

# Migration and movement patterns of green sturgeon (*Acipenser medirostris*) in the Klamath and Trinity rivers, California, USA

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**Abstract** Green sturgeon, *Acipenser medirostris*, movement and migration within the Klamath and Trinity rivers were assessed using radio and sonic telemetry. Sexually mature green sturgeon were captured with gillnets in the spring, as adults migrated upstream to spawn. In total, 49 green sturgeon were tagged with radio and/or sonic telemetry tags and tracked manually or with receiver arrays from 2002 to 2004. Tagged individuals exhibited four movement patterns: upstream spawning migration, spring outmigration to the ocean, or summer holding, and outmigration after summer holding. Spawning migrations occurred from April to June, as adults moved from the ocean upstream to spawning sites. Approximately 18% of adults, those not out migration in the spring, made spring post-spawning outmigrations. The majority of adults, those not outmigrating in the spring, remained in discrete locations characterized as deep, low velocity pools for extended periods during the summer and early fall. Fall outmigration occurred when fish left summer holding locations, traveled rapidly

downstream, and exited the river system. High river discharge due to the onset of winter rainstorms and freshets appear to be the key environmental cue instigating the fall outmigration.

**Keywords** Acipenseridae · Sonic telemetry · Radio telemetry · Summer holding · Outmigration · River discharge

## Introduction

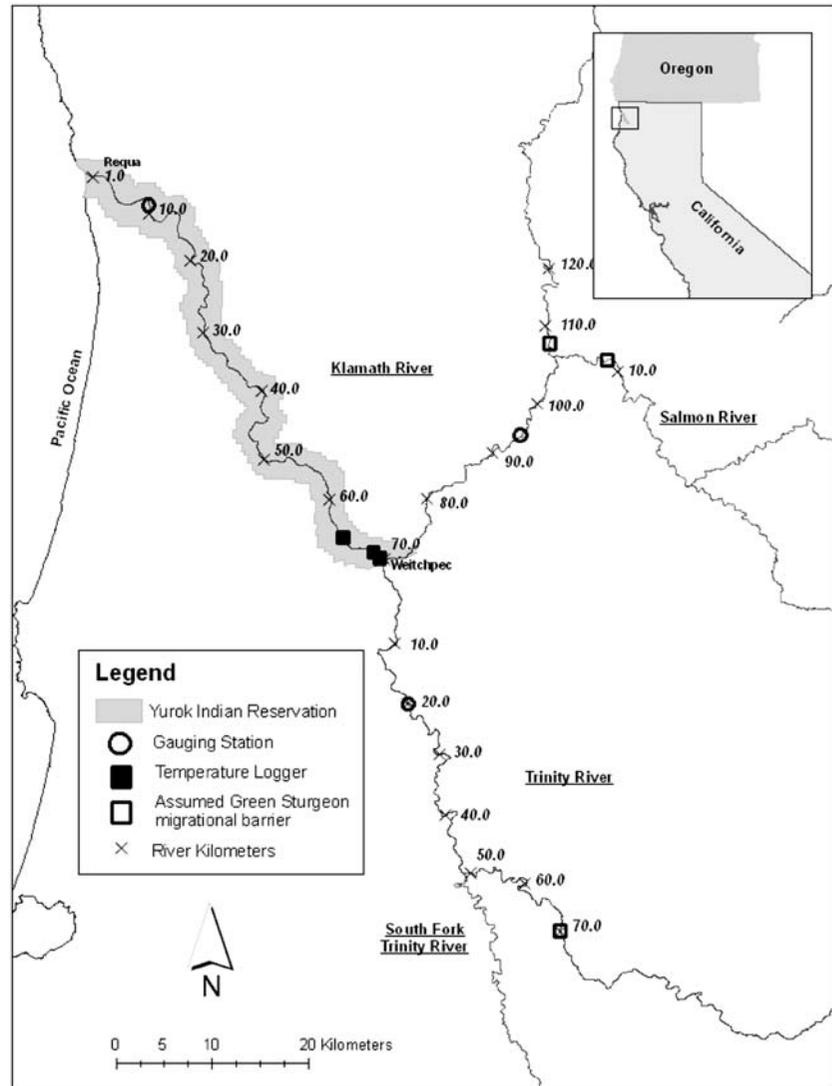
The green sturgeon, *Acipenser medirostris*, is an anadromous Pacific sturgeon whose primary spawning areas are in the Rogue River in Oregon, and the Sacramento and Klamath rivers in California (Moyle et al. 1995; Moyle 2002). The mainstem Klamath and Trinity Rivers are believed to be the principle spawning streams in California (Moyle 2002). Distribution within the Klamath Basin ranges from the Trinity River downstream of Gray's Falls (river kilometer (rkm) 70), the mainstem Klamath River downstream of Ishi Pishi Falls (rkm 108), and the lower Salmon River downstream of Wooley Creek (rkm 8) (Moyle et al. 1994; Moyle 2002) (Fig. 1). The Klamath and Trinity rivers both have major hydroelectric dams and irrigation diversions at the headwaters, which alter flow and temperature regimes downstream (Moyle 2002; National Research Council 2004).

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**Fig. 1** Map of the study area in the lower Klamath and Trinity rivers, California, USA. Ishi Pishi Falls, Wooley Creek, and Grays Falls are assumed to be migrational barriers to green sturgeon on the Klamath, Salmon, and Trinity rivers, respectively. Note that tributary river kilometers (rkm) begin at 0 at the confluence with the mainstem Klamath River



Green sturgeon life history, abundance, and distribution data are limited. Green sturgeon use freshwater primarily for spawning, incubation, and early rearing; with most of their life spent in saltwater and brackish estuaries of large coastal rivers (Scott and Crossman 1973; Parks 1978; Houston 1988). However, Erickson et al. (2002) documented stream residency during summer and autumn for up to 6 months in the Rogue River. Green sturgeon held positions in specific areas throughout the summer, presumably to conserve energy and to feed. Timing of emigration from the Rogue River was related to increased discharge, particularly winter freshets (Erickson

et al. 2002). Green sturgeon summer holding behavior and specific holding sites on the Klamath River have always been acknowledged by Yurok oral history (F. Meyers, Yurok Tribe, personal communication).

The status of green sturgeon populations in North America is considered by some to be vulnerable to endangered (Musick et al. 2000); however, the National Marine Fisheries Service determined that available information does not warrant listing Klamath/Trinity green sturgeon for protection under the Endangered Species Act. Presumed spawning populations in the Eel and South Fork Trinity rivers have been extirpated

within the last 25–30 years (Moyle et al. 1995). Mature spawners in other populations are reduced, with mature females numbering in the low hundreds (Musick et al. 2000; Moyle 2002). However, decline of green sturgeon stocks reported by Musick et al. (2000) may be based on outdated statistics (Adams et al. 2002). Anthropogenic activities may detrimentally affect green sturgeon populations, particularly dams and hydroelectric projects (Houston 1988; Moyle et al. 1995; Erickson et al. 2002). Until abundance, distribution, population dynamics, and ecological requirements are identified, green sturgeon should be considered rare and a species of special concern, especially due to the extreme vulnerability of sturgeons globally (Houston 1988; Birstein 1993; Birstein et al. 1997; Musick et al. 2000; Moyle 2002).

The Yurok Indian Reservation is located on the lower 70 km of the Klamath River (Fig. 1), and green sturgeon have been important to the Yurok People for subsistence and cultural purposes since time immemorial. Water management issues, declining salmon populations and the recent petition to list the green sturgeon under the Endangered Species Act, have elevated the need to understand green sturgeon in the Klamath River. Major questions remain regarding spawning locations, adult summer holding, frequency of spawning, duration of juvenile rearing, and population size. In this study we documented adult green sturgeon freshwater migration and movement, as well as summer holding locations.

## Materials and methods

### Tagging

We captured adult green sturgeon, presumably on their upstream migration, from 29 April to 10 June, 2002, 8 April to 26 May, 2003, and 28 April to 4 June, 2004. We used single- and multi-stranded monofilament gill nets with an 18.4-cm stretched mesh size. The nets were 37 meshes deep (approximately 6.5 m), and 15–30 m in length. Nets were fished for 24 h per day for several days each week, and checked 3–4 times per day. We fished up to six nets simultaneously

at various locations, from the estuary at Requa (rkm 1.00) to Weitchpec, downstream of the Trinity River (rkm 69.00) (Fig. 1).

Captured green sturgeon were either tagged immediately or held in black PVC culvert live wells overnight in the river. Occasionally, green sturgeon were tethered by the tail using cotton rope and placed in calm water to rest before tagging. Data collected from each green sturgeon included: weight, total length, sex, and mid-lateral scute count. Techniques similar to those used by Schaffter (1997) and Conte et al. (1988) provided an indication of sex for externally tagged green sturgeon, with some error. We also collected date, time, GPS coordinates, water temperature, and behavioral observations and condition of the green sturgeon upon release.

For surgically implanted transmitters, we placed captured green sturgeon ventral side up in an inclined sling with an attached hood that fitted over the head and provided a reservoir of water to keep the gills submerged. An assistant monitored operculum of each green sturgeon during the surgery, and filled the hood with fresh water as needed. Surgical technique was modified from that used for collection of ovulated eggs from white sturgeon, *Acipenser transmontanus* (Doroshov et al. 1994; Webb et al. 1999). We made a 7–10 cm incision immediately to the right of the ventral mid-line, starting approximately 10–12 cm anterior to the base of the pelvic fins. The exterior skin surface was pulled upward while making the insertion to protect the internal organs from accidental damage. After incision, we identified sex from visual inspection of the gonads, then inserted a body implant radio transmitter with a coil antenna anteriorly and a sonic transmitter posteriorly through the incision. We used four to six interrupted cross stitches using size 1 Polydioxanone (PDS II) violet monofilament suture 70 cm in length attached to a CP-1 36 mm, double-edged cutting needle to close the incision. In general, the surgery lasted an average of 5–10 min, but never exceeded 12 min. All green sturgeon were tagged with a disc dangler tag behind the dorsal fin for external identification purposes, using methods described by Guy et al. (1996).

We tagged three green sturgeon with an external tag and harness in 2002 using techniques

modified from Carr et al. (1996) and Fox et al. (2000). We constructed a harness to hold both tags by affixing each tag to a separate backing plate made from a 5 mm thick, plastic dive slate. After the tags were secured with cable ties, both sides of the tag harness were coated with a thick coat (4 mm) of marine grade, long drying epoxy, and finished by drilling holes for attachment. Each backing plate was positioned on opposite sides of the dorsal fin. We attached the harness by threading a section of saltwater fishing leader material (braided wire coated in Teflon™, 100 lb. tensile strength) through the base of the dorsal fin and fastening with cable crimps. In 2003 we modified this technique further by using external radio tags with pre-drilled holes and a flat profile for external attachment.

In 2002, we used body implant radio transmitter tags (Advanced Telemetry Systems, F-1250) with coil antennae, a diameter of 29 mm, length of 112 mm, a mass in water of 100 g, and a longevity of 555 days. We used coded pinger transmitter tags (Vemco Ltd., V-16-5H) with a diameter of 16 mm, length of 92 mm, a mass in water of 16 g, and a longevity of 602 days. The combined weight of these tags was approximately 0.1% of the average weight of sampled green sturgeon. In 2003 we used external mount transmitter tags (Advanced Telemetry Systems, F-2130) with trailing whip antennae, a width of 26 mm, depth of 10 mm, length of 64 mm, a mass in water of 28 g, and a longevity of 275 days. We used body implant transmitter tags (Advanced Telemetry Systems, F-1245) with a diameter of 18 mm, length of 102 mm, a mass in water of 40 g, and a longevity of 475 days. Coded pinger tags (Vemco Ltd., V-16-6H) had a diameter of 16 mm, length of 92 mm, a mass in water of 16 g, and a longevity of 1,300 days. In 2004, we exclusively used the V-16-6H sonic tags, implanted internally.

### Tracking protocol

All tagged green sturgeon were tracked and located bi-weekly through the end of June. After 1 July each green sturgeon was located weekly. We radio-tracked using either a Lotek SRX 400 receiver or an Advanced Telemetry Systems R4000 receiver tuned to 151 or 150 MHz. Some radio

telemetry data were collected with fixed Lotek listening stations used for a large-scale adult salmon migration project on the Klamath and Trinity rivers. We conducted manual tracking surveys in 2002 and 2003. In 2004, we did not track manually and all fish locations were from an acoustic receiver array.

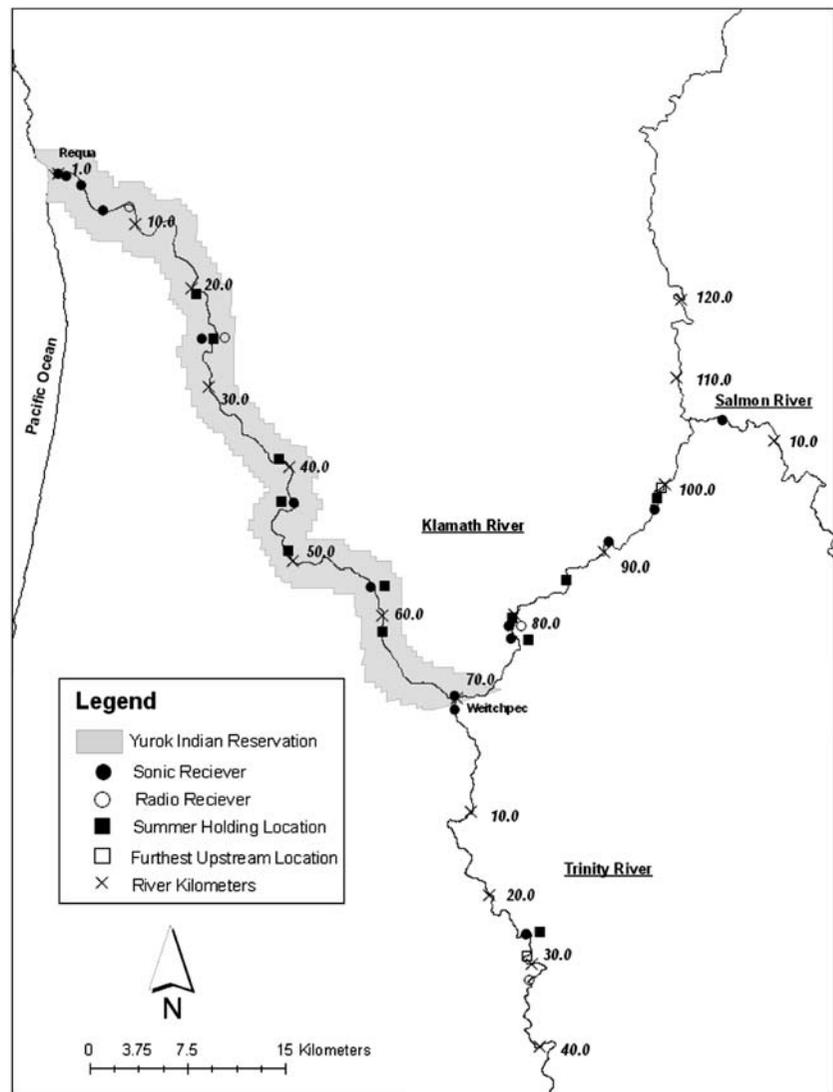
Fourteen Vemco Ltd. Vr2 sonic stationary receivers and four Lotek radio receivers were deployed strategically in the Klamath, Trinity, and Salmon rivers. The receiver array was established at the following locations: rkms 1.00–4.50, 26.50, 43.00, 57.50, 69.00–70.00, 78.5, 79.5, and 97.5 on the Klamath River, rkms 0.50 and 32.00 on the Trinity River, and rkm 4.00 on the Salmon River (Fig. 2). Occasionally we moved and re-deployed receivers in-season to increase the efficiency of the receivers when river conditions changed. We deployed sonic receivers in the estuary to collect information on estuary residence and departure times of tagged green sturgeon leaving the system. Each receiver was downloaded several times during the season and removed from the river before fall and winter flows arrived. We re-deployed each receiver the following spring to detect returns of tagged fish.

### Temperature and discharge

We compiled river flow data throughout the study from three United States Geological Survey and California Department of Water Resources gauging stations. Data used for flow analysis were collected at the Hoopa (no. 11530000) gauging station located at rkm 20.00 on the Trinity River, the Orleans (no. 11523000) gauging station located at rkm 95.00 on the Klamath River, and the Terwer Creek (no. 11530500) gauging station located at rkm 9.00 on the Klamath River (Fig. 1). Discharge below the Trinity River confluence was estimated by summing the Hoopa and Orleans gauge readings.

We monitored and recorded water temperature during the study period using an Onset Stowaway Tidbit Temp Logger (model no. 497097) on the Klamath River, just upstream of the confluence with the Trinity River at Weitchpec (rkm 69.50) (Fig. 1). Other temperature recorders were located downstream of the confluence (rkm

**Fig. 2** Map of the sonic and radio receiver array in the lower Klamath and Trinity rivers, California, USA. Summer holding locations and furthest upstream locations were documented using manual radio tracking



68.50) and at Martin’s Ferry (rkm 64.50) to assess the thermal influence of the Trinity River (Fig. 1). We recorded surface temperatures at all capture and tagging locations, and at confirmed green sturgeon locations using a standard handheld thermometer or portable water quality instrument.

**Results**

**Capture and tagging**

Between 29 April and 10 June 2002, we captured and tagged a total of 16 green sturgeon.

Of the 16 tagged green sturgeon, three were tagged externally and 13 tagged internally. One externally tagged green sturgeon was identified as a female, while the sex of the other two was unknown. Five of the internally tagged green sturgeon were female with a mean total length of 185 cm (range 173–197 cm) and a mean weight of 48 kg (range 39–59 kg). Eight internally tagged green sturgeon were male with a mean total length of 172 cm (range 150–198 cm) and mean weight of 33 kg (range 25–39 kg). One male, WS 1, was identified by mid lateral scute counts (R39 L36) as a white sturgeon, *A. transmontanus*, with a total length 188 cm and weight 43 kg.

Between 8 April and 26 May 2003, we captured and tagged 27 green sturgeon. Twenty-six green sturgeon received both radio and sonic tags, one green sturgeon received only a radio tag. Thirteen green sturgeon were tagged externally, and the other 14 were tagged internally. Of the 14 internally tagged green sturgeon, 6 were female and 8 were male. Of the 13 externally tagged fish, 11 were identified as male and 2 were identified as female. The mean total length and weight for males was 179 cm (range 155–196 cm) and 40 kg (range 31–61 kg). The mean total length and weight for females was 197 cm (range 177–223 cm) and 53 kg (range 35–75 kg). Two of the males were captured and tagged in the Trinity River. In 2003, we attempted to determine sex of externally tagged green sturgeon by characterizing the degree of abdominal distention. In addition, we predicted the sex of internally tagged green sturgeon before surgery to verify our external sex identification ability. The success rate using this technique was 79%.

Between 28 April and 4 June 2004, we captured and tagged eight green sturgeon; one male and seven females. All fish were tagged internally with sonic tags only. The total length and weight for the male was 188 cm and 50 kg. The mean length and weight for females was 190 cm (range 175–213 cm) and 55 kg (range 43–82 kg).

Two green sturgeon shed tags in 2002 (14%), and two shed tags in 2003 (7%). All shed tags were attached externally. One tagged green sturgeon was harvested in 2002 (7%), three were harvested in 2003 (11%), and one was harvested in 2004 (13%). We assumed the green sturgeon

was harvested in 2002, because the sturgeon was never detected after 5 June 2002, nor was the tag recovered.

## Movements

Movements observed for green sturgeon can be summarized into four distinct patterns: upstream spawning migration, spring outmigration to the ocean, summer holding, and outmigration after summer holding. The spawning migration is the upstream movement of sexually mature male and female green sturgeon. We assumed all tagged green sturgeon in the study were captured during the upstream spawning migration at various locations in the estuary and upstream. Spring outmigration is the downstream movement from spawning areas to the estuary and ocean before river flows drop to summer lows. Summer holding is characterized by little or no large-scale movement and the use of specific holding pools for extended periods during summer and fall. Outmigration after summer holding describes downstream movements to the estuary and ocean during the fall and early winter.

We documented full or partial spawning migrations for 11 green sturgeon in all years. This represents 11–60% of the tagged population for both males and females (Table 1). Mean ground speeds ranged from 1.18 to 2.15 km day<sup>-1</sup>, with females traveling slightly faster than males (Table 1). Results from 2004 were not included due to limitations of our sonic tracking protocol. Although there was no physical evidence of spawning activity, we assumed these upstream

**Table 1** Proportion of the tagged Klamath River green sturgeon population exhibiting four movement patterns and mean ground speed for each movement type

Year	Sex	% Spawning migration ( <i>n</i> )	Mean ground speed (km day <sup>-1</sup> )	% Spring outmigration ( <i>n</i> )	Mean ground speed (km day <sup>-1</sup> )	% Summer holding	% Fall outmigration ( <i>n</i> )	Mean ground speed (km day <sup>-1</sup> )
2002	M	11 (1)	1.28	0	–	78 (7)	44 (4)	29.62 (6.38–56.45)
2002	F	60 (3)	1.61 (1.29–2.10)	0	–	60 (3)	40 (2)	49.26 (21.01–77.50)
2003	M	26 (5)	1.18 (0.83–1.75)	32 (6)	5.09 (2.20–7.67)	42 (8)	16 (3)	6.57 (1.03–12.25)
2003	F	25 (2)	2.15 (2.22–2.27)	0	–	50 (4)	38 (3)	33.57 (16.20–64.00)
2004	M	0	–	0	–	100 (1)	0	–
2004	F	0	–	43 (3)	5.55 (2.68–11.17)	14 (1)	43 (3)	n/a

Ground speeds in parentheses indicate the range for individual green sturgeon

movements were related to spawning based on the time of the year and the presence of gravid females.

Movement was classified as an outmigration event when a green sturgeon was detected in or near the estuary, followed by no further detections for that individual. Nine green sturgeon made post-spawning spring outmigrations, where individuals exited the river system immediately after spawning. In 2003, 32% of tagged males were spring outmigrants. In 2004, 43% of tagged females were spring outmigrants (Table 1). Mean ground speeds were similar for each year (Table 1). Alternatively, apparent post-spawning spring outmigration may actually be a flight response to tagging and handling stress.

At least 24 green sturgeon exhibited a summer holding behavior. The proportion of the tagged population that held ranged from 14 to 100%, in all years for both males and females (Table 1). Mean holding time was 150 days in 2002 (range 116–178 days) and 170 days in 2003 (range 129–199 days). One male and one female green sturgeon demonstrated a summer holding pattern in 2004. However, the exact duration of holding could not be determined. In 2002, one male green sturgeon (GS 6) remained in a pool at rkm 43.00 for 34 days, then moved downstream and remained at rkm 26.50 for 82 days. We documented 12 discrete holding locations in the Klamath and Trinity rivers (Fig. 2). Typically, summer holding locations were in pools that are characterized by deep water, eddy currents, and a formative feature, which maintains the depth of the site through high flow events. Formative features can be, but are not limited to rapids, bedrock outcroppings, and large mid-channel boulders. In general, the summer holding period started at the beginning of June and continued until mid to late November.

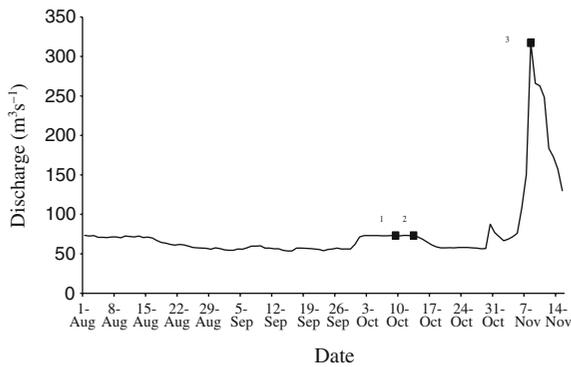
Two green sturgeon were tagged in the Trinity River, and six other green sturgeon moved into the Trinity River after being tagged and released in the Klamath River during the spawning migration. Both of the green sturgeon tagged in the Trinity were males, and exited the river within 2 weeks. One male and one female green sturgeon moved into the Trinity and exited by 4 June. These individuals held for the summer in the

Klamath River (rkm 57.50). Two males and one female made brief excursions into the Trinity River for 1 or 2 days, and were detected a maximum of 0.50 km upstream of the Trinity–Klamath confluence before returning to the mainstem Klamath River. One male green sturgeon was detected on the Trinity River, 0.50 km from the confluence, on 23 May and 19 June. This individual was detected only once on each day. It is likely this green sturgeon spent approximately one month in the Trinity River, traveling past the radio receiver once on the way up and once on the way back downstream. This individual likely stayed in the Trinity for approximately one month, and did not travel past Campbell Creek receiver station (rkm 26.00) (Fig. 2).

We documented fall outmigration for 15 green sturgeon in all years. This represents 16–44% of the tagged population for males and females (Table 1). Mean ground speeds in 2002 and 2003 ranged from 6.57 to 49.26 km day<sup>-1</sup>. In general, individuals initiated outmigration during the first major flow event of the season and entered the estuary 1–2 days later.

One male green sturgeon left the summer holding site on 9 October 2002, was first detected in the estuary at Requa on 13 October, and held there until 8 November before exiting the system. Estuary residence before ocean re-entry for this green sturgeon was a minimum of 25 days 18 h. Beginning 28 September 2002, discharge was increased at Iron Gate Dam for a 2-week-period in an attempt to alleviate a fish kill downstream (CDFG 2003; YTFP 2004). We speculate that premature outmigration may have been initiated when water released from Iron Gate Dam reached this section of the lower Klamath River, increasing discharge from 53 m<sup>3</sup> s<sup>-1</sup> to 70 m<sup>3</sup> s<sup>-1</sup> (Fig. 3). This green sturgeon was next detected in the estuary at Requa on 13 October as discharge decreased. The individual appears to have resumed a summer holding pattern until river flow increased again in early November in response to the first rainfall of the season (Fig. 3).

Outmigration of the remaining tagged green sturgeon occurred when river flow increased in excess of 100–200 m<sup>3</sup> s<sup>-1</sup> during the first significant rainfall event in November and December (Figs. 4, 5). GS 48 was the only other green



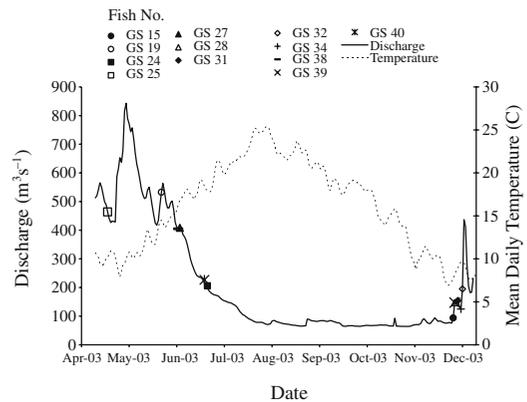
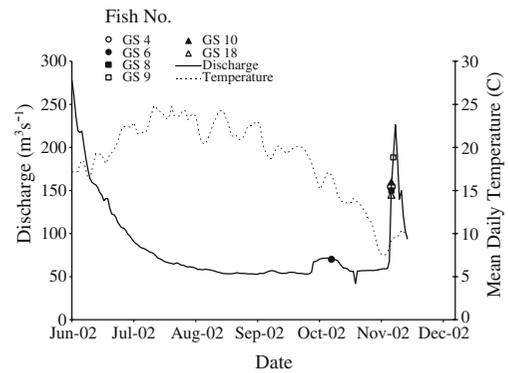
**Fig. 3** Movements of green sturgeon GS 6 during the Iron Gate Dam fish kill flow release in September and October 2002. Symbols represent significant receiver detections: (1) Exited summer holding at Blue Creek. (2) Entered estuary and was first detected at the Requa sonic receiver. (3) Exited system as river flow increased (last detection at Requa). Discharge was measured at rkm 9.00

sturgeon that outmigrated before the first significant rainfall. This individual was detected in the estuary in late October after a brief increase in discharge (Fig. 5). Several tagged green sturgeon were detected at the beginning and end of this flow-induced migration, allowing the calculation of hourly downstream outmigration rates. Mean hourly migration rates were  $2.19 \text{ km h}^{-1}$  and ranged from  $0.55$  to  $5.69 \text{ km h}^{-1}$ . The longest outmigration distance traveled was  $77.50 \text{ km}$  by a female green sturgeon, which held in Aikens Creek Hole during the summer and traveled to the estuary in  $36.5 \text{ h}$  at a downstream rate of  $2.12 \text{ km h}^{-1}$ .

## Discussion

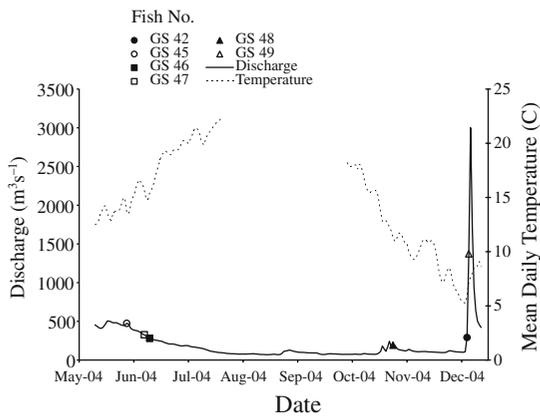
Houston (1988) suggested that green sturgeon rarely inhabit freshwater, except to spawn. However, recent research in the Rogue River indicates that green sturgeon reside up to 6 months in freshwater (Erickson et al. 2002). Our work in the Klamath River identified four adult green sturgeon movement patterns: (1) upstream spawning migration, (2) spring outmigration, (3) summer holding, and (4) fall outmigration after summer holding.

Green sturgeon in the Klamath River migrated long distances (up to  $110 \text{ km}$ ) from April to June. We assumed green sturgeon were migrating for



**Fig. 4** Initiation of green sturgeon post-spawning outmigration in relation to discharge and mean daily water temperature in the Klamath River in 2002 and 2003. Discharge was estimated at the confluence of the Klamath and Trinity rivers (rkm 69.50). Water temperature was measured at rkm 69.50 (2002), and rkms 64.50, 68.50, and 69.50 (2003)

spawning purposes. Other sturgeon species initiate upstream spawning migrations in the spring (Kohlhorst et al. 1991; Kieffer and Kynard 1993; Chapman and Carr 1995; McKinley et al. 1998; Fox et al. 2000). Some white sturgeon in the Sacramento River gather in the lower river and delta in autumn, then move up and concentrate in the upper river from March to May (Kohlhorst et al. 1991). Gulf sturgeon, *Acipenser oxyrinchus desotoi*, initiated migration from mid-February to April in the Suwannee River (Foster and Clugston 1997). Gulf sturgeon in the Choctawhatchee River commenced migration in late March into summer. The difference in timing is attributed to temperature differences and different warming rates between the two rivers (Fox et al. 2000). The



**Fig. 5** First appearance of tagged green sturgeon in the Klamath River estuary (rkm 1.00–4.50) in relation to discharge and mean daily water temperature in 2004. Discharge was measured at rkm 9.00. Temperature was measured at rkms 64.40 and 68.40

distance between wintering and spawning areas may determine timing for shortnose sturgeon, *Acipenser brevirostrum*, spawning migrations. When the distance was long (more than 50 km), most shortnose sturgeon began migrating during the preceding winter, while a few started in the spring. When the distance was short, all shortnose sturgeon started migrating in the spring (Kieffer and Kynard 1993).

We observed six male spring outmigrants (32% of the tagged male population), and three female spring outmigrants in 2004 (43% of the tagged female population). There was no clear pattern of spring outmigration based on sex, however, a biased sex ratio of tagged green sturgeon may be a confounding factor. For example, in 2003 we tagged almost twice as many males as females (19 M, 8 F). In 2004, we tagged only one male and seven females. The majority of spring outmigrants were detected in the estuary shortly after peaks in discharge, typically related to spring rainstorms. Rapid downstream outmigration may be common for post-spawning female white sturgeon in the Sacramento River (Schaffter 1997). The downstream movements occurred following elevated flows or pulses. Shortnose sturgeon moved downstream within 7 days after spawning. Downstream movement may have been prompted by increasing temperatures and rapid increases in river discharge (Kieffer and Kynard 1993). The environmental cues instigating post-spawning

outmigration is likely a combination of increased flow and temperature. This is a typical pattern for spring rainstorms and freshets, sudden overflows of a stream resulting from a heavy rain or a thaw.

It is possible that spring outmigration was a response to tagging and handling stress. Schaffter (1997) observed arrested and interrupted upstream migration after fish were tagged. He postulated that tagged individuals may have abandoned their spawning migration due to stress incurred during capture and tagging. Moser and Ross (1995) observed a similar behavior for shortnose sturgeon captured by commercial fishers. In this study, a total of 17-tagged individuals were located downstream from 1 to 21 days after tagging (50% in 2002, 26% in 2003, 38% in 2004). Five of the 17 were classified as spring outmigrants. Four of the spring outmigrants either continued migrating upstream or remained in close proximity to the tagging location for 3–4 weeks after tagging. Stress may have prompted spawning adults to abandon upstream migration. Alternatively, these individuals may have been captured while on their downstream post-spawning migration, another explanation presented by Schaffter (1997). Sampling in 2003 was conducted earlier in the season than other years. The higher percentage of downstream migrants immediately after tagging in 2002 and 2004 may be the result of sampling later in the season, when spawned adults were in the process of outmigrating. Alternately, green sturgeon may have terminated spawning migration due to drop in river flows. Kootenai River white sturgeon appeared to abandon spawning reaches after rapid reduction in discharge from Libby Dam (Paragamian and Kruse 2001).

In 2002 and 2003, we documented at least 25 green sturgeon (15 male, 9 female, 1 unknown) exhibiting a summer holding pattern in 12 discrete locations on the Klamath and Trinity rivers. Yurok oral accounts describe green sturgeon use of certain pools (i.e. Moore’s Rock, Aiken’s Creek Hole) extensively during the summer (F. Meyers, Yurok Tribe, personal communication). Duration of holding ranged from 44 to 199 days. Extended periods of inactivity and restricted movement in discrete areas have been documented for several sturgeon species (Wooley

and Crateau 1985; Kieffer and Kynard 1993; Moser and Ross 1995; Foster and Clugston 1997; Erickson et al. 2002; Knights et al. 2002). Gulf sturgeon did not move further than 0.6 km from holding sites (Foster and Clugston 1997). Atlantic sturgeon were re-located within 1 km 80% of the time (Moser and Ross 1995). Green sturgeon in the Rogue River stayed in holding sites for up to 6 months in the summer and fall. Some of these holding sites were as small as 50 × 50 m (Erickson et al. 2002). Occasionally, holding sturgeon moved between holding areas (Erickson et al. 2002; Knights et al. 2002). It appears green sturgeon in the Klamath River do move between summer holding sites, however, this behavior is less common than holding in a single location.

Sturgeon holding areas are typically deep (5–10 m) with low velocity (Wooley and Crateau 1985; Moser and Ross 1995; Erickson et al. 2002; Knights et al. 2002). Our results indicate similar physical characteristics for summer holding sites. It is hypothesized that sturgeon hold in these areas to feed and conserve energy (Kieffer and Kynard 1993; Erickson et al. 2002; Knights et al. 2002). An alternate purpose for holding behavior could be to seek thermal refugia, areas cooler than ambient river temperatures due to inflow of tributaries or springs (Chapman and Carr 1995; Moser and Ross 1995). However, Foster and Clugston (1997) found no evidence that Gulf sturgeon were differentially selecting for sites with cold spring water influences, even though they were readily available. Although we did not measure temperature profiles in the holding sites, it is unlikely green sturgeon were seeking thermal refugia. Several thermal refuges have been documented in the Klamath and Trinity rivers (YTFP unpublished data). Green sturgeon were never found within thermal refugia, even though several of these sites were a short distance to holding areas, and were readily available to sturgeon.

Initiation of fall outmigration appears to be related to temperature and discharge. Green sturgeon in the Klamath River initiated downstream migration when river temperature was 10–12°C. The initiation of downstream migration coincided with a significant increase in discharge, resulting from the onset of the fall and winter rainy season. River discharges for three years

were greater than 150–200 m<sup>3</sup> s<sup>-1</sup> when green sturgeon began migrating; an increase from summer base flows ranging from 50–100 m<sup>3</sup> s<sup>-1</sup>. Discharge appears to be the environmental cue initiating downstream migration, but decreasing temperatures may also play a role. Green sturgeon on the Rogue River began migrating when river temperatures reached 12–13°C. Two thirds of tagged individuals left after river temperature was below 10°C (Erickson et al. 2002). Wooley and Crateau (1985) also suggest temperature may be a factor. In addition, they observed significant Gulf sturgeon outmigration after a 15% increase in discharge. Erickson et al. (2002) found that most green sturgeon left the river when flows increased over 100 m<sup>3</sup> s<sup>-1</sup>. A striking example of discharge influenced outmigration was fish GS 6, which left summer holding after a brief pulse flow from Iron Gate Dam in 2002. This green sturgeon initiated outmigration when the pulse reached Blue Creek, then seemed to abandon the migration after the pulse was over. This individual remained in the Klamath River estuary until the fall rains, when it exited the system. Our data corroborates Yurok historical accounts of green sturgeon outmigrating with the first fall rains and resulting increase in discharge (F. Meyers, Yurok Tribe, personal communication).

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