# Morphometric Variation among Spawning Groups of the Gulf of Maine–Georges Bank Herring Complex

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## Abstract

The purpose of this study was to characterize morphometric variation between the two major spawning components of Atlantic herring, *Clupea harengus*, in the Gulf of Maine–Georges Bank stock complex and to evaluate the use of morphometric differences for stock discrimination. Morphometric characters, including both traditional and truss network distances, were measured on herring from pre- and postspawning aggregations on Jeffreys Ledge (inshore Gulf of Maine) and Georges Bank. Prespawning herring were morphometrically distinct from postspawning herring on the same spawning ground, principally due to differences in abdominal size. Many truss measurements were affected by spawning condition while most of the traditional measurements were not. The Jeffreys Ledge and Georges Bank stocks could not be effectively discriminated using morphometrics based on prespawning samples due to the confounding effects of spawning condition on morphometry. Extrinsic samples of postspawning herring were classified into their respective spawning groups using discriminant analysis of morphometric characters with 88% accuracy. This study indicates that morphometric characters can be used to distinguish spawning stocks of Atlantic herring in the northwest Atlantic with moderate accuracy. However, due to the confounding effects of spawning condition, these analyses can only be accomplished on postspawning fish.

# Introduction

Atlantic herring, *Clupea harengus*, that spawn off southwest Nova Scotia, on Georges Bank and Nantucket Shoals, and in coastal waters of the Gulf of Maine have historically been recognized as distinct stocks (Anthony 1972, Stephenson and Gordon 1990, NEFSC 1998), although the discreteness of these spawning grounds remains controversial (Stephenson 1990, Safford and Booke 1992). Assessments performed by the United States prior to 1991 were specific to either Georges Bank–Nantucket Shoals (GB-NS) or the Gulf of Maine (GOM) components. Since 1991, the stock complex has been assessed as a whole, because specific spawning components cannot be distinguished from survey samples and the mixed stock fisheries (NEFSC 1992). The Gulf of Maine–Georges Bank stock complex has been defined to include Atlantic herring from the southern extent of their northwest Atlantic range to the western shore of the Bay of Fundy, including Georges Bank (NEFSC 1998). The current stock assessment assumes all individuals are part of a single highly migratory population composed of distinct spawning stocks.

Geographic patterns in fishing effort and trends in abundance make assessment and management of the stock complex difficult. The Georges Bank spawning component collapsed in the 1970s due to intense fishing by distant water fleets (Anthony and Waring 1980), but low levels of exploitation following the collapse have allowed the resource to rebuild (Stephenson and Kornfield 1990; Smith and Morse 1993; Overholtz and Friedland 2002). As most catches of herring currently occur in the inshore waters of the Gulf of Maine, this portion of the stock complex likely has a higher rate of exploitation. If it is indeed a separate stock, distinct from the Georges Bank stock, then a reduction in the abundance of this population could be masked by the continued growth and larger size of the Georges Bank population. An alternative approach that would be more sensitive to changes in components is to conduct stock assessments on individual components of the stock complex. This requires the ability to discriminate between fish from the various stocks and to be able to assign removals and survey samples to individual stocks.

A number of methods have been used to discriminate herring stocks including genetic techniques (Kornfield et al. 1982, Grant 1984, King 1984, Kornfield and Bogdanowicz 1987, Safford and Booke 1992), parasite fauna (McGladdery and Burt 1985, Chenoweth et al. 1986, Moser 1990, Stephenson 1990), tagging (Harden-Jones 1968, Wheeler and Winters 1984), and meristics and morphometrics (Anthony 1972, Parsons 1975, Meng and Stocker 1984, King 1985, Schweigert 1990, Stephenson 1990, Safford and Booke 1992), with varying degrees of success. Of these methods, meristics and morphometrics have shown the most utility for stock discrimination. Morphometric analyses can likely be accomplished more quickly than meristic analyses, especially using image analysis equipment. Speed and ease of accomplishment is essential if stock discrimination needs to be performed between several stocks at several locations and times of year, as would be necessary to characterize mixed stock fisheries.

The purpose of this study was to characterize the morphometric variation within and between Atlantic herring from the two major spawning grounds in the stock complex (Jeffreys Ledge and Georges Bank) and further, to evaluate if morphometric differences could be used to discriminate these two stocks. Additionally, the effect of spawning condition and age on morphometric characters was examined.

# Materials and Methods

## *Data*

Atlantic herring were collected in September 1998, on Jeffreys Ledge and Georges Bank from a commercial midwater trawler fishing on prespawning aggregations (all fish were ripe or running ripe). Samples were taken at the dock and catch locations were obtained from the captain of the vessel. Each sample represented a single 2- to 3-hour tow. Samples of postspawning herring (spent or resting) were obtained during the National Marine Fisheries Service (NMFS) Autumn Bottom Trawl Survey in October 1998 from stations on Jeffreys Ledge and northeastern Georges Bank. Locations at which samples were obtained are presented in Fig. 1. An additional sample of unknown spawning affinity was obtained from the winter fishery near Block Island in southern New England during January 1999.

A digital image of the sagittal view of each fish was recorded and saved. A suite of morphometric characters was measured on the two-dimensional image using image analysis software (UTHSCSA ImageTool). Thirty straight-line measurements were made, including both traditional and truss network measurements (Strauss and Bookstein 1982; Table 1, Fig. 2). Sex and developmental stage were also recorded for each fish. Otoliths were removed and imbedded in Permount resin in black plastic trays and aged whole using standard methods (Dery 1988). The sample sizes were as follows: prespawning Jeffreys Ledge, 373; prespawning Georges Bank, 416; postspawn Jeffreys Ledge, 122; postspawn Georges Bank, 103.

## *Statistical Analysis*

All variables were natural log transformed prior to analysis. Data were screened for outliers by examination of bivariate scatter plots of individual variables on total length and by examination of Studentized residuals from linear regressions of each variable on total length. Additionally, a principal component analysis (PCA) (SAS PRINCOMP, SAS Institute Inc. 1989) was run and bi-plots of the first four principal components were examined for outliers. Ten fish with grossly aberrant measurements for one or more variables were identified through these methods and excluded from further analysis.

Several data sets were assembled to examine different facets of morphometric variation within and between the two spawning groups. The

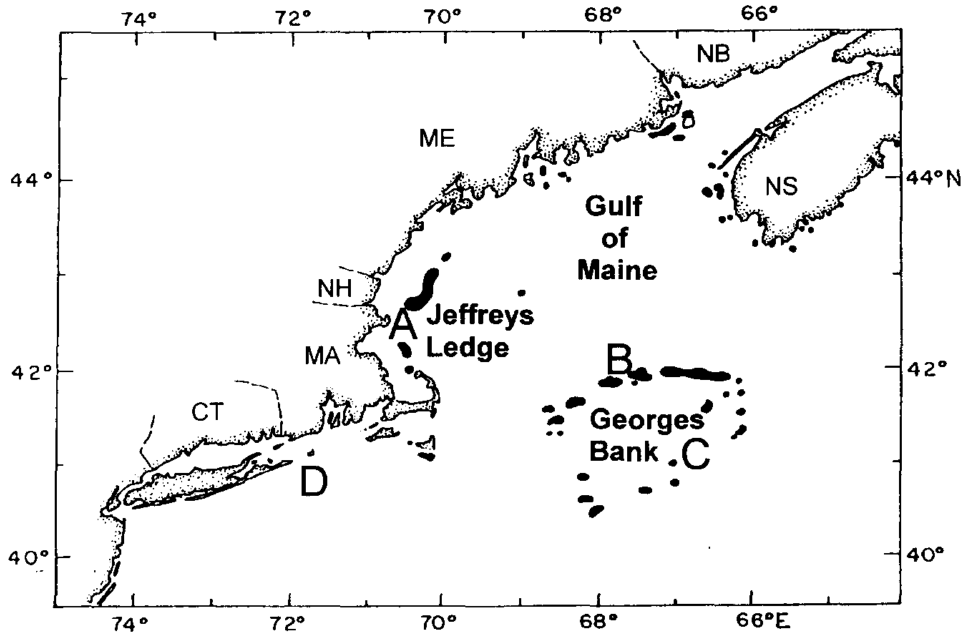


*Figure 1. Location of sampling sites and historic spawning areas. A = Jeffreys Ledge, both pre- and postspawn samples; B = Georges Bank, prespawn sample; C = Georges Bank, postspawn sample; D = sample from the winter commercial fishery, unknown spawning affinities.*

data sets were as follows: prespawning fish collected from the commercial fishery, postspawning fish collected from the NMFS Bottom Trawl Survey, postspawning fish from Georges Bank only, and pre- and postspawning fish from Jeffreys Ledge. Reduced data sets using only the most common age in all samples were also created.

Patterns of morphometric variation were initially examined using principal component analysis. Group discrimination was accomplished using discriminant analysis on size-adjusted data. The size adjustment was accomplished using multigroup principal component analysis (MGPCA; Thorpe 1988). Size components were removed from morphometric distances by setting first component scores to zero and transforming the adjusted score matrices back to the original variable space to derive size-adjusted data matrices (Burnaby 1966, Rohlf and Bookstein 1987). Discriminant analysis with equal prior probability was performed on the size-adjusted data with SAS DISCRIM using jack-knifed classification. Stepwise discriminant analysis (SAS STEPDISC) was used to select variables to use in the group discrimination. Multivariate analysis of variance (MANOVA) was used to examine shape differences among spent, resting, and immature herring in the Georges Bank postspawning sample.

**Table 1. List of morphometric characters measured (asterisk indicates characters used in the discriminant analyses).**

| Name | Description |
|---|---|
| TL | Total length |
| A* | Snout to front of eye |
| B | Snout to posterior edge of circumorbital bone |
| C | Snout to posterior of opercular bone |
| D | Snout to anterior dorsal fin |
| E* | Snout to pectoral fin |
| F* | Snout to pelvic fin |
| G | Length of pectoral fin |
| H* | Length of pelvic fin |
| I | Pectoral fin to anterior dorsal fin |
| J | Pectoral fin to pelvic fin |
| K* | Head height |
| L | Base of dorsal fin |
| M | Anterior dorsal fin to pelvic fin |
| N | Posterior dorsal fin to pelvic fin |
| O | Anterior dorsal fin to anterior anal fin |
| P* | Anterior dorsal fin to posterior anal fin |
| Q* | Caudal peduncle height |
| R | Anterior dorsal fin to dorsal peduncle |
| S* | Anterior dorsal fin to ventral peduncle |
| T | Base of anal fin |
| U* | Pelvic fin to anterior anal fin |
| V* | Pelvic fin to dorsal peduncle |
| W | Pelvic fin to ventral peduncle |
| X* | Posterior dorsal fin to anterior anal fin |
| Y | Posterior dorsal fin to posterior anal fin |
| Z* | Posterior dorsal fin to dorsal peduncle |
| AA* | Posterior dorsal fin to ventral peduncle |
| BB | Anterior anal fin to dorsal peduncle |
| CC* | Anterior anal fin to ventral peduncle |

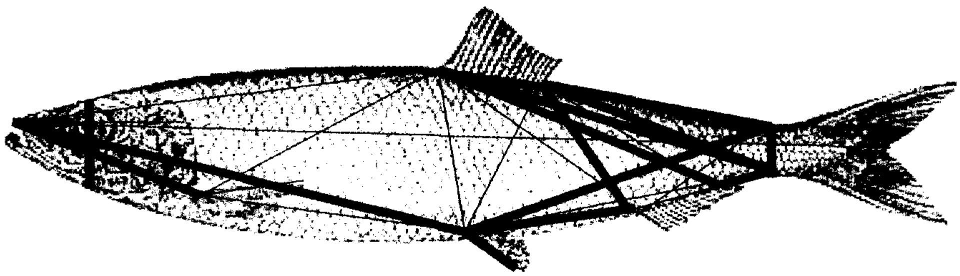

*Figure 2. Morphometric features of Atlantic herring. Bold lines indicate distances used in discriminant analysis.*

## Results

All samples were a mix of ages 3-7, but were dominated by age 4. Prespawning fish from both areas were in various stages of ripening, although the Jeffreys Ledge fish were, in general, more well developed. PCA of pre- and postspawning herring from Jeffreys Ledge showed clear separation along the second component (PC2; Fig. 3). Correlations between all variables and first principal component (PC1) scores were positive, indicating that PC1 can be interpreted as a size component (Table 2). Correlations between variables and PC2 scores were greatest for the truss measurements that captured the abdomen height (M, N). As a precaution, we eliminated M and N from further analyses because they were so greatly affected by spawning condition.

PCA of postspawning fish from Georges Bank and Jeffreys Ledge showed moderate separation along the PC1 axis (accounting for size differences between the samples) but little separation along the PC2 axis (accounting for shape variation; Fig. 4). Stepwise discriminant analysis resulted in the inclusion of 15 characters, and accurately classified 88% of extrinsic samples into their correct spawning group (Table 3). Characters important in the discrimination included E, H, K, Q, U, V, X, Z, and AA (Table 4). Inclusion of only age-4 fish decreased the classification success to 79%. A multivariate analysis of variance (MANOVA) found no significant difference between spent, resting and immature fish in the postspawn sample from Georges Bank (Wilk's Lambda = 0.0334, $P > 0.05$). All univariate comparisons between these fish were nonsignificant for all 15 characters. This analysis indicated that using postspawning fish effectively eliminated the confounding effect of differences in spawning condition.

Prespawning fish from Georges Bank and Jeffreys Ledge showed no clear separation based on PCA (Fig. 5). Discriminant analysis successfully classified 64% of individuals into their correct spawning group (Table 5). Characters important in the discrimination included E, I, P, S, U, V, AA, and CC (Table 6). Classification success did not improve when only age-4 fish were used.

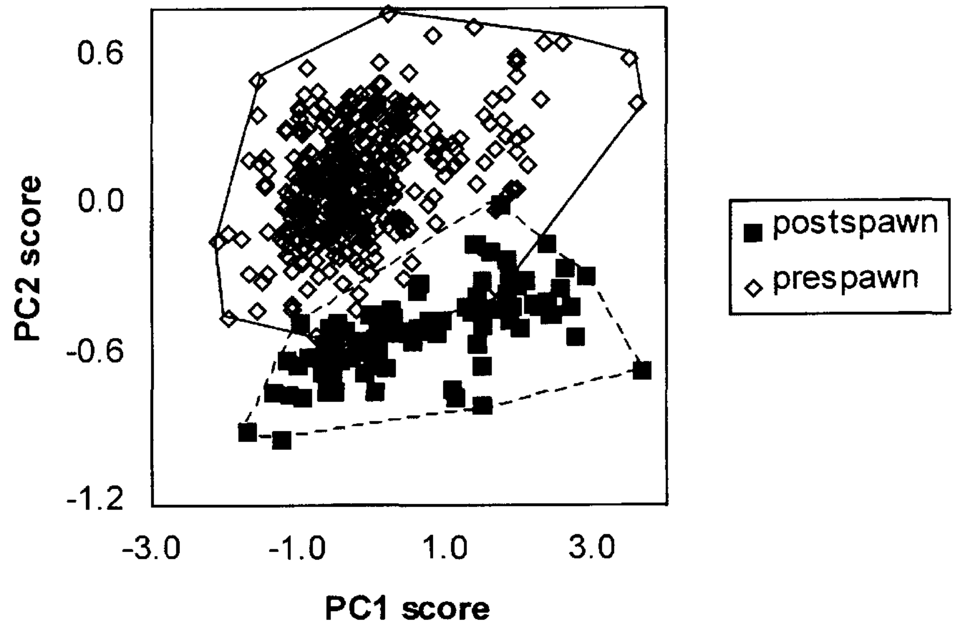


*Figure 3. PC scores of Atlantic herring from pre- and postspawning aggregations on Jeffreys Ledge.*

The sample of herring from the winter fishery in southern New England was classified using discriminant function based on the postspawning data set. The sample was classified as being 70% from the Georges Bank stock and 30% from the Jeffreys Ledge stock.

## Discussion

Atlantic herring showed clear morphometric differences between prespawning and postspawning individuals. Development of the gonads results in an expansion of the abdomen which was captured by the truss components and clearly seen in principal component or discriminant analyses. This led us to conclude that discrimination of stocks based on truss distances that measured abdominal size would be confounded by differences in spawning times. For instance, two putative stocks could be discriminated if their times of spawning, and consequently their gonadal development, were slightly different, even if these morphometric differences did not exist outside of the spawning period. Alternatively, if differences in abdomen height did exist between stocks, the difference may be hidden by the expansion due to developing gonads. This presents difficulties when trying to discriminate stocks, since spawning times are seldom synchronized among stocks. In fact, this is one characteristic that

**Table 2. Eigenvectors of the PCA using the pre- and postspawning data set from Jeffreys Ledge. Characters with high loadings are those that are most affected by spawning condition.**

| | PC1 | PC2 |
|---|---|---|
| A | 0.209 | –0.011 |
| B | 0.189 | –0.062 |
| C | 0.196 | –0.082 |
| D | 0.187 | –0.002 |
| E | 0.205 | –0.141 |
| F | 0.188 | 0.062 |
| G | 0.201 | –0.118 |
| H | 0.198 | –0.111 |
| I | 0.178 | 0.155 |
| J | 0.184 | 0.184 |
| K | 0.179 | 0.002 |
| L | 0.207 | –0.192 |
| M | 0.129 | 0.538 |
| N | 0.126 | 0.522 |
| O | 0.198 | 0.057 |
| P | 0.196 | –0.052 |
| Q | 0.178 | –0.073 |
| R | 0.192 | –0.049 |
| S | 0.193 | –0.065 |
| T | 0.192 | –0.305 |
| U | 0.191 | 0.203 |
| V | 0.172 | 0.095 |
| W | 0.188 | –0.012 |
| X | 0.178 | 0.188 |
| Y | 0.185 | 0.034 |
| Z | 0.185 | 0.019 |
| AA | 0.182 | 0.001 |
| BB | 0.165 | –0.092 |
| CC | 0.187 | –0.276 |
| Proportion of variance explained | 0.665 | 0.079 |

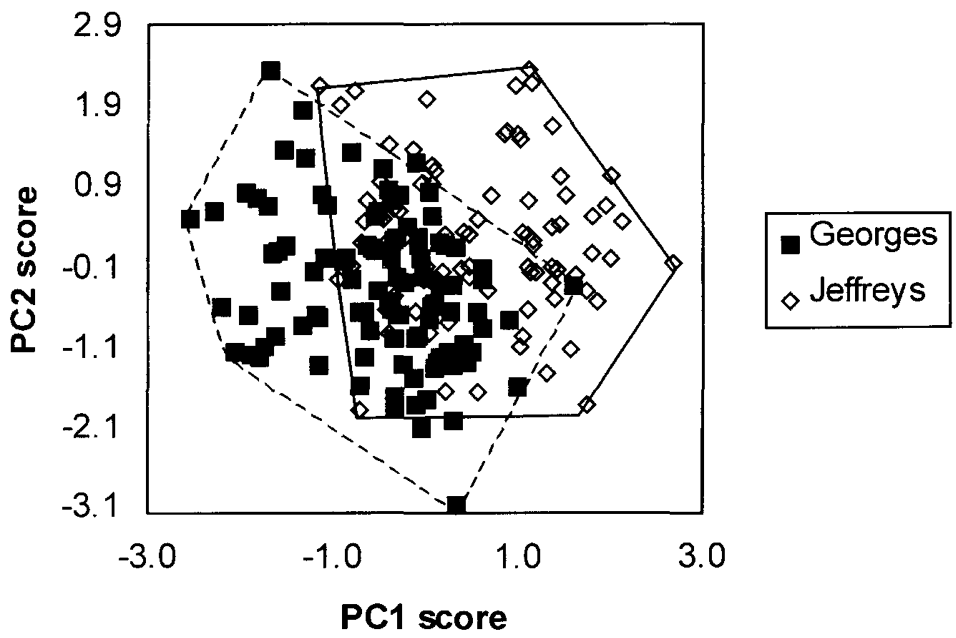


*Figure 4. PC scores of Atlantic herring from postspawning aggregations on Jeffreys Ledge and Georges Bank.*

**Table 3. Number of fish classified to spawning group as extrinsic samples and associated error rate using the size-adjusted discriminant function of the postspawning samples.**

| Sample area | Classified as Georges Bank | Classified as Jeffreys Ledge | *n* | Error rate |
|---|---|---|---|---|
| Georges Bank | 85 | 18 | 103 | 17.5% |
| Jeffreys Ledge | 10 | 112 | 122 | 8.2% |
| Overall error rate | | | | 12.4% |

**Table 4. Univariate test statistics (d.f. = 1, 787) for the 15 variables used in the discriminant analysis using the postspawning data set.**

| | *F* value | Test probability |
|---|---|---|
| A | 1.53 | 0.2177 |
| E | 120.08 | 0.0001 |
| F | 0.02 | 0.8871 |
| H | 38.44 | 0.0001 |
| I | 1.60 | 0.2067 |
| K | 5.73 | 0.0175 |
| P | 2.51 | 0.1143 |
| Q | 25.47 | 0.0001 |
| S | 1.90 | 0.1692 |
| U | 5.91 | 0.0159 |
| V | 34.78 | 0.0001 |
| X | 23.42 | 0.0001 |
| Z | 27.96 | 0.0001 |
| AA | 24.05 | 0.0001 |
| CC | 0.003 | 0.9574 |

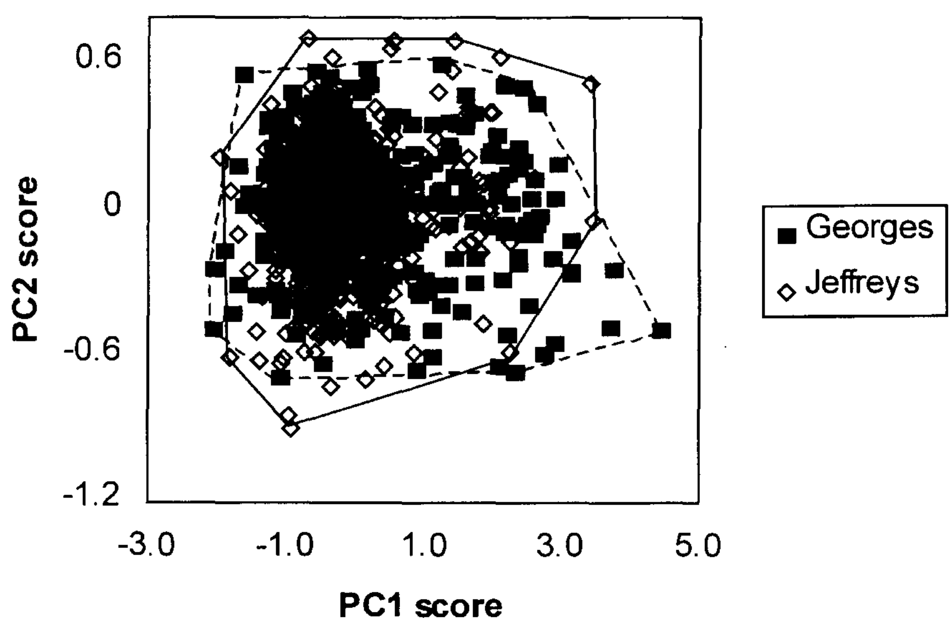


*Figure 5. PC scores of Atlantic herring from prespawning aggregations on Jeffreys Ledge and Georges Bank.*

**Table 5. Number of fish classified to spawning group as extrinsic samples and associated error rate using the size-adjusted discriminant function of the prespawning samples.**

| Sample area | Classified as Georges Bank | Classified as Jeffreys Ledge | *n* | Error rate |
|---|---|---|---|---|
| Georges Bank | 295 | 121 | 416 | 29.1% |
| Jeffreys Ledge | 166 | 207 | 373 | 44.5% |
| Overall error rate | | | | 36.4% |

**Table 6. Univariate test statistics (d.f. = 1, 787) for the 15 variables used in the discriminant analysis using the prespawning data set.**

| | *F* value | Test probability |
|---|---|---|
| A | 0.99 | 0.3209 |
| E | 22.74 | 0.0001 |
| F | 0.02 | 0.8955 |
| H | 0.01 | 0.9379 |
| I | 21.41 | 0.0001 |
| K | 8.06 | 0.0046 |
| P | 39.05 | 0.0001 |
| Q | 2.29 | 0.1309 |
| S | 10.62 | 0.0012 |
| U | 4.10 | 0.0431 |
| V | 22.99 | 0.0001 |
| X | 2.59 | 0.1081 |
| Z | 0.07 | 0.7951 |
| AA | 4.31 | 0.0383 |
| CC | 6.06 | 0.0141 |

has often been used to indicate discreteness of herring stocks. Because of the intermixing of stocks during nonspawning times, the only way to assure that individuals are members of a specific spawning group is to collect samples during spawning periods, preferably using only ripe or running ripe fish. However, these analyses show that abdominal measures from ripe herring cannot be used to discriminate stocks in a manner that will be applicable to nonspawning fish. In order to use fish in spawning condition, morphometric characters that are not affected by spawning condition must be used.

Discrimination of prespawning fish from Jeffreys Ledge and Georges Bank was poor (classification success 65%), likely because this analysis was confounded by differences in spawning condition between the two areas. Herring on Georges Bank spawn about 2-3 weeks later than the herring inshore on Jeffreys Ledge (M.P.A., unpublished data). This was evident from the samples where, even though the samples were taken only a few days apart, fish in the Jeffreys Ledge postspawn sample were all resting, while fish in the Georges Bank postspawn sample were a mix of resting and spent, indicating Jeffreys Ledge fish had completed spawning sooner, assuming no movement between areas. Although the two stocks can be discriminated based on morphometric characters as seen in the analysis with postspawn fish, the differences are confounded by the effects of spawning condition. Both Georges Bank and Jeffreys Ledge prespawn samples contained fish in various stages of ripeness. Overall, Jeffreys Ledge fish were more developed. However, because the classification was being driven by spawning condition rather than stock differences, less-developed fish from Jeffreys Ledge were classified into Georges Bank and more developed Georges Bank fish were classified as Jeffreys Ledge, resulting in low classification success.

Classification success was high using the postspawning data set. Many of the characters that showed differences between pre- and postspawners were also important in discriminating the stocks. In general, Georges Bank fish had a shorter pelvic fin (H), shorter but taller head (E and K), and a wider and longer area of the body (U, V, X, Z, AA) between the posterior edge of the dorsal to the caudal peduncle, although the peduncle itself (Q) was narrower than in Jeffreys Ledge fish. Overall, the Georges Bank fish could be described as "stockier" than the Jeffreys Ledge fish, especially in the head and caudal regions.

Using postspawned fish presents difficulties because there is less certainty that the fish are members of a specific spawning group. However, because our samples were taken shortly after spawning, this is less of a concern. It is likely that individuals from a specific spawning group maintain themselves as a school after spawning and remain in the area of spawning for at least a short time. As evidence of this, commercial purse-seine fishermen, who are prohibited by law from taking ripe and running ripe fish during the spawning season, target postspawning fish adjacent to spawning aggregations (M.P.A., personal observation). Nonetheless, it is possible that fish from other spawning groups contaminated our postspawning samples. Cross contamination between Jeffreys Ledge and Georges Bank would be less likely owing to their separation by greater than 150 miles. Any presence of herring from other spawning groups would violate our assumption that each sample comes from a single spawning group, and may have contributed to decreasing our classification success.

This study indicates that it is possible to discriminate Georges Bank spawners from Jeffreys Ledge spawners, with the caveat that the samples must be taken shortly after spawning rather than before spawning. Spawning condition greatly affects truss measurements and, unfortunately, traditional measurements that are unaffected by spawning condition such as head height, snout length, etc., show little discriminatory power by themselves.

Confining analyses to specific ages did not improve discriminatory power, suggesting that the differences between stocks maintain themselves over time and among cohorts. This will be an important consideration for future research when it may be necessary to process large numbers of fish. Simply taking morphometric measurements without removing, processing, and reading otoliths will reduce processing time.

The mix of stocks found in the sample from the winter fishery (30% Jeffreys Ledge, 70% Georges Bank) is in agreement with the relative size of these stocks (NEFSC 1998). This implies that both stocks winter in southern New England and form a well-mixed group. However, this analysis is purely exploratory. This classification does not consider that there may be fish from other spawning areas (e.g., eastern Maine, western Georges Bank, Nantucket Shoals) that may have morphologically distinct forms.

These results confirm morphological patterns in the Gulf of Maine-Georges Bank complex found by other researchers. Anthony (1972) examined counts of vertebrae and pectoral fin rays of herring from several locations around the Gulf of Maine including eastern and western Maine, Jeffreys Ledge-Stellwagen Bank, Nova Scotia, and Georges Bank. In general, he found counts to be highest in herring from Nova Scotia and lowest in Georges Bank herring. There were statistically significant differences in counts for both vertebrae and pectoral fin rays among the groups but the differences did not maintain themselves over the years for which he had samples. Anthony (1972) concluded that consistent differences in mean counts of meristic characters indicated limited mixing of groups of herring. Such separation means that, although the groups may not be genetic stocks, they can function as stock units in a herring management program.

Safford and Booke (1992) examined morphometric differences between herring from Trinity Ledge, Nova Scotia, and Jeffreys ledge. They found significant differences between the two spawning grounds but the discriminant function only performed well in one of two years. They also performed traditional starch gel electrophoresis of enzymes and found no stock structure.

The suggestion of stock structure indicated by the present study is not supported by previous genetic studies (Grant 1984, Kornfield and Bogdanowicz 1987, Safford and Booke 1992). The genetic studies indicate that there is enough mixing among spawning groups to prevent fixation of distinct alleles; thus, the morphometric differences seen between Jeffreys Ledge and Georges Bank spawners may be environmentally induced. Morphometric differences may result from differences in life history between the two groups, including perhaps migration and spawning patterns, trophic differences, and exposure to different environmental cues during important developmental periods. Although the spawning groups do not appear to be true genetic stocks, the presence of significant differences in morphometric characteristics indicates limited mixing of the stocks at spawning time, and so the spawning groups can be treated as unit stocks for management purposes.

Although we have successfully documented significant morphometric differences between two spawning groups in the Gulf of Maine, this is the first step in the stock identification process (Cadrin 2000) culminating in the ability to assign fishery catches and survey samples to individual stocks. There are many more discrete spawning areas in the Gulf of Maine and on Georges Bank and Nantucket Shoals that we have not yet sampled, and the degree of morphometric variation within and between all these spawning herring has yet to be determined.

## Acknowledgments

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