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WHITE STURGEON SPAWNING MIGRATIONS AND LOCATION OF SPAWNING HABITAT IN THE SACRAMENTO RIVER, CALIFORNIA

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Sixty sturgeon (59 white, *Acipenser transmontanus*, and one green, *A. medirostris*) were tagged with radio transmitters in the lower Sacramento River in late winter 1990 and 1991 and their movements during spawning migrations were followed. In spring 1991 and 1992, artificial substrate samplers were deployed in various habitats in areas of the Sacramento River used by spawning sturgeon. Upstream movement of tagged sturgeon could be quite rapid, up to 25 km/d, and was often stimulated by small increases in river flow. Downstream movement of females, assumed to be post-spawning migrations, were also rapid, as fast as 91 km/d. Sturgeon eggs were taken at artificial substrate sites where depths ranged from 1.8 to 4.6 m and flow velocities exceeded 1.0 m/s. Most spawning occurred from Knights Landing to several kilometers upstream of Colusa.

INTRODUCTION

The white sturgeon, *Acipenser transmontanus*, population in California is mainly associated with the Sacramento River and its combined estuary with the San Joaquin River. This population was commercially overfished in the last two decades of the 19th Century, prompting closure of the fishery by the California Fish Commission in 1901. Following brief re-openings in 1910 and 1916, the fishery was legislatively closed from 1917 to 1954. In 1954, a sport fishery was re-opened with a 102-cm total length (TL) minimum size limit and a daily creel limit of one fish. Under these regulations, annual exploitation rates were 0.056-0.083 in the 1970s, but increased to 0.087-0.115 in the 1980s (Kohlhorst et al. 1991). This increase in fishing mortality reduced population egg production by 35%. In response, the California Department of Fish and Game (CDFG) instituted a "slot" size limit of 117-183 cm TL designed to reduce annual fishing mortality of sturgeon > 102 cm TL to about 0.05, with only a negligible decrease in biomass yield. This action was also intended to increase egg production by reducing the harvest of females before first spawning and by protecting large, highly fecund females (Botsford and Hobbs 1986).

With adoption of this strategy to partially manage sturgeon on an eggs-per-recruit basis, it is assumed that the hatching success and mortality rates of young sturgeon to recruitment will not decline from present levels. Recruitment is positively associated with freshwater flow through the estuary (Kohlhorst et al. 1991), but little is known about the specific migration stimuli and spawning habitat requirements of white sturgeon in the Sacramento River. Specific spawning habitat criteria have been examined for white sturgeon in the Columbia River (Parsley and Beckman 1994); lake sturgeon, *A. fulvescens*, in the Lake Winnebago, Wisconsin system (Kempinger 1988); and shortnose sturgeon, *A. brevirostrum*, in the Connecticut River (Taubert 1980, Buckley and Kynard 1985). However, these studies have largely centered on populations spawning immediately below impassable barrier dams or in very restricted areas and may not be directly applicable to white sturgeon in the Sacramento River.

Identification and protection of spawning habitat is vital for the maintenance of the population and the sport fishery. Historical spawning habitat has been lost in California, mostly due to dam construction. The San Joaquin River may have supported a larger spawning population than at present before the upstream diversion of most of its flow for agricultural irrigation (Moyle 1976). In the Sacramento River, white sturgeon spawned upstream of Shasta Dam before it was constructed(1940-1945), as evidenced by the relic population above this impassable barrier (Fiske[1] 1963). However, Kohlhorst (1976) found no evidence of spawning upstream of Ord Ferry Bend (river kilometer [rkm] 297) in 1973. Hence, I report the results of a two-phased study using radio-telemetry to determine general spawning areas and artificial substrates to identify specific spawning habitats as evidenced by egg deposition.

STUDY AREA

The study area included the Sacramento River from Rio Vista (rkm 19) to Ord Ferry Bend (Fig. 1). At low flows (< 285 m^3/s) the river is tidal below Sacramento (rkm 95), with flow reversals upstream to Freeport (rkm 74); however, salinity seldom exceeds 1‰ at Rio Vista. From rkm 25 to Sacramento, the river is contained within rip-rap-armored levees. Depths at low water average about 6 m over sand substrates, ranging from 2 m in shoal areas to 15 m in the deepest holes. Widths range from about 125 m below major distributaries downstream of Walnut Grove (rkm 43) to about 300 m near Sacramento.

From Sacramento to Wilkins Slough (rkm 190) the river is low gradient (0.08 m/km), meandering, and confined within flood control levees. Between Sacramento and Verona (rkm 128) river width averages 150 m and depths range from 2 to 4 m during low flows. Rock wing dams, installed to maintain a navigation channel, are present in shoaling areas. Levees are generally rock armored and substrates are coarse and medium sands with some gravel in high velocity areas near wing dams. From Verona to Wilkins Slough the river narrows to about 75 m and is confined by armored and unarmored levees. Substrates are fine to medium sands and submerged snags are present. From Wilkins Slough to Colusa (rkm 231) the river gradient remains low, but substrates change to coarse sand and fine to medium gravels in areas with higher gradients. Snags are abundant in areas where flood control levees are set back from the river channel and the river is allowed to meander. Charted depths range from 0.3 m to 8.5 m at low flows.

[1] Fisk, L.O. 1963. The Shasta Lake sturgeon fishery. California Department of Fish and Game, Inland Fisheries Administrative Report No. 63-12.

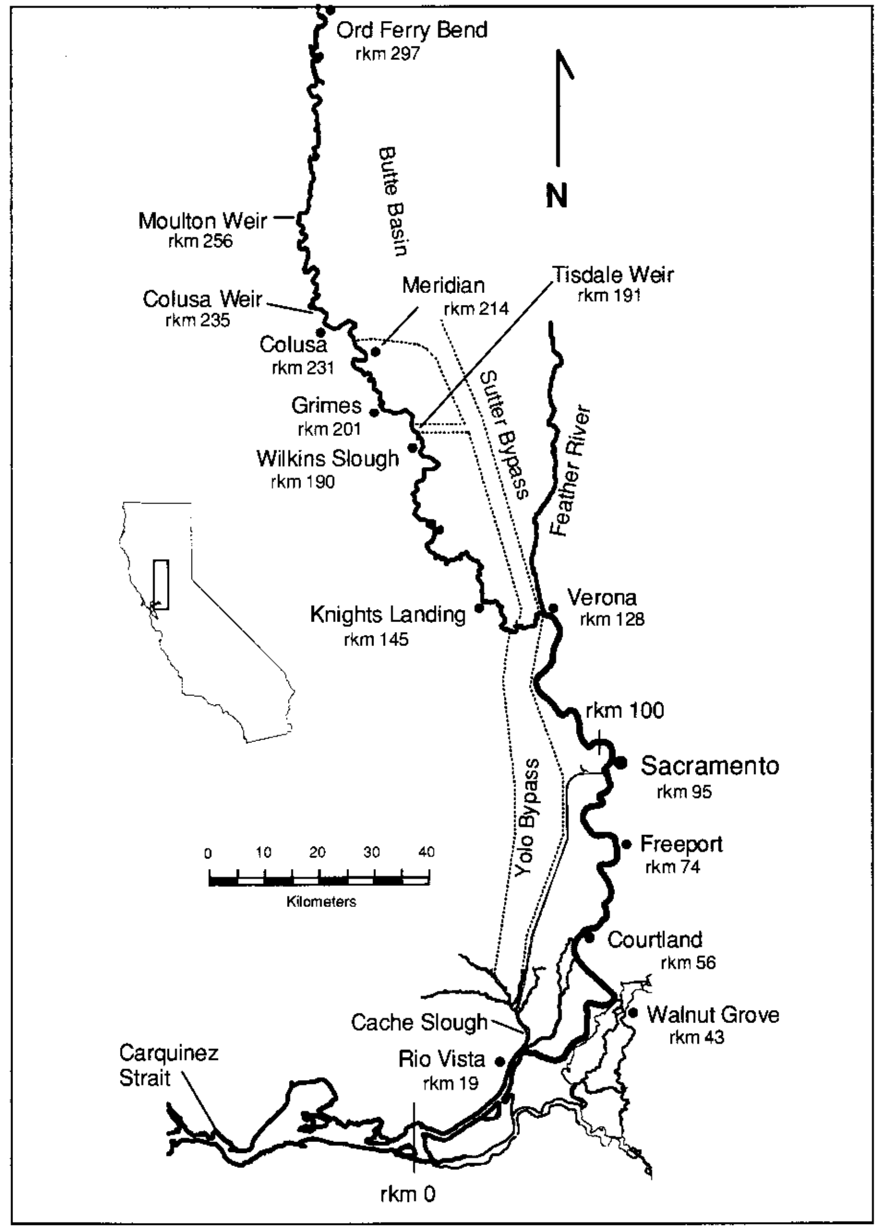

Figure 1. The white sturgeon radio-tagging and spawning habitat study area from Carquinez Strait to Ord Ferry Bend.

Between Colusa and Ord Ferry Bend (rkm 297) the river gradient averages 0.24 m/km and the river assumes a pool-riffle character. In this reach, flood control levees contain the river in a designated floodway 0.5-2.5 km wide and the river is free to meander between the floodway levees, except in areas where armored banks protect levees and deciduous orchards from bank erosion. In this region, substrates range from mud in backwater areas to coarse gravel-small cobble in riffles. Most levees in direct contact with the river are armored with rock $\leq$ 0.5 m in diameter and this armoring includes a toe extending into the river bottom.

River flows in the Sacramento River channel are highly controlled by large water storage reservoirs and an extensive system of designated floodways and bypasses. The major storage reservoirs tend to reduce flows in the wet winter and spring months and to augment flows in the dry summer and fall when stored water is released for downstream consumptive use. The bypass and floodway system is designed to transport flows in excess of the capacity of the main channel. Major diversion points from the main channel, where water is diverted into the Butte Basin and Sutter Bypass, are located at Moulton Weir (rkm 256), Colusa Weir (rkm 235), and Tisdale Weir (rkm 191) (Fig. 1). Water in this bypass joins with the lower Feather River and crosses the main channel of the Sacramento River into the Yolo Bypass at rkm 132, re-entering the Sacramento River through Cache Slough (rkm 24). Since all major features of this system of reservoirs and bypasses have been in place (1968), maximum in-channel flow has been approximately 3,200 m^3/s at Sacramento, 835 m^3/s between Verona and Wilkins Slough, 1,240 m^3/s between Wilkins Slough and Colusa, and 10,400 m^3/s at Ord Ferry Bend (CDWR[2] 1974). The amount of water bypassed around the Sacramento River channel can substantially exceed the main channel flow; in 1986 when 3,185 m^3/s were flowing in the main channel at Sacramento, 14,000 m^3/s were flowing through the Yolo Bypass several kilometers to the west (CDWR[3] 1987).

Water years 1990, 1991, and 1992 were extremely dry. Average daily flows in the Sacramento River at Sacramento from 1 February through 31 May in 1990 and 1991 were 370 and 371 m^3/s, 43% of the 1955-1993 average. When radio-tagged sturgeon were being monitored, water flowed into the Sutter Bypass on only 2 d (15 m^3/s over Tisdale Weir, 27 and 28 March 1991). In 1992, the overall season was dry (46% of average), but flows increased at Sacramento to 1,350 m^3/s during February storms.

METHODS

Migration

Radio transmitters were based on a "C" cell lithium battery and were approximately cylindrical, 2.8-cm diameter x 8-cm long. Two plastic-coated, 1.5-mm stainless steel cables were cast into the transmitter 7 cm apart. A quarter-round backing plate, cut from PVC pipe, completed the mounting harness. Each tag had a 40-cm trailing antenna of stainless steel cable. Transmitter weight with antenna, mounting cables and backing plate was approximately 100 g in air and 40 g in water. Transmitters had nominal 2- and 3-yr life spans (75 and 55 pulses/min) and transmitted on unique frequencies in the 48-50 MHz band. Although the time an individual sturgeon would spend in fresh water, where radio tags could be detected, was expected to be relatively brief each year, long-duration tags were selected to attempt to determine spawning periodicity.

White sturgeon were captured with setlines fished overnight in the Sacramento River between Courtland (rkm 56) and Freeport (rkm 74). Most white sturgeon that far upstream are thought to be mature fish moving upstream to spawning areas (Kohlhorst et al. 1991, Miller 1972). Approximately 400 hooks were spread over four 550-m setlines of 6.4-mm diameter soft-lay nylon rope. Initially, 12/0, 14/0, and 16/0 tuna circle hooks were used, but in 1990 they were replaced with 8/0, 10/0, and 12/0 straight shank "O'Shaughnessy" hooks similar to those used in the sport fishery. Hooks were attached to setlines using groundline clips with 1-m braided polyester leaders. Fish were lifted on the deck of the tagging boat with the aid of a soft noose slipped behind the pectoral fins, sexed by external examination, and measured to the nearest cm TL. The external characteristic used to sex sturgeon was abdominal distension; fish with noticeably distended abdomens were assumed to be females (Conti et al. 1988). Radio tags were attached by drilling holes through the base of the fourth and fifth dorsal scutes, slipping the mounting wires through the drilled holes and the PVC backing plate, then fastening the wires together with two crimp fittings. Sturgeon were normally out of the water for 2-3 min.

Fishing was usually conducted Monday through Thursday nights until the annual supply of 30 tags was exhausted. In 1990, every healthy sturgeon captured was tagged, without regard to sex. In 1991, female sturgeon were preferentially tagged.

Because the time from tagging to spawning and subsequent return to salt water was expected to be brief, the tracking strategy was to locate each tagged fish as often as possible. Radio-tagged sturgeon were tracked by automobile, airplane, and boat. Auto searches were effective from Rio Vista (rkm 19) to Verona and from Meridian (rkm 214) to Colusa, but were only partially successful in the remaining upstream reaches of the study area as public roads did not provide continuous access to the river. During auto searches, 8 to 10 frequencies were scanned for 2 s each while driving 45-50 km/h, allowing three opportunities to hear each tag within the 300-500-m reception range. Most auto searches initially proceeded upriver and, as fish were located, scanned frequencies were changed to include fish previously in upriver locations. If a previously known upriver fish was not located, its frequency was scanned in the lower river on the return trip.

Aerial surveys of the Sacramento River for radio-tagged white sturgeon were conducted on 34 d from 1990 to 1993. In late winter and spring 1990, 16 of 17 aerial searches were conducted during CDFG Sacramento River System Sport Fish Catch Inventory flights. All major tributaries in the Sacramento basin available to anadromous fish were searched, including the Feather, Yuba, and American rivers. In one additional flight in 1990, seven flights in 1991, seven flights in 1992, and three flights

[2] California Department of Water Resources (CDWR). 1974. Hydrological data: 1973. Bulletin 130-73, Volume II. Sacramento, California, USA.

[3] California Department of Water Resources (CDWR). 1987. Hydrological data for the Sacramento-San Joaquin Estuary. DAYFLOW program summary. Sacramento, California, USA.

in 1993, only the main stem Sacramento River from the downstream limit of fresh water to Ord Ferry Bend was searched.

Early aerial tracking indicated that tags could be detected for 30-50 s at normal flight speeds and altitudes (130-150 km/h, 50-200 m). Therefore, during angler survey flights, only seven to nine frequencies could be scanned for 2 s each by a single observer to allow two to three opportunities to hear a given tag. During dedicated study flights, the river was flown with two observers in both directions allowing up to 32 frequencies to be continuously scanned. One flight in 1991 and all flights in 1992 and 1993 searched for fish tagged in previous years. In 1990-1992, the downstream limit of telemetry observations was reached 5 km below Rio Vista because salt water absorbed radio signals. High freshwater flows in 1993 allowed reception of radio-tag signals as far downstream as 24 km below Rio Vista.

Most boat surveys were in the reach where fish were tagged. Four upriver boat surveys in 1990 and one upriver boat survey in 1991 primarily searched for fish that had disappeared between aerial and auto surveys or were last detected in areas where automobile searches were ineffective.

During auto, aircraft, and boat searches, the primary antenna was a 1/4-wavelength base-loaded whip. When more precise positioning was desired during auto or boat searches, a hand-held, tuned, diamond-loop, directional antenna was used.

Spawning Habitats

To determine spawning locations and sites of egg deposition more precisely than was possible by locating radio-tagged adults and to verify spawning at these specific locations, 0.9 x 0.75-m artificial substrate egg samplers of latex-coated animal hair (McCabe and Beckman 1990) were deployed. Between 16 April and 3 June 1991, two or three artificial substrates were fished across each of 16 transects between Grimes (rkm 201) and Moulton Weir (Appendix 1). Sites initially selected were in areas where local anglers are successful in catching fish (T. Shroyer, CDFG, pers. comm.) or downstream of deep locations, often associated with sharp river bends, where sturgeon had been located during daylight hours while radio tracking. Artificial substrates were examined twice weekly for attached eggs, cleaned of debris, and reset. As the season progressed, transects originally located in depositional areas, where artificial substrates filled with sediment, were moved to erosional or stable areas.

In 1992, substrates were installed at four transects between rkm 223 and rkm 251 on 4 February (Appendix 2). After high flows from mid-February through mid-March washed out or sedimented in artificial substrates at several transects, six transects were re-established upstream of Colusa between rkm 232 and 255 between 20 March and 14 April. These were examined biweekly through 15 May, when two transects were discontinued. All sampling ended on 22 May.

Substrate composition at each site was sampled with a clamshell dredge. Because of the somewhat imprecise nature of dredge sampling, sediments were classified according to the scale developed for the Instream Flow Incremental Methodology (Bovee and Cochnauer[4] 1977) rather than a more precise particle size distribution (Appendix 3). In 1991, depth was estimated by the amount of buoy line deployed until the substrate hit bottom. In 1992, depth was measured at each site by fathometer and water velocity was measured both at the surface and 30 cm from the river bottom with a propeller-driven, digital flowmeter. To estimate date of spawning, I aged individual eggs according to developmental stage (Beer[5] 1981), with compensation for temperature (Wang et al. 1985), and subtracted this age from sampling time.

Unless otherwise cited, river flow and stage data used in this paper were obtained from the California Data Exchange Center maintained by the California Department of Water Resources.

RESULTS

Migration

Capture and tagging

In 17 fishing days between 29 January and 10 March 1990, 14 adult female, 15 adult male and one subadult (95 cm) white sturgeon were radio tagged. Nineteen of the 30 fish tagged were captured between 6 and 9 March when flows at Freeport increased to 450-510 m^3/s. Previous flows during the fishing period had ranged from 350 to 425 m^3/s. Most fish were caught after circle hooks had been replaced by straight-shank hooks.

In 1991, 21 adult female and seven adult male white sturgeon and one adult white sturgeon of undetermined sex were radio-tagged during 11 fishing days between 4 March and 21 March. A single male green sturgeon was tagged on 7 March. Sturgeon were captured when daily flows at Freeport averaged 695 m^3/s (range: 375-1,070 m^3/s). No fish died during capture and tagging either year.

After tagging, 33 of 58 adult white sturgeon (57%) did not continue their upstream migration. In 1990, 18 of 29 white sturgeon (11 females and seven males) moved downstream either immediately after tagging (four females and four males) or after spending 1-10 d within 10 km of the tagging site (seven females: $\bar{x} = 4.1$, SD = 2.1; three males: $\bar{x} = 4.3$, SD = 5.8). Mean TL of females that moved upstream was 181 cm (SD = 5.1); mean TL of females moving downstream was 170 cm (SD = 13.0). For males, the respective TLs were 135 cm (SD = 16.4) and 158 cm (SD = 22.8).

In 1991, 15 of 29 sturgeon moved downstream either (i) immediately after tagging (three females and the white sturgeon of undetermined sex), (ii) after remaining near the tagging site for 1 d (two males), or (iii) after 1-26 d within 10 km of the tagging

[4] Bovee, K.D. and T. Cochnauer. 1977. Development and evaluation of weighted criteria, probability-of-use curves for instream flow assessments: Fisheries. U.S. Fish and Wildlife Service, Cooperative Instream Flow Services Group, Instream Flow Information Paper No. 3.

[5] Beer, K.E. 1981. Embryonic and larval development of white sturgeon (*Acipenser transmontanus*). M.S. Thesis, University of California, Davis, California, USA.

site (nine females: $\bar{x}$ = 7.1, SD = 9.1). The mean TL of females moving upstream after tagging was 158 cm (SD = 8.5); those that moved downstream averaged 151 cm (SD = 9.5).

Movements, 1990

In 1990, only three radio-tagged females migrated upstream (Table 1, Fig. 2a) after delays of 2-19 d ($\bar{x}$ = 13.0, SD = 9.5). During sustained, active migration, upstream travel rates ranged from 4.6 to 22.3 km/d ($\bar{x}$ = 13.8, SD = 8.9). A 182-cm female tagged on 30 January resumed an upstream migration 2 d after tagging (Fig. 2a), reaching a maximum recorded ascension of rkm 220 on 7 March. This fish was last located 45 h later downstream at rkm 137. It was not found in the lower river during ground searches the following 2 d. A 175-cm female tagged on 14 February (Fig. 2a) remained near the tagging site for 18 d, then moved upstream strongly during a slight rise in river flow, reaching rkm 179 on 9 March. Twenty-seven h later, it was found at rkm 103 moving downstream at a velocity estimated to be approximately equal to that of the river current. The third female (185 cm TL) tagged on 23 February (Fig. 2a), dropped downstream to rkm 21 eleven d after tagging, then moved back up into the tagging area. It resumed a definite upstream migration 19 d after tagging, reaching rkm 180 during initial upstream movement. After 16 d near this location, this fish resumed slow upstream movement and reached Colusa (rkm 233) in 2 weeks. It remained near Colusa for 1 month, then, between 24 May and 26 May, was tracked moving downstream as fast as 91 km/d, leaving the river within 3 d. This rapid downstream movement was preceded by a slight increase (22 m^3/s) in river flow at Colusa between 17 and 23 May.

Eight males made upstream migrations after tagging in 1990 following delays of 0-13 d ($\bar{x}$ = 4.0, SD = 4.3) (Table 1; Fig. 2b, c). Maximum ascension ranged from rkm

Table 1. Summary of white sturgeon upstream movements following tagging in 1990. Actual movements are shown in Fig. 2. F = female, M = male, rkm = river kilometer.

Total length (cm) and sex	Tagging date	Tagging location (rkm)	Migration delay (days)	Upstream limit of initial migration (rkm)	Date	Average upstream movement (km/d)	Ultimate maximum ascention (rkm)
182 F	30 Jan	63	2	220	7 Mar	4.6	220
175 F	14 Feb	63	18	179	9 Mar	22.3	179
160 M	21 Feb	69	5	113	2 Mar	7.2	113
127 M	21 Feb	69	13	106	10 Mar	9.1	106
185 F	23 Feb	68	19	182	23 Mar	14.7	234
144 M	7 Mar	66	0	248	24 Mar	10.7	248
116 M	7 Mar	66	6	183	24 Mar	10.4	191
129 M	9 Mar	64	4	212	21 Mar	19.1	212
157 M	9 Mar	64	1	142	16 Mar	19.2	157
121 M	9 Mar	64	0	230	19 Mar	16.9	233
129 M	9 Mar	64	3	188	21 Mar	11.2	188

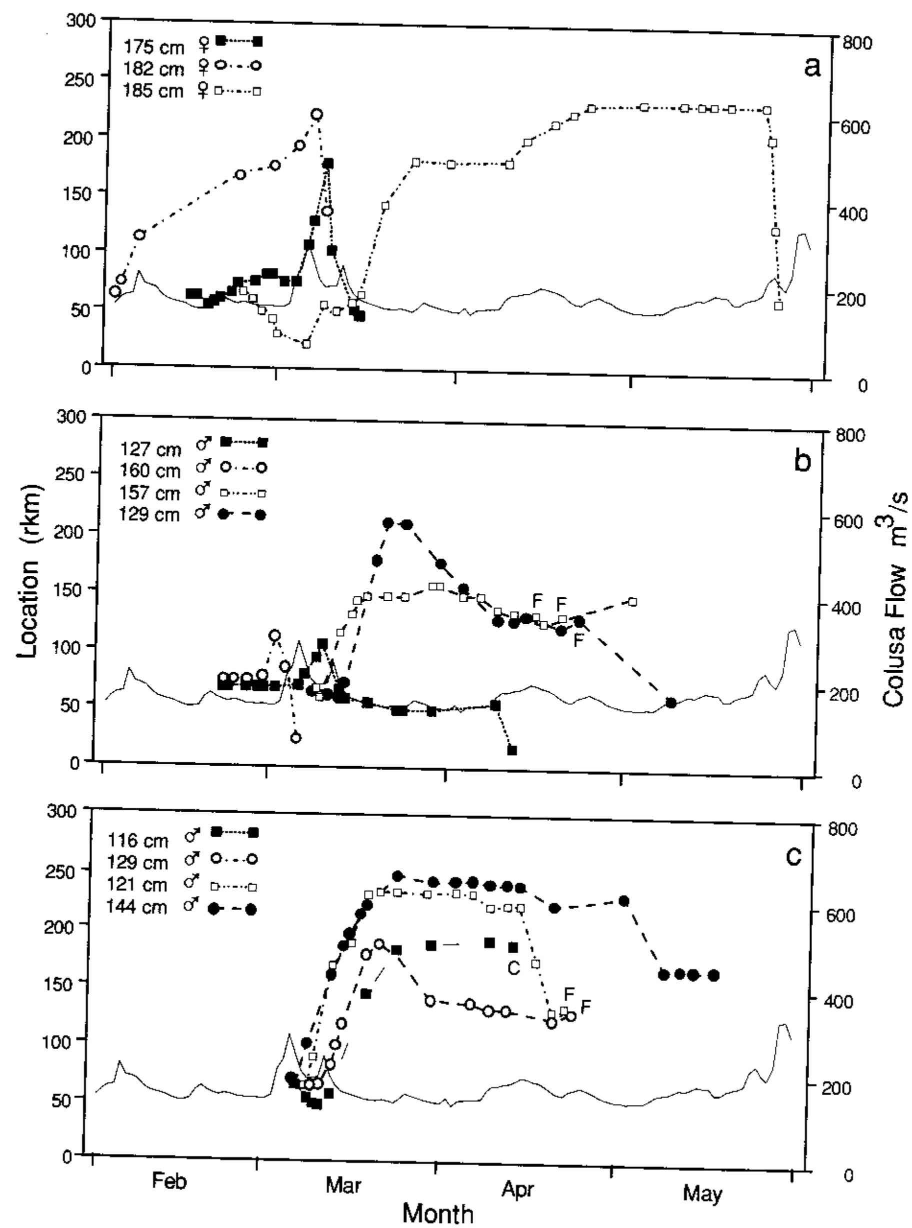

Figure 2. White sturgeon movements following 1990 tagging and Sacramento River flow at Colusa (solid line). Markers indicate observations; some observations have been deleted for clarity. "C" indicates the point of angler capture, if applicable. "F" indicates a location in the lower Feather River.

106 to 248, and upstream migration rates averaged 13.0 km/d (SD = 4.7, range = 7.2-19.1) during initial active migrations. Although some males made

apparently rapid downstream movements or disappeared from upstream locations between tracking surveys, no male was repeatedly located on a daily (or more frequent) basis while migrating downstream, so no downstream migration rate comparable to that observed for females was determined. In contrast to females, several males drifted irregularly downstream after reaching their maximum ascension point (Fig. 2b, c). Four males that had moved downstream below Verona were found in the Feather River 1-5 km upstream from its mouth between 14 April and 2 May when reservoir releases increased Feather River flow above that in the Sacramento River upstream of Verona (Fig. 2b, c). A 116-cm male (Fig. 2c) was caught by an angler on 13 April at rkm 179 after moving upstream. A 144-cm male (Fig. 2c), tagged on 7 March, moved rapidly upstream to rkm 248, remained near that location for at least 20 d, then drifted downstream to rkm 168, where it remained for 2 weeks. Sometime after 17 May, this tag was shed at that location, ≥ 73 d after capture.

Movements, 1991

In 1991, nine females resumed their upstream migration after delaying near the tagging site for 0-11 d ($\bar{x}$ = 2.4, SD = 3.9) (Table 2). Upstream migration rates ranged from 5.8 to 25.2 km/d ($\bar{x}$ = 11.5, SD = 6.8). Five females either moved back downstream (Fig. 3a) or were last located upstream during elevated flows in March. Those last located upstream in March are presumed to have moved rapidly downstream without being detected between tracking surveys. Of the four females remaining upriver after the March flow peaks, three were still upriver on the last aerial tracking survey on 6 May; one had moved downriver and was last found below the tagging site in mid-April (Fig. 3b). On 7 May, a 155-cm female was caught within 1 km of its 6 May location by an angler who affirmed the fish was a gravid female.

Table 2. Summary of white and green sturgeon upstream movements following tagging in 1991. Actual movements are shown in Figure 3. Where migration delay is unknown, the migration rate is calculated from the day of tagging. F = female, M = male, rkm = river kilometer.

Total length (cm) and sex	Tagging date	Tagging location (rkm)	Migration delay (days)	Upstream limit of initial migration (rkm)	Date	Average upstream movement (km/d)	Ultimate maximum ascention (rkm)
175 F	7 Mar	70	11	124	21 Mar	25.2	124
125 M	7 Mar	60	unk	164	22 Mar	9.0	164
184 M[a]	7 Mar	60	unk	108	13 Mar	8.0	108
147 M	8 Mar	66	1	266	22 Mar	14.3	293
142 M	8 Mar	62	0	221	22 Mar	11.4	233
155 F	12 Mar	69	0	213	29 Mar	8.5	213
146 F	13 Mar	66	0	122	20 Mar	7.9	128
130 F	14 Mar	70	2	149	29 Mar	6.1	149
187 F	14 Mar	66	7	154	29 Mar	10.8	154
146 F	16 Mar	62	1	219	3 April	9.8	219
188 F	19 Mar	66	1	188	26 Mar	20.2	188
152 F	19 Mar	70	0	113	24 Mar	8.5	116
133 M	19 Mar	58	unk	109	28 Mar	5.7	109
138 M	20 Mar	64	unk	124	4 April	10.4	124
144 F	21 Mar	66	0	113	29 Mar	5.8	136

[a] Green Sturgeon

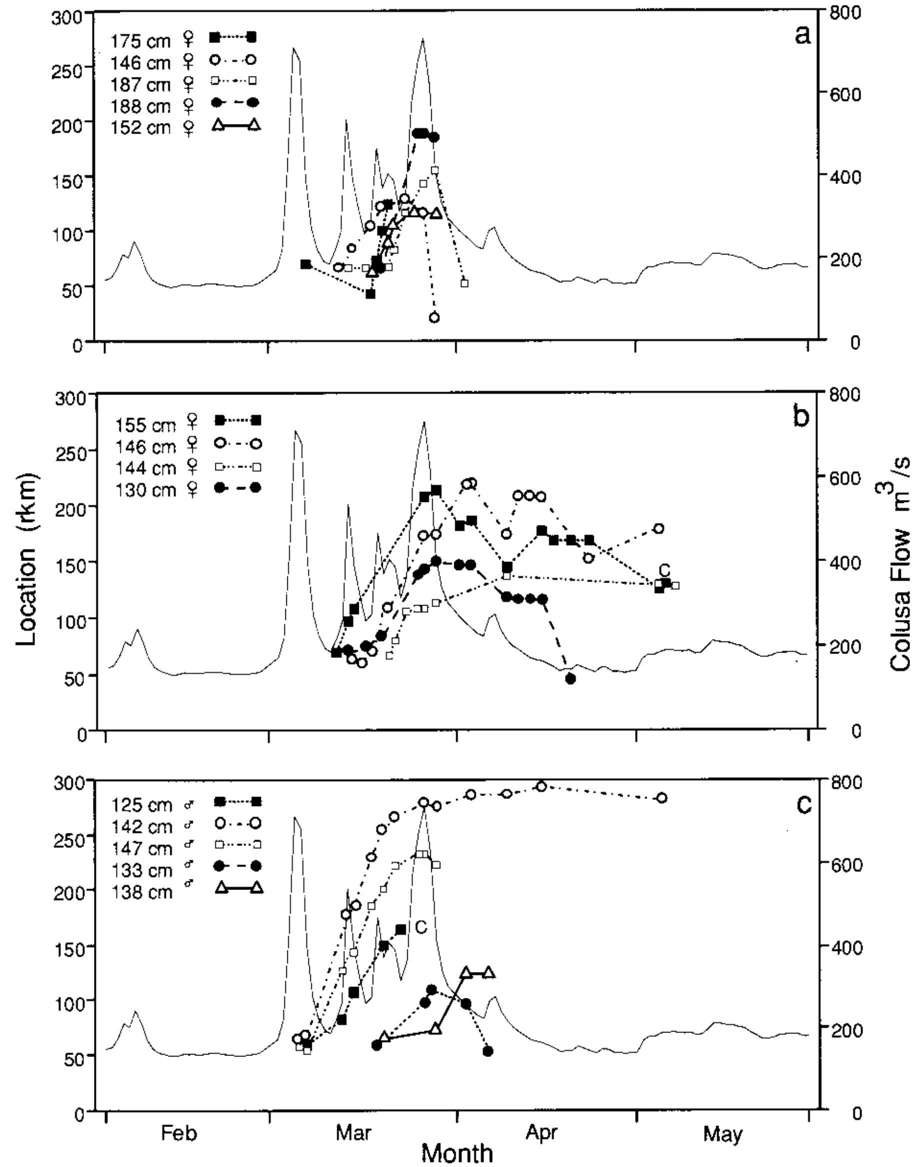

Figure 3. White sturgeon movements following 1991 tagging and Sacramento River flow at Colusa (solid line). Markers indicate observations; some observations have been deleted for clarity. "C" indicates the point of angler capture, if applicable.

Migration behavior of a 184-cm male green sturgeon and three male white sturgeon were not measured because the tagging area was not searched daily (Table 2). One male white sturgeon (142 cm) was found upstream of the tagging location the day after tagging and one other (147 cm) moved upstream after a 1-d delay, during which it drifted 7 km downstream (Fig. 3c). Upstream migration rates for two male sturgeon for which departure dates from the tagging area are known ranged from 11.4 to 14.3 km/d ($\bar{x}$ = 12.9, SD = 2.1). The male green sturgeon was only observed once (at rkm 107, 7 d after tagging) despite repeated air and ground searches of the Sacramento River and lower 10 km of the Feather River. A 125-cm male (Fig. 3c) was caught by an angler at rkm 164, apparently still actively migrating upstream. Two males moved upstream of Colusa (Fig. 3c), one ultimately ascending to rkm 293, the most upstream location of any tagged fish in the 2-yr study. It remained upriver through the last aerial survey on 6 May. Again, as in 1990, no males were repeatedly observed on a daily basis while migrating downstream and no comparison could be made with downstream migration rates of females.

Tag Shedding

In addition to the previously mentioned shed tag, at least six other tags are known to have been shed. Shed tags could be differentiated from tags on relatively stationary fish by the consistency of signal strength; tags still attached to a sturgeon tended to vary in signal strength as the orientation of the transmitting antenna changed, while signal strength of shed tags was unvarying. In 1990, tags applied to a 95-cm immature fish and a 149-cm female, neither of which ascended very far upstream of the tagging area, were repeatedly located near Rio Vista 120 and 35 d, respectively, after tagging. The tag applied to a 127-cm male in February 1990, which was tracked moving up to the Verona area and then downstream (Fig. 2a), was found in February 1991 at rkm 69 near the north end of the tagging area. This fish was not found in an aerial search of the river on 3 June 1990; presumably, it re-entered the river after that date. Tags applied to a 175-cm female in February 1990 (Fig. 2a) and to a 129-cm male (Fig. 2b) in 1991 were both repeatedly located 23 km downstream from Rio Vista in March and April 1993 when high outflows freshened this downstream area sufficiently to allow reception of radio signals. The tag applied to a 188-cm female (Fig. 3a) in March 1991 was recovered from a beach 35 km downstream of Rio Vista in June 1992 with the tagging harness intact. Barnacles on the tag indicate it was in salt water for some time before being recovered. All shed tags continued to transmit to the end of their 2- or3-yr life spans. No tags except these shed tags were detected during the 1992 and 1993 flights.

Spawning habitats

Between 7 and 14 May 1991, nine eggs were collected on artificial substrates at two locations near Colusa (Table 3). I estimated, based on degree of embryological development, that these eggs were spawned on 4 different d between 6 and 13 May. These spawnings followed a 40 m³/s increase in Sacramento River flows at Colusa, which had averaged 145 m³/s from the beginning of sampling through 2 May (Fig. 4a). This increase in flow was due to increased reservoir releases rather than precipitation. During these spawnings, average daily river flow ranged from 184 to 188 m³/s and temperatures ranged from 14 to 17°C; highest temperature was measured on 7 May. Seven of the eggs were taken immediately downstream from a deep (> 8 m) pool formed where the river makes a right-angled bend (rkm 222.9). The sample transect was approximately 20 m below the downstream end of this pool. Transect depth ranged from 1.5 to 2.5 m. Substrates were sand to gravel-sand mixtures. Eggs with intact egg membranes from this site were either evenly covered with sand grains, suggesting that they had contacted the river bottom before becoming trapped in the artificial substrate, or were noted in laboratory examination to be 3/4 covered with sand, suggesting that sediment adhesion occurred after the eggs became entrapped on the substrate.

Table 3. Date, location, and developmental stage of sturgeon eggs collected on artificial substrates in the Sacramento River in 1991.

Date collected	Location (rkm)	Developmental stage	Estimated age (h)	Estimated spawning date
7 May	234.2	2 Yolk plug	30-36	5-6 May
10 May	222.9	3 Neurulation complete	55-70	7-8 May
		1 Decomposed	—	—
14 May	222.9	1 Neurulation complete	55-70	11 May
		1 Yolk plug	30-36	13 May
		1 Decomposed	—	—

Between 24 March and 21 April 1992, 32 eggs were collected at two transects; these eggs represented at least six spawning events (Table 4). During these spawnings, river flow ranged from 180 m³/s to 350 m³/s (Fig. 4b) and temperatures ranged from 12 to 16°C. As in 1991, spawning seemed to be stimulated on 15 and 17 April by a small increase in flow starting on 13 April, following a period of relatively low and declining flows. Sturgeon eggs were taken from substrates placed at depths from 1.8 to 4.6 m where bottom flow velocities exceeded 1.0 m/s (Fig. 5). All eggs were collected over bottoms which were primarily gravel and cobble. As in 1991, eggs were 40-100% sand covered.

DISCUSSION

The externally attached radio tags worked well over the short duration of a single spawning season and only one tag was shed while a fish was in the spawning area. However, my attempt to assess spawning periodicity by using long-duration telemetry tags was not successful because of tag shedding. Kieffer and Kynard (1993) found that external telemetry tags were unsatisfactory for long-term studies of shortnose sturgeon

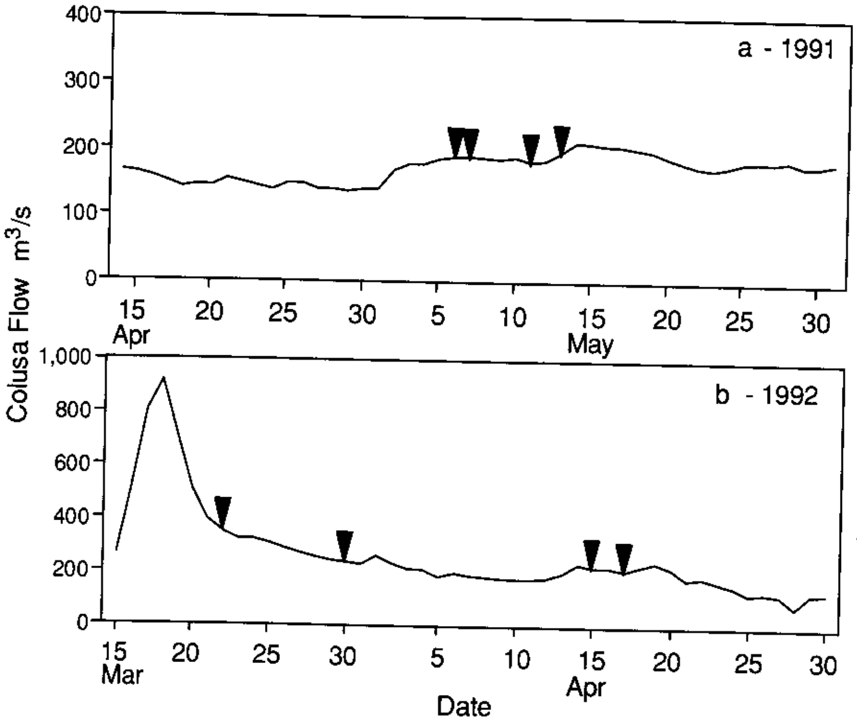

Figure 4. Estimated spawning dates (arrows) and Sacramento River flows at Colusa in 1991 and 1992.

Table 4. Date, location, and developmental stage of sturgeon eggs collected on artificial substrates in the Sacramento River in 1992.

Date collected	Location (rkm)	Developmental stage	Estimated age (h)	Estimated spawning date
24 March	251.2	1 Yolk plug	30-36	22-23 March
31 March	251.2	1 Gastrulation	18-24	30 March
17 April	252.2	4 Early cleavage 1 Early neurulation	6-8 40-48	17 April 15 April
17 April	251.2	8 Early cleavage 15 Late yolk plug-early neurulation	6-8 30-40	17 April 15 April
21 April[a]	251.2	2 S-heart	70-90	17 April

[a] Eggs were present on substrates on 17 April and missed during examination.

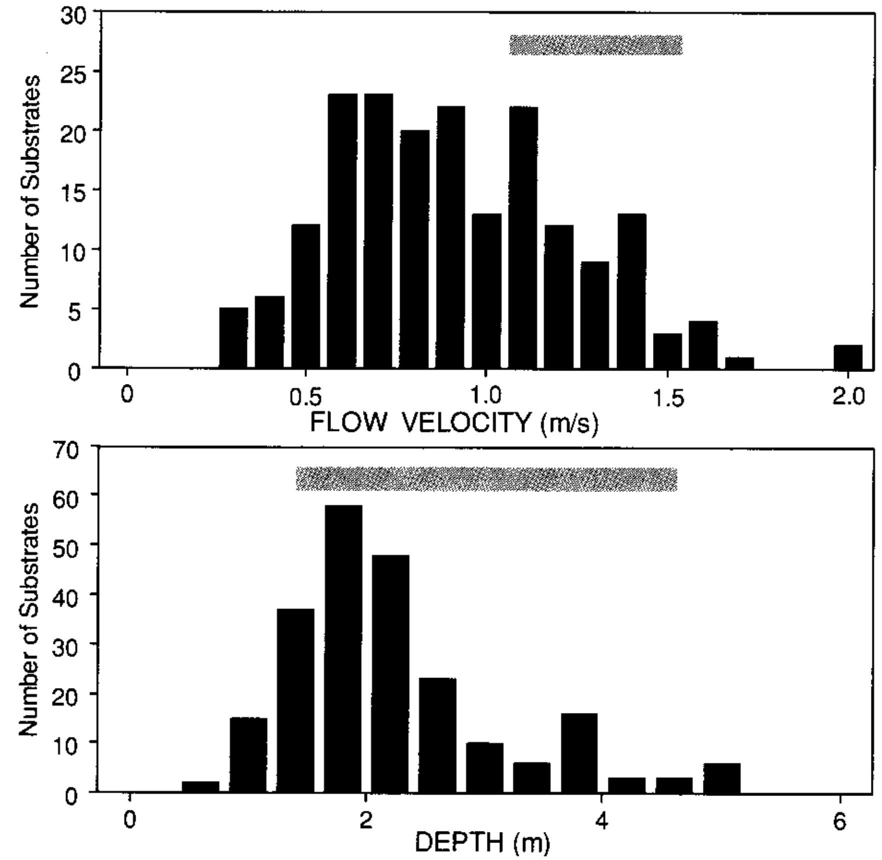

Figure 5. Distribution of bottom flow velocities (measured 30 cm above the substrate) and depths sampled with artificial substrates in the Sacramento River in 1991 and 1992. Shaded horizontal bars denote the range of velocities and depths where eggs were collected.

in the Merrimack River because all externally affixed transmitters were shed 14-134 d after release. Similarly, Moser and Ross (1995) found that seven juvenile (69-122 cm) Atlantic sturgeon (*A. oxyrhynchus*) retained external tags only 36-229 d. The shortest term of tag retention in my study was < 32 d; the longest verified term was 92 d. While delayed mortality after tagging could mimic a shed tag, the extreme tolerance of shortnose sturgeon to repeated gill-net capture and tagging suggests that fish of the genus *Acipenser* withstand handling and radio-tagging well (Kieffer and Kynard 1993).

Many sturgeon abandoned their upstream migrations after tagging and others interrupted their migration before proceeding upstream. Twenty-three of 35 female white sturgeon tagged either moved downstream immediately after tagging or after spending up to 26 d in the vicinity of the tagging site. This behavior was most likely due to stress induced by capture and tagging. In sturgeon aquaculture, 30-40% of ripe females collected from the wild for spawning fail to progress to final oocyte maturation in the hatchery because of capture stress (Conte et al. 1988). Moser and Ross (1995) also noted that excessively handled shortnose sturgeon moved rapidly downstream. Although my capture and tagging techniques were designed to minimize stress, undoubtedly my tagging was of some detriment to the fish.

It is also possible that some sturgeon were moving upriver for reasons other than spawning. From angler recaptures of white sturgeon tagged for population and mortality estimates, it is known that some sturgeon move into the lower Sacramento River from downstream portions of the estuary during fall (Miller 1972, Kohlhorst et al. 1991). Some of these fish, presumably mature and ready to spawn, move up the river, concentrating between Verona and Colusa. Both Miller and Kohlhorst et al. concluded that these fish were spawners because the mean length at tagging of fish recaptured by anglers upstream of Verona was significantly larger than the overall recapture sample. Through 1992, mean size at time of tagging of sturgeon recaptured upstream of Verona (139 cm) was significantly larger than the remainder of the recapture sample (125 cm) ($t = 8.96$, 1,776 df, $P < 0.001$). Conversely, mean length of sturgeon recaptured by anglers in the area where sturgeon were radio-tagged (Courtland to Verona) was 140 cm at time of tagging, not significantly different from recaptures above Verona ($t = 0.46$, 102 df, $P > 0.5$) (CDFG, unpubl. data). This suggests that most white sturgeon in the tagging capture area are migrants on their way to the spawning area upstream.

A third possible reason for apparent abandonment of spawning is that my sample may have included spent fish on their way downstream. This is most applicable to the sturgeon identified as males and may explain why "male" sturgeon that moved downstream after tagging (identified as males, but really females) tended to be larger than males that moved upstream.

The responses of sturgeon to changes in river flow in the dry winter and spring of 1990 may provide some insight into the minimum flow needs of white sturgeon in the Sacramento River. Prespawning adults tended to move upstream during periods of elevated flow. When Colusa flows decreased below 150 m^3/s, fish tended to cease their upstream migration or to drift downstream (Fig. 2). In 1991, this tendency was less distinct, probably because flows were higher during tagging and a greater portion of the tagged fish left the system during elevated flows in March and early April. Two females (Fig. 3b) did respond to a small flow pulse of 275 m^3/s on 7-8 April by moving upstream, then drifted downstream when flows dropped below 150 m^3/s between 18 April and 2 May.

Flow increases above low base levels may trigger spawning. In both 1991 and 1992, no spawning was detected by artificial substrate sampling in periods when mean daily flows were < 180 m^3/s; sturgeon spawned 1-3 d after flows increased above that level. Kieffer and Kynard (1993) also noted downstream migrations of shortnose sturgeon from the spawning area concurrent with pronounced increases in flow in the Merrimack River. Kohlhorst (1976) stated that there was no obvious flow threshold in the Sacramento River at which spawning was initiated, but in late winter and spring 1973, when his larva sampling was conducted, flows upstream of Colusa ranged from > 2,000 m^3/s in February to 300 m^3/s in late April and early May, much higher than the low flows of the drought years of 1991 and 1992.

My data suggest that downstream movement from the spawning area > 50 km/d may be common post-spawning behavior of female white sturgeon in the Sacramento River. Two females that were repeatedly tracked as they migrated downstream were moving at approximately the velocity of floating objects, suggesting a rather passive, but rapid, downstream migration. Similar rapid downstream movement following spawning has been noted for shortnose sturgeon spawning in the Connecticut and Delaware rivers (Buckley and Kynard 1985, O'Herron et al. 1993). Female sturgeon oocyte maturation and ovulation is preprogrammed by a release of pituitary gonadotropin and, once mature, eggs are viable only for a few hours (Conte et al. 1988). Hence, female sturgeon spawning is singular within a season and of relatively brief duration. A rapid outmigration is also suggested by three females that disappeared from the Sacramento River in the 2 or 3 d between repeated searches in March 1991. These rapid downstream movements or disappearances also coincided with or followed flow peaks or rises and occurred when Colusa flows were above the 180 m^3/s minimum flow when spawning was detected by egg capture. While completion of spawning is suspected as the cause of apparent rapid departures from the river, either unreported angler capture or equipment failure cannot be excluded as possible causes.

If the maximum ascension of female white sturgeon, or their last location before disappearing, corresponded to the approximate spawning location, then my results generally confirm previous findings suggesting that most white sturgeon spawning in the Sacramento River occurs from Knights Landing to several kilometers above Colusa (Kohlhorst 1976). This result is contrary to expectations because the river between Knights Landing and Colusa generally does not have the larger substrate material associated with sturgeon spawning areas (Gard[6] 1996), although the banks are often lined with cobble and larger rip-rap.

A difference from earlier findings is that, based on the movements of two female white sturgeon in 1991 (152 and 146 cm) (Fig. 3a) which were never found above Verona, some spawning potentially occurs below the Feather River. Sturgeon spawning below the Feather River has not been verified by egg capture, but numerous wing dams have been constructed of pilings and large rocks to reduce shoaling in the river between Verona and Sacramento. These dams may provide suitable sturgeon spawning habitat.

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Appendix 1. Artificial substrate sampling sites, 1991.

Location		Depth range		Substrate type[a]	
(river km)	Dates Sampled	(meters)	Right	Center	Left
202.5	19 Apr - 31 May	0.9 - 4.6	4.0	4.0	6.0
205.2	16 Apr - 26 Apr	2.7 - 3.0	4.0	4.0	4.0
206.2	16 Apr - 23 Apr	4.5 - 6.0	6.0	hard[b]	NS[c]
207.3	16 Apr - 3 June	0.9 - 3.0	4.0	4.1	5.0
211.1	16 Apr - 19 Apr	1.1 - 2.4	4.0	4.0	4.7
222.9	16 Apr - 3 June	0.9 - 3.7	4.0	4.7	4.7
232.1	1 May - 3 June	1.5 - 7.0	6.0	4.0	4.0
234.2	26 Apr - 31 May	0.9 - 3.6	4.2	hard[b]	6.0
237.5	16 Apr - 26 Apr	1.0 - 3.7	4.1	4.0	4.5
238.2	29 Apr - 31 May	0.6 - 4.6	hard[b]	4.0	4.6
239.1	16 Apr - 19 Apr	2.1 - 5.5	4.0	4.0	4.5
243.8	16 Apr - 23 Apr	1.5 - 5.5	6.0	4.0	4.5
244.6	26 Apr - 3 May	0.9 - 1.5	4.7	4.9	5.0
245.1	17 May - 3 June	1.5 - 2.5	4.7	4.9	5.0
245.4	16 Apr - 23 Apr	3.0 - 4.6	4.0	4.0	4.0
249.0	19 Apr - 14 May	0.6 - 4.6	4.5	4.8	6.0

[a] According to Instream Flow Incremental Methodology.
[b] Only material dredged was a small amount of sand; substrate was either bedrock or very hard clay.
[c] Not sampled

Appendix 2. Artificial substrate sampling sites, 1992.

Location		Depth range		Substrate type[a]	
(river km)	Dates Sampled	(meters)	Right	Center	Left
223.5	4 Feb - 11 Feb	2.1 - 2.4	NS	NS	NS
232.4	4 Feb - 22 May	1.2 - 3.0	4.5	4.5	4.0
244.2	7 Apr - 15 May	2.3 - 3.7	4.2	4.5	5.5
246.0	4 Feb - 11 Feb	1.3 - 2.8	4.0	4.0	4.0
251.2	4 Feb - 22 May	0.8 - 5.2	5.0	5.0	5.0
252.2	7 Apr - 15 May	1.5 - 2.6	4.0	5.0	5.0
252.7	20 Mar - 19 May	1.1 - 3.4	4.0	4.0	5.0
254.4	24 Mar - 19 May	0.9 - 3.4	5.0	5.0	5.0

Appendix 3. Substrate classifications developed for the Instream Flow Incremental Methodology. To describe a mixture of adjacent materials, the smaller material is listed with a decimal denoting the portion of larger material, e.g., 4.7 denotes a mixture of 30% sand and 70% gravel.

Code	Substrate	Particle size (mm)
1	Plant detritus/organic material	—
2	mud/soft clay	—
3	silt	<0.062
4	sand	0.062 - 2.0
5	gravel	2.0 - 64
6	Cobble/rubble	64 - 250
7	Boulder	250 - 4,000
8	Bedrock	—

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RELATIVE IMPORTANCE OF PREY ITEMS TO CALIFORNIA HALIBUT

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The relative importance of prey items in the diet of California halibut, *Paralichthys californicus*, was determined from 1,397 stomachs taken from fish ranging from 159 to 1055 mm total length (TL). Northern anchovy, *Engraulis mordax*, and mysids were the most important taxa in halibut < 300 mm TL. Halibut ≥ 300 mm TL were predominately piscivores, feeding on Pacific sardine, *Sardinops sagax*; northern anchovy; and white croaker, *Genyonemus lineatus*.

INTRODUCTION

California halibut, *Paralichthys californicus*, is a nearshore species that ranges from Magdalena Bay, Baja California to the Quillayute River, Washington (Miller and Lea 1972, Eschmeyer et al. 1983) and is a valuable commercial and sport fish in California (Schott 1971, Barsky 1990, Jow 1990).

Young California halibut are found in protected bays and estuaries; extensive research has been done on the feeding behavior and prey preference of juvenile halibut in these habitats (Haaker 1975, L.G. Allen 1988, Drawbridge[2] 1990). California halibut < 55 mm standard length (SL) feed predominately on small crustaceans (harpacticoid copepods, small gammarid amphipods, and mysids), while halibut between 55 and 230 mm SL feed increasingly on small fish, such as gobies; topsmelt, *Atherinops affinis*; and California killifish, *Fundulus parvipinnis* (Haaker 1975, L.G. Allen 1988). As juvenile California halibut increase in size and migrate out of protected bays and estuaries, they select larger and quicker prey (Drawbridge[2] 1990).

This trend towards larger and quicker prey continues among the larger California halibut found in open coastal waters. Large juvenile and young adult halibut (245-300 mm SL) have been found to forage predominately on northern anchovy, *Engraulis mordax*, and mysids (M.J. Allen[3] 1982, Roberts et al. 1982, Plummer et

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