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67	Abstract	<p>We conducted the first continuous shipboard tracking of southern Distinct Population Segment green sturgeon, <i>Acipenser medirostris</i>, 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.</p>	
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68	Keywords separated by ' - '	Acoustic telemetry - First-passage times - Habitat utilization - Site fidelity - <i>Acipenser medirostris</i> - Sacramento River	
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69	Foot note information		

4 **Behavior, movements, and habitat use of adult green sturgeon,**
5 ***Acipenser medirostris*, in the upper Sacramento River**6 **Michael J. Thomas · Matthew L. Peterson ·**
7 **Eric D. Chapman · Alex R. Hearn ·**
8 **Gabriel P. Singer · Ryan D. Battleson ·**
9 **A. Peter Klimley**10 Received: 22 December 2011 / Accepted: 12 March 2013
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13 **Abstract** We conducted the first continuous shipboard
14 tracking of southern Distinct Population Segment green
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19 Bluff, California. The recorded positions of acoustically
20 tagged green sturgeon were analyzed using First
21 Passage Time analysis to determine differences in hab-
22 itat use between suitable and non-suitable habitats.
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achieved by stationary acoustic monitors. 36**Keywords** Acoustic telemetry · First-passage times · 37
Habitat utilization · Site fidelity · *Acipenser medirostris* · 38
Sacramento River 39**Introduction** 40Green sturgeon, *Acipenser medirostris*, is one of two 41
sturgeon species found in the Sacramento/ San 42
Joaquin drainage. The green sturgeon is a long lived, 43
highly fecund, anadromous species (Moyle 2002). 44
Although little is known about the early life history 45
of green sturgeon it is believed that juvenile green 46
sturgeon migrate downstream at approximately age 47
one (Moyle 2002). Juvenile green sturgeon may spend 48
between 1 and 4 years rearing in the lower reaches of 49
their natal rivers, deltas, and estuaries before entering 50
the ocean (Moyle 2002). Sub-adults may then spend 51
between 6 and 10 years migrating along the continen- 52
tal shelf of the western Pacific between the Bering Sea 53
and Ensenada, Mexico, before returning to their natal 54
river to spawn (Moyle 2002; Erickson and Hightower 55
2007; Lindley et al. 2008). The green sturgeon is a late 56
maturing species. Males and females mature at slightly 57M. J. Thomas (✉) · M. L. Peterson · E. D. Chapman ·
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58 different rates, though maturation typically occurs be- 107
 59 tween age 13 and 27 years. The earliest reported age of 108
 60 maturity for males and females in Klamath River 109
 61 green sturgeon was 14 and 16 years respectively 110
 Q1 62 (Van Eenennaam et al. 2006a, b) and spawning migra- 111
 63 tions may occur every two to four (Moyle 2002; 112
 64 Erickson and Webb 2007). Recent genetic work on 113
 65 green sturgeon has shown a strong delineation of allele 114
 66 frequencies from northern and southern Distinct 115
 67 Population Segments (DPS) green sturgeon, suggesting 116
 68 that at least for the southern DPS, spawning is limited to 117
 69 natal rivers (Israel et al. 2004). There are currently only 118
 70 three known spawning population along the west coast. 119
 71 Spawning populations to the north in the Klamath River, 120
 72 California and Rogue River, Oregon are classified as the 121
 73 northern DPS due to genetic similarities between these 122
 74 two populations. The green sturgeon population from 123
 75 the Sacramento River watershed is classified as the 124
 76 southern DPS (NMFS 2009). 125

77 Adult green sturgeon typically arrive in the 126
 78 Sacramento River between the months of March and 127
 79 June (Heublein et al. 2009; M. Thomas unpubl. data). 128
 80 Green sturgeon, from the Klamath River, has been 129
 81 shown to be in the late stages of final maturation at the 130
 82 time of river entry. Therefore, mature green sturgeon 131
 83 which have entered the river are capable of spawning at 132
 84 any point (Van Eenennaam et al. 2006a, b). There is 133
 85 currently no description of green sturgeon spawning 134
 86 behavior. However, it is commonly thought that most 135
 87 North American sturgeon species exhibit similar 136
 88 spawning behaviors as those described for lake sturgeon 137
 89 (see Bruch and Binkowski 2002) where spawning 138
 90 timing and location appear to revolve around the female. 139
 91 Male white sturgeon, *Acipenser transmontanus*, a con- 140
 92 gener of green sturgeon have been shown to move onto 141
 93 the spawning grounds early with females following 142
 94 behind by several weeks (Paragamian and Kruse 143
 95 2001). Females may exhibit multiple spawning bouts 144
 96 each lasting several minutes in which multiple males 145
 97 may fertilize eggs. The green sturgeon is a broadcast 146
 98 spawner. Eggs have a sticky coating which adheres to 147
 99 substrate as they settle out of the water column (Dettlaff 148
 Q2 100 et al. 1993; Van Eenennaam et al. 2012). The polyga- 149
 101 mous mating behavior of green sturgeon may continue 150
 102 for several days until females have completed spawning. 151
 103 Males are polygynous, spawning with multiple females 152
 104 during the spawning season, and will thus continue 153
 105 seeking out additional females throughout the spawning 154
 106 season. In the case of lake sturgeon males have been 155

found to move about the spawning grounds continually 107
 searching for females with which to spawn (Bruch and 108
 Binkowski 2002). 109

Telemetry studies of adult green sturgeon have been 110
 conducted in the Rogue, Klamath, and Sacramento 111
 River using stationary receiver arrays (Erickson et al. 112
 2002; Benson et al. 2007; Heublein et al. 2009). 113
 Results from these course grain studies showed adult 114
 green sturgeon exhibited similar migratory patterns 115
 such as spawning run timing, in river residency, and 116
 outmigration timing. Similar methods have been 117
 used to identify spawning aggregation sites of 118
 Atlantic sturgeon (*A. oxyrinchus*; Hatin et al. 119
 2002) and of Kootenai River white sturgeon 120
 (*A. transmontanus*; Paragamian et al. 2002). White 121
 sturgeon were similarly shown to move between 122
 aggregation sites multiple times (Paragamian et al. 123
 2002), a behavior believed to be associated with 124
 males searching out ovulating females. 125

Within the Sacramento/ San Joaquin River drainage 126
 there has been no documentation of spawning in the 127
 Feather, Yuba and/or San Joaquin Rivers in recent 128
 history (Beamesderfer et al. 2007). This indicates that 129
 spawning may be restricted to the main-stem of the 130
 Sacramento River. As a caveat there has been relative- 131
 ly little attention paid toward monitoring other poten- 132
 tial spawning locations until the recent listing of sDPS 133
 green sturgeon. The Sacramento River has sustained a 134
 considerable amount of habitat loss and degradation, 135
 yet much of the habitat above rkm 400 (Fig. 1) is in 136
 relatively good condition when compared to the 137
 Feather, Yuba, or San Joaquin River. Nonetheless, 138
 there are many threats which have been identified as 139
 potential stressors to sDPS green sturgeon within the 140
 Sacramento River. Some of the threats identified in 141
 Adams et al. (2007) include impassable barriers, 142
 adult migration barriers, insufficient flows, increased 143
 temperatures, juvenile entrainment, exotic species, 144
 poaching, pesticides, and heavy metals. Many of 145
 these same threats were identified in in the ESA 146
 listing of the Sacramento River green sturgeon in 147
 2006 (NMFS 2006). 148

Fish passage and habitat improvements in major 149
 tributaries to the Sacramento River are likely to be 150
 crucial recommendations of recovery planning. 151
 However, limited information on behavior, habitat 152
 use, and aggregation site fidelity of adult green 153
 sturgeon in the upper Sacramento River currently 154
 exists. 155

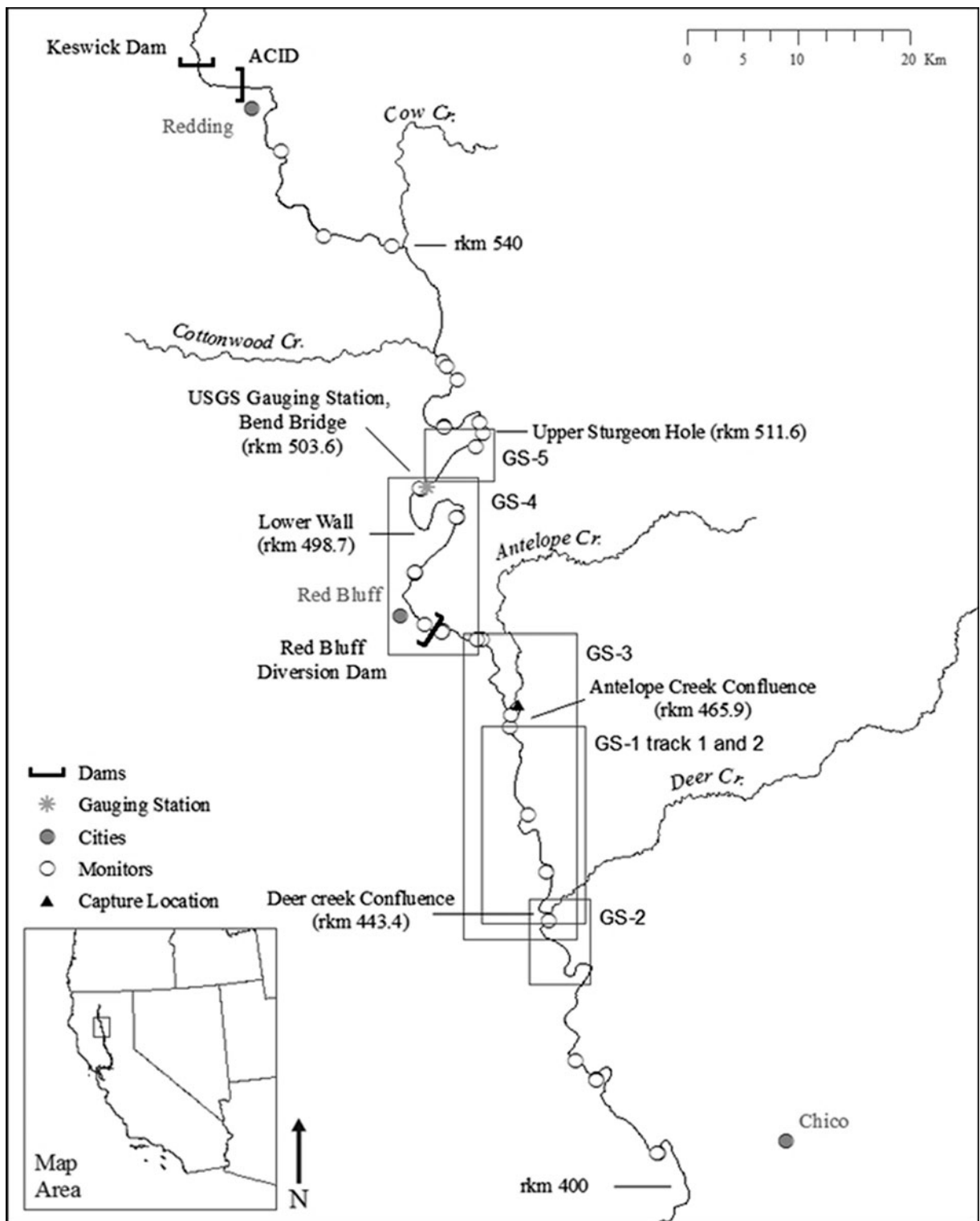


Fig. 1 The study area including locations of tracks (shown in boxes with fish identification numbers), capture location, gauging stations, dams, and stationary acoustic monitors

156 To address the lack of basic biological informa-
 157 tion available on southern DPS green sturgeon we
 158 conducted a telemetric study during spring 2008
 159 and 2010 with three objectives: (1) describe the
 160 behavior and movements between habitat units on
 161 the putative spawning grounds, (2) identify poten-
 162 tial aggregate sites, and (3) identify site fidelity
 163 and habitat use to potential or known aggregate
 164 locations.

165 **Materials and methods**

166 Study area

167 The Sacramento River is the largest river in California,
 168 with a watershed area of about 70 000 km². Major
 169 tributaries include the Pit, McCloud, Feather, Yuba,
 170 American and San Joaquin rivers. Brown (2007)
 171 described the reach of the Sacramento River from
 172 Keswick Dam to Colusa as the “upper” reach. The
 173 upper reach consists of pool-riffle-run types of habitats
 174 with increased leveed bank protection with increased
 175 distance downstream. Tracks were conducted from
 176 river kilometer (rkm) (rkm measured from the
 177 Golden Gate Bridge) 434.4 to rkm 511.7 (Fig. 1).
 178 The putative spawning grounds begins below the
 179 lowest track at a habitat unit located at rkm 424.
 180 To date the habitat unit at rkm 424 is the lowest
 181 unit where eggs have been sampled to confirm
 Q3 182 spawning (Poytress et al. 2011). The uppermost
 183 reaches of the historic spawning grounds are cur-
 184 rently blocked by Shasta and Keswick Dam
 185 (Fig. 1). Below Keswick are two seasonal barriers
 186 used for agricultural irrigation needs. Located at
 187 rkm 569 in Redding California, is the Anderson-
 188 Cottonwood Irrigation District (ACID) dam (Fig. 1).
 189 The ACID dam is a low head dam which operates
 190 between April and October. The ACID dam cur-
 191 rently only provides fish passage for salmonids
 192 during the periods when the dam is operated. Red
 193 Bluff Diversion Dam (RBDD) is the second of the
 194 seasonally operated dams located at rkm 479
 195 (Fig. 1). The RBDD is a gate-operated diversion
 196 used to move water to the adjacent irrigation canal.
 197 Gates of RBDD historically went down on May 15
 198 until 2009, and began going down on June 15 in
 199 2010. During the periods of gate operations there is
 200 no upstream passage for green sturgeon.

Capture, tagging and tracking procedures

201

202 We captured green sturgeon in both years of sampling
 203 using monofilament gill nets. Gill nets were between 5
 204 and 27 m in length, 2–5 m in depth, and mesh sizes
 205 ranged from 15 to 23 cm. Fishing efforts were primarily
 206 focused at Antelope Creek hole at rkm 465.9, a previ-
 207 ously identified aggregation site (USFWS 2009, 2010,
 208 2011; R. Corwin, United States Bureau of Reclamation
 209 [USBR], pers. comm.) (Fig. 1). Sampling at additional
 210 locations was performed on multiple occasions though
 211 was abandoned due to the inefficiency of the nets in
 212 these higher gradient locations. Surface water tempera-
 213 tures during the 2008 sampling season routinely reached
 214 16 °C late in the day. Individuals captured at the elevated
 215 temperatures, exhibited erythema, an indication of
 216 stress. Daily capture activities were suspended when
 217 river temperatures exceeded 16 °C in an effort to
 218 reduce any additional stress to the fish. During 2010,
 219 water temperatures did not exceed 16 °C during
 220 fishing activities.

221 Upon capture, fish were rotated ventral side up in a
 222 sling while a pump circulated water into the canvas
 223 hood that their head was placed in. A 20 mm incision
 224 was made approximately 1 cm off the mid-ventral line,
 225 between the third and fourth ventral scute. A continuous
 226 depth- and temperature-sensing ultrasonic transmitter
 227 (VEMCO, V16TP-4H) and a 69 kHz coded pinger
 228 (VEMCO, V16-6 L) was inserted into the coelomic
 229 cavity of each sturgeon (see Heublein et al. 2009 for
 230 surgical methods). Both transmitters had a diameter of
 231 16 mm; the former was 98 mm long, weighed 36 g in air,
 232 with tag life of 97 days; the latter was 71 mm long,
 233 weighed 25 g in air, and tag life of 3650 days (random
 234 delay of 60 s to 90 s). Gonads were visually inspected to
 235 determine sex and maturation (Van Eenennaam et al.
 236 2001; Van Eenennaam et al. 2006a, b). Incisions were
 237 closed using PDSII absorbable sutures (size #0 or 1,
 238 CP2 cutting needle) with three to four interrupted
 239 stitches. After completion of the surgery, sturgeon was
 240 reoriented and held upright until they swam away under
 241 their own volition.

242 A 6.7 m inboard jet boat equipped with a directional
 243 hydrophone and ultrasonic receiver (VR100, VEMCO,
 244 Halifax, Nova Scotia, Canada) was used for tracking. An
 245 integrated water quality sampler equipped with a water-
 246 quality sonde (Manta2, Eureka Environmental
 247 Engineering, Austin, Texas) interfaced with a fathometer
 248 (GP7000F, Furuno USA, Camas, Washington) was used

249 to collect environmental data. Surface water quality
 250 measurements were collected every minute along with
 251 a GPS position and depth measurement.

252 Each continuous transmitter's serial number, depth,
 253 and water temperature, at the transmitter, were typi-
 254 cally recorded every 3 s. The boat was positioned as
 255 close as possible to the fish based on signal strength
 256 and direction of the hydrophone. When the fish made
 257 sustained directional movements, we followed just
 258 behind the fish attempting to limit the distance be-
 259 tween the boat and fish. Proximity to the fish was
 260 subjectively determined by signal strength, the direc-
 261 tion of the detection, and physical features. An omni-
 262 directional signal with relatively equal signal strength
 263 when the directional hydrophone was rotated 360°
 264 indicated the fish was directly beneath the boat.
 265 There was no indication that the presence of the boat
 266 affected fish behavior as we observed no burst move-
 267 ments indicative of a flight response.

268 Rates of up-stream directed movements were esti-
 269 mated on seven occasions, whereas down-stream di-
 270 rected movements were not assessed due to difficulty
 271 in continuously and confidently detecting movements
 272 downstream (primarily due to boating safety during
 273 the night of the single sustained downstream move-
 274 ment of GS2). Rates of movement during milling
 275 behaviors were estimated on eight occasions by aver-
 276 aging rates between successive recorded positions dur-
 277 ing the behavior. We also calculated correlation
 278 between depths recorded from continuous transmitters
 279 and depths recorded from the depth-sounding unit to
 280 confirm fish were near or at the bottom.

281 **Habitat characteristics and environmental variables**

282 A rapid habitat assessment was conducted to identify
 283 potential holding habitat for adult green sturgeon from
 284 the State Highway 32 Bridge at rkm 415.0 to the
 285 Anderson-Cottonwood Irrigation District dam at rkm
 286 570.0. The study reach was selected as the putative
 287 spawning grounds based on two criteria; 1) habitats
 288 below rkm 415 are channelized by armored banks,
 289 with little current complexity. 2) Tag detections from
 290 passive monitoring has shown that green sturgeon on
 291 their upstream migration typically move quickly be-
 292 yond rkm 415 before exhibiting any long term holding
 293 patterns indicative of spawning behavior (Heublein et
 294 al. 2009; M. Thomas unpubl. data). The habitat as-
 295 sessment of the putative spawning grounds was

296 focused at the mesohabitat scale (see Maddock 1999
 297 for mesohabitat description). The methods used for the
 298 rapid habitat assessment were modified from protocols
 299 provided in Barbour et al. (1999).

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

318 **Data analysis**

319 The spatial distribution of points along a track can yield
 320 valuable information about the interaction between an
 321 animal and its habitat. If time intervals are approximately
 322 equal between recorded positions, then the in-between
 323 distance and the spatial pattern of points could be used to
 324 infer the type of interaction. A measure of the amount of
 325 time spent in a given area along a track, called first-
 326 passage time (FPT), has previously been used by re-
 327 searchers to infer the search effort and habitat prefer-
 328 ences of marine mammals (Fauchald and Tveraa 2003;
 329 Freitas et al. 2008). For each point in a track, a given
 330 circular area about that point is assumed. The difference
 331 between the time the fish entered and left that area would
 332 be an index of the total amount of time spent in the area.
 333 Individual points, and groups of points with low FPT
 334 values can be inferred as lacking some type of suitable
 335 resource for the fish. Conversely, groups of points with
 336 high FPT values could possess the suitable resource.
 337 Since FPT increases with a larger area about the point,
 338 ranges of areas (dependent on a given radius) are tested.
 339 The goal is to determine the radius that is best able to
 340 differentiate between areas with high and low FPT
 341 values. The radius resulting in the maximum natural
 342 log variance of FPT is the radius that is best able to

343 differentiate between areas with high and low FPT
 344 values. We then determined which variables were best
 345 associated with first-passage times of each recorded po-
 346 sition. First passage time values for any particular point
 347 are not actual times spent at that point, but rather an
 348 index of time spent within the given area. Only the first
 349 detection in any given minute interval was used.
 350 Distances (m) and rates of movement ($m \cdot s^{-1}$) were
 351 calculated by assuming straight-line distances and con-
 352 stant speed between recorded positions.

353 Classification and Regression Trees were utilized to
 354 estimate a regression relationship (applied to continu-
 355 ous variables) or a classification (of dichotomous vari-
 356 ables) by use of binary recursive partitioning. We used
 357 the programming language R (version 2.13.0, avail-
 358 able at: www.R-project.org) and routines from the
 359 packages rpart and rpart.plot (both available at:
 360 <http://CRAN.R-project.org>) to construct and evaluate
 361 the validity of constructed trees. Trees are constructed
 362 by repeatedly sorting variables to maximize homoge-
 363 neity within two groups and heterogeneity between the
 364 two groups. Trees can be displayed graphically with
 365 grouped data at the terminal nodes and/or displayed
 366 with typical distributional plots. First-passage time
 367 and CART analyses were performed on the complete
 368 track of each individual. The explanatory variables
 369 were depth of sensor tag, temperature of sensor tag,
 370 and habitat types. We also conducted 1000 indepen-
 371 dent cross-validations of each dataset to ensure we
 372 had not chosen an atypical tree (see De'ath and
 373 Fabricius 2000).

374 Measurements of discharge and water temperature
 375 were compiled from the United States Geological
 376 Survey (USGS) gauging station at Bend Bridge at rkm
 377 503.6 (USGS site no. 11377100, <http://water.usgs.gov/>)
 378 (Fig. 1). Water temperature data from below RBDD at
 379 rkm 479 was also compiled for comparison (USBOR,
 380 site RDB, <http://cdec.water.ca.gov>) (Fig. 1). Hourly
 381 measurements of above and below RBDD water tem-
 382 perature were compared using a Paired-*T* test.

383 **Results**

384 Behavior and movements

385 Five green sturgeon were continuously tracked during
 386 the spring of 2008 and 2010 for a total of six tracks
 387 (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).

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

405 The second behavior was characterized by random
 406 milling movements either restricted to a particular hab-
 407 itat unit or between adjacent habitat units. This behavior
 408 consisted of moderate movements, typically less than
 409 200 m. When sturgeon exhibited milling behaviors they
 410 would often return to specific locations within the pri-
 411 mary habitat unit being utilized. Movement rates during
 412 periods of milling ranged from 0.02 to 0.22 $m \cdot s^{-1}$
 413 (mean=0.07 $m \cdot s^{-1}$). Milling behavior was observed
 414 on four of the six tracks and made up about 5 % of the
 415 duration of the tracks (pooled across all tracks where
 416 milling observed), with GS-1 (second track) spending
 417 the most time milling (~ 12 %) and GS-3 spending the
 418 least amount of time milling (~ 2 %). Holding behavior
 419 consisted of the sturgeon staying within a single habitat
 420 unit for an extended period from 2 to 48 h, generally
 421 making small circling movements within a habitat
 422 unit of approximately 30 m or less. No movement
 423 rates were estimated while sturgeon were holding.
 424 Holding behavior was observed on all 6 tracks and
 425 made up about 61 % of the duration of the tracks
 426 (pooled across all tracks), with GS-5 spending the
 427 most time holding (~ 74 %) and GS-3 spending the
 428 least amount of time holding (~ 35 %).

429 Green sturgeon were tracked from rkm 434.4 to rkm
 430 511.7 an approximate distance of 77.3 km along the
 431 main stem Sacramento River (Fig. 2). Sturgeon GS-2
 432 was tracked most downstream and sturgeon GS-5 was
 433 tracked most upstream (Fig. 1). The distances moved by
 434 sturgeon ranged from a relatively short distance of
 435 6.5 km (GS-5) to 31.5 km (GS-3). The mean distance
 436 traveled by all tracked fish was 18.1 km (Fig. 3).

t1.1 **Table 1** Biological information and track data for five tracked adult green sturgeon on the Sacramento River (2008, 2010). Mean discharge ($\text{m}^3 \text{s}^{-1}$, standard deviation in parentheses) for each track was summarized from Bend Bridge (rkm 502.6, USGS site number 11377100)

t1.2	Fish ID	Tag ID	FL/TL (cm)	Sex	Capture date	Start of track	Duration (h:min)	Mean discharge (SD)
t1.3	GS-1	5452	198 / 217	UNK	4/23/2008	4/30/2008	53:45	251 (3)
t1.4	GS-1	5452	198 / 217	UNK	4/23/2008	5/6/2008	48:56	266 (2)
t1.5	GS-2	10820	171 / 186	M	6/11/2008	6/16/2008	79:58	352 (20)
t1.6	GS-3	48634	183 / 198	M	5/3/2010	5/11/2010	75:18	276 (9)
t1.7	GS-4	48419	165 / 176	M	5/3/2010	5/17/2010	92:31	301 (5)
t1.8	GS-5	48420	157 / 168	M	5/5/2010	6/1/2010	94:46	470 (69)

437 The length of the total directed movements
 438 (accounting for upstream and downstream move-
 439 ments) for each track ranged from 6.5 km for GS-5
 440 to 60.3 km for GS-3. The only sturgeon to pass
 441 through the open gates of RBDD was GS-4, which
 442 traveled a distance of 21.7 km (rkm 477.0 to rkm
 443 498.7) during that migratory movement. The first
 444 movement through the open gates of RBDD occurred
 445 at 19:20 h on 17 May 2010. This fish subsequently
 446 dropped back downstream of RBDD on the morning
 447 of 18 May 2010. GS-4 held at the downstream base of
 448 the open gates for approximately 3 h prior to moving
 449 above RBDD for the remainder of the track.

450 Positive correlation coefficients for transmitter
 451 depth and measured bathymetry were determined for
 452 the tracks of GS-3 and GS-5. When tag depths were
 453 plotted against sonar depths, most points fell above the
 454 line with slope 1, intercept 0. This indicated that any
 455 particular tag depth reading was generally greater than
 456 the sonar reading, suggesting that adult green sturgeon
 457 position themselves at or near the bottom of the water

column. We attribute depth readings greater than sonar 458
 readings to stationing the boats' position slightly away 459
 from the fishes' position, particularly when holding. 460

Habitat utilization 461

First-passage times were consistent with general obser- 462
 vations during tracks where adult green sturgeon held for 463
 long periods of time at several key sites (Figs. 2 and 4). 464
 Tracked sturgeon made sustained movements and 465
 recorded positions during these movements often had 466
 low to below average FPT values. However, five highly 467
 utilized aggregate sites had above average to high FPT 468
 values. Four of five of the sites were previously un- 469
 known as aggregate sites prior to 2008. These four sites 470
 included: 1) the reach above Deer Creek confluence at 471
 rkm 443.4; 2) the Lower Wall unit at rkm 498.7; 3) a 472
 large pool at rkm 505.2; and 4) upper Sturgeon Hole 473
 at rkm 511.6 (Figs. 2 and 4). Anecdotal information 474
 from recreational fishermen suggested that the 475
 Antelope Creek confluence at rkm 465.9 (Fig. 4) 476

t2.1 **Table 2** Biological information
 t2.2 of additional green sturgeon
 detected during continuous
 t2.3 tracking of green sturgeon listed
 t2.4 in Table 1

t2.5	Fish ID	Tag ID	FL/TL (cm)	Capture date	Sex	Capture location
t2.6	NT1	163	164/179	8/1/2008	UNK	Sacramento River
t2.7	NT2	5450	190/175	6/11/2008	UNK	Sacramento River
t2.8	NT3	219	165/151	6/27/2006	UNK	Sacramento River
t2.9	NT4	221	206/190	6/29/2006	UNK	Sacramento River
t2.10	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

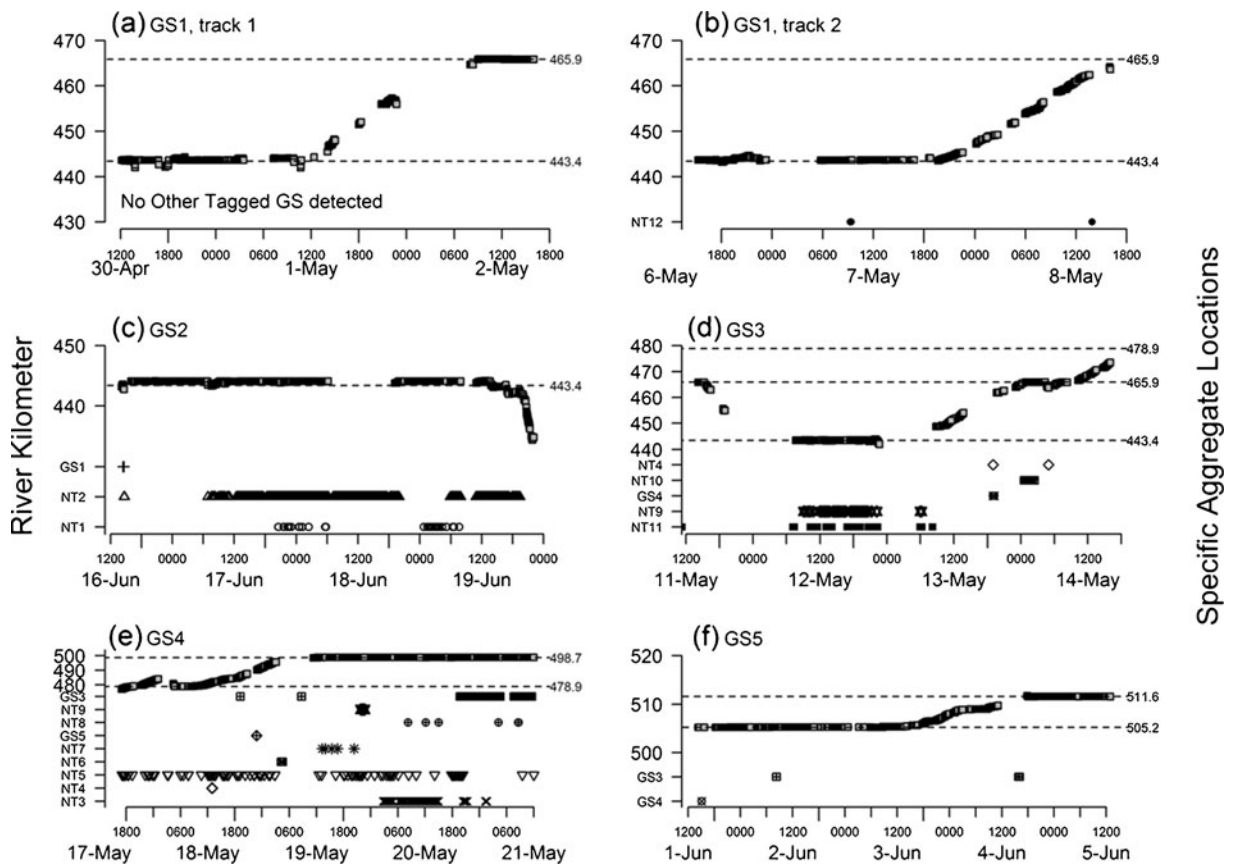


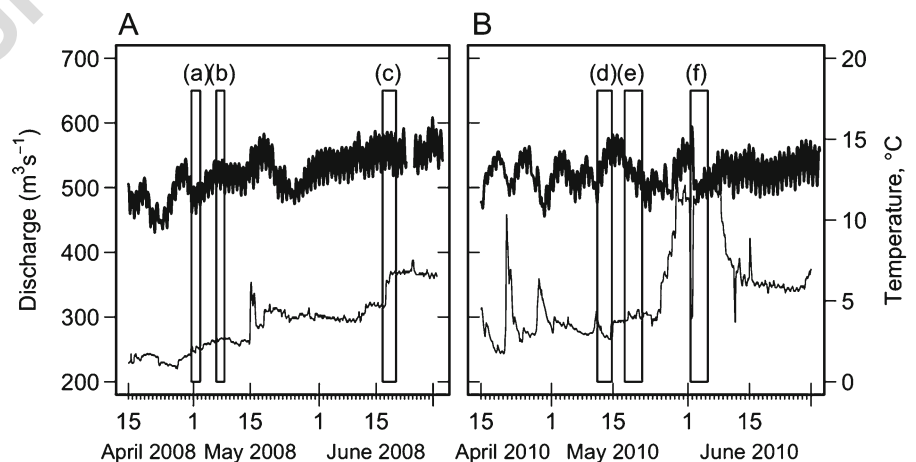
Fig. 2 River kilometer locations by date and time for each tracked green sturgeon conducted during spring 2008 and 2010 in the Sacramento River: **a** track 1 of GS-1; **b** track 2 of

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

477 was an aggregate site, though fidelity had not been
 478 documented until this study.
 479 Three of the five tracked sturgeon used the two habitat
 480 units near the confluence of Deer Creek (rkm 442.4 and

481 443.4; Deer Creek confluence area). Two of five indi-
 482 viduals used the Antelope Creek confluence unit, at rkm
 483 465.9. Two of five individuals exhibited what we de-
 484 scribe 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



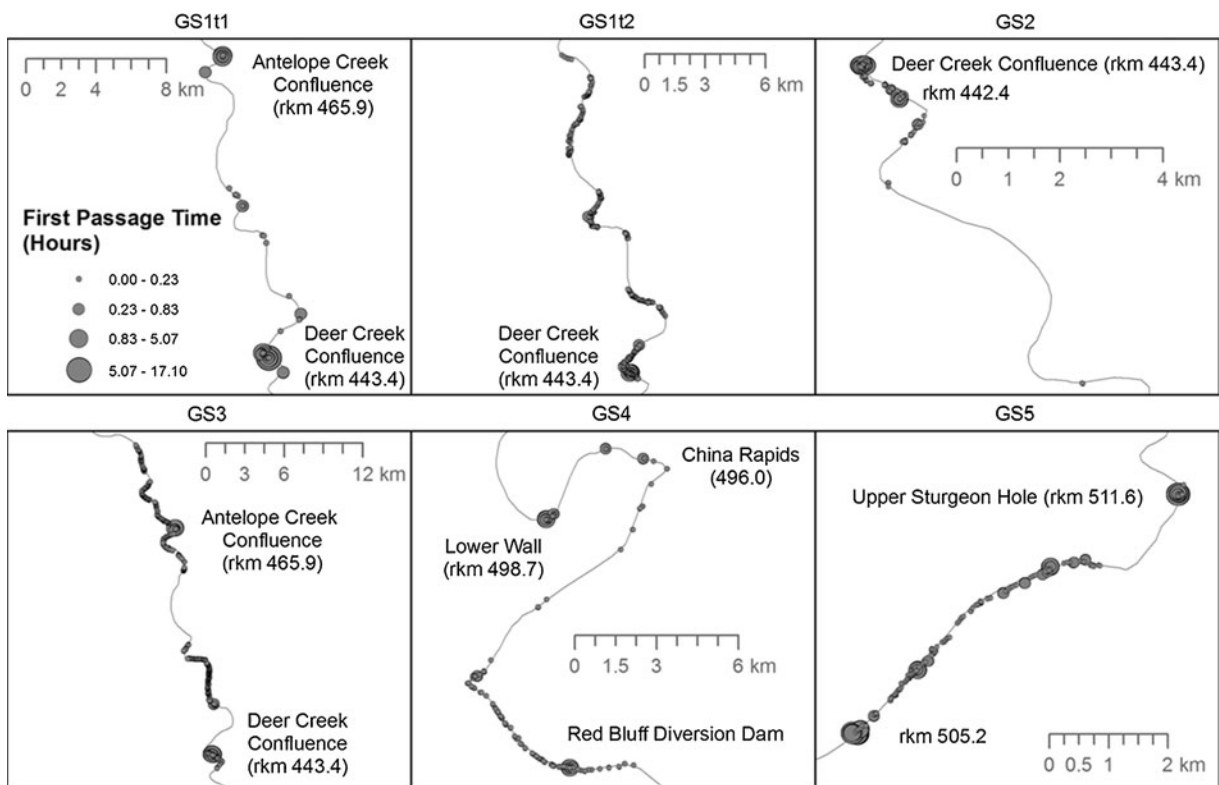


Fig. 4 Individual maps of tracks with first-passage time values depicted by amount of time spent at each recorded position. Note high usage of certain units (at rkm 442.4, 443.4, 465.9, 498.7, 505.2 and 511.6)

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

494 Classification and regression tree analysis was
 495 performed on the six tracks. Pruned regression trees
 496 for the six tracks contained two to five nodes or were
 497 three-branch to six-branch trees. Cross-validation

498 results showed that there was support for smaller or
 499 larger pruned trees, but that we chose the properly
 500 sized pruned tree in all cases.

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

t3.1 **Table 3** Habitat characteristics
 t3.2 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

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

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

522 In the single variable tree, using only depth of tag
 523 (D_{tag}) as the explanatory variable, the first split occurred
 524 at $D_{tag} < 5.85$ m with no further splits. When $D_{tag} <$
 525 5.85 m, the mean of first-passage time values was
 526 0.08 h ($n=843$ observations) and when $D_{tag} > 5.85$ m,
 527 the mean of first-passage time values was 1.4 h ($n=1784$
 528 observations). The general relationship of the splits indi-
 529 cated that first-passage times increased with increasing
 530 depth as measured from the sensor on the acoustic tag.

531 Water discharge measured at the nearest USGS gaug-
 532 ing station at Bend Bridge (Site number 11377100)
 533 showed that discharges were relatively stable throughout
 534 the tracks with the exception of during track GS-5
 535 (Table 1). Discharges in 2010 were more influenced by
 536 storm events compared to discharges in 2008. There also
 537 were high discharges recorded, prior to, during, and after
 538 the track of GS-3, likely due to increased agricultural
 539 demand (Fig. 3, right panel). Dissolved oxygen mea-
 540 surements recorded from all tracks ranged from 6.15 to
 541 10.69 mg/L depending on site and the time of day.

542 Mean water temperatures from above and below
 543 RBDD ranged from 11.6 °C to 15.1 °C (Table 4.) In

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

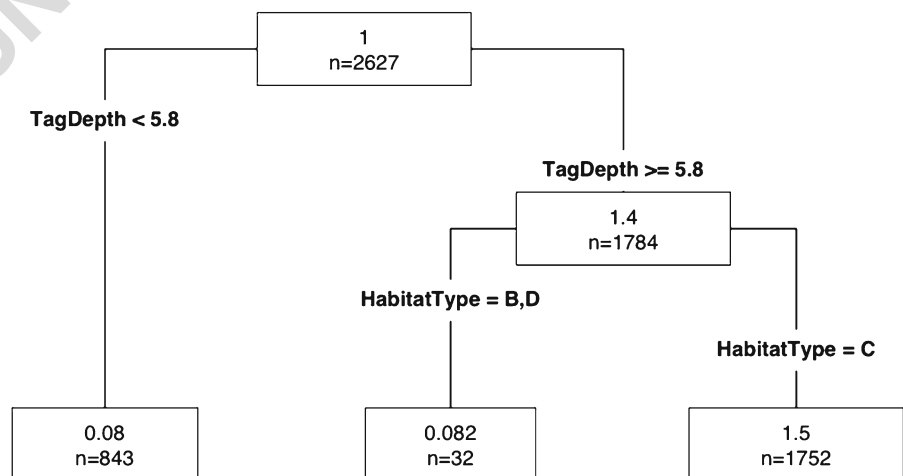
550 **Discussion**

551 Behavior and movements

552 This study provides new information on the move-
 553 ments and behaviors of southern DPS green sturgeon.
 554 Intensive, continuous shipboard tracking was effective
 555 as a method for understanding behavior, movement,
 556 and habitat use at an intermediate spatial scale such as
 557 the river reach or habitat unit. Prior to this research,
 558 results of green sturgeon movements have been pri-
 559 marily based upon broad scale spatial-temporal telem-
 560 etry, utilizing fixed station monitors (Benson et al.
 561 2007; Erickson and Hightower 2007; Heublein et al.
 562 2009). The methods used in this study compliment
 563 fixed station monitoring, providing new information
 564 about how green sturgeon move and behave beyond
 565 the range of acoustic monitors.

566 The migration of GS-1 between the Deer Creek con-
 567 fluence site and the Antelope Creek confluence site on
 568 consecutive weeks, illustrates sustained directed move-
 569 ments between specific aggregate sites, “Ping-Pong”
 570 behavior. It is likely that multiple sustained directed
 571 movements may be a mechanism by which males seek
 572 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 measure in meters from the surface. Habitat types are as follows: **b** Pool; **c** run; **d** glide



t4.1
t4.2

t4.3
t4.4
t4.5
t4.6
t4.7
t4.8

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	<i>t</i> value	<i>P</i> value
GS-1	4/30/2008	11.6 (0.6)	12.6 (0.7)	52	4.2	<i>P</i> <.01
GS-1	5/6/2008	12.7 (1.2)	13.5 (1.1)	47	6.4	<i>P</i> <.01
GS-2	6/16/2008	14.2 (0.9)	15.1 (0.3)	95	8.2	<i>P</i> <.01
GS-3	5/11/2010	13.5 (1.2)	14.1 (1.3)	95	5.4	<i>P</i> <.01
GS-4	5/17/2010	13.1 (0.7)	13.8 (0.6)	95	9.7	<i>P</i> <.01
GS-5	6/1/2010	12.7 (1.2)	13.5 (1.1)	95	11.0	<i>P</i> <.01

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

585 Hatin et al. (2002) found that male Atlantic stur-
586 geon moved large distances between potential
587 spawning sites. Similar behavior has been shown for
588 lake sturgeon (*A. fulvescens*), in the Winnebago sys-
589 tem of Eastern Central Wisconsin (Bruch and
590 Binkowski 2002). Sacramento River green sturgeon
591 showed similar movement patterns between aggregate
592 sites during the spawning season as those documented
593 for Atlantic and lake sturgeon.

594 Understanding the movement potential of this spe-
595 cies during the spawning season is a necessary compo-
596 nent of understanding potential population stressors. In
597 the case of the upper Sacramento River, much of the
598 remaining spawning habitat was blocked by RBDD
599 during a large portion of the spawning season. Due to
600 the movement potential that green sturgeon exhibit dur-
601 ing the spawning season, any blockage of spawning
602 habitat could fragment the population, interfering with
603 the necessary movement patterns by which males locate
604 ovulating females. Since the completion of this study,
605 RBDD has been replaced by a pumping facility, which
606 no longer blocks access to the spawning grounds.
607 However, understanding the behavior of these fish dur-
608 ing the spawning season may explain at least one effect
609 of the 46 year operation of RBDD.

610 All but one tracked individual made upstream
611 movements. It is possible that the downstream move-
612 ment of GS-2 was motivated by handling stress from
613 the capture and tagging procedure. Benson et al.
614 (2007) showed similar early outmigration for green
615 sturgeon in the Klamath River after only a few days
616 post tagging. It is possible this individual had com-
617 pleted spawning and was already out-migrating as the
618 time year was near the end of peak spawning activity.
619 Heublein et al. (2009) observed nine of ten green
620 sturgeon tagged in San Pablo Bay, that had moved
621 up to the spawning grounds, begin to migrate down-
622 stream before 24 August 2006. The earliest reported
623 outmigration by Heublein et al. (2009) occurred as
624 early as 22 May 2006.

Habitat utilization 625

626 We found strong evidence that green sturgeon seek
627 habitat units of depth >5 m. In most cases, habitat units
628 with high first passage times exceeded depths of 5 m
629 indicating that individuals sought out and resided
630 within the deeper habitat units Use of deep water
631 habitats has been shown for white and Atlantic stur-
632 geon (Hatin et al. 2002; Paragamian et al. 2002).
633 Northern DPS green sturgeon have been shown to
634 seek similar deep water habitats in the Rogue River,
635 Oregon (Erickson et al. 2002). However, caution
636 should be exercised when assuming that throughout
637 a species range there will be the same habitat require-
638 ments and preferences, particularly when populations
639 are genetically distinct and there is substantial spatial
640 separation. This study provides evidence suggesting
641 that despite the major alterations to the Sacramento
642 watershed, southern DPS green sturgeon continue to
643 seek out deep water habitat units. Northern DPS green
644 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 habit 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

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743 current complexities, velocity, depth, and substrate
 744 forming processes, and how each of these variables
 745 contribute to the use of known spawning sites and
 746 recruitment potential.

747
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 760

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UNCORRECTED PROOF

AUTHOR QUERIES

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