Summary

Following a variety of observations regarding a decrease in Black Sea Bass (*Centropristis striata*) abundance and reduced distribution coverage in the South Atlantic, the South Carolina Department of Natural Resources, with funding from the South Atlantic Fisheries Management Council, collected fin clips with partner surveys to re-assess genetic structure along the U.S. east coast. Fin clips were collected from central Florida to the Gulf of Maine in 2024 through the fishery-independent efforts of the Coastal Trawl Survey, Southeast Reef Fish Survey, Chesapeake Bay Multispecies Monitoring and Assessment Program, NorthEast Area Monitoring and Assessment Program, and Northeast Bottom Trawl Survey. Genomic DNA was isolated from fin clips and microsatellite loci amplified for genotyping for analysis along the full latitudinal coverage of samples. The resulting analyses are consistent with previous genetic stock structure findings indicating a difference in genetic composition between the South Atlantic and the Mid- and North Atlantic with a change around North Carolina / Virginia with continuing gene flow between areas. Despite the reduction in the South Atlantic stock abundance, genetic health (based on heterozygosity and inbreeding) remains high without a change since the last assessment with the same microsatellite panel. Therefore, given the lack of a change in either the location of the genetic shift in Black Sea Bass stocks or the degree of gene flow between stocks, it appears the southern stock is experiencing a constriction of its range under current climate conditions and not moving further north and introgressing with the northern stock.

Introduction

Black Sea Bass (*Centropristis striata*), occurs along much of the Atlantic coast of the United States in association with hard structured habitats (Wenner et al., 1986; Vaughan et al., 1995). The species has historically been managed as two stocks along the east coast of the United States, with a genetically and life history defined divide at Cape Hatteras (Drohan et al., 2007; SEDAR, 2011). The northern stock of Black Sea Bass has increased in abundance and landings over the past two decades, with the northern terminus of the range shifting from southern Massachusetts to the Gulf of Maine (Bell et al., 2015; McBride et al., 2018; National Marine Fisheries Service, 2022). Southern stock population numbers and geographic extent have varied over the past forty years with the highest estimated population in the 1980s and the lowest at present (SEDAR 2023).

Historically, the stock break between north and south was established as Cape Hatteras, NC (Mercer, 1978 and Shepherd, 1991). These stock designations are supported by life history and morphometric studies based on differences in seasonal migrations, growth and maturity, and spawning times (Kendall 1972; Musick and Mercer 1977; Mercer 1978; Wenner et al. 1986; O'Brien et al. 1993; Collins et al. 1996; Steimle et al. 1999; McGovern et al. 2002). Roy et al. (2012) and McCartney et al. (2013) found support for genetic differentiation between the southern and northern stocks, and evidence of limited gene flow between them. More recently, a genetic study supported that the southern stock has maintained high genetic diversity regardless of large shifts in their abundance over time and confirmed a single genetic stock occurs from FL to NC with samples through 2014 (O'Donnell and Darden, 2019).

Vecchio et al. (2025) recently examined the spatial dynamics of southern stock Black Sea Bass in the Marine Resources Monitoring Assessment and Prediction program and Southeast Reef Fish Survey (MARMAP/SERFS) chevron trap efforts before and during a phase of low recruitment and abundance. The southern stock constricted into the northern portion of the region when either recruitment is low (most recent years of survey data) or when bottom temperature is high (also the most recent years). Their observations and previous genetic structure suggest two potential scenarios may be occurring with the southern stock: 1) southern Black Sea Bass are still isolated from the northern stock by the shape and oceanography of Cape Hatteras and so this stock is contracting into a smaller range within the South Atlantic in response to changing conditions or 2) southern Black Sea Bass are shifting north past Cape Hatteras due to changing conditions in the South and Mid Atlantic, similar to the northward shift observed in the northern stock (McBride et al., 2018; Younes et al., 2020). If the range of the southern stock of Black Sea Bass is shifting north (scenario 2), we would expect that changes in the distribution of genetic composition would be occurring as well.

The objective of our study was to re-assess the genetic structure of Black Sea Bass along the U.S. Atlantic coast from Florida to Maine using contemporary samples and a nuclear genetic panel. Partner surveys were identified to provide genetic materials along the coast in 2024. These samples allow us to determine the recent genetic structure following and during observed changes in distribution, stock size, and regional conditions. The genetic results will either support or refute the competing hypotheses that the southern stock is not moving north but is contracting within the South Atlantic or if the southern stock is shifting into the Mid Atlantic region and either replacing or introgressing with the northern stock.

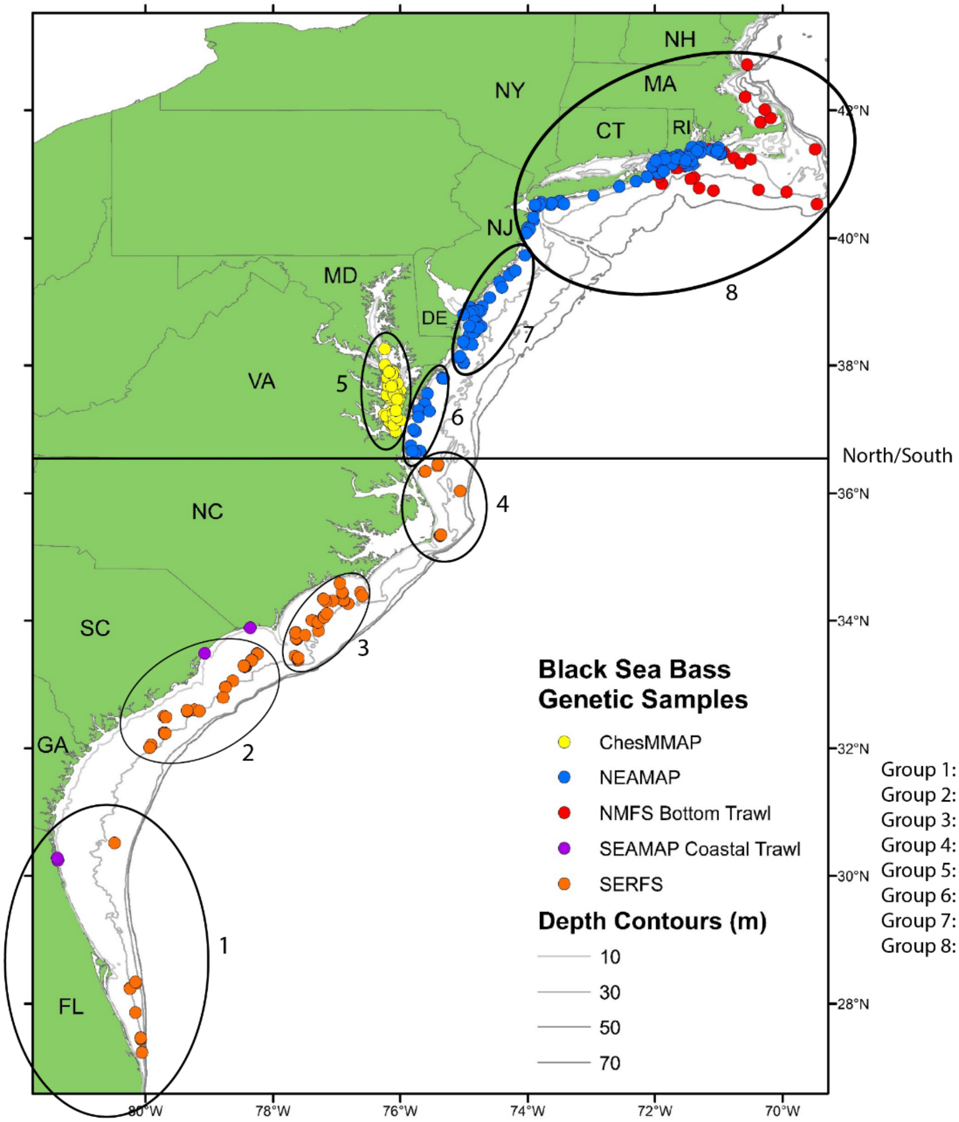
Material and Methods

Field Collection

In order to assess the contemporary genetic structure of Black Sea Bass along the U.S. east coast, we conducted fin clip collection through existing fishery-independent surveys that regularly encounter this species. Fishery-dependent sources would likely focus on older fish (and therefore less recent genetic characteristics) due to size limits for retention. Fishery-independent surveys that provided fin clips included the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), Coastal Trawl Survey (CTS), NorthEast Area Monitoring and Assessment Program (NEAMAP), NorthEast Bottom Trawl Survey (NEBTS), and Southeast Reef Fish Survey (SERFS). Each survey randomly selected fish from overall catches in accordance with standard operating procedures and collected detailed information for each individual fish including location and depth of capture and length and weight. Most fish were also dissected for otoliths to allow ageing.

Table 1. Number of Black Sea Bass (*Centropristis striata*) fin clips collected by fishery-independent surveys in 2024 for genetic stock structure analysis.

Survey	Genetic Samples Collected	Genetic Samples Processed
ChesMMAP	189	147
CTS	6	6
NEAMAP	564	293
NEBTS	144	144
SERFS	202	202
Totals	1,105	792



Group 1: FL_GA n=26
Group 2: SC n=102
Group 3: NC_South of Cape Lookout n=44
Group 4: NC_North of Cape Lookout n=28
Group 5: CHB n=145
Group 6: MD_VA Offshore n=33
Group 7: MD_DE_NJ Offshore n=30
Group 8: NJ_North n=335

Figure 1. Spatial distribution of Black Sea Bass (*Centropristis striata*) fin clips collected by fishery-independent surveys in 2024 for genetic stock structure analyses. Numbered black circles indicate collection groupings used for pairwise F_{ST} calculations (Table 4) and location priors used in *Structure* analysis in Figure 2.

Genetic Analysis

Fish fin tissue samples were stored in sarcosyl urea immediately upon collection to digest tissue and preserve genetic material. Processing priority was given to samples with the broadest spatial distribution, targeting up to 300 samples in each sample area: South Atlantic, Mid Atlantic, and North Atlantic. Additionally, priority was given to processing samples of small/young fish (Table 1).

Genomic DNA was isolated from fin clip sarcosyl urea lysate using a QIAcube HT automated DNA isolation system with QIAamp 96 DNA HT kits (Qiagen). For each sample, 13 microsatellite loci were amplified with polymerase chain reactions (PCR) in three multiplexed panels. Microsatellite loci were originally developed for Black Sea Bass (Chen et al. 2009) and three other serranid fishes including Gag Grouper (Chapman et al. 1999a), Convict Grouper (Zhao et al. 2009a), and Yellow Grouper (Zhao et al. 2009b) (Table 2) and optimized to run at identical PCR temperature cycling conditions. All amplifications occurred in 11 µL reaction volumes containing 1 × Type-it Microsatellite PCR Master Mix (Qiagen), 0.3 µM forward (5' labeled) and reverse primers, and 1 µL of isolated genomic DNA. Reactions were performed using C-1000 Touch thermal cyclers (Bio-Rad Laboratories, Hercules, California) with two no-template controls for each multiplex group at the following conditions: 5 min initial denature at 95°C, followed by 28 cycles of denaturing at 95°C for 30 s, annealing at 58°C for 90 s, and extending at 72°C for 30 s, with a final extension at 58°C for 30 mins. Following PCR, reaction products were separated by size on ABI SeqStudio Flex 24 capillary gel electrophoresis systems and genotyped using *GeneMapper* V6.1 (ABI) independently by two staff members. All discrepancies were resolved, or the samples were rerun.

Table 2. Microsatellite loci used for genotyping Black Sea Bass with repeat motif, number of samples (N), number of alleles (N_a), species for which each locus was developed, and the citation.

Locus	Repeat motif	N	N_a	Species of origin	Citation
Cest17	$(AC)_{27}$	756	37	*Centropristis striata*	Chen et al. 2009
Cest28	$(AC)_{12}$	773	27	*Centropristis striata*	Chen et al. 2009
Cest24	$(CT)_{5}TT(CT)_{11}$	773	13	*Centropristis striata*	Chen et al. 2009
Ese33	$(TG)_{6}TT(TG)_{7}$	772	14	*Epinephelus septemfasciatus*	Zhao et al. 2009a
GAG10	$(GT)_{*}$	769	26	*Mycteroperca microlepis*	Chapman et al. 2013
Ese44	$(CA)_{27}$	773	31	*Epinephelus septemfasciatus*	Zhao et al. 2009a
Ese28	$(GT)_{13}$	732	23	*Epinephelus septemfasciatus*	Zhao et al. 2009a
Cest37	$(AC)_{4}TT(AC)_{7}$	763	20	*Centropristis striata*	Chen et al. 2009
Ese52	$(CA)_{27}$	755	65	*Epinephelus septemfasciatus*	Zhao et al. 2009a
Cest7	$(TATC)_{20}$	741	37	*Centropristis striata*	Chen et al. 2009
Ese35	$(GA)_{10}CA(GA)_{9}$	770	17	*Epinephelus septemfasciatus*	Zhao et al. 2009a

Cest33	$(TATC)_5$	725	25	*Centropristis striata*	Chen et al. 2009
Epaw34	$(TG)_{21}$	763	14	*Epinephelus awoara*	Zhao et al. 2009b

*Repeat number not reported

Samples that were successfully genotyped at 10 or more loci were then evaluated for allelic richness, observed and expected heterozygosity, inbreeding coefficient, Garza-Williamson index, Hardy-Weinberg equilibrium (HWE), and linkage disequilibrium among loci and sampling locations using *Arlequin* 3.5.1.2 (Excoffier & Lischer, 2010) and *Genepop* 4.7.2 (Rousset, 2008). Two loci, Cest33 and Ese52, were consistently out of HWE and were excluded from analyses. Additionally, Ese52 could not be scored with the appropriate bin structure further justifying its removal. Loci Ese44 and Cest37 were dominated by a single allele shared ~equally across the geographic distribution of samples. All analyses were performed with and without Ese44 and Cest37 with no noticeable differences in results, therefore we conservatively chose to include 9 loci in evaluated analyses.

Analyses of population structure can be impacted by the presence of family groups within the dataset (Anderson and Dunham 2008; Rodríguez-Ramilo & Wang 2012), and we used *Colony* 2.0.6.2 (Jones & Wang 2010) to identify potentially related individuals. Three short-length runs were conducted using the full likelihood and pairwise-likelihood combined method with a polygamous breeding system, medium precision, weak priors, updating allele frequencies, and no genotyping errors assumed. Each short run was given a different random seed. No large family groups were identified within our dataset and therefore no samples were excluded on the basis of sibship or parentage.

We evaluated population structure and differentiation through pairwise F_{ST} statistics calculated in *Arlequin* and *GenAlEx*, and through clustering algorithms to identify the appropriate number of distinct populations (*K*) using *Structure* v. 2.3.4 (Pritchard et al., 2000). *Structure* simulations were performed with and without consideration for sampling location (*i.e.,* with locprior and without locprior in which individuals were assigned collection region- either north- and south- or finer geographical scale) for all analyses with 3-5 replicates for each *K* using a burn-in of 50,000 followed by 200,000 Markov chain Monte-Carlo post burn-in repetitions. The optimal number of ancestral populations (*K*) was selected using the delta-*K* method of comparison of log likelihood across iterative changes in *K*, as implemented in *StructureSelector* (Li & Liu, 2018). Multiple analyses were conducted by including sampling location priors for the simulations by either (1) state where collections occurred and clear breaks in sampling efforts, (2) by collector, or (3) divided into 'north' and 'south' populations with a break at the NC-VA border (Figure 1). Additionally, to rule out distinguishable year class genetic effects, analyses were performed with and without age 0-1 fish (TL < 175 mm) estimated by total length at time of capture. Other year classes could not be distinguished by length. A Mantel test for genetic isolation-by-distance was performed in *GenAlEx* v6.5 (Peakall & Smouse 2006, Peakall & Smouse 2012) and effective population size (N_e) was estimated with *LDNe* (Waples & Do 2008). We also estimated the effective number of migrants per generation between the north and south stocks based on our pairwise F_{ST} values as in Meirmans and Hedrick (2011).

Results

A total of 792 samples were successfully genotyped. Of these, 773 met criteria to include in analyses (Table 3). All *Structure* analyses indicated a *K* = 1 based on log likelihood plots (Figure 6); however, there is an obvious transition zone in proportional ancestry between northern and southern collections at the NC-VA border (Figures 2-5). *Structure* results were not influenced either by high proportion of young year classes (Figure 4) or collection program (Figure 5). Consistent with the observed shift in ancestry assignments, a significant difference in pairwise F_{ST} value (0.002, p = 0.001; Bonferonni corrected α = 0.025) was detected between the North and South collections. The estimated number of migrants per generation based on pairwise F_{ST} values (Meirmans and Hedrick 2011) was 116 migrants per generation. Expected and observed heterozygosity in the North and South collections were similar and high (~0.78-0.86) while the inbreeding coefficients in both were low (0.07-0.08). The G-W index in both the North and South (0.44 and 0.41, respectively) indicated the presence of historic bottlenecks in both collections (Table 3). Effective populations size (N_e) estimates from *LDNe* are large for both the North and South (14,571.4 [95% CI 3352.6 - ∞]; 15,889.7 [95% CI 1291.5 - ∞], respectively). The Mantel test for genetic isolation-by-distance showed no relationship between genetic and geographic distance (slope = 0.0002, Figure 6), suggesting the lack of a continuous genetic gradient which is consistent with the *Structure* and F_{ST} indications of two stocks.

Table 3. Genetic diversity statistics: number of samples, average number of all alleles (N_a), average number of effective alleles (N_e), observed heterozygosity (H_o), expected heterozygosity (H_e), inbreeding coefficient (F_{is}), and Garza-Williamson index (G-W). The South grouping includes all individuals collected from North Carolina to Florida, and the North grouping includes all individuals collected from Virginia and north.

Grouping	N	Na	Ne	Ho	He	Fis	G-W
South	200	19.56	9.87	0.789	0.860	0.084	0.415
North	573	22.11	9.77	0.798	0.861	0.074	0.441
Range wide	733	20.83	9.82	0.793	0.860	0.078	0.428

Table 4. Pairwise F_{ST} for 8 collection areas based on geographic features and sampling breaks. F_{ST} values are below the diagonal, and associated p-values are above the diagonal (Bonferonni corrected α = 0.0031). These areas are Florida and Georgia (FL_GA), South Carolina (SC), North Carolina south of Cape Lookout (NC_SCL), North Carolina north of Cape Lookout (NC_NCL), Chesapeake Bay (CHB), Maryland and Virginia offshore (MD_VA_Off), Maryland, Delaware, and southern New Jersey (MD_DE_NJ_Off), and northern New Jersey to Maine (NJ_North). These areas correspond to Groups 1 through 8 in Figure 1. Areas shaded in gray indicate F_{ST} estimates for population contrasts between northern and southern regions.

	1. FL_GA	**2. SC**	**3. NC_S**	**4. NC_N**	**5. CHB**	**6. MD_VA_off**	**7. MD_DE_NJ_Off**	**8. NJ_North**
1. FL_GA		0.192	0.238	0.253	**0.019**	**0.033**	**0.023**	**0.002**
2. SC	0.008		0.440	0.112	**0.042**	0.480	**0.042**	**0.002**
3. NC _SCL	0.009	0.005		0.230	**0.028**	0.055	0.092	**0.039**
4. NC_NCL	0.012	0.008	0.009		0.117	0.325	0.078	0.058
5. CHB	**0.009**	**0.003**	**0.006**	0.007		0.265	0.806	0.573
6. MD_VA_Off	**0.012**	0.005	0.010	0.010	0.006		0.522	0.476
7. MD_DE_NJ_Off	**0.010**	**0.005**	0.007	0.009	0.003	0.006		0.511
8. NJ_North	**0.010**	**0.003**	**0.005**	0.007	0.001	0.005	0.003	

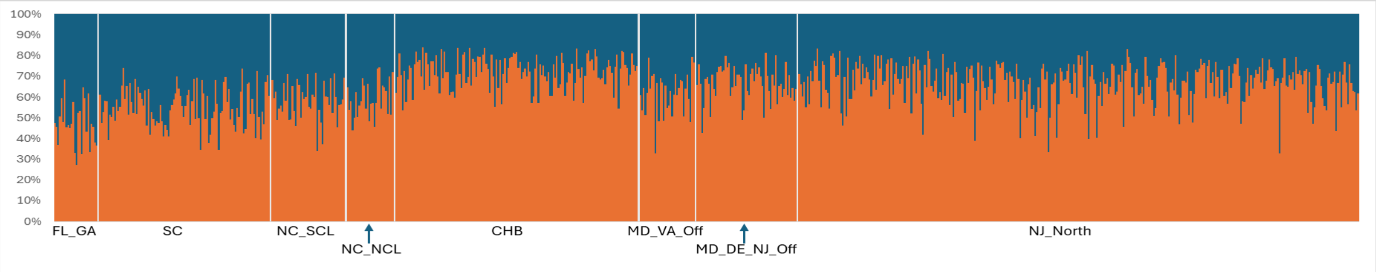


Figure 2. Individual ancestry plot for $K = 2$, estimated by *Structure* analysis performed with location priors for 8 collection areas (samples assigned to geographic regions). Vertical lines represent individual ancestry assignment, and individuals are arranged by collection latitude (south-to-north from left-to-right). Labels along the X-axis indicate collection origin: FL_GA, Florida and Georgia; SC, South Carolina; NC_SCL, North Carolina from

south of Cape Lookout; NC_NCL, North Carolina from north of Cape Lookout; CHB, Chesapeake Bay; MD_VA_Off, Atlantic coast of Maryland and Virginia; MD_DE_NJ_Off, Atlantic coast of Maryland to southern New Jersey; NJ_North, all collections north mid-New Jersey. These location prior groupings correspond to Groups 1 through 8 in Figure 1.

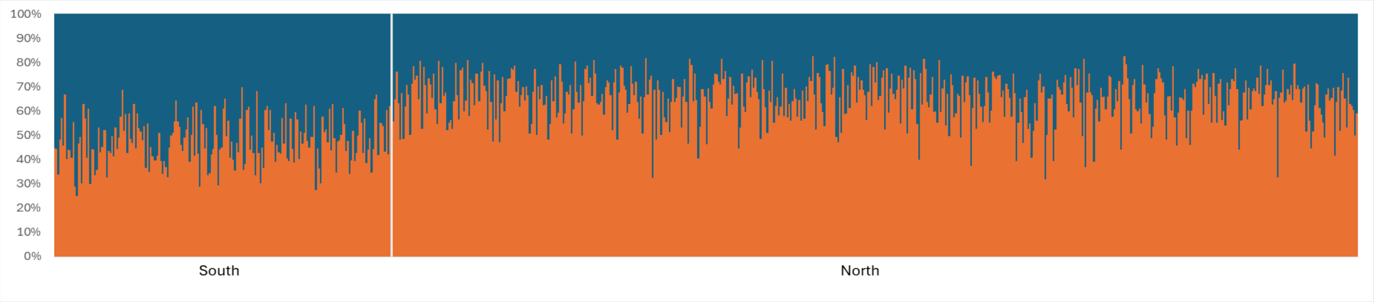


Figure 3. Individual ancestry plot for *K* = 2, estimated by *Structure* analysis performed with location priors for 2 populations, with specimens assigned to either a southern population (all specimens collected in North Carolina and south) or northern population (all specimens collected north of the North Carolina-Virginia border). Vertical lines represent individual ancestry assignment, and individuals are arranged by collection latitude (south-to-north from left-to-right).

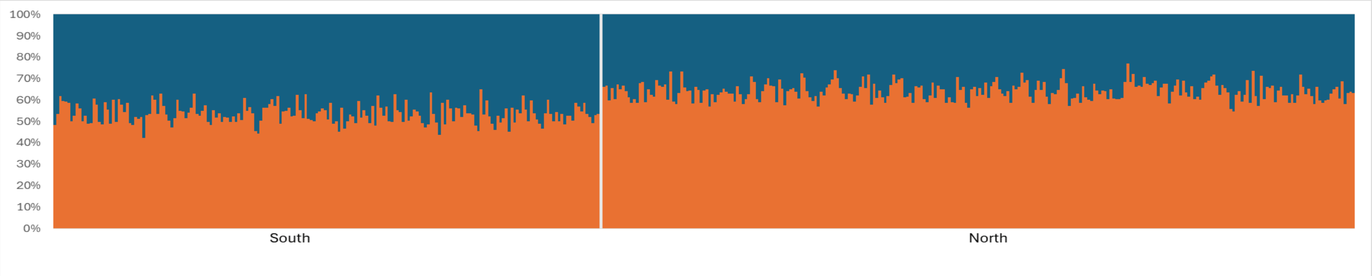


Figure 4. Individual ancestry plot for K=2, estimated by *Structure* analysis performed with location priors for 2 populations and excluding all fish smaller than 175 mm TL. Specimens were assigned to either a southern population (all specimens collected in North Carolina and south) or northern population (all specimens collected north of the North Carolina-Virginia border). Vertical lines represent individual ancestry assignment, and individuals are arranged by collection latitude (south-to-north from left-to-right).

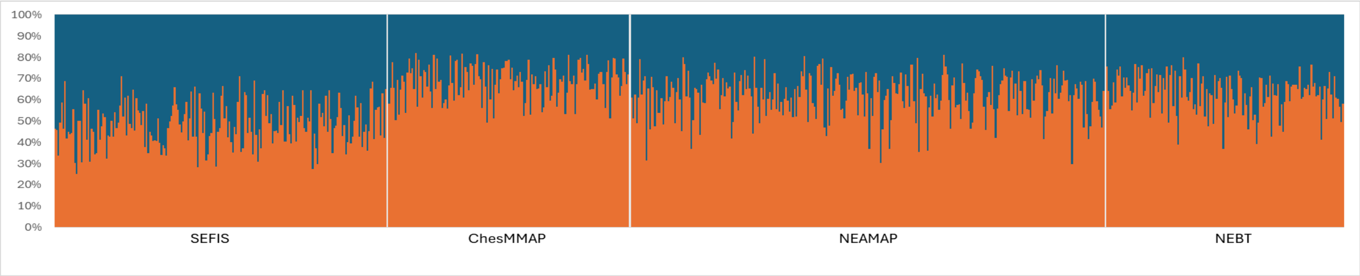


Figure 5. Individual ancestry plot for *K* = 2, estimated by *Structure* analysis performed with location priors for 4 groupings (samples assigned to collector/survey when a survey collected more than 10 samples). Vertical lines represent individual ancestry assignment, and individuals are arranged by collection latitude (south-to-north from left-to-right). Surveys were Southeast Reef Fish Survey (SERFS), Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), NorthEast Area Monitoring and Assessment Program (NEAMAP), and NorthEast Bottom Trawl Survey (NEBTS).

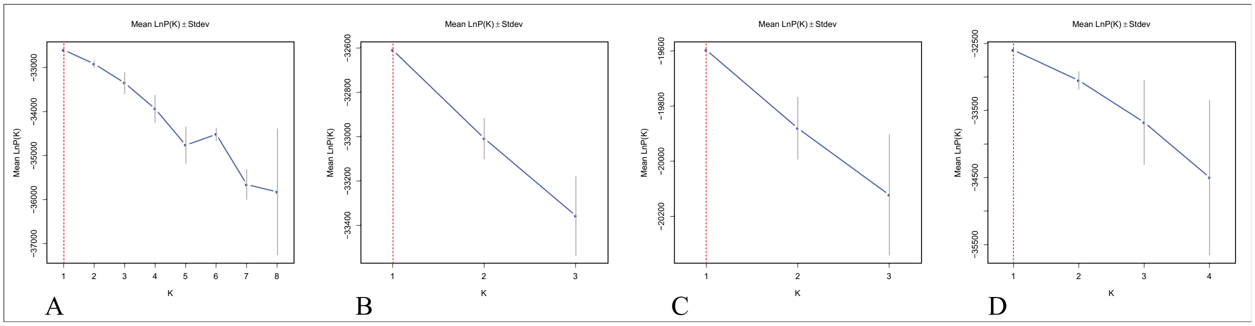


Figure 6. Log-likelihood plots for *Structure* analyses performed with (A) location priors for 8 collection areas (samples assigned to geographic regions); (B) location priors for 2 populations (samples assigned to either South or North with break at NC/VA border); (C) location priors for 2 populations (samples assigned to either South or North), excluding all fish smaller than 175 mm TL; (D) location priors for 4 groupings based on collector/survey.

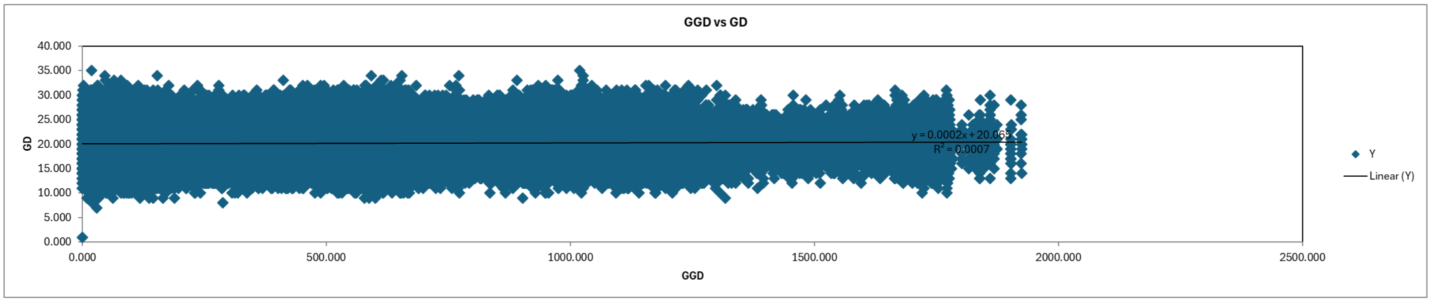


Figure 7. Isolation-by-distance plot with geographic distance on the x-axis and genetic distance on the y-axis.

Discussion / Conclusions

The results presented here provide the first multilocus assessment of the genetic variation of Black Sea Bass populations across the species' entire Atlantic coast distribution. Several approaches are commonly used to assess the geographic distribution of genetic diversity with multilocus datasets, including estimates of F_{ST}, genetic clustering analyses such as those performed in *Structure*, and Mantel tests to identify patterns of isolation by distance. Taken together, project results provide support for two genetic stocks of Black Sea Bass with weak genetic differentiation between the southern and northern populations with a transition occurring at approximately the North Carolina-Virginia border. The resulting genetic structure patterns would be consistent with a recent (in geological/evolutionary time) separation between northern and southern stocks followed by subsequent or contemporary gene flow.

Our analyses of Black Sea Bass population structure find patterns that are consistent with previously published studies that have similar geographic sampling along the Atlantic coast (Roy et al. 2012, McCartney et al. 2013). Both of the previous studies utilized a single locus, and gathered sequence data spanning ~340 base pairs (Roy et al. 2012) or ~580 bp (McCartney et al. 2013) of the mitochondrial control region to analyze the distribution of haplotypic diversity across the species' range. They also identified a shift in dominant haplotype frequencies at approximately the North Carolina – Virginia border. Although southern and northern stocks were dominated by different mitochondrial haplotypes, both studies found a low frequency of individuals in each region that exhibited the haplotype characteristic of the other region.

Roy et al. (2012) and McCartney et al. (2013) concluded strong genetic differentiation between northern and southern stocks on the basis of their calculation of significant F_{ST} values. Our dataset also infers significant F_{ST} values for pair-wise comparisons between northern and southern stock populations, although direct comparison of F_{ST} values among studies beyond the similarity in significant F_{ST} patterns is not appropriate due to the behavior of alternative data types on the metric's calculation. In general, the strength of the genetic distinctiveness is dependent on the characteristics of the genetic marker(s) evaluated. For instance, F_{ST} values calculated from datasets comprised of a single locus or multiple loci, and the number of alleles present at each locus can have a large influence on the scale of calculated values (Bird et al. 2011). Additionally, because it is inherited from only one parent, mitochondrial DNA reflects only 0.25 of the effective genetic population size compared to nuclear loci, and therefore diversity at mitochondrial loci can be more rapidly influenced by factors such as genetic drift. The differences in mitochondrial and nuclear markers between studies could potentially explain the increased genetic distinctiveness between southern and northern stocks reported in the Roy and McCartney studies.

The new microsatelite dataset also provides an inference of similar degree of gene flow between northern and southern stocks as reported in the previous studies based on calculated effective migration rates (116/generation in the current study; 63-179/generation from north to south of Cape Hatteras in Roy et al. [2012]; 179.5/generation from mid-Atlantic to North Carolina north of Cape Hatteras, and 19.2 from mid-Atlantic to south of Cape Hatteras in McCartney et al.[2013]). The southern directionality of migration rates inferred by both prior studies is presumably driven by either seasonal migratory behavior of adults in the northern stock, or through pelagic dispersal of larvae by southwesterly flowing inshore currents south of Cape Hatteras. The results of the current study are consistent with prior interpretations.

The assessment of heterozygosity, inbreeding, and effective population size of Atlantic Black Sea Bass populations suggest both are genetically healthy and have retained sufficient adaptive potential during population recovery/growth. While prior data are not available with the microsatellite data set for the northern population, the southern population metrics are highly consistent with data generated from 1985-2014 sample collection (O'Donnell and Darden, 2015) suggesting genetic diversity and adaptive potential is continuing to be maintained.

In summary, our project results are consistent with previous genetic stock structure findings indicating a difference in genetic composition between the South Atlantic and the Mid- and North Atlantic Black Sea Bass populations with a transition around North Carolina / Virginia with continuing gene flow between areas. Despite the reduction in the South Atlantic stock abundance, genetic health (based on heterozygosity, inbreeding, and effective population size) remains high without a change since the last genetic assessment with the same microsatellite panel. Therefore, given the lack of a change in neither the location of the genetic shift in Black Sea Bass stocks nor the degree of gene flow between stocks, it appears the southern stock is experiencing a constriction of its range under current climate conditions and not moving further north and introgressing with the northern stock.

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