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Sharks respond to climate change with a population-level shift in critical habitat

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ABSTRACT: Understanding how marine populations adapt to their environment is important for effective management. Range shifts can decrease genetic diversity, reducing species' ability to resist extinction. The bull shark *Carcharhinus leucas* is a large coastal predator that uses shallow water habitats as nurseries, the extent of which defines the adult range. In the northwest Atlantic, the historic northernmost nursery for bull sharks was in the Indian River Lagoon (IRL), Florida (USA). Recently, bull sharks were shown to have founded a new nursery in Pamlico Sound (PS), North Carolina, due to warming water. To describe the evolutionary patterns associated with this change, we investigated genetic connectivity and diversity using 15 microsatellite loci among juvenile bull sharks from both the historic and contemporary IRL, the novel PS nursery, and sites in southern Florida and the Gulf of Mexico. We identified connectivity between the historic IRL and PS populations, indicating an IRL origin for the new nursery. We also found significant structure between the historic and contemporary IRL populations, but not between the contemporary IRL and southern Florida, supporting a population-wide poleward shift. These results show that northwestern Atlantic bull sharks are altering their life history to cope with warming water, and demonstrate for the first time that a large coastal predator is undergoing a genetic response to climate change.

KEY WORDS: Bull shark · *Carcharhinus leucas* · Microsatellites · Genetic structure · Nursery habitat · Dispersal · Climate response

1. INTRODUCTION

Climate change can affect a multitude of life history traits at the individual and population levels, as well as the geographic distribution of species (Dulvy et al. 2008). Population-level responses to environmental change caused by anthropogenic warming in the last 50 yr are already being observed in many habitats (Anderson et al. 2013), including both terrestrial (Hickling et al. 2006) and marine systems (Ramos et al. 2018). Global sea surface temperatures have increased by 0.5°C over the last century (IPCC 2022, Thomas et al. 2023), with significant impacts on marine communities already observed (Last et al. 2011).

According to ecological theory, organisms are predicted to shift their critical habitat poleward under

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warming conditions (Parmesan 2006, Last et al. 2011). Indeed, such shifts have been observed via physical tracking in several marine species, including the gloomy octopus *Octopus tetricus* (Ramos et al. 2018) and several species of tuna (Erauskin-Extramiana et al. 2019), along with direct observations of the common snook *Centropomus undecimalis* (Purtlebaugh et al. 2020) in the Gulf of Mexico, and other fishes in eastern Florida (USA) waters (Adams et al. 2024). Such poleward movement creates a heterogeneity in the form of a leading or founding edge and a trailing edge of a population, which have implications for genetic diversity (Parmesan 2006). The leading edge is typically made up of a small number of individuals, and can be prone to founder effects, i.e. the rapid loss of diversity via genetic drift that follows an isolation event, depending on the speed of the range shift (Arenas et al. 2012). The rate of drift depends on the degree of connectivity with the larger, continuous population, which may be limited in less mobile species (Robalo et al. 2020). As the population continues to expand, the rear-edge of the population (composed of individuals that maintain a presence in the historical habitat) can become genetically isolated in the absence of gene flow (Hampe & Petit 2005). This decrease of gene flow can result in inbreeding depression, which in turn can lead to a loss in genetic diversity (Devloo-Delva et al. 2023). However, if connectivity is maintained as population habitats shift or expand, genetic diversity may be retained, providing a buffer against extinction risk. Therefore, understanding genetic diversity and connectivity is necessary to ensure population viability and effective conservation under anthropogenic climate change.

Recent observations of physical movement data generated via telemetry or catch data indicate that several shark species are shifting their distributions poleward in response to warming water. These include bull sharks *Carcharhinus leucas* (Bangley et al. 2018), tiger sharks *Galeocerdo cuvier* (Hammerschlag et al. 2022), and white sharks *Carcharodon carcharias* (Tanaka et al. 2021). Although these observations help to confirm climate theory, a behavior like a shift in movement patterns could be highly plastic, changing seasonally or annually based on weather patterns, and does not necessarily indicate long-term evolutionary adaptation (Price et al. 2003). However, genetic analyses can confirm a significant shift in allele frequencies between subpopulations, signaling that reproductive isolation has occurred (Avise 2000). Given the vulnerability of many species to extinction, understanding the response to climate-induced selection pressure on sharks is becoming an increasingly high priority (Pacoureau et al. 2021).

The bull shark is a relatively large (maximum total length [TL] = 400 cm) (Compagno 1984) requiem shark with a near-global distribution in warm temperate, tropical, and subtropical waters (Compagno 1984). Along the US Atlantic Coast, the bull shark is common in the Gulf of Mexico and western Atlantic, with adults observed from Massachusetts to southern Brazil (Castro 1993, Natanson et al. 2014). Tracking studies have demonstrated that female bull sharks are philopatric to nearshore estuarine and riverine environments that they use as nursery habitats, where juveniles and neonates reside year round until they near sexual maturity (Curtis et al. 2011, Matich & Heithaus 2012, Matich et al. 2020, Edwards et al. 2022). Because of their high mobility, adults can adjust to warming waters by changing their seasonal migration patterns (Hammerschlag et al. 2012, Rider et al. 2021), while the thermal range of nursery habitat typically encompasses the full seasonal variation experienced by resident juveniles, with some cold weather migrations occurring in temperate and subtropical latitudes (Curtis et al. 2011, Matich et al. 2024). Thus, the distribution of bull shark nurseries is considered to represent the permanent range of the species, as well as being Essential Fish Habitat for this and other fish species which are protected under special management conditions by NOAA Fisheries (NMFS 1999, 2003, 2006).

As identified with mitochondrial DNA, site fidelity of bull sharks to nurseries has resulted in fine-scale genetic structuring between the Gulf of Mexico and US Atlantic that indicates female natal philopatry (i.e. gravid females return to a specific location to give birth where they were born) (Karl et al. 2011, Chapman et al. 2015, Sandoval Laurrabaquio-A et al. 2019). Previous studies on various sharks have also examined genetic differentiation using microsatellite loci, which are bi-parentally inherited neutral nuclear DNA, but found genetic homogeneity across the regions, suggesting male-biased gene flow (Karl et al. 2011, Daly-Engel et al. 2012, Sandoval Laurrabaquio-A et al. 2019). However, male-biased dispersal is often overestimated in mixed-marker studies because samples are combined from different size classes, as genetic studies are often required to have sufficient statistical power, which will spuriously present as panmixia in microsatellite loci (Phillips et al. 2021). In addition, a relatively low number of microsatellite markers was used (5 loci by Karl et al. 2011 and 8 loci by Sandoval Laurrabaquio-A et al. 2019), so adding additional loci could boost the statistical power to

reveal any recent, fine-scale genetic structure (Phillips et al. 2021). For example, studies using high-resolution single nucleotide polymorphisms (SNPs) have identified weak but statistically significant differentiation between bull sharks in the Gulf of Mexico and US Atlantic coast (Devloo-Delva et al. 2023, Postaire et al. 2024), indicating that these regions have some reproductive isolation and have different evolutionary trajectories (Devloo-Delva et al. 2023).

Historically, the Indian River Lagoon (IRL) along the eastern coast of Florida has been the northernmost nursery habitat for bull sharks along the US Atlantic coast (Curtis et al. 2011). Sporadic, opportunistic parturition had been reported north of the IRL; for example, investigators reported neonate and juvenile bull sharks in the Altamaha River system in Georgia in 2008, and larger juveniles captured in 2009, ~350 km north of the IRL (Streich & Peterson 2011). However, the specific criteria established to define critical nursery habitat require evidence of seasonal, recurring, year-round presence of neonates and juveniles (Heupel et al. 2019, 2007), which was, until recently, never documented north of Florida (McCandless et al. 2002, Streich & Peterson 2011).

Based on long-term fisheries-independent data, Bangley et al. (2018) observed that bull sharks had founded a novel nursery in Pamlico Sound, North Carolina, >900 km north of the IRL. The consistent use of Pamlico Sound, where juvenile bull sharks were rarely captured in the past, was found to meet the criteria for a shark nursery habitat (Heupel et al. 2007, 2019, Bangley et al. 2018). Bangley et al. (2018) confirmed via fishery-independent survey data that this nursery range expansion was directly correlated with anthropogenic ocean warming within Pamlico Sound over the past 50 yr, the first time a climate response had been recorded in a large migratory shark. This response has likely created leading-edge dynamics within the population, but it is unknown whether these dynamics have had consequences for genetic diversity, or if connectivity is being maintained via gene flow between subpopulations.

The establishment of a new nursery habitat suggests a response to climate change (Crear et al. 2020), but it is unknown if this expansion has resulted in population-level genetic changes, including a loss of diversity that could reduce overall viability. We investigated the genetic patterns underlying the response to climate change in US Atlantic bull sharks using a suite of 15 polymorphic microsatellite loci to describe kinship and connectivity between 2 sites from the previously northernmost nursery in the IRL (historical IRL samples between 1994 and 1999, and contemporary IRL samples taken between 2007 and 2022), the novel nursery in Pamlico Sound, and sites to the west and south. Specifically, we sought to identify the source population for the new nursery by estimating levels of genetic differentiation between juveniles from the Gulf of Mexico and US Atlantic. If Pamlico Sound showed genetic structure separating it from all other sites, with little to no kinship identified, it would suggest that a different population founded this novel nursery, and there is little gene flow occurring between Florida and North Carolina, and likely less diversity observed due to a genetic bottleneck. Conversely, if no difference was detected between the historic IRL and contemporary IRL, it would suggest that no significant shift has occurred, and we would expect to see similar genetic structure amongst all sites, as well as full- and half-kinships. However, if differences are noted between the historic and contemporary IRL samples, it would suggest a population shift has occurred, with Pamlico Sound likely connected with the historic IRL population, and the contemporary IRL population connected with South Florida as populations move poleward. We also measured genetic diversity at each sampling site to explore the possibility of leading- and trailing-edge dynamics. In highly mobile animals, gene flow is expected to homogenize genetic diversity between nearby sites, but if nonrandom mating is occurring, curtailing gene flow in some parts of the range, this could create low-diversity conditions that increase extinction risk. Taken together, these findings have the potential to broadly expand our understanding of the patterns and implications of climate response in a large, slow-growing, migratory predator, with important insights for conservation and management.

2. MATERIALS AND METHODS

2.1. Sampling and microsatellite loci amplification

Previously collected bull shark tissue samples were acquired under permit from collaborators from the Caloosahatchee River in the Gulf of Mexico on Florida's west coast (CalR, N = 29), southern Florida (SF, N = 32), the IRL in eastern Florida (contemporary: coIRL, N = 61; historical: histIRL, N = 16), and Pamlico Sound, North Carolina (PS, N = 23) (Fig. 1). 'Contemporary' samples from all locations were taken between 2007 and 2022, while 'historical' IRL samples were collected between 1994 and 1999. Bull shark samples included neonates (<75 cm TL), age-zero (<90 cm TL), juveniles (<190 cm TL), sub-adults (<210 cm TL), and

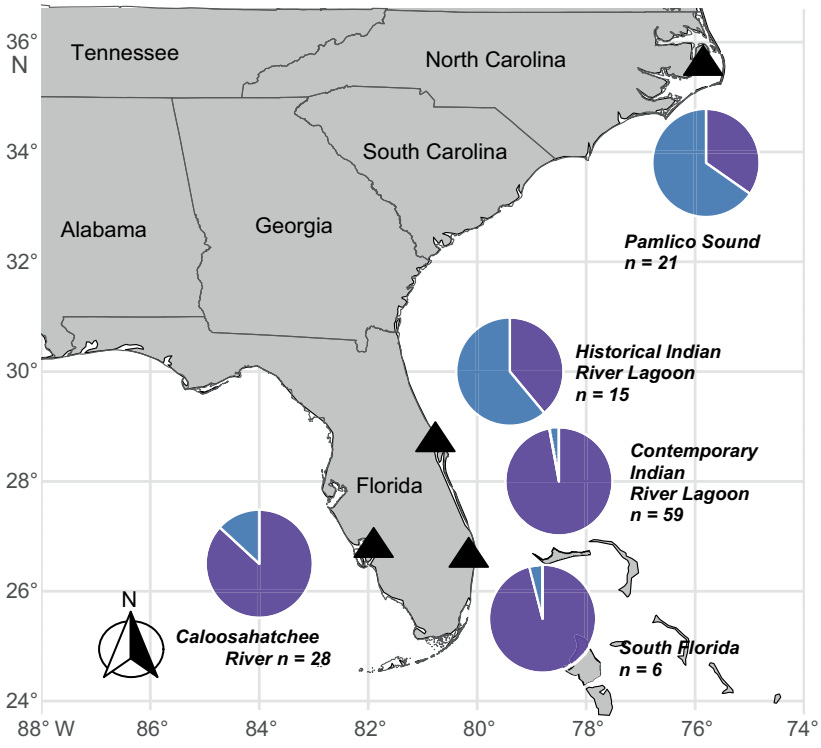

Fig. 1. Sampling locations, denoted by black triangles, and sample sizes for bull sharks *Carcharhinus leucas* within the Gulf of Mexico and US Atlantic. Pie charts represent STRUCTURE output of genetic clusters (*K*) for each individual within each sampling location (purple = Cluster 1, blue = Cluster 2)

adults (>210 cm TL) (Curtis et al. 2011), with 76 females and 74 males, and 11 of unknown sex. Samples provided were roughly 1 cm^3 of fin or muscle tissue, stored in 2 ml of 70% ethanol or dimethyl sulfoxide NaCl-saturated buffered solution. Total DNA was extracted using the DNeasy Blood and Tissue extraction kit (Qiagen) or through a modified salting out procedure (Sunnucks & Hales 1996).

A total of 26 microsatellite loci were tested for this study (Table S1 in the Supplement at www.int-res.com/articles/suppl/meps15095_supp.pdf). Of these, 20 were specifically developed for *Carcharhinus leucas* (Cle01–Cle20) (Pirog et al. 2015), 4 were successfully cross-amplified from *C. limbatus* (Cli007, Cli107, Cli108, and Cli166) (Keeney & Heist 2003), and 2 from *C. plumbeus* (CPL90 and CPL166) (Portnoy et al. 2007). Microsatellite loci were amplified via polymerase chain reaction (PCR) carried out in 10–20 µl reactions. Forward primers were indirectly labeled with a fluorescent tag (Applied Biosystems), and 10 µl reactions were run using 1.4× concentration of MyTaq Red MasterMix (Meridian Bioscience) with 2% bovine serum albumin (BSA). Primers were combined into a 3× solution using 4.4 µM of an unlabeled reverse primer, 4.4 µM of M13 primer tags labeled with 6-FAM, PET, NED, and VIC proprietary dyes obtained from ThermoFisher Scientific, and 1.1 µM of a labeled forward primer. For the PCRs, a total of 2 µl of the 3× primer cocktail was used, resulting in 0.88 µM of the reverse primer, 0.88 µM of the M13 proprietary dyes, and 0.22 µM of the labeled forward primer. A total of 10 ng of DNA was used for each PCR.

Fragment amplification was done on a BioRad T100 Thermal Cycler and consisted of an initial denaturation of 95°C for 3 min, followed by 30–35 cycles at 95°C for 30 s, optimal annealing of 51–62°C for 30–45 s (depending on the primer), and 1 min at 72°C, followed by a final extension at 72°C for 5 min. Products were pooled and analyzed on an ABI3730 DNA analyzer at the University of Arizona Genetics Core (Tucson, Arizona). Peak calling was done by eye using Geneious Prime v.2019.2.3. Any monomorphic loci were removed, leaving 17 loci for further analyses.

2.2. Quality control and kinship analyses

Deviations from Hardy-Weinberg equilibrium (HWE) were detected in GenePop v.4.7.5 (Rousset 2008). Significant deviations from HWE and the presence of null alleles were tested for using Microchecker v.2.2.3 (Van Oosterhout et al. 2004). Because studies have shown that microsatellites may not be as effective at detecting fine-scale genetic structure as SNPs even when in large numbers (Devloo-Delva et al. 2023), we performed a power analysis using Coancestry V1.0.1.9 (Wang 2011). Specifically, we used this program to calculate pairwise relatedness, inbreeding, and exclusion probability, which is the ability of our marker set to correctly assign kinship when 0, 1, or 2 parents are known. We compared 2 commonly used estimators to determine pairwise relatedness: Queller-Goodnight (QG) (Queller & Goodnight 1989) and Wang's unbiased estimator (Wang 2017). For inbreeding coefficients, we compared the TrioML and DyadML estimators. For all runs, 1000 reference individuals were used.

Kinship and relatedness were tested using Colony v.2.0 (Jones & Wang 2010), which uses overall likeli-

hood methods to infer sibship and parentage. Individuals were categorized as either offspring, potential mothers, or potential fathers by size when sampled. Those less than 190 cm TL were considered potential offspring, as they were not yet sexually mature and therefore not yet dispersive (Curtis et al. 2011). Potential parents were subadults and adults, individuals over 190 cm TL, given that they are more likely to be dispersive (Curtis et al. 2011). Given the time frame between those classified as potential parents from the histIRL and SF populations, there was a potential for histIRL individuals to be parents to SF individuals. Therefore, a preliminary Colony run was performed wherein only histIRL samples were designated as potential parents. Following this preliminary run, size was used to determine parents and offspring, as stated above. Colony runs were modeled after the 3-run protocol of Feldheim et al. (2017), wherein the first 2 runs assumed mating systems of female polygamy and male monogamy, due to the likelihood that half siblings are through the female, while the final run assumed both male and female polygamy. The Colony parameters were as follows: inbreeding populations, dioecious and diploid, long length of run, full-likelihood analysis, high likelihood when both males and females were polygamous with 4 runs. Loci probability was set to 1%, with a 1 and 25% probability of adults being a father or mother, respectively (Postaire et al. 2022). The second run incorporated known full or half siblings following the first run with a 95% or higher probability. Results from the first and second run were compared for consistency and quality control. The third run assumed both male and female polygamy, and included known sibling relationships identified from the first 2 runs. Parentage assignments were retained for those 95% and above.

2.3. Population-level analyses

Levels of genetic differentiation between locations were calculated using pairwise F_{ST} values in Arlequin v.3.5 (Excoffier et al. 2007, Excoffier & Lischer 2010) for all juvenile samples, with 1 individual from all sibling pairs removed, and a significance level of 0.05. Due to the uneven sizes of populations, 5 separate runs were performed by randomly selecting 15 individuals from PS, coIRL, and CalR populations. Once F_{ST} values were calculated, any locations lacking genetic differentiation among sites were combined into 1 population for an analysis of molecular variance (AMOVA) run in Arlequin v.3.5 5 (Excoffier et al. 2007, Excoffier & Lischer 2010). A discriminant analysis of principal components (DAPC) was run in R (v. 4.4.1, R Core Team 2025) using the R package 'adegenet' v.2.1.10 (Jombart 2008) to determine the structure between the Gulf and Atlantic non-dispersive groups. To identify the optimal number of genetic clusters (K), the function 'find.clusters' in 'adegenet' was used, which identified the best-fitting number based on the lowest Bayesian information criterion score. The number of PCs to retain was determined using the 'optim.a.score' function, also in 'adegenet'. Assignment testing was also conducted using STRUCTURE v.2.3.4 (Pritchard et al. 2000). STRUCTURE uses a Bayesian approach to determine the number of genetic clusters, K, within a data set. To identify structure between nursery habitats, only juveniles were analyzed (Klein et al. 2019, McClain et al. 2022). To avoid a bias in Hardy-Weinberg expectations, 1 individual from each sibling pair was removed. The number of clusters (K) analyzed was 1–7, to test the range of possible Ks (Evanno et al. 2005), with 20 independent runs of 100 000 Monte Carlo Markov chain (MCMC) replicates with a burn-in length of 10 000, and using both the admixture and LOCPRIOR settings. The admixture model was appropriate as we have strong confidence that bull sharks from PS originated from somewhere south, thus resulting in admixture of the populations (Porras-Hurtado et al. 2013). The LOCPRIOR setting is best used when weak population structure is expected, which was anticipated with these samples, as previous studies identified genetic variation when using mitochondrial DNA, but not with nuclear (Porras-Hurtado et al. 2013, Sandoval Laurrabaquio-A et al. 2019). Results were then uploaded to CLUMPAK (Kopelman et al. 2015), an online program package that can implement 2 different methods to determine best K (Evanno et al. 2005, Puechmaille 2016) and visualize the output.

2.4. Genetic diversity

Allelic richness (A_R), a genetic diversity measure that accounts for sample size, was estimated using FSTAT, with reported values based on the minimum sample size of n = 12 alleles, corresponding to the minimum number of genotyped individuals (Goudet 1995). We compared A_R between sampling locations to identify whether any populations exhibited reduced genetic diversity, which could indicate selection pressure or a possible loss of adaptation potential (Greenbaum et al. 2014). Arlequin v.3.5 (Excoffier et al. 2007, Excoffier & Lischer 2010) was used to estimate observed heterozygosity (H_o), expected het-

erozygosity (H_e), and total number of alleles (N_A). Isolation by distance (IBD) was assessed using a Mantel test between pairwise Nei's genetic and geographic distances, with significance calculated using 9999 permutations in the R package 'vegan' v2.6-8 (Oksanen et al. 2026).

3. RESULTS

3.1. Genotyping and kin relationships

A total of 159 bull sharks were successfully genotyped at 17 polymorphic microsatellite loci among 5 populations sampled from 4 different locations (including both historic and contemporary IRL, Table 1). Following a Bonferroni correction, an average 82% of loci were within HWE at every site, with the exception of Cle01, Cle05, CPL90, and CPL166. However, disequilibrium was rare across all populations, and given that departure from HWE suggests genetic structuring, all loci were retained for analyses. Null alleles were detected in significant proportions at 1 or more loci in all populations, but were common in just 2 loci (Cle01 and CPL166), so these were removed from further analyses. The remaining null alleles were measured at low frequencies (<0.2 for Oosterhout and <0.1 for Brookfield), and only in some populations, so these loci were retained for a total of 15 microsatellite loci.

After quality control, we assessed kin relationships between individuals using the final suite of 15 loci, which Coancestry showed has a non-exclusion probability of 2.22×10^{-3}, 6.51×10^{-5}, and 4.83×10^{-8} to discriminate kin when 0, 1, or 2 parents are known, respectively (Wang 2011). This non-exclusion probability refers to the likelihood that our set of loci will fail to exclude an unrelated parent or pairs of parents from parentage of a randomly selected offspring (Weng et al. 2021). With this, we were able to exclude non-kin with a confidence of 99.78% with zero parents known. Accordingly, 4 full sibling pairs were identified with >95% confidence (Table 2). All were full siblings caught within the same habitat, with no siblings detected between locations. Of the 4 full sibling pairs detected, 2 were sampled on the same date within PS, while the other 2 pairs were caught within 1 yr of each other in the CalR and IRL, respectively. We detected multiple pairs of half siblings with >90% confidence, although to be conservative, only 1 pair of half siblings that was detected with a level of 95% confidence was included in the final results. When calculating pairwise relatedness and inbreeding, the estimators with the lowest standard deviation and 95% confidence intervals were QG and Wang for r, and TrioML and DyadML for IR, and are the ones reported. Individual inbreeding values ranged from 0.000 to 0.566 (Table S2), while average inbreeding by population ranged from 0.038 to 0.161 (Table 1). Average pairwise relatedness ranged from −0.029 to 0.035 (Tables 1 & 2), with individual pairwise relatedness ranging from −0.773 to 0.765.

3.2. Population structure and diversity

A_R was similar among sampling sites, ranging from 5.4 to 5.9 (mean A_R = 5.78, standard deviation = 0.18; Table 1). H_o ranged from 0.46 (coIRL) to 0.59 (histIRL) (Table 1).

With pairwise F_{ST} and AMOVA, we observed low but statistically significant differentiation between most populations, with the exceptions of the histIRL

Table 1. Genetic diversity metrics of bull shark samples by location. Locations include contemporary samples from the Indian River Lagoon, Florida (CoIRL); historical samples from the Indian River Lagoon, Florida (HistIRL); Pamlico Sound, North Carolina (PS); Caloosahatchee River, Florida (CalR); and southern Florida (SF). Diversity metrics were taken on juveniles only, with 1 individual per sibling pair removed, and include the total number of alleles (N_A), observed heterozygosity (H_o), expected heterozygosity (H_e), and allelic richness (A_R), pairwise relatedness (r) for both Wang and Queller-Goodnight (QG) estimators expressed as a mean ± SE, and inbreeding (IR) for TrioML and DyadML estimators. Juveniles are defined as non-dispersive individuals less than 190 cm total length. Dispersive individuals are those in the sub-adult or adult categories over 190 cm total length

Location	N	Juveniles	Dispersive individuals	N_A	H_o	H_e	A_R	r (Wang)	r (QG)	IR (TrioML)	IR (DyadML)
CoIRL	61	61	0	9.1	0.460	0.519	5.75	−0.015 ± 0.003	0.035 ± 0.003	0.123	0.161
HistIRL	16	16	0	5.9	0.590	0.598	5.867	−0.025 ± 0.001	−0.021 ± 0.001	0.067	0.089
PS	23	23	0	6.3	0.521	0.562	5.49	−0.029 ± 0.001	−0.020 ± 0.001	0.081	0.11
CalR	29	29	0	7.6	0.545	0.552	5.949	0.001 ± 0.001	−0.017 ± 0.001	0.067	0.087
SF	32	6	26	4.4	0.543	0.533	5.894	0.007 ± 0.001	0.013 ± 0.001	0.038	0.054

Table 2. Related bull shark individuals. Grey highlight denotes individuals caught at different locations. All individuals were non-dispersive juveniles. Locations: PS, Pamlico Sound, North Carolina (Atlantic); CalR, Caloosahatchee River, Florida (Gulf Side); CoIRL, Contemporary Indian River Lagoon, Florida (Atlantic Side). Size is given in centimeters (cm) for total length (TL) with a handful of samples given in fork length (FL). r = pairwise relatedness. QG = Queller-Goodnight

	Individual ID	Location	Size (TL, cm)	Sex	Catch date	r (QG)	r (Wang)
Full sibling pairs	PS 236	PS	80.2	F	21 July 2016	0.6123	0.6432
	PS 237	PS	91	F			
	PS243	PS	84.6	F	27 July 2018	0.7649	0.8896
	PS244	PS	81.2	F			
	CalR 805	CalR	71 FL	F	28 July 2012	0.5382	0.6244
	CalR 813	CalR	96.5 FL	M	15 June 2013		
	CoIRL 107	CoIRL	84.5	F	6 December 2017	0.4516	0.5744
	CoIRL 131	CoIRL	93.3	M	12 April 2018		
Half sibling pair	CalR 800	CalR	66.5 FL	M	28 July 2012	0.1094	0.3664
	CoIRL 585	CoIRL	67.4	F	16 July 2012		

and PS, and histIRL and CalR. In addition, there was a lack of structure between the coIRL and SF, and SF and CalR (Table 3). Due to the low number of samples within the histIRL group, 5 runs to estimate pairwise F_{ST} were completed with 15 randomly selected individuals in the coIRL, PS, and CalR groups, and all individuals within the SF group. In each, we observed no evidence of genetic differentiation between PS and histIRL. F_{ST} p-values varied between locations across the 5 runs, ranging from 0.013 to 0.056, with the exception of PS and SF, and histIRL and SF, which consistently showed evidence of statistically significant structure, and PS and IRL, which showed a small amount of significant structure between them, but only in 1 run (Table S3). IBD testing indicated a significant pattern of IBD, with a Mantel test showing a significant positive correlation between genetic and geographic distances among sampling locations (n = 10 population pairs, Mantel r = 0.276, p = 0.0001)

The DAPC identified 2 genetic clusters, with 30 principal components retained and little overlap between the clusters (Fig. 2). Population assignment in STRUCTURE, evaluated using the ΔK method (Evanno et al. 2005), identified 2 distinct genetic clusters within non-dispersive juveniles (K = 2; Fig. 3), with both STRUCTURE and DAPC analyses congruent with individual assignments. While both clusters were present in all individuals, there was a strong partition of coIRL, SF, and CalR in Cluster 1, with most PS and histIRL individuals in Cluster 2 (Figs. 1 & 3; Fig. S1).

Table 3. Pairwise F_{ST} values by site. **Bold** indicates significance ($p < 0.05$); p-values are included above the diagonal. Locations: HistIRL: historical Indian River Lagoon, Florida (Atlantic); PS: Pamlico Sound, North Carolina (Atlantic); CoIRL, Contemporary Indian River Lagoon, Florida (Atlantic); SF: southern Florida; CalR: Caloosahatchee River, Florida (Gulf side)

	HistIRL	PS	CoIRL	SF	CalR
HistIRL		0.855	**0.0**	**0.005**	0.117
PS	−0.006		**0.0**	**0.009**	**0.0**
CoIRL	**0.021**	**0.022**		0.306	0.054
SF	**0.038**	**0.039**	0.006		0.117
CalR	0.007	**0.013**	0.007	0.010	

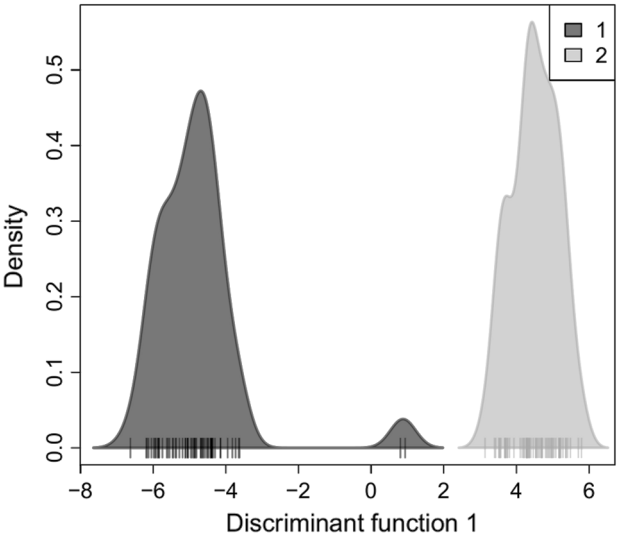

Fig. 2. Density plot of individual assignment of bull sharks along the first discriminant function (x-axis) from a discriminant analysis of principal components (DAPC) of K = 2. The 2 curves represent individual assignment to each cluster (Cluster 1 = dark grey; Cluster 2 = light grey). Tick marks along the x-axis represent each individual. The distance between the 2 curves reflects the strong genetic differentiation between the 2 clusters

4. DISCUSSION

4.1. Range shift and population structure

While Florida's IRL historically represented the northernmost known nursery ground for juvenile bull sharks, juveniles have been regularly encountered in North Carolina's PS since 2011, coinciding with rising water temperatures and salinity (Bangley et al. 2018). The repeated use of a nursery habitat, typically where the female was born (natal philopatry), is considered a form of maternal investment (Hussey et al. 2010, Chapman et al. 2015). These results suggest a recent climate-driven expansion in bull shark nursery habitat. Through genetic analysis of historical and contemporary samples of bull sharks, we found that bull sharks born in Florida's IRL in the late 1990s are genetically similar to individuals sampled in North Carolina's PS 30 yr later. By identifying genetic diversity between the histIRL and coIRL populations, while also finding genetic similarities among the histIRL and PS populations, we demonstrated that the population of bull sharks in the northwest Atlantic has shifted the northern bounds of its permanent, year-round range from the IRL to PS, over the past 50 yr.

Samples used for this study were opportunistic and acquired over a range of timeframes. The 'historical' designation for the IRL was given due to the likelihood of these samplings reaching sexual maturity when the coIRL samples were taken. While sampling for coIRL started in 2007, only 9 of the 61 coIRL samples were taken before 2016 (n = 3 in 2007; n = 5 in 2008, n = 1 in 2012). Because bull sharks are expected to reach sexual maturity at 15 yr for males and 15–17 yr for females (Natanson et al. 2014), we felt this designation was appropriate, if we assume the histIRL individuals were newborns at the time of sampling, they would be past, or just reaching, sexual maturity in 2016 and beyond, which is the timeframe in which a majority of the samples were supplied. That said, we recognize that a single generation timeframe would likely not result in a drastic genetic differentiation between locations. However, genetic variation, while significant, was low, and given the evidence for SF to coIRL migration, it is possible that the structure identified between locations could accumulate over the course of only a few generations if habitat shifts are occurring during that time as well.

The statistically significant genetic differentiation between the coIRL and histIRL samples indicates that most individuals born in the IRL in the 1990s are no longer using the IRL as their primary reproductive habitat. The absence of significant structure between the coIRL and SF suggests that gene flow is maintained between these populations. Given the range shifts of bull sharks noted here and by Bangley et al. (2018), and the predicted poleward movements of species responding to climate change (Walther et al. 2002, Robalo et al. 2020), we assume that SF individuals are moving northward. Separately, the signifi-

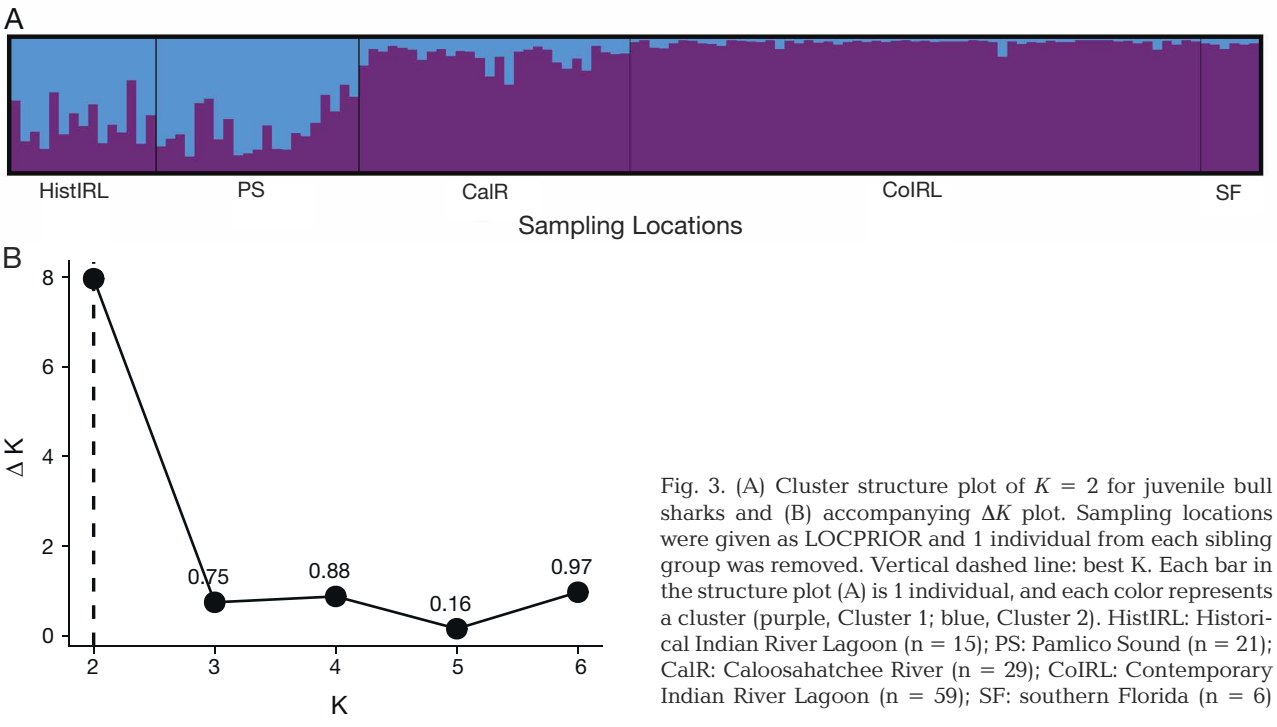

Fig. 3. (A) Cluster structure plot of K = 2 for juvenile bull sharks and (B) accompanying ΔK plot. Sampling locations were given as LOCPRIOR and 1 individual from each sibling group was removed. Vertical dashed line: best K. Each bar in the structure plot (A) is 1 individual, and each color represents a cluster (purple, Cluster 1; blue, Cluster 2). HistIRL: Historical Indian River Lagoon (n = 15); PS: Pamlico Sound (n = 21); CalR: Caloosahatchee River (n = 29); CoIRL: Contemporary Indian River Lagoon (n = 59); SF: southern Florida (n = 6)

cant IBD pattern indicates that as distance increases, genetic similarities decrease, a finding consistent with potential philopatric behavior. However, due to the low number of SF juveniles, more sampling is needed to validate this finding.

The evidence of genetic connectivity between the histIRL and PS individuals provides an evolutionary context to the fishery-independent surveys that show bull sharks recently expanding their range poleward (Bangley et al. 2018). This result is further supported by the distinct population clusters that STRUCTURE assigned within the Gulf of Mexico and US Atlantic populations, with cluster 2 largely found within the historical IRL and PS populations (Figs. 2 & 3). While statistically significant, the low F_{ST} values between sites, as well as the genotypic overlap between clusters (indicated by the admixture in each individual), suggests ongoing interbreeding between populations, or some flexibility in female philopatry. This is perhaps unsurprising given the high dispersibility of bull sharks, which theoretically allows them to easily maintain gene flow between distal regions. However, given the significant evolutionary partitioning observed here, such mixing is likely rare.

Due to the low sample sizes and low F_{ST} values, pairwise F_{ST} were re-run with sample sizes decreased to create equal population sizes. HistIRL and PS consistently showed no genetic structuring, which supported our initial results. Levels of statistically significant genetic structure varied between locations throughout the 5 additional runs, which does highlight that small sample sizes can produce variability when discerning genetic variation. That said, significant differentiation was consistently identified between PS and coIRL in 4 out of 5 runs, and no structure was identified between coIRL and SF in any of the 5 runs (Table S3). So, while some of the genetic variation results should be taken with caution, the main results identified (genetic structure between PS and coIRL, no structure between PS and histIRL or coIRL and SF) are better supported. When all samples were used, the CalR bull sharks had no genetic differentiation with the histIRL, coIRL, or SF populations (Table 3). Previous studies have shown a strong connection between Biscayne Bay (located in Miami, Florida) and the Gulf of Mexico bull shark habitats (Wiley & Simpfendorfer 2007, Rider et al. 2021). While Biscayne Bay has not been described as a nursery habitat for juvenile bull sharks, it has been suggested to be an important area for gestation for female bull sharks (Rider et al. 2021), and given the vagility of the species, it is likely that individuals move freely between these locations.

Because microsatellite DNA is nuclear and therefore with biparental inheritance, significant F_{ST} values between nursery areas suggest biparental philopatry, a phenomenon previously thought to be rare in sharks (Phillips et al. 2021). When both males and females of a species are philopatric, even sporadically, it limits the gene pool and causes genetic diversity to be lost. Bull sharks have been shown via telemetry to exhibit site fidelity as adults, although most studies have been limited to females (Brunnschweiler et al. 2010, Hammerschlag et al. 2012). Despite this site fidelity, we found consistent levels of A_R across the range. This finding is notable, as it runs counter to the theoretical expectation that a range shift would lead to reduced diversity and A_R within the leading- or trailing-edge population. Our results instead support our previous findings that indicate that gene flow is being maintained within the system. This could likely indicate that bull sharks are still early in their poleward movement, and genetic impacts of range expansion are not yet apparent. While we do see significant F_{ST} values within basins among both Gulf and Atlantic bull sharks, suggesting biparental philopatry, the significance is low (Table 3). Coupled with similar A_R values and low to moderate inbreeding values (Table S2) and what is known about physical dispersal among Gulf and Atlantic bull sharks, this suggests that genetic differentiation is slight, and some degree of reproductive admixture is ongoing, which could lead to higher genetic variation and increased fitness, a necessity for adaptation to future environmental changes (Ruck et al. 2024).

4.1. Kinship

We identified 4 pairs of full siblings in our data set (Table 2), which was surprising due to the opportunistic nature of our sampling. Relatedness values of the full siblings ranged from 0.452 to 0.890, although full siblings are expected to have a relatedness value of 0.5 (Table 2). Such high relatedness values, especially between the 2 PS individuals (PS 243 and PS 244) could suggest inbreeding, with an average inbreeding value across all samples of 0.112, and the highest individual inbreeding value of 0.566 (Table S2). Inbreeding for bull sharks within the Gulf and Atlantic was high compared to other shark species, e.g. an average of 0.038 in blacktip reef sharks *Carcharhinus melanopterus* (Mourier & Planes 2013), 0.048–0.077 in blue sharks *Prionace glauca* (Leone et al. 2024), and 0.002 in bonnethead sharks *Sphyrna tiburo* (Black et al. 2024), a surprising find for a highly mobile marine

species. While the inbreeding values were consistent, there is a possibility that the limited number of samples for this study may contribute to the magnitude of inbreeding detected. However, the inbreeding avoidance hypothesis states that if one sex is more dispersive, they decrease the chances of mating with close relatives (Pusey 1987). Given that studies have found adult male and female bull sharks to maintain relative site fidelity, with females more dispersive than males (Hammerschlag et al. 2012), it is likely that a lack of dispersal is contributing to the relatively high inbreeding rates, though more research is needed with larger sample sizes to confirm the inbreeding values of this population.

Two of the full sibling pairs were caught on the same day, and given that their size at the time of sampling indicates that these individuals were less than a year old (<90 cm TL) (Curtis et al. 2011), it is possible that they were grouping based on temperature and salinity preferences (Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008, Matich et al. 2020), a common occurrence among juvenile sharks (McClain et al. 2022). The likelihood of finding full sibling pairs, especially those sampled in different years, is low, given the dispersal capabilities of juvenile bull sharks within their nursery habitat. This study identifying 2 pairs of full siblings sampled in different years is surprising and highlights the juvenile tendency towards site fidelity within the nursery habitat (Edwards et al. 2022). Adult philopatry may be responsible for the lack of full siblings identified between sites, as female bull sharks will only pup at 1 site per an assumed 2 yr reproductive cycle (Brunnschweiler & Baensch 2011), which makes it unlikely to find full sibling young-of-year sharks between locations. Interestingly, the pair of half siblings detected were both sampled within the same month of the same year (July of 2012), yet one individual was caught in the CalR in the Gulf of Mexico, while the other was caught in the IRL on the Atlantic coast. Given the similar size of the juveniles at the time of sampling, this is likely a case of male-mediated dispersal, as it is unlikely that 1 female gave birth in both the CalR and IRL within a year. However, only detecting 1 pair of half siblings is surprising, considering the well documented occurrence of multiple paternity in bull sharks (Pirog et al. 2016, 2019). If females mate with multiple males, the likelihood of identifying half siblings within and between locations should increase, especially in species with reproductive philopatry. Since our sampling only detected one pair of half siblings with full confidence, it may be due to the relatively low numbers of samples per site, or there may be more kinship among sites than was detected. If both male and female bull sharks are using philopatry, as our results suggest, this could increase the chances of genetic monogamy and the frequency of full siblings. However, more work is needed, with the incorporation of mitochondrial DNA, to conclusively determine if biparental philopatry is indeed occurring.

4.2. Conservation Implications

Globally, sharks are facing a decline in abundance from a variety of pressures such as overfishing and habitat loss, with an estimated 71% decline of oceanic sharks in the last 50 yr, and an estimated one-third of all remaining species threatened with extinction (Dulvy et al. 2021, Pacoureau et al. 2021). Bull shark dependence on low-salinity nearshore habitats for breeding and parturition can result in increased vulnerability for an already-vulnerable group (Chin et al. 2010). Indeed, this species was recently listed as Vulnerable by the International Union for the Conservation of Nature (IUCN) (Rigby et al. 2021, Postaire et al. 2024). A shift in habitat can have deleterious consequences that include local extirpation, food web alteration, and changes to the physical and genetic patterning of populations (Daly-Engel et al. 2012, Cowman & Bellwood 2013, Devloo-Delva et al. 2023). Maintaining genetic diversity is essential for species' viability, especially when faced with climate change.

As the ocean temperatures continue to rise, bull sharks are likely to continue to expand their nursery habitat poleward, potentially into areas with no established size and catch limits established for bull sharks. For example, climate-driven changes to the extent and timing of tiger shark migrations have decreased their spatial protection from longline fishing (Hammerschlag et al. 2022). As populations of bull sharks in the Atlantic move northward, it is difficult to predict how bull sharks in the northern Gulf of Mexico will respond to climate change, as they are already at the physical limits of their habitat. Recent studies have shown a decrease in wintering migrations (Matich et al. 2024) and increases in habitat suitability in the northern Gulf of Mexico (Mullins et al. 2024). While findings from tracking studies show bull sharks swimming between the Gulf and Atlantic (Rider et al. 2021), and evidence from the present study shows that little genetic diversity exists between CalR and the US Atlantic sites, other studies do show inter-basin population differentiation, suggesting that the ability to physically disperse does not always result in reproductive admixture in this region (Devloo-Delva

et al. 2023, Postaire et al. 2024). Given that this study only incorporated one location within the Gulf of Mexico, we cannot rule out that genetic diversity may be greater in other populations more north and west within the Gulf. While it is possible that some bull sharks in the Gulf may switch to giving birth in the Atlantic, as the extent of genetic differentiation seen here is minimal, there may still be extensive evolutionary adaptation required for other populations, and further studies are needed to confirm this. Similarly, while we did not observe a loss of diversity in our study, inbreeding caused by biparental philopatry and genetic drift acting on depleted predator populations could rapidly lower the adaptive potential of Atlantic bull sharks. Either way, future conservation measures should consider evidence from both genetics and telemetry, in addition to fisheries-independent and -dependent monitoring, to form accurate long-term management goals and predict population-wide climate responses.

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