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Contemporary population structure and post-glacial genetic demography in a migratory marine species, the blacknose shark, *Carcharhinus acronotus*

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Abstract

Patterns of population structure and historical genetic demography of blacknose sharks in the western North Atlantic Ocean were assessed using variation in nuclear-encoded microsatellites and sequences of mitochondrial (mt)DNA. Significant heterogeneity and/or inferred barriers to gene flow, based on microsatellites and/or mtDNA, revealed the occurrence of five genetic populations localized to five geographic regions: the southeastern U.S Atlantic coast, the eastern Gulf of Mexico, the western Gulf of Mexico, Bay of Campeche in the southern Gulf of Mexico and the Bahamas. Pairwise estimates of genetic divergence between sharks in the Bahamas and those in all other localities were more than an order of magnitude higher than between pairwise comparisons involving the other localities. Demographic modelling indicated that sharks in all five regions diverged after the last glacial maximum and, except for the Bahamas, experienced post-glacial, population expansion. The patterns of genetic variation also suggest that the southern Gulf of Mexico may have served as a glacial refuge and source for the expansion. Results of the study demonstrate that barriers to gene flow and historical genetic demography contributed to contemporary patterns of population structure in a coastal migratory species living in an otherwise continuous marine habitat. The results also indicate that for many marine species, failure to properly characterize barriers in terms of levels of contemporary gene flow could in part be due to inferences based solely on equilibrium assumptions. This could lead to erroneous conclusions regarding levels of connectivity in species of conservation concern.

Keywords: conservation genetics, elasmobranchs, glacial refugia, secondary contact

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Introduction

Delineation of population structure is critical for conservation and management of exploited marine fishes, in part because separate management of subregional stocks, should they exist, is critical to avoid overexploitation and loss of adaptive genetic variation and in part because erosion of genetic resources via depletion of unrecognized spawning components can directly affect recruitment potential and adaptability (Begg *et al.* 1999; Hilborn *et al.* 2003). However, marine environments tend to be open, lacking obvious barriers to gene flow (Waples 1998), and documenting spatial genetic differences, particularly in migratory species, can therefore be difficult (Carvalho & Hauser 1998; Portnoy & Gold

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2013). Further, for some species, patterns of contemporary genetic variation may be affected by historical demography (Marko & Hart 2011). This is especially true for species impacted over the last two million years by repeated glacial events (Provan & Bennett 2008). Therefore, assessment of population structure must take into account the effect that historical processes may have had on contemporary genetic variation.

Understanding population structure is especially critical for conservation and management of elasmobranchs. Over one-quarter of coastal sharks and rays are estimated to be threatened (Dulvy *et al.* 2014) and approximately 13.5% of chondrichthyan fishes in waters of North America, Central America and the Caribbean Sea qualify for one of the three 'threatened' categories (Kyne *et al.* 2012). Further, many sharks tend to exhibit philopatry to nursery grounds (Portnoy & Heist 2012), which potentially enhances juvenile survival (Branstetter 1990) but also may increase localized extirpation if the species is exploited (Hueter *et al.* 2004).

The blacknose shark, *Carcharhinus acronotus*, is a tropical to warm-temperate, coastal species distributed in the Atlantic Ocean (hereafter Atlantic) from Virginia on the east coast of the United States (U.S.) through the Gulf of Mexico (hereafter Gulf) and Caribbean Sea to southern Brazil (Castro 2011). The coastal distribution of the species makes it highly available to both commercial and recreational fishing (Hazin *et al.* 2002) and susceptible to mortality as bycatch (Nichols 2007; NMFS 2007). The species had been managed in U.S. waters of the Atlantic and Gulf as a single management unit or stock and as a component of the small coastal shark (SCS) complex (NMFS 2007). A recent assessment, however, indicated that blacknose sharks are overfished along the U.S. Atlantic coast, with the consequence that the species was removed from the SCS complex and is now managed separately as Atlantic and Gulf units (NMFS 2013). Currently, the species is listed by the International Union for Conservation of Nature (IUCN) as near threatened with a decreasing population trend (Morgan *et al.* 2009).

Differences in life history and migratory behaviour between blacknose sharks in the U.S. Atlantic and Gulf support the hypothesis of separate populations. These differences include size and age at maturity (Driggers *et al.* 2004a,b), reproductive cycles and gestation times (Driggers *et al.* 2004a; Sulikowski *et al.* 2007). In addition, blacknose sharks in the U.S. Atlantic move northward from the east coast of Florida to the Carolinas in the summer, returning to Florida in the winter (Schwartz 1984; Ulrich *et al.* 2007), while blacknose sharks in the northeastern Gulf follow a similar pattern along the west coast of Florida, moving northward/onshore in the spring and summer and returning south/offshore in the winter (Clark & von Schmidt 1965; Carlson *et al.* 1999). These seasonal movements likely are associated with reproduction, as mating during the summer months is thought to occur along the coastline of South Carolina in the Atlantic and near the Florida panhandle in the northeastern Gulf (Driggers *et al.* 2004a; Sulikowski *et al.* 2007); neonates and juveniles are found in both regions (Ulrich *et al.* 2007; Grubbs, personal communication). In addition, there is suggestive evidence, based on tag-and-recapture studies and observational data (Kohler *et al.* 1998; W. B. Driggers, unpublished data), that there might be two populations of blacknose sharks in the Gulf.

In this study, we assessed patterns of genetic variation, using both nuclear-encoded microsatellites and mtDNA control-region sequences, between blacknose sharks sampled along the U.S. coastline, from South Carolina through Texas, from the Bay of Campeche in Mexico and from the Bahamas. The experimental design allowed us to assess patterns of population structure and search for potential barriers to gene flow in a migratory marine species across a potentially continuous sampling surface. In addition, we were able to assess the importance of male-mediated gene flow, thought to be common in coastal sharks (Portnoy & Heist 2012), in shaping patterns of genetic diversity. Finally, because the species is tropical to warm-temperate and its current range includes areas affected by recent glaciations, we examined the role that historical demography may have had in shaping contemporary patterns of genetic variation and divergence. While this dynamic has been well explored in terrestrial species and in some benthic/demersal and sessile marine species (Wilson 2006; Hoarau *et al.* 2007), it has not been well characterized in larger, migratory marine species such as sharks.

Materials and methods

Sample collection, DNA extraction, genotyping and sequencing

A total of 651 blacknose sharks were sampled between 2010 and 2012 (Figs S1 and S2, Supporting information) from near-shore localities in the U.S. Atlantic (South Carolina, SC; Georgia, GA; the east coast of Florida, NFL), the Florida Keys (KEY), the Gulf east of the Mississippi River (west coast of Florida, FL; Alabama, AL) and the Gulf west of the Mississippi River (Louisiana, LA; Texas, TX). Additional samples included 30 individuals from the Bay of Campeche (MX) and 36 individuals from the Bahamas (BAH). Most samples were taken during the summer months (May to September), when mature individuals are in the northern/inshore part of their range for parturition and mating. The

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exceptions were in the Florida Keys, where sampling occurred in both the summer and winter, and in the Bahamas where five individuals were sampled between October and November. Individual samples were a mix of older juveniles and adult males and females. Tissues (fin clips) were stored in 95% nondenatured ethanol or 20% DMSO buffer (Seutin *et al*. 1991). Sex was recorded for all individuals except for those from the Bay of Campeche. DNA was extracted following a modified Chelex extraction protocol (Estoup *et al*. 1996). After a final 2 min centrifugation at 13 000 *g*, 1–2 μL of supernatant was used as a template for PCRs.

A total of 23 microsatellites were assayed. The forward primer from each primer pair was labelled with one fluorescent label of 6-FAM, HEX or NED (Dye Set D; Applied Biosystems). Descriptions of primers and protocols of PCR amplifications may be found in Giresi *et al*. (2012). Amplicons were electrophoresed on 6% polyacrylamide gels, using an ABI Prism 377 sequencer (Applied Biosystems) and the GeneScan™ 400HD ROX™ Size Standard (Applied Biosystems) in each lane. Scoring was conducted manually, using GENESCAN v. 3.1.2 (Applied Biosystems) and GENOTYPER v. 2.5 (PerkinElmer).

The entire mitochondrial control region (Ctr; 1077 bp) was amplified using the primer Pro-L (5′-AGGG RAAGGAGGGTCAAACT-3′), complementary to a portion of the proline tRNA located on the light strand, and the primer 282H (5′-AAGGCTAGGACCAAACCT-3′), complementary to a portion of the 12S rRNA on the heavy strand (Keeney *et al*. 2003). To ensure accurate sequencing of rare haplotypes, internal primers CP5′ R (5′ACCTTAATGAACCAGATGAGCC-3′) and CP3′F (5′-CCTTTAATGGCATATTTATCC3′), described by Portnoy *et al*. (2010), were paired with primers Pro-L and 282H, respectively, to amplify overlapping fragments. Thirty-microlitre PCRs contained 1X reaction buffer (pH 8.5), 2 mM $MgCl_2$, 0.25 mM of each dNTP, 15 pmol of each primer, 0.1 U/μL *Taq* polymerase and 2 μL of template. Reaction conditions consisted of an initial denaturation at 95 °C for 4 min followed by 45 cycles of 95 °C for 1 min, 58 °C (Pro-L and 5′R) or 60 °C (3′F and 282H) for 45 s and 72 °C for 1 min, followed by a final extension of 72 °C for 10 min. Amplified products were gel-extracted using QIAquick® PCR gel extraction kits (Qiagen) and sent to University of Florida's Interdisciplinary Center for Biotechnology Research (http://www.biotech.ufl.edu/) for bidirectional sequencing.

Summary statistics

Conformance to expectations of Hardy–Weinberg equilibrium (HWE) was evaluated for each microsatellite in each sample locality, using GENEPOP v.4.0 (Raymond & Rousset 1995; Rousset 2008); significance was assessed at the 0.05 level, using exact tests with 1000 batches and 10 000 iterations per batch. Sequential Bonferroni adjustment (Rice 1989) was used to correct for multiple testing. MICROCHECKER v.2.2.3 (van Oosterhout *et al*. 2004) was used to screen for possible null alleles and/or genotyping error. Number of alleles, allelic richness and unbiased gene diversity (expected heterozygosity) were estimated for each microsatellite in each geographic locality, using FSTAT v.2.9.3.2 (Goudet 2001). Wilcoxon signed-rank tests, implemented in SYSTAT 8.0 (SPSS Inc.), were used to test for homogeneity in allelic richness and gene diversity between pairs of localities. For control-region sequences (mtDNA), nucleon diversity (h) and nucleotide diversity (π) at each locality were estimated using ARLEQUIN v.3.5.1.2 (Excoffier & Lischer 2010).

Population structure

Homogeneity in allele and genotype distributions (microsatellites) across localities was tested using a single-level analysis of molecular variance (AMOVA), as implemented in ARLEQUIN. Pairwise F_{ST} values between samples, based on microsatellites, also were estimated using ARLEQUIN. Significance of pairwise F_{ST} values at the 0.05 level was assessed by permuting individuals between localities 10 000 times. Correction for multiple testing was implemented using the false discovery rate (FDR) procedure of Benjamini & Hochberg (1995). LOSITAN (Beaumont & Nichols 1996; Antao *et al*. 2008) was used to screen for F_{ST} outliers (candidate loci under selection) by comparing observed mean F_{ST} values at each microsatellite, corrected for locus-specific gene diversity (expected heterozygosity), against a 95% confidence interval of F_{ST} values (corrected for diversity) generated by simulation. The run was implemented with a preliminary simulation of 50 000 steps, used to estimate the neutral mean F_{ST}, followed by a final simulation of 50 000 steps and a FDR of 0.05. Sequences of outlier microsatellites were screened using the BLASTN algorithm within NCBI's BLAST suite (Altschul *et al*. 1990) to identify putative function. Pairwise F_{ST} estimates, excluding outlier loci, were generated to assess whether any outlier microsatellites had a detectable effect on initial estimates of F_{ST}.

Homogeneity of haplotype (mtDNA) distributions among localities was tested using a single-level AMOVA, as implemented in ARLEQUIN. Genetic distances were calculated using a Kimura 2-parameter model (K2P, Kimura 1980), as selected by jMODELTEST 0.1.1 (Guindon & Gascuel 2003; Posada 2008). Pairwise Φ_{ST} values were estimated using ARLEQUIN, with significance

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determined as described previously for microsatellites. A minimum-spanning network was created with NETWORK v.4.510 (Fluxus-engineering.com), using the full median-joining algorithm (Bandelt *et al.* 1999), to visualize relationships of mtDNA haplotypes among localities. Maximum parsimony (MP) was used to remove unnecessary alternate connections (Polzin & Daneshmand 2003). Mantel tests (Smouse *et al.* 1986) were implemented in ARLEQUIN (100 000 permutations) to evaluate whether pairwise F_{ST} (microsatellites) and Φ_{ST} (mtDNA) estimates were correlated and whether F_{ST} and/or Φ_{ST} were correlated with geographic distance.

The geographic orientation of primary and higher-order barriers to gene flow among localities was visualized using BARRIER 2.2 (Manni *et al.* 2004). Genetic dissimilarity between pairs of localities (microsatellites) was calculated as one minus the proportion of shared alleles, using MSA ANALYZER 4.05 (Dieringer & Schlötterer 2003). Genetic distance between pairs of localities, based on Ctr sequences, employed a K2P model and was estimated as net mean divergence, using APE (Paradis *et al.* 2004). BARRIER was run iteratively to define primary and higher-order barriers; significance was assessed by bootstrapping over microsatellites or mtDNA haplotypes within localities and recalculating distances 1000 times.

Individual localities were grouped into the smallest genetic units (regions) defined by initial analysis: western Gulf, WG (TX, LA); eastern Gulf, EG (AL, NFL, KEY); Atlantic, ATL (FL, GA, SC); Bahamas (BAH); and Bay of Campeche (MX). A hierarchical AMOVA, as implemented in ARLEQUIN, was then carried out to test homogeneity of allele (microsatellite) and haplotype (mtDNA) distributions among regions and between/among localities within regions. Pairwise F_{ST} (Φ_{ST}) values between regions, based on microsatellites and mtDNA, also were estimated using ARLEQUIN. To facilitate comparisons between fixation indices made with different marker types (i.e. microsatellites and mtDNA), F_{ST} also was calculated to account for high diversity associated with microsatellites (Meirmans & Hedrick 2011).

Gene flow and historical demography

To assess the effects that male-mediated gene flow, a pattern commonly detected in large coastal sharks (Portnoy & Heist 2012), might have on the partitioning of genetic variation, pairwise F_{ST} values between regions were estimated, using ARLEQUIN, for females only and for males only. The sample from Bay of Campeche (MX) was excluded from this analysis as data on sex were not available. As an independent assessment of possible sex-specific migratory behaviour, Bayesian assignment tests were implemented in GENECLASS v.2.0 (Piry *et al.* 2004) and used to screen for first-generation migrants between all pairs of regions. Significance was assessed at $\alpha \leq 0.01$ by simulating 10 000 individuals (10 000 multilocus genotypes) for each region, using the Monte Carlo resampling algorithm described in Paetkau *et al.* (2004). Sex and source region were noted for each putative migrant.

Because rates of divergence are affected by connectivity and the rate of drift, we estimated M (average, long-term, mutation-scaled migration) and theta ($\theta = 4Ne\mu$) and their 95% highest posterior density (HPD) intervals for each region, using microsatellite data (sexes pooled) and the Bayesian approach implemented in MIGRATE-N v.3.2.16 (Beerli & Felsenstein 2001; Beerli 2006). Regions were subsampled ($n = 36$), except for MX ($n = 30$), and replicate runs assessed for consistency. Replicates were run using a burn-in period of 1 000 000 steps, followed by 10 000 000 steps, with trees recorded every 200 steps; a total of 50 000 trees were sampled. Average, long-term effective population size (N_{eLT}) and migration rate (m_{LT}) were estimated as $N_{eLT} = \theta/4\mu$ and $m_{LT} = M\mu$, respectively.

Estimates of divergence between BAH and all other regions were far greater than estimates of divergence between any other pair of regions. However, several individuals in ATL and EG had mtDNA haplotypes that were otherwise only found in BAH, a pattern that could reflect historical admixture. To explore whether a signal of historical admixture also was present in the nuclear genome, the spatially informed Bayesian clustering algorithm implemented in TESS 2.3.1 (Chen *et al.* 2007; Durand *et al.* 2009) was carried out using the microsatellite data. The number of clusters was set to $K = 2$, and degree of the trend surface was set to 1 (linear). Runs consisted of 25 000 burn-in sweeps followed by 80 000 sweeps. All runs were implemented using the Besag, York and Mollie admixture model (BYM; Besag *et al.* 1991), with θ proportional to the mean geographic distance between individual sampling localities and the variance term (initially set to 1) permitted to update during the course of runs. A total of 100 replicates were run and the 20 runs with lowest DIC scores (deviance information criterion; Durand *et al.* 2009) retained; results were combined using CLUMPP (Jakobsson & Rosenberg 2007).

To further understand how historical demographic processes may have helped shape current genetic variation, five divergence scenarios (Fig. 1a–e) were compared in a coalescent framework, using approximate Bayesian computation (ABC) as applied in DIYABC v2.0 (Cornuet *et al.* 2008, 2014), with microsatellite and mtDNA data merged. The first scenario involved a rapid split where sharks in all five regions diverged from an ancestral gene pool at time t in the past. The second scenario involved an early divergence of sharks in the

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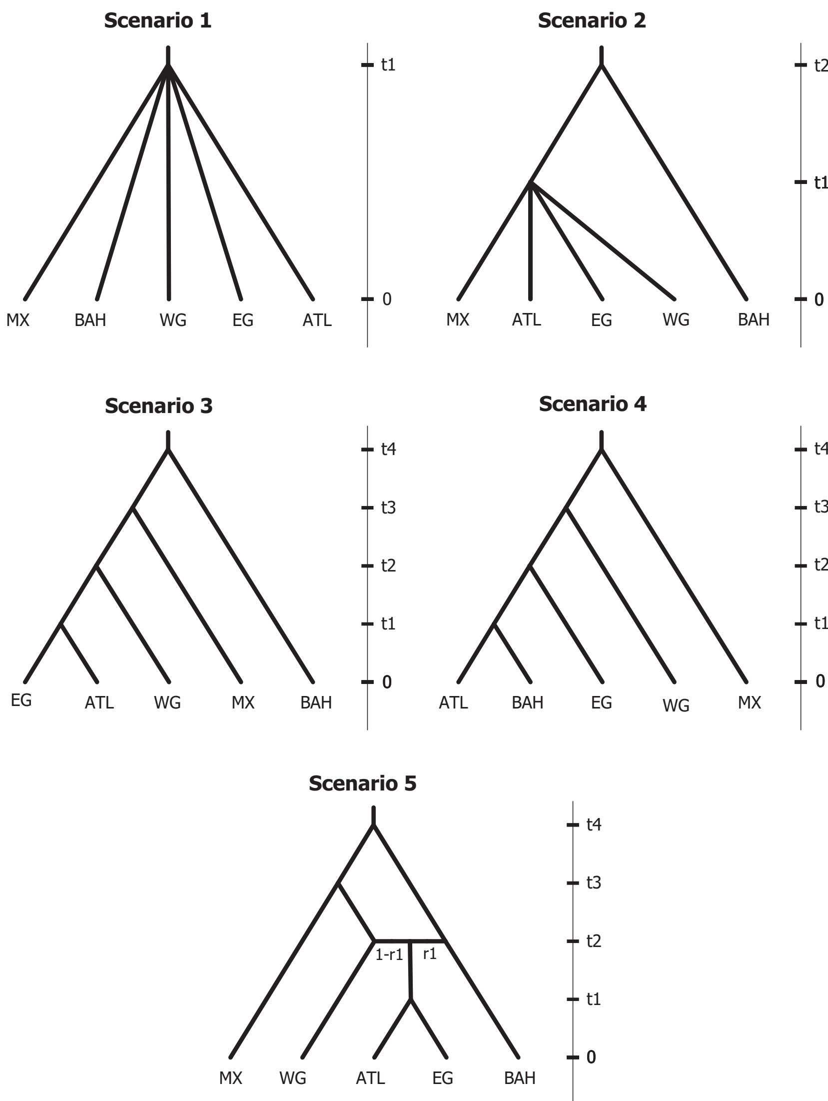

Fig. 1 Demographic scenarios, tested in an approximate Bayesian framework, for western Gulf (WG), eastern Gulf (EG), Atlantic (ATL), Mexico (MX), the Bahamas (BAH). For all scenarios, N_{eLT} was free to change immediately after a split event, t_j, is time step in the past measured in generations; *r* and 1-*r* are rate of immigration from donor populations.

Bahamas from the ancestral gene pool at time t_2 in the past, followed by divergence of populations in the other four regions at time t_1 in the past. The third and fourth scenarios involved treelike bifurcations occurring from t_4 to t_1 in the past. These scenarios differed in the placement of sharks in the Bahamas, which split at the base from the ancestral gene pool (Scenario 3) or was derived from a population along the southeastern U.S. Atlantic coast (Scenario 4). The final scenario involved a basal split between lineages leading to populations in Bay of Campeche and the Bahamas, followed by divergence from the population in Bay of Campeche of a population in the northwestern Gulf. In this last model, admixture of sharks from the Bahamas and the lineage leading to the population in the western Gulf led to a lineage that gave rise to populations along the southeastern U.S. Atlantic coast and the eastern Gulf. Each scenario was run with population sizes free to vary after splitting. Prior distributions for all parameters can be found in Table S1 (Supporting information). Runs consisted of five million simulated data sets (one million per scenario). Posterior probabilities of each scenario were then compared to determine which scenario was most consistent with the data. Posterior predictive simulations were then used to assess congruence between observed data and proposed models (Gelman *et al.* 1995). Briefly, 10 000 data sets were simulated using the posterior distributions of parameters from the selected model(s) and plotted along with observed data on the planes of a PCA. The planes of the PCA itself were defined by data sets that used priors of parameters. Finally, posterior distributions of all parameters were estimated from the selected model, based on the 100 000 simulated data sets closest to the observed data set.

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Results

Summary statistics

Summary statistics for each of the 23 microsatellites are presented in Table S2 (Supporting information). Genotypes at eighteen, microsatellite-locality pairings deviated significantly from HWE expectations prior to Bonferroni correction. Following correction, only genotypes at *Cac*58 (in nine of 10 localities) deviated significantly from HWE expectations. Analysis with MICROCHECKER indicated that the deviations at *Cac*58 could be due to null alleles; consequently, *Cac*58 was excluded from further analyses. Summary statistics for each population averaged across all retained loci (22 microsatellites) are presented in Table 1. The average number of alleles (22 microsatellites) assayed per locality (± SE) ranged from 11.6 ± 2.0 (FL) to 7 ± 1.2 (BAH). Allelic richness was highest in MX (9.2 ± 1.5) and lowest in BAH (6.5 ± 1.0), whereas gene diversity (expected heterozygosity) was highest in SC (0.681 ± 0.037) and lowest in BAH (0.578 ± 0.044). Pairwise tests of homogeneity in allelic richness (AR) and gene diversity (GD) indicated significantly less genetic diversity in blacknose sharks in BAH than in all other samples (AR: all P values ≤ 0.008, GD: all P values ≤ 0.022). Pairwise tests of homogeneity in allelic richness indicated significantly higher diversity for MX than four of the remaining eight samples (MX/LA: $T = 2.033$, $P = 0.042$; MX/KEY: $T = 2.549$, $P = 0.011$; MX/NFL: $T = 2.455$, $P = 0.014$; MX/GA: $T = 2.416$, $P = 0.016$). Summary statistics for mtDNA haplotypes also are presented in Tables 1 and S2 (Supporting information); geographic distributions of all haplotypes are presented in Table S3 (Supporting information). A total of 26 different haplotypes were found across all localities. Estimates of h and π ranged from 0.735 (BAH) to 0.227 (AL) and from 0.0010 (MX and BAH) to 0.0002 (NFL), respectively. The sample from Mexico (MX) was unique in having high levels of diversity for both microsatellites and mtDNA.

Population structure

Analysis of molecular variance, based on microsatellites, revealed significant heterogeneity among localities ($F_{ST} = 0.0153$, $P < 0.00001$). Estimates of F_{ST} (and tests of the null hypothesis $F_{ST} = 0$) between pairs of localities (Table S4, Supporting information) were highly significant for all comparisons involving BAH ($P < 0.00001$) after correction for multiple tests, with the magnitude of F_{ST} in comparisons involving BAH being more than an order of magnitude greater than F_{ST} values between pairwise comparisons of other localities. Comparisons between MX and the three localities from the Atlantic were significant after correction ($P < 0.0015$) as was the comparison between MX and TX and MX and FL ($P < 0.021$). All twelve estimates of F_{ST} involving a locality from the Atlantic vs. a locality from the Gulf were significant before correction; after correction, eight of these comparisons remained significant. None of the estimates involving KEY were significant (except between BAH and KEY). Two microsatellites were identified as outliers: *Cac*46 ($F_{ST} = 0.177$, $P = 1.00$) and *Cac*66 ($F_{ST} = 0.053$, $P = 0.999$). A BLASTN search did not identify any regions of high similarity between *Cac*46 or *Cac*66 and sequences stored in GENBANK. When pairwise estimates of F_{ST} were generated with these loci omitted, the results remained the same.

Single-level AMOVA, based on mtDNA haplotypes, revealed significant heterogeneity among all localities

Table 1 Summary statistics for each sampling locality (Texas, TX; Louisiana, LA; Alabama, AL; Gulf coast of Florida, FL; Florida Keys, KEY; Atlantic coast of Florida, NFL; Georgia, GA; South Carolina, SC; Bay of Campeche, MX; and the Bahamas, BAH) averaged across 22 microsatellite loci or for 1077 bp of the mitochondrial control region: n_a, mean number of individual genotyped; A, mean number of alleles; A_R, mean rarified allelic richness; H_E mean unbiased gene diversity; n, number of individual sequenced; H, number of haplotypes; h, nucleon diversity; π, nucleotide diversity

Microsatellite	TX	LA	AL	FL	KEY	NFL	GA	SC	MX	BAH
n_a	79.91	52.00	54.91	144.52	50.91	46.96	83.00	72.00	29.74	36.00
A	10.64	9.82	9.64	11.59	9.55	9.36	10.14	10.14	9.36	7.00
A_R	8.49	8.53	8.33	8.52	8.34	8.24	8.17	8.34	9.18	6.54
H_E	0.669	0.676	0.675	0.678	0.679	0.679	0.678	0.681	0.671	0.578
mtDNA	**TX**	**LA**	**AL**	**FL**	**KEY**	**NFL**	**GA**	**SC**	**MX**	**BAH**
n	25	23	25	25	25	24	27	29	26	23
H	3	5	3	7	6	3	7	5	10	4
h	0.290	0.324	0.227	0.660	0.623	0.236	0.504	0.318	0.671	0.735
π	0.00035	0.00048	0.00035	0.00079	0.00069	0.00023	0.00053	0.00032	0.00103	0.00102

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(Φ_{ST} = 0.2331, $P < 0.00001$). Estimates of Φ_{ST} (and tests of the null hypothesis $\Phi_{ST} = 0$) between pairs of localities (Table S4, Supporting information) were highly significant for all comparisons involving BAH ($P < 0.00001$) after correction for multiple tests, with the magnitude of Φ_{ST} in comparisons involving BAH being more than four times greater than Φ_{ST} values between pairwise comparisons of other localities. Of twelve pairwise Φ_{ST} values involving comparisons of localities from the Atlantic vs. localities from the Gulf, five were significant before correction and three were significant after correction. Estimates of Φ_{ST} also were significant after correction for comparisons between KEY and NFL ($P = 0.012$) and KEY and SC ($P = 0.015$). A Mantel test between F_{ST} and Φ_{ST} matrices was nonsignificant ($P = 0.224$). Mantel tests between fixation indices (F_{ST}, microsatellites; Φ_{ST}, mtDNA) and geographic distance were nonsignificant when all localities were included. When BAH was removed from the data set, the Mantel test between F_{ST} and geographic distance was significant ($P = 0.00059$).

The minimum-spanning network (Fig. 2) contained two major clades (1 and 2). Clade 1 was 'star-shaped' (Avise 2000; Calafell *et al.* 2002), with one central haplotype in highest frequency (≥58%) in all regions except BAH. Star-shaped phylogenies of mtDNA haplotypes generally indicate recent population expansion (Slatkin & Hudson 1991; Avise 2000). Therefore, we used the approach of Morral *et al.* (1994) to estimate the mean number of mutational steps (ρ) required to coalesce all haplotypes in Clade 1 to a single ancestral individual with the central haplotype. The estimate of ρ (0.153) was then divided by the number of mutations per year, following the approach used in Morral *et al.* (1994) and Saillard *et al.* (2000), to estimate the time to coalesce all haplotypes to a single ancestor. Based on the range of mutation rates estimated for mitochondrial control regions in two other carcharhiniform sharks (0.43% per MY, Keeney & Heist 2006; 0.8; % per MY, Duncan *et al.* 2006), the haplotypes in Clade 1 coalesced to an ancestral haplotype between 17.7 ± 1.3 (SE) kya to 35.5 ± 2.7 kya (SE).

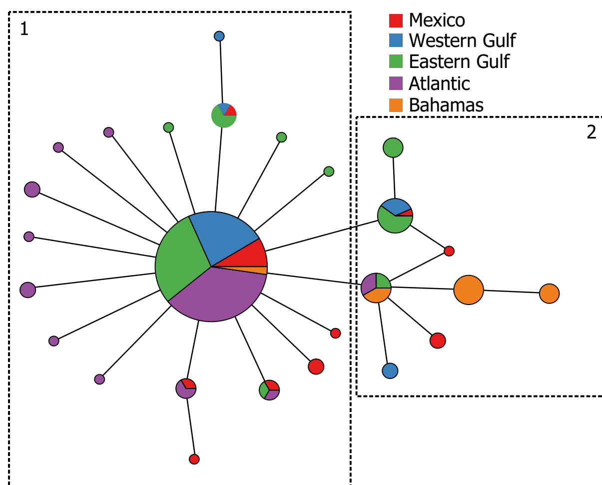

Fig. 2 Minimum-spanning network of 26 blacknose shark mtDNA control region haplotypes. Sizes of circles are proportional to haplotype frequencies, branch lengths are proportional to number of mutations, and boxes demarcate Clade 1 and Clade 2 discussed in text.

Bootstrap resampling of inferred barriers, based on microsatellites (Fig. 3a), indicated restricted gene flow between BAH and all other localities (primary barrier, 100% support) and between MX and Gulf plus Atlantic localities (secondary barrier, ≥99% support). A third barrier fell between LA and AL (tertiary barrier, >83% support), while Gulf and Atlantic localities were separated, with KEY placed in EG (quaternary barrier, >74% support). Bootstrap resampling of inferred barriers, based on mtDNA (Fig. 3b), also indicated restricted gene flow between BAH and all other localities (primary barrier, 100% support). Inferred barriers also separated Atlantic from Gulf localities plus MX (secondary barrier, ≥75%), and MX from localities in the Gulf (tertiary barrier, >56% support).

Based on these results, samples were grouped into regions and used in further analysis as follows: western Gulf (WG: TX and LA), eastern Gulf (EG: AL, FL and KEY), Atlantic (ATL: NFL, GA, and SC), MX and BAH. Hierarchical AMOVA, based on microsatellites and mtDNA, revealed significant heterogeneity among regions (F_{CT} = 0.019, $P = 0.0006$; Φ_{CT} = 0.272, $P = 0.0004$ respectively); the component of variance attributable to differences among localities within regions was not significant for either marker type (Table 2). Pairwise F_{ST} comparisons (microsatellites) between regions were significant after correction except for WG vs. EG and WG vs. MX (Table 3). Pairwise Φ_{ST} comparisons (mtDNA) were the same as comparisons with F_{ST} except that the comparison of WG with ATL was nonsignificant (Table 3). Pairwise F_{ST} estimates made using microsatellites with pooled (male and female) data, male-only data, and female-only data were similar in terms of magnitude and significance.

Gene flow and historical demography

Eight individuals were flagged at $P \leq 0.01$ as being potential first-generation migrants; of those, four were male, three were female, and one was unknown; details of potential migrants can be found in Table S5 (Supporting information). Admixture analysis ($K = 2$) indicated little admixture between BAH and the other regions. However, five individuals (one in SC, four in

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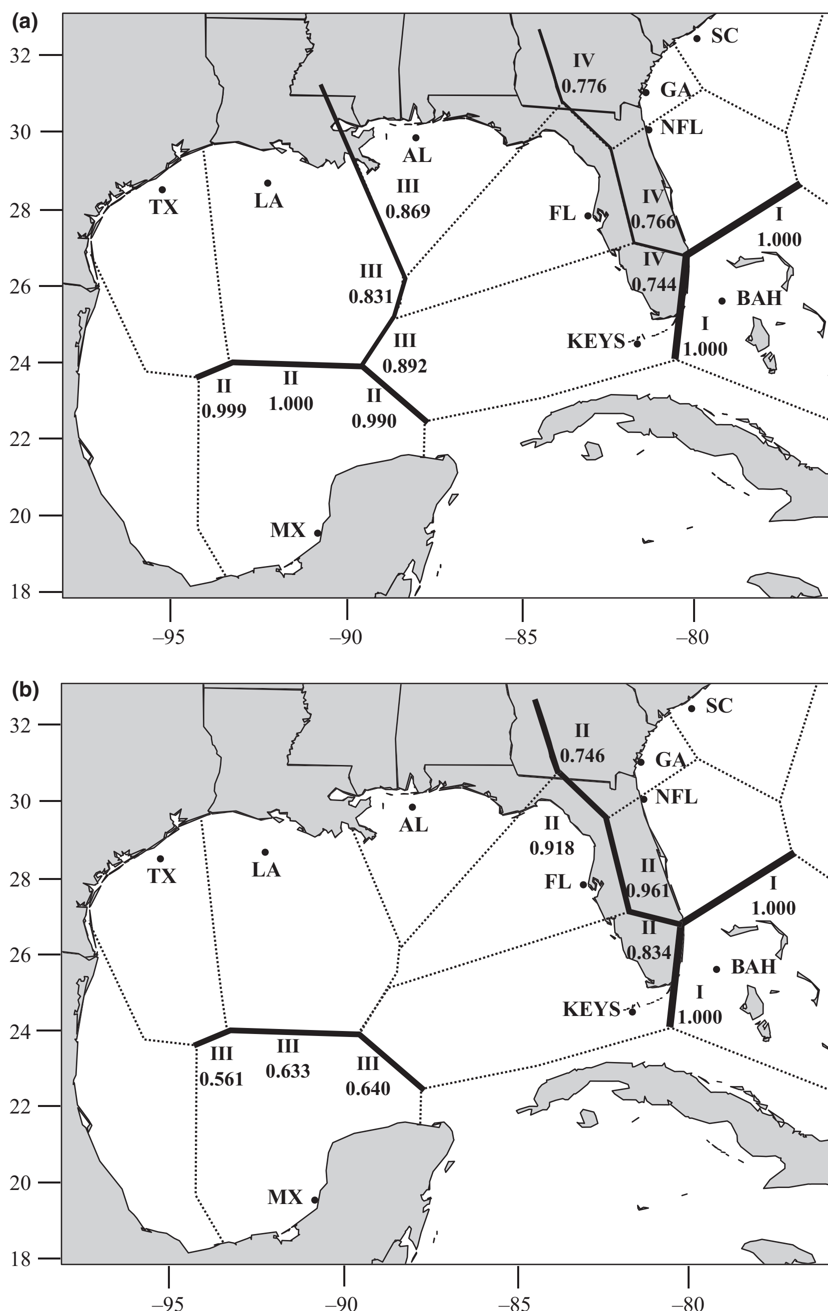

Fig. 3 Voronoi diagram and inferred barriers to gene flow: (a) microsatellites; and (b) mtDNA sequences. Edges separating nearest-neighbour localities are denoted by dotted lines; thick lines are identified barriers. Roman numerals identify ordination of identified barrier; numbers next to barriers are support index based on 1000 bootstrapped data sets.

FL) had 20% or greater assignment to BAH, suggesting some degree of historical admixture between sharks from BAH and the eastern Gulf and the U.S. Atlantic coast (Fig. 4).

Estimates of average, long-term effective population size (N_{eLT}) are shown in Table 4. The average mutation rate (μ) across all microsatellites, obtained from DIYABC and used to estimate N_{eLT}, was 6.14×10^{-4} (95% CI: 2.18×10^{-4} and 9.21×10^{-4}). The modal value of N_{eLT} for BAH (52) was one to two orders of magnitude less than values of N_{eLT} in all other regions. The modal value of N_{eLT} for WG was less than the lower confidence interval for MX and ATL, while the modal value of N_{eLT} for MX was about two times greater than values for WG and EG. Estimates of average, long-term migration rate (m_{LT}), shown in Table S6 (Supporting information), were similar and small (<1%) for all comparisons, well below the 10% rate beyond which populations may become demographically independent (Waples 2010). Modal values of m_{LT} ranged from 0.209% between MX and ATL (95% CI: 0.019–0.565%) to 0.461% between MX and WG (95% CI: 0.098–0.952%).

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Table 2 Results of hierarchical AMOVA for blacknose sharks, based on microsatellites and mtDNA. Regions are Atlantic (South Carolina, Georgia, east coast of Florida), eastern Gulf (Florida Keys, west coast of Florida, Alabama), western Gulf (Louisiana, Texas), Mexico and the Bahamas: d.f., degrees of freedom; SS, sum of squares; VC, variance component; and %V, per cent of variance

	d.f.	SS	VC	%V	Φ	*P* values
Microsatellites						
Among regions	4	158.25	0.139	1.86	0.019	<0.001
Among localities within regions	5	37.88	0.002	0.02	0.000	0.330
Within localities	1292	9472.88	7.332	98.12	0.019	<0.001
mtDNA						
Among regions	4	22.88	0.115	27.15	0.272	<0.001
Among localities within regions	5	1.29	−0.002	−0.49	−0.007	0.418
Within localities	242	75.00	0.310	73.34	0.267	<0.001

Table 3 F_{ST} (microsatellites, below diagonal) and Φ_{ST} (mtDNA, above diagonal) values for pairwise comparisons of regions: western Gulf of Mexico, WG; eastern Gulf of Mexico, EG; Atlantic, ATL; Mexico, MX; and Bahamas, BAH

	WG	EG	ATL	MX	BAH
WG	—	0.0092	0.0115	0.005	0.6071*
EG	0.0005 (0.0013)	—	0.0642*	0.0324*	0.5845*
ATL	0.0031 (0.0094)*	0.0031 (0.0095)*	—	0.0297*	0.6422*
MX	0.0029 (0.0095)	0.0034 (0.0107)*	0.0055 (0.0176)*	—	0.4465*
BAH	0.1061 (0.2956)*	0.0969 (0.2752)*	0.1108 (0.3158)*	0.1092 (0.2926)*	—

*Values significant after correction initial α = 0.005; values in parenthesis are F'_{ST}.

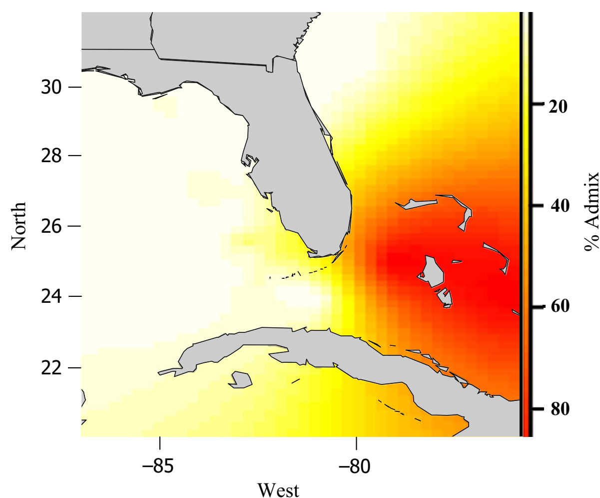

Fig. 4 Spatial interpolations of genetic admixture proportions for the data set that included all localities (K = 2). Spatial interpolations were made in R (R core development team), using the KrigAdmixProportions script provided with TESS 2.3.1 and the map data package (Becker & Wilks 1993, 1995). Heat map represents the proportion (% admix, scale on right axis) of ancestry in Cluster 1 (Bahamas).

Results of ABC analysis are shown in Figs S3 and S4 (Supporting information). Scenario one, where all populations diverged from an ancestral population at time t in the past, had the highest posterior probability (Fig. S3a,b, Supporting information) based on both direct and logistic regression-based estimates. Scenario two, which involved an early divergence of sharks in the Bahamas from the ancestral gene pool, occurring at time t_1, followed by divergence from the ancestral population of sharks in the other four regions, occurring at time t_2, had a slightly lower posterior probability based on direct estimates, and lower posterior probability based on logistic regression-based estimates (Fig. S3a,b, Supporting information). No other scenarios had statistical support. In addition, observed data for both scenarios fell within simulated data, suggesting good model fit (Fig. S4a,b, Supporting information). The posterior distribution of N_{eLT} for all five regions was estimated based on Scenario 1, as was the posterior distribution for the ancestral population and time since divergence (t). Estimates of N_{eLT} obtained from DIYABC were consistent in terms of both magnitude and pattern with those obtained from MIGRATE-N (Table 4). The modal value of N_{eLT} for BAH (538) was more than an order of magnitude smaller than values of N_{eLT} for any other region. The modal value for N_{eLT} for the ancestral population (494) was similar to that of BAH, while modal values of N_{eLT} for all other populations (regions) were one to two orders of magnitude greater than that for the ancestral population. The modal estimate of t

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was 168 generations (CI: 61–775). Given a generation time in blacknose sharks of approximately 13.5 years (Sulikowski *et al.* 2007), this translates to a divergence estimate of <10 463 kya.

Discussion

We assessed patterns of genetic variation in both nuclear-encoded microsatellites and maternally inherited mtDNA control-region sequences in a migratory marine species, the blacknose shark, sampled across a seemingly continuous range in the western North Atlantic. We also assessed the role that potential post-glacial demographic change may have had in moulding contemporary genetic variation. Tests of genetic homogeneity strongly supported existence of four genetic units corresponding to samples from the southern Gulf of Mexico, the Bahamas, the U.S. Atlantic Coast and the northern Gulf of Mexico. Secondary analyses, using microsatellites, suggested the presence of a fifth genetic unit, dividing the northern Gulf into eastern and western units. Further, sharks from the Bahamas were strongly divergent genetically from sharks in all other sample localities regardless of geographic distance. Average, long-term migration rates were similar and small in all comparisons, and little support was found for male-mediated gene flow. Demographic model testing in an ABC framework strongly supported recent population expansion in all samples except for the Bahamas, where long-term effective size was relatively small.

Barriers to gene flow

Occurrence of genetically distinct populations of blacknose sharks along the U.S. Atlantic coast and the northern Gulf is consistent with findings in other marine fishes where limited gene flow between the two regions has been observed (Avise 1992; Gold *et al.* 2002, 2009). The genetic discontinuity between the two regions is often attributed to the effect of surface currents in the Florida Straits on larval dispersal and/or to the absence of suitable habitat along the southern Florida coast (Avise 1992; Gold & Richardson 1998). For animals who have large dispersive adults, however, neither of these factors may prevent movement between the Gulf and the Atlantic, consistent with genetic data from large coastal sharks (Keeney *et al.* 2005; Portnoy *et al.* 2010).

A barrier to gene flow also separated sharks in BAH from those along the U.S. coast. Estimates of genetic divergence (F_{ST} and Φ_{ST}) between BAH and the other regions were at least four times greater than estimates of divergence between any other pair of regions. The magnitude of divergence is surprising, given the approximately 100 km that separate the Bahamas from the east coast of Florida and the reported occurrence of gene flow between the two areas in large coastal sharks (Feldheim *et al.* 2001; Karl *et al.* 2011, 2012). It may be that geophysical characteristics that restrict gene flow between the Gulf and Atlantic also impact movement between the U.S. coast and the Bahamas. The Gulf Stream in this area becomes constricted as it moves northward through the Florida Straits (Lynch-Stieglitz *et al.* 1999), resulting in a restricted, high-flow area that could potentially impede movement of smaller marine animals, such as blacknose sharks. Areas of deep open water (>600 m in depth) that separate the Bahamas from the east coast of Florida (Lynch-Stieglitz *et al.* 1999) and reduced amounts of shallow coastal habitat along the southeastern Florida coast also could represent zones of high predation risk for smaller marine species such as blacknose sharks. The possibility that open water can act as a barrier is consistent with phylogeographic studies that often have found open ocean expanses over large distances to be more effective barriers to gene flow than distances along continental shelves (Duncan *et al.* 2006; Portnoy *et al.* 2010).

Table 4 Estimates of average, long-term effective population size (N_{eLT}) for each group; western Gulf (WG), eastern Gulf (EG), Atlantic (ATL), Mexico (MX), the Bahamas (BAH) and an ancestral population (NA), based on microsatellites, with lower (0.025) and upper (0.975) bounds of 95% confidence intervals. Estimates were made using the Bayesian approach implemented in MIGRATE-N (Bayes) and an approximate Bayesian approach implemented in DIYABC (ABC)

	Bayes			ABC		
	0.25	Mode	0.975	0.25	Mode	0.975
WG	1995	3107	4173	4000	9890	18 700
EG	3054	4100	7614	5970	9050	9900
ATL	3339	5945	7879	5160	11 700	19 100
MX	4031	7980	8143	9090	17 000	19 700
BAH	0	52	1844	197	538	7970
NA	—	—	—	124	494	6140

Two other geographic barriers were inferred. The first, based on microsatellites, was between the western Gulf (TX and LA) and eastern Gulf (AL and FL); the second, based on microsatellites and mtDNA, was between the Bay of Campeche (MX) and all other localities. The genetic break between the western and eastern Gulf corresponds with the outflow from the Mississippi River, which produces a plume of freshwater that varies in magnitude seasonally but can be detected as far as 100 km offshore (Riley 1937). For stenohaline marine species, such as blacknose sharks which occur in waters with salinity between 31 and 35 (Ulrich *et al.* 2007), the freshwater plume from the Mississippi River could act

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as a barrier to gene flow. This finding is consistent with other studies (Rocha 2003; Floeter *et al.* 2008) which have shown that large riverine outflows can serve as biogeographic barriers for a variety of marine taxa. The nature of the barrier that appears to separate the Bay of Campeche (southern Gulf) from the western Gulf (TX, LA) is less clear. It could be related to the narrowing of the continental shelf in the region between Tamaulipas and Veracruz, which could limit available habitat, a possibility supported by catch data that show blacknose sharks are not common along the coast of Tamaulipas (Bonfil 1997).

Behaviour

For a variety of marine organisms, there appears to be a lack of congruence between dispersal potential and realized dispersal (Weersing & Toonen 2009) that may be attributable to aspects of adult ecology (Hellberg 2009). Site fidelity associated with reproductive behaviour has been found to be important for limiting gene flow in what would otherwise be open marine systems (Hutchinson *et al.* 2001; Portnoy *et al.* 2013). For live-bearing sharks, mating is typically thought to occur in locations remote from nursery areas that females utilize repeatedly across their lifespan to increase survivorship of their young (Springer 1967). In this model, males having less investment in individual offspring are free to move over larger areas. A number of studies have provided evidence for regional or site-specific fidelity in female sharks (Mourier & Planes 2013; Feldheim *et al.* 2014), and male-mediated gene flow in large coastal sharks is well documented (Keeney *et al.* 2005; Schultz *et al.* 2008; Portnoy *et al.* 2010; Karl *et al.* 2011).

We found no evidence of sex-biased gene flow. Estimates of pairwise F_{ST} from male-only data, female-only data or pooled data (male and female) between localities in both the Atlantic and Gulf were nearly identical, and the few, putative first-generation migrants detected were of mixed sex. Mating in blacknose sharks occurs in the proximity of nursery areas (Driggers *et al.* 2004a; Sulikowski *et al.* 2007), suggesting that females may show site fidelity to increase offspring survival, while males may show site fidelity to ensure mating opportunity. If both males and females are faithful to migratory pathways over time, genetic divergence at scales smaller than the species' dispersal potential might be expected. Genetic divergence in blacknose sharks at small spatial scales (e.g. 100 km between the Bahamas and peninsular Florida) is smaller relative to the distance (300 km) travelled by some tagged individuals in the Atlantic (Kohler & Turner 2001). Finally, when adult reproductive migratory behaviour plays a role in determining how genetic variation is partitioned, differences in life history can become correlated with genetic divergence (Ruzzante *et al.* 2006). This pattern appears to be present in blacknose sharks as the genetically divergent populations in the Atlantic, eastern Gulf and western Gulf differ in reproductive timing, cycles and gestation times (Driggers *et al.* 2004a; Sulikowski *et al.* 2007; W. B. Driggers, unpublished data).

Post-glacial demography

Historical demography also appears to have played an important role in shaping aspects of contemporary genetic variation in blacknose sharks. Model testing, using ABC, supported two scenarios of historical divergence. Both scenarios strongly supported recent divergence of all five regional populations from a common, ancestral gene pool, followed by expansion in each region except in the Bahamas. Both model testing and the Bayesian approach in MIGRATE indicated that average, long-term effective size of the population in the Bahamas was considerably smaller, possibly by an order of magnitude, than those of populations in the other regions. The minimum-spanning network, which featured a star-shaped network (Clade 1) with the central haplotype in the clade dominant in all regions except the Bahamas, is consistent with this inference. Star-shaped networks are thought to indicate recent distributional and/or demographic expansion (Slatkin & Hudson 1991; Avise 2000) where central haplotypes occurring in high frequency across a geographic range are generally considered ancestral (Avise 2000).

Estimated times of divergence/expansion based on ABC analysis were similar to those estimated from the mtDNA haplotype network, and the lower estimates for both approaches (10.4 and 17.7 ka, respectively) are near the end of or after the most recent glacial period in North America (~20 ka, Adams 1997). During the last glacial maximum (LGM), the northern Gulf and the shelf along the southeast U.S Atlantic coast were likely unsuitable habitat for many semitropical/temperate, shelf-associated species, in part because of reduced sea surface temperatures (Brunner & Cooley 1976) and in part because sea levels declined by as much as 150 m (Simms *et al.* 2007), greatly reducing appropriate shelf habitat (Kennett & Shackleton 1975; Davis 2011). In addition, periodic pulses of cold fresh meltwater from the Mississippi drainage caused by the recession of the Laurentide ice sheet from 16 to 9 ka (Aharon 2003) may have made portions of the northern Gulf inhospitable to a variety of marine species for thousands of years after the LGM (Portnoy & Gold 2012). The southerly location of the Bay of Campeche in Mexico (MX) and its comparatively high level of genetic variation in mtDNA and allelic richness in microsatellites, a genetic signal

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thought possibly to reflect glacial refugia (Widmer & Lexer 2001; Provan & Bennett 2008), seem to point to this region in the southern Gulf as a source population for post-glacial expansion into the northern Gulf and U.S. Atlantic coast.

The post-glacial history of the Bahamas in relation to the other samples seems less clear. It is possible that the Bahamas were colonized by a single, long-distance dispersal event, facilitated by decreased distance between shelf habitats in Mexico, South Florida and the Bahamas during the LGM (Hine 2013). This might explain the signal of admixture between the Bahamas and the U.S. Atlantic coast. Subsequently, the Bahamas may not have received migrants during the larger wave of colonization that appears to have occurred in the northern Gulf and U.S. Atlantic coast sometime after the LGM. Leptokurtic dispersal, where most colonization/dispersal events occur in geographically proximal regions, is thought to be common in both plants and animals and can lead to increased genetic divergence between areas that receive a few, long-distance migrants and areas that regularly exchange individuals with neighbouring demes (Ibrahim *et al.* 1996). In addition, the isolation by distance observed when the samples from the Bahamas were removed suggests that gene flow across the rest of the sampling surface is likely between nearest neighbours (Wright 1943), a dynamic that may make migration less homogenizing across the entire sampling surface (Wang 2004). Such a dynamic, in conjunction with a smaller, long-term effective population size, could account for the divergence between the Bahamas and all other regions. Alternatively, it may be that while the southern Gulf was a source for expansion of marine taxa into the northern Gulf, the Bahamas itself was a refuge or was seeded by a different refuge to the south. In either case, the data do indicate a different demographic history for blacknose sharks in the Bahamas as opposed to the other regions.

A number of studies involving taxa in the northern hemisphere have documented genetic signatures of recolonization following the LGM (Hewitt 2004). While the phenomenon is best documented in terrestrial and riverine biota (Hewitt 1999, 2004), there is growing evidence that marine biota also may display signs of post-glacial range expansion (Maggs *et al.* 2008; Marko *et al.* 2010). The majority of marine species thus far studied are either benthic (Luttikhuizen *et al.* 2003; Coyer *et al.* 2004; Hoarau *et al.* 2007) or demersal with limited dispersal potential (Chevolot *et al.* 2006; McCusker & Bentzen 2010; Woodall *et al.* 2011). The findings of this study demonstrate that highly mobile marine species also may have experienced range contraction and expansion associated with glacial cycles. Further, the majority of studies that examined post-glacial dynamics in marine species sampled organisms living at higher latitudes than blacknose sharks. Results of this study suggest that glacial cycles also affected the historical distribution of a subtropical species in the western Atlantic and Gulf of Mexico. Given the relatively short period of time since the LGM, there may be many such species where estimates of genetic divergence may reflect past demography as well as contemporary connectivity (Hauser & Carvalho 2008; Hellberg 2009).

Conclusions

We have shown that both contemporary barriers to gene flow, aspects of adult behaviour and historical genetic demography have contributed to observed patterns of population structure in a coastal migratory species living in an otherwise continuous marine habitat. The impact of historical genetic demography on contemporaneous population structure has been described in sessile, benthic, marine species with low dispersal potential (Maggs *et al.* 2008; Marko & Hart 2012) and also may be important in marine species with high dispersal potential. Failure to understand the influences of both historical and contemporaneous processes on patterns of genetic variation potentially could lead to erroneous conclusions regarding connectivity (Marko & Hart 2011), and this could be problematic for studies involving marine species of present-day conservation concern.

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D.S.P. had responsibility for study design, data collection, analysis and writing the manuscript. C.M.H. was involved in data collection and contributed to data analysis and writing. C.N.B., W.B.D. III, B.S.F., J.G. and R.D.G. had responsibility for coordinating sample collection in the field and contributed to writing. J.R.G. had responsibility for data analysis and writing.

Data accessibility

Sampling locations, mtDNA haplotypes and microsatellites genotypes may found at DRYAD (doi:10.5061/dryad.vv277) under the file name 'Full data, blacknose sharks.' Final aligned DNA sequences may be found a DRYAD (doi:10.5061/dryad.vv277) under the file name 'mtDNA haplotypes.' mtDNA sequences: GenBank Accession nos for blacknose sharks KM657065-KM657090.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Centroids of sampling localities for blacknose shark.

Fig. S2 Spread of sampling effort for blacknose shark.

Fig. S3 Results of model testing in an approximate Bayesian framework.

Fig. S4 Fit of observed data to models selected using ABC analysis.

Table S1 Prior distributions for each parameter used in approximate Bayesian computation.

Table S2 Summary statistics for microsatellite and mtDNA haplotype data.

Table S3 Spatial distribution of individual haplotypes and their GenBank Accession numbers.

Table S4 F_{ST} and Φ_{ST} values for pairwise comparisons of sample localities.

Table S5 Individuals identified as potential first generation migrants.

Table S6 Estimates of averaged long-term migration rate for each pair of groups.

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