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ARTICLE

Population Genetic Structure in Channeled Whelk *Busycotypus canaliculatus* along the U.S. Atlantic Coast

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Abstract

Globally, commercial fisheries for whelk (family Buccinidae) generally exhibit a boom-and-bust cycle that fuels overexploitation of resources. Channeled whelk *Busycotypus canaliculatus* is a commercially important species that supports a valuable fishery along the Atlantic coast of the United States. The fishery is managed at the state level, with minimum landing size varying by state. Biological studies of channeled whelk in New England and the mid-Atlantic region have indicated that females have a low probability of maturity upon entering their respective fisheries. The life history characteristics of channeled whelk, including slow growth, late maturation, and direct development paired with unsuitable minimum landing size, make this species vulnerable to overexploitation. Currently, the population genetic structure of channeled whelk is unknown, impeding the ability to appropriately inform management. This study used 2,570 single nucleotide polymorphisms to elucidate the population genetic structure of channeled whelk sampled from 10 locations ranging from Massachusetts to South Carolina. The data indicated seven genetically distinct populations across the sampled region of the U.S. Atlantic coast. Estimates of genetic divergence among populations spanned an order of magnitude (F_{ST} = 0.017–0.582), with higher levels of divergence observed when comparing populations separated by biogeographic barriers. Based on the magnitude of observed genetic differences, five regional management units are suggested. The results of this study will aid discussions among fisheries managers in Atlantic states aimed at the development of appropriate management plans. The complex population genetic structure revealed by this study underscores the need for more comprehensive sampling, including between fishing locations sampled in this study and among offshore locations, to better understand the population genetic structure of channeled whelk.

Globally, whelk species (family Buccinidae) are harvested as commercial fishing resources. Throughout the 1960s to 1980s, overall participation in commercial whelk fisheries increased due to the decline in more traditional fisheries (shrimp, crab, lobster) and changes in market demand (Davis and Sisson 1988; Fahy et al. 2005; Miranda

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et al. 2008; Power et al. 2009). Throughout the 1990s to 2010s, global whelk fisheries exhibited boom-and-bust cycles that fueled overexploitation, highlighting the need for regulatory changes that could enable stock recovery (Fahy et al. 2005; Shelmerdine et al. 2007; Miranda et al. 2008; Power et al. 2009; McIntyre et al. 2015; Shrives et al. 2015). This boom-and-bust cycle has been observed in fisheries for common whelk (also known as waved whelk) *Buccinum undatum* in European countries, Neptune whelk *Neptunea arthritica* in Japan, and knobbed whelk *Busycon carica* in the United States (Miranda et al. 2008; Power et al. 2009; McIntyre et al. 2015).

Within the United States, the channeled whelk *Busycotypus canaliculatus* is part of a multispecies commercial whelk fishery, colloquially known as a conch fishery, that also includes the knobbed whelk and lightning whelk *Busycon sinistrum*. Channeled whelk are found throughout the U.S. Atlantic coast from Cape Cod, Massachusetts, to Cape Canaveral, Florida. Since the 1970s, the majority of commercial landings and value have been in the New England and mid-Atlantic regions (Davis and Sisson 1988; Edwards and Harasewych 1988), and an unregulated commercial fishery developed in those regions in the mid-1980s. By the 1990s, landings in Virginia from post-production processed channeled whelk meat had reached 1.4 million pounds at US$1.80 per pound, generating approximately $2.5 million dollars in exvessel revenue (Fisher 2015). Although shellstock prices (the price of whole live whelk) have fluctuated, by the end of the 2010s prices were triple what they were in the 1990s (Fisher 2015). As other fisheries have become less profitable, the channeled whelk fishery has developed into an important source of diversity and income, particularly for New England and mid-Atlantic commercial fishermen.

Despite its economic importance, there have been few stock assessments of channeled whelk, largely due to the biological information gaps across the species' range. In 2009, Rhode Island reported the first stock assessment for channeled whelk in New England; channeled whelk from Rhode Island were not overfished and overfishing was not occurring (Gibson 2010; Angell 2018). In 2017, Rhode Island updated their stock assessment for channeled whelk and noted that whelk were overfished and overfishing was occurring (Gibson 2017; Angell 2020). In 2018, Massachusetts reported that channeled whelk populations in Nantucket Sound were likely overfished and overfishing was occurring (Nelson et al. 2018). While there has not been a stock assessment conducted in the mid-Atlantic region, the status of channeled whelk fisheries that have been assessed to date highlights the need for additional stock assessments throughout the species' range.

The age and growth of channeled whelk varies depending upon sex and location, with size at maturity being larger for females (Walker et al. 2008; Fisher and Rudders 2017; Nelson et al. 2018). In Buzzards Bay, Massachusetts, channeled whelk are estimated to mature between age 7 and age 8.5, with the maximum recorded age estimated at 14 years (Peemoeller and Stevens 2013). The average size at first maturity (L50) of reproducing females from Buzzards Bay is 155.3 mm shell length (SL), while males reach L50 at 115.5 mm SL (Peemoeller and Stevens 2013). In the mid-Atlantic region, channeled whelk are estimated to mature between age 5 and age 7, with the maximum recorded age estimated at 16 years (Fisher and Rudders 2017). Females from the mid-Atlantic region reach L50 at 148.9–158.6 mm SL, while males reach L50 at 121–134 mm SL (Fisher and Rudders 2017). Age and size at maturity have not been assessed for channeled whelk in the South Atlantic Ocean.

Channeled whelk along the U.S. East Coast are managed at the state level, and minimum landing size varies by state: 127 mm SL in New Jersey, 152.4 mm SL in Maryland and Delaware, and 139.7 mm SL in Virginia. A biological study conducted in the mid-Atlantic region found that females harvested at the minimum landing size of 139.7 mm SL in Virginia had a low probability (1% to 15%) of being sexually mature (Fisher and Rudders 2017). Females in Buzzards Bay, Massachusetts, were estimated to be entering the fishery at 6.3 years, approximately 2 years before sexual maturity based on shell width (Peemoeller and Stevens 2013). The disconnect between size at maturity and minimum landing size has led to a rising concern about the potential for the channeled whelk fishery to collapse due to recruitment overfishing (Fisher and Rudders 2017).

Management agencies have recognized that the long-term sustainability of the channeled whelk fishery is at risk and an understanding of stock boundaries could aid in developing appropriate management strategies (Fisher 2015). To support decision making about the appropriate scale of management for the channeled whelk fishery, we used DArTseq (Kilian et al. 2012) to investigate the population genetic structure of channeled whelk sampled from 10 commercial fishing areas from Buzzards Bay, Massachusetts, to Charleston, South Carolina.

METHODS

Sample collection and DNA isolation.— Sample collection took place throughout a large portion of the geographic range of channeled whelk, with a finer-scale focus on the mid-Atlantic region due to the range of harvest size regulations among neighboring states (Figure 1). Samples were collected from 10 commercial fishing locations between 2015 and 2019 (Table 1). Channeled whelk were collected opportunistically through dredging or baited pots with the help of commercial fishers, the South Carolina Department of Natural Resources, and the Massachusetts

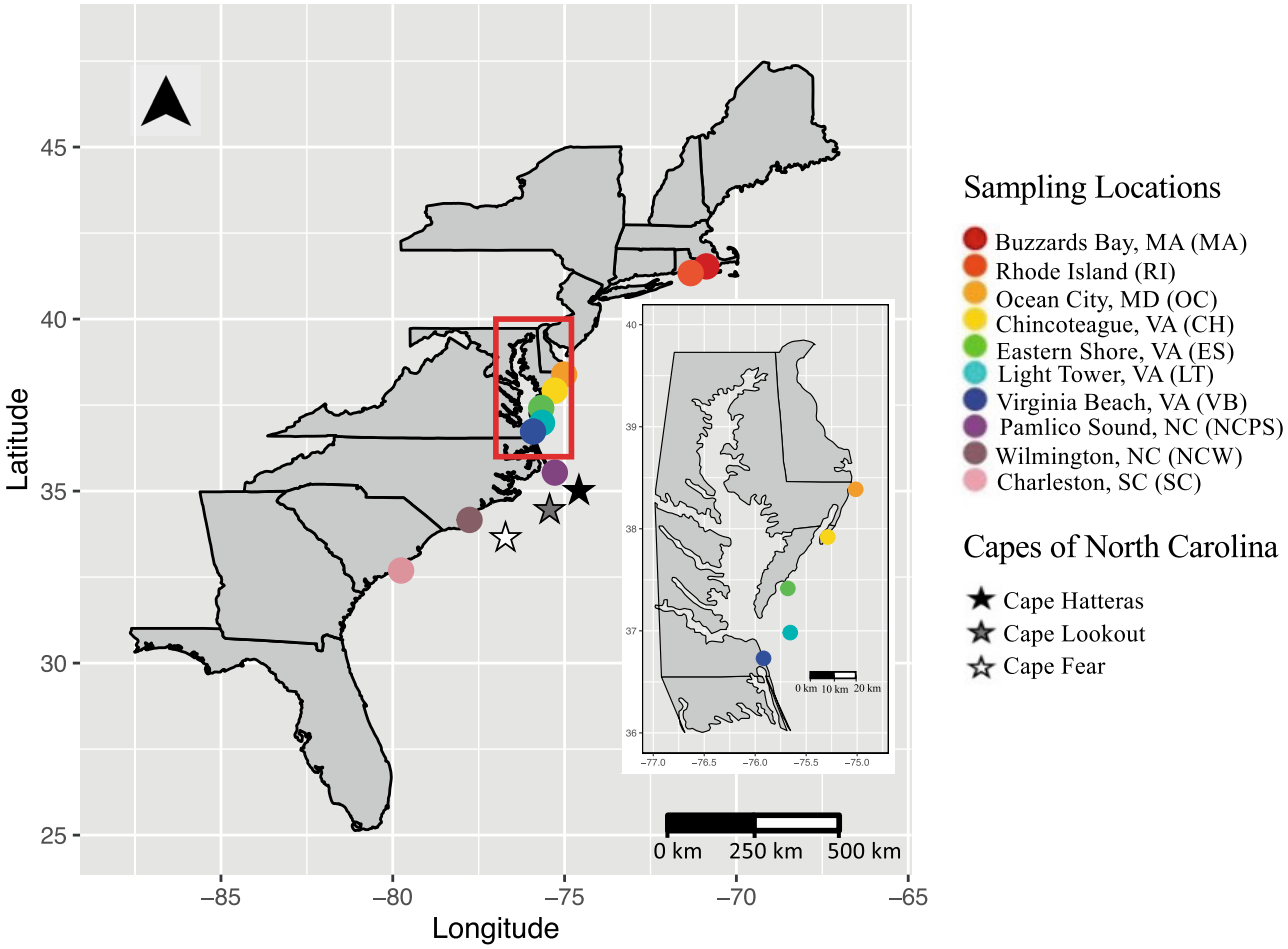

FIGURE 1. Geographic locations and abbreviations for the channeled whelk fishing locations that were sampled in this study. The inset displays the mid-Atlantic region where the sampling locations are more concentrated.

Division of Marine Fisheries. All sampled individuals were processed live, shell length and shell width were measured in millimeters, individuals were sexed, and a small piece of foot muscle was placed into 95% ethanol and stored at −20°C until DNA extraction.

Total genomic DNA was isolated from an approximately 25-mg piece of channeled whelk foot tissue using the Macherey-Nagel NucleoSpin Tissue DNA Extraction Kit according to the manufacturer's protocol (Macherey Nagle, Düren, Germany). To ensure that high-molecular-weight DNA was isolated, 5 µL of each sample was size-separated next to a 1-kb Plus DNA Ladder (Sigma-Aldrich, St. Louis, Missouri) on a 1% agarose gel that included GelRed Nucleic Acid Gel Stain (Biotium, Freemont, California) and visualized under UV light following standard protocols. The purity and concentration (µg/mL) of high molecular weight DNA was assessed using a Nanodrop 2000 spectrophotometer (Thermo Fisher Scientific, Waltham, Massachusetts).

Identification of loci using DArTseq.— To identify single nucleotide polymorphism (SNP) loci, high-quality DNA (50–100 ng/µL) was sent to the Diversity Arrays Technology facility (Canberra, Australia) for high throughput genotyping-by-sequencing using DArTseq (Kilian et al. 2012), a next generation sequencing approach that uses a restriction enzyme digestion step to reduce genome complexity and target low-copy-number sequences, allowing for the robust identification of thousands of SNP genotypes.

Filtering of SNPs.— Once the matrix of SNP genotypes for each individual was returned from Diversity Arrays Technology, additional filtering of the DArTseq data set was performed to minimize the probability of retaining inaccurate genotypes using "dartR" 9.9.1 (Gruber et al. 2018) in R version 3.6.1 (R Core Team 2020) (Table A.1 in the appendix). Loci that did not conform with the expectations of Hardy–Weinberg equilibrium were removed using "radiator" version 1.2.2 (Gosselin et al.

TABLE 1. Sampling locations, collection year, number of samples collected, number of samples retained after quality filtering, average shell length (SL), average shell width (SW), and the number of males and females for channeled whelk used in this study. The abbreviation N/A indicates information that was not available.

Sampling location and total	Abbreviation	Collection year	Number of samples collected	Number of samples fretained after filtering	Average SL (mm)	Average SW (mm)	Number of males	Number of females	Number of N/A
Buzzards Bay, Massachusetts	Massachusetts (MA)	2019	30	19	136.4	73.9	13	6	0
Rhode Island	Rhode Island (RI)	2018	12	12	N/A	N/A	N/A	N/A	N/A
Ocean City, Maryland	Ocean City (OC)	2018	34	34	150.6	81.0	7	27	0
Chincoteague, Virginia	Chincoteague (CH)	2018	25	17	169.8	93.4	10	7	0
Eastern Shore, Virginia	Eastern Shore (ES)	2018	32	11	146.6	73.9	6	5	0
Light Tower, Virginia	Light Tower (LT)	2018	25	21	149.0	74.8	9	12	0
Virginia Beach, Virginia	Virginia Beach (VB)	2018	34	34	162.5	87	17	17	0
Pamlico Sound, North Carolina	North Carolina Pam (NCPS)	2018	30	28	106.6	53.3	11	17	0
Wilmington, North Carolina	North Carolina Wilm (NCW)	2019	30	28	106.8	53.3	11	17	0
Charleston, South Carolina	South Carolina (SC)	2015–2018	30	23	N/A	N/A	10	6	7
Total			282 (total)	227 (total)	141.0 (total average)	73.8 (total average)	94 (total)	114 (total)	7 (total)

2020) in R. The *P*-value was set at the default (0.0001), and SNPs were removed if they were out of Hardy–Weinberg equilibrium in two or more sampling locations. Outlier loci were detected using "OutFlank" (Whitlock and Lotterhos 2015) and "pcadapt" version 4.3.3 (Luu et al. 2017). The OutFlank method, implemented in "dartR" infers the distribution of F_{ST} for loci unlikely to be strongly affected by spatially diversifying selection (Whitlock and Lotterhos 2015). The outlier function in the package "pcadapt" performs a principal component analysis and computes *P*-values to test for outlier loci based on the correlation between genetic variation and the first *K* principal components. The false discovery rate threshold for calculating *q*-values (adjusted *P*-values) was 0.05 for both detection methods.

Population identification.— Multiple individual-based clustering methods with different underlying assumptions were used to identify the most probable number of genetic clusters comprised by the data without prior information and to assign individuals to clusters. A principal component analysis (PCA) and a discriminant analysis of principal components (DAPC) were performed in the R package "adegenet" version 2.1.1 (Jombart 2008; Jombart and Ahmed 2011). The PCA was performed with uniformly weighted variables and samples, centered allele frequencies, and missing data imputed by mean allele frequencies. The DAPC uses PCA to maximize variation between groups while minimizing variation within groups to assign individuals to identified clusters using sequential *K*-means clustering. For DAPC, the optimal number of genetic clusters was evaluated using a successive number of *K*-means ($K = 1$–10), with the optimal number of clusters selected using the Bayesian information criterion (BIC).

The Bayesian clustering method implemented in STRUCTURE version 2.3.4 (Pritchard et al. 2000) was also used to group individuals into clusters that minimized departure from Hardy–Weinberg equilibrium. The most probable number of genetic groups (*K*) was assessed using 10 replicates, each with a burn-in of 250,000 Markov chain–Monte Carlo (MCMC) iterations followed by an additional 1,000,000 MCMC iterations allowing admixture and correlated allele frequencies. Structure Harvester (Earl and vonfHoldt 2012) was used to determine the likelihood value for each *K*, and the most supported *K* was identified through an analysis of ΔK (Evanno et al. 2005).

The optimal hierarchical grouping of sampling locations was assessed using an analysis of molecular variance (AMOVA) (Excoffier et al. 1992) in GenAlEx version 6.51b2 (Peakall and Smouse 2012) to identify the grouping of sampling locations that maximized the amount of genetic variance among groups (F_{SR}) using an infinite allele model. Significance was assessed using 9,999 permutations of the data.

Population summary statistics.— Once populations had been delineated, an unbiased estimator (Weir and Cockerham 1984) of Wright's *F*-statistic (F_{ST}) (Wright 1943) was calculated between pairs of sampled populations using "StAMPP" (Pembleton et al. 2013) in R. The significance of F_{ST} values was assessed using 10,000 bootstrap iterations of the data with $\alpha = 0.01$. Summary statistics for the evaluation of genetic diversity, including estimations of the inbreeding coefficient (G_{IS}) and observed (H_o) and expected (H_e) heterozygosity, were calculated in GenoDive version 3.0 (Meirmans 2020). Estimations of effective population size (N_e) were calculated for genetic populations of channeled whelk using a linkage disequilibrium model with random mating and critical values set at 0.05, 0.02, and 0.01 in NeEstimator version 2.1 (Do et al. 2014).

Isolation by distance.— Mantel tests were performed to identify whether the distribution of genetic divergence was consistent with an isolation by distance (IBD) pattern using a matrix of Euclidean geographic distances calculated from the closest known coordinates for sampling locations and a genetic distance matrix based on Slatkin's linearized F_{ST} (Slatkin 1995). Since Mantel tests of IBD are biased by the presence of hierarchical structure (Meirmans 2012), tests were conducted between vicariant barriers to gene flow identified by our clustering analyses. For each Mantel test, a total of 999 permutations of the data were used to assess the significance of the correlation between geographic and genetic distance using the R package "dartR."

RESULTS

Summary of Samples

A total of 282 samples was collected from Buzzards Bay, Massachusetts (MA), Rhode Island (RI), Ocean City, Maryland (OC), Chincoteague, Virginia (CH), Eastern Shore, Virginia (ES), Light Tower, Virginia (LT), Virginia Beach, Virginia (VB), Pamlico Sound, North Carolina (NCPS), Wilmington, North Carolina (NCW), and Charleston, South Carolina (SC) (Table 1).

Genotyping by Sequencing and SNP Filtering

Of the 282 samples collected, 252 had a sufficient amount of high-quality DNA and were sent for DArTseq, yielding 27,344 SNPs that passed standard Diversity Array Technology quality filtering procedures across all 252 individuals (Table A.1). A total of 2,570 SNPs from 227 individuals remained after additional quality filtering steps and comprised the full data set (Table 1). A total of 227 outlier loci was detected using PCA-based methods, but no outlier loci were detected using F_{ST}-based methods; therefore, all 2,570 SNP loci were retained.

Size and sex data were not recorded for channeled whelk sampled from RI or SC. The average shell length for the 227 channeled whelk remaining in the data set after quality filtering was 141.0 mm, and the average shell width was 73.8 mm (Table 1). The sex ratio was slightly skewed towards females; there were 1.02 females per male overall, ranging from 0.46 in MA to 3.85 in OC (Table 1). Additional biological information by sampling location can be found in Table 1.

Population Structure

For the PCA including all 10 sampling locations, the first two principal components explained 26.12% of the variability and clearly separated samples from the Carolinas (NCPS, NCW, and SC) from one another and from those taken further north (VB–MA), with the exception of a single NCW sample that clustered with the northern samples (Figure 2A). The high level of separation among the southernmost sampling locations resulted in tight clustering of VB–MA samples, so all clustering analyses were performed twice: once using all samples and once using only samples from VB–MA. A second PCA performed for the seven locations from VB to MA resulted in a "funneling effect," with the widest spread of individuals occurring in the southernmost sample retained (VB) and a gradual decrease in spread occurring northward (LT, ES, CH, OC, RI, MA) (Figure 2B). As compared with the PCA that included all sampling areas, less variation (3.9%) was explained by the first two principal components.

For the DAPC, the lowest BIC score (BIC = 1,008.2) supported $K = 4$ as the optimal number of clusters: (1) New England and mid-Atlantic regions (MA, RI, OC, CH, ES, LT, VB), (2) NCPS, (3) NCW, and (4) SC (Figure 3A). As with the PCA, the DAPC discriminated among the southernmost sampling locations and a single individual sampled from NCW was assigned to the north and mid-Atlantic cluster (Figure 3A). For the second DAPC plot using samples from the seven northernmost sampling areas (VB–MA), the lowest BIC score (BIC = 468.7) supported $K = 2$ as the optimal number of clusters, but $K = 3$ (BIC = 469.8) was also well supported and resolved additional groups: (1) MA and RI; (2) OC, CH, ES, and LT; and (3) VB (Figure 3B). However, not all individuals assigned to the geographic location from which they were sampled; four samples from the OC–LT group were assigned to the VB cluster, and eight samples from VB were assigned to the OC–LT cluster (Figure 3B).

In the Bayesian STRUCTURE analysis that included individuals from all 10 sampling areas, $K = 3$ was the most supported number of genetic lineages using ΔK (Evanno et al. 2005), with a likelihood value of $L(k) = -872{,}939.15$. Based on ancestry proportions, four genetic clusters were distinguished within the data. Results were consistent with the results of the DAPC using all sampling locations, resolving a single New England and mid-Atlantic (MA–VB) cluster and three separate clusters in the Carolinas (Figure 4A). However, $K = 4$ [$L(k) = -864{,}373.86$] was also well supported and resolved the New England samples (MA–RI) as a separate cluster from the mid-Atlantic region (OC–VB) (Figure 4A). When the samples from the Carolinas were excluded from analysis, $K = 3$ [$L(k) = -463{,}178.21$] was the most supported and resolved the same three groups identified by the DAPC but also indicated subtle differences in ancestry proportions between RI and MA (Figure 4B).

Five alternative groupings of sampling locations were tested with AMOVAs. All alternative groupings showed significant variance among groups ($F_{RT} = 0.279$–0.326, $P < 0.001$) but not among sampling locations within groups ($F_{SR} = -0.024$ to -0.014, $P = 0.991$–1.000) (Table 2). The optimal grouping resolved six groups, separating the two New England samples but retaining the mid-Atlantic region as a single group: (1) MA, (2) RI, (3) mid-Atlantic region (OC, CH, ES, LT, VB), (4) NCPS, (5) NCW, and (6) SC (Table 2, AMOVA 5).

Population Summary Statistics

Population-level summary statistics were calculated for seven genetically distinct groups identified by the previous analyses: (1) MA; (2) RI; (3) OC, CH, ES, and LT; (4) VB; (5) NCPS; (6) NCW; and (7) SC. All pairwise comparisons of F_{ST} values were significant ($P < 0.001$) (Table 3). Pairwise F_{ST} values ranged from 0.017 between OC, CH, ES, and LT and VB to 0.582 between VB and SC and (Table 3). Within the Carolinas, F_{ST} values ranged from 0.047 between NCW and SC to 0.280 between NCPS and SC. Comparisons between sampling locations in the Carolinas and all other locations (0.144–0.582) were an order of magnitude higher than comparisons within the New England and mid-Atlantic regions (0.017–0.086), and the magnitude of the difference increased with decreasing latitude: NCPS < NCW < SC (Table 3). Pairwise F_{ST} comparisons among all 10 sampling locations can be found in Table A.2. The average values of observed (H_o) and expected (H_e) heterozygosity across the seven groups were 0.098 and 0.097, respectively (Table 4). Expected heterozygosity (gene diversity) increased as latitude decreased, with a sharp discontinuity observed between populations north of the Carolinas ($H_e = 0.010$–0.030) and those in the Carolinas ($H_e = 0.121$–0.238) (Table 4). As with gene diversity, N_e estimates increased southward. The lowest N_e was found in MA (32.4; 95% CI = 27.7–38.8) and the highest N_e was found in SC (833.6; 95% CI = 664.2–1,117.5) (Table 4). Estimates of N_e for VB were more similar to estimates in the Carolinas than to estimates for samples further north. The total number of monomorphic loci per population also decreased from north to south, with MA having the highest number of monomorphic loci

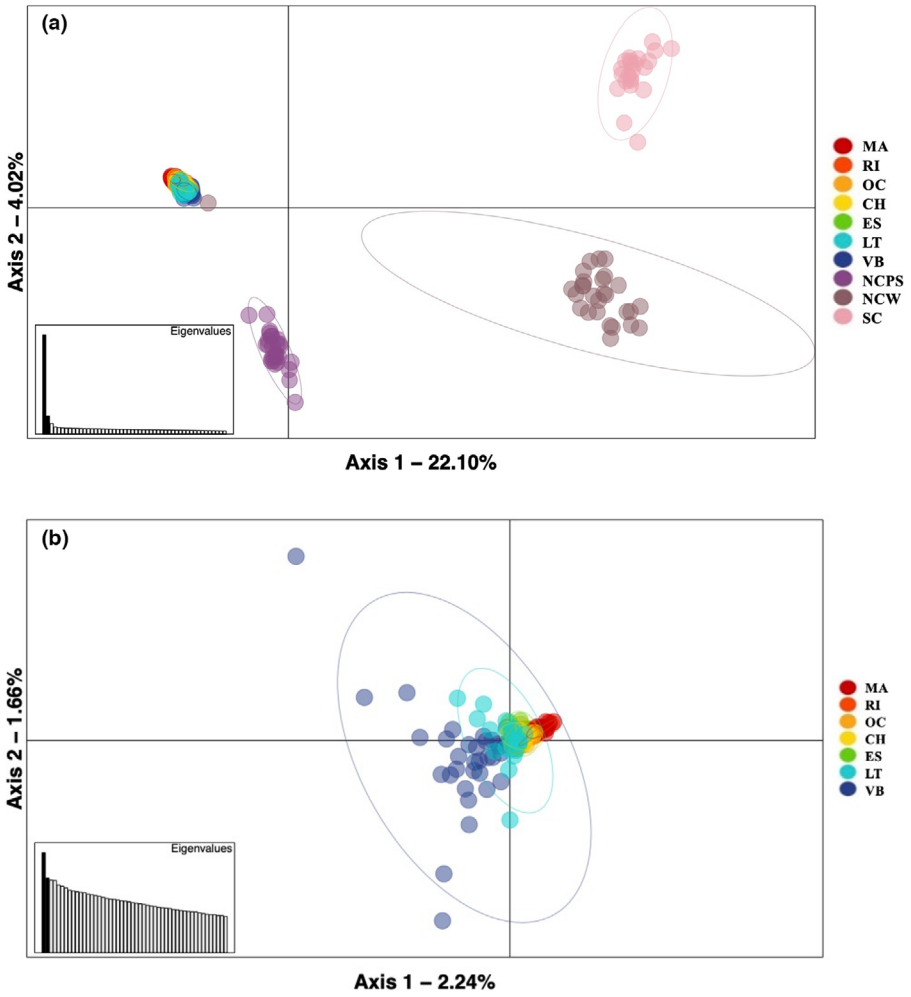

FIGURE 2. Principal component analyses plotting the relative positioning for **(A)** 10 and **(B)** 7 channeled whelk fishing locations along the U.S. Atlantic coast using the first two principal components. The ellipses surround 95% of individuals grouped by fishing location. The eigenvalues calculated for these plots are visualized as an inset boxplot in the lower left corner, with the first two axes used for the plot filled in black. For panel (A), axis 1 and axis 2 explained 22.10% and 4.02% of the variation in the data, respectively; for panel (B), axis 1 and axis 2 explained 2.24% and 1.66% of the variation in the data, respectively. Fishing region abbreviations are as follows: Buzzards Bay, Massachusetts (MA), Rhode Island (RI), Ocean City, Maryland (OC), Chincoteague, Virginia (CH), Eastern Shore, Virginia (ES), Light Tower, Virginia (LT), Virginia Beach, Virginia (VB), Pamlico Sound, North Carolina (NCPS), Wilmington, North Carolina (NCW), and Charleston, South Carolina (SC).

(2,373) and NCW having the lowest number of monomorphic loci (284) (Table 4).

Isolation by Distance

Patterns of IBD were examined for the seven northernmost sampling locations (MA, RI, OC, CH, ES, LT, VB) and within the mid-Atlantic region (OC, CH, ES, LT, VB) to reduce bias from the most prominent genetic breaks identified by the clustering analyses. A significant pattern of IBD was detected among the seven northernmost sampling locations ($r^2 = 0.6111$, $P = 0.011$); however, no significant pattern of IBD was detected among mid-Atlantic samples ($r^2 = 0.4686$, $P = 0.075$). Correlograms for Mantel tests of IBD can be found in Figure A.1 in the appendix.

DISCUSSION

Summary of Findings

This study was the first to assess the population genetic structure of channeled whelk throughout a large portion of its geographic range from Massachusetts to South Carolina. A total of 227 channeled whelk sampled from 10 commercial fishing locations along the U.S. Atlantic coast was used to estimate levels of genetic diversity and identify

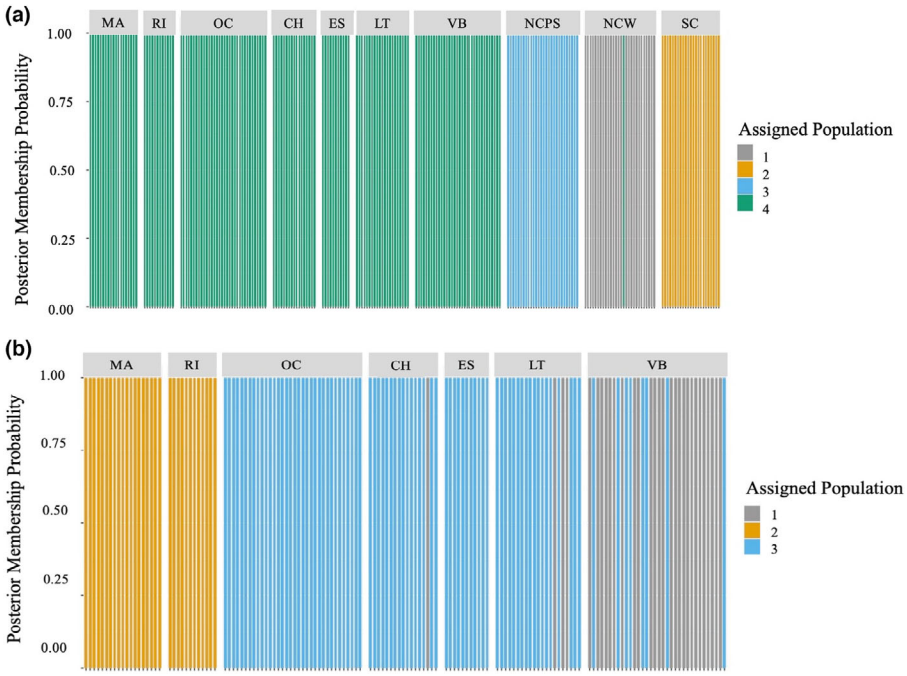

FIGURE 3. Discriminant analysis of principal components plotting the posterior membership probability for **(a)** 10 channeled whelk fishing locations along the U.S. Atlantic coast using four assigned populations and **(b)** 7 channeled whelk fishing locations using three assigned populations. See Figure 2 for fishing region abbreviations.

the presence of population genetic structure based on analyses of 2,570 SNP loci. Clustering analyses were used to identify high levels of population structure, while pairwise F_{ST} values were used to look for evidence of more subtle population structure within the mid-Atlantic region. The results of this study support the presence of seven genetically distinct populations with a wide range of population pairwise differentiation levels and intrapopulation diversity: (1) MA, (2) RI, (3) OC, CH, ES, and LT, (4) VB, (5) NCPS, (6) NCW, and (7) SC.

Barriers to Dispersal

The complexity of the marine environment can create multiple types of barriers that limit dispersal, including geographic barriers, currents, environmental limitations, and patchiness between suitable habitat (Treml et al. 2015), all of which are known to impact the dispersal potential of direct developing species (Weersing and Toonen 2009). The levels of divergence observed between populations of channeled whelk in this study spanned an order of magnitude, suggesting that multiple types of barriers have shaped the current population genetic structure.

The relatively higher levels of genetic divergence observed over short geographic distances in pairwise comparisons among sampling locations in North Carolina and South Carolina and between the Carolinas and all other sampling locations support the presence of substantial vicariant barriers to gene flow (dispersal) for channeled whelk in the Carolinas. The observed genetic discontinuities coincide with two well-known biogeographic features: Cape Hatteras, which separates the NCPS and VB sampling locations, and Pamlico Sound, bounded by Cape Lookout, which separates the NCPS and NCW sampling locations (Figure 1). Cape Hatteras is a well-known barrier for many other marine species, including Black Sea Bass *Centropristis striata*, Lined Seahorse *Hippocampus erectus*, and northern quahog *Merceneria merceneria* (Baker et al. 2008; Hale 2010; Briggs and Bowen 2012; McCartney et al. 2013; Boehm et al. 2015; Pappalardo et al. 2015). Although there is not a body of literature to support Cape Lookout as a common vicariant barrier for marine species, Cape Lookout defines the southern boundary of the Pamlico Sound estuary. Pamlico Sound is part of an extensive shallow lagoon estuary system, and exchange with the Atlantic Ocean is limited to the narrow Ocracoke, Hatteras, and Oregon inlets. Recent studies of circulation dynamics within the Albermarle–Pamlico Sound estuary have shown that bottom currents generally move westward towards the Pamlico and Neuse rivers (Jia and Li 2012), making advection of channeled whelk eggs and juveniles into the Atlantic Ocean, where they could be transported along the coast, unlikely. Within the Carolinas the level of divergence decreased an order of magnitude between NCW and SC, suggesting that Cape Fear, which separates these two sampling locations, is a less effective barrier to gene flow.

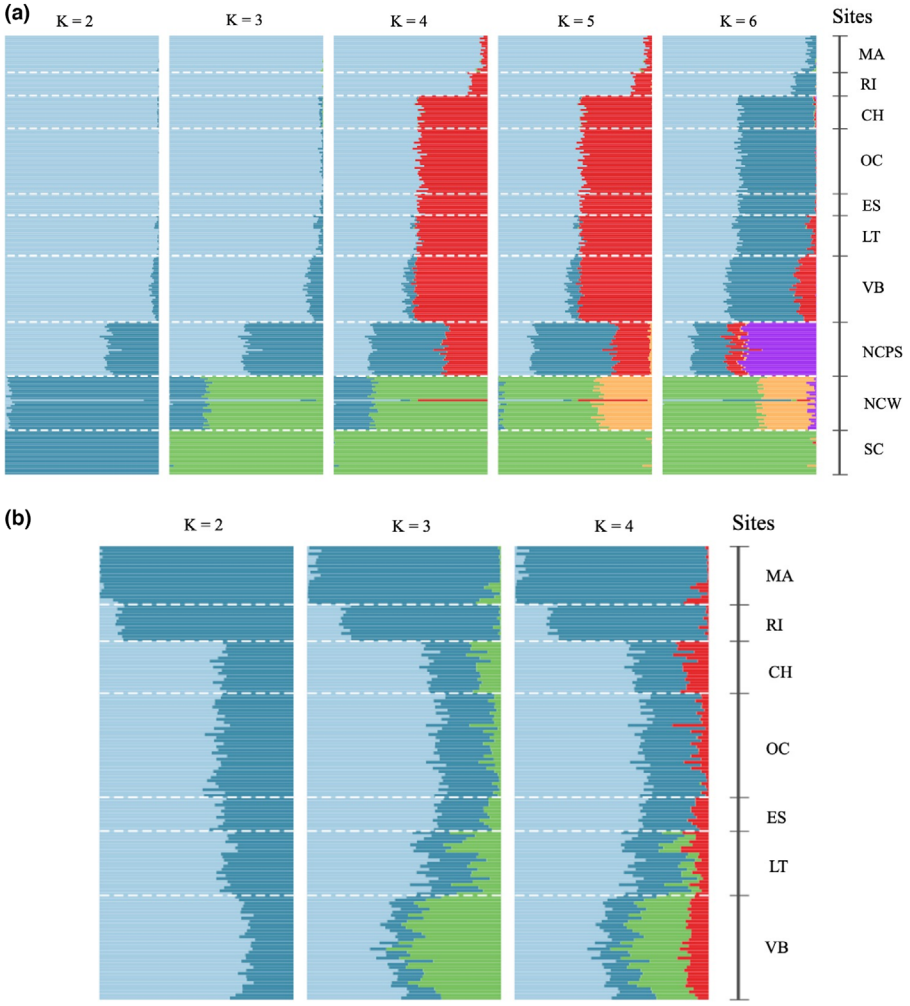

FIGURE 4. The STRUCTURE plot for **(a)** 10 channeled whelk fishing locations along the U.S. Atlantic coast with K set from 2 to 6 and **(b)** 7 channeled whelk fishing locations with K set from 2 to 4. Each K scenario was run with 10 replicates, each with a burn-in of 250,000 MCMC iterations followed by 1,000,000 MCMC iterations. Individual samples are represented by the bars and are grouped by fishing region. See Figure 2 for fishing region abbreviations.

While vicariant barriers may explain the highest levels of differentiation observed, physical parameters like ocean currents, temperature gradients, patchiness in suitable habitat, and geographic distance may also prove to be significant yet less extreme barriers to gene flow (Treml et al. 2015). Levels of differentiation among New England and mid-Atlantic populations were an order of magnitude lower than comparisons with populations south of Cape Hatteras, suggesting more subtle barriers to gene flow within and between these regions. The small but significant level of genetic differentiation observed between samples taken in New England and those taken in the mid-Atlantic region (average $F_{ST} = 0.058$) is concordant with the level of differentiation estimated between samples of a direct-developing snail, *Crepidula convexa*, from Massachusetts and Virginia using five microsatellite markers ($F_{ST} = 0.057$) (Cahill and Viard 2014). The authors of that study suggested that the observed difference was due to IBD. Although a significant pattern of IBD was detected by the current study when samples from MA–VB were considered, population pairwise F_{ST} values between MA and RI were similar to values between MA and the two mid-Atlantic groups and no significant pattern of IBD was present when only the mid-Atlantic sampling locations were considered. Taken together, this suggests that simple straight-line distance may not sufficiently explain the data.

Genetic differentiation may also arise in response to environmental factors that limit dispersal and may produce significant Mantel test results even when physical distance is not the main limit on dispersal (Meirmans 2012). For both Buzzards Bay and Chesapeake Bay, current

TABLE 2. Results from analyses of molecular variance (AMOVA) of channeled whelk fishing locations, including the variation explained (Est. var.), the *F*-statistic, and corresponding *P*-values. Significance was assessed using 9,999 permutations of the data. Statistically significant *F*-statistics are in bold.

Source of variation	Est. var.	*F*-statistic	*P*-value
AMOVA 1 (MA, RI, OC, [CH, ES, LT], VB, NCPS, NCW, SC)			
Among groups	47.279	$\mathbf{F_{RT} = 0.282}$	0.001
Among sampling locations	0	$F_{SR} = -0.016$	0.999
Among individuals	16.177	$\mathbf{F_{ST} = 0.270}$	0.001
Within individuals	106.207	$\mathbf{F_{IS} = 0.132}$	0.001
Total	169.663	$\mathbf{F_{IT} = 0.367}$	0.001
AMOVA 2 (MA, RI, OC, CH, [ES, LT], VB, NCPS, NCW, SC)			
Among groups	47.069	$\mathbf{F_{RT} = 0.283}$	0.001
Among sampling locations	0	$F_{SR} = -0.024$	1
Among individuals	16.177	$\mathbf{F_{ST} = 0.265}$	0.001
Within individuals	106.207	$\mathbf{F_{IS} = 0.132}$	0.001
Total	169.453	$\mathbf{F_{IT} = 0.362}$	0.001
AMOVA 3 (MA, RI, OC, [CH, ES], LT, VB, NCPS, NCW, SC)			
Among groups	46.39	$\mathbf{F_{RT} = 0.279}$	0.001
Among sampling locations	0	$F_{SR} = -0.019$	0.991
Among individuals	16.177	$\mathbf{F_{ST} = 0.265}$	0.001
Within individuals	106.207	$\mathbf{F_{IS} = 0.132}$	0.001
Total	168.773	$\mathbf{F_{IT} = 0.362}$	0.001
AMOVA 4 (MA, RI, [OC, CH, ES, LT], VB, NCPS, NCW, SC)			
Among groups	50.848	$\mathbf{F_{RT} = 0.296}$	0.001
Among sampling locations	0	$F_{SR} = -0.014$	1
Among individuals	16.177	$\mathbf{F_{ST} = 0.286}$	0.001
Within individuals	106.207	$\mathbf{F_{IS} = 0.132}$	0.001
Total	173.232	$\mathbf{F_{IT} = 0.381}$	0.001
AMOVA 5 (MA, RI, [OC, CH, ES, LT, VB], NCPS, NCW, SC)			
Among groups	58.535	$\mathbf{F_{RT} = 0.326}$	0.001
Among sampling Locations	0	$F_{SR} = -0.011$	1
Among individuals	16.177	$\mathbf{F_{ST} = 0.318}$	0.001
Within individuals	106.207	$\mathbf{F_{IS} = 0.132}$	0.001
Total	180.919	$\mathbf{F_{IT} = 0.409}$	0.001

patterns between the respective bays and the Atlantic Ocean may act as barriers to dispersal for channeled whelk; however, this has not been investigated. The absence of a significant pattern of IBD among the mid-Atlantic sampling locations and small F_{ST} values among mid-Atlantic sampling locations (within OC, CH, ES, and LT, the F_{ST} values ranged from 0.0001 to 0.007; Table A.2) relative to comparisons with other locations suggests that the distances encompassed by OC–LT are within the limits of dispersal for channeled whelk. A study using acoustic telemetry to track five channeled whelk in Lake Tashmoo, Massachusetts, over a 14-month period noted that adult whelk exhibited limited movement (0–133 m) and small home ranges (Edmundson 2016). The geographic distances among the OC, CH, ES, and LT sampling locations far exceeded the maximum estimated movement distance of Edmundson (2016), suggesting that longer-distance dispersal events are likely mediated by passive transport of egg cases and juveniles via currents, rather than vagility in larger, heavier adults.

Genetic Consequences of Direct Development

Species that exhibit direct development and reduced dispersal ability tend to have localized populations, a high level of genetic differentiation among populations, reduced genetic diversity, and high levels of inbreeding (Wright 1943; Martel and Chia 1991; Palumbi 2003; Sanford and Kelly 2011; Mariani et al. 2012; Underwood and Darden 2019). The high levels of population differentiation found for channeled whelk throughout the geographic range are consistent with what has been observed in other direct-developing gastropods. Comparison of two congeneric marine snails, *Littorina* spp., with different dispersal modes showed varying levels of population genetic

TABLE 3. Wright's *F*-statistics (F_{ST}) for the seven genetically distinct populations of channeled whelk. The F_{ST} values are on the lower diagonal of the table. Significance was assessed using 10,000 permutations of the data, with an asterisk denoting a *P*-value of <0.001. Population abbreviations are as follows: Buzzards Bay, Massachusetts (MA), Rhode Island (RI), Ocean City, Maryland (OC), Chincoteague, Virginia (CH), Eastern Shore, Virginia (ES), Light Tower, Virginia (LT), Virginia Beach, Virginia (VB), Pamlico Sound, North Carolina (NCPS), Wilmington, North Carolina (NCW), and Charleston, South Carolina (SC).

Populations	MA	RI	OC, CH, ES, LT	VB	NCPS	NCW	SC
MA		*	*	*	*	*	*
RI	0.084		*	*	*	*	*
OC, CH, ES, LT	0.086	0.031		*	*	*	*
VB	0.081	0.035	0.017		*	*	*
NCPS	0.184	0.144	0.249	0.151		*	*
NCW	0.337	0.292	0.496	0.357	0.197		*
SC	0.411	0.36	0.582	0.438	0.28	0.047	

TABLE 4. Estimates of effective population size (N_e) based on the linkage disequilibrium model with random mating and population summary statistics for the seven genetically distinct populations of channeled whelk. Critical values were set at 0.05, 0.02, and 0.01, and H_o is observed heterozygosity, H_e is the expected heterozygosity, and G_{IS} is the inbreeding coefficient. See Table 3 for population abbreviations.

Population	N_e	H_o	H_e	G_{IS}
MA	Allele frequency 0.01 = 32.4 (27.7–38.8) Allele frequency 0.02 = 32.4 (27.7–38.8) Allele frequency 0.05 = 137.7 (50.8–infinite) Monomorphic loci = 2,373	0.011	0.01	−0.033
RI	Allele frequency 0.01 = 65.6 (42.7–132.5) Allele frequency 0.02 = 65.6 (42.7–132.5) Allele frequency 0.05 = 19.9 (13.2–34.8) Monomorphic loci = 2,376	0.013	0.012	−0.035
OC, CH, ES, LT	Allele frequency 0.01 = 195.5 (184.4–207.9) Allele frequency 0.02 = 297.6 (256.2–353.6) Allele Frequency 0.05 = 1,612.5 (576.4–infinite) Monomorphic loci = 1,592	0.02	0.02	0.026
VB	Allele frequency 0.01 = 712.6 (534.6–1,063.3) Allele frequency 0.02 = 400.9 (307.7–571.6) Allele Frequency 0.05 = 68,382.3 (670.5–infinite) Monomorphic loci = 1,736	0.03	0.03	0.002
NCPS	Allele frequency 0.01 = 508.0 (434.8–610.2) Allele frequency 0.02 = 270.0 (242.7–304.0) Allele frequency 0.05 = 328.5 (283.6–389.7) Monomorphic loci = 981	0.124	0.121	−0.012
NCW	Allele frequency 0.01 = 227.9 (216.1–241.0) Allele frequency 0.02 = 206.2 (195.8–217.7) Allele frequency 0.05 = 193.1 (183.3–203.9) Monomorphic loci = 284	0.253	0.248	−0.007
SC	Allele frequency 0.01 = 833.6 (664.2–1,117.5) Allele frequency 0.02 = 833.6 (664.2–1,117.5) Allele frequency 0.05 = 904.6 (685.3–1,327.6) Monomorphic loci = 439	0.232	0.238	0.026
Overall		0.098	0.097	0.005

structure throughout their geographic range from northern California to Alaska. A moderate amount of population structure was observed in *L. subrotundata,* a direct developing species ($F_{ST} = 0.063–0.320$, $P = < 0.05$), while no population structure was resolved in *L. scultulata*, which has a pelagic larval phase ($F_{ST} = -0.003$ to $+0.006$,

$P > 0.05$) (Kyle and Boulding 2000). Significantly higher levels of divergence have been observed in species that exhibit direct development in many phyla, including Enchinodermata, Cnidaria, Arthropoda, Bryozoa, and Mollusca ($F_{ST} = 0.244–0.479$), as compared to the levels of divergence seen in species with pelagic larvae ($F_{ST} = 0.003–0.019$) (Cahill et al. 2017), consistent with reduced dispersal as a result of direct development.

A decline in genetic diversity in populations at the edge of a species' geographic range has generally been attributed to some combination of increased isolation, the relatively greater impact of genetic drift due to founder effects, and less than optimal conditions at the margins of the range (Eckert et al. 2008; Ackiss et al. 2018). The genetic diversity and N_e of channeled whelk sampled in this study declined moving northward, with a changeover in the level of diversity demarcated by the Carolinas. As compared to the Carolinas, VB–OC populations had average levels of genetic diversity that were approximately eight times lower, while average diversity levels in MA–RI populations were 18 times lower. Overall, this suggests that a combination of these factors have shaped the distribution of diversity in channeled whelk.

While increased levels of inbreeding can be a consequence of limited dispersal resulting from direct development, high levels of inbreeding were not observed in channeled whelk. The mean G_{IS} value (inbreeding value) for channeled whelk across all fishing locations sampled was lower than estimates of G_{IS} values found in other direct developing mollusks (−0.005 versus 0.184) (Addison and Hart 2005). Low levels of inbreeding have also been observed in *Crepidula convexa* (average $G_{IS} = -0.220$), a direct-developing marine snail that exhibits multiple paternity (Le Cam et al. 2014; Cahill and Levinton 2016). Multiple paternity can be classified as an inbreeding avoidance or it can act as a buffer against inbreeding when species have low dispersal rates (Pusey and Wolf 1996). While there are no current studies on mating strategies exhibited by channeled whelk, a study conducted on knobbed whelk, a closely related species, found evidence of multiple paternity (Power et al. 2009). Additional information to identify mating preferences in channeled whelk could be useful in understanding the low levels of inbreeding seen in this study.

Management Implications and Future Research

The long-term sustainability of the channeled whelk commercial fishery may be threatened by overharvest and removal of whelk before they are sexually mature. Management measures are inconsistent, with adjacent states having different or absent harvest regulations. The inconsistencies in minimum landing size by state provide an opportunity for a loophole fishery, allowing undersized channeled whelk harvested in a state with a higher minimum landing size to be landed in another state with a lower or absent minimum landing size. However, it may be appropriate for adjacent states to have different harvest regulations guided by differences in the biology (e.g., size at maturity), genetic structure, and stock status of channeled whelk. The current study elucidated seven genetically distinct populations along the U.S. Atlantic coast and inferred multiple potential drivers of population structure, including biogeographic barriers, physical distance, and current patterns. The substantial level of genetic stock structure present throughout the geographic range of channeled whelk examined in this study underscores the need for a more comprehensive look at this fishery to further delineate genetic stocks and assess whether there is a relationship between genetic differentiation and differences in size at maturity. Based on the magnitude of observed genetic differences, five regional management units are suggested: New England, the mid-Atlantic region, NCPS, NCW, and SC.

Multiple genetic stocks were identified within states, and a shared genetic stock was identified among states. In the mid-Atlantic region, the data are consistent with the presence of two genetic stocks in Virginia: one comprised of the Chincoteague, Eastern Shore, and Light Tower sampling areas and one comprised of Virginia Beach. The Chincoteague, Eastern Shore, and Light Tower fishing locations were found to be part of a larger genetic stock including Ocean City, Maryland. A high level of genetic differentiation was also found between samples from Pamlico Sound, North Carolina, and off Wilmington, North Carolina.

A more holistic view of the fishery, including assessment of the biophysical properties that limit dispersal for channeled whelk, is needed to better assess connectivity in the New England and mid-Atlantic regions. The addition of more sampling locations throughout the geographic range of channeled whelk, individual collection location data, and collection of environmental data for use in model development could be used to better understand the movement patterns and limits of dispersal for this species. Sampling effort should focus on the gaps between MA and RI and between RI and OC, which could provide a more fine-scale delineation of the population structure within New England and between New England and the mid-Atlantic region. While this study was able to obtain samples from inshore assemblages, future sampling should include known offshore assemblages (federal waters). A comparison of life history parameters among the genetic stocks identified in this study should be conducted to identify any differences in size at maturity and whether those differences correlate with genetic differences or with environmental parameters, which will be useful in deciding appropriate management recommendations. To highlight the challenges to the development of management plans,

our study found that channeled whelk in VB may represent a different genetic population than those in northern Virginia and Maryland, but Fisher and Rudders (2017) found that males matured at smaller sizes in VB and the eastern shore of Virginia (equivalent to our ES sample) than males in Ocean City, Maryland (OC). However, female size at maturity followed a similar pattern to the results of this study; VB differed from the other sites, and channeled whelk were found to be recruiting to the VB fishery at a smaller size than elsewhere. Based on the results of this study, it is recommended that a channeled whelk working group, including representatives of the channeled whelk fishery (scientists, commercial fishers, and management agencies) throughout the species range, be formed to further assess current regulations of the channeled whelk fishery and how state-by-state management may or may not align with findings from this study.

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Appendix: Additional Data A

TABLE A.1. The order of quality filtering performed on the 27,344-SNP data set provided by Diversity Arrays Technology (Canberra, Australia), including threshold for removal and the number of remaining SNPs and individuals postfiltering.

Filter	Threshold for removal	Number of SNPs remaining	Number of individuals remaining
Start		27,344	252
Call rate (loci)	<90%	20,097	252
Call rate (individual)	<80%	20,097	239
Monomorphic SNPs		18,500	239
Coverage depth	<5× and >25×	16,304	239
Repeatability	<100%	8,513	239
Hamming distance	<20%	7,290	239
Call rate (individual)	<95%	7,290	227
Monomorphic loci		6,797	227
Call rate (loci)	<96%	6,468	227
Minor allele frequency	<1%	2,572	227
Secondary SNPs	At random	2,572	227
Hardy–Weinberg equilibrium	Out of Hardy–Weinberg equilibrium in at least two locations with *P*-values = 0.0001	2,570	227
End		2,570	227

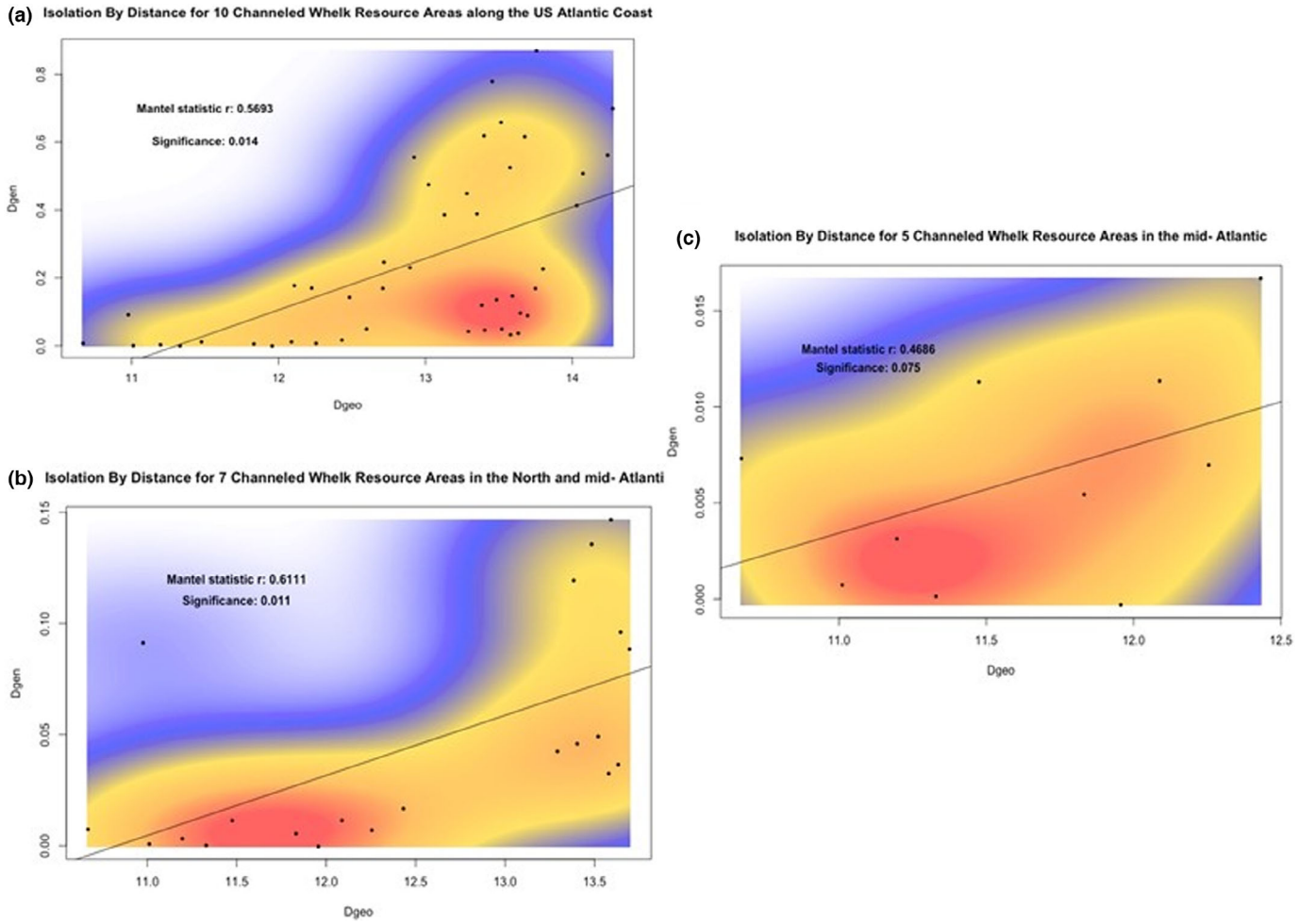

FIGURE A.1. Mantel test using a matrix between Euclidean distance (Dgeo) and genetic distance (Dgen) to examine patterns of isolation by distance for **(a)** 10 channeled whelk fishing locations, **(b)** 7 channeled whelk fishing locations, and **(c)** 5 channeled whelk fishing locations along the U.S. Atlantic coast. Significance was assessed using 999 permutations.

TABLE A.2. Wright's *F*-statistics (F_{ST}) for 10 channeled whelk fishing locations. The F_{ST} values are on the lower diagonal of the table. Significance was assessed using 10,000 permutations of the data, with an asterisk denoting *P*-values of <0.001. Population abbreviations are as follows: Buzzard Bay, Massachusetts (MA), Rhode Island (RI), Ocean City, Maryland (OC), Chincoteague, Virginia (CH), Eastern Shore, Virginia (ES), Light Tower, Virginia (LT), Virginia Beach, Virginia (VB), Pamlico Sound, North Carolina (NCPS), Wilmington, North Carolina (NCW), and Charleston, South Carolina (SC).

Population	MA	RI	OC	CH	ES	LT	VB	NCPS	NCW	SC
MA		*	*	*	*	*	*	*	*	*
RI	0.084		*	*	*	*	*	*	*	*
OC	0.107	0.041		0.032	0.564	*	*	*	*	*
CH	0.119	0.044	0.003		0.492	0.005	*	*	*	*
ES	0.128	0.047	0.0003	0.0001		0.396	*	*	*	*
LT	0.088	0.031	0.007	0.005	0.001		*	*	*	*
VB	0.081	0.035	0.016	0.011	0.011	0.007		*	*	*
NCPS	0.184	0.144	0.187	0.145	0.125	0.145	0.151		*	*
NCW	0.337	0.292	0.382	0.31	0.278	0.322	0.357	0.197		*
SC	0.411	0.36	0.465	0.381	0.344	0.397	0.438	0.28	0.047	