

ANALYSIS OF FLUCTUATING ASYMMETRY IN THREE POPULATIONS OF STRIPED
BASS

by

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ABSTRACT

Fluctuating asymmetry (FA) is commonly used to measure developmental instability and has been negatively correlated to genetic variation. Genetic variation in striped bass *Morone saxatilis* from two introduced populations, the Trinity River below Lake Livingston, Texas, and the Red River arm of Lake Texoma on the Texas-Oklahoma border, and from one naturally occurring population, the Congaree River, South Carolina, was examined using FA. Fluctuating asymmetry was measured as the difference in counts between the left and right sides of individuals for the following features: pectoral and pelvic rays, scale rows above, along, and below the lateral line, and gill rakers on the first branchial arch. All characters except scale rows below the lateral line exhibited significant differences in the median magnitude of asymmetry among the populations ($P < 0.001$ to 0.043). Although there was no consistent pattern in magnitude of asymmetry among populations, the Congaree River population had the least spread and numerically lower mean compared to the other populations. The values of FA reported here are higher than those reported for other fish species and may suggest some inbreeding.

INTRODUCTION

Striped bass is an important game fish that has been introduced into many reservoirs in the southeastern United States. Striped bass originally occurred in near-shore waters, bays, and coastal rivers along the Atlantic coast from the St. Lawrence River in Canada to the St. John's River in Florida and along the Gulf of Mexico from western Florida to Louisiana (Raney et al. 1952) or Texas (Matlock et al. 1984; Nicholson 1986). The first landlocked population of striped bass was in the Santee-Cooper system in South Carolina where fish were trapped following dam construction in 1941 (Scruggs and Fuller 1954). By 1957, the Santee-Cooper fishery drew national attention (Stevens 1957) and created interest in stocking striped bass in inland waters outside its natural range. Axon and Whitehurst (1985) reported that by 1981 striped bass fisheries were established in more than 100 lakes and reservoirs in the southeastern United States.

In Texas, striped bass were first introduced into inland waters in 1965 when the Oklahoma Department of Wildlife and Conservation (ODWC) stocked Lake Texoma on the Texas-Oklahoma border with 138 adult striped bass. Although this initial stocking apparently failed (J. Harper, ODWC, personal communication), Lake Texoma was subsequently stocked with more than 1.5 million striped bass of various sizes obtained through out-of-state sources through 1985 (ODWC, unpublished information). From 1967 through 1980, Texas Parks and Wildlife Department (TPWD) stocked 30 inland waters in Texas with approximately 13.3 million striped bass from out-of-state sources (TPWD, unpublished data). Though attempts were made to get these fish from diverse locations, the majority of striped bass used in Texas stockings came from two sources, the Santee-Cooper system and Kerr Reservoir on the Virginia-North Carolina border. With the exception of relatively small numbers of striped bass from California and Maryland, even those not directly obtained from South Carolina and Virginia represent offspring of fish from those same two sources. Although complete records were not obtained, the sources of fish for the Texoma stockings likely paralleled the Texas sources (e.g., see Mesinger 1970 and Kerby and Harrell 1990).

High individual fecundity of up to 176,000 eggs per kilogram of body weight (Lewis and Bonner 1966) coupled with limited sources of broodfish make introduced populations of striped bass vulnerable to inbreeding since hatcheries may meet production quotas with relatively few broodfish. Kerby and Harrell (1990) reported that, with few exceptions, annual stockings of striped bass fingerlings in individual east coast river systems consisted of progeny from 5 or fewer broodfish. In Texas, hatchery records indicate striped bass production is about 270,000 larvae per female (TPWD, unpubl. data). Eggs from each female are manually stripped and fertilized with milt from two males. These production numbers suggest that the entire Texas striped bass fishery could have been founded with approximately 400 broodfish, which could prevent unacceptable levels of inbreeding (Tave 1986). However, fish were distributed throughout the state over a period of years and in many locations such that individual populations were founded with much smaller numbers. Additionally, the effective population sizes likely would have been lower than founding numbers since variation in family size, unequal

contribution of male and female parents and genetic drift reduce effective population size (Tave 1986).

Annual production of striped bass in Texas relies on wild-caught fish usually collected from two sites, the Red River arm of Lake Texoma on the Texas-Oklahoma border and the Trinity River below Lake Livingston in east Texas. Lake Texoma received stockings of fry and fingerling striped bass totaling 1.6 million between 1967 and 1985 and natural reproduction was first verified in 1973 (Mauck 1991). Lake Livingston was stocked with approximately 8.3 million fry and fingerling striped bass between 1977 and 1993 and likely is the source of striped bass occurring below the dam. Natural reproduction in the Trinity River was first documented in 1988 (Kurzawski and Maddux 1991). The majority of broodfish used for striped bass production in Texas is collected in the Trinity River just below the Lake Livingston dam. Although the exact number is unknown, production data suggest that 3-21 broodfish were used to produce each cohort used to stock Lake Livingston and even fewer likely were used to produce fish for Lake Texoma. Such stocking histories suggest the potential for considerable inbreeding in these populations.

Loss of heterozygosity through inbreeding has been linked to reduced performance in a variety of traits for several fish species (Tave 1986). Kincaid (1976a, 1976b, 1983) reported that inbreeding in salmonids resulted in deleterious effects on several production characteristics including survival of eggs and young, growth, feed conversion, and body shape. Genetic variation also plays an important role in enabling a stock to adapt to different environments (Kapusinski and Jacobson 1987). Ryman (1970) reported inbred Atlantic salmon *Salmo salar* had significantly lower returns compared to non-inbred fish when stocked in natural waters and speculated that loss of genetic variation in hatchery-produced fish could lead to the failure of some restoration programs.

It has been proposed that genetic variation through heterozygosity increases an organism's ability to develop normally despite environmental variability (Lerner 1954). Fluctuating asymmetry is commonly used to measure developmental accidents (Van Valen 1962). Further, Leary et al. (1985a) suggested that FA is a useful indicator of the loss of heterozygosity in hatchery-reared fish. Fluctuating asymmetry occurs when there are differences between a character on the left and right sides of individuals, but those differences are non-directional (Van Valen 1962, Palmer and Strobeck 1986). Unlike the directional asymmetry exhibited by male fiddler crabs *Uca* spp., FA is not adaptive and results from inaccurate expression of genetically determined pathways (Graham et al. 1993). The left-right difference in a specific character usually is insignificant and may be considered as a random disruption (Ryabov and Kryshev 1990). However, increased levels of asymmetry may be associated with greater degrees of homozygosity through inbreeding. Fluctuating asymmetry has been used to measure developmental stability in salmonids (Leary et al. 1984; Alexander 1993; Wagner 1996), and is negatively correlated to fitness (Soulé 1982). Fluctuating asymmetry also has been used to evaluate environmental stress in fish (Valentine et al. 1972, Ames et al. 1979, Jagoe and Haines 1985, Ryabov and Kryshev 1990), disease effects (Escós et al. 1995), and as a monitoring and early warning tool to detect anthropogenic disturbances in natural ecosystems (Emlen et al.

1993). While FA has not been widely used to monitor inbreeding in fishes, at least two states, Wyoming and Utah, have explored evaluation programs of salmonid broodstocks that included analysis of FA (Alexander 1993; Wagner 1996).

The purpose of this study was to investigate FA in introduced populations used for striped bass production in Texas as an indirect measure of genetic diversity and to compare the Texas populations with a naturally occurring population strongly influenced by natural reproduction. The Congaree River of the Santee-Cooper system, South Carolina was chosen as a source for such a population. The Congaree River is the primary spawning tributary for the Santee-Cooper population (May and Fuller 1965, Bulak et al. 1993). It is likely the Congaree River population was founded with many more individuals than were used in hatchery introductions, although hatchery augmentation efforts were initiated there in 1984 (White 1989). Analysis of FA was selected because electrophoresis, a more conventional method to assess genetic variation, was not likely to be useful with an almost monomorphic species such as striped bass (Waldman et al. 1988).

MATERIALS AND METHODS

Adult striped bass (mean total length, 53 cm; range, 21 - 80 cm) used in hatchery spawning programs were collected by electroshocking in 1994 ($N = 52$), 1997 ($N = 38$), and 1998 ($N = 30$) from the Trinity River just below the Lake Livingston dam and in 1995 from the Red River arm of Lake Texoma ($N = 61$) and the Congaree River ($N = 26$). Males and females were examined from each population except for the Congaree River where only males were used. The following characteristics were counted on both sides of fish from each sample: pectoral rays, pelvic rays, scale rows above the lateral line, scale rows below the lateral line, scales along the lateral line, and gill rakers on the first branchial arch except for fish from the Trinity River in 1995, for which gill rakers were not counted. These meristic data were examined for the presence of FA (Mather 1953) and the mean magnitude of asymmetry per individual (absolute value of the difference between left and right character counts) and for each sample was calculated.

Since we had only males in the sample from the Congaree River, we checked for differences in magnitude of asymmetry between sexes for each character in the other populations using the Mann-Whitney test (U , Wilkinson 1998). To test for directional asymmetry and leptokurtosis, skewness (g_1) and kurtosis (g_2) of the signed asymmetry values (differences between left and right counts for each character of each group of fish) were calculated using SYSTAT (Wilkinson 1998) and tested for deviation from zero using the normal curve (Z) method in Zar (1999). Data distributions were evaluated for conformance to fluctuating asymmetry definitions (e.g., near normal distribution with a mean of zero). Distributions were tested for normality using the D'Agostino-Pearson test statistic K^2 (Zar 1999). Wilcoxon signed-rank tests with normal approximation (Z_T) were performed (Wilkinson 1998) to determine if the character counts had means of zero and to test pair-wise comparisons of right versus left character counts. Kruskal-Wallis tests (H) were performed (Wilkinson 1998) to determine if

differences in magnitude of asymmetry occurred among groups of fish. Statistical significance was set at $P \leq 0.05$ for all tests except nonparametric multiple comparisons using Dunn's method (Zar 1999), which followed the Kruskal-Wallis tests and was set at $P \leq 0.15$ (Daniel 1978).

RESULTS AND DISCUSSION

A total of 29 character-river-year comparisons were made (Table 1). Three of these combinations had count differences of zero, thus 26 character combinations remained. Only one character comparison by sex was significant; females from Lake Texoma had a higher median magnitude of asymmetry for scale rows above the lateral line ($U = 579$, $P = 0.029$, $df = 1$, $N = 61$). Leary et al. (1984, 1985a) also found no differences by sex so we pooled data for both genders.

Most character/river combination distributions exhibited some level of asymmetry characteristic of FA (Table 1). The exceptions were pelvic rays, which tended to be symmetric, except for the Trinity River sample from 1998, and gill rakers from the Congaree River. About half of the character distributions were not normally distributed ($K^2 > 5.99$, $P \leq 0.05$, $N = 22-61$). Although FA is usually described as having a normal distribution (Van Valen 1962), Jagoe and Haines (1985) suggested that asymmetric distributions would tend to be non-normal and biased toward the middle (i.e., leptokurtic) due to natural selection processes, which tend to eliminate individuals at the extremes. This contrasts somewhat with Sokal and Rohlf (1981), who define leptokurtic distributions as having more items near the mean and tails compared to a normal distribution with the same mean and variance. In the present study, 13 of the 26 character distributions were leptokurtic ($|Z_{g2}| > 1.96$, $P \leq 0.05$, $N = 22$ to 61). Seven of 26 character distributions showed significant skewness ($|Z_{g1}| > 1.96$, $P \leq 0.05$, $N = 22$ to 61), though 3 were to the left and 4 were to the right, which effectively balanced this hint of directionality. Additionally, only 3 of the 29 left-right comparisons were significant ($|Z_T| < 1.96$, $P > 0.05$, $N = 22$ to 61), substantiating a lack of directional asymmetry. Only 3 of 26 asymmetric character means did not equal zero, also a defining criterion for FA (Van Valen 1962). We conclude that the present data set substantially satisfies the criteria for FA.

All characters except scale rows below the lateral line exhibited significant differences among the populations ($H = 41.0$ to 9.8, $P < 0.001$ to 0.043, $df = 4$; Table 1). Gill rakers, followed by pectoral rays, had the greatest differences in magnitude of asymmetry between the Congaree River and other populations. Overall, the distribution of the magnitude of asymmetry for all characters combined (excluding gill rakers, which were not available for the Trinity River fish in 1994) was less dispersed for the Congaree River population than for the others (Figure 1). Additionally, the mean magnitude of asymmetry was significantly smaller for the Congaree River population than for the Trinity River population in 1994 and 1997, but not in 1998.

The levels of asymmetry described here, 2.4 to 4.2 (Figure 1), are greater than those previously described related to genetic causes. Although FA data sets may not be directly comparable due to an inextricable relationship with both the number of features measured and

the magnitude of counts for those features, trends likely are analogous. Leary et al. (1985a) reported that the mean asymmetry per individual generally ranged from 1.8 to 1.9 in both hatchery-reared and wild-ranging salmonids. Higher values of FA were observed among inbred and deformed fish; jaw and pelvic fin deformities occurred in rainbow trout *Oncorhynchus mykiss* and cutthroat trout *O. clarki* when mean magnitude of asymmetry exceeded 2.0 and an increase in deformities was associated with increasing asymmetry (Leary et al. 1984). However, Wagner (1996) reported mean asymmetry values up to 3.15 in cutthroat trout without a noted increase in the number of deformities or decrease in hatchery performance. Alexander (1993) reported FA values ranging from 1.44 to 2.24 in salmonids, also without apparent relation to deformities or performance. No obvious deformities were observed among the fish used in this study, although fishing guides have reported striped bass with missing pelvic fins from Lake Texoma (B. T. Hysmith, Texas Parks and Wildlife, personal communication).

Hubert and Alexander (1995) concluded that experimental error in counts of meristic characters limits their usefulness in assessing heterozygosity in salmonids. We used large, completely immobilized fish with easily counted characters compared to Hubert and Alexander who conducted counts on fingerling salmonids requiring the aid of a microscope. We believe that errors in counts, if they occurred, likely were essentially random, non-directional, and simply reduced our ability to detect FA differences among the striped bass populations. However, we cannot rule out the possibility that inaccurate counts adversely affected our results and interpretations.

Leary et al. (1985a) suggested the most valuable use of FA analysis would be to observe populations through time. An increase in asymmetry could indicate a loss of genetic variation in the population. According to Leary et al. (1985a), an ideal monitoring program would include examination of allele frequencies to detect the loss of genetic variation while simultaneously evaluating the effects of the loss on the population. In the present study, FA was measured at multiple points in time only in the Trinity River population, and there was no discernable trend. Although protein electrophoresis generally is not considered useful to examine genetic diversity in striped bass (Waldman et al. 1988), recently developed DNA markers (Dunham et al. 1989; Wirgin et al. 1989, 1990, 1991, and 1992; Diaz et al. 1998; Han et al. 2000; Roy et al. 2000) are proving useful and less ambiguous for examining genetic variation among and between populations of striped bass.

However, there is growing evidence that for some species, particularly those that are highly fecund and long-lived, it is not unusual for few individuals to contribute to each cohort and that this is a normal aspect of the evolutionary biology of those species (Hedgecock 1994). Indeed, this pattern of recruitment has been documented in striped bass (Secor and Houde 1995; Bulak et al. 1997). It also has been documented that, historically, the U. S. Atlantic coast of striped bass experiences "boom and bust" fluctuations in population densities (Van Winkle et al. 1979). Wirgin et al. (1990) hypothesized that periodic population bottlenecks may reduce genetic variation in individual striped bass populations. They also suggested that patterns of genetic diversity in striped bass were indicative of either fairly recent speciation or that all striped bass evolved from a single monomorphic population in the not-too-distant past. Alternatively, it

is possible that the striped bass genome tends towards fixation to a highly adapted genotype, as has been proposed for other monomorphic species (e.g., Carlson et al. 1982).

Biologists have long been aware of the dangers of inbreeding, though these concerns are not always addressed in management programs. This is evidenced by the use of relatively few broodfish, or large numbers of closely related fish, in many stocking programs. The Trinity River population has served as the primary source of striped bass broodfish for TPWD hatchery programs, followed in importance only by the Red River population. Although many fish were stocked over a number of years and each of these populations experiences some natural reproduction, each cohort likely was founded from relatively few parents. While it is probable that reproducing individuals comprise multiple cohorts, in exploited populations an overall decrease in average age diminishes the likelihood of individuals making a contribution to a cohort. Despite the considerable potential for inbreeding, FA analysis failed to identify clear differences between the two introduced populations in Texas and the naturally occurring population of striped bass from the Congaree River. It is unknown if this failure is due to maintenance of genetic variation, relatively small sample sizes, flawed counts, or fixation to an adaptive genotype. Additionally, recent genetic analysis found heterozygote deficiencies among Congaree River striped bass, suggesting this population itself might be inbred, although population admixture could also explain the deficiency (Diaz et al. 1998). While inbreeding was not clearly demonstrated herein, there were some noted differences between the Texas and South Carolina populations, with the Texas populations tending towards greater levels of asymmetry.

Although recruitment patterns and general lack of genetic diversity in striped bass populations could suggest that management programs for the propagation of striped bass mimic nature, prudent resource stewardship dictates that management programs be diligent and, in the absence of knowing which genetic characteristics are important for individual populations, strive to maintain genetic variation. It is not clear from the present study if the introduced populations of striped bass in Texas are inbred, though the somewhat higher levels of FA compared to the Congaree River population suggest higher levels of developmental instability in the Texas fisheries. Beginning in 2000, TPWD implemented a proactive management plan for the Trinity River striped bass population. Milt or male broodfish are acquired from out-of-state sources to fertilize eggs of females from the Trinity River. The resultant outcrossed offspring are stocked into Lake Livingston to help offset the potential for cumulative inbreeding and its deleterious effects in this important source of broodfish. The availability of more genetic marks, including microsatellite DNA (Han et al. 2000; Roy et al. 2000), will facilitate evaluating the efficacy of this program.

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Table 1.—Mean total count (upper number) and mean magnitude of asymmetry (lower number) for bilateral characters in five groups of striped bass. Different letters following means within a row indicate significant ($P \leq 0.05$) differences in corresponding medians (Kruskal-Wallis test).

| Character | Trinity River, Texas | | | | Red River, | Congaree River, |
|---------------------------|-----------------------------|-----------------|----------------------------|----------------|--------------------------|-----------------|
| | 1994 N = 52 | 1997 N = 38 | 1998 N = 30 | 1995 N = 61 | South Carolina N = 26 | |
| Pectoral rays | 30.5 0.56a | 29.2 0.82a | 32.2 0.50ab | 27.3 0.97a | 33.3 0.08b | |
| Pelvic rays | 10.2 0.10ab | 10.1 0.00a | 12.7 0.20b | 10.2 0.02a | 10.0 0.00a | |
| Scales above lateral line | 20.2 0.73ab | 17.9 0.82a | 20.5 ¹ 0.36b | 17.8 0.41b | 18.2 0.38b | |
| Scales below lateral line | 27.4 0.83 | 28.2 0.55 | 30.1 0.87 | 24.9 0.52 | 26.0 0.38 | |
| Scales along lateral line | 127.8 ² 2.16a | 123.3 1.74ab | 118.7 2.00a | 119.4 1.31b | 120.6 1.54ab | |
| Gill rakers | - - | 40.5 1.13a | 42.7 1.20a | 42.5 0.84a | 46.5 0.00b | |

¹N = 22

²N = 51

Figure 1. Magnitude of asymmetry, derived from scale and ray counts, for 3 populations (one sampled temporally for a total of 3 times) of striped bass (mean total length 53 cm, range 21-80 cm) sampled from the Congaree River, South Carolina, and the Red and Trinity rivers, Texas, 1994-1998. Means for each group are shown above dashed lines. Different letters indicate significant ($P \leq 0.05$) differences in corresponding means (Kruskal-Wallis test).

