

## Genetic Variation and Management of Striped Bass Populations in the Coastal Rivers of South Carolina

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*Abstract.*—The coastal rivers of South Carolina possess reproducing populations of striped bass *Morone saxatilis*. Historically, all of these populations have been augmented with hatchery stocks from the Santee–Cooper drainage. Concern has been expressed that locally adapted, reproductively isolated populations may exist in these coastal rivers. Thus, the objective of this effort was to assess the distinctiveness of reproducing striped bass populations in these coastal rivers. Tagging studies indicated that the interrivers movement of striped bass was minimal. A population estimate of 406 striped bass longer than 30 cm was obtained for the Combahee River, suggesting a relatively small breeding population. Genetic assays at three nuclear restriction fragment length polymorphism sites showed highly significant allele frequency differences among seven coastal rivers, suggesting reproductive isolation. Partially or fully isolated populations can develop beneficial adaptations to local environmental conditions. Thus, we recommend the use of endemic stock to augment striped bass populations in the coastal rivers of South Carolina.

The coastal rivers of South Carolina (Figure 1) possess reproducing populations of striped bass *Morone saxatilis*. As has been observed in other southeastern coastal rivers, these populations exhibit minimal anadromy, generally remaining in the fresh and estuarine waters of their natal rivers (Dudley et al. 1977). The largest population is found in the Santee drainage, which includes the Santee, Cooper, Congaree, and Wateree rivers and Lakes Marion and Moultrie. The state's striped bass hatchery is located on and generally obtains broodfish from the Santee River, which has a mean annual discharge of 330 m<sup>3</sup>/s (Cooney et al. 1996). To the north of the Santee drainage, striped bass are found in the Pee Dee drainage, which includes the Little Pee Dee, Sampit, Pee Dee, Black, Lynches, and Waccamaw rivers. To the south of the Santee drainage, the Edisto, Combahee, Ashepoo, Coosawhatchie, and New rivers possess striped bass. The Ashepoo, Combahee, and Edisto rivers

are generally referred to as the ACE drainage. The Combahee River is a relatively small drainage of the coastal plain, with a mean annual discharge of approximately 10 m<sup>3</sup>/s (Cooney et al. 1996). The Intracoastal Waterway and other coastal waters connect these river systems.

Genetic data defining population structure have only recently become available. Resource managers previously assumed that the coastal rivers of South Carolina contained a single population of striped bass; as a result, to augment population abundance, they intermittently stocked these rivers with hatchery-produced progeny from the Santee drainage (Table 1). As new information has begun to surface, however, concern has been expressed that locally adapted, reproductively isolated populations may exist in these coastal rivers.

A variety of information can help define the distinctiveness of populations. Determining the migration of striped bass among the various coastal rivers can help define the likelihood of genetic exchange among populations. A relatively low rate of gene flow is required to overcome the random effects of genetic drift (Hartl and Clark 1997). Knowledge of the size of the breeding population can also help to assess the probability of impacting

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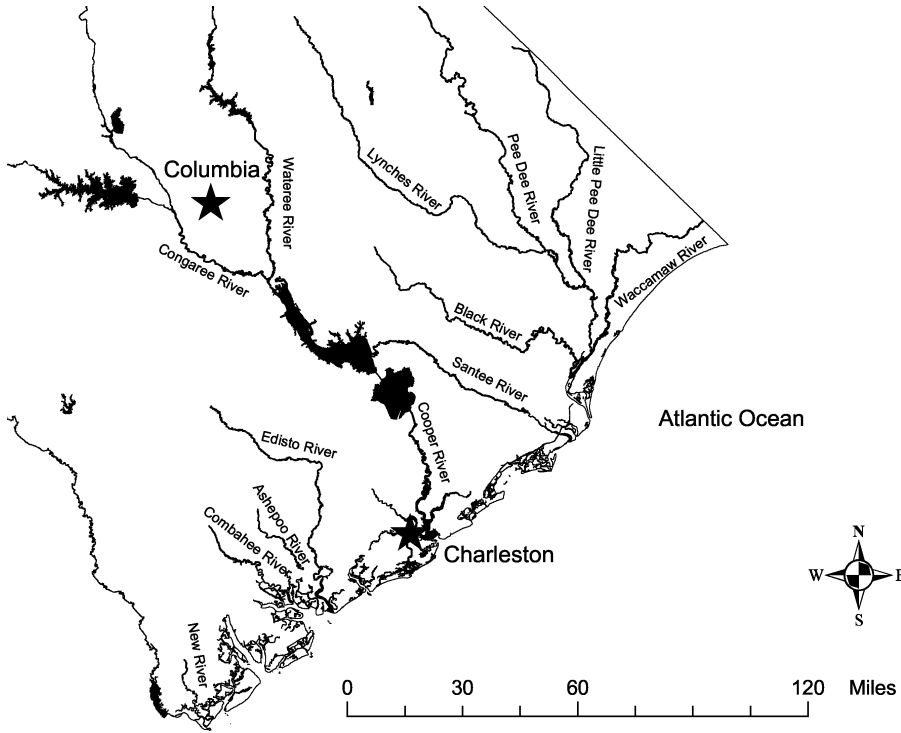


FIGURE 1.—Map showing the coastal rivers of South Carolina that support indigenous populations of striped bass.

population structure through management efforts, such as stocking. Small populations generally have a lower effective population size than large populations and thus are more susceptible to change in genetic structure (Ellner and Hairston 1994). However, the potential for multiple spawning opportunities by a species with overlapping generations, such as striped bass, can help offset the effects of a low effective population size. Assess-

ing the relative contribution of stocked progeny can also help to assess the potential influence of stocked fish.

Genetic assays can define the current level of divergence and reproductive isolation among population units. Genetic assessment of population structure is dependent on there being a sufficient amount of variation at assayed loci. Initially, allozymes at enzyme-coding loci were employed to

TABLE 1.—Number, in thousands, of striped bass stocked in three coastal river systems of South Carolina, 1986–1997. All stockings used broodstock collected from the Santee–Cooper basin except in 1997, when endemic parents were used for Combahee River stocking. Fingerling (F) and advanced fingerling (A) stockings are denoted in parenthesis; CWT = coded wire tagging.

Year	Combahee River	Edisto River	Santee River	Pee Dee River
1986	16 (A)	10 (A)	120 (F) 35 (A)	0
1987	18 (A)	16 (A)	183 (F) 38 (A)	0
1988	21 (A)	8 (A)	153 (F) 32 (A)	0
1989	0	0	64 (F) 14 (A; CWT)	0
1990	10 (A; CWT)	17 (A)	34 (F) 29 (A; CWT)	0
1991	0	0	113 (F) 13 (A; CWT)	0
1992	0	0	57 (F) 8 (A; CWT)	0
1993	10 (A)	10 (A; CWT)	5 (A; CWT)	0
1994	0	23 (F)	100 (F) 35 (A)	83 (F)
1995	0	0	231 (F) 14 (A)	12 (F)
1996	0	0	5 (A)	0
1997	438 (F); 10 (A)	2 (A)	1,111 (F)	0

investigate population structure. Allozyme surveys of migratory striped bass along the Atlantic coast revealed a low amount of variation relative to other species (Otto 1975), which limited their usefulness for examining population structure (Siddell et al. 1980; Rogier et al. 1985). Dunham et al. (1989), however, found relatively high levels of allozyme variability in riverine populations of striped bass from coastal Georgia, suggesting that allozymes possess sufficient variation for one to assess population structure in nearby South Carolina. If not, other genetic assays might reveal sufficient variation. For example, mitochondrial DNA assays of Atlantic coast striped bass have been used to establish the genetic identity of the Gulf of Mexico population (Wirgin et al. 1989).

The objective of this effort was to assess whether coastal basins should be defined as distinct management units for striped bass. Genetic assays were used to assess the genetic variation among these river systems. To get a more detailed look at one of these populations, we assessed migratory patterns and census size within the Combahee River. Based on the results obtained, the relative merits of potential management actions were evaluated.

### Methods

Two tagging programs were used to assess the migration of striped bass in the coastal rivers of South Carolina. Since 1974, the Marine Division of the South Carolina Department of Natural Resources (SCDNR) has conducted a coastwide, volunteer angler tagging program. Yellow polyethylene dart tags 8.9 cm in length are distributed to anglers who volunteer to maintain a log. Each tag has a unique six-digit number, the word "reward," and a return address. Anglers record the tag number and the release and recapture locations in their logs.

In a separate effort initiated in 1993 on the Edisto, Ashepoo, Combahee, and New rivers, numbered internal anchor tags were attached to striped bass captured by electrofishing. All striped bass greater than 30 cm in total length (TL) received a uniquely numbered tag. The yellow T-bar tags were 75 mm long, possessed a return address, and indicated that a reward was available. The date and location of recaptures were obtained from anglers and subsequent electrofishing surveys. A Schnabel mark-recapture population estimate was then obtained for the Combahee River. We used the original formula of Schnabel (Ricker 1975) to

estimate the population size ( $N$ ) of striped bass larger than 30 cm TL, that is,

$$N = \sum \frac{\text{daily captures} \times \text{total marked to that day}}{\text{total recaptures}}$$

The 95% confidence interval (CI) was estimated by treating total recaptures as a Poisson variable (Ricker 1975). The time period for the estimate was from October 17, 1995, to January 22, 1997. During this period, all electrofishing was conducted within a 16-km tidal freshwater section of the river, centered at the U.S. Highway 17 bridge crossing. All electrofished striped bass that were recaptures were noted and immediately returned to the river.

The relative contribution of a hatchery stocking was also assessed. In the fall of 1990, 10,000 advanced fingerling striped bass were stocked into the Combahee River. All stocked fish were marked with coded wire tags (CWTs). From July 1991 through February 1992, the 1990 cohort was re-sampled by electrofishing. The presence or absence of a CWT was assessed in the field. To verify age and cohort, otoliths were removed from all collected striped bass. At a later date, two independent readers determined age and cohort. The percentage of the 1990 cohort that possessed CWTs was calculated.

For allozyme assessment, striped bass were collected in 1991 and 1992 from the Combahee, Edisto, Pee Dee (Winyah Bay), Congaree, and Wateree rivers. In the Combahee, Edisto, and Pee Dee rivers, sampled fish were checked for the presence of CWTs, which was indicative of stocked fish from the Santee drainage. Fish possessing a CWT were not included in allozyme analysis. The liver, muscle, eyes, and heart were immediately removed from each sampled fish and placed on dry ice to prevent enzyme degradation. Tissues were stored in a  $-20^{\circ}\text{C}$  freezer. At a later date, allozyme analysis at 43 enzyme-coding loci was performed according to procedures defined by Norgren et al. (1988). Allele frequencies at each enzyme locus were evaluated by means of horizontal starch gel electrophoresis. At polymorphic loci with sufficient variability, the  $G$ -test (Sokal and Rohlf 1969) was used to evaluate whether allele frequencies were independent of drainage.

Allele frequency differences among five coastal (Combahee, Ashepoo, Edisto, Santee, and Pee Dee rivers) and two inland populations (Congaree and Wateree rivers) were evaluated at three unlinked anonymous nuclear loci, *SB83*, *SB14*, and *SB8-2*.

TABLE 2.—Striped bass tag return data from (1) a statewide angler tagging program conducted by the the Marine Division (MD), South Carolina Department of Natural Resources (SCDNR), in 1974–1995 and (2) electrofishing surveys conducted by the Freshwater Fishery Section (FWF) of SCDNR from November 12, 1993, to October 4, 1996. The electrofishing surveys were confined to the New, Ashepoo, Edisto, and Combahee rivers and were not applicable to studies in the Pee Dee and Santee–Cooper drainages.

Location		Number	
Tagging	Return	MD	FWF
New River	New River	0	1
Combahee River	Combahee River	83	31
Ashepoo River	Ashepoo River	0	6
Edisto River	Edisto River	2	5
Santee-Cooper <sup>a</sup>	Santee–Cooper	14	
Pee Dee <sup>b</sup>	Pee Dee	35	
New River	Combahee River	1	0
Ashepoo River	Combahee River	0	1
Santee–Cooper	Pee Dee	1	
Pee Dee	Santee–Cooper	8	

<sup>a</sup> Includes the Santee and Cooper rivers and the Santee–Cooper lakes.

<sup>b</sup> Includes Winyah Bay and the Little Pee Dee, Pee Dee, Wacamaw, Sampit, and Black rivers.

Congaree and Wateree river fish were collected by electrofishing during the spawning migrations of 1992–1994. Santee River tissue samples were obtained in 1992–1994 from female broodstock used at the Jack D. Bayless Striped Bass Hatchery, St. Stephen, South Carolina. Electrofishing was used to collect striped bass during November through April 1995–1996 and 1996–1997 from the Combahee, Ashepoo, Edisto, and Pee Dee rivers. Assay procedures for the three nuclear loci were developed and fully described by Leclerc et al. (1996). At the *SB14* and *SB8-2* loci, each locus was amplified by polymerase chain reaction using locus-specific primers. The resulting product was digested with a restriction enzyme that was capable of cutting the DNA of only one of the two alleles. The *SB14* locus contains a variable *Afl* II site and the *SB8-2* locus was variable at one of two *Mnl* I sites. At the *SB83* locus, amplification was followed by simultaneous digestion with *Rsa* I and *Pst* I to identify three alleles. Hardy–Weinberg equilibrium was evaluated for each locus with the chi-square test. Allele frequency differences among the studied rivers and the three major drainages (Pee Dee, Santee, and ACE) were evaluated with the *G*-test, as provided in the program Genes in Populations designed by B. May and C. Krueger and written in C by W. Eng and E. Paul ([www.bioweb.uncc.edu/faculty/leamy/popgen/geneinp.htm](http://www.bioweb.uncc.edu/faculty/leamy/popgen/geneinp.htm)).

TABLE 3.—Tagging and recapture data used to calculate a Schnabel population estimate of striped bass in the Combahee River, South Carolina.

Date	Number captured	Number marked	Number recaptured
Oct 17, 1995	17	17	0
Nov 8, 1995	8	7	0
Nov 9, 1995	7	6	0
Nov 28, 1995	3	2	1
Nov 30, 1995	5	4	1
Dec 13, 1995	5	5	0
Dec 14, 1995	7	5	2
Feb 14, 1996	14	9	3
Apr 18, 1996	19	15	3
Apr 22, 1996	3	1	2
Oct 30, 1996	1	1	0
Dec 4, 1996	8	8	0
Dec 17, 1996	3	3	0
Jan 21, 1997	8	6	0
Jan 22, 1997	9	8	1

## Results and Discussion

The statewide volunteer tagging program indicated that the interdrainage movement of striped bass was minimal in South Carolina (Table 2). This was especially true for the ACE drainage, where not a single striped bass that was tagged and released in these rivers was recaptured from another drainage. There was some interchange (9 of 58 returns) between the more northern Santee and Pee Dee drainages, which are separated by an 8-km section of the Intracoastal Waterway. This relative proximity may explain the greater migration between these two systems. While the electrofishing survey efforts of SCDNR were confined to the ACE drainage, it is interesting that 42 of 43 returns were from the river within the drainage where tagging took place (Table 2).

The Schnabel population estimate for striped bass larger than 30 cm in the Combahee River was 406 (95% CI = 236–764). A total of 97 striped bass were tagged and 13 recaptures were recorded (Table 3). Strictly speaking, the Schnabel method requires constant population size with no recruitment or mortality during the experiment, but it is often useful even if these conditions are only approximately satisfied (Ricker 1975). We assumed identical mortality rates for marked and unmarked fish. As Bjorgo et al. (2000) had used radiotelemetry to show that striped bass primarily used the section of the river we electrofished during the winter months, we assumed that marked striped bass become randomly mixed with the unmarked fish. We did not specifically evaluate the effects of recruitment of smaller fish into the studied population, emigration of marked fish from the study

TABLE 4.—Allele frequencies at the *sIDHP-2\** locus (Shaklee et al. 1990) of striped bass populations in South Carolina rivers.

Allele	Site				
	Pee Dee	Congaree	Wateree	Combahee	Edisto
*90	0	0	0	1	0
*100	14	4	2	7	1
*108	48	38	18	48	27

zone, tag loss, or tagging mortality. However, each of these factors would have produced an overestimate of actual population size. An underestimate of population size could only have been obtained if either the catchability of the unmarked segment decreased relative to the marked segment or the marked segment's catchability increased relative to that of the unmarked segment. There were no obvious scenarios that would have produced either of these results. Thus, from a management perspective, it appeared reasonable to assume that the Combahee River supported a relatively small population of adult striped bass during the study period.

In 1990, all stocked striped bass were marked with coded wire tags. Sampling of the 1990 cohort in 1991 showed that 3 of 14 (21%) striped bass possessed CWTs, indicating that stocking had made a contribution to this cohort. From 1985 through 1994, a total of 84,875 advanced striped bass fingerlings were stocked into the Combahee River during the fall of the year (Table 1). However, despite the stocking efforts of the last decade, the Combahee striped bass population still appeared to be relatively small. Ecological constraints may limit the population size of striped bass in the Combahee River. Bjorgo et al. (2000) showed that limited summer habitat exists in Combahee River, which may restrict population size.

#### Allozyme Survey

Allozymes were largely monomorphic and provided no evidence of genetic differentiation among drainages. Approximately 120 striped bass were collected from the five study rivers for allozyme assessment. Forty-three loci were assessed and only seven were polymorphic. Only the isocitrate dehydrogenase (*sIDHP-2\**; enzyme number 1.1.1.42; IUBMB 1992) locus was sufficiently variable to allow assessment of allele frequency differences among the five study sites. At this locus, allele frequencies were not significantly different among locations (Table 4).

#### Nuclear Genetic Survey

Assays of three nuclear restriction fragment length polymorphism (RFLP) sites were attempted on a total of 788 striped bass collected from the Congaree ( $N = 329$ ), Santee ( $N = 143$ ), Wateree ( $N = 130$ ), Combahee ( $N = 109$ ), Ashepoo ( $N = 29$ ), Edisto ( $N = 22$ ), and Pee Dee rivers ( $N = 26$ ). Genotypes were not in Hardy–Weinberg equilibrium at 7 of 21 locus–river combinations. Significant ( $P < 0.05$ ) departures were found at *SB83* (Santee and Combahee rivers) and *SB14* (Congaree, Santee, and Wateree rivers). Highly significant ( $P < 0.01$ ) departures were found at *SB83* (Congaree River) and *SB8-2* (Ashepoo River). Most departures were found in samples from the rivers of the Santee drainage. Diaz et al. (1998) suggested that recent stocking of Congaree and Wateree rivers with Santee River striped bass was partly responsible for the ongoing temporal changes in genotype composition. However, more recent data indicate that even the relatively large population in the Santee–Cooper system has a small effective population size, with estimates ranging from 26 to 65 for the 1992–1994 year-classes (Diaz et al. 2000). Thus, the observed departures from Hardy–Weinberg equilibrium are probably due to differences in breeding success and the relatively small number of parents contributing to each year-class. Since striped bass are long-lived and have multiple opportunities to breed, genetic diversity and allele frequencies in the population appear to be maintained by the summation of multiple year-classes rather than a high rate of annual reproductive success.

Highly significant allele frequency differences existed among the seven rivers (Tables 5, 6). There was not a significant overall difference in allele frequencies among samples from the Ashepoo, Combahee, and Edisto rivers (Table 6). Thus, data from these samples were pooled to describe the ACE drainage. There was a significant difference among the Santee, Congaree, and Wateree river samples. However, there was not a significant allele frequency difference when all possible two-way comparisons were evaluated (Table 6). Based on this latter result, we pooled Santee, Congaree, and Wateree river data to describe the Santee drainage. There was a highly significant difference in overall allele frequencies among the pooled samples from the Santee, Pee Dee, and ACE drainages (Table 6). Because the Santee and Combahee rivers were of special interest, samples from these two rivers were compared and a highly significant

TABLE 5.—Allele (*A<sub>n</sub>*) frequencies of striped bass at three nuclear RFLP sites, *SB83*, *SB14*, and *SB8-2*; *N* denotes the number of samples.

Location	<i>SB83</i>				<i>SB14</i>			<i>SB8-2</i>		
	A1	A2	A3	<i>N</i>	A1	A2	<i>N</i>	A1	A2	<i>N</i>
Congaree River	0.56	0.14	0.30	228	0.52	0.49	265	0.41	0.59	232
Santee River	0.57	0.18	0.24	128	0.61	0.39	115	0.38	0.62	124
Wataree River	0.50	0.13	0.37	107	0.59	0.41	102	0.43	0.57	91
Combahee River	0.58	0.23	0.19	103	0.20	0.80	109	0.52	0.48	96
Ashepoo River	0.60	0.35	0.05	29	0.14	0.86	28	0.58	0.42	26
Edisto River	0.50	0.39	0.11	22	0.19	0.81	21	0.57	0.43	22
Pee Dee River	0.54	0.15	0.31	26	0.50	0.50	26	0.80	0.20	25

allele frequency difference was observed. These differences indicate that distinctive reproductive populations are found in the major drainages of South Carolina.

For the nuclear RFLP assay, striped bass collected from the Combahee, Ashepoo, and Edisto rivers were generally screened for CWTs indicating that they were hatchery-stocked fish from the

Santee drainage. However, stocked fish were not tagged in 1990 on the Edisto River, in 1993 on the Combahee River, and in 1994–1995 on the Pee Dee River (Table 1). Thus, the possibility exists that some hatchery fish from the Santee drainage were present in samples obtained from the Combahee, Ashepoo, Edisto, and Pee Dee rivers. If so, the contribution was not large enough to mask allele frequency differences between drainages, especially the Santee and ACE drainages (Table 6).

Stocking of hatchery-reared fish to augment population size is a core tool of fishery managers. In recent decades, concern has been raised that stocking can negatively affect population fitness by the introgression of deleterious alleles into the receiving population. Purposely mixing (e.g., stocking) distinct populations can decrease the fitness of a locally adapted population through ecological (e.g., competition and disease) or direct genetic effects (e.g., hybridization and introgression; Waples 1991). On the other hand, a no-stocking policy removes a population augmentation tool from fishery managers and has genetic risks of its own since significant decreases in population size can result in a loss of genetic variation (Allendorf 1986). Thus, managers have had to weigh the genetic risks of a particular stocking program against the possible benefits of population augmentation.

The risk of enhancing a population with hatchery-produced fish and subsequently producing a negative genetic effect is variable and dependent on a number of factors. An examination of case studies reveals that stocking effects can range from minimal to severe. For example, Heggenes et al. (2002) found that a 40-year stocking program had a minimal effect on wild brown trout *Salmo trutta* in an Alpine lake. Koskinen et al. (2002) found clear genetic imprints of a stocking program on a population of the endangered Arctic grayling *Thymallus thymallus* yet suggested that there was minimal disruption of the evolutionary relationship

TABLE 6.—*G*-test evaluations of striped bass allele frequency differences among locations (CG = Congaree River, S = Santee River, W = Wataree River, CB = Combahee River, A = Ashepoo River, E = Edisto River, and PD = Pee Dee River) at three nuclear RFLP sites. The Congaree, Wataree, and Santee rivers are in the Santee drainage (SANTEE), the Ashepoo, Combahee, and Edisto rivers are in the ACE drainage (ACE), and the Pee Dee River is in the Pee Dee drainage (PD). Sidak's multiplicative inequality value was used when testing the significance of the *G*-value at all the three sites; *P* < 0.05\*, *P* < 0.01\*\*.

Locations	RFLP site			All 3 sites
	<i>SB83</i>	<i>SB14</i>	<i>SB8-2</i>	
<b>River comparisons</b>				
CG vs. S vs. W vs. CB vs. A vs. E vs. PD	**	**	**	**
S vs. CB		**	**	**
<b>Between-drainage comparisons</b>				
SANTEE vs. ACE vs. PD	**	**	**	**
SANTEE vs. ACE	**	**	**	**
SANTEE vs. PD		**	**	**
ACE vs. PD	**	**	**	**
<b>Within-drainage comparisons</b>				
SANTEE				
CG vs. S vs. W	*	*		*
CG vs. S		*		
W vs. S	**			
CG vs. W				
(CG + W) vs. S	*			
(CG + S) vs. W	*			
(S + W) vs. CG		**		
ACE				
CB vs. A vs. E	*			

within the population. In Spain, Almodovar et al. (2002) demonstrated extensive disruption of native brown trout by a long-standing stocking program. Nielsen et al. (2001) also showed extensive genetic change in a population of Atlantic salmon *Salmo salar*, though some "wild" genotypes remained. Habitat differences within a stream (Williams et al. 1997) have led to a stocking program's having differential effects within the stream. Englebrecht et al. (2002) suggested that anthropogenic disturbance is a specific factor that can influence the relative performance of hatchery and wild stocks within a stream.

In general, small populations with discrete population units are more likely to experience a reduction in effective population size (Tringali and Bert 1998) or a loss of genetic diversity (Quattro et al. 2002) than robust pelagic species with minimal population subdivision. However, Wang and Ryman (2001) demonstrated that supportive breeding programs could actually enhance effective population size when stocking increases census size. Thus, it is obvious that each stocking decision must weigh the unique characteristics of the species involved, the degree of difference between hatchery and wild stocks, and the unique habitats present at potential stocking sites.

Partially or fully isolated populations can develop beneficial adaptations to local conditions. These adaptations will, on average, improve a population's ability to survive and reproduce (i.e., lead to improved fitness) within a local habitat. During each of the years 1986–1988, 1990, and 1993, an average of 15,000 advanced striped bass fingerlings from the Santee drainage were stocked into the Combahee River, a coastal river with a relatively small census size. Nevertheless, our results obtained from 1995 to 1997 samples showed significant allele frequency differences between the Combahee and Santee samples. This suggests that there is some selective advantage for the native fish. Intentional stocking of Santee River striped bass into the Combahee River or other coastal drainages will, to some unknown degree, increase the risk of breaking down current reproductive barriers, possibly decreasing population fitness. Thus, for the immediate term, we recommended the use of endemic broodfish to augment striped bass census size within the ACE and Pee Dee coastal river drainages of South Carolina. The hatchery-stocked cohort should have an effective population size equal to or greater than that found in the receiving stream, which, according to the effective population size estimates obtained by Diaz et al. (2000),

appears to be a realistic goal. In the longer term, continued monitoring of genetic diversity and the success of stocking is needed to adaptively refine management strategies.

For the present, the level of adaptive divergence among these coastal river populations remains unknown. The differences in allele frequencies among basins may be due to genetic drift. If breeding populations are small, as they appear to be in the Combahee River, the effects of genetic drift can be rapid. On the other hand, reproductive isolation can foster the development of local adaptations within populations. Bergey et al. (2003), for example, found significant differences in striped bass egg composition that were related to watershed characteristics and thus they recommended the use of endemic fish for hatchery augmentation efforts. Additional evaluations of performance-related differences between populations are needed to determine whether adaptive traits are present among the populations analyzed in this study.

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