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Restoration of Gulf Striped Bass: Lessons and Management Implications

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Abstract.—Since the 1970s, the only known naturally reproducing population of native Gulf of Mexico (Gulf) striped bass *Morone saxatilis* occurs in the Apalachicola–Chattahoochee–Flint River system (ACF) in Florida, Georgia, and Alabama. To augment its depleted population, low numbers of fry and fingerlings of Atlantic coast ancestry were released into the ACF between 1965 and 1976. Restoration of Gulf striped bass was initiated in 1980 when putative Gulf fingerlings spawned from Apalachicola River (Gulf) broodfish were stocked back into the ACF. Since the initial stocking, approximately 10 million phase-I (25–50 mm) and 900,000 phase-II (150–250 mm) fingerlings have been released into Lake Seminole and the Apalachicola River, with hundreds of thousands more released into upstream reservoirs. Low levels of successful natural reproduction in the ACF were documented in 9 of the 10 years that natural reproduction was evaluated. Marked stocked fish have typically comprised 75–100% of fall age-0 samples. After stocking was initiated, striped bass harvest estimates increased as much as 10-fold during peak-season creel surveys conducted in the tailrace of Jim Woodruff Lock and Dam. A comparison of Atlantic-origin and Gulf striped bass co-stocked into an adjacent river-reservoir system over a 5-year period indicated no consistent differences in relative survival or growth through age 4. Gulf striped bass occupied coolwater thermal refuges during summer. Enhancement of thermal refuge habitats was successful, but results were short-lived. Small populations of Gulf striped bass, dependent on stocking of hatchery fish, now exist in several Gulf of Mexico tributary systems where adequate habitat is present. Genetic analysis of both mitochondrial and nuclear genomes revealed that a high percentage of fish from the ACF exhibit mitochondrial DNA (mtDNA) haplo-

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types and nuclear DNA (nDNA) alleles that are absent in Atlantic populations. However, significant introgression of Atlantic nDNA alleles was documented in the extant population. Knowledge of the life history of Gulf striped bass was improved as a result of this multi-state collaboration as well as a large stocking program, new Gulf broodfish repositories, extensive genetic cataloged database, and expanded trophy fisheries. ACF Gulf striped bass restoration goals and objectives were defined, adjusted, and revised throughout the collaborative process to meet the concerns and management needs of all participating agencies.

Introduction

Striped bass *Morone saxatilis* were reported from the river drainages and estuaries of the Gulf of Mexico (Gulf) during the late 1800s (Goode and Bean 1879; Bean 1883; Goode 1884). The historical range of striped bass in the Gulf region is considered to be from the Suwannee River, Florida, westward to the rivers of the Lake Pontchartrain basin, Louisiana (Pearson 1938; Merriman 1941; Barkuloo 1961, 1967; GSMFC 2006; Figure 1). Although striped bass is an anadromous species, populations at the northern and southern extremes of its range are generally potamodromous. Within the Gulf region, there are no records of specimens taken from coastal waters, and striped bass are riverine or estuarine in nature (Barkuloo 1967; McIlwain 1980). It is likely that striped bass populations within tributaries of the Gulf of Mexico were riverine and endemic to individual rivers (Barkuloo 1967; McIlwain 1980) because there is little documentation of occurrence in open Gulf waters and very limited evidence of interchange between river systems.

Striped bass in Gulf rivers were first differentiated from Atlantic coast striped bass by lateral line scale counts (LLSCs). Striped bass in the Apalachicola (Florida) and Alabama (Alabama) rivers exhibited mean LLSCs (66.7) significantly higher than those found in Atlantic coast populations (54.4–62.2; Raney and Woolcott 1955), and minimal overlap of LLSCs was observed between fish from the two coasts (Goode and Bean 1879; Bean 1883; Brown 1965; Barkuloo 1970). Barkuloo (1970) concluded that the native striped bass population from the Apalachicola–Chattahoochee–Flint (Florida–Georgia–Alabama) River system (ACF) was a distinct race from Atlantic coast striped bass and could be identified using LLSCs. The Gulf States Marine Fisheries Commission (GSMFC 2006) adopted “race” for referring to the unique form of striped bass found in the ACF or descended from the ACF population, and the term “race” is used herein.

Historical accounts indicate that Gulf race striped bass were never abundant. The largest populations likely occurred in the ACF and Mobile-Alabama-Tombigbee (Alabama) River system. In 1957, following closure of Jim Woodruff Lock and Dam (JWLD), forming Lake Seminole (Florida–Georgia) at the headwaters of the Apalachicola River, many young and adult striped bass were taken by anglers fishing in the tailrace (Barkuloo 1961). Young striped bass were so abundant that many were destroyed as a nuisance by anglers. Barkuloo (1961) concluded that the presence of young fish demonstrated natural reproduction and that striped bass angler success indicated that an important sport fishery might be developed in the tailrace area. An apparent reduction in Gulf striped bass occurred after the closure of JWLD in 1957. Following the closure of JWLD, Georgia Department of Natural Resources (GADNR) fisheries personnel (GADNR 1969; Gennings et al. 1970) described a declining striped bass fishery in Lake Seminole, which was attributed to the cessation of spawning runs and to gill netting in the reservoir. By the mid-1960s, native striped bass were considered extirpated from most river drainages in the Gulf region (McIlwain 1980; GSMFC 2006). Barkuloo

(1961, 1967) reported that striped bass occurred in all major rivers along Florida's Gulf coast, but populations in rivers outside the ACF were too small to maintain a sport fishery. By the 1970s, the only known remaining naturally reproducing population along the Gulf was in the ACF (Wooley and Crateau 1983). The decline of striped bass in Gulf drainages was attributed to the construction of dams that blocked spawning migrations and access to thermal refuge habitat, water quality degradation, and other anthropogenic impacts.

With the development of techniques to artificially propagate striped bass, fisheries managers began stocking striped bass of Atlantic origin into many Gulf rivers and reservoirs in the mid-1960s in efforts to re-establish or augment populations, and stocking Atlantic race fish continues in some Gulf of Mexico tributaries to the present. Striped bass (Atlantic race) stocking programs for the ACF were initiated by GADNR (GADNR 1969) for Lake Seminole in 1965 and Lake Blackshear (Flint River, Georgia) in 1967. The Florida Game and Fresh Water Fish Commission (now the Florida Fish and Wildlife Conservation Commission [FFWC]) also released fingerlings of Atlantic origin into the Apalachicola River in 1976 (Crateau et al. 1980). All fish stocked into the ACF were progeny of broodfish collected from the Santee–Cooper system, South Carolina. In total, about 1.8 million Atlantic fry (<15 mm) and 125,000 fingerlings or adults (25–750 mm total length [TL]) were stocked into the ACF from 1965 to 1976 (Pasch et al. 1973; Nicholson et al. 1986; Keefer 1986). Introduction of hybrid striped bass (palmetto bass [male white bass *M. chrysops* × female striped bass] and sunshine bass [female white bass × male striped bass]) into ACF reservoirs was also initiated during the 1970s and continued throughout the course of this restoration project.

In the 1980s, fisheries managers working on the ACF became interested in the conservation and restoration of the native striped bass population. The collection of several very large striped bass (27–32 kg) and the hypothesis by Wooley and Crateau (1983) that Gulf fish were longer-lived and better adapted to surviving the warm summer climate than introduced Atlantic striped bass brought attention to Gulf striped bass in the ACF. This interest was further motivated by Wooley and Crateau (1983), who estimated that the population of adult striped bass (>381 mm TL) in the Apalachicola River was between 1,500 and 2,000 individuals, with approximately 43% native Gulf fish (identified by LLSCs), 51% introduced Atlantic fish, and 6% intergrades. The U.S. Fish and Wildlife Service (FWS) began stocking putative Gulf striped bass into the ACF in 1980. Broodfish were collected from the ACF system, primarily in the JWLD tailrace, and identified as Gulf striped bass based on LLSC; only fish with a LLSC of 65 or greater were accepted for hatchery propagation. However, the ability to discriminate Gulf, Atlantic, and intergrade striped bass using LLSCs was challenged after 1983 and 1984 year-class phase-II (150–250 mm TL) fish exhibited LLSCs ranging from 60 to 71, even though they were progeny of high LLSC (>65) broodfish (Florida Fish and Wildlife Conservation Commission, unpublished data). Concerns of inbreeding depression resulted in a relaxation of the LLSC criteria from 65 to 63 scales so that additional broodfish could be used to make crosses in the hatchery. The scale count criterion was later discontinued and Gulf striped bass are currently defined as any striped bass, or progeny, originating from the ACF.

One of the major questions at the inception of this native restoration program was the genetic integrity of striped bass from the ACF when compared with those from Atlantic coast systems. Specifically, were genetic characters unique to striped bass from Gulf coast drainages, and could these be used as heritable markers to unequivocally distinguish Gulf striped bass in the ACF from introduced Atlantic fish? The identification of unique genetic characters in ACF fish would provide the justification for efforts to restore a genetically unique fish along the Gulf coast. By the early 1980s, techniques were being developed to inspect mtDNA for sequence variation using restriction fragment-length polymorphism analysis (RFLP). Thus, genetic description and cataloging became a major component of the Gulf coast striped bass restoration effort.

Biologists and fisheries managers from Florida, Georgia, Alabama, and the FWS first met together in 1982 to discuss the management of striped bass and hybrid striped bass in the ACF at the first annual ACF *Morone* workshop. In 1987, representatives of conservation agencies in Alabama, Florida, and Georgia and the regional director of the FWS entered into a cooperative agreement for Gulf striped bass restoration in the ACF. The emphasis of the agreement was to restore a self-sustaining population of (Gulf) striped bass to the maximum extent possible. Under the agreement, the ACF Striped Bass Technical Committee, comprised of representatives from each agency, was formed to develop and implement a striped bass restoration plan for the ACF. The agencies also agreed to provide hatchery space, technical support, and other personnel. Later, representatives from Mississippi, Louisiana, the Gulf States Marine Fisheries Commission, New York University School of Medicine, Gulf Coast Research Laboratory (a facility of the University of Southern Mississippi), and the U.S. Army Corps of Engineers became participants of the workshop series, and Gulf restoration efforts expanded to include all states within the species' historical range. The ACF *Morone* workshop has now met for 29 consecutive years (as of 2011) and is one of the longest running cooperative fishery restoration efforts in the country.

The first striped bass management plan for the ACF was finalized in 1996 (ACF Striped Bass Technical Committee 1996) and established a general goal of enhancing the native Gulf striped bass population within the river system. Project objectives included determining hatchery production requirements and optimum stocking rates and sizes; monitoring broodfish collections and stocking success; monitoring the sport fishery; identifying, enhancing, or protecting thermal refuge habitat; establishing broodfish repositories outside of the ACF; and participating in public outreach. The plan was revised in 2004 (ACF Striped Bass Technical Committee 2004) to include a goal of restoring and maintaining a population of native Gulf striped bass "leading to a self-sustaining population that will (1) provide a broodfish source for the ACF and other Gulf state restoration programs; (2) support recreational fishing opportunities at optimum yield levels consistent with carrying capacity of available, restored, and enhanced habitat; and (3) maximize natural reproduction and recruitment of Gulf striped bass."

Concurrent with development of Gulf striped bass restoration strategies in the ACF, the Gulf States Marine Fisheries Commission's (GSMFC) Anadromous Fish Subcommittee authored the "Striped Bass Fishery Management Plan" (Nicholson et al. 1986) for the Gulf of Mexico. This management plan set goals of achieving and maintaining optimum sustainable yield for striped bass throughout their historical range, determining the validity of the Gulf striped bass as a race, and restoring or maintaining Gulf striped bass populations in suitable rivers at levels that would meet state restoration programs Gulf-wide. The GSMFC plan was revised in 2006 (GSMFC 2006) and established restoration and management goals across the Gulf region. Gulf-wide, river-specific restoration goals for striped bass include striped bass fisheries—lower Mississippi River (Louisiana–Mississippi); striped bass put-grow-and-take fisheries—Wolf and Jourdan rivers, Biloxi and Tchouticabouffa rivers, and Old Fort Bayou (Mississippi); Gulf race put-grow-and-take fisheries—Tangipahoa and Tchefuncte rivers (Louisiana), Perdido River (Alabama), Blackwater and Yellow rivers (Florida), and Ochlockonee River (Florida–Georgia); and self-sustaining Gulf race populations—Pearl River (Louisiana–Mississippi), Pascagoula River (Mississippi), Tallapoosa River (Alabama, between R.L. Harris Dam and Lake Martin), Escambia–Conecuh rivers (Florida–Alabama), Choctawhatchee River (Florida–Alabama), and the ACF.

The goals of this paper are to present data addressing the major components of the 1996 and 2004 ACF striped bass restoration and evaluation plans, to assess how restoration efforts have met the objectives, and to discuss the future status of the Gulf race of striped bass.

Methods

The ACF is located in northwestern Florida, western Georgia, and eastern Alabama (Figure 1). The system drains approximately 50,700 km^2 (Light et al. 1998). There are four federal dams and nine private hydroelectric dams on the Chattahoochee River. The Flint River has two private hydroelectric dams near Albany, Georgia, and there are approximately 168 km of unimpeded river between Jim Woodruff Lock and Dam and the Flint River Hydroelectric Project (Albany Dam). The JWLD was constructed at the confluence of the Chattahoochee and Flint rivers, forming Lake Seminole on the Florida–Georgia border. Lake Seminole is a 15,200-ha run-of-the-river reservoir with a mean and maximum depth of 3.0 and 9.1 m, respectively, with a stable water level that typically varies in elevation less than 1 m/year. The nonnative, invasive plant hydrilla *Hydrilla verticillata* was first observed in Lake Seminole in 1967 and now dominates the submersed plant community, covering as much as 64% of the surface area (USACOE 1998; D. Morgan, U.S. Army Corps of Engineers, personal communication). The JWLD outlet becomes the Apalachicola

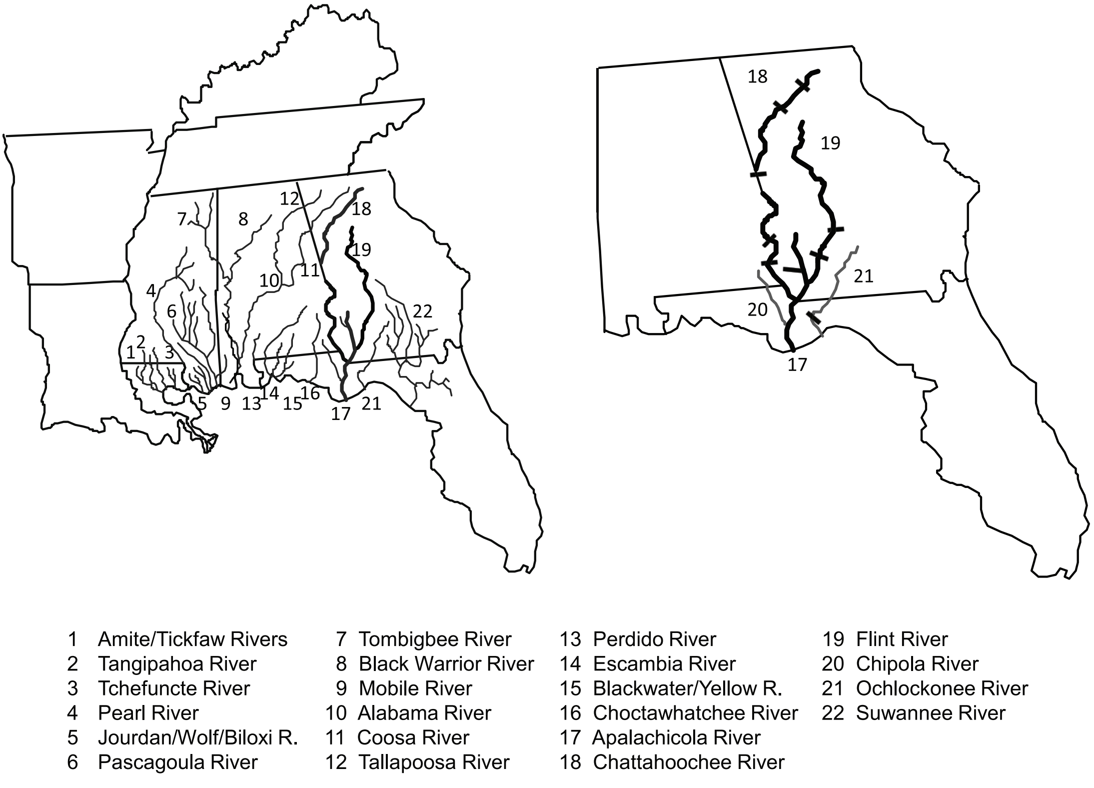

FIGURE 1. Left: Map of the Gulf of Mexico coast from Florida to Louisiana with the major tributaries that made up the historical range of Gulf striped bass. Right: Florida, Georgia, and Alabama with the location of the Apalachicola-Chattahoochee-Flint River system (17–20) and the Ochlockonee River (21), and the major dams located on these river systems. Six smaller dams (not indicated) also occur in the middle portion of the Chattahoochee River.

River, which flows approximately 171 km south to Apalachicola Bay and the Gulf of Mexico. The Apalachicola River is the largest in Florida in terms of discharge, with a mean annual discharge of 620 m^3/s measured at the U.S. Geological Survey gauge at Chattahoochee, Florida (Light et al. 2006). Its largest tributary is the Chipola River, which enters approximately 45 km upstream of the Apalachicola River mouth. The Chipola River, which was dammed at the mouth of Dead Lake from 1968 until 1988 (Hill et al. 1996), flows through lime rock topography and is highly influenced by springs and groundwater. Ambient water temperature in the upper Chipola River remains cooler than in the Apalachicola River during summer months.

From 1982 until 1996, Gulf striped bass restoration efforts were determined by state agency management and research needs, and efforts were reviewed by the ACF Striped Bass Technical Committee and at the annual ACF *Morone* workshop. The first ACF Striped Bass Restoration and Evaluation Plan (hereafter referred to as the ACFP) was completed in September 1996, and the revised ACFP was completed in 2004. The following items describe methods employed to address objectives and tasks of the two plans, but also incorporate activities collected prior to issuance of the 1996 ACFP.

Broodfish collections and indices

Objectives of both ACFPs (1996, 2004) were to annually produce phase-I and phase-II fingerlings to meet participating agency and restoration goals. Tasks included the collection of broodfish for hatcheries and conducting genetic analysis of the broodfish. To meet these objectives, striped bass broodfish were collected in several locations in the ACF basin. These included the tailrace of JWLD (i.e., Apalachicola River), the tailrace of George Andrews Lock and Dam (GALD; Chattahoochee River), and sections of the Flint River. Other tasks included a goal of meeting or exceeding an annual average of 0.7–1.0 adult fish (minimum size of 457 mm TL) per hour of electrofishing during broodfish collections in the ACF (1996) or to evaluate relative abundance of adult fish (2004). To meet these tasks, collected fish were measured (mm TL) and weighed. Mean catch per unit effort (CPUE) was calculated as mean number captured per hour (fish/h) of electrofishing time for small (>1.4 kg), medium (4.5–9.1 kg), and large (>9.1 kg) broodfish. We evaluated the potential association between time and mean catch rates overall and by size using Spearman correlation analysis. Only broodfish data collected since 1990 were used for our analysis as data collected prior to 1990 often lacked quantitative sampling effort. Fin clips were taken for genetic analysis from all fish that were transported to hatcheries. Sagittal otoliths were removed from broodfish that died or were sacrificed at the hatchery for age determination (Heidinger and Clodfelter 1987; Secor et al. 1995).

Stocking evaluation and young-of-year indices

Objectives of both ACFPs (1996, 2004) included determining the optimum stocking density, stocking locations, and sizes of stocked fish for restoration efforts in the ACF. Initial target numbers (1996) for striped bass annual stocking into the ACF were (all numbers are phase I unless specified otherwise) 500,000—Lake Seminole, 100,000—upper Apalachicola River, 170,000—Lake Blackshear, 100,000 phase II—lower Apalachicola River, 60,000—Bartlett's Ferry Lake (Georgia–Alabama), and 100,000—Walter F. George Lake (Georgia–Alabama). Stocking priority and numbers were reviewed annually at the ACF *Morone* workshop and adjusted as needed to fulfill study objectives for individual reservoirs, conservation agencies, or goals of the 1996 ACFP. An additional task of the 1996 ACFP was to establish broodfish repositories outside of the ACF by annually stocking phase-I fingerlings into Smith Lake (Alabama; 40,000), Lake Talquin (Florida; 250,000), Blackwater River (Florida; 100,000) and a domestic brood source housed in the National Fish Hatchery system (10,000). Gulf race phase-I (25–50 mm TL) fingerlings were stocked into Lake Seminole in 1980 and 1982 and then annually beginning in 1986, except in 1997 and 2006 when natural reproduction was evaluated. Phase-I fingerlings were stocked periodically into the upper Apalachicola River (UAR; U.S. Army Corps of Engineers navigation mile 77.5–106.4), lower Apalachicola River (LAR; navigation mile 0.0–20.0), and Apalachicola Bay (ARB) from 1982 to 1996. Age-0 phase-II (125–300 mm TL) fingerlings were also stocked into the LAR, ARB, Apalachicola River, and Intracoastal Waterway (ICW) near White City, Florida, during 16 years between 1980 and 2008.

Additional components of the 1996 and 2004 ACFPs were to develop an index to monitor survival, growth, condition, and age structure of striped bass in the ACF. Tasks included evaluating post-stocking survival and designing and implementing a relative abundance index of age-0 fish. To meet these tasks, approximately 50–100 fish from each delivery of phase-I fish to a stocking site (1992–2000) were held in receiving water in a 76-L aerated aquarium for 48–72 h to estimate short-term survival of stocked fish. Approximately 10–20 phase-II fish per delivery were also placed into live cars at stocking locations in the LAR and ICW.

Beginning in 2001, all phase-I fingerlings were marked with oxytetracycline (OTC; Secor et al. 1991) to determine the relative abundance of wild and hatchery fish. Phase-II fish were marked either with internal anchor tags, dart tags, T-bar tags, coded wire tags, fin clips, or OTC.

Relative abundance of stocked fish was monitored using electrofishing. Beginning in 1985, four fixed shoreline stations in Lake Seminole, UAR, and LAR were sampled for 10 min (Smith-Root Type 6A, GPP 5.0, or GPP 7.5 set to DC output) at night (Boynton et al. 1981) to estimate the relative abundance of age-0 fish. Stations were located on sand habitat in 0.6–1.2 m of water (Setzler et al. 1980; Boynton et al. 1981; Van Den Avyle et al. 1983). In 1985, sampling was conducted monthly from June through December. From 1986 to the present, except 1997, sampling was not initiated until the fall. Post 1986, stations were typically sampled twice, approximately 30 d apart, between late September and mid-November. The UAR and LAR were not sampled every year.

Catch-per-unit-effort (CPUE) values for age-0 fish were calculated as number of fish per minute (fish/min), and mean CPUE values were calculated for Lake Seminole, the UAR and LAR individually, and for all samples combined. We tested for differences in mean catch rates using Welch's t-test for unequal variances, and we evaluated the potential association between mean catch rates and time using Spearman correlation analysis. In addition, CPUE values of OTC-marked stocked age-0 fish and wild fish collected in Lake Seminole samples (2001–2004) were compared using Welch's t-test, as were CPUE values of wild age-0 fish collected in the absence of stocking (1985, 1997, and 2006) and values for wild fish collected during years when marked phase-I fish were stocked (2001–2004). In order to compare age-0 relative abundance in Lake Seminole from year to year, an age-0 relative abundance value (RAV) was calculated as the mean CPUE divided by the number stocked (Van Den Avyle and Higginbotham 1980) and then rescaled by multiplying by 100,000, similar to Brooks et al. (2002). Total length and weight were measured from collected fish. Based on comparison to previously aged fish (Florida Fish and Wildlife Conservation Commission, unpublished data), we assumed that all fish less than 250 mm TL were age 0, used otoliths to confirm the age of fish between 250 and 350 mm TL, and assumed that all fish greater than 350 mm TL were age 1or older. Catch per unit effort was calculated for all age-0 fish and separately for hatchery and wild age-0 fish. Wild age-0 fish were subtracted from the total catch prior to calculating the RAV for the 2001–2004 year-classes.

Relationships between mean annual CPUE of age-0 striped bass in Lake Seminole, the number of phase-I fish stocked annually and annual density of hydrilla (hectares) were calculated with multiple linear regression. Catch-per-unit-effort data were transformed as $\log_e(x + 0.0001)$ to normalize the distribution. The linear regression assumptions of normality and constant variance were evaluated by examining the normal quantile-quantile plot of residuals and the Studentized residuals plot. Both plots indicated that the normality and constant variation assumptions were met.

Mean relative weight (W_r) was calculated for age-0 fish (>150 mm TL; Brown and Murphy 1991a) using the standard weight (W_s) equation developed by Brown and Murphy (1991a). A correlation coefficient (r) was computed to evaluate the relationship, if any, between mean W_r and the number of fish stocked.

Creel census surveys

An objective of the 1996 ACFP was to restore striped bass populations in the ACF to a level that would meet management objectives of partner agencies. Agency objectives included development of recreational and trophy fisheries. This objective was omitted from the 2004 ACFP, but an objective to continue collecting fishery-dependent data was included. To meet these objectives, creel census surveys were conducted at several locations in the ACF. In the tailrace of JWLD, angler catch and harvest were monitored by continuing springtime roving creel surveys having nonuniform probability (Malvestuto 1983; Young 1987); they were initiated in 1980 and were conducted through 2009. Anglers were surveyed during a 3-h period (1000–1300, 1300–1600, or 1600–1900 hours eastern time) five times every 2 weeks—three times on weekdays and twice on weekend days. Surveys were conducted for 14 weeks between late February and early June. The area surveyed covered a river reach from the drive-up area at the powerhouse downstream for 11.3 km. Field data were statistically expanded to provide estimates of striped bass total catch (beginning in 1992), harvest, effort (hours), and angler success (striped bass catch or harvest per hour).

Randomly stratified roving creel surveys with nonuniform probability were initiated on the LAR and ICW in 1990. Anglers were surveyed during a 4-h period (morning or afternoon) six times every 2 weeks—three times on weekdays and three times on weekend days. Surveys were conducted for 10 or 12 weeks during the fall (October–December) and 16 weeks during the spring (March—June). Fall surveys were discontinued in 1999 and spring surveys in 2004. Field data were statistically expanded similarly to the JWLD tailrace survey. The area surveyed included the Apalachicola River from navigation mile 0.0 (U.S. Highway 98 Bridge) upstream 16.4 km, the major distributaries in the river delta, and the ICW from the LAR to Port St. Joe (approximately 40 km), Florida.

A nonuniform probability access creel survey (Malvestuto 1983) was conducted in the tailrace of George Andrews Lock and Dam on the Chattahoochee River and in the tailrace of Albany Dam on the Flint River from 1995 to 1998. Surveys were conducted for 26 weeks from November through April, which corresponded to the open season for striped bass angling and harvest at both locations. Survey periods were 2 weeks in length and were stratified by weekday and weekend. Four weekend days and six weekdays were sampled per period. The survey was conducted for 6 h, either in the morning or the afternoon. Access sites on the east and west side of the river were used for both surveys.

Thermal refuge habitat

Objectives of the 1996 and 2004 ACFPs were to pursue projects that would protect, enhance, or restore important striped bass habitats in the ACF. Because success of striped bass restoration in the ACF was assumed to depend on availability of summer thermal refuges, based on research on striped bass habitat usage conducted elsewhere (Coutant and Carroll 1980; Cheek et al. 1985; Coutant 1985), tasks of these plan objectives included identifying, protecting, or restoring/enhancing coolwater habitats in the ACF. To help meet these objectives, on four occasions, striped bass were tagged with temperature-sensitive radio or ultrasonic transmitters, and movements within sections of the ACF were monitored to locate thermal refuges and determine usage (Van Den Avyle and Evans 1990; Baker and Jennings 2001; Long 2001). Transmitters used on striped bass released into Lake Blackshear were also equipped with a 12-h mortality indicator. Fish used for telemetry studies were collected from the Apalachicola or Flint rivers or the ICW or were striped bass that had been spawned and housed at FWS national fish hatcheries. Transmitters were surgically implanted similar to Hart and Summerfelt (1975) or were attached externally (Baker and Jennings 2001). Fish were usually located by boat; however, fixed wing airplanes and/or helicopters also were used.

To sustain population enhancement efforts, several springs, spring runs, and coolwater creek tributaries in the Apalachicola and Flint rivers were renovated to increase flow or to enlarge thermal refuge volume by increasing pooling of cool water. In the Apalachicola River, five refuge creek and spring run tributaries identified by telemetry were de-snagged and excavated using either a dragline or clamshell dredge to provide 1 m of depth at typical low summer flows. The creeks were sampled by electrofishing during summer months, pre- and postrenovation, to determine utilization by striped bass. Between 1997 and 2007, eight springs in the Flint River between Lake Seminole and the Albany Dam were renovated using a pneumatic suction dredge. Annually, from 1997 through 2008, when ambient water temperature exceeded 27°C (typically June through September), monthly direct scuba counts of striped bass were conducted to evaluate the use of these springs and two nonrenovated springs as thermal refuges. During these surveys, two divers would position themselves as unobtrusively as possible within the opening of the spring, or on the edge of the refuge in the water-mixing zone, and count the number of striped bass observed during a 15-min time interval. Observed fish were categorized as either larger or smaller than 9.0 kg.

Gulf and Atlantic striped bass performance evaluation

Prior to issuance of the 1996 ACF plan, discussions at the *Morone* workshop prompted initiation of a study to compare growth and survival of Gulf and Atlantic race striped bass under similar conditions. A performance evaluation of co-stocked Gulf and Atlantic fish was conducted on Lake Talquin, a 6,561-ha run-of-the-river reservoir on the Ochlockonee River, Florida (Figure 1). Equal numbers of phase-I extant Gulf and Atlantic phase-I fingerlings were stocked into Lake Talquin from 1988 to 1993, and relative survival and growth were monitored through 1996. All stocking was done during daylight hours. Gulf fish originated from the ACF, and Atlantic fish were shipped as fry from the South Carolina Department of Natural Resources hatchery at Monks Corners (Santee–Cooper River system) to Welaka National Fish Hatchery for grow-out. Mitochondrial DNA from broodfish was analyzed to provide genetic tags to unequivocally identify the race of all sampled fish. All Atlantic fish exhibited the *Xba* I-1 haplotype, and all Gulf fish subsequent to the 1988 year-class exhibited the *Xba* I-2 haplotype unique to Gulf race fish (Wirgin et al. 1989). Gulf fish from the 1988 year-class that had the *Xba* I-1 haplotype D-1 also were characterized using nuclear DNA (nDNA) genotypes.

Striped bass from multiple year-classes were collected from Lake Talquin using experimental gill nets (38–254 mm stretch mesh, 2.4–4.3 m deep, and 91.4 m long) set overnight during November and December. Late fall was selected for sampling to help ensure that striped bass had vacated thermal refuges and would be redistributed within the reservoir. Mitochondrial DNA genotypes and race were determined according to Wirgin (1987). Total length, weight, and LLSCs were recorded for each fish. Otoliths were removed from all fish for age-class estimation (Heidinger and Clodfelter 1987; Secor et al. 1995). Relative survival of Gulf and Atlantic fish was compared using Pearson chi-square analysis to test for differences ($P < 0.05$) in the sample ratio of Gulf and Atlantic striped bass collected within each co-stocked year-class from ages 1 to 5. Because equal numbers of Gulf and Atlantic fish were stocked annually, we expected equal numbers of each race in our annual samples. As a result of small sample sizes, all lengths and weights at given ages for each race, and for all year-classes, were pooled to test for differences in mean length (millimeters total length) at age for each race using the Student's t-test. Differences in relative condition were tested by pooling data from the 1988 and 1989 year-classes for each race and comparing using analysis of covariance (ANCOVA) to determine differences in natural log transformed length–weight relations (least squared regressions). The comparison was limited to the 1988 and 1989 year-classes because they were the only ones from which sufficient numbers of fish older than age 4 were collected.

Genetic characterization

Since 1983, live fish or tissue samples (frozen liver or blood, fin clips preserved in 95% ethanol, or dried scales) from ACF and other Gulf coast striped bass were retained for genetic analysis. DNA isolated from these tissues was used to differentiate Gulf from Atlantic fish, characterize broodfish (1996 and 2004 ACFP) and wild fish, identify stocked fish, identify genetic tags (1996 ACFP), and compare the extant population with archived samples collected before the introduction of Atlantic striped bass (2004 ACFP). Several techniques, including mtDNA RFLP analysis (Wirgin 1987; Wirgin et al. 1989), nDNA fingerprinting (Wirgin et al. 1991), single nucleotide polymorphism (SNP; Wirgin and Maceda 1991), and microsatellite analysis (Roy et al. 2000; Wirgin et al. 2005) were developed and applied to the ACF population to assist in this restoration effort.

Results

Broodfish collections and indices

Since 1990, relative abundance has varied temporally (Figure 2). In the Apalachicola River, CPUE for all broodfish trended upward from 1990 (2.73 fish/h; SE = 0.48) until 1998 (11.90 fish/h; SE = 3.75), reached its high in 2003, and reached its low in 2007, the only year that CPUE did not meet the ACFP target of 0.7–1.0 fish/h. For the full period (1990–2009), there was no association between mean CPUE over time, but from the subset of 1990 to 2003, there was a significant positive association with all broodfish collected in the Apalachicola River and time ($r = 0.68$; $P = 0.002$). Mean CPUE for only medium-sized (4.5–9.1 kg) broodfish had similar trends to total broodfish mean CPUE, but no significant correlations were detected with medium or large broodfish collected over time in the Apalachicola River in either time set. In the Chattahoochee and Flint rivers, abundance of all broodfish tended to increase from 1990 to 2009 (Figure 2). Mean CPUE values for fish exceeding 1.4 kg increased significantly ($r = 0.81$; $P < 0.0001$) and ranged from 0.07 (1992) to 7.25 (2009; Figure 2). Mean CPUE of medium-sized broodfish in the Flint and Chattahoochee rivers also tended to increase over time ($r = 0.68$; $P = 0.02$). There was no association between mean CPUE of large broodfish and time, which ranged from 0.0 (1992) to 0.92 (2009), hitting peaks in 1997 and 1998 and again in 2009 (Figure 2).

Broodfish age and sex were indexed by fish sacrificed at hatcheries. Between 1993 and 2009, 94 female and 125 male striped bass broodfish from the ACF were sacrificed at the hatcheries and aged (Table 1). Females ranged from age 2 to 13 and males ranged from age 2 to 7. Sixty-five percent of the females were ages 4–6, and 67% of the males were ages 3 and 4. The youngest females were typically collected toward the end of the spawning season. The largest female collected was 21.6 kg, and the largest male was 16.2 kg

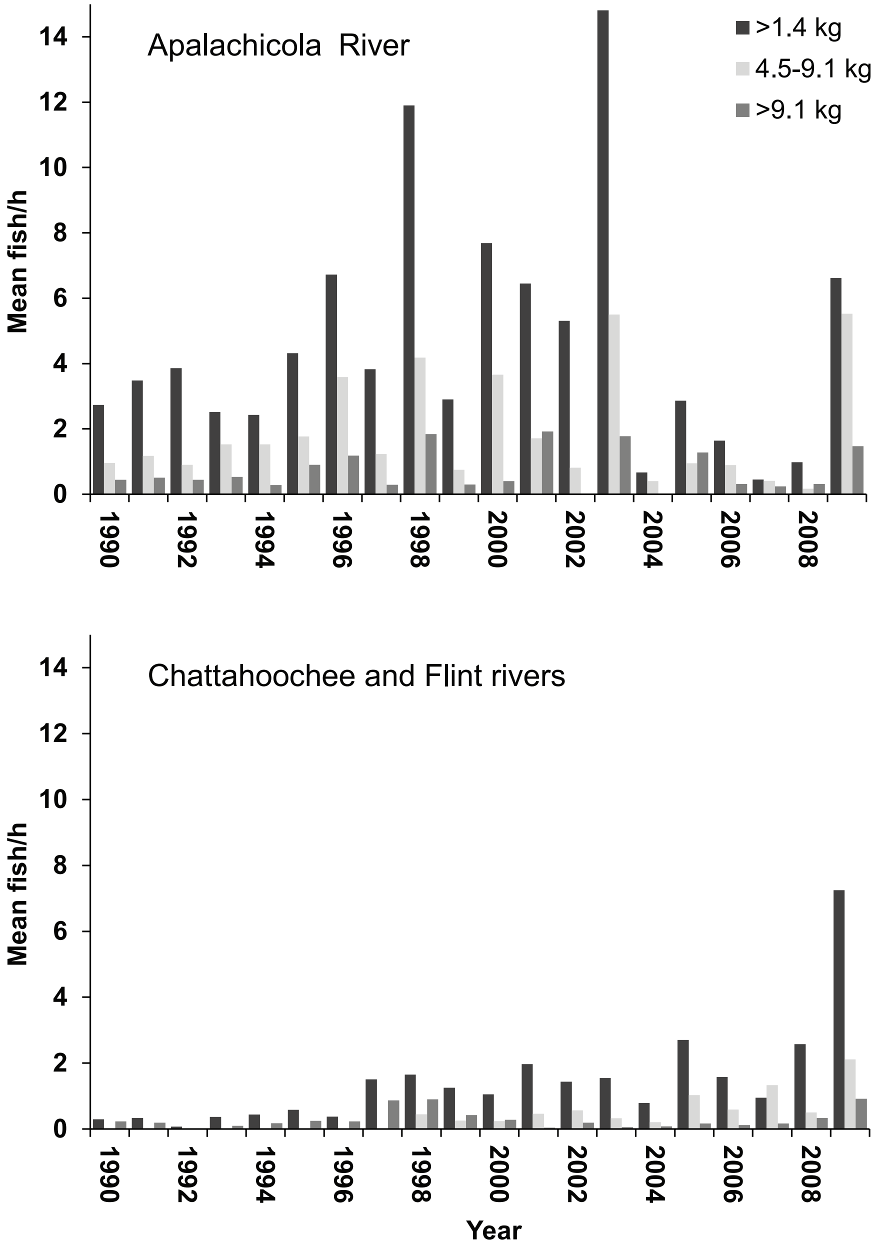

FIGURE 2. Mean catch per unit effort (fish/h) of striped bass caught for broodfish in the Aplalachicola (top) and the Chattahoochee-Flint rivers (bottom), 1990–2009, grouped by size (all >1.4 kg, 4.5–9.1 kg, and >9.1 kg).

and was not aged. Large males were typically released because hatchery managers preferred not to handle males greater than 9.1 kg, so males older than age 7 may have been collected and released.

Stocking evaluation

During the 28 years (1980–2008) since the first Gulf striped bass were stocked, more than 11,600,000 fingerlings were stocked into Lake Seminole, the Apalachicola River, and Apala-

TABLE 1. Numbers, weight (kg) range, and mean weight per age-class of Apalachicola-Chattahoochee-Flint striped bass broodfish sacrificed at hatcheries, 1993–2008. Numbers in parentheses represent one standard error.

	Female			Male		
Age	*N*	Weight range (kg)	Mean weight (kg)	*N*	Weight range (kg)	Mean weight (kg)
2	1	1.8		14	1.2–2.6	1.9 (0.5)
3	10	2.1–6.9	3.7 (1.3)	41	1.7–4.7	3.1 (0.8)
4	21	3.6–7.6	5.7 (1.0)	43	1.2–7.0	4.4 (1.1)
5	28	4.6–14.0	8.4 (2.2)	20	4.2–11.5	6.6 (2.0)
6	16	7.6–14.6	10.2 (2.2)	2	7.8–9.3	8.6 (1.1)
7	8	7.2–14.0	10.2 (2.2)	5	6.8–10.6	8.0 (1.5)
8	3	8.6–18.1	12.1 (2.2)			
9	1	21.6				
10	1	15.9				
11	4	11.0–15.9	14.1 (2.3)			
12	0					
13	1	21.0				

chicola Bay. Stocking numbers set in the 1996 ACFP were achieved for Lake Seminole for 3 of the 7 years from 1998 to 2004 that fish were stocked and were within 85% of the target number during the four other years (Table 2). Phase-II stocking numbers were achieved for the Apalachicola River during 5 of the 8 years from 1997 and 2004 and within 60% of the target for the other 3 years (Table 2). The goal of stocking 100,000 phase-I fingerlings into the LAR was dropped at the 1997 *Morone* workshop. Stocking numbers typically exceeded the target numbers for Lake Blackshear and Bartlett's Ferry Lake, but Lake Walter F. George was placed low on the priority list at ensuing *Morone* workshops and did not receive any fish until 2001and a full complement until 2004. Stocking phase-I fingerlings into Lakes Talquin and Smith and into the Blackwater River successfully resulted in establishment of broodfish repositories in these systems. In addition, a domestic broodfish source was developed at Warm Springs and Mammoth Springs national fish hatcheries (NFH).

Phase-I fingerlings were typically stocked between late April and mid-May at approximately 30 d posthatch. The total numbers of phase-I fish annually stocked into Lake Seminole ranged from 0 to 760,000; the average number stocked was 363,000 (24/ha). Short-term survival of phase-I fish stocked into the ACF from 1992 to 2000 ranged from 68% to 99% and averaged 86%.

There was no association between mean catch rates of age-0 fish and time. The mean CPUE for age-0 fish from Lake Seminole ranged considerably, from 0.08 (SE = 0.05) fish/min in 1993 to 4.64 (SE = 1.72) fish/min in 2000 (Figure 3).

There was a marginally significant difference (t = 2.52; df = 2; P = 0.06) between CPUE of wild fish in years of stocking and no stocking. Catch rates of wild fish were higher in years when no fish were stocked (mean of 0.5 fish/min) than years when fish were stocked (mean of 0.1 fish/min). Mean CPUE values of wild fish during years when no stocking occurred were 0.19 (SE = 0.05), 0.66 (SE = 0.48), and 0.52 (SE = 0.33) fish/min in 1985, 1997, and 2006, respectively. From 2001 to 2004, catch rates of OTC-marked stocked fish (range of 0.03–1.60 fish/min) were significantly higher (t = 2.93; df = 3; P = 0.03) than those of wild fish

Table 2. Number (rounded to the nearest 1,000) of phase-I and phase-II fingerling Gulf striped bass stocked into Lake Seminole and the Apalachicola River, 1980–2008. Number stocked per hectare (no./ha) for Lake Seminole is rounded to the nearest whole number. Stocking numbers are averaged for only the years in which stocking occurred.

	Phase I					Phase II		
	Lake Seminole		Appalachicola River			Lake Seminole		Apalachicola River
Year	number (x 1,000)	no./ha	upper (no. × 1,000)	middle (no. × 1,000)	lower (no. × 1,000)	number × 1,000)	no./ha	number × 1,000)
1980	100	7						13
1981								
1982			38					11
1983	80	5	53					
1984			20					
1985								
1986	273	18			180			13
1987	545	36						
1988	321	21	1					3
1989	516	34			135			
1990	374	25						17,000
1991	133	9			127			
1992	374	25	32		526			21
1993	200	13	55	50	430			30
1994	392	26	90					30
1995	345	23	60					54
1996	730	48	72					92
1997							129	
1998	533	35					148	
1999	428	28					150	
2000	520	34					149	
2001	476	31					110	
2002	199	13					74	
2003	494	33				46	3	71
2004	623	41				24	2	63
2005	145	10				32	2	59
2006							20	1
2007	169	11				42	3	
2008	372	24				55	4	14
Total	8,342	550	421	50	1,398	219	15	1,251
Average	363		24	47	280	37	2.5	62.5

(range 0.00–0.20 fish/min). Oxytetracycline-marked fish comprised 78–100% of the age-0 fish collected from Lake Seminole.

The abundance of age-0 striped bass in Lake Seminole (1986 to 2006) was positively correlated with the number of fish stocked and

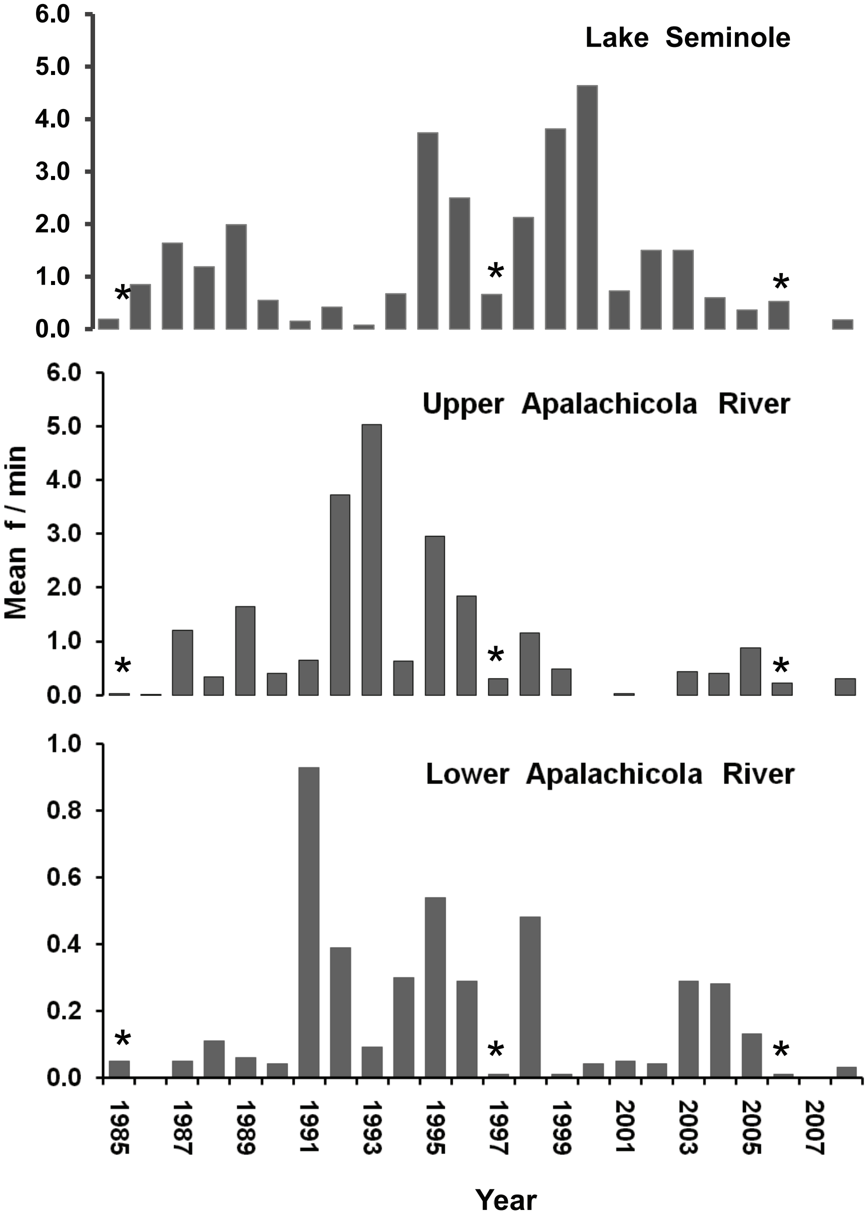

FIGURE 3. Mean catch per unit effort (fish/min [f/min]) of age-0 striped bass electrofished from fixed sites in Lake Seminole (top), the upper Apalachicola River (middle), and lower Apalachicola River (bottom), from 1985 through 2008. * denotes years when no phase-I stocking occurred. No electrofishing samples were collected in 2007.

negatively correlated with the surface area of hydrilla coverage (USACE 1998; D. Morgan, U.S. Army Corps of Engineers, personal communication). Multiple regression analysis described the relationship as

$$\log_e(\text{CPUE} + 0.0001) = 1.2534 + -0.0003689(\text{hydrilla}) + 0.00000403(\text{stocked})$$

(Adjusted $R^2 = 0.635$, $P < 0.001$).

Together, the surface area of hydrilla and the number of fish stocked explained about 63% of the variation in abundance of age-0 striped bass in Lake Seminole. Including hydrilla coverage in the model added significance over and above the variance explained by the number of fish stocked alone, which was 45%.

Age-0 relative abundance values (RAVs) for Lake Seminole exhibited wide variation among years, ranging from 0.04 in 1993 to 1.08 in 1995 (Figure 4). Relative abundance value was also significantly and negatively correlated (r = -0.59; df = 14; P < 0.05) with surface area of hydrilla. During the years 1986–1989, phase-I stocked year-classes that recruited well into the tailrace fishery had RAVs above 0.30 and we defined this value as indicative of a good year-class. Relative abundance value exceeded 0.30 in 11 of the 21 years

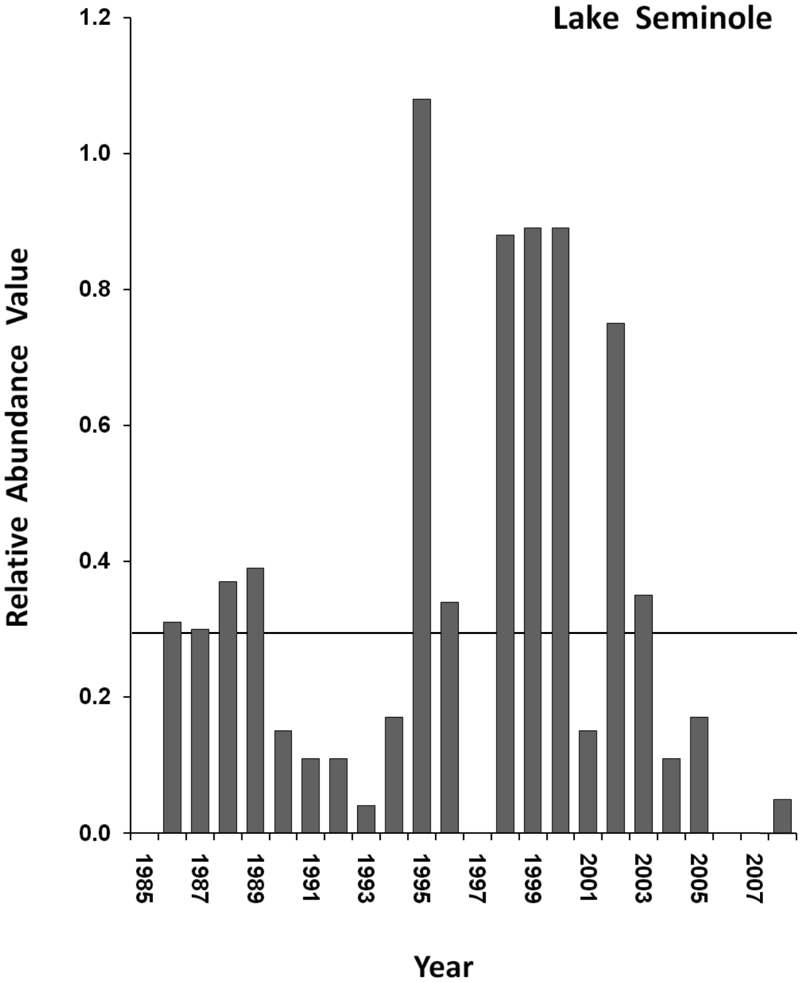

FIGURE 4. Relative abundance values (RAVs) of age-0 striped bass electrofished from Lake Seminole from 1986 through 2008. RAV was calculated as mean catch per unit effort (CPUE; fish/min) divided by the number stocked and multiplied by 100,000. The horizontal line represents the threshold level (0.3) considered to represent good survival through the fall. RAVs were not calculated for 1985, 1997, and 2006 because no phase-I striped bass were stocked. From 2000 through 2008, when all stocked fish were marked with oxytetracycline, wild striped bass were subtracted from total sample prior to calculating CPUE. No electrofishing samples were collected in 2007.

(1986–2008) that striped bass fingerlings were stocked into Lake Seminole.

Age-0 striped bass CPUE in the UAR and LAR trended higher in the 1990s, when phase-I fingerlings were being stocked, than during the 1980s or 2000s, when no stocking occurred (Figure 3). From 1985 to 2008, mean CPUE in the UAR ranged from 0.01fish/min (SE = 0.06; 1986) to 5.03 fish/min (SE = 1.91; 1993). Catch per unit effort in the UAR was highest during years that phase-I fingerlings were stocked into the upper river (1992, 1993, and 1995). However, mean values were above average (1.08 fish/min) during years that fingerlings were not stocked and floodgates at JWLD were open during the late spring or summer. In the lower Apalachicola River, mean catch rates ranged from 0.0 to 0.93 fish/min (SE = 0.51; 1991). Catch rates were higher during years that phase-I fingerlings were stocked, but stocking did not always result in higher CPUE than in nonstocking years. Mean CPUE in the LAR was almost always lower than in the UAR. Although CPUE in river samples tended to be higher during years when stocking occurred, stocking phase-I fingerlings did not contribute appreciably to the adult population and was discontinued in the LAR in 1993 and the UAR in 1996. From 2001 to 2008, stocked (Lake Seminole and upstream reservoirs) OTC-marked fish comprised 76–100% of the age-0 fish in river samples.

Mean W_r of age-0 fish in Lake Seminole was significantly correlated with numbers stocked ($r = 0.59$; df = 22; $P < 0.01$) but was not correlated with RAV or hydrilla coverage. Mean relative weight (W_r) derived for individual year-classes ranged from 74 to 97 (Figure 5), with only one year-class (1993) within the optimal 100 ± 5 range. From 1985 to 2008, mean total length of age-0 striped bass collected from Lake Seminole and the Apalachicola River during fall electrofishing ranged from 126.9 to 231.3 mm TL (Figure 6). Mean total length was not correlated with number stocked, RAV, or hydrilla.

Approximately 1,251,000 phase-II fingerlings were stocked into the Apalachicola River at various locations during 20 years between 1980 and 2008 (Table 2), with annual numbers stocked ranging from 3,000 (1988) to 149,000 (2000). Beginning in 2003, 20,000–60,000 (1–4/ha) phase-II fish were stocked annually into Lake Seminole. Short-term survival (48 h) of phase-II fish held in live cars at the stocking sites from 1995 to 2001 ranged from 61% to 94% and averaged 83%. Phase-II tag return data were collected from 1986 to 1988, 1993 to 1996, and 2000. A total of 26,477 phase-II fish received external tags with phone numbers, and 747 (2.8%) tag returns were reported. Angler returns were low for most year-classes (1–4%) but did reach 10% during 1 year. The vast majority of tagged fish were caught near the stocking location within a few months of release, and then tag returns dwindled to zero per month. Only seven externally tagged fish were captured two or more years poststocking. Phase-II stocking was considered unsuccessful and was discontinued in Lake Seminole and the Apalachicola River.

Creel census surveys

Upper Apalachicola River.—The creel survey results demonstrated that many anglers targeted striped bass during the 14-week survey period. Between 1982 and 2009, the number of striped bass anglers interviewed ranged from 24 to 416 and averaged 166 (Table 3), comprising 2–30% of the anglers interviewed each year. During the surveys conducted from 1980 to 2009, directed angling effort estimates for striped bass ranged from 1,098 (SE = 318) to 9,485 (SE = 2,936) hours, averaging 3,696 h.

Annual harvest estimates for striped bass during early stocking years from 1980 to 1992 increased 10-fold, from 152 (SE = 130) to 1,505 (SE = 474; Table 3). Prior to 1992, released striped bass were not documented in the survey data, and it was assumed that under prevailing harvest regulations, all caught fish were harvested. Catch and harvest estimates in 1992 (1,570 and 1,505, respectively) and 1993 (307 and 285, respectively; Table 3) supported

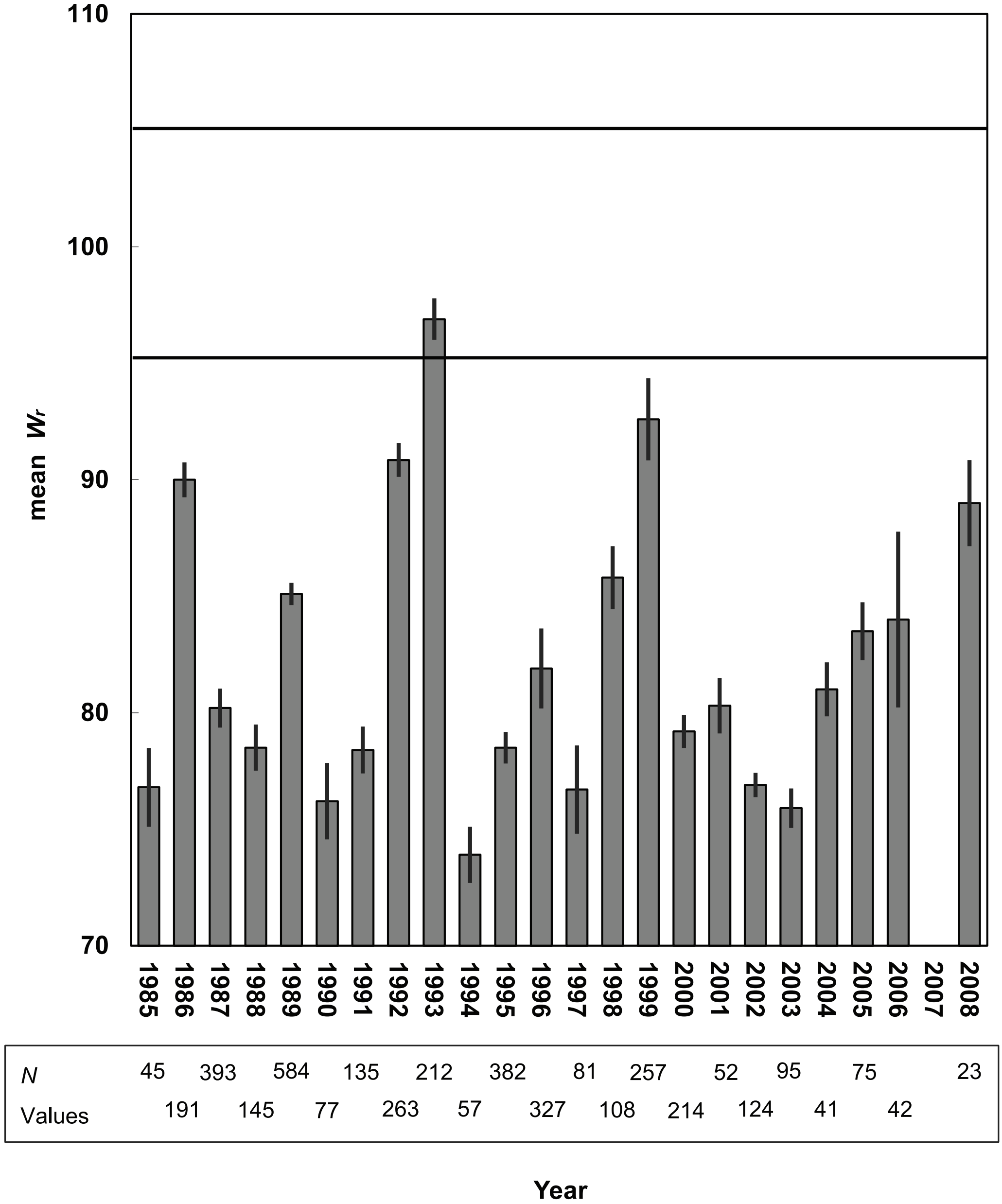

FIGURE 5. Mean relative weights (W_r) of age-0 striped bass greater than 150 mm total length electrofished from Lake Seminole and the Apalachicola River during September–December, 1985 to 2008. Vertical lines represent one standard error. Horizontal lines represent the optimal range of W_r (95–105; Brown and Murphy 1991).

this assumption. Following a change in harvest regulation (1994 to 2009) that reduced the bag and implemented a minimum size, estimates of striped bass total catch ranged from 311 (SE = 156) to 1,457 (SE = 346) and averaged 688 fish (Table 3). During this period, harvest estimates ranged from 134 (SE = 49) to 796 (SE = 214) and averaged 379 fish (Table 3).

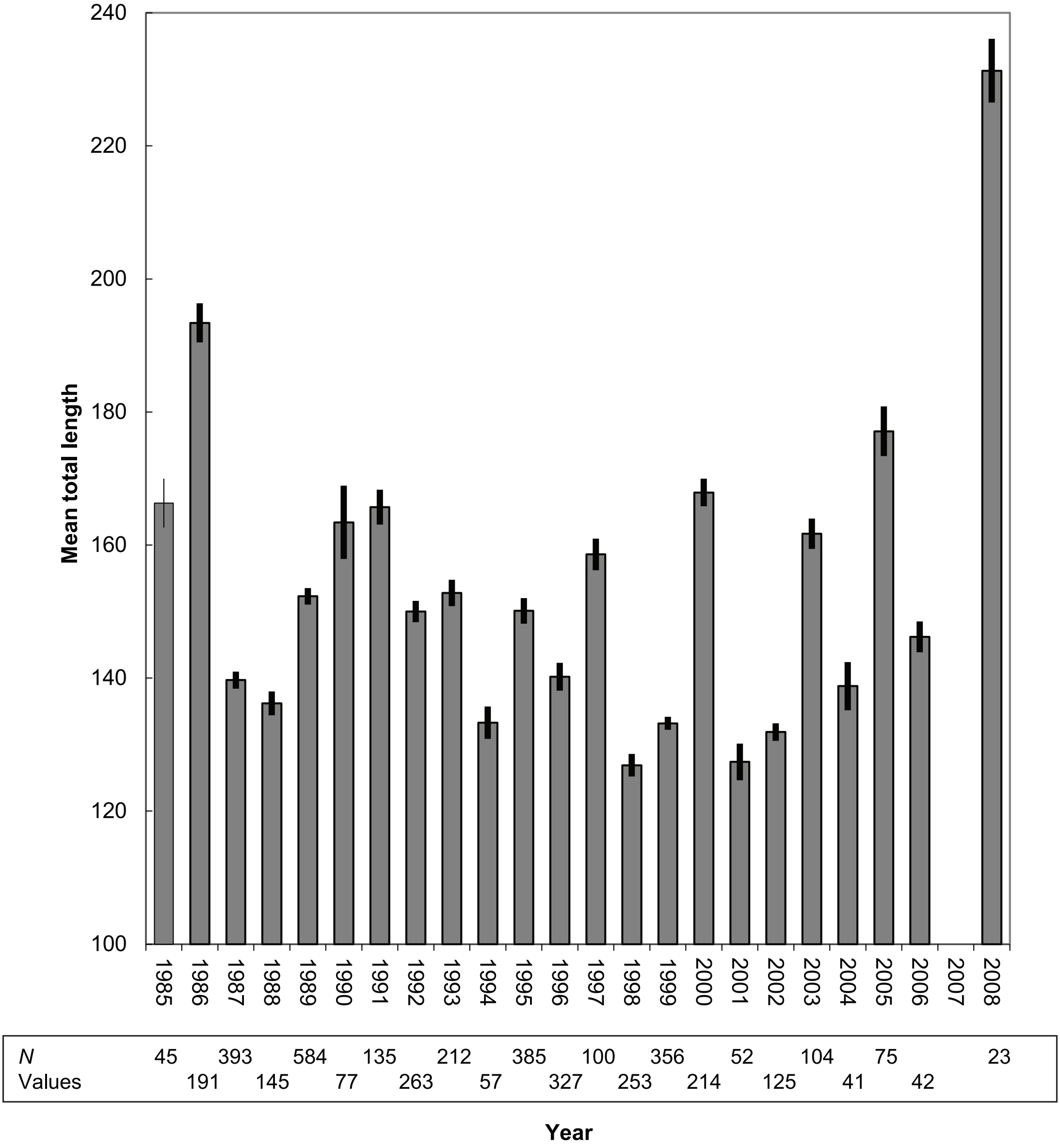

FIGURE 6. Mean total lengths of age-0 striped bass electrofished from Lake Seminole and the Apalachicola River during September–December, 1985 to 2008. Vertical lines represent one standard error.

Lower Apalachicola River/Intracoastal Waterway.—Few anglers targeted or harvested striped bass in the LAR/ICW area of the ACF. During spring (1990–2004) and fall (1990–1999) creel surveys, the number of anglers interviewed ranged from 250 to 550 and 225 to 502, respectively (Table 4). The most striped bass anglers encountered during any survey period was 24, which resulted in the highest estimate of effort (653 h; SE = 347; Table 4). Estimates of striped bass total catch ranged from 2 (SE = 2) to 1,458 (SE = 990) in the spring and 11 (SE = 12) to 1,521 (SE = 749) in the fall (Table 4). No harvest was

TABLE 3. Upper Apalachicola River 14-week spring creel census survey estimates, 1980–2009. Numbers in parentheses represent one standard error. Data for number of anglers and striped bass anglers were not available for 1980 and 1981.

Year	Number of anglers	Striped bass anglers	Harvest (SE)	Total catch (SE)	% released	Angling hours (SE)	Harvest success (SE)	Total success (SE)
1980			152 (130)			1,480 (514)	0.04 (0.03)	
1981			182 (60)			629 (162)	0.29 (0.05)	
1982	1,459	56	703 (467)			1,594 (720)	0.60 (0.13)	
1983	1,012	24	366 (124)			750 (274)	0.81 (0.51)	
1984	1,192	46	149 (68)			1,098 (318)	0.60 (0.20)	
1985	1,250	31	374 (118)			919 (156)	0.36 (0.02)	
1986	1,368	236	877 (337)			6,145 (682)	0.10 (0.03)	
1987	1,157	159	827 (129)			3,272 (507)	0.17 (0.02)	
1988	1,590	227	674 (177)			3,300 (1,275)	0.19 (0.05)	
1989	1,003	223	622 (121)			5,519 (1,032)	0.11 (0.02)	
1990	1,367	416	1,140 (205)			9,108 (1,049)	0.11 (0.03)	
1991	988	298	911 (161)			9,485 (2,936)	0.07 (0.02)	
1992	1,043	247	1,505 (474)	1,570 (516)	4	9,255 (3,378)	0.15 (0.04)	0.15 (0.04)
1993	1,077	179	285 (65)	307 (58)	7	3,163 (499)	0.06 (0.02)	0.07 (0.01)
1994	969	285	210 (69)	886 (104)	76	5,876 (703)	0.03 (0.01)	0.13 (0.02)
1995	1,009	297	134 (49)	311 (156)	57	5,951 (1,024)	0.02 (0.01)	0.03 (0.01)
1996	932	119	316 (97)	929 (226)	66	2,609 (474)	0.16 (0.03)	0.44 (0.09)
1997	518	271	196 (56)	823 (153)	76	4,180 (522)	0.05 (0.01)	0.20 (0.03)
1998	813	104	297 (49)	364 (74)	18	1,593 (380)	0.15 (0.07)	0.19 (0.09)
1999	896	158	500 (112)	700 (133)	29	4,250 (793)	0.12 (0.07)	0.15 (0.08)
2000	872	241	742 (189)	914 (225)	19	6,583 (2,200)	0.08 (0.02)	0.10 (0.02)
2001	1,078	34	722 (211)	1,199 (260)	40	968 (293)	0.22 (0.09)	0.34 (0.11)
2002	739	213	796 (214)	1,457 (346)	45	3,505 (457)	0.12 (0.03)	0.23 (0.05)
2003	1,155	206	257 (95)	598 (146)	57	4,275 (596)	0.06 (0.02)	0.17 (0.04)
2004	749	136	322 (81)	353 (82)	9	4,109 (651)	0.10 (0.02)	0.10 (0.02)
2005	1,085	51	303 (100)	313 (100)	5	1,716 (487)	0.25 (0.06)	0.25 (0.06)
2006	894	59	272 (95)	395 (166)	31	1,845 (489)	0.19 (0.03)	0.28 (0.06)
2007	810	129	236 (60)	389 (89)	39	3,139 (370)	0.07 (0.01)	0.10 (0.02)
2008	754	93	163 (61)	196 (64)	17	2,431 (325)	0.08 (0.02)	0.10 (0.03)
2009	670	102	150 (78)	219 (90)	32	2,135 (385)	0.09 (0.04)	0.12 (0.04)

recorded during five spring surveys and three fall surveys. Typically, striped bass were caught incidentally by anglers fishing for other species, and most anglers reported releasing their catch because the fish were shorter than the 457-mm-TL minimum size limit. During the 15 years that the spring surveys were conducted, only an estimated 1,484 (15%) of the 9,831 striped bass total catch estimate was harvested.

Flint and Chattahoochee rivers.—Creel surveys directed at the striped bass fishery in the Flint and Chattahoochee rivers were conducted from 1995 through 1998. The total number of angler trips during the 26-week creel surveys conducted at the Albany Dam tailrace on the Flint River ranged from 1,741 to 5,553 and averaged 3,855 (Georgia Department of Natural Resources, unpublished data). The estimated number of hours of directed fishing ef-

Table 4. Lower Apalachicola River spring and fall creel survey results. Numbers in parentheses represent one standard error.

Year	Number of anglers	Striped bass anglers	Harvest (SE)	Total catch (SE)	% released	Angling hours (SE)	Harvest success (SE)	Total success (SE)
				Spring creel surveys				
1990	393	3	25 (23)	84 (39)	70	109 (39)	0.02 (0.01)	0.65 (0.13)
1991	389	3	6 (4)	6 (4)	0	16 (12)	0.29 (0.04)	0.29 (0.04)
1992	291	0	0	2 (2)	100	0	0	0
1993	250	0	0	74 (81)	100	0	0	0
1994	298	0	0	151 (88)	100	0	0	0
1995	321	24	6 (6)	6 (6)	0	653 (347)	0.12 (0.04)	0.01 (0.04)
1996	861	1	365 (216)	1,311 (319)	72	133 (103)	2.00 (0.26)	2.00 (0.26)
1997	890	1	74 (57)	141 (99)	48	13 (10)	1.00 (0.13)	1.00 (0.13)
1998	855	0	8 (6)	379 (232)	98	0	0	0
1999	446	4	0	623 (104)	100	157 (73)	0	0.89 (0.24)
2000	397	0	0	1,458 (990)	100	0	0	0
2001	376	5	25 (19)	713 (268)	96	594 (576)	0	0
2002	452	1	2 (2)	430 (166)	99	253 (255)	0	0.11 (0.17)
2003	481	4	59 (65)	374 (246)	84	313 (343)	0	0.63 (0.12)
2004	421	0	0	0	0	0	0	0
				Fall creel surveys				
1990	301	19	381 (345)	595 (535)	36	332 (206)	0.83 (0.18)	1.28 (0.27)
1991	274	10	41 (45)	47 (53)	13	107 (65)	0.27 (0.16)	0.36 (0.21)
1992	296	8	11 (12)	44 (28)	75	67 (42)	0.13 (0.05)	0.13 (0.05)
1993	228	6	20 (22)	43 (48)	53	222 (161)	0.10 (0.02)	0.20 (0.05)
1994	225	6	0	11 (12)	100	659 (547)	0	0.01 (0.02)
1995	417	2	0	479 (209)	100	61 (48)	0	1.50 (0.24)
1996	502	10	256 (183)	1,521 (749)	83	256 (183)	0.56 (0.91)	1.56 (0.80)
1997	473	1	166 (95)	441 (211)	62	33 (23)	0	0.33 (0.04)
1998	421	3	39 (24)	755 (460)	95	94 (64)	0.57 (0.19)	1.16 (0.92)
1999	446	2	0	323 (199)	100	34 (27)	0	0

fort for striped bass averaged 801 h and ranged from 442 to 1,056 h. Expanded estimates of harvest for striped bass ranged from 15 to 37 fish and averaged 28 striped bass harvested. During the same time period, the total number of angler trips for the creel census conducted at the GALD on the Chattahoochee River ranged from 4,758 to 7,437 and averaged 6,134 angler trips. The number of hours of directed fishing effort for striped bass ranged from 0 to 466 h and averaged 192 h. Expanded estimates of harvest for striped bass ranged from 0 to 70 and averaged 30 fish. The timing of these surveys corresponded with the open season (1 November–31 May) for the harvest of striped bass. Harvest regulations for striped bass in these waters were 15 fish in combination, including striped bass, hybrid striped bass, and white bass, only two of which could be over 559 mm TL.

Thermal refuge habitat

Apalachicola River.—A total of 66 striped bass ranging in size from 0.7 to 9.6 kg were surgically implanted with temperature sensitive radio or ultrasonic transmitters and released into the UAR ($N = 13$; 2.5–9.6 kg; ages 2 and older), LAR and ICW (0.7–3.8 kg; age 1 $N = 1$, age 2 $N = 42$, age 3 $N = 1$), and Chipola River ($N = 9$; 1.8–5.4 kg). Ages of tagged fish released into the LAR and ICW were estimated based on comparison with aged fish of similar length and weight.

Ten radio-tagged striped bass released into the UAR located nine coolwater thermal refuges, which included two within-bank springs (22–25.5°C) and seven spring runs or canopied coolwater creeks (20–24°C) and began occupying these refuges when ambient temperature ranged between 23°C and 25.0°C. Medium (7.0–7.5 kg) and large (>9.0 kg) fish began to occupy thermal refuges between 28 April and 11 May. The smallest fish (2.7–3.8 kg) began using the refuges between 24 and 29 May. After taking residence in the refuge, only one fish (3.0 kg) was located outside of a refuge (twice), although several fish did move between two adjacent refuges located approximately 775 m apart. Only one fish (7.75 kg) survived over the summer of 1990. This fish remained in a refuge until 17 October (158 d after the first refuge relocation) when ambient temperature was 23.9°C. Three fish released into the UAR provided no data.

Nine tagged fish released into the LAR and ICW moved at least 160 km upstream to the UAR. Four were relocated in coolwater refuges in the upper river, four were relocated in the tailrace where several refuges occur, and one was harvested by an angler. One radio-tagged fish moved to the upper Chipola River where it was observed in a refuge by divers but was not relocated by telemetry. This fish was identified as a study fish by the trailing radio antenna and external tag. There was no apparent relationship between size (1–2.7 kg) and movement upstream. Of the 23 fish that remained in the LAR and ICW and were located at least once, four died (located 2–38 times) and six were caught by anglers (located 3–28 times). Several fish were relocated early in the study, disappeared, and were relocated in late summer or early fall. It was not clear whether these fish left the lower system and returned or occupied areas where the transmitter signal was occluded (e.g., deep holes or higher salinity). Of the 44 fish tagged (12 radio and 32 ultrasonic) and released into the LAR and ICW, 14 were never relocated or remained at the release site for several days and then disappeared, including five of the largest (2.0–3.8 kg) fish tagged. Fish tagged and released in this study were not relocated in thermal refuges in the lower part of the Apalachicola River system. However, several preferred areas were identified during telemetry that included bridge pilings and tidal mixing zones. Fish utilized these preferred areas, even though ambient temperature reached as high as 33°C during the summer. No fish tagged with ultrasonic transmitters (which could be detected in saline waters) were located outside of the main river, ICW, or distributary streams in the more saline areas of Apalachicola Bay (LAR) or St. Joe Bay (ICW).

Tagged fish released into the Chipola River were located in seven springs (21.6–22°C) and six coolwater creeks (22.8–25°C) that provided thermal refuge. While these fish preferred the discrete coolwater refuges, they frequently moved throughout the upper 85 km of the Chipola River, occupying water temperatures that ranged from 23°C to 26°C throughout the summer.

Lake Blackshear.—A total of 33 striped bass ranging in size from 2.7 to 15.0 kg were internally (22) or externally (11) fitted with temperature-sensing radio transmitters and released into Lake Blackshear (Flint River) during the fall of 1998 ($N = 16$), spring of 1999 ($N = 11$), and spring of 2000 ($N = 6$; Baker and Jennings 2001) to determine habitat use, movement patterns, and survival of adult striped bass in Lake Blackshear. Eight fish (25%) were detected at least once within 2 months of release but not during the remainder of the study and were considered to be missing. Mortality switches on the transmitters indicated that all of the 25 fish that remained within Lake Blackshear died during the summer following their release. Only five fish were ever detected within thermal refuges in the reservoir, and these fish survived longer than those that were never located within a thermal refuge.

In addition to the telemetry studies, known thermal refuges in Lake Seminole and the Flint River were qualitatively monitored during the summertime for striped bass usage by scuba divers. During monthly surveys of 10 Flint River springs (1997–2008), the average number of large fish (>9.0 kg) observed per dive ranged from 0.09 to 2.15 and the average number of small and medium fish (<9.0 kg) ranged from 1.4 to 19.8. The highest counts for both large and small striped bass occurred from 1999 to 2000, followed by a gradual decline through 2005 and then increases during the most recent years (Georgia Department of Natural Resources, unpublished data).

Thermal refuge renovation

Five spring runs and canopied coolwater creeks in the upper Apalachicola River identified as thermal refuges by telemetry were renovated by removing snags and excavating sediments from the mouths of the creeks during 2001. The amount of substrate material removed ranged from 190 to 1,900 m^3. The excavations partially filled in within 1 to 2 years, and as low summertime discharges persisted in the Apalachicola River because of drought conditions, availability of these refuges for striped bass returned to prerenovation levels (Florida Fish and Wildlife Conservation Commission, unpublished data).

Gulf and Atlantic striped bass performance evaluation

We did not find consistent differences in survival or growth between Gulf and Atlantic races of striped bass when co-stocked into Lake Talquin. From 1988 to 1992, a total of 277,000 Gulf and Atlantic race phase-I striped bass were co-stocked into the reservoir. During the study, size and health of fish at stocking varied within and between year-classes, resulting in highly variable survival and growth to age 1. Atlantic fingerlings tended to be larger at stocking, whereas sizes of Gulf fingerlings were more variable (900–4,400/kg) than Atlantic fingerlings (1,850–4,400/kg) among years. Incomplete air bladder inflation was observed for both races but appeared to be more prevalent among Gulf fish. For unknown reasons, one Gulf mtDNA haplotype (B2) that was stocked in 3 of the 4 years was absent from samples collected at age 1. Although numerous fish were collected from other year-classes, obtained sample sizes through age 4 limited the comparison of relative survival to the 1988, 1989, 1991, and 1992 year-classes.

Relative survival of Gulf and Atlantic race striped bass was similar from age 1 to age 5. Results of Pearson chi-square analysis revealed no difference ($P > 0.05$) in the number of Gulf and Atlantic fish collected for three of four year-classes evaluated (Table 5). However, Atlantic striped bass from the 1992 year-class demonstrated significantly higher (Table 5; $\chi^2 = 25.034$, df = 3, $P = 0.0001$) relative survival at age 3 (Atlantic $N = 34$; Gulf $N = 16$) and age 4 (Atlantic $N = 47$; Gulf $N = 6$).

Although we observed some significant differences in mean total length and weights between races, these differences were not consistent from ages 1 to 6. Early differences may have been linked to the size at stocking. Atlantic phase-I fingerlings were generally larger than Gulf fingerlings at the time of stocking, and we observed significantly greater mean total length ($P = 0.004$) and total weights ($P = 0.03$) for all Atlantic fish sampled at age 1 (Table 6). However, by age 4, Gulf striped bass had significantly ($P < 0.006$) greater mean total length than Atlantic fish, but no significant differences ($P > 0.05$) were observed at ages 5 or 6. ANCOVA revealed no differences ($P > 0.05$) in the elevation of the regression lines between races ($P = 0.155$) for the 1988 and 1989 year-classes. Also, no significant difference in the length–weight natural log regressions of the two races was found, suggesting similar growth and body conditions during the evaluation. These composite results suggested that Gulf

TABLE 5. Number of Gulf and Atlantic striped bass phase-I fingerlings stocked into Lake Talquin for the 1988, 1989, 1991, and 1992 year-classes and number of Gulf and Atlantic fish per year-class recaptured at ages 1 through 5 during November–December gill netting. The ratios of number of Gulf and Atlantic fish collected were evaluated using Pearson chi-square analysis ($P < 0.05$). Significant difference is indicated for the year class by *.

		Total number collected				
Race	Number stocked	Age 1	Age 2	Age 3	Age 4	Age 5
Year-class 1988 (χ^2 value = 5.76 df = 4.0 P = 0.22)						
Atlantic	100,000	18	21	39	31	22
Gulf	100,000	24	34	37	24	16
Year-class 1989 (χ^2 value = 0.20 df = 2.0 P = 0.91)						
Atlantic	50,000	28	25	18	14	5
Gulf	50,000	19	17	10	3	4
Year-class 1991 (χ^2 value = 1.33 df = 2.0 P = 0.51)						
Atlantic	42,000	23	17	15	4	5
Gulf	42,000	34	17	14	6	3
*Year-class 1992 (χ^2 value = 25.03 df = 3.0 P < 0.0001)						
Atlantic	85,000	29	47	36	47	–
Gulf	85,000	29	42	14	6	–

and Atlantic striped bass co-stocked into Lake Talquin performed similarly in terms of growth and condition from 1988 to 1996.

Genetic characterization

A pivotal question in justifying the restoration program was whether the ACF still harbored a population of native striped bass that was genetically distinct from Atlantic coast populations. Advances in genetic analyses in the decades since stocking began have identified unique features of the Gulf genotype, but also significant introgression by the Atlantic race into the current population. In the mid-1980s, allozymes had failed to reveal sufficient levels of genetic variation in striped bass to address population structure questions and the use of mtDNA was in its infancy. Using RFLP analysis, Wirgin (1987) demonstrated that approximately 55% of Gulf striped bass from the ACF exhibited a mtDNA haplotype with the restriction enzyme *Xba* I that was absent in Atlantic coast samples. Over a 24-year period (1983–2007), 40% to 79% of Gulf broodfish collected annually from the ACF exhibited the unique *Xba* I haplotype (Wirgin et al. 1997; I. I. Wirgin, unpublished data). Gulf striped bass mtDNA also showed a high frequency of a length variant (length A) that was present, but in low frequencies, in Atlantic populations. Additional studies also demonstrated that the Gulf-unique mtDNA *Xba* I haplotype was absent in Atlantic populations that extended from New Brunswick to Georgia and included the Santee–Cooper source of Atlantic-race introductions into the ACF (Wirgin et al. 1990, 1993). As a result, descendants of broodstock with this haplotype were preferred for reintroduction back into the ACF. Further studies that analyzed mtDNA in striped bass from other Gulf tributary rivers in Mississippi, Louisiana, and Texas

TABLE 6. Total numbers and mean lengths and weights of Gulf and Atlantic striped bass, by age-class, collected by gill netting from Lake Talquin during November–December 1988–1996. Standard deviations are provided. Differences were analyzed using Student's *t*-test and significant differences ($P < 0.05$) are denoted by *.

Race	Total number collected	(%)	Mean total length (mm)	SD	Mean weight (kg)	SD
			Age 1 ($N = 327$)			
Atlantic	150	46	*454	37	*1.18	0.29
Gulf	177	54	441	46	1.12	0.37
			Age 2 ($N = 263$)			
Atlantic	125	48	596	33	2.59	0.49
Gulf	138	52	590	35	2.53	0.51
			Age 3 ($N = 216$)			
Atlantic	134	65	688	34	4.06	0.69
Gulf	82	35	693	36	4.07	0.62
			Age 4 ($N = 136$)			
Atlantic	96	71	722	33	4.69	0.78
Gulf	40	29	*742	38	4.86	0.96
			Age 5 ($N = 56$)			
Atlantic	32	57	786	33	5.75	0.83
Gulf	24	43	781	30	5.37	0.87
			Age 6 ($N = 17$)			
Atlantic	9	53	788	34	5.96	0.96
Gulf	8	47	797	38	5.86	0.65

where the Atlantic race had been stocked failed to detect the Gulf-specific *Xba* I haplotype (Wirgin et al. 1997). Because the ACF was the only system along the Gulf to harbor striped bass with the *Xba* I mtDNA haplotype, it was presumed to have the only remaining stocks of true Gulf striped bass. Because of these results, efforts to restore Gulf populations with supplemental stocking were dependent on the ACF as the only source of Gulf fish having the unique genetic characteristics.

Although a high percentage of ACF fish had unique mtDNA haplotypes, the mtDNA genome comprises less than 0.1% of total genetic material in cells and its maternal heritability differs from that of biparentally transmitted nDNA. Therefore, it is possible that fish exhibited predominantly Gulf mtDNA haplotypes in the background of predominantly Atlantic nuclear genomes. Two different nDNA approaches, each interrogating different forms of nDNA variation, addressed this possibility, and both provided the same answer. First, two of four heterologous probes used with nDNA fingerprinting (multi-loci minisatellite analysis) revealed that more than 90% of ACF fish exhibited individual minisatellite DNA fragments that were absent from Atlantic striped bass (Wirgin et al. 1991). Second, striped bass-specific SNP markers, identified from a striped bass genomic DNA library, and using RFLP with Southern blot analyses, identified several polymorphisms that were unique to fish from the ACF population (Wirgin and Maceda 1991). Over the ensuing years, continued analysis of broodstock from the ACF, and additional Atlantic fish, confirmed that several SNP alleles were unique to the ACF population (Wirgin, unpublished data).

In summary, three different DNA approaches, focusing on two different genomes, demonstrated that the ACF population harbored a high percentage of fish that were genetically distinguishable from all Atlantic fish. Also, both minisatellite and microsatellite analyses revealed high levels of allelic diversity in the ACF, comparable to, if not higher than, diversity observed in all Atlantic populations investigated (Wirgin et al. 2005).

Although these studies confirmed that the ACF was genetically differentiated from Atlantic populations, they did not evaluate the genetic impact of the introduction of Atlantic fish into the ACF. To address this issue, museum-archived samples from the ACF whose collection predated Atlantic introductions were screened. MtDNA analysis of the *Xba* I haplotype showed that the allele frequencies did not differ significantly between the prestocking fish and extant ACF populations, indicating that significant introgression of the Atlantic mtDNA haplotype into the ACF population had not occurred (Wirgin et al. 1997). However, subsequent work with nuclear markers demonstrated significant introgression of nDNA into the Gulf genome.

The introgression of Atlantic striped bass nDNA alleles into the Gulf genome was addressed by comparing the frequencies of informative microsatellite DNA polymorphisms in archived ACF samples from prior to any stocking to the frequencies in the extant ACF population. Five microsatellite loci were identified from a striped bass genomic DNA library (Roy et al. 2000) that all exhibited fixed (two loci) or highly significant allelic frequency differences (three loci) between the extant ACF and Atlantic collections from the Hudson River, Chesapeake Bay, Santee–Cooper system, and St. Mary's River, Florida–Georgia (Wirgin et al. 2005). These diagnostic loci were then used as markers to evaluate the extent of nDNA introgression into the extant ACF population.

DNA was isolated from dried striped bass scales archived from the ACF (N = 48) prior to stocking and also the extirpated St. Johns River, Florida population (*N* = 40), which historically was the southernmost population along the Atlantic coast (Wirgin et al. 2005). When this DNA was analyzed for microsatellite variation at three (two fixed and one almost fixed) of the diagnostic microsatellite loci discussed in the preceding paragraph, fixed allelic differences were found at two of three loci between the archived ACF and St. Johns River samples. At these two loci, 45% and 67% of fish from the archived ACF sample exhibited genotypes that were absent from the St. Johns River sample. At the third locus, 80% of prestocking ACF fish exhibited genotypes that were observed in only 7% of St. John River specimens. Comparison of allelic frequencies at these three microsatellite loci in the prestocking versus extant ACF collection yielded highly significant differences ($P < 0.001$). Greater allelic diversity at all three loci was observed in the extant compared to the archived prestocking ACF samples, and all alleles were those commonly found in Atlantic populations. Results of a mixture model (ADMIX 2) suggested that at these three loci, the proportion of Atlantic alleles in extant ACF fish was approximately 51%, indicating that significant introgression of Atlantic nDNA alleles had occurred in the ACF population (Wirgin et al. 2005).

Discussion

Restoration of Gulf striped bass in the ACF system has been ongoing for 32 years (as of 2011), as conservation agencies from Alabama, Georgia, Florida, and the federal government have worked together to define, protect, and enhance the population of this unique race of striped bass. Knowledge of the life history of Gulf striped bass was improved as a result of this partnership. A large cooperative stocking program was implemented, and cooperative monitoring and evaluation programs were conducted. Alternative broodfish repositories were developed outside of the ACF in Lake Talquin, the Blackwater River, and Smith Lake and Lake Martin (Alabama). Genetic cataloging of broodfish and captive fish was accomplished. Thermal refuge habitats important to adult striped bass were identified, protected, and enhanced or rehabilitated. Recreational fisheries were developed or augmented in several reservoirs in the ACF (Walter F. George Lake, West Point Lake, Bartlett's Ferry Lake, and Lake Blackshear), and enhanced trophy fishing opportunities resulted in the catches of new state record fish. Restoration efforts in the ACF have been a catalyst for expansion of Gulf striped bass re-establishment throughout the Gulf region, including the Mobile-Alabama-Tombigbee system (Alabama), the Pascagoula and Pearl rivers (Mississippi), and the Tangipahoa and Tchefuncte rivers (Louisiana). Propagated Gulf striped bass fingerlings are now available for stocking programs across the Gulf region.

Stocking Gulf striped bass phase-I fingerlings into the ACF successfully resulted in an initial increase in the adult population evidenced by significant increases in broodfish catch rates in the tailrace of JWLD as well as in the Chattahoochee and Flint rivers and a 10-fold increase in estimated harvest in the JWLD tailrace fishery during the 1990s. From 1997 to 2000, estimated harvest and success rates for the UAR creel survey increased to the point that striped bass were the most sought species in the tailwater fishery. In addition, recreational fisheries were developed in the Chattahoochee and Flint rivers. Continued stocking in Lake Seminole and the Apalachicola River did not result in further enhancement to broodfish relative abundance or in catch and harvest estimates in the JWLD tailrace or in sustaining the elevated numbers of fish observed during the 1990s. Instead, broodfish CPUE and catch estimates oscillated off of their lows and highs through the remainder of this study. Age-0 CPUE in Lake Seminole suggested several weak year-classes during the mid-1990s, which likely affected broodfish relative abundance during the late 1990s and early 2000s. In addition, severe drought conditions in the ACF basin beginning in 1999 would have resulted in fewer fish being discharged from Lake Seminole and reduced thermal refuge capacity (e.g., reduced groundwater discharge and disconnection of tributaries from the channel) in the upper Apalachicola River. In contrast, in the Chattahoochee and Flint rivers, where thermal refuge habitat is more abundant, broodfish CPUE values continued to increase through the 2000s despite weak year-classes in Lake Seminole and the potential impacts (e.g., reduced groundwater discharge and water withdrawals for irrigation) to thermal refuges that resulted from drought conditions.

Available evidence suggests that natural reproduction remained at a relatively low level in the ACF during the study period despite the stocking program and enhancement in the broodfish population. Although CPUE of wild age-0 fish in Lake Seminole was higher in 1997 and 2006 than in 1985 (nonstocking years), catch rates during nonstocking years were similar to those observed during stocking years that relative abundance values indicated were weak year-classes (RAV < 0.30). Higher catch rates of wild age-0 fish during nonstocking years than during stocking years (2001–2004) also suggested that density dependent mechanisms could be affecting survival of wild fish during some years when stocking occurs. Catch per unit effort was above average (1.45 fish/min) in 2002 and 2003 and wild fish comprised about 13% of the total, while catch rates were well below average in 2001 and 2004 and wild fish comprised 0% and 25% of the total. Natural reproduction was also documented in the Chattahoochee River upstream of West

Point Lake, Alabama–Georgia (Hess and Jennings 2001, 2002) following the introduction of Gulf striped bass into West Point Lake in the 1990s, but only during one year. It is likely that stocking will be required to sustain higher numbers of adult fish in the population than wild fish abundances observed prior to restoration efforts.

Most wild, age-0 fish sampled during fall electrofishing were collected in Lake Seminole, suggesting that successful natural reproduction was primarily occurring in the Flint or Chattahoochee rivers, supporting Keefer's (1986) assessment that successful striped bass reproduction occurs in the Flint River. The predominance of OTC-marked, age-0 hatchery fish (stocked only above JWLD) collected during fall electrofishing in the Apalachicola River demonstrated that a large proportion of age-0 fish in the river were discharged to the Apalachicola River through turbines, flood gates, or the lock at JWLD. From 2001 through 2008, unmarked age-0 fish were collected from the Apalachicola River only in the presence of OTC-marked hatchery fish. Since most age-0 fish collected in the river are taken from the two uppermost sites below JWLD, it is likely that unmarked age-0 fish represent migrants from Lake Seminole rather than wild fish spawned in the Apalachicola River.

Other investigators have reported a negative relationship between phase-I stocking density and survival. Van Den Avyle and Higginbotham (1980) found that stocking density and survival were inversely correlated, though not significantly, for striped bass fingerlings stocked into Watts Bar Reservoir, Tennessee. These authors hypothesized that increased mortality at higher stocking rates may have been influenced more by the smaller size at stocking when stocking numbers were higher than by density dependent variables. Moore et al. (1991) found a significant inverse correlation between the survival and numbers of phase-I fingerlings stocked into Smith Mountain Lake, Virginia. Our analysis demonstrated a positive relationship between numbers stocked and relative abundance of age-0 striped bass in fall electrofishing samples. However, our results may have differed had we sampled during the spring following stocking when fish were age 1 (e.g., Moore et al. 1991).

Studies that evaluated the merits of stocking phase-I and phase-II striped bass or hybrid striped bass fingerlings into coastal rivers (Yeager 1988; Wallin and Van Den Avyle 1995; Wallin et al. 1995) have suggested that stocking phase-II fingerlings into coastal rivers is more efficient than stocking phase-I fingerlings (Yeager 1988). Stocking fingerlings into brackish areas resulted in higher initial survival than stocking into freshwater (Wallin and Van Den Avyle 1995). However, Wallin et al. (1995) reported that survival to age 2 was higher for fingerlings stocked into freshwater despite early survival advantages of fingerlings stocked into brackish water. Our results suggested that although initial survival (48–72 h; 83%) of fingerlings stocked into the UAR, LAR, ICW, and ARB was similar to that reported by others, survival to adulthood for both phase-I and phase-II fish stocked into riverine or brackish habitat was poor. Although we did not evaluate the reasons for poor survival, we believe that factors included predation, and in the case of phase-II fingerlings, extended (8–10 months) culture on artificial feed reduced their fitness for foraging on natural food and may have affected their ability to digest and assimilate natural food.

The invasion and expansion of hydrilla in Lake Seminole appeared to negatively affect the reproductive potential and carrying capacity of age-0 striped bass in the reservoir. Relative abundance of age-0 striped bass in Lake Seminole was inversely correlated with surface area of hydrilla. Dense hydrilla may impact primary productivity by filtering out nutrients, thus reducing phytoplankton (Carter et al. 1988; Jones 1990), or adversely impacting zooplankton communities (Maceina and Shireman 1985; Carter et al. 1988; Jones 1990; Tsai et al. 1991; Michaletz and Bonneau 2005). The effects of hydrilla on plankton communities would be most pronounced during summer months (Carter et al. 1988; Jones 1990), and the impact would be greatest on juvenile fish by reducing preferred sand habitat, available prey, and feeding efficiency (Maceina and Shireman 1985). Loss of sand habitat may concentrate age-0 striped bass into smaller areas of preferred habitat, resulting in poor growth, reduced condition, or starvation. We observed slower growth and low W_r values of age-0 striped bass in Lake Seminole after hydrilla expansion. In addition, the alteration or reduction in zooplankton populations may impact important forage fish species (Maceina and Shireman 1985; Michaletz and Bonneau 2005) such as threadfin shad *Dorosoma petenense*, gizzard shad *D. cepedianum*, skipjack herring *Alosa chrysochloris*, and Alabama shad *A. alabamae* that are important prey for older juvenile and adult striped bass. A reduction in shad populations could also result in increased predation on age-0 striped bass by other piscivores such as largemouth bass *Micropterus salmoides* (Michaelson et al. 2001), particularly given the close proximity of dense hydrilla to available sand habitat.

From a management perspective, the inverse relationship between relative abundance of age-0 fish and hydrilla density in Lake Seminole could be used to adjust annual stocking numbers based on the expected density of hydrilla. Although the effects of expanded hydrilla appear to be detrimental to young-of-year survival, the relationship suggests that losses could be offset by increasing stocking numbers, as occurred in the 1990s. For example, years having RAVs above 0.30 and high hydrilla estimates in the fall were typically associated with higher stocking rates (>33 fish/ha). Conversely, when fall hydrilla estimates were low or declining, stocking rates as low as 15 fish/ha resulted in RAVs similar to years when twice as many fish were stocked. In future years, stocking rates could be adjusted at the spring *Morone* workshop to adapt to expected hydrilla conditions in the reservoir.

Creel surveys conducted on the upper Apalachicola River, Chattahoochee River, and Flint River demonstrated directed effort towards striped bass and that stocking helped develop or enhance recreational fisheries below dams in the system. From 1997 to 2000, estimated harvest and success rates for the UAR creel survey increased to the point that striped bass were the most sought species in the tailwater fishery. Stocking phase-I and phase-II fingerlings into the lower Apalachicola River, Bay, and Intracoastal Waterway resulted in very little directed fishing effort towards striped bass.

The striped bass population in the Apalachicola River is largely dependent on hatchery fish stocked into Lake Seminole and the subsequent emigration of fish through JWLD at some time during their life history. Downstream emigration of *Morone* species has been well documented in the ACF. Young (1987) described the establishment of a palmetto bass fishery in the tailrace of JWLD through emigration of this hybrid stocked into Lake Seminole, but he did not address the life stage at which palmetto bass exited the reservoir. Mesing et al. (1999) investigated the movement of palmetto bass and sunshine bass stocked into Lake Seminole and documented emigration of both hybrid crosses from the lake through JWLD into the tailrace and recruitment into the fishery as early as age 1. Our results demonstrated that age-0 striped bass emigrated to the tailrace during periods of both low and high discharge, but we did not address emigration of subadult or adult fish through the dam. Other studies (Van Den Avyle and Higginbotham 1980; Henley 1998; Hightower et al. 2001; Thompson et al. 2007) found that adult striped bass emigrated downstream through turbines or locks from other reservoirs in the Southeast. Trash racks likely prevent passage of most adult fish downstream through the turbines at JWLD; however, adult fish emigrate through JWLD via the lock or floodgates during high water events. Van Den Avyle and Evans (1990) reported that the greatest number of contacts with radio-tagged adult striped bass in the lower portions of Lake Seminole occurred between November and January, a time when floodgates at JWLD are most likely to be open. We attempted to correlate broodfish indices and creel catch/harvest estimates in the tailrace with monthly discharge and lock usage at JWLD. Significant correlations occurred only when April discharge was included in the analysis, which indicated to us that we were only seeing the immediate effects of water discharge on angling or broodfish electrofishing efficiency during the peak concentration of striped bass in the tailrace and not the overall effects of discharge or lockages on emigration from Lake Seminole. Stewart and Burrell (2013, this volume) discuss the effects of emigration through dams, though the rate of emigration has not been quantified.

Striped bass along the Gulf coast occur on the southern fringe of their range in North America, and their habitats and existence in many Gulf of Mexico rivers has always been tenuous. Striped bass do not occur in peninsular Florida, except in the St. Johns River, their southernmost range on the Atlantic coast. Ware (1971) attempted to establish striped bass in five central Florida lakes and Lake Talquin (northwest Florida) by stocking phase-I Atlantic (Moncks Corners origin) fingerlings during 1968 and 1969. He reported excellent growth, with the most rapid growth occurring during cooler fall and winter months, and survival to age 2. However, at age 1, summer die-offs beginning in June were reported for the central Florida lakes. Die-offs were associated with low coefficients of condition (K ranged from 1.41 to 1.78) that was attributed to parasitism by the marine nematode *Goezia* sp. (Ware 1971; Gaines and Rogers 1972). The vector of infection was assumed to be diet supplementation using a marine herring during fingerling culture. However, die-offs were not reported for Lake Talquin, which was stocked with the same hatchery products. Die-offs in the central Florida lakes were more likely the result of thermal stress that may have also exacerbated the effects of parasitism. The survival of fish stocked into Lake Talquin was more likely due to the presence of coolwater habitat. Summer die-offs are also atypical for striped bass in the St. Johns River, an Atlantic population that utilizes coolwater habitats (springs and streams) during the summer, which has also been parasitized with Goezia sp. (Gaines et al. 1973; Florida Fish and Wildlife Conservation Commission, unpublished data). Stocking striped bass into central Florida lakes was discontinued after 1969 in lieu of more successful stocking with sunshine bass (Ware 1975), which tolerate warmer temperatures.

The hypothesis of a thermal niche for striped bass and size/age dependent thermal partitioning among striped bass was proposed by Coutant and Carroll (1980). After extensive literature review, Coutant (1985) further developed the hypothesis and concluded that cool, oxygenated water was a requirement for adult (age 2–3 or >5 kg) striped bass during hot summer months. Other researchers (Dudley et al. 1977; Cheek et al. 1985; Matthews 1985; Matthews et al. 1989; Zale et al. 1990; Schaffler and Isely 2002; Young and Isely 2002) provided supporting evidence that adult striped bass, particularly large individuals, select coolwater refuges when thermal habitat is constrained during summer in southeastern and southwestern rivers and reservoirs and suggested that cool, oxygenated water was important for large striped bass. Wooley and Crateau (1983), Moss (1985), Lamprecht and Shelton (1988), Van Den Avyle and Evans (1990), and Weeks and Van Den Avyle (1998) reported that striped bass in Gulf coast tributaries similarly select coolwater refuges during summer months, and their period of residence was longer than reported for other southeastern reservoirs and river systems (Lamprecht and Shelton 1988; Van Den Avyle and Evans 1990; Weeks and Van Den Avyle 1998). Our telemetry results demonstrated that adult Gulf striped bass in the Apalachicola River began occupying coolwater refuges as early as April and remained in the refuges through mid-October, consistent with findings by Van Den Avyle and Evans (1990) that striped bass in Lake Seminole and the Flint River began using coolwater refuges in May and occupied them as late as November.

Many state fisheries agencies that stock striped bass into freshwater lakes have reported the mortality of adult striped bass due to thermal stress from high temperatures and low dissolved oxygen concentrations as the most frequent management problem for this species (Axon and Whitehurst 1985). Nine agencies identified these issues as limiting factors for striped bass survival (Axon and Whitehurst 1985). Matthews (1985) conducted a survey of states that stock striped bass into reservoirs and found that summer die-offs of adult striped bass were reported for 27 of 80 reservoirs. Large adult fish (>5.0 kg) were most often included in the mortality reports, although mortalities of fish as young as age 1 were also included. In many southeastern and southwestern reservoirs, thermal refuges consist of a hypolimnetic stratum of cool, oxygenated water that often becomes thinner, smaller, and more confined as summer temperatures increase and the season is prolonged (Matthews et al. 1985, 1989; Zale et al. 1990; Van Horn et al. 1998; Jackson and Hightower 2001; Thompson et al. 2010). In each study, the stratum of preferred temperature and oxygen disappeared by mid to late August, and striped bass occupied suboptimal conditions for a short period during the remainder of the summer. Only Zale et al. (1990) reported significant mortality, but the duration of suboptimal conditions in Keystone Reservoir was longer than reported for other study lakes. In the ACF, and other Gulf tributaries that have been dammed, reservoirs are typically shallow and become isothermal early in the summer. In these systems, striped bass are reliant on springs and coolwater creeks for thermal refuge during the summer. Although these refuges may provide consistent habitat throughout the summer and fall, their size and availability may be a limiting factor for the adult population size (Wooley and Crateau 1983; Coutant 1987b; Lukens 1988; Van Den Avyle and Evans 1990; Weeks and Van Den Avyle 1998). Our telemetry results in the Apalachicola River indicated a high percentage of mortality among all sizes of fish during the summer that was not observed by Van Den Avyle and Evans (1990) in Lake Seminole and the Flint River.

Van Den Avyle and Evans (1990) reported that 96% of their summertime (May–October) locations of adult striped bass (3.2–30.0 kg) were in coolwater refuges in Lake Seminole and the Flint River, and the only exceptions were during a brief period of exceptionally high discharge during August. Although thermal refuges may ameliorate the effects of high summer temperatures, extended residence in refuges may be detrimental to Gulf striped bass because these summer habitats are typically void of forage species (Weeks and Van Den Avyle 1998). Striped bass may lose as much as 22% of their body weight while occupying refuges (Wooley and Crateau 1983; McDaniel et al. 1993; Florida Fish and Wildlife Conservation Commission, unpublished data). Ware (1971) suggested that a coefficient of condition (K) less than 1.70 would result in mortality of subadult striped bass. Loss of weight and condition during the summer may contribute to reduced spawning success the following spring (Coutant 1987a). Striped bass in the ACF and other Gulf tributaries have a short period of weight recovery between vacating the refuges (mid-October to early November) and the spawning season (mid to late March). There is also only a short period between the spawning season and occupation of refuges.

While our telemetry studies did not define the thermal tolerances of Gulf striped bass, they were consistent with findings by earlier investigators (Cheek et al. 1985; Coutant 1985; Moss 1985; Lukens 1988; Van Den Avyle and Evans 1990; GSMFC 2006) that coolwater refuges are important, if not essential, habitats for over-summer survival of adult striped bass. Our observations indicated that some small striped bass (1–3 kg) were able to over-summer in the brackish portion of the lower Apalachicola River and Intracoastal Waterway, without using known thermal refuges, and occupied habitats similar to those reported by Haeseker et al. (1996). However, this telemetry study also documented that small fish (age 2) that remained in the freshwater main stem of the river moved upstream and occupied coolwater refuges during the summer. While we cannot quantify the importance of thermal refuges to the ACF population, if reproduction by large individuals contributes disproportionately to recruitment, then thermal refuge availability may be a limiting factor for the striped bass population in the ACF, as well as for populations in other Gulf of Mexico tributary rivers.

Accessibility to tributaries that are known thermal refuges in the Apalachicola River has been impacted by entrenchment of the river channel and decreased water discharge through JWLD. Current water management and upstream consumptive use in the ACF basin has resulted in lower discharge into the Apalachicola River, particularly during summer months and periods of drought when coolwater refuge is most important. Riverbed entrenchment typically occurs below dams (American Rivers 2002; Poff and Hart 2002; Pizzuto 2002) and, in the case of the Apalachicola River, has been accelerated by navigation maintenance practices such as dredging, bendway easing, rock removal, and construction of training dikes (Light et al. 2006). Entrenchment of the riverbed has resulted in the need for higher water discharge through JWLD during summer months to maintain connectivity between thermal refuge tributaries and the main channel. When discharge from JWLD is less than 312 m^3/s, thermal refuge creeks and spring runs in the upper river become disconnected (Light et al. 1998), resulting in the loss of important habitat in the Apalachicola River during summer months. When discharge is less than 255 m^3/s, only three thermal refuge creeks or spring runs are connected to the main channel; below a discharge of 142 m^3/s (the prescribed minimum flow for JWLD), only one refuge stream is connected to the main channel (Light et al. 1998). Loss of thermal refuge habitat in the upper Apalachicola River emphasizes the need to maintain suitable water levels in the river during summer months and to investigate upstream passage of striped bass via the lock at JWLD, or by other means, for access to thermal refuges above the dam. It also underscores the need to protect thermal refuge habitat not only in the Apalachicola River, but in Lake Seminole and the Flint River as well, as a step toward conserving the last remnant of a naturally reproducing population of Gulf race striped bass along the Gulf of Mexico.

Thermal refuges provided by springs and other groundwater sources in the Flint River may have been impacted also by consumptive water use in the ACF. Demands for water have been increasing in this area to accommodate population growth in municipal areas and farmland irrigation in rural areas. Center-pivot irrigation has become widespread in southwestern Georgia and northwestern Florida, and the negative effects on spring discharges have been well documented (Albertson and Torak 2002; Golladay et al. 2007). The numbers of Gulf striped bass using the 10 monitored thermal refuges in Lake Seminole and the Flint River has varied over time. The severe drought that occurred from 1999 through 2002, in conjunction with increased groundwater usage in the basin, resulted in decreases in flow in some of the monitored springs and may be directly related to a decline in striped bass habitation in some thermal refuges. Georgia Department of Natural Resources fisheries personnel observed reversal of flow within a thermal refuge spring on the Flint River shortly after a center-pivot system approximately 1.5 km away began pumping groundwater for irrigation (J. Kilpatrick, Georgia Department of Natural Resources, personal communication). More recently, the numbers of fish observed using springs in the Flint River has been gradually increasing.

Renovation of thermal refuges appears to have provided only short-term gains as many renovated areas degraded relatively quickly, especially during drought conditions. There was no measurable increase in use by striped bass in eight refuges in the Flint River and Lake Blackshear following renovation. However, the removal of material constricting the flow of cool water should have increased the quantity of thermal refuge area available to striped bass. During the telemetry study in Lake Blackshear in the summer of 1999, two of three thermal refuges in the reservoir that were renovated by GADNR did not flow (Baker and Jennings 2001). Since the 2001 study, these springs have still not flowed, probably because of hydrostatic pressure, continued drought, and groundwater withdrawals (Weeks and Van Den Avyle 1998; Georgia Department of Natural Resources, unpublished data).

A co-stocking experiment conducted in Lake Talquin, Florida suggested that there were no major differences in performance of Gulf and Atlantic race striped bass. Atlantic race striped bass showed significantly better survival at ages 3 and 4 for a single year-class; however, no other differences in survival were noted across the four tested cohorts. Differences in mean length and mean weight at age between Atlantic and Gulf fish also were not consistent throughout the study. Atlantic fish were larger at age 1, which was attributed to differences in size at stocking. By age 4, Gulf fish were larger, but the difference was not significant at ages 5 and 6. It is likely that these differences in growth were not biologically significant relative to habitat limitations.

Indiscriminate stocking of nonnative striped bass conspecifics where natural reproduction persists has resulted in genetic consequences that are probably irreversible. Although the ACF striped bass population remains genetically unique from Atlantic populations, a pure Gulf race no longer exists. The long-term effects of introgression of Atlantic-origin alleles into the Gulf striped bass genome may never be fully known.

Genetic analysis has been an integral component of the ACF restoration program since its inception. The long-term commitment and support to the genetic component of this project was essential for successfully completing genetic components of the 1996 and 2004 ACF-Ps. The detection of numerous mtDNA and nDNA markers should prove informative in future performance evaluation tests. Additional diagnostic markers will provide more flexibility in the design of future studies. Darden et al. (2013, this volume) provide an up-to-date description of microsatellite markers and resultant genetic analysis that are available for striped bass. All DNAs and/or tissues analyzed in this program have been stored in a repository and provide a valuable resource. Molecular research techniques evolve over time, and questions that prove refractory to analysis can often be addressed in the future.

This effort showed that the analysis of DNA from archived collections in museums or other sources can provide a wealth of information regarding the genetic composition of extirpated populations or comparisons of extirpated with extant populations. Such information will permit retrospective analysis of long-term trends in genotypic composition of populations. For example, we can envision the use of such materials to compare the effective population size of the original versus extant ACF population. Minimizing the likelihood of the development of inbreeding depression in small populations such as in the ACF is a primary objective of conservation genetics programs. This can be achieved by preventing severe population declines and resulting bottlenecks. In cases such as the ACF where augmentation is used to supplement natural reproduction, hatchery programs can be optimized to prevent decreases in effective population size. Current restoration efforts seek to maximize genetic diversity in the ACF population and broodfish repositories by accepting progeny from all crosses originating from the ACF, regardless of genotypic or meristic characteristics, and stocking progeny from as many different crossings as feasible. Based on more than 25 years of genetic analyses, the ACF population appears to be more genetically diverse than Atlantic populations, perhaps resulting from its initial genetic isolation. More recently, introductions of nonnative Atlantic fish have also increased genetic diversity.

Lessons and management implications

Collaborative group discussions, planning, and cost sharing among multi-state and federal agencies provided a forum to address a declining native Gulf striped bass population in the ACF and ultimately other river systems along the Gulf of Mexico. Without the cooperative efforts of the conservation agencies involved with fish management on the ACF, many tasks of the ACFPs could not have been attempted or successfully completed. Collaborative efforts were also beneficial in establishing and maintaining small populations, through stocking, in several other river and reservoir systems along the Gulf of Mexico.

Monitoring programs used in the ACF restoration program demonstrated that we were able to enhance the Gulf striped bass population in the ACF through a large stocking program. However, benefits obtained through stocking large numbers of fish have not been consistently sustained through time and have not resulted in the ability of the population to self-sustain at a desired level that is substantially larger than previously observed from natural reproduction alone.

Striped bass along the Gulf coast occur on the southern extent of their range. Limited historical references suggest that populations were small, and given the ecological constraints (e.g., high temperature regime) and the alterations to riverine environments (e.g., segmentation, dredging, and water withdrawals), populations will likely remain small despite stocking large numbers of fish. The most challenging aspects of our restoration program were the recognition by all parties involved that historic populations were inherently small, the acceptance of the role of altered habitat on restricting Gulf striped bass populations, and that feasible opportunities for restoration of degraded habitat were limited.

Large perturbations to the environment, such as the construction of dams that block access to spawning grounds, disrupt spawning processes, and limit access to thermal refuges, were harmful and difficult to remediate. However, less obvious impacts, such as the diversion or deforestation of a canopied creek, or well and irrigation withdrawals from aquifers, may be equally detrimental to coolwater habitat that is beneficial to the continued existence of small adult populations. We were able to meet objectives of the ACF plans that pursued restoration or enhancement of important known striped bass habitat areas by physically renovating several thermal refuges in the Apalachicola and Flint rivers. However, in dynamic river systems, such as the ACF, renovation efforts have been small and short-lived. Protection and enhancement of remaining functional thermal refuges will require a broader water-management strategy encompassing dam releases and groundwater supplies as well as periodic maintenance of habitat enhancement projects.

The observed low levels of striped bass natural reproduction in the ACF resulted in a reliance on stocking large numbers of hatchery fish into the system in lieu of addressing the more challenging issues of segmented rivers and lost or degraded habitats. Stocking has resulted in the introgression of genetic material from the Atlantic race into the Gulf genome. Genetic analyses of archived and extant striped bass from the ACF demonstrated that there is no longer a pure Gulf race striped bass population. However, because the ACF is the only natural population to still harbor a vestige of the Gulf genome, efforts to protect and restore the unique ACF population, as well as those where ACF progeny have been introduced, are warranted. Florida fish managers have committed to stocking only Gulf striped bass into Gulf of Mexico tributaries within their historic range. Likewise, fish managers in Alabama have committed their stocking program in all river systems to Gulf striped bass (N. Nichols, Alabama Wildlife and Freshwater Fisheries, personal communication). Fish managers in Mississippi and Louisiana have also expressed a desire to stock only Gulf striped bass but with the caveat that they cannot sacrifice their established striped bass fisheries when Gulf fingerlings are not available for stocking. To this end, fish managers in Mississippi are developing a broodfish repository in Ross Barnett Reservoir.

The ACF Striped Bass Restoration and Evaluation Plan will be revised in 2012. As a result of the work described herein, sufficient information now exists to redefine appropriate management, research, and restoration goals in the revised plan.

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