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[Article]

Geometric Morphological Differences Distinguish Populations of Scup in the Northwestern Atlantic Ocean

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Abstract.—Scup *Stenotomus chrysops*, a commercially important marine species, are distributed from Nova Scotia to south Florida, and may represent morphologically distinct populations across their range. It was determined whether there were morphological differences between a North Atlantic Bight (NAB) population (41°N) and two South Atlantic Bight (SAB) populations (30°N and 32°N) of this species from April 2005 to July 2005, when the populations had formed spawning groups. Morphology was compared among populations by means of a geometric, landmark-based analysis of morphological and meristic traits for 180 individuals that were sexed and staged to maturity. A backward, stepwise discriminant functions analysis (DFA) produced a model that generated DFA scores that differed significantly between the NAB and SAB populations. Forehead and body depth dimensions differed among populations but not sexes. The DFA model predicted similar scores for 32 new NAB individuals and 31 new SAB individuals; however, scores were consistently underpredicted for the NAB individuals and overpredicted for the SAB individuals. We concluded that distinct northern and southern populations support a two-stock or two-species hypothesis; however, it is unclear whether this stock structure is related to reproductive or other life history traits. Either phenotypic plasticity or divergent selection may explain the morphological dissimilarities among these populations, but their influence on individual fitness remains unknown.

Scup *Stenotomus chrysops*, a commercially important marine species, are distributed from Nova Scotia to south Florida. In 2005, the U.S. commercial and recreational catch of scup was 5.3 million kg. This widely distributed species has historically been recognized as two or three distinct species (*S. chrysops*, *S. aculeatus*, and occasionally *S. versicolor*; Bigelow and Schroeder 1953). Early studies suggested that *S. chrysops* occurred north of Cape Hatteras, North Carolina, and *S. aculeatus* occurred south of Cape Hatteras (Johnson 1978), which may be a formidable barrier to gene flow between the North Atlantic Bight (NAB) and South Atlantic Bight (SAB) (Jones and Quattro 1999; Adams and Rosel 2006). *Stenotomus aculeatus* is not currently recognized as a distinct species (Robins et al. 1991; Carpenter 2002). Dispersal of larval fish between the NAB and SAB (Hare and Cowen 1996; Grothues et al. 2002) may prevent genetic isolation of these populations (Jones and Quattro 1999). However, no published studies have examined the level of morphological divergence between NAB and SAB populations. Our objective was to compare the size and shape of scup from the northern and southern extents of its range.

The science of morphometrics has a long history in quantifying phenotypes and has been radically changed by recent, widespread use of the digital processing of specimens (Cadrin and Friedland 1999). Phenotypic differences in size and shape within a species may exist because of sexual dimorphism (Love 2002) and ecological specialization (Sage and Selander 1975; Schluter and McPhail 1992). Size differences among fish within the same age-cohort may also reflect differences in reproductive capacity and growth, which are locally adaptive (Conover et al. 2005). Quantifying phenotypic differences among fish populations and identifying their causes and consequences may be informative of differences in natural history across a species' geographic range, which would have implications for both theoretical and applied work in ecological and fishery science.

This study sought to determine the extent to which morphological and meristic traits discriminate scup populations from the northern and southern extents of the species' range in the northwestern Atlantic Ocean. We tested the hypothesis that the size and shape of

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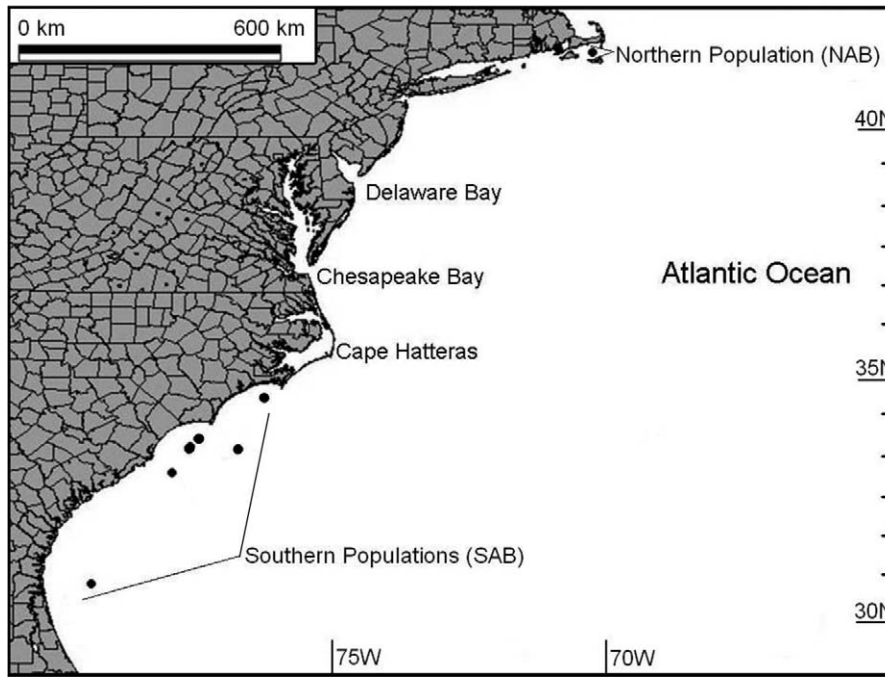

FIGURE 1.—Map of the northwestern Atlantic Ocean showing the latitudes at which scup were collected during their spawning season (late spring–early summer) in 2005 in the NAB and SAB.

similarly sized individuals differed between the populations from the NAB and the SAB.

Methods

Scup were collected from May to July 2005, when spawning aggregations were formed for the NAB (41°N) and SAB (30°N–34°N) populations (Figure 1). We compared populations from two SAB latitudes to evaluate the level of morphological difference across a relatively small spatial area. Adults were collected by means of a combination of trawling and trapping methods. Nine NAB specimens were collected during the Massachusetts Division of Marine Fisheries 2005 Spring Inshore Bottom Trawl Survey (1.8-cm-mesh otter trawl; 20-min tow at 2.5 knots during the day). Additional NAB specimens were collected by means of pot traps (60 cm wide × 60 cm deep × 60 cm high) that were soaked for 3 h. All SAB specimens were collected by means of wire fish traps (Collins 1990) set by the South Carolina Department of Natural Resources during surveys for their Marine Resources Monitoring Assessment and Prediction program. Collection depths ranged from 6 to 36 m. All individuals were frozen before processing. After thawing, each individual was measured, weighed, photographed for digital analysis (see below), and dissected to determine sex. Lateral line scales and other meristic traits were counted following Hubbs and Lager (2004). We counted the number of spines and rays for the dorsal, anal, and pelvic fins. Measurements for morphometric characters were made with a ruler (to the nearest 0.10 cm). These measurements included the length of the longest unbranched dorsal ray, the length of the pectoral fin, and the total length.

Additional measurements of shape were recorded from digital images. Digital images were taken of thawed fish with a Nikon Cool Pix 5.0 Mega Pixels camera and analyzed with TPSdig (version 2.04; Rohlf 2005). Before digital imaging, fish were pinned to a dissecting pan and 10% solutions of formalin were applied to their fins for stiffening. For each digital image, 17 landmarks that could be clearly represented on the body of the fish were chosen out of 55 originally examined (Figure 2; Table 1). A box truss of 28 lines connecting these landmarks was generated for each fish to represent the basic shape of the fish (Strauss and Bookstein 1982; Cadrin and Friedland 1999). Not all landmarks were used to generate a box truss in order to reduce the number of linear dimensions subjected to analysis and ease interpretation of the results. The effect of length on the linear dimensions was removed by means of linear regression. The residual variance was saved from individual regression models of length (independent variable) and the linear dimension

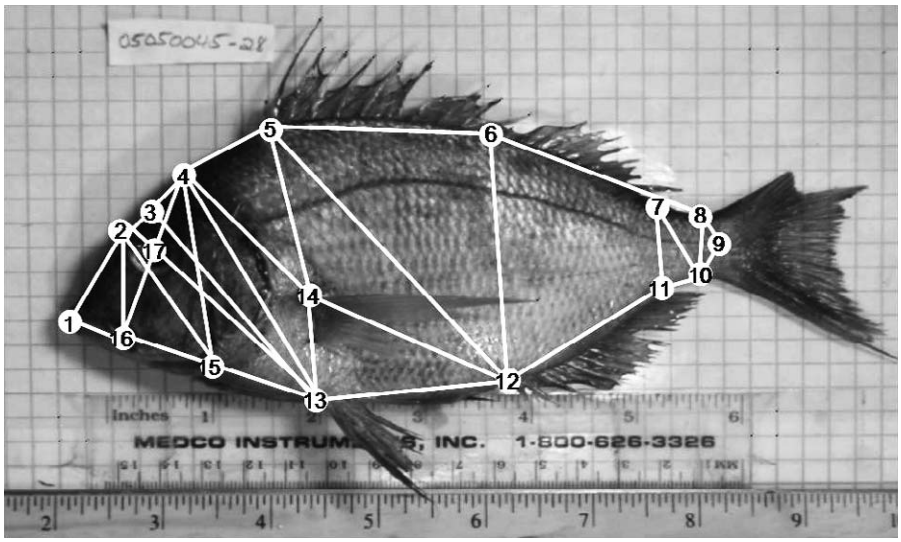

FIGURE 2.—Digital image of a scup depicting the 17 landmarks and associated box truss used to infer morphological differences among populations in the northwestern Atlantic Ocean.

(dependent variable). Kolmogorov–Smirnov tests for normality were performed for all variables. As there were significant departures from normality for all variables, the linear dimensions were $\log_{10}$ transformed to help normalize the variances, but in no case was normality achieved. However, histograms indicated approximate normality for each variable, probably as a result of the large sample sizes.

Thirty-two response variables subjected to a backward, stepwise discriminant functions analysis (DFA), the *P*-value to leave being 0.15 or more. The variables included 28 linear measurements from the box truss network, mass, the length of the longest unbranched dorsal ray, the length of the pectoral fin, and the lateral line scale count. The multivariate DFA reduced the dimensionality of the data set by systematically removing response variables that contributed little to discriminating among latitudinal populations. The relative importance of each response variable in the classification of the independent variable was indicated by its discriminant coefficient standardized by a constant. The coefficients were used to generate a DFA model for assigning additional individuals to particular latitudes (see below).

TABLE 1.—Landmarks and corresponding locations on scup (see Figure 2).

Landmark	Location
1	Distal tip of premaxillary bone, closed mouth
2	Nasal bone, bump over eye
3	Deepest part of frontal bone
4	Tip of supraoccipital bone
5	Origin of dorsal fin
6	Origin of unbranched rays
7	Termination of dorsal fin
8	Dorsal side of caudal peduncle, at the nadir
9	End of lateral line
10	Ventral side of caudal peduncle, at the nadir
11	Termination of anal fin
12	Origin of anal fin
13	Origin of pelvic fin
14	Dorsal origin of pectoral fin
15	Dorso-posterior tip of interopercle
16	Articulation of maxillary and dentary bones, closed mouth
17	Center of eye

The performance of the DFA was evaluated in three ways. First, scores from the DFA were saved after the analysis and plotted to interpret the level of separation among populations. If morphology differs between the NAB and SAB populations, the scores for individuals from these two regions should not overlap. The scores for individuals from both SAB latitudes were predicted to overlap. Second, Wilk's λ was used to evaluate the significance of the discriminant functions model for discriminating among populations. Significant λ values would indicate that discriminant function scores differ between groups. Third, the error rate for classifying individuals to each latitudinal population was evaluated by means of a matrix of classification errors computed from a DFA of a subset of the data (via jackknifing).

The variables important for discriminating among populations were determined by two methods. First, we used the magnitude of the standardized discriminant coefficient as an indication of the importance of each

TABLE 2.—Descriptive information for scup collected at both northern (41°N) and southern latitudes (30°N, 32°N; 2005). The values for the last four variables are means ± SDs.

Variable	41°N	32°N	30°N
Sample size	91	65	24
Proportion male[a]	37%[b]	49%[c]	46%[d]
Proportion female[a]	48%	51%	46%
Total length	21.3 ± 3.9	20.0 ± 1.6	21.1 ± 2.4
Mass	167.2 ± 101.1	123.2 ± 28.2	132.0 ± 50.5
Longest dorsal spine	31.4 ± 5.9	30.0 ± 7.1	28.5 ± 5.5
Scale count	48.9 ± 0.9	48.6 ± 1.4	46.0 ± 2.1

[a] Proportions do not include individuals that could not be sexed.
[b] χ^2 for comparing sex ratio = 1.28; $P = 0.26$.
[c] χ^2 for comparing sex ratio = 0.00; $P = 1.00$.
[d] χ^2 for comparing sex ratio = 0.02; $P = 0.90$.

response variable. Second, we subjected the shape-related variables that were selected by the DFA to a multivariate analysis of variance (MANOVA) and to subsequent univariate significance tests to determine which of these response variables differed significantly among populations and between sexes (the independent variables).

The robustness of the DFA model was determined by predicting DFA scores for 32 NAB individuals and 31 SAB individuals (20 from 33°N and 11 from 34°N). Following the procedures mentioned above, morphometric data were generated for new individuals collected from May to July 2005. Because new scores were calculated from the existing DFA model, the performance of the model could be assessed by (1) plotting the new predicted scores against the scores assigned originally (see above), (2) comparing the predicted DFA scores for the NAB and SAB by means of analysis of variance (ANOVA), and (3) conducting a nested ANOVA that tested for effects due to position (NAB versus SAB) and prediction error (original scores versus predicted scores) within positions. If the DFA model was effective, the plots of the new predicted scores should overlap the plot of the original scores. In addition, we hypothesized that there would be a significant difference in scores between the NAB and SAB populations but no significant nested effect (i.e., no difference between original and predicted scores for either the NAB or SAB). All analyses were performed in SYSTAT (version 10).

Results

We analyzed data for 180 specimens of scup (Table 2). There were 78 males, 87 females, and 15 of unknown sex. The number of males did not differ from the number of females between the NAB and SAB (Pearson $\chi^2 = 0.81$; $P = 0.67$) or at any latitude (Table 2). The total length of specimens also did not differ among latitudes.

Of the 32 morphological variables subjected to the backward, stepwise DFA, 20 variables had relatively high discriminant coefficients. These variables were retained in the final DFA model (Table 3), which performed well in discriminating the NAB and SAB populations (Wilks' $\lambda = 0.06$; $F_{40,312} = 24.3$; $P < 0.0001$; Figure 3). There was fairly high accuracy in predicting individual assignment to the northern populations (90%) and southern populations (83–84%; Table 4). Error rates were lower for classifying individuals to the NAB and SAB populations than for classifying them within the SAB, supporting a two-species or two-stock hypothesis of stock structure.

Of the 20 variables in the final DFA model, 8 variables differed significantly among populations (MANOVA: Wilk's $\lambda = 0.059$, $F_{40,308} = 23.9$, $P < 0.0001$; Table 2). Sex did not significantly explain the variation in shape (Wilk's $\lambda = 0.812$, $F_{40,308} = 0.884$, $P = 0.737$). Most significant variables were associated with body shape ($n = 2$) and forehead shape ($n = 3$). Forehead shape differences were related to the distance from a bump above the eye (point 2; see Figure 2) to other landmarks on the body. Foreheads for SAB individuals were typically less convex, the distance between the eye or the pelvic fin and the forehead being smaller than for NAB individuals. In addition to shape differences, the lateral line scale count was lower for an SAB population (30°N) than for the NAB population (see Table 2).

The DFA model was effective, in that the predicted scores for the NAB and SAB specimens differed from one another (DFA Axis 1: $F_{1,60} = 99.4$, $P < 0.0001$; DFA Axis 2: $F_{1,60} = 50.9$, $P < 0.0001$; Figure 3). However, the scores for the NAB were significantly underpredicted and those for the SAB significantly overpredicted (DFA Axis 1: $F_{2,236} = 43.4$, $P < 0.0001$; DFA Axis 2: $F_{2,236} = 18.2$, $P < 0.0001$; Figure 3).

Discussion

Scup populations differed in morphology between the NAB and SAB, supporting a two-species or two-stock structure for this species. However, most morphological differences were related to forehead shape, which may not be related to important growth or reproductive characteristics of interest in stock assessments. For other species of the family Sparidae (e.g., squirefish *Chrysophrys auratus*), forehead shape naturally differs among populations and sexes (Moran et al. 1999). Interestingly, there was no evidence of sexual dimorphism in forehead shape for our scup specimens. Other morphological differences between the NAB and SAB populations, such as mass and scale count, were slight or nonsignificant.

Morphological divergence in shape among conspe-

TABLE 3.—Canonical coefficients standardized for within-unit variance, as derived from a discriminant functions analysis of morphological data (see Table 1) from three populations (30°N, 32°N, and 40°N) of scup in the northwestern Atlantic Ocean in 2005. The variables listed remained in the discriminant functions model after backward, stepwise regression. Average measurements are given for linear dimensions that differed significantly among populations according to a multivariate analysis of variance. Significant differences among populations (Tukey–Kramer honestly significant difference test) are designated by different superscripts.

Variable	Axis 1	Axis 2	30°N	32°N	41°N
Body shape					
Points 1 to 2	0.381	0.327	−0.103[a]	−0.150[a]	0.134[b]
Points 2 to 3	0.362	−0.037	0.006	0.011	−0.009
Points 5 to 6	−0.943	0.090	0.066[a]	0.161[a]	−0.132[b]
Points 13 to 15	1.100	0.874	−0.040	0.017	−0.001
Caudal peduncle					
Points 9 to 10	0.293	0.234	−0.030[a,b]	−0.025[a]	0.026[b]
Body depth					
Points 6 to 12	−1.428	0.862	−0.006	0.012	−0.007
Points 5 to 12	2.191	−2.183	−0.028	0.006	0.003
Points 5 to 14	−1.194	0.520	−0.016	0.009	−0.002
Points 12 to 14	−0.734	0.142	0.013[a]	0.040[a]	−0.032[b]
Points 13 to 14	−0.883	−0.813	−0.042	0.006	0.007
Forehead shape					
Points 4 to 14	−1.890	−3.653	−0.056	0.007	0.010
Points 4 to 13	7.445	−3.493	−0.061[a]	−0.004[a,b]	0.019[b]
Points 2 to 13	−2.387	3.733	−0.069[a]	−0.014[a,b]	0.028[b]
Points 4 to 17	−1.086	0.695	0.003	0.027	−0.020
Points 3 to 17	−0.381	0.308	0.005	0.007	−0.006
Points 2 to 17	0.739	1.085	−0.053[a]	−0.021[a,b]	0.029[b]
Points 2 to 15	−2.258	1.443	−0.035	0.013	0.000
Mass	0.593	0.356	137.4	123.2	155.7
Pectoral ray length	−0.554	0.437	56.0	51.8	51.6
Lateral line scale count	0.221	−0.781	46.2[a]	48.6[b]	48.9[b]
Eigenvalue	6.82	1.14			

cific populations may be caused by a phenotypic plastic response to local environmental differences or be an adaption resulting from differences in resource use (Schluter and McPhail 1992; Snorrason et al. 1994; Langerhans et al. 2003). Larval fish may develop different morphologies because of local environmental conditions that vary by latitude, leading to differences in adult morphology as well. According to Cadrin and Silva (2005), the geographic variation in adult morphology for yellowtail flounder *Limanda ferruginea* may be explained by differences in ontogenetic rates among local populations if morphology is a product of ontogenetic history. Different prey resources for larvae and juveniles may lead to different adult body shapes, suggesting that there is a phenotypic plastic response to resource availability (Wimberger 1990). It is not clear whether there are differences in ontogenetic rates or resource availability for larvae and juveniles between the NAB and SAB populations. Cadrin and Silva (2005) ultimately determined that all

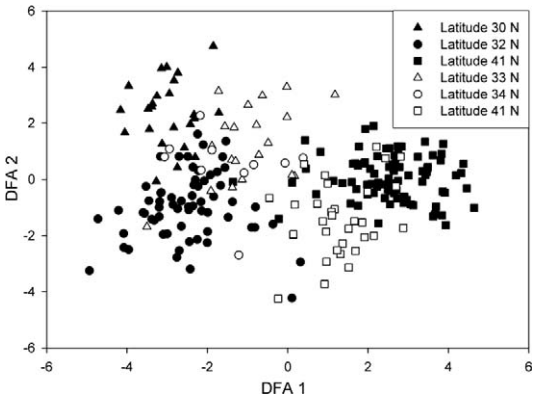

FIGURE 3.—Scatterplot of scores along two axes derived from a discriminant functions analysis (DFA) of morphological and meristic variables measured for scup from various latitudes in the northwestern Atlantic Ocean.

TABLE 4.—Jackknifed classification error rates derived from a discriminant functions analysis of a subset of morphological and meristic data for scup from three latitudes in the northwestern Atlantic Ocean in 2005. The first three columns show the number of individuals from a given latitude that were assigned to each of the three latitudes; the last column shows the percentage of correct assignments.

Latitude	30°N	32°N	41°N	% Correct
30°N	20	4	0	83
32°N	8	54	2	84
41°N	0	3	87	97

yellowtail flounder constitute a single stock despite the geographic variation in their morphology, largely because there is substantial gene flow among local populations.

Adult morphology may also be determined by diversifying selection and ecological adaptation. Costa and Cataudella (2007) found that shape differences were related to trophic ecology for several species of the family Sparidae, thus indicating local adaptation (Schluter and McPhail 1992; Langerhans et al. 2003) and possibly ecological radiations. However, there are no a priori reasons to expect that forehead shape is adaptive for scup. To discriminate between phenotypic plasticity and ecological adaptation as mechanisms explaining morphological divergence, a combination of laboratory studies and genetic tests using population markers (e.g., the D-loop and cytochrome *b*) could be useful. Laboratory studies designed to test the plastic response of larvae to diet or temperature conditions may be informative, particularly if shape differences are detectable at earlier ages than those examined here. Genetic tests may distinguish discrete population units, especially if rapidly mutating (e.g., D-loop) and relatively slowly mutating (e.g., cytochrome *b*) markers are used in concert to distinguish between population-level and species-level differences, respectively. Morphological differences, whether related to ontogenetic growth history or ecological adaptation, may be preserved under instances of low gene flow, such as that observed for metapopulations (Cadrin and Silva 2005), or high gene flow (Anderson et al. 2008); no work has addressed the gene flow between the NAB and SAB scup populations.

Our research represents an important advance in understanding scup biology and highlights the morphological divergence in this widely distributed marine species. Such divergence is commonly observed for freshwater and lacustrine populations (Schluter and McPhail 1992; Snorrason et al. 1994). We have identified significant differences in the shape of scup from populations at extremes of its range in the northwestern Atlantic Ocean. If shape is related to either environmental influences on larval development (Cadrin and Silva 2005) or diversifying selection and ecological adaptation at a trophic level (Costa and Cataudella 2007), then spatially or latitudinally different environmental factors (e.g., temperature and resource availability) may explain the variations in body shape among scup. Langerhans et al. (2003) found that the distance between habitats correlated positively with the level of divergence in body shape among conspecific populations of two neotropical fish species. Although our data support a two-stock or two-species model for scup, the morphological variation that we observed may be the result of an environmental gradient rather than genetic isolation or differences in the age structure and reproductive fitness of adults. Additional data on life history differences and gene flow between the NAB and SAB populations will better elucidate the management units required for this species and possibly those for other wide-ranging species in the northwestern Atlantic Ocean.

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