Lack of biochemical genetic and morphometric evidence for discrete stocks of Northwest Atlantic herring *Clupea harengus harengus*

Susan E. Safford

U.S. Fish and Wildlife Service, P.O. Box 796 Turner's Falls, Massachusetts 01376
Present address: Graduate Center of Toxicology, 204 Funkhouser Building
    University of Kentucky, Lexington, Kentucky 40506-0054

Henry Booke

U.S. Fish and Wildlife Service, P.O. Box 796, Turner's Falls, Massachusetts 01376

Historically, herring stock delineation has been based on spawning site because herring are presumed to return to their natal beds to spawn (Sindermann 1979). For example, Wheeler and Winters (1984) have estimated homing fidelity of spawning herring at 90%. Furthermore, some recognition of these historic stocks has been achieved through meristic studies (Anthony 1972, Parsons 1975, Cote et al. 1980), though these meristic differences disappear after several years, probably from environmental perturbations (Sindermann 1979). These means of defining a stock imply genetic differentiation, but do not measure it. A valid stock definition such as that in Booke (1981), "a species group, or population, of fish that maintains and sustains itself over time in a definable area," should include both genetic and geographic isolation. However, for managerial purposes it is often useful to divide large groups of a species into smaller groups, even if genetic or permanent geographic isolation cannot be demonstrated. Managerial units have sometimes been defined as stocks as in Anthony (1972), "a group of fish that remain sufficiently isolated so it can be managed as a unit separate from another one." A population can subdivide itself into discrete groups, which can be individually managed during the period of subdivision, such as a spawning season, even if these groups aren't genetically differentiated. Therefore, the goal of this study was to determine if the two spawning groups investigated constitute genetically differentiated stocks, and whether these groups could be identified either genotypically or phenotypically, regardless of stock status, outside the spawning grounds.

The first objective was to determine if herring which spawn in two geographically well-defined areas—Trinity Ledge, Nova Scotia, and Jeffries' Ledge, MA—constituted separate stocks through the demonstration of genetic differentiation by starch gel electrophoresis of enzymes. Electrophoretic studies on herring, including specimens from the two spawning grounds sampled in the present study, have been published (Kornfield et al. 1981 and 1982, Grant 1981 and 1984, King 1984). However, lack of standardization in technique, which has led to differences in the number and frequency of alleles at the same locus in different studies, makes it difficult to assess the true amount of electrophoretic differentiation among spawning groups. The second objective was to determine if these same groups of herring were separable phenotypically, whether or not genetic differences were detected. Included in this objective was the assessment of the temporal stability of a set of phenotypic characters measured over two years. This was important, as most morphometric and meristic studies which have indicated that significant phenotypic differences do exist between spawning groups of herring consist of only one year's data (Parsons 1975, Cote et al. 1980, Meng and Stocker 1984). The third and most important objective was to simultaneously measure the amount of electrophoretic and morphometric variation in the two spawning groups. Simultaneous performance of both kinds of analyses, previously done only by Ryman et al. (1984) on Northeast Atlantic herring, permits a better understanding of the level of variation between herring spawning groups.
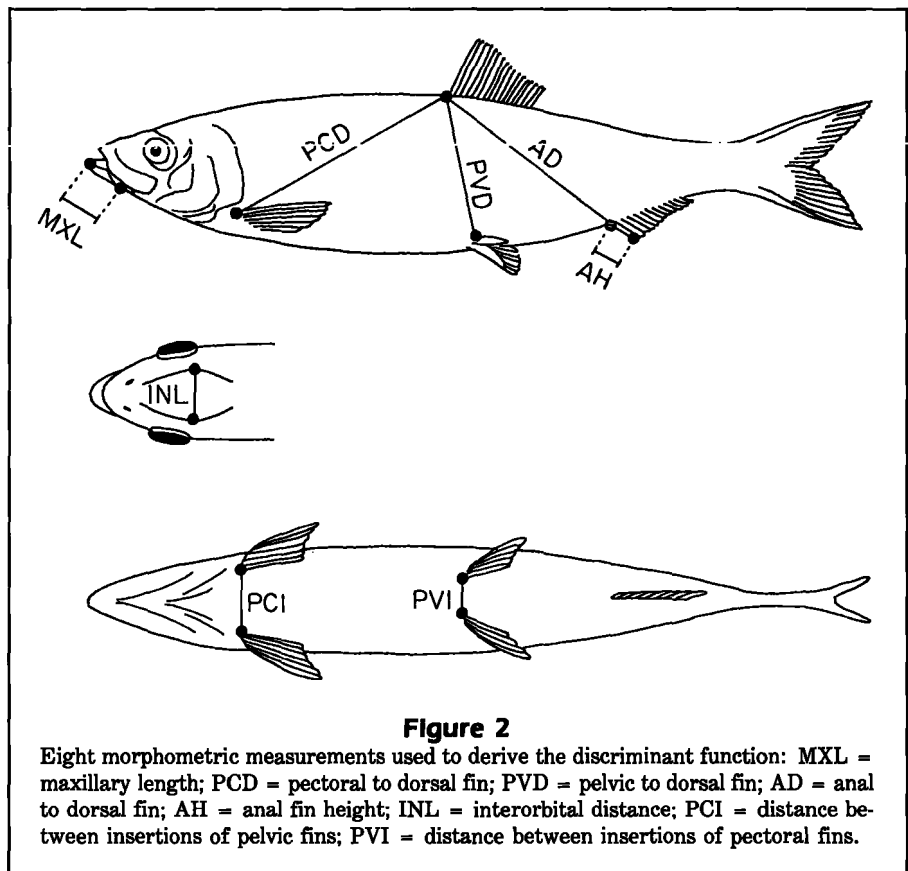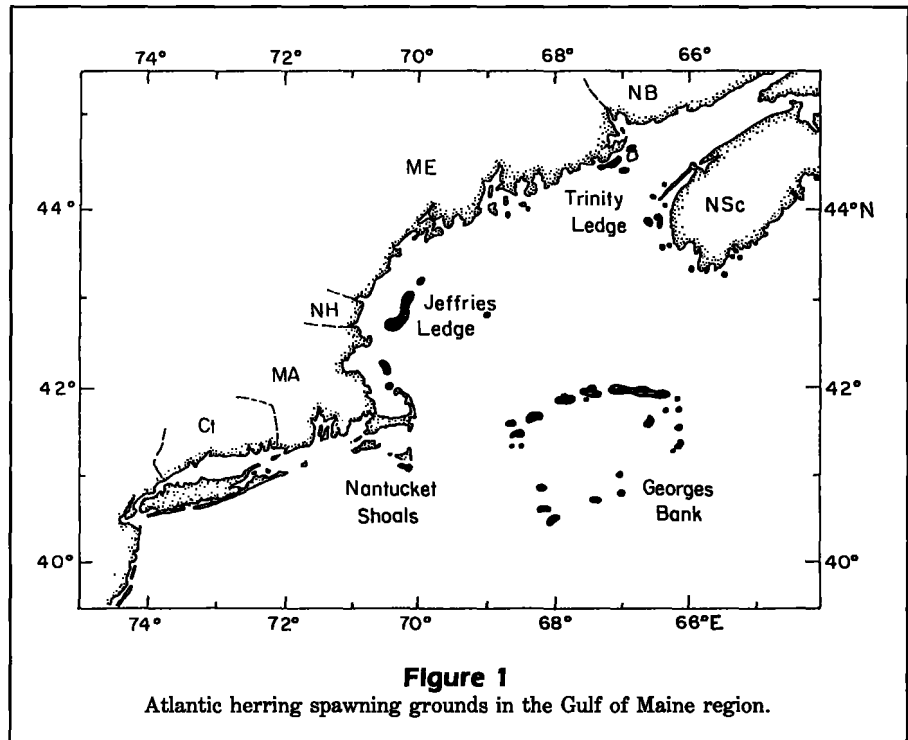
Materials and methods

Sampling

Trinity Ledge (TL) fish were collected on 31 August 1983 and 5 September 1984, and Jeffries' Ledge (JL) fish on 1 November 1983 and 11 October 1984. All fish were taken on spawning grounds (Fig. 1) by commercial fishermen. The fish were transported frozen or packed in ice, and stored at $-20°C$ for 1 week to 9 months until white muscle tissue samples were excised. The tissue samples were stored at $-80°C$ until analyzed electrophoretically. A sample of 100 fish from each collection (400 total) was analyzed electrophoretically. These same fish were also analyzed morphometrically, except for 50 TL fish collected in 1983. Poor packing conditions made these 50 fish difficult

to measure accurately, so an additional 50 herring were taken from the remaining TL 1983 sample for the morphometric analysis.

Morphometrics

Measurements Initially, 25 morphometric characters described by Meng and Stocker (1984) in their analysis of Pacific herring were measured on 100 Atlantic herring, 50 from each location, from the 1983 sample. The measurements followed Hubbs and Lagler (1958). Standard length (SL) was measured to the nearest 0.5mm on a measuring board. The other measurements were taken with vernier calipers to the nearest thousandth of an inch and converted to millimeters. Multivariate analyses were used to determine if the groups were different from one another and which characters contributed to these differences. To address length bias, multiple analysis of covariance, performed under the MANOVA subroutine in the statistical package for the social sciences, was used to remove the effect of SL on the other variables (Sokal and Rohlf 1969, Steel and Torrie 1980). The results of multiple analysis of variance of the adjusted measurements versus spawning group, performed under the same subroutine, showed that the two groups were significantly different from each other and identified eight characters whose means were significantly different (Snedecor and Cochran 1967, Safford 1985) (Fig. 2). The binomial distribution predicted the probability of eight significant characters out of 25 as 1.77 $\times 10^{-5}$, given a probability of 0.05 that a single character would be significantly different due to chance alone.

Figure 1

Atlantic herring spawning grounds in the Gulf of Maine region.

Figure 2

Eight morphometric measurements used to derive the discriminant function: MXL = maxillary length; PCD = pectoral to dorsal fin; PVD = pelvic to dorsal fin; AD = anal to dorsal fin; AH = anal fin height; INL = interorbital distance; PCI = distance between insertions of pelvic fins; PVI = distance between insertions of pectoral fins.

Discriminant function   These eight characters were used to derive a discriminant function (Snedecor and Cochran 1967, Sokal and Rohlf 1969). Each measurement in subsequent samples was adjusted to the SL of the original sample to eliminate bias due to differences in the SL. Details of the construct of the discriminant function and the formulae used to adjust the subsequent measures can be found in Appendix A and Safford (1985).

The discriminant function was tested for spatial and temporal stability with additional samples from both 1983 and 1984. The additional sample data were treated as described in Appendix A to yield a z-score so the fish could be classified according to spawning group. The cut-off value for the z-score was set at zero, where fish with a z-score > 0 were classified as Trinity Ledge fish and those with a z-score ⩽ 0 were classified as Jeffries' Ledge fish (Norusis 1979, Safford 1985).

Statistics   A stepwise function employing the F-value of each character, ($p < 0.05$), to accept or reject a character was derived to rank the variables. The distribution of phenotypic variation was measured by a nested analysis of variance (ANOVA), with years nested within groups, generated by nested procedures using PC-SAS packaged programs (SAS 1985). One-way ANOVA generated by the general linear models procedure in PC-SAS packaged programs (SAS 1985) was used to analyze differences in morphometric measurements, both between years within a spawning group and between spawning groups within a year.

Table 1
Means (mm), unadjusted for standard length, and 95% confidence intervals of the eight morphometric characters used in the discriminant function derived from 100 Atlantic herring from the 1983 samples.

Character	Jeffries' Ledge (n 50)	Trinity Ledge (n 50)
Maxillary length (MXL)	27.90 ± 0.57	31.06 ± 0.51
Pectoral to dorsal fin (PCD)	81.46 ± 1.98	93.44 ± 1.82
Pelvic to dorsal fin (PVD)	48.41 ± 1.53	59.43 ± 1.63
Anal to dorsal fin (AD)	70.56 ± 1.88	79.62 ± 1.59
Height of anal fin (AH)	14.35 ± 0.59	13.13 ± 0.47
Interorbital distance (INL)	10.34 ± 0.31	10.10 ± 0.25
Distance between insertions of pectoral fins (PCI)	13.16 ± 0.49	17.37 ± 0.71
Distance between insertions of pelvic fins (PVI)	8.41 ± 0.31	10.63 ± 0.35
Standard length (SL)	233.50 ± 18.03	251.50 ± 14.19

Electrophoresis

Enzyme visualization   Traditional starch gel electrophoresis of white muscle tissue samples as described by Utter et al. (1974), with some modifications, was used to resolve the enzymes. A detailed description of the gel composition and running conditions can be found in Safford (1985). Four polymorphic loci—phosphoglucomutase, *PGM-2** (5.4.2.2), glucose-6-phosphate isomerase, *GPI-2** (5.3.1.9), and two of lactate dehydrogenase, *LDH-1** and *LDH-2** (1.1.1.27)—were analyzed. The enzyme abbreviations and numbers follow the suggestions of Shaklee et al. (1989). Two buffer systems, Ridgway et al. (1970) and Markert and Faulhaber (1965), were used. The Ridgway gel buffer, used for LDH and GPI, was modified by doubling the amount of Tris (Sigma Chemical Co., St. Louis) in the recipe, which raised the pH to 8.5 and made the bands more distinct. The Markert-Faulhaber buffer was used for PGM because it improved band resolution. Stain recipes and techniques followed Shaw and Prasad (1970) with modifications which are detailed in Safford (1985). Photographs were taken immediately upon staining.

Statistics   Allelic frequencies were compared between samples by chi-square contingency table analysis. Genotypic frequencies were tested for conformation to the Castle-Hardy-Weinberg (C-H-W) equilibrium with a chi-square goodness-of-fit test (Zar 1974). Gene diversity analyses were conducted according to Nei (1973), Chakraborty (1980), and Chakraborty et al. (1982).

Results

Morphometrics

Group means of eight morphometric characters were found to be significantly different ($p < 0.01$) between samples taken from the two spawning areas in 1983. No overlap in range was found within the 95% confidence interval for seven of these variables, and overlap at the eighth variable was very small (Table 1). Therefore, it was concluded for this study that 50 fish from each sample were sufficient. The stepwise discriminant function accepted the first seven of these eight variables. Multiple analysis of variance of the eight characters versus locality for the 1984 samples revealed that only three of these characters—distance between insertions of the pelvic and dorsal fins (PVD), anal fin height (AH), and distance between the insertions of the pectoral fins (PCI)— were significantly different ($p < 0.01$) between the two groups. Two of these characters, PVD and PCI, were among the three which

Table 2

Discriminant function analysis results of different Atlantic herring samples from known spawning grounds.

Sample	Number from each spawning ground classified as:		Percent from each spawning ground classified as:		Overall correct classification
	Jeffries' Ledge	Trinity Ledge	Jeffries' Ledge	Trinity Ledge	
1983 discriminant function construction sample $(N = N_1 + N_2 = 100)$					
Jeffries' Ledge $(N_1 = 50)$	44	6	88%	12%	
Trinity Ledge $(N_2 = 50)$	7	43	14%	86%	87%
1983 Sample $(N = N_1 + N_2 = 100)$					
Jeffries' Ledge $(N_1 = 50)$	38	12	76%	24%	
Trinity Ledge $(N_2 = 50)$	11	39	22%	78%	77%
1984 Sample $(N = N_1 + N_2 = 198)$					
Jeffries' Ledge $(N_1 = 99)$	92	7	93%	7%	
Trinity Ledge $(N_2 = 99)$	84	15	85%	15%	54%

Table 3

Phenotypic variation of Atlantic herring in geographic and temporal hierarchies for each of eight morphometric characters. (*)$p \leqslant$ 0.01; (+)$p \leqslant 0.001$. See Figure 2 for definitions of morphometric characters.

Source of variation: Character	Between spawning groups			Between years within a spawning group			Within samples		
	df	mean square	variance component (%)	df	mean square	variance component (%)	df	mean square	variance component (%)
MXL	1	120.3+	0.0	2	597.3+	59.0	390	4.2	41.0
AH	1	38.2*	0.7	2	29.0*	3.3	390	6.6	96.0
PCD	1	2136.1+	0.7	2	7778.3+	58.5	390	55.7	41.5
PVD	1	2655.8+	0.7	2	4483.7+	57.1	390	34.0	42.9
AD	1	1379.7	0.0	2	4475.3	53.4	390	41.9	46.6
INL	1	0.0	0.0	2	131.0+	63.6	390	0.6	36.4
PCI	1	282.3+	0.0	2	383.9+	46.5	390	4.4	53.5
PVI	1	45.8+	0.0	2	136.2+	46.3	390	1.6	53.7

accounted for most of the between-group variation in the 1983 sample. The percent correct classification by spawning group of three sets of samples (two from 1983, one from 1984) separated by the derived discriminant function is found in Table 2. Overall misclassification of fish collected in 1983 was 18%, while that of fish collected in 1984 was 46%.

The phenotypic variation of the unadjusted measurements was partitioned similarly within each morphometric character, except AH (Table 3). The partitioning of the phenotypic variation averaged across all characters is found in Table 4. None of the variation was explained by differences between spawning groups, while approximately one-half was partitioned within a spawning group between years. The remainder of the variation was within a sample. One-way ANOVA of between-year differences within a spawn-

ing group showed that within the TL group the means of all the characters, except AH ($p \leqslant 0.02$), were highly significantly different ($p \leqslant 0.0001$) between 1983 and 1984. In contrast, within the JL group three characters—distance between the insertions of the pelvic fins (PVI), AH, and PCI—were not significantly different between years. The remaining characters were significantly different ($p \leqslant .05$) between years.

Electrophoresis

Allelic frequencies within each sample for the four loci chosen for analysis are found in Table 5. Other enzyme systems were also investigated, but few specimens expressed enzyme activity at these loci (Safford 1985). We chose these loci because they had previously been shown to be polymorphic and to follow Mendelian in-

heritance in herring (Grant 1981, Kornfield et al. 1981 and 1982, King 1984). The designation of alleles is taken from Kornfield et al. (1982) and is based on direction of migration of the enzymes on the gel and their distance from the origin. *LDH** is encoded by three anodally migrating loci. The fastest locus, *LDH-3**, was present only in eye tissue and activity was found in only some of the fish, so this locus was not used in the present analysis. Each of the other two loci were represented by two alleles. *PGM** is encoded by two anodally migrating loci. The slower locus, *PGM-1**, was fixed for the same allele in all samples. The polymorphic locus, *PGM-2**, was represented by three alleles. However, the slowest allele was found in only one specimen. *GPI** is encoded by one anodally migrating locus, *GPI-2**, which was represented by five alleles in our samples.

Chi-square contingency table analysis revealed that *GPI-2** was significantly different ($p \leqslant 0.05$) between JL 1984 and both TL 1984 and JL 1983. This was probably due to a greater frequency of allele 150 in the JL 1984 sample. Its frequency was double (0.18) that found in the JL 1983 sample (0.09) and the TL 1984 sample (0.10). The chi-square goodness-of-fit test showed that the JL 1984 sample was not in C-H-W equilibrium at the *GPI-2** locus, which contained an excess of 150/−3 heterozygotes. The gene-diversity analysis results for the individual loci were similar within each locus, and revealed that more than 99% of the genetic diver-

sity was found within a single sample. A comparison between the partitioning of the average gene diversity and the average phenotypic variation is shown in Table 4. The large between-year phenotypic variation is not reflected in the between-year genetic diversity index, as <1% of the gene diversity can be explained by between-year differences within a spawning group.

Discussion

In-depth discussions of the historical construct of herring stocks and the implications of recent electrophoretic findings can be found in Jorstad and Naevdal (1981), Smith and Jamieson (1986), and Kornfield and Bogdanowicz (1987). The traditional herring stock construct has not been supported by genetic stock structure analyses as none of the electrophoretic studies, including the present one, have found a large amount of genetic differentiation (Andersson et al. 1981, Grant 1981 and 1984, Jorstad and Naevdal 1981 and 1983,

Table 4

Distribution of relative gene diversity and phenotypic variation of Atlantic herring in geographic and temporal hierarchies. Gene diversity is based on four individual or pooled samples and four polymorphic loci. Phenotypic variation is averaged over 393 individuals, four individual or pooled samples, and eight morphometric characters.

	Gene diversity			Phenotypic variation	
Source of variation	Absolute	%	df	Mean square	Variance component (%)
Between spawning groups	0.00024	0.1	1	823.28	0.09
Between years within spawning groups	0.00074	0.4	2	2289.34	48.46
Within samples	0.20138	99.5	390	18.63	51.45

Table 5

Allelic frequencies of samples of Atlantic herring.

	Loci and alleles										
	LDH-1		*LDH-2*		*PGM-2*			*GPI-2*				
Location/Year	*100	0	100	72	112	100	95	150	100	40	−3	−75
Jeffries' Ledge (*N*)												
1983 (100)	0.980	0.020	0.955	0.045	0.025	0.975	0	0.090	0.630	0.140	0.120	0.020
1984 (100)	0.985	0.015	0.955	0.045	0.055	0.945	0	0.180	0.540	0.105	0.160	0.015
Trinity Ledge (*N*)												
1983 (100)	0.965	0.035	0.955	0.045	0.065	0.925	0.005	0.110	0.560	0.210	0.115	0.005
1984 (100)	1.000	0	0.945	0.055	0.025	0.975	0	0.100	0.630	0.120	0.130	0.020

* Allelic designations indicate direction of migration (+ anodal, − cathodal), and relative distance from origin (the farther away, the larger the number).

Kornfield et al. 1982, King 1984, Ryman et al. 1984). The conclusion that herring spawning groups are not discrete genetically-distinct stocks is further supported by the results of a recent study by Kornfield and Bogdanowicz (1987). They investigated the genetic relationships of ripe female herring from three locations, including Jeffries' Ledge and some of the 1983 Trinity Ledge samples analyzed in this study, by restriction endonuclease analysis of mitochondrial DNA (mtDNA). In other species, this technique has revealed genetic differentiation not uncovered by traditional enzyme electrophoresis (Avise et al. 1986). Kornfield and Bogdanowicz (1987) found that these spawning groups were not completely distinguished by the composite mtDNA digestion patterns generated, and no consistent geographic patterns were found for the unique composites. Therefore, they concluded that this approach also provided no evidence for the existence of genetically distinct stocks in the Gulf of Maine.

The significant departures from C-H-W equilibrium found in this and previous studies (Grant 1981, Ryman et al. 1984) may be considered contradictory to the hypothesis of the existence of a genetically homogenous herring population. However, these departures seem to be a feature of pelagic fish stocks (Smith et al. 1989). These disequilibria have been variously attributed to chance due to the low frequency of occurrence (Grant 1981, Ryman et al. 1984) and assortative mating (Smith et al. 1989). The significant departure in the present data has derived from an excess number of heterozygotes of one particular allelic combination in the JL 1984 data. One significant departure in 16 tests is slightly higher than would be expected by chance alone at the 5% probability level. An excess of heterozygotes can result from negative assortative mating; however, the data are not sufficient to support that hypothesis. Importantly, the C-H-W equilibrium applies to all generations in a population, thus significant departures may occur if sampling does not measure all generations in the same proportion in which they occur in the population. Based on SL, few immature and old fish were included, so this sample bias may have contributed to the significance level. Thus, the departure from C-H-W equilibrium is probably due to chance and perhaps some sampling bias. However, the distribution of alleles across generations within a population may warrant further investigation as disequilibrium, though explicable, is a feature of herring populations and some age-based selection may be occurring.

Although the genetic evidence argues for a single population of herring, significant phenotypic differences between spawning groups have been demonstrated (Parrish and Saville 1965, Burd 1969, Anthony 1972, Cote et al. 1980, Ryman et al. 1984). Morphometric and meristic characters, which have a complex underlying genetic structure, are believed to be greatly influenced by environmental parameters (Sindermann 1979, Ryman et al. 1984). Thus phenotypic differences may not reflect genetic differentiation, and small but detectable genetic differences may not significantly alter phenotypic characters. Differences in biochemical genetic and phenotypic variation can best be demonstrated when genetic and phenotypic analyses are performed on the same specimens. In their study, Ryman et al. (1984) screened 17 loci from herring caught in 17 locations ranging from the Gulf of Bothnia to the northeast Atlantic off Norway's western coast, and found significant allelic heterogeneity at only 4 loci. They concluded that the results resembled those of samples drawn from a single breeding population, as both the genetic diversity index and genetic distances were very small. They chose numbers of vertebrae and keeled scales as morphological characters. Morphological distances were used to construct a dendogram which differentiated herring in central Baltic fall spawning groups from a spring spawning Baltic group and the other fall spawning groups. Thus these meristic characters differed to some extent despite genetic similarities. Morphologic variation was partitioned by nested ANOVA with localities nested within larger geographic areas, and genetic variation was partitioned by genetic diversity analysis. They found over 99% of the gene diversity within a locality, compared with 50% of the phenotypic variation. Most important, <1% of the gene diversity was explained by between-geographic-group differences, while these differences explained 40% of the phenotypic variation.

The partitioning of variance in our samples was similar in many respects to that of Ryman et al. (1984). Over 99% of the genetic variance in our samples also occurred within a locality within a year, compared with approximately 50% of the morphometric variance component. However, the percent of the morphometric variance component explained by differences between spawning groups was similar for both the genetic and morphometric components (0.1%), in contrast to the large between-group morphometric variation found by Ryman et al. (1984). Results from both these studies demonstrate that most genetic diversity lies within a single locality at one point in time, further supporting the hypothesis that herring form a single panmictic population. Thus the current situation seems to be that despite the existence of discrete, defined spawning groups and apparent high homing fidelity, enough gene flow exists between spawning groups to prevent Northwest Atlantic herring from evolving into genetically distinct stocks. Alternatively, herring may have begun this process in recent geographic time, so that genetic differences have not had time to evolve. This lack of genetic differentiation also means that observed

phenotypic differences are most likely due primarily to differences in environmental conditions during development, and therefore will not be reliable indicators of stock identity. Further, if all measurable phenotypic characters are distributed similarly to those in the present study and Ryman et al. (1984), then the use of phenotypic characters to distinguish herring groups may be proscribed, as the large within-group variation would mask the subtler between-group differences.

These ideas need to be incorporated into current herring management policy. The results show that individuals from discrete spawning groups can not be reliably identified off the spawning grounds. Therefore, the contribution of each spawning group to various fisheries cannot be estimated. These results also suggest that the demise of a single spawning ground will not adversely affect the underlying genetic structure of the herring population, as few unique genes should be found exclusively within a spawning location. However, small discrete spawning grounds are apparently necessary to support a large population. Small spawning grounds may be necessary for appropriate spawning behavior or to ensure proper conditions for the larvae. Therefore, until the relationship between discrete spawning grounds and a healthy herring population is understood, management policy should include the maintenance of existing spawning grounds.

Acknowledgments

Citations

Andersson, L., N. Ryman, R. Rosenberg, and G. Stahl
    1981 Genetic variability in Atlantic herring (*Clupea harengus harengus*): Description of protein loci and population data. Hereditas 95:69–73.
Anthony, V.
    1972 Population dynamics of the Atlantic herring in the Gulf of Maine. Ph.D. diss., Univ. Wash., Seattle, 266 p.
Avise, J.C., G.S. Helfman, N.C. Saunders, and L.S. Hales
    1986 Mitochondrial DNA differentiation in North Atlantic eels: Population consequences of an unusual life history pattern. Proc. Natl. Acad. Sci. 83:4350–4354.

Booke, H.E.
    1981 The conundrum of the stock concept—Are nature and nurture definable in fishery science? Can. J. Fish. Aquat. Sci. 38:1479–1480.
Burd, A.C.
    1969 Trials with principal component analysis for herring racial studies. Int. Counc. Explor. Sea CM 1969/30, Pelagic Fish Comm., 11 p.
Chakraborty, R.
    1980 Gene-diversity analysis in nested subdivided populations. Genetics 96:721–726.
Chakraborty, R., M. Haag, N. Ryman, and G. Stahl
    1982 Hierarchical gene diversity analysis and its application to brown trout population data. Hereditas 97:17–21.
Cote, G., P. Lamoureux, J. Boulva, and G. Lacroix
    1980 Separation des populations de hareng de l'Atlantique (*Clupea harengus harengus*) de l'estuaire du Saint-Laurent et de la peninsule gaspienne. Can. J. Fish. Aquat. Sci. 37:66–71.
Grant, W.S.
    1981 Biochemical genetic variation, population structure, and evolution of Atlantic and Pacific herring. Ph.D. diss., Univ. Wash., Seattle, 135 p.
    1984 Biochemical population genetics of Atlantic herring, *Clupea harengus*. Copeia 1984(2):357–364.
Hubbs, C., and K. Lagler
    1958 Fishes of the Great Lakes region. Bull. 26, Cranbrook Inst. Sci., Bloomfield Hills, MI, 186 p.
Jorstad, K., and G. Naevdal
    1981 Significance of population genetics on management of herring stocks. Int. Counc. Explor. Sea CM 1981/4:64.
Jorstad, K.E., and G. Naevdal
    1983 Genetically distinct populations of herring. Contrib. XV Int. Cong. Genetics, New Delhi, India.
King, D.P.F.
    1984 Genetic analysis of enzyme polymorphisms in herring. Heredity 52:121–131.
Kornfield, I., and S.M. Bogdanowicz
    1987 Differentiation of mitochondrial DNA in Atlantic herring, *Clupea harengus*. Fish. Bull., U.S. 85(3):561–568.
Kornfield, I., P. Gagnon, and B. Sidell
    1981 Inheritance of allozymes in Atlantic herring. Can. J. Genet. Cytol. 23:715–720.
Kornfield, I., B. Sidell, and P. Gagnon
    1982 Stock definition in Atlantic herring: Genetic evidence for discrete fall and spring spawning populations. Can. J. Fish. Aquat. Sci. 39:1610–1621.
Markert, C.L., and I. Faulhaber
    1965 Lactate dehydrogenase patterns in fish. J. Exp. Zool. 159:319–332.
Meng, H.J., and M. Stocker
    1984 An evaluation of morphometrics and meristics for stock separation of Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 41:414–422.
Nei, M.
    1973 Analysis of gene diversity in subdivided populations. Proc. Natl. Acad. Sci. 70(12)Pt. I:3321–3323.
Norusis, M.J.
    1979 SPSS. Statistical algorithms. Release 8.0. SPSS, Inc., Chicago.
Parrish, B.B., and A. Saville
    1965 The biology of the Northeast Atlantic herring populations. Oceanogr. Mar. Biol. Annu. Rev. 3:323–373.
Parsons, L.S.
    1975 Morphometric variation in Atlantic herring from Newfoundland and adjacent waters. Int. Comm. Northwest Atl. Fish. Res. Doc. 11:73–92.

Ridgway, G.J., S.W. Sherburne, and R.P. Lewis
1970 Polymorphism in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99(1):147–151.

Ryman, N., U. Lagercrantz, I. Andersson, R. Chakraborty, and R. Rosenberg
1984 Lack of correspondence between genetic and morphological variability patterns in Atlantic herring (*Clupea harengus*). Heredity (53)3:687–704.

Safford, S.E.
1985 Stock identification through electrophoretic and morphometric analyses of two spawning populations of Northwest Atlantic herring (*Clupea harengus harengus*, Linnaeus). Master's thesis, Univ. Mass., Amherst, 111 p.

SAS
1985 SAS/STAT guide for personal computers, Version 6 Ed. SAS Inst., Inc., Cary, NC.

Shaklee, J.B., F.W. Allendorf, D.C. Morizot, and G.S. Whitt
1989 Genetic nomenclature for protein-coding loci in fish: Proposed guidelines. Trans. Am. Fish. Soc. 118:218–227.

Shaw, C.R., and R. Prasad
1970 Starch gel electrophoresis of enzymes: A compilation of recipes. Biochem. Genet. 4:297–320.

Sindermann, C.J.
1979 Status of Northwest Atlantic herring stocks of concern to the United States. Tech. Ser. Rep. 23, Sandy Hook Lab., NMFS, NOAA, Highlands, NJ, 449 p.

Smith, P.J., and A. Jamieson
1986 Stock discreteness in herrings: A conceptual revolution. Fish. Res. 4:223–234.

Smith, P.J., A.J. Birley, and A. Jamieson
1989 Electrophoretic studies and the stock concept in marine fishes. J. Fish. Biol. 35(Suppl. A):345–346.

Snedecor, G.W., and W.G. Cochran
1967 Statistical methods, 6th ed. Iowa State Univ. Press, Ames, 593 p.

Sokal. R.R., and F.J. Rohlf
1969 Biometry. W.H. Freeman, San Francisco, 776 p.

Steel, R.G.D., and J.H. Torrie
1980 Principles and procedures of statistics, biometrical approach, 2d ed. McGraw-Hill, NY.

Utter, F.M., H.O. Hodgins, and F.W. Allendorf
1974 Biochemical genetic studies of fishes: Potentialities and limitations. *In* Malins, D.C., and J.R. Sargent (eds.), Biochemical and biophysical perspectives in marine biology, Vol. 1, p. 213–238. Academic Press, NY.

Wheeler, J.P., and G.H. Winters
1984 Homing of Atlantic herring in Newfoundland waters as indicated by tagging data. Can. J. Fish. Aquat. Sci. 41: 108–117.

Zar, J.H.
1974 Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ, 620 p.

Appendix A

The values of the eight morphometric characters were linearly combined to form a single value, a z-score, which was used to classify an individual into a group (Sokal and Rohlf 1969, Norusis 1979). The general formula for a z-score is

$$Z = C1X1 + C2X2 + \ldots + CnXn + e$$

where each C is the unstandardized canonical discriminant function coefficient for each character (Norusis 1979).

The general formula used to adjust each measurement was

$$R_v = Vn - b_0 - b_i * SL$$

where R_v = adjusted measure,
V_n = original measure,
b_0 = intercept,
b_i = slope of the univariate covariance equation, with
SL = 242.5 (mean SL of original sample).