

Migration of green sturgeon, *Acipenser medirostris*, in the Sacramento River

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Abstract Adult green sturgeon, *Acipenser medirostris*, were collected in San Pablo Bay, California, and surgically implanted with ultrasonic acoustic tags from 2004 to 2006. An array of automated acoustic monitors was maintained in the Sacramento River to record movements of these fish. We presumed movements to known spawning areas (based on previous green sturgeon egg collections) or areas with potential spawning habitat (characterized by substrate, flow, and temperature criteria) represented a “spawning migration.” Three separate annual “spawning migrations” were recorded involving 15 individuals. The majority of the Sacramento River migrants entered the system in the months of March and April. Two different patterns of “spawning migration” and out-migration were observed. Six individuals potentially spawned, over-summered and moved out of the river with the first fall flow event. This is believed to be the common behavior of the green sturgeon. Alternative-

ly, nine individuals promptly moved out of the Sacramento River before 1 September, and any known flow or temperature cue. Some green sturgeon appeared to be impeded on their upstream movement by the 15 May closure of the Red Bluff Diversion Dam, and at least five passed under the dam gates during downstream migration. A delay in the closure of the Red Bluff Diversion Dam would likely allow upstream passage of spawning green sturgeon, further, the potential mortality affects of downstream passage beneath the Red Bluff Diversion Dam should be assessed. Specific protection should be also given to the large aggregation of green sturgeon located in the reach of the Sacramento River adjacent to the Glen Colusa Irrigation District pumping facility.

Keywords Ultrasonic telemetry · Acipenserids · Migration · Movement · Behavior

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Introduction

The green sturgeon, *Acipenser medirostris*, is considered a Species of Special Concern by the California Department of Fish and Game, and the Southern Distinct Population Segment (Southern DPS) of the species (e.g. green sturgeon spawning in the Central Valley basin of California) is listed by the National Marine Fisheries Service as Threatened under the Endangered Species Act (NOAA Federal Register April 2006). A major conservation concern for green sturgeon in the Sacramento River (California) is the historical and ongoing degradation of spawning and rearing habitat associated with land-use patterns and water management. Impassable dams block much of the historically utilized habitat, and the mainstem is impeded by Red Bluff Diversion Dam (RBDD), a seasonally-operated water diversion at river kilometer (Rkm) 391 that may prevent green sturgeon from reaching suitable spawning habitats that remain below Andersen Cottonwood Irrigation District Dam (ACID Dam, Rkm 482) (Fig. 1).

Little is known about the timing or location of spawning for southern DPS green sturgeon. In the Klamath (California) and Rogue (Oregon) rivers, green sturgeon initiate upriver spawning migrations in the spring (Benson et al. 2007; Erickson and Webb 2007), hold over summer in deep pools after spawning, and migrate downstream in late fall or early winter when flow increases occur. Spawning or ripe green sturgeon collected in the Klamath River ranged in size from 152 to 216 cm total length (TL) for males, and 162–242 cm TL for females (Van Eenennaam et al. 2001; personal communication J. Van Eenennaam, University of California, Davis (UC Davis)). It is thought that green sturgeon spawn on rocky bottoms in river reaches with high velocity, based on both sightings of adults in the wild and on the characteristics of the early life stages. Normal development in larval green sturgeon can occur in water temperatures up to 17°C (Van Eenennaam et al. 2005).

Our understanding of the timing and location of green sturgeon spawning in the Sacramento River is based primarily on anecdotal reports and a few collected specimens. Most significantly, sturgeon larvae were captured in rotary screw traps below RBDD in 1994 (517 individuals), and between 1996 and 2000 (291 individuals). The larvae were subsequently identified as green sturgeon by the Center of Aquatic Biology and Aquaculture (CABA) at UC Davis (Johnson and Martin 1997; Gaines and Martin 2001). Addition-

ally, two green sturgeon eggs were collected directly below RBDD and one larva below Bend Bridge (above RBDD on the Sacramento River, Rkm 415) in June and July of 2001 respectively (Brown 2007). The presence of these early life stages indicates that a spawning population of green sturgeon exists in the Sacramento River, and implies that the species migrates upriver above RBDD during spring.

Red Bluff Diversion Dam, constructed in 1966, is a seasonal irrigation dam with flow-control gates that are installed annually between 15 May and 14 September. A fish ladder, adequate only for salmonid passage, and a narrow gap (<0.5 m) between the river bottom and the flow-control gates are the only opportunities for passage during closure periods. No green sturgeon have been observed migrating up the fish ladder, and extreme water velocities below the flow-control gates are believed to prevent fish from moving upstream under the gates (Brown 2007). Consistent observation of green sturgeon directly below RBDD after the gates are closed annually suggest that some fraction of the spawning migration is impeded (pers. comm. Kurt Brown, U.S. Fish and Wildlife Service). The gonads of green sturgeon caught 60 km downstream of RBDD at the Glen Colusa Irrigation District (GCID) pumping facility (Rkm 331), prior to the opening of the Red Bluff gates in September, are often in post-spawn condition (personal communication Matt Manual, GCID, based on tagging efforts of green sturgeon from 2001 to present). This suggests that either the fish pass under the gates at RBDD after spawning above the dam, or that some fish spawn in reaches below the dam, as shortnose sturgeon (*A. brevirostrum*) have been reported to do when migratory passage was blocked on the Kennebec River, Maine (Kynard 1996).

We conducted an acoustic telemetry study to identify the timing of the migration of green sturgeon spawning in the Sacramento River, describe spawning habitat above the Red Bluff Diversion Dam, and locate aggregations and passage impediments in the river. Based on our existing understanding of Southern DPS green sturgeon, we expected that fish would enter the Sacramento River between March and May, migrate beyond RBDD prior to the 15 May closure, and spawn in high velocity reaches over rock substrate. After spawning, green sturgeon were expected to move downstream, below the RBDD flow-control gates, to reaches adjacent to the GCID pumping plant in the period between July and October, and migrate out of

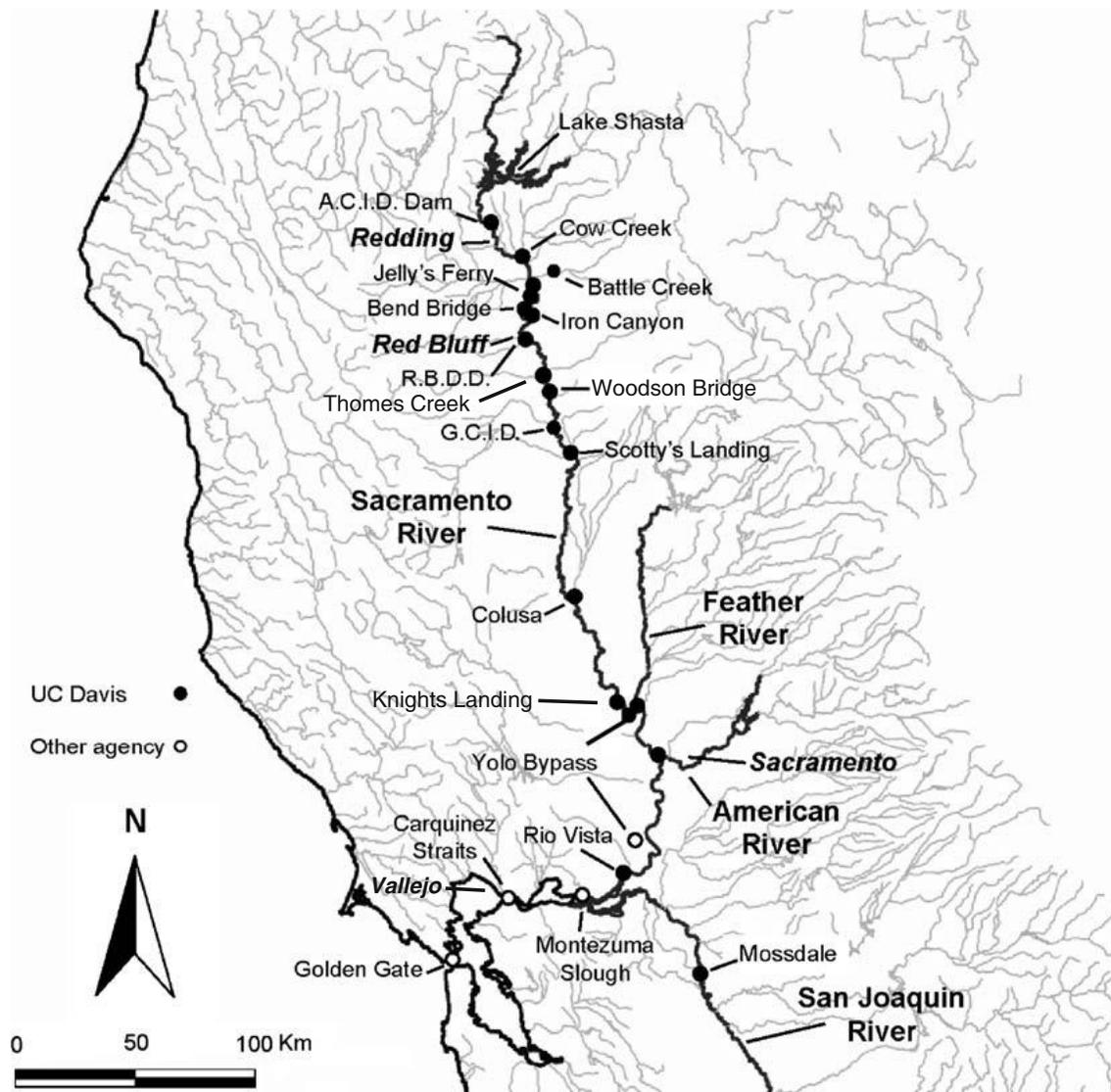


Fig. 1 Map of VR2 monitor sites. *Solid circles* indicate sites deployed and maintained in this study for green sturgeon detection. *Open circles* indicate monitor(s) maintained by other agencies

the Sacramento River in November and December. We also anticipated that green sturgeon entering the Sacramento River later in the season would encounter a barrier to upstream migration at RBDD, and either abort the migration or spawn in reaches below RBDD.

Methods

Green sturgeon were collected over five periods between 2004 and 2006: Spring 2004, Fall 2004, Spring 2005, Fall 2005, and Spring 2006. Each period lasted for 40 days with the exception of a shortened 18-day period in Spring 2006. Sampling occurred daily, weath-

er permitting. Fish were captured with monofilament gill-nets (274–365 m length, 19–24 cm mesh size) deployed from a commercial herring gill-net boat (*F/V Intrepid*) in San Pablo Bay. The gill nets ranged in depth from 18 to 35 mesh, depending on mesh size. The realized depth of the net depended on water depth as a function of billowing or stretching.

All but eight of the 178 10-h fishing days were carried out from approximately 04:00 to 14:00. Fishermen averaged three gill-net sets per sampling day, with 1.5 h of fishing for each set. We recorded the number of individuals per species captured and released, and undersized green sturgeon (<120 cm TL) were measured and released. Priority was placed on capturing and

tagging potentially mature fish (>150 cm TL) (Van Eenennaam et al. 2001); however, subadults >120 cm total length (TL) were tagged at some times in order to deploy the maximum number of tags per season.

Some green sturgeon tagged in southwestern Washington were also included in this analysis. These fish were collected in Willapa Bay, Grays Harbor, and the lower Columbia River from 2003–2005 using similar gillnetting methods. Details of the capture methods and summary information on tagged fish from these locations are reported by Lindley et al. (2008).

Tagging

Green sturgeon above the selected minimum size were held onboard the *F/V Intrepid* in a 500-L holding tank supplied with flow-through water and supplemental O₂, and were transported back to the Vallejo Marina at the completion of the fishing day. Green sturgeon were anesthetized in the onboard holding tank while at dock at the Vallejo Marina. During Spring 2004, Fall 2004, and Spring 2005, tricaine methane sulphate (MS-222) was used as an anesthetic. Preparation for surgery involved draining the holding tank to 100 L and adding 7.5 g of MS-222 to achieve a concentration of 0.075 g MS-222 L⁻¹. After approximately 5 min, the fish were rolled to an inverted position with their mouth and gills still below the water surface. The ventral surface of the fish was exposed, and swabbed with iodine disinfectant. A 4-cm longitudinal incision was made with a sterile scalpel (size #3 handle, #10 scalpel blade) adjacent to the third or fourth scute, and offset from the midline. The peritoneal cavity was inspected to determine, when possible, the sex of the fish and the maturity of the gonads, and an ultrasonic pinger (V16, Vemco Ltd.), which was 106 mm long, 16 mm in diameter, and 16 g weight, was inserted into the peritoneum. The incision was closed using PDSII monofilament sutures (size #0, CP-1 cutting needle) with three to four interrupted knots depending on incision length, and the green sturgeon was returned to a ventral-side down position. The fish was resuscitated in fresh water pumped into the tank along with diffused oxygen. An overnight holding period in flow-through water followed the surgery, and green sturgeon were checked for normal activity and good suture condition prior to release at the site of capture. Identical methods were used during Fall 2005 and Spring 2006 except sodium bicarbonate and acetic acid (buffer) were

substituted as anesthetic. The holding tank was again drained to 100 L and 270 g of NaCO₃ and 100 mL of acetic acid were mixed in 5 L of ambient water and introduced into the holding tank, achieving a concentration of 2.7 g NaCO₃ L⁻¹ (Peake 1998). In all cases, the fish recovered quickly from handling, and there were no known mortalities associated with the tagging procedure.

Fish captured in southwestern Washington were also tagged with Vemco V16 pingers. Surgical procedures were similar, with details given by Moser and Lindley (2007); the primary difference was that green sturgeon were released immediately after the completion of surgery.

Monitor placement

Tagged green sturgeon were detected by an array of automated data-logging monitors (VR2, Vemco Ltd.) deployed between the impassable Anderson-Cottonwood Irrigation District (ACID) water diversion dam in Redding, California, and the Golden Gate Bridge (Rkm-94 based on shortest path through estuary). The array consisted of approximately 50 monitors, the exact number varying depending on losses (Fig. 1, Table 1).

In rivers, monitor moorings were installed by fastening one end of an 18 m-long 0.63-cm stainless steel cable to the bank, usually around a large diameter tree, and extending the other end perpendicularly out into the river where it was attached to a 18-kg lead pyramid river anchor. Also shackled to the anchor was 1 m of 1.3-cm diameter polypropylene rope which was fastened to a buoy (2.95-kg buoyancy). Heavy gauge cable ties and stainless steel hose clamps were used to attach the VR2 onto the rope mid-way between the anchor and buoy with the hydrophone oriented towards the water's surface to maximize detection range. At the Golden Gate Bridge, VR2 hydrophones were deployed on subsurface moorings consisting of three hard plastic trawl floats (3.6-kg buoyancy per float), 3 m of 1.3-cm polypropylene line, an acoustic release (Model 111, InterOcean Systems Inc.), another 3 m of 1.3-cm polypropylene line, 2 m of anchor chain, and a 70-kg anchor. Moorings were spaced approximately 500 m apart along two lines roughly 1 km east of the Golden Gate Bridge at depths ranging from 25 to 90 m.

Monitor sites were selected based on a number of factors. General locations were chosen based on possible migration routes, proximity of potential spawning tribu-

Table 1 List of VR2 monitor locations by river kilometer (Rkm)

Site	Rkm
Golden Gate Bridge	-94
San Pablo Bay release site	-54
Carquinez Strait	-44
Montezuma Slough	-19
Rio Vista Bridge	21
Sacramento River at confluence with Ship Channel	22
Brannan Island	23
Cache Slough (lower)	25
Cache Slough (upper)	31
Knights Landing	145
Scotty's Landing	317
Adjacent to GCID diversion	331
Thomes Creek (below)	359
Thomes Creek (above)	365
Below Red Bluff Diversion Dam	391
Above Red Bluff Diversion Dam	393
China Rapids (below)	404
Bend Bridge (below)	414
Table Mountain	422
Jelly's Ferry	430
Battle Creek (above)	438
Cow Creek (below)	451
Mossdale (San Joaquin River)	n/a

The Mossdale site was selected to ensure that no green sturgeon moved into the San Joaquin River.

taries, expected or known sites that green sturgeon aggregate, and migration impediments (Fig. 1). Exact locations of receivers were chosen to maximize the likelihood of detection of fish passing the site, and monitors were paired at many sites. Tag detection ranges by VR2 monitors, when the water is calm and the ambient noise is low, extends to over 500 m (UC Davis Biotelemetry Lab, unpublished data). The Sacramento River only exceeds this width in the lowest downstream monitor sites; however, background noise, bottom contour and obstructions, and the observation that green sturgeon swim near the bottom when moving against the current (JTK, unpublished data) likely reduced the functional detection ranges of the monitors used in this study to less than this optimum value. Positions of some monitor sites were also adjusted during the study because of theft and loss.

The river above RBDD was intensively targeted based on earlier collection of green sturgeon eggs and larvae in that region (Johnson and Martin 1997; Gaines and Martin 2001; Brown 2007). Long stretches of high

velocity bedrock runs are present in the Sacramento River upstream of RBDD between Red Bluff and Jelly's Ferry (Rkm 430), including reaches such as China Rapids (Rkm 405) and Table Mountain (Rkm 421). River morphology and water temperature in these areas are similar to what is believed to be preferred green sturgeon spawning habitat (these conditions are not as prevalent below RBDD). Monitors were placed throughout this area in the anticipation that this was potential spawning habitat.

During our study period, other researchers were operating compatible equipment in the Yolo Bypass (California Department of Water Resources Division of Environmental Services: Zoltan Matica and William Harrell), Carquinez Straight and Montezuma Slough (California Department of Fish and Game Bay Delta Branch: Robert Vincik), and Monterey Bay (Moss Landing Marine Laboratory: Rick Starr), and we included data from these monitors in our analysis.

Data collection and treatment

Data were downloaded from monitors every 2–3 months. Extreme water levels prevented access to the monitors during some seasons, while dam-regulated agricultural flows during summer months generally permitted more routine downloads.

We examined relationships between movements of migrating green sturgeon with flow and water temperature data acquired from long-term monitoring stations administered by the California Data Exchange Center (CDEC) (California Department of Water Resources 2007). Flow data (cubic meter per second) were acquired for downriver sites from the station located at Verona (Rkm 135), mid-river at Woodson Bridge (Rkm 351), and upriver (in the potential spawning reach described by Brown (2007)) near Bend Bridge (Rkm 414). Water temperature records (°C) were acquired from the Red Bluff Diversion Dam (the nearest CDEC temperature site upriver of GCID), and Bend Bridge.

Results

Capture and tagging

We fished for green sturgeon on a total 178 days during five tagging periods from 16 April 2004 to 19

March 2006. In all, 212 green sturgeon were captured and 96 tagged, of which, 60 were detected later by a VR2 monitor.

Detections

Eleven fish tagged in San Pablo Bay were observed moving in the Sacramento River. An additional 15 green sturgeon tagged in southwestern Washington were detected in our study area (Table 2).

Green sturgeon traveling to or above the Knights Landing monitor location (Rkm 145) were categorized as “spawning migrants”. All green sturgeon detections at Knights Landing (Table 1; after the completion of the UC Davis array) were followed by a substantial upstream movement and sustained residence in reaches containing suitable suspected spawning habitat. Final detections of individuals at Knights Landing were also indicators of out-migrating green sturgeon. No green sturgeon remained at Knights Landing for more than 2 days and a rapid downstream migration to the Sacramento River Delta usually followed outbound detections at the Knights Landing site. Residence time in the Delta varied and sea-going detections at the Golden Gate Bridge sometimes occurred months after out-migration from the Sacramento River itself.

In the spring/summer 2004, only two green sturgeon (SP1, WB4) were detected moving upstream of Knights Landing, potentially migrating upriver to spawn; however, the monitor array was incomplete during this period and detections during this spring period were sporadic.

Fifteen green sturgeon (eight tagged in San Pablo Bay, four in Willapa Bay, and three in the Columbia River) were detected in the first complete season of 2005, and three of these fish moved upstream of Knights Landing for sustained periods (>3 months). Ten green sturgeon (seven tagged in Grays Harbor, Washington, and three in San Pablo Bay) were detected in the second season (2006–2007). All ten migrated into the Sacramento River above Knights Landing.

Upstream-migration and spawning

Of the two fish detected moving upriver in Spring 2004, SPB1 was known to be mature with ripe eggs, within 2–3 months of spawning (personal communication J. Van Eenennaam, UC Davis CABA.), when it was tagged on 19 April 2004 in San Pablo Bay. This

fish was later caught near Rio Vista by an angler on 6 February 2005, who reported that a few mature eggs remained in the abdominal cavity, indicating a spawn had occurred in the previous months (personal communication J. Van Eenennaam, UC Davis CABA). WB4, captured in Willapa Bay, Washington in August 2003, was above a minimum size length for maturity (Erickson and Webb 2007) but was not thought to be mature when tagged.

In Spring 2005, three tagged green sturgeon exhibited a movement pattern that we believe represents a spawning migration (CR2, CR3, and SPB8, Fig. 2). Of these, CR2 and CR3 were tagged in the Columbia River (CR) and detected at the Golden Gate Bridge on 14 March and 2 April, respectively. SPB8 was tagged in San Pablo Bay (SPB) on 11 April.

During the Spring 2005 season, we experienced some theft and loss of important monitors, leading to gaps in the record of detections of tagged fish. For example, although there were few monitor detections above Thomes Creek (below RBDD, Rkm 362) during this period, CR3 successfully passed RBDD and was later detected upriver just below Cow Creek (Rkm 450) on 27 June. Similarly, CR2 and SPB8 could have migrated above the RBDD before the 15 May closure, but detections are not conclusive in these reaches during this period. All green sturgeon had a long period in which there were no detections after the farthest upstream movement (Fig. 2). By late June to mid-July all three green sturgeon were detected again, now moving downstream to the GCID aggregation site. Water temperature was consistent during this period (<1°C change) (Fig. 3b and c). All of the fish had a prolonged residence time in the GCID aggregation area (Fig. 2).

Ten green sturgeon were detected migrating upriver during the 2006 spawning season. GH1 was the earliest detection in that year, entering the San Francisco Bay on 24 February (Fig. 4). Sacramento River flow increased substantially 21 February coincident with the time that GH1 started moving upriver (Fig. 5a). No passage of RBDD occurred, despite the absence of control gates, and a final detection at Thomes Creek was recorded on 18 May prior to a rapid out-migration.

Three fish tagged in San Pablo Bay and one in Grays Harbor (SPB10, SPB9, SPB11, GH7) successfully passed RBDD prior to the 15 May 2006 installation of the gates (Fig. 6). Of these fish, SPB10, SPB9, and GH7 were tagged in late summer 2005 and detected entering the estuary at the Golden Gate Bridge on 5

Table 2 Biological information of green sturgeon detected in the Sacramento River and Bay/Delta

Code	Date captured and tagged	Region captured and tagged	Total length (cm)	Fork length (cm)	Sex (M/F)
SPB1	19-Apr-04	San Pablo Bay	183	165	F ^a
SPB2	27-Apr-04	San Pablo Bay	144	128	
SPB3	25-May-04	San Pablo Bay	153	144	F
SPB4	9-Aug-04	San Pablo Bay	128	114	
SPB5	27-Aug-04	San Pablo Bay	130	118	
SPB6	31-Aug-04	San Pablo Bay	131	118	
SPB7	8-Sep-04	San Pablo Bay	149	136	
SPB8	11-Apr-05	San Pablo Bay	186	166	
SPB9	28-Aug-05	San Pablo Bay	156	145	
SPB10	31-Aug-05	San Pablo Bay	204	194	M ^a
SPB11	19-Mar-06	San Pablo Bay	206	189	F ^a
CR1	13-Jul-04	Columbia River	184		M
CR2	10-Sep-04	Columbia River	210	186	F
CR3	13-Sep-04	Columbia River	168	156	M
WB2	2-Sep-03	Willapa Bay	160	155	
WB3	5-Sep-03	Willapa Bay	144	131	F
WB4	26-Aug-03	Willapa Bay	186		M
WB5	28-Aug-03	Willapa Bay	137		
WB6	30-Jun-04	Willapa Bay	132		
GH1	29-Jun-05	Grays Harbor	190	174	
GH2	20-Jul-05	Grays Harbor	172		
GH3	20-Jul-05	Grays Harbor	167	155	
GH4	3-Aug-05	Grays Harbor	193		
GH5	3-Aug-05	Grays Harbor	165	150	
GH6	19-Aug-05	Grays Harbor	184	166	
GH7	1-Sep-05	Grays Harbor	188		
Range			128–210	114–194	
Mean			167	152	

Fish are described by codes based on capture location and order of detection. For example, SPB1 was the first green sturgeon tagged in San Pablo Bay that was detected by the UC Davis array, and WB4 was the fourth green sturgeon tagged in Willapa Bay that was detected by the UC Davis array.

^a Fish identified as mature

March, 8 March, and 11 March respectively, and SPB11 was tagged on 19 March 2006 in San Pablo Bay. All four green sturgeon appear to have entered the river system in early/mid-March, coincident with a rapid increase in flow (Fig. 5a). The movements of the three green sturgeon tagged in San Pablo Bay showed notably close temporal relation; for instance, all detections at RBDD occurred within the same 26 h period.

When it was tagged just prior to initiating its upriver migration, SPB11 was observed to be mature with abundant well-developed eggs. Eggs collected from this fish and analyzed at CABA (personal communication J. Van Eenennaam, UC Davis) indicated the fish was likely to spawn in 2–3 months. That time frame coincides with the apex of the up-migration conducted by this individual in the reach above Battle Creek (Rkm 436).

Four green sturgeon tagged in Grays Harbor (GH4, GH2, GH3, and GH6) that migrated upriver but did not pass RBDD also exhibited close temporal relation in movement. Up-stream movement was initiated by these four fish approximately one month after the green sturgeon that successfully passed RBDD, starting in early April through early May (Fig. 4). Another spike in Sacramento River flow appears to be closely related to this up-migration (Fig. 5a). GH6 was detected at the Golden Gate Bridge on 3 May and moved rapidly to GCID, where it remained for 4 days (16–20 May) before a quick out-migration. GH2 and GH3 were detected near the Rio Vista Bridge (Rkm 21) on 15 April and 23 April respectively. These fish remained downstream of RBDD in the reaches near GCID. GH4 was first detected at the Golden Gate Bridge on 4 April,

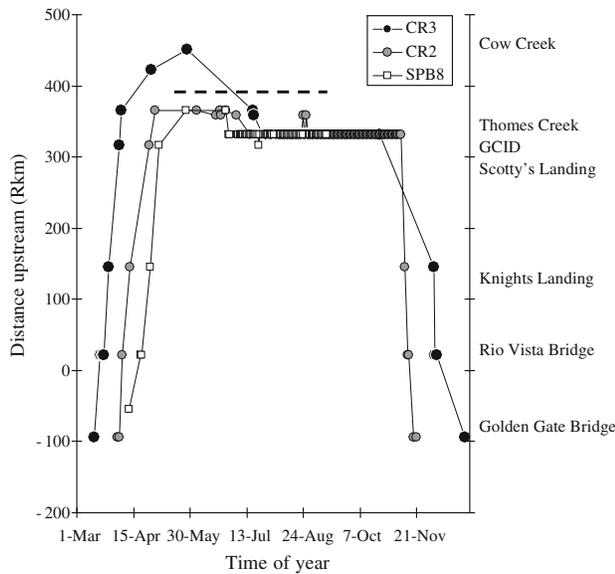


Fig. 2 2005 movements of tagged green sturgeon in the Sacramento River. Green sturgeon position by river kilometer (Rkm) is plotted with date. Symbols reference individual fish. For reference, selected river locations are indicated on the secondary y-axis. Bold dashed line indicates presence of flow control gates at Red Bluff Diversion Dam

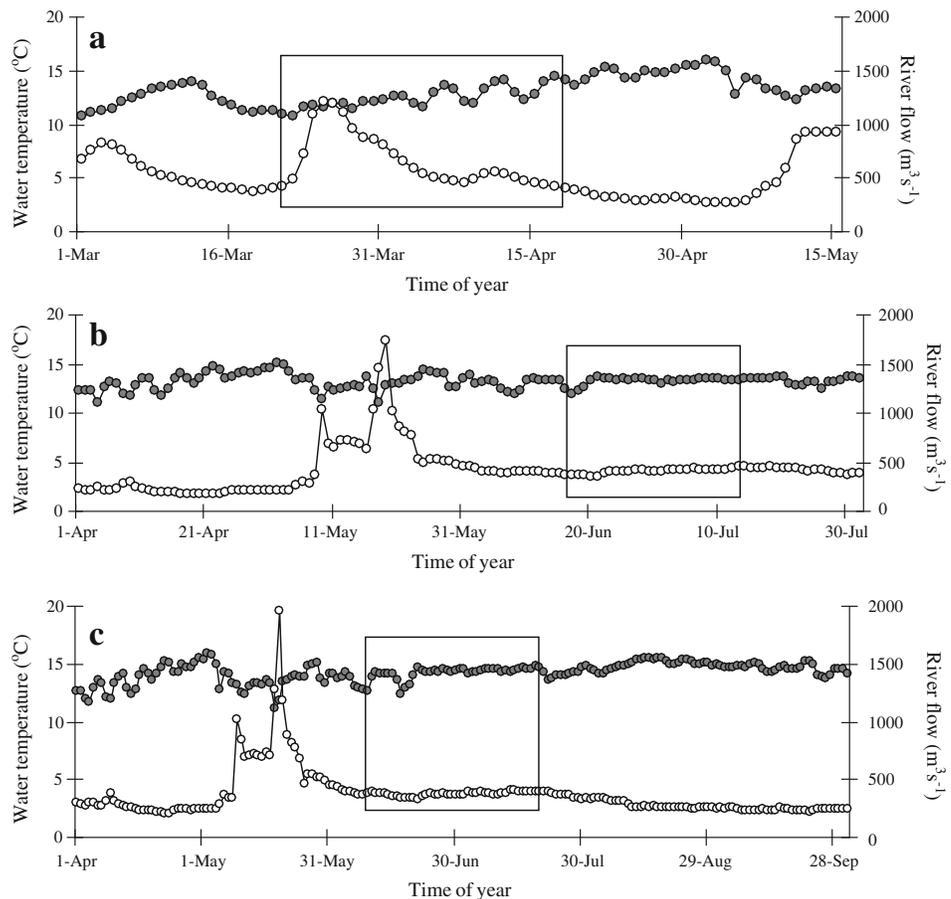
moved upriver as far as RBDD, then remained near GCID until 24 July. It is possible that these fish spawned during their residence in the region below the RBDD between mid-May and late-June.

The latest up-migrant of 2006, GH5, was detected at the Golden Gate Bridge on 7 May. A steep decrease in flow and increase in temperature occurred in the Sacramento River during this period (Fig. 5a). GH5 moved rapidly upriver and was detected on 28 May in the GCID aggregation site. A long period with no detections preceded a 26 July detection at Thomes Creek.

Fall out-migration

By fall of 2004, the UC Davis monitor array had been fully deployed in the Sacramento River, thus the movements of the two green sturgeon detected in Spring 2004 and later detected upriver (SP1, WB4) produced interpretable data regarding freshwater out-migrations. These individuals were both detected at Knights Landing on 10 December 2004. This was followed by

Fig. 3 Comparison of temperature and flow at representative locations in the Sacramento River in 2005: **a** RBDD temperature and Verona flow, **b** Bend Bridge temperature and flow, **c** RBDD temperature and Woodson Bridge flow. Water temperature (°C) is represented by solid circles and flow (cubic meter per second) is represented by open circles. Rectangle in **a** highlights the temperature and flow when tagged fish were first detected. Rectangle in **b** highlights temperature and flow during migration to GCID by CR3. Rectangle in **c** highlights flow and temperature during CR2 and SPB8 migration to GCID



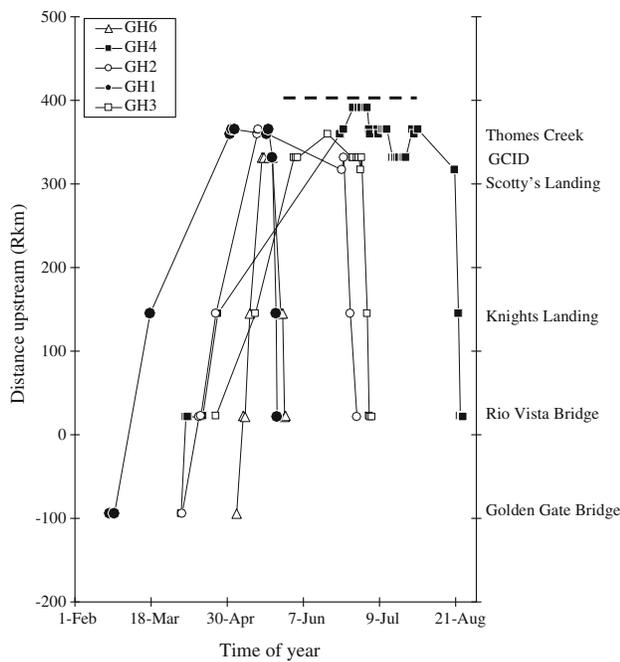


Fig. 4 2006 movements of tagged green sturgeon that were not detected above RBDD. Green sturgeon position by river kilometer (Rkm) is plotted with date. Symbols indicate movements of individual fish. For reference, selected river locations are indicated on the secondary y-axis. Bold dashed line indicates presence of flow control gates at RBDD

a downstream movement of a minimum of 125 km to the Rio Vista Bridge in less than 2 days. This suggests both green sturgeon initiated out-migration from the river system in relation to a similar cue. This downstream migration corresponds closely with the first spike of winter flow in the Sacramento River and a general downward trend in temperature (Fig. 7a).

In 2005, out-migration from the GCID aggregation site by CR2 and CR3 occurred in early November and early December respectively. Both green sturgeon appear to have exited the river in response to separate surges in river flow (Fig. 7b), and rapidly moved out of the San Francisco Bay entirely, with detections of CR2 on 18 November and CR3 on 28 December at the Golden Gate Bridge. The third fish, SPB8, was not detected at any location after 10 September 2005, likely due to tag failure, tag expression, or mortality.

Only one green sturgeon remained in the upper reaches of the Sacramento River until the fall of 2006 (GH5). After 4.5 months with no detections, GH5 was recorded at Scotty's Landing (Rkm 316) on 13 December. It rapidly moved downstream and was detected again at Knights Landing on 16 December, and Freeport (Rkm 76) on 17 December. This movement coincided

with the first large increase in Sacramento River flow of the fall (Fig. 7c). GH5 was detected almost daily at Freeport until the end of the year and ultimately the Golden Gate Bridge on 7 March 2007.

Summer out-migration

In contrast to the previous two years, most of the green sturgeon detected in the river in 2006 did not hold-over until winter. Of the ten fish detected in 2006, nine out-migrated prior to 24 August (Figs. 4 and 6) and only GH5 remained in the system until December.

The earliest out-migrants were two fish that did not pass upstream of RBDD: GH1 and GH6 were detected on 22 May and 26 May at Knights Landing, followed by 23 May and 27 May detections Rio Vista Bridge respectively (Fig. 4).

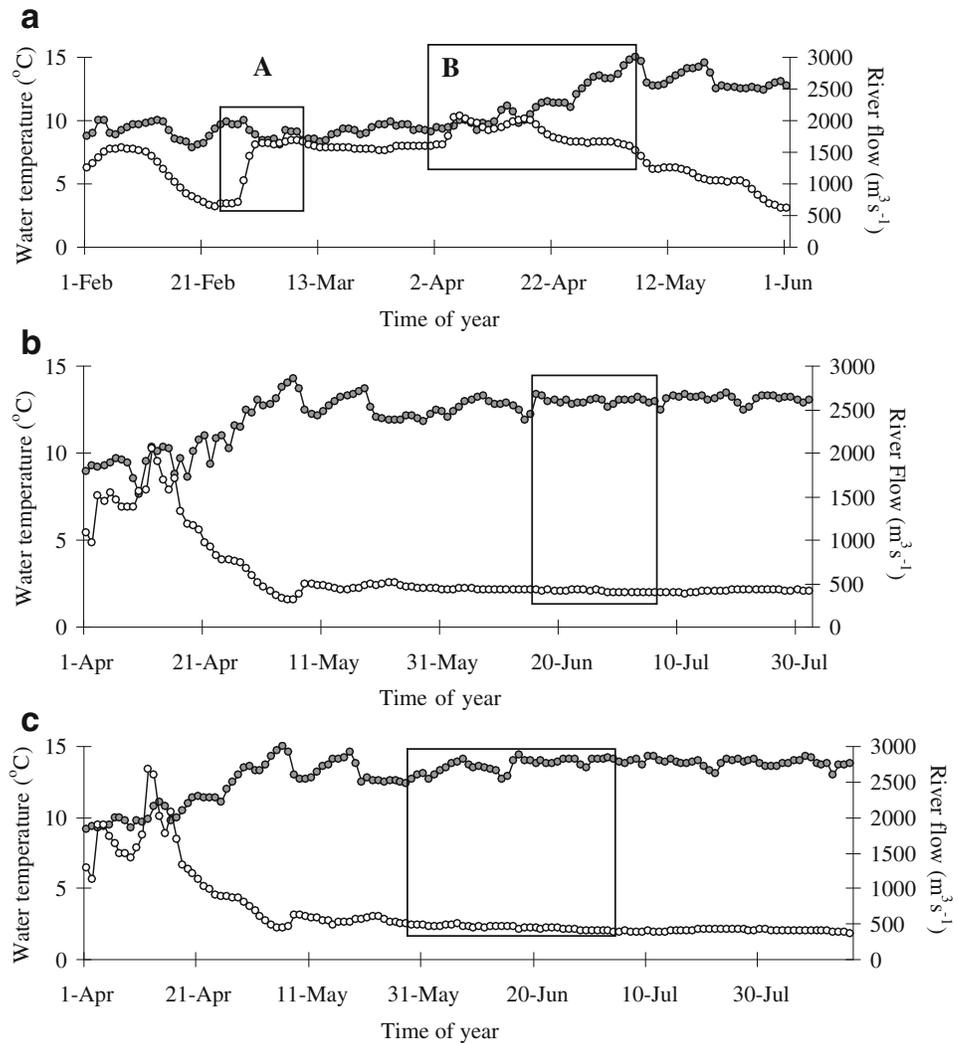
The three latest out-migrants of the 2006 summer also did not pass RBDD. GH2 and GH3 were detected passing Knights Landing within 8 days of one another on 25 June and 3 July; and Rio Vista Bridge on 28 June and 4 July respectively (Fig. 6). GH4 was detected at Scotty's Landing on 20 August, Knights Landing on 22 August, and ultimately at Rio Vista on 23 and 24 August.

The outbound movements of the four fish that did move upstream of RBDD were tightly clustered in time (Fig. 6). All started downstream in mid-June, passing Knights Landing within 10 days of one another. No holding period in the GCID aggregation reach was observed. The out-migration did not appear to coincide with a significant change in water temperature or flow; however, overall river flow was higher, and water temperature lower than in previous study years (Fig. 8a,b). There were no further detections of GH7 or SPB11 prior to the completion of the study on 1 April 2007 after they passed the Rio Vista station on 27 June and entered the Delta. SPB9 and SPB10 were detected at the Golden Gate Bridge on 1 August and 13 August respectively.

Discussion

Prior to this study, there were few empirical observations of green sturgeon movement in the Sacramento River. Both the timing of the species' migration and the location of spawning could only be inferred from the collection of only two green sturgeon eggs below

Fig. 5 Comparison of temperature and flow at representative locations in the Sacramento River in 2006: **a** RBDD temperature and Verona flow, **b** Bend Bridge temperature and flow, **c** RBDD temperature and Woodson Bridge flow. *Solid circles* indicate water temperature ($^{\circ}\text{C}$) and *open circles* indicate flow (cubic meter per second). *Rectangles in a* contain flow and temperature at first detections of green sturgeon that “A” successfully passed RBDD, or “B” did not pass RBDD. *Rectangle in b* contains flow and temperature during out-migration of fish that passed RBDD. *Rectangle in c* contains flow and temperature during out-migration of fish which were not detected above RBDD



RBDD (Brown 2007) and occasional anecdotal records of adult fish. Additionally, green sturgeon larvae have been periodically captured below RBDD in rotary screw traps (Johnson and Martin 1997; Gaines and Martin 2001). While these records do indicate that spawning is occurring in the river, extrapolating back from larval developmental stage in order to estimate the location of spawning would be extremely imprecise at best. Our study is the first to describe the characteristics of the adult green sturgeon migration in the Sacramento River, and to identify putative regions of spawning habitat, based on the recorded movements of free-swimming adults.

The timing of the upstream migration of Southern DPS green sturgeon in the Sacramento River appears to be similar, though slightly earlier, than that of the Northern DPS. There, green sturgeon were captured while initiating spawning migrations in the Klamath

River between April and June (Benson et al. 2007) and between May to July in the Rogue River (Erickson et al. 2002); whereas we observed that the Southern DPS green sturgeon enter San Francisco Bay in March and April and migrate rapidly up the Sacramento River to the region between Rkm 331–450 (from GCID to Cow Creek). The fish lingered at these regions at the apex of their migration for 14–51 days, presumably engaged in spawning behavior, before moving back downriver.

In the Northern DPS of green sturgeon, fish are typically observed to aggregate and over-summer in deep, low-velocity pools, out-migrating in the late fall coincident with increases in flow from the first significant rain events (Erickson et al. 2002; Benson et al. 2007). In the Southern DPS, we observed similar behavior in two green sturgeon in 2004 (SPB1 and WB4), two in 2005 (CR2 and CR3), and one in 2006

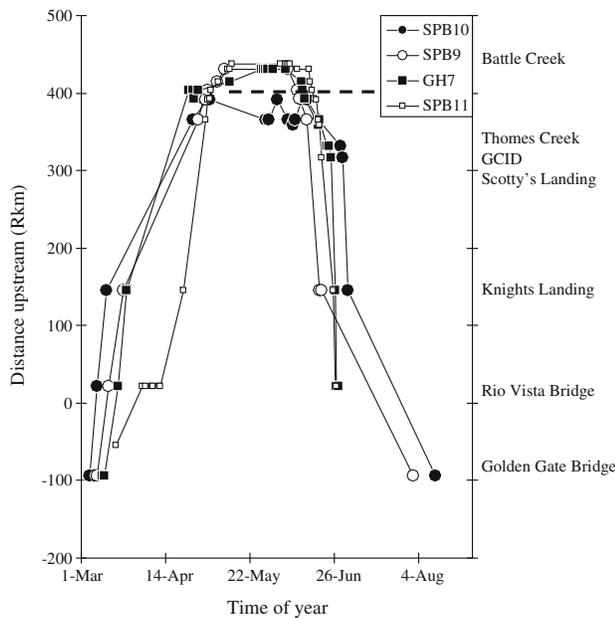


Fig. 6 2006 movements of the tagged green sturgeon that were detected above RBDD. Green sturgeon position by river kilometer (Rkm) is plotted with date. Symbols indicate movements of individual fish. For reference, selected river locations are indicated on the secondary y-axis. Bold dashed line indicates presence of flow control gates at RBDD

(GH5). In most cases, the fish are thought to have resided in the reach near GCID, and all appear to have out-migrated in response to increases in flow (Fig. 7a–c).

The GCID aggregation site is atypical of over-summering habitats in other systems, being an area of high water velocity. Aggregation sites on the Klamath River were described as scour pools created by high flows, which in turn exhibit low water velocity in the summer months (Benson et al. 2007), and aggregation sites on the Rogue River are similar (Erickson et al. 2002). In contrast, the GCID site is over 5-m deep with structural current refuges and eddy formations. It is possible that green sturgeon occupy lower-velocity subsections of the site; however, observations of green sturgeon capture, and manual tracking estimates, indicate that green sturgeon are found in, or in very close proximity to, high velocity areas.

The presence of green sturgeon exhibiting pre-spawn egg maturity (personal communication Matt Manual, GCID), coupled with high water velocities in the GCID reach could imply that green sturgeon use this area to spawn rather than over-summer. Throughout this study, river temperatures at RBDD (60 Rkm upstream of GCID) remained below 17°C, indicating that normal

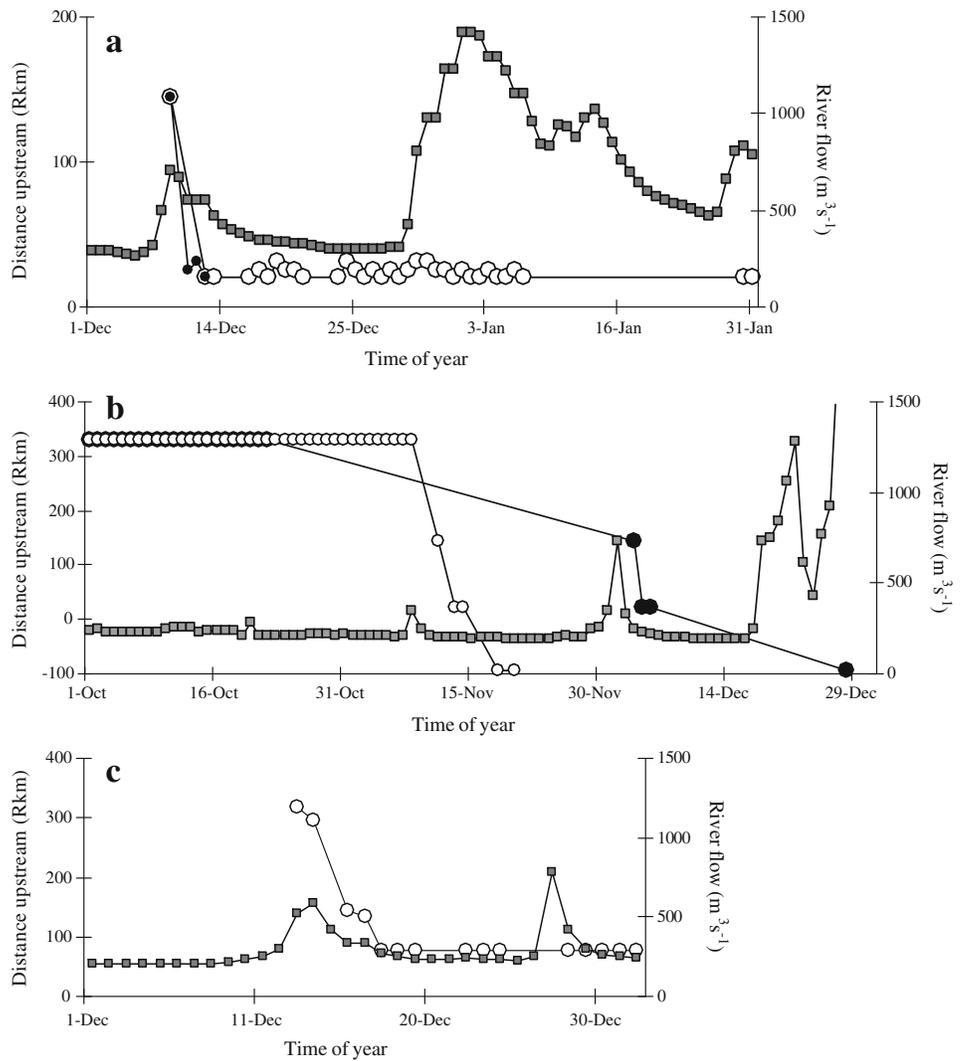
larval development could occur in the reaches below RBDD (Van Eenennaam et al. 2005). Of interest was the behavior of GH6, which migrated rapidly to GCID where it remained for only 4 days before out-migrating. It is possible that this movement represented a spawning event at GCID.

Whatever the reason, the Sacramento River adjacent to the GCID pumping plant routinely holds a large aggregation of green sturgeon during summer and fall months. In this small area, green sturgeon are vulnerable to sport angling and poaching. Protection measures for green sturgeon in the threatened Southern DPS need to address this area.

In contrast to both the behavior of Northern DPS green sturgeon and to our results from 2004–2005, the majority of out-migrants detected in 2006 displayed an entirely different movement strategy. Nine of the ten tagged fish detected that year exited the system with no extended hold-over period and with no apparent relation to flow increases, eight leaving before 4 July and the last on 22 August. Only two of those fish (both not detected above RBDD) were detected repeatedly in the GCID reach, and these detections were for a short duration prior to early out-migration. The number of green sturgeon captured at GCID declined noticeably after September 2006, indicating a marked lack of fish when compared to previous sampling years (pers. comm. Matt Manual, GCID). The rapid out-migration of green sturgeon in 2006, and the reduced aggregation period at the GCID site, could be a result of consistently higher flows and lower temperatures than previous study years (Fig. 8a, b). Alternatively, this could be an unusual behavior, related to unknown cues, that has not been documented in green sturgeon prior to this study.

The apex detections of individual fish indicate reaches and dates when spawning might have occurred during this study. The two green sturgeon from which egg samples were collected (SPB1, SPB11) were expected to be ready to spawn between May and July, and all apex detections fell within these months. Similarly, spawning is thought to have occurred in May or June in the only collection of green sturgeon eggs in the Sacramento River to date (Brown 2007). Of note, high water velocities and extensive bedrock habitat are found in all of the apex detection reaches. Furthermore, water temperatures did not exceed 17°C in these reaches during this study, which would have permitted normal green sturgeon larval development (Van Eenennaam et al. 2005).

Fig. 7 Fall out-migration of green sturgeon compared to Sacramento River flow: **a** movement of SPB1 and WB4 in 2004–2005 with flow at Verona, **b** 2005 movement of CR2 and CR3 with Woodson Bridge flow, **c** movement of GH5 in 2006 with Woodson Bridge flow. River flow (cubic meter per second) is represented as *filled squares*, sturgeon position is represented in river kilometer (Rkm) by day. *Open circles* represent SPB1, CR2, and GH5. *Filled circles* represent WB4 and CR3

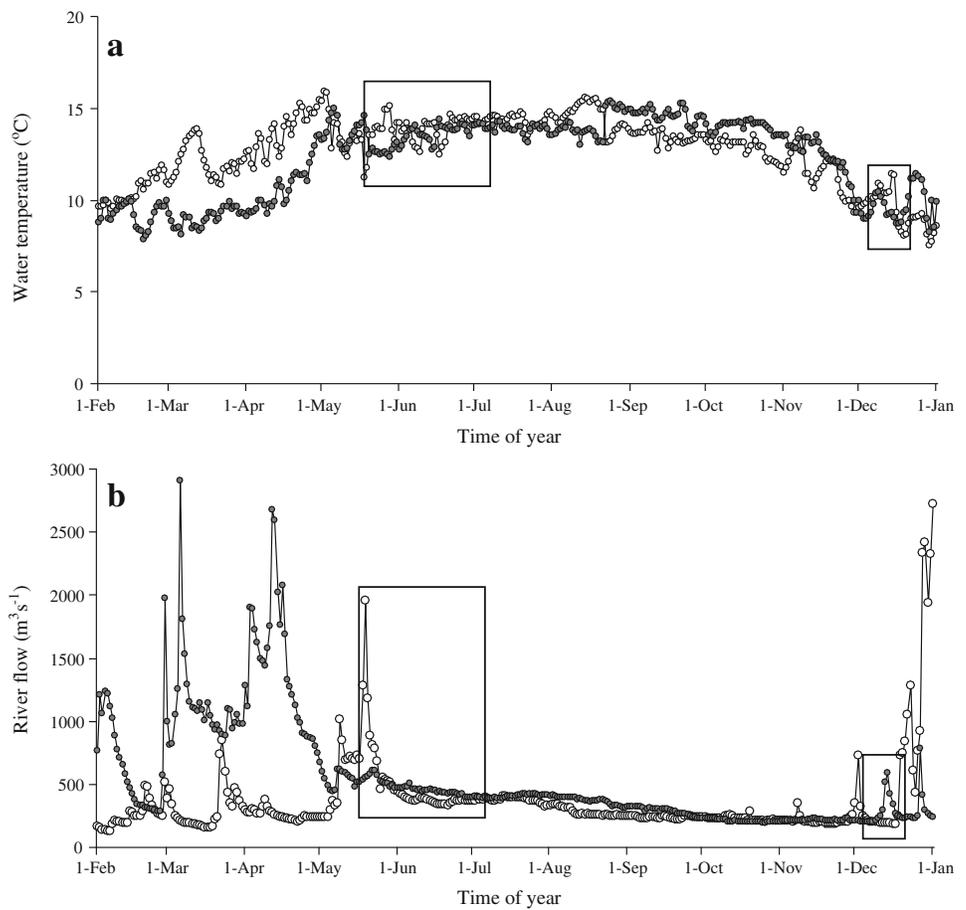


All of the green sturgeon in this study that initiated up-migration in the month of March were detected above RBDD. In contrast, all of the green sturgeon that entered the system later, in April and May, were not detected above RBDD. Fish entering later in the season (e.g. CR2 and SPB8 in 2005) appear to have been impeded by the closure of the diversion gates at RBDD. It is notable that only one of the green sturgeon that would have been physically obstructed by the 15 May closure of RBDD had it continued upriver (GH4), actually was detected immediately below the dam. It is possible that mature green sturgeon may curtail upstream migration upon reaching groups of conspecifics, and either abort their migration entirely, or spawn instead in the reaches below the dam, although this latter phenomenon has yet to be documented. Similar aggregations associated with impeded migration have been noted in shortnose sturgeon

in the Kennebec River, Maine, which are reported to form pre-spawn groups at Rkm 58 before spawning below the dam at Rkm 69 (Kynard 1996).

It seems clear that the timing of the operation of RBDD affects the migration of green sturgeon in the Sacramento River. Based on detections from this study, a 6 week delay in the closure of the gates would allow the majority of migrating green sturgeon an opportunity for safe upriver passage. Reaches above RBDD have consistently lower temperatures, and larger amounts of high-velocity bedrock habitats. Furthermore, the only physical evidence to date of spawning in the river was collected at RBDD (Brown 2007), suggesting that the reaches above the dam are important to the species. Interestingly, prior to this study, it was assumed that RBDD also presented a barrier to downstream migration in green sturgeon (Brown 2007); however, all of the green sturgeon that we

Fig. 8 Comparison of temperature and flow in the Sacramento River in 2005 and 2006: **a** water temperature (°C) at RBDD, **b** flow (cubic meter per second) at Woodson Bridge. The *open circles* indicate 2005, *solid circles* indicate 2006, *rectangles* highlight out-migration periods in 2006



recorded passing upstream of RBDD migrated downstream of the dam prior to the fall opening of the control gates. Based on these observations, an examination of the risks of injury to green sturgeon passing under the control gates of RBDD is also necessary. Green sturgeon captured at GCID were observed by the author (JCH) to display striations on the ventral surface, along with scute and fin damage, possibly due to trauma caused by passing under the RBDD gates. Sturgeon are not adept at passing shallow, high-velocity river reaches, and similar damage has been observed in shortnose sturgeon attempting to pass rapids on the Connecticut River (Kynard 1998). These marks were not observed in green sturgeon captured in San Pablo Bay; however, these injuries could also be incurred during the normal course of spawning or migration, and further investigation is needed to determine the cause.

Our results describe the timing and movement patterns of migrating green sturgeon in the Southern DPS, identify likely spawning reaches, and should be valuable in guiding future work to identify the specific

habitats in which spawning actually occurs. A better understanding of spawning habitat requirements is fundamental to assessing the degree to which anthropogenic alterations to the natural flow regime may be impacting this threatened population. This understanding could be obtained by adding high-resolution mobile tracking of tagged green sturgeon within the reaches identified by our fixed array, underwater video or sonar observations, and deployment of egg mats. Additionally, the success of spawning in different habitats might be assessed with particle dispersal and temperature-mortality models. Such information is urgently needed for effective management of this imperiled species.

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