12-10-2022

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Recommended Citation

Takacs, Molly Katherine, "Abundance and growth of juvenile Atlantic Sturgeon in the Edisto River, SC" (2022). *Electronic Theses and Dissertations*. 148.
https://digitalcommons.coastal.edu/etd/148

Abundance and Recruitment of Juvenile Atlantic Sturgeon (*Acipenser oxyrinchus*) in the Edisto River, SC

By

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Submitted in Partial Fulfillment of the
Requirements for the Degree of Master of Science in
Coastal Marine and Wetland Studies in
the School of the Coastal Environment
Coastal Carolina University
2022

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Acknowledgments

I would first like to thank Dr. Derek Crane for serving as my major advisor during my graduate studies at Coastal Carolina University. I thank him for the opportunity he has given me to work on this project as well as the guidance he has given over my three years at Coastal. I am forever grateful to him for pushing me to become a better scientist as it has prepared me to succeed in my future career. His encouragement and insight has gotten me to where I am today as a successful fisheries scientist.

Thank you also to Ellen Waldrop, Erin Burge, and Christopher Hill for serving as members of my committee and providing valuable input through my thesis project as well as editing my final thesis. I would like to thank Bill Post at South Carolina Department of Natural Resources (SCDNR) for the opportunity to be a part of this project as well as his valuable insight and involvement in the study. Thank you to my field crew at SCDNR, Danielle Carty, Caroline Devries, Claire Benson, and Emily Klimczak, for their help in collecting data each summer as well as data input and net building in the off season. Thank you for working hard though the early mornings, sweltering heat, and endless trees caught in our nets. I would like to thank the SCDNR and the many other employees involved in collection of the data used in this manuscript. I thank the NOAA Anadromous Fisheries Conservation Act and the Atlantic Coastal Fisheries Cooperative Management Act for research funding. Thank you to Coastal Carolina University for making this project possible. I am grateful to Lindsey Bell and Keshav Jagannathan for assisting with statistical analyses and their help with R.

Finally, I would like to thank my parents for their love and support throughout this entire journey. They have encouraged and pushed me to follow my dreams since day one when I decided to become a marine biologist in 5th grade. I could not be where I am today without them, and I am eternally grateful.

ABSTRACT

Information on abundance and body growth are important for understanding the status and health of populations, and this information can be used to guide and monitor conservation and recovery efforts for species of conservation concern. The Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) is an anadromous fish native to the Atlantic coast of the United States and Canada. Due to overfishing and habitat degradation, population levels declined, and Atlantic Sturgeon were placed on the Endangered Species list in 2012. Although there is substantial research on adult Atlantic Sturgeon, knowledge about their early life history is lacking. The objectives of this study were to estimate the annual abundance of juvenile Atlantic Sturgeon in the Edisto River, SC, over a 25-year period. I also investigated growth and growth rates of juveniles, what environmental factors were related to growth and growth rate, and if growth differed between seasonal cohorts. Drifted gill nets were used to sample juvenile Atlantic Sturgeon in the Edisto River, SC from 1994–2019. I estimated the number of juveniles in the river during May through September of each year based on daily and monthly encounter histories using the POPAN version of the Jolly-Seber open population model. I calculated average growth per day and growing degree days for each individual and a suite of linear models were used to determine what environmental factors (mean temperature, growing degree days [GDD], and discharge) and biological factors (initial length and seasonal cohort) were related to growth rate and overall growth between captures. The juvenile ($\leq$1050 mm) abundance averaged 845 individuals (range = 333–1,343, 95% CI = 644–1,046) based on the average of daily and monthly encounter history population estimates. Growth rate was weakly related to the environmental and biological variables investigated (most likely model $R^2 = 0.32$). Absolute growth between captures was related to initial TL at capture, mean temperature, discharge, GDD, seasonal cohort, and the interactions between GDD and mean temperature, and GDD and initial TL (most likely model $R^2 = 0.89$). The results of this study provide the first long-term abundance estimates for juvenile Atlantic Sturgeon in the southeastern United States and increase our understanding of juvenile Atlantic Sturgeon biology.

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List of Symbols and Abbreviations

AIC*c*	Second order Akaike Information Criterion
ASMFC	Atlantic States Marine Fisheries Commission
BIC	Bayesian Information Criterion
CI	Confidence interval
df	Degrees of freedom
FL	Fork length
GDD	Growing degree days
N	Superpopulation size
NOAA	National Oceanic and Atmospheric Administration
PIT	Passive integrated transponder
p	Capture probability for POPAN open population model
pent	Probability of entry into the population for POPAN open population model
r	Correlation coefficient
SCDNR	South Carolina Department of Natural Resources
SD	Standard deviation
TL	Total length
Φ	Apparent survival for POPAN open population model

Chapter 1: Introduction

Fishes typically follow a type III survivorship curve with high mortality early in life (Houde 1994). Small changes in mortality rates of larval and juvenile fish can have substantial effects on year class strength, greatly affecting the abundance and spawning success of the adult population (Houde 1987, 1994). Survival rates of juveniles directly influence recruitment to adulthood; however, the biotic and abiotic factors (which can vary in time and space) affecting recruitment variability in many populations are complex and dynamic (Anderson 1988; Myers et al. 1997). Factors controlling variability in recruitment likely differ between freshwater and marine fishes and may more strongly affect marine fishes during the larval stage and freshwater fishes during the juvenile stage (Houde 1994). Fluctuating abiotic factors such as temperature, dissolved oxygen, and river discharge can greatly affect year class strength (Houde 1994). For example, floods and droughts can affect the ability of many migratory species to move from hatch sites to down river nursery areas (Mion et al. 1998; Jensen and Johnsen 1999). Additionally, anthropogenic factors such as water pollution, loss of critical habitat, and barriers to migration can result in decreased recruitment and the population declines (Guy and Brown 2007).

The overall size and growth of larval and juvenile fish are considered major contributors to recruitment success, because faster growing, larger larvae and juveniles have increased swimming ability, better access to food resources, and are less vulnerable to predation

(Houde 1987; Miller et al. 1988). Hatch date is important for recruitment and first winter survival because larger, early hatched, juveniles are less susceptible to predators and exhibit greater degrees of piscivory (Ludsin and DeVries 1997; Pine et al. 2000). Juveniles are thought to prefer warmer temperatures compared to adults of the same species; however, growth may plateau or even decline when temperatures exceed thermal optima and the metabolic rates of juveniles decrease (Jobling 1996; Jonassen et al. 1999).

Growth and survival of anadromous fishes can be more complex than non-migratory species due to the necessity of movement between freshwater and saltwater (Stein et al. 2004). Once individuals reach sexual maturity, anadromous species will begin migrations from the ocean or estuaries into freshwater habitats when they are ready to spawn. The eggs that are fertilized will hatch and larvae and juveniles mature and grow within the freshwater environment until they are ready to begin their migration into the ocean, joining the adult population. Having a natural flow regime and its specific hydrologic components such as magnitude, frequency, timing, duration, and rate of change of flows can be critical to successful spawning and juvenile survival of anadromous fishes (Poff et al. 1997). For example, timing of spawning for spring cohorts of adult Atlantic Sturgeon (*Acipenser oxyrhynchus oxyrhynchus*) is positively related to lagged discharge in the Savannah River, GA (Vine et al. 2019). Furthermore, some anadromous fishes rely on seasonal peaks of river discharge to carry their larvae to optimal nursery areas (North et al. 2005). During this transportation process, abiotic factors such as water mixing and high or low river discharge can carry larvae and small juveniles to areas where they are unable to survive, potentially affecting year-class strength (Vinagre et al. 2009).

Therefore, timing of spawning migration is key to survival of larvae (Jensen and Johnsen 1999).

The Atlantic Sturgeon is an anadromous fish known to travel substantial distances within its range along the East Coast of the United States and Canada (Hatin et al. 2002; Stein et al. 2004; Dadswell 2006). Sturgeons are anatomically primitive fishes having a heterocercal tail, posteriorly placed dorsal fin, and three rows of bony plates or “scutes” along their body (McCord 2005). Among Atlantic Sturgeon, males mature between ages 5 and 20 and females between ages 7 and 30 , dependent on geographic location (Smith 1985). Populations of Atlantic Sturgeon in the southern part of their range have shorter life spans (25–30 years) and reach smaller maximum sizes (NOAA 2022) compared to populations in the northern portion of range where individuals can live up to 60 years. On average, southern populations of Atlantic Sturgeon migrate for spawning at 1–3 year intervals (Hager et al. 2020; Kahn et al. 2021). Additionally, greater energetic costs of eggs compared to sperm results in females spawning less frequently than males (Smith and Clugston 1997). In several coastal river systems, Atlantic Sturgeon spawn in the spring and fall within the same river system (i.e., dual spawning; Balazik and Musick 2015), creating separate spring and fall hatched juvenile cohorts. Genetically distinct dual spawning runs have recently been documented in the Ogeechee River, GA, Edisto River, SC, Great Pee Dee River, SC, and James River, VA (Balazik and Musick 2015; Farrae et al. 2017; White et al. 2021). Southern cohorts of Atlantic Sturgeon are observed to initiate spawning migrations in the spring in February or March at water temperatures 16–18°C and in the fall between May and October at water temperatures 24–29°C

(Ingram and Peterson 2016; Vine et al. 2019). Captures of adult Atlantic Sturgeon before or recently after a spawning event in the Edisto River, SC, occurred at ~13°C in the spring and 17–18°C in the fall (Collins et al. 2000). During spawning events, adult sturgeon release eggs over hard bottom substrate within the channel or off-channel habitats (Scott and Crossman 1976). Once sturgeon eggs hatch, the larvae move downstream towards nursery habitats located near the head of tide (Bahr and Peterson 2016). In southern rivers, juveniles forage over sand and mud substrates, feeding on small crustaceans, worms, and mollusks (Smith and Clugston 1997; NOAA 2022). Juvenile Atlantic Sturgeon remain in riverine and estuarine habitats until they reach ages 1–3, at which time they begin to migrate offshore into the marine areas occupied by the adult population (Bahr and Peterson 2016). Juveniles are considered fully recruited to the population and reside alongside the adults at ages 2–6, dependent on location (Dovel and Berggren 1983; Hilton et al. 2016).

Atlantic sturgeon were once widely abundant, serving as a food source and item of commerce for Native Americans and early European settlers in the 1600s and 1700s (Smith and Clugston 1997; NOAA 2022). In South Carolina, the Atlantic Sturgeon commercial fishery was established in the 1870s by Swedish immigrants primarily in Winyah Bay and the Edisto River (Hilton et al. 2016). Adult sturgeons were harvested during spring spawning migrations for meat, eggs (caviar), and oil (NOAA 2022). For example, in 1887 nearly 3 million kg of Atlantic Sturgeon were reportedly caught in the United States, and in 1897 South Carolina produced its highest annual catch of 190,000 kg of meat and 32,000 kg of caviar (Hilton et al. 2016; NOAA 2022). Beginning in the

1970s South Carolina catch-per-unit-effort began to decline (Hilton et al. 2016), and the commercial fishery was closed in 1985. In addition to range-wide population declines of Atlantic Sturgeon through directed fishing, bycatch in commercial fishing gear, including set and drifted gill nets, have also caused substantial mortality (Stein et al. 2004). Historical landing data of sturgeons were often inaccurate and lacked critical details, but today most subpopulations are estimated to occur at only a fraction of their historical levels (ASSRT 2007; NOAA 2022).

Alteration, loss, and degradation of Atlantic Sturgeon spawning and nursery habitats have also contributed to decline of their populations. Natal river systems such as the Savannah River, GA, James River, VA, and the Hudson River, NY, include some of the country's largest trade ports, industrial plants and shipping yards, which increase water temperature and decrease dissolved oxygen (Austin 2012; Bahr and Peterson 2016; Breece et al. 2021). To accommodate large cargo carriers and cruise ships, sections of main river channels have been dredged deeper, reducing water quality and degrading nursery habitat (Diaz 1989; Bahr and Peterson 2016). Records of lethal ship strikes have also increased over time at rates higher than expected and most often occur in narrow channels with substantial vessel traffic (Brown and Murphy 2010; Balazik et al. 2012; Bahr and Peterson 2016). Additionally, dams and impoundments have restricted access to historical spawning sites in rivers including the Savannah River, GA, Congaree River, SC, Connecticut River, CT, Merrimack River, NH, and the St. Lawrence River, Québec (Hoover 1938; Galligan 1960; Leland 1968; Murawski and Pacheco 1977). For example, Atlantic Sturgeon do not have access to 90% of the historical spawning habitat in the

Savannah River (NMFS 1998). When an impoundment blocks access to a free-flowing river, females will migrate as far upstream as they can but may spawn in unsuitable areas or even choose not to spawn, despite their internal drive to reach historical spawning areas (Kynard 1997).

As a result of the cumulative effects of fishing, boat strike mortality, and habitat degradation and loss, populations declined, and the United States commercial Atlantic Sturgeon fishery was closed in 1998 (NOAA 2018). Amendment 1 to the Atlantic States Marine Fisheries Commission (ASMFC) management plan placed a coast-wide moratorium on harvest of the species for 40 years beginning in 1998 (McCord 2000) and the Atlantic Sturgeon was listed under the Endangered Species Act (ESA) in 2012 by the National Oceanic and Atmospheric Association. Under the ESA, five distinct population segments (DPSs) were designated for Atlantic Sturgeon: Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic (NMFS 2007). All DPSs are listed as endangered except the Gulf of Maine DPS, which is listed as threatened (NMFS 2007). The Carolina and South Atlantic DPSs have defined four factors that are critical for species recovery: hard bottom substrate in low salinity waters, zones of downstream gradient with transitional salinity and soft substrate, absence of physical and anthropogenic barriers from spawning sites, and water conditions of appropriate temperature and dissolved oxygen (Wortzel 2017). With an interim outline of a Fishery Management Plan in place, the National Oceanic and Atmospheric Administration aims to improve understanding of population dynamics, distribution, abundance, trends, and structure, and continue research and monitoring of human-caused mortality (NOAA

2018). Initial steps towards conservation of extant populations also include research on fish passage designs that would allow spawning at historical grounds and standardizing methods for determining abundance indices. Long term recovery goals include region-wide initiatives to improve water quality and access to historical habitats by implementing fish passage (NOAA 2018). Sturgeon research efforts for the South Atlantic DPS have focused on estimating abundance of juvenile and adult sturgeons to evaluate their distribution, population status, and recruitment levels (Collins et al. 2002; Schueller and Peterson 2010; Bahr and Peterson 2016; Fox and Peterson 2019).

My studies focused on abundance and growth of juvenile Atlantic Sturgeon in the Edisto River, SC. The Edisto River, located in the ACE (Ashepoo-Combahee-Edisto) basin watershed, is one of the longest undammed blackwater rivers in the United States and is known to host both spring and fall spawning runs (Beasley et al. 1996; McCord 2005). Atlantic Sturgeon in the Edisto River have been sampled since 1994, yet the population is still poorly understood (McCord 2005). For populations to recover, research efforts must focus on the known threats to sturgeon populations along with expanding knowledge on juvenile sturgeon recruitment in southern rivers (Collins et al. 2002; Schueller and Peterson 2010). My study provides one of the first population estimates of juvenile Atlantic Sturgeon in South Carolina using long term capture-recapture data. Estimating abundance and measuring year class strength close to time of recruitment is critical for obtaining accurate indices of recruitment and understanding early life history (Stige et al. 2013). Research efforts to identify recruitment mechanisms and juvenile growth can provide a baseline for assessing trends in juvenile early life history for future surveys. My study also provides baseline data for overall growth and growth rates of age-0 Atlantic Sturgeon and how they relate to biological and environmental factors.

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Chapter 2: Abundance and growth of juvenile Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the Edisto River, SC

Abstract

Information on abundance and body growth are important for understanding the status and health of populations, and this information can be used to guide and monitor conservation and recovery efforts for species of conservation concern. The Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) is an anadromous fish native to the Atlantic coast of the United States and Canada. Due to overfishing and habitat degradation, population levels declined, and Atlantic Sturgeon were placed on the Endangered Species list in 2012. Although there is substantial research on adult Atlantic Sturgeon, knowledge about their early life history is lacking. The objective of this study were to estimate annual abundance of juvenile Atlantic Sturgeon in the Edisto River, SC, over a 25-year period. I also estimated growth and growth rates of juveniles, what environmental factors were related to growth and growth rate, and if growth differed between seasonal cohorts. Drifted gill nets were used to sample juvenile Atlantic Sturgeon in the Edisto River, SC from 1994–2019. I estimated the number of juveniles in the river during May through September of each year based on daily and monthly encounter histories using the POPAN version of the Jolly-Seber open population model. I calculated average growth per day and growing degree days for each individual and a suite of linear models were used to determine what environmental factors (mean temperature, growing degree days [GDD], and discharge) and biological factors (total length at initial capture and seasonal cohort) were related to growth rate and overall growth between captures. Juvenile (≤1050 mm) abundance averaged 845 individuals (range = 333–1,343, 95% CI = 644–1,046) based on the average of daily and monthly encounter history population estimates. Growth rate was weakly related to the environmental and biological variables investigated (most likely model $R^2 = 0.32$). Absolute growth between captures was related to initial TL at capture, mean temperature, discharge, GDD, seasonal cohort, and the interactions between GDD and mean temperature, and GDD and initial total length (most likely model $R^2 = 0.89$). The results of this study provide the first long-term abundance estimates for juvenile Atlantic Sturgeon in the southeastern United States and increase our understanding of juvenile Atlantic Sturgeon biology.

Introduction

The Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) is a long-lived (up to 60 years), anadromous species that spawns in rivers along the east coast of the United States and Canada (Stein et al. 2004). On average, Atlantic Sturgeon have spawning periodicities of 1–3 years (Hager et al. 2020; Kahn et al. 2021), and the timing of spawning is variable across systems, with some rivers only having a spring (e.g., Delaware River, DE, and Hudson River, NY) or fall (e.g., Satilla River, GA) spawning group and other rivers having both spring and fall spawning groups (e.g., Ogeechee River, GA, Edisto River, SC, Great Pee Dee River, SC, James River, VA; Balazik and Musick 2015; Farrae et al. 2017; White et al. 2021). Once sturgeon eggs hatch, larval sturgeon move downstream towards nursery habitats located near the head of tide (Bahr and Peterson 2016). Juvenile Atlantic Sturgeon remain in estuarine habitats until they reach ages 1–3 and then begin to migrate offshore into the marine areas occupied by the adult population (Bahr and Peterson 2016).

Atlantic Sturgeon were once widely abundant, serving as a food source for Native Americans and early settlers (Smith et al. 1984). Beginning in the late 19th century, commercial fisheries began harvesting adult sturgeons on a large scale for meat, oil, and caviar (Smith and Clugston 1997). Dams and habitat degradation and loss further added to the decline of Atlantic Sturgeon populations (Bahr and Peterson 2016, McCord 2005; Schueller and Peterson 2010). As a result, Atlantic Sturgeon were listed under the Endangered Species Act in 2012 (NMFS 2012).

Abundance of fish in a population and growth of individuals in the population are used to assess population health and better understand population dynamics. Natural disturbances and anthropogenic changes in an environment can alter fish populations, therefore understanding trends in abundance and growth are critical for conservation and management decisions (Pope et al. 2010). Increasing the understanding of population dynamics, distribution, and abundance, and developing standardized methods to create reliable abundance indices, are primary goals of the Atlantic Sturgeon interim recovery plan under the Endangered Species Act (NOAA Fisheries 2012). Similarly, the Atlantic States Marine Fisheries Commission listed development of standardized methods for abundance indices for adults and juvenile Atlantic Sturgeon as a high priority (ASMFC 2017). Juvenile Atlantic Sturgeon abundance analyses have typically been based on short-term sampling data (≤3 y; e.g., Schueller and Peterson 2010; Bahr and Peterson 2016). Estimating the abundance of juvenile Atlantic Sturgeon based on long-term capture-recapture data can be used to make more robust comparisons across populations and detect trends within a population over time.

Growth of individuals in a population is an important biological characteristic that can be used to assess fish population health and suitability of habitat. The overall size and growth of juvenile fish are considered major contributors to survival and recruitment success because faster growing, larger juveniles have increased swimming ability, better access to food resources, and are less vulnerable to predation (Houde 1987; Miller et al. 1988; Ludsin and DeVries 1997). Many environmental and biological factors can affect growth including water quality, nutrition, and competition (Viadero 2005). Additionally, growth rates of fishes are often affected by the ambient temperature (Bacon et al. 2005; Chezik et al. 2014; Markin and Secor 2020). The cumulative thermal conditions an individual experiences can be quantified using growing degree days (Neuheimer and

Taggart 2007; Markin and Secor 2020). The growing degree day (GDD) is the time integral of the daily temperatures a fish experiences greater than a species-specific minimum temperature needed for growth to occur (Neuheimer and Taggart 2007; Chezik et al. 2014), which is suggested to be ~4°C for juvenile Atlantic Sturgeon (Markin and Secor 2020 based on Niklitschek and Secor 2009). The sum of positive degree day values (thermal energy experienced) can be used to describe relationships between temperature and growth for juvenile Atlantic Sturgeon (Chezik et al. 2014). Although several juvenile Atlantic Sturgeon studies have quantified length at age (Schueller and Peterson 2010; Balazik et al. 2012; Bahr and Peterson 2016; M. Takacs, unpublished data), environmental effects on growth are not well understood. Determining growth rates and environmental and biological factors that may affect growth will improve our understanding of Atlantic Sturgeon early life history.

The South Atlantic distinct population segment (DPS) of Atlantic Sturgeon ranges from southern South Carolina to northern Florida and includes the Edisto, Combahee, Broad-Coosawatchie, Savannah, Ogeechee, Altamaha, Satilla, and St. Marys rivers (NMFS 2007). Juvenile length-at-age and abundance has been estimated in several Georgia rivers including the Altamaha (Schueller and Peterson 2010), Savannah (Bahr and Peterson 2016), and Ogeechee (Farrae et al. 2009); however, recent published data on juvenile Atlantic sturgeon in SC rivers is more limited. The Edisto and Combahee rivers support the third largest spawning subpopulation across all five distinct population segments (NOAA Fisheries 2012) and the Edisto River has two genetically distinct seasonal spawning runs (spring and fall; Farrae et al. 2017; White et al. 2021). Juvenile Atlantic Sturgeon have been sampled and individually marked annually in the Edisto River by the

South Carolina Department of Natural Resources since 1994, thus providing the unique opportunity to investigate abundance and growth of juvenile sturgeon using long-term data. Therefore, we used a 25-year data set from the Edisto River, SC, to investigate four questions related to abundance and growth of juvenile Atlantic Sturgeon: (1) How many juvenile Atlantic Sturgeon occupy the sampling area during May through September? (2) Are abundance estimates related to water quality?, (3) Are there differences in growth between seasonal cohorts of juvenile Atlantic Sturgeon (fall vs. spring spawned)?, and (4) What environmental factors influence juvenile growth rates and overall growth? The results of this study provide one of the first long-term abundance estimates for juvenile Atlantic Sturgeon in the United States and increase our understanding of juvenile Atlantic Sturgeon growth.

Methods

Fish Collection – Sampling was conducted annually (1994–2019) using drifted gill nets in the Edisto River, SC, near Jehossee Island (river kms 27–28; Figure 1). This section of river was chosen for sampling because it was the only straight and obstruction free section upstream of the salt wedge that was feasible for drift netting. Sampling occurred throughout the year (with a concentration of sampling during May through September). However, the timing of sampling, effort, and mesh sizes varied across the study period. From 1994–2003 effort ranged from 173–538 drifts per year, and mesh sizes ranged from 54–152 mm. During 2004–2019 sampling was standardized to five days per month from May–September with an average of five drifts per day. For the purposes of this study, captures for all years were standardized to only include individuals caught in 137 m dual panel gill nets, with a 4 m deep top panel consisting of 140 mm stretch mesh and a 2 m deep bottom panel consisting of 64 mm stretch mesh.

Growth analyses included fish captured from January 1st through October 17th (day-of-year 290) to maximize the range of temperatures and growing degree days experienced, while still allowing for separating cohorts and year classes based on plots of length at day of year. Population models only included fish captured during May–September so estimates could be compared across years. Captured Atlantic Sturgeon were weighed (g), and total length (mm TL), and girth (mm) were measured to the nearest mm. Sturgeon were then tagged with Biomark Model HPT12 (12.5 mm, 134.2 kHz ISO FDXB) passive integrated transponder (PIT) tags using a syringe-type injector (McCord 2000; Biomark, Boise, ID). Sturgeon ≤200 mm FL were tagged under the first post-cranial dorsal scute, and individuals >200 mm FL were tagged in the dorsal musculature below the base of the dorsal fin.

Abundance estimates - Previous studies of juvenile Atlantic Sturgeon in the southeastern United States have made age specific population estimates (ages 1–3+) for individuals up to 1,050 mm TL (Farrae et al. 2009; Schueller and Peterson 2010; Bahr and Peterson 2017). Age data were not available for fish collected in this study and therefore we based our annual population estimates on capture histories of individuals ≤1,050 mm TL (~900 mm FL) to make comparisons with other studies on juvenile Atlantic Sturgeon. Atlantic Sturgeon ≤1,050 mm TL will be considered and referred to as “juveniles” here. I used the ‘POPAN’ version of the Jolly-Seber open population model (Schwarz and Arnason 1996) in ‘RMark’ (Laake 2013, version 2.2.7; program Mark available from http://www.phidot.org/software/mark/, version 9.x) within Rstudio (RStudio Team 2020, desktop version 1.1.463) to estimate the superpopulation (parameter N in POPAN) of juveniles annually. Here, the superpopulation is an estimate of the total number of juveniles that occupied the sampling area during the May–September sampling period annually. In addition to a parameter for the superpopulation, POPAN includes parameters for apparent survival (Φ), capture probability (p), and probability of entry into the population (*pent*). The POPAN model assumes that sampling is instantaneous, and individuals retain their tags throughout the study. The model also assumes that tagged and non-tagged individuals are equally likely to be captured and survive to the next sampling occasion. Lastly, the model assumes that the study area remains constant for the duration of the study and any emigration from the study area is permanent. Pollock and Aplizar-Jara (2005) suggest that sampling events be as short as possible to limit the potential for heterogeneity of survival probabilities across individuals. Therefore, I used daily and monthly encounter histories (see below) to minimize the probability of heterogeneity in survival probabilities. Passive integrated transponder retention rates are high for Atlantic Sturgeon (100% within a sampling season; Kahn et al. 2019) and closely related Gulf Sturgeon (*Acipenser oxyrinchus desotoi*; ~90%; Clugston 1996) and PIT tags are the standard tag used in sturgeon studies (Kahn and Mohead 2010). The mobility of juvenile Atlantic Sturgeon facilitates mixing of tagged and untagged individuals and thus increased the probability that tagged and untagged individuals had an equal chance of being captured. Survival rates of juvenile Atlantic Sturgeon are suggested to be high despite capture using gill nets and surgical implantation of transmitters (Fox and Peterson 2019), therefore I had no reason to suspect differential survival between marked and unmarked individuals. The sampling area remained between Edisto River km 27–28 throughout the entire duration of the study; however, given the relatively small area of the study reach, temporary emigration undoubtedly occurred. Although temporary emigration occurred it was most likely to be random and therefore should not appreciably affect my estimates.

Previous studies have assumed closure and used closed population models to estimate the abundance of juvenile Atlantic Sturgeon, but I chose to use an open population model because (1) the Edisto River is an open system and juveniles are known to frequently travel within and between rivers (Smith 1982), (2) The annual sampling duration (5 months) in my study was longer than previous studies in other systems (Farrae and Schueller 2009; Schueller and Peterson 2010; Bahr and Peterson 2016), and (3) my sampling area was much more restricted than in other systems.

I estimated May–September superpopulation sizes and 95% confidence intervals each year based on daily and monthly encounter histories. For daily encounter histories, fish were recorded as captured or not captured for every day that sampling occurred. For monthly encounter histories, fish were recorded as captured or not captured for each of the 5 months that sampling occurred. A suite of time dependent and constant parameter models was then fitted for daily and monthly encounter histories and the most likely models for each year were selected using AIC_c (Akaike 1973). Time dependent parameter models allow each parameter to vary for each sampling occasion, whereas time constant models do not allow parameter estimates to vary across sampling occasions. How encounter histories are entered can affect population estimates, so I examined annual abundance estimates and calculated average abundance across years several ways. First, I examined abundance estimates over time and calculated average abundances for estimates (separately for daily and monthly encounter histories and then averaged between estimates from daily and month encounter histories) based on all years that there was enough data to produce a population estimate. These annual abundance estimates were assumed to reflect general trends in the population specifically within the sampling area during the sampling period but may or may not be reflective of the greater Edisto River (e.g., due to avoidance of the sampling area based on environmental conditions; see Discussion). Because estimates based on this criterion reflected general trends in abundance within the 1 km fixed sampling reach, they could be used to investigate the relationship between environmental conditions (e.g., salinity; see below) and abundance within the sampling area. Next, I examined population estimates and calculated average abundance (separately for daily and monthly encounter histories) based on years I considered to have reliable estimates, which were defined using the following criteria: (1) years with sufficient data to produce a population estimate, (2) years with estimates greater than the total number of individuals used for population analysis, (3) years with estimates that produced a standard error greater than zero, and (4) years with estimates that produced confidence intervals. Because juvenile sturgeon tend to concentrate and move about in areas with salinity of 0–10 and below the head of tide during the summer, population estimates from years that were deemed reliable based on the criteria defined above were assumed to be reflective of the number of individuals that were in the Edisto River, both within and outside the sampling area, at some point during the sampling period (i.e., sturgeon were concentrated in and around the sampling area and therefore sampling a 1 km fixed location was likely adequate for estimating abundance in the Edisto River and not just the sampling area). Finally, I averaged daily and monthly estimates across years for years where estimates based on the two encounter histories differed by <15%.

I examined relationships between abundance estimates (average of daily and monthly estimates for years where there were enough data to produce abundance estimates) and mean discharge (m^3/s) and salinity during the sampling period. I used mean daily discharge data from the Edisto River near Givhans, SC (USGS 02175000 EDISTO RIVER NR GIVHANS, SC; Available at waterdata.usgs.gov), and salinity data from the closest water quality gauge to the sampling site (ACEFCWQ-Fishing Creek, 6.2 rkm upriver) to calculate mean salinity and discharge during the May through September sampling period for each year. Because Fishing Creek was upriver from the sampling location salinity values were likely greater at the sampling location than Fishing Creek, but still reflective of annual trends in salinity. Salinity data are not available for Fishing Creek from 1995–2002, so I used linear regression to develop a model (in RStudio) to predict Fishing Creek salinity using discharge data from the Edisto River at Givhans, SC and salinity data from Saint Pierre Creek, SC (26 rkm downriver) as potential predictors (Fishing Creek and St Pierre Creek, SC data retrieved from the ACE Basin National Estuarine Research Reserve website, available from www.dnr.sc.gov/marine/NERR/long_term_monitoring.html). Next, I used AIC*c* to identify the most likely model, and then predicted mean daily salinity for each year with the following equation:

$$\text{Fishing Creek salinity} = -20.84 + 1.08(\text{St. Pierre Creek salinity}) + 0.00029(\text{discharge}) - 0.00014(\text{St. Pierre Creek salinity} \times \text{discharge})$$

Observed and predicted mean daily salinities for Fishing Creek from 2003–2019 were correlated (Figure 2; *r*: 0.72). I then averaged predicted mean daily discharge and salinity for each year to calculate the mean annual values for years where salinity data were missing. Next, I created a plots of annual discharge and salinity to visualize trends over time (Figure 3). Finally, scatterplots of population estimates vs. mean annual discharge and salinity were created and Pearson correlation coefficients were calculated to examine relationships between population estimates and environmental variables.

Growth Analyses – To investigate growth of assumed age-0 Atlantic Sturgeon, I first created length at day-of-year scatterplots based on total length at initial capture (or only capture). Individuals in their first year of life are predominately ≤600 mm TL, and are considered and referred to as “age 0” here. I visually examined length at capture data each year from 1994–2019 and assigned age-0 individuals to seasonal cohorts (fall or spring) based on noticeable length groupings in plots of length at day of year (Figure 3). Individuals from the fall cohort (larger individuals in Figure 3) started to be caught during late winter through early spring at 5–6 months old, whereas individuals from the spring cohort started to be caught in early summer at 2–3 months old. Examining plots for each year made it easier to see distinct separate seasonal cohorts without overlap in sizes (which occurs when all years are examined together). Genetic data allowing for assignment to a spring of fall cohort based on molecular techniques (Farrae 2017; Farrae, unpublished data) were available for a subset (n = 1,281) of individuals and thus provided a way to validate our visual method of assigning individuals to each seasonal cohort; only 0.7% (n = 9 out of 1,284) of individuals were incorrectly assigned. Visual examination of scatterplots suggested length at day of year followed a polynomial growth curve, thus I used linear regression and the poly() command in Rstudio (2019) to fit orthogonal polynomial growth curves for each cohort.

I investigated potential relationships between total growth (mm) or growth rate (mm day^{-1}) of age-0 individuals between captures as functions of environmental and biological characteristics using a subset of individuals that were also recaptured (within a sampling season) during the study. Total growth between captures was investigated as a function of mean temperature, growing degree days, cohort, initial length at capture, and discharge. I investigated growth rate as a function of mean temperature, discharge, initial length at capture, and seasonal cohort. No age-0 sturgeon were recaptured data during 1994 or 1995 and therefore these analyses focused on 1996–2019. To minimize the effects of likely measurement error I removed 2% of individuals (n = 11) with a negative growth rate or a growth rate greater than 3 mm/day. I used temperature data from the Fishing Creek water quality gauge for 2003–2019, but similar to salinity data described above, I needed to use the relationship between mean daily temperature (°C) for Fishing Creek, SC, and mean daily temperature at St. Pierre Creek, SC (ACESPWQ), to predict mean daily temperature at Fishing Creek, SC (Fishing Creek and St Pierre Creek, SC data retrieved from the ACE Basin National Estuarine Research Reserve website, available from www.dnr.sc.gov/marine/NERR/long_term_monitoring). I used linear regression in RStudio to develop a model to predict Fishing Creek temperature using discharge and Saint Pierre Creek temperature as potential predictors. Next, I used AIC*c* to identify the most likely model and then predicted mean daily temperature (ºC) for each year with the following equation:

$$\text{Fishing Creek temperature} = -0.59 + 1.01(\text{St. Pierre Creek temperature})$$

Observed and predicted water temperature for Fishing Creek from 2003–2019 were correlated (Figure 2; daily *r*: 0.98). I calculated temperature and discharge for each individual as the average value between initial capture and recapture. Growing degree days for a single day were calculated as:

$$DD = ((T_{Max} + T_{Min})/2) - T_0,$$

and then summed over the time between captures (inclusive of capture dates). T_{Max} and T_{Min} were the maximum and minimum daily water temperatures and T_0 was the base temperature threshold (Chezik et al. 2013). Based on laboratory experiments of thermal limits for growth (Niklitschek and Secor, 2009), the baseline temperature for Atlantic Sturgeon was set to 4°C following Markin and Secor (2020). Both mean temperature and GDD were included in the analysis of total growth because GDD is a function of both temperature and time. Therefore, two fish could have equal GDDs based on different thermal conditions (e.g., shorter period of time at warmer temperatures or longer period of time at cooler temperatures), which may affect growth. However, accumulated GDD was not included in the growth rate analysis because growth rate inherently accounts for time. Discharge was included because it could affect salinity, energy used for swimming, and prey availability. Finally, initial total length and cohort were included because I wanted to know if growth or growth rate decrease as length increases or if it differs between seasonal cohorts. For each response variable (growth or growth rate), I fit a suite of linear regression models in Rstudio (2020) and the most likely models were selected based on Bayesian Information Criterion (BIC; Schwartz 1978). The suite of models allowed for all possible combinations of variables and their two-way interactions. Prior to fitting models, I calculated variance inflation factors using the car package vif()

command in Rstudio (2019) to determine if multicollinearity was an issue in my set of predictor variables; multicollinearity was not an issue because variance inflation factor values were <5 (Tay 2017).

Finally, I investigated if annual GDD for spring and fall spawned Atlantic Sturgeon changed over the study period or if it differed between cohorts. First, I calculated the average number of accumulated GDD for each cohort and year and then calculated the average for each cohort across all years. Annual GDD was based on assumed hatch dates of October 1 for the fall cohort and March 15 for the spring cohort (E. Waldrop, SCDNR, personal communication). Finally, I used multiple linear regression at an alpha level of 0.05 to investigate if there was a trend in average annual GDD during 1995–2019 for each cohort.

Results

Netting efforts captured 6,410 Atlantic Sturgeon during 1994–2019 (Figure 4) with an average total length of 624 mm (range = 174–2102 mm; Table 1). Of these, 4,944 individuals were ≤1,050 mm and used to estimate juvenile abundance (Figure 4). During May–September from 1996–2019, monthly average water temperature in the study area was 27.3°C (range = 21.4–30.4 °C, SD: 0.7), average salinity was 11.0 (range = 1.3–30.3, SD: 4.6), and average discharge was 38.1 m^3/s (range = 6.71–246.8 m^3/s, SD: 31.5).

The most likely POPAN model varied across years and was dependent on whether daily or monthly encounter histories were used. Using encounter histories that could produce population estimates over the 25-year study, I estimated that the annual juvenile Atlantic Sturgeon superpopulation averaged 900 individuals based on daily encounter histories (range = 15–2,375, 95% CI = 628–1,172), 664 individuals based on monthly encounter histories (Table A1; Figure 5; range = 15–2,478, 95% CI = 411–917), and 783 individuals (range = 15–2,209, 95% CI = 548–1,017) based on the average of daily and monthly encounter histories. Population estimates from years considered reliable averaged 1,073 individuals (range = 6–2,530, 95% CI = 792–1,345) based on daily encounter histories with five unreliable years removed, 859 individuals (range = 100–2,471, 95% CI = 581–1,137) based on monthly encounter histories with seven unreliable years removed, and 845 individuals (range = 333–1,343, 95% CI = 644–1,046) based on twelve years where daily and monthly estimates differed by <15%. Discharge had a positive relationship (Figure 6; r: 0.45) with population estimates over the 25-year study period, but salinity had a negative relationship (Figure 6; r: -0.58).

Two thousand one hundred fifty-seven age-0 sturgeon (174–680 mm) were used to fit length at day-of-year growth curves. Inspection of length at day-of-year scatterplots suggested that juvenile Atlantic Sturgeon from both cohorts followed a 2nd degree polynomial growth curve with a decrease in growth rate during summer months (Figure 3). Four hundred eighty-nine age-0 sturgeon (182–627 mm) were used to calculate growth rate and overall growth. Overall growth and growth rate between captures for recaptured individuals did not differ between fall and spring cohorts (term for seasonal cohort not included in the most likely model). The fall cohort had an average growth rate of 0.86 mm d^{-1} (0.78 SD) during March–November (with most data from May–September) and the spring cohort had a growth rate of 0.87 mm d^{-1} (0.94 SD) during June through November. On average, juvenile Atlantic Sturgeon within the Edisto grew 0.04 mm GDD^{-1}, and the average number of accumulated GDD was 6002 per year (fall cohort

= 6004 GDD, spring cohort = 6000 GDD; Figure 7). On average, GDD increased by 19.1 per year for the fall cohort ($R^2 = 0.36$, $t = 2.07$, $df = 22$, $P = 0.0019$) and increased by 17.2 for the spring cohort ($R^2 = 0.29$, $t = 2.07$, $df = 22$, $P = 0.0063$) during 1995–2019. The most likely model for growth rate included terms for mean temperature and initial length at capture (Table 2; Figure 8). Mean temperature was negatively related to growth rate, and growth rate decreased by 0.09 mm day^{-1} for every 1°C increase in mean water temperature between captures (with initial length held constant). Initial length was negatively related to growth rate, and growth decreased by 0.03 mm day^{-1} for every 25 mm increase in initial length (with mean temperature held constant). The most likely model for overall growth included terms for accumulated GDD, mean temperature, initial length, and the interactions between accumulated GDD and mean temperature, and accumulated GDD and initial length (Table 3; Figure 9; Figure 10). As temperature increased, the positive effect of accumulated GDD on overall growth decreased (Figure 10). Similarly, larger size at initial capture was associated with a declining positive effect of accumulated GDD on overall growth (Figure 10).

Discussion

I estimated abundance and growth for juvenile Atlantic Sturgeon in the Edisto River using long term capture-recapture data. My population estimates are likely conservative in some years due to the small 1 km sampling area and changes in salinity in the sampling area within and across years. I observed that population estimates had a negative relationship with salinity and this relationship was stronger that what was observed for discharge. Even though age 0–1 Atlantic Sturgeon primarily remain within their natal habitats, they often move within the system following the freshwater-saltwater interface (Bahr and Peterson 2016). In the Ogeechee, Satilla, and Altamaha rivers of GA, juvenile Atlantic Sturgeon (~300–450 mm) had a more restricted range of habitat during the summer compared to other seasons and occupied areas of 0–10 salinity downstream of the head of tide (Fox and Peterson 2019). Similarly, in the Hudson River, NY, juvenile Atlantic Sturgeon were found in salinities of 0–5 in the summer but used habitats with salinities up to 18 in the winter (Bain et al. 2000). Since the sampling site in my study was fixed due to physical obstructions in the water (i.e., woody debris) which limited the ability to sample further upstream, the susceptibility of Atlantic Sturgeon to capture likely varied based on their use of the sampling area as a function of salinity levels. Absence of rain in a coastal rivers can reduce discharge, causing salinity levels to rise and the freshwater-saltwater interface to migrate upstream. Long term average median discharge was 40 m^3/s (range = 12–145 m^3/s) during May–September in the Edisto River, but median discharge was <40 m^3/s for 18 of the 25 years in my study, resulting in salinity levels of 10–28 at the study site during some years (Figure 11). Therefore, low abundance estimates during periods of low discharge and high salinity may not be indicative of low abundance in the Edisto River, but instead, avoidance of the study area due to high salinity levels, resulting in reduced catch rates.

My population estimates likely included juveniles from systems other than the Edisto River, because Atlantic Sturgeon are known to frequently travel between neighboring estuaries and rivers (Peterson et al. 2008). Juveniles > age-1 are commonly recaptured in rivers adjacent to where they were initially tagged. For example, in 2021, 18 out of 482 juvenile Atlantic Sturgeon <1,200 mm captured in the Winyah Bay system were previously tagged in the Edisto (3), Altamaha (7), or Savannah (8) rivers (M. Takacs, unpublished data). Similarly, juveniles from the Hudson River have been recaptured in rivers from Massachusetts to North Carolina (Dovel and Berggren 1983).

Despite our limited capture data, my estimates are smaller yet comparable to several other studies that included individuals of the same or similar size classes in other rivers. In the Altamaha River, GA, during 2004–2007, Schueller and Peterson (2010) estimated an annual average abundance of 2,257 juveniles (350–1050 mm). In the Savannah River, GA, during 2013–2015, Bahr and Peterson (2016) estimated there was an average annual abundance of 1,475 juveniles (300–1,050 mm). Similarly, ongoing research in the Winyah Bay estuary of SC resulted in an estimated abundance of 1,795 juveniles (189–1,050 mm) during 2021 (M. Takacs, unpublished data). Population estimates among all rivers differed by <1,500 individuals despite differing sampling years, time and season of sampling, and sampling protocol.

Although mean temperature and initial length were identified as factors related to growth rate, the most likely model only explained 32% of variation in growth rate and scatterplots indicated weak relationships between these variables and growth rate. The relatively weak relationship between growth rate and environmental variables may partly be explained by the coarse resolution of environmental data used in this analysis and limited variability in temperature data (mean temperature between captures was 22-30ºC for the vast majority of fish). Finer resolution data across a wider range of temperatures would allow for better understanding of the relationship between growth rate and temperature in a wild setting. Stronger relationships were observed between the predictor variables and overall growth between captures compared to what was observed for growth rate. I used a linear term to define the relationship between growth and mean temperature between captures; however, fishes have a unimodal relationship between growth and temperature, with peak growth occurring at varying temperatures depending on the thermal guild of a species (Lindmark et al. 2021). Niklitschek and Secor (2009) observed that that juvenile Atlantic Sturgeon growth was strongly related to temperature and fish experienced peak growth at ~20°C. I had limited data on growth at mean temperatures <20°C and preliminary analyses indicated that including a quadratic term to account for the unimodal relationship between temperature and growth did not improve model fit. As initial length increased, increases in GDD resulted in smaller increases in size, suggesting that age-0 sturgeon growth slows as individuals get larger. However, the influence of initial length on growth was less important than mean temperature and may also be due to seasonal changes in food availability.

Interestingly, lengths predicted for a given day of the year based on growth curves differ from lengths predicted from estimated growth rates. For example, by October 1st (day 274), individuals from the fall cohort were estimated to average 512 mm and individuals from spring cohort were estimated to average 324 mm based on growth curves. However, predicting total length at a given day of year results in a substantially smaller estimated size compared to what is estimated based on growth curves. Assuming an assigned hatch date of October 1st for the fall cohort (based on adult spawning migrations in the Edisto River) hatch size of 8 mm (Bath 1981), and growth rate of 0.86 mm day^{-1}, individuals are predicted to average 322 mm by October 1st of the following year. If the spring cohort is assumed to have a hatch date of March 15th and growth rate of 0.87 mm day^{-1}, individuals should reach 182 mm by day October 1st of the same year they hatched. Therefore, my estimated growth rates result in predicted total lengths that are 150 mm less than the mean lengths based on growth curves fitted to length at day-of-year data.

There are two potential (primary) explanations for discrepancies between lengths estimated from growth rates and lengths estimated from growth curves: (1) my assumption that the fish included in the growth analysis were age-0 is incorrect and they were actually age-1 and (2) my growth rates are not representative of growth over the course of a year. I do not believe my assumption about the age of the fish is incorrect and explain below. Several studies of Atlantic Sturgeon in coastal rivers of Georgia suggest that fish collected at similar sizes to assumed age-0 fish in the Edisto River are age 1, based on examination of pectoral fin spines (captured at 19–22 months in late spring through summer). For example, Bahr and Peterson (2016) indicated that age-1, fall-spawned Atlantic Sturgeon (19–21 months old) were 300–509 mm during their May–July sampling period in the Savannah River, GA. Schueller and Peterson (2010) indicated that age-1, fall-spawned Atlantic Sturgeon (20–22 months old) were 350–550 mm during their June–August sampling period in the Altamaha River, GA. Finally, Farrae et al. (2009) indicated that age-1, fall-spawned Atlantic Sturgeon (20–22 months old) were 242–361 mm during their July–September sampling period in the Ogeechee River, GA. Contrary to studies in Georgia rivers, Balazik (Virginia Commonwealth University, personal communication, 2021) followed a known age-0, fall-spawned cohort (2018) from the James River, Virginia, beginning at total lengths of <100 mm to 2 years of life and observed a mean length of 292 mm by June 1st (~8 months old), 424 mm by October 1st (~12 months old), 589 mm by June 1st of the following year (20 months old), and 664 mm by October 1st (24 months old). Although the mean length of James River fish at ~12 months old is smaller than what was observed for the Edisto River fall-spawned cohort, the James River experiences cooler winter water temperatures than the Edisto River, and growth curves for the James River indicate that growth is minimal or ceases during the winter there. If Edisto River fish were age 1 instead of age 0, they would need to be growing substantially slower than fish from the James River, which is unlikely given that mean winter water temperatures in the Edisto River are warm enough (~11ºC) to allow for growth. Examination of the spring cohort also provides evidence to suggest that my assumption about age is correct. I observed that fish from the spring cohort were 172 mm by June 1st (2–3 months old). If they were actually age-1 (14–15 months old), their length at age would be substantially smaller than what has previously been documented for Atlantic Sturgeon (Markin and Secor 2020). Additionally, my growth curve for the spring cohort indicates that average length increases by ~160 mm from June 1 to October 1 (4 months), and thus it is improbable that they would only average 167 mm by 14–15 months old.

I suspect that the Edisto River growth rates estimated from capture-recapture data are biased low and not reflective of growth rates throughout the entire year. Fish included in my growth analysis based on capture-recapture data were primarily at-large during May–September, whereas my growth models (length at day of year) were based on initial captures from January–October. Seasonal growth of fishes is species specific and varies dependent on location. My growth models indicated that growth was greatest in the spring and slower in the summer and early fall, which is likely explained by seasonal variation in water temperature. Summer and early fall water temperatures in the Edisto River are substantially greater (mean summer water temperature during 2003–2019 =

27ºC) than optimal water temperatures for juvenile Atlantic Sturgeon growth (~20ºC; Niklitschek and Secor 2009 [growth measured in weight]). Optimal water temperatures for growth in the Edisto River most commonly occurs during spring and again in late fall, which are periods where I had more limited capture-recapture data compared to late spring through early fall. Therefore, differences in the timing of sampling likely explains differences in lengths estimated from growth rates and lengths estimated from length at day-of-year growth curves.

Finally, the Savannah and Altamaha River studies (Schueller and Peterson 2010; Bahr and Peterson 2016) used sectioned pectoral fin and age-length keys to estimate ages of juvenile Atlantic Sturgeon. Questions about the reliability of age estimates based on pectoral spines and rays complicates my ability to understand growth of juvenile Atlantic Sturgeon. Age data were not available for fish in my study, but examination of fin spines and rays from juvenile Atlantic Sturgeon in the Winyah Bay, SC, system suggest age estimates from these structures during early life may be unreliable or at least variable in reliability across systems.

Variable growth across and within systems, dual spawning, and unknown and likely variable reliability of age estimates based on hard structures make understanding and describing growth of juvenile Atlantic Sturgeon challenging. For example, Sulak and Clugston (1998) caught 11 juvenile Gulf Sturgeon, in the Suwannee River, FL over three years of sampling and they were unable to determine if they were large age-0 spring-spawned fish, small age-1 spring-spawned fish, or average-sized fall-spawned fish. Discrepancies in the current understanding of growth could be resolved by incorporating sampling methods such as small otter trawls, epibenthic sleds, and fine mesh anchor or gill nets to target smaller age-0 fish (<100 mm) than what are caught with larger mesh gill nets that have historically been used for sampling in southeastern U.S. rivers. This would allow biologists to follow a cohort of fish throughout their river residency period and reduce any size-related biases in growth rate estimates. Additionally, sampling could occur throughout the year (where permitted) to better understand seasonal changes in growth and how it may vary across systems. Finally, there is a need for assessing the validity of using fin spines for age estimation of Atlantic Sturgeon during their first two years of life to better understand growth and early life history.

Acknowledgments

I would like to thank the South Carolina Department of Natural Resources and the many employees involved in the collection of the data used in this manuscript. I thank the NOAA Anadromous Fisheries Conservation Act and the Atlantic Coastal Fisheries Cooperative Management Act for research funding. I also thank the Atlantic Coastal Fisheries Cooperative Management Act. I am grateful to Lindsey Bell and Keshav Jagannathan for assisting with statistical analyses.

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TABLE 1: Total capture of Atlantic Sturgeon ≤ 1,050 mm TL and total initial and recaptured fish from seasonal age-0 cohorts in the Edisto River, SC, from 1994–2019. N is the sum of individuals form January–December.

Year	N ≤ 1050 mm TL	Cohort 1 initial captures	Cohort 1 recaptures	Cohort 2 initial captures	Cohort 2 recaptures
1994	98	1	0	0	0
1995	75	4	0	0	0
1996	711	290	103	1	0
1997	573	204	71	0	0
1998	741	409	105	9	1
1999	442	140	23	3	0
2000	279	171	23	0	0
2001	314	113	10	1	1
2002	75	14	0	0	0
2003	817	259	69	281	56
2004	285	16	0	0	0
2005	168	67	9	0	0
2006	189	3	0	0	0
2007	41	1	0	0	0
2008	35	2	0	0	0
2009	76	2	0	0	0
2010	33	4	0	6	0
2011	45	1	0	0	0
2012	64	1	0	0	0
2013	76	19	1	0	0
2014	103	10	1	0	0
2015	62	27	1	0	0
2016	129	1	1	0	0
2017	253	35	4	0	0
2018	188	21	3	1	0
2019	176	45	7	0	0
Total	6048	1860	431	302	58

TABLE 2: Linear models, BIC*c*, ΔBIC, BIC weight, and R^2 values for models describing the relationships between growth rate of juvenile Atlantic Sturgeon in the Edisto River, SC and environmental and biological factors from 1994–2019. Environmental factors include mean temperature and discharge. Biological factors include initial TL and seasonal cohort.

Model	**BIC**	**ΔBIC**	**weight**	R^2
Growth rate ~ mean temperature + TL	643.12	0.00	0.43	0.32
Growth rate ~ mean temperature + TL + discharge + (TL×discharge)	643.88	0.77	0.30	0.34
Growth rate ~ mean temperature + TL + discharge	646.06	2.94	0.10	0.32
Growth rate ~ mean temperature + TL + (TL×mean temperature)	647.06	3.94	0.06	0.32
Growth rate ~ mean temperature + TL + discharge + cohort + (TL×discharge)	647.52	4.40	0.05	0.34
Growth rate ~ mean temperature + TL+ cohort	648.89	5.78	0.02	0.32
Growth rate ~ mean temperature + TL + discharge + (TL×mean temperature)	649.46	6.34	0.02	0.33
Growth rate ~ mean temperature + TL+ cohort + (TL×mean temperature)	650.95	7.83	0.01	0.33
Growth rate ~ mean temperature + TL + discharge + cohort + (TL×discharge) + (TL×mean temperature)	651.46	8.34	0.01	0.34
Growth rate ~ mean temp + TL + discharge + cohort	652.25	9.14	0.00	0.32

1

TABLE 3: Linear models, BIC*c*, ΔBIC, BIC weight, and R^2 values for models describing the relationships between overall growth (mm) of juvenile Atlantic Sturgeon in the Edisto River, SC, and environmental and biological factors from 1994–2019. Environmental factors include mean temperature, discharge, and accumulated growing degree days (GDD). Biological factors include initial TL and seasonal cohort.

Model	**BIC**	**ΔBIC**	**weight**	R^2
Overall growth ~ accumulated GDD + mean temperature + initial TL + (accumulated GDD×mean temperature) + (initial TL×accumulated GDD)	4271.30	0.00	0.36	0.89
Overall growth ~ Initial TL + mean temperature + accumulated GDD + discharge + (initial TL×discharge) + (Initial TL×accumulated GDD) + (mean temperature×accumulated GDD)	4271.62	0.32	0.31	0.90
Overall growth ~ accumulated GDD + mean temperature + initial TL + (accumulated GDD×mean temperature)	4273.54	2.24	0.12	0.89
Overall growth ~ initial TL + mean temperature + accumulated GDD + (initial TL×mean temperature) + (initial TL×accumulated GDD) + (mean temperature×accumulated GDD)	4275.57	4.27	0.04	0.89
Overall growth ~ accumulated GDD + mean temperature + initial TL + discharge + (accumulated GDD×mean temperature) + (initial TL×discharge)	4275.93	4.63	0.04	0.89
Overall growth ~ accumulated GDD + mean temperature + initial TL + (accumulated GDD×mean temperature) + (initial TL×mean temperature)	4276.31	5.01	0.03	0.89
Overall growth ~ accumulated GDD + mean temperature + initial TL + cohort + (accumulated GDD×mean temperature) + (initial TL×accumulated GDD)	4277.01	5.72	0.02	0.89
Overall growth ~ initial TL + mean temperature + accumulated GDD + discharge + cohort + (initial TL×discharge) + (initial TL×accumulated GDD) + (mean temperature×accumulated GDD)	4277.0	5.77	0.02	0.90
Overall growth ~ accumulated GDD + mean temperature + initial TL + discharge + (accumulated GDD×mean temperature) + (initial TL×accumulated GDD)	4277.39	6.09	0.02	0.89
Overall growth ~ initial TL + mean temperature + accumulated GDD + discharge + (initial TL×discharge) + (initial TL×accumulated GDD) + (mean temperature×accumulated GDD) + (initial TL×mean temperature)	4277.76	6.46	0.01	0.90

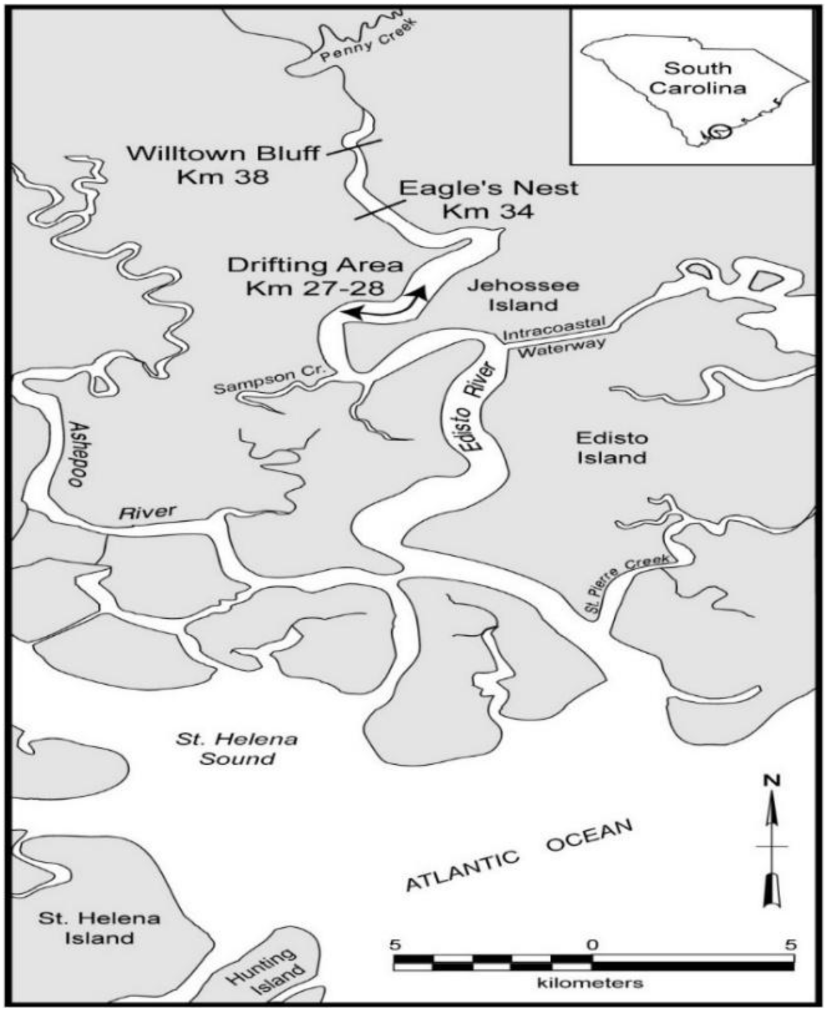


Figure 1: Study area for mark-recapture sampling of Atlantic Sturgeon using drifted gill nets during the 25-year study in the Edisto River, SC (map from McCord 2007).

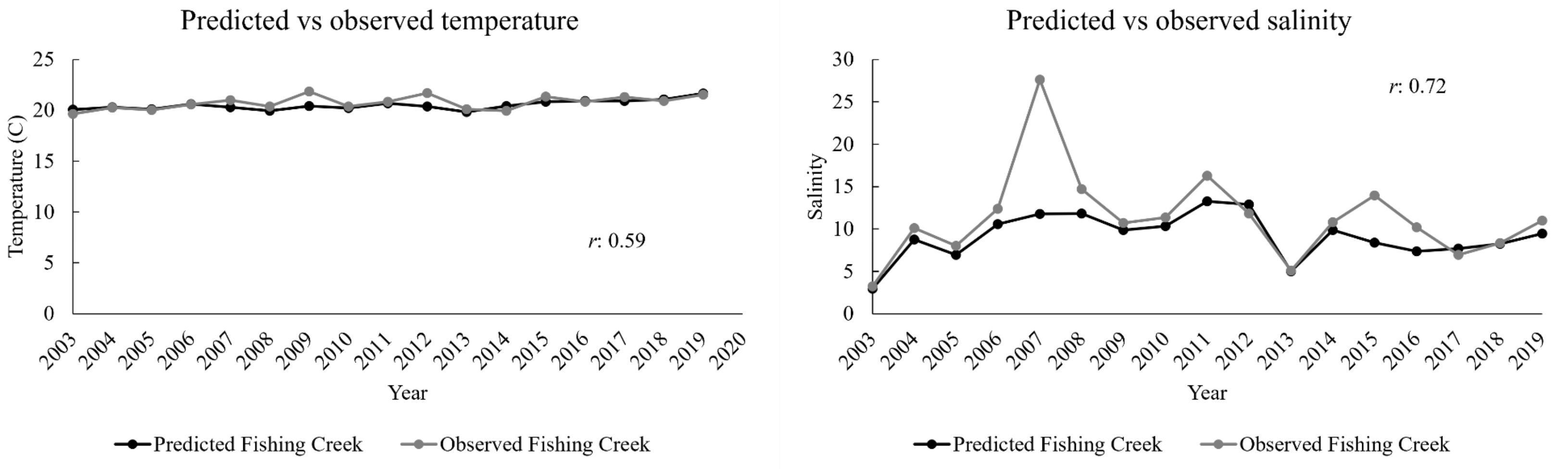


Figure 2: The relationship between observed and predicted average annual water temperature and salinity from January–December in the Edisto River, SC, from 2003–2019.

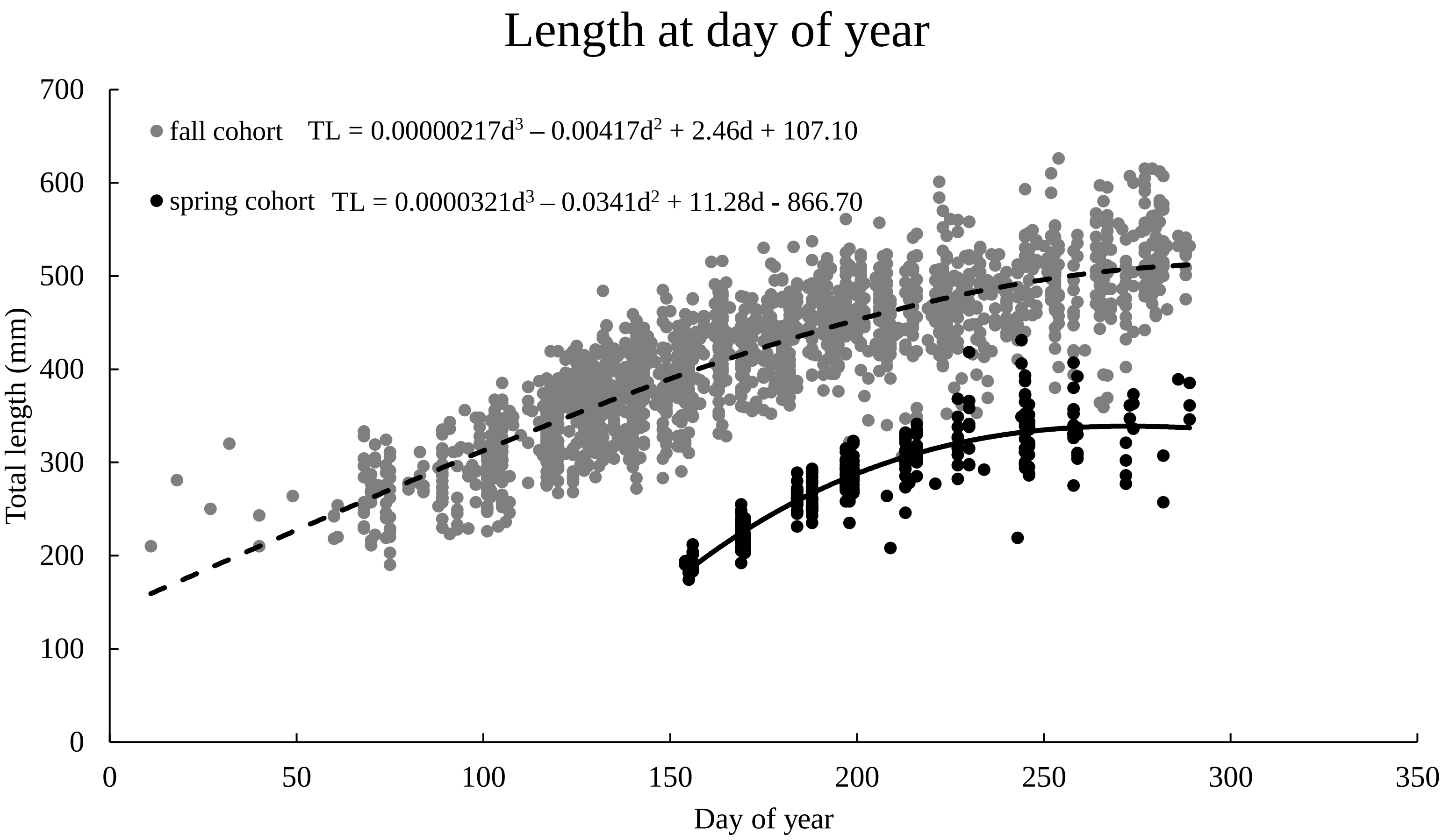


Figure 3: Length at day-of-year scatterplots for seasonal cohorts of juvenile Atlantic Sturgeon in the Edisto River, SC from 1995-2019. TL = the total length in mm and d = day of year in the equations. Recapture data were not available in 1994.

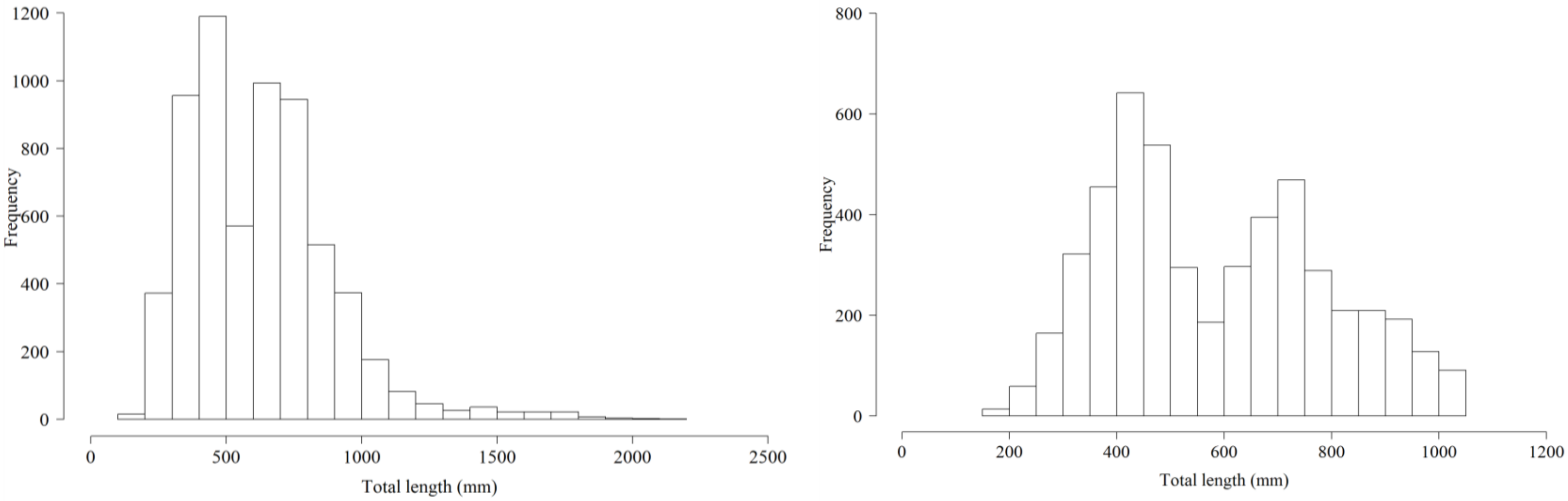


Figure 4: Histogram of lengths (mm) of total Atlantic Sturgeon collected in the Edisto River, SC, during 1994–2019 (n=6,410) on the left and lengths (mm) of Atlantic Sturgeon used for population analysis after standardization (n=4,944) on the right.

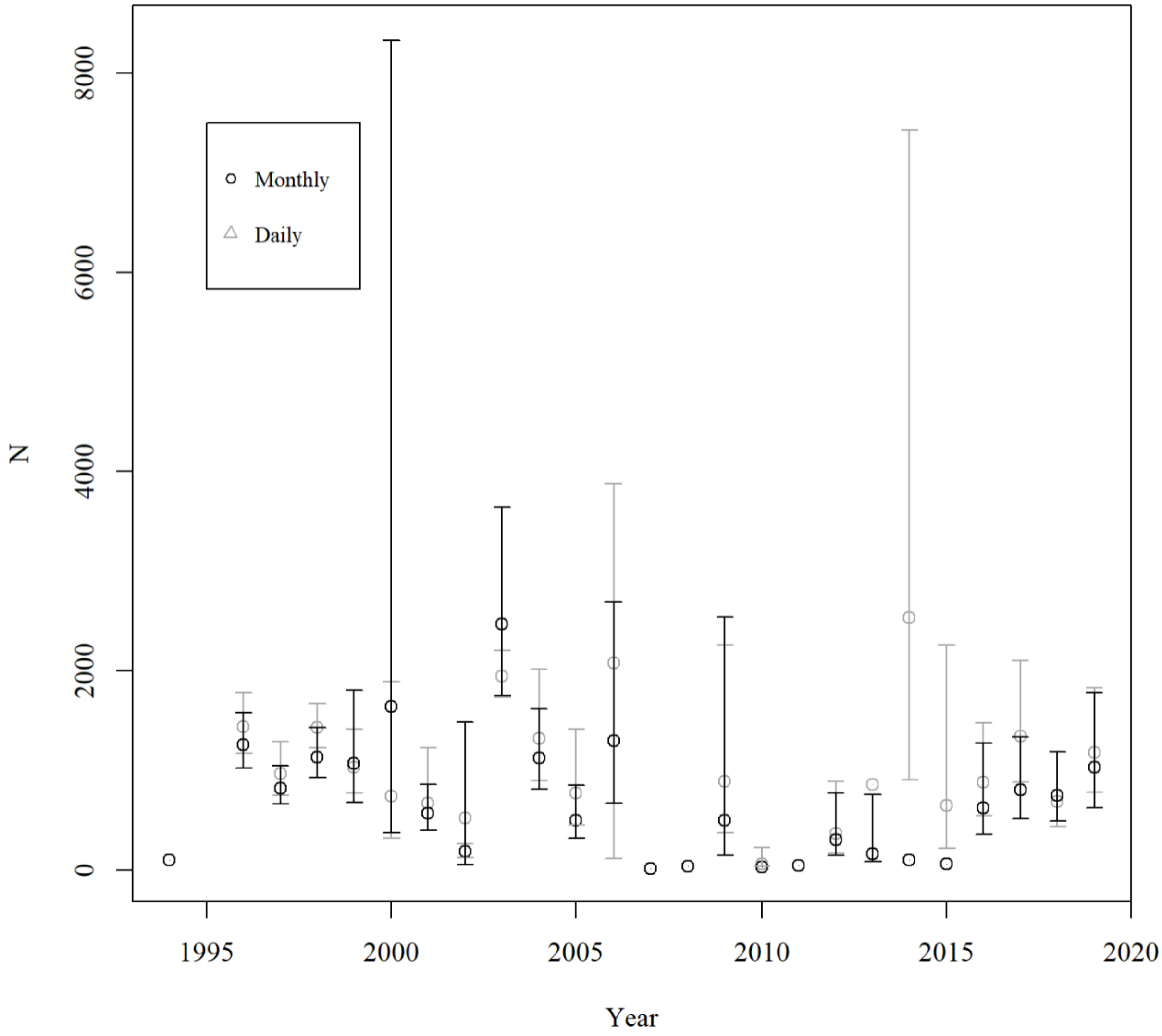


Figure 5: Population estimates by year for juvenile Atlantic Sturgeon in the Edisto River, SC, from 1994–2019. The points represent population estimates based on monthly (black) and daily (grey) encounter histories with error bars representing 95% confidence intervals. Capture-recapture data in 1995 did not fit our standardized methods May–September for population estimates.

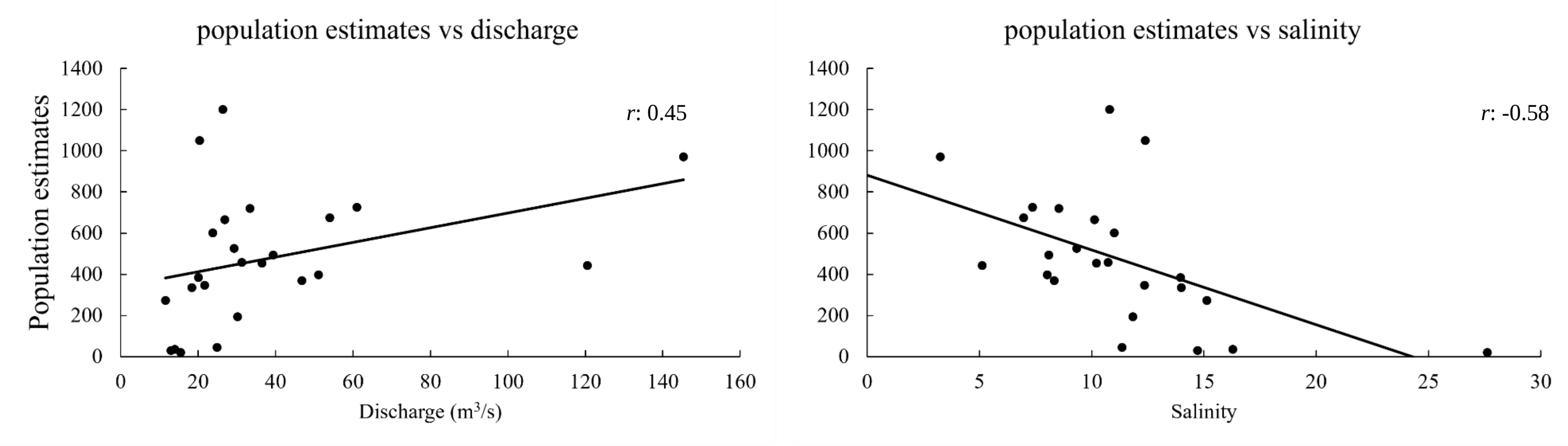


Figure 6: The relationship between yearly population estimates and salinity and discharge for juvenile Atlantic Sturgeon in the Edisto River, SC from 1996–2019. Population estimates are based on the average from models using daily and monthly encounter histories each year. Salinity data was not available in 1994 and capture-recapture data fit our standardized methods May–September in 1995 for population estimates.

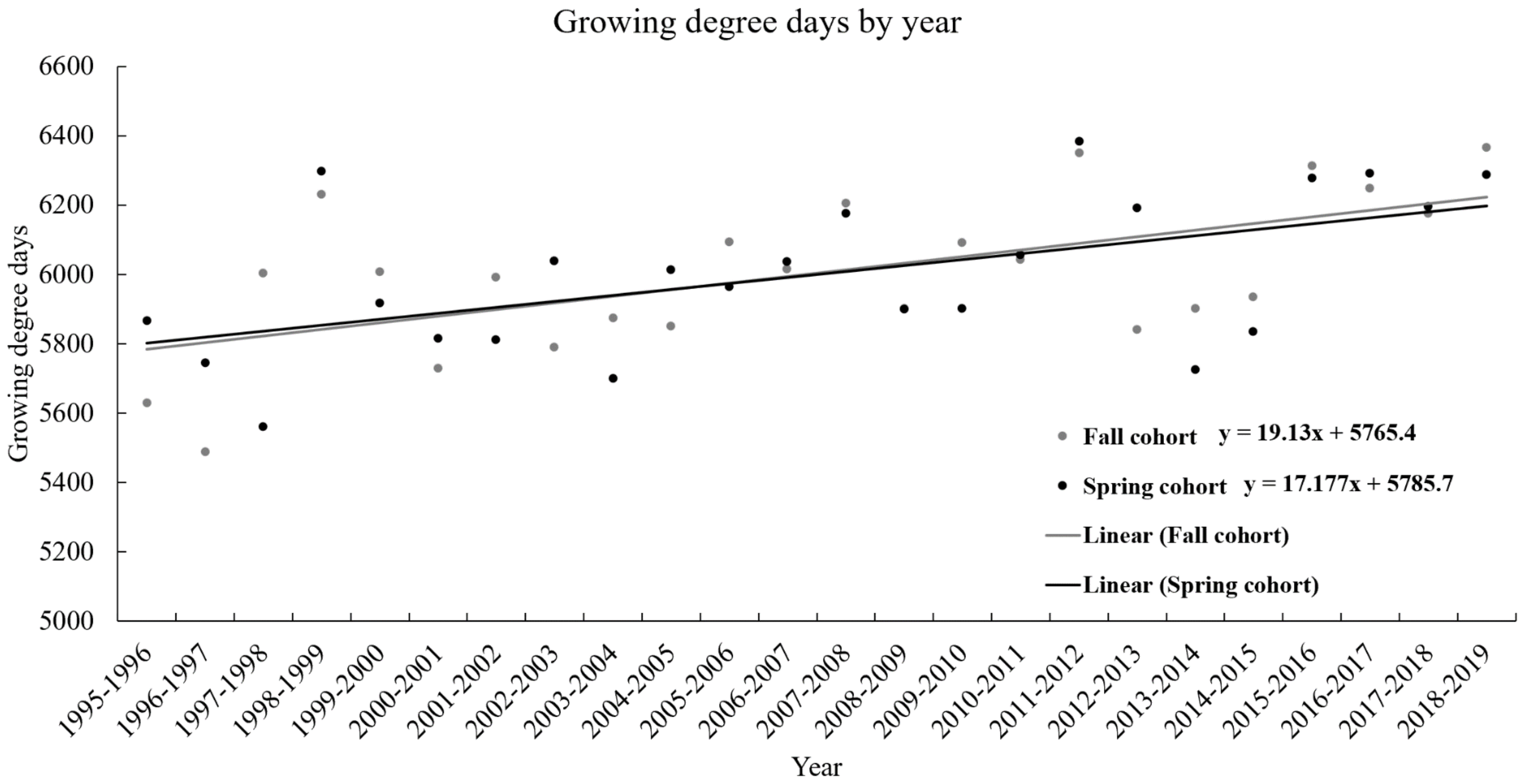


Figure 7: Accumulated growing degree days per year. Arbitrary hatch dates of March 15th and October 1st were assigned to spring and fall cohorts of Atlantic Sturgeon in the Edisto River, SC to determine number of GDD within the first year of life.

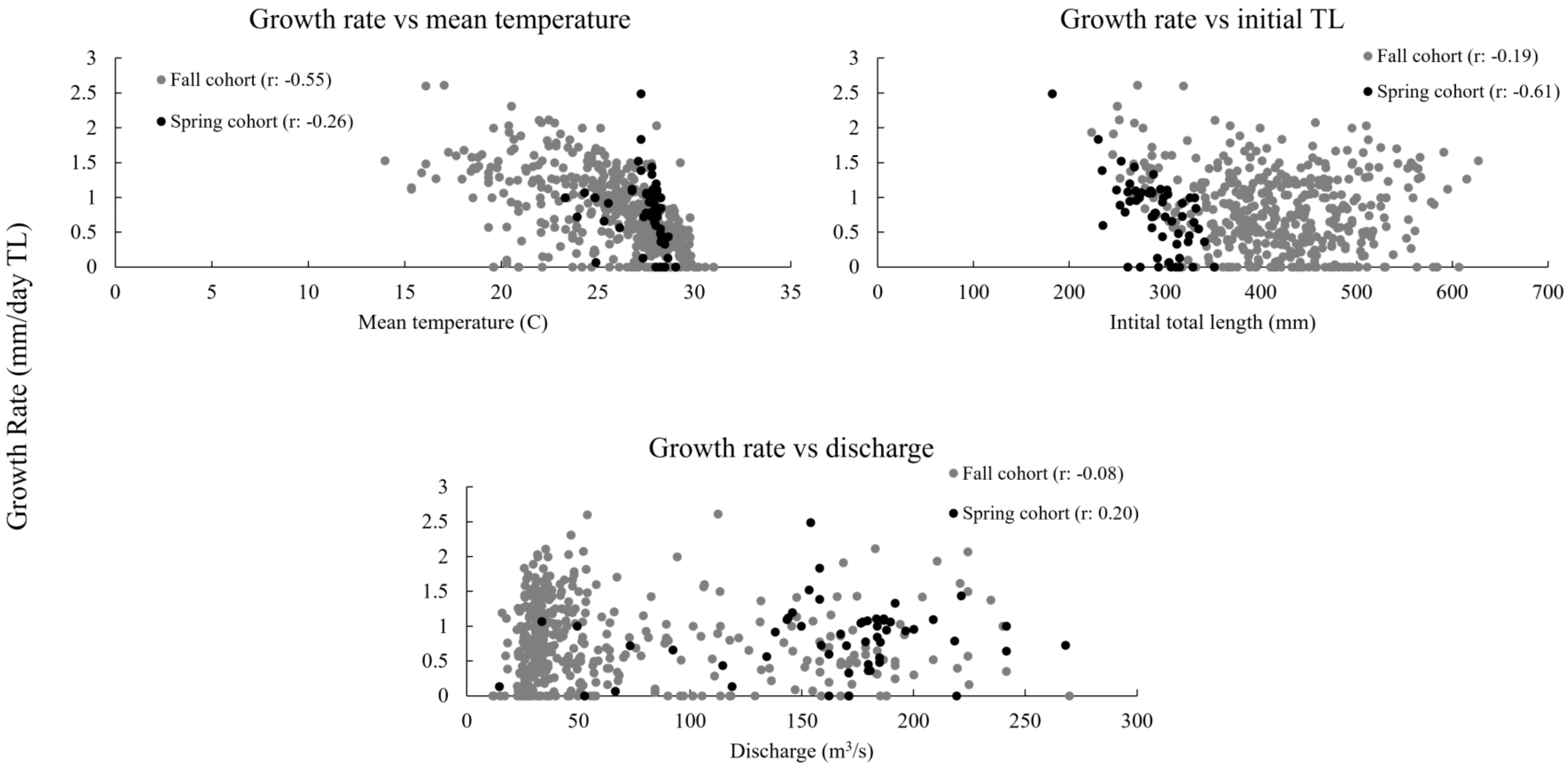


Figure 8: Growth rate in mm TL day^{-1} for juvenile Atlantic Sturgeon in the Edisto River, SC during 1994–2019 in relation to mean temperature (°C), discharge (m^3/s), and initial TL (mm).

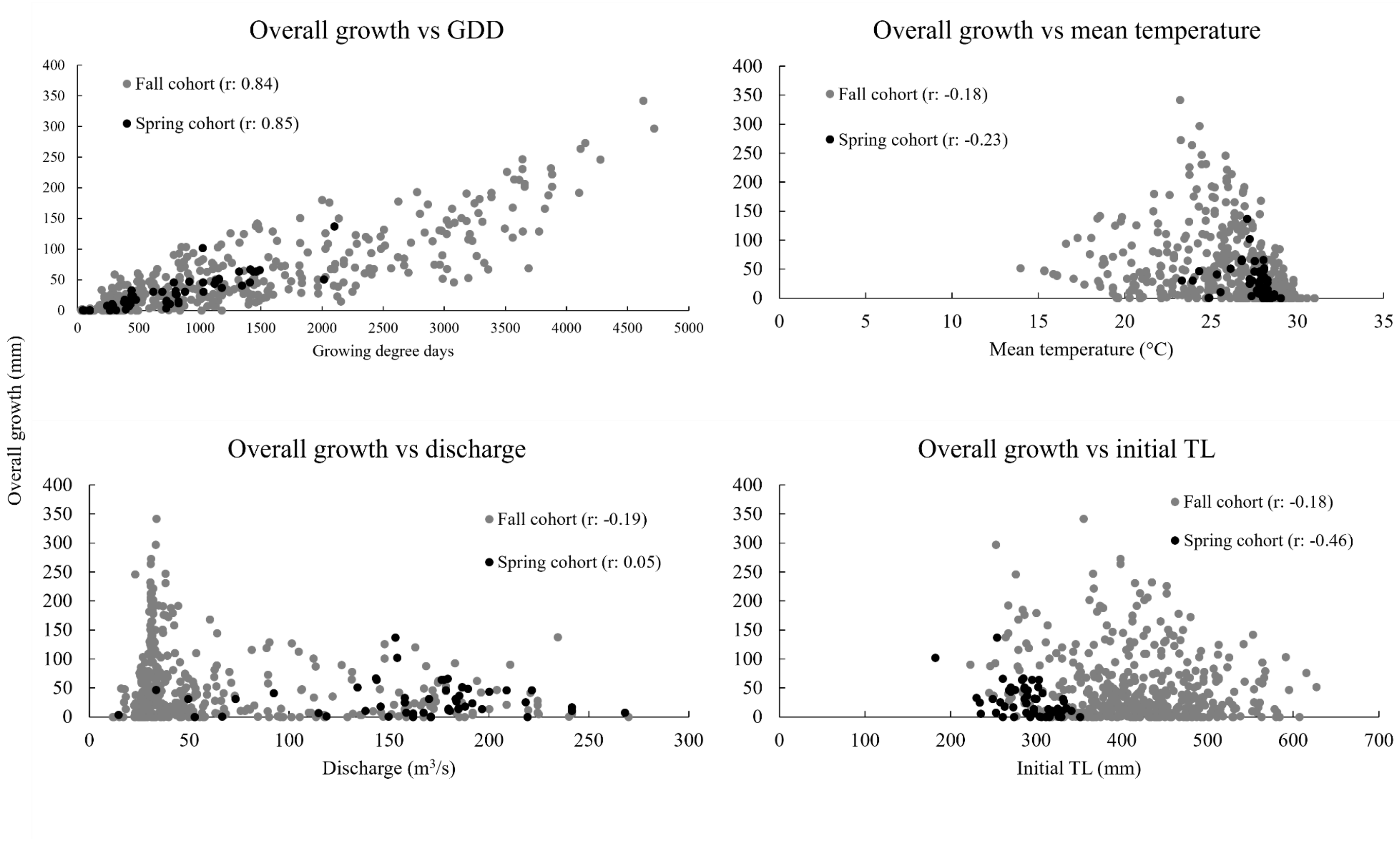
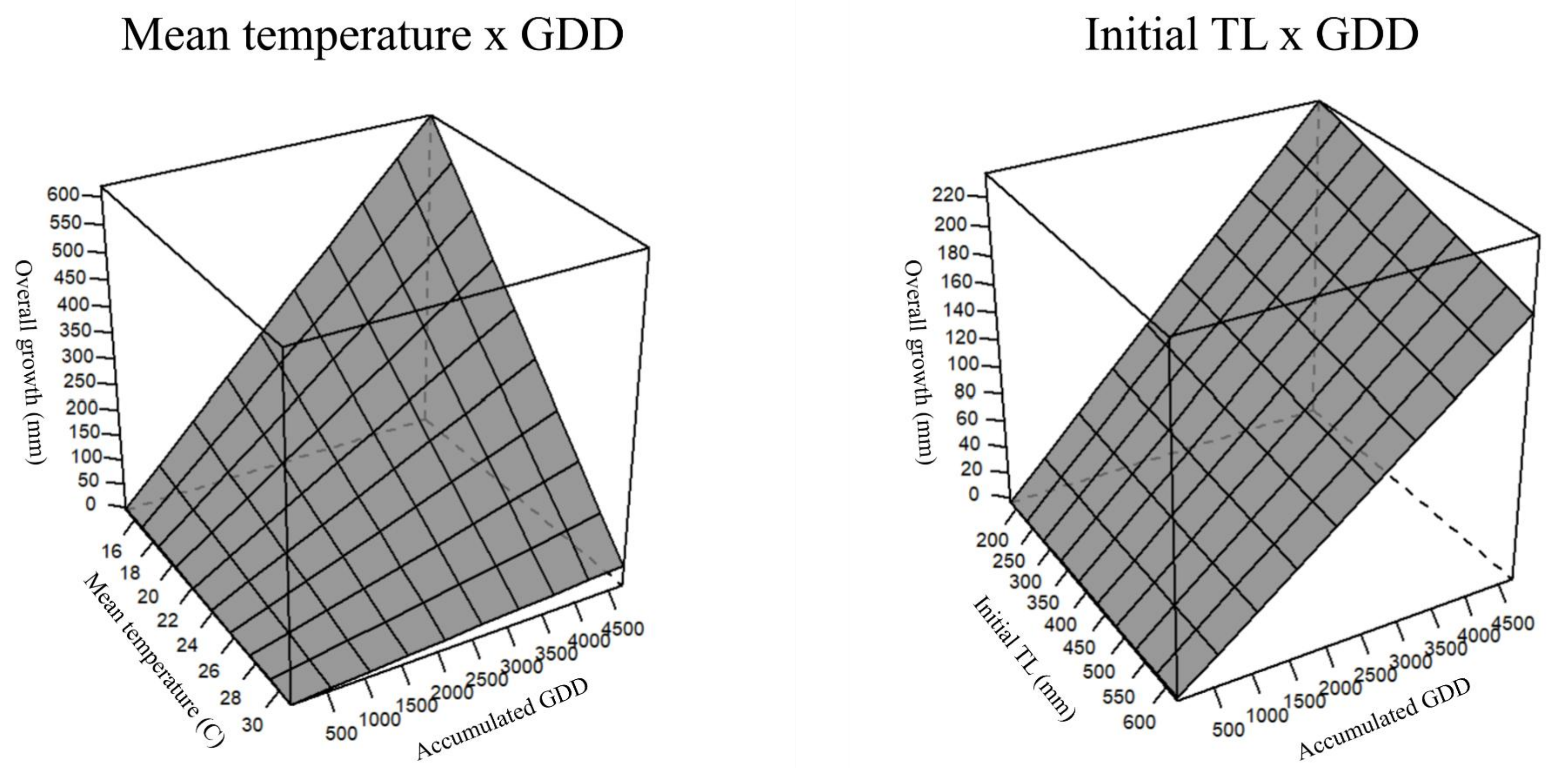


Figure 9: Scatterplots of the relationships between overall growth and accumulated growing degree days, mean temperature (°C), discharge (m^3/s), and initial TL (mm) for juvenile Atlantic Sturgeon collected from the Edisto River, SC during 1994–2019.



Mean temperature x GDD

Initial TL x GDD

Figure 10: Interaction plots for models of overall growth between captures for Juvenile Atlantic Sturgeon in the Edisto River, SC duirg 1994–2019. Interactions include accumulated growing degree days×mean temperature and accumulated growing degree days×initial TL.

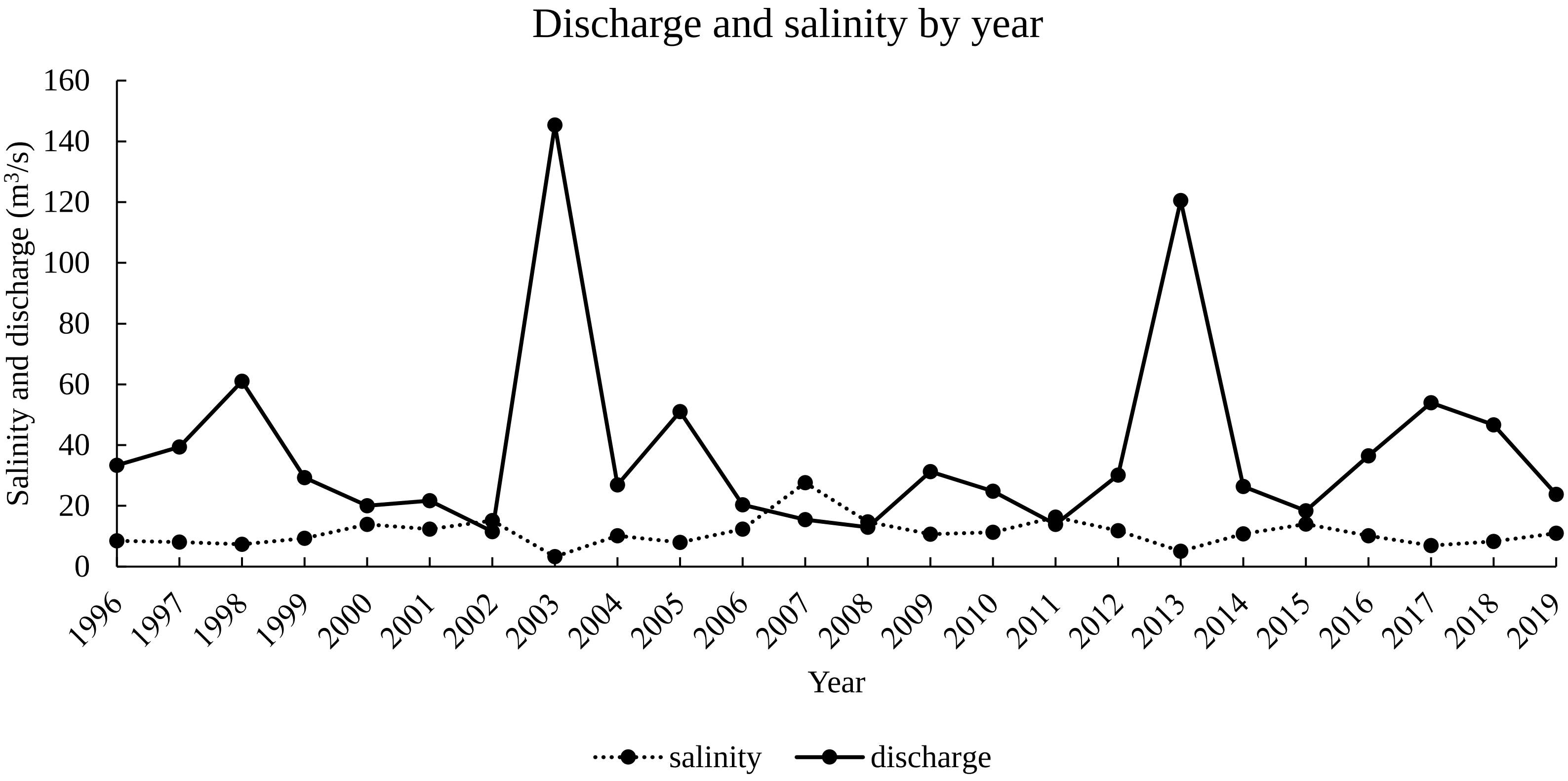


Figure 11: Mean discharge and salinity during the sampling period in the Edisto River, SC, from 1995–2019. Water quality data was not available in 1994.

APPENDIX:

TABLE A1: POPAN open population models and AIC*c*, ΔAIC*c*, weight, and number of independent variables for pooled and daily estimates each year. “time” represents time dependent, and “dot” represents time independent for each parameter.

Year	Daily Model	AIC*c*	ΔAIC*c*	w_i	*K*	Monthly model	AIC*c*	ΔAIC*c*	w_i	*K*
1994	phi.dot_p.dot_pent.dot	105.01	0.00	0.99	4	phi.dot_p.dot_pent.time	23.31	0.00	0.87	6
	phi.dot_p.dot_pent.time	122.09	17.08	0.00	23	phi.time_p.dot_pent.time	28.03	4.72	0.08	8
	phi.dot_p.time_pent.dot	131.70	26.69	0.00	24	phi.dot_p.time_pent.time	30.47	7.16	0.02	9
	phi.time_p.dot_pent.dot	158.11	53.10	0.00	23	phi.dot_p.time_pent.dot	30.98	7.67	0.02	7
	phi.time_p.dot_pent.time	214.00	108.99	0.00	42	phi.time_p.time_pent.time	35.54	12.23	0.00	11
	phi.dot_p.time_pent.time	220.74	115.73	0.00	43	phi.time_p.time_pent.dot	35.81	12.50	0.00	9
	phi.time_p.time_pent.dot	227.83	122.82	0.00	43	phi.dot_p.dot_pent.dot	56.51	33.20	0.00	4
	phi.time_p.time_pent.time	428.67	323.66	0.00	62	phi.time_p.dot_pent.dot	61.02	37.71	0.00	6
1996	phi.dot_p.time_pent.dot	1250.51	0.00	0.00	36	phi.dot_p.time_pent.dot	511.25	0.00	0.04	8
	phi.time_p.time_pent.dot	1317.61	67.10	0.00	67	phi.time_p.dot_pent.dot	511.43	0.18	0.04	7
	phi.dot_p.time_pent.time	1322.39	71.88	0.00	67	phi.time_p.dot_pent.time	515.41	4.16	0.00	10
	phi.time_p.dot_pent.dot	1332.51	82.00	0.00	35	phi.dot_p.time_pent.time	517.08	5.83	0.00	11
	phi.dot_p.dot_pent.time	1372.32	121.81	0.00	35	phi.dot_p.dot_pent.time	522.04	10.79	0.00	7
	phi.time_p.dot_pent.time	1377.04	126.53	0.00	66	phi.time_p.time_pent.time	522.71	11.45	0.00	14
	phi.time_p.time_pent.time	1399.10	148.59	0.00	98	phi.dot_p.dot_pent.dot	525.64	14.39	0.00	4
	phi.dot_p.dot_pent.dot	1742.92	492.41	0.00	4	phi.time_p.time_pent.dot	538.50	27.25	0.00	11
1997	phi.dot_p.time_pent.dot	779.86	0.00	1.00	26	phi.dot_p.dot_pent.dot	409.48	0.00	0.44	4
	phi.time_p.time_pent.dot	821.21	41.35	0.00	47	phi.dot_p.dot_pent.time	410.64	1.17	0.25	7
	phi.dot_p.dot_pent.dot	822.91	43.05	0.00	4	phi.dot_p.time_pent.dot	411.46	1.98	0.16	8
	phi.dot_p.time_pent.time	826.13	46.27	0.00	47	phi.time_p.dot_pent.dot	412.82	3.35	0.08	7
	phi.time_p.dot_pent.dot	839.08	59.22	0.00	25	phi.time_p.dot_pent.time	414.29	4.81	0.04	10
	phi.dot_p.dot_pent.time	847.25	67.38	0.00	25	phi.time_p.time_pent.dot	415.92	6.44	0.02	11
	phi.time_p.dot_pent.time	876.11	96.25	0.00	46	phi.dot_p.time_pent.time	416.95	7.47	0.01	11
	phi.time_p.time_pent.time	877.51	97.64	0.00	68	phi.time_p.time_pent.time	421.83	12.35	0.00	14

1998	phi.dot_p.time_pent.dot	1392.34	0.00	1.00	35	phi.dot_p.time_pent.time	665.89	0.00	0.31	11
	phi.dot_p.time_pent.time	1441.25	48.90	0.00	65	phi.time_p.time_pent.dot	666.29	0.40	0.25	11
	phi.time_p.time_pent.dot	1459.35	67.00	0.00	65	phi.time_p.dot_pent.dot	666.57	0.68	0.22	7
	phi.time_p.time_pent.time	1522.00	129.66	0.00	95	phi.time_p.dot_pent.time	667.56	1.67	0.13	10
	phi.dot_p.dot_pent.time	1546.18	153.83	0.00	34	phi.dot_p.dot_pent.dot	670.13	4.24	0.04	4
	phi.time_p.dot_pent.dot	1558.38	166.03	0.00	34	phi.dot_p.dot_pent.time	670.86	4.97	0.03	7
	phi.time_p.dot_pent.time	1563.52	171.17	0.00	64	phi.time_p.time_pent.time	671.42	5.53	0.02	14
	phi.dot_p.dot_pent.dot	1568.47	176.12	0.00	4	phi.dot_p.time_pent.dot	677.60	11.71	0.00	8
1999	phi.dot_p.time_pent.dot	721.86	0.00	1.00	29	phi.dot_p.time_pent.dot	296.79	0.00	0.50	8
	phi.dot_p.dot_pent.dot	739.32	17.45	0.00	4	phi.time_p.dot_pent.dot	297.67	0.89	0.32	7
	phi.time_p.dot_pent.dot	765.01	43.14	0.00	28	phi.dot_p.time_pent.time	300.83	4.04	0.07	11
	phi.dot_p.dot_pent.time	776.64	54.77	0.00	28	phi.time_p.dot_pent.time	300.83	4.05	0.07	10
	phi.dot_p.time_pent.time	779.89	58.02	0.00	53	phi.time_p.time_pent.dot	302.43	5.64	0.03	11
	phi.time_p.time_pent.dot	784.34	62.48	0.00	53	phi.dot_p.dot_pent.time	305.85	9.06	0.01	7
	phi.time_p.dot_pent.time	820.58	98.72	0.00	52	phi.time_p.time_pent.time	307.17	10.38	0.00	14
	phi.time_p.time_pent.time	857.39	135.52	0.00	77	phi.dot_p.dot_pent.dot	309.69	12.90	0.00	4
2000	phi.dot_p.dot_pent.dot	165.70	0.00	1.00	4	phi.time_p.dot_pent.dot	46.19	0.00	0.87	7
	phi.dot_p.time_pent.dot	176.71	11.01	0.00	24	phi.dot_p.time_pent.dot	50.93	4.74	0.08	8
	phi.dot_p.dot_pent.time	183.05	17.35	0.00	23	phi.time_p.dot_pent.time	53.05	6.87	0.03	10
	phi.time_p.dot_pent.dot	196.20	30.50	0.00	23	phi.time_p.time_pent.dot	55.68	9.50	0.01	11
	phi.time_p.dot_pent.time	295.36	129.66	0.00	42	phi.dot_p.dot_pent.time	56.38	10.20	0.01	7
	phi.time_p.time_pent.dot	302.05	136.35	0.00	43	phi.dot_p.time_pent.time	58.24	12.06	0.00	11
	phi.dot_p.time_pent.time	307.01	141.31	0.00	43	phi.time_p.time_pent.time	64.42	18.23	0.00	14
	phi.time_p.time_pent.time	866.44	700.74	0.00	62	phi.dot_p.dot_pent.dot	64.85	18.67	0.00	4
2001	phi.dot_p.dot_pent.dot	404.85	0.00	1.00	4	phi.dot_p.dot_pent.time	190.90	0.00	0.67	7
	phi.dot_p.time_pent.dot	416.43	11.58	0.00	29	phi.dot_p.dot_pent.dot	193.91	3.00	0.15	4
	phi.dot_p.dot_pent.time	436.40	31.55	0.00	28	phi.dot_p.time_pent.dot	194.55	3.64	0.11	8
	phi.time_p.dot_pent.dot	444.23	39.38	0.00	28	phi.time_p.dot_pent.dot	196.51	5.60	0.04	7
	phi.dot_p.time_pent.time	497.42	92.57	0.00	53	phi.time_p.dot_pent.time	197.34	6.44	0.03	10
	phi.time_p.dot_pent.time	504.15	99.29	0.00	52	phi.dot_p.time_pent.time	199.79	8.89	0.01	11
	phi.time_p.time_pent.dot	508.71	103.85	0.00	53	phi.time_p.time_pent.dot	201.01	10.11	0.00	11
	phi.time_p.time_pent.time	615.07	210.22	0.00	77	phi.time_p.time_pent.time	206.26	15.35	0.00	14

2002	phi.time_p.dot_pent.time	-406.89	0.00	1.00	36	phi.dot_p.dot_pent.dot	46.76	0.00	0.47	4
	phi.dot_p.time_pent.time	-340.12	66.78	0.00	37	phi.dot_p.dot_pent.time	47.01	0.26	0.42	7
	phi.time_p.time_pent.dot	-338.80	68.10	0.00	37	phi.dot_p.time_pent.dot	50.46	3.70	0.07	8
	phi.time_p.time_pent.time	-102.12	304.77	0.00	53	phi.time_p.dot_pent.dot	52.26	5.51	0.03	7
	phi.dot_p.dot_pent.dot	74.87	481.76	0.00	4	phi.time_p.dot_pent.time	56.77	10.02	0.00	10
	phi.dot_p.dot_pent.time	173.59	580.48	0.00	20	phi.time_p.time_pent.dot	61.41	14.65	0.00	11
	phi.time_p.dot_pent.dot	178.39	585.28	0.00	20	phi.dot_p.time_pent.time	62.16	15.40	0.00	11
	phi.dot_p.time_pent.dot	191.70	598.60	0.00	21	phi.time_p.time_pent.time	78.01	31.26	0.00	14
2003	phi.dot_p.time_pent.dot	1927.35	0.00	0.09	30	phi.dot_p.time_pent.dot	742.33	0.00	0.30	8
	phi.time_p.time_pent.dot	1935.02	7.66	0.00	55	phi.time_p.dot_pent.time	742.70	0.37	0.25	10
	phi.dot_p.time_pent.time	1947.54	20.18	0.00	55	phi.time_p.time_pent.dot	743.68	1.35	0.15	11
	phi.time_p.time_pent.time	1965.93	38.57	0.00	80	phi.dot_p.dot_pent.time	743.72	1.38	0.15	7
	phi.time_p.dot_pent.time	1991.39	64.03	0.00	54	phi.dot_p.time_pent.time	745.03	2.69	0.07	11
	phi.dot_p.dot_pent.time	2019.75	92.40	0.00	29	phi.time_p.time_pent.time	745.71	3.37	0.05	14
	phi.time_p.dot_pent.dot	2048.63	121.28	0.00	29	phi.dot_p.dot_pent.dot	828.75	86.41	0.00	4
	phi.dot_p.dot_pent.dot	2170.02	242.66	0.00	4	phi.time_p.dot_pent.dot	830.73	88.39	0.00	7
2004	phi.dot_p.time_pent.dot	489.34	0.00	0.09	22	phi.dot_p.dot_pent.dot	257.38	0.00	0.05	4
	phi.dot_p.dot_pent.dot	522.51	33.17	0.00	4	phi.time_p.dot_pent.dot	258.77	1.39	0.02	7
	phi.time_p.dot_pent.dot	526.20	36.85	0.00	21	phi.dot_p.dot_pent.time	260.13	2.75	0.01	7
	phi.dot_p.time_pent.time	526.88	37.54	0.00	39	phi.time_p.dot_pent.time	264.18	6.80	0.00	10
	phi.time_p.time_pent.dot	527.54	38.19	0.00	39	phi.time_p.time_pent.dot	265.79	8.41	0.00	11
	phi.dot_p.dot_pent.time	534.18	44.83	0.00	21	phi.dot_p.time_pent.time	266.68	9.29	0.00	11
	phi.time_p.dot_pent.time	541.91	52.56	0.00	38	phi.time_p.time_pent.time	272.23	14.85	0.00	14
	phi.time_p.time_pent.time	568.69	79.34	0.00	56	phi.dot_p.time_pent.dot	303.93	46.54	0.00	8
2005	phi.dot_p.time_pent.dot	348.64	0.00	0.76	23	phi.dot_p.dot_pent.time	153.59	0.00	0.27	7
	phi.dot_p.dot_pent.dot	350.99	2.34	0.24	4	phi.dot_p.time_pent.dot	153.65	0.06	0.26	8
	phi.time_p.dot_pent.dot	365.12	16.48	0.00	22	phi.time_p.dot_pent.dot	153.66	0.07	0.26	7
	phi.dot_p.dot_pent.time	365.33	16.68	0.00	22	phi.time_p.dot_pent.time	155.08	1.49	0.13	10
	phi.time_p.time_pent.dot	399.69	51.04	0.00	41	phi.dot_p.time_pent.time	156.52	2.93	0.06	11
	phi.dot_p.time_pent.time	400.85	52.21	0.00	41	phi.time_p.time_pent.dot	158.66	5.07	0.02	11
	phi.time_p.dot_pent.time	406.64	57.99	0.00	40	phi.time_p.time_pent.time	163.46	9.88	0.00	14
	phi.time_p.time_pent.time	474.20	125.56	0.00	59	phi.dot_p.dot_pent.dot	164.10	10.51	0.00	4

2006	phi.dot_p.time_pent.dot	245.88	0.00	1.00	24	phi.dot_p.dot_pent.time	111.25	0.00	0.41	7
	phi.dot_p.dot_pent.time	272.21	26.32	0.00	23	phi.time_p.dot_pent.time	111.96	0.70	0.29	10
	phi.dot_p.dot_pent.dot	272.83	26.94	0.00	4	phi.dot_p.time_pent.dot	111.97	0.72	0.29	8
	phi.time_p.dot_pent.dot	276.93	31.04	0.00	23	phi.time_p.time_pent.dot	117.96	6.70	0.01	11
	phi.time_p.time_pent.dot	298.22	52.34	0.00	43	phi.time_p.time_pent.time	121.01	9.76	0.00	14
	phi.dot_p.time_pent.time	304.52	58.64	0.00	43	phi.time_p.dot_pent.dot	134.47	23.21	0.00	7
	phi.time_p.dot_pent.time	308.93	63.05	0.00	42	phi.dot_p.time_pent.time	140.24	28.98	0.00	11
	phi.time_p.time_pent.time	378.48	132.60	0.00	62	phi.dot_p.dot_pent.dot	150.36	39.10	0.00	4
2007	phi.time_p.dot_pent.time	-62.84	0.00	0.94	22	phi.dot_p.dot_pent.dot	21.39	0.00	0.98	4
	phi.dot_p.time_pent.time	-57.00	5.83	0.05	23	phi.dot_p.dot_pent.time	30.51	9.12	0.01	6
	phi.time_p.time_pent.dot	-53.20	9.64	0.01	23	phi.time_p.dot_pent.dot	31.89	10.50	0.01	6
	phi.time_p.time_pent.time	-33.67	29.17	0.00	32	phi.dot_p.time_pent.dot	39.39	18.00	0.00	7
	phi.dot_p.dot_pent.dot	34.38	97.22	0.00	4	phi.time_p.dot_pent.time	48.01	26.62	0.00	8
	phi.dot_p.dot_pent.time	409.66	472.50	0.00	13	phi.dot_p.time_pent.time	62.01	40.62	0.00	9
	phi.time_p.dot_pent.dot	412.38	475.22	0.00	13	phi.time_p.time_pent.dot	63.39	42.00	0.00	9
	phi.dot_p.time_pent.dot	Inf	Inf	0.00	14	phi.time_p.time_pent.time	118.01	96.62	0.00	11
2008	phi.dot_p.dot_pent.dot	45.53	0.00	0.09	4	phi.dot_p.dot_pent.dot	23.70	0.00	0.09	4
	phi.dot_p.dot_pent.time	70.20	24.66	0.00	13	phi.dot_p.dot_pent.time	31.35	7.64	0.00	7
	phi.time_p.dot_pent.dot	75.01	29.47	0.00	12	phi.time_p.dot_pent.dot	32.62	8.92	0.00	7
	phi.dot_p.time_pent.dot	80.69	35.15	0.00	14	phi.dot_p.time_pent.dot	36.08	12.38	0.00	8
	phi.time_p.dot_pent.time	145.00	99.46	0.00	21	phi.time_p.dot_pent.time	42.60	18.90	0.00	10
	phi.time_p.time_pent.dot	166.58	121.04	0.00	22	phi.dot_p.time_pent.time	47.04	23.34	0.00	11
	phi.dot_p.time_pent.time	182.40	136.86	0.00	23	phi.time_p.time_pent.dot	48.32	24.62	0.00	11
	phi.time_p.time_pent.time	1080.00	1034.46	0.00	31	phi.time_p.time_pent.time	63.14	39.44	0.00	14
2009	phi.dot_p.dot_pent.dot	141.03	0.00	0.98	4	phi.dot_p.time_pent.dot	69.09	0.00	0.64	8
	phi.dot_p.time_pent.dot	148.59	7.56	0.02	19	phi.time_p.dot_pent.dot	71.82	2.72	0.17	7
	phi.time_p.dot_pent.dot	162.93	21.90	0.00	18	phi.dot_p.dot_pent.time	72.63	3.54	0.11	7
	phi.dot_p.dot_pent.time	165.06	24.03	0.00	18	phi.time_p.dot_pent.time	74.68	5.58	0.04	10
	phi.time_p.dot_pent.time	212.73	71.70	0.00	32	phi.time_p.time_pent.dot	75.70	6.60	0.02	11
	phi.dot_p.time_pent.time	214.76	73.73	0.00	33	phi.dot_p.time_pent.time	76.37	7.28	0.02	11
	phi.time_p.time_pent.dot	222.34	81.31	0.00	33	phi.time_p.time_pent.time	83.73	14.64	0.00	14
	phi.time_p.time_pent.time	357.94	216.91	0.00	47	phi.dot_p.dot_pent.dot	93.63	24.54	0.00	4

2010	phi.time_p.time_pent.time	-257.02	0.00	1.00	41	phi.dot_p.dot_pent.dot	38.01	0.00	0.54	4
	phi.dot_p.dot_pent.dot	71.14	328.15	0.00	4	phi.dot_p.dot_pent.time	38.49	0.49	0.43	7
	phi.time_p.dot_pent.dot	115.34	372.36	0.00	16	phi.time_p.dot_pent.dot	45.36	7.36	0.01	7
	phi.dot_p.dot_pent.time	115.74	372.76	0.00	16	phi.dot_p.time_pent.dot	45.42	7.41	0.01	8
	phi.dot_p.time_pent.dot	121.21	378.23	0.00	17	phi.time_p.dot_pent.time	48.32	10.31	0.00	10
	phi.time_p.dot_pent.time	506.21	763.23	0.00	28	phi.dot_p.time_pent.time	54.58	16.58	0.00	11
	phi.dot_p.time_pent.time	684.41	941.43	0.00	29	phi.time_p.time_pent.dot	56.93	18.92	0.00	11
	phi.time_p.time_pent.dot	684.64	941.65	0.00	29	phi.time_p.time_pent.time	69.65	31.64	0.00	14
2011	phi.time_p.time_pent.time	-488.46	0.00	1.00	53	phi.dot_p.dot_pent.time	30.12	0.00	0.97	7
	phi.dot_p.dot_pent.dot	88.50	576.96	0.00	4	phi.dot_p.time_pent.dot	38.21	8.09	0.02	8
	phi.dot_p.dot_pent.time	123.31	611.77	0.00	20	phi.time_p.dot_pent.time	39.68	9.56	0.01	10
	phi.dot_p.time_pent.dot	140.48	628.93	0.00	21	phi.dot_p.time_pent.time	43.26	13.14	0.00	11
	phi.time_p.dot_pent.dot	147.73	636.19	0.00	20	phi.time_p.time_pent.dot	48.89	18.77	0.00	11
	phi.time_p.dot_pent.time	446.54	935.00	0.00	36	phi.dot_p.dot_pent.dot	51.06	20.94	0.00	4
	phi.dot_p.time_pent.time	524.03	1012.49	0.00	37	phi.time_p.time_pent.time	55.49	25.37	0.00	14
	phi.time_p.time_pent.dot	527.28	1015.73	0.00	37	phi.time_p.dot_pent.dot	59.15	29.03	0.00	7
2012	phi.dot_p.dot_pent.dot	119.94	0.00	1.00	4	phi.time_p.dot_pent.dot	66.66	0.00	0.46	7
	phi.time_p.dot_pent.dot	146.70	26.76	0.00	17	phi.dot_p.time_pent.dot	68.06	1.40	0.23	8
	phi.dot_p.time_pent.dot	148.54	28.60	0.00	18	phi.dot_p.dot_pent.time	68.35	1.69	0.20	7
	phi.dot_p.dot_pent.time	151.59	31.64	0.00	17	phi.time_p.dot_pent.time	69.81	3.15	0.09	10
	phi.time_p.dot_pent.time	210.66	90.71	0.00	30	phi.time_p.time_pent.dot	73.61	6.95	0.01	11
	phi.time_p.time_pent.dot	218.69	98.75	0.00	31	phi.dot_p.time_pent.time	74.26	7.60	0.01	11
	phi.dot_p.time_pent.time	220.24	100.30	0.00	31	phi.dot_p.dot_pent.dot	75.89	9.23	0.00	4
	phi.time_p.time_pent.time	387.76	267.81	0.00	44	phi.time_p.time_pent.time	82.21	15.55	0.00	14
2013	phi.dot_p.dot_pent.dot	142.61	0.00	1.00	4	phi.dot_p.dot_pent.dot	70.07	0.00	0.52	4
	phi.dot_p.dot_pent.time	167.00	24.39	0.00	21	phi.dot_p.dot_pent.time	70.88	0.81	0.35	7
	phi.dot_p.time_pent.dot	168.17	25.56	0.00	22	phi.dot_p.time_pent.dot	73.50	3.43	0.09	8
	phi.time_p.dot_pent.dot	179.06	36.45	0.00	21	phi.time_p.dot_pent.dot	76.58	6.51	0.02	7
	phi.time_p.dot_pent.time	254.38	111.77	0.00	38	phi.time_p.dot_pent.time	77.49	7.42	0.01	10
	phi.dot_p.time_pent.time	263.36	120.75	0.00	39	phi.dot_p.time_pent.time	80.69	10.62	0.00	11
	phi.time_p.time_pent.dot	265.48	122.87	0.00	39	phi.time_p.time_pent.dot	80.88	10.81	0.00	11
	phi.time_p.time_pent.time	539.48	396.87	0.00	56	phi.time_p.time_pent.time	87.37	17.30	0.00	14

2014	phi.dot_p.dot_pent.dot	159.81	0.00	0.09	4	phi.dot_p.dot_pent.time	42.88	0.00	0.08	7
	phi.dot_p.time_pent.dot	186.45	26.64	0.00	28	phi.time_p.dot_pent.time	47.76	4.88	0.00	10
	phi.time_p.dot_pent.dot	196.16	36.34	0.00	27	phi.dot_p.time_pent.dot	49.63	6.74	0.00	8
	phi.dot_p.dot_pent.time	197.95	38.14	0.00	27	phi.dot_p.time_pent.time	52.64	9.76	0.00	11
	phi.time_p.dot_pent.time	301.97	142.16	0.00	50	phi.time_p.time_pent.dot	56.60	13.72	0.00	11
	phi.dot_p.time_pent.time	307.38	147.57	0.00	51	phi.time_p.time_pent.time	58.20	15.32	0.00	14
	phi.time_p.time_pent.dot	309.15	149.34	0.00	51	phi.dot_p.dot_pent.dot	73.91	31.03	0.00	4
	phi.time_p.time_pent.time	641.96	482.15	0.00	74	phi.time_p.dot_pent.dot	78.34	35.46	0.00	7
2015	phi.dot_p.dot_pent.dot	79.53	0.00	1.00	4	phi.dot_p.dot_pent.dot	22.62	0.00	0.94	4
	phi.dot_p.dot_pent.time	103.17	23.63	0.00	15	phi.dot_p.dot_pent.time	29.67	7.05	0.03	7
	phi.time_p.dot_pent.dot	104.15	24.62	0.00	15	phi.time_p.dot_pent.dot	30.07	7.46	0.02	7
	phi.dot_p.time_pent.dot	105.83	26.30	0.00	16	phi.dot_p.time_pent.dot	32.75	10.14	0.01	8
	phi.time_p.dot_pent.time	148.90	69.36	0.00	26	phi.time_p.dot_pent.time	38.06	15.44	0.00	10
	phi.time_p.time_pent.dot	154.32	74.79	0.00	27	phi.dot_p.time_pent.time	41.09	18.47	0.00	11
	phi.dot_p.time_pent.time	157.38	77.84	0.00	27	phi.time_p.time_pent.dot	41.49	18.88	0.00	11
	phi.time_p.time_pent.time	264.36	184.83	0.00	38	phi.time_p.time_pent.time	51.02	28.40	0.00	14
2016	phi.dot_p.dot_pent.dot	311.40	0.00	0.76	4	phi.dot_p.dot_pent.time	120.37	0.00	0.48	7
	phi.dot_p.time_pent.dot	313.73	2.34	0.24	29	phi.dot_p.time_pent.dot	121.16	0.79	0.32	8
	phi.dot_p.dot_pent.time	341.98	30.58	0.00	28	phi.time_p.dot_pent.time	122.81	2.44	0.14	10
	phi.time_p.dot_pent.dot	343.05	31.65	0.00	28	phi.dot_p.time_pent.time	126.39	6.02	0.02	11
	phi.time_p.time_pent.dot	406.97	95.57	0.00	53	phi.time_p.time_pent.dot	126.96	6.59	0.02	11
	phi.dot_p.time_pent.time	407.29	95.89	0.00	53	phi.dot_p.dot_pent.dot	129.53	9.16	0.00	4
	phi.time_p.dot_pent.time	415.77	104.37	0.00	52	phi.time_p.dot_pent.dot	130.27	9.90	0.00	7
	phi.time_p.time_pent.time	598.71	287.31	0.00	77	phi.time_p.time_pent.time	131.63	11.26	0.00	14
2017	phi.dot_p.dot_pent.dot	460.37	0.00	0.09	4	phi.time_p.dot_pent.time	162.14	0.00	0.44	10
	phi.dot_p.time_pent.dot	489.42	29.05	0.00	43	phi.time_p.dot_pent.dot	163.65	1.51	0.20	7
	phi.dot_p.dot_pent.time	526.87	66.50	0.00	42	phi.dot_p.time_pent.dot	164.04	1.89	0.17	8
	phi.time_p.dot_pent.dot	535.41	75.04	0.00	42	phi.time_p.time_pent.dot	165.93	3.79	0.06	11
	phi.dot_p.time_pent.time	646.49	186.12	0.00	81	phi.dot_p.dot_pent.time	166.03	3.88	0.06	7
	phi.time_p.time_pent.dot	649.33	188.96	0.00	81	phi.dot_p.time_pent.time	166.63	4.48	0.04	11
	phi.time_p.dot_pent.time	668.81	208.44	0.00	80	phi.time_p.time_pent.time	170.75	8.60	0.00	14
	phi.time_p.time_pent.time	976.29	515.92	0.00	119	phi.dot_p.dot_pent.dot	184.00	21.86	0.00	4

2018	phi.dot_p.dot_pent.dot	495.90	0.00	0.09	4	phi.dot_p.time_pent.dot	173.56	0.00	0.64	8
	phi.dot_p.time_pent.dot	514.06	18.16	0.00	37	phi.dot_p.dot_pent.time	177.25	3.68	0.10	7
	phi.dot_p.dot_pent.time	555.04	59.13	0.00	36	phi.time_p.dot_pent.dot	177.29	3.72	0.09	7
	phi.time_p.dot_pent.dot	563.82	67.91	0.00	36	phi.dot_p.dot_pent.dot	177.77	4.20	0.07	4
	phi.time_p.time_pent.dot	621.80	125.90	0.00	69	phi.time_p.dot_pent.time	178.84	5.27	0.04	10
	phi.dot_p.time_pent.time	627.24	131.34	0.00	69	phi.dot_p.time_pent.time	180.31	6.74	0.02	11
	phi.time_p.dot_pent.time	666.44	170.54	0.00	68	phi.time_p.time_pent.dot	183.42	9.85	0.00	11
	phi.time_p.time_pent.time	842.04	346.14	0.00	101	phi.time_p.time_pent.time	185.99	12.42	0.00	14
2019	phi.dot_p.dot_pent.dot	399.43	0.00	1.00	4	phi.time_p.dot_pent.dot	143.57	0.00	0.48	7
	phi.dot_p.time_pent.dot	421.86	22.43	0.00	37	phi.dot_p.dot_pent.dot	144.42	0.85	0.31	4
	phi.time_p.dot_pent.dot	447.81	48.39	0.00	36	phi.dot_p.dot_pent.time	146.33	2.76	0.12	7
	phi.dot_p.dot_pent.time	459.50	60.07	0.00	36	phi.dot_p.time_pent.dot	147.80	4.24	0.06	8
	phi.time_p.time_pent.dot	545.05	145.63	0.00	69	phi.time_p.dot_pent.time	150.25	6.68	0.02	10
	phi.dot_p.time_pent.time	549.24	149.82	0.00	69	phi.dot_p.time_pent.time	152.41	8.84	0.01	11
	phi.time_p.dot_pent.time	560.03	160.60	0.00	68	phi.time_p.time_pent.dot	152.69	9.12	0.01	11
	phi.time_p.time_pent.time	786.34	386.92	0.00	101	phi.time_p.time_pent.time	159.14	15.57	0.00	14