POPULATION DYNAMICS OF ATLANTIC STURGEON IN THE ALTAMAHA RIVER, GEORGIA

by

PAUL M. SCHUELLER

(Under the direction of Douglas L. Peterson)

ABSTRACT

The Atlantic sturgeon was commercially harvested in the United States until 1996. The current status of most populations since fishery closure is unknown as life history and habitat use have been the focus of most previous research. From 2004 to 2007, I collected mark-recapture data of both the juvenile and adult portion of the Altamaha River population of Atlantic sturgeon. Several hundred adults entered the river annually, but only a small portion of these were reproductively ripe. Annual mortality of adults may be higher than expected for an unharvested population. The juvenile population of Atlantic sturgeon exhibited a high turnover rate with high rates of per capita recruitment and low rates of apparent survival. The demographic parameters presented here could be incorporated into population projection models to make assessments of population recovery and predictions of future population trends.

Index words: Atlantic sturgeon, population assessment, population dynamics, mark-recapture

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DEDICATION

I would like to dedicate this thesis to my parents, Leo and Jeanie Schueller, and sister, Brenda Schueller, who provided me with the ability and support required to pursue my education. I would also like to dedicate this thesis to all of my friends who helped me keep a level head through my career in Georgia.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Atlantic sturgeon (*Acipenser oxyrinchus*) are large, long-lived fish with a history of commercial exploitation (Smith and Clugston 1997, Bain et al. 2000). Atlantic sturgeon were once highly abundant in most coastal rivers from St. Lawrence River, Canada to St. Johns River, Florida (Vladykov and Greeley 1963, Murawski and Pacicheo 1977). Commercial exploitation began in the late 19th century and quickly decimated many populations (Murawski and Pacicheo 1977, Bain et al. 2000). Thereafter, commercial landings continued at much lower levels until the 1970s when increased demand for caviar spurred a sharp increase in effort (Smith and Clugston 1997). Overexploitation and degraded habitats lead to further population declines, and US fisheries were closed in 1996 (ASMFC 1998). A highly regulated fishery has since persisted in Canadian waters, but US populations are not expected to be reopened for at least two more decades. Assessment of population recovery since fishery closure is needed to determine the effectiveness of these management actions.

Several differences in life history characteristics between northern and southern populations of sturgeon have been documented, but further studies are needed to better understand how these difference affect population dynamics and hence, restoration efforts (Dadswell et al. 1984, Bain 1997, Kynard 1997). In coastal rivers of North Carolina, South Carolina, and Georgia, Atlantic sturgeon mature earlier but have a shorter life spans than in northern rivers (Van Den Avyle 1984, Smith 1985). Differences in habitat preferences of both adults and juveniles also have been observed (Moser and Ross 1995, Collins et al. 2000, Hatin et al. 2002, Hatin et al. 2007). Unfortunately, fisheries dependent data are no longer available and few recent studies have provided information on adult or juvenile population dynamics, stocking assessments, or ecology of marine juveniles (also known as sub adults). Information regarding latitudinal variation in life history is largely lacking, yet this information is critical for proper protection and restoration of remaining populations.

Recent studies suggest that the Altamaha River may support the largest remaining population of Atlantic sturgeon south of the Hudson River; however, quantitative studies of recruitment, spawner abundance, and population structure are still needed to fully evaluate stock status (Peterson et al. 2008). As such, the Altamaha population offers a unique opportunity to learn more about the life history characteristics of Atlantic sturgeon at what is currently believed to be the southern extent of their extant range (Smith and Clugston 1997). In chapter two, I present a manuscript with four primary research objectives focused on the adult population of Atlantic sturgeon in the Altamaha River: 1) to estimate abundance, 2) to estimate annual mortality, 3) analyze sex ratio and age structure, and 4) to assess the potential effects of environmental variables on seasonal movement. I present a second manuscript, in chapter three, with three additional research objectives focused on juvenile Atlantic sturgeon; 1) to estimate annual age-specific abundance, 2) to estimate annual apparent survival and per capita recruitment, and 3) to identify key factors that influence recruitment processes. In the concluding chapter, the result of both studies are summarized and synthesized in the context of current information gaps and management need for species recovery throughout the Atlantic coast.

Life History

Atlantic sturgeon are large, long-lived, anadromous fish with a complex life history. Historically, their range extended from the St. Lawrence River, Canada south to the St. Johns

River, Florida (Vladykov and Greeley 1963), but their current distribution is diminished (Smith and Clugston 1997). Females may grow to 3.0 m in length while males only reach 2.1 m. The largest fish ever recorded was a 4.3 m, 368-kg female, caught in 1924 by a commercial trawler on Georges Bank in the North Atlantic Ocean (Vladykov and Greeley 1963). Maximum age reported from northern populations is 60 years (Smith 1985) and 30 years for southern stocks (Van Den Avyle 1984). In addition to differences in longevity, Atlantic sturgeon in southern rivers also mature earlier with females typically spawning by age-10 and males by age-8 (Smith 1985). In contrast, age at maturity in northern populations may require 20 years or more (Scott and Crossman 1973).

Adult Atlantic sturgeon select spawning sites well upriver from the saltwater interface of coastal rivers, usually at least 20 -100 rkm from the ocean (Van Eenennaam et al. 1996, Collins et al. 2000, Caron et al. 2002, Hatin et al. 2002). Presumably, this is because early life stages are intolerant of salinity (Van Eenennaam et al. 1996). The demersal, adhesive eggs are broadcast on rocky substrate, where they hatch after a 5 – 6 day incubation period at 18^{o} C (Gilbert 1989). After spawning, adults gradually return to saltwater where they may remain for 1 – 5 years before returning to spawn again (Vladykov and Greeley 1963). Larval development occurs at about eight days post-hatch, at which time downstream migrations begin (Kynard and Horgan 2002). As the larvae develop into early juveniles, they primarily use deep water habitats near the fresh/saltwater interface (Bain 1997, Moser and Ross 1995). Thereafter, juveniles remain in natal rivers for 2 – 6 years before out-migrating to marine environments (Dovel and Berggren 1983).

Growth

Atlantic sturgeon grow quickly during their first three years of life. At hatching, embryonic sturgeon are about 7 mm in length (Smith et al. 1980), and within 8 days of hatching begin exogenous feeding (Kynard and Horgan 2002). Once exogenous feeding begins, the larvae grow quickly; 20 mm by day 20; 100 mm by day 130 (Smith et al. 1980). By age-1 juveniles may exceed 500 mm TL in both northern and southern populations (Dovel and Berggren 1983, McCord et al. 2007). By age-3 Hudson River juveniles are over 700 mm, but thereafter, growth in the river slows, which probably triggers the onset of out-migration and the transition to the sub adult life stage (Dovel and Berggren 1983). While juvenile growth has been fairly well studied in northern populations, studies of juveniles in southern rivers are largely lacking.

The growth pattern of Atlantic sturgeon changes at maturity, and differences between sexes and regions are well documented. In the Hudson River, Atlantic sturgeon reach maturity at about 150 cm, after which somatic growth slows (Bain 1997). As adults, the adult growth becomes asymptotic (Stevenson and Secor 1999). In the Hudson River, asymptotic growth begins by age-11 for males and age-12 for females, which, not surprisingly, corresponds with the onset of maturity (Van Eenenaam et al. 1996). Males typically grow faster than females, but females obtain larger size. In southern populations, the longer growing season may lead to more rapid growth, and hence, earlier age at maturity (Stevenson and Secor 1999).

Juvenile Migrations and Habitat Use

Exact timing of larval downstream migration remains unknown; however, laboratory studies have revealed useful information regarding larval behavior (Kynard and Horgan 2002). Passive downstream migration, or larval drift, lasts about 12 days, and occurs mainly at night during the first 6 days; however little diel preference is shown thereafter. Nocturnal migrations likely decrease predation risk, and larvae may use daylight hours for foraging. As juvenile development progresses, the risk of predation decreases, and daytime migrations may become increasingly common (Kynard and Horgan 2002). Downstream migration continues until juveniles reach the nursery grounds, typically located near the fresh/saltwater interface. Once there, age-0 juvenile will forage with other older juveniles until they are 2-6 years old and ready to leave their natal estuaries (Dovel and Berggren 1983, Kynard and Horgan 2002).

Latitudinal and seasonal variations in habitat preferences also are well documented in juvenile Atlantic sturgeon. As pre-migratory or “river-resident” juveniles, the young fish use riverine habitats throughout the year; however, fish in northern populations tend to occupy different habitat zones depending on season, while those from southern populations show no distinct seasonal habitat preferences (Dovel and Berggren 1983, Lazzari et al. 1986, Moser and Ross 1995). In the Hudson, Delaware, and Chesapeake Systems, river-resident juveniles use upriver habitats from late spring until fall but over-wintering occurs in the more saline habitats of the lower estuary (Dovel and Berggren 1983, Lazzari et al. 1986, Secor et al. 2000). In contrast, Moser and Ross (1995) found that juveniles in the Cape Fear River, North Carolina, occupy a single river reach throughout the entire year; however, habitat use did expand during the winter months (Moser and Ross 1995). In northern populations, juveniles move upriver as water temperatures rise in late spring and summer, while in southern populations the young fish begin to gather in well-defined deep water areas above the fresh/saltwater inteface (Dovel and Berggren 1983, Lazzari et al. 1986, Moser and Ross 1995). In either case, these seasonal changes in habitat use may be linked to decreasing intolerance of saline conditions as water temperature increases (Zeigeweid et al. in press).

Despite seasonal differences in habitat use among northern and southern populations, several habitat preferences are common across the species range. Regardless of latitude, juvenile Atlantic sturgeon are frequently found in deep channel habitats, but they also have been captured over shoals and areas of swift current (Moser and Ross 1995, Bain 1997, Savoy and Pacileo 2003, Sweka et al. 2007). In the Hudson River, catch-per-unit-effort (CPUE) was significantly higher in deep water habitats than in shallow waters (Sweka 2007), and in Long Island Sound (LIS), juvenile Atlantic sturgeon selected deep water zones even though these habitats were relatively scarce (Savoy and Pacileo 2003). These findings suggest that juveniles captured in shallow water habitats may result more from fish movements rather than habitat preferences (Savoy and Pacileo 2003, Sweka et al. 2007). Ultimately, habitat preferences of juvenile Atlantic sturgeon may be largely influenced by food availability. Juveniles often inhabit areas of freshwater or low salinity just upstream of the fresh/saltwater interface (Moser and Ross 1995, Bain 1997, Hatin et al. 2007). However, location of juveniles in the Chesapeake Bay was not related to variation in water quality but rather, it was thought to be related to foraging behavior (Secor et al. 2000). In the Hudson River, catch rates of juveniles was often higher in soft bottom areas where prey availability was higher (Sweka et al. 2007).

Juvenile Atlantic sturgeon inhabit natal rivers for up to 6 years before out-migrating to marine environments. Juveniles younger than age-4 are commonly found in the Hudson River, but juvenile abundance decreases after age-3 (Dovel and Berggren 1983, Peterson et al. 2000). Recent studies in LIS and the Connecticut River determined that older juveniles were present in both systems even though no reproduction occurs in the Connecticut River. Savoy and Pacileo (2003) suggest that these fish are older juveniles from the Hudson River that are preparing for out-migration to marine environments (Savoy and Pacileo 2003). The specific age that out-migration occurs is unknown, but it has been hypothesized that out-migration occurs in the fall and that males out-migrate sooner than females (Dovel and Berggren 1983).

Marine habitats are used by both sub adult and adult Atlantic sturgeon, and lengthy coastal migrations are thought to be quite common. Fish tagged in the Hudson River, for example, have been recaptured in coastal rivers from North Carolina to Massachusetts (Dovel and Berggren 1983, Bain 1997). Sub adults tagged as river-resident juveniles in North Carolina and Georgia have been recaptured as far north as LIS (Smith 1985, Peterson, unpublished data). While multiple accounts of lengthy migrations exist, Waldman et al. (1996) suggests that most adults and sub adults remain close to their natal rivers. During coastal migrations, both marine life stages may enter non-natal estuaries, but they have never been observed upstream of a fresh/saltwater interface (Kieffer and Kynard 1993, Savoy and Pacileo 2003).

Spawning Migrations/Habitats

At maturity, Atlantic sturgeon enter coastal rivers and begin their freshwater spawning migrations. Smith (1985) reports that adult Atlantic sturgeon enter coastal rivers when water temperature reaches 7 – 10° C. In southern populations, spawning migrations begin in February, but in northern populations fish don't enter rivers until May (Vladykov and Greeley 1963). Male Atlantic sturgeon enter coastal rivers several weeks before females, and males are thought to spend more time in fresh water (Dovel and Berggren 1983, Van Eenennaam et al. 1996). Females make spawning migration every 3-5 years and males every 1-5 years (Smith 1985).

Atlantic sturgeons broadcast their eggs over coarse substrates consisting of gravel, cobble, and bedrock when water temperatures are 14 – 23° C (Smith 1985, Smith and Clugston 1997). While precise timing of spawning may vary with latitude, the range of water temperatures that induce female maturation is the same for both northern and southern populations (Bain et al. 2000, Collins et al. 2000, Hatin et al. 2002). Spawning typically occurs in the spring, but Collins et al. (2000) suggest that a second fall spawn may occur in South Carolina rivers. Hatin et al. (2002) suggest that spawning adults may use relatively discrete areas as spawning habitat. In the Hudson River, ripe adults are consistently captured during the spawning season from two specific locations (Bain et al. 2000).

After spawning, adults slowly return to the marine environment, often remaining in estuarine habitats for several weeks before returning to oceanic waters by late fall (Bain 1997, Hatin et al. 2002). In southern populations, however, adults are frequently observed in both estuarine and freshwater habitats throughout the year; however, the reasons for this behavior are unknown (Collins et al. 2000).

Population Declines and Management

Commercial exploitation of Atlantic sturgeon began in the late 1800s, and population declines quickly followed. Commercial fishing of Atlantic sturgeon in the United States began in the 1870s after European technologies enabled the production of high quality caviar and more efficient capture (Secor and Waldman 1999). During this era of uncontrolled exploitation, Atlantic sturgeon were harvested from both coastal rivers and in near-shore marine environments (Bain et al. 2000). In the early Delaware Bay fishery, male Atlantic sturgeon only comprised about 10% of the total harvest and 2.6 – 4.3% of biomass because females were selectively targeted for caviar production (Secor and Waldman 1999). Landings in the US fishery peaked in 1890 at 3,350 mt (Smith and Clugston 1997), 75% of which came from the Delaware River (Secor and Waldman 1999). Because adult sturgeon only enter spawning rivers every 3 – 5 years, the sustained harvests in the early years of the fishery may have misled fisherman into believing that harvest were sustainable indefinitely (Secor and Waldman 1999). Unfortunately, populations were grossly overexploited in short order and by 1900 landings had declined by 90% despite a steady increase in effort during the same period (Smith and Clugston 1997). Uncontrolled harvest continued to decimate remaining populations and by 1905 Atlantic sturgeon had been nearly extirpated from both the Delaware and Chesapeake Bays (Murawski and Pacicheo 1977).

Over-exploitation, combined with habitat degradation, likely contributed to localized extirpation. After the initial decline of most stocks around 1900, Atlantic sturgeon harvest remained at ~1% of peak harvest through most of the 1900s (Bain et al. 2000). Simultaneously, construction of dams on many coastal rivers prevented adult Atlantic sturgeon from reaching their historic spawning grounds (Smith and Clugston 1997). Industrial development along many rivers lead to channel alterations and increased pollution that severely altered both physical and chemical characteristics of critical sturgeon spawning and nursery habitats. The collective effects of these anthropogenic activities were a range wide decline in adult abundance and juvenile recruitment (Smith and Clugston 1997).

By the late 1900s, a few populations were showing signs of recovery. In the Hudson River, commercial landings in the 1980s increased to approximately 20% of the peak landings reported nearly a century earlier (Smith and Clugston 1997, Bain et al. 2000). However, the fishery remained relatively unregulated during this period and many juveniles and non-spawning adults were harvested (Smith and Clugston 1997, Bain et al. 2000). The resurgence in sturgeon harvest lead to increased management oversight by the Atlantic States Marine Fisheries Commission (ASMFC) and in 1990 a “sustainable harvest” level was established, with a management goal of limiting the commercial harvest to 10% of maximum landings reported in the 1890s. With regulatory authority delegated to the individual states, however, management goals were not uniform and hence, difficult to enforce (Smith and Clugston 1997, Bain et al. 2000). Most states restricted harvest or allowed an incidental harvest of Atlantic sturgeon in other fisheries. Some states, including both Georgia and Delaware, maintained their directed fisheries, but limited commercial harvest with minimum length limits. New York and New Jersey had the least restrictive regulations, allowing both directed and incidental fisheries, although they too established a minimum length limit to reduce the take on immature fish (Smith and Clugston 1997). Unfortunately, these management efforts proved to be too little, too late. In 1994, for example, harvest goals on the Hudson River were exceeded resulting in recruitment failure in the years following (Bain et al. 2000, Peterson et al. 2000). In December of 1995, the ASMFC placed an emergency moratorium on all US Atlantic sturgeon fisheries. Despite bitter protest from commercial interests, the moratorium was made permanent in 1998 (ASMFC 1998) with the intent of protecting 20 breeding cohorts. Although some debate remains about when the fishery could be reopened, Bain et al. estimate that the fishery will remain closed until at least 2038 (ASMFC 1998, Bain et al. 2000). Although stocking and other recovery efforts are now underway in some rivers, results have not been quantified (St. Pierre 1999, Peterson et al. 2000, Secor et al. 2000).

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CHAPTER 2

ABUNDANCE, SURVIVAL, AGE, SEX, AND IN-RIVER MOVEMENTS OF ADULT ATLANTIC STURGEON IN THE ALTAMAHA RIVER, GEORGIA[1]

Schueller, P. and D. L. Peterson *to be submitted to*

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Abstract

Atlantic sturgeon were once the target of commercial harvest along the Atlantic coast of the United States until a federal moratorium was implemented in 1996. Many populations lack sufficient records of historical abundance to allow for assessment of population recovery since fishery closure. From 2004 to 2007, I evaluated abundance, factors influencing in-river movement, annual survival, age, and sex of the adult population of Atlantic sturgeon in the Altamaha River. I used gill nets located in the main branches of the river system to capture adult Atlantic sturgeon. Over the four years of study I captured 320 individuals from 5 to 17 years old, with a mode of age-9 in all years. I used closed Schnabel and open POPAN models to estimate annual spring adult abundance, and POPAN models allowed for evaluation of environmental factors that influenced in-river movement. Abundance estimates from Schnabel models ranged from 192 to 324 individuals, while POPAN estimates ranged from 89 to 213 individuals. Catch curve analysis indicated that annual mortality was 23.9% throughout the study. Interactive effects of tide cycle and other environmental variables, such as temperature, discharge, and photoperiod, influenced in-river movement of adult Atlantic sturgeon. Estimated annual mortality was similar to those of estimates from a harvested population. No fish older than 20 years was captured in this study and at most, two individuals that were captured were exposed to previous commercial fishing. The adult population was composed of 79.5% and 68.6% males in 2006 and 2007 respectively. As a portion of the observed population is migratory, Schnabel abundance estimates in this and other studies may be biased high. This work indicates that few ripe individuals are found in the Altamaha River annually, and adult abundances may be overestimated in some systems.

Introduction

Atlantic sturgeon (*Acipenser oxyrinchus*) are a long-lived, anadromous species with a complex life history that require specific combinations of freshwater, estuarine, and marine habitats (Vladykov and Greeley 1963). Its life history is characterized by long life span, late age-at-maturity, and protracted spawning periodicity (Vladykov and Greeley 1963, Scott and Crossman 1973, Smith 1985, Smith and Clugston 1997). Although these characteristics have enabled the Atlantic sturgeon to survive virtually unchanged for millions of years, but they have also rendered the species particularly vulnerable to declines from commercial fishing and habitat alterations (Smith et al. 1984). Despite the 1996 closure of all US Atlantic sturgeon fisheries, a recent status review concluded that most US populations are currently at either moderate or high risk of becoming endangered within the next 20 yrs (Atlantic Sturgeon Status Review Team 2007). Although this report specifically identified the need for additional data on abundance and population dynamics, fisheries dependent data are no longer available and few studies have provided estimates of adult abundance in US waters (Peterson et al. 2008).

The Atlantic sturgeon population of the Altamaha River, Georgia is the second largest extant population in US waters and the largest remaining in the southern portion of the species range (Kahnle et al. 2007, Peterson et al. 2008). Although the Altamaha River is the longest unimpounded river system remaining on the US Atlantic coast, rapid development throughout the watershed has altered available fish habitat. These habitat changes have had dramatic implications for Atlantic sturgeon, which was once a major biotic component of the drainage (Colligan et al. 1998). Both chemical and physical changes have resulted from land development and industrial effluents. These changes threaten to further degrade critical habitats by increasing nutrient levels and changing natural thermal regimes (Colligan et al 1998). Degraded water quality may decrease reproductive success by reducing juvenile habitat and depressing survival of early life stages (Rochard et al. 1990, Beamesderfer and Farr 1997, Collins et al. 2000a, Niklitscheck and Secor 2005).

Management decisions that benefit population growth will require an understanding of current population status and variations in life history. Life history of sturgeons varies with latitude (Dadswell et al. 1994, Bain 1997, Kynard 1997), but Atlantic sturgeon life history in the southern portion of its range should be further described. Differences in life history between northern and southern populations may necessitate different management actions between the regions. Studies of adult habitat use in southern populations have been conducted (Collins et al. 2000), but no estimates of adult abundance have been made. Before limitations to population recovery can be addressed, current population parameters and status must be determined. The primary objectives of this study were to: (1) estimate abundance, (2) assess the potential effects of several environmental factors on behavior, (3) estimate annual mortality, and (4) analyze the sex and age structure of the adult population of Atlantic sturgeon in the Altamaha River, Georgia.

Methods

Study Site/Fish Sampling

The study was conducted entirely within the tidally influenced portion of the Altamaha River system, near Darien, Georgia (Figure 2.1). Adult Atlantic sturgeon were captured using anchored multifilament gill nets measuring 60.9 m long by 6.1 m deep with stretched mesh sizes of either 30.5, 35.6, or 40.6 cm. To estimate abundance during the spring run, fish were collected from each of the major branches within the Altamaha River delta, and at least 1 km upriver of all main branches. Nets were deployed perpendicular to flow and fished continuously (except for during routine repairs and maintenance) from March to May, 2004 – 2007. Effort was measured in net days and netting locations were chosen based on maximum water depth available where the bottom was free of obstructions. Although I tried to maintain the same netting sites throughout the study, movement of large woody debris during some high water events necessitated the selection of alternate netting sites in some years. In 2004 and 2005, one net was set in the Champney River (Figure 2.1; rkm 18.6), while two others were set in Lewis creek (rkm 26.2 & 26.6). In 2006 and 2007, nets were set in the Champney River, the Altamaha River (Figure 2.1; rkm 25.0 of the south branch), and just above the junction of these two branches (rkm 23.2 in 2006, rkm 21.9 in 2007). Nets were checked at each slack tide (four times daily) and captured fish were removed and placed in a 2.4 by 0.9 m aerated tank for transport to the nearest boat launch (rkm 15.9). Once there, the fish were transferred to a 1-m by 3-m floating net pen and allowed to recover for at least 30 minutes before being measured (fork length in mm) weighed (kg) and inspected for PIT tags. If no tag was found, one was injected beneath the fourth dorsal scute. A coping saw was used to remove a 1-cm section from the leading edge of the left pectoral fin spine for later age determination. In 2006 and 2007, sex was determined by inserting a laparoscope into the body cavity, facilitating visual inspection of the gonads to determine sex and reproductive condition as described by Conte et al. (1988). Fish were then allowed to recover in the water for 2-3 minutes before being released.

Data Analysis

I used the Schnabel model for estimating spring, in-river adult annual abundance as described by Ricker (1975). Only fish of fork length greater than 1 m were used in any mark-recapture models. Assumptions of the Schabel model include:

1. Marked fish do not lose their marks prior to recapture periods

2. Marked fish are not overlooked in recapture samples

3. Marked and unmarked fish are equally vulnerable to capture in recapture periods

4. There is no mortality of marked or unmarked individuals during sampling

5. After release, marked animals become randomly mixed with unmarked animals

6. There are no additions to the population during the study interval

To allow for random mixing of tagged and untagged fish, all captured individuals were released downstream of the sampling area. Individuals were released within one hour of capture. Mortality was assumed to be zero during the 3-mo sampling period, as this is a relatively short time frame in comparison to the known life-span of Atlantic sturgeon. Because nets were fished continuously, high and low tides were used to define sampling intervals within the Schnabel model. Ninety-five percent confidence intervals were established for annual abundance estimates using a Poisson distribution to account for low numbers of recaptures (Ricker 1975).

Abundance estimates from the closed Schnabel model were compared to similar estimates calculated using open models derived from a reparameterized Jolly-Seber model as described by Schwarz and Arnason (1996). This model, often referred to as POPAN, is based on the idea that a super-population of animals exists and that some animals enter the sample population and are available for capture during sampling. The POPAN reparameterization estimates the total number of individuals (N), marked or unmarked, available for capture, which represents estimates of the number of adults in a given year in the Altamaha River estuary. This approach also estimates capture probability (p), apparent survival (φ), and entry probability (pent). The entry probability parameter estimates the probability of unmarked individuals entering the population, and therefore, the Altamaha River estuary (Schwarz and Arnason 1996). Mark-recapture models including apparent survival assume that all emigration from the study area is permanent (Williams et al. 2002). Therefore, the apparent survival parameter represents the probability of an individual surviving and staying in the sample area from one period to the next. POPAN models are reliant on the following assumptions:

1. All marked and unmarked fish have the same probability of capture
2. All fish in the super-population have the same probability of entering the sample population
3. Every fish marked at time i has the same probability of surviving to $i + 1$
4. Marks are not lost or overlooked
5. Sampling occurs instantaneously, or over a short interval, and recapture fish are released immediately
6. All emigration is permanent
7. Fates of all fish, with respect to capture, survival and entry, are independent

The POPAN model has been developed in a likelihood framework, and linear covariates can be imposed on parameters of interest (Schwarz and Arnason 1996). POPAN models allowed me to estimate annual abundance, environmental factors influencing capture, and environmental factors influencing in-river movement of adults throughout the study.

A candidate set of POPAN models with varied parameters was constructed for each study year. The capture histories were pooled so that each day was considered a sampling period. Survival was modeled as constant to maintain model simplicity and because we had little evidence to support alternative models for survival. Capture probability was modeled as constant, as a function of total length of individuals, or as a function of water temperature, tide cycle, or their additive and interactive effects. Capture probability was not a parameter of primary interest, but was hypothesized to vary with the above environmental variables.

Use of covariates on the entry probability (pent) parameter of POPAN models allowed for inferences regarding in-river movements of adults throughout the sampling season. The entry probability parameter was modeled as either a function of environmental variables or held constant. Temperature data were obtained from the most downriver Georgia Coastal Ecosystem – Long Term Ecological Research (GCE-LTER) monitoring station (~rkm 14, in South Altamaha River), while discharge data were obtained from the closest upriver United States Geologic Survey (USGS) gaging station (~rkm 100; USGS #02226000). Photoperiod data were obtained from National Oceanic and Atmospheric Administration (NOAA) weather data (Appendix 1). Because these three predictor variables were highly correlated (Pearson's $r \geq 0.65$) they were never used together in the same model to avoid multicollinearity. I used maximum daily high tide (MDHT) to determine if fish were entering the study section of the river based on variation in tidal magnitude (referred to as tidal cycle). Because MDHT was not correlated with the other variables (Pearson's $r \leq 0.37$), it was incorporated into models with both additively and interactively with other variables. All predictor variables were standardized, with a mean of zero and standard deviation of one, prior to incorporation into models.

The relative likelihood of models and parameters was evaluated with an information-theoretic approach as described by Burnham and Anderson (2002). The plausibility of each model was evaluated based on Akaike's information criterion (Akaike 1973) with an adjustment for small sample size (AICc; Hurvich and Tsai 1989). I accounted for model selection uncertainty by model-averaging the recapture probability, apparent survival, and abundance parameters from all models in the candidate set. Many models carried relative support in 2007; therefore the relative support for different predictor variables thought to influence entry probability were assessed by calculating parameter importance weights, which were calculated by summing the relative model weights of all models the parameter appeared in (Burnham and Anderson 2002). Importance weights were calculated for all predictor variables individually, and for combinations of non-correlated predictor variables (additive and interactive effects). I also assessed the effect of different environmental factors on the entry parameter in a manner that allowed for interpretation of an effect size.

Expected entry probability values were estimated from model-averaged beta parameters and plotted across a range of predictor variable values. The $\hat{\bar{\beta}}$ model-averaging approach, as described by Burnham and Anderson (2002), was used to average the beta estimates. The range of values used for estimating entry probabilities was based on the observed range of all three variables. Expected entry probability values were predicted across the observed range at both high (1.5 standard deviations above mean) and low (1.5 standard deviations below mean) MDHT for all three predictor variables. Given a value for tidal cycle (-1.5 or 1.5) and a given predictor variable (-2.5 to 2.5 incremented by 0.1), the composite models were used to calculate log-odds (η), which were then back-calculated to expected entry probability. Plots of entry probabilities then were used to assess the relative sensitivity of the parameter to changes in temperature, photoperiod, discharge, and tidal cycle. The effect of tidal cycle between low and high levels was interpreted as the difference in probabilities, while holding the other variable constant. The effect of other variables was interpreted as the difference in probabilities across the range of values.

Population age structure and annual mortality was evaluated by assigning ages from cross-sections of pectoral fin spines as described by Cuerrier (1951). Sections were air dried for at least one month, after which they were cross sectioned to a thickness of ~300 µm with a Beulher Isomet® low-speed saw. Thermoplastic glue was used to attach each cross-section to a glass microscope slide. A variable magnification dissecting scope was used to aid in the counting of annuli. A catch-curve was then constructed using these data to estimate annual mortality of the adult population as described by Ricker (1975). To reduce variance in estimated mortality resulting from annual sampling variance, a hierarchical model with a random effect of year and a randomly varying intercept was created (Raudenbush and Bryk 2002). The x-intercept of the catch curve regression line of the sample population was considered the mean maximum age of individuals.

Results

Over the four years of study, 320 adult Atlantic sturgeon were captured in 243 net days (Table 2.1). Few fish were captured in March, but catch rates increased around the third week of April and remained high through the second week of May. Interestingly, water temperatures during the peak of the run were largely >23° C, the maximum reported spawning temperature for Atlantic sturgeon (Smith 1985; Figure 2.2). There was little difference in mean fork length or mean weight (Figure 2.3) of captured adults, among years; however, females were longer and heavier than males in both years when laparoscopic sex determinations were conducted (Figure 2.4).

Annual abundance estimates from Schnabel and POPAN models were different in each year of the study (Table 2.1). Schnabel estimates varied from 192 in 2007 to 386 in 2005, while those from POPAN models varied from 89 in 2004 to 213 in 2005 (Table 2.1). Based on AICc weights, the most plausible POPAN models had capture probability as a function of fish total length in all years, and entry probability as a function of various environmental covariates in all years; however, many models, with different parameters, carried some relative weight in all years (Table 2.2). Daily apparent survival varied from 0.13 to 0.45 annually, and recapture probability varied from 0.28 to 0.99 annually based on mean fish size (Table 2.3).

The environmental variables that most influenced entry probability varied by study year (Table 2.4). In 2004, the most important parameter combination was temperature and tidal cycle interactively, which was 2.79 times more plausible than the interactive effects of photoperiod and tide cycle. The additive effects of discharge and tidal cycle were most influential in 2005. Models with discharge and discharge with tide cycle additively carried similar importance weight values in 2006. In 2007, the most important parameterization of entry probability was photoperiod alone, which was 2.55 times more likely than photoperiod and tide cycle additively.

The effects of environmental variables on probability of river entry revealed several consistent patterns among study years (Table 2.5). In all four years of study, temperature and photoperiod had a positive effect on entry probability. Discharge and tidal cycle had negative effects on entry probability in all four years, although in 2004 the 95% confidence intervals of the discharge parameter overlapped zero, indicating that the estimate was not precise.

Predicted entry probabilities were most affected by interactions between tide cycle and other environmental variables (Appendix 1). The magnitude of environmental variable effects was greatest during high MDHT periods in all years except 2005. In many cases, environmental variables had little effect at low MDHT values. Differences resulting from changes in tidal cycle were less than those resulting from changes in environmental variables, suggesting that tidal cycle had little effect on entry probability by itself. For example, in 2007, expected entry probability changed from near 0.9 at low discharge and high MDHT, to less than 0.1 at high discharge and high MDHT. Conversely, expected entry probability at low discharge and low MDHT was about 0.75 and only decreased to about 0.2 at high discharge and low MDHT

(Figure 2.7; see appendix 1 for full results). In most years, the largest difference in entry probabilities resulted from the environmental variable that was most supported by importance weights; however, in 2007, changes in discharge, which did not carry the most importance weight, resulted in greater changes in entry probability.

Ages of captured Atlantic sturgeon varied from 5 to 17 years, with age-9 fish most common (Figure 2.5), and the majority of fish were males. Only individuals age-9 or greater were included in the catch curve analyses. Annual mortality from the catch curve was estimated at 23.9% with a mean maximum age of 18.9 years based on the grand mean regression. Randomly varying intercepts resulted in mean maximum age estimates varying from 18.1 in 2007 to 20.1 years in 2005 based on Bayes' estimates from individual years (Figure 2.6). In 2006 and 2007, sex determinations of 148 individuals (Table 2.6) revealed that males comprised 79.5% and 68.6% of the catch in each respective year. Only one male, captured in March of 2006, was observed to be in ripe condition, based on the presence of milt. In 2006 and 2007, 13 and 14 females respectively were observed in stage 3 condition (eggs were present but not ripe). Three females in 2006 and four females in 2007 had enlarged green/gray colored eggs, indicating a transition in maturation from stage 3 to stage 4. Although no ripe females were observed in 2006, four ripe (stage 4) females were captured in 2007.

Discussion

Lack of historical data complicates assessment of population recovery in Atlantic sturgeon, but annual run estimates and age structure of the adult population suggests that the Altamaha River population may be recovering. Based on the relative abundance of adult age-classes, recruitment to the adult population appears to be stable. Likewise, annual estimates suggest that adult abundance in the Altamaha is similar that of large northern rivers (Dadswell

2006). Nonetheless, juvenile recruitment in the Altamaha should be assessed to better understand current population trend, and hence, population status.

The majority of adults captured in this study did not enter the river until water temperatures were well above the 23° C maximum reported for spawning in Atlantic sturgeon (Smith 1985). Furthermore, most of the adults captured were not in spawning condition, suggesting that many adults use the estuarine and freshwater habitats of the Altamaha for foraging or other non-reproductive purposes. Although this behavior is unknown in northern populations, similar findings have been previously reported for South Carolina rivers, where adults frequently use both riverine and estuarine habitats throughout the summer and fall months (Collins et al. 2000). Corroborating studies of adult habitat use are needed; however, our results suggest that latitudinal variations in Atlantic sturgeon life history may significantly affect population dynamics, and hence interpretations of population data between northern and southern stocks.

Comparison of open and closed population models used in this study produced different estimates of annual adult abundance. However, estimates obtained using the open POPAN models were likely more accurate because they accounted for heterogeneity of capture probability and model selection uncertainty. Estimates from the POPAN models were more precise, and given that some individuals were ripe, migratory fish the assumption of population closure required for the Schnabel model was not likely met. Violations of the closure assumption, resulting from emigration would cause negative bias in capture probability and positive bias in the resulting abundance estimate (Williams et al. 2002). Schnabel estimates were consistently higher than those obtained from POPAN models, also suggesting that the requisite assumption of a closed population was violated. Hence, we suggest that future abundance assessments of adult Atlantic sturgeon employ open models to avoid the potential for inflated population estimates.

Specific environmental variables most influencing Atlantic sturgeon movements varied from year to year, but tidal cycle was always important. As tidal cycles are largely influenced by the lunar cycle, my results are consistent with those of Sulak and Clugston (1999) who concluded that movements Gulf sturgeon in the Suwannee River were largely influence by lunar phases (Sulak and Clugston 1999). While previous studies have documented a range of water temperatures during the onset of annual migrations (Smith 1985), temperature effects on riverine movements have not been quantified previously. The relative support for various environmental factors from year to year suggests that variation in annual sampling may have influenced the results, or there is additional random effects in the environment that were not accounted for. My results demonstrated that river entry was positively related to both photoperiod and river temperature and negatively related to discharge and tidal cycle. In the Altamaha River, adult Atlantic sturgeon are most likely to enter the estuary in late spring during periods of low flow, and at water temperatures >20^{o}C. Modeling of environmental variables also suggests that adult Atlantic sturgeon are more likely to enter the river when MDHT is low.

Although annual mortality rates of adult Atlantic sturgeon provided in this study establish a baseline for future status assessment, interpretation of these estimates is difficult because similar estimates from other southern populations have not been attempted since fishery closure more than 10 years ago. From 2001 to 2003, Berg et al. (2007) estimated annual mortality of Gulf sturgeon in the Yellow River, Florida, to be 11.9%. Similar analyses of the Suwannee River population of Gulf sturgeon estimated mortality at 17% during the mid 1980s to the mid 1990s (Pine et al. 2001), and 16% through the 1990s (Sulak and Clugston 1999). Like the

Altamaha River, the Suwannee system had been closed to commercial fishing for approximately ten years at the time of analysis. Sensitivity analysis showed that increases in adult mortality to 20% could result in population declines in the Suwannee River (Pine et al. 2001). Total annual mortality rates of Atlantic sturgeon in the Hudson River during the last years of commercial fishing (1993 – 1995) varied from 8 to 21% for females and 24 to 33% for males (Kahnle et al. 2007). A mortality rate of 23.9% obtained in this study is higher than those reported for Gulf sturgeon, but similar to those observed in exploited northern populations, suggesting that the Altamaha stock is probably still recovering from commercial exploitation.

Age structure of the Altamaha River population suggests that recruitment has been stable during the past 20 years, but effects of commercial fishing may still be evident. All adult age classes were captured in each year of the study, with young adults (age-7 – age-9) being most abundant. As such, many of the captured individuals were likely young adults that had not previously spawned (Smith 1985). Because the Georgia fishery was closed in 1996, most of the young adults captured in this study were progeny of adults that had either escaped harvest, or more likely, were not yet mature when the fishery was closed. Because Atlantic sturgeon are known to live for at least 30 years in southern rivers (Van Den Avyle 1984), the absence of fish age-20 and older is probably a direct result of past commercial exploitation. In fact, the oldest individual we captured, age-17 in 2005, would have been age-7 in 1995, during the last year of commercial harvest. Because males mature at 7 – 9 years and females mature at 9 – 12 in southern populations (Smith 1985), few, if any, of the fish we captured during the study were exposed to the commercial fishery. As the population recovers, the age structure should shift as older individuals become increasing abundant. Because older adults are typically more fecund, recruitment also may be expected to increase, further accelerating population recovery.

The sex ratios observed in this study were 79.5% and 68.6% males in 2006 and 2007, respectively, and no ripe females were captured in 2006. Because females were disproportionately selected in commercial fisheries, the percentage of males observed in exploited Atlantic sturgeon populations is typically 70-83% (Van Eenennaam et al. 1996, Collins et al. 2000, Caron et al. 2002). Extrapolation using numbers of late stage females observed and capture probabilities from the most plausible models, yielded an estimate of 5 spawning females in 2006, and 22 spawning females in 2007. While these analyses reveal that the current adult sex ratio of the Altamaha population is similar to those reported for exploited populations, female spawners were slightly more abundant, again suggesting the population may be in early stages of recovery.

The results of this study show that several hundred adults use the Altamaha River annually; however, ripe adults comprised only a small fraction (<5%) of the annual adult run. Similar results were reported for the St Lawrence population where only two ripe females were observed in a random sample of 200 migrating adults (Caron et al. 2002). These findings suggest that because the spawning periodicity of Atlantic sturgeon is both protracted and variable, mark-recapture estimates of annual spawner abundance may be confounded by the presence of non-spawning adults (Smith et al. 1984), unless adults can be sampled on or near spawning grounds and reproductive readiness can be verified. I suggest that future studies address effective population size, using modern genetic techniques, in addition to numerical abundance based on traditional mark-recapture approaches.

While the results of this study present a quantified and current description of the spring run of adult Atlantic sturgeon in the Altamaha River, future studies are needed to better assess population trends, and hence recovery. My results suggest that while the Altamaha stock is probably the largest remaining south of the Hudson River, the scarcity of spawning adults and absence of fish older than age-17 suggests that the population is still in the early stages of recovery. Similarly, mortality rates were higher than expected suggesting that the effects of chronic over-exploitation may still be evident 10 years after the fishery was closed.

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Table 2.1. Numbers of net days, fish captured, recaptured, Schnabel and POPAN abundance estimates, and lower (LCI) and upper (UCI) 95% confidence intervals of adult Atlantic sturgeon in the Altamaha River from 2004 – 2007.

				Schnabel			POPAN		
Year	# Net Days	# of Captured	# of Recaptured	Estimate	LCI	UCI	Estimate	LCI	UCI
2004	47	67	7	324	144	667	89	76	102
2005	62	93	11	386	216	787	213	169	258
2006	70	84	15	241	139	377	139	118	160
2007	64	76	17	192	120	330	92	82	101

Table 2.2. Relative likelihood of POPAN models, within 10% of the most plausible model, of capture probability (p) and entry probability (pent) with constant survival from 2004 to 2007.

Year	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	K
2004	p(TL)pent(temp*tide)}	260.837	0.000	0.65203	1	7
	p(TL)pent(pp*tide)}	262.886	2.049	0.23405	0.359	7
2005	p(TL)pent(disc+tide)}	245.801	0.000	0.53768	1	6
	p(TL)pent(disc*tide)}	247.362	1.561	0.24632	0.4581	7
	p(TL)pent(pp*tide)}	247.933	2.132	0.18521	0.3445	7
2006	p(TL)pent(disc)}	321.847	0.000	0.42753	1	5
	p(TL)pent(disc+tide)}	322.208	0.361	0.35694	0.8349	6
	p(TL)pent(disc*tide)}	323.248	1.401	0.21224	0.4964	7
2007	p(TL)pent(pp)}	375.903	0.000	0.57985	1	5
	p(TL)pent(pp+tide)}	377.793	1.890	0.22535	0.3886	6
	p(TL)pent(pp*tide)}	379.066	3.163	0.11925	0.2057	7

Table 2.3. Estimates of daily apparent survival and daily recapture probability (for mean fish size) from POPAN models from 2004 – 2007.

	Apparent Survival			Recapture Probability		
Year	Estimate	LCI	UCI	Estimate	LCI	UCI
2004	0.454	0.310	0.605	0.281	0.124	0.519
2005	0.132	0.070	0.235	0.999	0.999	1.000
2006	0.316	0.211	0.445	0.597	0.403	0.764
2007	0.577	0.446	0.699	0.595	0.395	0.767

Table 2.4. Parameter importance weights (w_i) of different models of entry probability for 2004 to 2007 POPAN models.

2004		2005		2006		2007	
Parameterization	w_i	Parameterization	w_i	Parameterization	w_i	Parameterization	w_i
Temperature*Tidal Cycle	0.652	Discharge + Tidal Cycle	0.538	Discharge	0.428	Photoperiod	0.623
Photoperiod*Tidal Cycle	0.234	Discharge*Tidal Cycle	0.246	Discharge + Tidal Cycle	0.357	Photoperiod + Tidal Cycle	0.244
Photoperiod + Tidal Cycle	0.041	Photoperiod*Tidal Cycle	0.185	Discharge*Tidal Cycle	0.212	Photoperiod*Tidal Cycle	0.128
Temperature + Tidal Cycle	0.040	Photoperiod + Tidal Cycle	0.031	Photoperiod + Tidal Cycle	0.001	Temperature	0.003
Tidal Cycle	0.016			Photoperiod	0.001	Temperature + Tidal Cycle	0.001
Discharge + Tidal Cycle	0.007			Photoperiod*Tidal Cycle	0.000	Temperature*Tidal Cycle	0.001
Discharge*Tidal Cycle	0.005			Temperature + Tidal Cycle	0.000	Discharge	0.000
Temperature	0.004			Temperature	0.000	Discharge + Tidal Cycle	0.000
Photoperiod	0.001			Temperature*Tidal Cycle	0.000	Discharge*Tidal Cycle	0.000
Discharge	0.000						

Table 2.5. Model-averaged parameter values used in composite models for entry probability predictions.

Year	Model Subset	Parameter	Estimate	Unconditional Standard Error	LCI	UCI
2004	Temperature	Intercept	0.123	1.013	-1.863	2.108
		Temperature	0.530	0.199	0.141	0.920
		Tidal Cycle	-0.389	0.155	-0.694	-0.084
		Temperature*Tidal Cycle	0.486	0.190	0.113	0.859
	Photoperiod	Intercept	0.084	1.013	-1.901	2.069
		Photoperiod	0.504	0.216	0.081	0.926
		Tidal Cycle	-0.432	0.146	-0.718	-0.146
		Photoperiod*Tidal Cycle	0.401	0.179	0.050	0.753
	Discharge	Intercept	0.162	1.010	-1.818	2.142
		Discharge	-0.122	0.148	-0.412	0.168
		Tidal Cycle	-0.347	0.204	-0.747	0.052
		Discharge*Tidal Cycle	-0.147	0.141	-0.423	0.129
2005	Photoperiod	Intercept	-0.722	1.032	-2.744	1.300
		Photoperiod	1.710	0.233	1.253	2.166
		Tidal Cycle	0.055	0.325	-0.582	0.692
		Photoperiod*Tidal Cycle	-0.539	0.243	-1.015	-0.062
	Discharge	Intercept	-1.653	1.096	-3.803	0.496
		Discharge	-3.262	0.543	-4.327	-2.198
		Tidal Cycle	-0.378	0.325	-1.016	0.259
		Discharge*Tidal Cycle	0.380	0.596	-0.787	1.548
2006	Temperature	Intercept	-0.037	1.009	-2.015	1.942
		Temperature	0.622	0.138	0.351	0.893
		Tidal Cycle	-0.225	0.137	-0.493	0.043
		Temperature*Tidal Cycle	0.163	0.137	-0.105	0.432
	Photoperiod	Intercept	-0.078	1.010	-2.057	1.901
		Photoperiod	0.700	0.140	0.424	0.975
		Tidal Cycle	-0.185	0.121	-0.421	0.052
		Photoperiod*Tidal Cycle	0.060	0.138	-0.210	0.329
	Discharge	Intercept	-0.266	1.016	-2.257	1.726
		Discharge	-1.092	0.221	-1.525	-0.658
		Tidal Cycle	-0.218	0.172	-0.556	0.119
		Discharge*Tidal Cycle	-0.256	0.234	-0.714	0.202
2007	Temperature	Intercept	-0.149	1.012	-2.132	1.834
		Temperature	0.725	0.155	0.421	1.028
		Tidal Cycle	-0.072	0.164	-0.393	0.250
		Temperature*Tidal Cycle	0.179	0.211	-0.234	0.593
	Photoperiod	Intercept	-0.268	1.014	-2.256	1.720
		Photoperiod	0.894	0.167	0.567	1.221
		Tidal Cycle	-0.084	0.165	-0.409	0.240
		Photoperiod*Tidal Cycle	0.176	0.211	-0.237	0.589
	Discharge	Intercept	-0.141	1.012	-2.125	1.844
		Discharge	-0.770	0.197	-1.156	-0.383
		Tidal Cycle	-0.062	0.181	-0.417	0.293
		Discharge*Tidal Cycle	-0.177	0.402	-0.965	0.610

Table 2.6. Sex, egg condition, and maturation stage of adult Atlantic sturgeon captured in 2006 and 2007 in the Altamaha River

Year	Sex	Egg Condition	Maturation Stage	No. Identified
2006	Female	White/Yellow	3	13
		Green/Gray	4-Mar	3
	Total			16
	Male			62
2007	Female	White/Yellow	3	14
		Green/Gray	4-Mar	4
		Black	4	4
	Total			18
	Male			48
Total	Female			34
	Male			110

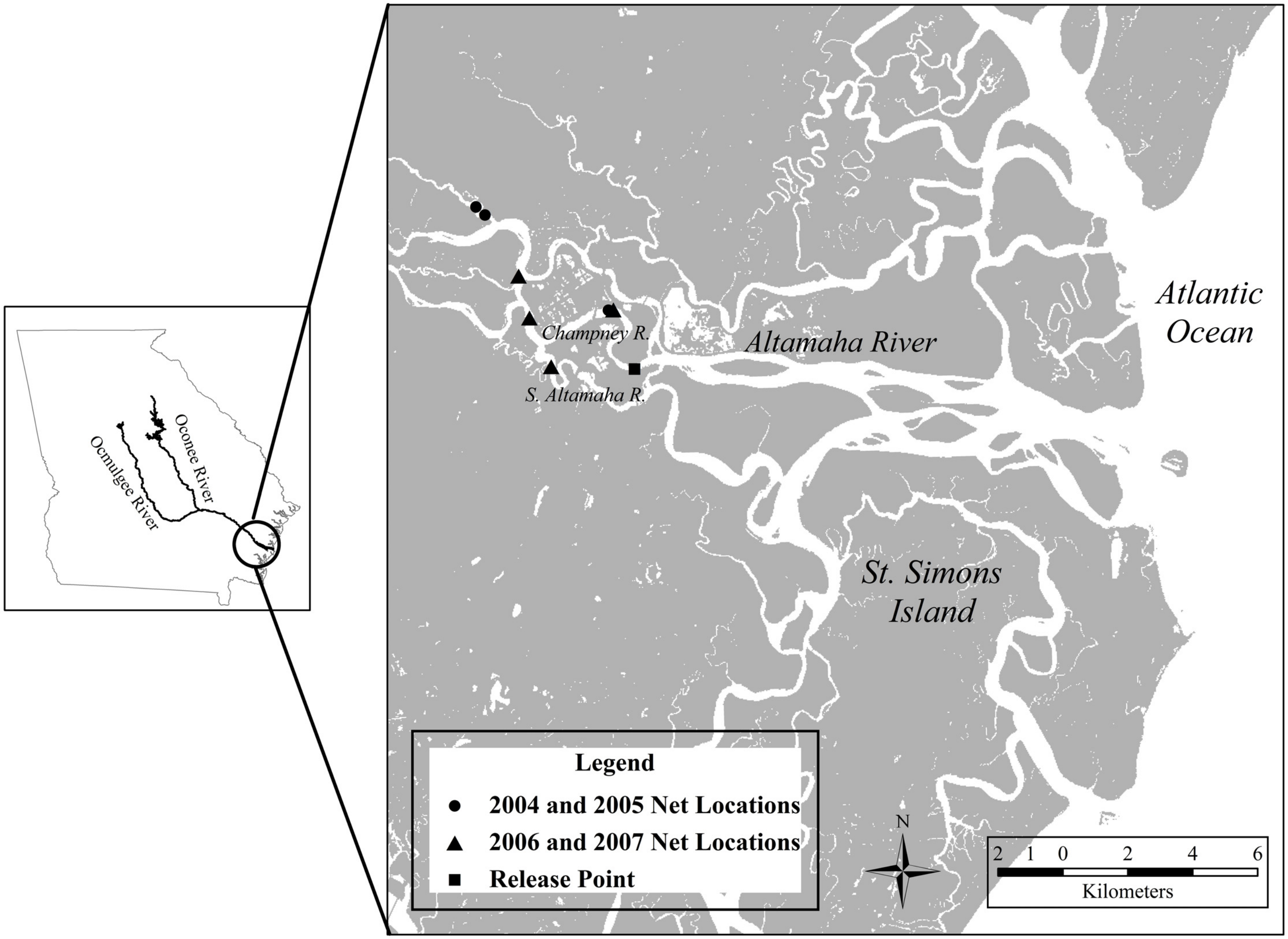

Figure 2.1. Netting locations of adult Atlantic sturgeon within the tidally influenced portion of the Altamaha River.

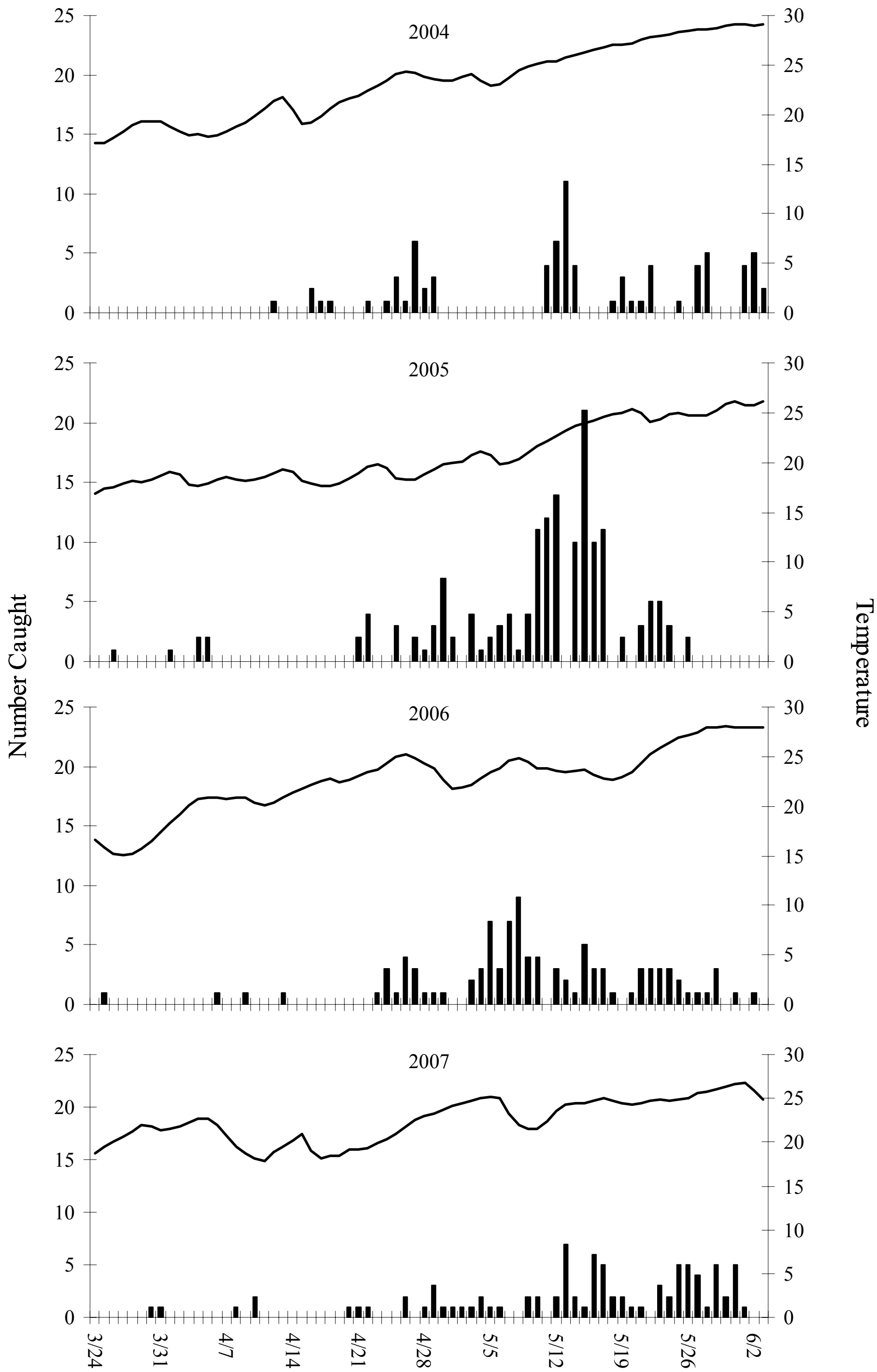

Figure 2.2. Number of adult Atlantic sturgeon caught by day (black bars) and average daily temperature (black line, °C) in the Altamaha River, Georgia in 2004 – 2007.

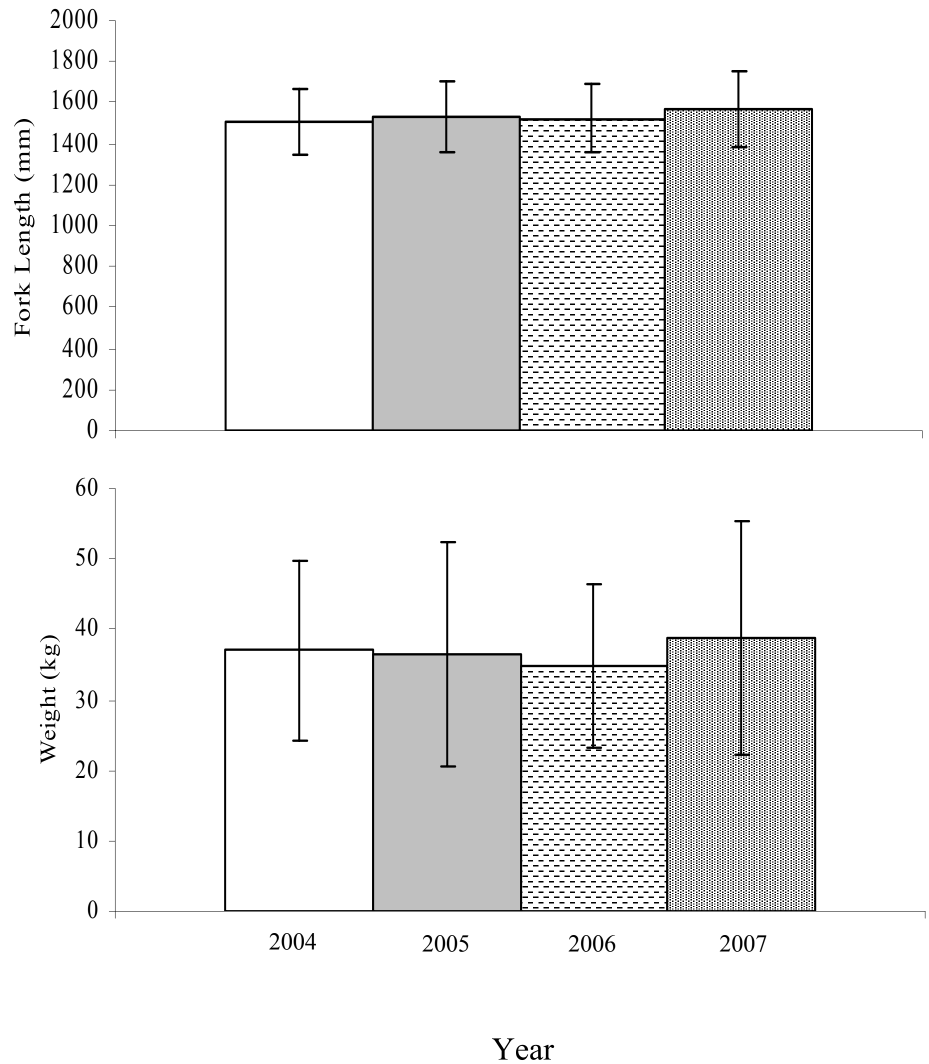

Figure 2.3. Mean (with standard deviation error bars) fork length and weight of captured Atlantic sturgeon in the Altamaha River from 2004 – 2007.

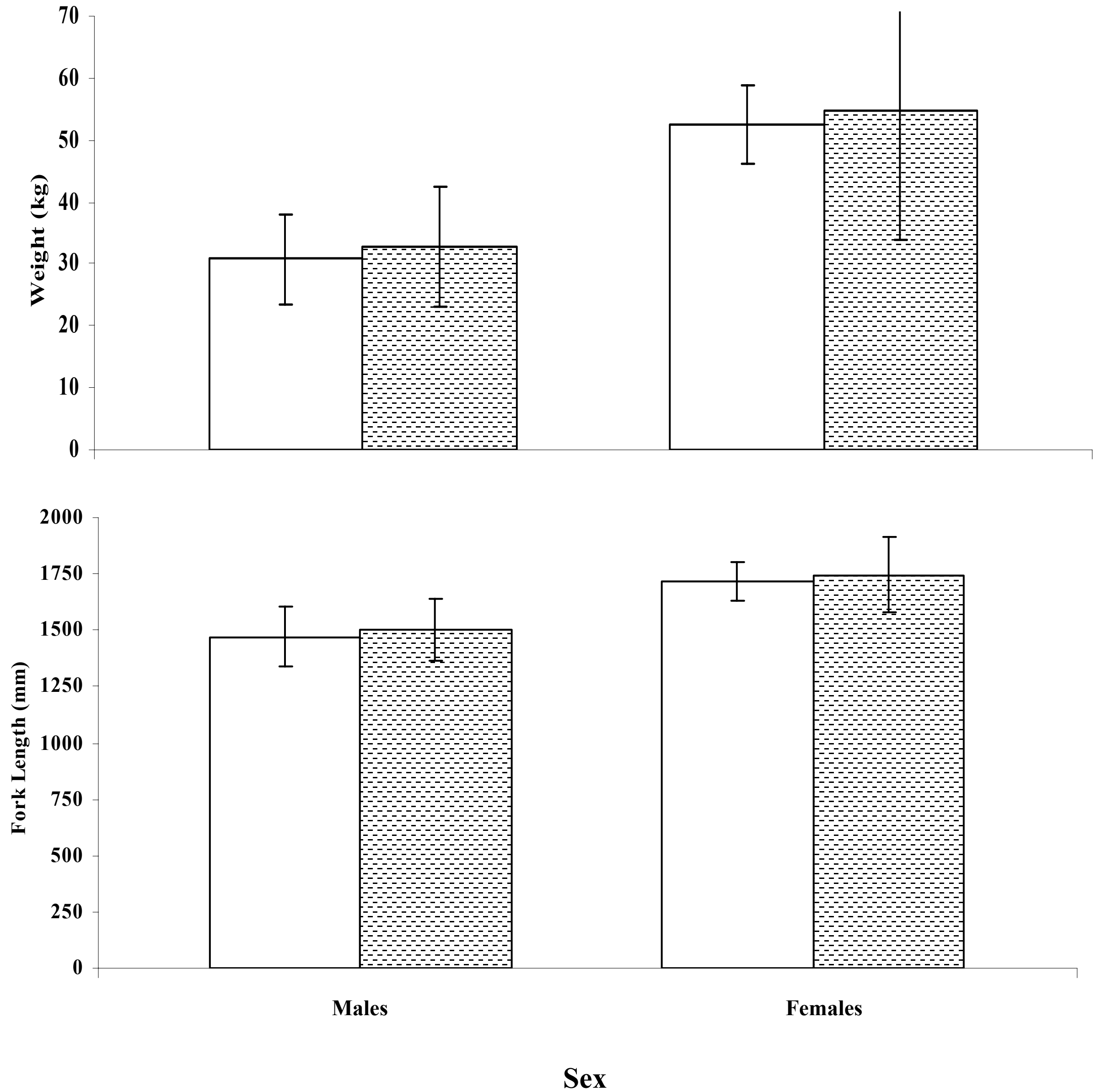

Figure 2.4. Mean (with standard deviation error bars) fork length and weight by sex of Atlantic sturgeon captured from the Altamaha River from 2006 (white bars) and 2007 (dashed bars).

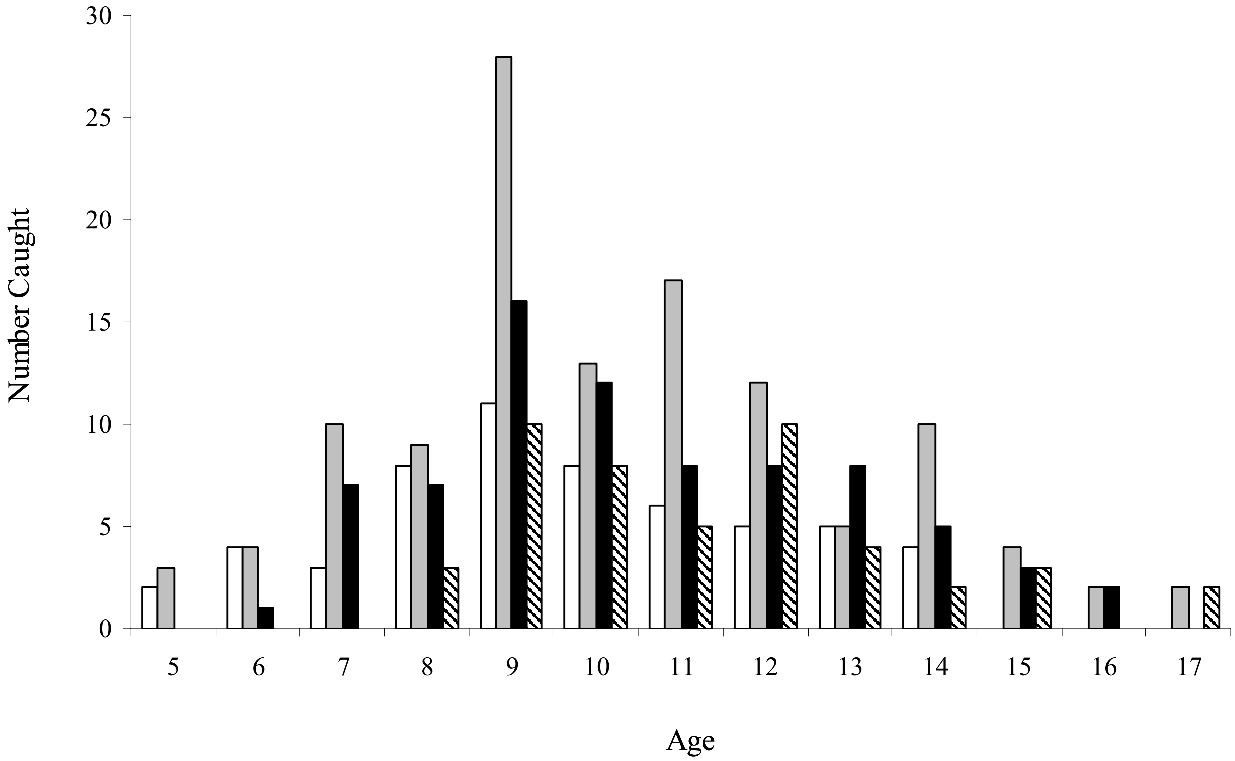

Figure 2.5. Age distribution of Atlantic sturgeon captured in gill nets within the Altamaha River, Georgia, during spring in 2004 (white bars), 2005 (gray bars), 2006 (black bars), and 2007 (lined bars).

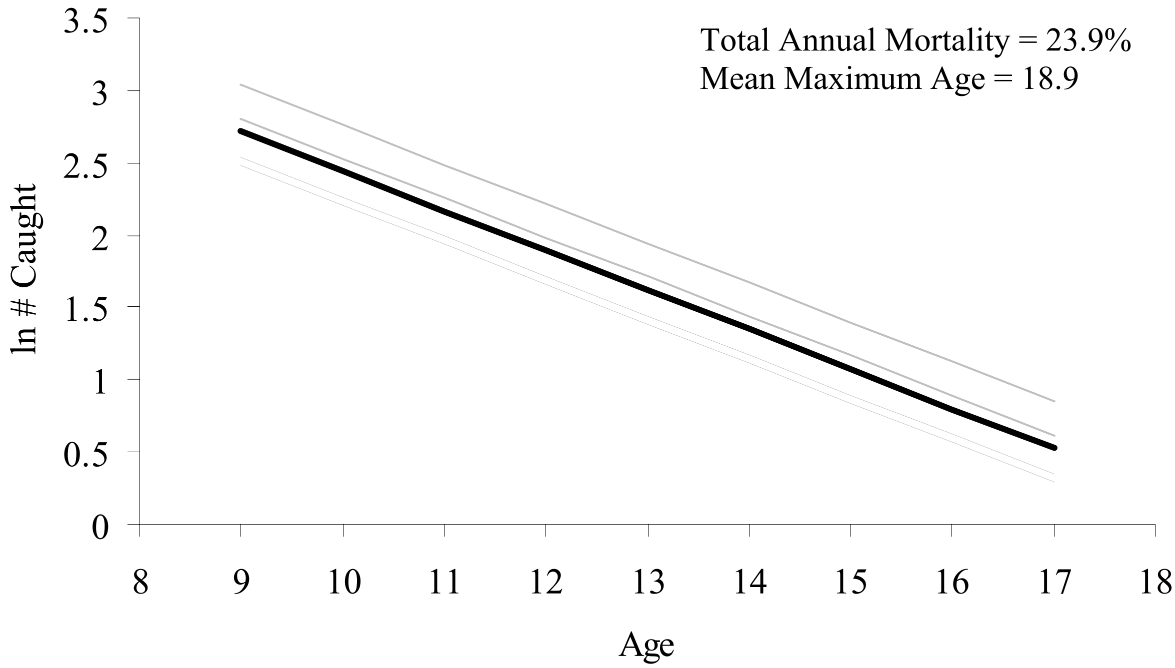

Figure 2.6. Catch curve ($\log_e$[numbers caught] versus age in years [y]) based on the grand mean, in black, and Bayes' estimates of individual years, in grey, of adult Atlantic sturgeon (ages 9–17) captured in gill nets within the Altamaha River, Georgia,
during spring in 2004 – 2007.

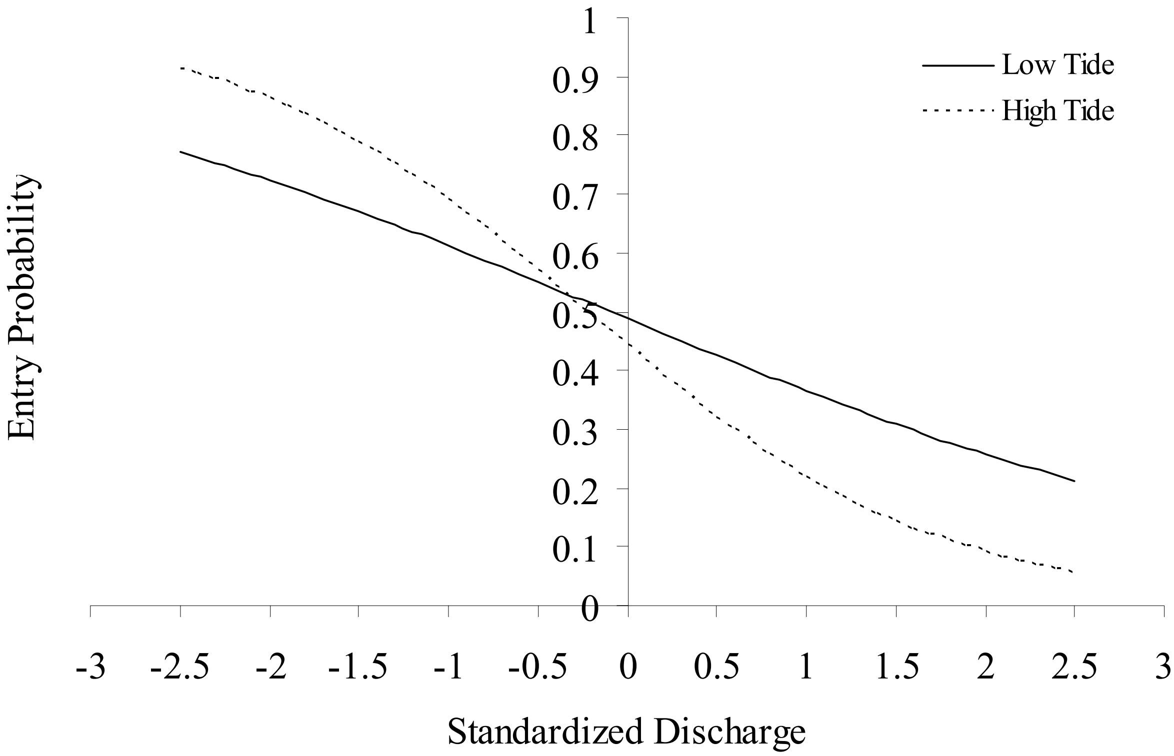

Figure 2.7. Composite model predictions of entry probability across a range of discharge values at low, solid line, and high, dashed line, tidal cycle levels in 2007.

CHAPTER 3

ABUNDANCE AND RECRUITMENT OF JUVENILE ATLANTIC STURGEON IN THE ALTAMAHA RIVER, GEORGIA[2]

[2]Schueller, P., and D. L. Peterson *to be submitted to*

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Abstract

Many populations of Atlantic sturgeon have suffered major declines resulting from commercial fishing. Juvenile Atlantic sturgeon remain in natal rivers for several years prior to out-migrating to marine environments during later portions of their life history. Data regarding river-resident juvenile population dynamics are lacking both historically and since fishery closure. During the summers of 2004 – 2007, I preformed mark-recapture of juvenile Atlantic sturgeon in the Altamaha River to assess age-specific abundance, apparent survival, per capita recruitment, and factors influencing recruitment. Abundance estimates indicated that juvenile abundance ranged from 1072 – 2033 individuals and age-1 and age-2 individuals comprised greater than 87% of the juvenile population, while abundance of age-3 or older individuals was less than 13% of the population. Estimates of apparent survival and per capita recruitment from Pradel models indicated that the juvenile population experiences high annual turnover, as apparent survival rates are low (< 33%) and per capita recruitment is high (from 0.82 to 1.38). Fall discharge, which had a positive relationship with recruitment, was the only factor assessed that significantly explained time variation in per capita recruitment. The findings of this study suggest that juvenile populations at the southern extreme of the Atlantic sturgeon's range may remain in natal rivers for less time than northern counterparts. The demographic parameters presented here, along with recently publish parameters of the adult portion of the population, could be used to create projection models to predict future abundance. Potential findings of density dependence could have major implications for both population recovery and management of this species.

Introduction

Atlantic sturgeon (*Acipenser oxyrinchus*) are a long-lived, anadromous species that spend the early portion of their juvenile stage in freshwater (Scott and Crossman 1973). Adults inhabit marine environments in most years, but females enter coastal rivers for spawning every 3 – 5 years while males spawn every 1 – 5 years (Smith 1985). Spawning occurs well upriver from the saltwater interface of most rivers (Van Eenennaam et al. 1996, Caron et al. 2002, Hatin et al. 2002), as embryos and larvae are intolerant of salinity (Van Eenennaam et al. 1996). At hatching, embryonic Atlantic sturgeon seek cover within interstitial spaces of rocky substrates, but after 8 – 10 d they emerge as true larvae and disperse downstream (Kynard and Horgan 2002). Larval migration continues for approximately 12 d, and although most movements occur at night during the first 6 d, little diel preference has been observed thereafter (Kynard and Horgan 2002). In early juvenile development, individuals primarily use deep water habitats near the fresh/saltwater interface (Moser and Ross 1995, Bain 1997). After 2 – 6 years in these habitats, juveniles leave their natal rivers for marine environments (Dovel and Berggren 1983).

As pre-migratory or “river-resident” juveniles, Atlantic sturgeon exhibit fast growth during their first few years (Dovel and Berggren 1983, McCord et al. 2007). In the Hudson River, for example, juveniles reach 50+ cm by age-1, 60+ cm by age-2, and 70+cm TL by age-3, but juvenile growth in river habitats typically slows in subsequent years (Dovel and Berggren 1983). Causal mechanisms for changes in growth stanzas of juvenile Atlantic sturgeon are unclear, but similar patterns have been linked to density dependent factors in other estuarine dependent fishes (Cushing 1974, Saborido-Rey et al. 2004). In southern populations, similar sizes of age-1 individuals have been observed (McCord et al. 2007), but growth of older juveniles has not been well studied. Nonetheless, understanding variations in growth patterns and other life history characteristics between northern and southern populations is important for assessing juvenile condition, recruitment, and other population processes that influence species recovery.

Although few studies of juvenile ecology in southern rivers exist, Dovel and Berggren (1983) suggest that out-migration of juvenile Atlantic sturgeon in the Hudson River occurs in the fall at 15 months of age. Subsequent studies in northern rivers have documented larger juveniles (>600 mm) in freshwater rivers (Dovel and Berggren 1983, Lazzari et al. 1986, Moser and Ross 1995, Peterson et al. 2000), suggesting out-migration is more likely to occur after age-2. Regardless, quantitative studies of precise timing of juvenile out-migration are lacking, particularly in southern populations. While quantitative studies of juvenile out-migration are lacking, all previous studies suggest that estimation of age-1 abundance is probably the only practical method of assessing annual recruitment in Atlantic sturgeon (Bain et al. 1999).

Throughout their range, Atlantic sturgeon populations have suffered declines resulting from decades of anthropogenic activities. Throughout much of 20th Century, adults were harvest during spring spawning migrations for both meat and caviar (Smith 1985). As northern stocks declined, commercial fishing shifted to southern rivers, particularly during the 1970s and 1980s (Colligan et al 1998). While overexploitation was likely a primary cause for population declines, habitat degradation may be impeding or limiting recovery of many populations (Smith 1985). Reduced water quality from introduced industrial effluents and poor land use practices have adversely affected both spawning and nursery habitats (Smith 1985, Colligan et al. 1998). Thermal effluents and pumping of ground water often degrades juvenile habitats by increasing water temperatures and lowering dissolved oxygen (Rochard et al. 1990, Collins et al. 2000, Niklitscheck and Secor 2005).

An understanding of recruitment mechanisms is a key element of assessing recovery for most Atlantic sturgeon populations. In the Hudson River for example, Peterson et al. (2000) estimated abundance of age-1 juveniles to demonstrate the severity of recruitment declines resulting from decades of overfishing. Unfortunately, studies of recruitment mechanisms in Atlantic sturgeon are rare, especially for southern populations. However, a recent study in the Suwannee River, Florida showed that annual recruitment in Gulf sturgeon (*Acipenser desotoi*), a subspecies of Atlantic sturgeon, can be significantly affected by mean river flows during September and December (Randall and Sulak 2007). Nonetheless, the stock-recruitment relationship for the species remains uncertain because abundance estimates for either juvenile or adults are lacking (Dadswell 2006, Peterson et al. 2008). Because quantified estimates of recruitment and recruitment mechanisms are needed to assess population recovery, the objectives of this study were to: 1) estimate annual age-specific abundance, 2) estimate annual apparent survival and per capita recruitment and 3) identify key factors that influence recruitment processes of juvenile Atlantic sturgeon in the Altamaha River, Georgia.

Methods

Study Site/Fish Sampling

The study was conducted entirely within the tidally influenced portion of the Altamaha River system, near Darien, Georgia (Figure 3.1). Specific sampling sites were randomly distributed within three contiguous 10-km strata compromising the lower 30 rkm of the Altamaha Estuary. Each stratum was sampled weekly from June to August, 2004 – 2007. Juvenile Atlantic sturgeon were captured using both trammel nets and experimental gill nets measuring 91 m by 3 m. Experimental gill nets consisted of three 30.5-m panels of 7.6, 10.2, and 15.2-cm monofilament mesh (stretch measure). Trammel nets were made from 7.6-cm mesh inner panel and two 30.5-cm mesh outer panels. Nets were deployed perpendicular to the current, anchored to the bottom, and fished for 25 – 90 min during slack tides only.

As nets were retrieved, juvenile Atlantic sturgeon were removed and placed in a floating net pen, where they were allowed to recover for 10-15 minutes prior to data collection. Each fish was then checked for PIT tags using a portable PIT tag reader. If no tag was detected, one was injected beneath the fourth dorsal scute. Measurements of total length (mm) and weight (kg) were then recorded for each fish. Prior to release a 0.5 – 1.0-cm section of the leading pectoral fin spine was removed from a random sub-sample of 32 and 25 fish in 2005 and 2006 respectively for subsequent age determination.

Data Analysis

Ages of juvenile Atlantic sturgeon were determined based on modal distributions of length frequency histograms as described by Peterson et al. (2000) and subsequently, McCord et al. (2007). Accuracy of modal distribution age assignments was verified from fin spines sections collected from a random sub-sample of captured fish. Using the basic methods described by Cuerrier (1951), pectoral fin spine sections were first air dried for at least one month, cross-sectioned using a Beulher Isomet® low-speed saw, and viewed under a dissecting scope to reveal growth annuli.

Robust design models have been generalized to incorporate additional model types. Traditional robust design models implement a combination of open and closed model types (Kendall et al. 1995). Open population models, such as the Cormack-Jolly-Seber model (or CJS; Cormack 1964, Jolly 1965, Seber 1965), are used between primary occasions that are widely spaced, such as annual sampling, to provide estimates of apparent survival. Within primary occasions, a series of sampling events, known as secondary occasions, are taken at shorter intervals, days or a week, which allows the use of traditional closed population abundance estimators (Otis et al. 1978). Robust design models have been modified to incorporate open multi-state models within primary periods (Kendall and Bjorkland 2001). The open robust design multi-state model can be modified to have closed secondary periods, enabling the use of traditional closed capture models to estimate state specific abundance within primary periods, while allowing for state transitions between primary periods (White et al. 2006). The assumptions of the open robust design multi-state model allowed for relaxing an assumption of closure during primary occasions (Kendall and Bjorkland 2001); however, the assumptions of the closed robust design multi-state model type are similar to those of the traditional robust design:

1. The conditional probability of surviving from primary period i to $i + 1$ is the same for all fish
2. The conditional probability of being caught at each primary period is the same for all marked fish
3. The fates of fish with respect to survival and capture are independent
4. Marks are retained and correctly recorded
5. Sampling periods are instantaneous, or very short, and recapture fish are released immediately
6. All emigration within primary periods is permanent

The closed robust design multi-state model type estimates state-specific apparent survival, state transition probabilities, capture and recapture probabilities, and state-specific abundance.

I used the closed robust design multi-state model to estimate annual age-specific abundance and identify factors influencing capture and recapture probabilities. Individual capture histories were constructed by using each sampling week during the summer as an individual sampling period. Eight secondary periods (4 weeks in June, and 4 weeks in July) within four primary periods (summers of 2004 – 2007) yielded a total of 32 sampling periods. Captured individuals were categorized into three different age strata: age-1, age-2, or age-3+. I then used the Huggins formulation of the multi-state robust design model (Huggins 1989; 1991) to estimate annual abundance of each age class. By using age as a state within the model, I was then able to estimate annual abundance of each age class, while evaluating the effects of sampling effort, water temperature, and river discharge on capture and recapture probabilities.

A candidate set of models with different combinations of parameters for capture and recapture probabilities were constructed to identify potential differences among age-classes, behavioral responses, and to quantify influences of environmental predictor variables. Survival and state transition probabilities were modeled as constant across time and ages in all models. Capture and recapture probabilities were modeled either as constants or as functions of predictor variables specific to secondary period sampling. Sampling effort was measured in net sets per week and weekly averages in water temperature and discharge were included as key environmental variables. Water temperature data were obtained from the Georgia Coastal Ecosystem – Long Term Ecological Research (GCE-LTER) monitoring station (~rkm 14, in South Altamaha River), while discharge data were obtained from the United States Geologic Survey (USGS) gaging station at rkm 100 (#02226000). All predictor variables were standardized, with a mean of zero and a standard deviation of one, across years before incorporating them into models. The effects of predictor variables on capture and recapture probabilities were modeled as either constant among primary periods or varying among primary periods. Behavioral response to capture (increased or decreased recapture rates after initial capture) was evaluated by rerunning all models with capture and recapture probabilities set equal. To test for potential heterogeneity in capture and recapture probabilities among age classes, all models were rerun with separate parameters for each age class.

The relative likelihood of each model was evaluated with an information theoretic approach (Burnham and Anderson 2002), by calculating Akaike's information criterion (Akaike 1973) with a small sample size adjustment (AICc; Hurvich and Tsai 1989). As survival and state transition probabilities were consistent among models, assessing model likelihoods allowed me to identify sources of variation in capture and recapture probabilities. The most plausible model was used for age-specific abundance estimates, with the corresponding parameterization of capture and recapture probabilities used in subsequent models to assess juvenile recruitment.

Pradel temporal symmetry models with robust design were used to estimate parameters specific to the entire juvenile population (Kendall et al. 1995, Pradel et al. 1996). Open mark-recapture models, such as the CJS, are conditioned on first capture and use observed capture histories to estimate apparent survival and recapture probability. Reverse time models are conditioned on last observation of individuals and the reverse capture history is used to make inference regarding the probability of an individual being in the population at a prior time period and recruitment of new individuals into the population. Pradel temporal symmetry models use both forward and reverse time approaches simultaneously to estimate recruitment, population growth, and seniority probability (Pradel 1996). Incorporation of Pradel models between primary periods of robust design models was used to estimate apparent survival, per capita recruitment, and juvenile population abundance. The Pradel Robust design model is reliant on the following assumptions:

1. All marked and unmarked fish have the same probability of capture

2. Every fish marked at time *i* has the same probability of surviving to $i + 1$
3. Marks are not lost or overlooked
4. Sampling occurs instantaneously, or over a short interval, and recapture fish are released immediately
5. All emigration is permanent
6. Fates of all fish, with respect to capture, survival and seniority probability, are independent

Assumptions for robust design models listed above are also applicable to the Pradel robust design models. Per capita recruitment was defined as number of new juveniles in the population at time *i* per juvenile in the population at time $i - 1$. Apparent survival was defined as the probability of an individual surviving and remaining in the river during the interval from time *i* to time $i + 1$. Apparent survival was modeled as constant or time varying. Capture and recapture probabilities were modeled using the same parameters as the best approximating closed robust design multi-state model.

A candidate set of models with different combinations of recruitment parameters were constructed to evaluate the effect of various predictor variables on annual variation in juvenile recruitment. The candidate set also included models with recruitment time varying without predictor variables. Predictor variables used to explain annual variation in recruitment included spawner abundance and the seasonal averages of water temperature and river discharge at time of age-0 (Appendix 2). Average water temperature and discharge during March – May (spring), June – August (summer), and September – November (fall) were used as predictor variables because these periods represented key seasonal changes in these variables that are recognized as critical to year-class strength in Atlantic sturgeon (Secor and Gunderson 1998). Estimates of spawner abundance were derived from previous population assessments of adult abundance (Peterson et al. 2008, Schueller and Peterson, unpub.). All predictor variables were standardized, with a mean of zero and standard deviation of one, among years prior to use in models.

As in closed robust design multi-state models, the relative plausibility of each model was determined with an information theoretic approach (Burnham and Anderson 2002). Models with recruitment predictor variables were only considered important if they were more likely than time varying recruitment models lacking a predictor variable. As model weights were dispersed among several models, model-averaged parameter estimates were used to account for model selection uncertainty (Burnham and Anderson 2002). Model-averaged estimates and unconditional standard error were calculated for both the apparent survival and recruitment parameters and juvenile population abundance estimates.

Results

In the four consecutive years of study, a total of 1,012 juvenile Atlantic sturgeon were captured in a total of 391 net sets (Table 3.1). Average number of nets set in a sampling week varied from 11.6 to 13.3 among sampling years. Catch-per-unit-effort varied from 2.04 to 3.75 juveniles per net from 2004 – 2007. Sizes of captured juveniles varied from 350 – 1050 mm total length, although 90% of juveniles measured less than 714 mm (Figure 3.2). While relative abundance of juvenile age-classes varied annually, the size distribution of juveniles within year classes was similar in each year of the study.

Length frequency analysis of the catch identified a distinct modal distribution of juveniles. Age-determination from the random sub-sample of fin spines confirmed that age-1 juveniles measured 350 – 550 mm, age-2 juveniles measured 550 – 750 mm, while age-3 juveniles measured 750 – 1050 mm (Figure 3.3). These results were consistent among all years of the study. After assigning ages to all juveniles captured in each year, I calculated that the total catch from 2004 to 2007 was comprised of 568 age-1, 403 age-2, and 63 age-3+ juveniles (Table 3.2). Although annual abundance of the total juvenile population varied from a low of 1072 in 2004 to a high of 2033 in 2006, ages 1-2 comprised 87-96% of the juvenile population in all years of the study (Table 3.2).

Closed robust design multi-state models revealed the best-fitting model had capture and recapture probabilities equal and as a function of weekly effort varying annually (Table 3.3). Model comparisons showed that this model was 10.5 times more plausible than the second best model, which also had capture and recapture probabilities equal but as a function of temperature varying annually. These analyses indicated that there was no significant behavioral response to capture, and there was no evidence that capture and recapture probabilities differed among age groups. During summer sampling, temperature and discharge varied only slightly across years, except in 2005 when river discharge was higher and water temperature was lower. In all other years, summer water temperatures remained near 30° C and discharge varied from 70.5 to 154.6 m^3/s.

The best-fitting Pradel model indicated that apparent survival and per capita recruitment estimates varied annually, with highest recruitment occurring in 2005 and highest apparent survival in 2006 (Table 3.5). The best-fitting model incorporated survival as time varying and annual recruitment was significantly influenced by fall discharge, which had a positive relationship with recruitment (Table 3.4). In fact, this model was 1.69 times more plausible than the second best model, which had survival and recruitment time varying with no predictor variables. The third ranked model included recruitment as a function of spring Schnabel adult abundance estimates, but as this model was less likely than time varying recruitment lacking a predictor variable, it was not considered to be important (Table 3.4).

Discussion

The ages assigned from length frequency histograms were easily verified using fin spines collected from randomly selected juveniles. Furthermore, average length at age-1 of Altamaha juveniles was virtually identical to that of age-1 juveniles from coastal rivers in South Carolina (McCord et al. 2007). While the use of histograms and age-estimates from fin spines can probably be used to accurately identify juvenile cohorts in other southern rivers, spatial and temporal variations in growth could potentially complicate age assignment in age-2 and older individuals. Hence, future studies using known age juveniles, possible from hatchery origin, should be considered for validation of juvenile age estimates derived from fin spines or length frequency histograms.

Closed robust design multi-state models provided estimates of age specific juvenile abundance and identified potential sources of variation in capture probability. Model results showed that individuals of all age classes were equally likely to be captured, and once tagged, individuals had an equal probability of being recaptured. The analyses also confirm the accuracy of the estimates by demonstrating that heterogeneity in capture probability was minimal, and hence, did not bias the abundance estimates. Consequently, I suggest that similar modeling approaches be used for other Atlantic sturgeon populations, so that results can be compared with those presented in this study. Provided that adequate numbers of juveniles can be captured over several consecutive years, such comparisons will greatly improve current knowledge of recruitment processes as they affect population recovery in many river systems.

Obtaining separate estimates of annual survival and out-migration rates was not possible in this study. In using the open population models to estimate apparent survival of juvenile cohorts in the Altamaha river, the requisite assumption was that emigration of juveniles was permanent (Williams et al. 2002). Consequently, apparent survival represented the probability of any individual surviving at time i and remaining in the river until time $i + 1$. As apparent survival is confounded with permanent emigration, mark-recapture methods will not be able to provide separate estimates of annual survival and out-migration rates, yet these rates are critical in understanding recruitment processes for the species. Hence, future studies are needed to obtain quantified recruitment data using alternative methods such biotelemetry and known fates models (Cox and Oakes 1984).

The use of Pradel robust design models allowed for direct estimates of apparent survival and per capita recruitment, which together revealed a high turnover rate of the juvenile population. Per capita recruitment estimates in this study ranged from 0.82 to 1.38, indicating that annual recruitment to age-1 is nearly equal to, or greater than, the abundance of the entire juvenile population in the proceeding year. Likewise, apparent survival was highest when recruitment was lowest, suggesting that a higher percentage of age-2 and older fish leave the river in years when age-1 fish are more abundant. The surprisingly high turnover rate of river-resident cohorts observed in this study is consistent with previous studies suggesting that life history of southern populations is accelerated (Van Den Avyle 1984, Smith 1985,) compared to northern stocks that exhibit later age at maturity and longer life span (Scott and Crossman 1973, Van Eenennaam 1996). These findings also suggest that out-migration of river-resident juveniles older than age-1 may be influenced by density dependent competition with younger cohorts. Because early juveniles are intolerant of ocean salinity they are likely unable to seek alternative foraging habitats in coastal waters if riverine food resources become limited. Older juveniles, however, have no such constraints, but may prefer the relatively predator free environments of brackish water estuaries as long as food resources are not limited.

Although I examined the potential effects of several environmental variables, fall discharge was the only predictor variable that significantly explained annual variation in recruitment. Adult abundance from the proceeding spring was the next best predictor variable, but these models were less likely than those with time varying recruitment lacking a predictor variable. Recent work on the Suwannee River population of Gulf sturgeon indicates that mean discharge during September and December is positively related to recruitment of age-0 juveniles (Randall and Sulak 2007). Randall and Sulak (2007) hypothesize that discharge during September improves oxygenation while high flows in December may help reduce salinity, thereby increasing potential foraging habitats available to age-0 fish. The effect of discharge on juvenile recruitment may be especially important in hydro-regulated river systems

The results of this study provide the first quantified recruitment data of a juvenile Atlantic sturgeon population in a southern river. Although further studies are needed to better understand recruitment mechanisms and variables affecting out-migration of river-resident juveniles, stage-based projection or population viability models can be used to assess population recovery of Atlantic sturgeon in the Altamaha and other Atlantic coast rivers. Similar approaches have been used in previous studies of other sturgeon species to project population trends (Pine et al. 2001), to identify survival bottlenecks at specific life history stages (Paragamian et al. 2005), and to quantify survival rates necessary to achieve recovery goals (Morrow et al. 1998). With regard to Atlantic sturgeon, however, current demographic data are needed to complete similar analyses. The results of this study provide quantified estimates of age-1 recruitment, apparent survival, and age-specific abundance, all of which could be used in simplified population viability analyses.

Proper assessment of population status and recovery will require proper sampling designs and statistical approaches. Although future studies of sub adult and adult life stages are needed, quantified assessment of river-resident juveniles can provide fisheries managers with the data necessary for making sound inferences about population trends. Previous studies of Atlantic sturgeon on the Altamaha River have shown that population inference based on adult spawning runs can be confounded by the presence of non-spawning adults and immature fish (Peterson et al. 2008). The results of this and other studies show that sampling of river-resident juveniles, particularly the age-1cohort, can provide reliable estimates of recruitment, a key aspect of aspect of evaluating population recovery (Bain et al. 1999, Peterson et al. 2000).

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Table 3.1. Number caught, catch-per-unit-effort (CPUE), and mean and range of effort (nets set per week), water temperature (° C), and discharge (m^3/s) values used to model capture probability of Atlantic sturgeon captured in the Altamaha River from 2004 to 2007.

			Effort		Temperature		Discharge	
Year	Number Caught	CPUE	Mean	Range	Mean	Range	Mean	Range
2004	190	2.04	11.6	3 - 21	29.8	29.1 - 30.8	154.6	80.2 - 258.3
2005	281	2.75	12.8	3 - 27	27.7	25.9 - 29.0	481.5	261.9 - 869.3
2006	335	3.72	11.3	5 - 15	30.0	28.6 - 31.5	70.5	54.3 - 90.4
2007	321	3.03	13.3	8 - 18	29.4	26.7 - 31.1	84.7	62.1 - 131.0

Table 3.2. Number of juvenile Atlantic sturgeon tagged in the Altamaha River per age class, age-specific abundance estimates from multi-state models, juvenile population abundance estimates from Pradel models, confidence intervals, and proportion of the population for 2004 to 2007.

Year	Age Class	Number Tagged	Abundance Estimate (95% CI)	Proportion of Population
2004	1	79	483 (368 – 643)	0.45
	2	89	544 (424 – 707)	0.51
	3	6	37 (9 – 294)	0.03
Total		174	1072 (815 – 1330)	
2005	1	226	1345 (1077 – 1697)	0.91
	2	18	107 (28 – 784)	0.07
	3	5	30 (6 – 935)	0.02
Total		249	1493 (1154 – 1833)	
2006	1	52	333 (246 – 460)	0.17
	2	250	1600 (1420 – 1808)	0.79
	3	13	83 (38 – 209)	0.04
Total		315	2033 (1582 – 2485)	
2007	1	211	1318 (1053 – 1668)	0.71
	2	46	287 (132 – 727)	0.16
	3	39	244 (101 – 711)	0.13
Total		296	1865 (1449 – 2282)	
Study Total	1	568		
	2	403		
	3	63		

Table 3.3. Top five closed robust design multi-state models using predictor variables to describe variation in capture and recapture probability of Atlantic sturgeon in the Altamaha River for 2004 to 2007.

Capture Probability	Recapture Probability	AICc	AICc Weights	Model Likelihood	K
Effort varying annually	Equal to capture probability	5251.59	0.845	1.000	7
Temperature varying annually	Equal to capture probability	5256.3	0.080	0.095	7
Effort constant annually	Equal to capture probability	5258.15	0.032	0.038	4
Effort varying annually	Effort varying annually	5259.4	0.017	0.020	12
Effort constant annually, varying by age class	Equal to capture probability	5259.75	0.014	0.017	6

Table 3.4. Top five Pradel robust design models using predictor variables to describe variation in apparent survival and annual per capita recruitment of Atlantic sturgeon in the Altamaha River for 2004 to 2007.

Apparent Survival	Per Capita Recruitment	AICc	AICc Weights	Model Likelihood	K
Time varying	Fall discharge	8003.94	0.587	1.000	10
Time varying	Time varying	8004.99	0.347	0.592	11
Time varying	Schnabel adult abundance	8009.57	0.035	0.060	10
Constant	Time varying	8011.89	0.011	0.019	9
Time varying	POPAN adult abundance	8013.06	0.006	0.010	10
Constant	Fall discharge	8013.70	0.004	0.008	8

Table 3.5. Parameter estimates, and lower (LCI) and upper (UCI) 95% confidence intervals for annual apparent survival and per capita recruitment of Atlantic sturgeon in the Altamaha River for 2005 to 2007.

Parameter	Estimate	LCI	UCI
Apparent Survival '04 - '05	0.030	0.003	0.226
Apparent Survival '05 - '06	0.338	0.182	0.539
Apparent Survival '06 - '07	0.125	0.060	0.243
Per Capita Recruitment '05	1.379	1.071	1.687
Per Capita Recruitment '06	0.980	0.000	1.000
Per Capita Recruitment '07	0.823	0.609	0.933

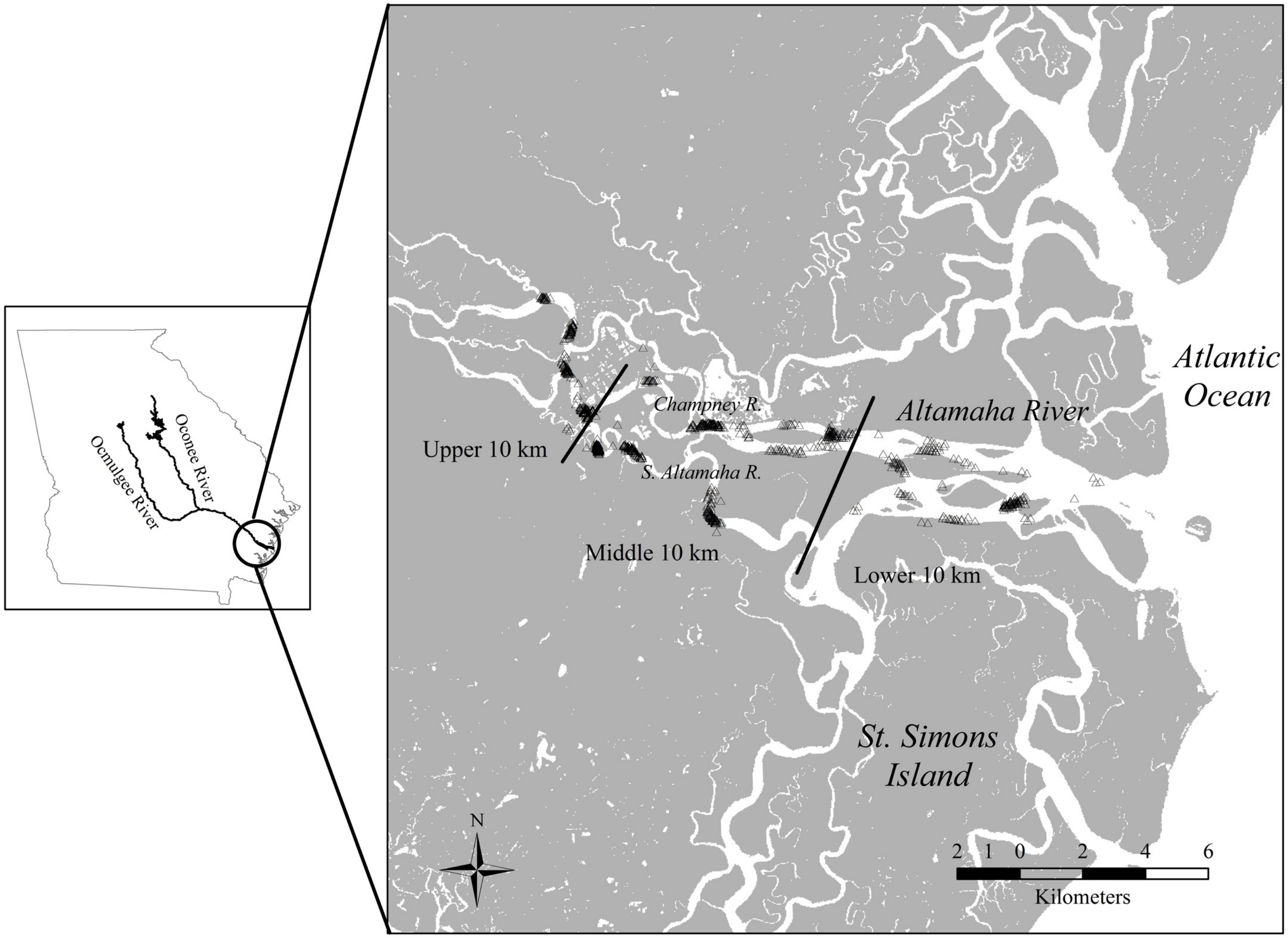

Figure 3.1. Netting locations (hollow triangles) and 10-km sampling strata (separated by black bars) for juvenile Atlantic sturgeon sampling within the Altamaha River, Georgia from 2004 to 2007.

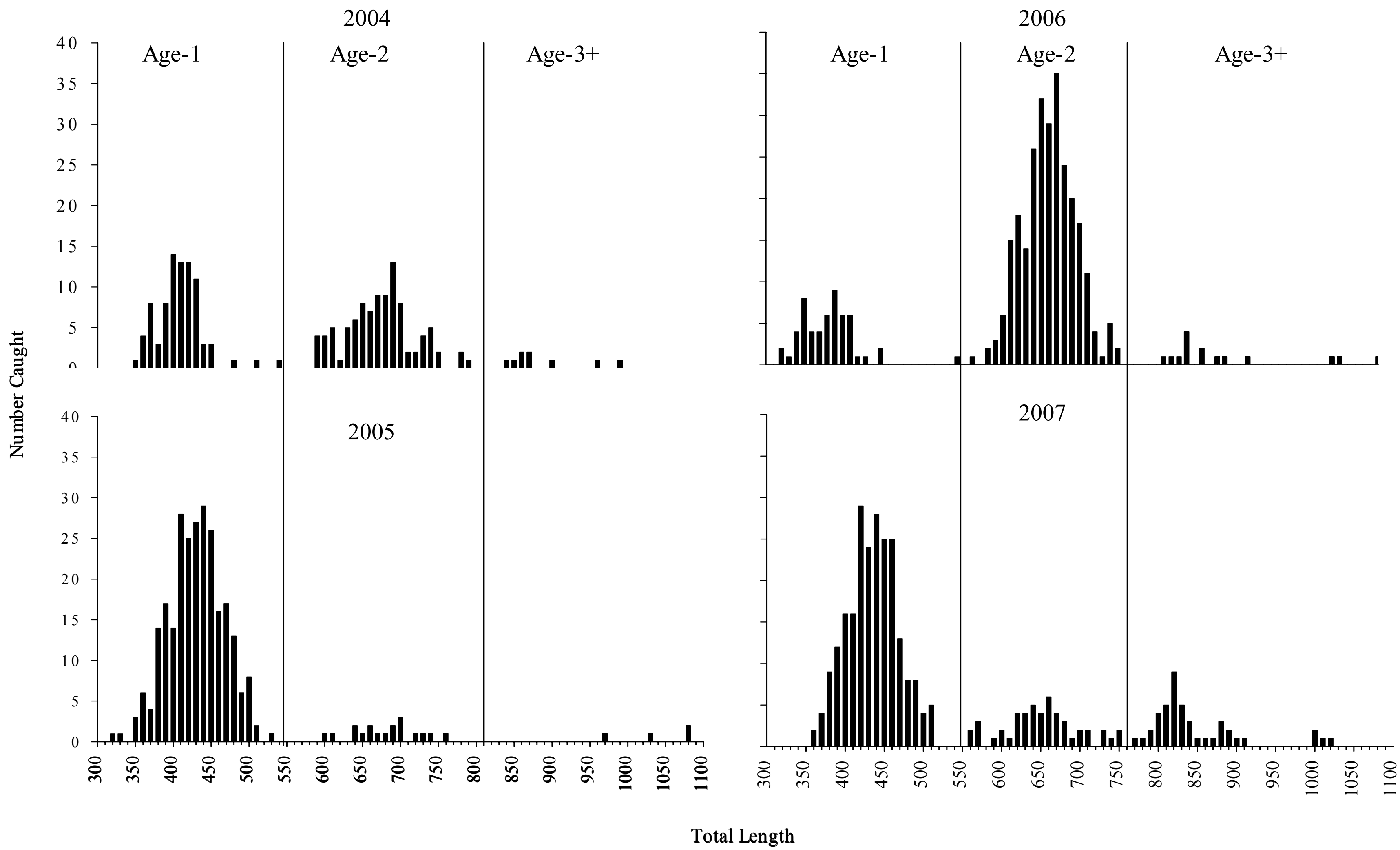

Figure 3.2. Length (mm) frequency histogram and age assignments of all captured juvenile Atlantic sturgeon in the Altamaha River from summer sampling in 2004 to 2007.

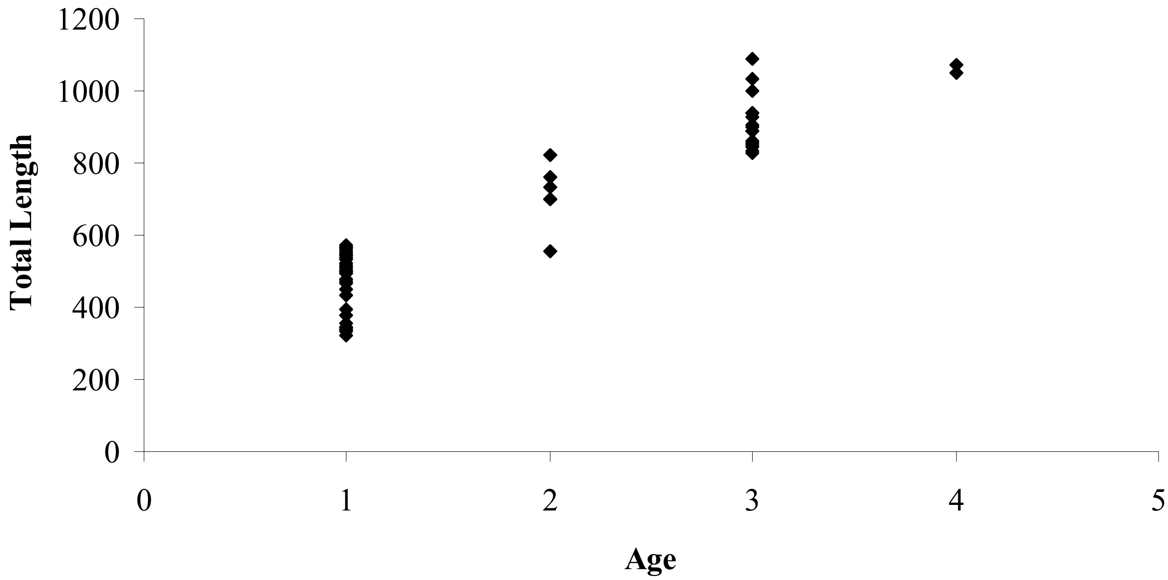

Figure 3.3. Total length (mm) at age of juvenile Atlantic sturgeon capture in the Altamaha River, Georgia.

CHAPTER 4

CONCLUSIONS

The Atlantic sturgeon population in the Altamaha River may be recovering from commercial harvest. Current population estimates suggest a recovering population, with increasing recruitment of juveniles and adults. I found that 85 –386 adult Atlantic sturgeon enter the river each spring. Altamaha River abundance estimates approach annual adult abundance in the St. Lawrence River, even though the Altamaha is a much smaller (Dadswell 2006). Similar to other studies, a limited number of captured females had ripe eggs (Caron et al. 2002). Juvenile abundance in the Altamaha River varied from about 1,000 to 2,000 annually and was composed largely of age-2 or younger fish. The juvenile population appears to be sustained by high annual recruitment and most juveniles leave the Altamaha River by age-3. The age distribution of the juvenile population was 1-2 years younger in the Altamaha River than that of the Hudson River (Dovel and Berggren 1983). Similar comparisons with southern populations were not possible because age specific abundance estimates have not been attempted on other southern rivers.

Annual mortality of adult Atlantic sturgeon was higher than expected; however, the current adult age structure suggested that recruitment has been consistent since the fishery was closed in 1996. In all four years of study, age-9 individuals were the most abundant age-group in the adult catch, indicating consistent recruitment to the adult population. Abundance of fish born since fishery closure suggests that the population is still in the early stages of recovery. Because many of the adults captured in this study were probably first-time spawners recruitment will likely increase in the near future; however, studies on spawning habitats and conditions are needed to better understand reproductive potential of adult Atlantic sturgeon in the Altamaha River.

Modeling results of this study indicated that several hundred adult Atlantic sturgeon enter the river annually and their probability of entering the river was significantly influenced by tidal cycles. Although no other studies have examined the influence of environmental variables on adult Atlantic sturgeon movements, my findings are similar to those reported for Gulf sturgeon movements (Sulak and Clugston 1999). Currently, Dadswell (2006) presents the only other estimate of annual in-river spring abundance of adult Atlantic sturgeon, but the estimate (>500 fish) comes from the St. Lawrence River, a much larger river system than the Altamaha. Annual estimates of adult abundance varied from 89 to 386, although only a few of these adults were in spawning condition. These results suggest that while the population is probably recovering from decades of overfishing, recruitment is currently being supported by a low number of adult spawners. Consequently, genetic analyses are needed to evaluate effective population size and to monitor future changes in genetic diversity as the number of spawning adults increases.

Dovel and Berggren (1983) reported the age structure of the juvenile population of Atlantic sturgeon in the Hudson River, but I present the first quantified analyses of juvenile population dynamics. By using mark-recapture models that accounted for heterogeneity in capture probability, I was able to make annual estimates of age-specific abundance and annual recruitment and apparent survival of juvenile Atlantic sturgeon. These analyses showed that the juvenile population of the Altamaha River is sustained through high per-capita recruitment, as most juveniles migrate to marine habitats by age-3. Despite high recruitment and turnover in the juvenile population, total juvenile abundance was consistent, suggesting that timing of juvenile out-migration may be density dependent.

Future study of the Altamaha River population of Atlantic sturgeon is needed to monitor population recovery while providing a better understanding of species biology within the southern portion of the range. I found that annual recruitment of juveniles was influenced by mean discharge in fall months, but these findings were based on only four years of data. By monitoring juvenile recruitment in future years the influence of environmental variables and spawner abundance on recruitment may be better understood. Incorporation of genetic approaches to estimate annual numbers of spawning females should be implemented as this could be a reliable predictor of juvenile recruitment. Because few tagged adults returned to the Altamaha within the four years of the study, super-population estimates for the entire adult stock were not possible. However, future studies could use annual incidence of adults captured in the river to scale up the open population models used in this study. These models could then be used to estimate abundance of the entire adult stock.

This study has provided new quantified data regarding several key demographic parameters of the Atlantic sturgeon population in the Altamaha River. More importantly, however, my results provide parameters that could be used in stage-based projection models to allow fisheries managers to predict future population trends. Likewise, future studies are needed to develop stochastic models capable of estimating survival to both sub adult and adult life stages. Thereafter, predictions of long-term adult abundance could be calculated using various annual survival rates. Subsequent modifications to the model could then be used to evaluate population responses to future changes in survival (ie. Harvest) and/or recruitment.

More than ten years after commercial fishery closure, the Altamaha River population of Atlantic sturgeon appears to be recovering, but further research is needed to monitor population trends. The current age structure of the adult population indicates recruitment is occurring at a relatively consistent rate, although the lack of comparable studies on other southern rivers makes interpretation of these finding difficult. Nonetheless, the results of this study have provided valuable information regarding Atlantic sturgeon life history, especially at the southern portion of its range. Future studies of juvenile annual survival and out-migration rates, habitat use studies, and stage based projection or population viability models will benefit future management of this species. A better understanding of Atlantic sturgeon biology at the southern end of its range, current population recovery potential, and limitations to population recovery will be critical for future management and recovery of the species.

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APPENDIX 1

SUPPLEMENTAL TABLES AND FIGURES FOR CHAPTER 2

Table A1.1. Observed and standardized values of temperature (° C), Maximum Daily High Tide (m above mean lower low water height), photoperiod (h), and discharge (m^3/sec) during adult Atlantic sturgeon sampling in spring of 2004 in the Altamaha River, Georgia.

	Temperature		Tidal Cycle		Photoperiod		Discharge	
Date	Actual	Standardized	Actual	Standardized	Actual	Standardized	Actual	Standardized
4/17/2004	19.889	0.786	2.256	1.051	13.017	0.956	160.840	1.249
4/18/2004	20.585	0.813	2.316	1.080	13.067	0.959	158.008	1.227
4/19/2004	21.215	0.838	2.316	1.080	13.100	0.962	156.875	1.218
4/20/2004	21.656	0.855	2.316	1.080	13.117	0.963	158.574	1.231
4/21/2004	21.914	0.866	2.256	1.051	13.150	0.965	161.972	1.257
4/22/2004	22.341	0.883	2.164	1.009	13.183	0.968	164.521	1.277
4/23/2004	22.957	0.907	1.737	0.810	13.200	0.969	164.804	1.279
4/24/2004	23.430	0.926	2.073	0.966	13.233	0.971	159.990	1.242
4/25/2004	24.014	0.949	2.012	0.938	13.267	0.974	151.212	1.174
4/26/2004	24.334	0.961	1.951	0.909	13.283	0.975	141.867	1.101
4/27/2004	24.253	0.958	1.920	0.895	13.317	0.978	133.939	1.040
4/28/2004	23.821	0.941	1.920	0.895	13.350	0.980	126.859	0.985
4/29/2004	23.557	0.931	1.951	0.909	13.367	0.981	120.347	0.934
4/30/2004	23.470	0.927	1.981	0.924	13.400	0.984	117.515	0.912
5/1/2004	23.409	0.925	2.134	0.995	13.433	0.986	118.931	0.923
5/2/2004	23.775	0.939	2.316	1.080	13.450	0.987	120.913	0.939
5/3/2004	24.076	0.951	2.469	1.151	13.483	0.990	126.293	0.980
5/4/2004	23.392	0.924	2.530	1.179	13.517	0.992	132.806	1.031
5/5/2004	22.883	0.904	2.560	1.193	13.533	0.993	138.469	1.075
5/6/2004	23.089	0.912	2.499	1.165	13.550	0.995	142.434	1.106
5/7/2004	23.699	0.936	2.469	1.151	13.583	0.997	145.832	1.132
5/8/2004	24.405	0.964	1.981	0.924	13.617	1.000	146.681	1.139
5/9/2004	24.875	0.983	2.347	1.094	13.633	1.001	148.097	1.150

5/10/2004	25.122	0.992	2.256	1.051	13.650	1.002	150.362	1.167
5/11/2004	25.358	1.002	2.164	1.009	13.683	1.004	149.230	1.158
5/12/2004	25.412	1.004	2.103	0.980	13.700	1.006	144.133	1.119
5/13/2004	25.738	1.017	2.042	0.952	13.733	1.008	136.487	1.059
5/14/2004	26.033	1.028	2.134	0.995	13.750	1.009	127.992	0.994
5/15/2004	26.303	1.039	2.195	1.023	13.767	1.011	119.214	0.925
5/16/2004	26.467	1.046	2.256	1.051	13.800	1.013	112.135	0.870
5/17/2004	26.771	1.058	2.286	1.066	13.817	1.014	107.887	0.837
5/18/2004	26.993	1.066	2.316	1.080	13.833	1.015	107.038	0.831
5/19/2004	27.072	1.069	2.286	1.066	13.850	1.017	113.551	0.881
5/20/2004	27.193	1.074	2.225	1.037	13.883	1.019	119.780	0.930
5/21/2004	27.583	1.090	2.164	1.009	13.883	1.019	117.798	0.914
5/22/2004	27.811	1.099	2.103	0.980	13.917	1.022	113.551	0.881
5/23/2004	27.997	1.106	1.646	0.767	13.933	1.023	110.153	0.855
5/24/2004	28.106	1.110	2.042	0.952	13.950	1.024	107.321	0.833
5/25/2004	28.368	1.121	1.981	0.924	13.967	1.025	108.170	0.840
5/26/2004	28.447	1.124	1.951	0.909	14.000	1.028	112.135	0.870
5/27/2004	28.521	1.127	1.951	0.909	14.000	1.028	112.418	0.873
5/28/2004	28.560	1.128	1.981	0.924	14.017	1.029	108.737	0.844
5/29/2004	28.686	1.133	2.073	0.966	14.033	1.030	103.356	0.802
5/30/2004	28.928	1.143	2.012	0.938	14.050	1.031	99.392	0.772
5/31/2004	29.156	1.152	2.042	0.952	14.050	1.031	95.145	0.739
6/1/2004	29.049	1.148	2.073	0.966	14.067	1.033	92.030	0.714
6/2/2004	29.022	1.146	2.073	0.966	14.083	1.034	88.915	0.690
Average	25.314		2.145		13.623		128.824	
Standard Deviation	2.543		0.198		0.321		21.590	

Table A1.2. Observed and standardized values of temperature (° C), Maximum Daily High Tide (m above mean lower low water height), photoperiod (h), and discharge (m3/sec) during adult Atlantic sturgeon sampling in spring of 2005 in the Altamaha River, Georgia.

	Temperature		Tidal Cycle		Photoperiod		Discharge	
Date	Actual	Standardized	Actual	Standardized	Actual	Standardized	Actual	Standardized
3/26/2005	17.498	-1.099	2.225	0.244	12.350	-1.777	659.783	-0.455
3/27/2005	17.888	-0.945	2.256	0.395	12.367	-1.743	722.080	-0.380
3/28/2005	18.161	-0.838	2.256	0.395	12.400	-1.676	787.208	-0.303
3/29/2005	18.069	-0.874	2.225	0.244	12.433	-1.609	883.486	-0.188
3/30/2005	18.286	-0.789	2.164	-0.059	12.467	-1.542	1189.308	0.178
3/31/2005	18.731	-0.614	1.829	-1.721	12.500	-1.475	1633.882	0.709
4/1/2005	19.100	-0.468	2.134	-0.210	12.533	-1.408	1951.031	1.088
4/2/2005	18.748	-0.607	2.103	-0.361	12.550	-1.374	2098.278	1.263
4/3/2005	17.814	-0.975	2.103	-0.361	12.600	-1.273	2197.387	1.382
4/4/2005	17.582	-1.066	2.134	-0.210	12.617	-1.240	2375.783	1.595
4/5/2005	17.858	-0.957	2.195	0.093	12.650	-1.173	2588.160	1.849
4/6/2005	18.344	-0.766	2.286	0.546	12.683	-1.105	2698.595	1.981
4/7/2005	18.588	-0.670	2.408	1.151	12.717	-1.038	2721.249	2.008
4/8/2005	18.266	-0.797	2.438	1.302	12.750	-0.971	2675.942	1.953
4/9/2005	18.213	-0.818	2.438	1.302	12.783	-0.904	2610.813	1.876
4/10/2005	18.318	-0.776	2.408	1.151	12.800	-0.870	2559.843	1.815
4/11/2005	18.604	-0.664	2.286	0.546	12.833	-0.803	2494.714	1.737
4/12/2005	18.988	-0.512	1.890	-1.419	12.867	-0.736	2381.447	1.602
4/13/2005	19.282	-0.397	2.164	-0.059	12.900	-0.669	2245.526	1.439
4/14/2005	19.067	-0.481	2.042	-0.663	12.933	-0.602	2078.457	1.240
4/15/2005	18.100	-0.862	1.951	-1.116	12.967	-0.535	1900.060	1.027
4/16/2005	17.868	-0.953	1.890	-1.419	12.983	-0.501	1704.674	0.793
4/17/2005	17.625	-1.049	1.859	-1.570	13.017	-0.434	1512.120	0.563

4/18/2005	17.633	-1.046	1.859	-1.570	13.050	-0.367	1333.723	0.350
4/19/2005	17.953	-0.920	1.890	-1.419	13.067	-0.333	1180.813	0.168
4/20/2005	18.451	-0.724	1.951	-1.116	13.100	-0.266	1047.723	0.009
4/21/2005	18.989	-0.512	2.103	-0.361	13.150	-0.165	923.129	-0.140
4/22/2005	19.516	-0.305	2.225	0.244	13.167	-0.132	821.189	-0.262
4/23/2005	19.804	-0.191	2.316	0.697	13.200	-0.064	750.396	-0.347
4/24/2005	19.392	-0.353	2.377	0.999	13.233	0.003	682.436	-0.428
4/25/2005	18.450	-0.724	2.408	1.151	13.250	0.036	634.297	-0.485
4/26/2005	18.222	-0.814	2.377	0.999	13.283	0.103	605.981	-0.519
4/27/2005	18.223	-0.813	2.316	0.697	13.317	0.171	594.654	-0.533
4/28/2005	18.789	-0.591	1.920	-1.268	13.350	0.238	583.327	-0.546
4/29/2005	19.254	-0.408	2.256	0.395	13.367	0.271	566.337	-0.566
4/30/2005	19.768	-0.205	2.195	0.093	13.400	0.339	555.010	-0.580
5/1/2005	19.941	-0.138	2.164	-0.059	13.433	0.406	540.852	-0.597
5/2/2005	20.149	-0.055	2.134	-0.210	13.450	0.439	518.198	-0.624
5/3/2005	20.776	0.191	2.134	-0.210	13.467	0.473	498.377	-0.648
5/4/2005	21.077	0.310	2.225	0.244	13.500	0.540	487.050	-0.661
5/5/2005	20.686	0.156	2.347	0.848	13.517	0.574	489.881	-0.658
5/6/2005	19.769	-0.205	2.408	1.151	13.550	0.641	478.555	-0.671
5/7/2005	19.902	-0.153	2.438	1.302	13.583	0.708	461.565	-0.692
5/8/2005	20.292	0.001	2.408	1.151	13.600	0.741	461.565	-0.692
5/9/2005	20.938	0.255	2.347	0.848	13.617	0.775	470.060	-0.681
5/10/2005	21.601	0.516	2.256	0.395	13.650	0.842	478.555	-0.671
5/11/2005	22.148	0.731	2.164	-0.059	13.683	0.909	470.060	-0.681
5/12/2005	22.625	0.919	1.737	-2.174	13.700	0.943	436.079	-0.722
5/13/2005	23.198	1.144	2.042	-0.663	13.717	0.977	385.109	-0.783
5/14/2005	23.642	1.319	1.981	-0.965	13.750	1.044	342.634	-0.834
5/15/2005	23.935	1.435	1.920	-1.268	13.767	1.077	322.812	-0.857
5/16/2005	24.182	1.532	1.859	-1.570	13.783	1.111	317.149	-0.864

5/17/2005	24.568	1.683	1.859	-1.570	13.817	1.178	314.317	-0.868
5/18/2005	24.787	1.770	1.890	-1.419	13.833	1.212	300.159	-0.884
5/19/2005	24.940	1.830	2.042	-0.663	13.850	1.245	261.648	-0.930
5/20/2005	25.382	2.004	2.164	-0.059	13.883	1.312	227.951	-0.971
5/21/2005	25.003	1.855	2.286	0.546	13.883	1.312	207.279	-0.995
5/22/2005	24.057	1.483	2.408	1.151	13.917	1.379	201.616	-1.002
5/23/2005	24.345	1.596	2.469	1.453	13.917	1.379	221.438	-0.978
5/24/2005	24.906	1.817	2.469	1.453	13.950	1.447	237.012	-0.960
5/25/2005	24.976	1.844	2.469	1.453	13.967	1.480	229.366	-0.969
5/26/2005	24.724	1.745	2.408	1.151	13.967	1.480	206.996	-0.996
Average	20.290		2.176		13.232		1040.566	
Standard Deviation	2.541		0.202		0.496		837.170	

Table A1.3. Observed and standardized values of temperature (° C), Maximum Daily High Tide (m above mean lower low water height), photoperiod (h), and discharge (m3/sec) during adult Atlantic sturgeon sampling in spring of 2006 in the Altamaha River, Georgia.

Date	Actual	Standardized	Actual	Standardized	Actual	Standardized	Actual	Standardized
3/25/2006	15.856	-2.112	2.134	-0.221	12.300	-1.831	300.159	1.105
3/26/2006	15.155	-2.329	2.225	0.212	12.317	-1.800	322.812	1.367
3/27/2006	15.077	-2.353	2.316	0.646	12.367	-1.708	348.297	1.663
3/28/2006	15.226	-2.307	2.469	1.368	12.400	-1.646	368.119	1.893
3/29/2006	15.688	-2.164	2.530	1.656	12.417	-1.615	385.109	2.089
3/30/2006	16.491	-1.916	2.530	1.656	12.450	-1.554	396.436	2.221
3/31/2006	17.335	-1.655	2.469	1.368	12.483	-1.493	396.436	2.221
4/1/2006	18.287	-1.361	2.377	0.934	12.517	-1.431	387.941	2.122
4/2/2006	19.154	-1.093	1.951	-1.087	12.550	-1.370	379.446	2.024
4/3/2006	20.066	-0.812	2.225	0.212	12.583	-1.308	370.951	1.925
4/4/2006	20.732	-0.606	2.073	-0.510	12.617	-1.247	365.287	1.860
4/5/2006	20.882	-0.560	1.981	-0.943	12.650	-1.185	353.961	1.728
4/6/2006	20.867	-0.564	1.890	-1.376	12.683	-1.124	334.139	1.499
4/7/2006	20.756	-0.599	1.859	-1.520	12.700	-1.093	297.327	1.072
4/8/2006	20.866	-0.565	1.890	-1.376	12.733	-1.032	261.081	0.652
4/9/2006	20.903	-0.553	1.920	-1.231	12.783	-0.939	243.525	0.448
4/10/2006	20.395	-0.710	2.012	-0.798	12.800	-0.909	228.800	0.278
4/11/2006	20.087	-0.805	2.103	-0.365	12.833	-0.847	225.685	0.241
4/12/2006	20.367	-0.719	2.195	0.068	12.867	-0.786	227.384	0.261
4/13/2006	20.890	-0.557	2.225	0.212	12.883	-0.755	228.234	0.271
4/14/2006	21.329	-0.422	2.225	0.212	12.917	-0.694	228.517	0.274
4/15/2006	21.737	-0.296	2.225	0.212	12.967	-0.601	227.667	0.264
4/16/2006	22.147	-0.169	2.195	0.068	12.983	-0.571	223.420	0.215
4/17/2006	22.549	-0.045	2.164	-0.076	13.017	-0.509	215.774	0.127
4/18/2006	22.744	0.015	1.798	-1.809	13.050	-0.448	206.430	0.018

4/19/2006	22.413	-0.087	2.103	-0.365	13.067	-0.417	197.368	-0.087
4/20/2006	22.675	-0.006	2.103	-0.365	13.100	-0.356	189.157	-0.182
4/21/2006	23.019	0.100	2.073	-0.510	13.133	-0.294	178.679	-0.303
4/22/2006	23.404	0.219	2.103	-0.365	13.150	-0.263	168.768	-0.418
4/23/2006	23.634	0.290	2.164	-0.076	13.183	-0.202	161.406	-0.504
4/24/2006	24.334	0.506	2.286	0.501	13.217	-0.140	156.026	-0.566
4/25/2006	24.954	0.698	2.438	1.223	13.250	-0.079	152.628	-0.605
4/26/2006	25.237	0.785	2.530	1.656	13.283	-0.018	152.911	-0.602
4/27/2006	24.842	0.663	2.560	1.801	13.317	0.044	157.725	-0.546
4/28/2006	24.332	0.506	2.530	1.656	13.333	0.075	163.955	-0.474
4/29/2006	23.829	0.350	2.469	1.368	13.350	0.105	175.564	-0.340
4/30/2006	22.608	-0.027	2.347	0.790	13.383	0.167	181.794	-0.267
5/1/2006	21.703	-0.306	1.859	-1.520	13.400	0.198	183.493	-0.248
5/2/2006	21.848	-0.262	2.195	0.068	13.433	0.259	182.360	-0.261
5/3/2006	22.143	-0.170	2.073	-0.510	13.467	0.320	178.679	-0.303
5/4/2006	22.758	0.020	1.951	-1.087	13.500	0.382	173.016	-0.369
5/5/2006	23.398	0.217	1.890	-1.376	13.517	0.413	163.671	-0.477
5/6/2006	23.881	0.366	1.859	-1.520	13.550	0.474	150.646	-0.628
5/7/2006	24.566	0.578	1.859	-1.520	13.583	0.536	137.903	-0.776
5/8/2006	24.867	0.671	1.981	-0.943	13.583	0.536	129.125	-0.878
5/9/2006	24.487	0.554	2.073	-0.510	13.617	0.597	125.444	-0.921
5/10/2006	23.828	0.350	2.164	-0.076	13.650	0.658	129.974	-0.868
5/11/2006	23.856	0.359	2.225	0.212	13.667	0.689	141.301	-0.737
5/12/2006	23.563	0.268	2.286	0.501	13.700	0.751	157.725	-0.546
5/13/2006	23.442	0.231	2.316	0.646	13.717	0.781	166.786	-0.441
5/14/2006	23.550	0.264	2.316	0.646	13.733	0.812	163.105	-0.484
5/15/2006	23.690	0.307	2.286	0.501	13.767	0.874	162.822	-0.487
5/16/2006	23.156	0.143	2.225	0.212	13.783	0.904	164.238	-0.471
5/17/2006	22.782	0.027	1.829	-1.665	13.800	0.935	169.618	-0.408

5/18/2006	22.719	0.008	2.195	0.068	13.817	0.966	182.360	-0.261
5/19/2006	22.883	0.058	2.164	-0.076	13.850	1.027	191.988	-0.149
5/20/2006	23.478	0.242	2.134	-0.221	13.867	1.058	185.475	-0.225
5/21/2006	24.376	0.520	2.134	-0.221	13.883	1.089	166.220	-0.448
5/22/2006	25.226	0.782	2.225	0.212	13.917	1.150	147.531	-0.665
5/23/2006	25.822	0.966	2.347	0.790	13.917	1.150	133.089	-0.832
5/24/2006	26.390	1.141	2.438	1.223	13.950	1.212	124.594	-0.930
5/25/2006	26.966	1.319	2.469	1.368	13.967	1.242	126.293	-0.911
5/26/2006	27.220	1.398	2.469	1.368	13.967	1.242	124.028	-0.937
5/27/2006	27.415	1.458	2.469	1.368	14.000	1.304	116.382	-1.026
5/28/2006	27.879	1.601	2.377	0.934	14.000	1.304	110.153	-1.098
5/29/2006	27.933	1.618	2.256	0.357	14.017	1.334	105.905	-1.147
5/30/2006	28.009	1.642	2.134	-0.221	14.050	1.396	101.941	-1.193
5/31/2006	27.978	1.632	1.737	-2.098	14.050	1.396	97.693	-1.242
6/1/2006	27.991	1.636	2.042	-0.654	14.067	1.427	95.145	-1.272
6/2/2006	27.941	1.620	1.951	-1.087	14.083	1.457	92.313	-1.305
Average	22.694		2.180		13.293		204.856	
Standard Deviation	3.238		0.211		0.542		86.268	

Table A1.4. Observed and standardized values of temperature (° C), Maximum Daily High Tide (m above mean lower low water height), photoperiod (h), and discharge (m3/sec) during adult Atlantic sturgeon sampling in spring of 2007 in the Altamaha River, Georgia.

	Temperature		Tidal Cycle		Photoperiod		Discharge	
Date	Actual	Standardized	Actual	Standardized	Actual	Standardized	Actual	Standardized
3/30/2007	21.823	-0.284	2.012	-0.769	12.450	-1.828	184.343	1.036
3/31/2007	21.396	-0.454	2.103	-0.335	12.483	-1.760	175.281	0.873
4/1/2007	21.472	-0.424	2.164	-0.045	12.517	-1.692	166.220	0.710
4/2/2007	21.831	-0.281	2.195	0.099	12.550	-1.624	158.858	0.577
4/3/2007	22.275	-0.104	2.195	0.099	12.567	-1.590	153.194	0.475
4/4/2007	22.723	0.074	2.164	-0.045	12.600	-1.522	148.097	0.383
4/5/2007	22.743	0.082	2.103	-0.335	12.633	-1.454	143.283	0.296
4/6/2007	21.890	-0.258	2.042	-0.624	12.667	-1.386	139.319	0.225
4/7/2007	20.790	-0.696	1.737	-2.071	12.700	-1.318	137.337	0.189
4/8/2007	19.437	-1.234	2.012	-0.769	12.733	-1.250	135.921	0.164
4/9/2007	18.762	-1.503	1.951	-1.058	12.750	-1.217	135.355	0.154
4/10/2007	18.171	-1.738	1.951	-1.058	12.800	-1.115	135.921	0.164
4/11/2007	17.915	-1.840	1.981	-0.914	12.833	-1.047	137.054	0.184
4/12/2007	18.836	-1.473	2.012	-0.769	12.850	-1.013	137.620	0.194
4/13/2007	19.471	-1.221	2.103	-0.335	12.883	-0.945	135.355	0.154
4/14/2007	20.127	-0.959	2.256	0.389	12.917	-0.877	130.824	0.072
4/15/2007	20.954	-0.630	2.438	1.257	12.933	-0.843	126.576	-0.005
4/16/2007	18.983	-1.415	2.560	1.836	12.967	-0.775	124.594	-0.040
4/17/2007	18.124	-1.757	2.621	2.126	13.017	-0.673	126.293	-0.010
4/18/2007	18.374	-1.657	2.621	2.126	13.033	-0.639	145.265	0.332
4/19/2007	18.477	-1.616	2.530	1.691	13.067	-0.571	182.077	0.996
4/20/2007	19.126	-1.358	2.042	-0.624	13.100	-0.503	225.685	1.782
4/21/2007	19.098	-1.369	2.438	1.257	13.117	-0.469	258.250	2.369
4/22/2007	19.378	-1.258	2.286	0.534	13.150	-0.401	278.071	2.726

4/23/2007	19.941	-1.034	2.134	-0.190	13.183	-0.333	276.656	2.700
4/24/2007	20.392	-0.854	2.042	-0.624	13.217	-0.265	260.798	2.414
4/25/2007	20.899	-0.652	1.981	-0.914	13.233	-0.231	240.976	2.057
4/26/2007	21.772	-0.305	1.920	-1.203	13.267	-0.163	210.394	1.506
4/27/2007	22.525	-0.005	1.981	-0.914	13.300	-0.095	181.511	0.985
4/28/2007	22.932	0.157	2.073	-0.479	13.317	-0.061	158.858	0.577
4/29/2007	23.196	0.262	2.164	-0.045	13.350	0.007	142.434	0.281
4/30/2007	23.686	0.457	2.225	0.244	13.383	0.075	130.257	0.062
5/1/2007	24.165	0.648	2.256	0.389	13.400	0.109	122.046	-0.086
5/2/2007	24.490	0.777	2.256	0.389	13.433	0.177	115.533	-0.204
5/3/2007	24.767	0.887	2.225	0.244	13.467	0.245	110.153	-0.301
5/4/2007	25.050	1.000	2.164	-0.045	13.483	0.279	105.622	-0.382
5/5/2007	25.236	1.075	2.134	-0.190	13.517	0.347	101.091	-0.464
5/6/2007	25.001	0.981	1.768	-1.927	13.550	0.415	97.976	-0.520
5/7/2007	23.242	0.280	2.073	-0.479	13.550	0.415	94.861	-0.576
5/8/2007	21.964	-0.228	2.042	-0.624	13.583	0.483	92.030	-0.627
5/9/2007	21.481	-0.421	2.042	-0.624	13.617	0.551	90.048	-0.663
5/10/2007	21.498	-0.414	2.042	-0.624	13.650	0.619	88.632	-0.689
5/11/2007	22.448	-0.036	2.073	-0.479	13.667	0.653	86.933	-0.719
5/12/2007	23.498	0.382	2.225	0.244	13.683	0.687	85.800	-0.740
5/13/2007	24.295	0.700	2.377	0.968	13.717	0.755	86.366	-0.729
5/14/2007	24.433	0.755	2.499	1.547	13.733	0.789	88.349	-0.694
5/15/2007	24.375	0.731	2.591	1.981	13.750	0.823	86.933	-0.719
5/16/2007	24.683	0.854	2.621	2.126	13.783	0.890	84.384	-0.765
5/17/2007	24.968	0.968	2.560	1.836	13.800	0.924	82.968	-0.791
5/18/2007	24.767	0.887	2.469	1.402	13.817	0.958	81.553	-0.816
5/19/2007	24.504	0.783	2.377	0.968	13.850	1.026	79.570	-0.852
5/20/2007	24.244	0.680	1.890	-1.348	13.850	1.026	78.154	-0.877
5/21/2007	24.392	0.739	2.256	0.389	13.883	1.094	77.305	-0.893

5/22/2007	24.706	0.863	2.134	-0.190	13.900	1.128	77.305	-0.893
5/23/2007	24.867	0.928	2.012	-0.769	13.917	1.162	77.022	-0.898
5/24/2007	24.733	0.874	1.951	-1.058	13.933	1.196	75.606	-0.923
5/25/2007	24.814	0.906	1.920	-1.203	13.950	1.230	73.624	-0.959
5/26/2007	25.079	1.012	2.012	-0.769	13.967	1.264	71.358	-1.000
5/27/2007	25.588	1.215	2.073	-0.479	14.000	1.332	68.527	-1.051
5/28/2007	25.793	1.296	2.164	-0.045	14.000	1.332	66.261	-1.092
5/29/2007	25.995	1.376	2.195	0.099	14.017	1.366	64.562	-1.122
5/30/2007	26.325	1.508	2.225	0.244	14.033	1.400	62.863	-1.153
5/31/2007	26.665	1.643	2.225	0.244	14.050	1.434	61.448	-1.179
6/1/2007	26.802	1.698	2.225	0.244	14.067	1.468	60.032	-1.204
Average	22.537		2.174		13.347		126.837	
Standard Deviation	2.512		0.211		0.490		55.482	

Table A1.5. Relative likelihood of POPAN models with constant apparent survival and various parameterization of recapture probability (p) and entry probability (pent) from 2004.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	K
p(TL)pent(temp*tide)	260.837	0	0.65203	1	7
p(TL)pent(pp*tide)	262.886	2.0491	0.23405	0.359	7
p(TL)pent(pp+tide)	266.387	5.5498	0.04066	0.0624	6
p(TL)pent(temp+tide)	266.419	5.5813	0.04002	0.0614	6
p(TL)pent(tide)	268.249	7.4119	0.01602	0.0246	5
p(TL)pent(disc+tide)	269.789	8.9516	0.00742	0.0114	6
p(TL)pent(disc*tide)	270.709	9.8715	0.00468	0.0072	7
p(TL)pent(temp)	271.197	10.3599	0.00367	0.0056	5
p(TL)pent(pp)	273.465	12.6278	0.00118	0.0018	5
p(TL)pent(.)	277.782	16.9445	0.00014	0.0002	4
p(TL)pent(disc)	278.105	17.2679	0.00012	0.0002	5
p(temp*tide)pent(temp*tide)	300.796	39.9592	0	0	9
p(temp+tide)pent(temp*tide)	300.94	40.1023	0	0	8
p(temp)pent(temp*tide)	305.612	44.775	0	0	7
p(tide)pent(temp*tide)	305.683	44.8458	0	0	7
p(temp+tide)pent(pp+tide)	306.127	45.2894	0	0	7
p(temp+tide)pent(temp+tide)	306.128	45.2903	0	0	7
p(temp*tide)pent(pp+tide)	306.526	45.6883	0	0	8
p(temp*tide)pent(temp+tide)	306.541	45.704	0	0	8
p(temp)pent(pp*tide)	307.427	46.5897	0	0	7
p(temp+tide)pent(pp*tide)	307.427	46.5897	0	0	7
p(temp*tide)pent(pp*tide)	307.427	46.5897	0	0	7
p(temp+tide)pent(tide)	307.577	46.7394	0	0	6
p(tide)pent(pp*tide)	307.752	46.9148	0	0	7
p(temp*tide)pent(tide)	307.899	47.0617	0	0	7
p(temp+tide)pent(disc+tide)	309.271	48.4333	0	0	7
p(temp*tide)pent(disc+tide)	309.605	48.7674	0	0	8
p(temp+tide)pent(temp)	309.98	49.1431	0	0	6
p(temp+tide)pent(disc*tide)	310.323	49.4861	0	0	8
p(temp*tide)pent(disc*tide)	310.378	49.5412	0	0	9
p(temp*tide)pent(temp)	310.487	49.6494	0	0	7
p(tide)pent(temp+tide)	310.996	50.159	0	0	6
p(tide)pent(pp+tide)	311.022	50.1843	0	0	6
p(temp)pent(temp+tide)	311.487	50.65	0	0	6
p(temp)pent(pp+tide)	311.506	50.6684	0	0	6
p(temp+tide)pent(pp)	312.046	51.2083	0	0	6

p(temp*tide)pent(pp)	312.551	51.714	0	0	7
p(tide)pent(tide)	312.702	51.8649	0	0	5
p(temp)pent(tide)	312.774	51.9369	0	0	5
p(.)pent(temp*tide)	313.78	52.9432	0	0	6
p(tide)pent(disc+tide)	314.326	53.4885	0	0	6
p(temp)pent(disc+tide)	314.578	53.7403	0	0	6
p(tide)pent(temp)	314.616	53.7791	0	0	5
p(temp)pent(disc*tide)	315.295	54.4578	0	0	7
p(tide)pent(disc*tide)	315.363	54.5255	0	0	7
p(.)pent(pp*tide)	315.689	54.8522	0	0	6
p(temp+tide)pent(.)	315.701	54.8637	0	0	5
p(temp)pent(temp)	316.114	55.2766	0	0	5
p(temp*tide)pent(.)	316.164	55.3269	0	0	6
p(temp+tide)pent(disc)	316.397	55.5602	0	0	6
p(tide)pent(pp)	316.72	55.8829	0	0	5
p(temp*tide)pent(disc)	316.852	56.0145	0	0	7
p(temp)pent(pp)	318.324	57.4868	0	0	5
p(.)pent(temp+tide)	319.426	58.5889	0	0	5
p(.)pent(pp+tide)	319.501	58.6642	0	0	5
p(tide)pent(.)	320.562	59.7248	0	0	4
p(.)pent(tide)	321.06	60.2228	0	0	4
p(tide)pent(disc)	321.167	60.3296	0	0	5
p(temp)pent(.)	321.852	61.0146	0	0	4
p(temp)pent(disc)	322.742	61.9044	0	0	5
p(.)pent(disc+tide)	322.839	62.0017	0	0	5
p(.)pent(disc*tide)	323.706	62.8684	0	0	6
p(.)pent(temp)	323.845	63.0076	0	0	4
p(.)pent(pp)	326.193	65.3557	0	0	4
p(.)pent(.)	330.031	69.194	0	0	3
p(.)pent(disc)	330.898	70.0605	0	0	4

Table A1.6. Relative likelihood of POPAN models with constant apparent survival and various parameterization of recapture probability (p) and entry probability (pent) from 2005.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	K
p(TL)pent(disc+tide)	245.801	0	0.53768	1	6
p(TL)pent(disc*tide)	247.362	1.5613	0.24632	0.4581	7
p(TL)pent(pp*tide)	247.933	2.1315	0.18521	0.3445	7
p(TL)pent(pp+tide)	251.522	5.7207	0.03078	0.0572	6
p(TL)pent(disc)	269.594	23.7926	0	0	5
p(TL)pent(pp)	272.365	26.5642	0	0	5
p(.)pent(disc+tide)	272.589	26.7876	0	0	5
p(temp)pent(disc+tide)	272.996	27.1954	0	0	6
p(tide)pent(disc+tide)	273.656	27.8546	0	0	6
p(.)pent(disc*tide)	274.145	28.3437	0	0	6
p(temp+tide)pent(disc+tide)	274.548	28.7465	0	0	7
p(temp)pent(disc*tide)	274.556	28.7552	0	0	7
p(.)pent(pp*tide)	274.74	28.9389	0	0	6
p(temp)pent(pp*tide)	275.081	29.2799	0	0	7
p(tide)pent(disc*tide)	275.22	29.4194	0	0	7
p(tide)pent(pp*tide)	275.811	30.0099	0	0	7
p(temp+tide)pent(disc*tide)	276.096	30.2947	0	0	8
p(temp*tide)pent(disc+tide)	276.509	30.7078	0	0	8
p(temp+tide)pent(pp*tide)	276.614	30.8131	0	0	8
p(temp*tide)pent(disc*tide)	278.05	32.249	0	0	9
p(.)pent(pp+tide)	278.343	32.5418	0	0	5
p(temp*tide)pent(pp*tide)	278.563	32.7624	0	0	9
p(temp)pent(pp+tide)	278.698	32.8966	0	0	6
p(tide)pent(pp+tide)	279.386	33.5847	0	0	6
p(temp+tide)pent(pp+tide)	280.271	34.4697	0	0	7
p(TL)pent(temp*tide)	281.836	36.0349	0	0	7
p(temp*tide)pent(pp+tide)	282.241	36.4404	0	0	8
p(TL)pent(temp+tide)	287.092	41.2911	0	0	6
p(.)pent(disc)	296.301	50.5003	0	0	4
p(temp)pent(disc)	296.871	51.07	0	0	5
p(TL)pent(temp)	297.5	51.6993	0	0	5
p(tide)pent(disc)	297.779	51.9776	0	0	5
p(temp+tide)pent(disc)	298.689	52.8876	0	0	6
p(.)pent(pp)	299.098	53.2971	0	0	4
p(temp)pent(pp)	299.577	53.7763	0	0	5

p(tide)pent(pp)	300.548	54.7473	0	0	5
p(temp*tide)pent(disc)	300.685	54.8836	0	0	7
p(temp+tide)pent(pp)	301.403	55.6016	0	0	6
p(temp*tide)pent(pp)	303.402	57.6007	0	0	7
p(.)pent(temp*tide)	308.606	62.8046	0	0	6
p(temp)pent(temp*tide)	309.033	63.2316	0	0	7
p(tide)pent(temp*tide)	309.717	63.9157	0	0	7
p(temp+tide)pent(temp*tide)	310.559	64.7582	0	0	8
p(temp*tide)pent(temp*tide)	312.495	66.6943	0	0	9
p(.)pent(temp+tide)	313.86	68.0594	0	0	5
p(temp)pent(temp+tide)	314.288	68.4872	0	0	6
p(tide)pent(temp+tide)	314.952	69.1511	0	0	6
p(temp+tide)pent(temp+tide)	315.885	70.0839	0	0	7
p(temp*tide)pent(temp+tide)	317.855	72.0537	0	0	8
p(.)pent(temp)	324.22	78.4191	0	0	4
p(temp)pent(temp)	324.685	78.8835	0	0	5
p(tide)pent(temp)	325.597	79.7957	0	0	5
p(temp+tide)pent(temp)	326.465	80.6643	0	0	6
p(temp*tide)pent(temp)	328.461	82.66	0	0	7
p(TLpent(tide)	368.743	122.942	0	0	6
p(TL)pent(.)	381.434	135.633	0	0	5
p(.)pent(tide	391.906	146.105	0	0	4
p(tide)pent(tide)	393.001	147.2	0	0	5
p(temp)pent(tide)	393.708	147.907	0	0	5
p(temp+tide)pent(tide)	395	149.199	0	0	6
p(temp*tide)pent(tide)	396.45	150.649	0	0	7
p(.)pent(.)	404.377	158.576	0	0	3
p(tide)pent(.)	405.762	159.961	0	0	4
p(temp)pent(.)	406.21	160.409	0	0	4
p(temp+tide)pent(.)	407.762	161.961	0	0	5
p(temp*tide)pent(.)	409.596	163.795	0	0	6

Table A1.7. Relative likelihood of POPAN models with constant apparent survival and various parameterization of recapture probability (p) and entry probability (pent) from 2006.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	K
p(TL)pent(disc)	321.847	0	0.42753	1	5
p(TL)pent(disc+tide)	322.208	0.3609	0.35694	0.8349	6
p(TL)pent(disc*tide)	323.248	1.4006	0.21224	0.4964	7
p(TL)pent(pp+tide)	333.279	11.432	0.00141	0.0033	6
p(TL)pent(pp)	333.464	11.6172	0.00128	0.003	5
p(TL)pent(pp*tide)	335.434	13.5869	0.00048	0.0011	7
p(TL)pent(temp+tide)	340.122	18.2745	0.00005	0.0001	6
p(TL)pent(temp)	340.609	18.7613	0.00004	0.0001	5
p(TL)pent(temp*tide)	340.95	19.1025	0.00003	0.0001	7
p(.)pent(disc)	348.766	26.9186	0	0	4
p(.)pent(disc+tide)	349.053	27.2057	0	0	5
p(temp)pent(disc)	349.815	27.9675	0	0	5
p(.)pent(disc*tide)	350.028	28.1803	0	0	6
p(temp)pent(disc+tide)	350.16	28.3123	0	0	6
p(tide)pent(disc)	350.81	28.9627	0	0	5
p(tide)pent(disc+tide)	351.098	29.2505	0	0	6
p(temp)pent(disc*tide)	351.216	29.3688	0	0	7
p(temp+tide)pent(disc)	352.077	30.2293	0	0	6
p(tide)pent(disc*tide)	352.121	30.2742	0	0	7
p(temp+tide)pent(disc+tide)	352.455	30.6082	0	0	7
p(temp+tide)pent(disc*tide)	353.559	31.7115	0	0	8
p(temp*tide)pent(disc)	353.934	32.0865	0	0	7
p(temp*tide)pent(disc+tide)	354.358	32.5109	0	0	8
p(temp*tide)pent(disc*tide)	355.608	33.7604	0	0	9
p(.)pent(pp+tide)	360.05	38.2026	0	0	5
p(.)pent(pp)	360.314	38.4664	0	0	4
p(TL)pent(.)	360.733	38.8862	0	0	4
p(temp)pent(pp+tide)	361.004	39.1566	0	0	6
p(temp)pent(pp)	361.188	39.3406	0	0	5
p(tide)pent(pp+tide)	362.055	40.2081	0	0	6
p(.)pent(pp*tide)	362.144	40.2963	0	0	6
p(tide)pent(pp)	362.328	40.4812	0	0	5
p(temp)pent(pp*tide)	363.164	41.3169	0	0	7
p(temp+tide)pent(pp+tide)	363.287	41.4401	0	0	7
p(temp+tide)pent(pp)	363.443	41.5954	0	0	6
p(tide)pent(pp*tide)	364.204	42.357	0	0	7

p(temp*tide)pent(pp+tide)	365.187	43.3396	0	0	8
p(temp*tide)pent(pp)	365.267	43.42	0	0	7
p(temp+tide)pent(pp*tide)	365.501	43.6541	0	0	8
p(.)pent(temp+tide)	366.923	45.0761	0	0	5
p(.)pent(temp)	367.484	45.6367	0	0	4
p(temp*tide)pent(pp*tide)	367.492	45.6448	0	0	9
p(.)pent(temp*tide)	367.677	45.8295	0	0	6
p(temp)pent(temp+tide)	367.878	46.0309	0	0	6
p(temp)pent(temp)	368.355	46.5079	0	0	5
p(temp)pent(temp*tide)	368.72	46.8724	0	0	7
p(tide)pent(temp+tide)	368.949	47.1013	0	0	6
p(tide)pent(temp)	369.521	47.6742	0	0	5
p(tide)pent(temp*tide)	369.745	47.8978	0	0	7
p(temp+tide)pent(temp+tide)	370.171	48.3236	0	0	7
p(temp+tide)pent(temp)	370.619	48.7714	0	0	6
p(temp+tide)pent(temp*tide)	371.053	49.2062	0	0	8
p(temp*tide)pent(temp+tide)	372.082	50.2352	0	0	8
p(temp*tide)pent(temp)	372.453	50.6062	0	0	7
p(temp*tide)pent(temp*tide)	373.141	51.2934	0	0	9
p(.)pent(tide)	387.505	65.6577	0	0	4
p(.)pent(.)	387.541	65.6937	0	0	3
p(temp)pent(.)	387.7	65.853	0	0	4
p(temp)pent(tide)	387.778	65.9312	0	0	5
p(tide)pent(tide)	389.464	67.6167	0	0	5
p(tide)pent(.)	389.507	67.6597	0	0	4
p(temp+tide)pent(.)	389.917	68.07	0	0	5
p(temp+tide)pent(tide)	390.03	68.1828	0	0	6
p(temp*tide)pent(.)	391.551	69.7039	0	0	6
p(temp*tide)pent(tide)	391.792	69.945	0	0	7

Table A1.8. Relative likelihood of POPAN models with constant apparent survival and various parameterization of recapture probability (p) and entry probability (pent) from 2007.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	K
p(TL)pent(pp)	375.903	0	0.58235	1	5
p(TL)pent(pp+tide)	377.793	1.8902	0.22633	0.3886	6
p(TL)pent(pp*tide)	379.066	3.163	0.11977	0.2057	7
p(.)pent(pp)	382.582	6.6789	0.02065	0.0355	4
p(.)pent(pp+tide)	384.308	8.4055	0.00871	0.015	5
p(tide)pent(pp)	384.48	8.5771	0.00799	0.0137	5
p(temp)pent(pp)	384.578	8.6751	0.00761	0.0131	5
p(.)pent(pp*tide)	385.734	9.8311	0.00427	0.0073	6
p(tide)pent(pp+tide)	386.171	10.2678	0.00343	0.0059	6
p(temp)pent(pp+tide)	386.304	10.4013	0.00321	0.0055	6
p(temp+tide)pent(pp)	386.48	10.577	0.00294	0.005	6
p(TL)pent(temp)	386.496	10.5937	0.00292	0.005	5
p(tide)pent(pp*tide)	387.555	11.6525	0.00172	0.003	7
p(temp)pent(pp*tide)	387.733	11.8304	0.00157	0.0027	7
p(temp*tide)pent(pp)	387.962	12.0591	0.0014	0.0024	7
p(temp+tide)pent(pp+tide)	388.17	12.2676	0.00126	0.0022	7
p(TL)pent(temp+tide)	388.423	12.5201	0.00111	0.0019	6
p(temp+tide)pent(pp*tide)	389.551	13.648	0.00063	0.0011	8
p(TL)pent(temp*tide)	389.612	13.7097	0.00061	0.001	7
p(temp*tide)pent(pp+tide)	389.721	13.8183	0.00058	0.001	8
p(temp*tide)pent(pp*tide)	391.332	15.429	0.00026	0.0004	9
p(TL)pent(disc)	392.061	16.1582	0.00018	0.0003	5
p(.)pent(temp)	393.038	17.1357	0.00011	0.0002	4
p(TL)pent(disc+tide)	393.989	18.0861	0.00007	0.0001	6
p(tide)pent(temp)	394.84	18.9371	0.00004	0.0001	5
p(.)pent(temp+tide)	394.914	19.0108	0.00004	0.0001	5
p(temp)pent(temp)	394.995	19.0919	0.00004	0.0001	5
p(TL)pent(disc*tide)	395.759	19.8563	0.00003	0.0001	7
p(.)pent(temp*tide)	396.572	20.6692	0.00002	0	6
p(tide)pent(temp+tide)	396.683	20.7805	0.00002	0	6
p(temp+tide)pent(temp)	396.826	20.9237	0.00002	0	6
p(temp)pent(temp+tide)	396.87	20.9674	0.00002	0	6
p(.)pent(disc)	397.198	21.2954	0.00001	0	4
p(tide)pent(temp*tide)	398.333	22.4303	0.00001	0	7
p(temp*tide)pent(temp)	398.4	22.4968	0.00001	0	7
p(temp)pent(temp*tide)	398.56	22.6573	0.00001	0	7

p(temp+tide)pent(temp+tide)	398.672	22.7693	0.00001	0	7
p(temp)pent(disc)	398.864	22.9612	0.00001	0	5
p(.)pent(disc+tide)	399.066	23.1632	0.00001	0	5
p(tide)pent(disc)	399.193	23.29	0.00001	0	5
p(temp*tide)pent(temp+tide)	400.291	24.3879	0	0	8
p(temp+tide)pent(temp*tide)	400.333	24.4303	0	0	8
p(temp*tide)pent(disc)	400.656	24.7533	0	0	7
p(.)pent(disc*tide)	400.693	24.7898	0	0	6
p(temp)pent(disc+tide)	400.744	24.8411	0	0	6
p(temp+tide)pent(disc)	400.862	24.9595	0	0	6
p(tide)pent(disc+tide)	401.054	25.1516	0	0	6
p(temp*tide)pent(temp*tide)	402.162	26.2589	0	0	9
p(temp)pent(disc*tide)	402.369	26.4666	0	0	7
p(temp*tide)pent(disc+tide)	402.588	26.6856	0	0	8
p(tide)pent(disc*tide)	402.659	26.7564	0	0	7
p(temp+tide)pent(disc+tide)	402.744	26.841	0	0	7
p(temp*tide)pent(disc*tide)	404.354	28.4516	0	0	9
p(temp+tide)pent(disc*tide)	404.367	28.4643	0	0	8
p(TL)pent(.)	411.539	35.6367	0	0	4
p(TL)pent(tide)	413.539	37.6366	0	0	5
p(.)pent(.)	414.946	39.0431	0	0	3
p(tide)pent(.)	416.641	40.738	0	0	4
p(temp)pent(.)	416.745	40.8423	0	0	4
p(.)pent(tide)	416.871	40.968	0	0	4
p(temp+tide)pent(.)	418.517	42.6139	0	0	5
p(tide)pent(tide)	418.526	42.6232	0	0	5
p(temp)pent(tide)	418.664	42.7615	0	0	5
p(temp+tide)pent(tide)	420.402	44.4995	0	0	6

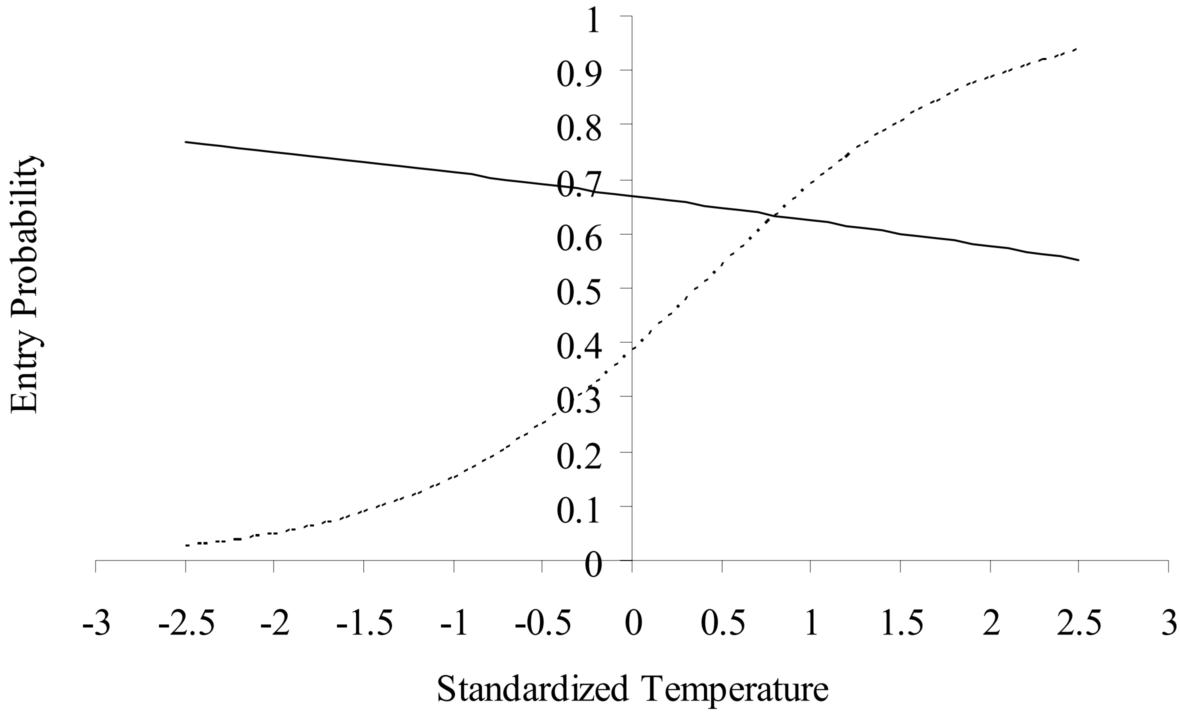

Figure A1.1. Composite model predictions of entry probability across a range of temperature values at low, solid line, and high, dashed line, tidal cycle levels in 2004.

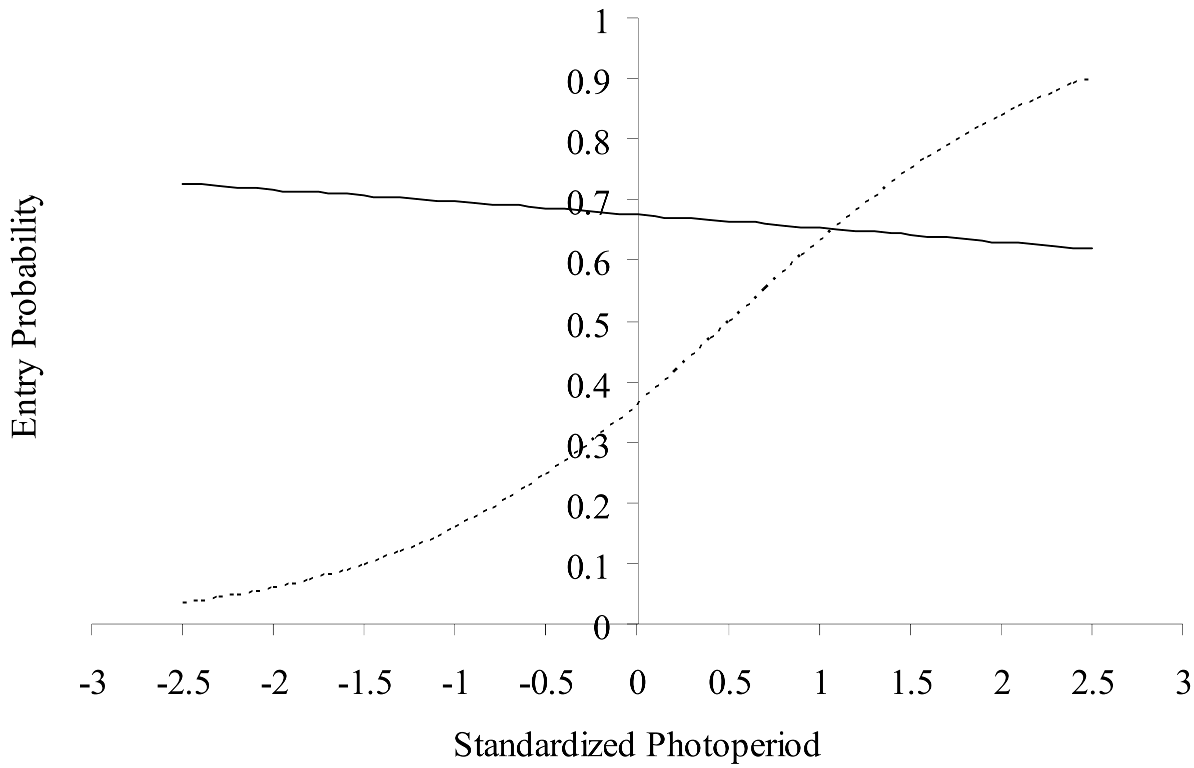

Figure A1.2. Composite model predictions of entry probability across a range of photoperiod values at low, solid line, and high, dashed line, tidal cycle levels in 2004.

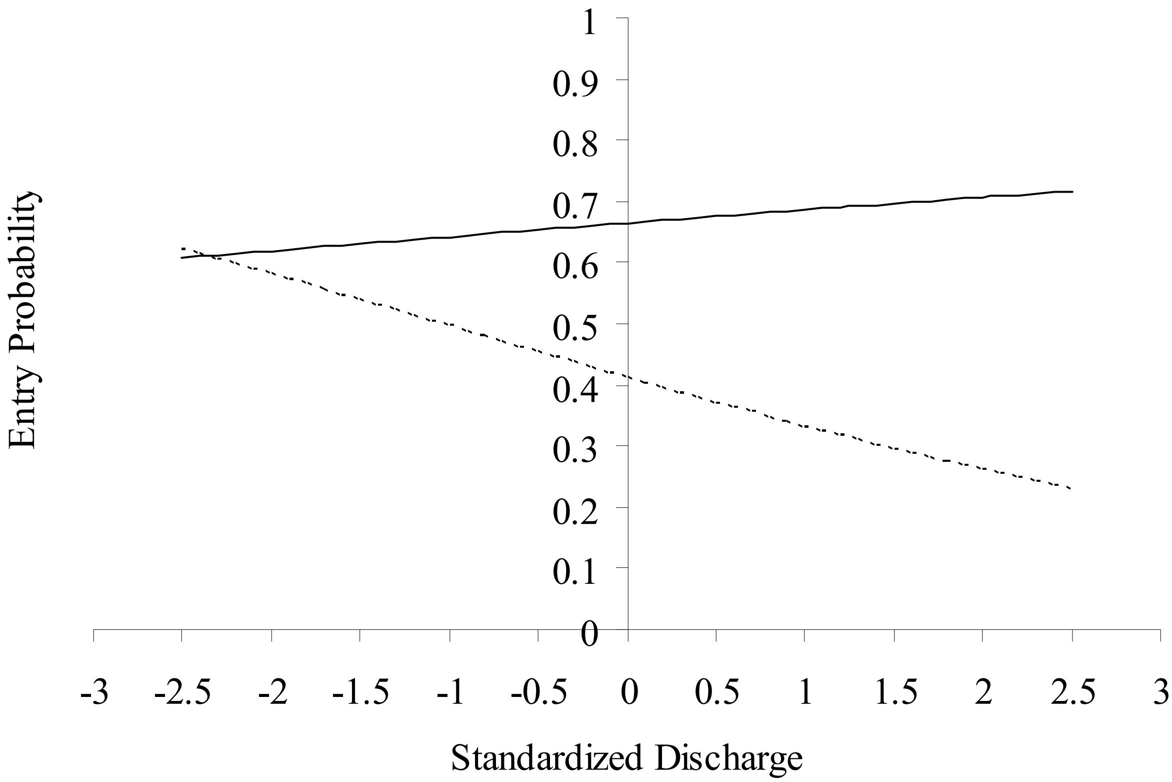

Figure A1.3. Composite model predictions of entry probability across a range of discharge values at low, solid line, and high, dashed line, tidal cycle levels in 2004.

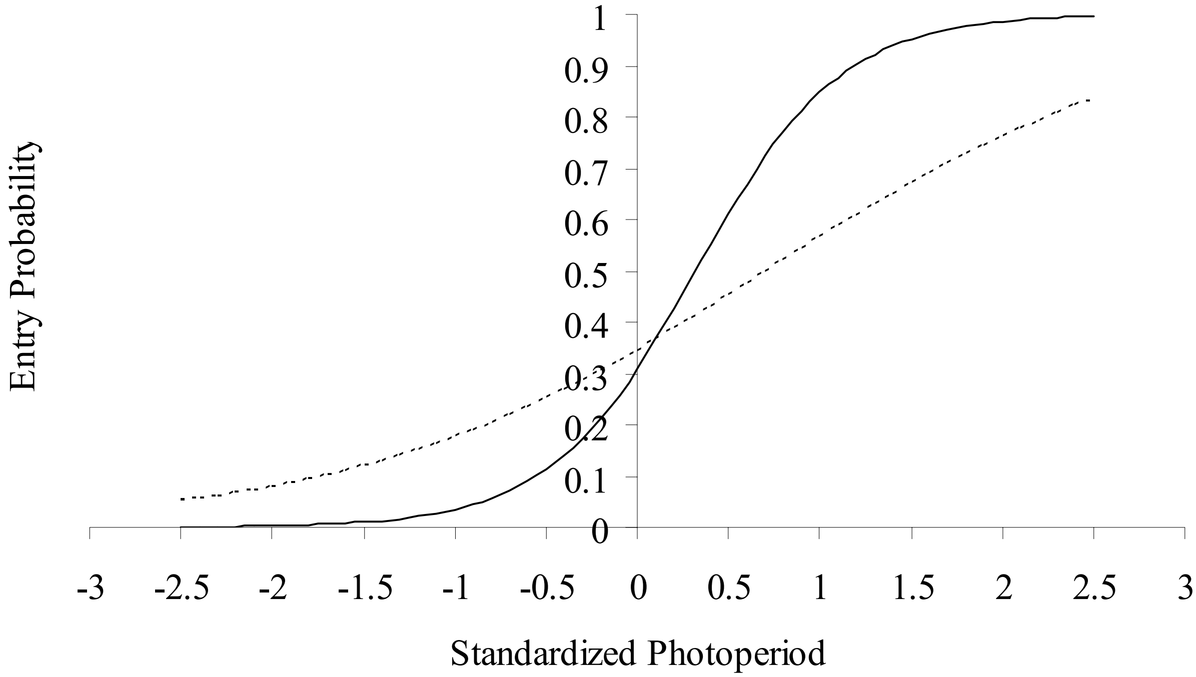

Figure A1.4. Composite model predictions of entry probability across a range of photoperiod values at low, solid line, and high, dashed line, tidal cycle levels in 2005.

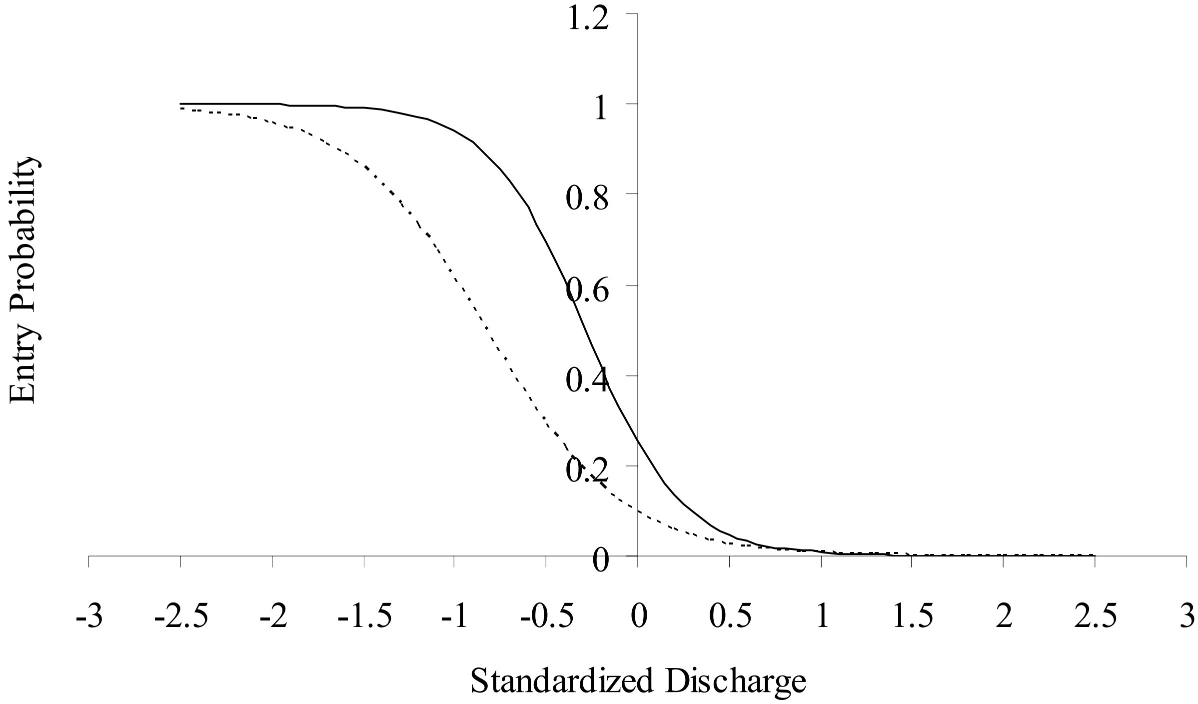

Figure A1.5. Composite model predictions of entry probability across a range of discharge values at low, solid line, and high, dashed line, tidal cycle levels in 2005.

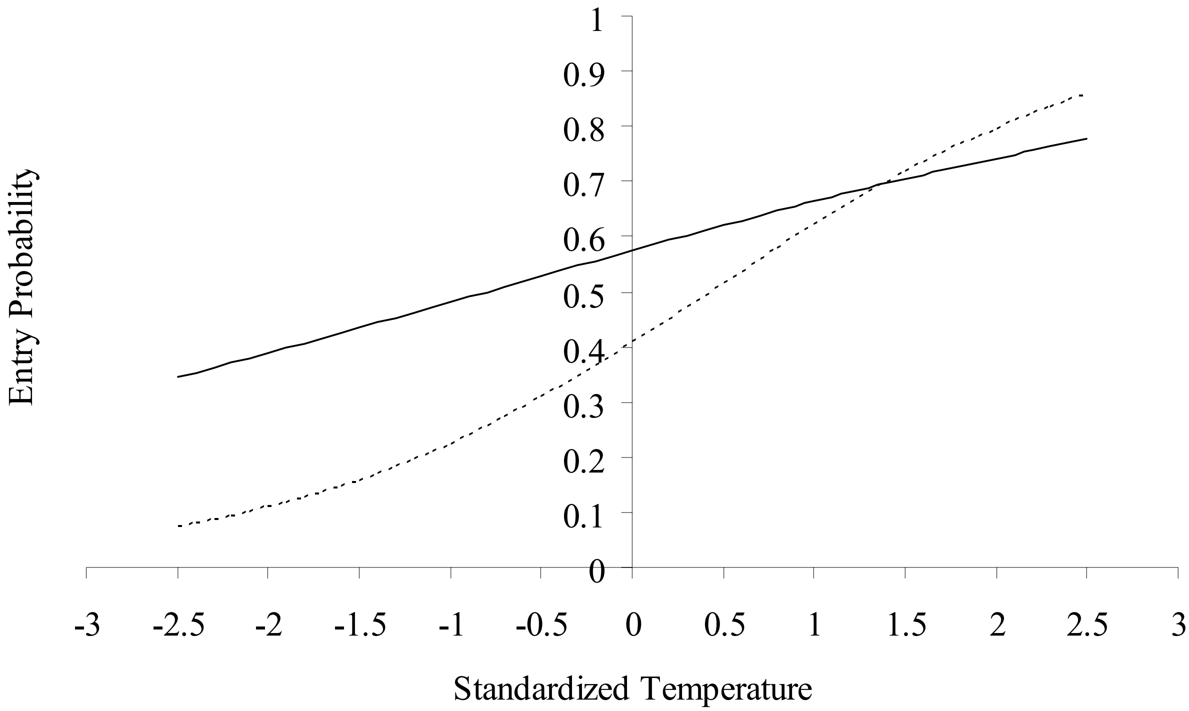

Figure A1.6. Composite model predictions of entry probability across a range of temperature values at low, solid line, and high, dashed line, tidal cycle levels in 2006.

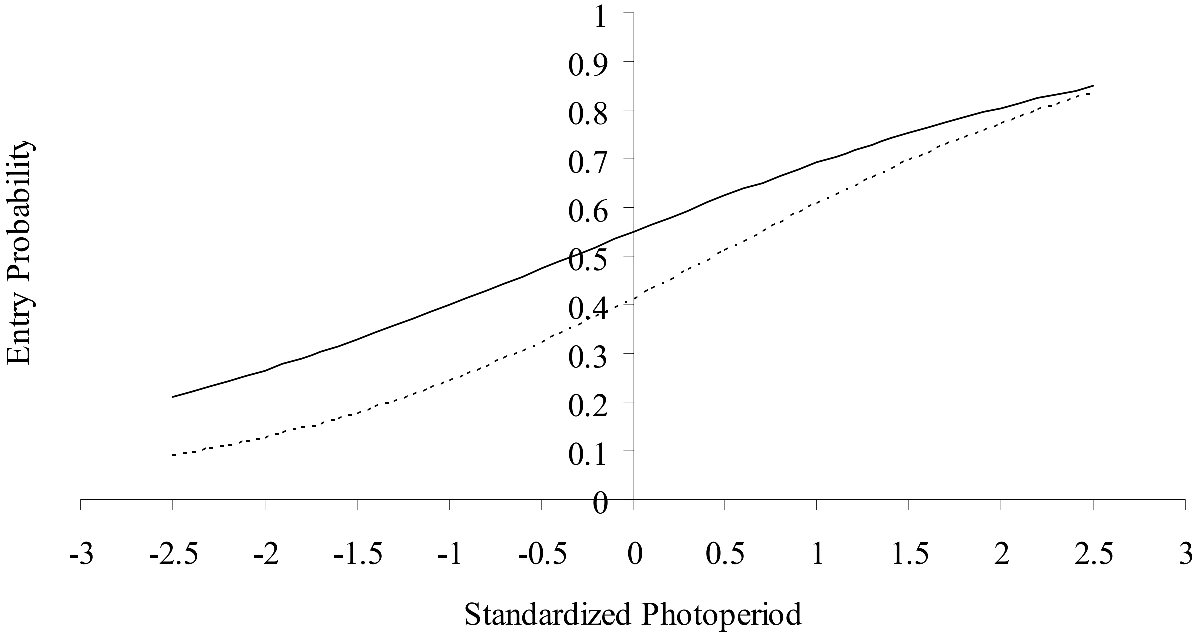

Figure A1.7. Composite model predictions of entry probability across a range of photoperiod values at low, solid line, and high, dashed line, tidal cycle levels in 2006.

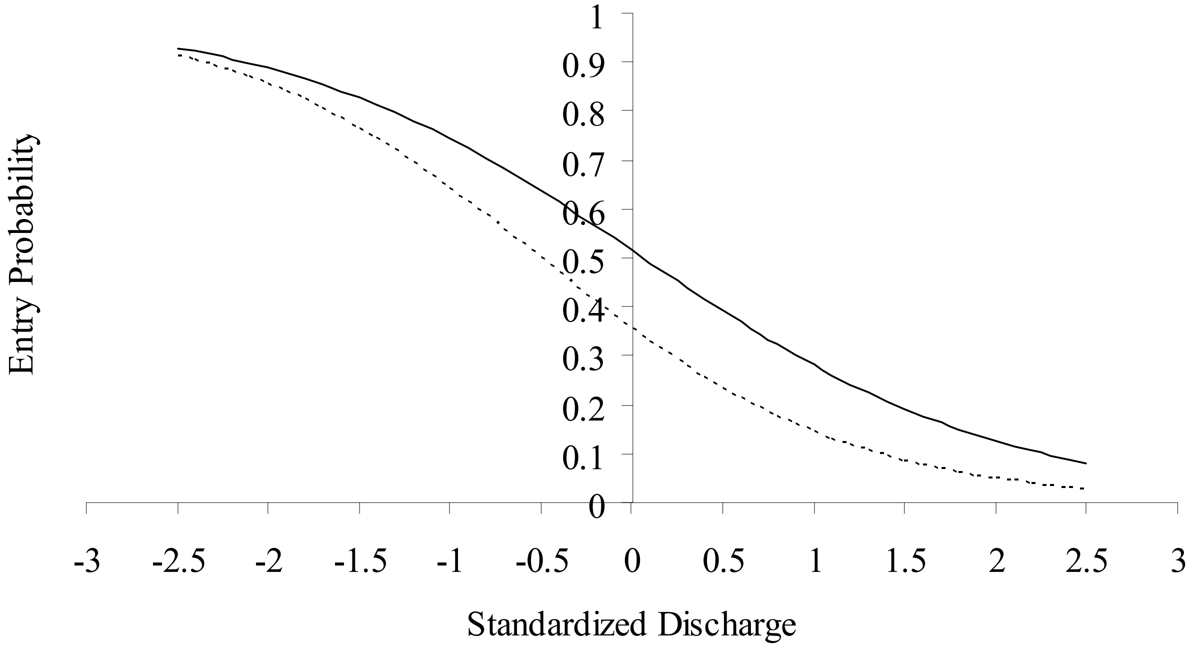

Figure A1.8. Composite model predictions of entry probability across a range of discharge values at low, solid line, and high, dashed line, tidal cycle levels in 2006.

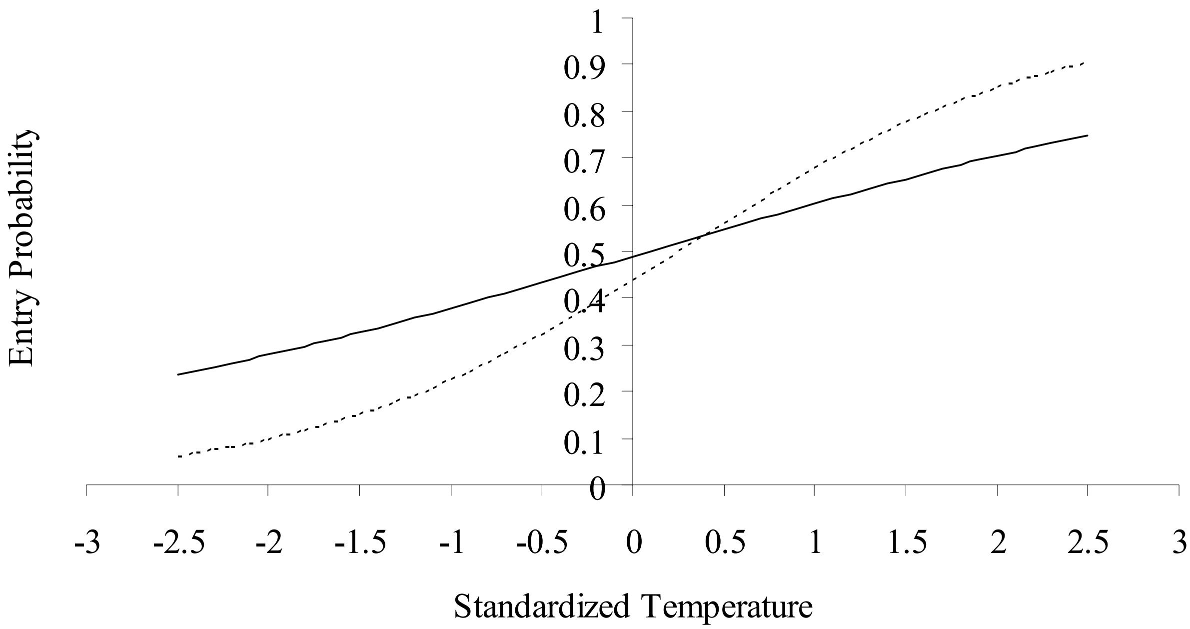

Figure A1.9. Composite model predictions of entry probability across a range of temperature values at low, solid line, and high, dashed line, tidal cycle levels in 2007.

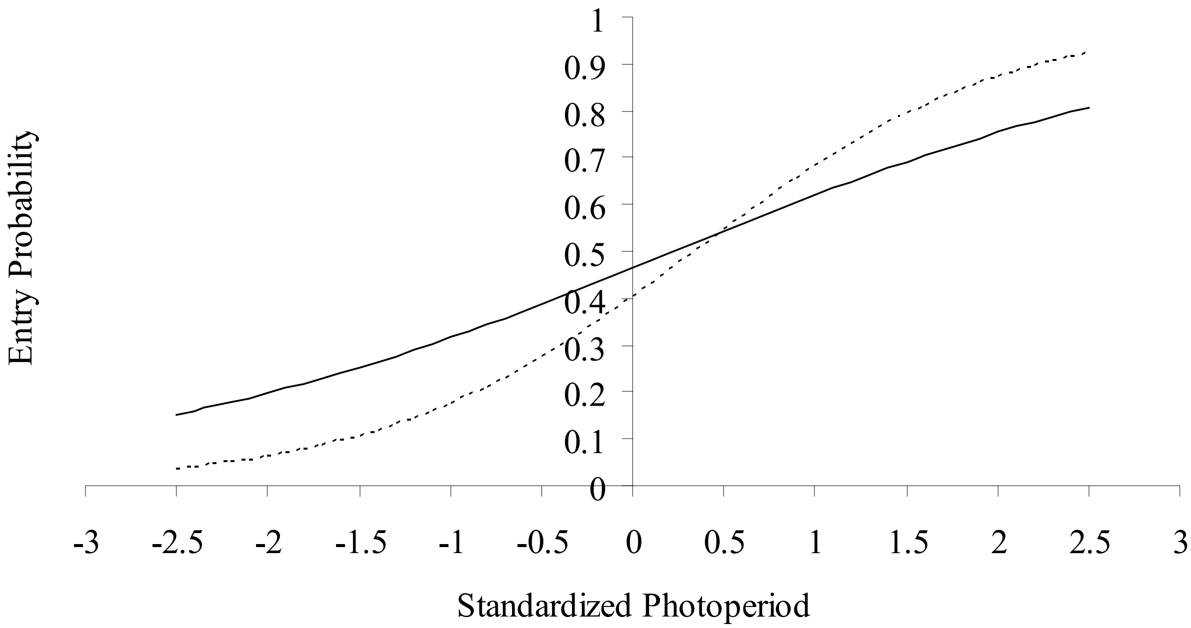

Figure A1.10. Composite model predictions of entry probability across a range of photoperiod values at low, solid line, and high, dashed line, tidal cycle levels in 2007.

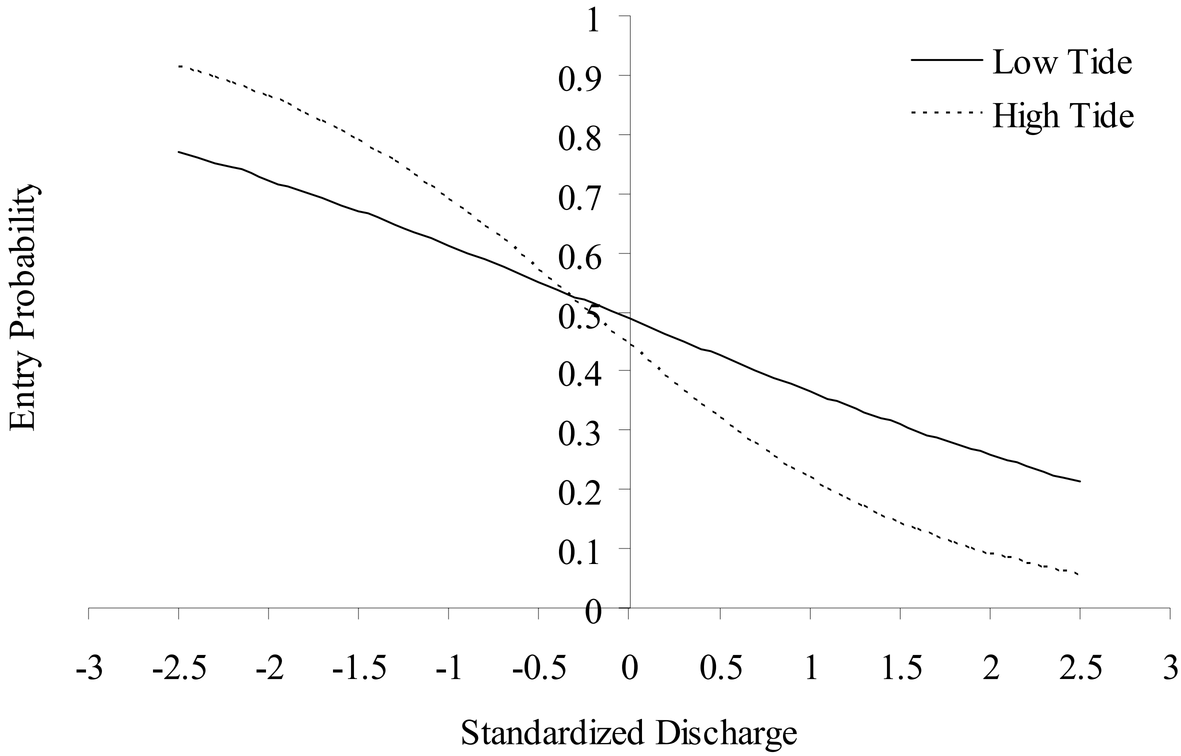

Figure A1.11. Composite model predictions of entry probability across a range of discharge values at low, solid line, and high, dashed line, tidal cycle levels in 2007.

APPENDIX 2

SUPPLEMENTAL TABLES FOR CHAPTER 3

Table A2.1. Values of water temperature (° C) and discharge (m^3/s) from various seasons, and spring adult abundance from Schnabel and POPAN models used to model per capita recruitment of juvenile Atlantic sturgeon in the Altamaha River from 2005 to 2007.

Variable	Season	2004	2005	2006	Mean	Standard Deviation
Water Temperature	Spring	21.2	18.9	21.0	20.4	1.3
	Summer	29.2	28.2	29.7	29.0	0.8
	Fall	22.3	23.0	22.4	22.6	0.4
Discharge	Spring	228.9	859.5	293.1	460.5	347.0
	Summer	133.6	460.3	67.4	220.4	210.4
	Fall	530.7	156.2	76.3	254.4	242.6
Adult Abundance (Schnabel)	Spring	324	386	241	317.0	72.8
Adult Abundance (POPAN)	Spring	99	230	158	162.3	65.6

Table A2.2. Relative likelihood of closed robust design multi-state models using predictor variables to describe variation in capture and recapture probability of Atlantic sturgeon in the Altamaha River for 2004 to 2007.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{S(.)Psi(.)p=c(effort*y)}	5251.59	0	0.84465	1	7	5237.49
{S(.)Psi(.)p=c(temp*y)}	5256.3	4.7104	0.08014	0.0949	7	5242.2
{S(.)Psi(.)p=c(effort)}	5258.15	6.5562	0.03184	0.0377	4	5250.11
{S(.)Psi(.)p(effort*y)c(Effort*y)}	5259.4	7.8067	0.01704	0.0202	12	5235.11
{S(.)Psi(.)p=c(effort*age)}	5259.75	8.1625	0.01426	0.0169	6	5247.68
{S(.)Psi(.)p(effort)c(effort)}	5261.85	10.2624	0.00499	0.0059	6	5249.78
{S(.)Psi(.)p(temp*y)c(Temp*y)}	5262.72	11.1292	0.00324	0.0038	12	5238.44
{S(.)Psi(.)p=c(age*efort*y)}	5263.16	11.5682	0.0026	0.0031	15	5232.72
{S(.)Psi(.)p(effort*age)c(effort*age)}	5265.61	14.0222	0.00076	0.0009	10	5245.41
{S(.)Psi(.)p=c(age*temp*y)}	5266.61	15.0221	0.00046	0.0005	15	5236.18
{S(.)Psi(.)p(disc*y)c(disc*y)}	5273.75	22.1557	0.00001	0	12	5249.46
{S(.)Psi(.)p(age*temp*y)c(age*temp*y)}	5277.75	26.1587	0	0	26	5224.46
{S(.)Psi(.)p(age*effort*y)c(age*effort*y)}	5284.02	32.4324	0	0	28	5226.53
{S(.)Psi(.)p=c(temp)}	5284.15	32.556	0	0	4	5276.11
{S(.)Psi(.)p(temp)c(temp)}	5286.14	34.5538	0	0	6	5274.07
{S(.)Psi(.)p=c(temp*age)}	5286.57	34.9782	0	0	6	5274.49
{S(.)Psi(.)p(age*disc*y)c(age*disc*y)}	5289.77	38.1784	0	0	26	5236.48
{S(.)Psi(.)p(temp*age)c(temp*age)}	5290.47	38.8772	0	0	10	5270.27
{S(.)Psi(.)p=c(.)}	5290.72	39.1276	0	0	3	5284.7
{S(.)Psi(.)p=c(disc)}	5291.07	39.4829	0	0	4	5283.04
{S(.)Psi(.)p=c(disc*age)}	5292.06	40.4728	0	0	6	5279.99
{S(.)Psi(.)p(.)c(.)}	5292.55	40.9542	0	0	4	5284.51
{S(.)Psi(.)p(age)c(age)}	5292.6	41.0095	0	0	8	5276.47
{S(.)Psi(.)p(disc)c(disc)}	5293.27	41.6808	0	0	6	5281.2
{S(.)Psi(.)p=c(age)}	5293.51	41.9182	0	0	5	5283.46

{S(.)Psi(.)p=c(disc*y)}	5296.09	44.5008	0	0	7	5281.99
{S(.)Psi(.)p(disc*age)c(disc*age)}	5296.91	45.3165	0	0	10	5276.71
{S(.)Psi(.)p=c(age*disc*y)}	5304.45	52.8581	0	0	15	5274.01

Table A2.3. Relative likelihood of Pradel robust design models using predictor variables to describe variation in apparent survival and annual per capita recruitment of Atlantic sturgeon in the Altamaha River for 2004 to 2007.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{phi(t)f(fall disc)p=c(effort*y)}	8003.94	0	0.58671	1	10	7983.74
{phi(t)f(t)p=c(effort*y)}	8004.99	1.049	0.34724	0.5918	11	7982.75
{phi(t)f(spring schnabel)p=c(effort*y)}	8009.57	5.6359	0.03504	0.0597	10	7989.37
{phi(.)f(t)p=c(effort*y)}	8011.89	7.953	0.011	0.0187	9	7993.73
{phi(t)f(spring AdultAbund)p=c(effort*y)}	8013.06	9.126	0.00612	0.0104	10	7992.86
{phi(.)f(fall disc)p=c(effort*y)}	8013.7	9.7643	0.00445	0.0076	8	7997.57
{phi(t)f(.)p=c(effort*y)}	8015.28	11.3459	0.00202	0.0034	9	7997.12
{phi(t)f(summer temp)p=c(effort*y)}	8015.34	11.4029	0.00196	0.0033	10	7995.14
{phi(t)f(summer disc)p=c(effort*y)}	8015.68	11.7443	0.00165	0.0028	10	7995.48
{phi(t)f(fall temp)p=c(effort*y)}	8017.17	13.2322	0.00079	0.0013	10	7996.97
{phi(t)f(spring temp)p=c(effort*y)}	8017.32	13.3783	0.00073	0.0012	10	7997.12
{phi(t)f(spring disc)p=c(effort*y)}	8017.32	13.3822	0.00073	0.0012	10	7997.12
{phi(.)f(summer temp)p=c(effort*y)}	8017.77	13.8353	0.00058	0.001	8	8001.64
{phi(.)f(summer disc)p=c(effort*y)}	8018.16	14.2213	0.00048	0.0008	8	8002.03
{phi(.)f(.)p=c(effort*y)}	8020.08	16.141	0.00018	0.0003	7	8005.98
{phi(.)f(spring temp)p=c(effort*y)}	8020.97	17.0284	0.00012	0.0002	8	8004.84
{phi(.)f(spring disc)p=c(effort*y)}	8021.05	17.1097	0.00011	0.0002	8	8004.92
{phi(.)f(fall temp)p=c(effort*y)}	8021.58	17.6442	0.00009	0.0002	8	8005.45