National Marine
Fisheries Service
NOAA

Fishery Bulletin
established in 1881

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Recruitment and survival of juvenile Gulf sturgeon (*Acipenser oxyrinchus desotoi*) in the Apalachicola River in Florida

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Abstract—The Gulf sturgeon (*Acipenser oxyrinchus desotoi*) is an anadromous fish found in drainages of the Gulf coast from Louisiana to Florida and is federally listed as threatened under the Endangered Species Act. Estimates of abundance of adult Gulf sturgeon from several studies have been reported, but direct quantification of juvenile abundance has not been attempted—although such information regarding annual recruitment and juvenile population trends is critical. Our objectives were to quantify recruitment of Gulf sturgeon in the Apalachicola River in Florida by estimating age-1 juvenile abundance and to investigate their survival. During May–August in 2013–2018, we used entanglement gear to conduct a mark-recapture assessment of juvenile Gulf sturgeon. Using Huggins closed population models, we estimated that the Apalachicola River produces 28–210 age-1 juveniles annually (mean: 70 individuals [standard deviation 69.4]). Acoustic telemetry data collected from a subset of age-1 fish indicate that the study area was closed during sampling. We conservatively estimated overwinter survival on the basis of detections and recapture of age-2+ fish acoustically tagged at age 1. Survival varied among years from 33% to 90%. These results indicate that direct estimates of recruitment of Gulf sturgeon to age 1 are feasible, but it is difficult to determine whether this population is recruitment limited without similar data for other populations of Gulf sturgeon.

Manuscript submitted 13 April 2021.
Manuscript accepted 14 October 2021.
Fish. Bull. 119:243–254 (2021).
Online publication date: 12 November 2021.
doi: 10.7755/FB.119.4.4

The Gulf sturgeon (*Acipenser oxyrinchus desotoi*) is a large-bodied, anadromous fish found in drainages of the Gulf coast of the United States from Louisiana to Florida. Like most members of Acipenseridae, the Gulf sturgeon has a late age at maturity, a protracted spawning interval, and a long lifespan (Huff[1]; Nelson et al., 2013). These life history traits make sturgeon particularly vulnerable to anthropogenic disturbances (Rochard et al., 1990), and, as a result of population declines caused by overharvesting and habitat alteration, the Gulf sturgeon was listed as threatened under the Endangered Species Act in 1991 (Federal Register, 1991).

Reproducing populations of Gulf sturgeon currently exist in 7 coastal river systems from the Suwannee River, in Florida, to the Pearl River, in Louisiana (USFWS and NMFS, 2009). Research and monitoring of these populations has largely focused on the capture of juveniles (>900 mm in total length [TL]) and adult fish (≥1350 mm TL), by using gill nets with large mesh (≥12.7 cm stretch) (Sulak et al., 2016). Results of these efforts indicate that the Suwannee River has the largest population, with an estimated abundance of 5000–10,000 adults and juveniles (Chapman et al., 1997; Sulak and Clugston, 1999; Sulak et al., 2016). As summarized by Sulak et al. (2016), most recent estimates of juvenile and adult abundance in other rivers are substantially lower. Although quantifying juvenile and adult abundance does provide insights into long-term population trends, these estimates are not useful in assessing the effects of recovery actions aimed at improving the reproductive success of Gulf sturgeon because these changes will not be reflected in the adult population for many years.

[1] Huff, J. A. 1975. Life history of the Gulf of Mexico sturgeon, *Acipenser oxyrinchus desotoi*, in the Suwannee River, Florida. Fla. Dep. Nat. Resour., Mar. Resour. Publ. 16, 30 p. [Available from Fla. Dep. Environ. Protection, 3900 Commerce Blvd., Tallahassee, FL 32399-3000.]

Monitoring recruitment to age 1 could provide an alternative method for investigation of bottlenecks to population growth that occur during reproduction and early life and could provide managers with forward-looking, quantitative measures for monitoring biological responses to restoration actions that target such bottlenecks (Pine et al., 2001; Schueller and Peterson, 2010). Indeed, some of the core goals of the Programmatic Damage Assessment and Restoration Plan (DHNRDAT[2]), which was developed to restore injury caused by the Deepwater Horizon Oil Spill of 2010, are to improve access to spawning habitats and to boost the reproductive success of Gulf sturgeon by increasing rates of survival during early life.

One approach to gathering recruitment data for sturgeon species is to capture larval sturgeon as they disperse from spawning areas. This method has been used to collect larvae of several sturgeon species (Braaten et al., 2008; Dumont et al., 2011; McAdam, 2011), although it requires precise knowledge of spawning locations and timing to effectively target larvae with fishing gear. Spawning has been confirmed at a handful of sites across the range of the Gulf sturgeon (Parauka and Giorgianni[3]; Heise et al., 2004; Kreiser et al., 2008; Flowers et al., 2009; Sulak et al.[4]). However, larvae do not appear to disperse from spawning areas in a synchronized, predictable fashion, as has been observed for other sturgeon species (Kynard and Parker, 2004), and it remains to be determined whether they can be reliably captured with drift nets.

A second method for monitoring recruitment involves the capture of young-of-the-year (YOY) sturgeon by using bottom-trawling gear. This method has proven effective for large river species like the pallid sturgeon (*Scaphirhynchus albus*) and shovelnose sturgeon (*S. platorynchus*) (Herzog et al., 2005; Doyle et al., 2007), where occupied habitats have been identified (Braaten and Fuller, 2007). However, given the dispersal behavior of Gulf sturgeon, YOY are likely distributed throughout the entire system during their first summer after hatching (Kynard and Parker, 2004; Sulak et al., 2016), rendering capture with trawling gear unlikely. Indeed, efforts to capture Gulf sturgeon with bottom-trawling gear have had little success (Sulak and Clugston, 1999; Kirk and Killgore[5]).

A third method for gathering recruitment data is to estimate the abundance of age-1 juveniles by using gill nets and a mark-recapture approach. This method is now routinely used to assess populations of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) (Schueller and Peterson, 2010; Bahr and Peterson, 2016; Hale et al., 2016) and is also effective for monitoring small populations (e.g., Farrae et al., 2009). Despite success with Atlantic sturgeon, a fellow subspecies of *A. oxyrinchus*, quantitative estimation of age-1 juvenile recruitment has not been attempted for any population of Gulf sturgeon (USFWS and NMFS, 2009). Several researchers have back-calculated recruitment by using data on the age structure of populations (Sulak and Clugston, 1999; Randall and Sulak, 2007; Pine and Martell[6]), but those studies provided only general information about historical population trends and shed no light on current trends in recruitment of Gulf sturgeon.

In addition, little is known about the seasonal habitat requirements of juvenile Gulf sturgeon, although habitat and access may be impediments to species recovery (USFWS and GSMFC[7]; Zehfuss et al., 1999; Flowers et al., 2009). During the summer months, both adult and juvenile (i.e., age 1 and older) Gulf sturgeon reside in main-channel aggregation sites of their natal rivers (Wooley and Crateau, 1985; Hightower et al., 2002), and the majority of individuals do not actively forage (Sulak et al., 2012). During late fall, juvenile Gulf sturgeon move downriver to forage for benthic macrofauna in the estuary (Mason and Clugston, 1993; Sulak and Clugston, 1999; Sulak et al., 2009), while adults disperse more widely to feed in the nearshore, marine waters of the Gulf of Mexico (Odenkirk, 1989; Sulak and Clugston, 1999).

Abiotic conditions may limit habitat access and utilization by juveniles; young juveniles have a lower tolerance for salinity than older fish (Altinok et al., 1998; Kynard and Parker, 2004). Juvenile Gulf sturgeon may remain inshore for up to 6 years (Clugston et al., 1995), possibly because of an intolerance to full ocean salinity. Regarding one potential determinant of year-class strength of Gulf sturgeon, Randall and Sulak (2007) proposed the *salinity barrier* hypothesis, which is that growth and survival of juvenile sturgeon may be enhanced during years when elevated river discharge reduces the salinity of the receiving estuary for longer durations, thereby providing juveniles greater access to benthic resources during the foraging period. Monitoring the year-class strength of

[2] DHNRDAT (Deepwater Horizon Natural Resource Damage Assessment Trustees). 2016. Deepwater Horizon oil spill: final programmatic damage assessment and restoration plan and final programmatic environmental impact statement. [Available from website.]

[3] Parauka, F. M., and M. Giorgianni. 2002. Availability of Gulf sturgeon spawning habitat in northwest Florida and southeast Alabama river systems, 77 p. [Unpublished technical report. Available from Panama City Field Off., U.S. Fish Wildl. Serv., 1601 Balboa Ave., Panama City, FL 32405.]

[4] Sulak, K. J., M. Randall, J. P. Clugston, and W. Clark. 2013. Critical spawning habitat, early life history requirements, and other life history and population attributes of the Gulf sturgeon (*Acipenser oxyrinchus desotoi*) in the Suwannee River, Florida, 99 p. Final report to the Florida Fish and Wildlife Conservation Commission. Proj. Rep. TAL-NG95-125-2013. [Available from the Fla. Fish Wildl. Conserv. Comm., 620 S. Meridian St., Tallahassee, FL 32399.]

[5] Kirk, J. P., and K. J. Killgore. 2008. Gulf sturgeon movements in and near the Mississippi River Gulf outlet. U.S. Army Corps Eng., ERDC/EL TR-08-18, 9 p. [Available from website.]

[6] Pine, W. E., III, and S. Martell. 2009. Status of Gulf sturgeon *Acipenser oxyrinchus desotoi* in the Gulf of Mexico, 34 p. [Unpublished report prepared for 2009 Gulf sturgeon annual working group meeting; Cedar Key, 17–19 November.]

[7] USFWS and GSMFC (U.S. Fish and Wildlife Service and the Gulf States Marine Fisheries Commission). 1995. Gulf sturgeon recovery/management plan, 170 p. Southeast Reg., USFWS, Atlanta, GA. [Available from website.]

age-1 juvenile cohorts over time could enable an investigation of environmental factors, like salinity, that have been thought to influence recruitment during the first year of life of Gulf sturgeon (e.g., Nilo et al., 1996).

Yet another unknown is the overwinter survival rate of juvenile Gulf sturgeon during the foraging period. While foraging in the estuary, juvenile sturgeon may be taken by bottom fisheries, such as shrimp trawling fisheries (Wooley and Crateau, 1985; Collins et al., 2000). Although this potential source of mortality has been noted over the years (USFWS and GSMFC[7]; USFWS and NMFS, 2009), estimation of the overwinter survival of juvenile sturgeon has not been attempted. Monitoring the overwinter survival of age-1 Gulf sturgeon may provide insight into what happens to young juveniles after they recruit to the population and may allow comparisons of mortality across river systems that experience different pressures (e.g., bycatch in other fisheries or dredging).

The goal of this 6-year study, therefore, was to investigate juvenile Gulf sturgeon in order to elucidate gaps associated with this life stage. We selected the Apalachicola River system for this investigation because information on where to target juvenile Gulf sturgeon was available from historical records of their incidental capture during monitoring of adults. The specific objectives of this study were to estimate the abundance of age-1 annual cohorts as a quantified measure of recruitment and to calculate a conservative estimate of the survival of age-1 juveniles during their estuarine overwintering period.

Materials and methods

Study site

The Apalachicola River is the largest river by discharge in the state of Florida (Iseri and Langbein, 1974). The river is formed by the confluence of the Flint and Chattahoochee Rivers, although this junction is now inundated by the reservoir created by construction of the Jim Woodruff Lock and Dam (JWLD). Downstream of the JWLD, the Apalachicola River flows freely for 171 river kilometers (rkm) through the Florida Panhandle to Apalachicola Bay in the Gulf of Mexico (Fig. 1). Sampling efforts were concentrated in the Brothers River, a tributary that flows into the Apalachicola River 21 rkm upstream of the bay. The Brothers River has a deep (9–15 m) channel that has been identified as a summer habitat for juvenile Gulf sturgeon (Wooley and Crateau, 1985; Kirk and Killgore[5]; A. Kaeser, unpubl. data). Additional sampling was conducted in several areas located in the lower and upper sections of the main stem Apalachicola

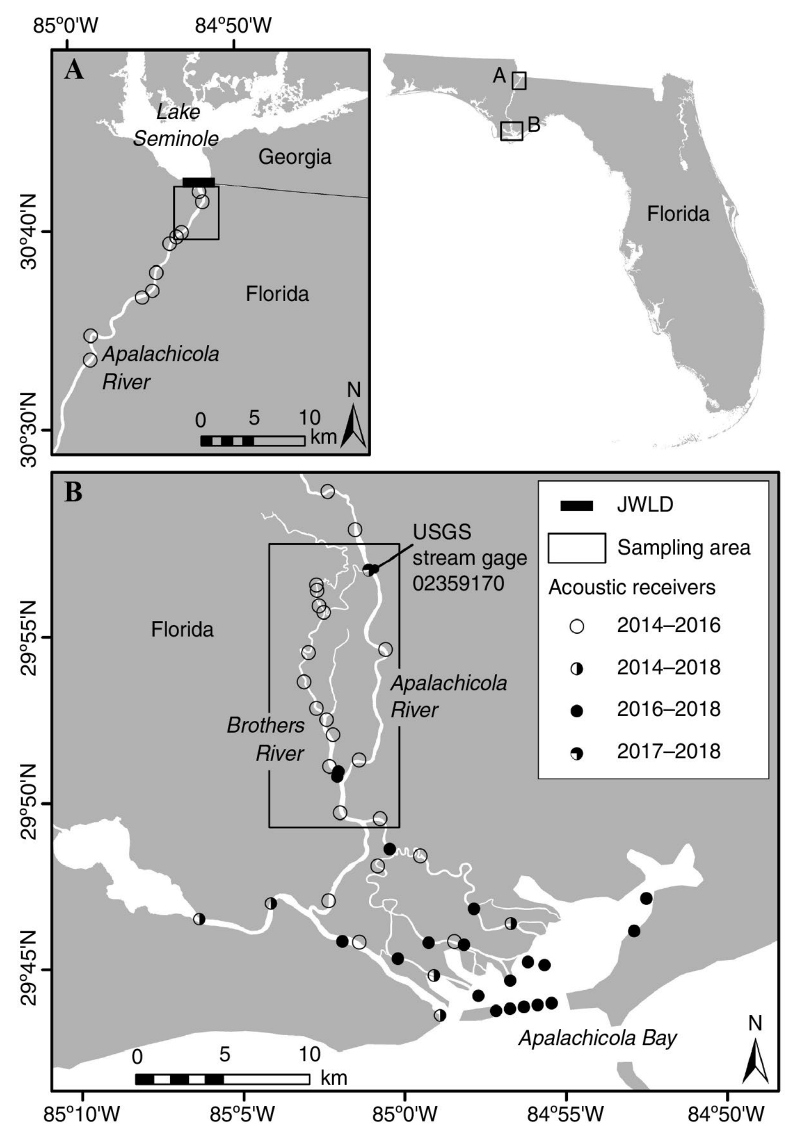

Figure 1

Maps of the study site in the Apalachicola River in Florida: (**A**) the Apalachicola River downstream of the Jim Woodruff Lock and Dam (JWLD, indicated by a black rectangle) and (**B**) the Brothers River and lower Apalachicola River. Sampling for juvenile Gulf sturgeon (*Acipenser oxyrinchus desotoi*) in 2014–2018 occurred within the boxes outlined in black. Circles indicate locations of acoustic receivers within the array installed for this study—open for receivers deployed during 2014–2016, black for those deployed during 2016–2018, half black for those deployed during 2014–2018, and three-fourths black for the receiver deployed during 2017–2018. In panel B, the location of U.S. Geological Survey (USGS) stream gage 02359170 on the Apalachicola River near Sumatra, Florida, is indicated.

River where juvenile and adult Gulf sturgeon have previously been captured (A. Kaeser, unpubl. data), as well as in other nearby reaches of the river (Fig. 1).

Fish tagging

From May through August of 2013–2018, we sampled for Gulf sturgeon 4–5 d/week. Each day, we deployed 6–12 anchored monofilament gill nets throughout the river channel at depths of 4–18 m. All nets comprised three 50-m panels consisting of 7.6-, 8.9-, and 10.2-cm monofilament mesh (stretch measure). Net design was based on nets proven to capture juvenile Atlantic sturgeon in rivers in Georgia (Schueller and Peterson, 2010). Nets were typically soaked for 60–120 min, depending on conditions. To ensure that sampling occurred within the recommended water-quality ranges (Kahn and Mohead, 2010), we used a YSI Pro2030[8] meter (YSI Inc., Yellow Springs, OH) to measure water temperature (in degrees Celsius), dissolved oxygen (in milligrams per liter), and salinity (using the practical salinity scale) at each netting location. River discharge data were obtained from the nearest U.S. Geological Survey stream gage (02359170 on the Apalachicola River near Sumatra, Florida; data available from website.).

As nets were retrieved, all captured Gulf sturgeon were immediately removed and placed into a floating net pen where they could recover before being brought on board the vessel for data collection. Each individual was examined for marks indicating previous capture; if no mark was present, the fish was marked with a passive integrated transponder (PIT) tag inserted into the musculature at the base of the dorsal fin or under the fourth dorsal scute. The fish was then weighed to the nearest gram, measured to the nearest millimeter (in fork length [FL]), and released at the site of capture within 30 min of initial capture.

Fish ages were first assigned from modal distributions on length–frequency histograms of catch of Gulf sturgeon for each year of the study, by using the method described by Peterson et al. (2000) and Schueller and Peterson (2010). To validate assigned ages, we obtained sections of second marginal fin rays from the pectoral fins of a subsample of captured fish; these samples were prepared by using techniques described by Baremore and Rosati (2014). Ages were determined on the basis of consensus of 3 independent readers (if consensus could not be reached, we removed that sample from the validation data set). Because there was essentially no overlap in lengths at age, we were able to assign a length range for age-1 and age-2 Gulf sturgeon.

Acoustic telemetry

To investigate the closure of the summer aggregation site in the Brothers River during the fishing period and to examine overwinter survival, we tagged up to 20 age-1 juveniles (age estimated on the basis of length) with a surgically implanted acoustic transmitter (Vemco V7-4X, Innovasea Systems Inc., Boston, MA) in May and June of each study year. To implant the transmitter, we placed each fish in a V-shaped surgical platform, with a battery-powered pump supplying fresh river water to its gills. An incision of 2–3 cm was made along the midline of the abdomen by using a sterile scalpel, and through this incision the sanitized transmitter (~1.6 g) was inserted into the body cavity. The incision was then closed with a 2/0 absorbable monofilament suture (Monoswift L943, CP Medical, Norcross, GA) by using a single interrupted pattern (Boone et al., 2013; Baremore and Rosati, 2014). After the surgical procedure, each fish was placed in a floating pen. Once a fish had regained its orientation and ability to swim, it was released at its capture site. Ping rate and battery life of transmitters varied among the study years (Table 1). The transmitters deployed in 2017 had a 120-d delay before they began transmitting, extending the battery life of those tags through the summer of 2018, allowing us to confirm fish survival and improve estimates of overwinter survival.

To detect the tagged juveniles after their release, we deployed an array of acoustic receivers throughout the Brothers and Apalachicola Rivers, their distributaries, and the East Bay subunit of Apalachicola Bay (Fig. 1). The array consisted of 30 stationary acoustic receivers (Vemco VR2W, Innovasea Systems Inc.). Receivers were anchored to the bottom with concrete weights and held upright (hydrophone upward) in the water column with a PVC float. Receivers were attached to trees, navigational markers, or other pilings by using stainless steel cables. Some were secured to pilings with aluminum U-channel, and others were deployed in open water, where they were anchored with cinder blocks. Every 2–3 months throughout the study period, the entire receiver

Table 1

Specifications for acoustic transmitter tags implanted in age-1 juvenile Gulf sturgeon (*Acipenser oxyrinchus desotoi*) captured and tagged from May through August in 2013–2018 in the Brothers River and other areas of the Apalachicola River system in Florida. All tags were Vemco V7-4X transmitters with a frequency of 69 kHz. Minimum and maximum delays, and delay before activation, were set by the manufacturer. Transmitter lifespan was estimated by the manufacturer.

Year	Min. delay between signals (s)	Max. delay between signals (s)	Lifespan (d)	Delay before activation (d)
2014	80	160	305	0
2015	170	310	426	0
2016	170	310	426	0
2017	80	160	374	120

[8] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

array received routine maintenance and data were downloaded from each receiver. Routine maintenance included replacing batteries and cleaning of any biofouling. Supplemental telemetry data were obtained by periodically sweeping the study area with a portable receiver and hydrophone (Vemco VR100, Innovasea Systems Inc.) to detect fish between receivers or outside of the array. Between December and May in 2016, our receiver array was restructured to include more receivers outside of the Brothers River, leaving a gate (i.e., receivers that covered the river channel) where the Brothers River flowed into the Apalachicola River; in the spring of 2017, another gate was added at the cut connecting the upper Brothers River to the main stem Apalachicola River. The purpose of these gates was to detect fish as they left or reentered the aggregation site.

Data from the acoustic receiver array were carefully checked for any spurious detections (e.g., simultaneous detections of a single fish at disparate receiver stations), and such detections were removed. Raw detection data were converted into detection days (one detection per fish per receiver per day). If a fish was not detected on a study day but was known to be alive because of detections on subsequent days, that fish was assigned the location of its last known detection until it was detected elsewhere (this method was applied by Fox and Peterson, 2019, to telemetry data from tagged juvenile Atlantic sturgeon). We used these telemetry data to determine whether and how often tagged fish left the Brothers River during our mark-recapture sampling season or to determine if fish tagged elsewhere in the system entered the Brothers River—the lack of such movements into or out of the Brothers River would indicate closure of the aggregation site. Additionally, we used telemetry data to calculate overwinter survival, as described later in the "Survival analysis" section.

Abundance estimation

To estimate the annual abundance of age-1 juvenile Gulf sturgeon, we fit a Huggins closed capture model (Huggins, 1989, 1991) to mark-recapture data from the gill-net surveys. Models were fit to data by using the RMark package (Laake[9]) in statistical software R (vers. 3.5.1; R Core Team, 2018). Each week of the study was considered a sampling period in the capture history for each year, and in each sampling period, an individual was classified as either absent or present, regardless of the actual number of times it was captured that week. The model includes the assumption that the population was closed, meaning that there were no births or deaths and that no immigration or emigration occurred throughout each summer in the study period, and the assumption that tags were not lost or overlooked. We primarily used telemetry data to look for violations to the assumption of closure, but we also used the program CloseTest (vers. 3; Stanley and Burnham, 1999) for an alternative way to investigate closure.

After we compiled individual capture histories for each juvenile caught during the study, each fish was assigned to an age group (i.e., age 1, age 2, or age 3+) on the basis of its length. A set of candidate models was produced to estimate juvenile cohort abundances in each of the 6 study years. The candidate set of models and their main settings were as follows:

- M_o, in which capture probability was constant;
- M_t, in which capture probability varied with time;
- M_a, in which capture probability varied by fish age;
- M_{t+a}, in which capture probability varied by an additive effect of time and age; and
- M_{t*a}, in which capture probability varied by an interactive effect of time and age.

In all models, capture probability was set as equal to recapture probability because no evidence indicates that capture history had any influence on recapture probability for sturgeon—this method has been used in other studies in which recruitment of sturgeon was estimated to age 1 (e.g., Bahr and Peterson, 2016). Akaike information criterion (Akaike, 1973), corrected for small sample size (AIC_c) (Hurvich and Tsai, 1989), was then used to evaluate the relative likelihood of each model. For each year of the study, all models were averaged by using Akaike information criterion model weight to estimate abundance of age-1 Gulf sturgeon, to reduce bias in the event of several candidate models being plausible (i.e., the top model carried a weight <0.90) (Burnham and Anderson, 2002).

Survival analysis

We estimated overwinter survival by comparing the number of acoustically tagged age-1 juveniles detected leaving the summer aggregation sites in the fall and winter with the number of fish from that cohort that returned the following spring. Detection of the fish that by then were age 2 was done through acoustic detection or physical capture. Survival was calculated as the percentage of tagged age-1 fish that were confirmed to still be alive at age 2 (or an older age). Because this survival analysis does not include detection probabilities, it has a necessarily conservative approach, in that survival is likely underestimated because it is not possible to distinguish between fish that died and fish that remained alive but were not detected.

Results

Over 6 years of sampling, we set 1834 nets for a total of 2205 net-hours of sampling effort within the Brothers River. Because anchored gill nets did not sample Gulf

[9] Laake, J. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Process. Rep. 2013-01, 25 p. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA. [Available from website.]

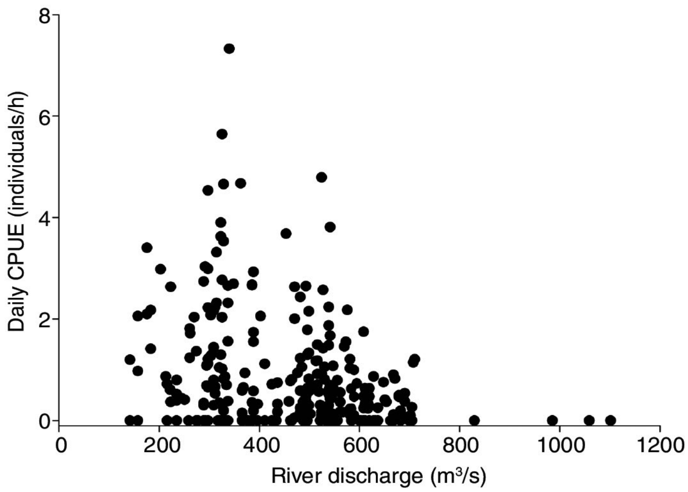

Figure 2

The relationship of catch per unit of effort (CPUE) for sampling of Gulf sturgeon (*Acipenser oxyrinchus desotoi*) and discharge of the Apalachicola River in Florida between May and August in 2013–2018. Catch per unit of effort was calculated as number of sturgeon captured per hour of netting effort. River discharge data are from U.S. Geological Survey (USGS) stream gage 02359170 on the Apalachicola River near Sumatra, Florida. Data in this figure are a subset of all catch data, consisting of catch for the 2 sites most frequently sampled in the Brothers River tributary, which had a wide variety of river discharge conditions in 2013–2018.

sturgeon effectively when river discharge exceeded ~850 m^3/s (Fig. 2), we generally did not set nets when flows exceeded this threshold. Therefore, sampling period varied among study years, from just 4 weeks in 2013 to 15 weeks in 2018 (Table 2). In 2013, netting locations were dispersed entirely within the Brothers River. During 2014–2018, 192 net-hours (10% of all net-hours in the period) were expended in other areas of the Apalachicola River system. Water quality in netting areas remained relatively consistent throughout all summer sampling periods (Suppl. Table 1). The interquartile temperature range was 26.7–29.1°C, and the interquartile range for dissolved oxygen was 4.34–5.79 mg/L. Salinity in all sampling locations was <0.1, with the exception of several sets in the lower Apalachicola River, from which no sturgeon were caught.

Over the 6 years of sampling, 2029 Gulf sturgeon were captured in the Apalachicola and Brothers Rivers, including 1100 unique individuals (Table 2). Of those fish, 288 were identified as age-1 juveniles. Results of length–frequency analysis (validated by pectoral fin ray analysis) indicate that age-1 fish had FL of 370–530 mm, although there was some variation among years in median length (Suppl. Fig. 1). Most age-1 juveniles (number of samples [n]=282, 97.9%) were captured within the Brothers River. During this study, only 6 age-1 fish were ever captured in other reaches of the Apalachicola River—all were observed just below the JWLD in 2017 and 2018 (although we sampled in that area in 2015–2018).

In May and early June during 2014–2017, we tagged 50 age-1 juveniles with acoustic transmitters (Fig. 3). All but 1 fish were captured within the Brothers River; the exception was a fish captured at the JWLD. We detected 76% (n=38) of tagged fish on our acoustic array after tagging; detection rates varied, with 42–100% of fish detected per study year and 21–25,360 detections per fish. We also physically recaptured 16 acoustically tagged individuals within the year they were tagged or in subsequent years. In 2016, we found infections of the sutured surgery site on several tagged fish that were

Table 2

Effort, catch, and other details for sampling of Gulf sturgeon (*Acipenser oxyrinchus desotoi*) in the Apalachicola River, in Florida, during May–August in 2013–2018. The total number of Gulf sturgeon captured includes all ages and all recaptured fish. Abundance of age-1 fish was calculated by using Huggins closed capture models, and values are presented as point estimates of number of individuals with 95% confidence intervals (CIs). We tested for closure of the age-1 population by using the program CloseTest; P-values ≤0.05 indicate statistical significance and a population that was not closed.

	Effort				No. of age-1 juveniles		Abundance of age-1 fish		
Year	Nets set	Net-hours	Sampling periods	Total no. of fish captured	Marked	Recaptured	Abundance	95% CI	CloseTest *P*-value
2013	167	287	4	101	33	12	46	37–70	0.34
2014	291	465	9	602	151	62	218	190–241	0.63
2015	318	348	9	341	25	6	54	34–119	0.75
2016	270	270	9	333	34	23	51	35–67	0.06
2017	291	311	13	198	24	22	28	24–36	0.72
2018	497	524	15	156	21	9	31	21–48	0.11

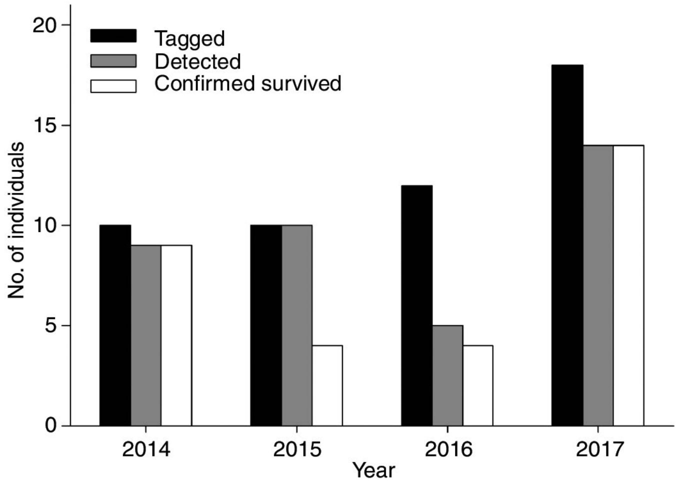

Figure 3

Deployment and detection of acoustic tags on and fate of age-1 Gulf sturgeon (*Acipenser oxyrinchus desotoi*) captured and tagged in the Apalachicola River in Florida during 2014–2017. Black bars indicate the number of age-1 fish implanted with acoutic transmitters in each year of this study, and gray bars indicate how many of those transmitters were subsequently detected by the acoustic receiver array. Open bars indicate the number of individuals confirmed to have survived to at least age 2, through a combination of detections with telemetry data and physical recapture of fish.

recaptured in nets—something we did not observe in any other study year.

During summer months, individuals tagged in the Brothers River remained there almost exclusively. In 2014, one fish was briefly detected by a receiver in the main stem Apalachicola River near the mouth of the Brothers River but returned to the Brothers River within about 3 h of that detection. In 2017, another tagged fish was detected at a receiver at the mouth of the Brothers River and may have entered the Apalachicola River (it was never detected by receivers there); that fish was detected again at the same gate receiver 18 d later. Recapture of fish (in gill nets) and sporadic active tracking of tagged fish confirmed their presence in the Brothers River even when fish were not detected by the acoustic receiver array (e.g., they were between 2 receivers and out of the detection range of both). During opportunistic hydrophone sweeps, tagged age-1 fish were never detected outside of the Brothers River. The juveniles moved out of the Brothers River in the fall and were detected with receivers in the main stem Apalachicola River and its distributaries as they moved toward Apalachicola and East Bays. Tagged fish were detected moving back up these same channels toward and into the Brothers River the following spring. The single Gulf sturgeon acoustically tagged at the JWLD was never detected in the Brothers River, but it was detected with receivers in the Apalachicola Estuary as it moved downriver in the fall.

Recruitment

Model selection on the basis of AICc values indicates that the M_{t+a} model (with the additive effect of time and age) held almost all of the weight in most years of the study; the M_{t*a} model (with the interactive effect of time and age) held the most weight in only 2 years (Suppl. Table 2). For the age-1 cohort, weighted averaging of all models resulted in estimated abundance of 28–54 individuals in each year of the study, except for 2014, for which the estimated abundance of age-1 fish was 210 individuals (Fig. 4).

Survival

Of the 38 acoustic transmitters that we deployed on Gulf sturgeon and later detected in our array, 24 transmitters were last detected in March or later of the following calendar year (i.e., the fish implanted with the transmitters survived the winter after tagging). An additional 7 tagged fish that were never detected by the array were physically recaptured ≥1 sampling season after tagging. We have confirmed that 31 fish (62% of all tagged fish) survived to at least age 2. Our conservative estimates of overwinter survival varied annually from a low of 33.3% to a high of 90.0% (mean: 60.2% [standard deviation (SD) 27.8]) (Fig. 3).

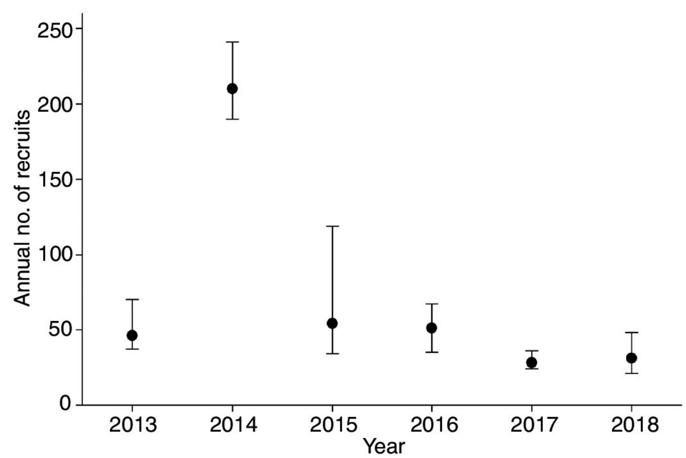

Figure 4

Estimates of abundance of age-1 juvenile Gulf sturgeon (*Acipenser oxyrinchus desotoi*), by year that a cohort was sampled, in the Apalachicola River in Florida during 2013–2018. Abundance is measured as the number of recruits. Error bars indicate 95% confidence intervals.

Discussion

Recruitment

This study is the first to directly estimate annual recruitment of any population of Gulf sturgeon. Across the 6 years of this study, age-1 recruits were observed every year, and mean annual recruitment was relatively stable. The Apalachicola River produced approximately 50 age-1 Gulf sturgeon in most years, although recruitment was substantially greater in 2014, when we estimated that there were 210 age-1 sturgeon.

Although there are no direct recruitment estimates for Gulf sturgeon to which our results can be compared, Pine and Martell[6] used an age-structured, mark-recapture model to back-calculate recruitment on the basis of the adult population, and they reported annual recruitment in the Apalachicola River to be 100–300 individuals/year, slightly greater than our estimates. However, direct recruitment estimates do exist for Atlantic sturgeon in several southern rivers. The largest populations of Atlantic sturgeon in the southeastern United States have annual recruitment that is an order of magnitude greater than what we generally observed in the Apalachicola River: the Altamaha River, in Georgia, produces 500–2500 age-1 juveniles every year (Schueller and Peterson, 2010), and the Savannah River, in Georgia and South Carolina, produces 500–600 juveniles annually (Bahr and Peterson, 2016). Recruitment of Gulf sturgeon in the Apalachicola River appears more similar to that observed in small rivers in Georgia's coastal plain, rivers where annual recruitment is <100 age-1 juveniles per year, if any, such as in the Ogeechee River (Farrae et al., 2009), Satilla River (Fritts et al., 2015), and St. Marys River (Fox et al., 2018). These populations are considered particularly small and imperiled (ASSRT, 2007).

Although recruitment of Gulf sturgeon in the Apalachicola River was substantially lower than recruitment of Atlantic sturgeon in similar large, Piedmont river systems (e.g., the Savannah and Altamaha Rivers), all 3 river systems did produce new recruits every year, indicating that spawning occurred every year. In contrast, small populations of Atlantic sturgeon (e.g., those in the Satilla and St. Marys Rivers) did not produce age-1 recruits every year. This comparison to recruitment of Atlantic sturgeon indicates that, although Gulf sturgeon in the Apalachicola River spawn successfully every year, recruitment may be limited. Analysis of recruitment across other populations of Gulf sturgeon will be necessary to determine how the population in the Apalachicola River compares to others of the same subspecies.

We tagged fish largely within the Brothers River; therefore, our recruitment estimates pertain primarily to the population of juveniles that reside in this part of the river system. Over many years of historical sampling by the U.S. Fish and Wildlife Service (A. Kaeser, unpubl. data), juvenile Gulf sturgeon have been captured in only one other location outside the Brothers River—below the JWLD. Moreover, in this study, we set nets in the Apalachicola River, including in many reaches with characteristics (e.g., depth, salinity, and temperature) similar to those of the Brothers River and, in most years, caught no age-1 juveniles outside of the Brothers River. Our capture of several age-1 juveniles below the JWLD indicates that juveniles can (sometimes) be found at this location. Because our estimates are specific to the geography we sampled, we acknowledge that the presence of age-1 fish in undiscovered aggregation sites, should they exist, would mean that we have underestimated true, population-level recruitment in the Apalachicola River system. However, unless there are unknown aggregation sites that contain dozens or hundreds of unsampled age-1 fish, it seems likely that our estimates either accurately represent or provide a robust indicator of recruitment to age 1 in the river system. Annual recruitment in the Apalachicola River appears to be measured in dozens of fish, not hundreds or thousands.

The validity of the abundance estimates produced in this study relies heavily on the assumption of population closure (demographic and geographic)—no births, deaths, immigration, or emigration can occur during the sampling period (Huggins, 1989). Under this assumption, capture rates could fluctuate throughout the sampling season (as they did during this study), resulting in more accurate estimates than values produced with an open model (Stanley and Richards, 2005). Although the assumption of closure can never be proven per se, there are several reasons why we believe the population was essentially closed during our sampling. For numerous studies (e.g., Wooley and Crateau, 1985; Hightower et al., 2002) in which the life history of Gulf sturgeon was examined, results indicate that all juveniles returned to aggregation sites in their natal river during summer months. We conducted our sampling mainly in the summer at the aggregation site in the Brothers River. CloseTest results (Table 2) indicate that age-1 cohorts likely met the closure assumption in most years of the study—the lack of closure in 2016 could have been a result of elevated mortality due to exceptionally warm water temperatures (see discussion of survival in the next section).

The telemetry data collected during this study largely support the assumption of closure for the Brothers River. No tagged age-1 juveniles were detected outside the aggregation site in that river for more than a short period (<4 h), and no individuals marked (i.e., acoustically tagged) near the JWLD were observed in the Brothers River during the summer in which they had been tagged. The JWLD appears to have a separate aggregation site that is occupied by only a few, if any, age-1 fish. However, if the population was not closed, our estimates of annual recruitment would be lower than the true number of recruits.

Mark-recapture models also include the assumption that marks (i.e., tags) were not lost or overlooked. In lake sturgeon (*Acipenser fulvescens*), PIT tag retention is 99% (Briggs et al., 2019), and we would expect similar results for other species in Acipenseridae. Each Gulf sturgeon we captured was thoroughly scanned for PIT tags, and many marked fish were captured more than once within a single summer. Although we cannot prove that no fish rejected PIT tags, the repeated capture of tagged fish within and among summers indicates that sturgeon retained their PIT tags and that tags were not overlooked.

Survival

Overwinter survival of juvenile Gulf sturgeon from age 1 to age 2 appears quite variable, with high survival in some years (e.g., 90% in 2014) and substantially lower rates in others (e.g., 40% in 2015 and 33% in 2016). However, these estimates are conservative (i.e., biased lower than the true values) because we were unable to differentiate actual mortality of tagged fish from transmitter failure or lack of detection. We were able to supplement acoustic detections with physical recapture events to confirm that—after as long as several years at large—some fish had actually survived. Although we are unable to ascertain the fates of individuals that were not detected or recaptured at age 2 or beyond, it is unlikely that these fish utilized another aggregation site outside of our receiver array because they were not detected moving upriver in the spring or in the main stem Apalachicola River. No tagged juveniles were detected outside of the Brothers River in surveys with the portable receiver, and many tagged fish were eventually recaptured in gill nets within the aggregation site in the Brothers River.

The probability of detecting tagged fish in our array was undoubtedly <1. Although results of preliminary testing of the detection range of receivers indicate that receivers could detect a Vemco V7-4X transmitter at ranges of up to 800 m, we recognize that in most cases detection range is probably substantially smaller. Detection range also likely varied with condition and orientation of receivers, with river conditions at each site in the array, and even with ambient weather. Therefore, fish could certainly have swum past acoustic receivers in the array without detection. Additionally, distribution of receivers within the array changed over the course of this study. Beginning in 2016, many receivers in the Brothers River were moved to locations lower in the estuary. Our transmitter specifications also differed among study years, both in signal delay and activation delay, creating additional differences in probability of detection across study years.

Despite imperfect detection, our survival analysis required only that we detect each tagged fish at least once in the year after tagging—to indicate that it had survived and moved back upriver. Most surviving tagged fish likely would have been detected at least once during the several months in which this detection could occur. Indeed, 77.5% of all fish confirmed to have survived to ages ≥2 were detected by the array (and most of those fish were detected hundreds of times). Additionally, if a fish did survive, each year it remained at large provided an additional sampling season in which we might catch it and confirm survival. Continued long-term monitoring of Gulf sturgeon in the Apalachicola River may yet reveal the survival of some fish that are currently presumed dead by this model, increasing the rate of survival beyond what we report in this paper.

This study was not intended to identify sources of overwinter mortality for Gulf sturgeon in the Apalachicola River. However, some mortalities may have resulted from transmitter implantation, especially in substandard environmental conditions. In 2016, water temperatures reached as high as 31.3ºC (Suppl. Table 1). Although we did not conduct surgeries in temperatures above 28ºC, exposure to very warm water shortly after being tagged may have facilitated the infections we observed at surgery sites of recaptured fish in 2016. These infections likely explain the decreased survival of tagged fish in 2016. Commercial fisheries in the area may also be responsible for some mortality of Gulf sturgeon. Wooley and Crateau (1985) documented incidental capture of juvenile and adult Gulf sturgeon (>800 mm TL) in shrimp trawls and other commercial fishing gears; juveniles are also potentially susceptible to these threats.

Despite the conservative bias and potential inaccuracies of our estimates of overwinter survival, examining mean annual survival still has utility. During this study, the mean annual survival rate was 60.3% (SD 27.8)—which translates to annual mortality of 39.7% (*mortality*=1–*survival*). This rate of mortality is roughly comparable to previous estimates of mortality for juvenile Gulf sturgeon: Morrow et al. (1998) found an annual mortality of 34% for fish at ages 3–9 in the Pearl River, and Pine et al. (2001) estimated that annual mortality was 25% for Gulf sturgeon at ages 1–3 in the Suwannee River. If we omit data for 2016 from our survival analysis (presuming that low survival in that year was due to surgery site infections), mean mortality across this study was 30.7%., a value that is even more congruent with the reports in the literature. Tate and Allen (2002) simulated responses of populations of Gulf sturgeon to several rates of juvenile mortality and found that, at 30% annual mortality, populations remained stable over 200 years but that, at 35% annual mortality, the population slowly collapsed. Refining the accuracy of survival estimates remains an important goal for researchers and managers of Gulf sturgeon, and the ability in future studies to adjust survival estimates for imperfect detection should lead to estimates of true overwinter survival that are more accurate and higher than those we have reported.

Conclusions

The results of this study indicate that direct estimates of annual recruitment of Gulf sturgeon are feasible. In the Apalachicola River, we observed age-1 juveniles recruiting to the population in every year of our study, but abundance of age-1 fish was low: only about 50 individuals in 5 of the 6 years of this study.

The methods employed in this study can be used to obtain recruitment data for other populations of Gulf sturgeon, once juvenile aggregation sites have been located.

To capture juveniles, we recommend that researchers set small-mesh gill nets and initially focus sampling on river reaches with water-quality characteristics similar to those of the aggregation site in the Brothers River (see Suppl. Table 1). Sampling with anchored nets should occur only in appropriate flows—we recommend that researchers attempt to determine the relationship between discharge and catch per unit of effort of juvenile Gulf sturgeon in each river in order to maximize sampling efficiency. Once age-1 fish have been located, acoustic telemetry can be used to identify the extent of aggregation sites. Mark-recapture sampling then should target the identified aggregation sites, with additional sampling occurring in other river reaches.

Quantitative estimates of recruitment of Gulf sturgeon in other rivers will allow direct comparison between populations, as well as comparisons across time within each population. Additionally, telemetry data from age-1 fish will help fill important data gaps about juvenile habitat utilization. Researchers and managers will be able to assess the effects of restoration actions (e.g., dam removal, fish passage, and habitat restoration) or environmental catastrophes (e.g., oil spills and hurricanes) on recruitment quickly, rather than having to wait a decade to see any changes reflected in the adult population. Additionally, multiyear sets of recruitment data will allow investigation of how variation in annual recruitment relates to environmental conditions, such as temperature and river discharge (both of which, in the Apalachicola River, are influenced by the JWLD).

Acknowledgments

We would like to thank the USFWS for funding this work and the USFWS Panama City Field Office, St. Joseph Bay State Buffer Preserve, and D. Higginbotham for providing support. This project was conducted under Florida Fish and Wildlife Conservation Commission special activity licenses SAL-14-1481-SRP and SAL-15-1481A-SRP. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the USFWS.

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