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K.J. Sulak
Wetland and Aquatic Research Center, ksulak@usgs.gov

F. Parauka
US Fish and Wildlife Service

W. T. Slack
U.S. Army Engineer Research and Development Center

R. T. Ruth
Louisiana Department of Wildlife and Fisheries

M. T. Randall
Wetland and Aquatic Research Center

See next page for additional authors

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Authors

K.J. Sulak, F. Parauka, W. T. Slack, R. T. Ruth, M. T. Randall, K. Luke, and M. E. Price

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Supplement Article

Status of scientific knowledge, recovery progress, and future research directions for the Gulf Sturgeon, *Acipenser oxyrinchus desotoi* Vladykov, 1955

By K. J. Sulak[1,*], F. Parauka[2,*], W. T. Slack[3], R. T. Ruth[4], M. T. Randall[1], K. Luke[2], M. F. Mettee[5,*] and M. E. Price[6]

[1]*Wetland and Aquatic Research Center, US Geological Survey, Gainesville, FL, USA;* [2]*US Fish and Wildlife Service, Panama City, FL, USA;* [3]*U.S. Army Engineer Research and Development Center, Vicksburg, MS, USA;* [4]*Louisiana Department of Wildlife and Fisheries, Inland Fisheries, Lacombe, LA, USA;* [5]*Geological Survey of Alabama, Tuscaloosa, AL, USA;* [6]*University of Florida, Gainesville, FL, USA*

Summary

The Gulf Sturgeon, *Acipenser oxyrinchus desotoi*, is an anadromous species of Acipenseridae and native to North America. It currently inhabits and spawns in the upper reaches of seven natal rivers along the northern coast of the Gulf of Mexico from the Suwannee River, Florida, to the Pearl River, Louisiana, during spring to autumn. Next to the Alligator Gar *(Atractosteus spatula)*, the Gulf Sturgeon is currently the largest fish species occurring in U.S. Gulf Coast rivers, attaining a length of 2.35 m and weights exceeding 135 kg, but historically attained a substantially larger size. Historically, the spawning populations existed in additional rivers from which the species has been wholly or nearly extirpated, such as the Mobile and Ochlockonee rivers, and possibly the Rio Grande River. Most Gulf Sturgeon populations were decimated by unrestricted commercial fishing between 1895–1910. Subsequently most populations remained unrecovered or extirpated due to continued harvest until the 1970s–1980s, and the construction of dams blocking access to ancestral upriver spawning grounds. Late 20th Century harvest bans and net bans enacted by the several Gulf Coast states have stabilized several populations and enabled the Suwannee River population to rebound substantially and naturally. Hatchery supplementation has not been necessary in this regard to date. Sturgeon are resilient and adaptable fishes with a geological history of 150 million years. Research undertaken since the 1970s has addressed many aspects of Gulf Sturgeon life history, reproduction, migration, population biology, habitat requirements, and other aspects of species biology. However, many knowledge gaps remain, prominently including the life history of early developmental stages in the first year of life. Natural population recovery is evident for the Suwannee River population, but seems promising as well for at least four other populations. The Pascagoula and Pearl River populations face a challenging future due a combination of natural and anthropogenic factors. These two populations, and perhaps the Escambia River population, are particularly vulnerable to periodic mass mortality due to major stochastic events including hurricanes, flooding, hypoxia, and toxic spills. The present manuscript provides a comprehensive synthesis of knowledge regarding the Gulf Sturgeon at the organismal and population levels, identifying knowledge gaps as priorities for future research. Topics not treated in the present synthesis include morphology, internal biology, physiology, and endocrinology. Topics only briefly treated include parasites and diseases, contaminants, and sturgeon aquaculture.

Introduction

The present manuscript has been prepared based on the accumulated scientific knowledge of the Gulf Sturgeon (GS) to the present time. It builds upon a paper (Sulak et al., 2009b) with that same goal originally presented in the symposium 'Acipenseriformes in North America – where do we stand in 2009?', convened at the American Fisheries Society (AFS) 139th Annual Meeting, Nashville, TN), 30 August-3 September. The symposium was organized by the North American Chapter of the World Sturgeon Conservation Society (WSCS), now the North American Sturgeon and Paddlefish Society (NASPS) (Haxton et al., 2016 – this volume). An outgrowth of the 2009 symposium, this resultant manuscript provides a comprehensive synopsis of all that is known about the GS and identifies knowledge gaps to guide future research.

Materials and Methods

This manuscript relies both on published research and important unpublished technical reports prepared by resource agencies and academic institutions, as well as historical reports, photographs, and oral history recordings of

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sturgeon fishermen from the early 20th century. Key unpublished information sources comprise the extensive mark and recapture databases consolidated by the U.S. Geological Survey – Wetland and Aquatic Research Center (USGS-WARC). A database has been assembled for each GS natal river population based on research undertaken since 1977 by the U.S. Fish and Wildlife Service (USFWS), U.S. Geological Survey (USGS), U.S. Army Corps of Engineers (USACE), Mississippi Museum of Natural Sciences (MMNS), Louisiana Department of Wildlife and Fisheries (LDWF), other state natural resources agencies, several universities, and several non-government organizations (NGOs). These consolidated databases, maintained in Microsoft Excel©, are current up to and including 2008, except for the Suwannee River database which is current through 2015. They have been used herein to prepare species distribution maps, length frequency distribution plots, weight-length plots, and to provide fundamental summary information that has not otherwise been published.

Life history stage terminology for the GS

Life history stage terminology employed for the GS in the present manuscript are defined in terms of age (days or months) and/or TL, recognizing however that these criteria are approximate with wide individual variation. Certain stages are illustrated in Fig. 1 and are defined as follows:

Ova = unfertilized eggs retained in the ovaries prior to spawning.

Black eggs = recently spawned, unfertilized or just-fertilized eggs (embryos) attached to substrate.

Brown or yellow-brown eggs = fertilized eggs (embryos) in advanced stages of embryo development, attached to substrate.

Embryo = developing stage within the egg.

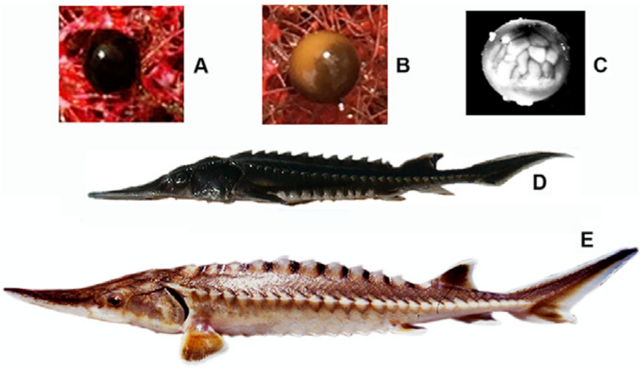

Fig. 1. Gulf Sturgeon early life history stages: (a) 2.1 mm recently-spawned black egg deposited on a fiber matrix floor buffer pad egg sampler in the Suwannee River (USGS photograph); (b) 2.8 mm diameter fertilized and hydrated late development egg (embryo) similarly collected (USGS photograph); (c) ~3.0 mm diameter wild-spawned egg (embryo) in fourth cleavage, 16-cell, stage with some adherent sand particles (USGS photograph, K. Sulak); (d) Conecuh River 80 mm TL, 2.5 month old, black-stage YOY (Alabama Department of Conservation and Natural Resources photograph, S. Rider); (e) Yellow River 313 mm TL, 4.5 month old YOY in bicolor-stage (brown dorsolaterally, cream-white ventrolaterally with white lateral scutes) (Alabama Geological Survey photograph, M. Mettee)

Free embryo = hatched embryo after emerging from the egg at ca 6.8–8.8 mm TL (in the literature alternately termed yolksac larva, pre-larva, or eleutheroembryo [Balon, 1971]). This is a non-dispersal stage in the GS.

Larva = exogenously-feeding individual after consumption of the yolksac and expulsion of the yolksac plug at age 5–8 days, 14.7–17.5 mm TL. This is the GS stage that is initially a free-swimming hemi-benthic, hemi-pelagic dispersal stage, later transforming to a completely benthic existence.

Young-of-the-Year (YOY). YOY = all age-0 stages from larva through first migration to the estuary in January-February (at age 9 months, 330–450 mm TL).

Black-stage YOY = YOY of age 2–4 months, ~85–150 mm TL, in which the body is pigmented dull black dorso-laterally. This is apparently a non-dispersal stage that occupies riverbed deposits of black decaying leaf litter.

Bicolored-stage YOY = YOY of age 4–9 months, ~150–450 mm TL, in which the body acquires the typical adult bicolored pigmentation, tan to gray dorsolaterally, cream colored ventrally, scutes light gray to whitish. This is a foraging stage that disperses widely within the natal river.

Juvenile = age-0 through ~age-6 individual, <900 mm TL, in which gonads remain undeveloped. This stage conducts an annual seasonal movement back and forth between riverine freshwater and estuarine brackish water.

Subadult = age-6 through ~age 9–12 (sex dependent) individual, >900 mm TL, <~1350 mm TL. This stage, in which early stages of gonad development are observed, conducts an annual seasonal movement between the river and the open Gulf of Mexico (GOMEX).

Adult = individual >~1350 mm TL in which gonads mature and spawning occurs, and which conducts an annual seasonal movement between the river and the open GOMEX.

Taxonomy and phylogeny

Scientific name: *Acipenser oxyrinchus desotoi* Vladykov, 1955.
AFS English common name: Atlantic Sturgeon (subspecies vernacular names are not official AFS common names).
Vernacular names: Gulf Sturgeon, Gulf of Mexico Sturgeon.

When described by Vladykov (1955), sturgeon specimens from the GOMEX were designated as a subspecies of the Atlantic Sturgeon (AS), based on morphological criteria confirmed by later studies (Vladykov and Greeley, 1963; Wooley, 1985). Subsequently, GOMEX specimens have been distinguished from Atlantic specimens by use of the vernacular names Gulf of Mexico Sturgeon and Gulf Sturgeon. Both have been widely applied, especially the latter. However, neither name has official AFS common name status. Results of nuclear DNA analyses (King et al., 2001) have demonstrated substantial genetic distance between the two nominal subspecies (below). The authors have observed that these genetic distances are more consistent with phylogenetic differentiation at the species level, rather than subspecies level, a matter which begs formal resolution. Furthermore, results of recent life history investigations (e.g., Kynard and Parker, 2004) reinforce developmental and behavior distinctions between the GOMEX and Atlantic counterparts in the earliest developmental stages. Overall, recent evidence suggests that elevation of the GS to species level taxonomic status would be appropriate. In the present paper, and in the *Status of Scientific Knowledge of North American Sturgeon* volume, the GS is treated as a distinct taxonomic entity.

Distribution, abundance, mortality, and population trends

General distribution – rangewide

Prior to fishery exploitation beginning in 1886, and subsequent range contractions and natal river extirpations due to habitat alterations, the GS home range probably extended from Southwest Florida to South Texas. Originally, reproductive populations probably inhabited most of the larger Gulf Coast Rivers, with the exception of the Mississippi River, from the Suwannee River to the Rio Grande River. Spawning populations currently inhabit seven rivers from northwestern Florida to eastern Louisiana (Fig. 2). Proceeding from east to west, these include the Suwannee, Apalachicola, Choctawhatchee, Yellow, Escambia/Conecuh, Pascagoula, and Pearl/Bogue Chitto rivers. Commercial landings (Townsend, 1900, 1902; Alexander, 1905) and historical accounts indicate that the Ochlockonee River (Townsend, 1901; Florida Outdoors 1959; Swift et al., 1977), Mobile-Alabama-Tombigbee river system, and possibly the Rio Grande River (Townsend, 1900) also originally supported spawning populations. Whether or not the present small Ochlockonee River population (probably numbering at least 100 individuals) (Table 1) spawns in that impounded river remains uncertain. Despite occasional records (Reynolds, 1993), the species has probably been extirpated from the extensively impounded, fragmented, and dredged Mobile River system, where one of the largest ever commercial GS catches was reported in 1902 (Alexander, 1905). A spawning population may also have been present in the Rio Grande River, based on a large commercial sturgeon catch in 1897 from estuarine and coastal waters, Cameron County, Texas (Townsend, 1900). The historical population known from Tampa Bay was extirpated in three years of commercial fishing (Townsend, 1902). This fishery was conducted in winter (Huff, 1975), rather than during the spring spawning immigration when most sturgeon fisheries were conducted. This suggests that GS were using the Tampa Bay estuary only for winter feeding. If derived from the Suwannee River, these winter transients would have returned to that natal river in spring, explaining the absence of a spring immigration fishery in Tampa Bay. Reynolds (1993) compiled a small number of anecdotal records of the GS in the Mississippi River, suggesting occasional straying into that river. Otherwise, the GS appears not to utilize this river, home to three other freshwater sturgeon species, the Lake Sturgeon (LS) (*Acipenser fulvescens*), Shovelnose Sturgeon (SVS) (*Scaphirhynchus platorynchus*), and Pallid Sturgeon (PS) (*S. albus*).

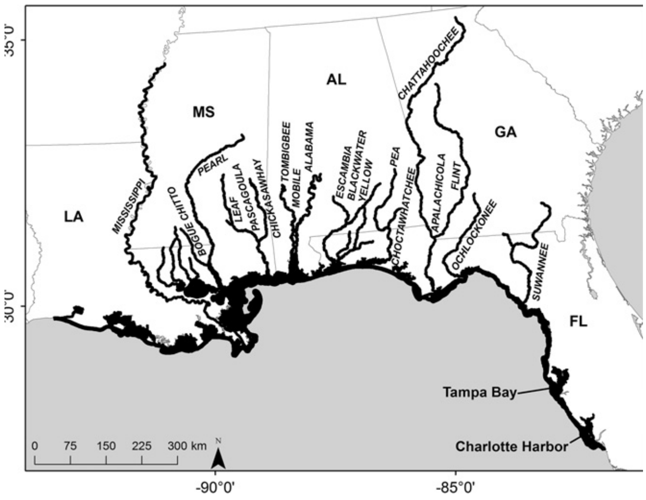

Fig. 2. Contemporary geographic range of the Gulf Sturgeon (excluding rare extralimital records from Texas and from Florida Bay). See several map figures that follow for detail of contemporary and historical distributions within individual natal rivers

Winter straying and spring to autumn probing excursions up numerous smaller coastal rivers results in an overall extralimital GS distribution from South Florida to South Texas. Coastal rivers that are too short (Randall et al., 2013) to provide YOY habitat or lack appropriate upriver habitat required for spawning nonetheless may serve as suitable summer holding habitat or as temporary use habitat. Widespread incidental records in many small rivers, Texas to South Florida, have been well documented (Reynolds, 1993). Incidental records from non-spawning GOMEX rivers have been reported for the Perdido (M. Mettee, AGS, unpubl. data), St. Marks, and Styx rivers in Florida; the Blakely, Magnolia, and Tensaw rivers in Alabama; the Escatawpa in Mississippi; and the Atchafalaya, Amite, Tangipahoa, Tchefuncte, and Tickfaw rivers in Louisiana (Davis et al., 1970; Jue,1989; Reynolds, 1993; Rogillio et al., 2001). Gulf Sturgeons have never been reported from several small coastal Florida rivers between the Ochlockonee River and Tampa Bay, including the Econfina, Fenholloway, Steinhatchee, Waccasassa, and Withlacoochee (south) rivers. The Weeki Wachee and Aucilla rivers are exceptions. The mouth of the Weeki Wachee River at Bayport, FL, was the site of an early historical record of the species (Fowler, 1923). And in 2012, following the atypically early Tropical Storm Debby (24–28 June), a subadult GS got stranded and died in the brackish lower reach of that river (J. Wilcox, Florida Wildlife Conservation Commission [FWC], pers. comm., 9 August 2012). There is also one record from the lower Aucilla River where a 142 cm TL GS was captured on baited hook and line in November 2000 (Woods 'N Water, 2000).

Typically in winter, there have been sporadic reports of GS from coastal and estuarine areas well south of Tampa Bay, including Charlotte Harbor, the Caloosahatchee River, Florida Bay, and Florida Keys (Reynolds, 1993; USFWS, GSMFC and NMFS, 1995). These may represent extralimital records of Suwannee River GS in years when exceptionally cold winters expanded the thermally-suitable GS marine feeding zone further south than normal (Wooley and Crateau, 1985, citing C. R. Robins, Univ. Miami, pers. comm.).

However, use by GS of certain other non-spawning rivers is more than incidental. For example, large numbers of GS consistently use one small Blackwater River area 12 river kilometers (rkm[1]) from the river mouth as a seasonal

Table 1
Abundance and mortality estimates (or total number of unique individuals in a sampling period) for net-vulnerable Gulf Sturgeon populations from the seven known spawning rivers, plus Ochlockonee and Blackwater rivers

River Sample period	Bar mesh (cm)	Population estimate (mean N & CI range)	Size (mm) or age (year) criterion	Model & (type)	Mortality estimate (%)	Reference
Apalachicola 1983	5.7-15.2	282 181–645 CI	>450 FL	S closed	NA	Wooley and Crateau (1985)
Apalachicola 1983–1988	NA	60–282 37–645 CI	>450 FL >755 FL (1985 only)	Not specified	NA	Barkuloo (1988)
Apalachicola mid-1980s	NA	>500	Age 2+	ASMR (3)	(5–7) assumed	Pine and Martell (2009a)
Apalachicola 1982–1991	2.5–10.2	88–218[a] 61–321 CI	>450 TL	JS – model B open (2)	33	Zehfuss et al. (1999)
Apalachicola 1983, 1985, 1990	2.5–15.2	101–149[a]	>450 mm TL	CAP model M_t closed (1)	NA	Zehfuss et al. (1999)
Apalachicola 1993	2.5–15.2	19–77[a] −23 to 127 CI	>450 TL	JS – model D closed (1)	21	Zehfuss et al. (1999)
Apalachicola 1998	3.8–11.4	~250 ~180–320 2SE from graph	>700 FL	CAP model M_t closed (1)	(6) assumed ages 4–30	Pine and Allen (2005)
Apalachicola 1998	3.8–11.4	270 NA	>635 TL	MS closed (1)	NA	USFWS (1999)
Apalachicola 1999	3.8–11.4	~260 ~230–310 2SE from graph	>700 FL	CAP model M_t Closed (1)	(6) assumed ages 4–30	Pine and Allen (2005)
Apalachicola 1999	3.8–11.4	321 199–1010	>635 TL	MS closed (1)	NA	USFWS (1999)
Apalachicola 2004	3.8–11.4	~350 ~260–440 2SE from graph	>700 FL	CAP model M_t closed (1)	(6) assumed ages 4–30	Pine and Allen (2005)
Apalachicola 2003	3.8–11.4	350 221–648 CI	>660 TL	MS closed (1)	NA	USFWS (2004)
Apalachicola 2005	NA	~1000	Age 2+	ASMR (3)	(5–7) assumed	Pine and Martell (2009a)
Apalachicola 2006	3.8–12.7	N = 216 unique fish (N_t = 289)	NA	Actual 'N' from net samples	NA	USFWS (2006); USFWS unpubl. data
Apalachicola 1982–2006	2.5–15.2	NA	>600 TL	ERD (2)	37.5	USGS 2010 unpubl. data from Apalachicola database
Apalachicola 2010	5.7–15.2	1282	NA	P closed	NA	USFWS unpubl. F. Parauka
Apalachicola 2014	7.6–12.7	503 450–570	<900 FL (juveniles)	MS closed	NA	USFWS unpubl. A. Kaeser
Apalachicola 2014	7.6–12.7	785 631–1037	>900 FL (subadults & adults)	MS closed	NA	USFWS unpubl. A. Kaeser
Blackwater 2013	12.7	328[b] 164–661 CI	>900 FL	Program Mark POP open	0.18	USFWS 2015 unpubl. A. Kaeser
Choctawhatchee 1999–2000	6.4–15.2	2000–3000	>610 TL	P closed (1)	NA	USFWS (2001)
Choctawhatchee 2001	6.4–15.2	2800	>610 TL	MP open (2)	16	USFWS (2002)
Choctawhatchee 2007	6.4–15.2	2800	>890 FL	MP? open (2)?	NA	USFWS (2009)
Escambia 2003	6.4–15.2	687 316–1058 CI	NA	NR closed (1)	NA	USFWS (2003) (uncorrected)
Escambia 2003	6.4–15.2	558 83–1033 CI	NA	NR closed (1)	NA	USFWS (2004) (2003 estimate corrected)
Escambia 2003	6.4–15.2	554 373–735 CI	NA	NR closed (1)	NA	USFWS (2008) (2003 estimate revised)
Escambia 2004	6.4–15.2	573 402–745 CI	>483 TL	NR closed (1)	NA	USFWS (2004)
Escambia 2006	6.4–15.2	451 338–656 CI	>610 TL	NP closed (1)	NA	USFWS (2008)

Table 1
(Continued)

River Sample period	Bar mesh (cm)	Population estimate (mean N & CI range)	Size (mm) or age (year) criterion	Model & (type)	Mortality estimate (%)	Reference
Escambia 2015	6.4–12.7	373 253–548 CI	>900 FL	Program Mark POP open	0.03	USFWS 2015 unpubl. A. Kaeser
Ochlockonee 1991–2012	6.4–12.7	N = 156 unique fish	650–2060 TL	Actual 'N' from net samples	NA	USFWS unpubl. (and USGS database)
Pascagoula 1999	10.0–18.0	162 34–290 CI	>1180 TL	MS closed (1)	NA	Ross et al. (2000, 2001a)
Pascagoula 1999	10.0–18.0	200 120–381 CI	>1180 TL	CAP model M_o closed (1)	NA	Ross et al. (2001a)
Pascagoula 2000	10.0–18.0	181 38–323 CI	>690 TL	MS closed (1)	NA	Ross et al. (2001a)
Pascagoula 2000	10.0–18.0	216 124–429 CI	>690 TL	CAP model M_o closed (1)	NA	Ross et al. (2001a)
Pascagoula 1999	7.6–18.0	193 117–363 CI	>615 FL	CAP model M_t Closed (1)	NA	Ross et al. (2000, 2001a); Heise et al. (2002)
Pascagoula 2000	7.6–18.0	206 120–403	>615 FL	CAP model M_t closed (1)	NA	Ross et al. (2001a) Heise et al. (2002)
Pascagoula 1997–2002	7.6–18.0	234 142–394	>615 FL	JS open (2)	NA	Heise et al. (2002)
Pearl 1993	7.0–11.4	67 28-∞	>320 FL	S closed (1)	NA	Morrow et al. (1996)
Pearl 1994	7.0–11.4	88 59–171	>320 FL	S closed (1)	NA	Morrow et al. (1996)
Pearl 1995	7.0–11.4	124 85–236	>320 FL	S closed (1)	NA	Morrow et al. (1996)
Pearl 1992–1996	3.8–17.8	292 202–528	>age 2	S closed (1)	34	Morrow et al. (1998)
Pearl 2000–2001	5.1–10.2	430 323–605	>623 FL	NP closed (1)	7	Rogillio et al. (2001)
Pearl 2000–2003	5.1–11.5	503 actual 'N'	>381 FL	NA sample 'N'	NA	Rogillio et al. (2007)
Pearl 1986–2007[c]	5.1–11.5	224–376 168–603 CI	>350 TL	CJS, Phi p_t open (2)	40.5	USGS unpubl., Sulak and Randall (2009)
Suwannee 1972–1973	12.7	NA	Age 8–12	NA	46.2	Huff (1975)
Suwannee 1976–1979	NA	3500	NA	NA	NA	Meylan (1977)[d]
Suwannee 1976–1979	NA	3000–4000	NA	NA	NA	Hollowell (1980)
Suwannee 1987–1992	12.7	1504–3066 2285 ± 398 SE	NA	JS open (2)	NA	Rago (1993)
Suwannee 1986–1994	12.7	1504–3066 2285 ± 398 SE	>869 TL	JS open (2)	NA	Carr et al. (1996b)
Suwannee 1986–1997	12.7	2097–5312 3152 ± 369 SE	>759 FL	JS open (2)	NA	Chapman et al. (1997)
Suwannee 1986–1998	10.2–12.7	7650	>600 TL	ERD (1)	16	Sulak and Clugston (1999)
Suwannee 1986–1995	12.7	5500	>1000 TL	TSopen (2)	17	Pine et al.(2001)
Suwannee mid-1980s	12.7	2000	Age 2+	ASMR (3)	NA	Pine and Martell (2009a)
Suwannee mid-1990s	12.7	3000–5000	Age 2+	ASMR (3)	(10–20) assumed	Pine and Martell (2009a)
Suwannee 2006	10.2	9728 6488–14 664 CI	≥1000 TL	CJS open (2)	12.9	USGS unpubl.
Suwannee 2006	10.2	14 496 7745–27 428[e] CI	≥400 TL	CJS open (2)	11.3	Randall and Sulak (2008)
Suwannee 2007	1.9–15.2	8877 6351–12 446	>1000 TL	PMMS open	11.01	USGS unpubl. 2016 M. Randall
Suwannee 2012–2013	1.9–15.2[f]	9743 3437–29 653[e] CI	≥1000 TL	PMMS open	11.04	USGS unpubl. 2016 M. Randall
Yellow 2001–2003	10.0–17.0	500–911 378–1550 CI	>880 FL (~1000 TL)	CJS open (2)	11.9	Berg et al. (2007)

Table 1
(Continued)

River Sample period	Bar mesh (cm)	Population estimate (mean N & CI range)	Size (mm) or age (year) criterion	Model & (type)	Mortality estimate (%)	Reference
Yellow 2010–2011.	6.4–15.2	1036 724–1348	All vulnerable to 6.4–15.2 cm bar mesh net	P closed	NA	USFWS unpubl. A. Kaeser

ASMR = Age-structured mark-recapture model, CAP = Program Capture, CJS = Cormac-Jolly-Seber model, ERD = Exponential recapture decay rate analysis, JS = Jolly-Serber model, MP = Modified Peterson model, MS = Modified Schnabel model, NR = NOREMARK program, P = Petersen model; PMMS = Program Mark, Multi-State model; POP = POPAN open model; S = Schnabel model; TS = Temporal symmetry model; NA = data or method not provided, or mortality estimate not available from cited reference; Nt = total captures; SE = standard error of the estimate; CI = 95% confidence interval around estimate(s).

[a] Abundance and mortality estimates are based on the samples obtained immediately below the JWLD.

[b] Abundance and mortality estimates are based on samples of Yellow River and Escambia River GS occupying the Cooper Basin holding area in the Blackwater River.

[c] Abundance and mortality estimates are composite estimates for all samples obtained over the period of 1986–2007.

[d] Meylan, 1977; cited in Chapman et al. (1997)

[e] Recapture and survival probabilities are confounded for the last year of a CJS model, making them unreliable. The 95% CIs are large due to the greatly uneven 'N' for catches and effort over the sampling years.

[f] Nets used varied in mesh bar dimension from 1.9 to 15.2 cm, with nets of 10.2 cm used predominately. For the multistate model mesh size used is not a factor since individual fish tracked through the analysis may have been captured and recaptured in different size meshes.

holding and/or migration staging area (USFWS, 2005, 2008; A. Kaeser, USFWS unpubl. data; N. Craft, Northwest Florida Aquatic Preserves, unpubl. data; USGS-WARC unpubl. database). GS aggregate in Cooper Basin (Carr, 1983; Craft et al., 2001), a lake-like river basin which may formed as an old meander got cutoff at its upper end, widened and remained connected at its lower end to the Blackwater River, or may have formed by sink hole subsidence (Jue, 1989). The rectangular 6 m deep portion of this basin was deepened in the late 19th century to serve as a timber catchment area. The Blackwater River, probably several deep basins in the lower river, was extensively targeted in early commercial GS fishery (Alexander, 1905), and Cooper Basin in particular for decades thereafter (Carr, 1983). It appears to serve the same lower river holding-resting-staging area function for the Yellow and Escambia River GS populations (Craft et al., 2001; Berg, 2004) as does the deep Brothers River tributary of the Apalachicola River (Wooley and Crateau, 1985), 23–31 rkm from its mouth. In both systems, these deep lower river holding/staging areas lie within tidal reaches, but above the influence of salinity. Stewart et al. (2012) have identified three summer holding areas in the lower 30 rkm of the Escambia River, all close enough to the river mouth to serve a pre-emigration staging function.

Sturgeon records reported from Bermuda as 'common sturgeon' or as *Acipenser sturio* (European Sturgeon or Sea Sturgeon), (Jones, 1876; Hurdis, 1897; Beebe and Tee-Van, 1933; Smith, 1997) and French Guiana (as *Acipenser guianensis* Bertin, 1940), most probably pertain to the AS, not the GS, which typically limits its migrations to movements along the inner continental shelf, with maximum movements of typically <200 km away from the natal river (Edwards et al., 2007; Parauka et al., 2011). Unlike its GOMEX counterpart, the AS has displayed some remarkable long distance oceanic movements. Hudson River adults have been recaptured as far south as North Carolina along the U.S. East Coast (Dovel and Berggren, 1983; Waldman et al., 1996; Bain, 1997) – a distance of approximately 900 km. Bay of Fundy satellite-tagged AS have been detected 1500 km away in Quebec, having traveled a mean of 44 km day^{-1} (Taylor et al., 2016). Microsatellite DNA (mtDNA) investigations have documented even wider coastal spread of Hudson River fish from the St. Lawrence River, Canada, to the Altamaha River, Georgia (King et al., 2001; Wirgin et al., 2015). The species has also undertaken at least one trans-Atlantic excursion to Europe. Genetic and archeological evidence shows that AS originating from northern North American colonized the Baltic Sea approximately 1200 years ago, flourished, and were exploited by humans until fished out (Ludwig et al., 2002, 2008; Ludwig and Gessner, 2007). Additional evidence of further AS excursions to Europe and apparent hybridization with the European Sturgeon has recently been reported (Chassaing et al., 2013; Nikulina and Schmölcke, 2016). Records from Bermuda and French Guiana suggest additional trans-oceanic migrations.

General abundance – major river populations

Currently, GS natal river populations decrease in abundance in this approximate order based on gill net sampling programs: Suwannee, Choctawhatchee, Yellow, Escambia, Apalachicola, Pearl, and Pascagoula rivers (Table 1). However, the presumed non-spawning population in the Ochlockonee River may be larger than that in either the Pearl or Pascagoula rivers. Knowledge of river-specific abundance may change in the near future as Sidescan SONAR (SSS) remote sensing surveys are conducted to estimate total numbers of GS within a given river. It has been repeatedly stated (Huff,1975; Wooley and Crateau, 1985; Pine and Martell, 2009a,b; Ahrens and Pine, 2014) that the Apalachicola and Suwannee rivers originally sustained the largest GS fisheries at the turn of the 20th century. Thus, it has been assumed that these two rivers originally supported the largest GS river populations prior to exploitation. However, the largest GS commercial landings in the peak year of 1902 were instead reported from Escambia County, Florida (Alexander, 1905). Most of this record catch probably came from the Escambia River and Yellow River GS populations, plus fish using the Blackwater River holding area (rivers fished were not specified by Alexander). Additionally, some GS netted in the Choctawhatchee River and transported to Pensacola may also have been included (Cason et al., 1985). Nonetheless, the 1902 'Escambia-Blackwater' Escambia County landings of 259 171 lb (117 664 kg) exceeded the peak Apalachicola River catch (1902) by 3.5 times, that of the Mobile River (1902) by 2.6 times, that of the Suwannee River (1900) by 5.9 times, and that of the Pascagoula River (1902) by 10.7 times. Accordingly, contemporary river population abundances are not a good index of the historical natal river GS population carrying capacity prior to the depredations of commercial fisheries and dams. Nor were the largest landings correlated with the original unimpounded lengths of natal sturgeon rivers. As per Table 2, maximum river length, arranged in approximate order of longest to shortest would be Mobile, Apalachicola, Suwannee, Pascagoula, Escambia, and Yellow. Even when combined, the lengths of the Escambia and Yellow rivers fall short of the length of the Apalachicola River.

However, commercial fisheries landings from Gulf Coast states must be viewed with some caution. At best, these uneven and infrequently conducted surveys provide equivocal evidence of the historical abundance of GS in the various coastal rivers. Landings of GS from the turn of the 20th century GOMEX commercial fisheries were reported only infrequently and mainly for Florida, Alabama, and Mississippi. The source river was sometimes equivocal as well. For example, GS fished in the Choctawhatchee River or bay may have been transported to Pensacola, FL (above), and thus reported as Escambia County landings. Also, except for first landings reported for the Ochlockonee River in 1900 (Townsend, 1901), GS from that river were thereafter transported to the town of Apalachicola (Florida Outdoors, 1959; Swift et al., 1977; Fichera, 1986) for shipment to New York and were probably reported with landings for the Apalachicola River (or Franklin County).

Turn of the 20th century GS landings during the 1890–1920 heyday of the fishery were reported only once from Texas [1897 from the vicinity of Rio Grande River mouth (Townsend, 1900)], and never from Louisiana. Indeed, the only commercial GS landings reports for Louisiana have been small catches (100–1000 lb or 45–454 kg) between 1939–1951 (Anderson and Power, 1946, 1951; Anderson and Peterson, 1953, 1954; Barkuloo, 1988).

History of the GS commercial fishery and pre-fishery abundance

Prior to the onset of commercial sturgeon fisheries in the U.S. in the 1880s, sturgeon were rarely fished or utilized for food. In the early colonial period, sturgeon caught in New England and Virginia were netted, pickled, and shipped to England (Wood, 1634; Wharton, 1957). This early trade was short-lived. Subsequently sturgeon were shunned, considered unworthy for human consumption (Saffron, 2004) except as a survival food of last resort (Smith, 1623). Indeed, along the Atlantic coast, they were considered trash fishes (Meehan, 1893; Cobb, 1900), destructive to shad nets (Hamlen, 1884), and subject to both purposeful and profligate eradication (Smith, 1914). This attitude continued until the late 1800s (Jordan and Evermann, 1905) when a sturgeon fishery was re-kindled in the northeastern U.S. in response to a German market for caviar.

In the GOMEX states, sturgeon did not appear in a comprehensive report on coastal and inshore fisheries and species harvested up to 1891 (Collins and Smith, 1893). Indeed, U.S. Commissioner of Fisheries interest in GS was not apparent until the report of Brice (1897). In the absence of a directed fishery, GS abundance data were not available from the Suwannee River or any other Gulf Coast river prior to 1886. No commercial landings outside of Florida were reported until 1902. Beginning with the Tampa Bay 1886–1888 harvests (Collins, 1892; Townsend, 1902), sturgeon landings in GOMEX fisheries were summarized sporadically and inconsistently through 1939 in reports of the U.S. Commissioner of Fisheries. Thereafter, landings were reported in the USFWS 'Statistical Digest' through the 1940s. Subsequently, annual Florida sturgeon landings were reported through 1985 by the University of Miami Marine Laboratory, Florida State Board of Conservation, or the National Marine Fisheries Service. Historical landings for all Gulf Coast states from 1950 onward can now be accessed via online query (NMFS, 2011). The initial 1886–1888 Tampa Bay landings were reported as numbers of fish (Townsend, 1902). Thereafter, catches were reported in pounds (round weight), without specifying numbers of fish landed. This makes determination of historical population abundances difficult.

Nonetheless, numerical abundance for the pre-fishery population can be estimated indirectly, if very approximately, from weight of annual landings reports, using the mean weight of fish netted in the early fishery. Fortunately, both total catch weight and numbers are uniquely available for the Tampa Bay fishery in 1897, the second year of commercial GS fishing in the GOMEX. Weight of catch was 50 294 lb (22 833 kg) (Collins, 1892), and number of fishes landed was 1500 (Townsend, 1902), yielding a mean weight of 33.6 lb (15.2 kg). However, mean weight in the winter net fishery in Tampa Bay was undoubtedly skewed low since an estuarine winter feeding aggregation would be biased toward subadults and smaller adults. Comparative GOMEX marine aggregations would comprise primarily large adults (Fox et al., 2002). Adjusting for such bias, the mean weight of adult GS, the target of the early commercial gill net fishery (using 8.0 in [20.3 cm] bar mesh nets) (Cook, 1959) can be hypothesized to have been at least ~50 lb (22.7 kg). Odlund (1958) stated that GS of 200–300 lb (91–181 kg) were common in the Suwannee River spring gill net catches in the early 1900s. The 22.7 kg mean weight estimated for the historical GS fishery compares to the 2012–2013 mean weight of 18.3 kg (40.3 lb) from USGS scientific sampling in the Suwannee River after 28–29 years of protection from harvest, and a mean weight of 33.4 kg (73.6 lb) from scientific

Table 2
Major attributes of Gulf Sturgeon spawning rivers and additional probable historic spawning rivers

River	Watershed area (km^2)	Mainstem length (rkm)	Estuary area (km^2)	Mean daily flow (m^3 s^{-1})	Major tributaries	Type of river	Lowermost barrier to migration (rkm from mouth) & elevation [m][a]	Spawning grounds (rkm)
Spawning Rivers:								
Apalachicola	50 688–64 291	805–1018	629	664–759	Flint River, Chattahoochee River Chipola River Brothers River	Alluvial	Jim Woodruff Lock & Dam 171 [13]	160–171
Choctawhatchee	12 033	280–370	335	204–212	Pea River, Holmes Creek East, West, and Little Choctawhatchee rivers	Alluvial	Elba Dam Pea River 239 [49]	Choc. R. 140–155 Pea R. 155
Escambia	10 963	384–386	377[b]	178–196	Conecuh River Sepulga River Patsaliga River	Alluvial & Blackwater	'Point A' Dam 222 [42]	160–177
Pascagoula	24 599–25 123	~430	29	350–432	Black Creek Bouie River Leaf River Chickasawhay River Escatawpa River	Alluvial & Blackwater	None [26]	Bouie R. 250
Pearl	21 999–22 688	659–772	2774[c]	373	Bogue Chitto River Yockanookanay River Strong River Tchefuncte Tangipahoa Tickfaw Amite	Alluvial	Bogue Chitto Sill 78[d] [14] Pool's Bluff Sill 80[d] [17]	Unknown
Suwannee	24 967–25 771	394–451	81	294–350	Withlacoochee River, Alapaha River, Santa Fe River	Blackwater & Groundwater	None (273)[e] [26 at Big Shoals]	202–221[f] 158–162[f]
Yellow	3133–3535	176–196	377[b]	33–62	Shoal River	Alluvial & Blackwater	None [46]	91 & 134
All spawning rivers	3133-50 668	177–1018	29–2453	33–759	All spawning rivers	All river types	78–273 [13–49]	91–250
Non-Spawning Rivers:								
Mobile	111 369	1245–1691	1051	1914	Alabama River, Tombigbee River, Black Warrior River, Coosa River, Tallapoosa River, Cahaba River, Sipsey River, Tensaw River	Alluvial	Claiborne Dam Alabama River 207 [5] Coffeeville Dam Tombigbee River 193 [2]	NA
Ochlockonee	5828	331	29	51	None	Blackwater	Jackson Bluff Dam 105 [10]	NA

Data sources: United States Study Commission (1963), Beck (1965), Livingston et al. (1974), Wooley and Crateau (1985), Barkuloo et al. (1987), Jue (1989), McPherson and Hammett (1990), Nordlie (1990), Dynesius and Nilsson (1994), Marchant and Shutters (1996), Morrow et al. (1998), Sulak and Clugston (1998, 1999), Fox et al. (2000), Tillis (2000), Craft et al. (2001), Parauka et al. (2001), Rogillio et al. (2001), Ross et al. (2004), Benke and Cushing (2005), Heise et al. (2005), Kreiser et al. (2008), Scollan and Parauka (2008). Key: NA = data not available; rkm = river kilometer.

[a] Elevation of the riverbed above sea level (m) at the first barrier (manmade dam, natural shoals or falls) to upstream migration, or river mainstem headwater elevation where no barrier exists.

[b] Total estuarine area available to the Escambia River and Yellow River GS populations is that of Escambia, Blackwater, East and Pensacola bays combined.

[c] Total estuarine area is that of Lake Pontchartrain, Rigolets, Lake Borgne, and Lake Maurepas combined. Rivers flowing into Lake Pontchartrain are included in the list of Pearl River system tributaries.

[d] The Pools Bluff and Bogue Chitto sills are manmade impediments to upstream migration, impassable for up to 280 days per year (Morrow et al., 1998); passable only during unusually high river stages. If the sills are ultimately removed, the next upriver barrier on the Pearl River is the Ross Barnett Dam at rkm 486.

[e] A natural impediment to upstream migration occurs at Big Shoals, rkm 273 (Fig. 5), impassable except during unusually high river stages.

[f] Telemetry and egg collections indicate the existence of two spawning reaches, including rkm 202–235 and rkm140–165.

sampling in the Pascagoula River 23–28 years after the State of Mississippi GS harvest ban in 1974 (Ross et al., 2002) (Table 3). Such recent mean weights 2–3 decades after elimination of fishing mortality provide perspective on probable pre-fishery (pre-1880) mean weight. However, 'fishing down' of maximum size cannot be accounted for in such a retrospective mean weight analysis. Armstrong and Hightower (2002) provide some insight in that regard, reporting that the mean weight of the sister-subspecies AS captured in the historical 1901–1907 North Carolina haul seine fishery as 41 kg (90.3 lb) (Table 3).

River populations – east to west across the species range

Suwannee River population – abundance, mortality, and trend. The Suwannee River maintains the largest contemporary GS population (Table 1). As with other North American sturgeon, that population was rapidly fished down between 1897–1917. An exploratory commercial fishing party was deployed to the Suwannee River in 1895 (Brice, 1897), with directed net fishing initiated the year thereafter (Cobb, 1898; Townsend, 1900), resulting in the first reported landings of 9254 lb (4201 kg) in 1897 (Townsend, 1900). The largest reported landings were 44 400 lb (20 158 kg) in 1900 (Townsend, 1901; Barkuloo, 1988). By 1902, however, GS were already reported as 'becoming scarce' according to the U.S. Fish Commission (Townsend, 1902; Alexander, 1905). However, a thriving sturgeon fishery was still in force in 1912, as reported by Odlund (1958). Nonetheless, commercial landing reports indicate that GS catches declined precipitously over a period of two decades. The last big catch reported in the early fishery was 40 000 lb (18 160 kg) from 1917 (Barkuloo, 1988). Only 4915 lb (2231 kg) were reported in 1918 (Radcliffe, 1920, 1921), just 1.4% of the largest reported Florida catch of 343 291 lb (155 854 kg) in 1902 (Alexander, 1905) [elsewhere reported by Sette (1926) as 348 082 lb (158 029 kg)]. Thereafter, a highly variable harvest continued, ranging from 74 to 26 196 kg annually until Florida implemented a GS harvest ban in 1984, but <1000 kg annually after 1977 and more than 10 000 kg only in 1968 (Huff, 1975; Barkuloo, 1988; NMFS, 2011).

The first GS mark-recapture program in the Suwannee River was undertaken by Archie Carr in 1976–1981 (Carr,1983), resulting in 253 fish tagged and 103 recaptured

Table 3
Mean weight estimates for Suwannee River Gulf Sturgeon from net samples using 4–5 in (10.2–12.7 cm) bar mesh gill nets, 1897 to 2013, with one comparative mean weight from the Pascagoula River historical fishery, and one from the Atlantic Sturgeon historical U. S. East Coast fishery

Period	Location & method	Catch or sample (N)	Mean weight (lb)	Mean weight (kg)	Source	Comment
Gulf Sturgeon						
1897	Tampa Bay estuary gill net	1500	33.6[a]	15.2[a]	Collins (1892), Townsend (1902)	Historical GS fishery
1896–1917	Suwannee River gill net	NA	Probably ≫ 33.6[a]	Probably ≫ 15.2[a]	—	Historical GS fishery
1972–1973	Suwannee River gill net	632	38.5[b]	17.5[b]	Huff (1975)	Pre-1984 harvest ban Florida
1981–1984	Suwannee River gill net	279	50.5[c]	22.9	Tatman (1984)	Pre-1984 harvest ban Florida
1986–1995	Suwannee River gill net	1670	39.7[c]	18.0	Carr and Rago unpubl. – cited in USFWS, GSMFC and NMFS, 1995	Post-1984 harvest ban Florida
1986–1997	Suwannee River gill net	1115	24.7–44.8[d] (34.7)[e]	11.2–20.3[d] (15.8) [e]	Chapman et al. (1997)	Post-1984 harvest ban Florida
2006–2007	Suwannee River gill net	543	60.6[b]	27.5	USGS database unpubl.	Post-1984 harvest ban Florida
2012–2013	Suwannee River gill net	791	40.3[b]	18.3	USGS database unpubl.	Post-1984 harvest ban Florida
1997–2002	Pascagoula River gill net	251	73.6	33.4	Ross et al. (2002)	Post-1974 harvest ban Mississippi
Atlantic Sturgeon						
1901–1907	North Carolina	—	90.3	41.0	Armstrong and Hightower (2002)	Historical AS fishery

[a] The 1897 gill net fishery in the Tampa Bay estuary targeted winter feeding GS, which would have been comprised of juveniles and subadults, thus probably under-estimating mean weight of the overall Suwannee GS population from which the Tampa Bay sub-group may have been derived. After 1897 landings were reported in round weight only without number of fish reported such that mean weight could be determined.

[b] Mean weight determined from total catch weights in Fig. 3 of Huff (1975) and total sample N = 632 during a period when adults were depleted from the population due to size-selective fishing.

[c] Mean weight determined only from first captures of wild GS, hatchery fish captures excluded.

[d] Range in mean weights determined for each of 12 sampling years; pooled 'N' = 1115.

[e] Mean of 12 annual sample means.

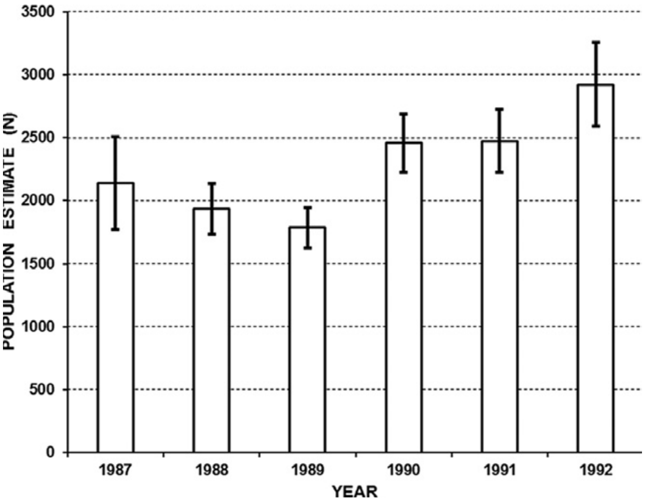

Fig. 3. Estimated Suwannee River Gulf Sturgeon population size (Jolly-Serber open model), 1987–1993, based on Rago (1993). Key: open bars = population estimate, number of individuals; vertical bars show ±95% SE

through 1981. Field notes and data from that study, funded by the Caribbean Conservation Corporation (CCC) have apparently been lost. However, those data were used, method unspecified, to arrive at the first estimate of Suwannee River GS abundance prior to the 1984 harvest ban. That estimate, 3000–4000 GS (Table 1), was reported by a consultant to CCC (Hollowell, 1980). The next abundance estimate, using the Jolly-Seber open model, was performed by Rago (1993) based on data from scientific mark-recapture sampling in 1987–1992 using 4–5 in (10.2–12.7 cm) bar mesh commercial gill nets. Rago's analysis resulted in an estimated, net-vulnerable (fish >1000 mm TL) population of 2285 ± 398 (mean ± SE) (Table 1). A duplicate estimate from the same data was reported by Carr et al. (1996b) (Table 1). Chapman et al. (1997) reported a third population estimate of 3152 ± 369 from 1986 to 1994 data. The GS population in the unimpounded Suwannee River, relatively unaltered by major human 20th century impacts, apparently responded positively and rapidly to cessation of commercial fishing. Rago's (1993) mean 1990, 1991, and 1992 estimates were each significantly greater than either the 1988 and 1989 abundance estimates (Fig. 3). The 1992 estimate (2921) was significantly greater ($P < 0.05$) than the 1990 and 1991 estimates (2458–2475). Rago (1993) also reported a statistically significant increase in recruits added to the population in 1989–1990 vs 1987–1988. Continued mark-recapture sampling, 1986–1997, resulted in an estimated mid–1990s population of 5500–7650 fish (>1000 mm TL) with an annual natural mortality rate of 16–17% (Sulak and Clugston, 1999; Pine et al., 2001). The most recent estimates from 2007 and 2013 (Randall and Sulak, USGS unpubl.) range from 8877 to 9743 GS >1000 mm TL (Table 1) with adults comprising 48% of the combined 2012–2013 sample, and an annual natural mortality rate of 11.04% (essentially identical to the 11.0% estimate of Pine and Martell, 2009a). When GS juveniles (>400 mm TL) are included in the mark-recapture histories, the 2006 USGS estimate was 14 496 (95% CI = 7745–27 428) with an annual mortality rate of 11.3% (Table 1). Length frequency data from the most recent USGS population census in 2013 (Table 1) displays strong year-class modes occurring almost annually (Fig. 4). Correspondingly, the present population is comprised of mixed-size, mixed-age fish, regularly and robustly recruiting to the adult spawning population.

Huff's (1975) pioneering study of the Suwannee population in 1972–1973 revealed a total annual mortality rate (combined natural plus fishing mortality) of 42% (Huff, 1975) in a population selectively depleted of large adults by large-mesh gill netting. Such a high mortality rate is unsustainable for sturgeons (Boreman,1997; Pine et al., 2001; Tate and Allen, 2002), reflecting the highly overfished state of the GS fishery prior to harvest prohibition in Florida in 1984.

Suwannee River population– historical context and pre-fishery population size. *Historical context:* The 394–451 rkm long Suwannee River is unimpounded. However, a natural barrier at Big Shoals (rkm 271.5) just upstream of White Springs (Fig. 5) limits GS passage to periods of exceptionally high water. The river is considered only moderately impacted by anthropogenic change. However, between 1830 and 1930 the primeval North Florida giant conifer forests were completely logged out (Miller, 1998) and the ecosystem irreversibly changed. By 1879, the annual harvest of bald cypress (*Taxodium distichum*) and longleaf pine (*Pinus palustris*) exported from Florida was 247 million board feet (BF), by 1899 it was 790 million BF, and in 1909 harvest peaked at 16 billion BF (Miller, 1998). The Suwannee River riparian conifer-dominated forest of giant 1000–3000 year-old cypress and longleaf pine forest (Fig. 6a–c) that was gone by 1930 and subsequently replaced by a second-growth oak-dominated mixed hardwood forest (oak, gum, ash, maple, birch). Canals from the river were dug and elevated rail trams constructed deep into the floodplain forests to enable complete

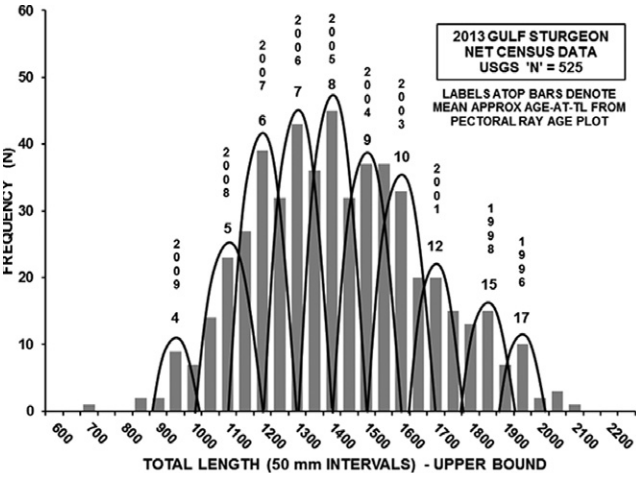

Fig. 4. Length frequency distribution in 100 mm TL intervals for Suwannee River Gulf Sturgeon first captures (excluding recaptures) sampled by USGS 2013 (USGS-WARC unpubl. database). Apparent year-class recruitment modes in the population are indicated by confining parabolas with approximate age and spawned year indicated for each mode. Age scale is based on pectoral fin spine length-at-age

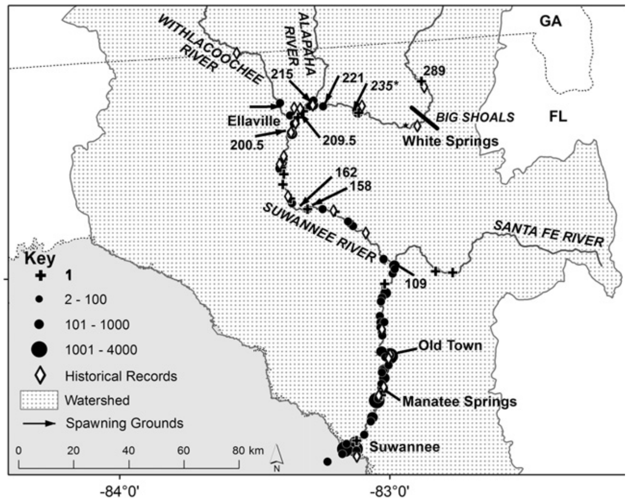

Fig. 5. Map of the Suwannee River, showing the known distribution of the Gulf Sturgeon, including individual historical records (pre-1986) and total scientific sampling records by location, 1986–2015. Known spawning grounds are identified with arrows; an additional suspected spawning ground with an asterisk. Distances from the river mouth are indicated by rkms for spawning grounds within the Suwannee River mainstem. Rkm 109, not a spawning site, is labeled to denote the confluence of the Santa Fe River tributary

exploitation of timber. At the same time, early American settlers rapidly and extensively converted the upland watershed from longleaf pine forest and scrub habitat to row crop and pasture agriculture, with native swamp habitat and savannah used for free-range foraging by non-indigenous feral hogs and bush cattle. The impact of highly altered habitat upon the low-tannin clear-water Suwannee River was profound. Colonial naturalist William Bartram on his botanical collection expedition in 1774 William Bartram (1793) described the pre-settlement river thus:

> “The river Little St. Juan [Suwannee] may, with singular propriety, be termed the pellucid river. The waters are the clearest and purest of any river I ever saw, transmitting distinctly the natural form and appearance of the objects moving . . . on its silvery bed.”

Conversion to a second-growth oak and mixed hardwood dominated riparian forest resulted in the contemporary high-tannin blackwater ecosystem amenable to colonization by GS, a fish species not observed in the Suwannee River by Bartram (1793) in summer 1774, but abundantly present where he had camped and canoed one hundred years later (Cobb, 1898) and now.

Pre-fishery population size: Analysis of fish stock reduction in the early fishery can be used to estimate abundance in a pre-fishery GS population. Accordingly, Pine and Martell (2009a) estimated the biomass of the original pre-fished Suwannee River GS stock of the late 1800s as 600 000–700 000 kg. From this estimated biomass and the USGS 2013 estimated mean weight of 22.7 kg, the pre-1886 GS population abundance range for the Suwannee River population can be estimated as 26 400–30 800 fish >1000 mm TL.

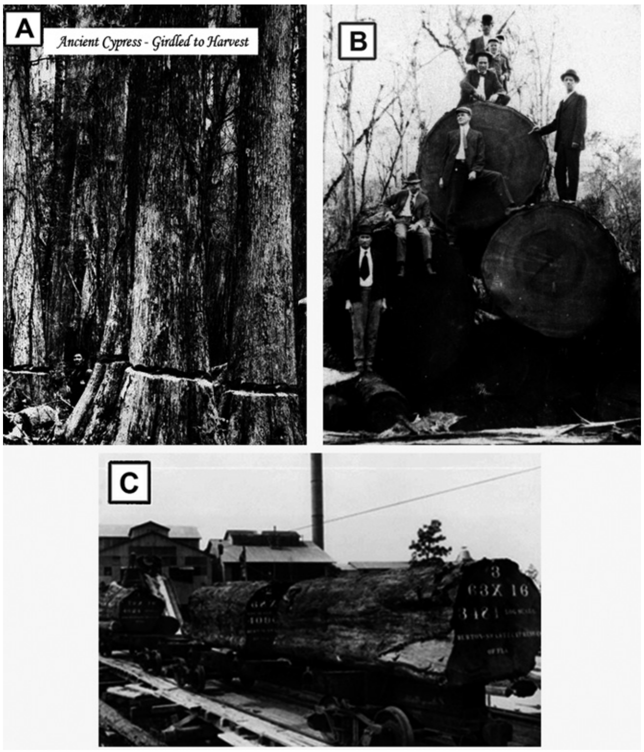

Fig. 6. Photographic documentation of the primeval Suwannee River giant cypress and longleaf pine conifer forest ecosystem, logged out between 1830–1930: (a) Cypress ‘brake’ (impassable barrier) riparian forest along the lower river: Image RC13193: ‘O.M. Anderson in a cypress forest – Dixie County, Florida. 192-‘ (https://www.floridamemory .com/items/show/35552, accessed 22 September 2016); (b) 2-m diameter logs felled in 1916: Image PR05039, ‘Fallen trees ca 1916’ (https://www.floridamemory.com/items/ show /4442, accessed 22 September 2016); (c) Three sections of a 203+ ft (62+ m) tall 3000-year old cypress, 16 ft (5 m) diameter at top cut: Image PR05108, ‘Burton-Swartz Cypress Company: Perry, Florida. 1926’ (https://www. floridamemory.com/ items/ show/ 4484, accessed 22 September 2016); Public record images obtained for educational use as per Section 257.35(6) of the Florida Statutes from the online ‘State Archives of Florida, Florida Memory’ website

Allowing for substantial under-reporting in the commercial landings data (with a typical range of 2–3 times the reported landings) a probable total of 50 000–100 000 GS were removed from the Suwannee River from 1896 through 1917, a 22-year period approximating one full 25-year GS generation span (Sulak and Randall, 2002). That is, the mixed-age stock of sturgeon that sustained the early Suwannee River fishery for two decades, until it was exhausted, can be estimated as 50 000–100 000 GS vulnerable to capture in large mesh gill nets.

Ochlockonee River population – abundance, mortality, and population trend. Prior to impoundment by the Jackson Bluff Dam (rkm 105) in 1927, the Ochlockonee River undoubtedly supported a spawning population of GS. Townsend (1902) reported that commercial fishing was conducted on the river in 1898, 1899, and 1900, with reported landings of 37 100 lb (16 843 kg) in 1900. Commercial fishing in the

Ochlockonee River was again reported for 1902 (Alexander,1905). However, GS landings of 74 120 lb (36 650 kg) reported for Franklin County, FL, combined those for both the Apalachicola and the Ochlockonee rivers. Beyond the impacts of the initial intensive fishery (1898–1902), and subsequent construction of the dam, the population remained sufficiently resilient to sustain commercial fishing at least through 1959 (Florida Outdoors, 1959; Swift et al., 1977). That fishery was conducted from a sturgeon fish camp at Hitchcock Lake on the lower river (40 rkm from the river mouth, very probably a GS seasonal holding area), with the catch being sold to the Taranto Fish Company in Apalachicola (Florida Outdoors, 1959; Swift et al., 1977; Fichera, 1986). The longevity of the post-impoundment fishery strongly suggests the prior existence of a self-sustaining population. After the end of the commercial fishery, GS continued to be harvested by angling (using filamentous algae twisted onto treble hooks as bait) below the Jackson Bluff Dam (Ingle and Dawson, 1952; Swift et al., 1977; USFWS, GSMFC and NMFS, 1995) where they have frequently been sighted (Reynolds, 1993).

In recent decades USFWS and USGS have conducted infrequent and limited scientific gill net sampling in the Ochlockonee River (USGS-WARC unpubl. database), targeting the same sites previously used by commercial fishermen. Between 1991–2012, 156 unique GS (TL range 620–2060 mm; bimodal at 800–900 mm and 1200–1600 mm) (Fig. 7) have been netted and tagged, providing a rough minimum estimate of the existing population (Table 1). Documented summering of adults in substantial numbers suggests spawning may occur in the Ochlockonee River. The length frequency distribution of first captures (excluding recaptures) suggests a mixed age-class, unimodal population (Fig. 7) including large adults (>1800 mm TL) as potential resident spawners. Alternately, acoustic telemetry suggests that GS occupying the Ochlockonee River may simply use that river as seasonal resting habitat, migrating to the Suwannee River to spawn. For example, five adult GS tagged by USFWS in the Ochlockonee River in 2011 were detected entering the Suwannee River the following spring, and proceeding directly to spawning grounds above rkm 200 past a series of acoustic receivers (USGS-WARC unpubl. data).

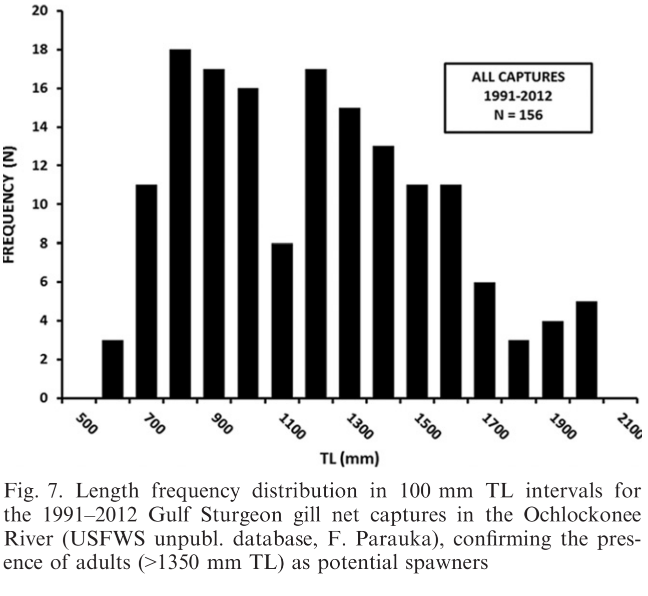

Fig. 7. Length frequency distribution in 100 mm TL intervals for the 1991–2012 Gulf Sturgeon gill net captures in the Ochlockonee River (USFWS unpubl. database, F. Parauka), confirming the presence of adults (>1350 mm TL) as potential spawners

Both USFWS and USGS have conducted very preliminary acoustic telemetry efforts to monitor movements of adults in the Ochlockonee River to potentially pinpoint holding areas (resting areas where GS congregate from spring to autumn, detailed below) and upriver migrations suggestive of spawning behavior. However, telemetry has not yet detected movements to the base of the dam, where substrate is suitable for spawning (Parauka and Giorgianni, 2002). Thus, without recent scientific documentation of spawning in the Ochlockonee River, that river was not included in the U.S. Endangered Species Act (ESA) critical habitat designation for the GS (USFWS and NOAA, 2003; NOAA, 2004). The current small, poorly-studied Ochlockonee River population (Table 1) represents either a seasonal (summer holding and winter feeding) population derived from the genetically closely-related Apalachicola and Suwannee rivers populations, or a small functional spawning population. The capture of juveniles in a size range (700–1000 mm TL) that do not normally enter fully marine GOMEX waters (Fleming, 2013) reinforces the later interpretation. Moreover, several GS have been recaptured in the Ochlockonee River multiple times over intervals spanning 1–4 years, indicating long-term residence and river fidelity. On the other hand, a small number of fish originally tagged with a Passive Integrated Transponder (PIT) tag or acoustically tagged in either the Apalachicola River or Suwannee River have been recaptured in the Ochlockonee River (F. Parauka, USFWS, pers. comm.; USGS-WARC, unpubl. mark-recapture database[2]), indicating some in-migration from other river populations.

The reach of river available as YOY developmental habitat and summer holding habitat below the Jackson Bluff Dam at rkm 105 is nearly equivalent to that available below the known spawning grounds in the Yellow River (rkm 91–134), and is substantially longer than the 68–78 rkm unimpounded reach below the sills in the Pearl River. The size of the present Ochlockonee River GS population may be constrained both by limited upriver habitat for spawning and limited estuarine habitat available to support winter feeding by juveniles in Ochlockonee Bay, a bay much smaller in area than either Pensacola-Escambia Bay, Choctawhatchee Bay, or Apalachicola Bay (but larger than Suwannee Sound) (Table 2).

Apalachicola River population – abundance, mortality, and population trend. Historically, the Apalachicola River supported a large and economically important sturgeon fishery (Huff, 1975; Wooley and Crateau, 1985). GS fishing in the Apalachicola River system began in 1899, with large landings reported for 1900 (84 000 lb or 38 136 kg) (Townsend, 1902) and 1902 (74 120 or 33 650 kg) (Alexander, 1905). However, the fishery declined rapidly and dramatically. Annual catches reported from 1928 (Fiedler, 1930) onward were under 10 000 lb (4540 kg) per year, dwindling steadily to a final report of 149 lb (68 kg) in 1954 (Luce and Greer, 1955). Commercial fishing continued at a low level through the late

1950s, finally ending in the 1970s when the fishery became unprofitable (Barkuloo, 1988). Recreational fishing using snatch-hooks (snagging or snitching) or algae-baited catfish rigs in late summer became popular just below the Jim Woodruff Lock and Dam (JWLD) (Fig. 8) during the late 1950′s to 1960's (Burgess, 1963; Swift et al., 1977; Reynolds, 1993), continuing near Blountstown as well until at least 1975 (Tallahassee Democrat, 1963; Carr, 1978, 1983). However, Barkuloo (1988) reported that snatch-hook fishing continued into the 1980s, serving as a source of study material for Wooley and Crateau (1982). Sport fishing for GS in Florida ended with the 1984 harvest ban, although a low level of illegal poaching by snatch-hook and 'rubbing' probably continued for some years thereafter. Rubbing is another form of snag-hooking formerly used in Gulf Coast rivers. A series of large hooks are driven into a water-logged log anchored to the river bottom (Reynolds, 1993). Sturgeon with a habit of rubbing against hard objects to relieve skin irritations get snagged on the protruding hooks.

Construction of the JWLD at rkm 172 (Fig. 8) in 1957 denied GS upstream access to 78% of the originally available habitat in the Flint and Chattahoochee rivers above the dam (Carr, 1978; USFWS, GSMFC and NMFS, 1995). Before river impoundment, GS were known to ascend an additional 320 rkm (Smith, 1917), as documented by historical capture records (Fig. 8). Currently, GS spawn in three locations from immediately below to a few rkm below the dam, areas which probably served as ancestral spawning grounds. The entire riverine phase of GS life cycle, including spawning and YOY development, must now be completed within the unimpounded 172 rkm reach of the Apalachicola River. This reach, from the river mouth to the dam, has been substantially modified to facilitate commercial shipping (Odenkirk et al., 1988). Streambed modifications included periodic dredging of the 30.5 m wide navigation channel to a uniform depth of 2.7 m along the entire Apalachicola River until halted by the State of Florida in 2005[3] (as well as the lower reaches of the Chattahoochee and Flint rivers above the dam) (Bass and Cox, 1985; Wakeford, 2001). Habitat modifications included removal of rock shoals (potential GS spawning grounds), filling in of deep holes (potential GS seasonal holding/resting areas), and elimination of many low-velocity oxbows (potential YOY feeding habitat). Habitat and water quality has been further degraded by agriculture and silviculture impacts in the Chattahoochee and Flint watersheds. Erosion of the steep river banks has resulted in elevated turbidity, suspended solids, and bacteria (Wakeford, 2001). In recent decades, fertilizer-intensive, water-intensive center-point agriculture in the watershed above JWLD has resulted in reduced flow accompanied by elevated pollutant, nitrate, and suspended sediment levels. A growing GS habitat threat is elevated salinization of winter feeding habitat in the Apalachicola Bay estuary due to the combined effects of freshwater withdrawals and reservoir holdbacks, exacerbated by encroaching marine waters due to sea-level rise. These synergistic processes have progressively raised the salinity of Apalachicola Bay (R. Lehnert, FWRI, pers. comm., 2007), constricting the winter feeding habitat of GS juveniles which avoid high salinity habitats.

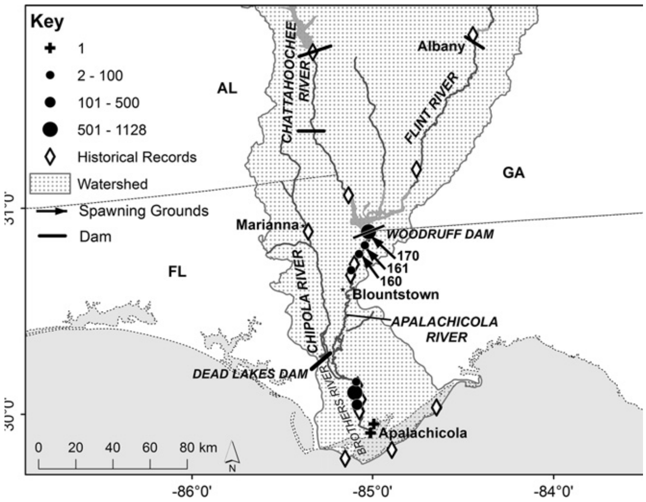

Fig. 8. Map of the Apalachicola River, showing the known distribution of the Gulf Sturgeon, including individual historical records (pre-1993) and total scientific sampling records by location, 1978–2008. Dams are indicated by bars across the river. Spawning grounds are identified with arrows. Distances from the river mouth are indicated by rkms for spawning grounds

In the Apalachicola River, impacts of GS overfishing at the turn of the 20th century preceded impacts from dam construction by several decades. The GS population declined precipitously in the fishery as documented in the U.S. Commissioner of Fisheries report series. This decline in abundance precisely paralleled that in the Suwannee River GS population at the same time, with a simultaneous Apalachicola landings high point of 84 000 lb (38 136 kg) reported in 1900 (Townsend, 1902), and low point of 1215 lb (552 kg) in 1918 (Radcliffe, 1920). Thereafter, catches were reported irregularly until construction of JWLD, fluctuating between 2087 and 12 121 lb (947–5503 kg) annually.

The Apalachicola River currently sustains a GS population that is probably the fourth most abundant for the species. A series of abundance estimates from closed models, 1983–2003, yielded a range of 19–350 fish, with an upper confidence limit of 1010 (Table 1). More recently, an age-structured model yielded a 2003–2005 population estimate of 500–1000 GS (Pine and Martell, 2009a) (Table 1). The latest closed-population estimate (A. Kaeser, USFWS, pers. comm., 2016) from mark-recapture data is 503 (95% CI = 450–570) juveniles <900 mm TL, plus 785 (95% CI = 631–1037) subadults and adults >900 mm TL Analysis of mDNA genetic diversity among GS eggs collected in 2008 from Apalachicola River spawning grounds suggest that population size is probably greater than estimated by mark-recapture results (Saarinen et al., 2011). All Apalachicola population estimates to date are constrained by the use of closed models, generally inappropriate to an unconfined anadromous species. Moreover, the most recent population modeling exercise (Pine and Martell, 2009a) assumed an unrealistically low 5–7% mortality rate, which also better fits a closed population with low within-river, within-season mortality. The mortality rates of 21–33% determined by Zehfuss et al. (1999) appears to be a much better fit to a population in which population size appears to have been static over several decades. Mark-recapture data in the USGS-WARC database for the Apalachicola River population indicates an annual mortality rate of 37.5% (Table 1). These higher mortality rates match up well with the abnormally truncated distribution curve (Fig. 9a), displayed for Apalachicola population data from 1997 to 2006 (F. Parauka, USFWS, pers. comm.). Although early juveniles were well represented over this 12-year period, subadults were notably under-represented, suggesting disproportionately high size-selective mortality among large juveniles and small adults. The pattern of under-representation after fish have entered the phase of full marine anadromy is also evident as a deep valley in the length frequency distribution of 2006 first captures (Fig. 9b). Currently, the trajectory of the Apalachicola River population remains equivocal (Flowers, 2008; Flowers et al., 2009; Pine and Martell, 2009a). However, two of the most recent estimates from 2006 and 2014 are similar. Sampling in 2006 yielded 216 individuals primarily from the Brothers River holding area (F. Parauka, USFWS, pers. comm.) (Table 1), with a within-year, within-river recapture rate of 28%. That would indicate an estimated population ~3.6 times larger, or 771 net-vulnerable fish (>1000 mm TL), closely matching the 2014 closed model estimate of 785 GS >900 mm FL (Table 1). Application of open population models to the existing mark-recapture data, with no assumptions regarding mortality rates, would serve to test these recent population estimates. Good proportional representation of small juveniles (<800 mm TL) across 1977–2006 samples (Fig. 9a) suggests frequent spawning success and juvenile survival success. Thus, the population seems poised to rebound if mortality among subadults could be reduced.

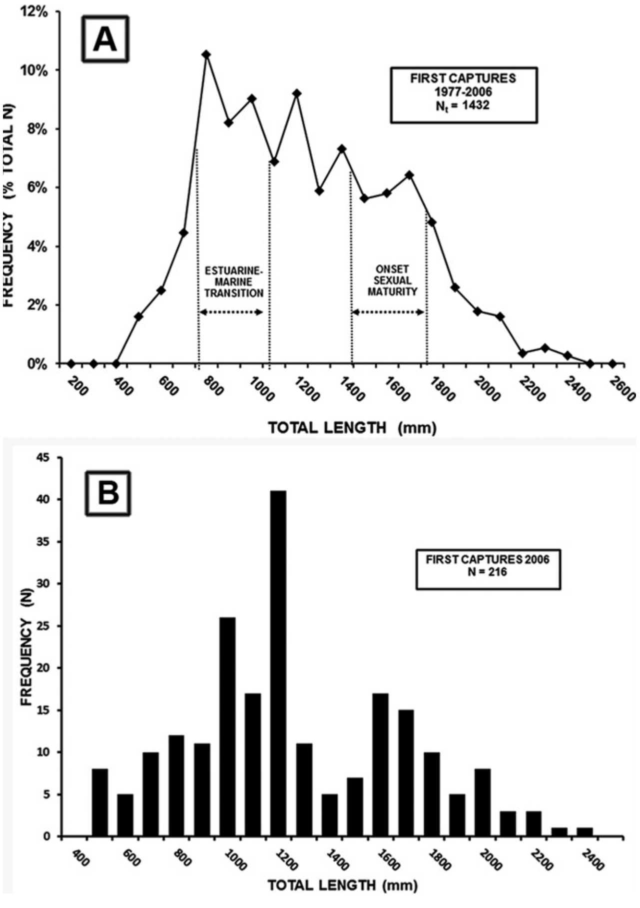

Fig. 9. Length frequency distribution plots in 100 mm TL intervals for the Apalachicola River Gulf Sturgeon population (USFWS unpubl. database, F. Parauka): (a) All gill net first capture data, 1997–2006, as percent of all first captures (recaptures excluded) for all sampling years, displaying abnormal truncation in the 800–1700 mm TL range in relation to TL at transition to full marine anadromy, and at onset of sexual maturity; (b) Length frequency distribution plot for 2006 first captures displaying abnormal gap in the young adult TL range of 1300–1600 mm TL

In the earliest (1981–1984) comprehensive study of the Apalachicola River GS population, Wooley and Crateau (1985) had identified the Brothers River, 23–31 rkm upstream of the Apalachicola River mouth with a mean depth of 11 m, as an important holding area. Others include a deep hole at Ocheese Bluffs (rkm 148) and the deep area immediately below the Jim Woodruff Lock and Dam (rkm 171). Gill nets set in the deep hole below the dam in 1982–1983 captured 228 GS (Wooley and Crateau, 1985). Use of the 'migration resting area' deep hole at Ocheese Bluffs, and of the Brothers River 'deep fall migration staging area' was identified from the detected relocations of 17 GS fitted with radio tags (Wooley and Crateau, 1985). The Brothers River area was targeted in the early GS commercial fishery (Fichera, 1986).

Choctawhatchee River population – abundance, mortality, and population trend. No GS landings were ever reported in the U.S. Commissioner of Fisheries report series from the Choctawhatchee River. Nonetheless, commercial sturgeon fishing certainly took place (Cason et al., 1985). Indeed, Swift et al. (1977) reported that large catches were taken from this river. Shell middens and historical narratives (Cason et al., 1985) provide evidence that Choctawhatchee Bay had been saline at some period in the past. However, during the early part of the 20th century, prior to creation (with human assistance) of a new inlet, Destin Pass, during the 1929 flood, Choctawhatchee Bay was essentially a freshwater body of water isolated from direct communication with the GOMEX (Cason et al., 1985). Choctawhatchee River outflow reached the Gulf only through Santa Rosa Sound and out via Pensacola Pass. Alternating episodes of semi-isolation from the GOMEX, then more direct reconnection of Choctawhatchee Bay to the GOMEX, seem likely as the barrier islands were repeatedly re-shaped. This alternation of GOMEX access probably influenced the historical presence and abundance of GS in the river during any given time interval. Currently, low to mid-salinity nearshore areas of the bay represent the preferred winter feeding habitat for juvenile and adult males in the Choctawhatchee River GS population (Parauka et al., 2001; Fox et al., 2002). Thus, fluctuating salinity regimes may influence GS population trajectory with respect to expansion or contraction of the available shallow low to mid-salinity estuarine feeding habitat required by juveniles, and apparently also preferred by adult males in this population.

Abundance estimates for the Choctawhatchee River GS population from 1999 through 2007 range from 2000 to 3000 individuals >610 mm TL (USFWS, 2001, 2002, 2009) (Table 1). This currently represents the second largest GS population. While no trend over time is apparent from the available abundance estimates, population size appears to either be stable or increasing. Annual natural mortality has been estimated at 16% (USFWS, 2002), which is at the upper limit necessary to maintain stability in sturgeon population size (Boreman, 1997; Morrow et al., 1998; Pine et al., 2001). The Choctawhatchee River mainstem is unimpounded, although there is a dam on the Pea River tributary, 191 rkm from the river mouth (Fig. 10). Thus, it appears that riverine habitat availability does not impede population increase. Length frequency distribution from one large sampling year, 2007 (F. Parauka, USFWS, unpubl. data, 2011), displays a population containing at least four year-class modes (Fig. 11), indicating periodic reproduction and successful recruitment. The focus of recent research has been on defining movements and habitat use in the river and within the Choctawhatchee Bay estuary (Fox et al., 2000, 2002; Fox, 2001).

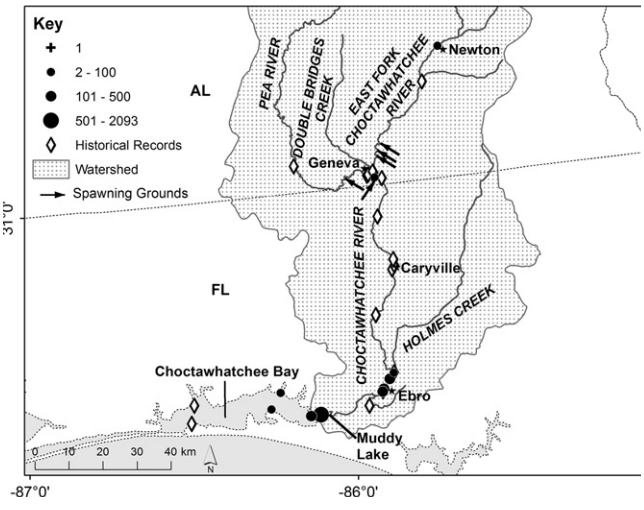

Fig. 10. Map of the Choctawhatchee River system, showing the known distribution of the Gulf Sturgeon, individual historical records (pre-1993) and total scientific sampling records by location, 1977–2008. The Elba Dam is located at rkm 239 on the Pea River, just off the map. Known spawning grounds are identified with arrows

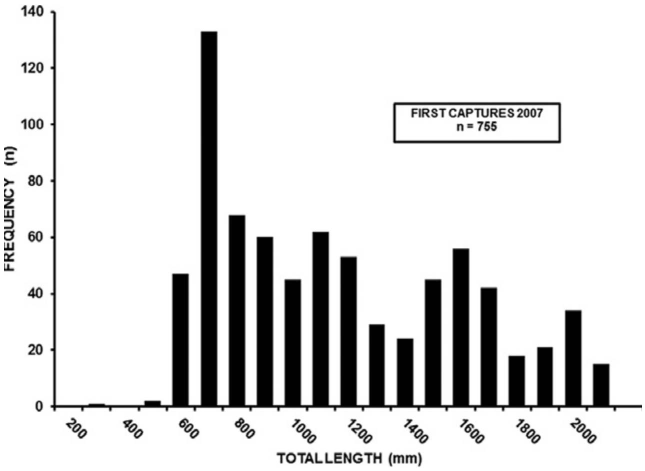

Fig. 11. Length frequency distribution in 100 mm TL intervals for Choctawhatchee River 2007 Gulf Sturgeon first captures (recaptures excluded) sampled by USFWS (USFWS unpubl. database). Apparent over-representation of juveniles (600–900 mm TL) is due to routine use of gill nets with mesh as small as 2.5 in bar (6.4 cm bar)

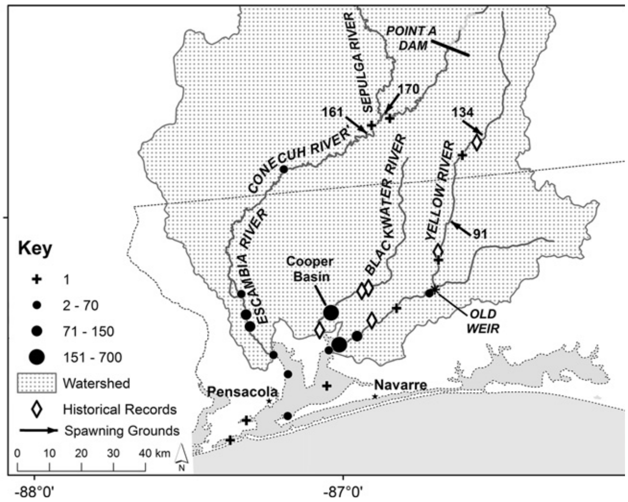

Fig. 12. Map of the Yellow, Blackwater, and Escambia rivers, showing the known distribution of the Gulf Sturgeon, including individual historical records (pre-1993) and total scientific sampling records by location, through 2010. Known spawning grounds on the Yellow and Escambia rivers are identified with arrows. The 'Point A' Dam is located at rkm 222 on the Conecuh River near Andalusia, AL

Yellow River (including Blackwater River) population – abundance, mortality, and population trend. Barkuloo (1988) reported that GS were occasionally harvested commercially in the Yellow River prior to the 1984 Florida harvest ban. While commercial landings have otherwise never been reported from this river, harvested GS may have been combined with those reported for the Escambia River (Alexander, 1905), due to close geographic proximity of both river mouths (Fig. 12). Reynolds (1993) reported that sightings of GS jumping in several locations in the lower Yellow River were common in the 1980–1990s. The eroded wooden pilings of a fishing weir remain as a testament to presumed but undocumented GS commercial harvest at rkm 54 in the lower river (Figs 12 and 13). The effort required to construct and maintain such a permanent post weir suggest that substantial numbers of GS were harvested over a span of several years. Anecdotal reports to USGS fisheries biologists from several local residents confirm that a local-market meat fishery was conducted in the Yellow River in the 1950s and 1960s.

The USFWS conducted mark-recapture GS sampling in the Yellow River from 1993 to 2005 (USFWS, 1994a,b, 1998, 2002, 2004, 2005, 2006) and from 2009 to 2012 (W. Tate, USFWS, pers. comm.). The USGS conducted sampling in 2001–2003 (Berg, 2004; Berg et al., 2007) to estimate population abundance. Berg et al. (2007) reported length

Fig. 13. Abandoned remains of a wooden post fish weir at rkm 54 on the lower Yellow River, Florida, evidence that a substantial undocumented Gulf Sturgeon fishery existed historically in this river (USGS-WARC photograph)

frequency distributions for 2001–2003 samples of GS >880 mm FL. Each annual plot displays a mixed-size, mixed-age sample, dominated however by well-separated recruitment modes (Fig. 14). Abundance across three sampling years was estimated at 500–911 individuals (95% CI = 378–1550) (Table 1) with dominant modes at 1300–1500 mm and 1650–1800 mm FL, including abundant juveniles. Annual natural mortality was estimated at 11.9% (Berg et al., 2007), a rate comparable the 11.0–12.9% rates recently determined for the Suwannee River (Table 1). Population metrics reported in Berg et al. (2007) indicate a self-sustaining spawning population with periodically successful year-classes, and a very high proportion of adults (78.8% in net samples) (USGS-WARC unpubl. database). The Yellow River sustains the third most abundant GS population across the species range (Table 1).

Escambia River population – abundance, mortality, and population trend. Alexander (1905) reported the largest single-river GS catch ever (above) from the Escambia County, FL, in 1901, and refers to the Escambia Bay in text. Thus, landings recorded in Pensacola probably included GS from the Escambia, Yellow, and Blackwater rivers, and possibly from the Choctawhatchee River). Subsequent landings reports were sporadic, but indicate that a small GS fishery continued (e.g. 3604 lb, or 1636 kg, in 1918) (Radcliffe, 1921) beyond the early commercial fishery heyday (last report: Greer and Cohen, 1953). The apparent pre-fishery abundance of GS in the Escambia Bay system seems surprising, given an Escambia River watershed of modest dimensions, less than half the size of the Suwannee River watershed for Escambia River alone (only slightly larger if combined with the Yellow River watershed), one-fifth the size of the Apalachicola River watershed, and one-tenth the size of the Mobile River watershed (Table 2). This puzzling situation illustrates the current lack of understanding of what factors actually determine GS population carrying capacity in any given river. Current models are inadequate in relating GS carrying capacity to length of the unimpounded lowermost reach of a natal river (e.g., Ahrens and Pine, 2014). Nor would watershed area serve as a substitute metric in this regard.

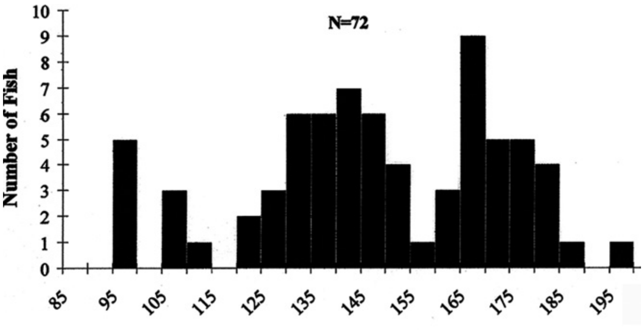

Fig. 14. Length frequency distribution in 50 mm FL intervals for Yellow River 2002 Gulf Sturgeon captures (recaptures included) (from Berg, 2004, Fig. 11, with permission), displaying at least three distinct modes, evidence of infrequent recruitment

Based on USFWS sampling in 2003–2006, Escambia River GS population abundance was estimated (USFWS, 2004, 2008) as 451–573 individuals (95% CI = 83–1003) (Table 1). The most recent estimate from 2015 is within the same range (373 GS >900 mm TL, 95% CI = 243–548) (Table 1). This is <2.0% of the late 19th century pre-fishery GS population of 5000–10 000 based on the total weight of reported Escambia Bay 1902 landings (probably combined Escambia, Blackwater, and Yellow rivers landings), divided by a hypothesized pre-fishery mean weight of 22.7 kg (above). A small commercial fishery still existed on the Escambia River until the 1984 Florida harvest ban. Landings of 259 kg were reported in 1982 (NMFS, 2011), suggesting a severely depleted population. Reynolds (1993) reported that GS sightings in the lower Escambia River were common in the 1960s, but rare thereafter. Estimates available for 2003–2015 (Table 1) reveal no trend in either increase or decrease. No open model mortality rate has yet been estimated. The 2015 within-river, within-summer closed model annual natural mortality rate estimate of 0.03% (Table 1) simply confirms that most mortality takes place in saline habitats during the winter feeding period.

Population recovery in the Escambia/Conecuh River system may also have been impacted by the ‘Point A’ Dam at rkm 222 on the Conecuh River in Alabama (Fig. 12), which may limit access to ancestral upriver spawning and YOY nursery habitat. Telemetry relocations have documented GS movements upstream as far as rkm 204, and into the Sepulga River, a major tributary of the Escambia system (Fig. 12). Urbanization and industrialization of Escambia-Blackwater-Pensacola Bay may impact the extent and quality of winter estuarine feeding habitat available to juvenile GS. Based on reports of large number of sturgeon carcasses (F. Parauka, USFWS, pers. comm., 2005), the population may also be periodically depleted by stochastic mortality from hypoxia in the Escambia River, e.g., following Hurricane Ivan in 2004.

The length frequency distribution of the Escambia GS from USFWS, 2002–2003 samples displays two dominant adult modes at 1600–1800 mm TL and 2000–2100 mm TL (Fig. 15) within a mixed-age adult (>1350–1500 mm TL) spawning population. Furthermore, good representation of juveniles in the distribution documents spawning success in several years prior to 2002–2003. It appears that the population was on a promising trajectory for natural increase prior to Hurricane Ivan. Prior to the 1980s, as in the adjacent Yellow River basin (Wakeford, 2001), sedimentation, agricultural runoff, non-point-source pollutants, and gravel mining may have seriously affected water quality and benthic habitat in the Escambia River basin (Livingston et al., 1974; USEPA, 1975; Hand et al., 1996), potentially resulting in a decline in fisheries (Wakeford, 2001). Despite water quality improvement in the 1980s and 1990s (FDEP, 1998a), GS mass mortalities may still periodically result from riverine and estuarine hypoxia following major stochastic anthropogenic or weather events. Thus, hypoxia during flooding from Hurricane Ivan in 2004 may have very negatively impacted GS population recovery. Anecdotal reports following the storm suggest high mortality that was differentially selective for large adults (F. Parauka, USFWS, pers. comm.).

Pascagoula River population – abundance, mortality, and population trend. Historically, the Pascagoula River appears to have sustained a large GS population, based on GS commercial landings of 24 100 lb (10 930 kg) in 1902 (Alexander, 1905). However, after the range-wide species demise in the turn-of-the century commercial fishery, only small and infrequent catches were reported from the Pascagoula River until Mississippi closed the fishery in 1974. Reported commercial landings are limited to those from 1930, 1950 and 1952, ranging from 73 to 3300 lb (33–1498 kg) (Fiedler, 1933; NMFS, 2011). In the earliest report on GS in Mississippi rivers, Cook (1959) observed that captures were rare and inferquent, suggesting chance occurrence, with 'no orderly migration'. The first scientific survey for GS in the Pascagoula River in June 1987 (Miranda and Jackson, 1987) suggested a seriously depleted population. Only one GS was captured from 30 nights (~600 net-hours) of gill net sampling in three locations chosen based on information from commercial fishermen and state fishery biologists. Subsequently, Murphy and Skaines (1994) captured only seven juveniles and subadults (464–1118 mm FL) in 37 475 net-ft-hr of gill net sampling at the river mouth in April and May 1993. A repeat effort conducted by the USFWS in January to June 1994 yielded another juvenile (620 mm FL) from 240 net-hr of sampling. The USFWS collected nine GS (three juveniles, five subadults, one adult, FL range 767–1308 mm, including one 1993 tag recapture) in the Pascagoula River (junction of Black Creek and Pascagoula River) during a 2-days (60 net-hr) in July 1995. Subsequently, the MMNS initiated a multi-year GS research program in 1997. In the initial sampling year Slack and Ross (1998) reported the first evidence of adults in the contemporary population, capturing them on or near upriver spawning grounds. Four GS (1390–1650 mm TL) were captured in a gravel pit area in the Bouie River tributary (250 rkm from the Pascagoula River mouth) (Fig. 16) in April 1997. One net mortality was a male with testes in spawning condition. In spring 1998, 155 700 net-ft-hr of gill net sampling in the river mouth returned no GS, while 77 740 net-ft-hr resulted in capture of seven adults (1300–1730 mm FL) from the Bouie River site. An additional 23 subadults and adults (1160–2040 mm FL) were captured from holding areas (Heise et al., 2004) in Big Black Creek, the lowermost reach of Black Creek, and in the lower Pascagoula River (Fig. 16).

The most recent estimates for the Pascagoula River GS population, prior to Hurricanes Katrina and Rita in 2005, were accomplished by Ross et al. (2001a) and Heise et al. (2002). Abundance estimates for 1997–2002 ranged from 162 to 234; 95% CI ranged from 34 to 429 (Table 1). Major stochastic mortality appeared to accompany hypoxic conditions in the Pascagoula River resulting from Hurricane Katrina in 2005 (Havrylkoff, 2010). Numerous sturgeon mortalities were observed in both Louisiana and Mississippi in

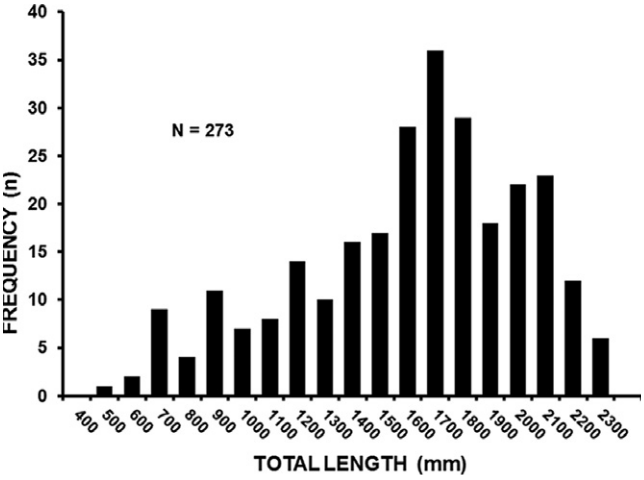

Fig. 15. Length frequency distribution in 100 mm TL intervals for Escambia River 2002–2003 Gulf Sturgeon first captures (recaptures excluded) sampled by USFWS (USFWS unpubl. database, F. Parauka)

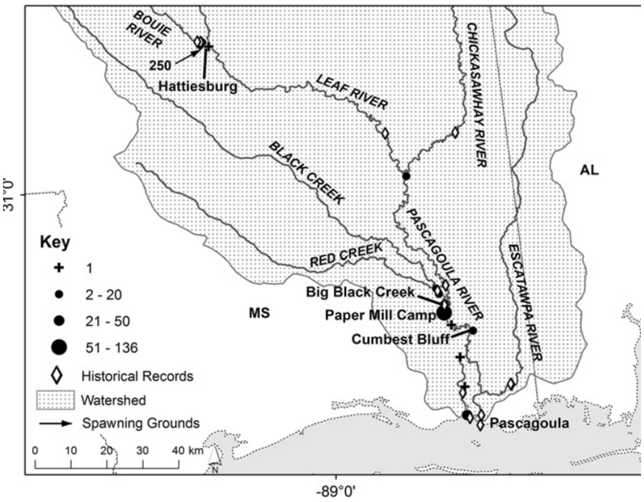

Fig. 16. Map of the Pascagoula River system, showing the known distribution of the Gulf Sturgeon, including individual historical records (pre-1993) and total scientific sampling records by location, 1977–2008. Known Bouie River spawning ground at rkm 250 is identified with an arrow

the wake of that hurricane (Peterson et al., 2008). Scientific sampling in 1997–2003 totaled 281 captures of 201 unique individuals, with a mean of 45 captures per year (Ross et al., 2004). After the two 2005 hurricanes, 2008–2009 combined MMNS and Gulf Coast Marine Laboratory (GRCL) scientific sampling yielded a mean of <4 individuals per year. In 2008, 85 259 net-ft-hr of gill net sampling in the lower river yielded only one GS. In 2009, 81 947 net-m-hr of sampling further upriver yielded six GS (810–1960 mm TL) (Havrylkoff, 2010). Prior to the 2005 hurricanes, captures from 2000 to 2003 suggested a population skewed toward adults (bimodal at 1700 and 2000 mm TL) (Fig. 17). Post-hurricanes captures from 2008 to 2009 did not alter this pattern. The 2000–2003 length frequency distribution is biased toward >900 mm TL GS due to the net mesh size employed. Nonetheless, juveniles and subadults (800–1350 mm TL) still appear underrepresented in the Pascagoula River population, displaying a somewhat different pattern than for the Apalachicola River (Fig. 9) and Pearl River populations (Fig. 18). In those comparative population samples, from a range of net mesh sizes, juveniles and adults are well represented, but subadults are disproportionately underrepresented.

Despite hurricane depredations, and despite a limited rate of recruitment from a depleted population, prospects for GS recovery remain good since habitat quality is very good for all life history stages in the Pascagoula River. The watershed (Fig. 16) is comparable in area to that of the Suwannee River, with a 430 rkm long mainstem, and five major tributaries (Table 2). The river remains unimpounded (Dynesius and Nilsson, 1994) and only moderately impacted by late 19th century to present anthropogenic alterations. However, by 1930 the ancient bald cypress and longleaf pine lowland and riparian forest typical of Gulf Coast rivers was completely logged out, probably permanently altering the riverine ecosystem. Currently, much of the riparian habitat along the lower Pascagoula River (south of latitude 31°N) is bottomland forest and swamp cooperatively conserved by The Nature Conservancy and the Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP) (Schueler, 1980). Thus, habitat in present-day lower Pascagoula River watershed remains relatively immune to human disturbance.

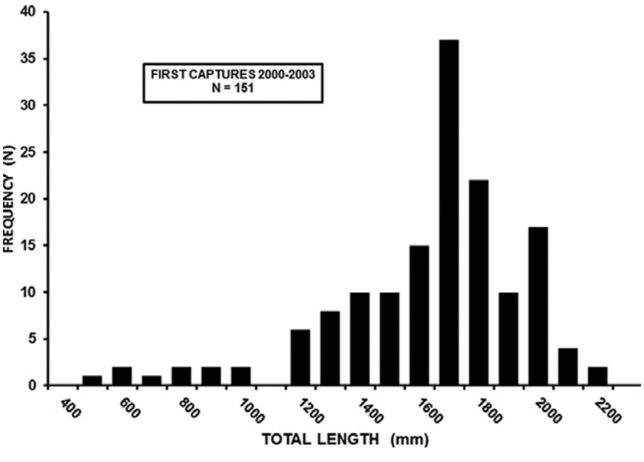

Fig. 17. Length frequency distribution in 100 mm TL intervals for Pascagoula River Gulf Sturgeon first captures (recaptures excluded) sampled in 2000–2003 (data from W. T. Slack, Mississippi Museum of Natural Science, pers. comm., 2010)

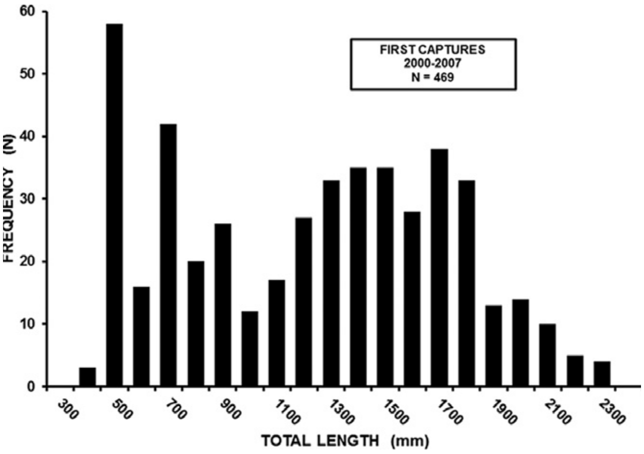

Fig. 18. Length frequency distribution in 100 mm TL intervals for Pearl River first captures (recaptures excluded) sampled in 2000–2007 [data from Louisiana Department of Wildlife and Fisheries (LDWF), H. Rogillio and W. T. Ruth, LDWF, pers. comm.]

Three major Pascagoula River tributaries are extensively utilized by GS for staging, holding, summering, or spawning (Dugo et al., 2004; Heise et al., 2004). GS occur as far upstream at rkm 387 in the Chickasawhay River (Fig. 16) (Ross et al., 2002; Heise, 2003). Spawning has been documented by egg collections (Table 4) at rkm 250 in the Bouie River (Fig. 16) (Slack et al., 1999; Heise et al., 2004) where adult GS were captured every spring, 1997–2003 (Ross et al., 2004). Spawning is also suspected to occur in the Chickasawhay River (Dugo et al., 2004; Heise, 2003).

Pearl River population – abundance, mortality, and population trend. There is no record of a late 1800s to early 1900s GS commercial fishery on the Pearl River. It was not until the 1940s through early 1950s that commercial landings were subsequently reported (Anderson and Power, 1949; Anderson and Peterson, 1953; NMFS, 2011), ranging from 100 lb (45 kg) in 1945 to 1000 lb (454 kg) in 1950. However, an artisanal GS fishery has undoubtedly been continuously conducted in the Pearl River. Reynolds (1993) provides numerous reports of incidental GS captures in trawls, river hoop nets, and by angling. Additionally, GS were frequently taken as bycatch in the commercial shrimp trawl fishery in Lake Pontchartrain. Bycatch is probable as well in entanglement gill nets, which are still legal in Louisiana. Morrow et al. (1998) and Tate and Allen (2002) have suggested that bycatch in the commercial shrimp fishery is a major contributor to total mortality in the Pearl River GS population. Reporting of such bycatch appears to have been stymied by legal penalties accompanying the GS harvest ban imposed by Louisiana in 1990, and by the federal ESA listing in October 1991.

The presence of early juveniles among scientific samples over the past three decades demonstrates that the river still supports a spawning population (Miranda and Jackson, 1987; Morrow et al., 1996, 1998; Rogillio et al., 2001, 2007),

Table 4
Gulf Sturgeon embryo and egg collections by river, date, and location, with associated physical, chemical, and hydrological data

River & GS Stage	Year	Period (all years)	Location (rkm) [outlier]	Conductivity (μS cm^{-1}) Ca^{++} [mg L^{-1}]	DO (mg L^{-1})	Temp (°C) [outlier]	pH	Substrate description	Depth (m)	Flow velocity (m s^{-1}) or volume [m^3 s^{-1}]
Free Embryos:										
Apalachicola[a] 1 free embryo, 9.71 mm TL 1–2 days old	1977	11 May	167.3	—	—	23.9	—	Captured in plankton net	4.2	0.67 [365]
Apalachicola[a] 1 free embryo, <10 h old	1987	1 May	167.3	—	—	21.6	—	Captured in plankton net	4.2	[437]
Apalachicola[a] 1 free embryo, 1–1.5 days old	1987	3 Apr	18.7	—	—	16.1	—	Captured in plankton net	7.9	0.96
Suwannee[b]1 free embryo, 10.0 mm TL, 0-d old (next to egg shell)	1996	19 Apr	215	158	—	17.5	—	Found adhering to anchor shaft	—	—
Eggs:										
Apalachicola[c]	2005–2008	4 Apr–14 May	160.1–170.6	108–178	7.49–12.21	18.96–25.31	7.44–8.02	Limestone, hard clay, gravel	0.15–7.43	0.14–1.15 [183–1047]
Choctawhatchee & Pea[d]	1997	18 Apr–1 May	140–155	32–70	7.4–8.4	18.4–22.0	—	Limestone, gravel	1.4–7.9	0.25–1.08 [~15–82]
Escambia[e]	2001	3–11 May	161–170	92.9–113.4	7.72–9.67	21.8–23.4	7.01–7.18	Limestone, hard clay	2.1–7.6	—
Pascagoula (Bouie)[f]	1998	21 Apr	250	—	7.90	18.2	—	Gravel	2.1–3.3	—
Pascagoula (Bouie)[f]	1999	7–14 Apr	250	—	6.41	22.7–23.9	—	Gravel	2.3–3.4	—
Suwannee[g]	1993	22 Apr	215	—	5.5	18.3	—	Fine to coarse sand & cobble	5.5–8.1	[320]
Suwannee[g]	1994	28 Mar	202–221	—	6.3–6.6	18.8–20.0	—	Very fine to coarse sand & cobble	4.2–9.5	—
Suwannee[h]	1995–1998	26 Mar–21 Apr	209–221	40–135 [6–15]	4.3–7.2	17.0–21.5 [14.9]	7.0–7.2	Limestone gravel 2–10 cm	1.5–12.2	0.2–1.5
Suwannee (Withlacoochee)[i]	2005	Early May	~206	—	—	—	—	Limestone	—	—
Suwannee[j]	2015	24–27 Mar	158–162	166–178	5.6–5.8	19.9–20.3	—	Limestone gravel	2.7–2.9	—
Yellow[k]	2005	4 May	134	40.2	7.06	18.1	—	Limestone, cobble	2.1–3.0	[105]
Yellow[l]	2010	5 May	91	—	—	20.5	—	Limestone cluster	2.0–4.0	[19.2–62.3]
All rivers combined	1977–2008	26 Mar–14 May	~95–250 [18.7]	32–135 [6–15]	4.3–12.21	16.1–25.31	7.0–8.02	Limestone, hard clay, gravel, cobble	0.15–9.5	0.14–1.5 [~15–1047]

Rkm = river kilometer.
Data sources:
[a] Wooley et al. (1982), Foster et al. (1988), USFWS (1988), USFWS, GSMFC, NMFS (1995).
[b] Sulak and Clugston (1998).
[c] Scollan and Parauka (2008), USFWS (2005), Pine et al. (2006), Flowers et al. (2009).
[d] Fox and Hightower (1998, Fox et al., 2000), Parauka and Giorgianni (2002). Flow rate data obtained graphically from Fox et al. (2000, Fig. 5).
[e] Craft et al. (2001), Parauka and Giorgianni (2002).
[f] Ross et al. (2001a), Heise et al. (2004).
[g] Marchant and Shutters (1996).
[h] Sulak and Clugston (1998, 1999), Sulak et al. (2013), USGS unpubl. data.
[i] Parkyn et al. (2007), D. Parkyn, Univ. Florida, pers. comm., 2016.
[j] USGS unpublished.
[k] USFWS (2005), Kreiser et al. (2008).
[l] J. Van Vrancken and W. Tate, USFWS, pers. comm.

although spawning grounds remain undiscovered. The Pearl River sustains a small reproductive population of GS adults (Table 1). Gill-net samples from 1992 to 1996 suggest a population dominated by juveniles of age 2–5, 780 mm mean FL, and 4300 g mean weight (Morrow et al., 1998), compared to 1967–1969 samples (mean FL = 1140 mm and mean weight = 11 200 g) (Davis et al., 1970; reported in Morrow et al. (1998). However, it is now known that the areas sampled in 1992–1996 are areas frequented by juveniles, while those sampled in 1967–1969 are subadult and adult holding areas (W. T. Ruth, LDWF, pers. comm.). More recently, length frequency data for 2000–2007 first captures (LDWF, unpubl. data) suggest a promising population trajectory (Fig. 18). Thus, large subadults and adults are well represented across a broad range of 1100–1800 mm TL, with modes in the juvenile range (<900 mm TL) displaying evidence of frequent recruitment. The Pearl River plot of GS first captures is similar to the corresponding Apalachicola River plot. In both, the component of the population that appears underrepresented is comprised of late juvenile through early subadult stages. Those life history stages would be particularly vulnerable to mortality as bycatch in the estuarine shrimp trawl fishery.

Population recovery appears to have been retarded not only by fishery bycatch mortality (Morrow et al., 1998; Tate and Allen (2002), but by loss of access to upriver habitat above two low-head sills at rkms 78 (Pearl River) and 80 (Bogue Chitto River, 17 rkm upstream of the conjunction with the Pearl River) (Fig. 19) constructed in 1956 as part of the West Pearl River Navigation Canal project. The Bogue Chitto sill bars upstream migration during low water conditions prevailing for >200 day year^{-1} (Kirk et al., 1998). Occasional records from above the two sills indicate that GS do surmount these barriers during high water (W. T. Slack, USACE, pers. comm.). A further obstacle to upstream migration and habitat access is the impassable Ross Barnett Dam at rkm 486. Prior to its construction at in the 1960s, there were records of GS from the vicinity of the dam and reservoir site and further upstream (Fig. 19, Table 5). In addition to loss of upriver habitat access, the population has also been periodically impacted by stochastic mass mortality, e.g., hypoxia following Hurricanes Katrina and Rita in 2005, and toxicity following from the August 2011 Bogalusa, LA, pulp mill effluent spill (Reuters, 2011). Morrow et al. (1998) additionally identified habitat degradation and eutrophication of Lake Pontchartrain as potentially pertinent to the status of the Pearl River GS population. Given the current small population size, and a correspondingly small mark-recapture database, the model of Morrow et al. (1999) was unable to determine if the population was either declining or increasing.

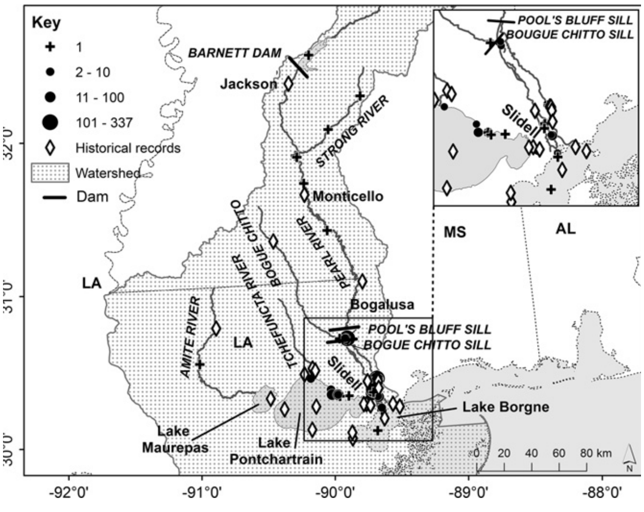

Fig. 19. Map of the Pearl River system, showing the known distribution of the Gulf Sturgeon, including individual historical records (pre-1993) and total scientific sampling records by location through 2008. Low-head sills on the Pearl River (Pool's Bluff Sill, rkm 78) and Bogue Chitto River (Bogue Chitto Sill, 80 rkm upstream of Pearl River mouth), and the Ross Barnett Dam at rkm 486, are denoted with black bars

Extirpated historical populations and problematic populations. *Tampa Bay:* A three-year winter GS commercial fishery conducted between 1887–1889 (Townsend, 1902) apparently extirpated the species from Tampa Bay. In middle 1900s there were occasional small GS catches from the area between the Suwannee River and Tampa Bay (e.g., Greer and Cohen, 1953, 1954). Since the 1960s, there have been sporadic GS observations or reported mortalities in the Tampa Bay area (Reynolds, 1993; Wakeford, 2001; St. Petersburg Times, 19 March 2002). Most recently, USGS acoustically-tagged GS from the Suwannee and Ochlockonee rivers have been detected in an acoustic array in the GOMEX off the mouth of Tampa Bay [(S. Barbieri, Florida Wildlife Research Institute (FWRI), pers. comm., 2011, 2013)].

The Tampa Bay population was probably a winter migratory feeding aggregation derived from the Suwannee River population. If any of the rivers emptying into Tampa Bay (Hillsborough, Manatee, Little Manatee, and Alafia rivers) had been a GS spawning river, the fishery would have been conducted instead in spring to target fish during the spawning run. Moreover, it should have taken many years to fish down a natal river population. Historically, none of the rivers feeding Tampa Bay appears to have the appropriate combination of characteristics (sufficient river length, a hydroperiod yielding high spring flow, sufficient headwaters gradient and gravel substrate for spawning) typical of a GS spawning river (Table 2). In particular, the West Central Florida hydroperiod (60% of an annual precipitation of 55 in or 140 cm coming in June-September, with lowest precipitation in January to May) is out of synchrony with GS spring spawning requirements for high flow over upriver gravel beds. The best candidate as a historical GS natal river would have been the 95 rkm long Hillsborough River, but that river has been impounded at rkm 16 since 1897, chanelized below the dam in 1910 to facilitate logging operations, and shorelines hardened and riprapped in that same lower reach thereafter. Indeed, all remaining Tampa Bay rivers have also been highly modified by impoundment or phosphate mining operations. In the modern context, as the Suwannee River GS population continues to increase,

Table 5
Notable historical and scientific captures of Gulf Sturgeon listed chronologically: reports of very large (>90 kg) sturgeon and/or records from far upriver (above river kilometer 300). English lengths and weights are retained to correspond with original reports

Locality	Date	Length (ft & in) [cm]	Weight (lb) [kg]	Notes	Photograph	Source or Citation
Mobile River system, Black Warrior River, Tuscaloosa, AL, above City Wharf	05/–/1872	7 ft 3 in	~200 lb [~91 kg]	Caught in fish trap	No	Tuscaloosa Times (8 May 1872)
Mobile River system, Black Warrior River, University Shoals pool, Tuscaloosa, AL	05/01/1889	—	211 lb [98 kg]	Caught by angler	No	Tuscaloosa Times (1 May 1889)
Mobile River system, Black Warrior River, AL, about 4–5 mi (5–6.5 km) from Eutaw, AL	1894	5 ft [152 cm]	135 lb [61 kg]	Butchered and sold to local citizens.	No	M. Mettee, AGS, pers. comm. 3 February 2009. Article in Eutaw Mirror newspaper (date unknown), reprinted from Tuscaloosa Times (18 April 1894)
Mobile River system, Black Warrior River, Tuscaloosa, AL	04/–/1897	—	100 lb [45 kg]	—	No	M. Mettee, AGS, pers. comm., 26 January 2009
Pascagoula River, MS	3–4 years prior to 1905	~14 ft [356 cm]	500–600 lb [227–272 cm]	Killed by a tug boat	No	Alexander (1905), pp. 455
Pascagoula River, MS	1902	8 ft 10 in [269 cm TL]	—	—	No	Alexander (1905), fisheries of MS section
Mobile River system, Coosa River, Coopers, AL	1924	9 ft 6 in [290 cm]	400 lb [182 kg]	—	Yes	Reynolds (1993) pp. 19, based on Birmingham News (15 June 1924)
AL	~1920–1930 based on vehicle in photograph	[~200–250 cm] based on photograph	—	One Gulf Sturgeon	Yes	M. Mettee, AGS, pers. comm., 2009 (file photograph #1).
AL	~1920–1930 based on vehicle in photograph	[~200–250 cm] based on photograph	—	2 large Gulf Sturgeon	Yes	M. Mettee, AGS, pers. comm., 2009 (file photograph #2)
Mobile River sytstem, Coosa River, one mile below Wetumpka, AL, 315 mi (507 km) upstream from Mobile River mouth	1930	7 ft 8 in TL [234 cm]	265 lb [120 kg]	Caught on baited hook and line. Sold to fish market	Yes	Alabama Game and Fish News (May 1930a), pp. 8
Mobile River, AL, confluence with Alabama & Tombigbee rivers	1930s	12–14 ft [370–430 cm]	~1000 lb [~454 kg]	—	No	Reynolds (1993) based on commercial fisherman interview
Mobile River system, Tallapoosa River, AL, 4 mi (5 km) south of Tallassee, AL	07/–/1930	—	417 lb [189 kg]	Gigged in a 3-ft deep pool.	No	Alabama Game and Fish News, (July 1930b), pp. 14. Caught by G. W. Lambert of Tallassee, AL
Mississippi River mouth, LA	prior to 1933	9 ft 3 in [282 cm]	503 lb [228 kg]	—	Yes	Gowanloch (1933), p 408; Cited in USFWS, NOAA and GSMFC (1995), pp. 4

Table 5
(Continued)

Locality	Date	Length (ft & in) [cm]	Weight (lb) [kg]	Notes	Photograph	Source or Citation
Mississippi River mouth. LA, Cow Horn Reef	09/–/1936	9 ft [274 cm]	503 lb [228 kg]	Caught on hook and line	Yes – New Orleans newspaper article, 20 Sept. 1936	Reynolds (1993). Caught on hook and line. Cited in USFWS, GSMFC and NOAA (1995), pp. 4. Photograph obtained from F. Parauka, USFWS, Panama City, FL 2006.
Mobile River system, Coosa River, AL, below Jordan Dam	1938	9 ft [274 cm]	306 lb [139 kg]	Trapped in pool below Jordan Dam. Shot and killed	Yes	P. Harper, USFWS, pers. comm. (letter and photograph from Prof. Harvey H. Jackson III, Jacksonville State Univ., AL)
Strong River, Pearl River system	4/–/1939	6 ft [183 cm]	225 lb [102 kg]	Stranded on rocks	No	Cook (1959), Donated to MS Game and Fish Museum.
Mobile River system, Cahaba River, AL, one mile north of Centreville bridge.	4/23/1941	8 ft [244 cm]	360 lb [163 kg]	Caught on trot line	Yes	Centreville Press (8 November 1984). Repeat of original 1941 article. Also Birmingham News (19 July 1959)
Pearl River, 14 mi (24 km) above Jackson, MS, 300 mi (483 km) upstream from river mouth	4/28/1942	7 ft 8 in TL [234 cm]	340 lb [163 kg]	Captured by Ben Britton, stranded on a sandbar	Yes	Ross et al. (2002), pp. 73, Fig. 6.6; Cook (1959):Letter from Parauka, 22 April 2008
Mobile River system, Black Warrior River, West Blocton, AL	1944	7 ft 11 in [241 cm]	296 lb [134 kg]	Persons in photograph are Bob Riley and C. L. Lawley	Yes	Source unknown.
Mobile River system, Coosa River, AL	~1930–1950	[~200 cm] based on photograph	—	—	Yes	M. Mettee, AGS, pers. comm., 2009 (photograph #3)
Apalachicola River system, Flint River, near Albany, GA	Before 1950	—	461 lb [209 kg]	Reported by J. Taranto, fish house owner, Apalachicola, FL	No	Swift et al. (1977), USFWS, GSMFC and NMFS, 1995, pp. 11
Pascagoula River, below Cumbest Bluff, Jackson County, MS	Spring 1951	—	255 lb [116 kg]	—	No	Cook (1959)
Mobile River system, Cahaba River, Montevalle, AL	1952	~8 ft [~244 cm]	—	Caught on snatch hook	No	Reynolds (1993), Appendix 5
Ochlockonee River, FL	1954 based on license plate of truck	~ 7 ft [~213 cm] via width of truck tailgate in photograph	2 GS – each 200 lb [91 kg]	Sold in Blountstown, FL? 60 lb [27 kg] of caviar taken	Yes	Florida Outdoors (1959). Florida Memory online historical photograph archive: Image #CO25131, 1957
Ochlockonee River, FL	1956	—	297 lb [135 kg]	—	No	Florida Outdoors (1959)
Pearl River system, Bogue Chitto River, St. Tammany Parish, LA	Unknown (~1960?)	—	200 lb [91 kg]	Caught by Cloise Blackledge 'Grandpa Catfish'	Yes	LDWF news clip, H. Rogillio. LDWF, pers. comm
Pascagoula River system, Chickasawhay R., MS	1969	7 ft 11 in [241 cm]	296 lb [134 kg]	—	No	Reynolds (1993). Based on 1969 newspaper article

Table 5
(Continued)

Locality	Date	Length (ft & in) [cm]	Weight (lb) [kg]	Notes	Photograph	Source or Citation
Pascagoula River system, Bowie River, MS	January-February 1973 or 1974	NA	370 lb [168 kg]	Caught in gill net set for carp	No	Reynolds (1993), Appendix 5
Pearl River, MS, below Ross Barnett Dam spillway	1976	7 ft 3 in [220 cm]	263 lb [119 kg]	Caught by commercial fisherman	No	Cited in USFWS, GSMFC, and NOAA (1995), pp. 6
Lake Borgne, LA, Pearl River estuary	1978	[~200–250 cm] estimate from photograph	387 lb [176 kg]	Caught in shrimp trawl, 1978 Robert Kenny	Yes	H. Rogillio, LDWF, pers. comm
Apalachicola River, FL	9/8/1989	[240 cm^{a}]	205 lb 93 kg	Scientific net collection	No	USGS Apalachicola River database
Apalachicola River, FL	6/18/1998	[250 cm^{a}]	—	Scientific net collection	No	USGS Apalachicola River database
Pearl River system, Bogue Chitto River, LA, Paige Lake	6/11/2002	[227 cm]	~325 lb [148 kg]	Scientific net collection	Yes	H. Rogillio, LDWF, pers. comm. 2002
Pearl River system, Bogue Chitto River, near McComb, MS	7/14/2005	6 ft 9 in [206 cm]	—	Caught by kayakers	Yes	Enterprise-Journal (21 July 2005); W. T. Slack, USACE, pers. comm., 2016

NA, not available.

approaching contemporary carrying capacity, it can be hypothesized that out-migration will increase, potentially resulting in renewed use of the Tampa Bay estuary as an important GS winter feeding ground.

Mobile River: Historically, one of the largest GS populations may originally have inhabited the Mobile River system (including the Alabama and Tombigbee rivers, and their major tributaries). For 1902, the first year of commercial GS fishing in the Mobile River, landings of 100 000 lb (45 400 kg) were reported (Alexander, 1905). The Mobile system is the largest and geographically most extensive southeastern U.S. river watershed east of the Mississippi (Table 2) (Fig. 20), potentially providing the largest amount of GS riverine habitat. Historical records substantiate the occurrence of large GS in far upper reaches (Tuscaloosa Times, 1872, 1889; Alabama Game and Fish News, 1930a,b; Mettee et al., 1996) of tributary rivers including the Coosa, Cahaba, Tallapoosa, and Black Warrior rivers (Table 5). However, the Mobile river system has been highly fragmented by dam construction that began on the Alabama River in 1887. By the turn of the 20th century 17 dams had been constructed on that river alone. They were subsequently replaced by five higher dams by 1915, and again replaced by three still higher dams constructed in the 1960s–1970s. Currently, there are 17 major dams on the Alabama, Tombigbee and Black Warrior rivers combined (locations of ten shown in Fig. 20), leaving only the lower 220–227 rkm of the Mobile River system unimpounded below the Claiborne and Coffeeville dams. However, the unimpounded reach has been extensively altered by dredging for navigation. Blockage of upriver migration by dams was already a factor when commercial sturgeon fishing was subsequently initiated. For a more comprehensive synopsis of negative physical and hydrological impacts upon sturgeon species

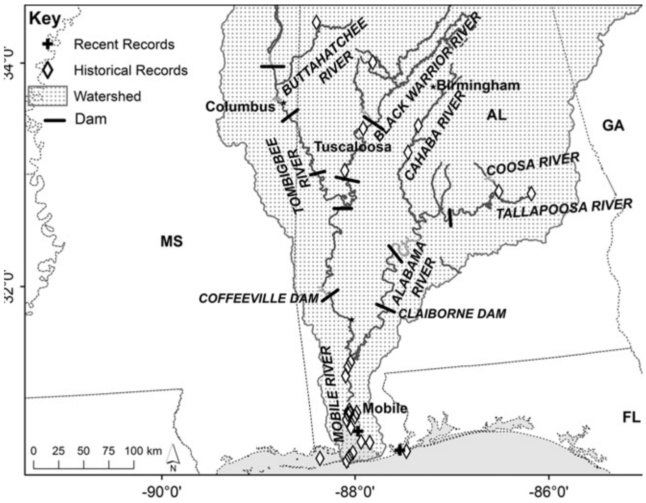

Fig. 20. Map of the Mobile/Alabama/Tombigbee River system, showing the known Gulf Sturgeon historical and recent records through 2008. Ten of the largest dams are denoted by black bars. The two lowermost barriers to GS migrations are the Coffeville Dam (rkm 193) and Claiborne Dam (rkm 207)

from human alternation of the Mobile River system, refer to Kuhajda and Rider (2016), this volume.

Together, denial of access to upriver habitat, river fragmentation, and commercial fishing rapidly depleted the Mobile River system GS population. It is impossible to determine how abundant the species may have been historically in the Mobile system. After the report of large landings in 1902, more than two decades passed before landings of only 9666 lb (4388 kg) were again reported (Fiedler, 1930) for 1928, the last landings ever reported. Recent GS Mobile River records from fishermen or scientific sampling have been few, limited to single individuals, and restricted to the lower river and estuary (Fig. 20) (Reynolds, 1993; Mettee et al., 1994, 1995, 1996). Net sampling surveys in recent decades have been inadequate to determine the status of the species in the unimpounded reaches of the Mobile system. However, recent environmental DNA (eDNA) analysis of river water suggests the presence of GS in those reaches (S. Rider, ADCNR, pers. comm., 2015). There is an equal or more extensive unimpounded reach (220–227 rkm) available as GS habitat in the Mobile River system below the Coffeeville and Claiborne dams (Fig. 20) than is available in the 171 rkm reach below the JWLD on the Apalachicola River, the 78–80 rkm braided reach available below the Bogue Chitto and Pool's Buff sills on the Pearl River, or the 222 rkm reach below the 'Point A' Dam on the Conecuh River (Fig. 12). All three of those comparative river systems support GS spawning populations. Additionally, Mobile Bay represents the second largest estuary potentially available as juvenile GS winter feeding habitat (Table 2). Thus, it appears that habitat should be sufficient to support population recovery. However, the Mobile River has been highly altered by dredging and channelization. Deep holes to serve as critical seasonal holding habitat may have been eliminated by dredging. Moreover, dredging has so reduced the river gradient in the unimpounded reaches below the first dams (Randall et al., 2013) that flow may be insufficient (Kynard, 1997) to attract adult GS as potential spawners, and YOY nursery habitat may be adversely impacted. Finally, extensive industrialization and pollution of the Mobile Bay estuary over many decades may represent another re-population obstacle of undetermined impact. The city of Mobile boomed as a major shipbuilding and manufacturing center during World War II.

Mississippi River: The rarity of historical records or recent reports of GS in the Mississippi River (Reynolds, 1993; Ross et al., 2001a) seems curious, particularly given the regular use of Lake Pontchartrain and Lake Borgne by Pearl River GS. Only occasional records of GS have been reported from the Mississippi-Atchafalaya River system (Reynolds, 1993; Ross et al., 2001a. When the ancestral AS source species expanded its range into the GOMEX, large GOMEX rivers lacking competing sturgeon species were colonized by the GS. However, the Mississippi River may have posed an obstacle to colonization due to competitive exclusion from three previously established freshwater sturgeon species LS, SVS, and PS. All three competitors appear to have existed in enormous numbers prior to human exploitation. For example, in 1899, LS and SVS (probably including PS) commercial landings of 178 881 lb (81 212 kg) and 496 614 lb (225 463 kg), respectively, were reported from the Mississippi River (Townsend, 1902). An instructive parallel of competitive exclusion is the case of the AS and LS where the species ranges meet in the St. Lawrence River. The zone of sympatric overlap is very small, consisting of the low salinity estuarine transition zone (ETZ) nursery. Moreover, it is only the juveniles of the two species that co-exist by partitioning the benthic food resource (Guilbard et al., 2007). Facing an established LS freshwater competitor, adults of the anadromous AS do not ascend further into the freshwater reaches of the St. Lawrence River. A further obstacle to GS colonization of the Mississippi River as a spawning river may have been the great distance upstream that would have to be traversed to find gravel substrate suitable for spawning.

Rio Grande River: The only species of sturgeon reported to inhabit Texas freshwaters is the SVS in the Rio Grande River (Evermann and Kendall, 1894). However, a commercial catch of 22 400 lb (10 170 kg) of 'sturgeon' was landed in Cameron County (probably the port city Brownsville), Texas in 1897 (Townsend, 1900). This catch came from seines set in estuarine bays (probably in the vicinity of the Rio Grande River mouth), and thus the species was undoubtedly the GS. Fowler (1923) reported the 'common sturgeon' (= GS, referred to as AS in the early literature) as occurring rarely in Texas. Catches of riverine SVS, a species confined to freshwater, were always listed as 'Shovelnose Sturgeon' in the U.S. Commissioner of Fisheries landings reports, or otherwise referred by the old vernacular name 'hackleback'. However, no landings of SVS were ever reported from Texas, nor any further 'sturgeon' landings. More recently, there have been only two incidental records of the GS in Texas waters, one angled in the open GOMEX off Galveston, and a large adult reported fisheries biologists far upriver in the Rio Grande during electrofishing operations (Reynolds, 1993). If a historical GS spawning population did inhabit the Rio Grande River, as suggested by the 1897 catch, it was extirpated early on. The river is now too highly fragmented, altered, and depleted of flow in the lower reaches to sustain a GS population.

Sabine River: The Sabine River, which forms the border between Louisiana and Texas, lies within the historical geographic range of the GS. It appears to have suitable GS habitat in the contemporary unimpounded 246 rkm reach below the Toledo Bend Dam, and would have provided substantially greater upriver habitat prior to impoundment. Given the paucity of early commercial fishing activity, and hence fishery landings reports, from western Louisiana and Texas, it is impossible to determine if GS ever inhabited this river. No anecdotal records of GS have yet been discovered for the Sabine River. The only historical report on the fish fauna of this river is that of Evermann (1899), who observed that very little commercial fishing took place in the Sabine River region, and what did was conducted with baited hoop nets and for local consumption. He commented that shad (*Alosa* spp.) were not caught in the local fishery since methods appropriate for capture of shad (i.e., anchored gill nets), were not employed. Thus, without gill net fishing or seining, neither shad nor GS would have been caught.

In recent times, pollution from the oil refinery complex at Port Arthur along the shores of Lake Sabine adversely impacts water quality in the low salinity Sabine River estuary. That estuary may once have served as juvenile winter feeding habitat for a hypothetical historical GS population. Riverine habitat appears to satisfy all GS habitat requirements (Randall et al., 2013: Categorical Habitat Attribute Acceptability Tool, or CHAAT). The five necessary attributes, i.e., those required by the GS to support sustained residence of a reproducing population in a given river (with minimum [negative] criteria specified below which a self-sustaining population is unlikely) are: (i) Elevation at barrier or head ≥10 meters (negative at 9 m); (ii) Average annual discharge (for spawning) ≥2232 cubic feet per second [cfs] (negative at 1148 cfs); (iii) Watershed area ≥6257 km^2 (negative at 4133 km^2); (iv) Mainstem length to river mouth ≥280 km (negative at 227 km); and (v) Anthropogenic barrier distance (un-impounded length to river mouth) ≥80 km.

Population metrics and trajectories

Natural recruitment, mortality and survival

With a relatively long lifespan, several spawnings per lifetime, and very high fecundity, the GS life history strategy is one that can withstand infrequent and often low recruitment success, punctuated by periodic high recruitment success. Thus, GS populations tend to be dominated by strong year-classes spaced at intervals of several years, against a background of generally weak year-classes (e.g., Figs 9b, 11 and 14). When an adequate sample of a GS population can be obtained, the length frequency distribution typically reveals one or more abundance modes representing those strong year-classes that dominate population structure for many years. In the strongly recovering Suwannee River population, a substantial increase in effective breeding population size has resulted in nearly annual frequency of strong year-classes (Fig. 4). For the Suwannee River GS population in 2013, net samples have revealed successive length frequency modes now occurring almost annually (Fig. 4), contrasting with the mid-1990s samples displaying only two dominant length frequency modes separated by 6–7 years (Fig. 21) (Sulak and Randall, 2002).

Generally, in fish species that do not undertake egg, nest, or brood protection, egg through age-1 mortality normally exceeds 99.9% (Miller et al., 1988), close to the 99.96% mortality assumed for age-0 GS in population modeling by Pine et al. (2001). Miller et al. (1988) hypothesize that most larval fish die in the first week of life. Thus, even in a good GS spawning year, only a very small percentage of the spring-spawned eggs survive to participate in the first emigration to the estuary in January-February. As advanced by Miller et al. (1988) successful spawning alone is insufficient to determine successful recruitment to the spawning population.

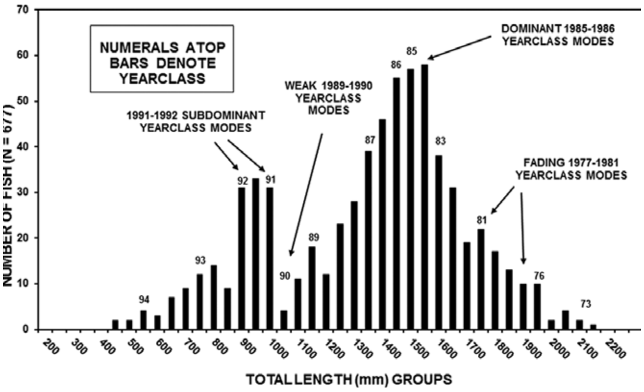

Fig. 21. Length frequency distribution in 50 mm TL intervals for Suwannee River Gulf Sturgeon 1995 first captures (after Sulak and Randall 2002, Fig. 9). Modes in the population have been annotated with approximate year-class year (e.g., 91 = 1991). Approximate age-at-length is based on pectoral fin spine ring count

In sturgeon, survival to age-1 is probably much less consequential than subsequent survival through the subsequent 7–11 juvenile-subadult years before a given year-class contributes to the spawning population. In the early post-harvest ban period in Florida, Rago (1993) estimated a mean annual addition of 517 (95% CI = 367–701 recruits to the Suwannee River adult population for the period of 1987–1991. In a model scenario for the Suwannee River GS population, with parameter values approximating empirical data (i.e., 20% annual natural mortality, 5% of adults spawning, and at least 99.96% egg through age-1 mortality), Pine et al. (2001) predicted an annual addition to the Suwannee River population of approximately 1000 recruits per year. Based on a logistic regression model fitted to abundance estimates through 2007, Sulak and Randall (2009) estimated an annual addition of 500–600 recruits to the adult GS population, conforming closely to Rago's (1993) estimate. These three estimates provide a range of 367–1000 fish per year added to the Suwannee River adult population, providing a basis for projecting future population growth. In any year, 100 females with modest fecundity (300 000 ova) would spawn a total of ~30 million eggs, requiring a survival rate of only 0.17–0.33% to age-1 (age 9–10 months) to result in the range of estimated annual GS juvenile population increment in the Suwannee River.

Thus, while good spawning success and survival to age-1 is an initial hurdle that must be surmounted to form a potential strong GS year-class, that result is not of the overwhelming importance argued by Gross et al. (2002). In a long-lived species with a 'periodic' reproductive strategy (Winemiller and Rose, 1992) and high fecundity, many years of total age-0 year-class failure can be tolerated. Surviving the first winter of estuarine feeding in age-1 yearlings probably represents a much more critical hurdle. How many of those juveniles survive to age-2, gaining sufficient size to be relatively invulnerable to predation and to carry a substantial energy store sets the stage for contributing measurably to the adult spawning population many years later. Huff (1975) reported a minimum age to first gonad ripening of 9 and 12 years, with means of 12.2 and 16.8 years, for males and females, respectively.

From analysis of 19 years of Suwannee River mark-recapture data, Randall and Sulak (2007) found that year-class success in surviving to adulthood (i.e., the formation of a strong year-class) was positively correlated with river flow in September and December for age-1 fingerlings. These authors hypothesized that access to low-salinity estuarine feeding grounds by high-salinity avoiding age-1 GS is greatly expanded during periods of high river flow. Intercepted in the middle Suwannee River during the January-February downriver migration, YOY are very lean (relatively low weight vs TL), having subsisted upon the sparse prey resources of a blackwater river. In contrast, after a few months of winter estuarine feeding, GS transitioning from age-0 to age-1 become heavy relative to body length (i.e., display better 'condition'), with full taut abdomens (M. Randall, USGS, pers. obs.). Access to estuarine benthic macrofaunal prey, twice as abundant and six-fold denser in biomass per unit area than in riverine benthos (Sulak et al., 2007), appears to be key to the success of yearlings foraging in the estuary for the first time. Wet Septembers occur with uneven frequency, depending on the stochastic arrival of late summer or autumn tropical storms. October is predictably one of the driest months of the year in North Florida. It seems probable that high precipitation in September, resulting in high fresh water delivery rate to the estuary, sustained by further mid-winter precipitation to maintain high flow, is perhaps the most critical threshold determining GS year-class success. Supporting the hypothesized high autumn freshwater flow relationship with GS recruitment success (Randall and Sulak, 2007), Scheuller and Peterson (2010) have reported an equivalent flow-related recruitment success paradigm for AS in the Altahama River.

A third critical threshold along the path to sexual maturity is encountered at about age-6 to age-8 when juvenile GS transition to full marine feeding in the open nearshore GOMEX. First marine emigration adds new and substantially elevated mortality risks, including increased predation, exposure to stochastic mortality from storms and red tides, potential failure to transition to different prey, and potential failure to navigate back to the natal river to join the spawning population. Multi-year scientific monitoring of 1192 PIT-tagged hatchery-reared GS (from Suwannee parents) experimentally released into the Suwannee River at age 9 months in 1992 (Chapman et al., 1993) provided evidence (Sulak et al., 2014) of a marked drop in survival rate beginning at age-6, the age of onset of first marine migration.

Mortality due to predators. Field logs of the USGS-WARC (1986–2015) document scientist visual observations of large predators capturing and feeding upon juvenile GS in the Suwannee River, including the Bald Eagle (*Haliaeetus leucocephalus*), Osprey (*Pandion haliaetus*), and American Alligator (*Alligator mississippiensis*). A professional sportfisherman reported to the USGS field biologists that he frequently found juvenile GS in the stomachs of Channel Catfish (*Ictalurus punctatus*) angled in the upper Suwannee River. Juveniles are probably also preyed upon by bullhead catfishes (*Ameiurus* spp.), Bowfin (*Amia calva*), and Flathead Catfish (*Pylodictis olivaris*) in GOMEX rivers, the last species distributed from the Apalachicola River west to the Pearl River. Fishery biologists have observed catfishes in the Mississippi River regurgitating SVS upon capture (W. Slack, USACE, pers. comm.), suggesting that juvenile GS would also be probable catfish prey. However, there has been no systematic investigation of predator fish stomach contents to evaluate predation on GS. Barred owls (*Strix varia*), abundant along GS rivers, were reported by fish farmers as troublesome nocturnal predators of fingerling GS being experimentally raised in ponds in Florida in the early 1990s. Large size and protective scutes do not render adult GS completely immune to predation. USGS field biologists have observed large sturgeon being devoured by alligators, observed scars of unsuccessful alligator attacks in netted GS bearing healed deep impressions of alligator teeth on the head and body, and investigated dismembered carcasses of large sturgeons obviously fed upon by alligators. Sharks are probably important GS predators in the GOMEX. Evidence of partially successful attacks (e.g., large semi-circular bites to the body that have healed, and missing pectoral or caudal fins) have been observed by USGS fish biologists in captured GS. The head and scutes of a GS have been reported from the stomach of a 161 cm FL Tiger Shark (*Galeocerdo cuvier*) caught by an angler off Cedar Key, Florida in 2001 (F. Parauka, USFWS, pers. comm.).

The eggs, free embryos, and larvae of the GS are probably preyed upon by a range of predators that feed opportunistically over open sand substrates, and in upper river mosaic of rock, gravel and sand riffle habitats. These probably include several species of bullhead catfishes, madtom catfishes (*Noturus* spp.), Blackbanded Darter (*Percina nigrofasciata*), and predatory dragonfly (Odonata) larvae. Deng and Xu (1991) and Zhuang et al. (1997) reported that eggs of Chinese Sturgeon (*Acipenser sinensis*) and Dabry's Sturgeon (*Acipenser dabryanus*) are preyed upon by several species of catfishes and cyprinids. Qing (1993) and Gao et al. (2009) reported that the majority (up to 90%) of Chinese Sturgeon eggs deposited below the Gezhouba Dam were consumed by the same types of bottom-feeding fishes. Caroffino et al. (2010) found that freshwater crayfishes (*Orconectes* spp.) consumed an estimated 300 000 LS eggs during the incubation period within the lake sturgeon spawning habitat in the Peshtigo River. Parenthetically, the loss of GS eggs to predators is not without ecosystem benefits and reciprocal trophic benefits to YOY GS. The millions of eggs annually spawned by GS in any natal river undoubtedly represent a substantial caloric transfer to oligotrophic muddy and blackwater riverine ecosystems of energy acquired in estuarine and marine habitats.

Other sources of adult mortality, natural and anthropogenic. Most incidental GS mortalities encountered by field biologists (Parkyn et al., 2006) or reported to state and federal resource agencies by the public have been of single, large adults with no apparent injuries. Old age may be responsible. Occasionally, large old individuals captured display notably poor condition, with discolored skin, a thin and flabby body that is disproportionately emaciated relative to head size (USGS unpubl.). Others appearing otherwise healthy may bear multiple old injuries acquired over a long life, including predator bites, split rostrums in males from courtship rubbing, motorboat prop scars, and missing scutes and deep cuts suggesting monofilament fishing gear entanglement. Other potential sources of mortality are death from angling (Fig. 22), dredge and power plant impingement, boat collisions, and occasional poaching.

Mortality from scientific net sampling and tagging stress was a substantial problem during GS research prior to 2000 (Tatman, 1984; Carr et al., 1996b; Fox et al., 2000) when large mesh commercial nets and long sets were employed. Chapman et al. (1997) reported net mortality of up to 5% in GS catches from anchored 12.7 cm bar mesh gill nets. The combined USGS-WARC database for all multi-agency scientific sampling in the Suwannee River, 1986–1999 documents 425 mortalities, mainly subadults and adults, representing 5.9% of total captures. Removal of that number of potential spawners from the breeding population undoubtedly had a substantial negative impact on population recovery. However, sampling mortality has almost been eliminated by contemporary sampling and tagging methods using small mesh gill nets (≤10.7 cm bar mesh), multifilament rather than monofilament twine nets, and much smaller implanted telemetry tags. Nonetheless, occasional mortalities have been reported following gill net capture or surgical implantation of telemetry tags (Ross et al., 2001b), or upon release after artificial spawning (Parauka et al., 1991). Safe sampling and handling precautions to reduce scientific mortalities, developed by the NMFS (Kahn and Mohead, 2010) in consultation with GS researchers, have now been adopted for most field sampling. Additional measures in common use (not all specified in the NMFS safe handling protocol) include reducing use of anchored gill nets, using less injurious multifilament nets, tending nets continuously, holding landed sturgeon on board in sufficiently large tanks or net pens – or secured on tail ropes in the river – during tagging operations, returning landed fish rapidly to the water after tagging, and suspending sampling and tagging during periods of high (>28°C) water temperatures when GS are otherwise physiologically stressed (W. T. Slack, MMNS, pers. comm., 1999; J. Berg, pers. comm., 2002).

Fig. 22. Juvenile Gulf Sturgeon, 618 mm TL, hooked on catfish trot-line (‘bush-hook’) in the Blackwater River, FL (Berg, 2004, with permission), released by field biologists

Mass mortalities have been observed accompanying red tides and toxic algal blooms, during riverine and estuarine hypoxia following tropical storm flooding, and following toxic chemical spills (Reuters 2011). Large adults seem particularly vulnerable to such stochastic fish kills which can exert a major negative impact on a GS population. Small pods of GS sometimes succumb to stranding in river pools during droughts, if not rescued (World Fishing Network, 2010). Eggs, free embryos, and larvae are also vulnerable to mortality from siltation on spawning grounds and nursery habitat due to stormwater runoff from unpaved roads, construction activities, and unsound riparian agricultural practices.

Aside from acute mass mortalities from a toxic chemical spill (e.g., Reuters, 2011), direct impacts of contaminants upon sturgeon would probably be sublethal, resulting either in impaired growth and physiological function, altered behavior, or impaired or failed reproduction (refer to reports in Berg, 2006). Mortality impacts upon early life history stages (eggs and larvae) from chronic low-level environmental contaminants would be nearly impossible to detect. Those acting upon gonad function would also be difficult to assay in live GS. Such effects upon the GS have not been studied for any life history stage. However, to gain insight into potential impacts of environmental contaminants upon the GS in Florida rivers, USFWS conducted studies to analyze the concentrations of metals and organic pollutants in muscle and blood of juvenile GS, and assess the impact of excessive environmental nutrients (Bateman and Brim, 1994, 1995; Alam et al., 2000). The same agency also contracted a literature synopsis of contaminant impacts upon sturgeon (Berg, 2006) Specific pollution issues in the several GS natal rivers have been briefly detailed in Wakeford (2001). Contaminants or excess nutrients may impact the GS indirectly by altering the abundance and composition of macrofaunal prey (Peterson et al., 2013). Direct and indirect contaminant impacts have received considerable research attention in other North American species, e.g., the White Sturgeon (WS) (*Acipenser transmontanus*), and Green Sturgeon (GRS) (*Acipenser medirostris*) (refer to Hildebrand et al., 2016; Moser et al., 2016 – this volume).

Again, aside from acute fish kills during red tides or from a virulent disease epidemic, the impacts of parasites and diseases upon individual sturgeon or populations are typically subtle, difficult to detect or assess, and in the GS barely studied. In an exhaustive bibliography of all known publications and reports on the GS through August 2015, Price et al. (2015), no studies dealing with GS diseases, and only one with parasites (Heard et al., 2002) were listed. However, most sturgeon species are susceptible to the same fish diseases and parasitic organisms. A good treatment of these issues for the LS is presented in Bruch et al. (2016, this volume).

Mortality impacts upon GS year-class strength

The natural mortality rates estimated for the Yellow, Choctawhatchee, and Suwannee river GS populations (11–17%) after enactment of state harvest bans (Table 1) are mathematically consistent with self-sustaining sturgeon populations

(Boreman, 1997). Higher rates (21–40.5%) determined for the Apalachicola, Pascagoula, and Pearl River GS populations (Table 1) are not (Boreman, 1997; Pine et al., 2001; Tate and Allen, 2002). The highest reported Pearl River rate (40.5%) approaches the mortality rate estimated for the Suwannee River population (46.2%) (Table 1) while GS harvest was still ongoing (Huff, 1975). Commercial bycatch mortality in river trap fisheries, industrial pet food fisheries, and coastal shrimp fisheries, prior to GS harvest bans, state net bans, and the ESA listing has been amply documented (Roithmayr, 1965; Swift et al., 1977; Wooley and Crateau, 1985; Reynolds, 1993; and USFWS, GSMFC and NMFS, 1995). Continued bycatch mortality has been hypothesized as an obstacle to GS population recovery in the Pearl and Apalachicola rivers (Wooley and Crateau, 1985; Kirk et al., 1998; Morrow et al., 1998; Tate and Allen, 2002). Fishery mortality is one of two major sources of mortality identified for sturgeon species in the southeastern U.S. (Collins et al., 2000). Wooley and Crateau (1985) estimated an incidental GS mortality of 7.1% during the autumn and winter commercial shrimp trawl fishery in Apalachicola Bay in the early 1980s. Winter estuarine and coastal feeding presents a period of particular vulnerability to trawl capture and to dredging activities. For example, shrimp trawl operations undertaken to protect and relocate GS during dredging for beach nourishment in winter 2012–2013 yielded 32 GS from the near-shore GOMEX between Pensacola Pass and Mobile Bay (F. Parauka, USFWS, pers. comm.).

However, quantitative evaluation of net bycatch as a major source of GS mortality is impossible due to the lack of GOMEX fisheries observer programs. Nonetheless, a significant positive correlation has been found in the Pearl River population between mortality rate and commercial fishing effort measured as the number of commercial licenses issued (Kirk et al., 1998; Morrow et al., 1998). From the mid-1960s to the mid-1980s, licenses issued increased approximately six-fold. Simultaneously, mean FL of Pearl River GS declined from ~1400 mm to ~750 mm, suggesting size-selective removal of subadults and adults. The mode in the age frequency distribution in the Pearl River in the mid-1990s was comprised of age-3 to age-4 juveniles, with a notably low number of adult GS in the population (Fig. 18).

It is difficult to quantify the indirect but chronic GS mortality impacts from natal river habitat alterations including impoundment, channelization, dredging, and bulkheading. Riverine habitat in the Apalachicola, Pearl and Mobile systems has been highly altered by dams and navigation projects (Wooley and Crateau, 1985). Alterations may limit GS carrying capacity in these systems not only by habitat fragmentation and diminution, but also by reducing flow needed for spawning and larval drift, eliminating deep holding/resting and migration staging areas required by juveniles and adults (Wooley and Crateau, 1985), and diminishing freshwater input. These alterations thereby elevate salinity in estuaries, and periodically contribute to hypoxia during periods of diminished releases through dams. Thus, uncontrolled and/or uncorrected habitat alterations may limit the ultimate success of a promising year-class at various stages in the GS life cycle.

Population recovery – Example of the Suwannee River population

Boreman (1997) determined the fundamental vulnerability of sturgeon populations to varying rates in fishing mortality. Vulnerability to mortality, population trajectory, population viability, and recovery potential recovery of the GS in specific river populations, or theoretically, has been variously explored and modeled (Morrow et al., 1999; Pine et al., 2001; Flowers et al., 2009; Ahrens and Pine, 2014). The theoretical effect of early juvenile mortality upon sturgeon populations has been by evaluated by Tate and Allen (2002) and Gross et al. (2002).

To date, mathematically demonstrable GS population recovery is evident only in the Suwannee River among the seven natal river populations (Table 1). From an 11-year mark and recapture study in the Suwannee River, Chapman et al. (1997) concluded that the GS population was stable at ~3000 subadults and adults, but was not increasing. However, following the harvest ban in 1984, a statistically significant positive response was already evident by 1990–1992 (Fig. 3) (Rago, 1993). Between 1984 and 2012, the population has increased 3–5 fold. The observed rate of population increase plotted from population estimates from the early 1990s through 2006 (Table 1) (Sulak and Randall, 2008, 2009) best fits ($R^2 = 0.9904$) an exponential growth model (Fig. 23). This suggests an absence of density-dependent effects upon population growth through at least 2006. However, application of a biologically more realistic logistic growth model (Sulak and Randall, 2008, 2009) indicates that the Suwannee population will top out at ~15 200 net-vulnerable individuals (~11 200 > 900 mm TL) before 2020 (Fig. 24a). According to this analysis the rate of annual population increase post-1987 has varied according to a polynomial parabolic rate function (Fig. 24b), initially increasing, peaking in 2000–2002, declining thereafter. Adults have accumulated in the recovering population from a low of 25.3% of sampled individuals in 1972–1973 (Huff, 1975), rising to 64.6% in 2006 (USGS-WARC database, N = 404), subsiding

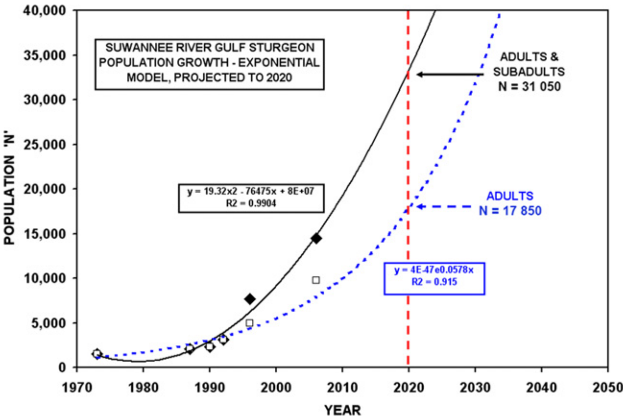

Fig. 23. Suwannee River Gulf Sturgeon population recovery and forward projection (Sulak and Randall, 2008, 2009). Mark-recapture population estimates through 2006 are drawn from Table 1, present manuscript. Data most closely fit an exponential curve model ($R^2 = 0.9904$) when estimates of both adults and subadults were included

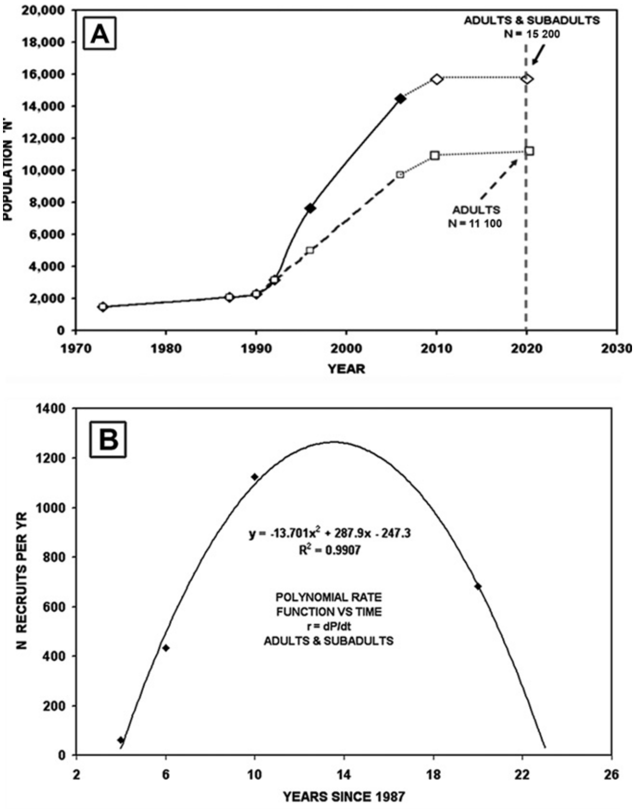

Fig. 24. (a) Suwannee River Gulf Sturgeon population projection, with data from Fig. 21 fitted to a logistic regression model (Sulak and Randall, 2008, 2009). (b) Population growth (number of recruits per year entering the adult population) rate change over time, 1987–2006, fitted to best-fit function = a parabolic (polynomial) function (Sulak and Randall, 2008, 2009)

to 55.5% in 2012–2013 as subadults have also recruited, increasing their proportional representation (USGS database, N = 791) 28–29 years after the harvest ban. The apparently declining juvenile recruitment rate since the peak in 2000–2002 can be hypothesized to represent an inverse response to the accumulation of adults. Indeed, density-dependent Mathusian effects on juvenile survival (i.e., increased mortality rate) can be anticipated in a rapidly growing mixed-age adult population that theoretically produces an increasing number of YOY annually.

Density-dependency seems to be signaled as well by recent expansion of habitat use for spawning (Parkyn et al., 2007; USGS-WARC unpubl. data) and for seasonal holding area (USGS-WARC, unpubl. data) in the upper Suwannee River and major tributaries. Investigations prior to 2002 did not reveal GS spawning or holding activity in these same areas. Two boat collisions with large jumping sturgeons in the Santa Fe River in 2015, (K. Parker, FWC, pers. comm. 7 July 2015) the first ever such reports, confirmed unprecedented adult excursions into that tributary. Detections of five acoustically-telemetered adults well above rkm 225 during the spring spawning period for the first time ever in 2015 are also unprecedented. The same is true for recent adult excursions into the Alapaha River tributary (Fig. 5) over the past decade, resulting in GS strandings during mid-summer low water (World Fishing Network, 2010), and increased public reports of GS in the Withlacoochee River.

Population carrying capacity

The abundance of GS in any natal river, when the population is fully recovered, would ultimately be limited by carrying capacity of present day essential habitat (riverine, estuarine, and coastal marine). Due to landscape use change and riverine and estuarine environmental degradation and eutrophication (Morrow et al., 1998), current carrying capacity can be hypothesized to be substantially lower than it was historically. Comparative analysis of historical fishery data vs contemporary scientific sampling data provides insight into carrying capacity.

Present day GS carrying capacity for all natal river populations can be hypothesized to be diminished from the pre-fished era, particularly due to historical watershed alterations. Based on early historical 1898–1902 landings reports, a GS mean weight in the fishery was estimated as 22.7 kg (above, and Table 3). When used to convert reported landings weights to estimated numbers of fish caught over the 1898–1917 heyday of the fishery (prior to the 1918 crash), the number of GS harvested from the Suwannee River population would equal 26 400–30 800 fish >1000 mm TL (above). Accordingly, a Suwannee River population of 10 000–15 000 would represent 18–31% of the pre-fished Suwannee River GS population in the 1880s. Pine and Martell (2009a,b) estimated that the current Suwannee River population biomass is probably about 20–30% of original pre-fishery (pre-1895) biomass, a surrogate for abundance. Applying a ‘structured Stock Reduction Analysis’ (sSRA) method to the same question, Ahrens and Pine (2014) arrived at a carrying capacity of ~10 000 net-vulnerable GS, closely matching the prior estimate of Sulak and Randall (2008, 2009) and similarly suggesting that the population had already topped out at full carrying capacity by 2014. Ahrens and Pine (2014) based their computations on assumptions which counter knowledge of the early GS fishery and GS habitat requirements. They assumed that the Apalachicola and the Suwannee rivers produced the largest historical GS landings, and thus originally supported the largest GS populations prior to human impacts. They also hypothesized that length of river habitat correlates with carrying capacity, a faulty assumption for an anadromous fish that does not feed within the river, except in the larval and YOY stages. As reported by the Bureau of Commercial Fisheries, the largest early GS fishery catch in the peak year of 1902 did not come from the three longest unimpounded commercially fished GS rivers at the time (the >800 rkm Apalachicola River, the >400 rkm Pascagoula River, or the >390 rkm long Suwannee River [273 rkm long below Big Shoals (Fig. 5), a natural barrier except during high water]. Instead, it came from the ~380 rkm long Escambia River [222 rkm long below the ‘Point A’ Dam near Andalusia, AL (Fig. 12), the location of rapids which were probably a natural barrier to GS prior to dam construction]. In that 1902 banner harvest, the weight of the Escambia River catch was 3.5 times that of the Apalachicola River, 3.1 times the largest ever Apalachicola River landings in 1900, and 5.9 times that of Suwannee River landings in the same year (Townsend, 1901; Alexander, 1905). Thus, river length did not correlate with fishery yield, a surrogate for original GS carrying capacity. Accordingly, river length cannot readily be correlated with GS carrying capacity.

However, Ahrens and Pine (2014) essentially contradicted Pine and Martell (2009a,b) who had earlier concluded that the current Suwannee GS population represented only 20–30% of historical pre-fishery abundance. In contrast to both Sulak and Randall (2008, 2009) and Pine and Martell (2009a,b), Ahrens and Pine (2014) assert that present abundance '… is similar to current estimates of population size suggesting that this population is approaching the pre-exploitation levels'. They concluded that natal river carrying capacity, hypothesized to be a function of river length, has remained unchanged since the 1880–1890s. Ahrens and Pine (2014) advanced that thesis as a basis for setting contemporary population recovery targets for resource managers.

The present authors suggest that this thesis may not be well-grounded and deserves critical scrutiny before being adopted for GS management. Infrequent port surveys and suspected under-reporting by fishermen render the historical landings data unreliable, most probably substantially lower than the actual GS catches. Moreover, the conclusion of unchanged carrying capacity was forced by a fundamentally untested premise that carrying capacity is determined by length of river habitat available as juvenile habitat below the first barrier to migration (among seven river habitat metrics evaluated). However, Ahrens and Pine (2014) erred at the outset in stating that the Apalachicola and the Suwannee rivers produced the largest historical GS landings, and thus originally supported the largest GS populations prior to human impacts. They erred as well in their hypothesized correlation of length of river habitat with carrying capacity (above) for an anadromous fish that does not feed in the river, except for the first year of life.

Nonetheless, based on a CHAAT model analysis of 38 river habitat attributes (Randall et al., 2013), length of free-running river below the first natural or manmade obstacle to GS migration is indeed one of five determinants of whether or not a self-sustaining GS population can exist in a given river in the first place. Moreover, the extent of the freshwater river reach below the first obstruction to migration (otherwise unimportant to subadults and adults) is important to YOY in delimiting nursery habitat. The extent of river reach is improbable as a determinant of carrying capacity of a given river since age-1 and older GS do not feed in the river (Mason and Clugston, 1993; Gu et al., 2001; Sulak et al., 2007). Instead, number and extent of seasonal holding/resting areas (energetic refugia) for GS (Sulak et al., 2007) may be the factor that ultimately limits subadult-adult carrying capacity. Beyond a critical minimum threshold of river length for GS river occupancy, river length is not statistically significant to recruitment of juveniles to the overall river population (Randall et al., 2013). Neither river length, nor any of the other model habitat metrics used by Ahrens and Pine (2014) determines carrying capacity. A more probable determinant is the extent of oligohaline to mesohaline shallow estuarine habitat available to age-1 to age-6 juvenile GS during the critical winter feeding period that is important. Success in growth, survival, and ultimate recruitment of juveniles depends on volume of river outflow in autumn and winter (Randall and Sulak, 2007), i.e., the effective dilution of GOMEX marine waters as a determinant of the areal extent of the estuarine feeding zone. Volume of freshwater outflow determines the size of low to medium salinity area in the estuary and adjacent shallow GOMEX available to salinity-intolerant juvenile GS (which may be smaller or larger than the geographic area of a given bay or sound). In particularly favorable winters, high Suwannee River outflow extends the 'estuary' into the GOMEX well beyond the fringing oyster reef, the normal physical barrier to influx of high salinity marine water. A high rate of delivery of fresh water probably insures optimal dissolved oxygen conditions on the feeding grounds. Paralleling the conclusions of Randall and Sulak (2007), but for juvenile AS in the Altamaha River, Georgia, Scheuller and Peterson (2010) similarly determined that 'fall discharge was the only predictor variable that significantly explained variation in annual year-class strength.'

Habitat and trophic requirements and preferences

Food habits and feeding chronology

Free embryo, larvae and YOY food habits. The hatchling GS free embryo emerges from the egg membrane in late-development, but is still dependent upon the yolksac for nutrition, and lacking respiratory organs. The yolk of sturgeon eggs is a rich, high-energy food source. In terms of percent composition by weight, eggs of commercially cultured sturgeons are composed of 48–56% crude protein dry weight (including up to 28 amino acids) and 24–31% lipids (Gong et al., 2013). Free embryos of the GS initially avoid light and seek dark cover (Kynard and Parker, 2004) under gravel, a behavioral stage typical of the free embryos of several other sturgeon species. In this regard, Boglione et al. (1999) have reported that the newly hatched free embryos of Adriatic Sturgeon (*Acipenser naccarii*), are similarly photonegative. Laboratory hatched GS free embryos emerge at 6.6–8.3 mm long and weigh ~8.0 mg (Parauka et al., 1991; Bardi et al., 1998). Free embryos do not swim or disperse upon hatching. They seek cover (Kynard and Parker, 2004), hiding beneath spawning ground gravel, lying on their sides and vibrating the tail to facilitate gas exchange. Only four GS free embryos, with their habit of hiding interstitially among spawning ground gravel, have been collected in the wild (Table 4).

Exogenous feeding begins with the free-swimming GS larval stage (sensu Kynard and Parker, 2004), about 5–8 days posthatch at a TL of 14.7 mm (Bardi et al., 1998; Kynard and Parker, 2004). The melanin plug at the posterior end of the alimentary canal is shed within one day of initiation of feeding (Bardi et al., 1998). First feeding larvae, ca 15.5–17.5 mm TL (Bardi et al., 1998) disperse downstream and initiate drift foraging. During downstream dispersal, GS larvae display an optionally benthic-pelagic mode of plankton feeding, which by day 10 becomes largely pelagic, swimming at an altitude of 40–90 cm above bottom (Kynard and Parker, 2004). This distinctive larval feeding ontogeny appears to be unique to the GS among other sturgeon species investigated (Kynard and Parker, 2004). When larvae swim up into the water column, they maintain position facing into the current, suggesting a visual, drift-plankton foraging mode. Laboratory-reared GS larvae readily consumed brine shrimp (*Artemia* sp.) nauplii (Foster et al., 1995; Bardi, 1997; Bardi et al., 1998). The presence of brine shrimp nauplii and cysts elicited strong larval swimming and searching behavior in the water column (Bardi et al., 1998). In the early larvae of the Russian Sturgeon (*Acipenser gueldenstaedtii*), Boiko et al. (1993) have shown that chemical imprinting, either olfactory or gustatory (or both), over the developmental interval of yolksac larvae (free embryos) is important in subsequent food acceptance by exogenous-feeding sturgeon larvae.

Free embryos and early YOY use a pause-move foraging mode while gradually migrating downstream, facing into the current and maintaining position while feeding, turning to face downstream when moving (Kynard and Parker, 2004). By age ~50 days, GS YOY transition to a fully benthic (ventrum parallel to the substrate, barbels skimming the sand) foraging mode. The YOY extended downstream migration lasts for at least 5 months (Kynard and Parker, 2004). During the first 10 months of life in freshwater, YOY probably consume primarily aquatic insect larvae (Mason and Clugston, 1993). In the laboratory YOY attain a uniformly dark pigmentation by age 85 days (Kynard and Parker, 2004). Wild GS of age 2–4 months from the Suwannee River are jet black (dull charcoal-black) dorsally and laterally, and have the underside of the rostrum level with the underside of the abdomen (Fig. 1d). The few black-stage YOY obtained in trawls in this river (N = 5, 82–149 mm TL) have always been found in association with masses of blackened decaying leaf and twig debris (USGS-WARC, unpubl. data). The same association has been observed (W. T. Slack, USACE, pers. comm.) for three black-stage YOY collected by trawl in the Apalachicola River (Kirk et al., 2010). This habit suggests a cryptic and perhaps sedentary existence in the black color phase. The snout and abdomen present one continuous flat horizontal surface, suggesting the use of currents to maintain a fixed position by hydrodynamically appressing the body against the substrate. Decaying vegetative litter, accumulated in swales, crevices, and depressions in the riverbed, is inhabited by epibenthic invertebrates such as gammarid amphipods and aquatic insect larvae that are probable black-stage YOY prey (Mason and Clugston, 1993). Larger bicolored-stage YOY (Fig. 1e) display the brown to gray above, off-white below counter-shaded pattern typical of adults, and have the underside of the rostrum notably angled up relative to the underside of the abdomen. The shift from black-stage YOY to bicolored-stage YOY probably accompanies a switch to mobile foraging on open sand substrate in the river (Sulak and Clugston, 1999). Observations of bicolored-stage YOY show that they use the up-tilted snout like a kite when lifting off the substrate into a current (K. Sulak, USGS-WARC, pers. obs.).

Allen et al. (2014) have identified salinity as a potential constraint on juvenile AS habitat use. That is, osmoregulation in high salinity waters exacts an energetic toll in terms of growth rate and weight gain. In the GS, early YOY confine their feeding to freshwater reaches of the natal river (Table 6). At age 10–11 months (late January-early February) spring-spawned YOY migrate to the estuary for the first time (Sulak and Clugston, 1998, 1999) to initiate a lifelong seasonal cycle of winter feeding in saline waters, followed by fasting in freshwater (Mason and Clugston, 1993; Gu et al., 2001; Sulak et al., 2012). Juveniles up to 900–1000 mm TL (~age-6) confine winter feeding to oligohaline to mesohaline estuarine waters. Except for a small percentage of juveniles and subadults that continue to feed during the post-immigration and pre-emigration periods, all feeding in freshwater ceases after the YOY stage (Sulak et al., 2012).

Few YOY have been examined for stomach contents or isotopic evidence of food sources. Thus, knowledge of prey consumed by is very limited. One 300 g YOY from rkm 221 in the Suwannee River contained insect larvae (mayflies, chironomids, and three other insects), a bivalve, detritus, and biofilm (Mason and Clugston, 1993). Gammarid amphipods are also important YOY GS prey (Mason and Clugston, 1993) as is true larger GS juveniles (Huff, 1975), and for several other sturgeon species (Dadswell, 1979; Holcik, 1989; Nigro, 1991; Hatin et al., 2007). Stable isotope analysis of muscle tissue from two YOY confirmed a diet based entirely on terrestrial carbon from freshwater prey (Sulak et al., 2012).

Juvenile, subadult and adult food habits. Marine and estuarine prey eaten by age-1 (spring-spawned GS are actually 8–9 months old upon migration to the estuary) and older GS have been analyzed directly from stomach contents using harvested fish (Huff, 1975), sacrificed individuals (Mason and Clugston, 1993), and mortalities from netting or tagging (Carr et al., 1996b; Fox et al., 2000). Stomach contents have been analyzed by gastric lavage (Haley, 1998) of live adults netted on winter feeding grounds (Murie and Parkyn, 2002; Harris, 2003; Harris et al., 2005), and released thereafter. Much of the available evidence of GS food habits comes from stomach contents of large individuals netted during the spring immigration, still retaining food items from recent marine and estuarine feeding (Huff, 1975; Mason and Clugston, 1988, 1993; Carr et al., 1996b; Peterson et al., 2013).

Mason and Clugston (1993) hypothesized that GS store sufficient energy during feeding in saline waters such that they become ‘indifferent’ to feeding upon riverine prey. They found that most juveniles and subadults sampled in freshwater reaches of the Suwannee River had empty stomachs. Sparse prey resources in light-limited, low productivity tannic and muddy Gulf Coast rivers render freshwater foraging energetically mal-adaptive beyond the YOY stage. Cessation of feeding in freshwater represents an accommodation to the energetic expense of active foraging for macrofaunal prey that is four times less abundant, and six times lower in biomass, per unit area in freshwater reaches, than in the estuary (Sulak et al., 2007). Stable carbon isotope studies confirm that, beyond the larval and YOY stages, most GS cease to feed in freshwater, and subsist almost exclusively on prey of estuarine and marine origin (Gu et al., 2001; Sulak et al., 2012). Nonetheless, Sulak et al. (2012) found that 6% of juveniles and subadults (600–1400 mm TL), but no adults,

Table 6
Post-larval and age-0 YOY (>25 mm TL, ≤450 mm TL) Gulf Sturgeon captured or reported from freshwater reaches in all natal rivers, 1972–2015

River	N	TL (mm)	Date range	Location (rkm or rkm range) [tributary]	Conductivity (μS cm^{-1})	DO (mg L^{-1})	Temp (°C)	Substrate	Depth (m)
Captures in Scientific Sampling:									
Apalachicola[a]	1	264	8/10/1976	9.6 [Jackson River]	—	—	28.0	—	—
Apalachicola[b]	2	445, 445	8/06/2006–9/28/2006	~23 [Brothers River]	—	—	—	—	—
Apalachicola[c]	1	32	5/–/2008	~23 [Brothers River]	—	—	—	—	—
Apalachicola[d]	3	60–125	6/11/2009	~23 [Brothers River]	—	—	—	—	—
Apalachicola[e]	2	38, 30 FL	5/06/2013	~13 [East River]	—	—	—	—	—
Choctawhatchee[f]	1	(~7 in TL) ~178 mm TL	1957	Below Geneva, AL	—	—	—	—	—
Choctawhatchee[g]	7	222–427	6/23/1990–8/29/2007	~35–~125	—	—	—	—	—
Choctawhatchee[h]	6	152–419	10/–/1974–7/–/1992	~69–~125	—	—	—	—	—
Escambia[i]	2	80 149	6/21/2010–7/21/2010	~70	109	8.1	32.0	Sand, gravel & detritus	0.70–0.75
Pearl[j]	53	370–450	6/19/1985–9/30/2009	0–80	—	—	—	—	—
Suwannee[k]	56	82–449	6/29/1989–12/06/2006	12.5–237.5	89–385	1.6–8.8	14.2–28.0	Sand to leaf litter	0.5–7.5
Suwannee[l]	7	176–310	8/23/1993–9/17/1993	~213	—	—	22.0–23.9	Coarse to muddy sand	~1.0
Suwannee[m]	2	306, 313	12/02/1991–1/14/1992	215–237.5	—89	—8.5	17.2–14.2	——	——
Suwannee[n]	1	422	8/28/1990	221	—	—	—	—	—
Suwannee[o]	1	152	9//17/1990	213	—	—	—	Sand flat	0.70
Suwannee[o]	1	114	8/09/1990	210	—	—	—	Sand flat	—
Suwannee (Santa Fe)[p]	1	426	12/06/2006	142 [Santa Fe River]	—	—	—	—	—
Suwannee (Santa Fe)[q]	1	250 TL234 SL	1/–/1974	129 [Santa Fe River]	—	—	—	—	—
Yellow[r]	1	313	4/19/2000	~50	—	—	—	—	—
Yellow[s]	1	300 TL 261 FL	11/4/2003	~72	72	8.7	20.3	Fine sand, silt	0.2
Yellow[t]	1	~150	Late 1990s	~134	—	—	—	—	—
Visual Field Observations:									
Choctawhatchee[h]	2–3	280	–/–/1972	~97	—	—	—	—	—
Mobile[u]	2	381, 440	–/–/1970	~50	—	—	—	—	—
Suwannee[k]	1	~356	–/–/1989	~162	—	—	—	—	—
Suwannee[l]	40	~100–300	8/23/1993–9/17/1993	~213	—	—	22.0–23.9	Coarse sand to muddy sand	~1.0
Suwannee[v]	1	~203	–/–/1994	289	—	—	—	—	<0.5

Table 6
(Continued)

River	N	TL (mm)	Date range	Location (rkm or rkm range) [tributary]	Conductivity (μS cm^{-1})	DO (mg L^{-1})	Temp (°C)	Substrate	Depth (m)
Suwannee[w]	1	~125	8/30/1993	184	360	5.2	25.0	—	—
Suwannee[x]	1	350	5/31/1995	184.5	—	—	23.0	Fine sand	1.0
Yellow[t]	2	~150	Late 1990s	~134	—	—	—	—	—
All rivers: all records	196–197	32–449	–/–/1957 12/6/2006	0–289	72–385	1.6–8.8	14.2–32.0	Mainly sand	0.2–7.5

Total YOY collected ≤450 mm TL from all rivers from 1974 through 2015 = 151 (excluding visual records); subtotal ≤150 mm TL = 17. Length of three specimens was measured as SL or FL instead of TL. Location is determined from the mouth of the mainstem river of the system. rkm = river kilometer.

Data sources:

[a] Wooley and Crateau (1982), a mid-summer record from brackish water.

[b] USFWS data unpubl.

[c] R. Lehnert, FWRI, pers. comm.

[d] Kirk et al. (2010).

[e] FWC, A. Smith pers. comm. to USFWS, May 2013 (including photographs of trawled specimens).

[f] J. Barkuloo, USFWS, pers. comm. to J. Clugston, USFWS, 18 December 1986.

[g] USFWS data unpubl.; USGS Choctawhatchee River database through 6 November 2008, unpubl.

[h] Reynolds (1993).

[i] S. Rider, ADCNR, pers. comm., 2010 (including photographs).

[j] USGS Pearl River database through 30 September 2009, unpubl. (including three records from potentially brackish water near the mouth of the Pearl River).

[k] Sulak and Clugston (1998); USGS Suwannee River database through 31 December 2015, unpubl. (including records from Reynolds, 1993).

[l] Carr et al. (1996a)

[m] Clugston et al. (1995).

[n] Mason and Clugston (1993).

[o] FWC officers, pers. comm. to USFWS J. Clugston, USFWS, 1990 (FWC hand caught and angler caught YOY); USGS Suwannee River database through December 2015, unpubl.

[p] Flowers and Pine (2008).

[q] Reynolds (1993); Cited in Flowers and Pine (2008): Florida State Board of Conservation (FSBC), FWRI Museum Collection number F08847, St. Petersburg, FL; USGS database unpubl.

[r] M. Mettee, AGS, pers. comm. to USGS, 13 January 2005 (including photograph).

[s] USGS field log record, 4 November 2003; Berg (2004, Fig. 9); M. Randall, USGS, pers. comm.

[t] Berg et al. (2004), based on P. Kilpatrich, ADCNR, pers. comm.

[u] Reynolds (1993); USGS Mobile River database through March 2008, unpubl.

[v] M. Williams, Univ. Florida, pers. comm. to USGS Sulak, 1996.

[w] S. Marchant and M. Shutters, pers. comm. to USFWS, 1993.

[x] USGS field log record, 31 May 1995.

continued to feed for 1–3 months after spring immigration from saline waters, or resumed feeding in freshwater prior to autumn emigration. It may be hypothesized that such smaller individuals are not always able to store enough energy during the winter feeding period to suffice for multiple months of fasting. Further evidence of juveniles feeding in freshwater (captured on baited hook and line) has been reported (Burgess, 1963; Berg, 2004). Mason and Clugston (1993) found that the stomachs of 5–17 kg GS from middle reaches of the Suwannee River were either empty (29 of 40 examined) or contained a small number of freshwater prey. Predominant prey included aquatic insect larvae (chironmids and mayflies), and oligochaetes. Occasional gastropods and amphipods were found along with greenish mucus, detritus, and sand. As the GS abundance increases in recovering populations, and particularly following poor food resource years on estuarine and marine feeding grounds, freshwater feeding may become more common.

Aside from certain juveniles or subadults, a small subset of individuals within a population, or a large segment of an entire GS river population may deviate from the overall species norms, adapting to local natal river or estuary conditions, including food resources. Thus, Fox et al. (2002) reported that some Choctawhatchee River adults may not migrate offshore to feed in winter, but instead remain within Choctawhatchee Bay, which is sufficiently populated by ghost shrimp and haustoriid amphipods to sustain the entire GS population (Heard et al., 2000, 2002). More recent and robust telemetry data (Fleming, 2013) indicate that about 20% of the population remains in the bay in winter. Similarly, Duncan et al. (2011) reported extended periods (up to 80 days) of GS winter residency within Santa Rosa Sound (as opposed to feeding in the open GOMEX), the mesohaline seaward backbay extension of the Pensacola Bay estuary.

Dietary breadth is wide in the GS, with species from at least 24 major taxa being consumed (Mason and Clugston, 1993). Peterson et al. (2013, supplemental material) provide a compendium of documented GS prey by drainage and life history stage. However, a much smaller suite of prey taxa predominate in the diet. Among the marine food items preferentially selected by subadult and adult GS are soft-bodied invertebrates (Mason and Clugston, 1993), including brachipods (*Glottidia pyramidata*), ghost shrimp (*Lepidophthalmus louisianensis*), lancelets (*Branchiostoma caribaeum*), and gammarid amphipods (Boschung and Mallory, 1956; Carr, 1983; Carr et al., 1996b; Fox et al., 2000; Murie and Parkyn, 2002), while amphipods, polychaetes, and other smaller benthos are important in the estuarine diet of juvenile GS. Additional prey available to and probably consumed by juvenile, subadult and adult GS feeding in marine, estuarine and oligohaline river mouth waters include other amphipods (Haustoriidae, Corophiidae, Amplescidae), cumaceans, isopods (*Cyathura*), mysids, grass shrimp (*Palaemonetes*), insect larvae (Chironomidae, Ceratopogonidae), polychaetes (Arenicolidae, Nereidae, Orbiniidae, Sabellidae, Capitellidae), oligochaetes (Tubificidae), brittlestars, starfishes, keyhole urchins (*Mellita*), sea cucumbers, globular bivalves (Cardidae, Tellinidae), gastropods, small fishes, decapod crustaceans, bryozoans, diatoms, fibrous plant material, filamentous algae, and detritus (Boschung and Mallory, 1956; Huff, 1975; Mason and Clugston, 1993; Heard et al., 2002; Murie and Parkyn, 2002; Ross et al., 2009; Peterson et al., 2013).

Certain prey types appear to generally be avoided by GS. Thus, despite the abundance and availability of hard-shelled benthic organisms [e.g., the freshwater snail (*Elimia floridensis*), the freshwater Asiatic clam (*Corbicula fluminea*), and numerous estuarine and marine bivalve species] in GS habitats, such organisms are minor items in the diet. The same is true for species armed with sharp projections, like the blue crab (*Callinectes sapidus*), except that crabs in the softshell or parchment shell stages may be important prey. Also under-represented in GS stomach contents are encrusting organisms or those inhabiting hardened tubes (Mason and Clugston, 1993). Certain abundant polychaetes (e.g., *Laeonereis* and Ampharetidae), as well as fishes, are also apparently avoided as prey. Small fishes have been reported, but only as minor GS stomach contents (Huff, 1975; Mason and Clugston, 1993).

As in most other bottom-feeding sturgeon species, the GS depends upon suction-feeding (Carrol and Wainwright, 2003) to accomplish prey ingestion through a highly-protrusible siphon-like mouth Miller (2004). This mode of feeding places a limit on the maximum size of prey that can be ingested (Mason and Clugston, 1988) at any given life history stage. It would generally be ineffective for capture of wary, large, or highly-mobile organisms. Thus, GS necessarily display size-limited prey selectivity, with emphasis on small benthic invertebrates of low mobility. Moreover, even large adults of most sturgeon species continue to consume very small prey items (Miller, 2004). The tubular mouth in the GS is relatively narrow (compared to head width at the level of the mouth) and nearly circular in cross-section when protruded. This morphology corresponds with a diet dominated by small invertebrates. In contrast, sturgeon species that feed more extensively on fishes, like the LS (Stelzer et al., 2008; Bruch et al., this volume), PS (Coker, 1930; Carlson et al., 1985; Jordan et al., 2016, this volume), and WS (Galbreath, 1979) have a relatively much wider mouth with a more elliptical cross-section.

Benthic macrofaunal sampling to identify high prey density areas with in combination with acoustic telemetry to define GS habitat use areas has been applied to circumscribe juvenile winter feeding areas within the Suwannee estuary (Edwards et al., 2003; Brooks and Sulak, 2005; Sulak et al., 2009a) and in the Pascagoula river mouth estuary (Peterson et al., 2013). Similarly coupled methods have defined probable adult feeding areas in the nearshore GOMEX off the Suwannee River (Harris, 2003; Harris et al., 2005), in Choctawhatchee Bay (Fox et al., 2002; Heard et al., 2002), in Mississippi Sound (Rogillio et al., 2007; Ross et al., 2009), and in the Pascagoula river mouth estuary (Peterson et al., 2013, 2016). In Choctawhatchee Bay deeply-burrowing shrimp have been hypothesized to represent the dominant food item of subadult and adult GS (<1000 mm TL and 10 kg) wintering in Choctawhatchee Bay (Heard et al., 2000, 2002; Fox et al., 2002), and in Mississippi Sound (Ross et al., 2009). Ghost shrimp density has been estimated at

20 individuals m^{-2} or a total abundance in that shallow bay of ~500 million (Heard et al., 2002). Also important as food items are the alpheid shrimp (*Leptalpheus forceps*), a commensal living in ghost shrimp burrows (Fox et al., 2000, 2002) and haustoriid amphipods (*Lepidactylus* spp.), abundant inhabitants of sandy substrate. Heard et al., 2002 reported that the stomach of a single adult GS mortality from Choctawhatchee Bay contained 65 adult ghost shrimps and 100 haustoriid amphipods. Ghost shrimps may be important winter prey in other mesohaline coastal bays and estuaries as well (Carr et al., 1996b). Fox et al. (2000) reported adults from marine waters captured upon re-entry into the Choctawhatchee River in spring expelled large numbers of blue crabs and ghost shrimp.

Contrary to expectations, Fox et al. (2002) found a negative spatial correlation between benthic infaunal (macrofaunal) density (abundance m^{-2}, excluding ghost shrimp) and density of relocations of acoustically-tagged GS in Choctawhatchee Bay during the winter feeding season. While depth, salinity, and vegetation were habitat factors at play, this correlation nonetheless suggests that when ghost shrimp are abundantly available, smaller macrofaunal invertebrates were ignored. These authors hypothesized that deep-burrowing ghost shrimp, not captured in benthic grabs, are vulnerable to powerful GS suction-feeding. Where ghost shrimp are less prevalent, GS may selectively target alternate preferred prey.

A strong positive spatial correlation between the density and biomass (per m^2) of brachiopods (*G. pyramidata*) and concentrations of telemetry relocations of acoustically-tagged subadult GS was reported in the nearshore GOMEX off the Suwannee River (Harris, 2003; Harris et al., 2005). Carr (1983) and Mason and Clugston (1993) had earlier reported brachiopods and lancelets as important GS food items, among an array of estuarine and marine prey items. Heard et al., 2002 hypothesized that razor clam (*Tagelus plebius*), lugworm (*Arenicola cristata*), and acorn worm (*Balanoglossus* sp.), three large and very abundant macroinvertebrates, may be exploited by GS in Choctawhatchee Bay. However, based on GS telemetry, Fleming (2013) reported that juvenile and subadult occupancy in the bay appeared to be positively correlated with amphipod abundance. Harris (2003), Harris et al. (2005), and Peterson et al. (2013) reported a significant positive correlation between GS telemetry relocations and estuarine areas of highest abundance and biomass of brittle stars (*Amphipholis* and *Ophiactis*), bivalves (*Corbula, Crassinella*, and *Parvilucina*), and crabs (*Euryplax* and *Portunus*). However, such a correlation may simply denote rich substrate areas that are generally densely populated by multiple species of macroinvertebrates and by GS, rather than identifying a GS prey preferences. Nonetheless, density and spatial concentration (clumping) of benthic prey, both of which change seasonally, may be important factors in selectivity. What Chiasson et al. (1997) have elegantly written for LS is equally true for GS. That is, they are: '...generalist, opportunistic predators foraging almost exclusively on macroinvertebrates.' At any given time and location, GS opportunism may be expressed in targeting the most abundant prey available, in effect prioritizing the maximum biomass return for foraging effort. Thus, in both spring and autumn, Harris (2003) found a significant positive correlation between GS telemetry relocations and abundance and biomass per unit area of brachiopods. Autumn relocations in 2001 were similarly correlated with abundance and biomass of the brittle stars *Amphipholis* and *Ophiactis*; the molluscs *Corbula*, *Crassinella*, and *Parvilucina*; and the crabs *Euryplax* and *Portunus*. However, spatial correlations between GS locations and potential prey abundance and biomass in spring 2002 shifted to the amphipod *Ampelisca* and the clam *Ensis*. A high positive correlation was found between frequency of Suwannee River population GS relocations (76.4–86.4%) and sand substrate, identifying the preferred nearshore marine feeding habitat of subadult and adults. In the same nearshore region off the mouth of the Suwannee River, Sulak et al. (2008) reported spatial congruence between areas of high overall benthic infaunal density (Brooks and Sulak, 2005) in sand substrate and areas of high-use habitat by juvenile GS (Sulak et al., 2008; Figure 9) (Fig. 25). On the other hand, for GS from the Pascagoula River and Pearl River populations, Peterson et al. (2013) reported an affinity for marine sediments with high silt and clay fractions. Overall, findings from coupled GS telemetry and benthic prey resource quantification studies suggest GS target densely populated patches of individual benthic prey taxa of proportionally high biomass per individual prey item. Open, unstructured habitat is preferred, either sand or silt/clay, depending upon density of contained benthic prey. McLelland and Heard (2004, 2005) analyzed the benthic macrofauna at two Florida coastal sites (off Perdido Key near the Florida-Alabama border, and off Panama City) where winter foraging concentrations of GS have been identified by telemetry (Edwards et al., 2007; Parauka et al., 2011). The benthos sampled by both conventional bottom grabs and corers and 'Yabby' suction pump samplers was dominated by polychaete worms. However, bottom grabs are unsatisfactory for collection of deep-burrowing ghost shrimp, which have been effectively sampled only with the 'Yabby' sampler (Heard et al., 2000; McLelland and Heard, 2004, 2005).

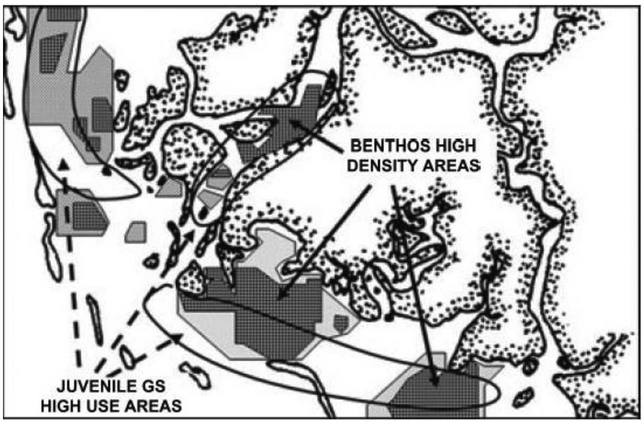

Fig. 25. Spatial correspondence between areas of densest concentrations of potential Gulf Sturgeon benthic prey (dark shading) and areas of highest juvenile use (ellipses) from acoustic telemetry in the Suwannee river mouth estuary, winter 2007–2008 (adapted from Sulak *et al.* 2008, Fig. 9)

Most adult GS feed in marine waters in winter, with individuals from different river populations often congregating in the same localized areas. Thus, acoustically-tagged Pearl River and Pascagoula River adults from the westernmost natal rivers depart summer riverine habitat, rapidly traverse Mississippi Sound, and then co-occupy winter feeding ground in the passes between and shoals around GOMEX barrier islands for several months (Ross et al., 2009). These feeding grounds have been found to be richly supplied with benthic prey preferred by GS, prominently including lancelets (*Branchiostoma floridae*). In the middle of the species range, GS adults from several populations (Escambia, Yellow, Blackwater and Choctawhatchee rivers) congregate in a 45 km stretch of GOM coastline from west of Pensacola Pass to east of Mobile Bay (Parauka et al., 2011). Further east, GS adults from several Florida populations (Apalachicola, Choctawhatchee, Blackwater, Yellow, and Escambia rivers) co-occur along a 25 km stretch of coastline from offshore of Panama City east to Mexico Beach (Edwards et al., 2007; Parauka et al., 2011). Rakocinski et al. (1993, 1998) reported very high densities of lancelets off both Perdido Key and Santa Rosa Island. It has been hypothesized that such winter GS concentrations, often panmictic, are driven by benthic prey availability (Edwards et al., 2003; Ross et al., 2009), as similarly suggested for winter offshore concentrations of AS (Stein et al., 2004). The winter distribution of Suwannee River GS presents an exception, spreading along the West Florida shelf to the south and northwest, but rarely far enough northwest to mix with GS from natal river populations west of Apalachicola Bay.

While the open nearshore GOMEX is the ultimate winter feeding habitat for adults, their first stop upon leaving natal rivers is often the same estuary used by juveniles. Thus, several telemetry studies (Carr et al., 1996b; Edwards et al., 2003; Parkyn et al., 2007), have determined that Suwannee River adults stayed in Suwannee Sound estuary for 2 weeks–3 months before leaving for the open GOMEX. Rogillio et al. (2001) reported that Pearl River adults spent 2–49 days in the brackish waters of the Rigolets before moving out to Mississippi Sound. An extended period of initial adult winter feeding within mesohaline estuaries is also known from Choctawhatchee Bay (Parauka et al., 1991; Fox et al., 2002) and the Pascagoula River estuary (M. Peterson, GCRL, pers. comm., August 2016). However, acoustically-tagged adults in the Apalachicola River rapidly traversed Apalachicola Bay, exiting into the GOMEX (Sulak et al., 2009a).

In both saline and riverine environments, habitat attributes influence GS behavior and thus prey selectivity, regardless of availability of potential prey. Thus, Sbikin and Bibikov (1988) reported that juvenile sturgeon observed in aquaria avoided vegetation, suggesting that sturgeon avoid structured habitat that may impede orientation and movement. Diver observations confirm avoidance of submerged vegetation in juvenile LS (Kempinger, 1996), and much lower use of cobble-wood foraging habitat vs open sand habitat. Clean, medium grain size sand appears to be the preferred GS feeding habitat. Fine, coarse, and muddy sand are utilized much less frequently in Florida (Harris, 2003), but not in western populations (Peterson et al., 2013). However, regardless of prey availability and substrate preference, anthropomorphic habitat alteration may alter where GS feed. Thus, Peterson et al. (2013) have suggested that urbanization and industrialization in the estuarine mouth of the Pascagoula River may reduce GS use of feeding habitat in the eastern distributary of that river.

Subadult and adult GS are tolerant of full GOMEX salinity and use coastal bays and nearshore coastal habitats in depths generally <10 m as primary winter feeding habitat (Fox et al., 2002; Edwards et al., 2003, 2007; Ross et al., 2009; Parauka et al., 2011). Important nearshore wintering grounds are soft substrate (sand, mud, or muddy sand) areas supporting a rich prey base of macrofaunal benthos (Fox et al., 2002; Brooks and Sulak, 2005; Harris et al., 2005; Ross et al., 2009). However, it is currently unknown if GS occasionally or routinely descend to greater depths where similar soft substrate habitat occurs. The closely-related AS in the Atlantic Ocean has been documented from depths as great as 40–110 m by trawling (Timoshkin, 1968; Collins and Smith, 1997). In the Bay of Fundy, AS occupy depths primarily between 40–70 m (with a maximum of 120 m) from November to April based on depth-recording satellite telemetry tags (Beardsall et al., 2016). Other anadromous sturgeon species including the GRS (Erickson and Hightower, 2007) and the European Sturgeon (Rochard et al., 1997) descend to and forage at depths of 100 m. Holcik (1989) reported that in the Caspian Sea Stellate Sturgeon (*Acipenser stellatus*) occur down to 100–130 m and Siberian Sturgeon (*Acipenser baerii*) down to 100–150 m. In the Black Sea Russian Sturgeon descend as deep as 140 m (Holcik, 1989). Khodorevskaya and Krasikov (1999) have reported that Russian Sturgeon occur to depths of 60 m, Stellate Sturgeon to 80 m, and juvenile Beluga (*Huso huso*) to 100 m. Watanabe et al. (2008) used accelerometer tag telemetry to monitor routine locomotion in Chinese Sturgeon at maximum depths 106–122 m. These several reports suggest a maximum biomechanical depth of 100–150 m for physostomous sturgeons. That is, in order to maintain buoyancy control at depth (Watanabe et al., 2008), sturgeon must return to the surface periodically to replenish swimbladder gas. It is probable that GS are thus capable of descending to and foraging at comparable depths. Whether deep feeding behavior actually occurs is probably determined by coastal bathymetry and prey availability as suggested for the AS (Stein et al., 2004). Potential GS use of GOMEX offshore habitats in depths >20–30 m is an important question that remains to be researched.

Feeding chronology (seasonal and ontogenetic): The annual trophic cycle of the GS may be visualized as a ‘trophic ratchet’, a pattern of alternating winter weight gain while in saline waters vs spring-to-autumn weight loss while in riverine freshwaters (Sulak and Randall, 2002). This pattern (Fig. 26a–c) was first observed by Carr (1983), quantitatively evaluated by Wooley and Crateau (1985), and definitively confirmed by subsequent studies (Clugston et al., 1995; Ross et al., 2002; Sulak and Randall, 2002). Several mark-recapture investigations have shown dramatic weight gains within a single winter season (Fig. 27a–b), ranging up to 137%

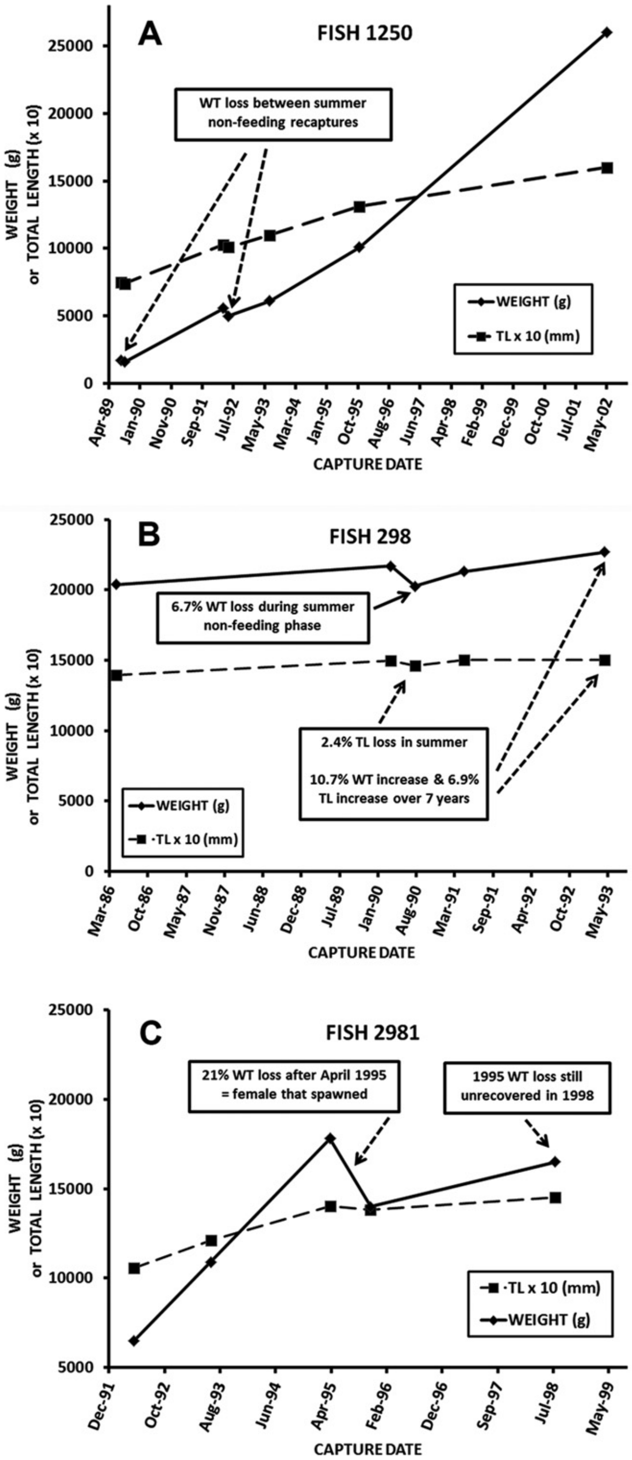

Fig. 26. 'Trophic ratchet' pattern of weight gain in multiply-recaptured Suwannee River Gulf Sturgeon (after Sulak and Randall, 2002): (a) Winter gain alternating with summer loss over 13 years in a putative female (>1500 mm TL); (b) Same over 7 years but for a putative male topped out <1500 mm TL; (c) Putative small adult female that spawned in April 1995, losing 21% weight, lost not fully regained by 3 years later

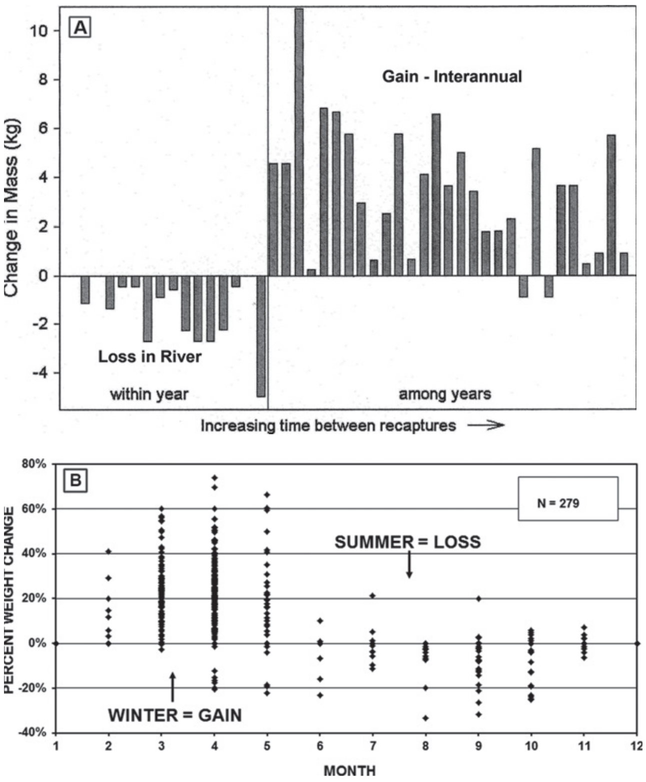

Fig. 27. Seasonal pattern of winter weight gain alternating with summer weight loss in the Gulf sturgeon populations, based on tagged and recaptured fish: (a) Pascagoula River (after Ross *et al.* 2002, Fig. 4, courtesy of Mississippi Department of Fisheries, Wildlife and Parks, and the Mississippi Museum of Natural Science), (b) Suwannee River (after Sulak and Randall, 2002, Fig. 3)

(Wooley and Crateau, 1985), followed by more modest seasonal losses of 0–40% during the period of trophic dormancy (Table 7). Accordingly, growth in length and weight proceeds via a series of large winter gains alternating with smaller summer losses (Sulak and Randall, 2002). In the anadromous GS, this may represent an evolutionary life history accommodation to comparatively low prey densities in riverine habitats (Brooks and Sulak, 2005; Sulak et al., 2007) vs much higher densities in saline habitats. Southeastern and GOMEX region blackwater and muddy alluvial rivers offer rather meager prey resources in contrast to those of productive rivermouth estuaries (Brooks and Sulak, 2005; Sulak et al., 2007) and bays (Heard et al., 2002; Ross et al., 2009; Peterson et al., 2013). Indeed, it can be hypothesized that anadromy in sturgeons evolved to take advantage of the generally much greater benthic prey resources in saline waters vs natal rivers. The energetic advantage gained apparently compensates for increased predation risks and the increased physiological expense of osmoregulation (lowered standard metabolic rate and decreased growth rate) in salt water (McKenzie et al., 1999, 2001; Singer and Ballantyne, 2004). The trophic advantage of anadromy has been confirmed from growth rate studies on comparative populations of the Volga-Caspian Russian Sturgeon. Fish in the anadromous population grow much more rapidly than those in the river-resident population (Holcik, 1989). For the GS, invertebrate prey resources in the Suwannee River consist of very sparsely distributed organisms of low individual biomass (e.g.,

Table 7
Seasonal gain or loss of weight from marked and recaptured Gulf Sturgeon available for four river populations

River	Study Period	Sample N	Mean winter TL gain (cm per unit time)	Mean winter weight gain (kg per unit time)	Mean winter weight gain (% ± SD) [range]	Mean summer weight loss (%) or [kg]
Apalachicola[a]	1981–1984	12	—	6.8 ± 2.0 year^{-1}	93.6 ± 30.2 [35–137]	10.5 ± 3.2 [1.4 ± 0.5 summer^{-1}]
Choctawhatchee-Pascagoula[b]	1999–2000	1	5.66[c] per 218 days	7.27 per 218 days	—	—
Pascagoula[c]	1997–2001	29	6.44 ± 4.12[c] year^{-1}	3.41 year^{-1}	3.65 ± 3.03	3.87 [2.12 month^{-1}]
Pearl[d]	1992–1995	36	—	2.60 × 10^{-3} day^{-1}	—	1.44 × 10^{-3} day^{-1}
Suwannee[e]	1972–1973	Subset from N = 343 total	6.3 year^{-1}	—	—	—
Suwannee[f]	1972–1973	Subset from N = 343 total	1.4 months^{-1}	—	—	—
Suwannee (subadults & adults)[g]	1976–1981	NA	—	—	30	—
Suwannee (subadults & adults)[h]	1986–1994	54[h]	8.0–8.7 year^{-1}[i]	3.0–3.3 year^{-1}[h]	—	—
Suwannee (subadults & adults)[h]	1986–1994	98[i]	8.0 year^{-1}[j] 1.7 months^{-1}	2.8 year^{-1}[i] 0.5 months^{-1}	—	—
Suwannee (subadults & adults)[h]	1986–1994	25[k]	—	—	—	[0.33 months^{-1}]
Suwannee (juveniles >age-2)[h]	1986–1994	27[l]	2.8 months^{-1}[l]	0.3 months^{-1}[l][max 1.0 months^{-1}]	—	—
Suwannee (juveniles age-1 to age-2)[h]	1986–1994	14[n]	1.4 months^{-1}[n]	0.14–0.16 months^{-1}[n]	—	—
Suwannee (subadults & adults)[m]	1986–1994	197 13	7.1 ± 3.7 year^{-1}	2.7 ± 1.6 year^{-1}	20.1 ± 13.6	3.7 ± 2.5

NA = data not available.

[a] Wooley and Crateau (1985).

[b] Ross et al. (2000) reporting FL and weight increase for an individual tagged in the Choctawhatchee River, recaptured 282 days later in the Pascagoula River.

[c] Ross et al. (2002) reporting FL and weight changes.

[d] Morrow et al. (1996)

[e] Clugston et al. (1995) reporting an estimated annual FL increase derived from Huff (1975, Fig. 9) FL-weight regressions for fish in a weight range of 8–18 kg (subadults and adults).

[f] Clugston et al. (1995) reporting an estimated growth rate between age 1–2 from Huff (1975, Fig. 9) FL-weight regressions.

[g] Carr (1983).

[h] Clugston et al. (1995).

[i] TL and weight increase determined from 54 subadults and adults at large 2–5 years between capture and recapture.

[j] Annual rates, but with TL and weight increases occurring over the 6 months winter feeding period only.

[k] Rate of summer weight loss determined from 25 subadults and adults in the 5–17 kg weight range.

[l] TL and weight increase determined from 27 juveniles at large 4–5 months (winter to spring) between capture and recapture.

[m] TL and weight rates of increase determined from 14 age-1 to age-2 juveniles at large ~12 months (successive winter-spring periods), captured and recaptured in the estuary.

[n] Carr et al. (1996b).

chironomid larvae) (Mason and Clugston,1993) compared to densely concentrated estuarine and marine organisms of higher mean biomass per individual (Harris, 2003; Brooks and Sulak, 2005; Harris et al., 2005; Sulak et al., 2008; Ross et al., 2009). The energetic cost of foraging is reduced in saline environments, not only due to denser prey abundance and concentration of prey in patches, but also due to the much larger comparative size of individual marine prey items.

Sulak et al. (2007) tested and refuted the hypothesis of feeding cessation due to elevated summer river temperatures (Mason and Clugston, 1993; Chapman and Carr, 1995; Carr et al., 1996b; Gu et al., 2001). Except for a minor percentage of juveniles and subadults, feeding actually ceases upon immigration in February-April (Sulak et al., 2012) when water temperatures are near their coldest of the year, not when water temperatures peak months later. A temperature threshold (~13–17°C) upon entry into the river in spring may serve as a cue to the initiation of feeding cessation, but elevated temperatures are probably not a causal factor. Many species of sturgeons display extended periods of trophic dormancy and/or reduced activity during various times of the year (Magnin, 1963; Dadswell, 1979; Holcik, 1989; Wei et al., 1997), including mid-winter or prior to spawning (Haynes et al., 1978; Barannikova, 1991; Krykhtin and Svirskii, 1994; McLoed et al., 1999). The evolution of large body size enables the GS and other anadromous sturgeons to store sufficient energy in the form of fat and muscle to endure long periods of fasting in freshwater after periods of intense feeding in saline waters. The seasonal cycle of intense estuarine/marine feeding, followed by extended freshwater fasting, represents an appropriate energetic adaptation to food availability vs the energetic cost of foraging.

While hiding under gravel, GS free embryos rely upon the yolksac as the initial food source and do not feed exogenously until the yolk supply is consumed. Free embryos up to age day-4 do not migrate, but remain in hiding (Kynard and Parker, 2004) During the free embryo yolksac period, larval teeth and a functional digestive tract develop in preparation for exogenous feeding at 5–8 days post-hatch. The yolksac melanin plug occluding the anus is expelled one day prior (Bardi et al., 1998). First-feeding GS larvae remain associated with the substrate, displaying salutatory swim-up excursions into the water column to attack planktonic prey. Altitude above substrate of swim-up excursions increases from an initial mean of 30–40 cm to a mean of 90 cm on days 12–13 (Kynard and Parker, 2004). *Acipenser* larvae are equipped with impressive conical larval teeth, large eyes, and large nasal capsules (Ryder, 1890), the morphology of capable predators (Fig. 28). Minute teeth are also present on the pharyngeal floor (Ryder, 1890), tongue, and roof of the mouth (Boglione et al., 1999), presumably used in trituration of food items. Olfaction is probably predominant in prey detection and in triggering feeding search behavior. Indeed, it may be the primary sense used by early GS free embryos to locate and pursue prey. In that regard, Boglione et al. (1999) have reported that olfactory sensors in the Adriatic Sturgeon are already functional at age day-4, but that electroreception and vision develop no sooner than day-12. Regardless of the sensory system used to locate prey, laboratory-reared GS free embryos actively pursue live planktonic prey introduced into culture vessels (Foster et al., 1990; Bardi, 1997; Bardi et al., 1998). Ryder (1890) reports that the stomachs of larval AS and Sterlet (*Acipenser ruthenus*), feeding *ad libitum* in rearing ponds, contained freshwater plankton including *Daphnia* and *Cladocera*.

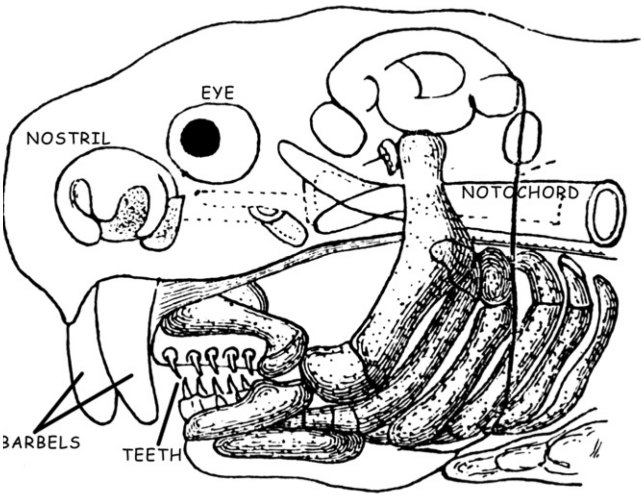

Fig. 28. Head of sterlet, *A. ruthenus* free embryo (13.5 mm TL) just prior to shedding of yolksac, with jaw teeth and sensory systems (eyes, nasal capsule, ootic capsule, barbels) developed and poised to begin exogenous feeding. After Ryder (1890, pp. 291, plate XLI, Fig. 17)

Confirming the intolerance of YOY to saline water (see Table 6 regarding rare exceptions), stable ^{13}C isotope analysis (Sulak et al., 2012) has confirmed that YOY derive their carbon from wholly terrestrial sources. Sporadic captures of single individuals in small bottom trawls (Sulak and Randall, 2005) suggest that during this life history stage in tannic blackwater rivers (e.g., the Suwannee River) or muddy alluvial rivers (e.g., the Apalachicola River), GS YOY forage individually in a food-poor environment. Solo foraging is probably enforced by the low abundance, biomass, and sparse distribution of epibenthic prey, primarily chironomid larvae. Records for YOY captured or positively observed in the Suwannee River show that they use the entire non-saline reach available to them (Sulak and Clugston, 1998), from rkm 12.5 to rkm 289 (Fig. 5; Table 6). Thus, YOY nursery habitat has been lost where impassable manmade barriers (dams or sills) have been placed in GS natal rivers below the first natural barrier (falls or impassable shoals). The distribution and abundance of potential GS benthic prey for YOY feeding in the Suwannee River, spring to autumn, has been analyzed by Mason (1991). Larval GS soon shift from water column plankton feeding to benthic cruising, with barbels skimming the substrate (Kynard and Parker, 2004). Correspondingly, the larval teeth are lost accompanying the switch to benthic suction feeding. Bicolor-stage YOY have occasionally been captured in trawls, gill-nets, or by electrofishing on open sand habitat (Table 6). In the Suwannee River, spring-spawned (March-April) GS descend to the river mouth estuary for the first time in late January and early February (Sulak and Clugston, 1998), switching to feeding in saline waters for the first time, remaining in the estuary until March. Shallow (<4 m), sandy, low-salinity habitats tolerable to 9-month old YOY (Altinok, 1997; Altinok et al., 1998) offer comparatively much greater density and biomass of benthic food per unit area than does the freshwater river (Brooks and Sulak, 2005; Sulak et al., 2009a). Arriving from upriver, YOY of 330–450 mm TL (only 2% under 350 mm TL) are relatively thin, carrying low biomass. However, without substantial increase in length, they rapidly increase in weight, storing sufficient biomass by March-April to subsequently fast from spring to autumn. Thus, the annual cycle of alternating feeding and fasting is initiated for the first time.

Benthic macrofaunal sampling to identify high prey density areas with acoustic telemetry to define habitat use areas has been applied to circumscribe juvenile winter feeding areas within the Suwannee estuary (Edwards et al., 2003; Brooks and Sulak, 2005; Sulak et al., 2009a) and in the Pascagoula river mouth estuary (Peterson et al., 2013). Similarly coupled methods have defined probable adult feeding areas in the nearshore GOMEX off the Suwannee River (Harris, 2003; Harris et al., 2005), in Choctawhatchee Bay (Fox et al., 2002; Heard et al., 2002), in Mississippi Sound (Rogillio et al., 2007; Ross et al., 2009), and in the Pascagoula river mouth estuary (Peterson et al., 2013, 2016).

Prey detection and ingestion: In sturgeons (Buddington and Christofferson, 1985), as in fishes generally (Pavlov and Kasumyan, 1990), the full gamut of sensory systems is brought into play in the detection, location, and acceptance of prey. Ontogeny and environmental context are both important determinants of which sensory system predominates in prey detection. In laboratory experiments, Boiko et al. (1993) demonstrated that early larvae of the Russian Sturgeon reacted strongly and positively to olfactory stimuli. However, the above-bottom, head into the current, drift-feeding mode of larval GS (Kynard and Parker, 2004) suggests that vision is used in prey detection during the planktivorous phase of life, probably in combination with olfaction and electroreception (Boglione et al., 1999), and finally gustation upon barbel or snout contact with prey. The food selected by early larvae of cultured sturgeon when both benthic (chironomid larvae) and planktonic prey (*Daphnia* and copepods) were available suggests a predominance of visual prey detection of swimming planktonic prey (Baranova and Miroshnichenko, 1969), with larval teeth used to grasp prey. However, all dentition is lost before early YOY transition to benthic suction feeding. Transitioned YOY, juveniles, and adult GS appear to be non-visual feeders, corresponding to observations in other sturgeon species (Sbikin, 1974; Buddington and Christofferson, 1985). Morphological evidence suggests that adult sturgeon lack object discrimination and color vision capability, as well as the ability to adjust focus (Pavlov, 1979; Kasumyan and Kazhlayev, 1993). Under laboratory culture, with constant low velocity current, natural sand substrate, and subdued illumination, benthic YOY and early juvenile GS passed within close visual range of live food items (e.g., *Lumbriculus variegatus* blackworms) with no apparent reaction. But when the barbels happened to contact a blackworm, it was immediately ingested (K. Sulak, USGS, pers. obs.). Taste and touch sensors of sturgeon barbels require direct contact to trigger ingestion. Location of distant prey is primarily by olfaction (Pavlov and Kasumyan, 1990; Kasumyan, 1995, 1999). Additionally, olfaction may serve to sensitize other sensory modalities once the presence of prey is signaled (Pavlov and Kasumyan, 1990). Detection of prey by smell in sturgeons is accompanied by a switch in swimming mode. When exometabolites of food organisms were released in aquaria, young (38-days old to 1.5-year old individuals) of five sturgeon species displayed searching trajectories consisting of swimming in circles and S-shaped loops while the head oscillated from side to side (Kasumyan, 1995, 1999). Correspondingly, Foster et al. (1990) reported that early juvenile GS displayed excited swimming when minced blackworms were introduced into culture tanks. Ampullary organs are abundantly present on the underside of the snout and dorso-lateral margins of the rostrum in sturgeons (Teeter et al., 1980; Boglione et al., 1999, 2006). These organs are morphologically and functionally homologous to the electroreceptors of Paddlefish (*Polyodon spathula*) (Jorgenson et al., 1967; Teeter et al., 1980) and elasmobranchs. Thus, a second 'distant' sense may supplement smell to home in on benthic prey, particularly at close range. In paddlefish, the ampullary sensory system of YOY (120–170 mm TL) is the primary short-range sense (for distances up to 10 cm) used to detect and locate plankton (Wilkens et al., 2001). In sturgeons, the final stage of food acceptance is probably accomplished by with taste and touch sensors on the four sensory barbels, head, lips, inside and outside of the mouth, and on the tongue. Thus, ingestion and retention (or rejection) is probably mediated by sensors requiring physical contact with potential food items (Kasumyan, 1997). Utilization of multiple non-visual sensory systems in prey detection confers a particular competitive advantage to sturgeon vs other benthic-feeding fishes. That is, sturgeon can forage as effectively at night as in the day. Indeed, there is evidence of increased GS foraging activity at night during the winter feeding period (Wrege et al., 2011).

The GS forages in the mode of a mobile 'benthic cruiser' (Findeis, 1997), swimming along very close to the substrate. When food is encountered, the highly protrusible tubular jaw mechanism projects downward and forward (Carrol and Wainwright, 2003). Simultaneously, the orobranchial chamber is expanded as the gill covers are flared outward. The powerful suction generated by this process draws in benthic prey along with sediment. As in all sturgeons, the GS jaws are toothless. Prey is ingested whole, then held in the buccal cavity and crushed by pressing the large muscular tongue against the roof of the mouth (Findeis, 1997; Miller, 2004). The tongue is provided with a series of hard transverse ridges (Boglione et al., 2006) used in trituration of ingested food. As food is manipulated and swallowed, sediment is expelled through the mouth and gill openings. Given the relatively small diameter of the GS mouth opening, large prey are not regular food items. Sturgeon are unique in having evolved retrograde gill ventilation via an accessory respiratory shunt

(Findeis, 1997) allowing them to ventilate the gills while the mouth is occupied with feeding (Burggren and Randall, 1978). They do this by taking in water 'backwards' through the curious crescent-shaped opening along the upper rear margin of the gill cover. Such an adaptation enables uninterrupted high-intensity benthic prey intake in the GS when a patch of prey is encountered. The GS, along with all other sturgeon species, sharks, and certain other primitive bony fishes, retains a spiral valve in the intestine, an ancient adaptation to increase residence time of food in the gut and the absorptive area of the digestive tract.

On estuarine and nearshore winter feeding grounds, the spatial congruence between juvenile and subadult GS with concentrations of benthic prey (Brooks and Sulak, 2005; Harris et al., 2005; Peterson et al., 2013) indicates an ability to home in precisely upon prey concentrations, at least on a local scale. The ability of adult GS to detect ghost shrimp in deep burrows and lancelets and small benthos buried in sand suggests the use of smell, perhaps accompanied by electroreception. Lack or paucity of GS telemetry relocations over deeper areas of Mississippi Sound (Ross et al., 2009) and Choctawhatchee Bay (Fox et al., 2002) have been interpreted to suggest that rapid, directed movement occurs from coastal rivers to known shoal feeding grounds around offshore barrier islands and in adjacent passes. While this may be true in general, more recent telemetry evidence (M. Peterson, GCRL, pers. comm., August 2016) has revealed that certain individuals remain in Mississippi Sound for extended periods, apparently foraging there. In contrast to direct movements to known feeding grounds, Edwards et al. (2003) reported that while searching for prey in marine waters, the tracks of adult GS plotted via acoustic telemetry approximate a Lévy search pattern (Viswanathan et al., 1996), a special class of random walk that is particularly efficient at exploiting randomly distributed food patches in a seascape that lacks landmarks. That is, an individual GS heads off linearly along a randomly selected compass direction for a search distance that follows a power-law probability distribution until a concentration of prey is located, then forages randomly in place within the patch for hours to days, before again departing in a random compass direction. The telemetry tracks for individual GS were remarkably similar to those for wandering albatrosses (Viswanathan et al., 1996; Fig. 4). Such a random-direction, scale-invariant search pattern suggests no advance knowledge of where prey is located, (c.f., when the predator navigates directly toward prey concentrations from a distant starting point). If a prey-seeking GS uses a Lévy search pattern, it would proceed on a fundamentally linear trajectory until one or more sensory systems detected the presence of a patch of prey.

Although descended from freshwater Chondrostean ancestors (Berg, 1948; Krayushkina et al., 2001), sturgeons are slightly hyper-osmotic relative to freshwater, but hypo-osmotic relative to seawater Low salinity brackish water in estuaries provides not only greater sturgeon prey densities, but conforms most closely to GS physiology and metabolic efficiency. A preference for juvenile feeding in brackish water may reflect greater digestive efficiency (food conversion ratio and energy absorption efficiency) in low-salinity estuarine water (3–9 ppt) that is close to isotonic with GS internal fluids (Altinok and Grizzle, 2001). However, at 20 ppt, juvenile Adriatic Sturgeon displayed reduced food conversion efficiency (McKenzie et al., 1999). Cataldi et al. (1999) found that while 1–1.5 year old Adriatic Sturgeon could withstand 20–30 ppt salinities for up to 60 days, exposed juveniles encountered both physiological and morphological stress, and increased susceptibility to mortality. The example here is instructive regarding the closely-related GS. Residence and feeding within reduced salinity waters may be due more to physiological preference than to absolute marine salinity intolerance. Thus, telemetry documented (Sulak et al., 2009a, b) that juveniles wintering in Suwannee Sound suddenly departed to deeper, full-salinity marine water during a severe cold spell in January 2008. When temperatures moderated five days later, they returned to the estuary. The ability to tolerate polyhaline salinities for short periods appears to be adaptively advantageous relative to potential cold-event mortality in shallow water.

Age and growth

Growth through early life stages

Upon hatching in the laboratory (Bardi et al., 1998) GS free embryos were 8.30 ± 0.05 mm TL and weighed 8.00 ± 0.08 mg. Upon transition to the first feeding stage at age 7–10 days (Foster et al., 1990; Bardi et al., 1998) (one day after extrusion of the anal melanin plug), larvae will have grown to 15–17 mm TL (Foster et al., 1990; Bardi, 1997) and a weight of 18–22 mg (Foster et al., 1990; Bardi et al., 1998). Growth in length for wild YOY proceeds rapidly over the first year of life, a TL of 350–450 mm being attained by age 9–10 months, when the first downriver migration to the estuary takes place in late January and early February.

The 'trophic ratchet' growth pattern

After spending the first 9–10 months of life in freshwater reaches of the river, YOY GS transition morphologically and physiologically such that they can initiate feeding in brackish water in the estuary. Upon doing so, young GS essentially become age-1 juveniles, and initiate the anadromous pattern of migration and feeding that will continue for the rest of their lives. Thus, upon entering the estuary, age-1 fish begin winter (November-March) feeding in the estuary, a lifelong pattern that in later years will extend into open bays and the GOMEX as full salinity tolerance is achieved. Thereafter, 5–6 months of intense winter feeding will alternate with summer (April-October) resting and trophic dormancy in freshwater GS rivers. Spawning fits into this same cycle for ripe fish, with spawners undertaking upriver excursions to spawning grounds in both spring (Sulak and Clugston, 1998) and autumn (Randall and Sulak, 2012; Sulak et al., 2013). The annual migration pattern, with alternation between extended periods of feeding and periods of fasting, results in the lifelong pattern of stepwise increase in weight (Sulak and Randall, 2002) (Fig. 26a–c). That is, despite the small summer losses, the individual fish gradually continues to make annual weight gains throughout its life. The major exception to this lifelong pattern is the periodic (probably every 3–4 years) loss of substantially greater weight by females upon spawning. That major weight loss upon shedding the mass of eggs may take two or more years of recovery before further somatic growth is evidenced (Fig. 26c). Another exception of smaller consequence is that having achieved a TL of 1350–1500 mm, growth in adult males slows considerably, with both TL and weight reaching an asymptote (Fig. 26b).

In the laboratory, under conditions of constant food availability and minimal foraging energy expenditure, GS are capable of much faster growth than in the wild where food is limiting and swimming against currents and foraging widely to locate prey requires greater energy expenditure. Mason et al. (1992) reared two hatchery GS in laboratory tanks with natural substrates, good oxygenation, and dim illumination. The fish were initially fed live brine shrimp nauplii and blackworms, then switched to homogenized live prey for 7 months, then live earthworms *ad libitum* for 10 months. At age 12 months, laboratory juvenile one had grown to 719 mm TL and 1870 g, while juvenile two had grown to 634 mm TL and 1410 g. Wild GS of comparable age 12 months captured in the Suwannee River estuary in several years had a TL range of 450–550 mm, and a weight range of only 400–600 g (USGS-WARC, unpubl. database). At age 17 months, laboratory juvenile one had grown to 849 mm TL and 3060 g, laboratory juvenile two to 787 mm TL and 2680 g Mason et al. (1992). In contrast, captured wild Suwannee River GS did not achieve comparable TL and weight until age ~36–40 months (USGS-WARC, unpubl. database). There is a wide range in both TL and weight among individuals in the same cohort.

Historical reports and photographs document that GS regularly attained substantially greater lengths and weights in the 1870–1950 period than have been recorded in the last four decades (Table 5). Alexander (1905) reported a 14 ft (427 cm) GS weighing 602 lb (273 kg) killed by a tug boat in the Pascagoula River in 1899. Odlund (1958) reported 200–300 lb (91–136 kg) GS as common in early 20th Century Suwannee River commercial catches using 8.0 in (20.3 cm) bar mesh nets. Newspaper articles from 1897 to 1941 reported four GS weighing 265–417 lb (120–189 kg), with the longest measuring 9 ft 6 in TL (274 cm). These large GS were caught by anglers in the Coosa, Tallapoosa, and Cahaba rivers of the upper Mobile/Alabama River system (Table 5). Based on fisherman interviews and further newspaper reports, Reynolds (1993) reported additional historical records of GS ranging from 7 ft 11 in to 8 ft 0 in (241–244 cm) TL and 296–370 lb (134–168 kg) weight. As late as the 1950s, a GS weighing 209 kg (461 lb) was reported from the Flint River, a major tributary of the Apalachicola River (Swift et al., 1977), and another of 135 kg (297 lb) from the Ochlockonee River (Florida Outdoors, 1959).

There has been sufficient time since state harvest bans in the 1970s–1980s for GS to grow to sizes formerly attained. USGS has recaptured tagged Suwannee River GS that have been at large for as long as 26 years (potential actual ages 30–35 years) without exceeding 230 cm TL or 200 lb (USGS-WARC, unpubl. database). The use of large mesh nets in the early fishery apparently effectively 'fished down' maximum size. Size-selective harvesting (Fenberg and Roy, 2008; Christensen, 2015) typically targets large spawners (Coleman et al., 1996), simulating natural selection favoring maturation at a younger age and smaller size. The early commercial fishery would have been selective for GS exceeding 100–150 cm TL, particularly large egg-bearing females (which get larger than males) given the selectivity of the very large mesh nets used in the early fishery for both meat and caviar.

The trend in mesh size employed over time closely tracks the trend of size reduction in GS. In the first two decades of the fishery, nets of 8 in (20.3 cm) bar mesh were used (Alexander, 1905; Cook, 1959), even as late as 1912 (Odlund, 1958). Later, nets of 6 in (15.2 cm) bar mesh became standard. By 1920 and thereafter average fish size had been so reduced that nets of 4.5–5.0 in bar mesh were employed (Florida Outdoors, 1959; Fichera, 1986) through the end of the Florida sturgeon fishery in 1984 (Tatman, 1984; Rago, 1993). Gulf Sturgeon exceeding 200 lb (91 kg) were reported fairly frequently in the Suwannee and Apalachicola rivers from the early 1900s up to the 1950s–1960s (Odlund, 1958; Fichera, 1986) (Table 5), but not subsequently. It is probably not coincidental that the Pearl River population, with no history of an early GS commercial net fishery targeting large adults, has uniquely retained exceptionally large individuals (>300 lb or 136 kg) as recently as 2002 (Table 5).

Maximum TL (straight line distance, tip of snout to tip of tail) recorded for an individual GS netted since 1972 is 239 cm, equivalent to a fish of 250 mm TL measured over the round from the Apalachicola River (USFWS, Panama City, FL, unpubl. data). In the Suwannee River population, from among >13 000 net captures (1986–2013), maximum recorded TL is 227 cm, and maximum weight 90.9 kg (200.4 lb). Among the 9726 individuals captured primarily in large mesh (10.2–12.7 cm bar mesh) gill nets over the same time period, only 1.17% weighed more than 45.5 kg (100 lb). Similarly, individuals exceeding 45.5 kg are uncommon in sampling databases for the other natal populations. The heaviest GS caught in scientific gill net samples since sampling started in 1972 (Huff,1975) was 147.6 kg (325 lb) 227 cm TL fish from the Bogue Chitto River, LA, in 2002 (R. T. Ruth, LDWF, pers. comm.). Another Pearl River system GS weighing 387 lb (176 kg) was captured in a shrimp trawl in Lake Borgne, LA, by a commercial fisherman in 1978 (Fig. 29). Both of these records are truly exceptional for captures since 1960.

Faster growth rates have been suggested for GS in the Pearl River population (Ross et al., 2002; a) and the Yellow River population (Berg, 2004; Berg et al., 2007), compared with rates in other river populations. However, the period of time when sampling took place relative to the rise or fall in the population of a dominant year class mode can substantially bias apparent growth rate data. The limited sample sizes for pectoral fin spine ring-count ages from comparative river length-at-age data introduce another source of bias. Since GS older than age-0 feed in GOMEX estuaries, and

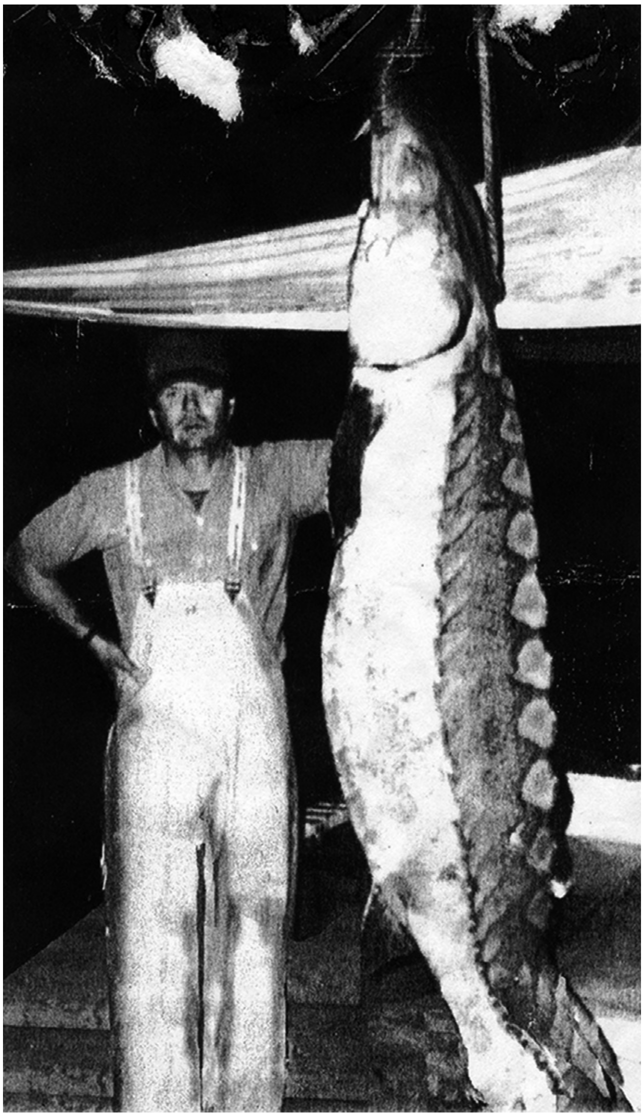

Fig. 29. Commercial fisherman R. Kenny, with 387 lb (176 kg) Pearl River Gulf Sturgeon caught in a shrimp trawl in Lake Borge, LA, in 1978

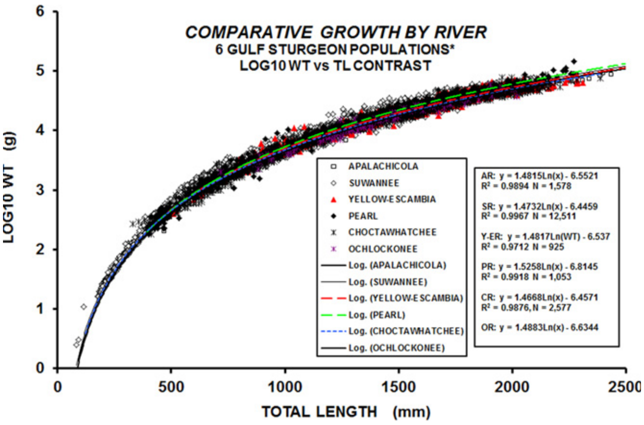

Fig. 30. Contrast in comparative Log_{10} weight (g) versus TL (mm) for individual Gulf Sturgeon in net samples, 1986 through 2007–2009 for six comparative river populations. For purposes of this contrast Yellow and Escambia sample have been combined

those older than age 6–8 feed either in estuarine/marine bays or in open GOMEX marine habitats, growth in length and weight with age (beyond age-0) does not depend upon natal river food resources. Winter feeding upon abundant benthic prey in saline waters accounts for almost all somatic growth. Accordingly, when all available weight vs length data are plotted, there is negligible difference in growth patterns among the various natal river GS populations. Weight-length (TL) regressions for the several GS river populations prove to be statistically identical. (Fig. 30).

Given the close similarity in the weight-length regressions for all GS rivers, the relationship determined by USGS for Log_{10} weight as a function of TL for Suwannee River GS can also be generally applied to all other GS river populations. That formula (N = 13 567 captures, TL range in mm = 82–2273 mm, weight expressed in g) is:

$$\text{Log}_{10}\text{Weight} = [1.4727 \times (\text{Log}_{10}\text{TL} \times 2.302585)] - 6.4427$$

For the Pearl River, the relationships between TL and FL, and Weight as a function of FL, have been determined by Morrow et al. (1996), as follows:

$$\text{TL (mm)} = 1.10 \times \text{FL(mm)} + 17.1$$

$$\text{Weight } (g) = 2.786 \times 10^{-6}\left[\text{FL(mm)}^{3.204}\right]$$

A second set of Pearl River weight-length formulas (N = 110 captures, FL range 635–2057 mm), have been provided by Rogillio et al. (2001):

$$\text{Weight } (g) = 2.35 \times 10^{-7} \times \text{TL(mm)}^{3.454}$$

$$\text{Weight } (g) = 1.12 \times 10^{-6} \times \text{FL(mm)}^{3.285}$$

A FL from TL conversion formula is also available from Suwannee River GS captures (N = 13 031) (USGS-WARC, unpubl. database):

$$\text{FL (mm)} = 0.8984 \times \text{TL(mm)} - 9.6971$$

Aging and longevity

Sturgeon species have generally been aged by counting concentric rings in cross-sectioned pectoral fin spines. In the GS, Morrow et al. (1996) determined that counted rings (dark bands) were annuli laid down in March-July (the period of arrested growth). Huff (1975) reported the following length-at-age relationship for Suwannee River GS using pectoral spine ring counts, but few adults were available in his sample from 1972 to 1973.

$$\text{FL (mm)} = 369.2326 \times \text{Age(year)}^{0.5284}$$

Maximum GS age estimated by Huff from pectoral spine rings was 42 years. A second fish was aged as 31 years. Ripe adults from 1973 sampling ranged in age between 12–26 years. For 35 Pearl River GS, Morrow et al. (1996) provided a table of mean ± SD FL at age over a FL range of 378–1143 mm. Based on pectoral spine ring counts from polished thin sections, Sulak and Randall (2002) determined length at age formulas in two formats:

$$\mathrm{TL}\,(\mathrm{mm}) = [697.01\ \ln\ \mathrm{age(year)}] - 37.405\left[R^2 = 0.7131\right]$$

$$\mathrm{TL}\,(\mathrm{mm}) = 565.86(\mathrm{age})^{0.4247}$$

However, pectoral fin spine counts are unreliable beyond approximately age 8–10, due to marginal convergence of rings and erosion of core rings. Also, mature males tend to slow down in increasing in length, and perhaps top out with age. Thus, a 1500–1600 mm TL male could alternately be 10, 15, 20, or 30 years old. Females, however, continue to grow until reaching an asymptotic TL of ~2200 mm, getting larger and older than males. Thus, a single empirical length-at-age curve works poorly for GS older than age 8–10. A further problem is that double rings may sometimes be formed per year (Sulak and Randall, 2002). These authors estimated that only 0.5% of adults live beyond age 20 in the Suwannee River.

Ontogenetic and seasonal migrations

Seasonal immigration and emigration in the anadromous GS

The GS is one of only three fully anadromous North American sturgeon species. Fully anadromous sturgeon must migrate back and forth annually, unimpeded between riverine spawning habitat and marine feeding habitat to complete the life cycle. The GS is thus an obligate estuarine/marine feeder that cannot survive land-locked or dam-locked above impassable barriers. Descended from freshwater Chondrostean ancestors, sturgeon internal physiology and reproduction is more akin to that of freshwater fishes. However, some sturgeon species have adapted physiologically to tolerate full marine salinity. Anadromy enables exploitation of rich and broadly distributed marine benthic prey, despite the necessity to return to freshwater to reproduce and undergo early development. Adults feeding in the GOMEX in winter sometimes venture as far from their natal rivers as 180 rkm, with fish from several natal river populations co-occurring in the same offshore areas (Edwards et al., 2007; Vick et al., 2016). At the same time, anadromy allows anadromous and amphidromous or potadromous sturgeon species pairs to co-exist in the same spawning river. In effect, such pairs partition the overall aquatic prey resource available regionally while sharing the same natal spawning river. North American examples include the AS and Shortnose Sturgeon (SNS) along the East Coast, the WS and GRS along the West Coast, and the AS and LS in the ETZ of the St. Lawrence River (Guilbard et al., 2007). Before the nearly complete extirpation of sturgeon from the Mobile River system (Kuhajda and Rider, 2016, this volume), the GS, LS, and the Alabama Sturgeon (ALS) probably co-existed as a unique sympatric North American anadromous/potadromous triad.

The long-held seasonal paradigm for GS movements is an early spring immigration into natal freshwater rivers (including upriver spawning migration for mature adults), late spring through autumn residence in freshwater (resting and fasting), then late autumn-early winter emigration to saline winter feeding habitats. Many tagging and telemetry studies have confirmed this general paradigm (e.g., Huff, 1975; Wooley and Crateau, 1985; Odenkirk, 1989; Hightower et al., 2002; Edwards et al., 2007). The standard post-emigration feeding habitat for juveniles is the low to mid-salinity estuary, while subadults and adults typically occupy full salinity GOMEX coastal marine habitat or mesohaline to polyhaline bays and sounds. For age-1 and older GS, spring through autumn habitat is normally the freshwater river.

However, there is considerable deviation from the accepted seasonal movement and habitat use paradigm within a given river population and between populations. That paradigm provides only a general framework. Both immigration and emigration are complex, extended phenomena, confounded by great inter-annual variations in environmental factors, sex and maturity differences among migrants, individual variation in GS behavior, and infrequent large stochastic disturbances.

Spring immigration. After wintering 4–7 months (October-November through February-April) on marine feeding grounds, most subadult and adult GS return to their natal river. However, natal river fidelity is not absolute (Carr et al., 1996b; Fox et al., 2000; Dugo et al., 2004; Heise et al., 2004; Berg et al., 2007; Ross et al., 2009; Duncan et al., 2011). Indeed, exploratory straying resulting in some level of permanent translocation (below) is essential in an anadromous fish species to maintain and opportunistically expand the species range as conditions change over geological time. Telemetry and genetic fingerprinting of immigrating and summering GS demonstrate that a small percentage of adults enter, explore, and often stay within a river other than their natal river, with evidence as well of spawning in the adopted river.

Immigration and spawning migration cues. The annual immigration period from marine and estuarine waters extends from late January through early May in the several natal rivers (Huff, 1975; Wooley and Crateau, 1985; Odenkirk, 1989; Clugston et al., 1995; Carr et al., 1996b; Foster and Clugston, 1997; Fox et al., 2000; Heise et al., 2004; Havrylkoff et al., 2012), with exceptional late returnees (Fox et al., 2000). For ripe adults, immigration coincides with the spring upriver spawning migration. In the Suwannee River, automated listing-post telemetry has revealed that the first returnees (presumably males in spawning readiness) enter in late January to mid-February (USGS-WARC, unpubl. telemetry database[4]), and swim rapidly and directly to staging areas just below upriver spawning grounds. The majority of GS, including ripe females, return to the river in March and April. Ripe females enter rivers in spawning readiness, i.e., with oocytes already in late stage vitellogenesis (Conte et al., 1988). They may either ‘stage’ in place in the lower river for several days, proceed to spawning grounds directly without major stops (Fig. 31a), or move upstream in a series of stop and go stepwise movements. Most unripe adults, subadults, and juveniles of both sexes settle into one of eight major seasonal holding-resting areas, depicted as plateaus in telemetry tracks (Fig. 31a–c) below the spawning grounds.

Knowledge of which factors serve as immigration and spawning run cues remains problematic. Those most frequently implicated by correlation with GS movements have been flow and temperature. Seasonally increased current flow or river discharge has also frequently and traditionally been advanced as the cue for spring immigration and/or spawning immigration, and/or onset of spawning activity in various sturgeon species, including the GS (Chapman and Carr, 1995; Foster and Clugston, 1997; Ross et al., 2001b). Correlations have been drawn between timing of river entry, initiation of spawning, or peak in egg deposition with either the peak or the descending limb of the hydrograph resulting from the spring freshet. Pine et al. (2006) reported that the majority of GS eggs collected in the Apalachicola River in 2006 followed increases in discharge. Scolland and Parauka (2008) reported that the majority of GS eggs from the same river were collected following decreases in discharge. Ross et al. (2001b) hypothesized that high flows in early March served as the cue for GS upstream migration in the Pascagoula River. However, correlation does not necessarily correspond with causation. Over five consecutive telemetry study years (1997–2001) in that river, Heise (2003) and Heise et al. (2004) found that GS arrived on the upriver spawning grounds at the same time every year, early April (Fig. 32), regardless of flow conditions. They arrived in early April in 1999 ahead of the major spring freshet, and again in early April in the low-water year of 2000, when the freshet was barely evident (Fig. 32, arrow). Similarly, in a Choctawhatchee River two-year telemetry study, Fox et al. (2000) found no clear relationship between flow and river entrance.

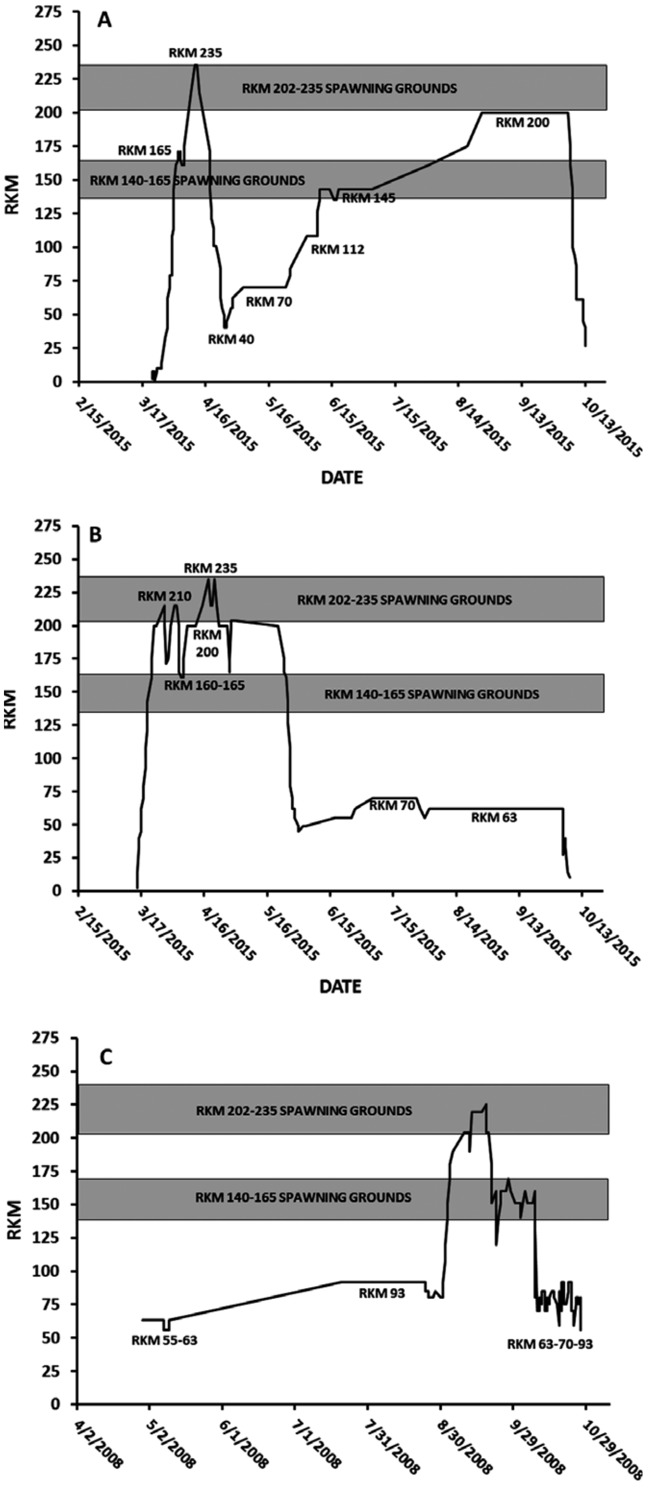

Fig. 31. Acoustic telemetry tracks of adult Gulf Sturgeon ascending to Suwannee River spawning grounds in spring 2015 (a, b) and in autumn 2008 (c) (USGS-WARC unpubl.). Key: a = putative spring-spawning female 29 846 entering in mid-March, spawning, dropping down, then occupying a series of holding areas at rkm 40, 55, 63, 70, 93, 112, 145, and 200; b = putative male 29 863 entering the river in mid-March and proceeding rapidly to upriver spawning grounds; c = putative autumn-spawning male 6773

Indeed, since the typical natural hydrograph for most North American rivers displays maximum flow in spring due to snow melt and spring rains, followed by a decline, a cause and effect relationship between hydroperiod and sturgeon seasonal migratory and reproductive behavior would be difficult to distinguish from phenological coincidence. Thus, regarding cueing of WS spawning in the Sacramento River, Kohlhorst (1976) has stated: ‘While most spawning occurred during periods of decreasing flows, this is the dominant flow regime during the spring. There was no obvious flow threshold at which spawning was initiated’. In a study of WS spawning in the Snake River, Lepla and Chandler (2001) found that eggs were deposited during the peak and the descending limb of the hydrograph, as well as in drought years with no spring freshet, and no peak in the hydrograph.

A minimum water temperature has been advanced as the spawning initiation cue in North American sturgeon including the LS (LeHaye et al., 1992; Bruch and Binkowski, 2002; Bruch et al., 2016; this volume) and WS (Golder Associates Ltd., 2010; Hildebrand et al., 2016; this volume). Accordingly, river water temperature has similarly been deemed the cue for GS spring immigration and spawning migration in a number of studies. Cueing would operate either as a minimum temperature threshold, a period of rapidly rising

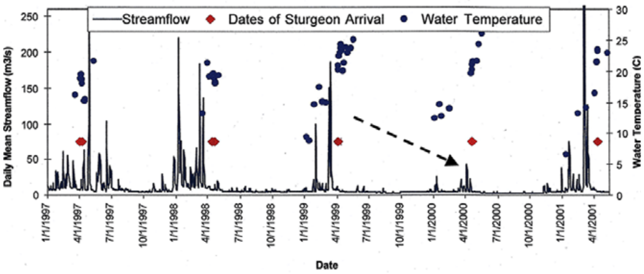

Fig. 32. Gulf Sturgeon arrival at the Bouie River spawning site in the Pascagoula River in relation to flow, temperature, and date,1997–2001, based on first spring captures Discharge data are from USGS gauge #2472500. Figure has been adapted from Ross *et al.* (2001a, Fig. 6, courtesy of Mississippi Department of Fisheries, Wildlife and Parks, and the Mississippi Museum of Natural Science). Dashed arrow denotes the very low streamflow discharge in spring 2000

temperature, or a period of convergence between GOMEX and river temperatures. Clugston et al. (1993) found that GS began migrating into the Suwannee River in mid to late February as the river warmed to 16–19°C, with immigration peaking at 20°C. Sulak and Clugston (1999) proposed a minimum 17°C threshold for upriver migration following river entrance. Chapman and Carr (1995) reported that return immigration from the GOMEX to the Suwannee River began when river water temperature reached 14.8°C and peaked in March and April at 17.2°C, with marine to riverine immigration coinciding when nearshore marine and river water temperatures fell within 1–2°C of each other. However, their 1986–1991 study period was characterized by a series of cold springs. In contrast, automated telemetry data showed that, despite January-April river mouth water temperatures continuously remaining at 19–22°C in 2012, immigration occurred during the normal February-April window (USGS-WARC unpubl.). Elevated temperatures (16.5–22.0°C) prevailed again in December through March 2014 without altering the timing of the main GS immigration. In the Choctawhatchee River, Fox et al. (2000) found GS entering the river in 1996 at 11.2–24.9°C, but in 1997 at 18.3–27.1°C. In the Pascagoula River mouth, Heise et al. (2004) captured returning March-April immigrants between 10.4–20.8°C. Across all GS immigration studies, observed temperatures have spanned a range of 10.4–27.1°C, nearly the complete thermal tolerance range of the species. Using temperature logging archival tags, Parkyn et al. (2007) found an annual range of 8.1–28.5°C experienced by Suwannee River GS. In the Pascagoula River, GS regularly experience midsummer holding area temperature maxima of 32–33°C, with a reported mean of 28.4°C (Heise et al., 2005). Therefore, it appears that no particular river mouth water temperature threshold provides a reliable cue to the timing of GS immigration. Additionally, the hypothesis that immigration is cued as river and GOMEX temperatures converge (Chapman and Carr, 1995) is not well supported. Neither is the hypothesis (Sulak and Clugston, 1999) that a minimum threshold of 17°C is a pre-requisite for upriver migration. Nonetheless, river temperature in spring is probably still biologically important. If it remains below the critical (undetermined) threshold needed to trigger pre-spawning vitellogenesis in GS, the upriver spawning migration in ripe females may be delayed.

As putative temporal cues, both flow and temperature vary widely from year to year, and often fluctuate erratically in spring as well (Foster and Clugston, 1997), suggesting unreliability in coordination of GS life history. The one environmental factor that is absolutely reliable as a cue is day length (photoperiod), as has been identified for the SNS (Kynard et al., 2012). Indeed, in a PCA test of factors determining GS arrival on spawning grounds, day length has been statistically identified (Heise, 2003; Ross et al., 2004) as the first and most dominant principal component (together with temperature accounting for >95% of variation) among five habitat factors evaluated (day length, temperature, stream flow, dissolved oxygen, and depth). It is true that the GS main spring immigration and the onset of spawning generally coincide with mean ambient river temperature and flow trends, the former increasing from a December-February minimum, and the latter decreasing after a February-March peak. But in the phenology of spring events, the same correlation is true of the blooming of red maples and the departure from Florida of sandhill cranes, neither of which species is cognizant of river temperature or flow. What maples, cranes, many other species, and probably the GS all use as their cue to initiate spring activity is day length (photoperiod). Indeed, in the GS, it is informative that the late March peak of spring spawning coincides very closely with the spring Equinox, while the late September onset of autumn spawning coincides very closely with the autumnal Equinox – when neither a remarkable thermal nor flow cue is typically evident. At the same time, and also without a notable change in river conditions, GS residing in summer holding areas begin to exude copious slime (Sulak and Clugston, 1999) and display a heightened swimming mode during net capture, presumably a pre-emigration staging feature. As a life history coordinating and priming cue, photoperiod is reliable, sufficient, and measurable within combined visual-cranial integration capability; GS may need no other seasonal cues.

However, inter-annual differences in environmental factors including temperature and flow may nonetheless determine the duration of immigration. Fleming (2013) reported that the 2010 and 2011 Choctawhatchee River spring immigrations of acoustically-tagged GS began on the same day in both years, 3 March, but lasted only 76 days in 2010 vs 94 days in 2011. Despite a rather constant date for the onset of annual immigration, consistent with a hypothesized photoperiod cue, timing of river entrance for individual GS may differ depending upon life stage, sex, and gonad ripeness. Thus, Odenkirk (1989) found that small adults (presumed males) entered the Apalachicola River in advance of large adults (presumed females). Fox et al. (2000) reported that male GS generally entered the Choctawhatchee River ahead of females, beginning at a lower minimum water temperature (11.2°C vs >15°C). Additionally, ripe GS entered the river from March to mid-April, while non-ripe individuals entered from March-September. Although immigration is seasonally coordinated, net sampling and telemetry results generally indicate that for any population there is no coordination of movements among individuals. The same pattern has been observed in other sturgeon species. Thus, in Dabry's Sturgeon Zhuang et al. (1997) observed that ripe adults neither aggregate nor swim upstream together, but instead move individually.

Telemetry data for Suwannee River GS (Carr et al., 1996a,b; USGS-WARC unpubl.) show that a subset of males (presumably ripe) arrive a month or more in advance of the general immigration of all other fish, juveniles to adults, both male and female, ripe and unripe. The early male run takes place in late January through mid-February regardless of water temperature in either the GOMEX or the Suwannee River, which has varied from 13–22°C inter-annually, 1996–2015 (USGS-WARC unpubl. data). Ripe males in the early run, and ripe males entering during the peak March-April immigration, proceed rapidly and directly to temporary holding areas near upriver spawning grounds where they remain for as long as two months (Fig. 31b) awaiting the arrival of females mainly in late March through mid-April. Extended upriver residence of GS males after spring immigration was also observed in the Choctawhatchee River by Fox et al. (2000), although those authors found no difference by sex in spring arrival. Nonetheless, differential onset of spring migrations between ripe males and ripe females may be a common phenomenon among sturgeon species. Indeed, an early river entrance and/or upriver spawning run by ripe males, 2–3 weeks ahead of the first adult females, has also been reported in the AS (Dovel and Berggren, 1983; Van Eenennaam et al., 1996), LS (Cuerrier, 1966; Bruch and Binkowski, 2002; Bruch et al., 2016), in the European Sturgeon (Classen, 1944), and in the Sterlet (Holcik, 1989). After overwintering in the estuary, juveniles join the main GS March-April upriver migration (Sulak et al., 2009a), but typically ascend only to seasonal holding areas rather than to upriver spawning reaches.

A further modifier of the basic pattern of immigration is individual behavior. For example, three acoustically-monitored GS that had overwintered in the GOMEX, and had returned to the oligohaline Choctawhatchee River mouth in spring, did not move upriver. Instead, they remained at the river mouth continuously from mid-June through mid-August (Fleming, 2013), matching an earlier and similar report (Fox et al., 2000). Similarly, Duncan et al. (2011) found that three telemetry-equipped adult GS spent the summer of 2006 in northeastern Escambia Bay, instead of immigrating upriver. Large adult GS have also been observed in mid-summer in Suwannee Sound at the river mouth entrance during low altitude helicopter reconnaissance (K. Sulak, USGS-WARC, pers. comm.).

Emigration. The long-standing paradigm for GS seasonal exodus has been that all fish, except YOY, depart to the estuary (juveniles) or the open GOMEX (subadults and adults) in October-November. Clugston et al. (1995) and Foster and Clugson (1997) reported that radio-tagged GS moved downstream in the Suwannee River in October-November as water temperature dropped from 26°C to 17°C. Edwards et al. (2003) found that acoustically-tagged GS left the same river in early November as river water temperature fell below 20°C, within the temperature range (19–21°C) also observed by Carr et al. (1996b). In the Apalachicola River a range of 18.5–19.0°C for emigration was reported by Odenkirk (1989). Parauka et al. (1991) suggested a drop in temperature below 19°C and increased flow as emigration cues. In the Pascagoula River, from 1998 to 2002, telemetry-tagged GS departed freshwater from late September through mid-October over a temperature range of 21–26°C, with river exit in most years coinciding with elevated streamflow (Heise et al., 2005). Emigration in that study coincided with decreasing day length, decreasing water temperatures, and increasing river flow. However, recent data from remote datalogging receivers show that departure from seasonal holding areas, emigration to estuarine and bay waters, and subsequent movement into fully marine waters, is complicated and variable (Grammer et al., 2015; Peterson et al., 2016) – with no readily demonstrable relationship with individual environmental cues. Important variables may include individual behavior, sex and maturity, co-varying environmental factors, differential population adaptation to a given natal river, and unpredictable stochastic events.

Individual behavior is a key element in emigration timing. Indeed, occasionally a certain individual or a pair of GS does not move downriver at all, instead overwintering upstream in the natal river. For example, Wooley and Crateau (1985) reported two radio-tagged adult GS overwintering near rkm 172 (below JWLD), spending a total of 9 and 13 months, respectively, in freshwater. Similarly, Ross et al. (2001b) reported telemetry GS overwintering in the Bouie River in the upper Pascagoula River system, not departing until as late as January or March. Overwintering in freshwater has also been hypothesized in the Suwannee River (A. Huff, pers. comm., cited in Wooley and Crateau, 1985). Furthermore, among those subadult and adult GS moving to the river mouth estuary or adjacent mesohaline bay, a certain percentage may remain in the bay or sound for an extended period, as in Mississippi Sound (M. Peterson, GCRL, and W. T. Slack, USACE, pers. comm.) or for the entire winter season, not exiting into the open GOMEX, as in Choctawhatchee Bay (Fleming, 2013).

The typical pattern and timing of GS emigration may be altered by stochastic events, prominently including late summer or early autumn tropical storms. Major precipitation events rapidly and substantially raise river water level and current velocity prompting early departure from seasonal holding areas and from the natal river by GS. Flooding scavenges nutrients from riparian lowlands and swamps, agricultural lands, and urban sewage plants, resulting in dissolved oxygen crashes that apparently trigger downriver movement by oxyphilic GS. For example, up to 73 cm of rain fell on the Suwannee River watershed during the passage of Tropical Storm Debby on 26–27 June 2012. The upper river rose 10 m (3 m above flood stage), reaching its highest level since 1964, third highest since 1906. Dissolved oxygen measured in the rkm 7–40 reach downriver fell progressively to a low of 2.1–2.7 mg L^{-1} by 16–17 July (USGS-WARC unpubl. data). As the wave of hypoxic flood water proceeded down the river, seven USGS remote datalogging receivers deployed between rkm 204 to rkm 7 documented that at least 90% of

49 acoustically-tagged GS departed holding areas and rapidly moved downriver. Of those, 23% remained within the river mouth (below rkm 7) while 67% departed the Suwannee River to enter the GOMEX, with 10% remaining undetected (M. Price, USGS, pers. comm.). One to two months after departure, all GS GOMEX refugees returned to the Suwannee River, later exiting again during the normal October-November emigration window. However, prematurely truncated river residence (i.e., early departure, 2–3 weeks ahead of the normal mid-October emigration onset) from the Choctawhatchee River to the GOMEX has been reported in response to late September 1998 flooding from Hurricane Georges, when river discharge rate increased from 63 cms to 2175 cms over 10 days (Parauka et al., 2001). During the same regional storm event, 75% of acoustically-tagged GS in the rkm 57 holding area of the Pascagoula River exited to the GOMEX within one week (Slack et al., 1999; Heise et al., 2005). Again, Ross et al. (2001b) observed an early departure of a telemetry GS following late August flooding in the same river.

Young-of-the-Year follow a different schedule for downriver migration. After spending the first 9–10 months of life in freshwater reaches of the Suwannee River, YOY descend to the brackish estuary for the first time in late January through early February, proceeding downriver at the same time as early arrival males swim upriver.

Staging in the lower river during immigration or preceding emigration. Staging is an extended precursor to or interruption of either GS immigration or emigration for a period of multiple days to multiple weeks (Grammer et al., 2015). Staging in various GS life history contexts has been documented from telemetry evidence in various rivers. During the spring immigration in the Suwannee and Pascagoula rivers, Carr et al. (1996b) and Ross et al. (2000) have documented GS lower river or rivermouth staging via telemetry. Fish entering the Choctawhatchee River may spend up to a week in the 'Muddy Lake' staging area, 7.5 rkm above the river mouth (Fig. 10) (Parauka et al., 1991). Typically, staging during spring consists of either cessation of migration or a series of short distance (up to ~25 rkm) up and back movements within the staging area over a period of hours or days prior to a definitive migration upriver to a holding area (Fig. 33). It may be hypothesized that such movements serve an olfactory probing function, in an attempt to recognize the chemical signature of the natal river. An alternative hypothesis is that a period of accommodation to freshwater is necessary for certain individuals arriving from marine waters. However, many immigrating individuals display no period of staging, proceeding directly upriver (Fig. 31a,b). Odenkirk (1989) observed that immigrating GS did not linger at the saltwater – freshwater interface, but moved steadily upstream into the Apalachicola River.

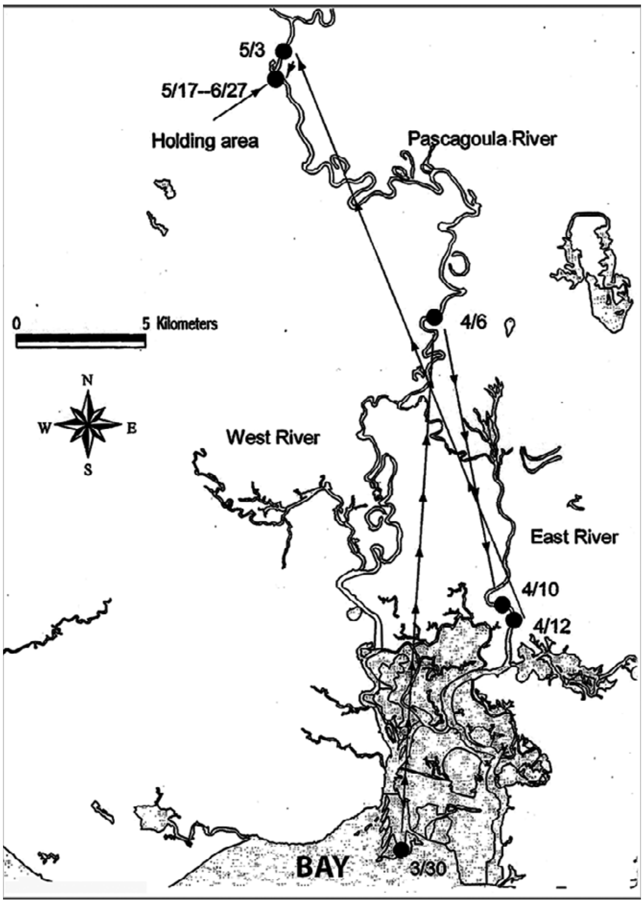

Fig. 33. Telemetry track of an individual Gulf Sturgeon immigrating into the Pascagoula River on 30 March, thereafter displaying up and back river mouth staging until at least 12 April before finally ascending upriver and settling into a seasonal holding area at rkm 56 on 17 May, remaining there through 27 June (adapted from Ross et al., 2000, Fig. 10, courtesy of Mississippi Department of Fisheries, Wildlife and Parks, and the Mississippi Museum of Natural Science)

Pre-emigration staging has been observed in several GS rivers. Odenkirk (1989) hypothesized that an extended period (multiple days) of staging may be required in emigrating GS to allow for adjustment to saline water after spending several months in freshwater. Such a seasonal acclimation process in emigrating juvenile through adult stages may recapitulate the initial ontogenetic process of physiological and cellular accommodation to salinity at the YOY to age-1 transition in anadromous sturgeon species (Altinok, 2007; Allen et al., 2011, 2014). The last two studies referenced speculated that this preparatory period was stimulated by natural photoperiod. Telemetered GS moving down the Choctawhatchee River in mid-October stopped and staged in 'Muddy Lake' for 2 weeks before emigrating into Choctawhatchee Bay (Parauka et al., 2001). In the Pascagoula River, Slack et al. (1999). Heise et al. (2005) and Grammer et al. (2015) found that GS moved >150 rkm downriver over 2.5–16 days in late September-early October stopping at staging areas between rkm 38 and 24, remaining in that reach for several weeks before exiting the river in early November. Rogillio et al. (2001) observed that GS emigrating from the Pearl River remained in the Rigolets area, a brackish interface between the mouth of the Pearl River and the adjacent more saline waters of Lake Pontchartrain and Lake Borgne (Fig. 19). In the Apalachicola River, the deep Brothers River tributary, starting 23 rkm above the river mouth (Fig. 8), serves as a pre-emigration staging area (Wooley and Crateau, 1982, 1985; Odenkirk, 1989). The same is true of the Cooper Basin (Fig. 12), a major GS aggregation area adjoining the Blackwater River 14 rkm from the river mouth (Carr, 1983; A. Kaeser, USFWS unpubl. SSS data; N. Craft, Northwest Florida Aquatic Preserves, unpubl. data). Lower river staging areas have also been identified in the Escambia River (Craft et al., 2001; Stewart et al., 2012). In the Yellow River, the aptly-named 'Sturgeon Lake' at rkm 14 may also serve as a migratory staging area.

Upriver aggregation/staging prior to spawning and prior to emigration. In the Suwannee River, anecdotal observations in September in several years indicate that GS aggregate at rkm 204, in the area of conjunction of the Withlacoochee River tributary with the Suwannee River (Fig. 5). Although such aggregations precede the onset of downriver emigration, the nature of aggregation behavior is uncertain. It is now known from acoustic telemetry (USGS-WARC unpubl. data) that males in autumn-spawning readiness occupy this same area for up to two months (Fig. 31c), waiting to escort arriving females to spawning grounds just upriver in the Suwannee River mainstem or 6 rkm up the Withlacoochee River (Fig. 5).

Natal river fidelity, straying, exploration, and inter-river translocations. Generally, high recapture rates between GS tagging years within a given river, together with genetic determinations of river of origin, indicate a high degree of natal river fidelity for a given GS population (Wooley and Crateau, 1985; Stabile et al., 1996; Foster and Clugston, 1997). Accordingly, Wooley and Crateau (1985) reported a between year recapture rate of 43%; Sulak and Clugston (1999) a rate of 36%. It has been hypothesized that genetic population structure within the anadromous GS is maintained by strong homing fidelity (Stabile et al., 1996; Wirgin et al., 1997; Waldman and Wirgin, 1998). Stabile et al. (1996) estimated an exchange of only 0.45 females per generation (~20–25 years) in a mtDNA genetic analysis of inter-population gene flow between the Choctawhatchee population and the Escambia/Yellow River complex.

On the other hand, data from tagging mark-recapture programs and telemetry relocation studies suggest a higher rate of inter-river translocations. Microsatellite DNA studies (Dugo et al., 2004; Kreiser, 2012) have detected a strong degree of genetic structure (natal river population differentiation) and hence a high degree of reproductive fidelity among river stocks. However, some individuals that stray from their natal river systems may not remain or spawn in the host river. This matter requires further resolution. Relocation data confirm that movement of individuals from one natal river to another via the marine corridor is a regular feature of GS life history. For example, in an early tagging study, Carr et al. (1996b) reported that six Apalachicola River tagged GS were recaptured in the Suwannee and one Suwannee River tagged GS was recaptured on the rkm 171 spawning ground below JWLD in the Apalachicola River. The minimum distance between the two rivers is 180 km. A coastal migration of even greater distance is evident from a 123 mm FL GS collected and tagged in the Suwannee River in 2001 (K. Sulak, USGS, pers. comm.), recaptured in Choctawatchee Bay in 2012, and later found dead in St. Andrews Bay in 2014 (N. Willett, Delaware State Univ., pers. comm.). This is the only evidence to date of a Suwannee River GS moving west of the Apalachicola River mouth. Mark-recapture and acoustic telemetry investigations by USGS have frequently detected Apalachicola and Ochlockonee River-tagged fish in the Suwannee River over two decades of research (USGS-WARC unpubl. database). Fox et al. (2000, 2002) found that a ripe male acoustically-tagged in the Choctawhatchee River in 1997 and detected on the spawning grounds that year, was subsequently detected in the Escambia River in 1998, then back in the Choctawhatchee River in 1999. Ross et al. (2002) reported a Choctawhatchee River tagged GS was recaptured in the Pascagoula River, and several Pascagoula River tagged GS were recaptured in the Pearl River. Exchange both ways between the Pearl River and Pascagoula River has been reported earlier by Rogillio et al. (2001). Translocations between the Pascagoula River and Yellow River, and Yellow River and Choctawhatchee River have been reported by Ross et al. (2009) and Edwards et al. (2007). Berg et al. (2007) reported that eight of 25 recaptures from among 77 GS tagged by USFWS in the Yellow River in 1993–2005, were fish originally tagged in the Blackwater, Escambia, and Choctawhatchee rivers, suggesting a higher rate of straying than estimated genetically by Stabile et al. (1996). Fox et al. (2002) also noted that the actual straying rate may be higher than the Stabile et al. (1996) estimate. River assignment by more recent molecular genetic fingerprinting suggests that the admixture of GS populations within a given river may indeed be more prevalent than earlier gene flow estimates suggested (Dugo et al., 2002, 2004; Kreiser, 2012). However, evidence of admixture among adults may simply represent temporary visits away from the natal river, rather than a permanent translocation with subsequent spawning in a host river.

Movement into non-natal rivers has been termed straying, but exploratory excursions sometimes result in a permanent change in river of residence and spawning. Co-occurrence of adult GS from several natal rivers on shared marine feeding ground hotspots (Edwards et al., 2007; Ross et al., 2009; Vick et al., 2016) may facilitate return migration to non-natal rivers. Permanent translocations probably insure maintenance of genetic diversity among the GS natal river populations, as well as maximal longitudinal spread of the species range. They would also serve as an adaptive hedge against sea-level changes that could merge river channels at low stands, or divide them at high stands. Temporary translocations may serve a different purpose. Thus, the majority of Pearl River GS relocated in the Pascagoula River appeared to be using the non-natal river only for seasonal holding. The same may be true of Yellow and Escambia River GS occupying the Cooper Basin holding area in the Blackwater River. In either case, individual translocations away from the natal river reinforce observations that a certain percentage of the population deviates from the norm in almost every aspect of the highly-adaptive life history of the GS.

Holding areas, congregation, and holding behavior

Sturgeon engage in an energetically-conservative life style characterized by a distinctively poikilothermic strategy of energy acquisition, expenditure, and conservation. They balance periods of migration and active foraging with opposing periods of spatially limited movement and trophic dormancy. This is particularly true for the anadromous sturgeon species, including the GS. The period of intense migratory and feeding activity spans 4–7 months, from the October-November emigration through the February-April emigration and spring spawning interval, or a somewhat modified version for autumn spawners. In the GS, the period of heightened energy expenditure and acquisition is balanced by February-April through September-October seasonal holding and resting behavior accompanied by cessation of feeding. The ontogenetic and annual cycles of probably all sturgeon species are so punctuated by periods of spatially-confined holding and energy conservation accompanied by trophic dormancy. Dadswell (1979) reported a similar multi-month period of intense feeding and dramatic weight gain in female SNS in New Brunswick, Canada, countered by a winter period of inactivity and fasting in deep holding areas. During such intervals, energy stored in oil and muscle tissue is consumed, growth in length is halted, and weight is lost. In the GS, these coordinated phenomena are evident in the GS 'trophic ratchet' growth pattern (Fig. 26) resulting from dramatic differences in seasonal weight loss and gain (Fig. 27).

In some species, holding coincides with extreme low winter temperatures, as in northern latitude populations of SNS (Dadswell, 1979), LS (McLoed et al., 1999), and WS (Hildebrand et al., 1999). Correspondingly, it has been hypothesized that holding in the GS represented a parallel southern latitude response to limiting high water temperatures in summer (Mason and Clugston, 1993). Within the logistic limitations of infrequent boat-tracking telemetry, GS were described as moving only infrequently with movements typically of only 1–2 km upstream or downstream once settled into seasonal holding areas (Wooley and Crateau, 1985; Chapman and Carr, 1995; Clugston et al., 1995; Carr et al., 1996b; Foster and Clugston, 1997; Heise et al., 2005) Indeed, this logic culminated in a 'thermal barrier hypothesis' stating that GS were 'trapped' within cool spring-water 'thermal refugia' (Chapman and Carr, 1995; Carr et al., 1996b). However, using temperature-sensing radio tag telemetry, Foster (1993) found no significant differences between temperatures recorded from tagged fish in holding areas and ambient water temperatures in the river mainstem. She concluded that GS do not use areas receiving spring water as thermal refugia. Furthermore, (Sulak et al., 2007) robustly tested the 'thermal barrier hypothesis'. Testing three independent lines of evidence, they determined that neither were GS trapped within holding areas, nor were those holding areas significantly cooler than adjacent reaches of the mainstem river. Indeed, GS frequently moved from one holding area to another during summer (Sulak et al., 2007), sometimes in progressive hops over several months (Fig. 31c). Movements between holding areas of as much as 54 rkm upstream and 139.5 rkm downstream were documented by sequential within-summer net recaptures.

The ultimate post-immigration and post-spawning spring-autumn destination for all non-YOY GS in all river populations are freshwater holding/resting areas. One or more such areas have been identified in each natal river, plus the non-natal Blackwater and Ochlockonee rivers. They have been discovered and delimited based on knowledge from the early commercial fishery, scientific net sampling surveys, radio and acoustic telemetry, and by SSS surveys.

The single outstanding characteristic that all holding areas have in common in all GS rivers, and indeed for all sturgeon species, is depth. Wooley and Crateau (1985) were the first to state that depth was the most important requirement of 'summer dormant areas' preferentially occupied by GS. Subsequently, Foster and Clugston (1997) described 'summer areas' or 'congregation areas' as 'a depression about 1–2 m deeper than the main channel.' Morrow et al. (1996) reported that 92% of Pearl River GS captures came from the West Middle River, from areas characterized by deep holes and low current velocity. Investigations of habitat selection during periods of relative inactivity in other sturgeon species have similarly identified depth as the key and common factor (e.g., Haynes et al., 1978; Dadswell, 1979; McLoed et al., 1999). Depth greater than average depth of the river creates natural topographic pockets of reduced current flow and reverse eddies, allowing sturgeon to conserve energy otherwise needed to swim against the prevailing current. Adams et al. (1997) have most eloquently captured the rationale of energetically-adaptive sturgeon habitat use as in their interpretation of substrate-tending behavior in the SVS. Thus, they have written: 'Substrate appression….is likely utilized by shovelnose sturgeon under natural conditions and may enhance exploitation of low velocity microhabitats within high velocity macrohabitats in rivers.' Seasonal holding in deep riverbed pockets and runs for the GS may be much the same, an adaptive escape into low velocity microhabitats during a period of energy conservation. Sulak et al. (2007) have described a typical Gulf sturgeon holding area in the Suwannee River as consisting '…of a 500–2000-m-long, 3–4-m-deep, sand-bottom run lying just below a 4–7-m-deep scour hole that is limited downstream by a 1–2-m-deep sand shoal.' Stewart et al. (2012) similarly found that holding areas in the lower Escambia River represented scour holes.

In various GS telemetry studies, by mid-summer nearly all tagged GS have been found residing within holding areas (e.g., Wooley and Crateau, 1985; Carr et al., 1996b; Foster and Clugston, 1997; Heise et al., 2005). Sidescan SONAR surveying (conducted continuously from rkm 140 to rkm 30 down the Suwannee River in mid-September 2015) showed GS densely congregated within known holding areas (Fig. 34a,b), in contrast to only scattered individuals being found in reaches between holding areas (USFWS and USGS-WARC unpubl. data). Sonar imagery showed that GS are highly congregated. Within the Suwannee River holding area adjacent to Manatee Springs (Fig. 34a), a mean density of one individual per 17 m^2 was determined from SSS imagery.

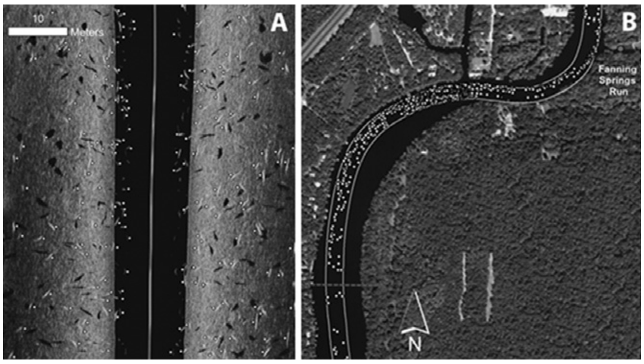

Fig. 34. Sidescan SONAR imagery of Gulf Sturgeon seasonal holding areas in the Suwannee River (provided by A. Kaesar, USFWS): (a) A 65 m long reach in the Manatee Springs holding area, center line showing survey boat path. Scanned areas are in gray to the right and left of the dark central SONAR void. Whitish elliptical returns denote Gulf Sturgeon hovering above the river bottom. Dark fish-shaped objects are the sturgeon SONAR shadows. White dots are inserted to mark each fish SONAR return (and its matching shadow) for enumeration. Mean density is one fish per 17.5 m^2. Note random orientation of individuals. (b) A 1.9 km reach of the 2.5 km long Fanning Springs holding area, dots show ~400 Gulf Sturgeon residing within

Most holding areas appear to be of natural origin due to geological history and hydrological sculpting of the riverbed. However, in some cases man has intervened by damming, diverting, dredging, and otherwise reconfiguring riverbed morphology and thereby altering hydrography as well. Such human reshaping has sometimes inadvertently created energetic refugia conducive to sturgeon holding. Examples include scour holes below high dams (e.g., the deep hole at rkm 172 below the JWLD on the Apalachicola River), deepened basins (e.g., the Cooper Basin timber catchment in the Blackwater River), and excavated holes (e.g., gravel pits in the Bouie River) beneficial to GS. Eddy zones behind river wingdams (e.g., such structures in the Missouri River) serve a parallel function for the SVS (Hurley et al., 1987). On the other hand, man has alternately intervened in eliminating natural holding areas in GS rivers, as with USACE channel modification for vessel navigation, e.g., dredging and filling of a 30.5 m wide channel to the uniform 2.7 m control depth in the Apalachicola River (Bass and Cox, 1985; Wakeford, 2001). In addition to destroying natural holding habitat, humans have also exploited GS congregations within holding areas. Thus, the turn-of-the-20th-century commercial fishery targeted aggregations of GS in holding areas in the Apalachicola, Suwannee, and Blackwater rivers (above).

In each GS natal river, and a few non-natal rivers, researchers have identified deep holes or runs used by GS as seasonal holding/resting areas. Some of these double as post-immigration, pre-emigration, or pre-spawning staging areas that serve as low-velocity energetic and physiological accommodation rest-stops. Telemetry has revealed that not all holding areas are occupied every year. On the other hand, additional deep areas not previously identified as holding areas have begun to be occupied by the growing Suwannee River population. This suggests that holding area habitat availability may be an important factor in determination of GS population carrying capacity in a given natal river.

Reproduction and spawning

Fecundity

Once a female GS achieves sexual maturity, she will continue to spawn periodically throughout her life. Among all species of sturgeon, no indications of female gonadal senescence have been observed. Fecundity is positively correlated with body mass, and thus generally increases with age, although data are limited. For example, Parauka et al. (1991) reported fecundities of 317 800–400 000 in two GS females of 68.1 kg weight each, with a mean of 101–103 eggs g^{-1} ovary weight (mean egg diameter 2.1 mm). Chapman et al. (1993) reported fecundity in three sexually mature GS females as 274 680–475 000, with a mean of 9366 eggs kg^{-1} body weight. Thus, for the largest wild females (~91 kg) typically found in any GS natal river fecundity would be >580 000 ova.

Spawning substrate choice

Balon (1975), who further refined the fish spawning guild established by Kryzhanovsky (1949), assigns sturgeon to the ‘open substratum lithophil’ guild. This guild includes fishes, like the GS, in which adhesive eggs are selectively deposited on rocky substrate, without a nest or parental guarding, and with benthic, lecithotrophic free embryos developing into pelagic larvae. Sturgeon have typically been termed ‘broadcast’ spawners, a term that is somewhat misleading since eggs are not released *ad hoc* into the water column nor randomly strewn over the substrate. For example, in WS on the Waneta spawning grounds, Pend d’Oreille River, BC, Golder Associates Ltd. (2008) observed that eggs deposited on riverbed collection mats were highly aggregated, suggesting egg release had occurred near the river bottom. Hard substrate is essential in order for the adhesive eggs to immediately adhere to the substrate, and not get swept downstream. Lithophilic spawners like the GS require clean, hard substrate (Mapes et al., 2015) upon which to directly deposit eggs. Neither sand nor clay substrate is satisfactory, since GS eggs would roll and get coated with sand or silt particles, get battered, swept downstream, and removed from essential post-hatching interstitial gravel developmental habitat.

Females are very selective regarding spawning ground location, homing to the same short (typically <500 m long) river reaches every year. They are also very selective in choice of egg deposition substrate within spawning grounds. In the upper Suwannee River, Sulak and Clugston (1998, 1999) and Sulak et al. (2013) deployed egg samplers over a mosaic of rock, gravel, coarse sand, and fine sand substrate. Eggs were collected only from samplers deployed on gravel substrate. Gravel is essential to provide the interstices into which free embryos will descend and hide immediately upon hatching and for the next 4–5 days. Evaluating the spatial distribution of eggs found on artificial substrate samplers, Sulak and Clugston (1998, 1999) and Sulak et al. (2013) determined that females chose only subareas with abundant, clean, sub-angular, heterogeneous gravel of major dimension

2–10 cm (Fig. 35a). Immediately adjacent subareas containing gravel with sub-optimal attributes (Fig. 35b–d) were not utilized, nor were subareas of fine to coarse sand, cobble and boulders, or rock ledge. Optimal particle size has similarly been found to be important in other sturgeon species. Thus, Holcik (1989) reported that Sterlet selectively deposit eggs on pebbles of 1–7 cm diameter, a range comparable to that of the GS (Sulak et al., 2013). LeHaye et al.'s (1992) study revealed elements of similarity in spawning substrate choice between the LS and GS. These authors described spawning habitat used by LS as comprising 'moderately heterogeneous substrates composed of fine to medium gravel or coarse gravel with scattered cobbles and boulders.' Within such areas, LS eggs were found most frequently where mean particle size ranged between 1.70–6.45 cm.

While gravel substrate is scarce as potential spawning substrate in the Suwannee River, it is abundant and ubiquitous in some alluvial rivers like the Pearl and Pascagoula. In-channel pit-mining in the Bouie River, Pascagoula system, has deepened the riverbed and exposed gravel, providing manmade staging and spawning areas for the GS (Ross et al., 2001a; Heise et al., 2004). In the Suwannee River gravel accumulates only where particular geological and hydrological settings occur. Such settings include cross-channel ridges formed by upfaults, eddy zones below boulders that retard current transportation of gravel, catchment pockets eroded into a horizontal rock shelves, and the upstream ends of mid-river islands that serve as depositional catchments. The hydrographic context is important as well. Turbulence and high flow velocity is required to prevent sand from accumulating and covering gravel beds. However, stochastic flood events can completely bury a gravel spawning ground under a thick layer of sand.

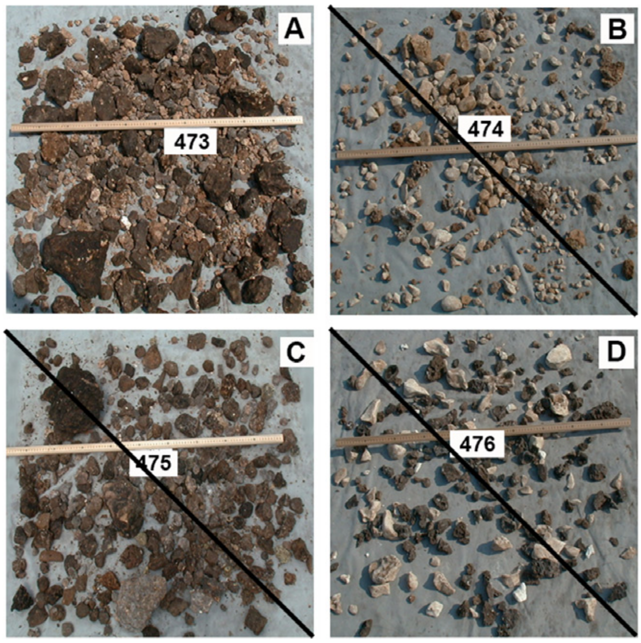

Fig. 35. Gravel samples from four 1.0 m^2 quadrats representing four subareas of the Suwannee River rkm 215.5 spawning ground in 1996 (Sulak et al., 2013). Size reference is a meter stick. (a) sample from subarea 473, were Gulf Sturgeon eggs were deposited almost exclusively, (b–d) samples from subareas 474–476, not selected for egg deposition

Hydrographic and water chemistry context of spawning habitat

Current velocity and turbulence. The presence of gravel, even with optimal attributes for egg deposition, is alone inadequate in the determination of GS spawning habitat. Hydrography and water chemistry are probable further determining factors. It is instructive that in the GS, all known spawning grounds lie 91–250 rkm from the river mouth (Table 2) where an optimal combination of substrate, flow and water chemistry pertains for egg and embryo development and survival. A high and continuous rate of current flow (generally >1.5 m s^{-1}) has been observed on sturgeon spawning grounds in many investigations. Rapid flow rate is essential (Wooley and Crateau, 1985) to insure sufficient delivery of oxygen to developing embryos. Nonetheless, rapid current velocity alone may be insufficient if flow is predominantly laminar. Turbulent flow over the gravel bed may be required to insure adequate oxygenation of the eggs and removal of waste CO_2. Perhaps relevant in this regard are observations that current breaks created by boulders were features attractive to LS spawners (LeHaye et al., 1992). On the rkm 215 gravel bed in the Suwannee River, GS eggs were found almost exclusively on substrate samplers (Sulak and Clugston, 1998, 1999) deployed on the south side of the river. Acoustic Doppler Current Profiling (ADCP) during the spring spawning period showed that the south side is characterized by abundant eddies and highly turbulent flow vs very laminar flow on the north side (Sulak and Clugston, 1998). It can be hypothesized that turbulence is essential to facilitate gas exchange across the egg membrane (O_2 delivery and CO_2 removal) for the developing embryo in a viscous medium. Water depth does not seem to be important. On the rkm 215 spawning ground in the Suwannee River, eggs have been collected on artificial substrate samplers in both very low water (<1.5–2.0 m depth) and exceptionally high water conditions (>10 m depth) (USGS-WARC unpubl. data). In the Apalachicola River, Scollan and Parauka (2008) collected eggs on samplers at depths ranging from 1.0 to 5.4 m (median depth 3.2 m).

Ionic properties of spawning site water. Divalent ion concentration, pH, and conductivity may be used to identify river reaches chemically suitable for spawning. Specific ranges in Ca^{++} ion concentration and pH appear to define water optimal for sturgeon spawning. Cherr and Clark (1984, 1985) reported a pH range of 5.5–8.5 for the WS sperm acrosome reaction, with sperm failing at higher and lower pH levels. Optimal pH for sturgeon eggs appears to lie in the near-neutral range (pH = 7.0) to slightly alkaline (pH < 8.0) range. In the European Sturgeon, a close relative of the GS, Holcik (1989, citing Ninua, 1976), reported a pH range of 7.4–7.6 on spawning grounds in the Rioni River, Republic of Georgia. Holcik (1989) reported a range of 6.8–7.2 as optimal for Sterlet eggs, and a range of 6.6–7.7 empirically observed for Russian Sturgeon eggs. The actual role of pH may be indirect, determining the concentration of dissolved Ca^{++} ions in river water within spawning reaches. Calcium ions are important in mediating the union of sturgeon gamete during fertilization (Detlaff and Ginsburg, 1963). Conductivity is a useful, easily-measured surrogate for Ca^{++} ionic concentration, otherwise not readily measured in the field. Sulak and Clugston (1999) determined a very tight positive linear correlation ($R^2 = 0.9481$) between Ca^{++} concentration and electrical conductivity in the Suwannee River, which courses through calcium carbonate bedrock. A Ca^{++} ion concentration range of 6–18 mg L^{-1} was observed from water samples taken during egg collections (Sulak and Clugston, 1998, 1999), corresponding to an observed range in electrical conductivity of 40–110 μS cm^{-1} (Sulak and Clugston, 1999; Sulak et al., 2013). Cessation in spawning coincided with a marked increase in conductivity. Similarly, Parkyn et al. (2006) reported that conductivity in the Suwannee River from March through June, spanning the spawning interval, was lowest (90–122 μS cm^{-1}) in April, rising rapidly in May (201–350 μS cm^{-1}). These authors suggested that decreased conductivity on spawning grounds during the spring season may be a factor in successful GS spawning. Fox et al. (2000) reported a conductivity range of 32–70 μS cm^{-1} during GS egg collections in the Choctawhatchee River. Scollan and Parauka (2008) reported the conductivity range of 108–169 μS cm^{-1} during April-May egg collections in 2008 in the Apalachicola River. In the earliest scientific study of the GS, Huff (1975) noted that low water hardness (due to Ca^{++} ions) was peculiar to upper river reaches that he hypothesized were used for spawning (a hypothesis subsequently confirmed). Conductivity in the low range of 70–125 μS cm^{-1} has been indicated as a water chemistry factor of importance during spawning in other sturgeon, including the LS (Auer, 1996) and SNS (Dadswell, 1979). It is highly probable that a specific chemical milieu, expressed by pH, Ca^{++} ion concentration, and conductivity is essential in GS selection of locations of upper river spawning grounds. Bull (1940) reported the ability to perceive slight changes in pH (0.04–0.10 pH units) among 20 species of marine teleosts. Given the apparent importance of electro-chemical properties of river water to GS spawning, it may be hypothesized that the electroreceptive ampullary organs are involved in spawning grounds selection and homing.

Spawning behavior

Telemetry has determined that male GS either stage below spawning grounds to await the arrival of ripe females, or accompany females during the upriver ascent. Males may make multiple ascents to spawning ground from their staging areas (Fig. 31b), spawning several times with different females over a period of up to six weeks. Female GS spawn once and drop back downriver to holding areas immediately (Fig. 31a), as has similarly been reported in the Sterlet (Holcik, 1989).

Due to the dark tannic or muddy water characteristic of GS natal rivers, and the secretive nocturnal habits of the species, actual spawning has not been observed. However, it can be hypothesized that mating in the GS is similar to that observed for the LS in Wolf River, WI, which is observable in shallow water during the daytime. Mating in LS, WS (Triton Environmental Consultants, 2004), and probably the GS is polyandrous. Several LS males compete vigorously for physical proximity to a female, rubbing her with the body and snout to stimulate release of eggs, as similarly reported in the AS by Dean (1893a). As the female releases a batch of eggs, attending males release clouds of sperm. There is no elaborate courtship ritual, although LS males vocalize during mating (Bocast et al., 2014). Vocalization (serial clicks) has also been recorded in GS aggregated in seasonal holding areas (USGS-WARC unpubl. data), but it is unknown if GS also utilize acoustic communication during spawning. Lateral rubbing, snout nuzzling, and forceful prodding are typical behaviors in courting male sturgeons, resulting in red abrasions in both sexes (Dean, 1893a,b; Borodin, 1925; Holcik, 1989). In the GS, males with red, bloody snouts and females with reddish lateral abrasions have commonly been observed in net captures just after the spring and autumn spawning seasons (USGS-WARC unpubl. data).

Spawned eggs, embryos, and hatchling free embryos

Although unfertilized sturgeon eggs become immediately adhesive upon contact with freshwater when spawned, Cherr and Clark (1985) report full adhesion in WS eggs only develops within five minutes of fertilization. Sturgeon egg adhesion to the substrate is reported as very strong (Markov, 1978), as also observed in the GS (Chapman et al., 1993; Parauka, 1993). Black when deposited, fertilized GS eggs hydrate, swell to 2.8–3.2 mm diameter, and turn brown to gray. The animal pole rotates to the top, initially appearing as a light-colored bullseye consisting of a polar spot surrounded by 3–4 concentric rings (Detlaff et al., 1993; Plate1, stage 2) later forming into the crescent shape of the embryo. It appears that eggs are spawned in batches, a few thousand at a time. Cleavage stages observed for GS eggs (embryos) collected between 08:00–10:00 hours on Suwannee River spawning grounds suggest that spawning occurs between 00:00–04:00 hours. Eggs (embryos) 1–2 days old become tan in color, on day 3 before hatching they become translucent yellow. Unfertilized eggs remain black; non-viable eggs become clear or shriveled (Sulak and Clugston, 1998). In laboratory culture of sturgeon eggs (embryos), fatal infection with furry white *Saprolegnia* fungus is common (Ryder, 1890; Kynard, 1997; Holcik, 1989), including in the GS (Parauka et al., 1991). However, this fungus has only been observed at a very low rate of occurrence on wild-spawned eggs (embryos) of the GS (Sulak and Clugston, 1998) or other North American sturgeon (Kynard, 1997).

Time to hatching is temperature dependent. At typical ambient river water temperatures on the spawning grounds in spring (20–21°C), GS hatching occurs in ~72 h. In the laboratory, Parauka et al. (1991) determined a range of 54.4–85.5 h at temperatures of 23.0–18.4°C, respectively. Chapman and Carr (1995) reported a range of 15–20°C for maximum egg, embryo, and larval survival under laboratory culture conditions, with highest embryo survival at 15°C. That is a water temperature 1–10°C below the range reported for wild GS egg collections from various natal rivers (Table 4). These authors reported high egg hatching failure and complete embryo mortality within a week at 25°C. At temperatures exceeding 23°C, development goes awry and the embryo dies (F. Chapman, Univ. Florida, pers. comm.). Actual duration until hatching depends upon a species-specific, genetically-set quantity of heat, measured in total CTU (cumulative thermal units[5]) required for embryonic development within the egg. The GS requires 7.5 CTU compared to 11.7 for its AS sister subspecies (Kynard and Parker, 2004). Accordingly, the AS requires a long period until hatching, 94 h at 20°C (Dean, 1893b) to as much as 168 h at 16–19°C (Vladykov and Greeley, 1963; Smith et al., 1980).

Documentation of spawning grounds

Spawning has been confirmed in six of seven natal rivers by the collection of eggs on gravel beds using artificial substrate samplers in spring. Locating spawning grounds has been facilitated by tracking the upriver movements and furthest upriver stopping points of adults using acoustic and radio telemetry. The first wild spawned GS eggs were collected on anchored floor buffer pads on gravel beds at rkms 202, 215 and 221 in the Suwannee River (Marchant and Shutters, 1996) (Table 4). Additional eggs have been collected at these same sites, at rkms 158–162 and 209 in the Suwannee River mainstem (Sulak and Clugston, 1998, 1999; USGS-WARC unpubl. database), and 4 rkm up the lower reach of the tributary Withlacoochee River (Parkyn et al., 2006) (Fig. 5). Recent telemetry suggests the presence of another spawning ground above rkm 235, the furthest upriver stopping point of telemetered adults in 2016 (USGS-WARC unpubl. data). In the Pascagoula River system, spawning has been documented by egg collections (Table 4) at rkm 250 in the Bouie River (Fig. 16) (Slack et al., 1999; Heise et al., 2004) where adult GS were captured every spring, 1997–2003 (Ross et al., 2004). Spawning is also suspected to occur in the Chickasawhay River tributary based on genetic sub-structure within the population (Dugo et al., 2004) and movements of adults. Spawning in the Yellow River has been confirmed by collection of GS eggs (Kreiser et al., 2008; W. Tate and J. Van Vrancken, USFWS, pers. comm., 2009) (Table 4), and by collection of three YOY (Table 6). Eggs have been collected in the Escambia River at five sites between rkms 161–170 (Fig. 12) (Craft et al., 2001), Choctawhatchee River at five sites between rkms 140–155 (Fig. 10) (Fox et al., 2000), and in the Apalachicola River at three sites below the JWLD between rkms 160–171 (Fig. 8) (Pine et al., 2006; Scollan and Parauka (2008); J. Ziewitz, USFWS, pers. comm., 2006). In the Pearl River, spawning grounds remain undiscovered, and no GS eggs have been collected. However, the presence of YOY and early juveniles among scientific samples over the past three decades demonstrates that the river still supports a spawning population (Miranda and Jackson, 1987; Morrow et al., 1996, 1998; Rogillio et al., 2001, 2007; USGS-WARC, 2009, unpubl. data). No attempt has been made to sample eggs in the Ochlockonee River.

Autumn spawning

It has now been established that a portion of the GS population in the Suwannee River spawns in the autumn (Sulak and Clugston, 1999; Randall and Sulak, 2012), a phenomenon recently documented as well in the sibling AS (Balazik et al., 2012; Balazik and Musick, 2015), and known in other sturgeon species (cites in Randall and Sulak, 2012). While autumn spawned eggs have yet to be collected in the Suwannee River, spawning has been confirmed by telemetry documentation of autumn upriver runs by adults (Fig. 31c), the collection of YOY in a TL range six months out of phase with the TL range of spring-spawned YOY, and by collection of motile sperm from males and fully vitellogenic ovulated black eggs extruded from ripe females in autumn collections. Histological examination showed that such eggs were ready to be fertilized. That condition is evident in a 2.5 mm full-term ovulated black ovum extruded by a 1914 mm TL female upon capture, 28 October 1995 in the Suwannee River, as shown in sagittal section in Figs. 36a, b. The 3-layer egg membrane and micropyles had already formed, and the ovum had already polarized (Conte et al., 1988) with germinal vesicle having migrated to the animal pole (= ovum in late maturity Stage IVc of Doroshov et al., 1983) and in the process of breaking down (Fig. 36a), i.e., releasing nuclear material in anticipation of fertilization. It is unknown if autumn spawning also takes place in any of the other GS natal river populations. If so, there could be management actions to consider in controlled-flow rivers, e.g., the scheduling of water releases from the JWLD in the Apalachicola River. Dual spring and autumn spawning is known in other sturgeon species. Thus, dual spawning has been confirmed in the AS (Balazik and Musick, 2015), as earlier reported for Dabry's Sturgeon (Zhuang et al., 1997).

Nocturnal spawning

Spawning in the Suwannee River appears to take place nocturnally. Cleavage stages observed in eggs (embryos)

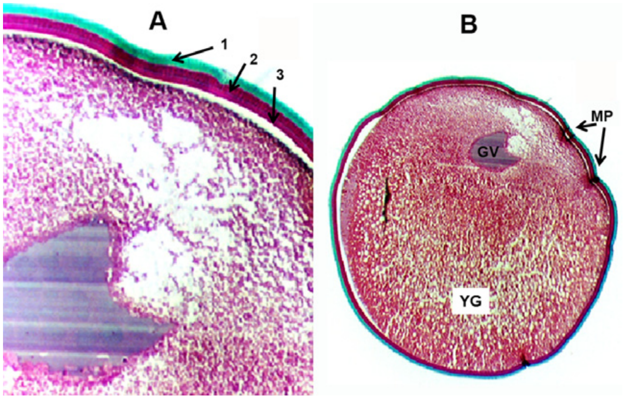

Fig. 36. Sagittal wax-mounted section (stained with Masson's trichrome method) through a 2.5 mm full-term black ovarian ovum extruded by a 1914 mm TL Gulf Sturgeon female upon capture, 28 October 1995, in the Suwannee River. This female was a putative autumn spawner, with fully vitellogenic eggs a few hours from being spawned. Key: (a) Enlargement shows detail of 3-layer egg membrane, layers labeled 1–3; (b) GV = germinal vesicle, already migrated to the animal pole and breaking down to release nuclear material in anticipation of fertilization; MP = egg micropyles, YG = yolk granules. Adapted from Sulak et al. (2013)

collected from sampler pads in early morning hours suggest spawning occurs between midnight and 04:00 AM (Sulak and Clugston, 1999). Nocturnal spawning may confer some initial protection against egg predation by visual predators, or may be just another behavioral expression of the tendency in GS for heightened activity at night (Grammer et al., 2015). The temperature range that has been observed during collection of viable, developing black to yellow eggs (embryos) in six natal rivers is 16–25°C (Table 4).

Effective breeding population size

Based on egg collections on Suwannee River spawning grounds in the mid-1990s, Sulak and Clugston (1998) estimated that the number of females spawning annually, i.e., the effective female spawning population was 80 individuals. Using mtDNA nucleotide diversity data, Bowen and Avise (1990) independently estimated the evolutionary effective breeding female population size for the Suwannee and Apalachicola rivers populations combined as 50. Subsequently, Pine et al. (2001) estimated that 5% of the adult females spawn annually. Since the Suwannee River GS population has grown to ~10 000 by 2011–2013, the percentage of adults has increased accordingly. Applying Pine et al.'s (2001) percentage would yield a current Suwannee River spawning population of 500 adults. Moreover, the population now comprises a mix of multiple year-classes, insuring that despite an apparent 3-year maturation cycle, substantial numbers of mature females are available to spawn each year.

What actually constitutes a minimum effective breeding population size to sustain a GS population in any natal river is unknown. Current breeding populations in the Escambia, Pascagoula, and Pearl rivers probably number in the tens of ripe adults annually. However, sturgeon seem to have inherently high immunity to the negative effects of small breeding population size. A review of published estimates of minimum viable population size (MVP) for >200 sexually-reproducing vertebrate species determined a median 'N' of 4169 (95% CI = 3577–5129) (Traill et al., 2007). However, such estimates do not seem to apply to extant sturgeon populations, many of which have survived depletion to a few hundred individuals. The most recent estimates of net-vulnerable (generally >900 mm TL) population abundances for all GS natal rivers, except the Suwannee River (Table 1), are well below the median MVP and lower 95% CI reported by Traill et al. (2007). Moreover, in the 1970s through mid-1990s, the Suwannee River population was also below the median MVP. A very instructive case regarding the resilience and rebound potential of sturgeon from small population size is that of the Medieval colonization of the Baltic Sea by a very small group of AS (refer to 'Population recovery potential section below'). That founder group subsequently expanded into a long-lasting population that supported a sturgeon fishery. Sturgeon populations that have been considered extirpated have often proven otherwise, such as the now substantially recovering AS in several Chesapeake Bay rivers (e.g., Balazik et al., 2012; Balazik and Musick, 2015). Thus, the prognosis for eventual recovery of small GS natal river populations is encouraging.

Early life history

Life history details for age-0 GS in freshwater from the free embryo stage through first migration to the estuary (330–450 mm TL) are generally lacking. In laboratory flow tank experiments, Kynard and Parker (2004) reported that free embryos do not drift during dispersal. Instead, they swim in directed and purposeful fashion (e.g., head pointing downstream when swimming downstream). But they can also maintain station and even swim upstream for brief periods.

Following adoption of a fully benthic mode, age-0 GS disperse widely in the Suwannee River (Table 6). Captures during the first 9–10 months of life display no apparent relationship in size (TL) as a function of rkm (Fig. 37). That is, there is no downriver trend in increasing TL as would be predicted in a passive downstream drift model. Moreover, capture records suggest that age-0 GS disperse widely, individually, and randomly, using the entire freshwater reach of the river available from Big Shoals (or further upstream during high water) (Fig. 5) to the ETZ (~rkm 10). They disperse not only downstream from spawning grounds as per the classical drift dispersal model for YOY of anadromous fishes, but also as far as 54–68 rkm, respectively, above the uppermost documented (rkm 221) or suspected (rkm 235) spawning grounds (Table 6, Fig. 5).

Collections of YOY have been sporadic in all GS rivers, despite 40 years of sampling effort with trawls, gill nets, traps and electrofishing (Table 6). Low density plus cryptic and solitary habits mean that YOY are typically captured one at a time in any sampling gear. However, Carr et al. (1996a) reported a singular visual observation of aggregation. Physical data accompanying YOY captures in all rivers (Table 6) displays wide tolerances to temperature (14.2–32.0°C), DO (1.6–8.8 mg L^{-1}), conductivity (72–

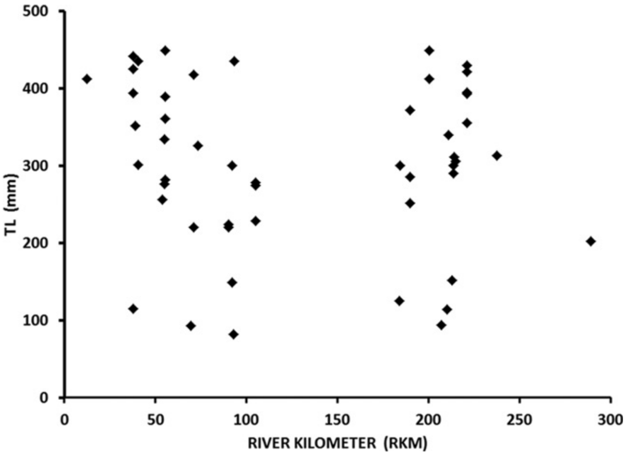

Fig. 37. Relationship between capture location (rkm) and total length (TL) for Gulf Sturgeon YOY in freshwater reaches of the Suwannee River (N = 50 captures). Absence of captures between rkm 105 and 180 is due to limitations of sampling in this shallow reach with numerous rocky shoals (USGS-WARC unpubl. data)

385 μS cm^{-1}), and depth (0.2–7.5 m). Broad dispersal of GS YOY may be an essential survival strategy when foraging competitively in food-poor GOMEX rivers. Such an adaptation enables maximal exploitation of arthropod prey occurring in low density per unit area (Sulak et al., 2007) in oligotrophic blackwater rivers like the Suwannee. Prey density on open sand habitat may limit the number of age-0 GS that can survive to age-1. McCabe and Tracy (1994) similarly reported that WS, larvae in the lower Columbia River disperse widely, facilitating utilization of available feeding habitat and minimizing competition for limited prey resources. Except for the single report of Carr et al. (1996a), GS YOY do not normally appear to school or aggregate. Chan et al. (1997) reported that age-0 GS observed in aquaria avoided contact with each other, maintaining horizontal separation over the substrate.

Carr et al. (1996a) hypothesized that age-0 GS are specifically associated with springs or spring outflows, based upon a singular observation downstream of the Alapaha Rise spring run in the Suwannee River. Otherwise, there is only one other report (by a SCUBA diver) of two or three small (~180 mm TL) YOY occurring within 100–200 m of Morrison Spring (Choctawhatchee River system) in 1972 (Reynolds, 1993) (Table 6). The hypothesis of Carr et al. (1996a) has not been substantiated by YOY captures or observations in springs, spring runs, or spring outflows in any other natal river. Nor have divers reported YOY (or any GS life history stage) observed in any of the ~200 springs or spring runs discharging into the Suwannee River, despite decades of snorkeling and sport SCUBA diving in Florida springs. Moreover, all YOY ≥450 mm TL collected in fresh water reaches of all natal rivers since 1974 (N = 150) have come from open riverine habitats, none from springs or spring runs (Table 6). However, there is empirical evidence of association of age-0 GS with particular substrate types. The eight black-stage YOY captured in the Suwannee and Apalachicola rivers (Table 6) have been found in association with blackened, decaying leaf and twig debris filling troughs in open sandy substrate. Black body color represents effective camouflage within such troughs. Larger bicolor-stage YOY are found on open, unvegetated, sand shoal habitats where a countershaded color pattern probably serves as effective camoflauge. Sturgeon appear to avoid structured or vegetated habitat (Sbikin and Bibikov, 1988; Kempinger, 1996), preferring open sand substrate. Diver observations of LS YOY (Kempinger, 1996) in the wild indicate that they lead a solitary existence. Observations of GS YOY maintained in low numbers in living stream tanks on river sand substrate under subdued lighting display mutual avoidance (K. Sulak, USGS, pers. obs.).

Genetics

Genetic differentiation of GS and AS

Based on mtDNA phylogenetic analyses (Peng et al., 2007; Krieger et al., 2008), the AS and the European Sturgeon form an ancient basal group, the 'sea sturgeon lineage', genetically distinct from all other sturgeon taxa within the Acipenseriformes. Estimated genetic distance suggests this group arose about 171 MYA, with the AS and European Sturgeon separating about 58–60 MYA (Peng et al., 2007; Ludwig et al., 2008) as sea-floor spreading pushed North America and Europe apart. Peng et al. (2007) hypothesized that anadromy is a basal acipenseriform condition characteristic of early sturgeon, including the ancient 'sea sturgeon lineage'. If so, anadromy has been lost in other sturgeon species now wholly adapted to life in lakes and rivers.

By logical inference, the GS is also a member of the ancient anadromous 'sea sturgeon lineage' since genetically it is very close to the AS (Bowen and Avise, 1990; Avise, 1992; Ong et al., 1996; Stabile et al., 1996; Krieger et al., 2000; Ludwig et al., 2008). Evolution of the GS arose by two major vicariant events: (i) Splitting of the Northern Hemisphere supercontinent Laurasia to form the Atlantic Ocean, resulting in two isolated sister species, the AS and the European Sturgeon, (ii) Emergence of the subtropical Florida peninsula due to postglacial sea level lowering, vicariously splitting the originally continuously distributed AS into isolated East Coast vs Gulf Coast populations. These isolated populations diverged over time into two reproductively isolated cognate entities. A large number of such disjunct Carolinian temperate vs GOMEX sub-tropical cognate fish species or subspecies pairs exist.

The present taxonomic status of the GS as a subspecies of the AS merits reconsideration. The totality of evidence suggests these cognate taxa represent genetically distinct species, as expressed phenotypically as well in terms of differential morphology, morphometrics, and behavior. Status of the GS as a subspecies of the AS was originally based primarily on differences in spleen morphology and the architecture of dorsal scutes (Vladykov, 1955; Vladykov and Greeley, 1963), later supported by a more robust analysis of these and morphometric characters (Wooley, 1985). When the GS was first described, genetic data were unavailable to evaluate degree of differentiation of the two sister taxa. Subsequently, mtDNA studies have reported varying degrees of genetic distinction of the GS and AS (Bowen and Avise, 1990; Avise, 1992; Ong et al., 1996; Stabile et al., 1996; Krieger et al., 2000). However, King et al. (2001) reported compelling evidence of trenchant divergence in the nuclear genomes of GS and AS:

> "Allele frequencies, diversity, and average genetic distance (0.557) suggest substantial divergence between the nuclear genomes of *A. o. oxyrinchus* and *A. o. desotoi*, supporting the differentiations previously documented using a morphological character (Wooley, 1985) and the mitochondrial genome (Bowen and Avise, 1990; Ong et al., 1996; Stabile et al., 1996). Average genetic distance between the putative subspecies is twice to three times that observed between populations of *A. o. oxyrinchus*."

Pairwise comparisons of allele frequency distributions for seven mDNA loci from East Coast AS populations vs from Suwannee River GS revealed a large and statistically significant difference between the 'subspecies' (King et al., 2001). Suwannee River GS were found to have significantly fewer alleles per locus than East Coast AS (3.9 vs 6.5). The average genetic distance reported in the same study separates the AS from the GS at a level ($\hat{D}$ = 0.52–0.58) comparable to the genetic distance (mean $\hat{D}$ = 0.63) separating congeneric fish species and substantially greater than that separating subspecies of centrarchid sunfishes (mean $\hat{D}$ = 0.17) (Avise and Smith, 1977). Similarly, within ten genera of teleost fishes, Avise and Aquadro (1982) reported an interspecific genetic distance mean $\hat{D}$ = 0.2–0.6. The research of Ludwig et al. (2008), combining both mtDNA and mDNA methods, again substantiates that the GS is markedly distinct from comparative East Coast populations of the AS.

Further support for specific-level genetic distinction of the GS and AS is provided by Kynard and Parker's (2004) report of trenchant early life history differences. Thus, free embryos of GS have a light gray body and black tail, while those of AS from the Hudson River have a uniform gray-black body and tail color. Additionally, in controlled experiments, CTU required for development differed markedly for GS and AS larvae (above). Larvae of GS vs AS also differ in foraging behavior, and downstream migration pattern (Kynard and Parker, 2004). Unlike the bottom-hugging larvae of the AS, the larvae of the GS routinely forage high in the water column. Additionally, among species of genus *Acipenser* that have been studied (including the AS), the GS displays a unique extended (multi-month), 1-step downstream migration of free-larva through juvenile stages, resulting in continuous broad dispersal along the entire river below the spawning grounds. This is distinctly different from the punctuated 2-step migration of age-0 AS, where free embryos initially move to a well-defined foraging reach just below the spawning grounds (step-1), later dispersing further downstream as YOY juveniles (step-2). Larval coloration and developmental CTU requirement are fixed early life history characters that could readily be hypothesized to be genetically determined and conservative. However, foraging behavior and downstream migration pattern may be more plastic, expressing ecophenotypic adaptation to the exigency of food availability in different rivers (Kynard and Parker, 2004). Early life history differences add substantial weight to taxonomic distinction of AS and GS based on the original morphological and morphometric characters. Recognition of the GS as distinct species would be consistent with the suite of genetic, morphological, and behavioral features that distinguish the GS from the AS.

Several genetic analyses have revealed fundamental geographic differentiation of the GS into distinct regional metapopulations. Additionally, finer scale differentiation is expressed as high natal-river fidelity among each population comprising the larger metapopulation. In their Restriction Fragment Length Polymorphism (RFLP) analyses of mtDNA, Stabile et al. (1996) reported homogeneity in haplotype frequencies for an eastern natal river metapopulation comprised of the Suwannee-Apalachicola-Ochlockonee river populations. This same grouping was also resolved by King et al. (1999) who applied multilocus mDNA genotyping to discriminate genetic stock structure within the GS across its geographic range. Three natural 'management units' (i.e., metapopulations with high genetic integrity) were robustly resolved, with very little evidence of gene exchange among the regional drainages: (i) a Suwannee-Apalachicola-Ochlockonee rivers unit, (ii) a Yellow River unit (including the Escambia River by inference), and (iii) a Pearl River unit (including the Pascagoula River by inference). However, the mtDNA study of Stabile et al. (1996) had suggested at least four genetically-distinct geographic GS stocks, adding the Choctawhatchee River 'stock' as a distinct metapopulation, with agreement otherwise with King et al. (1999). Most recently, Dugo et al. (2004) provided additional mDNA evidence robustly supporting a split in genetic distance between a Pearl-Pascagoula metapopulation and all Florida natal river populations sampled (Apalachicola, Choctawhatchee, Yellow and Escambia).

River population genetic structure

Individual-level genetic signature analyses have enabled discrimination of non-natal outlier individuals captured within host river populations, either as new immigrants or as the offspring of an immigrant x resident spawning. Additionally, recent studies have evaluated genetic substructure among individuals sampled within a given natal river population. In an analysis of fine-scale mDNA structure of GS in the Pascagoula River, Dugo et al. (2004), discriminated two genetic stocks or sub-populations within that river. Radio telemetry has identified a second group of GS that migrate up the Chickasawhay River tributary (Heise, 2003), 350 rkm distant from the Bouie River spawning site (Ross et al., 2004). Combined results suggest spawning probably also occurs in the Chickasawhay River (Dugo et al., 2004).

Miracle (1993) assessed mtDNA control region d-loop genetic sequence and length variation within the Suwannee River GS population. This study reported 100% sequence homology, indicating no evidence of within-river differentiation, i.e., no genetically distinct spawning sub-populations. More recently, however, mDNA results indicate the existence of two sub-populations within the overall Suwannee-Ochlockonee population (Kreiser, 2012). It may be hypothesized that genetic differentiation here corresponds to separate spring-spawning vs fall-spawning groups.

Population impacts and recovery potential

Anthropogenic impacts upon the GS

The list of major human impacts upon the GS is essentially the same long, much-published list for all North American sturgeon species. Attention to selected impacts, such as bycatch, has been given above. In addition to the established list, emerging threats and impacts for the GS include: nitrification of rivers; massive filamentous algal blooms, hypoxia, and toxicity accompanying nitrification; reductions in river flows and levels due to agricultural and industrial groundwater withdrawals; sea-level rise resulting in salinization of oligohaline-mesohaline juvenile estuarine feeding habitat; and sturgeon-boat collisions. From the established list, the next topic (below) deserves special consideration as perhaps the main obstacle to GS recovery in the Pearl River and perhaps the Apalachicola River.

Navigation and hydropower projects – dams, sills, impoundments, and channel reconfigurations

Secor et al. (2002) have astutely observed that there are two demographic categories of sturgeon populations: '…those that retain reliable or at least periodic natural recruitment and those that do not.' However, for GS a third category needs to be added: populations that reproduce periodically with abundant early juveniles, but which display poor survival in subadult and young adult life history stages. Thus, the fundamental dichotomy among GS populations is between the first and third categories, as displayed in annual mean natural mortality estimates (determined via open models or exponential decay rate) for the Suwannee, Yellow and Choctawhatchee river populations (11–17%) vs those of the Apalachicola and Pearl populations (33–40.5%), and possibly the Escambia and Pascagoula (Table 1). The first three rivers are unimpounded and minimally engineered, providing migratory and YOY access to upriver spawning and developmental habitat well beyond rkm 200–250. Lack of impoundments also provides unimpeded delivery of freshwater to the juvenile estuarine feeding grounds. Furthermore, isolated deep holes and pools remain intact and available as spring-autumn holding and resting habitats in middle and lower river reaches.

Over the 25-years post-harvest-ban interval, vigorous population rebound is evident at least in the well-studied Suwannee GS population (Table 1). In the Apalachicola and Pearl rivers, spawning grounds and YOY nursery/feeding habitat are confined to the unimpounded reaches below the JWLD, and the Bogue Chitto and Pools Bluff sills, respectively. This represents a loss of 78% of historical GS habitat in the Apalachicola/Chattahoochee/Flint River system (Zehfuss et al., 1999), and probably even greater loss in the Pearl/Bogue Chitto River system. Moreover, both systems have been dredged and otherwise highly altered by channelization and canals constructed for navigation purposes. Accordingly, many low velocity deep holes, rock platforms, and oxbows, resting habitats important to GS, have been eliminated. Accordingly, the fundamental dichotomy in recovery status and potential of GS populations appears to relate not to inherent GS life history failures or genetic diversity bottlenecks, but to loss of critical habitat following human re-engineering of these rivers (Wooley and Crateau, 1985). The extreme result of anthropomorphic change to a historical GS natal river population has been realized in the Mobile/Alabama/Tombigbee river system. A 1902 commercial landing of 100 000 lb (45 359 kg) of GS and 5000 lb of GS caviar reported by Alexander (1905) confirms that a large GS spawning population formerly inhabited that system. Multiple historical reports also confirm the use of far upriver habitat (>300–400 rkm from the Mobile River mouth) by large sturgeons (in the Coosa, Cahaba, Tallapoosa, and Black Warrior tributaries) (Table 5). Individuals weighing 61–189 kg occurring far upriver were probably engaged in spawning runs. But fragmentation of the Mobile River system by multiple dams starting in the late 1800s, culminating with the current set of 17 high dams, has resulted in a total loss of GS habitat above the lowermost (Coffeeville and Claiborne) dams. Moreover, in the reaches below those two dams the riverbed has been so dredged down that almost no vertical gradient exists along the 220–227 rkm of the Mobile River (Randall et al., 2013). Compared with the river reaches actually used by or available to GS in other rivers (for example, the 171 rkm reach below the JWLD dam in the Apalachicola River), the Mobile River system would seem to have sufficient unimpounded reach to the mouth to support a GS spawning population. However, the low gradient may equate to seasonally low attraction flow and accompanying low dissolved oxygen, or to insufficient gradient to provide for sorting of gravel to build and maintain spawning reefs. Together, such conditions resulting from human habitat modifications may synergistically interact to prevent GS immigration and spawning.

Although dam removal to restore sturgeon access to riverine spawning and nursery habitat is ongoing for some North American sturgeon species, no dams impacting the GS have yet been removed. Neither have sturgeon fishways have been installed on any impounded GOMEX river which currently supports or formerly supported a GS population.

Stochastic natural impacts

A fundamentally unstudied area of natural impacts is that of major stochastic events. Mass GS mortalities have been reported following hurricanes and tropical storms, and red tides. However, given priority in disaster response to human needs, counts of dead GS per event have typically not been accomplished. Large adult GS are frequently reported as riverine, estuarine, or coastal mortalities during such events in the Pearl and Pascagoula populations, suggesting differentially greater impact upon the effective spawning populations. However, this may be an artifact of greater visual detectability of large carcasses. Nonetheless, particularly for the westernmost GS river populations subject to more frequent major storm events, periodic mass mortalities may essentially reset the population recovery clock by stochastically reducing the spawning pool (Rudd et al., 2014). Recovery potential models and population management recovery targets will need to take into account the frequency and magnitude of major stochastic mortality.

Population recovery potential

The encouraging news for depleted river populations of the GS (and other sturgeons) comes from a historical colonization event forensically documented for the closely-related AS. Genetic diversity evidence indicates that a very small AS founder group was sufficient to establish a viable population in the Baltic Sea in the Middle Ages. That is, mtDNA and molecular DNA investigations (Ludwig et al., 2008) have determined that a group of only approximately 20 AS individuals from Canada made a single colonization excursion to Europe approximately 1200 years ago (Ludwig et al., 2002).

That event resulted in establishment of a self-sustaining and thriving AS population that supported a sturgeon fishery well into the early 20th Century before it was extirpated by human impacts. Ludwig et al. (2008) concluded that beyond any first generation bottleneck of the small founder population, given that a single female can produce a huge number of progeny, a sturgeon population can thereafter increase dramatically if the environment is suitable. Moreover, sturgeon polyploidy provides mutiple-allele diversity (i.e., intra-individual genetic variation) at a given gene locus, representing a unique hedge against small-population genetic diversity bottlenecks (Krieger et al., 2006). Thus, recovery of a highly depleted GS natal river population may be possible starting from a very small remnant population. This also suggests that transplanting a small number of sexually mature adult sturgeons would be a much more viable and rapid human-manipulation recovery strategy than the release of large numbers of highly vulnerable hatchery fingerlings. Such fingerlings face a minimum of 12 years period to attain sexual maturity in females (Huff, 1975).

The single most effective action taken to conserve and restore the GS has been cessation of direct net harvest of sturgeon in Florida, Alabama, Mississippi, and Louisiana. Total net bans or gill net bans in the first three states have also helped eliminate incidental bycatch in other fisheries. Protection of adult spawners has enabled strong recovery in the Suwannee River and stabilized GS populations in the Apalachicola, Yellow, and Choctawhatchee rivers. Factors inhibiting rebound in the Escambia, Pascagoula, and Pearl rivers remain either unidentified or unquantified.

Controlled propagation as a recovery option

Hatchery rearing of fishes for replenishment of depleted fishery stocks or for introduction of 'desirable' species into non-native rivers has had a long history in the U.S., as does rearing for commercial aquaculture purposes. As early as 1888, with commercial fishing in the Delaware River rapidly decimating the wild AS population (Smith, 1914), the U.S. Fish Commission began experimental culture of sturgeon (Ryder, 1890). Artificial propagation of the GS began in 1989 with river-side spawning on the lower Suwannee River (Parauka et al., 1991; Parauka, 1993) as a cooperative endeavor between the USFWS and the University of Florida (UF). Culture operations were subsequently moved to the USFWS laboratory in Gainesville and continued through 1999 by university researchers. The original objective was to develop the technology in order to be prepared to undertake supplementation of depleted wild GS populations in natal rivers, should such action be deemed necessary (USFWS, GSMFC and NMFS, 1995). Researchers at UF supported implementation of as artificial propagation program for GS population augmentation, contending that the Suwannee River population was not increasing (Chapman et al., 1997), with other river populations being even more seriously depleted.

However, a secondary objective emerged as UF scientists and the State of Florida (under the auspices of the Department of Environmental Protection, later the Department of Agriculture and Consumer Affairs) shifted from GS conservation aquaculture to parallel development of commercial sturgeon aquaculture for meat and caviar (Chapman et al., 1993; Chapman and Lazur, 1998). The State created a 'Florida Sturgeon Production Working Group' charged with preparation of an 'Implementation Plan for the Commercial Culture and Conservation of Native Sturgeon in Florida' (FDEP, 1999). The Florida Legislature passed sturgeon aquaculture enabling legislation (Florida Statutes, 1998). However, concerns had been raised regarding multiple risks accompanying hatchery culture and stocking into the wild, including reducing the effective breeding size of small GS populations by mining of wild adults as hatchery broodstock, diminishing genetic diversity resulting from artificial selection in the laboratory, swamping and eventual loss of wild alleles upon stocking large numbers of hatchery GS into wild populations, potential disease transfer from the cultured fish to wild fish, etc. Relative to such risks, the GS Recovery Plan committee (USFWS, GSMFC and NMFS, 1995) had already determined that '…stocking should be secondary to other recovery efforts that identify essential habitats and emphasize habitat restoration.' Similarly, Tringali and Bert (1998) and Morrow et al. (1998) had recommended against stocking of hatchery GS in the Suwannee and Pearl rivers, respectively, due to the risk of loss of genetic diversity in the wild population and depletion of wild breeding adults. In a multi-species evaluation of genetic population structure, including the AS and GS, Avise (1992) similarly emphasized the loss of genetic diversity that accompanies stocking programs. Such concerns and cautions led to convening of a sturgeon culture risk assessment workshop in Florida in 2000 (Metcalf and Zajicek, 2001). In response, the State of Florida sponsored research into wild GS population viability (relative to the risks of GS mining to provide hatchery broodstock) conducted by Pine et al. (2001). These authors concluded that even a modest increase in adult mortality rate (simulated by removal from the population of adult females as hatchery broodstock) would be detrimental to recovery of the wild Suwannee River population. They advised against any exploitation of wild adults for use as hatchery broodstock. Taken together, the multiple risks to wild native GS from hatchery rearing and supplementation were deemed prohibitive. Accordingly, all further development of commercial GS aquaculture was halted in Florida. The focus then shifted to rearing of non-indigenous species, primarily Russian Sturgeon, Siberian Sturgeon, Sterlet, and viable hybrids like Bester. Currently there are a small number of experimental and commercial sturgeon aquaculture farms operational in Florida, producing both meat and caviar.

Although GS artificial propagation intended for supplementary stocking was discontinued, the rearing program did provide specimens used to conduct laboratory investigations into reproduction, early life history, feeding and nutrition, physiology, and the viability of hatchery fingerlings released into a natal river. In the course of collaborative USFWS and UF early experimental Suwannee River GS culture, an excess of cultured fingerlings was produced in 1992. An experimental release of 1192 hatchery-reared, individually Passive Integrated Transponder (PIT) tagged, 220-day old (29–337 mm TL) GS was undertaken in 1992 to evaluate comparative survival rates of cultured GS vs wild 1992 cohort GS, and comparative growth rates. A 19-year follow-up recapture investigation (Sulak et al., 2014) found that hatchery GS performed poorly with a marked decline in recapture rate over time compared to their wild counterparts. Annual recapture rate of hatchery Gulf sturgeon dropped markedly from 1993 through 2011. Additionally, hatchery fish growth rates were significantly lower than those of wild GS through age 3000 days. Finally, mortality rate estimates for the 19-year period (1993–2011) were 26.7% for hatchery fish vs 11.2% for their wild counterparts. At the hatchery GS rate of mortality, compounded over the minimum 12-years span to female sexual maturity (Huff, 1975), few hatchery fish would have survived to contribute to the adult spawning population.

Aside from the Suwannee River release experiment, there has been only two other substantive stocking of hatchery GS into the wild. The FWRI conducted an experimental release of 46 acoustically-tagged, hatchery-reared 2-year old juvenile GS (mean TL 877 mm, progeny of Suwannee River parents) into the Hillsborough River in 2000–2001 both above and below the dam at rkm 16. These fish were equipped with acoustic tags. The objective was to evaluate survival and thus the potential for establishing a sustaining GS population in the Tampa Bay system via stocking (Gainesville Sun, 2000; Neidig et al., 2002). A small number (unspecified) of released GS were acoustically detected through 2001 (Florida Fish and Wildlife Conservation Commission, 2016), but no further results were subsequently published.

A second release of eleven hatchery-reared sterilized juveniles (811–1281 mm TL, progeny of Suwannee River parents) with radio telemetry tags was conducted in 2002 in the Apalachicola River system to assess GS habitat use, movements, and potential passage through the JWLD. Three were released in the river immediately below the dam, eight were released into the Flint or Chattahoochee rivers above the Lake Seminole reservoir behind the dam (USFWS, 2002; Weller, 2002; Bakal et al., 2003), and an additional five wild Apalachicola River GS (990–1610 mm TL) were telemetry tagged and released below the dam. The main outcome was that six of the GS released into Lake Seminole passed downstream through the JWLD lock within 8–83 days of release, while two stationary tags in the reservoir suggest the remaining two died (USFWS, 2002; Weller, 2002).

Learning

Observations of notable behaviors in the GS and other sturgeon species suggest social facilitation or learning, as well as great behavioral plasticity. For example, Holcik (1989) has reported that some immature Sterlet accompany sexually mature adults to upriver spawning grounds. Accordingly, the hypothesis that sturgeon navigate to spawning grounds via olfaction, based on the example of anadromous salmonids, may not be entirely correct. The same phenomenon, juveniles accompanying spawning adults to far upriver spawning grounds, was indicated from early GS telemetry (Huff, 1975; Wooley and Crateau, 1982). Similarly, 'test spawning' runs among non-ripe adults has been reported in GRS (Webb and Erickson, 2007). More definitive confirmation of GS juvenile false spawning runs came in 2014 and 2015 from four Suwannee River acoustically-tagged ~3-years old juvenile GS (USGS-WARC unpubl. telemetry database). In 2014, two juveniles (712 and 782 mm TL when tagged in 2013) mimicked a fall spawning run, ascending to the rkm 200 prespawning staging area in late July. One remained there 8 days into early August, typifying ripe male behavior but without evidence of further ascents to the rkm 202–235 spawning grounds. The second juvenile arrived at rkm 200, then immediately and rapidly dropped back down to the vicinity of the rkm 93 holding area, approximating spawning female behavior. In 2015, two juveniles (595 and 704 mm TL when tagged in 2014) mimicked a spring spawning run, ascending to the rkm 160 spawning ground area in late March, both remaining in that vicinity for 2–4 weeks. Such juvenile behavior suggests learning of staging and spawning grounds locations by moving at the same time as and potentially in company of actual adult spawners.

Learning in the form of net avoidance by previously tagged individuals has been observed by several GS researchers (e.g., F. Parauka, USFWS, pers. comm.). It is truly exceptional for any individual GS netted and tagged in the Suwannee River to be recaptured within the same season within the same year – even within a heavily sampled holding area (K. Sulak, USGS, pers. comm.). Repeat netting in a given area within the same day typically follows a pattern of rapidly diminishing captures that may persist for several days to weeks. This response among tagged GS is so prevalent that NOAA and USFWS have abandoned Catch-Per-Unit-Effort (CPUE) as a realistic metric in quantifying GS during net sampling.

Life history plasticity, individualistic behavior, and intrapopulation variability are recurring adaptive themes in sturgeon species. With respect to any life history theme, there is always a small percentage of GS behaving differently from the majority of the population. This may simply reflect expression of genetically-based variation among individuals (Stelzer et al., 2008; Hammerschlag-Peyer and Layman, 2010), or it may demonstrate learning. Either way, it suggests a high degree of behavioral and habitat adaptability in sturgeons, a probable explanation of their extraordinary persistence over 150 million years despite limited deviation from the sturgeon morphological plan. Examples of individual, group, or population plasticity are frequent in the GS (above), as in WS (Hildebrand et al., 2016; this volume), challenging accepted life history paradigms. Departure from the normal pattern of juvenile feeding in the estuary being confined to winter months (October to April) has been observed in years of unusual age-1 to age-2 juvenile abundance. Thus, juvenile GS gillnet captures were frequent in the Suwannee River mouth estuary in the summers of 1993 and 1994, where they atypically continued to reside, feed, and gain weight (USFWS, J. Clugston, pers. comm; USGS-WARC database). Residence in the estuary falsified the hypothesis that GS must move to freshwater holding areas to escape high summer water temperatures in the estuary. It also falsified the hypothesis that high summer temperatures preclude feeding. Individuals recaptured one or more times within summer demonstrated substantial weight gains. Even GS early life history stages display individuality in habitat selection. Thus, in laboratory experiments Chan et al. (1997) reported that early YOY (75–148 mm TL) displayed mixed preferences for velocity regimes under high flow conditions.

Jumping behavior

All sturgeon are physostomes, retaining the primitive pneumatic duct connecting the swimbladder to the esophagus. In freshwater environments, where depth is generally much <150 m, a physostomous swimbladder is an effective mechanism for controlling buoyancy and depth (altitude above substate) when swimming or hovering in midwater. Gas lost either by diffusion through the swimbladder wall, or via the pneumatic duct must be replenished by returning to the surface from depth. Thus, the GS and all other Acipenseriformes, must periodically return to the surface to gulp air.

Rapid vertical ascents to the surface, potentially resulting in breaching, have been reported in telemetry-tagged Chinese Sturgeon (Watanabe et al., 2008), GRS Erickson and Hightower, 2007), AS (Taylor et al., 2016), and GS (N. Whitney, Mote Marine Laboratory, pers. comm.). Jumping in the GS is well-known and has been frequently reported (Reynolds, 1993; Sulak et al., 2002). Additionally, GS have also been observed to 'porpoise' breaking the surface of the water with the head only (Slack et al., 1999). Jumping has been observed in many of the world's sturgeon and paddlefish species. Catesby (1731) provided one of the earliest and the most eloquent descriptions of jumping in North American sturgeon:

> "…in May, June and July, the rivers [Savannah River] abound with them [AS], at which time it is surprising, though very common to see such large fish elated in the air, by their leaping some yards out of the water; this they do in an erect posture, and fall on their sides, which repeated percussions are loudly heard some miles distance in still evenings; it is also by this leaping action that many of them are taken, for as some particular parts of the rivers afford them most food, to those places they resort in greater plenty. Here the inhabitants (as the Indians taught them) place their canoes and boats, that when the sturgeon leap, these boats and canoes may receive them at their fall. It is dangerous passing over these leaping holes, as they are called, many a canoe, and small boat having been overset by the fall of a sturgeon into it."

Catesby's description applies quite well to that observed in the GS.

Jumping is most frequently observed when GS are congregated within seasonal holding areas. It may be hypothesized that the primary purpose for jumping and breaching is to come to the surface to replenish swimbladder gas. Saunders (1953) found that the swimbladder gas of freshwater physostomes in deep water contains an excess of nitrogen gas (up to 94% vs atmospheric content of 78%). This implies that metabolically-active oxygen and carbon dioxide are lost into the tissues by diffusion. In the GS, swimbladder gas thus lost can only be replaced by swallowing air at the surface. Jumping facilitates recompression during a rapid power descent upon re-entry.

Jumping also generates a loud splash sound with a characteristic sonogram signature (Sulak et al., 2002). Additionally, it is now known from further underwater acoustic recording that the GS produces endogenous click sounds with a highly characteristic acoustic signature when congregated in holding areas (C. Phillips, USFWS and K. Sulak, USGS-WARC, pers. comm.). It can be hypothesized that GS also utilize jumping secondarily to contribute the splash sound to a series of clicks to form a patterned acoustic signal used in group cohesion. The splash sound as a form of acoustic communication was originally proposed by S. Carr (CCC, pers. comm. to USFWS, 1986).

Synopsis of key management actions regarding protection and recovery of GS populations

A detailed chronological listing of all federal, regional, state, university, and NGO investigations and management actions regarding the GS through 1995 is provided in the GS Recovery Plan (USFWS, GSMFC and NMFS, 1995). The brief narrative that follows summarizes key actions taken through 2015, as well as pending actions.

By the early 1900s all GS populations that had sustained commercial fishing had been seriously depleted. However, small scale commercial and recreational fisheries continued through the early 1970s to mid-1980s. Brief flourishes occurred roughly every two decades (one GS generation span) as populations rebounded briefly before again declining (e.g., in the Suwannee River in the 1960s). No protections were enacted for GS populations until 1972 when Alabama became the first state to impose a complete GS harvest ban (ADCNR, 1972), followed by Mississippi in 1974 (Mississippi Legislature, 1974), Florida in 1984 (Florida Legislature, 1984), and finally Louisiana in 1990 (Louisiana Legislature, 1990, 1993). Additionally, protection against bycatch was provided in 1994 in Florida by a ban on all fishing with nets larger than 500 ft^2 in area, effectively ending most commercial trawl, seine, and gill net fisheries. Additional protection against bycatch came with bans on the use of entanglement nets in Florida and Mississippi (still legal however in Alabama and Louisiana).

Anticipating the harvest ban, the State of Florida had sponsored a holistic GS life history study of the Suwannee River population in 1972–1973 (Huff, 1975), with catches provided by a contracted commercial fisherman. Subsequently, the CCC sponsored a mark-recapture population abundance study from 1976 to 1981 (Carr, 1983). Concurrently, the USFWS initiated mark-recapture netting in the Apalachicola River in 1979, and telemetry investigations of migrations thereafter. Finally, in advance of the harvest ban, the last commercial GS fisherman in the Suwannee River was contracted by CCC in 1981–1984 to provide gill net catch data on sturgeon abundance, size, maturity and food habits (Tatman, 1982, 1983, 1984). After cessation of GS fishing, the CCC continued to sponsor multi-purpose GS research in the Suwannee River through the early 1990s, in conjunction with UF. The USFWS embarked upon long-term mark-recapture, artificial rearing, migration, and spawning site studies beginning in 1986.

The Gulf States Marine Fisheries Commission (GSMFC) developed an interjurisdictional plan for GS management in 1990, a prelude to the 1991 ESA listing of the GS as a threatened species (with USFWS and National Oceanic and Atmospheric Agency, NOAA, given shared ESA responsibility), and to the collaboratively formulated 1995 GS Recovery Plan (USFWS, GSMFC and NMFS, 1995). Research coordination among federal and state agencies and researchers began in earnest in 1998 when USFWS hosted the first interagency workshop on GS science, conservation, management, and recovery at Mississippi Gulf Coast Community College, Gulfport, MS. This workshop has continued every year subsequently, formalized as the annual Gulf Sturgeon Recovery Workshop in 2000. It has become the main forum for GS research collaboration, cooperation, and planning across the species range, successfully achieving facile cooperation, collaboration, and data sharing among all concerned entities, including NGOs. As required under ESA provisions, GS critical habitat was defined in 2003 (USFWS and NOAA, 2003). Beginning approximately in 2008, NOAA began to consolidate GS mark-recapture data from all seven natal river populations into a common standardized central database. In 2009 USFWS and NMFS jointly undertook and published a '5-year review' (USFWS and NMFS, 2009) of progress according to recovery priorities specified in the 1995 Recovery Plan. GS researchers formalized a relationship with the 'Integrated Tracking of Aquatic Animals in the Gulf of Mexico' telemetry network (iTag) in 2014 to promote reporting and sharing of acoustic telemetry relocation data via a common FWC-maintained interactive database.

Currently, the GS Recovery Plan is undergoing revision. Research objectives and methodologies will be prioritized. Management and recovery actions will be reformulated based upon scientific knowledge gained since 1995, including the trajectories determined for individual natal river meta-populations across the subspecies range. The subspecies was listed as one overall population for ESA purposes, without delineation of 'Distinct Population Segments' (DPSs). However, based on differential mortality rates estimated among the several GS natal river populations, Rudd et al. (2014) have recommended that the GS needs to be managed instead on a river-specific basis. Differential mortality rates find a general equivalence in the well-established pattern of genetic differentiation of regional metapopulations (genetically related groups of river-specific populations). In the original plan, a potential de-listing date of 2023 was established, based upon the status of the overall species population. Criteria for de-listing will be re-evaluated in the forthcoming revised GS Recovery Plan. Based upon current evidence of genetic differentiation and geographic separation of GS metapopulations, consideration of designation of DPSs might be an option to enable potential regional delisting on a metapopulation basis.

Gulf Sturgeon research priorities

The following research priorities have been identified by the chapter lead author alone (apart from the overall co-author group) to identify critical life history knowledge gaps across all of the natal river populations, among a much larger host of topics remaining to be explored. Emphasis is on whole fish and whole population life history knowledge gaps. Many more priority topics need to be explored at the organ, tissue, cellular, and physiological levels – a matter beyond the scope of this list. The order below does not equate to relative order of research priority. All topics are deemed equally important.

(1) Empirical testing of factors hypothesized to determine GS population carrying capacity in a given natal river and its estuary, rather than relying on models based on multiple non-objective assumptions.

(2) Applying periodic SSS to efficient and rapid whole river enumeration of subadult and adult population abundance, supplanting time-consuming, labor-intensive net census methods that yield estimates with limited river coverage and high inherent variance.

(3) Monitoring expansion of and shifts in habitat use (spawning areas, holding areas, winter feeding areas) as depleted populations recover.

(4) Monitoring out-migration to other river systems as depleted populations recover.

(5) Conducting laboratory experiments to determine the tolerance ranges and optimal ranges in pH and divalent ion ($Ca{+}{+}$ and/or $Mg{+}{+}$) concentrations for GS gametes, embryos, and yolksac larvae.

(6) Determining the habitat attributes critical to GS choice of holding and staging areas, potentially as a guide to restoration of such areas.

(7) Determining the behavioral responses of GS subjected to sub-optimal and potentially lethal conditions while in holding areas (responses to extremes in temperatures, DO, pH, current velocity, illumination, turbidity)

(8) Determining the nursery habitat and food resources of 1–3 month old black-phase YOY, the black hole in knowledge of GS life history.

(9) Conducting carefully planned acoustic telemetry, full duplex PIT tag passage detection, and SSS monitoring of GS habitat use and movements before and after planned dam or sill removal, and before and after planned construction of a fish bypass.

(10) Assessing GS bycatch and mortality in the coastal and estuarine shrimp fisheries.

(11) Assessing if holding/resting area access limits population recovery, perhaps by experimental holding area excavation.

(12) Determining if GS behavior and activity is diurnally/nocturnally coordinated for various life cycle stages.

(13) Assessing mortality rates across the critical age 6–8 estuarine to marine feeding habitat life history transition.

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Notes

1. For any given GS river, two or more competing systems (or none) may exist for designating 'rkm' distances from the river mouth, depending on selection of the 0-rkm starting point, and the method applied to follow the river course. Thus, different 'rkms' may appear in publications for the same physical location. In the manuscript, the rkm system most widely used for a selected river has been adopted. File name and full directory path: \igsbacesgs016/CEC-Raid/Suwannee-Sturgeon-1988-2013 -population-database/USGS-2012-2013-GS-Census_excel_database-updates/Suw-GS-1986-2013 Data-31 Mar2015-validationMP.xls.
2. The USGS-WARC Suwannee River GS mark-recapture database is a 13 000+ record Excel® database in machine-readable.xlsx format. It consolidates all known and validated scientific capture records from USGS field sampling, with those contributed by USFWS, UF, FWC, CCC and other sources. This publicly-available database is maintained on the USGS-WARC main server in the care of lead GS researcher M. T. Randall (co-author, this manuscript) and chief information technology specialist T. Boozer. The database will become fully accessible online from USGS in 2017.
3. In 2015, resumption of dredging was proposed again.
4. The USGS-WARC maintains several project-specific Vemco® digital acoustic telemetry databases in machine-readable.xlsx format. Databases include all validated detections of acoustically-tagged GS from within the Suwannee River, Suwannee Sound estuary, and the adjacent coastal GOMEX. This database is maintained on the USGS-WARC main server in the care of lead GS researcher M. T. Randall (co-author, this manuscript) and chief information technology specialist T. Boozer.
5. 1 CTU = 1.0°C for 1.0 days

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Author's address: Kenneth J. Sulak, Coastal Ecology and Conservation Research Group, Wetland and Aquatic Research Center, U. S. Geological Survey, 7920 NW 71 St. Gainesville, FL, 32653, USA.
E-mail: ksulak@usgs.gov;
jumpingsturgeon@yahoo.com