Abstract. – To investigate the genetic basis of stock structure of the weakfish *Cynoscion regalis*, a total of 370 individuals was collected from four geographic sites along the mid-Atlantic coast of the United States over a period of 4 years. Restriction fragment length polymorphism (RFLP) analysis of weakfish mitochondrial DNA, employing either 6 or 13 restriction endonucleases, demonstrated a low level of intraspecific mtDNA variation, with a mean nucleotide sequence divergence of 0.13% for the pooled samples. The common mtDNA genotype occurred at a frequency of 0.91–0.96 in all samples, and no significant heterogeneity was found among samples in the occurrence of the common mtDNA genotype or rare variants. The lack of spatial partitioning of rare mtDNA genotypes among collection sites suggests considerable gene flow along the mid-Atlantic coast. Together these data are consistent with the hypothesis that weakfish comprise a single gene pool, and indicate that the fishery should be managed as a single, interdependent unit.

A genetic analysis of weakfish *Cynoscion regalis* stock structure along the mid-Atlantic Coast*

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The weakfish *Cynoscion regalis* is broadly distributed along the Atlantic coast of the United States. It is common from Long Island NY to Cape Canaveral FL, and has occasionally been reported from as far north as Nova Scotia and as far south as the Gulf of Mexico (Bigelow and Schroeder 1953, Weinstein and Yerger 1976). Weakfish abundance varies considerably on both a spatial and temporal basis, especially in the northern part of the species' range (Bigelow and Schroeder 1953).

The life history of the weakfish has been well studied (reviewed in Wilk 1979). Spawning occurs in estuarine and coastal waters from late spring through early fall, with a peak of activity in late May and early June. There appears to be little offshore transport of the early-life-history stages, and young-of-the-year remain in shallow estuarine and coastal waters during their first summer. Like many fishes along the mid-Atlantic coast, weakfish move offshore to overwinter as coastal waters cool during the fall, returning in the spring when inshore temperatures increase.

The seasonal inshore and offshore movements of weakfish could lead to significant mixing of fish from different coastal areas. Tagging studies by Nesbit (1954) showed that a large proportion of weakfish tend to return to the same coastal region in which they were tagged, although many fish were recaptured in areas distant from the original tagging location. The differential size distribution of weakfish along the mid-Atlantic coast is consistent with the hypothesis that mixing of weakfish from different coastal areas occurs. Larger (older) weakfish are more predominant in northern waters during the summer, and the mean size of weakfish tends to decrease as one moves down the Atlantic coast (Wilk and Silverman 1976). Whether this represents an ontogenetic change in seasonal movements or differential survival or growth of fish from different coastal areas is not known.

Weakfish support an important commercial and recreational fishery. Commercial landings over the past 110 years have undergone dramatic fluctuations. Combined commercial and recreational landings were at a recent peak during 1980 at 36,400 metric tons (t) and subsequently dropped to about 19.1t over a period of 2 years (Vaughan et al. 1991). The total catch has remained fairly constant for the last 8 years, although a significant decline in landings from northern waters has been noted over the period (Vaughan et al. 1991). For example, the combined commercial

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and recreational catch in New York dropped from 840 t in 1982, to 224 t in 1986, to 10 t in 1990 (NMFS Current Fishery Statistics Series). The recreational catch typically represents a sizable fraction of the total landings, and at times surpasses the commercial catch (Wilk 1979).

Many weakfish are lost from the fishery as incidental bycatch in shrimp trawling operations. The incidental weakfish bycatch, which is greatest in the southern part of the species' range, consists mostly of young-of-the-year fish. It is difficult to determine the magnitude of the weakfish bycatch, but it is estimated that it exceeds the combined recreational and commercial catch in the southern states (South Carolina, Georgia and Florida) and may approach 30% of the total coastal fishery for adults (Keiser 1976, Mercer 1983, Vaughan et al. 1991).

The Fishery Management Plan for Weakfish was adopted in 1985 by the Atlantic States Marine Fisheries Commission (Mercer 1985). At that time, the genetic basis of weakfish stock structure was not well understood, and most states have independently managed their weakfish fisheries. As a result, different gear restrictions and minimum sizes are enforced along the mid-Atlantic coast. For example, Florida, Georgia, South Carolina, North Carolina, New Jersey, and Connecticut have no recreational minimum size limit, but a 9-inch size limit is enforced in Virginia, 10 inches in Maryland and Delaware, and 12 inches in New York and Rhode Island.

A thorough understanding of weakfish stock structure is essential for effective management of the fishery. Several management decisions require knowledge of the interdependence of fishery resources from different coastal areas. The recent decline in landings from northern waters has coincided with increased catches of large weakfish in the North Carolina winter offshore (sinknet) fishery (Vaughan et al. 1991), but it is not known if the two fisheries operate on the same stock of fish. On a larger geographic scale, the relationship between bycatch mortality of young weakfish in southern waters and landings of older weakfish in northern waters in subsequent years has not been determined. A detailed genetic analysis of weakfish stock structure would provide information required to test hypotheses of the independence of weakfish from different coastal areas.

Several studies have investigated weakfish stock structure employing a variety of ecological and morphological techniques including mark and recapture data (Nesbit 1954), scale circuli patterns (Perlmutter et al. 1956), morphological characters (Seguin 1960, Scoles 1990), and relative growth rates and reproductive characters (Shepherd and Grimes 1983, 1984). Most of these studies concluded that weakfish comprise two or more stocks; however, the inability to distinguish between ecophenotypic and genetic character variation in these studies has confounded interpretation of the results.

There are few studies on the biochemical genetics of the weakfish. Crawford et al. (1989) analyzed water-soluble protein variation using starch gel electrophoresis. They found no significant genetic differentiation between weakfish collected from Buzzards Bay MA to Cape Hatteras NC, and so were unable to disprove the null hypothesis that weakfish along the mid-Atlantic coast share a common gene pool. Of the 25 protein-encoding loci surveyed in the Crawford et al. (1989) study, only two were polymorphic within the pooled sample, and the mean heterozygosity was low relative to other marine fishes.

Studies of protein variation have been extremely useful in demonstrating the intraspecific genetic structure of many marine fishes (reviewed in Ryman and Utter 1987). For those species which display little intraspecific variation, like the weakfish, sample sizes must be very large to detect significant differentiation between putative stocks, if it exists. In such cases, analysis of a more rapidly evolving set of molecular characters may provide a better estimate of population structure with a more manageable number of samples. Restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA) has provided such a tool, and the technique has been useful in resolving stock structure within species which exhibit little protein variation (reviewed by Ovenden 1990).

This paper reports the results of an RFLP analysis of weakfish mtDNA to determine if fish along the mid-Atlantic coast share a common gene pool. The study began as a spatial and temporal investigation of a large number of individuals from a few collection sites along the central mid-Atlantic coast with 6 restriction endonucleases. Because there was a high degree of genetic homogeneity among these samples, we expanded the investigation to include an intensive analysis of weakfish from the northern and southern ends of the species' range with 13 restriction endonucleases.

Materials and methods

For our sampling protocol we assumed that if separate genetic stocks of weakfish exist, they should be separated at the time of spawning. We therefore restricted our collections to female weakfish that were ready to spawn as evidenced by high gonadosomatic indices (GSI). For example, the mean GSI of the New York 1988 sample was 7.7% ± 3.1 SD.

Ripe, female weakfish were obtained from commercial fishermen, sportfishing tournaments, and the

National Marine Fisheries Service Inshore Trawl Survey. Dates and locations of capture, and the size composition of the collections are presented in Table 1. Freshly-caught weakfish were measured for standard length and then dissected. Ovaries were removed and quickly frozen at −20°C.

Mitochondrial DNA was obtained by the rapid isolation procedure of Chapman and Powers (1984) for the initial survey of mtDNA genetic heterogeneity. After ethanol precipitation, the mtDNA-enriched DNA pellet was rehydrated in 75 μL of distilled water, and the yield from ~7g of ovarian tissue was usually sufficient for at least 7 restriction digestions visualized with ethidium bromide.

The 1988 and 1989 samples were surveyed with the following six restriction endonucleases: *Ava*I, *Bam*HI, *Bgl*I, *Hind*III, *Nci*I, and *Pvu*II. Restriction fragments were separated by horizontal gel electrophoresis on 0.8–1.5% agarose gels run at 2v/cm for 16h. Gels of restriction digestions of isolations containing high yields of mtDNA were visualized after ethidium bromide staining with ultraviolet light illumination (Maniatis et al. 1982) and photographed with a Polaroid CU-5 camera using a Wratten #5 filter. For those samples in which there was not sufficient mtDNA for direct visualization, restriction digestions were endlabeled before electrophoresis with the appropriate ^{35}S nucleotide triphosphate using the Klenow fragment (Maniatis et al. 1982). After electrophoresis, the gels were rinsed with a scintillation enhancer, dried, and autoradiographed at −70°C for 5d.

To compare the genetic relationship of weakfish from the northern and southern ends of their range in greater detail, mtDNA was purified from ovarian tissues using the CsCl density-gradient centrifugation protocol of Lansman et al. (1981). The mtDNA from these samples was surveyed with the 6 restriction endonucleases listed above and the following 7 enzymes: *Apa*I, *Ava*II, *Ban*I, *Bcl*I, *Eco*RV, *Hinc*II, and *Hha*I. The restriction digestions were endlabeled, separated on agarose gels, and autoradiographed as described above.

The different fragment patterns produced by each restriction endonuclease were each assigned a letter. A composite mtDNA genotype, consisting of the letters representing the fragment patterns generated by each restriction endonuclease, was then constructed for each

Table 1

Weakfish *Cynoscion regalis* collection data.

Sample	Location	Date	N	Standard length Mean, range (mm)
NY88	Long Island NY	6/88	58	560, 254–750
NY89	Long Island NY	5/89	65	619, 216–750
DE88	Lewes DE	5/88	74	597, 256–761
DE89	Lewes DE	5/89	51	521, 290–744
DE91	Lewes DE	6/91	25	522, 390–670
NC88	Hatteras NC	6/88	72	278, 221–342
SO91	SC, GA, FL	5/91	25	201, 174–273

Table 2

Distribution of weakfish *Cynoscion regalis* mtDNA genotypes based on 6 restriction endonucleases among the different collections. The order of restriction enzyme morphs, represented from left to right, is *Hind*III, *Pvu*II, *Bgl*I, *Bam*HI, *Nci*I, and *Ava*I. Fragment sizes for each restriction pattern are available from the senior author upon request.

| Genotype | Sample | | | | | | | Total |
	NY88	NY89	DE88	DE89	DE91	NC88	SO91	
AAAAAA	55	60	67	48	22	69	24	345
AAAAAC	0	2	2	0	1	1	0	6
AAAAAB	0	0	2	0	1	0	1	4
AAAAFA	1	0	0	1	0	1	0	3
AAAADA	0	2	0	1	0	0	0	3
ABAAAA	1	1	0	0	0	0	0	2
AAAABA	1	0	1	0	0	0	0	2
AAAACA	0	0	2	0	0	0	0	2
DAAAAB	0	1	0	0	0	0	0	1
AAAAEA	0	0	0	0	0	1	0	1
CAAAAA	0	0	0	0	0	1	0	1
Total	58	66	74	50	24	73	25	370

individual. The nucleon diversity (Nei 1987) was calculated for each sample and for the pooled samples. The percent nucleotide sequence divergence between mtDNA genotypes was estimated by the site approach of Nei and Li (1979) and the percent mean nucleotide sequence divergences within and among weakfish samples were calculated following the method of Nei (1987), with the latter value being corrected for within-group heterogeneity. The distribution of genotypic frequencies was evaluated for homogeneity between collections using the G-test (Sokal and Rohlf 1981).

Results

Weakfish mtDNA demonstrated very little variation. Of the 370 weakfish surveyed with 6 restriction endonucleases, 345 shared a common mtDNA genotype (Table 2). Ten variant genotypes were encountered in

the analysis, distributed among the remaining 25 individuals. In each case, variant genotypes were closely related to the common genotype, differing by no more than two restriction site changes. Restriction site gains or losses were inferred from completely additive changes in fragment patterns. No length polymorphisms or heteroplasmy were observed. A total of 43 restriction sites were detected in the 6-enzyme survey, and the average individual was scored for 29 sites, representing about 1.0% of the weakfish mtDNA genome.

The common mtDNA genotype, AAAAAA, occurred in the great majority of fish in all samples, ranging in frequency from 0.905 (DE88) to 0.960 (DE89, SO91), with a value of 0.932 for the pooled sample (Table 2). The next most-common genotype, AAAAAC, occurred in the pooled sample at a frequency of 0.017, and was present in 4 of the 7 samples. Because of the predominance of a single genotype in all samples, nucleon diversities were relatively low (Table 3), ranging from 0.079 (DE89) to 0.180 (DE88), with a value of 0.130 for the pooled samples. As all variant mtDNA genotypes were related to the common genotype by no more than 2 restriction site changes, the percent mean nucleotide diversity within each sample was also quite low (Table 3), ranging from 0.06 (DE89) to 0.18 (NY89).

Little genetic differentiation was detected among weakfish samples collected at the same location over 2 or more years (Table 4). Among samples collected in Delaware during 1988, 1989, and 1991, and in New York during 1988 and 1989, the percent mean nucleotide sequence divergences, corrected for within-sample variation (Nei 1987), ranged from 0.00 (DE88/DE91, NY88/NY89) to 0.01 (DE89/DE91).

Little genetic differentiation was encountered among samples of weakfish collected along the mid-Atlantic coast. The nucleotide sequence divergences among samples collected at geographically distant sites during the same spawning season ranged from 0.00 (NY88/NC88) to 0.03 (NY89/DE89). These values are of the same magnitude as those found among samples of weakfish collected at the same site over 2 or more years, indicating a lack of spatial genetic structuring.

An analysis of the distribution of mtDNA genotypes also revealed no significant heterogeneity among temporal or spatial collections. To avoid a bias caused by including expected values <1, we initially pooled all alternate genotypes for an analysis of heterogeneity. The results of a G-test (Sokal and Rohlf 1981) revealed no significant spatial or temporal differences in the distribution of the common and pooled rare genotypes among the 7 samples (G_H 2.88, $0.75 > p > 0.50$). Expanding the analysis to include the common genotype and all 10 rare genotypes separately (each with expected values <1 in one or more collections) did not

Table 3

Genotypic diversity and percent mean nucleotide sequence diversities for 7 weakfish *Cynoscion regalis* collections. Values for both 6 and 13 restriction enzyme surveys are listed for the Delaware (DE) 1991 and southern (SO) 1991 samples.

Sample		Nucleon diversity	Percent mean nucleotide sequence diversity
NY88		0.102	0.09
NY89		0.171	0.18
DE88		0.180	0.15
DE89		0.079	0.06
DE91	(6)	0.163	0.19
	(13)	0.239	0.10
NC88		0.107	0.11
SO91	(6)	0.080	0.09
	(13)	0.080	0.04
Total		0.130	0.13

Table 4

Percent mean nucleotide sequence divergences between weakfish *Cynoscion regalis* collections. Values are based on results from 6 restriction endonucleases and have been corrected for within-group sequence diversity (Nei 1987).

	NY89	DE88	DE89	DE91	NC88	SO91
NY88	0.00	0.00	0.00	0.01	0.00	0.00
NY89	—	0.00	0.03	0.00	0.00	0.00
DE88	—	—	0.00	0.00	0.00	0.00
DE89	—	—	—	0.01	0.02	0.00
DE91	—	—	—	—	0.00	0.00
NC88	—	—	—	—	—	0.00

significantly change the outcome. Once again, the null hypothesis of homogeneity could not be disproved (G_H 51.62, $0.50 > p > 0.25$).

The low level of variation detected in our analysis of weakfish mtDNA could be the result of many factors. After reviewing the 1988 and 1989 results, we felt that we might have biased our estimates of mean nucleotide sequence divergence by using 6 restriction endonucleases that, by chance, were not variable within weakfish. To test this hypothesis, we analyzed the DE91 and SO91 weakfish collections with an additional 7 restriction endonucleases. The average individual in the 13-enzyme analysis was scored for 65 restriction sites, or approximately 2.4% of the weakfish mtDNA molecule. Of the 49 fish in the two samples surveyed, only one variant mtDNA genotype was found (one fish from the SO91 sample with the common 6-enzyme mtDNA genotype exhibited a site gain relative to the common pattern for the enzyme *Bcl*I). As a result,

the nucleon diversity, which is sensitive to the number of enzymes employed, increased for only one of the two samples. The within-sample percent mean nucleotide sequence diversity, which is not as sensitive to the number of restriction sites surveyed, was slightly lower for both samples (Table 4), and the corrected values of percent mean nucleotide sequence divergence between the DE91 and SO91 samples was essentially the same whether based on 6 or 13 informative restriction enzymes.

Discussion

The presence of alleles unique to samples from particular geographic locations has been used to infer intraspecific genetic structuring and to determine levels of gene flow among collection sites (Slatkin 1989). This model assumes that increased frequencies of "private" alleles are a direct result of limited gene flow. An inspection of the above data reveals several genotypes that are present at very low frequencies (Table 2); however, it is interesting to note that most genotypes represented by more than a single individual occur in two or more geographic samples. For example, the genotype AAAAFA was encountered three times in the analysis of 370 weakfish, occurring in the NY88, NC88, and DE89 samples. The lack of spatial partitioning of rare alleles is strongly suggestive of a high rate of gene flow among collection locations.

The level of mtDNA variation found within the weakfish is among the lowest reported for any species of fish. While it is difficult to compare nucleon diversities from different studies because the value is dependent upon the number of restriction sites surveyed, relative levels of variability can be determined from comparisons of studies involving about the same numbers and types of restriction endonucleases. The nucleon diversity of the 1991 weakfish samples surveyed with 13 enzymes was 0.157, a value that falls well below the range of 0.473–0.998 reported by Avise et al. (1989) for other fishes analyzed with about the same number of enzymes. The nucleon diversity of the weakfish was also substantially below the mean value of 0.943 reported for the red drum *Sciaenops ocellatus* (Gold and Richardson 1991). Relatively low values of nucleon diversity have been found for the black drum *Pogonias cromis* (0.584) and the spotted seatrout *Cynoscion nebulosus* (0.531), a congener of the weakfish (C. Furman and J.R. Gold, Texas A&M Univ., College Station, pers. commun., Aug. 1991). However, these values are still substantially larger than those we found for the weakfish. Comparisons of nucleotide sequence diversities among these species also indicate that the weakfish is relatively depauperate in terms of mtDNA

variation. The mean percent nucleotide sequence diversities within 7 black drum samples (0.142) and 5 spotted seatrout samples (0.222) are substantially higher than that within the 7 weakfish samples (0.10) surveyed in this study.

The finding of relatively low levels of mtDNA variation within the weakfish is consistent with the lack of allozyme variation reported by Crawford et al. (1989). Low levels of mtDNA variation have generally been attributed to small effective population sizes of females, resulting in relatively rapid sorting of gene trees (Nei 1987, Avise et al. 1988, Chapman 1990, Bowen and Avise 1990). Variations in weakfish abundance over the last 110 years have been reflected in commercial catches, which have fluctuated from a high of 44.5 million pounds in 1908 to a low of 3.1 million pounds in 1967 (Vaughan et al. 1991), but it is unlikely that such variations over recent history have drastically reduced the effective population size of female weakfish. Population bottlenecks on a larger time-scale (e.g., glaciation events) or cyclical fluctuations in population size may have resulted in the reduced genetic diversity within the weakfish, but such explanations are merely speculative and do not necessarily agree with the observation that other sciaenids with similar distributions and life histories do not exhibit such low levels of mtDNA diversity.

Reductions in effective population size can also occur due to differential reproductive contribution, resulting from skewed sex ratios, limited mating opportunities, or varying of survival among progeny. While little is known of weakfish spawning behavior or differential recruitment success, the sex ratio tends to be very close to 1.0 (Wilk 1979). Thus, the cause or causes contributing to the low genetic variation observed among weakfish relative to other fishes is problematic.

In addition to low levels of within-sample variation, we detected little temporal or spatial genetic differentiation among weakfish samples. Because there were few variant mtDNA genotypes, and almost all of the rare variant genotypes occurred in more than one population, the uncorrected mean nucleotide sequence divergences among weakfish samples were of the same magnitude as mean nucleotide diversities found within samples. Thus, the mean difference among mtDNA genotypes randomly drawn from within a single sample was equivalent to the mean difference among mtDNA genotypes drawn from different samples.

Low levels of within-group mtDNA variation do not preclude the occurrence of significant between-group differentiation. Bowen and Avise (1990) recently reported low values of mtDNA diversity within samples of Atlantic and Gulf of Mexico black sea bass *Centropristis striata* (within-sample percent nucleotide sequence diversity of 0.03), yet their study revealed

significant differentiation between the two populations (an uncorrected percent mean sequence divergence of 0.75). The lack of significant population structuring within the weakfish relative to the black sea bass is evidenced in a comparison of the ratio of between-group to within-group sequence divergences: For the black sea bass the ratio is 24, while for the weakfish it is ~1.

The results of our investigation suggest that weakfish comprise a single genetic stock throughout the species' range. No significant genetic differentiation was found among geographic samples or among samples taken at the same site over several years. Consequently, at the level of genetic resolution we employed, we cannot disprove the null hypothesis that weakfish share a common gene pool. The inference that gene flow occurs throughout the species' range is supported by the homogeneous distribution of rare mtDNA genotypes.

The genetic homogeneity found within the weakfish in this study and in the allozyme analysis of Crawford et al. (1989) contrast with the geographical variation of morphological and life-history characters reported in other studies (Perlmutter et al. 1956, Seguin 1960, Shepherd and Grimes 1983 and 1984, Scoles 1990). The degree of plasticity of weakfish morphological and life-history characters to different environmental conditions has not been determined, but in light of research on other fishes (Barlow 1961), it would not be surprising if much of the geographic variation previously described among weakfish is ecophenotypic.

Our inference that there is sufficient gene flow among weakfish along the mid-Atlantic coast to prevent even minor genetic differentiation from occurring has several management implications. There is clearly some interdependence among areas, a conclusion also supported by the tagging data of Nesbit (1954). To obtain a meaningful estimate of the magnitude of the interdependence between these areas would require a tagging study much more extensive than that of Nesbit (1954), which would involve considerable time and expense. Until such information is available, it would be best to manage the weakfish resource conservatively, as a single interdependent stock.

Acknowledgments

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