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Philopatry influences the genetic population structure of the blacktip shark (*Carcharhinus limbatus*) at multiple spatial scales

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Abstract

Understanding how interactions among microevolutionary forces generate genetic population structure of exploited species is vital to the implementation of management policies that facilitate persistence. Philopatry displayed by many coastal shark species can impact gene flow and facilitate selection, and has direct implications for the spatial scales of management. Here, genetic structure of the blacktip shark (*Carcharhinus limbatus*) was examined using a mixed-marker approach employing mitochondrial control region sequences and 4339 SNP-containing loci generated using ddRAD-Seq. Genetic variation was assessed among young-of-the-year sampled in 11 sites in waters of the United States in the western North Atlantic Ocean, including the Gulf of Mexico. Spatial and environmental analyses detected 68 nuclear loci putatively under selection, enabling separate assessments of neutral and adaptive genetic structure. Both mitochondrial and neutral SNP data indicated three genetically distinct units—the Atlantic, eastern Gulf, and western Gulf—that align with regional stocks and suggest regional philopatry by males and females. Heterogeneity at loci putatively under selection, associated with temperature and salinity, was observed among sites within Gulf units, suggesting local adaptation. Furthermore, five pairs of siblings were identified in the same site across timescales corresponding with female reproductive cycles. This indicates that females re-used a site for parturition, which has the potential to facilitate the sorting of adaptive variation among neighbouring sites. The results demonstrate differential impacts of microevolutionary forces at varying spatial scales and highlight the importance of conserving essential habitats to

maintain sources of adaptive variation that may buffer species against environmental change.

KEYWORDS
conservation genomics, elasmobranch, local adaptation, male philopatry, parturition site fidelity

1 | INTRODUCTION

Genetic population structure is determined by differences in the distribution of alleles among contemporary populations that result from interactions of microevolutionary forces (Laikre et al., 2005). Because genetic drift and gene flow influence allele frequencies on a genome-wide scale, selectively neutral loci exhibit patterns of variation that can be used to understand historical and contemporary demographic processes (Luikart et al., 2003). By contrast, selection acts upon variation at specific genes and/or genomic regions, and often produces patterns of structure distinct from those observed at neutral loci (Gagnaire et al., 2015; Nielsen, 2001). Disentangling these patterns is especially informative for the management of exploited species. While neutral structure can inform the designation of management units (Waples et al., 2008), loci under selection can be used to infer local adaptation across heterogeneous environments within management units (Nielsen et al., 2009). Understanding levels of gene flow among and within units is also critical because the adaptive potential of populations can facilitate the persistence of species confronted with environmental change (Bowen & Roman, 2005; Garant et al., 2007).

Examining the interplay of microevolutionary forces is challenging in marine systems because barriers to gene flow are fewer and often cryptic and they can be more difficult to study than many terrestrial systems (Grummer et al., 2019; Palumbi, 1994). In addition, marine species typically exhibit weak structure that is difficult to detect (Waples, 1998), resulting from the potential for long-distance dispersal (via adults and/or larvae), high fecundity, and large effective population sizes that reduce the magnitude of genetic drift (Poulsen et al., 2006). However, large population sizes and high fecundities provide more opportunities for mutation and increase the efficacy of selection relative to drift (Allendorf et al., 2010; Cormack et al., 1990). Further, many marine species have broad geographic ranges and are distributed across heterogeneous environments, increasing the potential for local adaptation (Bernatchez, 2016). Therefore, selection acting with varying degrees of strength upon a small number of loci can lead to fine-scale adaptive structure while neutral processes produce weaker, genome-wide structure across broader geographic scales (Gagnaire & Gaggiotti, 2016; Hoey & Pinsky, 2018).

The life history characteristics of elasmobranchs (i.e., sharks, skates, and rays) have an important role in shaping patterns of genetic structure. In contrast to many bony fishes and marine invertebrates, elasmobranchs mature late, have long life spans, and produce relatively few progeny within and across reproductive efforts (Conrath & Musick, 2012). Frequently, this leads to smaller effective sizes that are more coupled to census sizes (Portnoy et al., 2009). Though elasmobranchs lack a dispersive larval stage, they retain the potential for high levels of gene flow because they can move vast distances during juvenile and adult life stages (Kohler & Turner, 2019). However, many species display fidelity to specific habitats where they mate and give birth or deposit eggs (Chapman et al., 2015; Flowers et al., 2016). Furthermore, this behaviour can extend across generations, causing individuals to reproduce in their region of birth (i.e., regional philopatry; Pardini et al., 2001) and even result in females giving birth in the same habitat in which they were born (i.e., natal philopatry; Feldheim et al., 2014).

Female philopatry is common among coastal shark species that give birth in bays and estuaries where progeny may remain for extended periods (Heupel et al., 2007; Karl et al., 2011; Keeney et al., 2005). Female regional philopatry has the potential to limit gene flow mediated by females compared with males, and evidence for this has been documented in multiple species based on discrepancies in maternally and biparentally inherited DNA (Phillips et al., 2021). Because coastal sharks are heavily exploited around the world (Dulvy et al., 2017), understanding how philopatry influences neutral genetic structure by impacting gene flow is vital for delineating management units that will promote persistence. In addition, parturition sites can be environmentally heterogeneous (Bethea et al., 2015; Matich et al., 2017) and newborn sharks can be subject to higher rates of mortality than other life stages (Heupel & Simpfendorfer, 2002; Lowe, 2002; Manire & Gruber, 1993). Therefore, natal philopatry could drive selection for locally adaptive phenotypes and lead to fine-scale adaptive structure (Portnoy et al., 2015; Portnoy & Heist, 2012). This could have further implications for management because parturition sites harbouring novel adaptive variants may require individually tailored policies.

The blacktip shark (*Carcharhinus limbatus*) is a coastal shark species with a circumglobal distribution in tropical and warm temperate latitudes that is harvested for meat, fins, and liver oil (Compagno et al., 2005; Rigby et al., 2021). In waters of the United States (hereafter U.S. waters), blacktip sharks are found along the Atlantic coast from Florida to Massachusetts and throughout the Gulf of Mexico, where they are targeted by commercial and recreational fisheries (Castro, 1996; SEDAR, 2018, 2020). Commercial fisheries operate year-round and harvest adults in federal and state waters; however, recreational fisheries also operate in state waters, and some may land smaller blacktip sharks closer to shore (SEDAR, 2020). Male and female blacktip sharks mature after 4 and 6 years (respectively) and females produce one to eight pups (four on average) every 2 years

(Baremore & Passerotti, 2013; Natanson et al., 2019). Moreover, the species is highly migratory: males and females can move ~1200 km in fewer than 100 days (Weber et al., 2020) and males have been recorded travelling over 3400 km per year (B. Bowers & S. Kajiura, unpublished data). In the spring and early summer, females move into bays and estuaries to give birth (Castro, 1996; Hueter & Tyminski, 2007). Young-of-the-year (YOY) remain in their parturition site until the autumn of their birth year and migrate south and/or offshore when water temperatures decrease (Castro, 1996; Heupel, 2007; Heupel et al., 2004), and many return to the vicinity of their parturition site the following spring (Hueter et al., 2005).

Based in part on population genetics studies, the U.S. National Marine Fisheries Service (hereafter NOAA Fisheries) currently manages blacktip sharks as two stocks—one in the Atlantic and one in Gulf—but the Gulf stock is split into two subregions (eastern and western), with the dividing line through Mobile Bay, Alabama (SEDAR, 2018, 2020). An assessment of genetic structure based on YOY sampled in parturition sites from Texas, Florida, and Georgia/South Carolina identified three genetic units using the mitochondrial control region, but did not find significant differences using eight nuclear-encoded microsatellites, suggesting female regional philopatry (Keeney et al., 2005). However, the discordance between nuclear and mitochondrial data could also be due to limited resolution (i.e., too few loci) or insufficient time for differences to accrue (Whitlock & McCauley, 1999). Thus, to inform appropriate management and avoid loss of genetic variation resulting from localized depletion, it is vital to accurately characterize blacktip shark population structure and adaptive potential. An assessment of genetic structure at neutral and putatively adaptive loci is therefore warranted.

Here, the genetic structure of blacktip sharks in U.S. waters of the western North Atlantic Ocean was examined using mitochondrial control region and double digest restriction-site associated DNA sequencing (ddRAD-Seq) data. The sampling design targeted YOY within or just outside parturition sites during their spring-autumn residency to ensure that structure reflected differences among reproductive units. By examining thousands of loci spread throughout the genome, a higher resolution assessment of genetic structure at nuclear-encoded loci is possible, and the data can also be used to identify siblings captured in the same habitats across years, a pattern indicative of parturition site fidelity by females. Moreover, by screening for loci putatively under selection, the approach facilitates an assessment of the influence of genetic drift, gene flow, and selection in structuring genomic variation, providing a means to identify habitats harbouring adaptive variants that may facilitate the species' persistence.

2 | MATERIALS AND METHODS

2.1 | Sampling

Tissue samples were collected as fin clips from 503 individual blacktip sharks captured within or near 11 estuaries (sites) off the U.S. Atlantic Coast (hereafter Atlantic) and throughout the northern Gulf of Mexico (hereafter Gulf). The three sites in the Atlantic were along the coast of South Carolina. In the Gulf, there were three sites along the west coast of Florida, one on the coast of Alabama, and four along the coast of Texas. Mobile Bay, the site in Alabama, straddles the 88th meridian that separates the eastern and western blacktip shark Gulf stock subregions (NMFS, 2006). Fin clips were immersed in 20% DMSO-0.25 M EDTA NaCl-saturated buffer (DMSO; Seutin et al., 1991), or ethanol and then transferred into DMSO, and stored at room temperature until DNA extraction. All sharks were captured between March and November 2012–2019. The location of capture (latitude and longitude) was recorded for each individual, and sex was recorded for all but seven individuals. Body measurements (i.e., at least one of pre-caudal, fork, total, and stretch total lengths) were also recorded. If a fork or total length was not recorded, a customized R script (v3.6.0; R Development Core Team, 2008) was used to assign missing values based on observed relationships among length measurements (Carlson et al., 2006). Of the 503 individuals sampled, 488 were YOY: 227 (~47%) were classified as YOY based on the presence of an umbilical scar (Castro, 1993) and 261 (~53%) were classified as YOY using fork length (<593 mm) if sampled in the Atlantic (Ulrich et al., 2007) or total length (≤800 mm) if sampled in the Gulf (Parsons & Hoffmayer, 2007). Based on observations that YOY blacktip sharks in the Atlantic and Gulf remain in or near their parturition site into the autumn months of their first year of life (Castro, 1996; Heupel et al., 2004), these 488 individuals were assumed to have been sampled in their parturition site (Table S1).

2.2 | ddRAD-Seq library preparation and genotyping

High molecular weight genomic DNA was extracted from fin clips using either Mag-Bind® Blood and Tissue DNA Kits (Omega Bio-Tek) or phenol-chloroform extraction (Sambrook et al., 1989). A modified version of ddRAD-Seq (Peterson et al., 2012) was used to prepare genomic libraries containing the 488 YOY individuals plus 31 technical replicates spread across sites and libraries and sequenced using 11 lanes of an Illumina HiSeq 4000 (paired-end 150 bp; see Supplementary Methods for more information).

To map and improve the genotyping efficacy of HiSeq data, a separate library consisting of 27 individuals sampled across Atlantic and Gulf locations at multiple life history stages (Table S2) was prepared using the same protocol and sequenced on a single Illumina MiSeq lane (paired-end 300 bp). Of these 27 individuals, 12 were included in the HiSeq libraries. All raw HiSeq and MiSeq reads were demultiplexed using *process radtags* (Catchen et al., 2011) and quality-trimmed using default parameters implemented in dDocent (Puritz et al., 2014). dDocent was also used to assemble MiSeq reads into a reference of contiguous sequence alignments (i.e., contigs) representing putatively single-copy (orthologous) loci. dDocent was subsequently used to map HiSeq reads to the MiSeq reference and genotype SNPs.

2.3 | ddRAD-Seq data filtering

Raw SNPs were filtered using VCFTOOLS (v0.1.14; Danecek et al., 2011) and R functions in a customized workflow, following practices laid out in O'Leary et al. (2018). Filtering initially removed genotypes with <5 reads and quality <20 while applying a minor allele count of three. Loci were further filtered based on allele balance, mapping quality, ratio of reference vs. alternate allele, consistency of scoring in forward and reverse directions, proper pairing, depth/quality ratio, and excess heterozygosity to remove potential paralogs and other technical artefacts. Individuals with >20% missing data or very negative F_{IS} (<−0.13) indicative of cross-contamination (Petrou et al., 2019) were removed. Retained loci had a mean depth >20 and were called in at least 90% of individuals, 80% of individuals in each site, and 50% of individuals in each library. Haplotypes were then generated by collapsing SNPs on the same contig to produce a dataset of multi-allelic SNP-containing loci (Willis et al., 2017). In addition, the composite genotypes of technical replicates included within and across libraries were compared to characterize locus-specific genotyping error. Replicates were confirmed by assessing relatedness between each pair of individuals using the dyadic likelihood estimator (Milligan, 2003) executed using the R package *related* (Pew et al., 2015). Loci with systematic genotyping error (i.e., in >1 replicate pair) and one individual from each pair were removed, along with monomorphic loci. To minimize genotype inconsistencies across libraries (i.e., library effects), individuals were grouped by library and BAYESCAN (Fischer et al., 2011; Foll et al., 2010; Foll & Gaggiotti, 2008) executed to identify and remove loci contributing to differences among libraries.

2.4 | Mitochondrial sequencing and haplotyping

A 915 bp portion of the mitochondrial control region (1070 bp total length) was amplified for a subset of individuals (323) using a pair of primers within the proline (Pro: GCCCTTGGCTCCCAAAGC) and phenylalanine (Phe: TCATCTTAGCATCTTCAGTGCCA) tRNA genes (Table S3). These primers were designed to amplify the mitochondrial control region of multiple shark species (see Supplementary Methods and Table S4). Amplification was performed using polymerase chain reaction (PCR) in 50 µL reactions with 1× Green GoTaq buffer (Promega), 2 mM $MgCl_2$, 200 µM of each dNTP, 0.5 µM of each primer, and 1.25 units of GoTaq DNA Polymerase. Amplification consisted of an initial denaturation at 95°C for 2 min, followed by 40 cycles of denaturation at 94°C for 30 s, annealing at 54°C for 60 s, and extension at 72°C for 90 s, with a final extension of 72°C for 10 min. PCR products were visualized using gel electrophoresis before being cleaned, quantified, and standardized to 20 ng/µL. Mitochondrial sequence data was generated by unidirectional Sanger sequencing using the Pro primer and an ABI 3730xl platform.

Mitochondrial sequences were aligned using CLUSTAL OMEGA (Sievers et al., 2011) and edited manually in BIOEDIT (Hall, 1999). The R package *haplotypes* were used to identify unique haplotypes. To visualize the distribution of haplotypes among sites, a TCS network (Clement et al., 2000) was produced using POPART (Leigh & Bryant, 2015).

2.5 | Relatedness

To identify full- and half-siblings, pairwise relatedness was assessed using Wang's estimator corrected for sample size (Wang, 2002) executed using the R package *demerelate* (Kraemer & Gerlach, 2017). Because female blacktip sharks are thought to display regional philopatry (Keeney et al., 2005) and relatedness analysis used to confirm technical replicates already screened for kin sampled between regions, relatedness between individuals was assessed for each region separately (i.e., Atlantic, eastern Gulf, and western Gulf). For each region, 1000 pairs of simulated full- and half-sibling relationships were generated using empirical allele frequencies. To identify full- and half-siblings, minimum relatedness thresholds were set after trimming the lowest 1% of simulated values to reduce instances of false positives. Mitochondrial haplotypes were then compared for observed sibling pairs to determine if any half-siblings were paternally related (i.e., had distinct haplotypes). Removal of randomly sampled siblings can reduce the precision of population genetics analyses, as can the inclusion of siblings that are non-randomly sampled (Waples & Anderson, 2017). Therefore, full- and half-siblings were considered non-randomly sampled if both individuals were captured in the same site on the same day, in which case one individual from each pair was removed for all downstream analyses.

2.6 | F_{ST} outlier analysis

Three methods were used to screen for F_{ST} outlier loci putatively under directional selection with individuals grouped by site. The first approach, implemented in *OutFLANK* (Whitlock & Lotterhos, 2015), identifies F_{ST} outliers (q-value < 0.05) based on an inferred distribution of neutral F_{ST} after trimming the lowest and highest 5% of F_{ST} values, thus avoiding implicit assumptions of population structure and demography. The second method generates a null distribution of F_{ST} for neutral loci using a Bayesian approach implemented in BAYESCAN (Fischer et al., 2011; Foll et al., 2010; Foll & Gaggiotti, 2008). This method assumes an island model where allele frequencies in each group are correlated through a common ancestral gene pool. BAYESCAN was executed with prior odds of 1000 and a burn-in of 200,000 iterations; 25 pilot runs of 5000 iterations were used to tune MCMC parameters and following 35,000 sampling iterations with a thinning interval of 50, significance was evaluated using a q-value of 0.05. Finally, the FDIST method (Beaumont & Nichols, 1996), implemented in ARLEQUIN v3.5 (Excoffier & Lischer, 2010), identifies loci with elevated F_{ST} for simulated background heterozygosity under two models: an island model and a hierarchical island model in which sites in the Atlantic and Gulf were grouped. For both models, 50,000 simulations were executed, 100 demes were simulated per

group, and significance was evaluated using α of .05 corrected for multiple comparisons (Benjamini & Hochberg, 1995) by the *p.adjust* function of the R package *stats*.

2.7 | Spatial and environmental analysis

To examine the effects of spatial and environmental variation on genetic structure, correlations among genomic variation, spatial position, and environmental variables were assessed using redundancy analysis (RDA), as implemented in the R package *vegan* (Oksanen et al., 2018). RDA is a constrained ordination method based on multivariate regression that models how linear combinations of explanatory variables explain variation at a series of response variables, thereby enabling the identification of loci that co-vary with multivariate predictors (Legendre & Legendre, 2012). This approach is particularly useful when applied to genomic datasets because it can be performed without grouping individuals by location and does not rely on assumptions of equilibrium between microevolutionary forces, both of which are inherent components of F_{ST}-based analyses. Thus, RDA provides an alternative approach to assess population structure while screening for loci putatively under selection (Forester et al., 2018).

The genomic dataset was transformed into a response matrix detailing the allelic composition of each individual across loci (i.e., the number of copies of each allele at each locus for each individual). Two explanatory matrices describing relative spatial positions and environmental measurements for each sampling location were then produced. To ensure that each individual had a unique sampling location, the R package *geoR* (Ribeiro & Diggle, 2001) was used to jitter latitudes and longitudes for individuals caught in the same sampling effort. To generate the spatial matrix, Moran's eigenvector maps (MEMs; Dray et al., 2006) were calculated using the R package *adespatial* (Dray et al., 2019) based on coastal distances estimated between all sample locations using the R package *gdistance* (Van Etten, 2017). The environmental matrix encompassed measurements for coastal locations (Table S5) that were procured from the MARSPEC (35 variables; Sbrocco & Barber, 2013) and Bio-ORACLE (447 variables; Assis et al., 2018; Tyberghein et al., 2012) databases using the R package *sdmpredictors* (Bosch & Fernandez, 2021). For each explanatory matrix, forward model selection was used to identify the combination of variables that best explained genomic variation based on adjusted R^2 and significance testing (999 permutations; $\alpha < .01$; Blanchet et al., 2008). Because collinearity is likely among environmental variables, model selection prohibited the inclusion of variables with variance inflation factors (VIF) > 3 (Zuur et al., 2010).

The significance of each axis of the spatial and environmental RDA models was assessed using 999 permutation tests with α of .05. To visualize the differential effects of space and environment on genetic structure, the approach outlined by Forester et al. (2018) was used to produce individual biplots depicting how spatial and environmental RDA clustered individuals based on the combination of variables that were selected by each analysis. However, because environmental data is almost always spatially autocorrelated (Legendre, 1993), it is vital to disentangle spatial and environmental signals when identifying loci putatively under selection (Hoban et al., 2016). Therefore, partial RDA (pRDA), in which the linear effects of one set of variables are adjusted by accounting for covariables (Capblancq & Forester, 2021), was used to identify alleles most strongly correlated with environmental variables adjusted for spatial position. Allele loadings should form a distribution in which alleles at the centre show no relationship with environment, while those with loadings in the tails are strongly associated, and may therefore be considered putatively under selection (Forester et al., 2018). Environmentally associated loci were defined using a function that sets thresholds three standard deviations from the mean (equivalent to a two-tailed *p*-value of .0027; Forester et al., 2018). The significance of the full environmental pRDA model and each axis was assessed using 999 permutation tests with α of .05.

2.8 | Population structure

Allele frequencies of neutral and adaptive loci are shaped by different sets of interactions among microevolutionary forces and may provide for distinct patterns of genetic structure (Luikart et al., 2003). Therefore, nuclear loci flagged as being putatively under selection by either of the F_{ST} outlier methods or determined to be environmentally associated using pRDA were designated as adaptive. The nuclear data was then divided into adaptive and neutral (i.e., all other loci) datasets.

For each of the three datasets (mitochondrial control region, neutral, and adaptive nuclear loci), hierarchical AMOVA (Excoffier et al., 1992) was executed separately using Arlequin. For the mitochondrial data, standard AMOVA was performed. For neutral and adaptive datasets, locus-by-locus AMOVA was performed, with *F*-statistics calculated as weighted means of locus-specific values to account for uneven levels of missing data among loci (Weir & Cockerham, 1984). Sites were grouped as Atlantic and Gulf, with significance assessed ($\alpha < .05$) by permuting individuals among sites 10,000 times and by bootstrapping the nuclear data 20,000 times to create 95% confidence intervals. For each dataset, single-level AMOVA was also executed for Atlantic and Gulf sites separately. Subsequently, *post-hoc* estimates of pairwise Φ_{ST} and F_{ST} between sites were calculated using Arlequin, with 95% confidence intervals produced and significance assessed as above, but corrected for multiple comparisons (Benjamini & Hochberg, 1995). For the nuclear datasets, pairwise F_{ST} was estimated on a locus-by-locus basis. Finally, to test for isolation-by-distance, linear regression was used to determine if pairwise Φ_{ST}, neutral F_{ST}, and adaptive F_{ST} increased with coastal distance between sites.

2.9 | Genetic diversity and effective population size

The diversity of mitochondrial sequence data was assessed for each site based on the number of haplotypes, as well as haplotype (*h*) and

nucleotide sequence (π) diversities (Nei, 1987) calculated in ARLEQUIN. For neutral and adaptive nuclear loci, diversity was assessed separately for each site using Nei's gene diversity (H_e; Nei, 1978) and rarified allelic richness (A_r; El Mousadik & Petit, 1996) using the R packages *hierfstat* (Goudet, 2005) and *poppr* (Kamvar et al., 2014), respectively. For each nuclear diversity estimate, differences among sites were assessed using Friedman's rank-sum test ($\alpha < .05$), and Wilcoxon signed-rank tests were used to assess for *post-hoc* pairwise differences ($\alpha < .05$), with *p*-values corrected for multiple comparisons (Benjamini & Hochberg, 1995).

Contemporary effective population size (N_e) was estimated for each site using the linkage disequilibrium method (Hill, 1981) implemented in NEESTIMATOR (v2.1; Do et al., 2014). To ensure that the effective sample size was the same for each pair of loci, N_e was estimated using 1823 neutral nuclear loci with no missing data. Singleton alleles were also removed for each site. In addition to point estimates, 95% confidence intervals were estimated using a method that jackknifes over individuals (Jones et al., 2016). To account for downward bias resulting from physical linkage among loci, N_e estimates were adjusted based on the haploid number of chromosomes (43; Asahida et al., 1995) for the blacktip shark, following Waples et al. (2016).

All figures were produced in R using the package *ggplot2* (Wickham, 2016).

3 | RESULTS

3.1 | ddRAD-Seq data filtering

After demultiplexing and trimming, the mean number of HiSeq and MiSeq reads per sample was 3,796,003 and 1,121,052, respectively (standard deviation: 2,240,246 and 322,556). Filtering removed 47 individuals with missing data >20% and 31 individuals with $F_{IS} < -0.13$. Also, one sample was removed from each of 17 pairs of technical replicates confirmed using the dyadic likelihood estimator. After filtering, 424 individuals genotyped at 4339 SNP-containing loci (1.54 SNPs and 2.39 alleles per locus on average) were retained for subsequent analyses.

3.2 | Mitochondrial sequencing and haplotyping

Sixteen unique mitochondrial haplotypes were identified among 323 individuals, seven of which were previously identified by Keeney et al. (2003, 2005).

3.3 | Relatedness

Minimum values of relatedness used to identify siblings, as determined by simulations, were 0.44–0.45 for full-siblings and 0.19–0.20 for half-siblings (Figure S1). No siblings were identified in the Atlantic. Non-randomly sampled siblings included one full-sibling pair in Terra Ceia Bay (eastern Gulf) and a group of six full- and half-siblings in San Antonio Bay (western Gulf; Table S6). Randomly sampled siblings were detected only in Terra Ceia Bay and included three pairs of full-siblings and 15 pairs of half-siblings (Table S7). Notably, three pairs of half-siblings were sampled 2 years apart and two pairs were sampled 4 years apart. All other siblings were sampled within the same year or 1 year apart. Parent-offspring and avuncular relationships can produce similar relatedness values to full- and half-siblings (respectively). However, blacktip sharks do not mature until after 4 years, and because all kin were sampled within 4 years, pairs of kin identified in this study are most likely siblings. Mitochondrial haplotypes were assessed for 12 pairs of siblings (67%) and two pairs of half-siblings were found to have distinct haplotypes.

After an individual from each non-randomly sampled sibling pair was removed, 418 individuals remained, 77% of which (323) were also haplotyped using the mitochondrial control region (Figure 1).

3.4 | F_{ST} outlier analysis

Zero F_{ST} outliers were detected by *OutFLANK*, BAYESCAN, or ARLEQUIN.

3.5 | Spatial and environmental analysis

Ten MEMs describing spatial differences were generated based on coastal distances between sampling locations, and the first two MEMs were chosen by model selection: MEM1 (adjusted $R^2 = .00123$; $p < .01$; Figure 2c) and MEM2 (adjusted $R^2 = .00188$; $p < .01$; Figure 2d). The full spatial RDA model and both axes were significant ($p < .001$), and linear combinations of MEMs produced three groups (Figure 2a). While MEM1 clustered individuals into Atlantic and Gulf groups, MEM2 divided Gulf individuals into eastern and western groups. Individuals from Mobile Bay—which straddles the boundary between the eastern and western Gulf stock subunits—grouped predominantly with individuals from Florida. Model selection chose two environmental variables with VIF < 3 (Table S8): minimum annual sea surface temperature (°C; adjusted $R^2 = .00133$; $p < .01$; Figure 2f) and mean sea surface salinity in June (unitless; adjusted $R^2 = .00193$; $p < .01$; Figure 2g). The full environmental RDA model and both axes were significant ($p < .001$), and linear combinations of environmental variables also produced three groups (Figure 2b). Like MEM1, temperature grouped Atlantic and Gulf individuals separately, and salinity split Gulf individuals into two groups; however, in contrast to MEM2, salinity grouped individuals from Mobile Bay with those from the western Gulf. Furthermore, while 69% of loci (9/13) with high loadings for MEM1 also had high loadings for temperature, an additional 15 loci had high loadings only for temperature (Table S9), and structured Mobile Bay and western Gulf sites by latitude. MEM2 and salinity each had 11 loci with high loadings, including six loci for both variables, and a latitudinal pattern was also observed among Florida sites due to salinity.

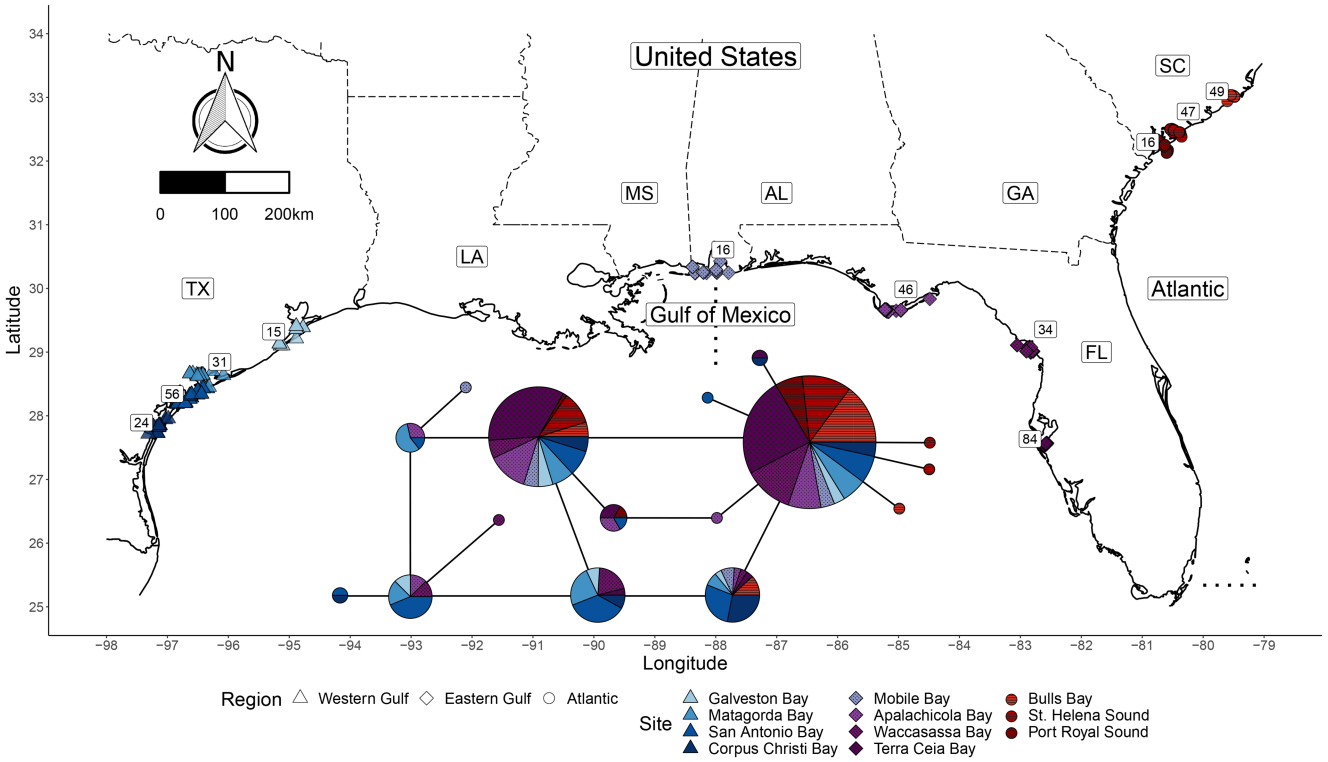

FIGURE 1 Haplotype network of the mitochondrial control region and map of sampling locations in the U.S. Atlantic and Gulf of Mexico for the blacktip shark (*Carcharhinus limbatus*). Dotted lines denote regions that follow designations by NOAA Fisheries. Mobile Bay, Alabama straddles the 88th meridian which separates the eastern and western Gulf stock subregions. Mobile Bay was found to be part of the eastern Gulf in this study. Numbers refer to the sample size for each site included in the ddRAD-Seq data. Abbreviations of U.S. States: AL, Alabama; FL, Florida; GA, Georgia; LA, Louisiana; MS, Mississippi; SC, South Carolina; TX, Texas.

The full pRDA model (i.e., the effect of temperature and salinity adjusted by MEMs 1 and 2) and each axis were significant ($p < .05$). Allele loadings resembled a normal distribution (Figure S2) and 68 environmentally associated loci (1.6%) were identified and removed to produce putatively adaptive (68 loci) and neutral nuclear datasets (4271 loci).

3.6 | Population structure

For the mitochondrial dataset, heterogeneity was observed among groups (Atlantic and Gulf; $\Phi_{CT} = 0.0997$; $p < .05$) and among sites within groups ($\Phi_{SC} = 0.0795$; $p < .0001$; Table 1). Heterogeneity was also observed at neutral nuclear loci among groups ($F_{CT} = 0.0015$; $p < .0001$) and among sites within groups ($F_{SC} = 0.0006$; $p < .001$; Table 1). By contrast, heterogeneity was observed at adaptive nuclear loci among sites within groups ($F_{SC} = 0.0069$; $p < .0001$), but not among groups ($F_{CT} = 0.0002$; $p = .3641$; Table 1). Within the Gulf, heterogeneity was observed for the mitochondrial (Φ_{ST}: 0.0826 and $p < .0001$), neutral nuclear (F_{ST}: 0.0007 and $p < .0001$), and adaptive nuclear (F_{ST}: 0.0085 and $p < .0001$) datasets based on single-level AMOVA (Table 1). By contrast, homogeneity was found in the Atlantic for all three datasets (Φ_{ST}: 0.0246 and $p = .1768$; neutral F_{ST}: 0.0004 and $p = .1871$; adaptive F_{ST}: 0.0006 and $p = .4687$; Table 1).

Post-hoc estimates of pairwise neutral F_{ST} between sites were statistically significant ($p < .05$ after corrections) for all but two Atlantic-Gulf comparisons (92%; Table S10). A similar, albeit weaker pattern was observed for the mitochondrial dataset, with differences found for 63% of Atlantic-Gulf comparisons (Table S11). Furthermore, the neutral nuclear dataset indicated differences within the Gulf between Terra Ceia and Waccasassa Bays (both eastern Gulf), as well as between Terra Ceia Bay and each of the four sites in the western Gulf (Table S10). However, after excluding siblings randomly sampled in Terra Ceia Bay, the difference with Waccasassa Bay was no longer significant (Table S12). A similar pattern was observed in the Gulf using the mitochondrial data, but in addition to Terra Ceia Bay being different from all four sites in the western Gulf, Apalachicola Bay was significantly different from San Antonio and Corpus Christi Bays (Table S11). Terra Ceia Bay was also significantly different from Waccasassa Bay, but not after the removal of randomly sampled siblings (Table S13). Consequently, estimates of pairwise Φ_{ST} and F_{ST} calculated after removing randomly sampled siblings from Terra Ceia Bay were used to assess for relationships between pairwise genetic differences and coastal distances between sites. Linear regression demonstrated a positive relationship between pairwise coastal distances and genetic differences for eastern and western Gulf sites based on the mitochondrial (adjusted $R^2 = 0.2360$; $p < .05$) and neutral nuclear datasets (adjusted $R^2 = 0.5168$; $p < .01$; Figure 2e). By

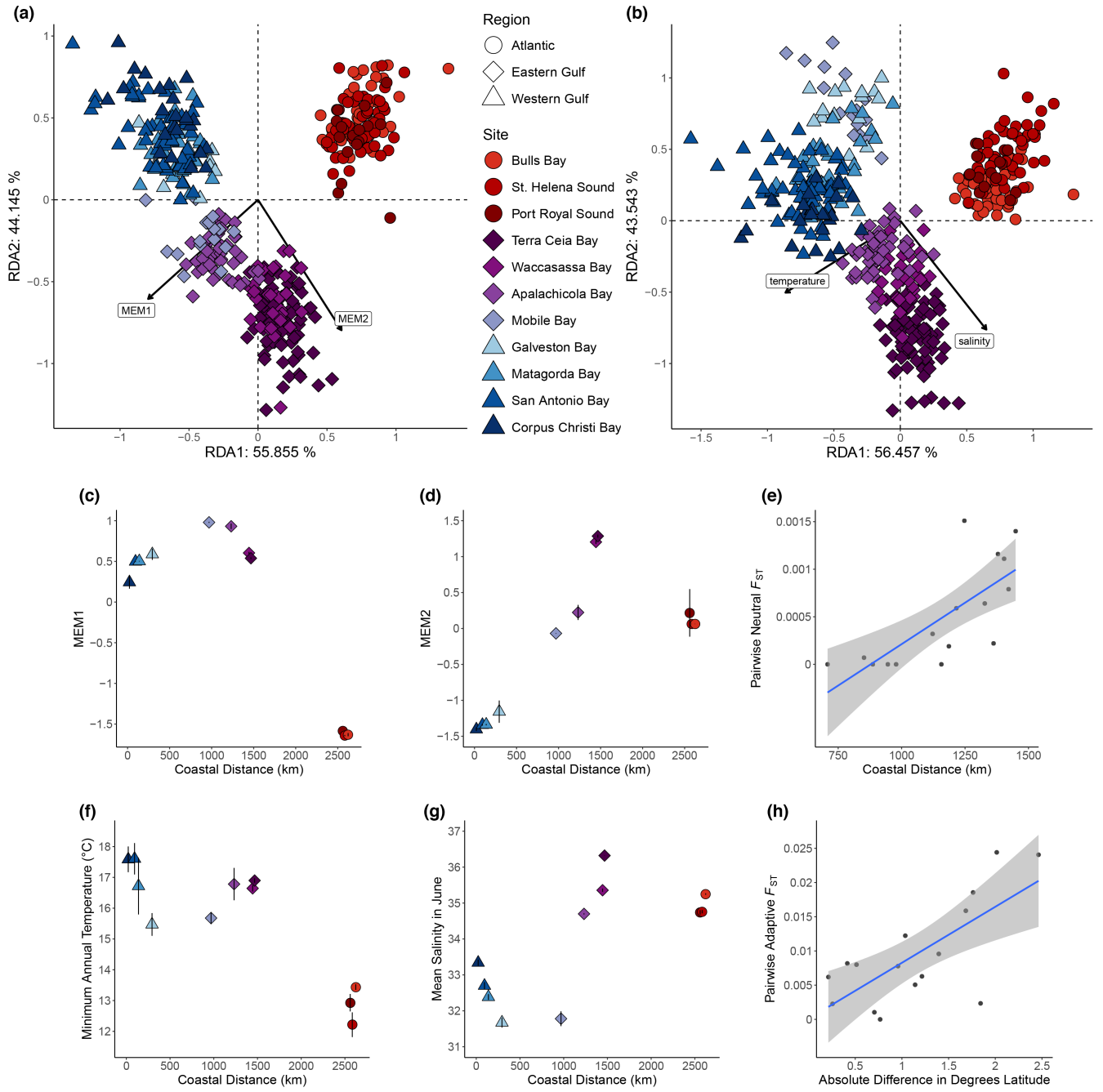

FIGURE 2 The differential effects of spatial and environmental differences on genetic population structure of blacktip sharks (*Carcharhinus limbatus*). (a) Biplot showing ordination space loadings determined by MEM1 and MEM2 from the full spatial redundancy analysis (RDA). (b) Biplot showing ordination space loadings determined by minimum annual temperature and mean salinity in June from the full environmental RDA. (c) Mean ± 1 standard deviation value for MEM1 by site vs. coastal distance. (d) Mean ± 1 standard deviation value for MEM2 by site vs. coastal distance. (e) Pairwise neutral F_{ST} between eastern and western Gulf sites versus pairwise coastal distance between sites. (f) Mean ± 1 standard deviation value for minimum annual temperature by site versus coastal distance. (g) Mean ± 1 standard deviation value for mean salinity in June by site versus coastal distance. (h) Pairwise adaptive F_{ST} between eastern and western Gulf sites versus absolute difference in latitudinal degrees between sites.

contrast, no such relationship was observed for Atlantic-eastern Gulf nor Atlantic-western Gulf comparisons (Figure S3).

For the adaptive dataset, estimates of pairwise F_{ST} were much larger, but statistically significant comparisons were fewer and predominantly observed between Gulf sites with the greatest latitudinal differences (Table S14). For example, Mobile Bay (the most northern Gulf site) was different from all other Gulf sites except Waccasassa and Galveston Bays; Terra Ceia Bay (the most southern Gulf site) was different from all Gulf sites but Waccasassa, San Antonio, and Corpus Christi Bays. Furthermore, in contrast to the mitochondrial and neutral nuclear datasets, linear regression demonstrated a negative relationship between pairwise genetic differences and coastal

TABLE 1 Results from hierarchical and single-level AMOVA using the mitochondrial control region, 4271 neutral, and 68 putatively adaptive SNP-containing nuclear loci.

Dataset	Sites	Source of variation	Variance components	Per cent variation	Φ/*F*-statistic	*p*-value
Mitochondrial control region	All	Among groups (i.e., Atlantic and Gulf)	0.0585	9.9700	0.0997	<.05
		Among sites within groups	0.0420	7.1500	0.0795	<.0001
	Atlantic	Among sites	0.0065	2.4600	0.0246	.1768
		Among individuals within sites	0.2592	97.5400	–	–
	Gulf	Among sites	0.0495	8.2600	0.0826	<.0001
		Among individuals within sites	0.5502	91.7400	–	–
Neutral nuclear loci	All	Among groups (i.e., Atlantic and Gulf	0.5151	0.1542	0.0015	<.0001*
		Among sites within groups	0.1993	0.0597	0.0006	<.001*
	Atlantic	Among sites	0.1167	0.0353	0.0004	.1871
		Among individuals within sites	330.1258	99.9647	–	–
	Gulf	Among sites	0.2182	0.0652	0.0007	<.0001*
		Among individuals within sites	334.5166	99.9348	–	–
Adaptive nuclear loci	All	Among groups (i.e., Atlantic and Gulf	0.0012	0.0242	0.0002	.3641
		Among sites within groups	0.0340	0.6858	0.0069	<.0001*
	Atlantic	Among sites	0.0028	0.0568	0.0006	.4687
		Among individuals within sites	4.9062	99.9432	–	–
	Gulf	Among sites	0.0423	0.8510	0.0085	<.0001*
		Among individuals within sites	4.9233	99.1490	–	–

Note: Underlined *p*-values denote statistically significant heterogeneity. For nuclear datasets, * denotes lower 2.5% of bootstrapped *F*-statistics were greater than zero.

distances for eastern and western Gulf sites (adjusted $R^2 = .4428$; $p < .01$). Consequently, linear regression was then used to determine if pairwise adaptive F_{ST} increased with latitudinal differences between eastern and western Gulf sites, and a positive relationship was observed (adjusted $R^2 = .4757$; $p < .01$; Figure 2h).

3.7 | Genetic diversity and effective population size

Each Atlantic site had fewer mitochondrial haplotypes (3–4) than all but one Gulf site (Mobile Bay; 4), and haplotype and nucleotide diversities were lower in Atlantic sites than in all Gulf sites (Table 2). Though similar numbers of haplotypes were observed within the eastern (4–7) and western Gulf (5–9), haplotype and nucleotide diversities were greater in the western Gulf. For the neutral and adaptive nuclear datasets, gene diversity (H_e) and allelic richness (A_r) differed among the 11 sites ($p < .0001$; Table 2). Estimated neutral H_e was lowest in Port Royal Sound (0.1537; Atlantic) and smaller ($p < .05$) than all sites except St. Helena Sound (Atlantic); estimated neutral H_e was greatest in San Antonio Bay (0.1584; western Gulf) and greater ($p < .05$) than all but three Gulf sites (i.e., Waccasassa, Mobile, and Corpus Christi Bays). Estimated adaptive H_e was lowest in San Antonio (0.1370; western Gulf) and greater in Mobile Bay (0.2076; eastern Gulf) than all other sites ($p < .001$). Estimated neutral A_r was lowest in Port Royal Sound (2.8174; Atlantic) and lower ($p < .05$) than three Gulf sites (i.e., Mobile, Galveston, and San Antonio Bays); estimated neutral A_r was greatest in San Antonio Bay (2.8545; western Gulf) and greater ($p < .05$) than six sites. Estimated adaptive A_r was lowest in San Antonio Bay (2.8332; western Gulf) and greater in Mobile Bay (3.5343; eastern Gulf) than all other sites ($p < .001$).

While finite upper and point N_e estimates were obtained for only one and six sites, respectively (Table S15), lower N_e estimates were obtained for all sites and varied considerably, with no obvious pattern among regions (Figure 3).

TABLE 2 Estimates of genetic diversity based on the mitochondrial control region, 4271 neutral, and 68 putatively adaptive SNP-containing nuclear loci.

		Mitochondrial control region				Neutral loci			Adaptive loci	
Region	Site	*n*	Haplotypes	*h*	π	*n*	H_e	A_r	H_e	A_r
Atlantic	BLB	30	4	0.4483 ± 0.1021	0.000538 ± 0.000528	49	0.1551	2.8273	0.1434	2.8932
	SHS	29	4	0.5345 ± 0.0725	0.000635 ± 0.000587	47	0.1544	2.8199	0.1445	2.8771
	PRS	12	3	0.3182 ± 0.1637	0.000513 ± 0.000540	16	0.1537	2.8174	0.1466	2.9122
Eastern Gulf	TCB	70	6	0.5706 ± 0.0314	0.000705 ± 0.000615	84	0.1547	2.8234	0.1373	2.8397
	WAB	32	6	0.6492 ± 0.0794	0.001260 ± 0.000930	34	0.1574	2.8448	0.1373	2.8521
	APB	31	7	0.7333 ± 0.0534	0.001208 ± 0.000904	46	0.1568	2.8399	0.1533	2.9057
	MOB	12	4	0.7424 ± 0.0842	0.001275 ± 0.000992	16	0.1578	2.8470	0.2076	3.5343
Western Gulf	GAB	13	5	0.8205 ± 0.0661	0.001429 ± 0.001070	15	0.1572	2.8420	0.1393	2.8943
	MAB	30	6	0.8253 ± 0.0334	0.001455 ± 0.001035	31	0.1562	2.8362	0.1450	2.8881
	SAB	44	9	0.8478 ± 0.0204	0.001606 ± 0.001101	56	0.1584	2.8545	0.1370	2.8323
	CCB	20	6	0.8000 ± 0.0537	0.001427 ± 0.001038	24	0.1578	2.8525	0.1465	2.8988

Note: Mean estimates are given for all, with ±1 standard deviation estimates for the mitochondrial control region only. *n* refers to sample size per site. *h* and π refer to mitochondrial haplotype diversity and nucleotide diversity, respectively. H_e and A_r refer to Nei's gene diversity and allelic richness, respectively.

Abbreviations: APB, Apalachicola Bay; BLB, Bulls Bay; CCB, Corpus Christi Bay; GAB, Galveston Bay; MAB, Matagorda Bay; MOB, Mobile Bay; PRS, Port Royal Sound; SAB, San Antonio Bay; SHS, St. Helena Sound; TCB, Terra Ceia Bay; WAB, Waccasassa Bay.

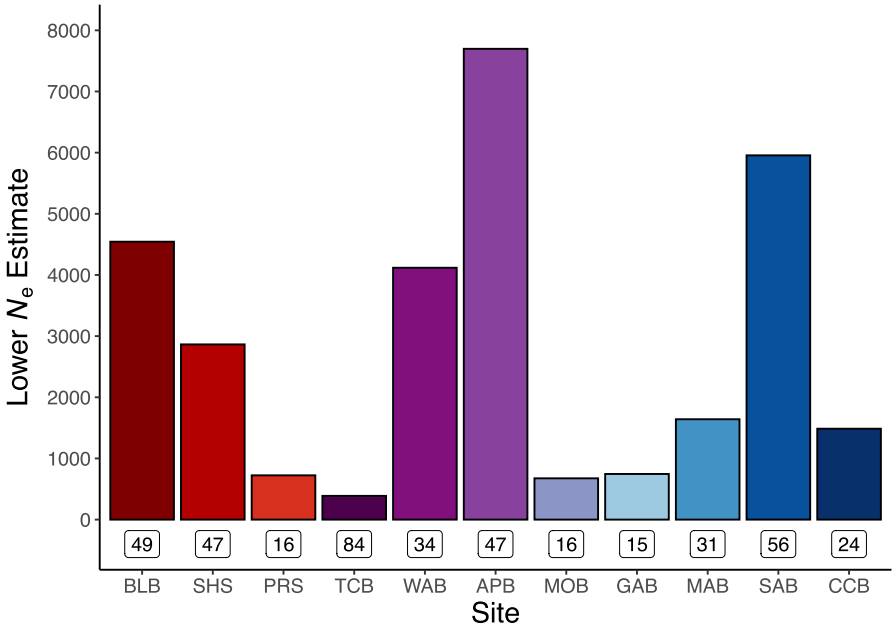

FIGURE 3 Lower 95% confidence interval estimates of contemporary effective population size (N_e) of blacktip sharks (*Carcharhinus limbatus*) by site. Numbers above the *x*-axis denote the sample size per site. Site abbreviations: APB[¥], Apalachicola Bay; BLB*, Bulls Bay; CCB[§], Corpus Christi Bay; GAB[§], Galveston Bay; MAB[§], Matagorda Bay; MOB[¥], Mobile Bay; PRS*, Port Royal Sound; SAB[§], San Antonio Bay; SHS*, St. Helena Sound; TCB[¥], Terra Ceia Bay; WAB[¥], Waccasassa Bay. Symbols denote regions: Atlantic*, eastern Gulf[¥], and western Gulf[§].

4 | DISCUSSION

The results of this study highlight how philopatry can influence genetic population structure at multiple spatial scales by restricting gene flow and facilitating the sorting of adaptive variants by selection. Mitochondrial and neutral genetic structure indicated that blacktip sharks in the U.S. Atlantic and Gulf of Mexico constitute three genetically distinct units with little to no gene flow between them. Structure within Gulf units at putatively adaptive loci, correlated with variation in sea surface temperature and salinity, suggested local adaptation to environmental conditions. Instances of parturition site fidelity were documented based on the sampling of maternally related siblings, and if this behaviour extends across generations (i.e., natal philopatry), it could contribute to the observed patterns of adaptive structure.

4.1 | Neutral genetic structure

Results from mitochondrial and neutral nuclear data confirm that blacktip sharks in the Atlantic and Gulf are genetically distinct. The

first MEM of the spatial RDA grouped Atlantic and Gulf individuals separately (Figure 2a) and genetic structure was also observed between these groups based on hierarchical AMOVA and *post-hoc* estimates of Φ_{ST} and F_{ST} between sites. In addition, genetic diversity was generally lower in the Atlantic than in the Gulf. The finding of genetically distinct blacktip shark units in the Atlantic and Gulf is consistent with previous assessments of mitochondrial DNA (Keeney et al., 2003, 2005) and life history traits such as maximum length and growth rate (Carlson et al., 2006). This observation is also consistent with studies of other marine fishes (Gold et al., 2009; Leidig et al., 2015; Seyoum et al., 2017), including coastal sharks (Dimens et al., 2019; Portnoy et al., 2015, 2016), and aligns with the Florida Vicariance Zone (Neigel, 2009), where constriction of the continental shelf from Miami to West Palm Beach has reduced nearshore habitat (Avise, 1992; Neigel, 2009). Consequently, suitable parturition sites for coastal sharks are lacking in southeastern Florida and may dissuade female movement across the vicariance zone. Although gene flow via males should be less affected, tagging data suggest that male blacktip sharks do not move between the Atlantic and Gulf either (Kohler & Turner, 2019), thus additional factors likely limit connectivity.

Neutral genetic structure was also found within the Gulf, but not within the Atlantic. YOY blacktip sharks occupy U.S. Atlantic estuaries from northern Florida to southern North Carolina (Castro, 1996; McCallister et al., 2013), so the lack of observed structure in the Atlantic could be due to limited spatial sampling. For the Gulf, single-level AMOVA indicated heterogeneity, and differences in both pairwise Φ_{ST} and F_{ST} were observed between the most eastern and the four western sites. This could indicate an isolation-by-distance effect (Laikre et al., 2005), which is supported by positive relationships between pairwise Φ_{ST}/F_{ST} and coastal distances (Figure 2e). However, the spatial RDA clustered Gulf individuals into eastern and western groups, with individuals from Mobile Bay grouping predominantly with those from Florida (Figure 2a). This division aligns with a biogeographic break in the northern Gulf (McClure & McEachran, 1992), centred on an area of transition from carbonate sediments in the east to mostly terrigenous sediments in the west (McClure & McEachran, 1992; Neigel, 2009). Further, low salinity outflows from the Mississippi and Atchafalaya rivers to the west of Mobile Bay could act as a barrier to gene flow for blacktip sharks. This has been suggested for other stenohaline sharks in the Gulf (Portnoy et al., 2014), as well as a variety of marine species around the world (Rocha, 2003; Volk et al., 2021). In addition, spatial RDA and estimates of pairwise Φ_{ST} and F_{ST} are consistent with the idea that straying by females occurs mostly among neighbouring parturition sites, as suggested by other studies of coastal sharks (Duncan et al., 2006; Keeney et al., 2003). Nevertheless, it should be noted that this study did not include sites between Mobile and Galveston Bays because a sufficient number of samples could not be collected in Louisiana. Thus, neutral structure in the Gulf may follow an isolation-by-distance pattern and the lack of samples from Louisiana could have facilitated the finding of discrete eastern and western Gulf groups by spatial RDA. The pattern of neutral structure documented by this study has been observed in multiple marine fishes in the northern Gulf (Karlsson et al., 2009; Portnoy et al., 2014; Seyoum et al., 2018). In particular, the results are similar to those of a genomic assessment of red drum (*Sciaenops ocellatus*; Hollenbeck et al., 2019), which do not give live birth but display spawning site fidelity to estuaries to which juveniles recruit after the larval period (Lowerre-Barbieri et al., 2019; Matlock, 1990). This is in contrast with the patterns seen in genomics studies of two species that spawn offshore, red snapper (*Lutjanus campechanus*; Portnoy et al., 2021) and southern flounder (*Paralichthys lethostigma*; O'Leary et al., 2021), and suggests that habitat use may be an important predictor of genetic structure for fishes of the Gulf of Mexico.

A previous assessment of blacktip shark genetic structure found differences among the Atlantic, eastern, and western Gulf in mitochondrial DNA, but not nuclear DNA, and the authors hypothesized that this reflected female regional philopatry and male-mediated gene flow (Keeney et al., 2005). While this study found similar patterns of mitochondrial DNA structure among the Atlantic, eastern, and western Gulf, heterogeneity was also detected among these regions at neutral nuclear loci. Inconsistencies in the observed patterns of neutral nuclear structure are likely due to the greater resolution offered by thousands of SNP-containing loci as compared to the eight microsatellite loci used by Keeney et al. (2005). Thus, it appears that male blacktip sharks also display regional philopatry, or that male-mediated gene flow is insufficient to homogenize allele frequencies among these regions. Evidence of male regional philopatry is noteworthy because it suggests that the widespread notion of male-biased dispersal in elasmobranchs—which developed from mixed-marker studies typically using microsatellites and mitochondrial DNA—may be overemphasized (Phillips et al., 2021). Taken together, the results suggest that regional philopatry by both male and female blacktip sharks has contributed to the formation of genetically distinct units in the Atlantic, eastern Gulf, and western Gulf that align well with the current stock subregions defined by NOAA Fisheries.

4.2 | Adaptive genetic structure

Genetic structure at putatively adaptive loci was observed on a more localized scale in the Gulf. Environmental RDA structured Gulf individuals into two groups along latitudinal gradients based on minimum annual temperature and mean salinity in June, and in contrast to spatial RDA, Mobile Bay individuals grouped with those from Texas (Figure 2b). These groups correspond with a transition in environmental conditions and a break in the coastal shark assemblage of the northern Gulf that has been described by multiple studies (Bethea et al., 2015; Drymon et al., 2020). Significant pairwise F_{ST} estimates based on adaptive loci were observed between sites within each group, and the greatest F_{ST} values were observed between sites with the greatest latitudinal differences (Figure 2h), indicating local adaptation among parturition sites. Furthermore, estimates of adaptive H_e and A_r were highly elevated in Mobile Bay, which could

be related to the spatial and temporal environmental heterogeneity that characterizes this estuary (Kim & Park, 2012; Orlando Jr et al., 1993). However, Mobile Bay is proximal to a marine-suture zone (Portnoy & Gold, 2012), an area of overlap between biotic assemblages (Remington, 1968), so greater diversity could also reflect contact between the eastern and western Gulf.

While the lack of a suitable reference genome precludes assessments of putative function, aspects of blacktip shark biology provide potential explanations for the fine-scale adaptive structure observed here. Adaptive differences associated with minimum annual temperature could reflect temporal variation in YOY migration out of parturition sites when waters cool in the autumn. Sea surface temperatures in Gulf estuaries are colder seasonally in the north than in the south and can vary considerably due to a variety of climatic factors. A gradient exists along the Texas coast because temperature differences are predominantly influenced by seasonal heat flux and river discharges (Portela et al., 2018), whereas differences along the Gulf coast of Florida appear less stark. Blacktip sharks born in Terra Ceia Bay were thought to remain until late October to late November, with emigration following dramatic decreases in water temperature (1.5–2°C) to approximately 21°C (Heupel, 2007). It now appears that some remain until January because water temperatures do not decrease sufficiently until then (Goldner, 2022). If there is a fitness cost to a shorter residency period, local adaptation could lead to individuals born in estuaries further north being more tolerant of lower temperatures. However, blacktip shark emigration from an Atlantic coast estuary (i.e., Bulls Bay, South Carolina) also coincides with ~21°C (Castro, 1996). Therefore, it appears that similar temperature changes stimulate emigration, and blacktip sharks born in more northern Gulf estuaries should migrate earlier in the year when those temperatures are reached. This is observed along the Texas coast where YOY blacktip sharks are found in Corpus Christi Bay until mid-November (Matich et al., 2021), weeks after they have emigrated from Galveston Bay (P. Matich & Texas Parks and Wildlife, unpublished data). Likewise, the species is mostly absent in Mobile Bay after October (Parsons & Hoffmayer, 2007). A similar pattern of migratory timing is seen when Atlantic salmon (*Salmo salar*) leave nurseries in the spring/summer (Hodgson & Quinn, 2002; Hvidsten et al., 1998), with individuals from southern habitats migrating weeks before those found further north because the temperatures that stimulate emigration are reached earlier (Otero et al., 2014; Vollset et al., 2021).

Salinities also vary among Gulf estuaries and adaptive differences associated with mean salinity in June—immediately after the peak period of parturition (Baremore & Passerotti, 2013)—could indicate local adaptation based on salinity tolerance. Peninsular Florida estuaries are relatively saline because conditions are predominantly influenced by precipitation, with little freshwater inflow compared with estuaries to the west. Conditions are less saline in the Florida panhandle due to lower evaporation rates and freshwater discharge from the Apalachicola, Chattahoochee, and Flint rivers that flow into Apalachicola Bay (Orlando Jr et al., 1993). Mobile Bay is relatively hyposaline because of the large freshwater influx via the Mobile River (Orlando Jr et al., 1993), and June salinities in Texas estuaries are similar to Mobile Bay because precipitation is greatest in May (TexasET, 2022). Also, the major river systems (e.g., Mobile, Mississippi, Rio Grande) that drain into the Gulf are distributed from Alabama to the border with Mexico (USGS, 1990). Nonetheless, a salinity gradient exists along the Texas coast because estuaries in the north receive hyposaline waters from the central Gulf via westerly currents, while isolated freshwater pulses lead to more saline conditions in the south (Orlando Jr et al., 1993). Consequently, blacktip sharks born in estuaries on the lower Texas coast may experience higher salinities, consistent with the conditions at which individuals have been captured in Corpus Christi (mean: 25.0–33.4) and Galveston Bays (mean: 16.1–22.3; Matich et al., 2017). By contrast, the species has been captured in Mobile Bay at salinities as low as 11 (Parsons & Hoffmayer, 2007) and is usually found at salinities of 22.3–34.2 in Florida estuaries (Bethea et al., 2009).

A limitation of this study is that the available data sources provide insufficient resolution to describe environmental variation within estuaries. The MARSPEC and Bio-ORACLE databases reflect coastal conditions for which differences are predominantly driven by latitude, and consequently, environmental heterogeneity among the sites is underestimated. Additionally, the environmental measurements are unable to account for habitat usage by blacktip sharks because these individuals are highly mobile, only use a subset of the available estuarine habitat, and move with environmental conditions (Froeschke et al., 2010). Even so, the environmental RDA shows latitudinal gradients in both the eastern and western Gulf, thus the results may reflect local adaptation to conditions that are not described by the environmental data but also vary with latitude.

4.3 | Philopatry and local adaptation

Two pairs of half-siblings had distinct mitochondrial haplotypes, demonstrating they had different mothers and thus were paternally related. For one pair, both siblings were sampled (born) in the same year, meaning a male reproduced with two females in the same breeding season that each gave birth in Terra Ceia Bay (eastern Gulf). This suggests that breeding sites may be proximal to parturition sites, which is consistent with what is understood about breeding locations in the U.S. Atlantic (Castro, 1996). For the other sibling pair, the individuals were sampled (born) 1 year apart, providing direct evidence that a male blacktip shark reproduced in the eastern Gulf in consecutive breeding seasons. This observation suggests that male blacktip sharks might display breeding site fidelity and is consistent with the indirect evidence of male regional philopatry based on patterns of neutral genetic structure.

Five pairs of half-siblings with the same mitochondrial haplotypes were captured 2 and 4 years apart in Terra Ceia Bay, accordant with the biennial reproductive period of female blacktip sharks (Baremore & Passerotti, 2013; Castro, 1996). This implies that five females re-used the habitat for parturition. It is important to note that all randomly sampled siblings were detected in Terra Ceia Bay, and N_e estimates indicated that the number of breeders using this habitat is much smaller than in other sites (Figure 3). Hence, blacktip

sharks may exhibit parturition site fidelity to additional estuaries, but the behaviour may be easier to detect in Terra Ceia Bay because there is a higher probability of catching siblings. Females that re-use the same estuary for parturition display a strong degree of habitat fidelity, but for this behaviour to constitute natal philopatry, the estuary that is re-used must be the habitat in which females were born. Multiple studies have demonstrated that sharks can navigate to their place of birth (Edrén & Gruber, 2005; O'Gower, 1995; Sundström et al., 2001), including blacktip sharks (Gardiner et al., 2015; Heupel et al., 2003), and while natal philopatry has been speculated to occur in this species (Hueter et al., 2005), the behaviour has been demonstrated directly only in the lemon shark (*Negaprion brevirostris*) in Bimini, The Bahamas (Feldheim et al., 2014). This was possible because lemon sharks in Bimini are captured in a nearly exhaustive manner, relatively few females give birth there, and genetic profiling has been ongoing for decades (Feldheim et al., 2004; Gruber et al., 2001; Postaire et al., 2022). The results presented here indicate that long-term studies focused on identifying kin among blacktip sharks in Terra Ceia Bay may demonstrate a second example of natal philopatry by coastal sharks.

While the observation of three genetically distinct units in the Atlantic and Gulf suggests male and female blacktip sharks reproduce in the region of their birth (i.e., regional philopatry), this behaviour cannot explain the fine-scale adaptive structure observed within Gulf units. Adaptive variation could sort among neighbouring estuaries if alleles adapted to local conditions conferred phenotypes with greater fitness and matrilines carrying these alleles re-used the same estuaries as parturition sites in subsequent generations (i.e., natal philopatry). Under this scenario, YOY with phenotypes locally adapted to their parturition site would have a higher probability of surviving and reproducing. Differential selection pressures among parturition sites would drive selection for locally adapted phenotypes and overcome gene flow of maladapted alleles from neighbouring estuaries via patrilines and/or female straying. Given the heterogeneity in conditions like temperature and salinity among Gulf estuaries and the high rates of mortality experienced by YOY blacktip sharks (Heupel & Simpfendorfer, 2002), directional selection and natal philopatry could facilitate the sorting of adaptive alleles (Kawecki & Ebert, 2004), generating the patterns of adaptive structure observed in this study.

5 | CONCLUSIONS

The genetic structure found among parturition sites within management units highlights the importance of policies that focus on the preservation of adaptive variation (Funk et al., 2012). Estuaries in which progeny are born and/or reside as juveniles are considered essential because they are fundamental to life cycles (Fluharty, 2000), but if neighbouring habitats are environmentally heterogeneous and sources of novel adaptive variants, it may be necessary to individually evaluate their contributions to ensure future persistence (Stiebens et al., 2013). These considerations are particularly important for species displaying fine-scale philopatry because the loss of certain habitats could lead to irreversible declines in recruitment and adaptive potential (Hess et al., 2013; Hueter et al., 2005). Furthermore, as environmental conditions continue to shift with climate change, the capability of organisms to adapt and persist will depend on existing genetic variation and levels of gene flow among habitats.

AUTHOR CONTRIBUTIONS

Dominic G. Swift: conceptualization; funding; sample collection; molecular laboratory work; data analysis; writing; writing-review and editing. **Shannon J. O'Leary**: data analysis, writing-review and editing. **R. Dean Grubbs**: collection funding, sample collection, writing-review and editing. **Bryan S. Frazier**: conceptualization; funding; sample collection; writing-review and editing. **Andrew T. Fields**: molecular laboratory work; data analysis; writing-review and editing. **Jayne M. Gardiner**: collection funding, sample collection, writing-review and editing. **J. Marcus Drymon**: sample collection, writing-review and editing. **Dana M. Bethea**: sample collection, writing-review and editing. **Tonya R. Wiley**: sample collection, writing-review and editing. **David S. Portnoy**: conceptualization; funding; data analysis; writing; writing-review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts.

DATA AVAILABILITY STATEMENT

Genetic data: Raw MiSeq and HiSeq reads are available in the NCBI SRA (BioProject PRJNA996573). Analysis scripts and data are available on GitHub (https://github.com/dgs108/blacktip_philopatry) and DataDryad (http://doi.org/10.5061/dryad.vmcvdnczp), respectively.

Sample metadata: Metadata associated with raw reads are available in the NCBI SRA (BioProject PRJNA996573) and Tables S1 and S2.

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