Multiple population bottlenecks and DNA diversity in populations of wild striped bass, *Morone saxatilis*

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Abstract.—Striped bass, *Morone saxatilis*, in the Coos River, Oregon, are derived from natural colonists from San Francisco Bay, which in turn were intentionally transplanted from the Hudson River. Because of founder effects, this unusually well-documented colonization sequence should have resulted in diminished genetic variability in the penultimate and ultimate populations, which may have been further compounded in the Coos River population by subsequent drastic reductions in its abundance. To test whether these sequential bottlenecks reduced genetic diversity we surveyed both nuclear DNA (nDNA) and mitochondrial DNA (mtDNA) variation in the Coos River population and in both populations along the historical pathway that led to its founding. There was no evidence of reduced nDNA diversity among these populations at the three loci examined. However, the number of mtDNA haplotypes revealed decreased from 8 in the original Hudson River population, to 5 in the San Francisco Bay population, to only 1 in the Coos River population. This pattern of conserved nDNA diversity and reduced mtDNA diversity is consistent with a recent population bottleneck. Coos River striped bass have shown increasing levels of pathological hermaphroditism. We speculate that the reduced genetic diversity of the Coos River striped bass population may have led to a depensatory cascade involving hermaphroditism that inhibited reproduction and recruitment, followed by increased levels of inbreeding as the population declined.

Manuscript accepted 20 October 1997.
Fishery Bulletin 96:614–620 (1998).

Population bottlenecks are often invoked to explain lower than expected levels of genetic diversity in wild populations of fishes (e.g. Bernatchez et al., 1989; Brown et al., 1992; Richardson and Gold, 1997), but rarely is there detailed information available on the degree and duration of the bottlenecks. Striped bass (*Morone saxatilis*) offer an exception because sequentially established populations (Fig. 1) in historical times have experienced unusually well documented bottlenecks.

Striped bass were introduced to the Pacific coast at San Francisco Bay in 1879 and 1882 (Stevens et al., 1987). The two plantings totaled approximately 430 individuals (132 in 1879; approximately 300 in 1882). All were yearlings collected in the Navesink and Shrewsbury rivers, New Jersey. The Navesink and Shrewsbury rivers are minor systems that do not support reproduction by striped bass and that are located near the mouth of the Hudson River; the transplants were almost certainly part of the proximal Hudson River striped bass population. The transplanted yearlings rapidly established a population in San Francisco Bay which reproduced in its two main tributaries: the Sacramento and San Joaquin rivers. The introduction of striped bass to San Francisco Bay has been viewed as one of the few highly successful introductions of non-native fishes (Raney, 1952); within 10 years of the original introduction striped bass were available in commercial quantities in California waters.

The first striped bass captured in Oregon waters were two adults taken in Coos Bay in 1914 (Morgan and Gerlach[1]). These fish were vagrants (or less likely, the offspring of vagrants) from the San Francisco Bay population, the only possible source along the Pacific coast. Since 1914, reproducing populations of striped bass became established in Oregon in the Coos, Coquille, Umpqua, Smith, and Siuslaw estuaries. Of these, the Coos River population was the largest and most studied.

[1] Morgan, A. R., and A. R. Gerlach. 1950. Striped bass studies on Coos Bay, Oregon in 1949 and 1950. Oregon Fish Commission Contribution 14, 31 p.

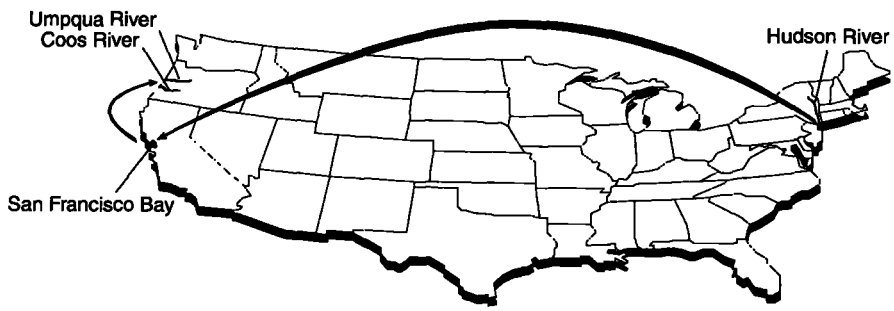

Figure 1
Colonization pathway of striped bass populations surveyed.

By the mid-1920s, striped bass were being commercially harvested in Coos Bay, and in 1945, annual landings from Coos Bay reached a high of 231,000 lb. The adult population also appeared to peak in 1945 at about 69,000 individuals (≥age-3), based on catch-per-unit-of-effort sampling. Pathological hermaphroditism was noted, but it was rare among Coos River striped bass during this period; Morgan and Gerlach[1] reported a 3% (n=124) incidence in 1950.

Since 1945, the Coos River striped bass population has crashed, whereas the incidence of hermaphroditism has increased dramatically. Between 1950 and 1975, population estimates of adults ranged from as many as 43,000 in 1963 to as few as 7800 in 1973. No adult population estimate is available for 1980, but in that year Moser et al. (1983) found 11 of 42 (26%) wild fish to be hermaphrodites. Population size of Coos River adult striped bass was not evaluated again until 1988 and 1989, when estimates of between 1000 and 3000 for both years were obtained. Estimates to date for the 1990s are of an adult population size under 1000. Furthermore, virtually no natural recruitment appears to be occurring (but supplemention is occurring through stocking of hatchery-produced offspring of San Francisco Bay broodstock). A standardized seine-haul survey of juvenile production begun in 1978 showed a decline in catch-per-unit-of-effort from 2.9 in 1978 to between 0.3 and 0.1 until 1986, and then only infinitesimal levels or zero through 1995. Recent estimates are that hermaphrodites make up 30% of the naturally produced adult population in the Coos River system (Reimers et al.[2]). Additionally, during 1993, an angling guide captured a hermaphroditic striped bass from the Umpqua River, the first reported from that system.

We hypothesized that Coos River striped bass would show reduced genetic diversity because both the history of the population's establishment and its subsequent demographics favored inbreeding. To test this hypothesis, we surveyed both nuclear DNA (nDNA) and mitochondrial DNA (mtDNA) variation in the Coos River population, the similarly non-native San Francisco Bay population (the source of the Oregon populations), and the source for the San Francisco Bay population, the Hudson River, New York. We also examined mtDNA variation in a second Oregon population (Umpqua River).

Methods

Coos River striped bass (both wild fish and fish that were originally hatchery-cultured) were captured in gill nets during spring 1993. These fish were distinguished on the basis of size; significant stocking of hatchery-cultured striped bass (age-0 only) did not begin until 1989. Only wild Oregon striped bass were used as broodstock until 1991, when broodstock from California were used. Umpqua River specimens were collected in 1992 by angling. San Francisco Bay samples were collected by means of gillnetting in the lower Sacramento and San Joaquin rivers during 1991 and 1992. Collections of striped bass from the Hudson River are described in Wirgin et al. (1990, 1993).

Total DNA was isolated from livers or blood by the CTAB method (Saghai-Maroof et al., 1984; Wirgin et al., 1990), phenol-chloroform extractions, and ethanol precipitations. To determine mtDNA haplotypes, DNAs were digested with *Acc* I, *Hind* III, and *Rsa* I, electrophoretically separated in 1.2% agarose gels, and visualized in Southern blot analyses by using ^{32}P

[2] Reimers, P. E., R. E. Bender, J. A. Johnson, T. Rumreich, D. J. Van Dyke, T. A. Confer, R. C. Smith, J. A. Hutado, and R. S. Boots. 1990. Tenmile-Coos-Coquille Fish District: a review of stocks of concern. State conservation department report, Oregon Department of Fish and Wildlife, 41 p.

Table 1

Genotypic frequencies for three single copy, nuclear DNA loci. Heterozygosity values in parentheses.

	Locus 25 *Dra* I				Locus 27 *Eco*R V				Locus 22 *Hinf* I			
Population	*N*	AA	AB	BB	*N*	AA	AB	BB	*N*	AA	AB	BB
Hudson River	35	0	11 (0.314)	24	123	6	42 (0.342)	75	80	47	24 (0.300)	9
San Francisco Bay	64	6	23 (0.359)	35	49	3	22 (0.449)	24	65	41	20 (0.308)	4
Coos River (wild)	27	1	12 (0.444)	14	32	3	14 (0.438)	15	34	11	9 (0.265)	14
Coos River (hatchery)	23	1	11 (0.478)	11	25	6	7 (0.280)	12	19	6	5 (0.263)	8

radiolabelled DNA probes (Feinberg and Vogelstein, 1983). Each of the three enzymes generates a diagnostic fragment which was used to characterize mtDNA major length-variant haplotypes (defined as differences of more than 100 base pairs; Wirgin et al., 1990). In addition, *Acc* I digestion revealed an informative, single base substitution. Probes were either highly purified mtDNA isolated from a single striped bass liver (Wirgin et al., 1990) or a gel-purified 1.7 kb PCR product containing the striped bass mtDNA control region (Wirgin et al., 1995). To determine nDNA genotypes, DNAs (10 µg) were digested with *Dra* I, *Eco*R V, and *Hinf* I, and analyzed in Southern blot analysis with the single copy probes developed from a striped bass genomic DNA library: DSB 25, DSB 27, and DSB 22, respectively (Wirgin and Maceda, 1991). Each of these enzyme-probe combinations revealed a single restriction site polymorphism with two alleles. Analysis of controlled laboratory matings demonstrated the Mendelian inheritance and nonlinkage of loci.

Genotypic frequencies derived from nDNA analysis were tested for deviations from Hardy-Weinberg equilibrium with the disequilibrium coefficient approach (Weir, 1990). Mitochondrial DNA haplotype diversity was calculated with the formula of Nei and Tajima (1981). Chi-square significance ($P<0.05$) of the differences between striped bass populations in nDNA allele frequencies and mtDNA haplotype frequencies was tested by using the randomization approach of Roff and Bentzen (1989).

Results

Nuclear DNA

Genotypic frequencies (Table 1) at two loci of samples from the Hudson River, San Francisco Bay, and Coos River (wild and hatchery) did not deviate significantly ($P>0.05$) from Hardy-Weinberg equilibrium; however, locus 22 did differ significantly from Hardy-Weinberg equilibrium for the Coos River wild ($P<0.01$) and hatchery ($P<0.05$) samples. Allelic frequencies for the three nDNA loci did not differ significantly ($P>0.05$) between the Hudson River and San Francisco Bay collections. Of the three nDNA loci, only locus 22 differed significantly in allelic frequencies between the San Francisco Bay and Coos River collections ($\chi^2=19.21$; $P<0.0001$).

Mitochondrial DNA

Mitochondrial DNA haplotypic diversity (based on mtDNA length variants) showed a clear pattern of reduction (0.810 to 0.0) among the striped bass populations along the historical path that led to and includes the wild Coos River population (Table 2). The number of mtDNA haplotypes revealed decreased from 8 among Hudson River specimens to 5 in the San Francisco Bay collection, to 2 in the Umpqua, and 1 in the wild and hatchery-cultured Coos River samples. The third most common haplotype (C-1) found in the Hudson River collection (17%) was observed in the great majority of San Francisco Bay specimens (81%) and in all Coos River specimens. Also, the three least common haplotypes in Hudson River striped bass were those absent in striped bass from San Francisco Bay. Mitochondrial DNA haplotype frequencies were significantly different between the Hudson River and San Francisco Bay samples ($\chi^2=71.47$; $P<0.0001$) and between the San Francisco Bay and Coos River samples ($\chi^2=8.21$; $P<0.05$).

Discussion

Extensive allelic surveys of Atlantic coast striped bass have shown extreme monomorphism at the pro-

Table 2

Mitochondrial DNA composite haplotype frequencies (letters represent length polymorphisms; numerals represent site polymorphisms; percentages in parentheses) and genotypic diversity indices.

Population	*N*	Haplotype								Genotypic diversity
		A-1	A-2	B-1	B-2	C-1	C-2	D-1	D-2	
Hudson River	110	3 (0.03)	2 (0.02)	25 (0.23)	7 (0.06)	19 (0.17)	32 (0.29)	17 (0.15)	5 (0.04)	0.810
San Francisco Bay	63			4 (0.06)	4 (0.06)	51 (0.81)	2 (0.03)	2 (0.03)		0.340
Coos Bay (wild)	38					38 (1.0)				0.0
Coos Bay (hatchery)	27					27 (1.0)				0.0
Umpqua River	12					11 (0.92)	1 (0.08)			0.167

tein level both within and among populations (reviewed in Waldman et al., 1988). For example, Otto (1995) reported mean heterozygosity levels of Atlantic striped bass of approximately 1.0%, and 0.75% for the Hudson River population. Very low genetic diversity for Atlantic coast striped bass has also been shown by several mtDNA studies (Chapman, 1990; Wirgin et al., 1990, 1993; Waldman and Wirgin, 1994). For example, Wirgin et al. (1990) estimated the proportion of nucleotides that differed for the most divergent individuals among mid-Atlantic striped bass stocks at 0.0004, one of the lowest values for any animal species. What mtDNA variation does exist in striped bass primarily is length, rather than site variation (Waldman and Wirgin, 1995). Four mtDNA major length variants have been found in striped bass from the Hudson River (Wirgin et al., 1990, 1993; Waldman and Wirgin, 1994).

Thus, the substrate of genetic variation available among striped bass from the Hudson River and other Atlantic coast estuaries was extremely low in comparison with most fishes (e.g. Waldman et al., 1996). From this unusually narrow gene pool some 430 or so yearlings were collected and transplanted in 1879 and 1882 to San Francisco Bay. It is not known how many of the female yearlings survived to reproduce as founders of all Pacific coast striped bass, but about 215 represents an approximate upper limit (assuming an unrealistic 100% survival rate), and 5 the lower limit, given the 5 haplotypes detected. Estimates of annual expectation of death from natural causes of the San Francisco Bay striped bass population obtained during a period of exploitation (summarized in Westin and Rogers[3]) ranged between 0.31 and 0.12, and averaged about 0.2. Moreover, female striped bass have variable maturation schedules (Berlinsky et al., 1995); in San Francisco Bay, it has been found that females mature at ages 4 and 5 (Stevens et al., 1987). Therefore, a more reasonable estimate for the number of transplanted females that survived to found the San Francisco Bay striped bass population is about 100.

Striped bass then appeared in Coos Bay some 35 years after their introduction to San Francisco Bay. It is not possible to determine the number of founders of the Oregon populations nor their initial genetic makeup. Present Oregon striped bass are restricted to mtDNA length haplotype C. It is not known what the mtDNA haplotype frequencies of the San Francisco Bay stock were circa 1915, but if their present haplotype frequencies are used as an approximation, then the chance of a single female founder having a haplotype other than the C haplotype is only 16%. We believe that given the historical scarcity of striped bass in north Pacific coastal waters (Forrester et al., 1972) and the concordance between the dominant haplotype of the San Francisco Bay stock and the single (major length variant) haplotype of the Coos River and Umpqua River stocks, it is reasonable to assume that the Oregon populations were founded by one or a very low number of female striped bass with the C-haplotype.

Founding of the Oregon striped bass populations by a limited number of females from California, following the initial bottleneck of transplantation from the Atlantic, would have resulted in a greatly reduced level of genetic variation in comparison with the

[3] Westin, D. T., and B. A. Rogers. 1978. Synopsis of biological data on the striped bass, *Morone saxatilis* (Walbaum) 1792. Technical Report 67, Graduate School of Oceanography, Univ. Rhode Island, 154 p.

Hudson River stock. However, genetic variation may have been pared further, i.e. the subsequent history of the Coos River population suggests that some of the demographic and life history factors that contribute to low levels of genetic variation among native populations of striped bass were pronounced in the Coos River population.

The Coos River population has experienced its own bottleneck; recent estimates suggest a reduction in its order of magnitude from 10^4 to 10^3 or 10^2. Fluctuating levels of annual spawning success also reduce the effective population size (N_e). Over generations N_e is approximated by the harmonic mean of each generation and strongly reflects periods of low abundance (Crow and Kimura, 1970). Many striped bass populations are sustained by occasional, extremely successful or "dominant" year classes (Raney, 1952). Dominant year classes have been rare but important for the Coos River population, occurring in 1940 and 1958 (McGie and Mullen[4]).

Other factors that may have contributed to a reduced N_e for the Coos River population are intrinsic to all populations of the species. Among these is skewed sex ratios. Males greatly outnumbered females on the Coos River spawning grounds (Morgan and Gerlach[1]). Estimates of male to female ratios on spawning grounds of other systems range from about 10:1 to 100:1 (Chapman, 1990). Another factor is variance in progeny production among females, i.e. nonrandom family size (Gall, 1987). Large female striped bass can produce on the order of 10^6 eggs per year. Because of variable environmental conditions within a spawning season, some cohorts of eggs may show low or no survival whereas other cohorts may flourish (Dey, 1981; Secor and Houde, 1995). Thus, inordinate success by a few females would cause particular genotypes to be overrepresented (Chapman, 1990).

The significant difference in allele frequencies for nDNA locus 22 between the San Francisco Bay and Coos River collections indicates either a founder effect or subsequent genetic drift. Also, the deviation from Hardy-Weinberg equilibrium of one of the three loci in the Coos River population is suggestive of small N_e or some other violation of the assumptions that lead to Hardy-Weinberg frequencies (Weir, 1990). In general, however, it appears that nDNA diversity was not strongly affected by the multiple bottlenecks that the Oregon populations experienced. In contrast, we have shown a stark decrease in mtDNA diversity. Our findings concerning nDNA and mtDNA diversity in Oregon striped bass are congruent with their having experienced a recent population bottleneck. A single breeding pair of diploid animals contains four nuclear genomes and one transmissible mtDNA; thus, a population that goes through an extreme bottleneck can lose all of its mtDNA; variability while still retaining a significant fraction of its nuclear variability (Wilson et al., 1985). A pattern of highly reduced mtDNA diversity and little altered nDNA diversity is consistent with a recent and unprolonged population bottleneck, as we hypothesize to have occurred during the establishment and history of the Coos River striped bass population.

There is an intriguing inverse relationship between genetic diversity (reflected in mtDNA) of the striped bass populations investigated and the frequency of hermaphroditism. Inbreeding depression has been firmly associated with detrimental effects in captive vertebrate populations (e.g. Kincaid, 1976, Laikre and Ryman, 1991), and recently, strong evidence of reduced fitness and reproductive impairments due to inbreeding depression in wild vertebrates has emerged (e.g. Jimenez et al., 1994; Keller et al., 1994; O'Brien, 1994).

Moser et al. (1983) investigated the phenomenon of hermaphroditism in Coos River striped bass in some detail. Protandry was suspected because young hermaphrodites had ripe, motile sperm and immature eggs, whereas older hermaphrodites (ages 7 to 10) had normal appearing eggs and only small patches of testes. Reproductive impairment of older hermaphrodites was evident. Hermaphrodites with small testes and large ovaries showed annual accretions of eggs and one or more ovarian ducts blocked by adhesions. Each egg mass, representing previous spawning seasons, became progressively more degenerated toward the interior of the gonad. Moser et al. (1983) also found that the oldest hermaphrodites had more constricted stomachs and intestines and more swollen abdomens than normal prespawning females. The four oldest hermaphrodites, 10 years old, had retained their eggs for up to 5 years. Also, it is possible that the absence of hermaphrodites among striped bass greater than 10 years of age (n=7) indicates earlier mortality of hermaphroditic individuals, perhaps as a consequence of numerous annual egg mass accretions.

We are aware of only a single observation of hermaphroditism among Atlantic coast striped bass. Westin (1978) reported one hermaphrodite among wild individuals from Chesapeake Bay that were sacrificed after being held in captivity for one year. However, in addition to surveying Coos River striped bass for evidence of hermaphroditism, Moser et al. (1983) also examined striped bass from San Francisco Bay. Of more than 500 individuals, two were hermaphrodites. Thus, hermaphroditism in striped bass appears to be exceedingly rare in native, out-

[4] McGie, A. M., and R. E. Mullen. 1979. Age, growth, and population trends of striped bass, *Morone saxatilis*, in Oregon. Oregon Department of Fish and Wildlife Information Report Series, Fisheries 79-8, 57 p.

bred populations, barely detectable in a non-native, outbred, but somewhat genetically constrained population, and pronounced in a non-native, inbred population. Moreover, the inverse association between abundance and hermaphroditism of the Coos River population suggests (but does not demonstrate) that a depensatory relationship exists because of these factors. That is, demographic influences that continued to reduce genetic diversity of the Coos River population may have promoted this pathological reproductive response, which then hindered reproduction, further reducing abundance and leading to higher levels of inbreeding.

Furthermore, no strong competing hypotheses have emerged to account for hermaphroditism of the Coos River striped bass stock. Chemical contamination is one conceivable cause. However, the Hudson River—the original source of Coos River striped bass—is a heavily polluted estuary, yet hermaphroditism has not been observed in its population. Also, the Coos River is home to American shad (*Alosa sapidissima*), similarly transplanted from the Atlantic (in 1871 to the Sacramento River; Mansueti and Kolb, 1953). In its native east coast rivers, including the Hudson River, American shad overlap with striped bass both spatially and temporally on their spawning runs. Nonetheless, whereas the Coos River striped bass population has approached extinction, its American shad population is flourishing.

It is clear that populations of striped bass in Oregon would benefit from broader genetic diversity (although there is considerable controversy concerning maintenance of non-native fish populations; e.g. Courtenay, 1995). If perpetuation of the Coos River population is desired, consideration should be given to the introduction of striped bass to Oregon waters from one or more additional Atlantic coast stocks. A combination of intention and serendipity resulted in the establishment of striped bass in California and then Oregon; however, the ultimate effect was to promulgate northern, hypothermal, nonmigratory populations from individuals originally obtained from a midlatitude, mesothermal, migratory population. There is some evidence that striped bass from northern latitudes are better adapted to the ambient environmental conditions of those latitudes (Conover, 1990). We suggest that Atlantic coast striped bass from northerly latitudes such as the Canadian Maritimes would be more preadapted to Oregon habitats.

Acknowledgments

We are grateful to Don Stevens for providing tissue samples from California striped bass and to Terry Jarmain for Umpqua River samples.

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