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Atlantic coastwide population structure of striped bass *Morone saxatilis* using microsatellite DNA analysis

Isaac Wirgin[a,*], Lorraine Maceda[a], Matt Tozer[b,c], Joseph Stabile[d], John Waldman[b,c]

[a] Department of Environmental Medicine, NYU School of Medicine, 341 East 25th Street, New York, NY, 10010, USA
[b] Department of Biology, Queens College, 65-30 Kissena Boulevard, Queens, NY, 11367, USA
[c] Graduate Program in Biology, City University of New York, New York, NY, 10016, USA
[d] Department of Biology, Iona College, 715 North Avenue, New Rochelle, NY, 10801, USA

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ABSTRACT

Striped bass *Morone saxatilis* support one of the most popular and important inshore recreational and commercial fisheries along the Atlantic Coast of North America. Populations at both extremes of its distribution are largely resident while those in the center of its range (Hudson River, New York, to Roanoke River, North Carolina) are seasonally migratory, ranging from the Bay of Fundy, Canada, to the Outer Banks of North Carolina. Historically, population abundances of striped bass fluctuated widely, sometimes resulting in the imposition of severe management measures to restrict their harvest. Detailed knowledge of its rangewide population structure would aid in more effective management; however, most genetic studies addressing the structure of the migratory coastal stock have largely failed to achieve this goal. To address this need, we used multi-loci microsatellite DNA analysis. We identified six, and posibly one more, genetically distinct populations across the species' distribution, including the Miramichi, Shubenacadie, Hudson, Delaware-Chesapeake, Roanoke, and Santee-Cooper rivers. We also report significant genetic differentiation between the Nanticoke and Choptank rivers along the eastern shore of the Chesapeake Bay and collections from tributaries along the western shore of the Bay. The Annapolis and Saint John rivers, tributaries of the Bay of Fundy, historically hosted striped bass aggregations that were extirpated, or nearly so, by anthropogenic stressors in the late 20th century. No specimens with unique genotypes were found in collections from either river; instead the vast majority were admixed with genotypes of Shubenacadie River, Hudson River, Chesapeake Bay, and Roanoke River lineages. Finally, we show in simulations that these genetic markers should be informative in quantifying the contributions of the Hudson River, Chesapeake Bay-Delaware, and Roanoke River to mixed-stock harvests that occur within the range of the coastal migratory stock.

1. Background

Striped bass *Morone saxatilis* has been the subject of numerous studies to delineate its stock structure. In fact, nearly all methods used in fisheries science to discriminate stocks of fish have been applied to this species. These include such "classic" morphological approaches as meristics and morphometrics, and other phenotypic methods based on scale shape, trace element composition of scales, fatty acids, and parasite assemblages (reviewed in Waldman et al., 1988). Genotypic techniques have included cytogenetics (Rachlin et al., 1978), protein electrophoresis (Morgan et al., 1973), isoelectric focusing of eye lens protein (Fabrizio, 1987), restriction fragment length polymorphism analysis (RFLP) of mitochondrial DNA (mtDNA) (Wirgin et al., 1990), DNA fingerprinting (Wirgin et al., 1991), single nucleotide polymorphisms (SNPs) (Wirgin et al., 2005), microsatellite DNA (Robinson et al., 2004; Gauthier et al., 2013; Anderson et al., 2014), immunogenetics (Schill and Dorazio, 1990), and next generation single nucleotide polymorphism analyses (Leblanc et al., 2018). However, even such robust and widely used molecular approaches as RFLP analysis of mtDNA and DNA fingerprinting have not proved completely satisfactory as applied to some populations of striped bass.

Most of these efforts have focused on the "coastal migratory stock," i.e., the anadromous populations that migrate between rivers and the sea, co-occurring in marine waters, (Berggren and Lieberman, 1978; Wirgin et al., 1993a, 1993b; Wirgin et al., 1997; Mather et al. 2008). The two primary populations contributing to the coastal migratory stock originate in the Chesapeake Bay and the Hudson River. However, the Chesapeake Bay stock is an amalgam of some 12 tributary-specific

* Corresponding author.
E-mail address: isaac.wirgin@nyumc.org (I. Wirgin).

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subpopulations which may vary across time in their contributions to the larger Chesapeake stock (Waldman and Fabrizio, 1994). Also, striped bass are functionally anadromous and need not migrate, e.g., members of the Hudson population do not all maintain the same behavior; "male contingents" have been identified that vary from non-migratory to ones that make long coastal migrations (Secor et al., 2001). Furthermore, individuals may switch behaviors among these contingents. Migration from the Hudson is complicated by evidence indicating that the distance of migration from the river is density dependent (Waldman et al., 1990).

In addition to these two primary contributors, the coastal migratory stock also includes lesser populations from the Roanoke (Callihan et al., 2015) and Delaware (Waldman and Wirgin, 1994) rivers. Historically, the Delaware River was probably a major contributor to the migratory stock until its near extirpation in the mid 20th century and is likely a meaningful contemporary contributor with the recent rebuilding of its stock (Kneebone et al., 2014). Recent evidence from acoustic telemetry studies suggest that adult Roanoke River-spawned striped bass also undergo seasonal migrations in U.S. coastal waters from Massachusetts to North Carolina and likely contribute to mixed-stock ocean fisheries (Callihan et al., 2015).

Striped bass along the Atlantic Coast also occur south of the Roanoke River as far as the St. Johns River, Florida (Cheek et al. 1984). These populations are believed to be strictly non-migratory. Striped bass also are native to rivers entering the Gulf of Mexico, between the Suwannee River to the east and the Mississippi River to the west (Striped Bass Technical Task Force, 2006). All of these original populations also were non-migratory (Wirgin et al., 1989). All Gulf populations with the exception of that in the Apalachicola-Chatahoochee-Flint (ACF) rivers were believed to have been extirpated and subsequently restored with individuals from South Atlantic populations (Wooley and Crateau 1983). The ACF population persisted, but, was introgressed with genes from Atlantic Coast populations (Wirgin et al., 2005). Striped bass populations in California and Oregon along the Pacific Coast are non-native and are derived from the Hudson River population (Waldman et al., 1998).

Breeding populations of striped bass are also found north of the Hudson River, from the Kennebec River, Maine, to the St. Lawrence River. Historically, the Kennebec River supported a naturally reproducing population that was believed extirpated by the 1920 s–1930 s (Flagg and Squiers, 1994). However, efforts began in 1982 and continued through at least 1991 to reestablish a spawning population by the introduction of juvenile striped bass of Hudson River origin (ASMFC, 1993). Canadian populations occur in marine waters but appear more riverine than those that constitute the coastal migratory stock. An exception is the population of the Miramichi River, members of which have been found in waters of Nova Scotia and Prince Edward Island, and recently, as far as Labrador and Newfoundland (Andrews et al., 2019). The St. Lawrence population was extirpated in the 1960s (Rulifson and Dadswell, 1995) and has since been restored with broodstock from the Miramichi River (Robitaille et al., 2011).

Of particular current interest in Canada is the historical and contemporary genetic status of striped bass populations in the Annapolis and the Saint John rivers, which both empty into the Bay of Fundy. The Annapolis River, on the southeastern shore of the Bay, hosted a small reproducing striped bass population that supported a popular recreational fishery. However, it was extirpated by the mid 1990s (Douglas et al., 2003), apparently because of the construction of a tidal dam which altered estuarine circulation and early life-stage success and the construction of a tidal hydroelectric station whose turbines caused significant adult mortality (Dadswell et al., 2018). Similarly, the Saint John River, on the western shore of the Bay, once hosted reproducing striped bass until the completion of the Mactaquac Dam in 1968. Repeated efforts over the following decades failed to capture young life-stages that would be indicative of spawning success in the Saint John.

The genetic architecture of native populations of striped bass is not only influenced by the complexity of their freshwater watersheds and their varying tendencies to migrate to marine waters (and thus, more likely to stray when homing to their natal rivers), but they have life history attributes that strongly influence genetic characteristics. These include later maturation of females, a greater likelihood of females migrating in some populations, multiple males spawning with individual females, spawning of overlapping year classes, and highly variable inter-annual recruitment that may have led to bottlenecking (Waldman et al., 1998). Moreover, as the focus of intense fisheries, the Atlantic coastal migratory stock, particularly that emanating in the Chesapeake Bay, was reduced to alarmingly low abundances in the 1980s, primarily due to coastwide overharvesting and recruitment failures (Richards and Rago, 1999). It is possible that stocking of hatchery-produced striped bass in Chesapeake Bay further eroded differences among its subpopulations.

The modern molecular tool of mitochondrial DNA (mtDNA) analysis might have been expected to parse population differences among native striped bass populations, but the combination of life history characteristics described above appears to have limited mtDNA haplotype diversity (Waldman et al., 1998). Striped bass do display mtDNA molecular length differences and these have proved somewhat useful in stock discrimination and identification among some populations (e.g., Wirgin et al., 1989, 1993a, 1993b; Waldman et al., 1997; Robinson et al., 2004) although their use in management has proved controversial (Waldman and Wirgin, 1995).

Interrogation of nuclear DNA; however, is a favorable alternative to more sensitively define the population structure of striped bass and to estimate the contributions of populations to mixed aggregations (Wirgin et al., 1997; Waldman et al., 2012). Alternative approaches are available that focus on different types of nDNA, including single nucleotide polymorphisms (SNPs), minisatellite DNA, and microsatellites. All of these have been applied to striped bass to varying degrees. Surprisingly though, despite its popularity in other taxa, ease of application, and high levels of variation revealed, microsatellite analysis has rarely been applied to striped bass and never to address population structure across the species' complete coastwide distribution.

We used microsatellite analysis to better understand the population structure of striped bass across almost their entire native range. We also sought to evaluate the genetic distinctiveness of adult striped bass collected from the Annapolis River prior to its extirpation and the genetic status of recently collected juvenile striped bass from the Saint John River.

2. Methods

2.1. Sample collections

Samples of striped bass DNA were analyzed from 15 drainages known to currently support striped bass spawning, including 7 of the Chesapeake Bay (summarized in Table 1). Of note, several collections were made several decades ago, dating to the late 1970s. Many of these samples have previously been used for genetic analysis (Robinson et al., 2004; Wirgin et al., 1993a;1993b; Wirgin et al., 2005; Waldman et al., 2012). Sample collections newly analyzed in this study are from the Miramichi River, Hudson River, Delaware River, Upper Chesapeake Bay, and the Roanoke River. Analysis of paired collections each from the Miramichi River (1990 and 1997–1998), Hudson River (1990 and 2015), Upper Chesapeake Bay (1989, 2011, and 2016), Rappahannock River (1979 and 1989), Roanoke River (1989 and 2014), and Santee-Cooper system (1979 and 1982) separated by up to 27 years, allowed us to evaluate the long-term temporal stability of diagnostic genotypes in these systems. But their use also introduced the possibility that our genetic characterization of these spawning rivers would not accurately reflect their contemporary genetic compositions.

Sample collections targeted either adults near spawning areas during spawning season or age-0 juveniles to age-1 yearlings within

Table 1
Seventeen locales where striped bass were collected for this study, collection dates, gear type used, sample size (N), and total length mean and range for specimens in that collection.

Locales	Collection date(s)	Gear type	N	Total Length Mean, (Range) cm
Miramichi River	10/18/-11/2/90	Smelt bag net	24	15.3 (14.7–16.7)*
Miramichi River	8/12/97	Beach seine	20	4.6
Miramichi River	7/8/98	Beach seine	20	2.2
Shubenacadie River	9/6/91	Beach seine	14	10.5 (7.2–23)*
Shubenacadie River	8/27/92	Beach seine	40	8.7 (5.5–12.7)*
Saint John River	2014	Angling, gill and fyke nets	42	ND (12–112)*
Kennebec River	8/11/-11/23/94	Beach seine	24	8.6 (5.0–16.5)
Kennebec River	8/95	Beach seine	25	11.5 (7.7–17.2)
Annapolis River	9/94	Angling	25	81.5 (50.8–119.4)*
Annapolis River	5/20-9/6/95	Angling	55	92.4 (54.1–119.4
Annapolis River	6/20-6/23/96	Angling	14	39.1 (35.6–43.2)*
Hudson River	5/31-6/20/89	Haul seine, Angling, Electrofishing	82	48.5 (19.5–60.8)*
Hudson River	5/07	Haul seine	32	78.8. (53–108.1)
Hudson River	4-5/15	Haul seine	53	81.6 (53.8–101.5)
Delaware River	4/15/-5/24/10	Electrofishing	77	59.9 (26.1–115.4)
Upper Bay	4/26/89	Drift gill net	47	41.4 (31.5–66)*
Upper Bay	4-5/11	Gill net	30	78.6. (35.3–116.4)
Upper Bay	4-5/16	Gill net	48	69.1 (33.8–102.5)
Choptank River	4/11/89	Drift gill net	41	42.3 (29.3–68.3)*
Potomac River	4/11-4/21/89	Drift gill net	51	42.7 (30.7–56.4)*
Rappahannock River	5/1/89	Pound net	43	34.0(21.2–54.5)*
Rappahannock River	11/79	Pound net	22	ND
York River	11/79	Pound net	23	ND
Patuxent River	7-9/97	Beach seine	41	8.6 (4.8–14.5)
Nanticoke River	7-8/97	Beach seine	54	ND (6.2–8.3)
Pocomoke River	7/97	Beach seine	19	5.5 (4.5–7)
Roanoke River	5/8-9/89	Angling	31	38.2 (34.3–59.2*
Roanoke River	7-10/10	Gill net	51	119.8 (77.0–174)
Roanoke River	8-9/14	Gill net	62	80.9 (56–116)
Santee Cooper Reservoir	9/24-9/26/79	Gill net	29	60.8 (39.8–78.8)
Santee Cooper Reservoir	4/89	Gill net	24	ND
Santee Cooper Reservoir	4/92	Gill net	48	70.8 (60.0–83.5)
*fork length				

their natal river system. In general, juvenile striped bass have been considered to be restricted to natal rivers and estuaries (Merriman, 1941; Nichols and Miller, 1967; Rulifson and Dadswell, 1995).

Older collections from the 1970s, 1980s, and 1990s consisted of liver tissues that were frozen until analysis. Collections made in 2010 from the Delaware River and 2010 and 2014 from the Roanoke River consisted of fin clips that were stored in 95 % EtOH until processing. The 2015 and 2017 Hudson River collections, and the 2011 and 2016 Upper Chesapeake Bay collections consisted of archived dried scales.

We also analyzed collections from two rivers in Canada whose native populations may have been extirpated because of anthropogenic disturbances in the mid-to- late 20th century, including the Annapolis River, Nova Scotia, and the Saint John River, New Brunswick. Samples from the Annapolis River were primarily adults (mean TL = 36.4 in.) collected by angling between 1994 and 1996. Striped Bass were collected from three locations in the Saint John River, including the Kennebecasis River, Grand Lake, and the Mactaquac Dam. Grand Lake and Mactaquac Dam juveniles were caught in 2015. Kennebecasis River juveniles were caught in 2014, 2015, and 2016.

2.2. DNA isolations

Total DNA was isolated from all tissue and scales samples by their incubation in hexadecyltrimethylammonium bromide buffer (CTAB) (Saghai-Maroof et al., 1984) and digestion with proteinase K at 65 °C, followed by standard phenol-chloroform extractions and alcohol precipitations. DNA concentrations were evaluated and quantified using a Nanodrop ND-100 spectrophotometer (NanoDrop Technologies, Wilmington Delaware) and adjusted to 25 ng/μL for standardization of subsequent procedures.

2.3. DNA analysis

Eight microsatellite loci were selected for analysis, including *SB91, SB108, SB113,* and *SB117D* (Roy et al., 2000), that were shown to be useful in distinguishing some striped bass populations (Robinson et al., 2004; Wirgin et al., 2005). Four additional loci, (*MSM1334, MSM1357, MSM1584,* and *MSM1598*) were selected from the battery developed by Rexroad et al. (2006), giving preference to those that showed high levels of heterozygosity. This was done to improve resolution power in population discrimination and assignment tests (Estoup et al., 1998) and because previous genetic studies have shown low levels of genetic diversity among populations of striped bass (Wirgin et al., 1993a, 1993b; Diaz et al., 1997; Brown et al., 2005).

Polymerase chain reactions (PCRs) for *SB91, SB108, SB113,* and *SB117D* were as performed as described in Robinson et al. (2004). Remaining PCRs were conducted in 12.5-μl total volumes that contained 50 ng of total DNAs, 0.5 μL of each primer (1 μM stock) (Integrated DNA Technologies, Coralville, IA), 0.1 μL of deoxynucleotide triphosphates (dNTPs) (250-μM stock of each) (GE Healthcare, Chicago, IL.), 1.25 μL of KlenTaq1 reaction buffer, and 0.0125 μL (0.75 units) of KlenTaq1 enzyme (AB Peptides, Inc., St. Louis, Missouri). All forward primers were labeled with Well-Red dyes on their 5′ end (Sigma Aldrich, St. Louis, MO). Cycling parameters were as follows: initial denaturation at 95 °C for 5 min, followed by 65 cycles of denaturation at 94 °C for 30 s, annealing at 58 °C (*MSM 1357* and *MSM1584*), 62 °C (*MSM 1334*), or 63 °C (*MSM 1598*) for 30 s, extension at 72 °C for 45 s, and a final extension at 72 °C for 7 min.

Characterization of microsatellite genotypes was performed using a Beckman Coulter CEQ8000 capillary-based DNA sequencer (Beckman Coulter, Inc., Fullerton, CA). To make economical use of the sequencer 0.75–6.0 μL of product from each of up to four PCR reactions were multi-pooled and loaded onto 96-well plates along with 0.5 μL of

Beckman Coulter CEQ DNA Size Standard-400 and 40 μL of Sample Loading Solution (Beckman Coulter). All analyses were performed using the FRAG 1 program (Beckman Coulter).

2.4. Statistical analysis

Departure from Hardy-Weinberg equilibrium and linkage disequilibrium were assessed with GENEPOP version 4.1.0 (Rousset, 2008) using the default parameters; dememorizatiion number = 1000, batches = 100 batches, and iterations = 1000. Allele frequency heterogeneity among all pairs of spatial collections was analyzed using log-likelihood G-statistics with 999 permutations implemented in GenoDive V.20b27 (Meirmans and Van Tienderen, 2004). Genetic differences among spatial collections were also quantified using Wier and Cockerham's (1984) F_{ST} analogue θ calculated in FSTAT v 2.9.3.2 (Goudet, 1995). F_{ST} is highly dependent on within-population diversity (Hedrick, 1999; Balloux and Lugon-Moulin, 2002; Meirmans and Hedrick, 2011). When loci with large numbers of alleles are examined and population diversity is high the maximum value of F_{ST} is severely deflated, complicating comparisons between populations or different loci. Thus, F'_{ST} tests that corrected the F_{ST} estimates for heterozygosity within populations were conducted using GenoDive (Meirmans and Van Tienderen, 2004). In all instances, Bonferonni corrections were used to account for multiple tests (Rice, 1989). Inbreeding coefficients for each population were also calculated in Genodive.

Temporal stability among temporally separated years of collections from the Miramichi River, Hudson River, Upper Chesapeake Bay, Rappahannock River, Roanoke River and the Santee-Cooper system were evaluated using the F_{ST} analogue θ calculated in Genodive (Meirmans and Van Tienderen, 2004). The statistical significance of these temporal comparisons were Holm-Sequential Bonferroni corrected using Gaetano's (2013) calculator.

Underlying population structure within the genotypic data was analyzed using STRUCTURE v.2.3.4 (Pritchard et al., 2000). STRUCTURE infers the number of genetic clusters, K, within a set of genetic data using a Monte Carlo-Markov chain Bayesian method that maximizes within-cluster Hardy–Weinberg and linkage equilibria. We used the admixture model with sampling locations as a prior with allele frequencies correlated (Hubisz et al. 2009). In all instances, we used burn-in lengths of 100,000 and run lengths of 100,000. Ten replicates were run for each K at K = 1–15. The best value of K was determined from optimum values of lnP(D) (Pritchard et al., 2000), ΔK (Evanno et al., 2005), MedMeaK', MaxMeakK', MedMedK', and MaxMedK' (Puechmaille, 2016) all determined in StructureSelector (Li and Liu, 2018). STRUCTURE figures were generated in StructureSelector (Li and Liu, 2018).

Discriminant Analysis of Principal Components (DAPC) was done using the R package adegenet (v2.1.1) (Jombart, 2008) to further define population structure. DAPC clusters by transforming genetic data using a principal component analysis (PCA) that has the largest between-group variance and smallest within-group variance (Jombart and Collins, 2015). Bayesian Information Criterion (BIC) values were used to determine the most appropriate range of clusters. The a-score function of adegenet determined the optimal range of principal components (PCs) that must be retained to have sufficient power of discrimination while avoiding the retention of too many dimensions that lead to overfitting of the data set. The optimal number of PCs to retain was calculated by measuring the difference between the proportion of successful reassignments and values obtained using random groups (Jombart and Collins, 2015). DAPC analyses were run on the coastwide striped bass data set and the coastal migratory stock (Hudson River, Delaware, Chesapeake tributaries and Roanoke) data set with the lower number of PCs retained in each analysis.

We were also interested in determining if the extent of genetic differentiation among the Hudson River, Delaware-Chesapeake Bay, and Roanoke River collections observed in this study would accurately estimate the contributions of these populations to mixed-stock aggregations. To do this, we used the "100 % simulation" option which is a tool to evaluate the accuracy of genetic stock identification analysis in ONCOR (Kalinowski et al., 2008). In this form of analysis, a fishery sample is simulated in which all of the specimens are from the same population. We used a fishery sample size of 2000, 1000 simulations, and the "same sample size as baseline" option which used the method of Anderson et al. (2007) to simulate mixture genotypes and estimate their probability in base populations. We followed this with the "Realistic fishery simulation" (1000 sample size and 1000 simulations) in ONCOR (Kalinowski et al., 2008) which simulates samples from a fishery and tests how well the baseline data can identify the origin of each specimen. We evaluated three realistic fishery composition scenarios for the coastal migratory stock in which all three populations (Hudson, Chesapeake-Delaware, and Roanoke) were represented, but in varying proportions: a) large Hudson and small Chesapeake-Delaware contributions; b) large Chesapeake-Delaware and small Hudson contributions; c) equal Hudson and Chesapeake-Delaware contributions. All three scenarios contained small Roanoke contributions. All three of these scenarios are representative of what has been reported in previous empirical mixed-stock studies of the coastal migratory stock of striped bass (Berggren and Lieberman, 1978; Fabrizio, 1987; Wirgin et al., 1993a, 1993b).

3. Results

3.1. Summary statistics

Our ability to successfully score these microsatellites across the 17 collections was high, with a mean failure rate across all loci of 0.88 %. The failure rate ranged from 0 % at MSM1584 to 2.3 % at SB91. There was evidence of linkage disequilibria between nine pairs of loci, however, only the combinations of MSM1357 and SB108, MSM1584 and MSM1334, and SB91 and SB113 exhibited disequilibria in more than one population. The combinations of MSB1357 and SB108, MSM1584 and 1334, and SB91 and SB113 showed linkage disequilibria in 3, 2, 2 collections, respectively. All loci were in Hardy-Weinberg equilibrium in all populations with the exception of SB117, which exhibited disequilibrium in four populations. In summary, all loci were retained for the population analyses described below because none of them exhibited disequilibria singly or in pairs across many collections.

Overall genetic diversity was generally lower in populations at the northern and southern extremes of the species' range and higher in those populations at the center of its distribution (Table 2). For example, all three measures of allelic diversity were lower in the Miramichi River and Shubenacadie River than in populations nearer the center of the species' distribution. Similarly, allelic diversity was also somewhat lower in the Santee-Cooper system than in the neighboring Roanoke River and most tributaries of the Chesapeake Bay. However, two Canadian collections, those from the Annapolis and Saint John rivers, displayed levels of diversity that were comparable to populations in the mid-Atlantic Bight.

3.2. Temporal stability analysis

We also tested the long-term (4-26 years) temporal stability of genotypes among paired collections from the Miramichi River (1990, 1998), Hudson River (1989, 2007, 2015), Upper Chesapeake Bay (1989, 2011, 2016), Rappahannock River (1979, 1989), Roanoke River (1989, 2010, 2014), and the Santee-Cooper system (1979, 1989, 1992). There was no evidence of significant temporal instability of genotypes within these populations after sequential Bonferroni correction, with the exception of the 1990–2011 collections comparison from the Upper Chesapeake Bay (Table 3). However, both of these Upper Chesapeake Bay collections fell within the same genetic clusters in the coastwide (Fig. 2A) and Chesapeake Bay-specific (Fig. 2b) STRUCTURE analysis

Table 2
Genetic diversity in 17 striped bass collections coastwide determined by microsatellite DNA analysis at eight loci.

Collection Locale	Mean Number Alleles	Effective Number Alleles	Allelic Richness	Observed Heterozygosity	Expected Heterozygosity	Inbreeding Coefficient
Miramichi	8.875	4.447	5.75	0.712	0.695	−0.024
Shubenacadie	9.625	5.164	6.61	0.735	0.771	0.047
Saint John	12.875	7.245	8.42	0.732	0.834	0.122
Annapolis	17.750	8.950	9.21	0.818	0.877	0.067
Kennebec	15.000	8.704	8.88	0.854	0.873	0.022
Hudson	17.625	9.003	8.89	0.838	0.873	0.040
Delaware	15.500	8.262	8.90	0.837	0.862	0.029
Upper Bay	18.000	8.461	8.96	0.824	0.852	0.033
Choptank	12.875	7.218	8.47	0.845	0.842	−0.003
Nanticoke	14.125	7.640	8.54	0.818	0.853	0.041
Pocomoke	11.375	7.441	8.95	0.826	0.863	0.043
Patuxent	13.125	7.420	8.50	0.840	0.845	0.005
Potomac	15.250	8.580	9.07	0.889	0.869	−0.023
Rappahannock	15.125	7.907	8.68	0.848	0.861	0.014
York	12.375	7.841	9.10	0.810	0.873	0.072
Roanoke	17.875	8.966	8.87	0.873	0.873	0.025
Santee-Cooper	12.750	4.611	6.83	0.774	0.774	0.026

Table 3
An evaluation of the long-term stability of genotypes between the temporally separate paired collections of striped bass from six spawning populations. *P* values from F_{ST} analysis were Holm-sequentially Bonferroni corrected using Gaetano's (2013) calculator. Only the F_{ST} value for the 1990 and 2011 Upper Chesapeake Bay comparison proved statistically significant after correction.

Collection Locale	Years Compared	F_{ST}
Miramichi River	1990-1997-8	0.005
Hudson River	1989-2015	−0.000
	1989-2007	0.007
	2007-2015	0.005
Upper Chesapeake Bay	1990–2011	*0.011*
	1990-2016	0.002
	2011-2016	0.007
Rappahannock River	1979-1989	0.007
Roanoke River	1989-2010	0.002
	1989-2014	0.001
	2010-2014	0.001
Santee Cooper	1979-1992	0.007
	1979-1989	0.002
	1989-1992	0.002

figures.

3.3. Population structure analyses

After Bonferroni correction, most pairwise comparisons among collections using either G statistics, F_{ST}, or F'_{ST} showed strong significant allelic heterogeneity, with the following exceptions (Tables 4–6). The Kennebec River collection was not significantly different than that from the Hudson River. The Delaware River sample was not significantly different from any individual collection within the Chesapeake Bay, except for that from the York River. Similarly, comparison of the Delaware River collection with the pooled Chesapeake Bay collection was not significant (F_{ST} = 0.001; p = 0.306). Most pairwise comparisons among tributaries of the Chesapeake Bay were not significantly different, with the exception of all comparisons of the Nanticoke and some comparisons of the Choptank on the eastern shore of the Bay versus all tributaries of the western side of the Bay. In contrast, there was strong allelic differentiation among all comparisons at both extremes of the species' distribution, including both collections from Canadian rivers, the Roanoke River, and the Santee-Cooper system.

We used leave-one-out tests implemented in ONCOR to quantify our accuracy in assigning specimens to the systems in which they were collected (Table 7). For the Chesapeake Bay, we pooled all collections for this analysis. Our assignment accuracy was perfect for the Miramichi River (100 %) and almost so for the Shubenacadie River in Canada (98 %). Similarly, our assignment accuracy for the Santee-Cooper system was very high at almost 98 %. The assignment accuracy to other systems was much lower, ranging from 73.6 % for the Hudson River to 65.2 % for the Roanoke River system. The largest misidentification for Hudson River collections was the Chesapeake Bay (11.9 %) and conversely for the Chesapeake Bay it was the Hudson River (14 %). The largest misidentification for the Roanoke River collection was the Chesapeake at 20.3 %.

STRUCTURE analysis was performed to determine the number of genetic clusters within the species' almost complete coastwide distribution from the Miramichi River, New Brunswick to the Santee-Cooper system, South Carolina. Six metrics were used to identify genetic clusters from the STRUCTURE results including: ln Pr(X|K, ΔK, MedMeaK', MaxMeakK', MedMedK', and MaxMedK'. The last four metrics are less sensitive to uneven sampling of genetic populations than ln Pr(X|K and, particularly ΔK (Puechmaille, 2016). We obtained quite different estimates of K with the six metrics. ΔK provided the lowest estimate, K = 3, ln Pr(X|K suggested that K = 6, and the four new metrics all indicated that K = 7. We provide STRUCTURE figures for the three results in Fig. 2 below.

In the K = 3 figure (Panel 1), major clusters included (1) the two most northern collections in Canada (Miramichi River and Shubenacadie River) in Canada, (2) a mid-Atlantic cluster from the Kennebec River, Maine to the Roanoke River, North Carolina and (3) a cluster that only included the Santee Cooper system, South Carolina. In the K = 6 figure (Panel 2), the six major clusters that were identified included the Miramichi River, Shubenacadie River, Hudson River, Delaware River-Chesapeake Bay, Roanoke River, and Santee Cooper collection. In the K = 7 figure (Panel 3), the six major clusters identified in the K = 6 figure remain well differentiated but there is some indication of division within the Chesapeake Bay with the Choptank River and Nanticoke RIver collections from the eastern shore of Chesapeake Bay being differentiated from the Delaware River and Chesapeake Bay collections from the western shore of the Bay.

We further explored the possible heterogeneity within the larger Chesapeake Bay cluster by performing STRUCTURE analysis of collections from the eight Chesapeake tributaries and Delaware River alone with K = 1-9. The ΔK method and the other four newer approaches (but not the (ln Pr(X|K method) all suggested that the larger Chesapeake Bay-Delaware Bay cluster identified previously was actually comprised of two clusters, with the Choptank River and Nanticoke River collections on the eastern side of the Bay well differentiated from the Delaware River and other collections from the western side of the Bay. The existence of two clusters among the eight Chesapeake Bay collections is well-supported in the STRUCTURE figure depicted in Fig. 2B. Furthermore, the Delaware River collection appears to be

Table 4
Pairwise comparisons of allelic frequencies at eight microsatellite loci among 17 coastwide collections of striped bass using log-likelihood G-statistics implemented in GenoDive 2.0b27. G statistics are depicted below the diagonal and *p* values for comparisons above the diagonal.

Locale	Mir	Shu	Sai	Ann	Ken	Hud	Del	UB	Cho	Nan	Poc	Pat	Pot	Rap	Yor	Roa	San
Miramichi		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Shubenacadie	788.5		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Saint John	616.7	307.2		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Annapolis	1127	752.5	354.4		0.002	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.256	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Kennebec	812.9	576.5	252.2	246.1		0.003	0.002	< 0.001	< 0.001	< 0.001	0.092	0.002	0.074	< 0.001	0.018	< 0.001	< 0.001
Hudson	1263	860.8	417.8	348.7	215.3		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Delaware	1041	791.6	373.9	317.8	221.7	464.6		0.130	0.008	0.029	0.412	0.010	0.237	0.004	< 0.001	< 0.001	< 0.001
Upper Bay	1264	869.3	421.3	333.7	264.4	541.2	188.1		0.006	0.002	0.774	0.010	0.043	0.014	< 0.001	< 0.001	< 0.001
Choptank	848.6	678.9	345.0	346.6	245.0	442.8	178.7	205.8		0.009	0.021	< 0.001	< 0.001	0.002	< 0.001	< 0.001	< 0.001
Nanticoke	991.5	732.2	371.5	330.1	230.6	467.9	174.3	229.3	177.6		0.364	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Pocomoke	579.7	425.9	253.7	167.0	162.3	215.4	143.0	136.5	165.0	137.8		0.939	0.361	0.540	0.107	0.006	< 0.001
Patuxent	771.6	583.6	332.0	253.8	202.4	306.8	188.8	208.9	215.2	242.7	100.9		0.213	< 0.001	< 0.001	< 0.001	< 0.001
Potomac	837.4	654.4	332.0	238.7	171.4	302.2	160.5	192.9	204.8	218.4	146.0	156.9		0.146	0.016	< 0.001	< 0.001
Rappahannock	1055	751.3	369.0	242.7	221.8	382.2	201.4	202.4	202.5	259.0	133.3	185.7	168.0		< 0.001	< 0.001	< 0.001
York	620.1	524.7	284.7	218.3	185.1	302.6	247.9	221.0	239.4	251.9	168.8	211.6	184.8	211.1		< 0.001	< 0.001
Roanoke	1368	1031	507.3	391.8	274.3	583.9	329.0	445.7	346.4	379.1	196.7	276.5	234.6	293.2	219.7		< 0.001
Santee Cooper	1897	1400	995.5	1135	931.6	1379	1112	1374	840.2	1025.2	472.0	831.3	943.7	1000.7	605.5	1326.5	

homogenous with the remainder of the collections from the western shore of the Chesapeake Bay.

Bayesian information criteria values of DAPC analysis of coastwide population structure supported a range of 8–12 clusters as reasonable explanations of the data set. The number of PCs retained varied from 40 to 70 and final analyses were run with the lowest number as indicated by the a-score. Fig. 3 illustrates the DAPC analysis of the coastwide data set retaining 42 PCs and using 10 clusters. In this analysis, the Shubenacadie River collection formed a distinct cluster. The Miramachi River and Saint John River samples were intermediate to the Shubenacadie River collection and all other river samples. The collections from the Kennebec, Hudson, Delaware, Chesapeake tributaries and Roanoke rivers overlapped with one another. The southernmost sample, the Santee Cooper collection, formed the most distinct cluster in the coastwide analysis. DAPC analysis was also conducted on the coastal migratory stock to assess population structure among the rivers that overlapped in the coastwide analysis. The number of PCs retained in the coastal migratory stock analysis was 50 and BIC values clearly supported 10 clusters. The DAPC plot of the coastal migratory stock illustrated in Fig. 4 is consistent with the coastwide analysis in that there is a high degree of overlap among collections from these rivers. However, the Hudson River formed a fairly distinct cluster and the Roanoke River was distinguishable from the Chesapeake Bay tributaries. Consistent with all of the previous analyses, the Delaware River sample overlapped with collections from the Chesapeake Bay tributaries.

3.4. Genetic status of the Saint John River population

In both the $K = 6$ and $K = 7$ figures, the collection from the Saint John River exhibited mixed ancestry. The majority of the individual specimens in the Saint John River collection seemed to be of mixed ancestry representing genetic signatures that were common in the Shubenacadie River, Hudson River, and Chesapeake Bay collections. Therefore, we further explored the ancestry of specimens in the Saint John River collection using Individual Based Assignment (IBA) testing. Interestingly, of the 42 specimens in the Saint John River collection, 11 specimens exhibited pure Shubenacadie River ancestry, 7 displayed pure Chesapeake Bay ancestry, and 2 showed pure Hudson River ancestry, each with greater than a 99 % probability (Table 8). The remaining 22 specimens exhibited hybrid lineages with 17 specimens showing mixed Hudson-Chesapeake ancestry, 4 specimens exhibiting mixed Shubenacadie-Hudson ancestry and 1 specimen showing mixed Shubenacadie-Chesapeake ancestry.

3.5. Genetic status of the Annapolis River population

Samples from the Annapolis River were collected just prior to the population's apparent extirpation in the mid to late 1990s. Similar to the Saint John River, the collection from the Annapolis River exhibited mixed ancestry under both the $K = 6$ and $K = 7$ scenarios. Of the 20 (21 %) specimens that exhibited pure ancestry with > 99 % probability, 10 (10.5 %), 6 (6.3 %) and 4 (4.2 %) were of Chesapeake Bay, Hudson River, and Shubenacadie River ancestry, respectively (Table 8). The remainder of specimens (79 %) displayed hybrid genotypes with Hudson-Chesapeake specimens (41 %) predominating. Surprisingly, many of the admixed individuals contained genotypes with a strong Roanoke River component. Ten specimens (10.5 %) showed a hybrid Roanoke-Chesapeake profile while another 9 (9.5 %) displayed a hybrid Roanoke-Hudson genetic signature. Only 1 specimen exhibited a hybrid profile that contained a Shubenacadie component.

3.6. Genetic status of the Kennebec River population

The Kennebec River sample clustered with mid-Atlantic collections under all three scenarios described above ($K = 3$, $K = 6$, $K = 7$), consistent with a likely Hudson River origin to its contemporary

Table 5
Pairwise F_{ST} values among collections of striped bass from 17 coastwide rivers based on microsatellite DNA analysis at eight loci. *P* values in bold are significant after Bonferroni correction at $p = 0.000368$.

Locale	Mir	Shu	Sai	Ann	Ken	Hud	Del	UB	Cho	Nan	Poc	Pat	Pot	Rap	Yor	Roa	San
Miramichi																	
Shubenacadie	**0.090**																
Saint John	**0.590**	**0.017**															
Annapolis	**0.960**	**0.053**	**0.022**														
Kennebec	**0.090**	**0.052**	**0.018**	**0.006**													
Hudson	**0.097**	**0.057**	**0.029**	**0.008**	0.002												
Delaware	**0.097**	**0.061**	**0.029**	**0.008**	**0.007**	**0.013**											
Upper Bay	**0.101**	**0.065**	**0.033**	**0.010**	**0.013**	**0.019**	0.001										
Choptank	**0.100**	**0.071**	**0.034**	**0.015**	**0.016**	**0.026**	0.004	0.004									
Nanticoke	**0.109**	**0.065**	**0.034**	**0.011**	**0.009**	**0.017**	0.002	0.006	0.006								
Pocomoke	**0.108**	**0.060**	**0.027**	0.002	0.005	**0.011**	−0.004	−0.002	0.005	−0.003							
Patuxent	**0.105**	**0.067**	**0.034**	**0.009**	0.011	**0.015**	0.003	0.004	**0.010**	**0.008**	−0.006						
Potomac	**0.093**	**0.061**	**0.025**	0.005	0.004	**0.011**	0.002	0.002	**0.008**	**0.008**	0.001	0.003					
Rappahannock	**0.108**	**0.068**	**0.033**	0.004	**0.008**	**0.013**	0.002	0.002	0.007	**0.009**	−0.001	0.004	0.001				
York	**0.099**	**0.075**	**0.029**	0.004	0.008	**0.020**	**0.013**	**0.012**	**0.014**	**0.017**	0.002	0.014	0.006	0.009			
Roanoke	**0.114**	**0.071**	**00.41**	**0.008**	**0.010**	**0.013**	**0.012**	**0.016**	**0.023**	**0.017**	0.008	**0.014**	**0.010**	**0.008**	**0.010**		
Santee-Cooper	**0.203**	**0.148**	**0.121**	**0.076**	**0.090**	**0.076**	**0.076**	**0.092**	**0.099**	**0.098**	**0.082**	**0.098**	**0.091**	**0.085**	**0.083**	**0.067**	

population. However, in addition to the expected Hudson River signal, many of the Kennebec River specimens exhibited an admixed profile consistent with a partial Chesapeake Bay origin.

3.7. Utility of these markers in mixed stock analysis

We used both 100 % single assignment unit simulations and more realistic fishery mixture simulations to quantitatively evaluate the potential effectiveness of our markers in mixed stock analysis. In the 100 % single unit simulation, assignment accuracy exceeded 93 % for all populations except the Roanoke River, were it was 82 % (Table 9). In the three more realistic fishery simulations, mean assignment accuracies were within 1.2 %, 2.6 %, and 4.5 %, respectively, of the actual assigned values (Table 10).

4. Discussion

4.1. Coastwide genetic population structure

Based on the STRUCTURE and DAPC analyses our study demonstrated that there are at least six and possibly seven genetic clusters of striped bass across its almost complete Atlantic Coast distribution. These clusters correspond well with six extant spawning populations, including the Miramichi River, Shubenacadie River, Hudson River, Delaware Bay-Chesapeake Bay, Roanoke River, and Santee-Cooper

Table 7
Proportion of baseline individuals correctly assigned to the river in which they were collected based on results at eight microsatellite loci and leave-one-out tests implemented in ONCOR. The population to which the largest percentage of specimens were misidentified is included. Specimens from tributaries of the Chesapeake Bay were pooled for analysis.

Collection Locale	N	% Correct	Largest Misidentification	%
Miramichi	61	100 %	None	NA
Shubenacadie	50	98 %	Chesapeake	2.0 %
Hudson	159	73.6 %	Chesapeake	11.9 %
Chesapeake	387	72.1 %	Hudson	14.0 %
Roanoke	138	65.2 %	Chesapeake	20.3 %
Santee-Cooper	89	97.8 %	Chesapeake	1.1 %

Table 8
Ancestry of striped bass collected from the Saint John River and Annapolis River based on microsatellite DNA analysis at 8 loci.

Collection Locale		Lineage							
	N	Shub	Huds	Ches	Shub-Huds admix	Shub-Ches admix	Huds-Ches admix	Huds-Roan admix	Ches-Roan admix
Saint John	42	11	2	7	4	1	17	0	0
Annapolis	95	4	6	10	0	1	39	14	21

Table 6
Pairwise F_{ST}^{I} values among collections of striped bass from 17 coastwide rivers based on microsatellite DNA analysis at eight loci.

Locale	Mir	Shu	Sai	Ann	Ken	Hud	Del	UB	Cho	Nan	Poc	Pat	Pot	Rap	Yor	Roa
Miramichi																
Shubenacadie	0.333															
Saint John	0.243	0.085														
Annapolis	0.457	0.308	0.154													
Kennebec	0.409	0.291	0.122	0.046												
Hudson	0.464	0.329	0.198	0.064	0.013											
Delaware	0.441	0.334	0.193	0.061	0.050	0.100										
Upper Bay	0.456	0.350	0.208	0.073	0.091	0.134	0.008									
Choptank	0.420	0.364	0.204	0.110	0.110	0.185	0.023	0.022								
Nanticoke	0.474	0.342	0.214	0.080	0.066	0.125	0.010	0.040	0.038							
Pocomoke	0.454	0.311	0.170	0.010	0.030	0.077	−0.033	−0.019	0.024	−0.029						
Patuxent	0.439	0.336	0.199	0.064	0.066	0.105	0.016	0.018	0.051	0.045	−0.073					
Potomac	0.419	0.339	0.165	0.036	0.029	0.085	0.014	0.015	0.052	0.058	−0.000	0.015				
Rappahannock	0.486	0.371	0.212	0.031	0.060	0.094	0.015	0.013	0.046	0.062	−0.012	0.023	0.004			
York	0.434	0.406	0.193	0.033	0.061	0.155	0.095	0.082	0.090	0.119	0.002	0.083	0.044	0.066		
Roanoke	0.546	0.405	0.279	0.064	0.080	0.101	0.088	0.114	0.160	0.122	0.059	0.094	0.073	0.061	0.077	
Santee-Cooper	0.771	0.648	0.606	0.435	0.500	0.433	0.462	0.495	0.505	0.516	0.428	0.502	0.500	0.460	0.449	0.382

Table 9
A 100 % simulation performed in ONCOR to evaluate the accuracy of a suite of eight microsatellite markers in mixed stock analysis. In this simulation, a fishery sample was simulated in which all the individuals were from the same population. The proportion of individuals from each baseline population that were assigned to that population along with 95 % CI are indicated.

Population Estimates			
Collection	Average	95 % CI	
Miramichi	0.999	0.996	1.000
Shubenacadie	0.998	0.991	1.000
Hudson	0.930	0.872	0.981
Chesapeake-Delaware	0.977	0.922	0.999
Roanoke	0.819	0.741	0.895
Santee-Cooper	0.999	0.991	1.000

system. Furthermore, in STRUCTURE analysis we found evidence of genetic heterogeneity among Chesapeake Bay tributaries with two of the eastern shore populations being discrete from all the populations along the western shore of the Bay. Moreover, in both STRUCTURE and DAPC analyses, there was no evidence of genetic differentiation between the Delaware River collection and either individual or pooled collections from tributaries of the Chesapeake Bay. However, the Delaware River population was discrete from the Hudson River population to its immediate north.

Interestingly, populations at the extremes of the species' range exhibited far greater genetic differentiation from proximal populations than those towards the center of its distribution. For example, the Miramichi River and Shubenacadie River populations were highly divergent from each other and all populations in U.S. waters. The strong differentiation among the Miramichi River, Shubenacadie River, and all U.S. populations observed in this study with microsatellites confirms results from our earlier studies with mtDNA (Wirgin et al., 1993a, 1993b) which reported similar divergence among these same populations. Similarly, the Santee-Cooper population was highly distinct from the neighboring Roanoke River and all other populations coastwide. In contrast, populations nearer the center of the species' distribution in the Roanoke River, tributaries of the Chesapeake Bay, Delaware River, and Hudson River showed much lower levels of genetic divergence among them. While the individual and pooled Chesapeake Bay collections were significantly genetically differentiated and formed distinct genetic clusters from the Hudson River population to their north and Roanoke River to their south, there was no evidence of genetic divergence between either the pooled or individual Chesapeake collections and the proximal Delaware River population.

We suggest that the contrast in levels of genetic divergence between populations at the extremes of the species' distribution and those at the center reflect their different migratory behaviors or their degree of geographic isolation, or both. Those populations at the center of the range i.e., the Hudson, Delaware, and Chesapeake and possibly, to a lesser degree, the Roanoke (Waldman and Fabrizio, 1994; Callihan et al., 2015) are highly migratory within coastal waters, with recaptures of tagged individuals from as far north as the upper Bay of Fundy (Waldman et al., 1990). This presents opportunities for strays to recolonize or augment populations within that reach, including the Kennebec, Saint John, and Annapolis rivers, as demonstrated in our study. However, such recaptures are unknown from the east coast of Nova Scotia, despite the regular presence of striped bass there of unknown stock origin (Andrews et al., 2019). This migratory behavior provides greater possibilities for gene flow among these populations and thus reduced levels of genetic discontinuity among them. This migratory behavior also may have resulted in the admixed legacy of the coastal migratory stock in estuaries at the northern extremes of the species' range in the Saint John and Annapolis rivers.

The Miramichi River population had a low abundance of about 5000 spawners over the period from 1996 to 2000, when it exploded to a modern high with as many as one million in 2017 (DFO, 2019). Though individuals ranged through the southern Gulf of St. Lawrence (Robinson et al., 2004) and its tributaries as far as Prince Edward Island and, possibly, to the east coast of Nova Scotia, the population did not display the recent regular occurrence to the eastern end of the Gaspe Peninsula, a likely outcome of density-dependent migrations, as seen for Hudson River striped bass (Waldman et al., 1990). However, even this expanded distribution would not cause admixture with other stocks (with the possible exception of the rebuilding St. Lawrence River population) given their isolation in the remote Gulf of St. Lawrence.

At the southern end of their Atlantic coastal distribution, south of Cape Hatteras, striped bass appear to be completely riverine, with virtually no movements into marine waters (Dudley et al., 1977; Bjorgo et al., 2000). Also, wintering adults occur on the inner continental shelf from Long Island southward but ending at Cape Hatteras (Waldman et al., 2012). Thus, there would be no apparent opportunity for genetic mixing of populations from South Carolina, Georgia, and Florida with stocks from rivers north of Cape Hatteras.

Several studies have used microsatellite analysis to investigate the population structure of striped bass along selected regions of the North American Atlantic coast. Initially, employing four microsatellites and mtDNA variants, Robinson et al. (2004) reported strong genetic differentiation between striped bass from the Miramichi River and Shubenacadie River populations in Canada; a finding consistent with our current study. They also reported that the Miramichi River was the likely source of age-0 aggregations in other rivers in the southern Gulf of St. Lawrence. Anderson et al. (2014) focused on striped bass populations in the southeastern U.S. Using R_{ST} and STRUCTURE analyses, they too reported strong genetic differentiation between their aggregated Santee-Cooper collection and one from the Roanoke River; a finding consistent with our results. The study by Brown et al. (2005) surveyed microsatellite variation in striped bass from five Chesapeake tributaries that largely overlapped with those included in our study. These included the Choptank, Nanticoke, Potomac, and Rappahannock, in addition to a small number from the Mattaponi. Using STRUCTURE and other methods, they concluded that the Chesapeake Bay population should be managed as a single unit. The reason they failed to detect any within-Chesapeake population differences is not apparent but may be

Table 10
Three realistic simulations of stock composition of mid Atlantic striped bass fisheries implemented in ONCOR. In each case, the mixture size was n = 200 and the number of simulations was 100.

Collection Locale	Stock Composition Scenarios					
	A		B		C	
	Actual Value	Estimate	Actual Value	Estimate (95 % CI)	Actual Value	Estimate (95 % CI)
Shubenacadie	0.00	0.000 (0.000-0.001)	0.00	0.000 (0.000-0.001)	0.00	0.000 (0.0-0.004)
Hudson	0.20	0.188 (0.156-0.218)	0.45	0.411 (0.375-0.449)	0.78	0.712 (0.641-0.777
Chesapeake	0.78	0.773 (0.737-0.811)	0.45	0.482 (0.443-0.524)	0.20	0.244 (0.176-0.327)
Roanoke	0.02	0.039 (0.018-0.060)	0.10	0.106 (0.077-0.136)	0.02	0.043 (0.002-0.082)

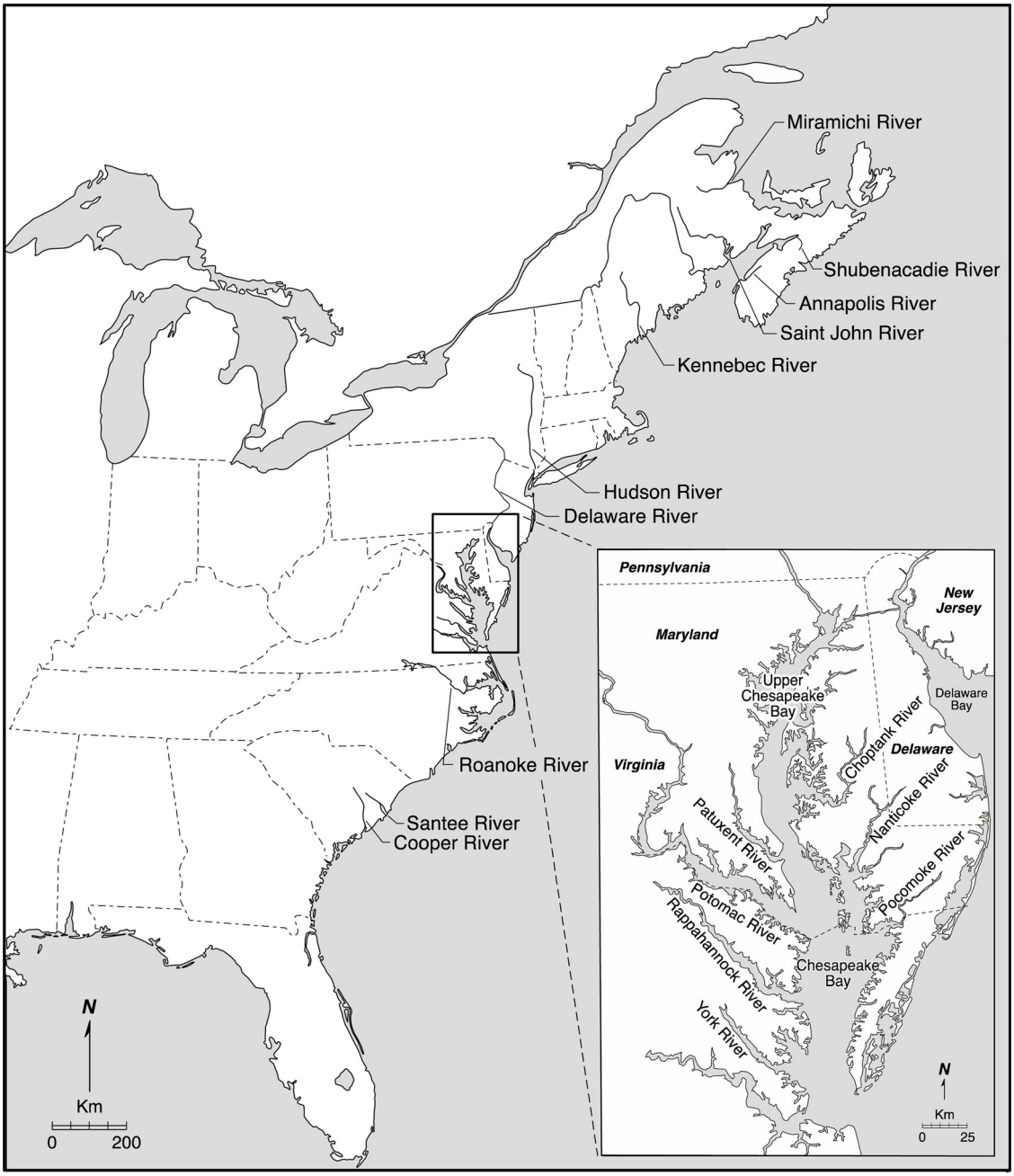

Fig. 1. Map of the Atlantic Coast of North America depicting 17 rivers from which striped bass were collected for microsatellite DNA analysis in this study.

due to stochastic issues for individual specimens collected in the presence of actual marginal differentiation, the mix of microsatellites employed, or unknown factors.

In the most geographically extensive study, Gauthier et al. (2013), primarily based on F_{ST} analysis concluded that the Hudson River, Delaware River, pooled Chesapeake Bay collections, Roanoke River, and Santee-Cooper all supported genetically distinct populations of striped bass. Our F_{ST} values for the same population comparisons using a different suite of microsatellites were similar to theirs, but in both STRUCTURE and DAPC analyses the Delaware River collection and individual or pooled Chesapeake Bay collections formed a single distinct genetic cluster. Therefore, we concluded that the Delaware River and Chesapeake Bay do not host genetically distinct populations of striped bass despite their having distantly discrete spawning reaches. Earlier analysis of mitochondrial DNA length variants was equivocal on whether the Delaware stock represented expansion of a relic population or recolonization from the Chesapeake, or both, but it favored the former (Waldman and Wirgin, 1994). This microsatellite analysis does not settle this question, but it does suggest meaningful contributions of Chesapeake Bay specimens to a recently rebuilt relic stock in the Delaware or to substantial historical exchange between them

Most pairwise comparisons of collections from the Chesapeake Bay proved genetically indistinguishable in both Gauthier et al.'s (2013) and our studies. In fact, the mean F_{ST} value among the five Chesapeake Bay populations characterized by Gauthier et al. (2013) was lower than what we report for the eight Chesapeake populations that we screened (Mean F_{ST} = 0.00073 versus Mean F_{ST} = 0.00548). But we did find evidence of genetic heterogeneity between the Nanticoke River and less so the Choptank River and collections from western tributaries of the Chesapeake Bay using both F_{ST} and STRUCTURE analyses. Similarly, Gauthier et al. reported little genetic differentiation among their five Chesapeake Bay collections except when they compared two pooled

northern collections and three pooled southern collections from the Bay. We also found that the York River collection at the southern end of the Bay was significantly different than our three collections from the northern end of the Bay (Upper Bay, Choptank River, and Nanticoke River) in F_{ST} analysis but did not cluster separately in STRUCTURE.

Concern to managers of results from our study may be that our analysis of population collections date back several decades and therefore potentially may not accurately represent their contemporary population structure. It may be that our analysis of collections made over several decades may present a more dynamic and accurate picture of their population structure than single shot contemporary collections that are typically analyzed. We addressed this issue by statistically evaluating the temporal stability of genotypes within six populations for which we have data on temporally disjunct collections (Table 3). In these 14 comparisons of collections that were separated by 4–27 years, one comparison proved to be statistically significant—the 1990 and 2011 samples of adults from the Upper Chesapeake Bay. We speculate that this difference may be due to the dramatic decline of the Chesapeake Bay population in the late 1970 and early 1980s which prompted the total moratorium on their harvest. As a result, it is possible that adults collected in 1990 were the offspring from a limited number of adults that spawned during the period of the historic population decline and therefore were not representative of full population's genetic composition.

4.2. Genetic relatedness of the Kennebec River to other populations

The Kennebec River historically supported a small reproducing population of striped bass (Foster and Atkins, 1869; Flagg and Squiers 1994). The Kennebec River population was believed to have been extirpated in the late 1920s to early 1930s because construction of the Edward's Dam in 1837 reduced spawning habitat by about 50 % and because of degraded water quality, which at times dropped dissolved oxygen levels to near zero. As a result, surveys in the 1960s did not observe any striped bass in the Kennebec estuary (Flagg and Squiers, 1994). In response, wild and hatchery-reared young-of-the year striped bass of Hudson River origin were stocked in the Kennebec River annually between 1982 and 1991 and spawning success was first observed in 1987 and annually through 2006.

By all means of statistical analyses in our study, the Kennebec River collection was indistinguishable from the Hudson River collection. However, this does not demonstrate that they were exclusively descendants of these stockings from the Hudson River, given the Kennebec's geographic location within the migratory range of the overall Mid-Atlantic stock and its proximity to populations of rivers in the Bay of Fundy. Our STRUCTURE results with $K = 6$ or $K = 7$ (Fig. 1ab) indicate the presence of a Chesapeake Bay signature in a Hudson River background across most of the Kennebec River collection. At this point, it is impossible to determine if this resulted from the hybridization of the Hudson River-stocked fish with parents of a remnant persistent population or with contemporary migrants of Chesapeake Bay ancestry.

4.3. Genetic composition of Canadian populations

The status and management of striped bass populations in Canada has been of considerable interest in recent years as they have become more numerous and have appeared in new geographic areas (reviewed in Andrews et al., 2019). The dramatically expanded Miriamichi River population was found as distant as Newfoundland and Labrador in 2017 (although not in 2018), and there is concern about its effects on the Atlantic salmon *Salmo salar* population of the Miramichi River (Daniels et al., 2018).

Similarly, the past and current genetic status of populations in the Annapolis River and Saint John River tributaries of the Bay of Fundy are issues of management concern (Andrews et al., 2019). Historically, the Annapolis River was thought to have supported a naturally reproducing population of striped bass (Williams et al., 1984) that was believed extirpated by the mid-to late 1990s, mainly because of the siting of a hydroelectric generating station near the entrance to the estuary in 1985, which may have made conditions inhospitable to young life-stages and caused acute mortality to adults (Dadswell et al., 2018). Critical in evaluating the consequences of operation of the facility is knowledge of the genetic status of its historic striped bass population. In examining adult striped bass collected from the Annapolis River between 1994 and 1996, we found that while its population was genetically distinct, it did not contain any genotypes that were unique to the Annapolis River. Instead, the majority of specimens in the collection (n = 75; 78.9 %) exhibited genotypes that were reflective of admixture among individuals of Shubenacadie River, Hudson River, Chesapeake Bay, and Roanoke River origin. The remaining 20 specimens (21.1 %) had genotypes that were of pure Chesapeake Bay (n = 10; 10.5 %), Hudson River (n = 6; 6.3 %), and Shubenacadie River (n = 4; 4.3 %) ancestry. The diverse genetic origins of our Annapolis River collection was also reflected in its much higher levels of genetic diversity than seen in the nearby Shubenacadie River population (Table 2). Thus, the propensity of striped bass from mid-Atlantic coast populations to migrate to distant locales likely resulted in frequent historic admixture events resulting in the establishment of a population in the Annapolis River comprised of individuals of predominantly mixed origin. Surprisingly, among the 75 individuals with admixed genotypes, only a single individual's genotype contained a signature of the proximal Shubenacadie River.

Historically, the Saint John River also hosted a naturally reproducing population of striped bass (Andrews et al., 2017). However, successful recruitment was impaired by chemical pollution and the building of the Mactaquac Dam in 1968, which may have prevented adults from reaching their historic spawning grounds and likely altered the downstream hydrological dynamics of the system, thereby compromising early life-stage success (Andrews et al., 2017). Periodic efforts during the late 20th century to locate eggs and juveniles that would be indicative of reproductive success usually failed (Andrews et al., 2017). As a result, the Saint John River striped bass population was listed as endangered in 2012 by COSEWIC. While the population was highly depressed, the question remained whether it was extirpated or persisted at low levels of abundance. We addressed this question by genotyping a contemporary collection of striped bass from the Saint John River that were possibly natal to the system. Similar, to the Annapolis River, we found that while the Saint John River collection was genetically distinct from all other populations, it too was comprised of individuals with predominately hybrid genotypes (n = 22; 52.4 %). By far, the greatest number of individuals with admixed genotypes exhibited combinations of Hudson River and Chesapeake Bay profiles (n = 17; 40.5 %). However, there were more admixed specimens with Shubenacadie River genetic signatures in the Saint John (n = 5; 11.9 %) than observed in the Annapolis River collection. In contrast to Annapolis River results, there was no contribution of the Roanoke River to admixed genotypes in the Saint John River sample.

Our results are somewhat, but not in total agreement, with those of Leblanc et al. (2018) who used the double-digest RAD-seq approach to identify 4700 single nucleotide polymorphisms that they surveyed in striped bass from the Saint John River (collected in 2014–2016; n = 21), Shubenacadie River, Hudson River, and the Upper Chesapeake Bay. They reported, as we did, that based on F_{ST} analysis their collection of Saint John River juveniles was genetically distinct from the other three collections. They also found that 6 of their 21 juvenile specimens exhibited admixed genotypes that included genetic contributions from the Shubenacadie and Hudson rivers and Upper Chesapeake Bay. However, they observed evidence of an additional genetic cluster in the remaining 15 specimens which they did not observe in their Shubenacadie River, Hudson River or Chesapeake Bay collections. They concluded that the presence of this third genetic cluster suggested

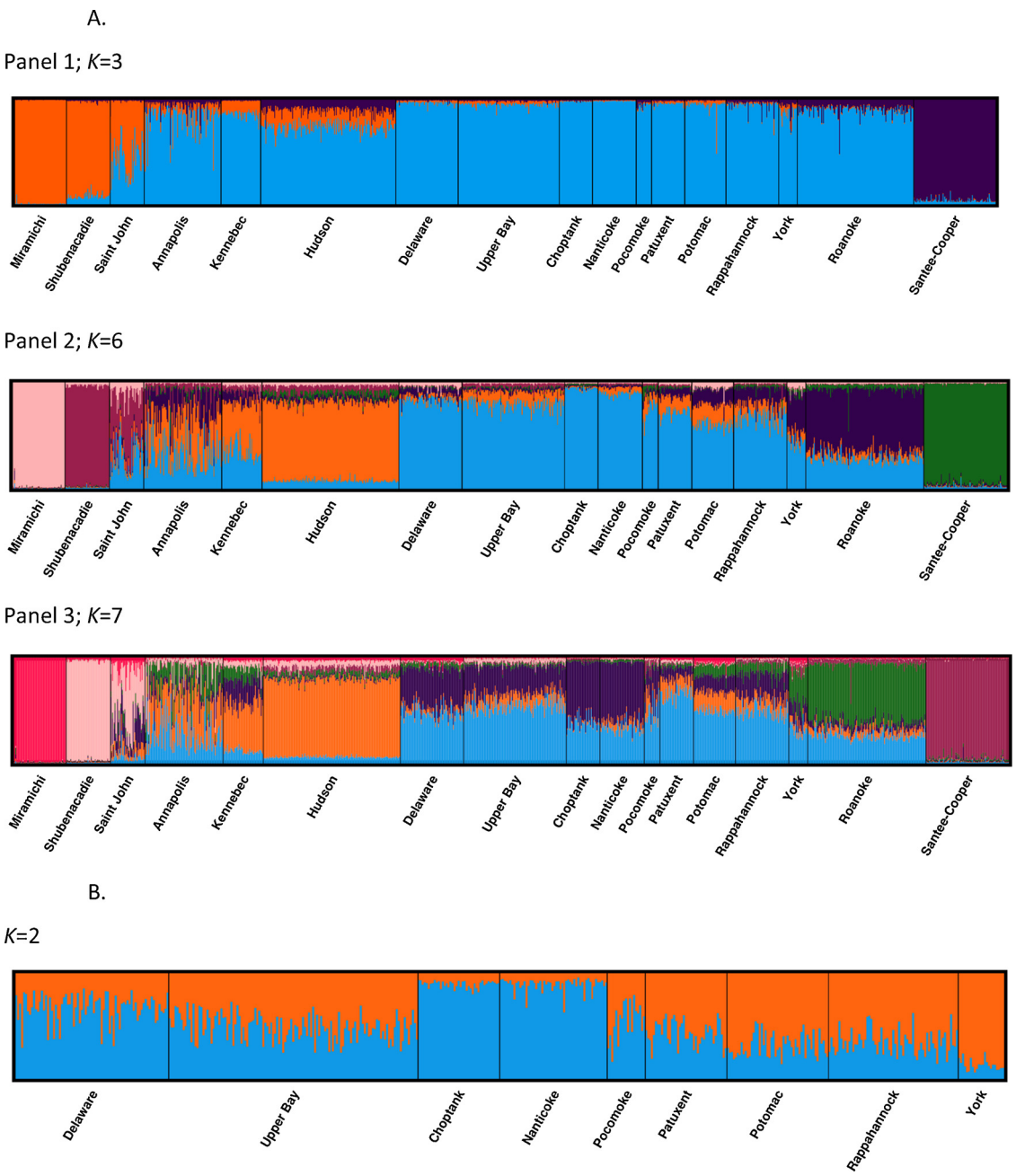

Fig. 2. Panel A.
STRUCTURE analysis of the coastwide population structure of striped bass based on microsatellite analysis of 8 loci from 17 collection sites ranging from the Miramichi River, New Brunswick to the Santee-Cooper system, South Carolina. Each vertical bar represents a single individual and different colors represent the contribution of each K genetic cluster to each specimen's genotype. The number of clusters depicted include; Panel 1 $K = 3$; Panel 2 $K = 6$; and Panel 3 $K = 7$. Panel B
STRUCTURE analysis of the population structure of striped bass among eight tributaries of the Chesapeake Bay and the Delaware River based on microsatellite analysis at eight loci. Each vertical bar represents a single individual and different colors represent the contribution of both genetic clusters ($K = 2$) to each specimen's genotype.

the continued presence of a remnant Saint John River genotype in their contemporary collection. We saw no evidence of this unique Saint John River genetic cluster in our Saint John River sample.

4.4. Potential use of microsatellite markers in mixed stock analysis

For their effective management, it is important to elucidate the genetic population structure of species with wide-ranging distributions such as striped bass. Genetic characterizations of individual migratory populations may allow for quantification of their contributions to mixed stock fisheries in coastal waters. For striped bass, it is known that the Hudson, Chesapeake, Delaware, and perhaps Roanoke rivers populations are highly migratory with their coastal movements extending seasonally from the Bay of Fundy to the Outer Banks of North Carolina. Furthermore, at many locations throughout this range they are subject to coastal harvest, however, the population composition of these mixed fisheries is dynamic, and in most cases, has never been addressed. Mixed Stock Analysis and Individual Based Assignment testing provide complimentary approaches to quantify the contributions of individual migratory populations to coastal harvests; however, their application

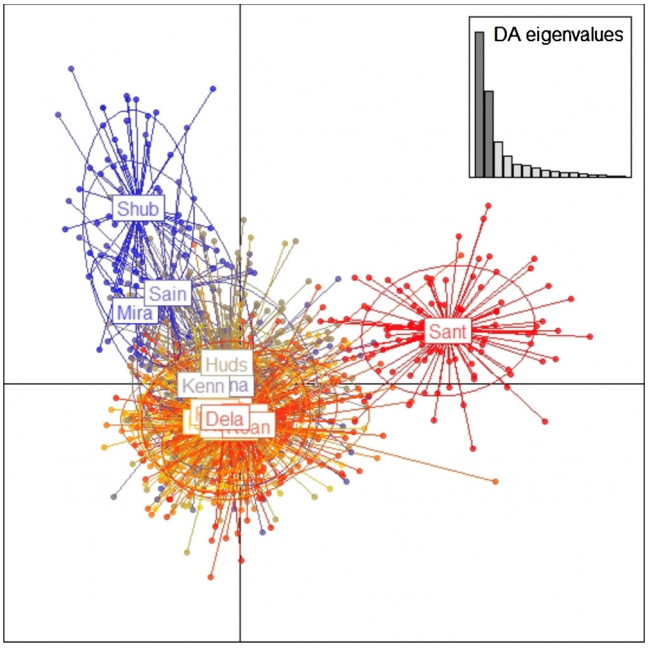

Fig. 3. Discriminant analysis of principal components (DAPC) plot of eight microsatellite loci across 17 collections of striped bass from the Atlantic coast of North America. The eigenvalue inset shows the relative amount of variance for each discriminant function. Specimens from each collection locale are depicted in different colors. Each dot represents an individual specimen and the line connects the dot to the location at which it was sampled. Shub = Shubenacadie; SJR = Saint John; Mira = Miramichi; Hud = Hudson; Kenn = Kennebec; Roan = Roanoke; SnCo = Santee-Cooper.

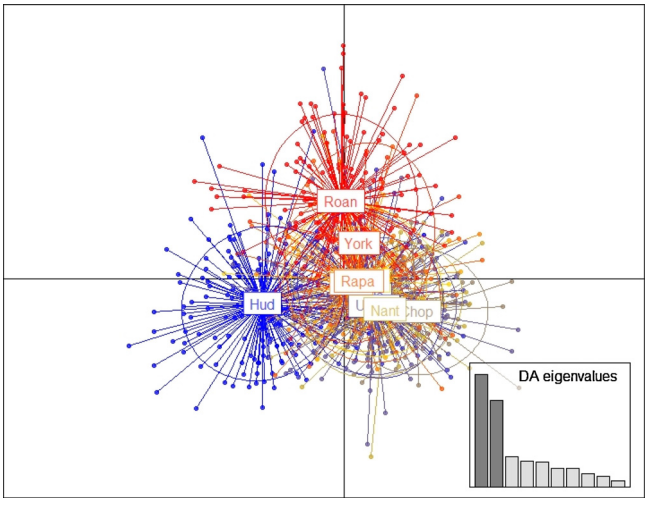

Fig. 4. Discriminant analysis of principal components (DAPC) plot of eight microsatellite loci across 11 collections of striped bass from the coastal migratory stock. The eigenvalue inset shows the relative amount of variance for each discriminant function. Specimens from each collection locale are depicted in different colors. Each dot represents an individual specimen and the line connects the dot to the location at which it was sampled. Collections included are from the Hudson (Hud); Delaware; Upper Bay; Choptank (Chop); Nanticoke (Nant); Pocomoke; Patuxent; Potomac; Rappahannock (Rapa); York; Roanoke (Roan) rivers.

requires sufficient genetic differentiation among contributing populations to reliably estimate their contributions. Was there sufficient genetic differentiation among the Hudson River, Chesapeake Bay, and Roanoke River collections to be informative in this management context? In the 100 % simulations, 93.2 %, 96.5 %, and 81.6 % of the Hudson River, Chesapeake Bay-Delaware River, Roanoke River collections were correctly assigned to the correct baseline populations, respectively. In the three realistic model simulations, 94 %, 97.5 %, and 95.5 % of specimens were assigned to the correct baseline population. It should be cautioned that these simulations may have provided somewhat optimistic results of the potential use of these markers in mixed stock analysis of these populations (i.e., smaller errors than they should) (Anderson et al., 2008). Nonetheless, we feel that these loci provide sufficient resolution to be valuable tools in mixed stock analyses of striped bass.

5. Conclusions

In summary, we have demonstrated that there are at least six and possibly seven genetically distinct populations of striped bass along its almost complete Atlantic Coast distribution. The extent of genetic differentiation among populations negatively reflects their tendency to migrate and, thus, is greatest among populations at both extremes of its range and lowest among the four populations that comprise the coastal migratory stock. Interestingly, this proclivity of individuals from the Hudson, Chesapeake, and Roanoke to migrate northward has resulted in their admixture in Canadian rivers distant from their natal estuaries and has contributed to the rebuilding of these distant populations. Based on results from simulation studies, the markers utilized in this study should prove informative in future mixed stock and individual based assignment analyses.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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