated water quality sampler equipped with a water-quality sonde (Manta2, Eureka Environmental Engineering, Austin, Texas) interfaced with a fathometer (GP7000F, Furuno USA, Camas, Washington) was used to collect environmental data. Surface water quality measurements were collected every minute along with a GPS position and depth measurement.

Each continuous transmitter's serial number, depth, and water temperature, at the transmitter, were typically recorded every 3 s. The boat was positioned as close as possible to the fish based on signal strength and direction of the hydrophone. When the fish made sustained directional movements, we followed just behind the fish attempting to limit the distance between the boat and fish. Proximity to the fish was subjectively determined by signal strength, the direction of the detection, and physical features. An omnidirectional signal with relatively equal signal strength when the directional hydrophone was rotated 360° indicated the fish was directly beneath the boat. There was no indication that the presence of the boat affected fish behavior as we observed no burst movements indicative of a flight response.

Rates of up-stream directed movements were estimated on seven occasions, whereas down-stream directed movements were not assessed due to difficulty in continuously and confidently detecting movements downstream (primarily due to boating safety during the night of the single sustained downstream movement of GS2). Rates of movement during milling behaviors were estimated on eight occasions by averaging rates between successive recorded positions during the behavior. We also calculated correlation between depths recorded from continuous transmitters and depths recorded from the depth-sounding unit to confirm fish were near or at the bottom.

Habitat characteristics and environmental variables

A rapid habitat assessment was conducted to identify potential holding habitat for adult green sturgeon from the State Highway 32 Bridge at rkm 415.0 to the Anderson-Cottonwood Irrigation District dam at rkm 570.0. The study reach was selected as the putative spawning grounds based on two criteria; 1) habitats below rkm 415 are channelized by armored banks, with little current complexity. 2) Tag detections from passive monitoring has shown that green sturgeon on their upstream migration typically move quickly beyond rkm 415 before exhibiting any long term holding patterns indicative of spawning behavior (Heublein et al. 2009; M. Thomas unpubl. data). The habitat assessment of the putative spawning grounds was focused at the mesohabitat scale (see Maddock 1999 for mesohabitat description). The methods used for the rapid habitat assessment were modified from protocols provided in Barbour et al. (1999).

The habitat assessment was accomplished by surveying the river and recording depths as well as the coordinates for the upper and lower limits of each habitat with a side-scan sonar and GPS [997C SI combo, Humminbird, Eufaula, Alabama (R. Corwin, USBR, unpubl. data)]. Units were then classified as a riffle, pool, run, glide, eddy, or backwater. We identified 126 potential suitable habitat units during the survey. Suitable habitat units were defined as a unit having depths≥5 m and mapped in ARC GIS 9.3 (ESRI, Redlands, CA.). We chose to identify potential suitable habitat using this depth criteria based on depth preferences taken from results of northern DPS green sturgeon telemetry studies (Erickson et al. 2002). In addition, depth ranges greater than 5 m were noted as being important to the species during the critical habitat designation issued by National Marine Fisheries Service (NMFS 2009).

Data analysis

The spatial distribution of points along a track can yield valuable information about the interaction between an animal and its habitat. If time intervals are approximately equal between recorded positions, then the in-between distance and the spatial pattern of points could be used to infer the type of interaction. A measure of the amount of time spent in a given area along a track, called first-passage time (FPT), has previously been used by researchers to infer the search effort and habitat preferences of marine mammals (Fauchald and Tveraa 2003; Freitas et al. 2008). For each point in a track, a given circular area about that point is assumed. The difference between the time the fish entered and left that area would be an index of the total amount of time spent in the area. Individual points, and groups of points with low FPT values can be inferred as lacking some type of suitable resource for the fish. Conversely, groups of points with high FPT values could possess the suitable resource. Since FPT increases with a larger area about the point, ranges of areas (dependent on a given radius) are tested. The goal is to determine the radius that is best able to differentiate between areas with high and low FPT values. The radius resulting in the maximum natural log variance of FPT is the radius that is best able to differentiate between areas with high and low FPT values. We then determined which variables were best associated with first-passage times of each recorded position. First passage time values for any particular point are not actual times spent at that point, but rather an index of time spent within the given area. Only the first detection in any given minute interval was used. Distances (m) and rates of movement ($m \cdot s^{-1}$) were calculated by assuming straight-line distances and constant speed between recorded positions.

Classification and Regression Trees (CART) were utilized to estimate a regression relationship (applied to continuous variables) or a classification (of dichotomous variables) by use of binary recursive partitioning. We used the programming language R (version 2.13.0, available at: www.R-project.org) and routines from the packages rpart and rpart.plot (both available at: http://CRAN.R-project.org) to construct and evaluate the validity of constructed trees. Trees are constructed by repeatedly sorting variables to maximize homogeneity within two groups and heterogeneity between the two groups. Trees can be displayed graphically with grouped data at the terminal nodes and/or displayed with typical distributional plots. First-passage time and CART analyses were performed on the complete track of each individual. The explanatory variables were depth of sensor tag, temperature of sensor tag, and habitat types. We also conducted 1000 independent cross-validations of each dataset to ensure we had not chosen an atypical tree (see De'ath and Fabricius 2000).

Measurements of discharge and water temperature were compiled from the United States Geological Survey (USGS) gauging station at Bend Bridge at rkm 503.6 (USGS site no. 11377100, http://water.usgs.gov/) (Fig. 1). Water temperature data from below RBDD at rkm 479 was also compiled for comparison (USBOR, site RDB, http://cdec.water.ca.gov) (Fig. 1). Hourly measurements of above and below RBDD water temperature were compared using a Paired-*T* test.

Results

Behavior and movements

Five green sturgeon were continuously tracked during the spring of 2008 and 2010 for a total of six tracks (Table 1). During the course of these tracks an additional 12 green sturgeon were detected throughout the study area (Table 2). The onset of continuous tracks occurred from 5 days to 29 days after tagging. Track durations ranged from 48 h 56 min to 94 h 46 min (Table 1).

Three types of short-term movement patterns of tracked sturgeon were observed: 1) sustained directed movements, 2) milling, and 3) holding. The first behavior consisted of sustained swimming movement upstream that often lasted several hours or more over large distances. At least one directed movement was observed during all six tracks. Upstream movement rates ranged from 0.15 to 0.57 $m \cdot s^{-1}$ (mean=0.33 $m \cdot s^{-1}$). Downstream and upstream directed movements made up about 34 % of the duration of the tracks (pooled across all tracks), with GS-3 spending the most time moving (~ 63 %) and GS-2 spending the least amount of time moving (~ 10 %).

The second behavior was characterized by random milling movements either restricted to a particular habitat unit or between adjacent habitat units. This behavior consisted of moderate movements, typically less than 200 m. When sturgeon exhibited milling behaviors they would often return to specific locations within the primary habitat unit being utilized. Movement rates during periods of milling ranged from 0.02 to 0.22 $m \cdot s^{-1}$ (mean=0.07 $m \cdot s^{-1}$). Milling behavior was observed on four of the six tracks and made up about 5 % of the duration of the tracks (pooled across all tracks where milling observed), with GS-1 (second track) spending the most time milling (~ 12 %) and GS-3 spending the least amount of time milling (~ 2 %). Holding behavior consisted of the sturgeon staying within a single habitat unit for an extended period from 2 to 48 h, generally making small circling movements within a habitat unit of approximately 30 m or less. No movement rates were estimated while sturgeon were holding. Holding behavior was observed on all 6 tracks and made up about 61 % of the duration of the tracks (pooled across all tracks), with GS-5 spending the most time holding (~ 74 %) and GS-3 spending the least amount of time holding (~ 35 %).

Green sturgeon were tracked from rkm 434.4 to rkm 511.7 an approximate distance of 77.3 km along the main stem Sacramento River (Fig. 2). Sturgeon GS-2 was tracked most downstream and sturgeon GS-5 was tracked most upstream (Fig. 1). The distances moved by sturgeon ranged from a relatively short distance of 6.5 km (GS-5) to 31.5 km (GS-3). The mean distance traveled by all tracked fish was 18.1 km (Fig. 3).

Table 1 Biological information and track data for five tracked adult green sturgeon on the Sacramento River (2008, 2010). Mean discharge ($m^3 s^{-1}$, standard deviation in parentheses) for each track was summarized from Bend Bridge (rkm 502.6, USGS site number 11377100)

Fish ID	Tag ID	FL/TL (cm)	Sex	Capture date	Start of track	Duration (h:min)	Mean discharge (SD)
GS-1	5452	198 / 217	UNK	4/23/2008	4/30/2008	53:45	251 (3)
GS-1	5452	198 / 217	UNK	4/23/2008	5/6/2008	48:56	266 (2)
GS-2	10820	171 / 186	M	6/11/2008	6/16/2008	79:58	352 (20)
GS-3	48634	183 / 198	M	5/3/2010	5/11/2010	75:18	276 (9)
GS-4	48419	165 / 176	M	5/3/2010	5/17/2010	92:31	301 (5)
GS-5	48420	157 / 168	M	5/5/2010	6/1/2010	94:46	470 (69)

The length of the total directed movements (accounting for upstream and downstream movements) for each track ranged from 6.5 km for GS-5 to 60.3 km for GS-3. The only sturgeon to pass through the open gates of RBDD was GS-4, which traveled a distance of 21.7 km (rkm 477.0 to rkm 498.7) during that migratory movement. The first movement through the open gates of RBDD occurred at 19:20 h on 17 May 2010. This fish subsequently dropped back downstream of RBDD on the morning of 18 May 2010. GS-4 held at the downstream base of the open gates for approximately 3 h prior to moving above RBDD for the remainder of the track.

Positive correlation coefficients for transmitter depth and measured bathymetry were determined for the tracks of GS-3 and GS-5. When tag depths were plotted against sonar depths, most points fell above the line with slope 1, intercept 0. This indicated that any particular tag depth reading was generally greater than the sonar reading, suggesting that adult green sturgeon position themselves at or near the bottom of the water column. We attribute depth readings greater than sonar readings to stationing the boats' position slightly away from the fishes' position, particularly when holding.

Habitat utilization

First-passage times were consistent with general observations during tracks where adult green sturgeon held for long periods of time at several key sites (Figs. 2 and 4). Tracked sturgeon made sustained movements and recorded positions during these movements often had low to below average FPT values. However, five highly utilized aggregate sites had above average to high FPT values. Four of five of the sites were previously unknown as aggregate sites prior to 2008. These four sites included: 1) the reach above Deer Creek confluence at rkm 443.4; 2) the Lower Wall unit at rkm 498.7; 3) a large pool at rkm 505.2; and 4) upper Sturgeon Hole at rkm 511.6 (Figs. 2 and 4). Anecdotal information from recreational fishermen suggested that the Antelope Creek confluence at rkm 465.9 (Fig. 4)

Table 2 Biological information of additional green sturgeon detected during continuous tracking of green sturgeon listed in Table 1

Fish ID	Tag ID	FL/TL (cm)	Capture date	Sex	Capture location
NT1	163	164/179	8/1/2008	UNK	Sacramento River
NT2	5450	190/175	6/11/2008	UNK	Sacramento River
NT3	219	165/151	6/27/2006	UNK	Sacramento River
NT4	221	206/190	6/29/2006	UNK	Sacramento River
NT5	2211	165/148	8/6/2005	UNK	Sacramento River
NT6	2228	156/145	8/28/2005	UNK	Sacramento River
NT7	2234	163/none	11/3/2005	UNK	Sacramento River
NT8	48423	184/172	5/3/2010	F	Sacramento River
NT9	48630	200/187	5/7/2010	F	Sacramento River
NT10	1132	200/none	7/13/2004	UNK	Columbia River
NT11	48633	191/176	5/6/2010	M	Sacramento River
NT12	5448	170/157	5/8/2008	UNK	Sacramento River

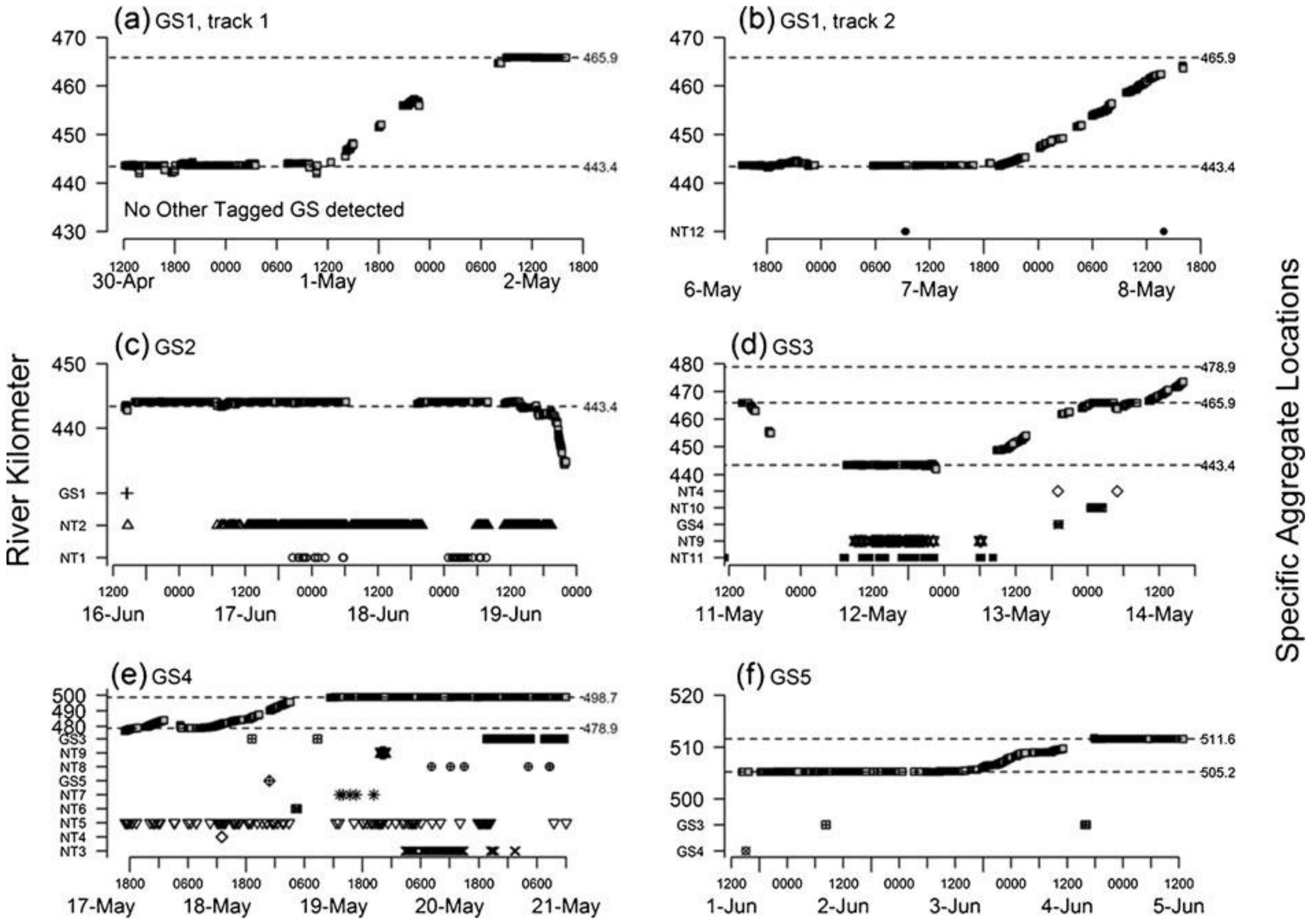

Fig. 2 River kilometer locations by date and time for each tracked green sturgeon conducted during spring 2008 and 2010 in the Sacramento River: **a** track 1 of GS-1; **b** track 2 of GS-1; **c** GS-2; **d** GS-3; **e** GS-4; **f** GS-5. Additional green sturgeon detected at the same rkm as the primary subject tracked for that week denoted by (NT or GS#) on the Y-axis

was an aggregate site, though fidelity had not been documented until this study.

Three of the five tracked sturgeon used the two habitat units near the confluence of Deer Creek (rkm 442.4 and 443.4; Deer Creek confluence area). Two of five individuals used the Antelope Creek confluence unit, at rkm 465.9. Two of five individuals exhibited what we describe as “ping-ponging” between aggregate sites such as

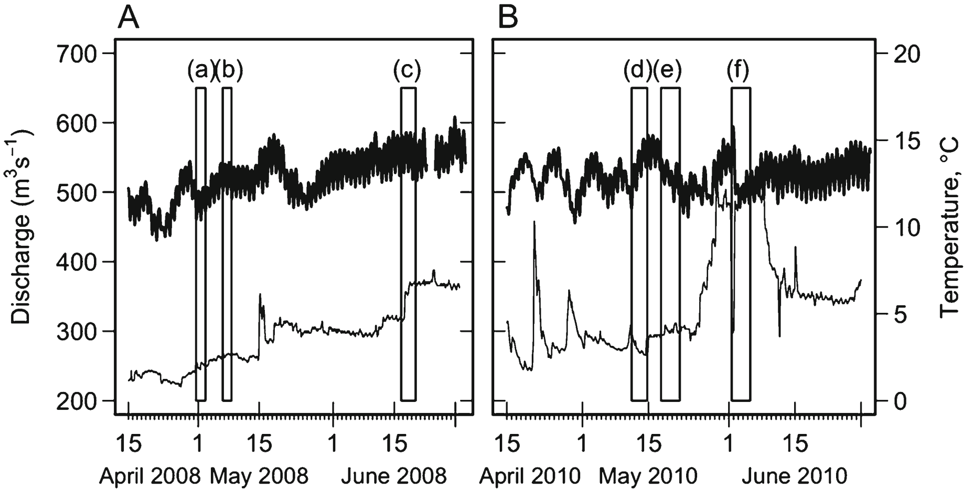

Fig. 3 Discharge (*light solid line*) and temperature (*bold solid line*) measured at rkm 503, (USGS gauging station at Bend Bridge, Site number 11377100), during spring 2008(A) and spring 2010(B). The beginning and end of tracks are denoted by solid rectangles for each green sturgeon: **a** GS-1, track 1; **b** GS-1, track 2; **c** GS-2; **d** GS-3; **e** GS-4; **f** GS-5

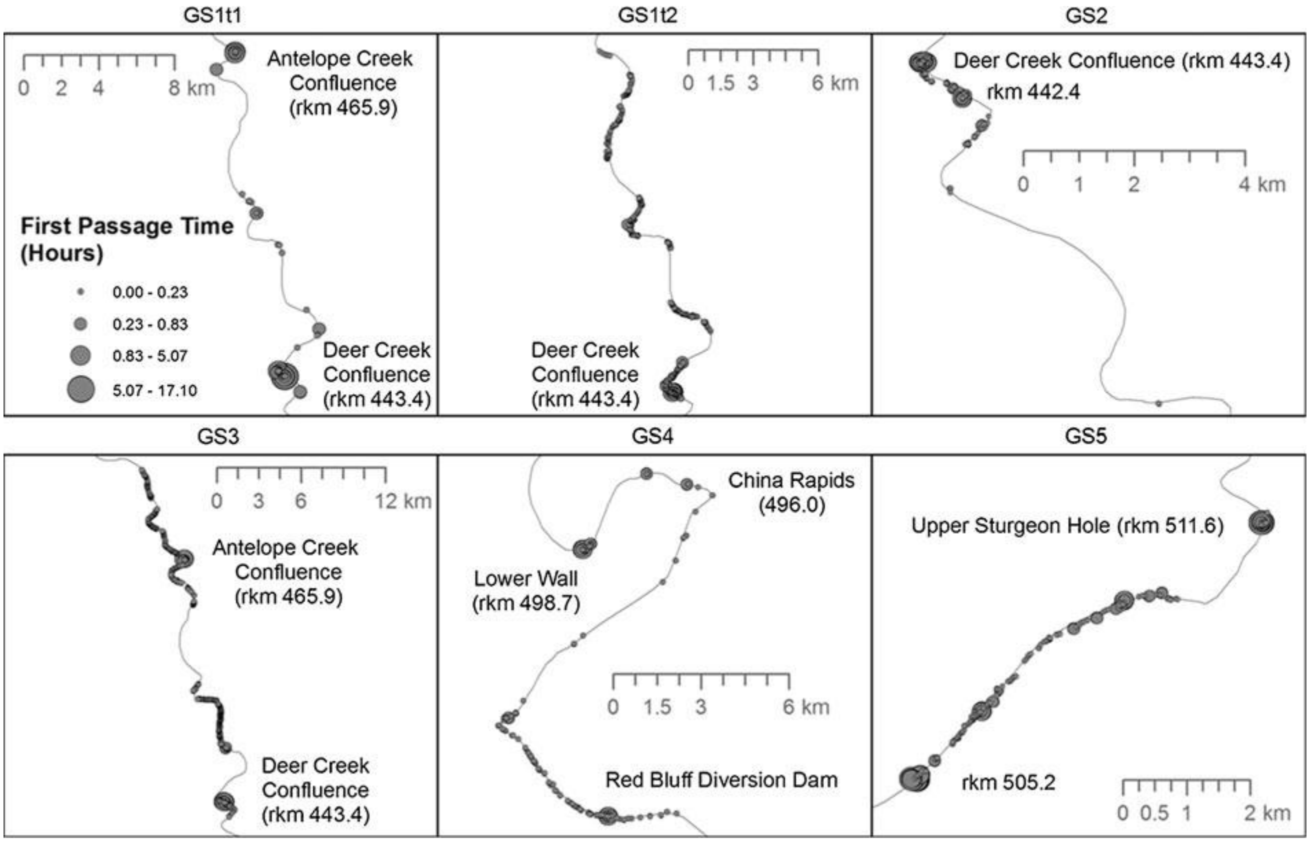

Fig. 4 Individual maps of tracks with first-passage time values depicted by amount of time spent at each recorded position. Note high usage of certain units (at rkm 442.4, 443.4, 465.9, 498.7, 505.2 and 511.6)

Deer and Antelope creek confluence areas. GS-3 used the Antelope Creek confluence area three separate times in 3 days. Similarly, GS-1 used both Deer and Antelope creek confluence sites on both tracks. In all cases the habitat units which received above average use conformed to the ≥ 5 m depth criteria (Table 3). However, in total sturgeon only exhibited fidelity to six of 60 hypothesized suitable habitat units (≥ 5 m) encountered.

Classification and regression tree analysis was performed on the six tracks. Pruned regression trees for the six tracks contained two to five nodes or were three-branch to six-branch trees. Cross-validation results showed that there was support for smaller or larger pruned trees, but that we chose the properly sized pruned tree in all cases.

Surface water temperature and depth of the tag were chosen at least twice as explanatory variables at the primary-level split. There was also a consistent relationship between the depth readings of the continuous tag and first-passage times for all tracks. The relationship was consistent within regression trees, regardless of the location of depth readings either at the primary-level or secondary-level split and was always positive. We verified this relationship by constructing and pruning the regression trees using

Table 3 Habitat characteristics of each of the five sites identified as aggregate locations

Unit name	River kilometer	Max depth (m)	Habitat type
Deer Creek confluence	443.4	6.5	Run
Antelope Creek confluence	465.9	12.3	Pool
Lower Wall	498.7	7.6	Run
Unit 85	505.2	19.7	Run
Sturgeon Hole	511.6	14.1	Pool

only tag depth as the explanatory variable. Again, this correlation existed for all pruned trees.

The pruned tree of GS-4 is given as an example of this relationship (Fig. 5). A pruned tree containing two splits, which produces a three-leaf tree, was chosen by the 1-SE rule as the "best" tree (Fig. 5). Permutations of the results indicated that 987 out of 1000, approximately 99 %, of the cross-validated trees contained two splits, suggesting that a pruned tree with two splits was the most likely tree. However, approximately 1 % of the cross-validated trees split three times.

In the single variable tree, using only depth of tag (D_{tag}) as the explanatory variable, the first split occurred at $D_{tag}<5.85$ m with no further splits. When $D_{tag}<5.85$ m, the mean of first-passage time values was 0.08 h ($n=843$ observations) and when $D_{tag}>5.85$ m, the mean of first-passage time values was 1.4 h ($n=1784$ observations). The general relationship of the splits indicated that first-passage times increased with increasing depth as measured from the sensor on the acoustic tag.

Water discharge measured at the nearest USGS gauging station at Bend Bridge (Site number 11377100) showed that discharges were relatively stable throughout the tracks with the exception of during track GS-5 (Table 1). Discharges in 2010 were more influenced by storm events compared to discharges in 2008. There also were high discharges recorded, prior to, during, and after the track of GS-3, likely due to increased agricultural demand (Fig. 3, right panel). Dissolved oxygen measurements recorded from all tracks ranged from 6.15 to 10.69 mg/L depending on site and the time of day.

Mean water temperatures from above and below RBDD ranged from 11.6 °C to 15.1 °C (Table 4.) In all cases comparisons of above and below RBDD water temperatures showed a statistically significant difference ($P<.01$, Table 4). However, the difference in mean temperatures between the upper and lower sampling site only represented a fraction of a degree and ranged from 0.6 °C to 0.9 °C.

Discussion

Behavior and movements

This study provides new information on the movements and behaviors of southern DPS green sturgeon. Intensive, continuous shipboard tracking was effective as a method for understanding behavior, movement, and habitat use at an intermediate spatial scale such as the river reach or habitat unit. Prior to this research, results of green sturgeon movements have been primarily based upon broad scale spatial-temporal telemetry, utilizing fixed station monitors (Benson et al. 2007; Erickson and Hightower 2007; Heublein et al. 2009). The methods used in this study complement fixed station monitoring, providing new information about how green sturgeon move and behave beyond the range of acoustic monitors.

The migration of GS-1 between the Deer Creek confluence site and the Antelope Creek confluence site on consecutive weeks, illustrates sustained directed movements between specific aggregate sites, "Ping-Pong" behavior. It is likely that multiple sustained directed movements may be a mechanism by which males seek out ripe females as suggested by Hatin et al. (2002) for

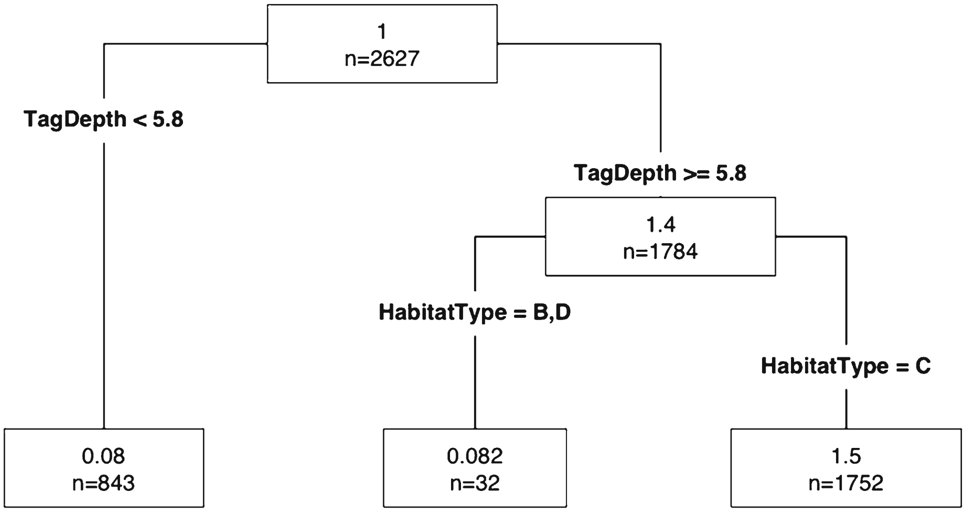

Fig. 5 Pruned regression tree (GS-4) with explanatory variables and cutoffs shown at each split, mean of first-passage times, and number of observations shown at each node. Tag depths were measured in meters from the surface. Habitat types are as follows: **b** Pool; **c** run; **d** glide

Table 4 Comparison of hourly water temperatures (°C) above and below Red Bluff Diversion Dam. Water temperatures were obtained from Bend Bridge (rkm 502.6, USGS site number 11377100) and below Red Bluff Diversion Dam (rkm 479, USBOR, site GDB) monitoring stations

Fish ID	Start of track	Mean temperature at Bend Bridge (SD)	Mean temperature below Red Bluff Diversion Dam (SD)	df	*t* value	*P* value
GS-1	4/30/2008	11.6 (0.6)	12.6 (0.7)	52	4.2	$P<.01$
GS-1	5/6/2008	12.7 (1.2)	13.5 (1.1)	47	6.4	$P<.01$
GS-2	6/16/2008	14.2 (0.9)	15.1 (0.3)	95	8.2	$P<.01$
GS-3	5/11/2010	13.5 (1.2)	14.1 (1.3)	95	5.4	$P<.01$
GS-4	5/17/2010	13.1 (0.7)	13.8 (0.6)	95	9.7	$P<.01$
GS-5	6/1/2010	12.7 (1.2)	13.5 (1.1)	95	11.0	$P<.01$

Atlantic sturgeon. During the tracks conducted on GS-1, eggs were collected on 6 May 2008 and 9 May 2008 at the Antelope site, estimated spawning dates based on embryogenesis were 3 May 2008, 8 May 2008, and 9 May 2008 (Poytress et al. 2009). Estimated spawning dates for the collection of eggs correspond with the upstream movement and presence of GS-1 at the Antelope Creek site. Individual GS-4 showed similar behavior, moving a total of 21.7 km to the Lower Wall unit at rkm 498.7, where it stayed with six other tagged individuals, including two females identified to be in reproductive condition.

Hatin et al. (2002) found that male Atlantic sturgeon moved large distances between potential spawning sites. Similar behavior has been shown for lake sturgeon (*A. fulvescens*), in the Winnebago system of Eastern Central Wisconsin (Bruch and Binkowski 2002). Sacramento River green sturgeon showed similar movement patterns between aggregate sites during the spawning season as those documented for Atlantic and lake sturgeon.

Understanding the movement potential of this species during the spawning season is a necessary component of understanding potential population stressors. In the case of the upper Sacramento River, much of the remaining spawning habitat was blocked by RBDD during a large portion of the spawning season. Due to the movement potential that green sturgeon exhibit during the spawning season, any blockage of spawning habitat could fragment the population, interfering with the necessary movement patterns by which males locate ovulating females. Since the completion of this study, RBDD has been replaced by a pumping facility, which no longer blocks access to the spawning grounds. However, understanding the behavior of these fish during the spawning season may explain at least one effect of the 46 year operation of RBDD.

All but one tracked individual made upstream movements. It is possible that the downstream movement of GS-2 was motivated by handling stress from the capture and tagging procedure. Benson et al. (2007) showed similar early outmigration for green sturgeon in the Klamath River after only a few days post tagging. It is possible this individual had completed spawning and was already out-migrating as the time year was near the end of peak spawning activity. Heublein et al. (2009) observed nine of ten green sturgeon tagged in San Pablo Bay, that had moved up to the spawning grounds, begin to migrate downstream before 24 August 2006. The earliest reported outmigration by Heublein et al. (2009) occurred as early as 22 May 2006.

Habitat utilization

We found strong evidence that green sturgeon seek habitat units of depth>5 m. In most cases, habitat units with high first passage times exceeded depths of 5 m indicating that individuals sought out and resided within the deeper habitat units. Use of deep water habitats has been shown for white and Atlantic sturgeon (Hatin et al. 2002; Paragamian et al. 2002). Northern DPS green sturgeon have been shown to seek similar deep water habitats in the Rogue River, Oregon (Erickson et al. 2002). However, caution should be exercised when assuming that throughout a species range there will be the same habitat requirements and preferences, particularly when populations are genetically distinct and there is substantial spatial separation. This study provides evidence suggesting that despite the major alterations to the Sacramento watershed, southern DPS green sturgeon continue to seek out deep water habitat units. Northern DPS green sturgeon in summer and fall months were most frequently relocated in low gradient pools with little to no water current (Erickson et al. 2002). In contrast, the habitat units that southern DPS green sturgeon utilized in the spring were most frequently characterized as high gradient, with complex hydraulic currents. These differences in habitat use may be attributed to the seasonal differences in which northern and southern green sturgeon were tracked. Alternatively, differences in habitat use may be explained by population level differences. However, it is more likely that such differences in seasonal habitat use are best explained by the temporal motivation of the fish, such as spawning versus post-spawning use of the freshwater environment.

Among the North American sturgeon species, Atlantic sturgeon *A. oxyrinchus*, have the most similar life history to that of green sturgeon. Hatin et al. (2002) utilized fixed station monitoring and shipboard tracking to identify movements and fidelity to three potential Atlantic sturgeon spawning aggregates. Similarly, our results suggest preference to limited number of habitat units. In a similar study, Kootenai River white sturgeon *A. transmontanus*, were shown to occupy specific aggregation sites and exhibited patterns of moving between spawning locations multiple times (Paragamian et al. 2002). Results from southern DPS green sturgeon movements and behavior seem to suggest some level of similarity in movement behavior between closely related sturgeon species.

Among the preferred habitat units depth was the best explanatory variable for above average FPT values, we recognize it may be but one parameter in site selection. Despite movements through many habitat units characterized by a depth>5 m, green sturgeon remained in only a few of these units for extended periods of time. Modeling efforts have shown that bottom roughness, riverbed slope, and to a lesser extent, depth are important habitat features for non-spawning white sturgeon (Hatten and Parsley 2009). Paragamian et al. (2002) has suggested that recruitment failure of white sturgeon may be attributed to a lack of suitable substrate and current velocities. Southern DPS green sturgeon have been shown to spawn in deep pools in the Sacramento River (USFWS 2009, 2010, 2011). Each of the habitat units where egg collection has occurred is characterized as having above average current velocities, complex hydraulics, and substrate of either, gravel, cobble, or bedrock (USFWS 2009, 2010, 2011). It is likely that depth alone does not determine optimal spawning habitat, but a combination of specific depths, gradients, and substrates, which form a habitat unit of varying complexity.

While water temperatures above and below RBDD were statistically different, it did not appear that water temperatures in either year deviated from the reproductive optimum of between 12 and 16 °C (Van Eenennaam et al. 2005). It is our opinion that the differences in water temperatures observed during tracks are not biologically significant. Eggs can survive between 11 and 22 °C, however, at the extremes of this range, reproductive success is diminished (Van Eenennaam et al. 2005). Erickson et al. (2002) found that Rogue River green sturgeon began the upstream migration when water temperatures were between 12 and 13 °C. It is likely that temperature plays a much larger role for upriver migration timing.

One of the primary objectives of this study was to find potential spawning aggregate sites. In doing so we were able to identify at least five new potential locations. While Hatin et al. (2002) identified three new sectors of the St Lawrence River as potential spawning ground, they also express their concern regarding the size of the area for refining future monitoring such as substrate sampling for eggs. Our study area while large by western standards is small enough compared to the St Lawrence River that we were able to distinguish use of specific habitat units. In doing so future egg and larval monitoring will be focused on specific sites rather than reaches of river.

Currently, work is being performed in the major tributaries of the Sacramento River to determine the potential availability of suitable habitat for green sturgeon. Our results are important in providing a starting point for identifying where and in which kinds of habitat green sturgeon may be found in these tributaries. Habitat models for green sturgeon in the Sacramento River watershed are currently in development. The results of this study are important to that process, as there is currently only one other published study on the movements and habitat use of green sturgeon in the Sacramento River (see Heublein et al. 2009). Information contained in this study are currently being utilized in intensive habitat characterization and flow modeling. Future research should focus more intensely on describing the relationship between current complexities, velocity, depth, and substrate forming processes, and how each of these variables contribute to the use of known spawning sites and recruitment potential.

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