

TEMPORAL AND SPATIAL PATTERNS OF SHORTNOSE STURGEON (*ACIPENSER
BREVIROSTRUM*) AND ATLANTIC STURGEON (*ACIPENSER OXYRINCHUS
OXYRINCHUS*) SPAWNING MIGRATIONS IN THE ALTAMAHA RIVER SYSTEM,
GEORGIA

by

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(Under the Direction of Douglas L. Peterson)

ABSTRACT

Sturgeon species in the U.S. are endangered or threatened because of various anthropogenic factors, and the identification of critical habitat and spawning migrations are crucial to their management and protection. The objectives of this study were to document and describe seasonal spawning migrations of endangered Shortnose and Atlantic Sturgeon in the Altamaha River system, Georgia. Using passive acoustic telemetry, the movements of 40 adult Shortnose Sturgeon and 45 adult Atlantic Sturgeon were monitored from April 2011 to March 2014. Upstream movements to suspected spawning habitat occurred during winter for Shortnose sturgeon and corresponded with changes in water temperature and discharge. Atlantic Sturgeon used spring two-step and fall one-step migrations, arriving at suspected spawning habitat in the fall as river temperatures dropped. These findings illustrate clinal variations in the life history of both species and highlight the need to manage sturgeon as distinct population segments with regionally specific recovery goals.

INDEX WORDS: Shortnose Sturgeon, Atlantic Sturgeon, *Acipenser brevirostrum*, *Acipenser oxyrinchus*, Acoustic telemetry, Spawning, Migration, Altamaha River, Ocmulgee River, Oconee River

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CHAPTER 1
LIFE HISTORY AND ECOLOGY OF ATLANTIC STURGEON AND SHORTNOSE
STURGEON

The sturgeon family, Acipenseridae, is composed of four genera and 27 extant species worldwide (Bemis and Kynard 1997). These species are considered “living fossils” (Gardiner 1984; Birstein 1993) and are characterized by a life history that is both long-lived and late maturing (Vladykov and Greeley 1963). Sturgeons are primarily cartilaginous fishes that have retained some ossification. They have several distinctive morphological characteristics, including a body covered in five rows of bony scutes, a heterocercal tail, and the retained presence of a notochord. All species of sturgeon are iteroparous, though most mature females will not spawn annually, and several species regularly migrate upstream to spawn at freshwater sites in fast-flowing water (Auer 1996; Bemis and Kynard 1997). Depending on species and habitat, sturgeon spawning migrations can cover distances of several thousand kilometers (Qiao et al. 2006) and access to high quality spawning habitat is among the most critical factors affecting their reproductive success (Auer 1996).

The status of sturgeons is in question worldwide and almost all species are either endangered or threatened because of many anthropogenic factors (Birstein 1993). Along with overharvest and pollution, an increase in hydropower development throughout the 20th century has been identified as a major cause of the dramatic declines suffered by many sturgeon populations (Williot et al. 2002; Lenhardt et al. 2006). Because dams currently limit upstream

migration and access to historic spawning grounds on many rivers worldwide, the identification of critical habitat and the timing of spawning migrations are crucial to the restoration and long-term conservation of many populations.

Although many North American sturgeon populations appear to be more secure than those found in Europe and Asia (Birstein 1993), they are equally susceptible to the same anthropogenic effects (Collins et al. 2000a). Along the Atlantic coast, Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*, Mitchell 1815) and Shortnose Sturgeon (*Acipenser brevirostrum*, LeSeur 1818) are native to most major coastal river systems from the Saint John River in Canada southward to the Saint Johns River, Florida (Vladykov and Greeley 1963; Kynard 1997; Smith and Clugston 1997). Both species are long-lived, late maturing, and diadromous, requiring access to both fresh and saltwater habitats at some point during their life cycles. Maximum size, maximum age, and age at maturity vary latitudinally in both species, and several genetically distinct populations have been identified (Grunwald et al. 2008; Wirgin et al. 2010). Despite several recent advances in our understanding of the basic life history of both species, important knowledge gaps remain. The timing, locations, and extent of spawning migrations have yet to be identified for either species in many rivers.

Atlantic Sturgeon

Atlantic Sturgeon are large, long-lived fish that are broadly distributed along the Atlantic coast of North America (Vladykov and Greeley 1963). They are anadromous throughout their range; they use riverine, estuarine, and marine habitats during their lives (Collins and Smith 1997; Savoy and Pacileo 2003). Although the majority of their life history is spent in marine and coastal waters, mature adults will return periodically to freshwater rivers to spawn. These

migrations extend to the uppermost navigable section of the river, often represented by the Atlantic Seaboard Fall Line; however, dams and impoundments can act as barriers to migration (Smith and Clugston 1997).

All populations of Atlantic Sturgeon within the U.S. are considered threatened or endangered as a consequence of various anthropogenic factors (Birstein 1993). Increased hydropower development throughout the 20th Century has been identified as a reason for the dramatic decline of Atlantic Sturgeon (Williot et al. 2002; Lenhardt et al. 2006), as dams have blocked upstream migrations and access to spawning sites. Unregulated harvest, coupled with the large-scale degradation of riverine habitats also contributed to population declines (Smith and Clugston 1997), and commercial fisheries were banned in U.S. waters in 1998. In 2012, all U.S. populations were listed under the Endangered Species Act (ESA). This federal listing also identified populations in the Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and the South Atlantic as distinct population segments (DPS) that met ESA listing criteria. Under the ESA, each DPS was listed separately as threatened (Gulf of Maine) or endangered (New York Bight, Chesapeake Bay, Carolina, and South Atlantic).

Although federally protected in the U.S., significant information gaps in the life history of Atlantic Sturgeon still exist. Despite a recent increase in federally funded research on the species, current information on the timing and extent of adult spawning movements and habitats is incomplete or contradictory for many rivers (ASSRT 2007). Likewise, the interbasin movements of Atlantic Sturgeon are not well understood yet these data are essential to proper management of this species.

Riverine and Estuarine Distribution

Until the 20th Century, Atlantic Sturgeon were common in major estuarine and riverine waters along the Atlantic coast of North America (Smith and Clugston 1997) and the Baltic region of northern Europe (Smith and Clugston 1997; Dadswell 2006). The historical range of the species in North America was extensive, spanning nearly 15 degrees of latitude. The northern limit of this range was considered generally to be the Hamilton Inlet on the coast of Labrador, Canada (Bachus 1951), although Scott and Scott (1988) identified historical populations of Atlantic Sturgeon in Ungava Bay, Labrador.

In the U.S., Atlantic Sturgeon were found historically in large river systems along the Atlantic coast as far south as the Saint Johns River, Florida (Vladykov and Greeley 1963). This range included approximately 38 rivers, 35 of which were thought to support spawning populations (ASSRT 2007). Currently, spawning populations have been confirmed in fewer than 20 Atlantic coast rivers, the most southern of these being the Altamaha River, Georgia, (ASSRT 2007). The Hudson River, New York, and the Altamaha River are currently believed to support the two largest remaining populations with estimated annual runs of approximately 870 (Bain 1997) and 350 fish (Schueller and Peterson 2010) respectively.

Marine Distribution

As adults, Atlantic Sturgeon spend a majority of their lives in marine environments, only returning to natal rivers to spawn. Relatively few studies, however, have focused on their marine movements. The U.S. commercial fishery, which extended from both coastal to freshwater habitats (Waldman et al. 1996), has provided the majority of data currently available regarding marine distributions (Bain 1997; Smith and Clugston 1997). Although these fisheries-dependent data are no longer available, adults and marine juveniles are still encountered frequently as

bycatch in a number of Atlantic coast fisheries (Collins et al. 1996). In the northeast Atlantic, the species is commonly caught in shallow inshore areas of the continental shelf at depths less than 60 m (Stein et al. 2004). At the southern end of the range, Atlantic Sturgeon are caught by trawl gear in nearshore marine waters of South Carolina at depth of 20–40 m (Collins and Smith 1997). Evidence suggests that Atlantic Sturgeon are distributed in marine waters along all bottom types that support successful foraging (Stein et al. 2004). Typically, these include sand and gravel substrates, but they may also contain varying mixtures of softer materials such as silt and clay. Coastal features such as river mouths, bay mouths, and inlets are thought to provide productive feeding areas for Atlantic Sturgeon (Johnson et al. 1997), as evidenced by seasonal aggregations that are commonly reported in these areas throughout the range (Dovel and Berggren 1983; Kynard et al. 2000; Dadswell 2006).

Spawning Migrations

As adults, Atlantic Sturgeon are primarily a marine species; however, they regularly migrate into freshwater for spawning. Their anadromous life history is important for optimizing reproductive success by partitioning resources at different life stages and preventing intraspecific competition (McDowall 1987; Auer 1996). The ability to efficiently and successfully osmoregulate allows Atlantic Sturgeon to move between sea water (salinity of 28–33‰) and freshwater (salinity of 0–3‰) (Krayushkina 1998).

Although southern populations have not been well studied, spawning runs in northern rivers are known to occur in the spring and early summer (Bain 1997). These runs have been previously characterized as a short, two-step migration, followed by upstream spawning (Bemis and Kynard 1997). A second spawning run, occurring in the fall, has been suggested for southern populations (Smith and Dingley 1984) and mature adults have been documented in upriver

habitats during fall months (Collins et al. 2000b), but confirmation of fall spawning is still lacking.

Adult Atlantic Sturgeon are capable of spawning several times during their lifespans. The frequency of these spawning events, however, is highly variable at both the population and individual level (Bemis and Kynard 1997). Because growth is more rapid in southern rivers the fish typically mature at an earlier age in southern rivers (Smith and Clugston 1997). Spawning periodicity varies depending on sex and population and yields broad estimates of spawning frequency for males (every 1–5 years) (Smith 1985; Collins et al. 2000a; Caron et al. 2002) and females (every 2–5 years) (Vladykov and Greeley 1963; Van Eenennamm et al. 1996; Stevenson and Secor 1999).

Spawning adults migrate upstream to habitats located between the fresh–saltwater interface and the Fall Line. Spawning occurs in the uppermost reaches of accessible river channels at flows of 46–76 cm/s and depths of 11–27 m (Smith and Clugston 1997; Bain et al. 2000). The adhesive eggs are broadcast over hard-bottom substrates composed of gravel and cobble (Smith and Clugston 1997; Sulak et al. 2000); the adults often selecting spawning sites in large pools below sharp bends of major tributaries (Secor et al. 2000). Once located, suitable spawning sites are often revisited and used annually (Bain et al. 2000); however, annual variations in flow are thought to be an important variable in spawning site selection.

Most information on Atlantic Sturgeon spawning is known from research of the Hudson River population, where spawning occurs from May through August (Bain 1997). Females enter the river and migrate directly to the spawning grounds, whereas males appear to migrate upstream only on incoming tides (Dovel and Berggren 1983). Despite these behavioral differences, males typically reach the spawning grounds before females as water temperatures

reach 5.6–6.1 °C. In contrast, females arrive much later, as water temperatures climb to 12.2–12.8 °C (Smith 1985). Specific spawning sites of Atlantic Sturgeon have not been identified in the Hudson, but spawning adults have been captured from the salt wedge (rkm 55) as far upstream as rkm 182 (Dovel and Berggren 1983; Van Eenennaam et al. 1996). The newly hatched embryos are found from rkm 60 to 148 (Dovel and Berggren 1983); however, the precise location of spawning has not been verified by the collection of fertilized eggs. Spawning behaviors and habitats in southern rivers are poorly understood (ASSRT 2007). Although possible spawning sites have been identified in South Carolina river systems (Collins et al. 2000b), corroborating evidence is lacking.

Intercoastal and Marine Migrations

The migratory patterns of Atlantic Sturgeon in marine waters are almost completely unknown (Erickson et al. 2011). The paucity of marine migratory data is a common problem that is not limited to sturgeon, as fish movements are notoriously difficult to document in the open ocean (Arkhipkin et al. 2012). Most current knowledge regarding the marine and intercoastal movements of Atlantic Sturgeon has been inferred from captures in marine fisheries (Dovel and Berggren 1983; Bain 1997; Smith and Clugston 1997), yet these data are known to underestimate habitat use while overestimating migration extent (Hunter et al. 2004).

Regardless of data source, marine migrations of Atlantic Sturgeon often are inferred from limited observations and small sample sizes. Erickson et al. (2011) examined the oceanic-migratory behavior of adult Atlantic Sturgeon from the Hudson. Of the 23 tagged fish, 15 were observed in U.S. marine waters dispersed from the Bay of Fundy, Nova Scotia, to the coast of Georgia, which indicates that populations may undertake long-range migrations. Although these

data provide evidence of the extent of marine habitat use, the sample sizes were too small for any kind of meaningful quantitative inference.

Recent advances in technology have been used to address the inherent difficulties of studying marine migrations (Metcalf and Craig 2012). Modern acoustic telemetry methods now allow researchers to monitor long-term movements of migratory species without recapture, which have provided new information on the intercoastal movements of Atlantic Sturgeon (e.g., Fernandes et al. 2010). In marine waters, satellite archival tagging has provided broad-scale data on the marine migrations of adult Atlantic Sturgeon (Erickson et al. 2011). These methods allow researchers to monitor sturgeon over large temporal and spatial scales, facilitating the identification of critical habitats, interbasin movements, distribution, and long-term migratory patterns.

Shortnose Sturgeon

Shortnose Sturgeon are an amphidromous species that occur in large coastal rivers along the eastern seaboard of North America (Vladykov and Greeley 1963). Their life history is well adapted to the dynamic nature of coastal riverine habitats and is characterized by long life, delayed maturity, and iteroparous reproduction (Dadswell 1979; Dadswell et al. 1984; Kynard 1997). Spawning occurs in freshwater, but regular migrations to nearshore estuarine or marine habitats are common. Spawning populations were historically found in coastal rivers ranging from the Saint John River, Brunswick, Canada, to the Saint Johns River, Florida (Vladykov and Greeley 1963; Kynard 1997); however, many populations have declined or been extirpated, particularly in rivers along the southern periphery of their range.

Shortnose Sturgeon are among the most endangered of North American sturgeons (Birstein 1993). Throughout the 19th and 20th centuries, the species was exploited for their meat and roe (NMFS 1998). Despite being federally listed as an endangered species in 1967 (NMFS

1998), most populations have not recovered over the past several decades (Bain et al. 2007). Habitat losses from dams that block spawning runs as well as alter flow and temperature regimes continue to hamper species recovery (NMFS 1998; Collins et al. 2000a; Cooke and Leach 2004; Wirgin et al. 2005).

The designation of critical habitat, particularly spawning habitat, is essential to the recovery of Shortnose Sturgeon and is a requirement for all endangered species listed under the ESA. Unfortunately, the timing and extent of spawning migrations is poorly understood in many rivers, and specific spawning sites have been identified in only a few locations (Hall et al. 1991). Data on Shortnose Sturgeon spawning behaviors and movements in southern rivers are conspicuously absent, yet this information is essential to effective recovery of the species.

Shortnose Sturgeon are well-adapted to a broad latitudinal range of estuarine habitats and the dynamic conditions and annual variations within. During the past century, however, many populations have been extirpated and at present only 16 coastal rivers are thought to support spawning populations (Kynard 1997). Under their original ESA listing, 19 individual populations have been recommended as separate DPS (NMFS 1998). Of these, at least nine are significantly discrete from their neighboring populations (Wirgin et al. 2010). Although quantified population assessments are lacking for most rivers systems, several Shortnose Sturgeon populations are known to be either precariously small or entirely extirpated from several rivers in Delaware, New Jersey, and North Carolina (Kynard 1997). The largest populations are found in northern rivers, specifically the Hudson (>38,000 adults; Bain et al. 1995), the Delaware (~14,000 adults; Hastings et al. 1987), and the Saint John (~18,000 adults; Dadswell 1979). The southern extent of their range is currently considered to be the Altamaha River, Georgia (~2,000 adults; Peterson and Bednarski 2013).

Shortnose Sturgeon spend the majority of their time within the tidally influenced portions of rivers. Upstream of the fresh–saltwater interface, juveniles and adults are found typically in main channel habitats characterized by soft substrates where they feed on available benthic crustaceans or insects (Dadswell 1979; Dadswell et al. 1984). During the winter months, however, the fish tend to prefer more brackish waters where they forage for amphipods and other crustaceans over silt and gravel substrates anywhere from 5 to 15 m deep (Dadswell 1979). In the Altamaha River, Shortnose Sturgeon have been observed moving upriver to lower salinities as temperatures rise during the summer months (Flournoy et al. 1992); however, the reasons for this seasonal movement pattern are unclear.

The seasonal occurrence of Shortnose Sturgeon in riverine and nearshore estuarine habitats has been commonly observed by many researchers (e.g., Fernandes et al. 2010; Peterson and Bednarski 2013; Farrae et al. 2014), although individuals have been documented in salinities of 30–31 ppt (Holland and Yelverton 1973). In the Connecticut River, Massachusetts, a landlocked population has persisted for several decades in the Holyoke Pool (Taubert 1980). Although that population was isolated by anthropogenic factors, its persistence illustrates the plasticity of Shortnose Sturgeon with respect to the types of riverine habitat they can use. Regardless, the seasonal pattern of habitat use varies greatly depending on latitude. In the northern part of the range, populations spend more time in marine and brackish water habitats than is typical for those in southern rivers (Kynard 1997).

Although often characterized as amphidromous, the degree and type of diadromy exhibited by Shortnose Sturgeon is often disputed. Despite their regular use of coastal marine habitats, Shortnose Sturgeon are rarely captured in non-natal rivers (Bemis and Kynard 1997). Although marine movements have not been well studied, several hatchery-reared individuals

released into the Savannah River during the 1980s were subsequently documented in several other rivers in both Georgia and South Carolina (Smith et al. 2002). Not only did these fish mix with extant native populations in the Ogeechee and Cooper rivers, but they also recolonized the Edisto River, whose population had been previously extirpated. Despite the extensive marine dispersal of these hatchery-reared individuals, recent genetic analyses of southeastern populations suggest that these movements were probably not typical for wild populations (Wirgin et al. 2010). Regardless, recent improvements in sonic telemetry methods, combined with additional mark-recapture studies, have helped facilitate closer examination of marine habitat use by Shortnose Sturgeon. Fernandes et al. (2010) used an extensive passive acoustic receiver array to document the movements of adult Shortnose Sturgeon between the Penobscot and Kennebec rivers in Maine – a migration that covered approximately 150 km of marine waters. Similarly, Peterson and Farrae (2011) used mark-recapture techniques to document that Shortnose Sturgeon in Georgia were moving between the Altamaha and Ogeechee rivers.

Spawning

The reproductive ecology of Shortnose Sturgeon is highly variable both within and among populations. Clinal variation in the timing of spawning has been well documented (Kynard 1997) and appears to be influenced by several environmental factors including water temperature, current velocity, and substrate. Length at maturity is similar throughout their range; however, because growth rates are faster in the south than in the north, age at maturity varies in a similar manner (Dadswell et al. 1984). Regardless of geography, males typically mature at 450–500 mm fork length (FL), whereas females mature at 500–700 mm FL (Dadswell et al. 1984). Bain (1997) advised a criterion of 500 mm FL to assign sexual maturity in wild caught Shortnose Sturgeon because of the difficulty of sexing fish in field conditions. In Georgia, males obtain this

size and begin spawning at 2–3 years whereas females often don't begin spawning until age 6 (Dadswell et al. 1984). Although iteroparous, the spawning interval in southern populations is typically 1–3 years for males, and 2–5 years for females (Dadswell 1979).

Although the upstream extent of spawning migrations is largely influenced by river length and morphometry (Hall et al. 1991; Kieffer and Kynard 1993; Kynard 1997), adults typically spawn near the fall line or at least at the most upstream main channel habitat that is accessible (Dadswell et al. 1984; Taubert 1980). Specific spawning sites can be located below dams (Buckley and Kynard 1985; Cooke and Leach 2004) or at river junctions above the head of tide (Dadswell 1979). Substrate composition, depth, and water velocity are widely recognized as the most important variables affecting the quality and supply of spawning habitat for Shortnose Sturgeon. In the Savannah River, Hall et al. (1991) identified likely spawning sites by the presence of submerged timber and gravel substrates at depths of 6–9 m and bottom velocities of 0.82 m/sec). In contrast, spawning has been documented over silt and sand substrates at the base of the Pinopolis Dam on the Cooper River, South Carolina (Cooke and Leach 2004). In the Altamaha, Rogers and Weber (1994) suggested that gravel, cobble, and boulder substrates were likely selected – especially where these substrates occurred contiguous to bluff formations.

Temperature and discharge appear to be the main factors influencing the timing of spawning migrations (Hall et al. 1991; Kieffer and Kynard 1996). Previous studies suggest that as adults, Shortnose Sturgeon spend most of the spring and summer months near the freshwater-saltwater interface of their natal rivers, moving upstream to spawn during winter and early spring as water temperatures reach 8–12 °C (Hall et al. 1991; Rogers and Weber 1994). Few researchers have studied spawning behavior; however, successful spawning has been reported at 12–18 °C (Dadswell et al. 1984, Kynard 1997). Although many studies suggest that moderate to

high flows are favorable for spawning (e.g., Taubert 1980; Kieffer and Kynard 1993), excessively high discharges are suspected to adversely affect spawning success (Dadswell 1979; Taubert 1980; Buckley 1982).

Despite several decades of research, there are still many gaps in knowledge regarding the spawning migrations of Shortnose and Atlantic Sturgeon, particularly in the southern portion of the range. These gaps include basic life history information essential for development of effective restoration strategies. Quantified data on spawning habitat, timing and extent of annual migrations, and marine habitat use are either incomplete or entirely lacking for southern populations and have been identified as key research needs by the National Marine Fisheries Service (NMFS 1998; ASSRT 2007). The unifying goal of this research thesis was to provide new information regarding the timing, extent, and specific locations of the seasonal movements and habitat use of Shortnose Sturgeon (Chapter 2) and Atlantic Sturgeon (Chapter 3) in the Altamaha River, Georgia.

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CHAPTER 2

TEMPORAL AND SPATIAL PATTERNS OF SHORTNOSE STURGEON (*ACIPENSER
BREVIROSTRUM*) SPAWNING MIGRATIONS IN THE ALTAMAHA RIVER SYSTEM,
GEORGIA¹

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Abstract

Spawning populations of Shortnose Sturgeon (*Acipenser brevirostrum*) have declined or been extirpated, particularly in rivers along the periphery of their range. Understanding the spatial and temporal dynamics of spawning migrations within natal rivers is a critical information gap with regard to habitat protection and ultimately, species recovery. The objectives of this study were to document and describe seasonal distribution and spawning migrations of Shortnose Sturgeon in the Altamaha River system, Georgia. Passive acoustic telemetry were used to monitor the movements of 40 adult Shortnose Sturgeon from April 2011 through March 2014. Telemetry data revealed that during much of the year, Shortnose Sturgeon resided within the tidally influenced portion of the river, with the most detections occurring near the freshwater–saltwater interface. Upstream movements to potential spawning habitat occurred during winter and early spring, with most fish returning to the lower estuary by April. Migrations appear to be triggered by environmental cues and were initiated when mean weekly temperature was 11.6–16.9 °C. During upstream migrations, fish occupied both the Ocmulgee and Oconee tributaries and were detected as high as 408 river kilometers above the mouth of the estuary. Unlike spawning migrations in northern rivers, the pattern of movement observed in the Altamaha was a single-step migration without a resting or staging period. Upstream migrations during the non-spawning months were observed in years two and three and appeared to correspond with increasing discharge, which potentially resulted in increased habitat availability. This study further illustrates the clinal variation in life history typical of the species and may have important implications on river-specific strategies to recover the species.

Introduction

Shortnose Sturgeon (*Acipenser brevirostrum*, Acipenseridae) are considered the most endangered of the North American sturgeons (Birstein 1993). Like many other sturgeon species, Shortnose Sturgeon are well-adapted to a broad range of environmental variables that are found along the latitudinal distribution of their range. Historically, Shortnose Sturgeon occupied all major Atlantic coast rivers of North America (Vladykov and Greeley 1963; NMFS 1998), from the Saint John River, Brunswick, Canada, to the Saint Johns River, Florida (Vladykov and Greeley 1963; Kynard 1997). However, a review by Kynard (1997) suggests that the historical range of Shortnose Sturgeon has been greatly diminished, and as few as 16 rivers are currently thought to host populations of this once abundant species (Kynard 1997). Nineteen river populations of Shortnose Sturgeon have been recommended as distinct population segments (DPS; NMFS 1998). Of these, at least nine are significantly discrete from their neighboring populations (Wirgin et al. 2010). Shortnose Sturgeon populations are notably small or entirely absent in rivers located between the Delaware River, New Jersey, and the Cape Fear River, North Carolina (Kynard 1997). The largest populations occur in the northern rivers, particularly the Hudson River, New York (>38,000 adults; Bain et al. 1995), the Saint John River, Canada (~18,000 adults; Dadswell 1979), and the Delaware River, New Jersey (~13,000 adults; O'Herron et al. 1993). The southern extent of their range is currently the Altamaha River, Georgia (~2,000 adults; Peterson and Bednarski 2013).

The timing and extent of Shortnose Sturgeon spawning migrations are not well understood, particularly in southern rivers, yet this information has been identified as a key information gap in the federal recovery plan for the species (NMFS 1998). Studies employing mark-recapture and biotelemetry have been effective in characterizing the movements and

habitat use of other diadromous sturgeon species (e.g., Foster and Clugston 1997; Fox et al. 2000), yet relatively few studies have examined the spawning migrations of Shortnose Sturgeon. Synthesis of the available literature suggests adults typically spend most of the year near the freshwater–saltwater interface of their natal rivers, moving upstream to spawn in the winter and spring when water temperatures reach 8–12 °C (Hall et al. 1991; Rogers and Weber 1995). Successful spawning has been documented at 12–18 °C (Dadswell et al. 1984; Kynard 1997). At the northern end of their range, adults have been documented overwintering near spawning sites (Bain 1997) as part of a two-step spawning migration (Bemis and Kynard 1997); however, in southern rivers, Shortnose Sturgeon typically exhibit a one-step migration (Hall et al. 1991; Rogers and Weber 1995). Although Rogers and Weber (1995) suggested that both fall and spring migrations occur in the southern populations, fall migrations have been documented only in populations north of Cape Hatteras. Environmental cues for spawning are not well understood; however, most research suggests that moderately high flows are favorable for spawning (Dadswell 1979; Taubert 1980; Buckley 1982, Buckley and Kynard 1985; Kynard 1997; Peterson and Bednarski 2013).

In contrast to many of the large river systems along the Atlantic coast, the Altamaha River system is a relatively pristine habitat for Shortnose Sturgeon (NMFS 1998). Isolated rocky shoal habitats are abundant in the upper river and in both the Oconee and Ocmulgee tributaries. Although both of these major tributaries are impounded, the dams are located at or above the fall line, providing more than 750 km of unimpounded habitat for migratory fishes. As such, the Altamaha provides a unique opportunity to better understand spawning migrations of a relatively undisturbed population of Shortnose Sturgeon within the southern portion of the range. Documentation of the timing and extent of Shortnose Sturgeon spawning migrations in the

Altamaha may provide critical new information regarding habitat use and requirements for southern populations. The objectives of this study were to document and describe the seasonal movements and spawning migrations of adult Shortnose Sturgeon in the Altamaha River.

Methods

Site Description

The Altamaha River System, located entirely within Georgia, is formed by the confluence of the Oconee and Ocmulgee rivers (Figure 2.1). The mainstem flows across the Atlantic coastal plain in a southeasterly direction for 207 km to the coast where it empties into the Atlantic Ocean near Darien, Georgia. Mid-channel depths average 2–3 m, with a maximum of 18 m in Altamaha Sound (Heidt and Gilbert 1978). The lower Altamaha Estuary is characterized by a tidally flooded salt marsh that gradually gives way upstream to cypress swamp. The location of the freshwater–saltwater interface is highly variable, occurring less than 50 km upstream of the mouth during low-flow conditions and as far as 25 km offshore under flood conditions (Rogers and Weber 1995). Tidal range averages 2 m, and tidal influence can persist as far upstream as rkm 60 above the sound (Sheldon and Alber 2002). Most of the Altamaha’s total discharge is contributed by the Ocmulgee (40%) and Oconee (36%) tributaries (Rogers and Weber 1995). Isolated rocky shoal habitats occur above rkm 80 and throughout the lower reaches of both tributaries (Flournoy et al. 1992). Although both of these tributaries are impounded above the Fall Line, the biological effects of these dams are considered only moderate (Dynesius and Nilsson 1994).

Fish Sampling

Anchored gill nets measuring 30.48 m in length by 3.3 m deep were used to capture adult Shortnose Sturgeon in the Altamaha River from February–April of 2011 through 2013. The nets were constructed of 12.7-cm and 15.2-cm monofilament mesh (stretch measure). Netting locations were selected within the tidally influenced portion of the estuary wherever preliminary sonar surveys identified clean bottom, but not farther than 15 km upriver of the freshwater–saltwater interface. Nets were fished for 30–60 min during slack tide to maximize capture efficiency while minimizing gear damage.

Upon capture, Shortnose Sturgeon were immediately removed from the nets and transferred to a floating net pen (1x1.5 m) where they were allowed to recover for approximately 15 min until netting activities had been completed. All fish were then examined for internal and external tags. If none was found, a passive integrated transponder (PIT) tag was inserted into the body musculature beneath the fourth dorsal scute. Measurements of total length (TL), fork length (FL), and weight were recorded (Table 2.1), and 1–2 cm sample of dorsal fin was collected for subsequent genetic analyses.

Coded acoustic transmitters (Vemco V16-4H) were surgically implanted into 40 individual Shortnose Sturgeon (15 in 2011; 15 in 2012; 10 in 2013). Transmitters had an estimated battery life of 1,248 d. Each transmitter broadcast at 69 kHz with a random signal repeat interval between 30 and 90 s to minimize signal overlap. All acoustic transmitter surgeries were conducted during February–May when water temperatures were below 28 °C. Surgical implantation of transmitters was conducted using methods modified from Moser et al. (2000). Initially, MS-222 (tricaine methanesulfonate) was used to anesthetize fish for surgery. However, to minimize handling time and eliminate the risk of anesthesia overdose under field conditions,

the use of anesthesia was discontinued after the first week of the study. Instead, fish were immobilized ventral side up in a padded cradle suspended above a 350 L holding tank onboard the research vessel. During the surgical procedure, a small bilge pump placed inside the tank was used to pump fresh river water continuously over the fish's gills. All surgical instruments and transmitters were sanitized with an antiseptic wipe (70% isopropyl alcohol) immediately prior to use. Transmitters were inserted through a 4–5 cm incision made along the midline of the ventrum, approximately 4–6 cm anterior to the vent. An interrupted pattern was used to close the incision with 4–6 absorbable Monocryl sutures (2-0 needle; Ethicon, Inc.) as described by Boone et al. (2013). Once the incision had been closed, the fish were immediately returned to the net pen and monitored for 5–10 min until they had fully recovered. They were then returned to the river at their original capture site.

Passive Acoustic Telemetry

A stationary array of 112 acoustic receivers (Vemco VR2W) was deployed over a total of 670 km throughout the Altamaha River system (Figure 2.1). Acoustic receivers were equipped with omnidirectional hydrophones to provide continuous monitoring for transmitted Shortnose Sturgeon. Receivers were placed at sites approximately 10 km apart, except at the confluence of the Ocmulgee and Oconee rivers and in Altamaha Sound, where they were placed at 2–3 km intervals—areas previously identified as high-use habitats for Shortnose Sturgeon (Rogers and Weber 1995; DeVries 2006). To document potential movements to or from other river systems, researchers from University of Georgia and South Carolina Department of Natural Resources deployed and maintained similar receiver arrays in the Ogeechee, Saint Marys, and Satilla rivers, Georgia, and the Edisto and Savannah rivers, South Carolina.

Stationary receivers were attached to anchored buoys and deployed so that they were suspended approximately 1 m from the river bottom in an upright position (Figure 2.2). To ensure efficient retrieval of the submerged receivers, anchors were tethered to the nearest structure with a 32-mm stainless steel cable. Within riverine habitat, receivers were positioned in the river channel and tethered to trees on the adjacent bank. In open water habitats, receivers were opportunistically tethered to channel markers or pilings. Receivers were downloaded at least every three months throughout the study, except when environmental conditions made the river unnavigable.

Data Processing

At the conclusion of each field season, all telemetry data were carefully reviewed to identify and remove any spurious detections that were evident from the spatial and temporal chronology of individual fish movements. Detections considered to be spurious were those resulting from simultaneous detections of a single transmitter at two geographically separate locations; or those that occurred consecutively at nonadjacent receivers (> 3 stations apart). Mean daily locations of each transmitted fish were then calculated based on all telemetry detections during each 24-h period. From these mean daily rkm values, mean weekly rkm values for individual fish were then calculated to construct box plots with 25th, 50th, and 75th percentiles of weekly river distributions. When mean weekly rkm values were unavailable because of limited fish movement, the last known position of the fish was used for that week. To maintain chronological consistency, the study year was defined by the beginning and end dates of each project year rather than calendar year (e.g., year one was April 1, 2011–March 31, 2012).

Side-scan sonar data for the Altamaha system showing composition of bottom substrate were obtained from Georgia Department of Natural Resources (Litts 2013). Data were available

for the Altamaha River (rkm 44–207), Ocmulgee River (rkm 207–541), and Oconee River (rkm 207–418). From these data, potential spawning habitat for Shortnose Sturgeon was identified based on the percentage of available hard-bottom substrates (i.e., rocky fine, rocky boulder, and/or bedrock) as described in the literature (Taubert 1980; Hall et al. 1991; Collins and Smith 1993). Mean weekly temperature (MWT) for the Altamaha River was obtained from the LTER GCE-7 hydrographic monitoring station at rkm 20 near Darien, Georgia. Temperature data were available through November 21, 2013. Mean weekly river discharge (MWD) was obtained from the USGS gauging station near Baxley, Georgia (rkm 181).

Results

Over the three years of the study, a total of 40 adult Shortnose Sturgeon were captured and tagged with acoustic transmitters (Table 2.1). Telemetry data indicated that the fish remained in the Altamaha River system throughout the entire study (April 22, 2011–March 14, 2014). The total number of valid detections for individual fish in the Altamaha system ranged from 5,266 to 296,130, with a total of 3,164,468 valid detections over the course of the study. In 2011 and 2012, all tagged fish were documented on receivers within the study site. In 2013, however, only 32 of the tagged fish were found, which suggests that eight fish either died, their transmitters failed, or that they simply remained stationary during the last year of the study.

Although individuals exhibited different movement patterns throughout the year, several seasonal patterns were evident. From April–December of year one, the 50th percentile of mean weekly locations of transmitted fish remained below the head of tide, without any (>100 km) upstream movements (Figure 2.3). During this period in years two and three, upstream movements were more varied, although the 75th percentile of mean weekly locations of

transmitted fish remained below rkm 100. During this estuarine residence period, sturgeon occupied relatively small (< 5 km) segments of river for extended periods (> 90 d). An interesting exception to this pattern was displayed by four individuals that moved above the head of tide during the spring/summer of study year two, and seven other fish that moved upstream almost to the Ocmulgee-Oconee confluence during the spring/summer of year three (Figure 2.3). In all these instances, the fish remained at these upriver sites until late October or early November, before returning back downstream to the freshwater–saltwater interface. In both years, these departures from tidally influenced habitats were rapid and appeared to be site specific in that the fish eventually returned downstream to the same approximate locations they had occupied before leaving. These temporary migrations appeared to correspond with either seasonal changes in MWT (Figure 2.3) or annual variations in MWD (Figure 2.4); upstream movements typically occurred during increasing temperature followed by downstream movements that occurred as temperature declined. These movements were most obvious during year three when peaks in MWD were observed.

Putative spawning migrations were observed in 25 of the 40 transmitted Shortnose Sturgeon (Table 2.2). These migrations encompassed at least > 160 rkm and culminated at sites near or above the Oconee-Ocmulgee confluence. In total, this pattern was observed at least once in 8 of 15 (53%) fish tagged in year one, 10 of 15 (67%) fish tagged in year two, and 7 of 10 (70%) fish tagged in year three. This movement pattern was similar in all years and was characterized by rapid and direct movements (e.g., 217 km in 10 d) that began in the tidally influenced reach of the lower river. These migrations appeared to correspond with late-winter increases in both MWT (Figure 2.3) and MWD (Figure 2.4). Migrations were initiated in January and February at MWT 11.6–16.9 °C. In all three years, the onset of upriver migrations occurred

in January as MWD was increasing, which suggests that increasing flows may provide an environmental cue to initiate spawning migration (Figure 2.4).

Shortnose Sturgeon were documented in both the Ocmulgee (n=20) and Oconee (n=18) tributaries and often moved between the two rivers during migrations. In study year one, four individuals were documented on receivers above the confluence from January 23, 2012 to March 10, 2012. In the following year, 10 individuals were detected above the confluence from January 14, 2013 to March 18, 2013. During these periods, the fish migrated into both the Ocmulgee (three fish in year one; eight fish in year two) and Oconee (three fish in year one; seven fish in year two) tributaries, and several fish (two fish in year one; five fish in year two) used both tributaries during their upstream migration. In year three, four Shortnose Sturgeon were detected near or above the confluence for much of the year, although the 50th and 75th percentiles of all weekly mean detections showed that most fish remained in the lower river until mid-February (Figure 2.3). From January 1, 2014 to March 14, 2014, 12 fish were detected above the confluence. The 50th percentile of all weekly mean detections occurred above rkm 207 during the weeks of February 14, 2014, and February 21, 2014. The farthest upstream Shortnose Sturgeon migration was documented on the Ocmulgee tributary where one individual moved upstream to at least rkm 408 (201 rkm above the confluence) from February 21 to February 23, 2014. In the Oconee, three sturgeon were detected at rkm 399 (192 rkm above the confluence)—only 19 km downstream of Sinclair Dam (rkm 211 above the confluence). These detections represent the longest known upriver migrations of Shortnose Sturgeon throughout their range.

Several Shortnose Sturgeon made upstream migrations in multiple years of this study (Table 2.2). Three of the fish tagged in year one were detected upstream in consecutive years. Similarly, four fish tagged in year two and two fish tagged in year three made upstream

migrations in consecutive years. Although the timing and extent of spring migrations were similar for all tagged fish during each year of the study, migration patterns varied among individuals. For example, SNS-2 and SNS-3 migrated upstream to rkm 350 in the Ocmulgee River during February in consecutive years whereas SNS-6 and SNS-14 moved back and forth between the confluence and the lower reaches of the Oconee and Ocmulgee during the same years—never reaching rkm 300 in either river.

Despite the individual variation in upstream migrations, downstream migrations to areas below the head of tide were rapid (<15 days) and direct. In each year of the study, all individuals had returned to their downstream habitats by April, regardless of how far upriver they had traveled during the preceding months. All four sturgeon observed above the confluence in year one returned downriver during February–March 2012. The last of these left the confluence on March 10, 2012 and was detected in the estuary only four days later. Downstream migrations in year two were similar to those observed in year one. Fish began moving back downstream in early February and the 75th percentile of mean weekly detections occurred below the head of tide by the first week in March. In the first two years of the study, these downstream migrations coincided with annual peaks in discharge (Figure 2.4). In year three, however, only 5 of the 13 fish that made upstream migrations returned back downstream by March 6, 2014. The remaining fish were last detected above the confluence prior to conclusion of the study (March 14, 2014).

Substrate composition in both mainstem and tributary reaches visited by migrating Shortnose Sturgeon consisted of discrete patches of hard-bottom substrate (i.e., rocky fine, rocky boulder, and/or bedrock). Data from side scan sonar showed that the highest percentage of hard-bottom substrate occurred at or just downstream of the confluence and in the lower reaches of the Oconee and Ocmulgee tributaries (Figure 2.5). Increased density of hard-bottom substrate was

located at rkm 287–358 in the Oconee and rkm 339–438 in the Ocmulgee, which suggests that these areas may have contained large shoal complexes.

Discussion

The results of this study address key research needs identified by NMFS (1998) and provide new information regarding the seasonal migratory patterns of Shortnose Sturgeon in the Altamaha River. Telemetry data revealed that adult Shortnose Sturgeon remain in the lower tidally influenced portion of the river for 9–10 months of the year (Figure 2.3); seasonal congregations of adult fish occurred in brackish water near the freshwater–saltwater interface. Previous studies have identified the freshwater–saltwater interface as important foraging areas (Hall et al. 1991; Kynard 1997) and have been linked with higher growth rates (Taubert 1980). In the Altamaha, Shortnose Sturgeon move upriver to lower salinities as temperatures rise during the summer months (Flournoy et al. 1992; DeVries 2006). Similar observations in this and previous studies (Dadswell et al. 1984; Hall et al. 1991; Rogers and Weber 1995) suggest a possible relationship between increasing temperatures and salinity preference, although the factors governing these movements are unknown. Seasonal extremes in temperature and salinity have been theorized to limit habitat availability for Shortnose Sturgeon, particularly in the southern portion of the range (Jenkins et al. 1995). Although the interactive effects of salinity and temperature on adults are unknown, Ziegeweid et al. (2008) showed that increased temperature and salinity significantly affected young-of-year survival, which could directly influence habitat preferences as well as annual recruitment. Further studies are needed to better understand the environmental tolerances of Shortnose Sturgeon so that managers can better define seasonal habitat needs in southern rivers.

The documentation of upriver migrations during this study indicated that Shortnose Sturgeon used most (80%) of the habitat available to them within the Altamaha system below the Fall Line. During the winter, upriver migrations to at least the confluence (rkm 207 above the mouth of the estuary) were common. Although none of the tagged individuals migrated upstream to the Fall Line in either tributary (rkm 541 in the Ocmulgee; rkm 418 in the Oconee), several individuals regularly entered the lower reaches of both the Ocmulgee and Oconee tributaries. In previous studies, Shortnose Sturgeon were not observed in the Oconee (Heidt and Gilbert 1978; Rogers and Weber 1995). The presence of fish in the Oconee at rkm 399 (192 rkm above the confluence) and the Ocmulgee at rkm 408 (201 rkm above the confluence) represents the longest upriver migrations of Shortnose Sturgeon within the U.S. Previously, Heidt and Gilbert (1978) observed ripe adults only as far upstream as rkm 16 above the confluence in the Ocmulgee. By comparison, in the Hudson River, only 246 km of river habitat is accessible (Bain 1997). Likewise, in the Savannah River, the maximum upriver spawning site of Shortnose Sturgeon is rkm 275–278 (Hall et al. 1991). These findings suggest that the location of Shortnose Sturgeon spawning is river specific and is likely variable depending on annual variations in flow, temperature, and other environmental variables.

Upstream migrations by Altamaha Shortnose Sturgeon that were documented during January and February were largely consistent with results from previous studies that indicate spawning in southern rivers occurs during the late winter (Heidt and Gilbert 1978; Hall et al. 1991; Rogers and Weber 1995). These migrations were typical of the long, one-step migrations described by Kynard (1997); but unlike the results of Rogers and Weber (1995) we did not find evidence of a fall spawning migration. Although five individuals did move upstream to sites near the confluence in the fall of 2013, water temperatures in the lower Altamaha were 24–28 °C at

that time—well above the maximum documented spawning temperature of 18 °C (Kynard 1997) for the species (Figure 2.3).

Although telemetry data alone do not provide direct evidence of spawning, the extent and timing of the late-winter migrations documented in this study, along with the types of habitats visited and the water temperatures during those visits, provides strong circumstantial evidence that these movements were, in fact, spawning runs. Despite the empirical evidence, however, the use of passive telemetry in this study precluded the collection of fine-scale movement data necessary for identifying specific spawning sites. The results of this study, however, should provide the broad overview of shortnose sturgeon spawning migrations that is needed to design future studies that will provide the fine-scale movement data needed to identify specific timing and locations of Shortnose Sturgeon spawning in the Altamaha System.

Similar studies of Shortnose Sturgeon in other river systems have helped depict clinal variations in the timing and patterns of Shortnose Sturgeon spawning migrations. In northern rivers, adults migrate upstream in mid-spring (March–April); whereas in southern systems, those migrations begin in January (Dadswell et al. 1984; Buckley and Kynard 1985; Hall et al. 1991; O’Herron et al. 1993; Kieffer and Kynard 1996). The timing of the putative spawning migrations observed in this study further corroborates these latitudinal patterns in spawning, which suggests that temperature regime probably plays a large role in determining the timing of Shortnose Sturgeon spawning migrations (Figure 2.3). In the Altamaha, Shortnose Sturgeon began their upstream migrations during the late-winter months of 2012, 2013, and 2014 as MWT declined to 11.6–16.9 °C. In previous studies of Shortnose Sturgeon in other southern rivers, adults were observed moving upstream to spawning sites at 8–12 °C (Hall et al. 1991; Rogers and Weber 1995), spawning at 10.5 °C (Heidt and Gilbert 1978), and returning downstream at 12–15 °C

(Dadswell et al. 1984)—temperature ranges well below those documented in this study.

Although other environmental variables could also be important, the temperatures of spawning activities observed in this study are likely another example of clinal variation in the ecology of Shortnose Sturgeon.

In addition to water temperature, the results of this study suggest that other environmental variables may also be important as proximate cues for Shortnose Sturgeon spawning migrations. In all three years of the project, putative upriver spawning migrations were observed during peak winter flows (Figure 2.4)—an observation that seems to corroborate previous studies of Shortnose Sturgeon in other river systems (Taubert 1980; Buckley and Kynard 1985; Kieffer and Kynard 1996; Cooke and Leach 2004), as well as laboratory studies that have linked ovulation and spawning to flow regime (Buckley and Kynard 1985). These studies show that in northern rivers spawning occurs during periods of moderate discharge immediately after spring flows have peaked. Although higher flows were observed in the Altamaha during this study, river-by-river comparisons are difficult because of the dynamic and discrete nature of different river systems. Further complicating these comparisons is the fact that many of these previous studies occurred on rivers with regulated flows.

In February and early March of all three years of this study, adult Shortnose Sturgeon left their suspected spawning areas above the confluence and returned downstream below the head of tide—another key movement pattern considered to be characteristic of spawning migrations in other rivers (Buckley and Kynard 1985; Hall et al. 1991; Kieffer and Kynard 1996). Although downriver movements observed in this study occurred earlier than previously reported (Heidt and Gilbert 1978; Rogers and Weber 1995), water temperatures during the migrations were

similar (18–19 °C), providing further circumstantial evidence regarding the importance of water temperature as a proximate cue for spawning.

The availability of hard-bottom substrate above the confluence provides further evidence that migrations documented in this study were used for spawning purposes and suggests there is substantially more potential spawning habitat available to Shortnose Sturgeon in the Altamaha System than was previously known (Figure 2.5). Although side-scan sonar data showing substrate composition may provide a useful proxy for locating suitable spawning habitat, the coarse resolution of the data makes identifying specific spawning sites impossible. Although several previous studies have described Shortnose Sturgeon spawning habitat, specific criteria defining the percentage of hard-bottom substrate required is still lacking—probably because other environmental factors may affect the specific spawning sites selected by spawning fish. Future studies are needed to quantify these variables and to define the criteria that can be used to quantify potential spawning habitat in coastal rivers throughout the species range.

The spawning periodicity of Shortnose Sturgeon is poorly understood and wide variation has been reported throughout the range (e.g., Dadswell 1979; Kieffer and Kynard 1996). In this study, several fish migrated upriver in consecutive years, and one individual did so in all three years. These results suggest that Altamaha Shortnose Sturgeon may have a much shorter spawning interval than previously reported (Table 2.2). Although few studies have documented individual fish spawning in successive years (Dovel et al. 1992; Collins and Smith 1993; Kieffer and Kynard 1993), the variability of spawning frequency within and among populations has not been well studied. Because males spawn more frequently than females in other river systems (Dadswell 1979), the fish that were observed upriver in consecutive years were likely males; however, future studies of Shortnose Sturgeon spawning movements on the Altamaha and other

river systems should attempt to determine the sex of the transmittered fish at the time of tagging. The acquisition of sex-specific data on spawning migrations would greatly enhance the current understanding of spawning periodicity and habitat requirements.

Upriver movements of Shortnose Sturgeon to discrete reaches above the head of tide during the late summer and fall in years two and three were somewhat puzzling. In both years, these directed upriver movements were followed by prolonged residency at upriver sites located approximately 100–150 km from the estuary. Despite previous reports of fall spawning migrations in the Altamaha (Rogers and Webber 1995), water temperatures during the fall migrations observed in this study were well above the maximum known spawning ranges for the species, which suggests that the fish used these upriver sites for some other purpose. Although the sites were likely used as summer foraging areas or possibly for thermal refugia, future studies will be needed to better understand the ecological importance of these non-spawning movements and to characterize the relevant environmental conditions at these upriver sites.

Reproductive straying has been suggested as an important adaptation of Shortnose Sturgeon for recolonization and for maintenance of genetic diversity throughout the range (Wirgin et al. 2010). In this study, however, none of the tagged individuals left the study area at any point. Given the relatively small sample size ($n=40$) of adults tagged in this study, however, these observations suggest that straying by Altamaha Shortnose Sturgeon is probably rare—a conclusion that is consistent with recent genetic evidence that characterized the Altamaha population as discrete from those in other southern rivers (Wirgin et al. 2005; Wirgin et al. 2010).

Understanding the timing and extent of the spawning migrations of Shortnose Sturgeon has important implications for the management of the species. The findings of this study further

illustrate the important clinal variations in the life history of Shortnose Sturgeon and underscore the need to manage the species as DPS with regionally specific recovery goals. Marked variations in basic life history patterns associated with the unique environmental conditions encountered by Shortnose Sturgeon within the Altamaha illustrate why river-specific research is critical for an accurate assessment of species recovery throughout the range. Within the Altamaha, future research is still needed to quantify spawning dynamics and to identify the specific habitat characteristics of spawning sites.

Acknowledgements

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Tables and Figures

Table 2.1. Means and ranges of lengths and weights of 40 adult Shortnose Sturgeon tagged with sonic transmitters in the Altamaha River, Georgia, 2011-2013.

Year	Sample Period	n	Mean (Range) TL mm	Mean (Range) FL mm	Mean (Range) Weight kg
2011	April 22–May 11	15	828 (732–973)	726 (635–830)	2.9 (1.7–4.8)
2012	March 2–March 12	15	784 (658–897)	690 (591–800)	2.5 (1.6–3.7)
2013	February 6–February 11	10	776 (656–945)	681 (574–819)	2.6 (1.4–4.5)
Overall		40	799 (656–973)	701 (574–830)	2.7 (1.4–4.8)

Table 2.2. Surgery dates, telemetry detections, and putative spawning migrations for 25 adult Shortnose Sturgeon in the Altamaha River system, Georgia, from April 22, 2011–March 31, 2014. Putative spawning migrations of individual fish were defined as directed upstream movements of > 160 km during each year of the study.

Surgery ID	Date	Valid Detections	Putative Spawning Migrations		
			2012	2013	2014
SNS-1	5/2/2011	244032		x	
SNS-2	5/3/2011	147548		x	x
SNS-3	5/5/2011	181429		x	x
SNS-4	5/5/2011	88170	x		
SNS-5	5/6/2011	296130	x		
SNS-6	5/6/2011	119567	x	x	x
SNS-7	5/10/2011	132606		x	
SNS-8	5/11/2011	180105	x		
SNS-9	3/2/2012	97466		x	
SNS-10	3/3/2012	124892		x	
SNS-11	3/3/2012	31249			x
SNS-12	3/11/2012	113566		x	
SNS-13	3/11/2012	12329			x
SNS-14	3/11/2012	141132		x	x
SNS-15	3/11/2012	122395		x	x
SNS-16	3/11/2012	138558			x
SNS-17	3/12/2012	67032		x	x
SNS-18	3/12/2012	71969	x	x	
SNS-19	2/6/2013	29390		x	x
SNS-20	2/8/2013	16448		x	x
SNS-21	2/8/2013	15958			x
SNS-22	2/9/2013	9812		x	
SNS-23	2/10/2013	39022			x
SNS-24	2/11/2013	23711		x	
SNS-25	2/11/2013	20427		x	

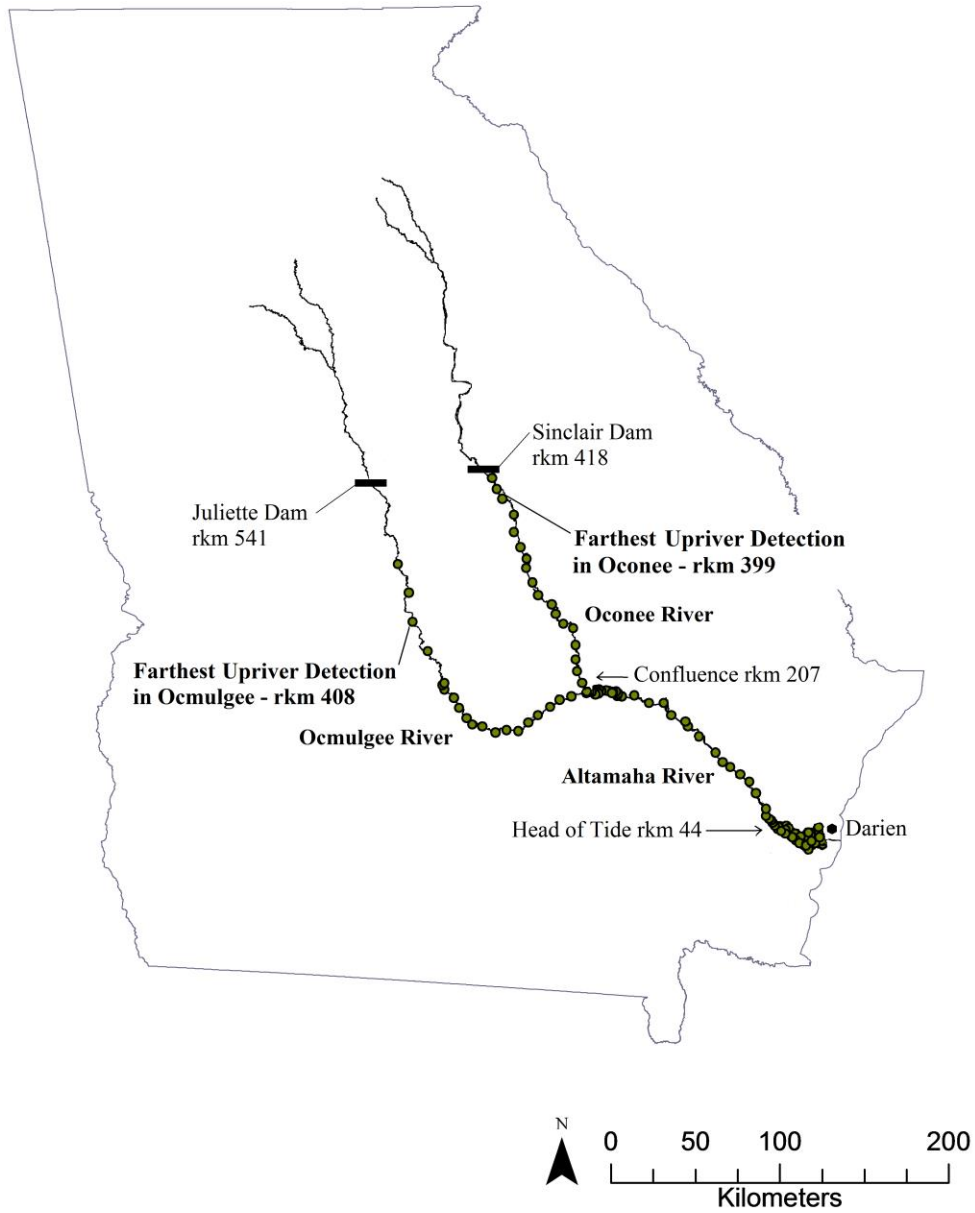


Figure 2.1. Map of the Altamaha River watershed, Georgia. Unique receiver station locations are represented by dots. Dams delineate the upper boundary of habitat accessible to Shortnose Sturgeon in the Ocmulgee and Oconee tributaries. Maximum upstream detections of Shortnose Sturgeon in both tributaries and other relevant river kilometer (rkm) locations are indicated.

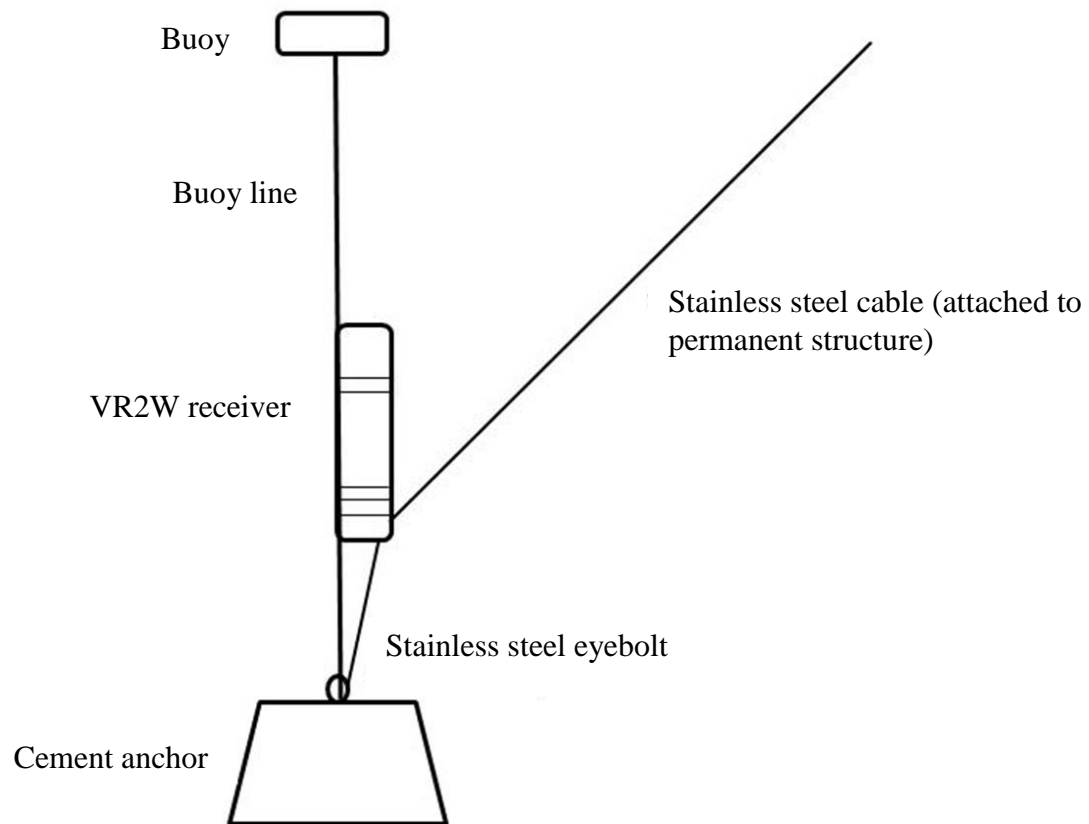


Figure 2.2. Diagram showing setup of stationary acoustic receivers deployed to monitor movements of sonic-tagged Shortnose Sturgeon in the Altamaha River system, Georgia, 2011–2014.

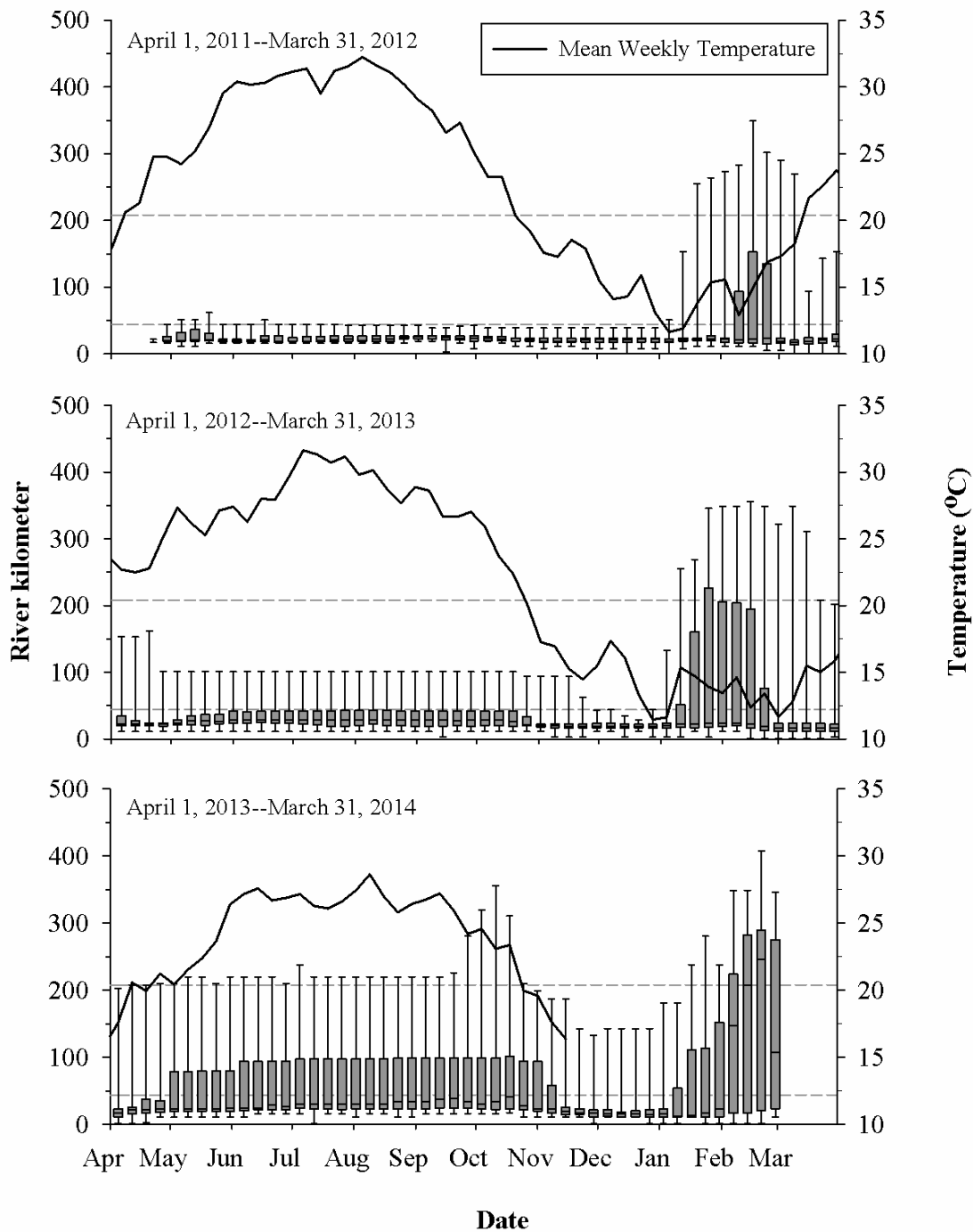


Figure 2.3. Box plots of mean weekly locations of Shortnose Sturgeon (primary axis) in the Altamaha River system, Georgia, 2011–2014 (box ends = 25th and 75th percentiles of ultrasonic tag detections; line within box = median; error bars [whiskers] = minimum and maximum rkm detections). Dashed lines at river kilometer (rkm) 44 and rkm 207 denote the head of tide and confluence, respectively. Mean weekly water temperature (secondary axis) is shown as measured from LTER GCE-7 mooring in the lower Altamaha River.

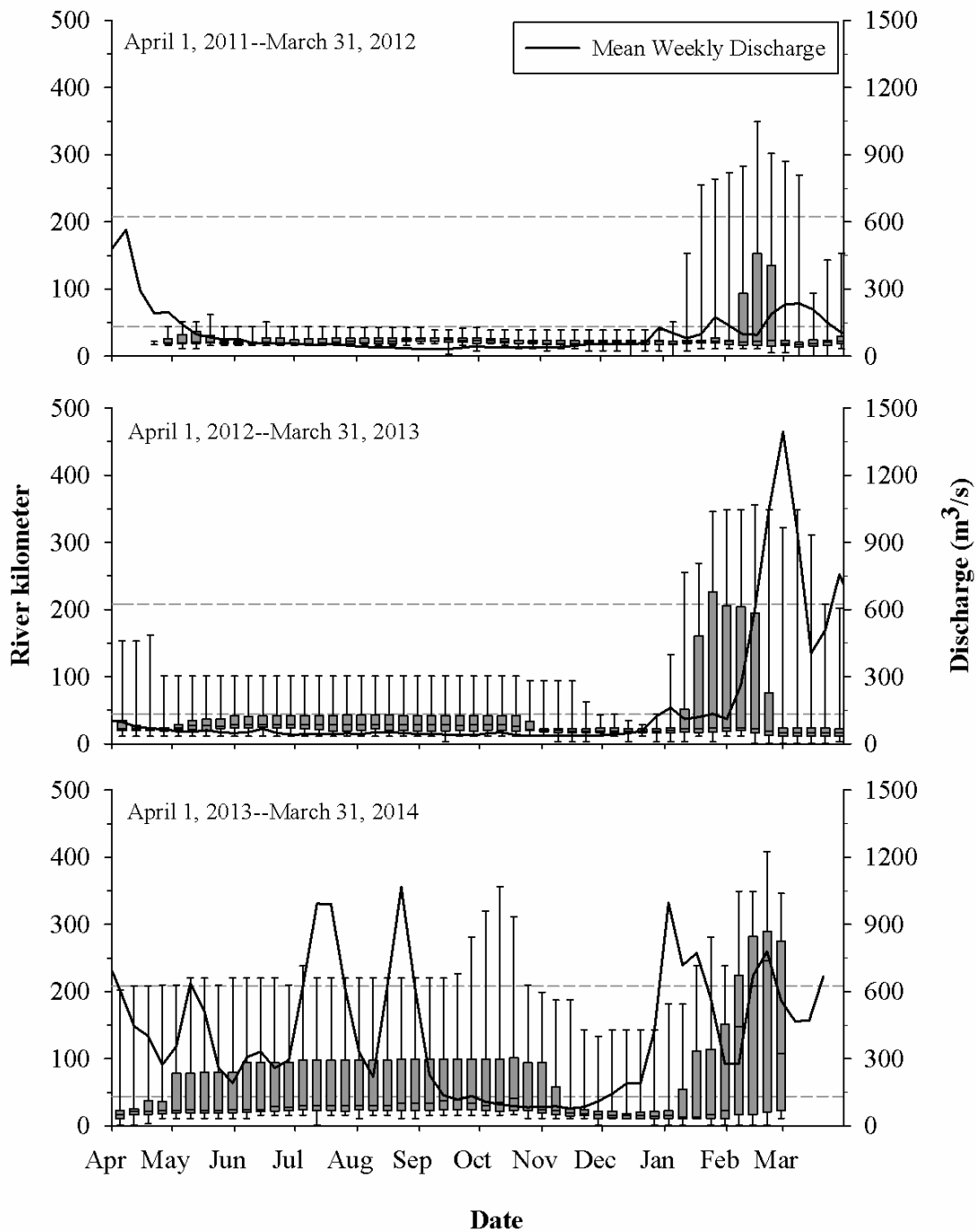


Figure 2.4. Box plots of mean weekly locations of Shortnose Sturgeon (primary axis) in the Altamaha River system, Georgia, 2011–2014 (box ends = 25th and 75th percentiles of ultrasonic tag detections; line within box = median; error bars [whiskers] = minimum and maximum rkm detections). Dashed lines at river kilometer (rkm) 44 and rkm 207 denote the head of tide and confluence, respectively. Mean weekly discharge (secondary axis) is shown as measured from the USGS gauging station at Altamaha rkm 181.

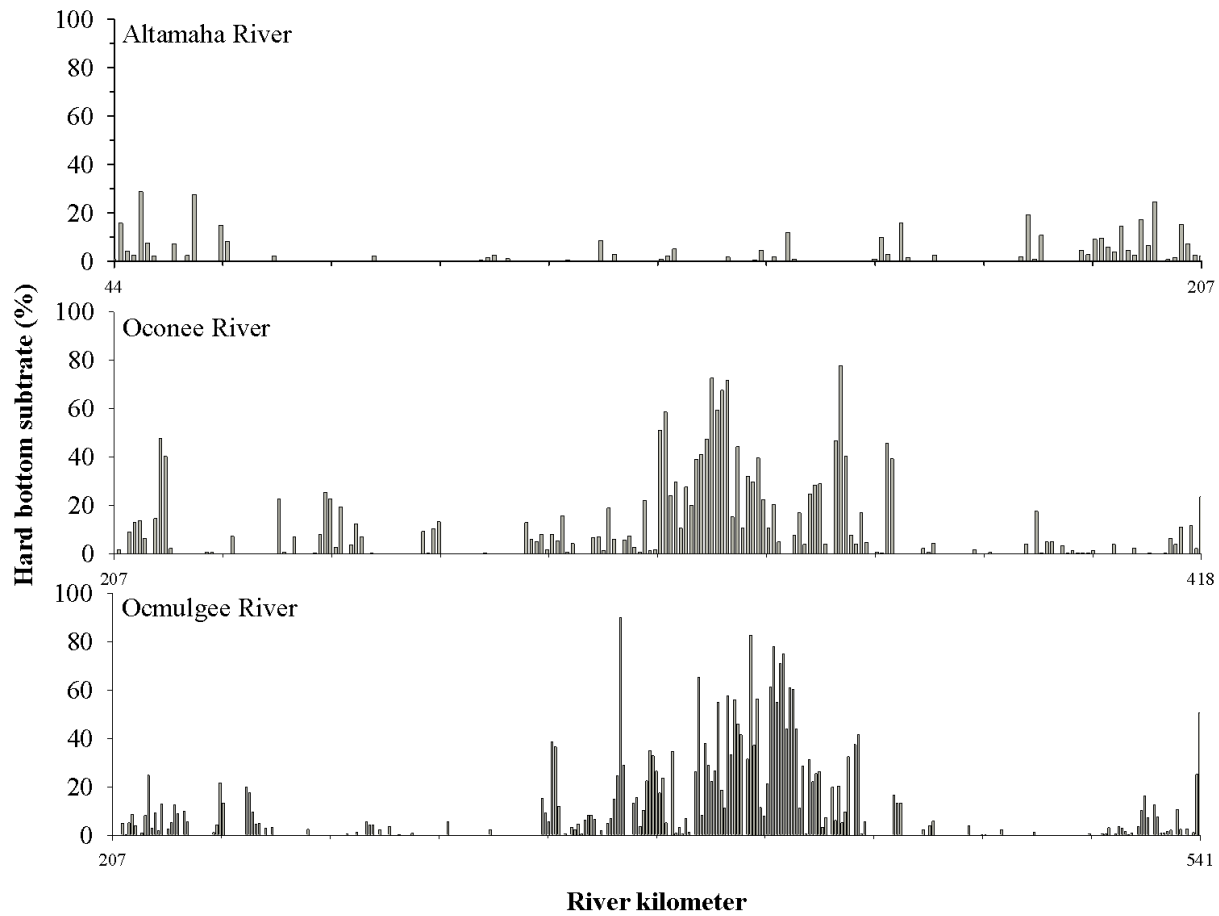


Figure 2.5. Spatial distribution of hard bottom substrate in the Altamaha (rkm 44–207), Oconee (rkm 207–418), and Ocmulgee (rkm 207–541) rivers, Georgia. Data from Litts (2013).

CHAPTER 3

TEMPORAL AND SPATIAL PATTERNS OF ATLANTIC STURGEON (*ACIPENSER OXYRINCHUS OXYRINCHUS*) SPAWNING MIGRATIONS IN THE ALTAMAHA RIVER SYSTEM, GEORGIA¹

¹ Ingram, E. C., and D. L. Peterson. To be submitted to *Transactions of the American Fisheries Society*.

Abstract

The Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) has declined throughout its range as a result of various anthropogenic factors and the species is now protected under the U.S. Endangered Species Act. Information on spawning migrations and spawning habitat is essential for effective recovery strategies. The objectives of this study were to document and identify the seasonal movements and spawning migrations of Atlantic Sturgeon in the Altamaha River system, Georgia. A stationary array of acoustic receivers was used to monitor the movements of 45 adult Atlantic Sturgeon from April 2011 through March 2014. Telemetry data revealed that adult Atlantic Sturgeon exhibited two distinct patterns of upriver migration: a spring two-step migration and a fall one-step migration. During the spring two-step migration, sturgeon appeared to stage in the upper Altamaha during the spring and early summer, before migrating to suspected spawning habitats in the Ocmulgee and Oconee tributaries during the fall. During the fall one-step migration, fish entered the river and migrated at least 207 km upriver to suspected spawning habitats in the Ocmulgee and Oconee tributaries. Regardless of which pattern was used during the upstream migration, all fish returned downstream and left the system by February. We found that Atlantic Sturgeon may spawn in the Altamaha River but only during the fall months when water temperatures decline to < 25 °C. The results of this study further illustrate the clinal variation in the life history of Atlantic Sturgeon and provide new evidence of a fall spawning run that contradicts previous interpretations of Atlantic sturgeon spawning migrations. These findings highlight the need to manage the species as distinct population segments with regionally specific recovery goals.

Introduction

The Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*, Acipenseridae) is a large, long-lived fish that is broadly distributed along the Atlantic coast of North America. Historically, spawning populations of Atlantic Sturgeon occurred in large river systems along the Atlantic coast as far south as the Saint Johns River, Florida (Vladykov and Greeley 1963). This range included approximately 38 rivers, 35 of which supported individual spawning populations (ASSRT 2007). In 1996, all U.S. fisheries were closed (Smith and Clugston 1997); and in 2012, the species was listed under the U.S. Endangered Species Act (ESA). Spawning populations are currently supported in less than 20 rivers along the Atlantic coast (ASSRT 2007). The Hudson River, New York (Bain 1997), and the Altamaha River, Georgia (Schueller and Peterson 2010; Moyer et al. 2012) are suspected to contain the healthiest U.S. populations of Atlantic Sturgeon, but a lack of abundance estimates for other spawning populations makes river-specific comparisons difficult (ASSRT 2007).

Atlantic Sturgeon are strictly anadromous, using riverine, estuarine, and marine habitats throughout their range. Although the majority of their life history is spent in marine and coastal waters, mature adults will return periodically to freshwater rivers to spawn. These migrations are important to optimizing reproductive success by partitioning resources at different life stages and preventing intraspecific competition (Smith et al. 1982; Bain 1997). Despite decades of research, many knowledge gaps remain regarding Atlantic Sturgeon spawning migrations, particularly in southern populations. Mark-recapture and telemetry studies have shown that spawning events are highly variable at both the population and individual levels (Bemis and Kynard 1997). Spawning occurs in the uppermost reaches of accessible river channels that are characterized by moderate flows of 46–76 cm/s and depths of 11–27 m (Smith and Clugston 1997; Bain et al. 2000). Eggs

are adhesive and are broadcast over hard-bottom substrates composed of gravel and cobble (Gilbert 1989; Smith and Clugston 1997; Sulak et al. 2000). Previous studies, including both lab and field research suggest that water temperatures of 13–23 °C are optimal for spawning (Borodin 1925; Smith 1985; Kieffer and Kynard 1993; Hatin et al. 2002). Specific spawning sites have been identified in only a few river systems—mostly within the northern portion of the range (ASSRT 2007). South Carolina is the only southern state where potential spawning sites have been located (Collins et al. 2000). Most information on the timing of Atlantic Sturgeon spawning is the result of research in the Hudson, where spawning occurs from May–August (reviewed in Bain 1997). A fall spawn, however, has been suggested to occur in southern rivers (Smith and Dingley 1984; McCord et al. 2007), and recent studies have documented fall migrations in South Carolina (Collins et al. 2000) and Virginia (Balazik et al. 2012) rivers.

In contrast to many of the other large river systems along the Atlantic coast, the Altamaha River system is a relatively pristine habitat for Atlantic Sturgeon (ASSRT 2007). Isolated rocky shoal habitats are abundant in the upper river and in both the Oconee and Ocmulgee tributaries. Although both of these major tributaries are impounded, the dams are located at or above the fall line. The position of these dams provide more than 750 km of unimpounded habitat and compose the largest and least-altered migratory route for spawning Atlantic Sturgeon within the southern portion of their range (ASSRT 2007). As such, the Altamaha provides a unique opportunity to better understand spawning migrations of a relatively undisturbed population within the southern portion of the species' range. The objectives of this study were to document and describe the seasonal movements and spawning migrations of adult Atlantic Sturgeon in the Altamaha River.

Methods

Site Description

The Altamaha River System, located entirely within Georgia, is formed by the confluence of the Oconee and Ocmulgee rivers (Figure 3.1). The mainstem flows across the Atlantic coastal plain in a southeasterly direction for 207 km to the coast where it empties into the Atlantic Ocean near Darien, Georgia. Mid-channel depths average 2–3 m, with a maximum of 18 m in Altamaha Sound (Heidt and Gilbert 1978). The lower Altamaha estuary is characterized by a tidally flooded salt marsh that gradually gives way upstream to cypress swamp. The location of the freshwater–saltwater interface is highly variable; it occurs less than 50 km upstream of the mouth during low-flow conditions and as far as 25 km offshore under flood conditions (Rogers and Weber 1995). Tidal range averages 2 m, and tidal influence can persist as far upstream as rkm 60 above the sound (Sheldon and Alber 2002). Most of the Altamaha’s total discharge is contributed by the Ocmulgee (40%) and Oconee (36%) tributaries (Rogers and Weber 1995). Isolated rocky shoal habitats are found above rkm 80 and throughout the lower reaches of both tributaries (Flournoy et al. 1992). Although both of these tributaries are impounded above the Fall Line, the biological effects of these dams are considered to be moderate (Dynesius and Nilsson 1994).

Fish Sampling

Adult Atlantic Sturgeon were captured during April–June of 2011 through 2013 with drift nets deployed in the lower portion of Altamaha Sound. These nets, constructed of multifilament mesh (stretch mesh lengths of 30.5 cm, 35.6 cm, and 40.6 cm; each 3.05 m high x 91.44 m long), were deployed during the last 30 min of running tides and fished through the end of the subsequent slack tide (~ 1 hr). Nets were tended continuously so that entangled fish could be removed immediately while the nets continued fishing.

Upon capture, Atlantic Sturgeon were immediately transferred to a floating net pen (1x3x1 m) stationed near the vessel where they were allowed to recover until netting activities had been completed. All fish were then examined for internal and external tags. If none was found, a passive integrated transponder (PIT) tag was inserted into the body musculature beneath the fourth dorsal scute. Measurements of total length (TL), fork length (FL), and weight were recorded (Table 3.1), and a 2–4 cm sample of dorsal fin tissue was collected for subsequent genetic analyses.

Coded acoustic transmitters (Vemco V16-6H) were surgically implanted into 45 individual Atlantic Sturgeon (17 in 2011; 13 in 2012; 15 in 2013). Transmitters had an estimated battery life of 1,633 d. Each transmitter broadcast at 69 kHz, with a random signal repeat interval between 30 and 90 s to minimize signal overlap. Acoustic transmitter implantation was conducted in April–June of each year when water temperatures were < 28 °C. Surgical implantation of transmitters was conducted using methods modified from Moser et al. (2000). Although MS-222 (tricaine methanesulfonate) was used during the first few surgeries, its use was discontinued after the first week of sampling to expedite the procedure and recovery of the fish. Instead, the fish were simply immobilized, ventral side up, in a padded cradle suspended above a 350-L holding tank onboard the research vessel. During the surgical procedure, a small bilge pump placed inside the tank was used to pump fresh river water continuously over the fish's gills. All surgical instruments and transmitters were sanitized with an antiseptic wipe (70% isopropyl alcohol) immediately prior to use. Transmitters were inserted through a 4–5 cm incision made along the midline of the ventrum, approximately 4–6 cm anterior to the vent. Once the transmitter had been inserted into the body cavity, an interrupted pattern was used to close the incision with 4–6 absorbable Monocryl sutures (0-0 needle; Ethicon, Inc.) as described by

Boone et al. (2013). The fish were then returned to the net pen and monitored for 5–10 min until they had fully recovered. They were then released at their original capture site.

Passive Acoustic Telemetry

A stationary array of 112 acoustic receivers (Vemco VR2W) was deployed over a total of 670 km throughout the Altamaha River system (Figure 3.1). Acoustic receivers were equipped with omnidirectional hydrophones to provide continuous monitoring for transmitted fish. Receivers were placed at sites approximately 10 km apart, except at the confluence of the Ocmulgee and Oconee rivers and in Altamaha Sound, where they were placed at 2–3 km intervals. To document potential movements to or from other river systems, researchers from University of Georgia and South Carolina Department of Natural Resources deployed and maintained similar receiver arrays in the Ogeechee, Saint Marys, and Satilla rivers, Georgia, and in the Edisto and Savannah rivers, South Carolina.

Stationary receivers were attached to anchored buoys and deployed so that they were suspended approximately 1 m from the river bottom in an upright position (Figure 3.2). To ensure efficient retrieval of the submerged receivers, anchors were tethered to the nearest structure with 32-mm stainless steel cable. Within riverine habitat, receivers were positioned in the river channel and tethered to trees on the adjacent bank. In open water, habitats receivers were opportunistically tethered to channel markers or pilings. Receivers were downloaded at least every three months throughout the study, except when environmental conditions made the river unnavigable.

Data Processing

At the conclusion of each field season, all telemetry data were carefully reviewed to identify and remove any spurious detections that were evident from the spatial and temporal

chronology of individual fish movements. Simultaneous detections of a single transmitter at two geographically separate locations were filtered out and removed. Mean daily locations of each transmitted fish were determined by calculating mean rkm based on all telemetry detections during each 24-h period. From these mean daily rkm values, mean weekly rkm values for individual fish were then calculated to construct box plots with 25th, 50th, and 75th percentiles of weekly river distributions for fish that made significant upstream movements (> 160 km). When mean weekly rkm values were unavailable because of limited fish movement, the last known position of the fish was used for that week. To simplify data processing, study year was defined by the beginning date of the project, rather than calendar year. Thus, study year one comprised April 1, 2011–March 31, 2012, study year two comprised April 1, 2012–March 31, 2013, and study year three comprised April 1, 2013–March 31, 2014.

Side-scan sonar data for the Altamaha system showing composition of bottom substrate were obtained from Georgia Department of Natural Resources (Litts 2013). Data were available for the Altamaha River (rkm 44–207), Ocmulgee River (rkm 207–541), and Oconee River (rkm 207–418). From these data, potential spawning habitat for Atlantic sturgeon was identified based on the percentage of available hard-bottom substrates (i.e., rocky fine, rocky boulder, and/or bedrock) as described in the literature (Smith and Clugston 1997). Mean weekly temperature (MWT) for the Altamaha River was obtained from the LTER GCE-7 hydrographic monitoring station at rkm 20 near Darien, Georgia. Temperature data were available through November 21, 2013. Mean daily river discharge (MWD) was obtained from the USGS gauging station near Baxley, Georgia (rkm 181).

Results

During three years of the study, 45 adult Atlantic Sturgeon were captured and tagged with acoustic transmitters (Table 3.1). Size of tagged fish ranged from 1,255 to 2,030 mm FL, with a mean (\pm SD) FL of $1,618 \pm 178$ mm. Forty-two of the fish were subsequently documented within the study area; the other three were identified as inactive and removed from subsequent analyses. The number of valid detections for individual fish in the Altamaha System ranged from 1 to 120,420, yielding a combined total of 515,814 valid detections for all fish over the course of the study. Data from acoustic telemetry indicated that the tagged fish were present in the Altamaha River system from April–December in each year of the study (Figure 3.3). Seven (16.7%) individuals left the study area within a few days of being tagged and did not return to the Altamaha. Twenty-six (42%) fish made significant upstream migrations (>160 rkm)—eight of these migrated upstream in at least two years of the study; four migrated upstream in all three years (Table 3.2). The extent of these upstream migrations varied among individuals and study years. Although some individuals were detected upriver in multiple years, there was no evidence of site fidelity. A few of the upriver sites, however, were visited by multiple fish in multiple years, particularly the area near the confluence and rkm 340–350 in the Ocmulgee River. The number of fish entering the Oconee and Ocmulgee tributaries was also variable among years; however, the vast majority of fish entered the Ocmulgee River. Fish were not detected in the Oconee in year one, only one fish in year two, and 13 fish in year three. The maximum extent of these upriver migrations was documented at rkm 408 on the Ocmulgee River and rkm 356 on the Oconee River (Figure 3.1). In total these migrations covered 557 km of the 752 km (74%) of free flowing habitats within the Altamaha River System.

Although each individual migration was unique, most fish adhered to one of two common movement patterns with regard to the timing and duration of their upriver migration: (1) early-year migrations that occurred in two discrete steps or (2) late-year, one-step migrations (Figure 3.4). Early upriver migrations that began in April–May typically occurred in two steps, with fish remaining at mid-river locations during the summer months before continuing upstream in the fall. The late-year migrations, however, were typically initiated in August or September and were generally non-stop. Most fish (six of eight) that made upriver migrations in multiple years used the same movement pattern; however, two individuals followed different patterns in different years. Regardless of which migration pattern was used during upstream migration, all fish exhibited a one-step pattern of migrating downstream in December and early January. After leaving the Altamaha River in late winter, 15 (36%) of the tagged fish were subsequently documented in other river systems in Georgia, South Carolina, and Florida.

Migrating Atlantic Sturgeon that entered the Altamaha River during April and May always used a two-step migration pattern (Figure 3.4a). This pattern was used by three of eight (38%) migrating fish in year one, four of 11 fish (36%) in year two, and five of 19 (26%) in year three. The first-step of these two-step migrations was characterized by rapid upstream movement to mid-river sites located above the head of tide (rkm 44). Once there, the fish exhibited little movement throughout the summer, as water temperatures exceeded 30 °C (Figure 3.3). Specific locations of over-summering sites were variable, although several sites were used repeatedly throughout the study—particularly deep holes located near rkm 162 and between rkm 205–207. Regardless of which specific over-summering sites were used, the median of mean weekly detections always occurred between the head of tide and confluence (Figure 3.3). The second-step of these spring migrations occurred when fish left their over-summering sites and moved

upstream to sites above the confluence in the Ocmulgee and Oconee tributaries in late August and September. These movements were rapid and direct and always occurred as water temperatures began to decline from their summer highs (Figure 3.3).

In contrast to the two-step migration pattern exhibited by spring migrants, most migrating fish—five of eight (62%) in year one, seven of 11 (64%) in year two, and 14 of 19 (74%) in year three used a fall one-step pattern (Figure 3.4b). These fall migrations were characterized by a long (>200 km), single-step migration from the estuary upstream to tributary reaches above the confluence. These migrations typically were initiated in August and September as MWT began to decline from summer maxima (Figure 3.3). Although fish exhibiting this pattern typically mixed with the one-step migrants during the second-step of their migrations, their movement patterns were distinctly different in that there were not staging or resting periods. Once the fall, one-step migrants reached their presumed spawning areas above the confluence, the median of their mean weekly detections was similar to that of the two-step migrants throughout the late summer and fall months. The farthest upriver detection occurred in the Ocmulgee River at rkm 408. Regardless of which migration pattern was exhibited, migrants remained in the lower tributary habitats near the confluence throughout the fall before returning back downriver between late November and early January.

All upstream migrants documented during the study concluded their downstream migrations in the Altamaha System by early January, as water temperatures approached their annual minimums (Figure 3.3). In the first two years of the study, the last detection in Altamaha Sound occurred on January 4. In year three, the last detection occurred on December 15. Downstream migrations typically were rapid and direct, occurring over only a few weeks. One

fish traveled 330 km in only eight days before exiting the system. Regardless of the rate of downstream movement, all fish left the system by early January.

After leaving the Altamaha River, 15 (33%) of the tagged Atlantic Sturgeon were detected on receiver arrays in other river systems including the Ogeechee and Satilla Rivers, Georgia, the Savannah, Cooper, Sampit, and Waccamaw Rivers in South Carolina, and the Nassau River in Florida. These intercoastal movements required a minimum linear distance traveled of 80 (Ogeechee River) to 350 km (Winyah Bay in South Carolina). Although the timing and duration of detections in these systems were variable, movements within systems were limited to estuary and lower river habitat, which indicated that the fish did not likely spawn in these other rivers.

Discussion

The putative spawning migrations documented in this study showed that Atlantic Sturgeon used approximately 74% of the free flowing habitats available to them within the Altamaha System below the Fall Line, including both major tributaries. Telemetry data revealed that 32% of putative spawners entering the system in the spring appeared to stage below the confluence during the late spring and summer (Figure 3.4). During the fall, freshwater migrations of at least 207 km (to the confluence) were common (68% of putative spawners). No individuals migrated all the way to the Fall Line in either tributary (rkm 541 in the Ocmulgee; rkm 418 in the Oconee); however, one individual migrated to at least rkm 408 (200 rkm above the confluence) of the Ocmulgee. This constituted the longest documented migration of an Atlantic sturgeon within a U.S. spawning river. Several fish moved into the lower reaches of the Ocmulgee in all years of the study and into the Oconee in two of three years. In the Oconee

River, fish traveled upstream as far as rkm 356—149 km above the confluence and only 62 km below Sinclair Dam. By comparison, adult spawning runs in the Hudson River only reach rkm 182 (Van Eenennaam 1996). Likewise, in the James River, Virginia, the highest upriver extent Atlantic Sturgeon have been documented was near the Fall Line at rkm 155 (Balazik et al. 2012). Observations in the Altamaha likely represent a superior analog of historic spawning availability and conditions when compared to other systems where factors such as limited reach size or impoundments exist.

The presence of adult Atlantic Sturgeon within the Altamaha River proper and in both main tributaries during all three years of this study indicated that the estuarine and riverine habitats found within the Altamaha system were used regularly for spawning runs. Despite the presence of isolated rocky shoal habitats in its lower reaches (Figure 3.5), the Oconee was used to a lesser extent than the Ocmulgee. The paucity of habitat use in the Oconee could be attributed to low flows in that tributary during the first two years of the study. Regardless, substrate data suggest that spawning habitat in the Oconee (Rogers and Weber 1995) is probably used by Atlantic Sturgeon at least in some years.

Previous studies of Atlantic Sturgeon in northern river systems suggest that spawning typically occurs in late spring and early summer (e.g., Dovel and Berggren 1983; Van Eenennaam et al. 1996); however, the movement patterns of Atlantic Sturgeon documented in this study indicated that spawning in the Altamaha system occurred only in the fall. Although the telemetry data do not provide direct evidence of spawning, the extent and timing of these movements in relation to the seasonal temperature regime provide strong circumstantial evidence that these movements were in fact spawning migrations. Although non-spawning adults are often encountered in freshwater at various times of the year (Van Eenennaam 1996; Sulak and Randall

2002), previous studies have demonstrated clinal variation in the timing of Atlantic Sturgeon spawning migrations; April–May in northern systems and February–March in southern systems (Smith 1985; Bain 1997). In this study, the two-step migrants entered the river in April–May (Figure 3.3)—later than described in previous studies of other southern populations. The timing of fall migrations (for both one- and two-step migrants), however, was consistent with a previous study in South Carolina rivers (Collins et al. 2000), yet the use of two different migration patterns has not been previously documented for Atlantic Sturgeon. Furthermore, the duality in migration patterns documented in this study helps explain the persistent confusion regarding spawning seasons of the species throughout the range by illustrating that, although Atlantic sturgeon may be present in the Altamaha River system in the spring and summer, they are only documented upstream near potential spawning habitat in the fall.

Putative spawning migrations documented in this study adhered to one of two distinct patterns: spring two-step or fall one-step. One-step migrations were initiated in the late summer and early fall (August–September) and were characterized by fish moving directly upstream to suspected spawning areas before returning downstream in the winter. Two-step migrations were initiated in the late spring–early summer (April–May) and were characterized by an initial upstream migration to mid-river sites followed by a prolonged staging period during summer before migration to spawning sites in early fall. Although these migration patterns have been described previously for other species of sturgeon (Bemis and Kynard 1997), the results of this study are the first documented evidence of their use by Atlantic Sturgeon.

Because of their extensive latitudinal range along the Atlantic coast, Atlantic Sturgeon encounter significant clinal variations in environmental conditions. Previous studies (e.g., Fox et al. 2000; Collins et al. 2002) of other sturgeon have identified water temperature as an important

factor in determining the timing of spawning migrations. Chapman and Carr (1995) hypothesized that Atlantic Sturgeon spawning migrations may be timed to coincide with river conditions that are optimal for egg and larva survival. Although the optimal temperature range for Atlantic Sturgeon eggs and larvae has not been determined empirically, aquaculture studies have reported successful incubation of eggs at temperatures 15–20 °C (Smith et al. 1980; Dean 1895; Chapman and Carr 1995) and significant mortality of eggs and larva above 25 °C (Chapman and Carr 1995). Results of this study show that fall spawning migrations placed the fish over hard substrates near or just above the Altamaha confluence just as water temperatures declined to < 20 °C in October. Although water temperatures also reached this range in early spring, telemetry data showed that few tagged fish had even entered the river at that time of year. Because temperatures remained > 28 °C for most of the summer, these data suggest that the timing of spawning migrations in the Altamaha allows the fish to maximize the duration of favorable water temperatures for early life stages.

Previous research on Atlantic Sturgeon within southern U.S. rivers has focused primarily on population dynamics (Peterson et al. 2008; Schueller and Peterson 2010); however, little is known about their seasonal movements and habitat use. Understanding the linkages between habitat use and population dynamics is a critical information gap in developing effective management strategies for this species, yet data regarding the timing and locations of spawning are scarce or even contradictory in some instances. Unfortunately, this information is critical for development of effective species recovery strategies. The results of this study provide new information regarding the seasonal migratory patterns and habitat use of adult Atlantic Sturgeon in the Altamaha River. Although previous studies in northern river systems indicate that adults typically spawn in late spring or early summer (e.g., Smith and Clugston 1997; Bain et al. 2000),

all telemetry data in this study indicated that the Altamaha population spawns in the late fall, as water temperatures declined from summer highs. Although some researchers have suggested that spawning may occur in both spring and fall in southern rivers (Smith and Dingley 1984; McCord et al. 2007), data from this study contradict that conclusion and provide strong evidence of a solitary fall spawn—at least for the Altamaha population.

Understanding the timing and extent of the spawning migrations of Atlantic Sturgeon has important implications for the management of this species. The findings of this study illustrate the clinal variation in the life history of Atlantic Sturgeon and highlight the need to manage the species as distinct population segments with regionally specific recovery goals. Marked variations in basic life history patterns of Atlantic Sturgeon migrations observed within the Altamaha compared to other rivers in the South Atlantic Bight suggest that river-by-river assessments are crucial, and further delineation of distinct population segments may be necessary. Within the Altamaha, future research is required to document spawning and identify the specific characteristics of spawning sites. Although this study provides the first evidence of a fall-only spawning run of Atlantic Sturgeon, it is only the first step in developing a better understanding of this population. Verification of upriver spawning habitats is necessary, using this study as a framework for identifying key spawning sites used during the fall months.

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Tables and Figures

Table 3.1. Means and ranges of lengths and weights for 45 adult Atlantic Sturgeon tagged with sonic transmitters in the Altamaha River, Georgia, 2011–2013.

Year	Sampling Period	n	Mean (Range) TL mm	Mean (Range) FL mm	Mean (Range) Weight kg
2011	April 21–May 10	17	1,828 (1,585–2,310)	1,622 (1,430–2,030)	47.8 (26.3–90.7)
2012	April 21–June 15	13	2,005 (1,640–2,240)	1,765 (1,460–2,000)	52.2 (22.7–90.7)
2013	April 25–May 8	15	1,641 (1,442–1,860)	1,470 (1,255–1,670)	43.9 (29.5–65.8)
Overall		45	1,825 (1,442–2,310)	1,618 (1,255–2,030)	48.0 (22.7–90.7)

Table 3.2. Surgery dates, telemetry detections, and putative spawning migrations for 26 adult Atlantic Sturgeon tagged in the Altamaha River system, Georgia, from April 1, 2011–March 31, 2014. Putative spawning migrations of individual fish were defined as directed upstream movements of > 160 km during each year of the study.

Surgery ID	Date	Valid Detections	Putative Spawning Migrations		
			Year 1	Year 2	Year 3
ATS-1	4/21/2011	27,275	x	x	x
ATS-2	4/22/2011	28,806	x	x	x
ATS-3	4/25/2011	7,465	x	x	
ATS-4	4/25/2011	8,968	x		
ATS-5	4/26/2011	18,191		x	
ATS-6	4/29/2011	24,268	x		x
ATS-7	4/29/2011	7,990			x
ATS-8	4/29/2011	12,471		x	x
ATS-9	5/4/2011	22,343	x	x	x
ATS-10	5/4/2011	15,085	x		
ATS-11	5/9/2011	16,197	x	x	x
ATS-12	4/21/2012	5,122		x	x
ATS-13	5/14/2012	5,703			x
ATS-14	5/25/2012	60,276		x	
ATS-15	5/31/2012	120,420		x	
ATS-16	6/11/2012	3,158		x	
ATS-17	4/25/2013	2,277			x
ATS-18	4/30/2013	62,226			x
ATS-19	4/30/2013	5,415			x
ATS-20	4/30/2013	1,449			x
ATS-21	5/7/2013	8,513			x
ATS-22	5/7/2013	9,235			x
ATS-23	5/7/2013	12,487			x
ATS-24	5/8/2013	2,065			x
ATS-25	5/8/2013	2,451			x
ATS-26	5/8/2013	3,932			x

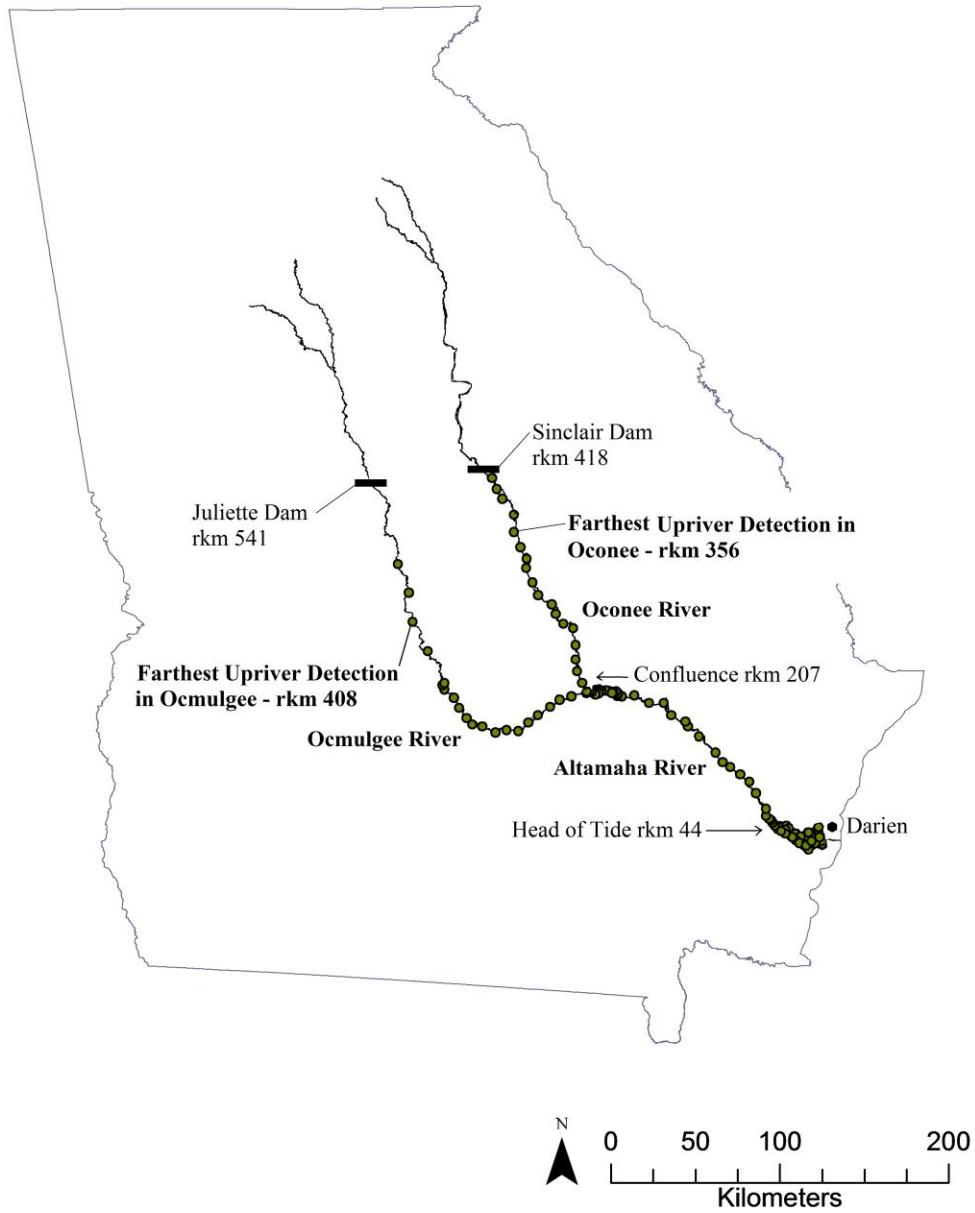


Figure 3.1. Map of the Altamaha River watershed, Georgia. Unique receiver station locations are represented by dots. Dams delineate the upper boundary of habitat accessible to Atlantic Sturgeon in the Ocmulgee and Oconee tributaries. Maximum upstream detections of Atlantic Sturgeon in both tributaries and other relevant river kilometer (rkm) locations are indicated.

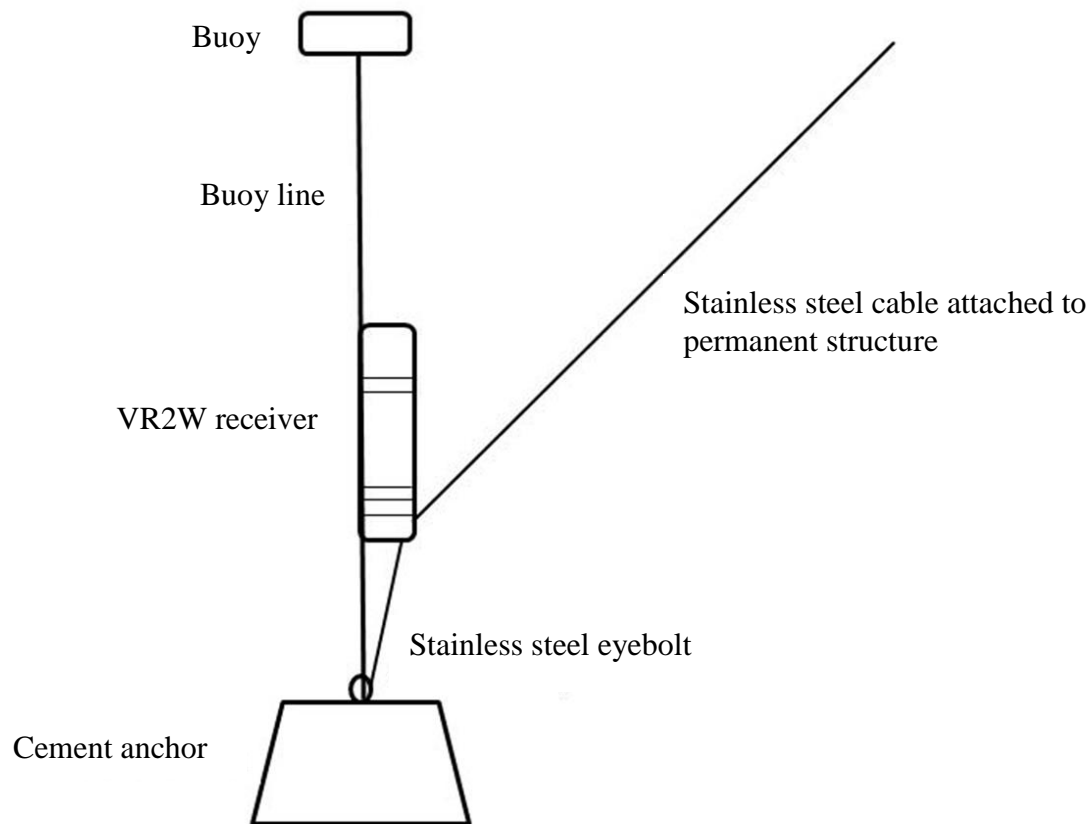


Figure 3.2. Diagram showing setup of stationary acoustic receivers deployed to monitor movements of sonic-tagged Atlantic Sturgeon in the Altamaha River system, Georgia, 2011–2014.

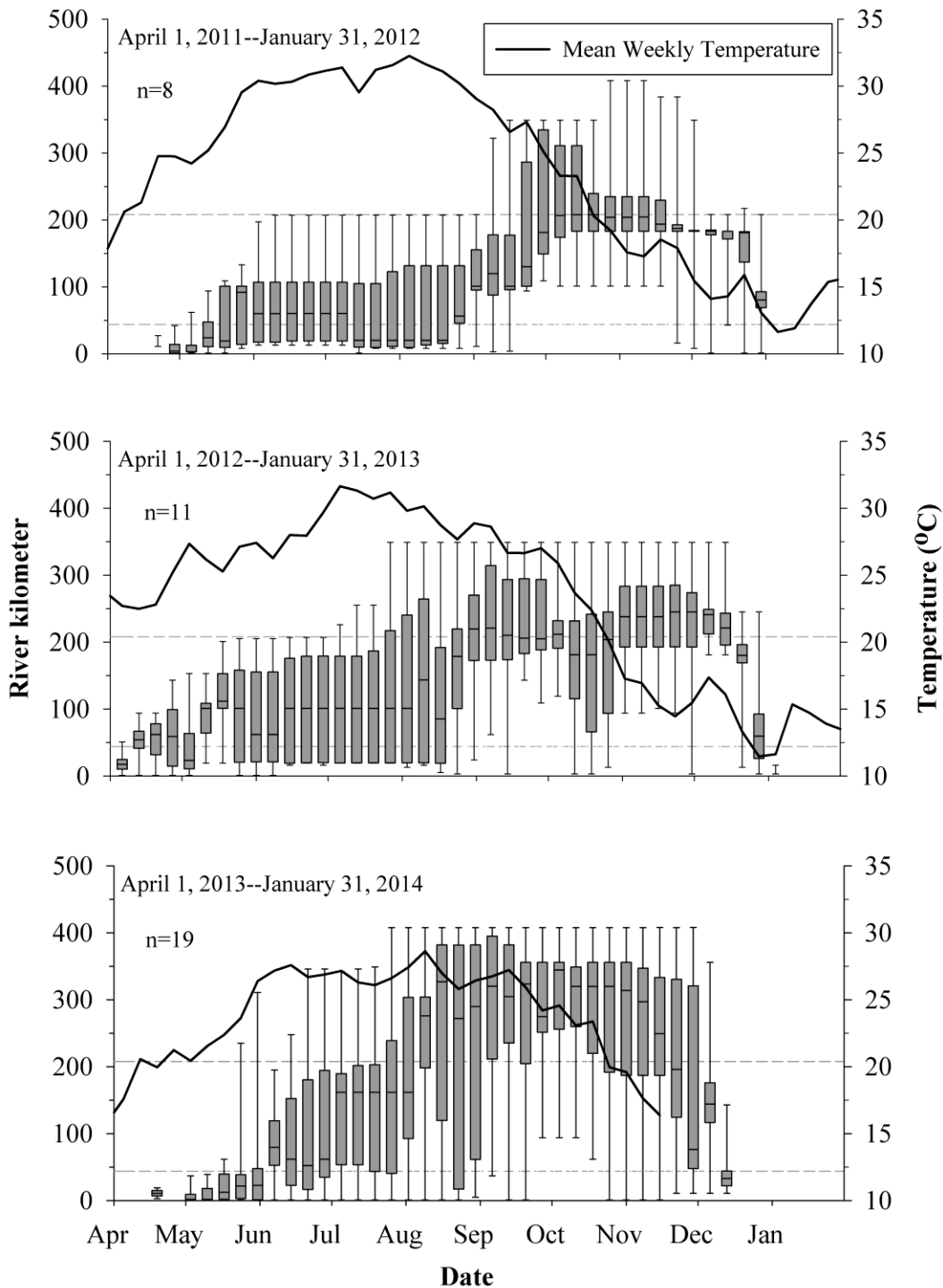


Figure 3.3. Box plots of mean weekly locations of Atlantic Sturgeon (primary axis) in the Altamaha River system, Georgia, 2011–2014 (box ends = 25th and 75th percentiles of ultrasonic tag detections; line within box = median; error bars [whiskers] = minimum and maximum rkm detections). Dashed lines at river kilometer (rkm) 44 and rkm 208 denote the head of tide and confluence, respectively. Mean weekly water temperature (secondary axis) is shown as measured from LTER GCE-7 mooring in the lower Altamaha River.

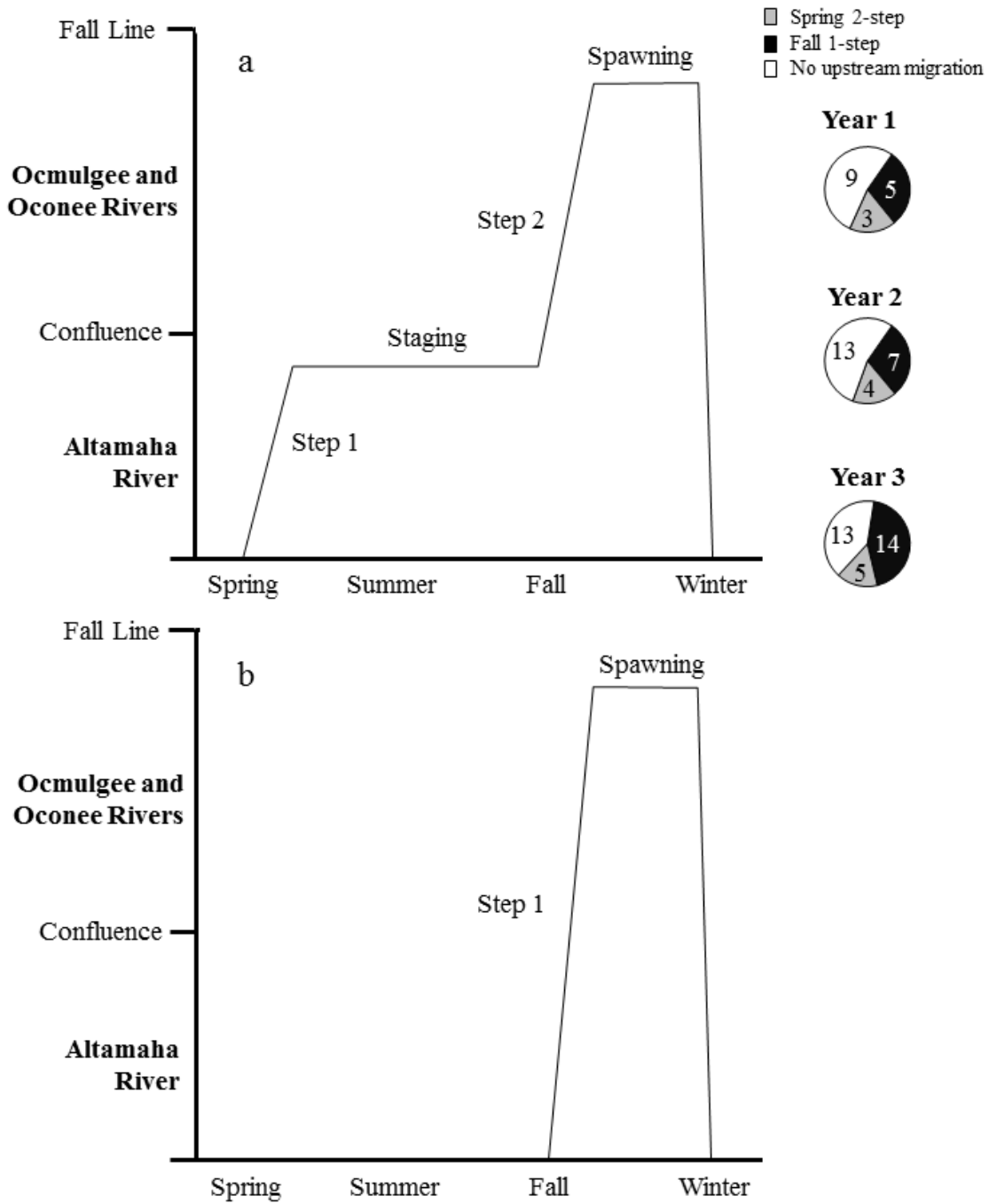


Figure 3.4. Diagram of (a) spring two-step and (b) fall one-step spawning migrations of Atlantic Sturgeon in the Altamaha River system, Georgia. Pie charts show prevalence of each migration strategy documented using acoustic telemetry from year one (April 1, 2011–January 31, 2012), year two (April 1, 2012–January 31, 2013), and year three (April 1, 2013–January 31, 2014).

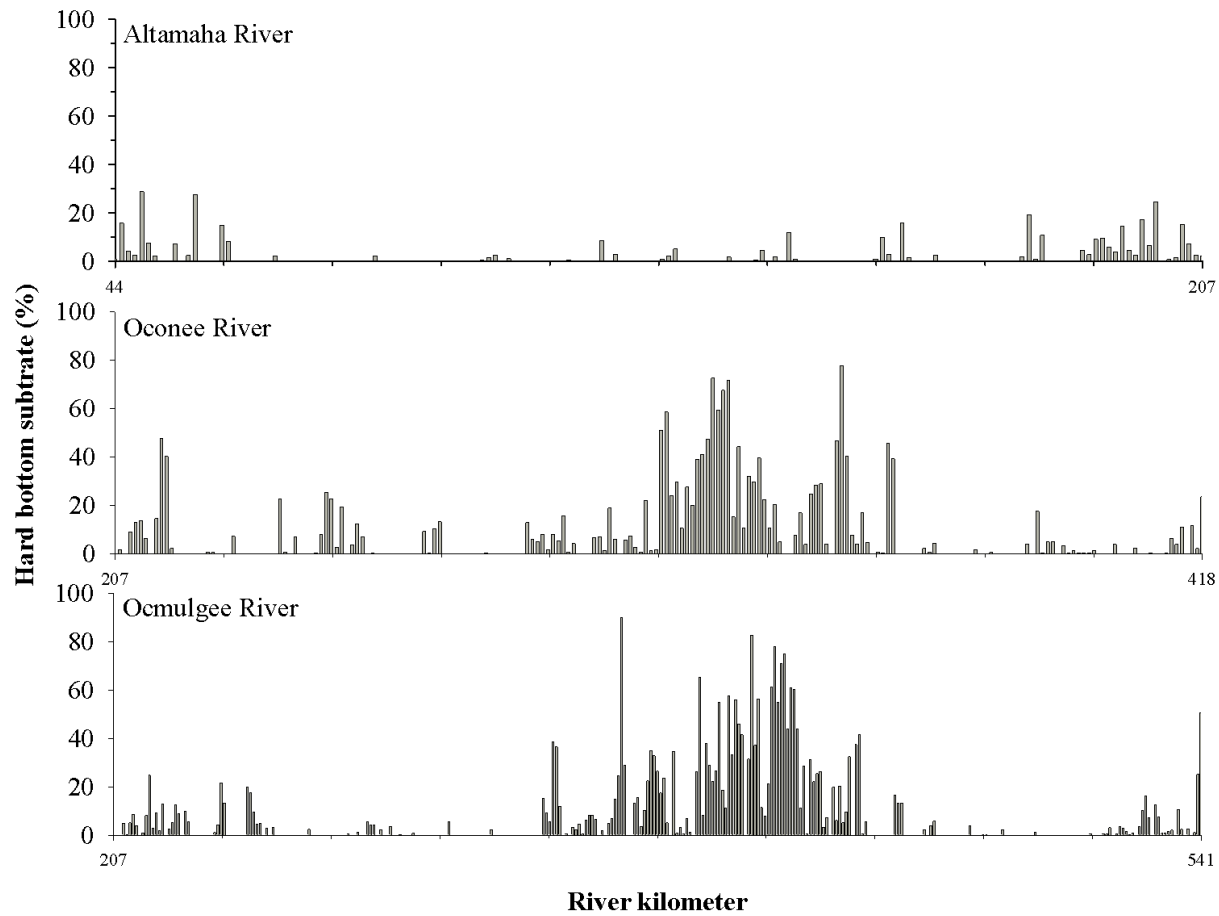


Figure 3.5. Spatial distribution of hard bottom substrate in the Altamaha (rkm 44–208), Oconee (rkm 208–420), and Ocmulgee (rkm 208–543) rivers, Georgia. Data from Litts (2013).

CHAPTER 4

CONCLUSIONS

This study was initiated in response to key research needs identified by the National Marine Fisheries Service (NMFS 1998; ASSRT 2007) and provides new information regarding the temporal and spatial patterns of spawning migrations of two federally endangered sturgeon species in the southern periphery of their ranges. Telemetry data revealed clinal variations in life history of Shortnose and Atlantic Sturgeon, typical of species with such a broad latitudinal range. Findings from this study may have important implications on river-specific strategies to recover these species. Although sturgeon spawning dynamics are known to be highly variable at both population and individual levels (Bain 1997; Bemis and Kynard 1997), the migratory patterns identified in this study were atypical or contradictory when compared to previous findings in both timing and extent. Telemetry data revealed that Atlantic Sturgeon in the Altamaha River spawn only during the fall, as opposed to the spring, and that during their upstream migrations both Atlantic Sturgeon and Shortnose Sturgeon utilize a larger percentage of available upstream habitat than previously thought. Although my findings could be an artifact of the dynamic nature of coastal river systems, observations in the Altamaha likely represent a superior analog of historic spawning availability and conditions than other southern systems where limiting factors such as impoundments and less ideal environmental conditions exist.

Although the implementation of critical habitat designation in the recovery process has been criticized (Hoekstra et al. 2002; Greenwald et al. 2012), this process is required for species

listed under the ESA. Information on the timing and extent of seasonal migrations documented in this study should be used to facilitate the designation of critical habitat for both Atlantic and Shortnose Sturgeon in the Altamaha and other southern river systems. Because of the variety of habitats used by both sturgeon species, definitions of their habitats must be sufficiently broad to account for system-wide conditions, rather than just site-specific conditions (Beamesderfer and Farr 1997). The presence of adult Shortnose and Atlantic Sturgeon within the Altamaha proper and in both main tributaries indicates that the estuarine and free-flowing riverine habitats found within the entire system are likely essential for these species—at least on a seasonal basis. Although both species can also use nearshore marine habitats, long-distance coastal migrations appear to be common only for Atlantic Sturgeon. Riverine and estuarine habitats below the head of tide in the Altamaha are used extensively by both species, whereas upriver spawning sites are used by Shortnose Sturgeon from January–March and by Atlantic Sturgeon from April–December.

Understanding the timing and extent of the spawning migrations of both Shortnose and Atlantic Sturgeon has important implications for management and recovery of each species. The findings of this study illustrate the clinal variations in the life history of both and further highlight the need to manage both species as distinct population segments (DPS) with regionally specific recovery goals. A better understanding of interbasin movements is necessary to facilitate the management of Shortnose and Atlantic Sturgeon within the U.S. Currently, the listing status of Shortnose Sturgeon is under review and the management of individual rivers as DPS has been suggested (NMFS 1998; Wirgin et al. 2010). Although Atlantic Sturgeon are currently managed as DPS, these designations may require revisions (Grunwald et al. 2008) as more data become available regarding population status and coastwide genetic structuring. Wide variations in life

history and seasonal habitat use documented in this study suggest that river-specific assessments will be critical to meeting recovery goals for both species. Within the Altamaha, additional studies are needed to document the specific timing and locations of spawning and to better understand what environmental factors affect spawning success. The identification of a discrete Atlantic Sturgeon fall spawning run in the Altamaha, along with the lack of a traditional spring spawning event, suggests that the environmental conditions found in the Altamaha system may be very different from those typical of rivers in the northern part of the species range. All sturgeons are likely locally adapted to such conditions, but future studies are needed to better understand the broader patterns of latitudinal variations in the environmental tolerances—particularly for early life stages. Although this study has provided important new information regarding the timing and locations of Atlantic and Shortnose Sturgeon spawning migrations within the Altamaha System, future research is needed to identify and characterize specific spawning sites through the active tracking of spawning adults and the collection of fertilized eggs at specific spawning sites. Additional research comparing cohort sizes of young-of-year and age-1 populations to the river conditions present during spawning may provide insights into the environmental variables that determine spawning success.

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