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ORIGINAL PAPER

A genomic assessment of movement and gene flow around the South Florida vicariance zone in the migratory coastal blacknose shark, *Carcharhinus acronotus*

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Abstract

South Florida has been identified as a genetic break for multiple mobile marine taxa but the mechanisms that impede gene flow largely remain unknown. To understand how South Florida functions as a barrier for blacknose shark, a highly migratory species that has genetically diverged Atlantic and Gulf populations, patterns of genetic variation were assessed in 212 individuals sampled from the Atlantic, eastern Gulf, and Florida Keys at 2213 nuclear-encoded SNP-containing loci. Results support divergence between the Gulf and Atlantic ($F_{ST} \sim 0.002$, $P < 0.05$), and 51 individuals caught in the Keys were assigned to the Gulf, as compared to only two individuals that assigned to the Atlantic, indicating that Florida Keys is largely composed of Gulf individuals. Further, two to three migrants were identified, all of which were Gulf individuals captured in the Atlantic. The results indicate that South Florida does not prevent individual movement between the Gulf and Atlantic and that the Keys may be a seasonal mixing zone. However, the Gulf and Atlantic remain genetically independent, suggesting that region-specific reproductive behavior/compatibility, or aspects of movement ecology, such as swimming energetics or temperature-driven interannual variability in migratory range, may maintain divergence rather than a physical barrier in South Florida.

Introduction

Historically, it was assumed that because of large population sizes, the potential for long-distance dispersal and the lack of visible barriers, most vagile marine species would be genetically and demographically homogeneous across large geographic areas (Palumbi 1994; Shaklee and Bentzen 1998; Begg et al. 1999). Though homogeneity is observed in some species (Sang et al. 1994; Broughton and Gold 1997; Mariani et al. 2005), research has revealed that many species are less homogeneous than expected in terms of both life history traits (Conover 1992; Blanck and Lamouroux 2006) and genetics (Hauser and Carvalho 2008), indicating the presence of contemporary barriers to gene flow in apparently open expanses. These barriers can be physical, such as large ocean expanses (Benavides et al. 2011) and landmasses (Lessios 1998; Marko 2002; Rocha et al. 2007), and restrict gene flow because migration across them is not possible. Conversely, other barriers exist that restrict gene flow even though organisms can potentially traverse them, including trenches (Portnoy and Gold 2013), habitat transitions (Sotka et al. 2004; Hollenbeck et al. 2018), and oceanographic features, such as salinity gradients (Nielsen et al. 2004; Riginos and Cunningham 2005; Kijewska et al. 2016), currents (Baltazar-Soares et al. 2014), and temperature fronts (Quesada et al. 1995). While physical barriers tend to be conspicuous, these other barriers are often cryptic, making a priori identification of likely population units challenging. Nonetheless, cryptic barriers have been identified in a wide range

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of marine organisms, including bluefin tuna (Carlsson et al. 2006), limpets (Johnson and Black 1982), cod (Berg et al. 2015; Kijewska et al. 2016), crabs (Han et al. 2015), corals (Tsounis et al. 2006), and copepods (Burton 1986).

South Florida is a well-characterized barrier to gene flow for many marine species, sometimes referred to as the Florida Vicariance Zone (Neigel 2009), that separates the southern US Atlantic (hereafter Atlantic) from the Gulf of Mexico (hereafter Gulf). It is speculated that swift currents moving through the Straits of Florida into the Atlantic, coupled with a reduction in nearshore habitat in South Florida, may restrict movement between the Atlantic and Gulf for estuarine and demersal shelf fishes (Bowen and Avise 1990; Gold and Richardson 1991; Seyoum et al. 2017). The barrier, however, appears less effective for larger, migratory, coastal-pelagic fishes, such as king mackerel and amberjack, which appear genetically homogeneous between the Gulf and Atlantic (Gold and Richardson 1998; Gold et al. 2002). Coastal sharks differ from most bony fishes in that they exhibit high migratory capabilities as adults but often return to specific nearshore areas to give birth to young in nursery habitat (Hueter et al. 2004; Chapman et al. 2015). South Florida seems to function as an effective barrier to gene flow for some coastal sharks (scalloped hammerhead, Daly-Engel et al. 2012; bonnethead shark, Portnoy et al. 2015; finetooth shark, Portnoy et al. 2016), but not others (blacktip shark, Keeney et al. 2005; sandbar shark, Portnoy et al. 2010; bull shark, Karl et al. 2011; Sandoval Laurrabaquio-A et al. 2019) and it is unclear why this is the case.

The blacknose shark (*Carcharhinus acronotus*) is a small (< 1.6 m) coastal shark found in tropical to warm-temperate waters of the western Atlantic Ocean, from Virginia to Florida (Atlantic), through the Gulf of Mexico (Gulf) and in the Caribbean Sea to southern Brazil (Castro 2010). The species occupies both soft and hard-bottom habitat and occurs in a salinity range of ~ 26–38 (Carlson 2002; Hueter and Tyminski 2007; Ulrich et al. 2007). A recent assessment of patterns of genetic variation in this species in the Atlantic and Gulf, using mitochondrial DNA (mtDNA) and microsatellites, identified significant heterogeneity between blacknose caught along the Atlantic coast and those from the Gulf (Portnoy et al. 2014). However, the relationship between individuals sampled off the Florida Keys (hereafter Keys) and the two populations was equivocal, as the Keys did not differ significantly from the Gulf or the Atlantic.

Several possibilities might explain the observed ambiguity for blacknose sharks in the Keys. First, in the eastern Gulf and Atlantic, these sharks migrate seasonally (Castro 1993; Hueter et al. 2004), southward and/or offshore in the fall and inshore or northward in the spring (Clark and Von Schmidt 1965; Dodrill 1977; Schwartz 1984; Driggers et al. 2007; Sulikowski et al. 2007; Heithaus et al. 2007). Unlike large coastal sharks, both sexes of blacknose appear as part of inshore aggregations in the summer and mating has been documented during this period (Driggers et al. 2004; Sulikowski et al. 2007). This may indicate that adult blacknose of both sexes demonstrate philopatry to regions in the summer not only for pupping, but also for mating, but are free to stray at other times. The Keys, therefore, may be an area where Gulf and Atlantic populations mix without mating during periods of reproductive inactivity. Alternatively, individuals from the Atlantic and Gulf may breed in the Keys, making it a spatially limited zone of admixture between the two populations. Finally, the species are caught year-round near the Keys, leading to speculation that they represent a third population (Driggers et al. 2007), a hypothesis unsupported by previous work (Portnoy et al. 2014) and the apparent absence of newborn individuals in this region (Grubbs, pers. obs.).

The objectives of this study were to test whether sharks sampled in the Keys are part of the Gulf or Atlantic population and whether admixture is occurring by using a population genomics approach and including a more robust year-round sample of individuals caught in the Keys. South Florida has been identified as a physical barrier to dispersal for many shelf species, but if blacknose sharks from both stocks are found in the Keys, this would indicate that some other process (or processes) are responsible for maintaining genetic differences between Atlantic and Gulf populations.

Materials and methods

A total of 261 individual blacknose sharks captured 2009–2013 were used in analysis, including a subsample of those used by Portnoy et al. (2014). Individuals were chosen to represent seven geographic samples (grouped based on proximity of collection), including three samples in the Atlantic, three samples in the eastern Gulf, along with the Florida Keys. The samples included mature and immature individuals of both sexes and from a range of lengths (Fig. 1, Supplemental Table 1). Atlantic Ocean samples consisted of 31 individuals caught off South Carolina (SC) from May to August, 31 individuals caught off Georgia (GA) from May to October, and 25 individuals caught off Cape Canaveral, Florida (CC) from December to March. Samples from the Gulf included 30 individuals caught in the southeastern Gulf (SEG; Tampa Bay to Florida Bay, but not including the Keys) from February to August, 31 individuals caught in the coastal waters of the mid-eastern Gulf (MEG; Panama City, FL to Tampa Bay) from May to October, and 31 individuals caught in the northeastern Gulf (NEG; Mississippi to Panama City, FL, USA) from July to November. A final sample consisted of 77 individuals caught year-round within 60 km of the Florida Keys (KEY). To mitigate sex-specific

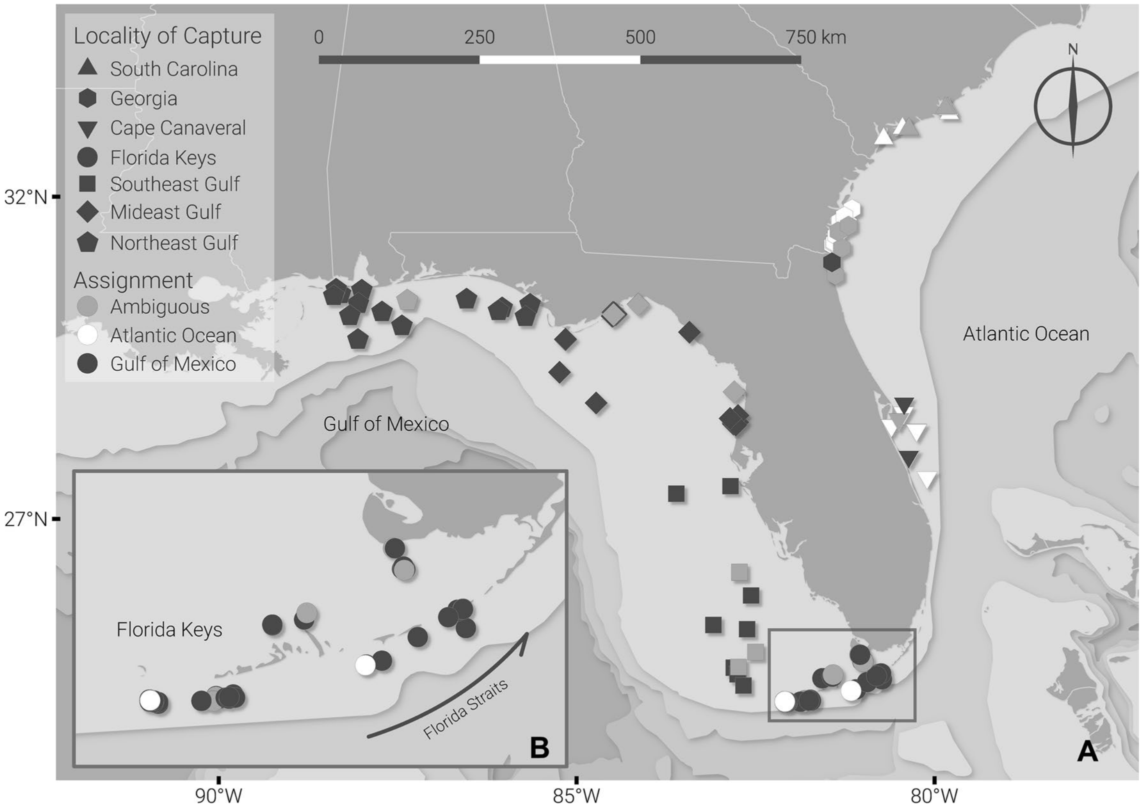

Fig. 1 Map of catch locations and geographic samples (represented by shapes) of *C. acronotus* individuals for used in analyses after filtering. **a** Population assignments of *C acronotus* individuals captured year-round in the Atlantic and Gulf resulting from Bayesian clustering and **b** in the Florida Keys. Individuals assigned to home population (Gulf or Atlantic) had a membership probability > 90%

biases, geographic samples included an even representation of individuals of each sex when possible.

A modified double digest restriction-site associated DNA (ddRAD) protocol (Peterson et al. 2012; Portnoy et al. 2015) was used to simultaneously discover and genotype individuals at thousands of single nucleotide polymorphisms (SNPs). Briefly, high molecular weight DNA was extracted from individual fin clips and digested using the enzymes *Sph*I and *Eco*RI (New England Biolabs). Barcoded adapters were ligated onto the digested fragments and fragments pooled and size selected. Flow cell adapters with one of four index-identifiers were ligated to each set of pooled individuals using 12 cycles of PCR, prior to sequencing on an Illumina HiSeq 2500. Raw sequences were demultiplexed, trimmed, and mapped onto a de novo reference assembly. Full details about methods used to create the final SNP dataset, including data filtering, can be found in the Electronic Supplement. The final SNP dataset was screened for outlier-loci putatively under selection using the Bayesian modeling framework implemented in Bayescan (Foll and Gaggiotti 2008). This analysis included 20 pilot runs with 5000 iterations each followed by a burn-in of 50,000 steps, and a sample size of 5000, with a thinning factor of 10. Significance of outlier loci was determined by using a q value that corresponded to a false discovery rate of 0.05.

Non-assumptive cluster identification was performed by cross-validated Discriminant Analysis of Principal Components (DAPC) implemented in the R- package Adegenet (Jombart et al. 2010; R Core Team 2019). Keys individuals were omitted and individuals were grouped based on geographic sampling locality but with ocean basin identity excluded, the analysis also did not consider spatial location of geographic samples. Cross-validation was performed over a range of 1–170 principal components with 500 replicates. Once an optimal number of principal components was identified, a second cross-validation was performed for a narrower range of principal components ± 10 of the previously identified optimum. Partitioning of genetic variation was assessed using a hierarchical, locus-by-locus AMOVA, with a priori groupings of localities into eastern Gulf and Atlantic based on the findings of Portnoy et al. (2014), and with the Keys sample excluded. Significance was assessed at the $\alpha = 0.05$ level using 20,000 permutations as implemented in Arlequin v. 3.5 (Excoffier and Lischer 2010). Pairwise F_{ST} values were then estimated between all geographic samples (including the Keys) and between regions using Genodive (Meirmans and Van Tienderen 2004), with significance assessed using an alpha of 0.05

and adjusted for multiple comparisons (Benjamini and Hochberg 1995).

Membership of each Keys individual was assessed using the Bayesian clustering algorithm implemented in Structure v.2.3.4 (Hubisz et al. 2009). The three Atlantic localities were used as one reference population and the three eastern Gulf localities as a second reference population, with the Keys unassigned to either. Analysis involved four replicate runs, each with 1,000,000 burn-in steps and another 1,000,000 sampling steps, and used the no-admixture model which is preferred when levels of divergence between populations are low (Hubisz et al. 2009). Individual assignments to the Atlantic or Gulf were determined by examining membership probabilities for every individual caught in the Keys, as well as for individuals caught in the Atlantic and Gulf. The saddlepoint approximation method, as implemented in Geneplot (McMillan and Fewster 2017), was used as a second method for assessing population membership of Keys individuals, as well as individuals caught in the Atlantic or Gulf. The saddlepoint approximation method assesses and visualizes genetic fit of individuals to candidate populations as the probability of individual *I* occurring in a given reference population *R* versus an alternative reference population *Q*. Population assignment in Geneplot was determined by visualizing the multilocus log genotype probability of every individual for each of the reference populations. To further test for putative migrants within the eastern Gulf and Atlantic, likelihood ratios were calculated as the likelihood of an individual's multilocus, composite SNP-genotype originating in the population of origin over the likelihood of that genotype originating in the alternate population ($L' = L_{\text{home}}/L_{\text{not\_home}}$) in GeneClass v.2.0 (Piry et al. 2004), using a Bayesian approach (Rannala and Mountain 1997). Significance was determined by simulating 10,000 individual multi-marker genotypes based on estimated population allele frequencies (Paetkau et al. 2004) and generating a null distribution of L' values; significance was assessed at the 0.01 level. Due to computational limitations, this analysis was run with a reduced dataset made up of 146 loci identified as significantly differentiated between the Atlantic and Gulf reference populations ($P \leq 0.05$). Individuals identified as migrants were examined for trends in sex, length, date of capture, and maturity.

Results

Variant calling of demultiplexed and aligned reads produced 657,986 raw reference contigs across 261 individuals plus duplicates. Rigorous filtering and haplotyping (described in the Supplemental Materials and Methods) produced a final dataset of 2484 SNPs in 2213 putatively orthologous loci from 212 individuals (Supplemental Table 1). Supplemental Table 2 contains details of filtering parameters and the number of SNPs at each step. Bayescan identified no significant outlier loci in the filtered dataset.

Excluding basin information and spatial data, individuals from the six sampling localities clustered by basin on the PCA plot (Supplemental Fig. 2), lending evidence to the assumption of genetic discontinuity between basins. Consistent with this observation, the component of variation attributable to differences among basins (Atlantic, eastern Gulf) was significant ($F_{\text{CT}} = 0.0025$, $P < 0.001$, Table 1), while the component of variation attributable to differences among populations within regions was not ($F_{\text{SC}} = 0.0001$, $P = 0.385$, Table 1). Twelve of 21 pairwise estimates of F_{ST} were significant before correction and nine after correction. All comparisons between Atlantic and Gulf localities were significant, while no comparisons between localities within regions were significant (Table 2). Comparisons between the Keys and Atlantic localities were all significant, while no comparisons between the Keys and Gulf were significant.

A probability threshold of > 90% was used for assigning Keys individuals to the Atlantic or Gulf. Fifty-one individuals assigned to the Gulf, two individuals assigned to the Atlantic and twelve were ambiguous (Fig. 1). Assignment using Geneplot indicated 53 Keys individuals belonged to the Gulf population, six individuals assigned to the Atlantic (including the same two identified previously), and six were ambiguous (difference in log-likelihoods < 1; Supplementary Fig. 1).

Individuals caught outside the Keys were divided into three categories based on membership probability calculated using Bayesian clustering: non-migrants (> 90% membership probability to region where sampled), putative migrants (< 10% membership probability to region where sampled), and ambiguous (between 10 and 90% membership probability to region where sampled). Bayesian clustering

Table 1 AMOVA for geographic samples (localities) nested within regions

Level	SS	VC	%*V*	*F*	*P*
Among regions	276.373	0.51077	0.25327	0.00253	< 0.0001
Among localities within regions	809.664	0.02632	0.01305	0.00013	0.3847
Within localities	57388.544	201.12919	99.73367	0.00266	< 0.0001

SS the sum of squares, *VC* variance component, %*V* percent variance, *F* F statistic, and *P P* value

Table 2 Pairwise F_{ST} values between localities (below diagonal) and corresponding P values (above diagonal)

	SC	GA	CC	KEY	SEG	MEG	NEG
SC	–	0.867	0.641	< 0.001	0.021	< 0.001	0.05
GA		–	0.169	< 0.001	0.006	< 0.001	0.04
CC	0.000	0.001	–	< 0.001	0.001	< 0.001	0.046
KEY	0.002**	0.002**	0.003**	–	0.723	0.233	0.594
SEG	0.002**	0.002**	0.003**	0.000	–	0.237	0.145
MEG	0.003**	0.004**	0.004**	0.000	0.001	–	0.593
NEG	0.001*	0.001*	0.003*	0.000	0.001	0.000	–

The localities are *SC* South Carolina, *GA* Georgia, *CC* Cape Canaveral, *KEY* Florida Keys, *SEG* Southeast Gulf, *MEG* Mideast Gulf, *NEG* Northeast Gulf

*Significance at 0.05 before correction (Benjamini and Hochberg 1995) and **significance after correction

analysis identified three putative migrants, two caught off Cape Canaveral (♀ $_{\text{November}}$, ♀ $_{\text{December}}$) and one caught off Georgia (♂ $_{\text{July}}$), and nineteen individuals that were ambiguous (Fig. 2; Table 3). Only two individuals were identified as putative, first-generation migrants using likelihood-ratio testing ($P < 0.01$): the same Cape Canaveral individuals identified using Bayesian clustering (Table 3; Fig. 1). While no explicit maturity assessment was provided in the catch metadata for these individuals, they were larger than the size at 50% sexual maturity for both males and females (Table 3; and see Hendon et al. 2014).

Discussion

Analysis using 2213 putatively-neutral genetic markers confirmed the findings of Portnoy et al. (2014), that there are discrete Atlantic and Gulf populations of blacknose sharks, and with a similar magnitude of divergence between populations. Estimates of pairwise F_{ST} were significant for all comparisons between the Keys and Atlantic samples but never between the Keys and Gulf samples, indicating that the Keys are a part of the eastern Gulf population. Consistent with this, the majority of blacknose caught in the Florida Keys were assigned back to the Gulf population (78% or 83%) with only two to six individuals assigning to the Atlantic. In addition, two to three migrants from the Gulf were identified in the Atlantic, indicating that South Florida does not completely prevent movement between the regions.

Estimates of pairwise F_{ST} and the assignment of most Keys individuals to the Gulf indicates that the Keys represent the southern extent of the eastern Gulf population, rather than an independent population as suggested by Driggers et al. (2007). Gulf blacknose were found as far east as 80.725° West longitude on the Florida Straits side of the Keys, suggesting that the dividing line between Gulf and Atlantic stocks of blacknose falls somewhere between Cape Canaveral and the Florida Keys. This is consistent with the current assessment of two separate stocks, defining individuals from the Florida Keys as part of the Gulf stock (NMFS 2011c). A division between Atlantic and Gulf populations is seen in a number of marine species (Neigel 2009; Felder and Camp 2009), and for estuary-dependent species a break associated with fragmented estuarine habitat has been proposed to occur on the Atlantic side of Florida near Biscayne Bay (Seyoum et al. 2017, 2018). While estuarine habitat would not be expected to be a limiting factor for blacknose sharks, the southeastern edge of the Florida Shelf is relatively narrow (4–8 km) between West Palm Beach and Miami, limiting the amount of available nearshore, marine

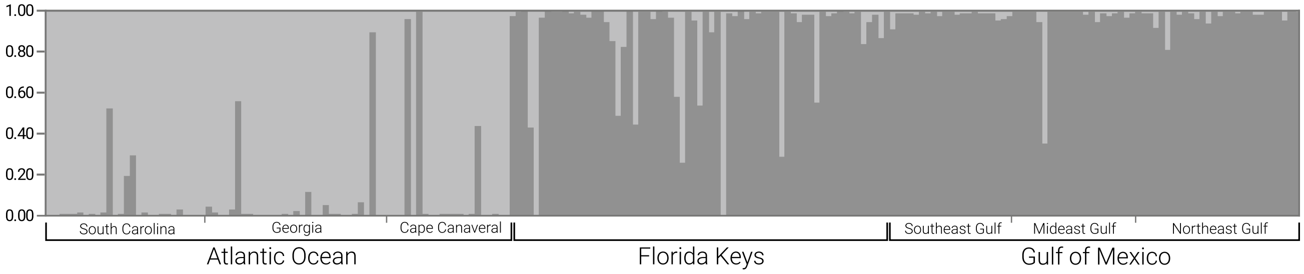

Fig. 2 Barplot representing population membership probabilities from Bayesian clustering of *C acronotus* individuals (one vertical bar per individual) captured year-round in the Florida Keys assigned to either Atlantic Ocean (light) or Gulf of Mexico (dark) reference populations. See also electronic Supplementary Materials for interactive version with associated metadata

Table 3 Putative migrants and ambiguous individuals identified with associated metadata Listed are membership probabilities inferred from Bayesian clustering that indicate whether an individual arose from the region (Atlantic or Gulf) in which it was sampled (Home) Metadata include month and year of samples, sex of individual, maturity status (Maturity) and fork length (FL) Individuals identified as first-generation migrants by GeneClass ($P < 0.01$) are bolded italicized A cross (+) indicates maturity inferred from comparing fork length (FL) to size at 50% maturity at the assigned population

Region	Individual	Home	GeneClass	Month	Year	Sex	Maturity	FL
Atlantic	cc_005	0.011	0.0018	11	2009	F	Mature	900
Atlantic	cc_008	0.001	< 0.0001	12	2009	F	Mature	880
Atlantic	cc_019	0.373	0.5133	4	2013	M	Mature	890
Atlantic	ga_006	0.26	0.5138	6	2010	M	Mature+	797
Atlantic	ga_020	0.74	0.5152	10	2010	F	Mature	820
Atlantic	ga_023	0.866	0.0116	5	2011	F	Mature	820
Atlantic	ga_031	0.839	0.0167	10	2010	F	Mature	660
Atlantic	ga_033	0.039	0.5134	7	2010	M	Mature	875
Atlantic	sc_011	0.271	0.5137	8	2010	F	Mature	862
Atlantic	sc_015	0.655	0.5142	6	2011	F	Mature+	1115
Atlantic	sc_016	0.557	0.514	6	2011	M	Mature+	1063
Atlantic	sc_032	0.878	0.5147	6	2011	M	Mature+	1056
Gulf	meg_005	0.814	0.5495	7	2012	M	Immature+	590
Gulf	meg_007	0.663	0.5493	7	2012	F	Immature+	375
Gulf	meg_012	0.892	0.5501	7	2010	M	Immature+	390
Gulf	meg_014	0.852	0.5549	7	2010	F	Immature+	360
Gulf	meg_028	0.881	0.5514	8	2012	M	Mature+	880
Gulf	neg_006	0.868	0.5524	8	2011	M	Mature+	866
Gulf	neg_007	0.204	0.5487	11	2011	F	Mature+	865
Gulf	neg_025	0.865	0.5527	9	2011	F	Immature+	506
Gulf	seg_028	0.885	0.5508	2	2011	M	Mature+	850
Gulf	seg_029	0.886	0.5512	2	2011	M	Mature	980

habitat (Walker 2009). Consistent with this idea, blacknose sharks have been not sampled in this area during tagging studies (Kohler and Turner 2007).

While habitat along the southeastern coast of Florida may play a role in limiting dispersal of blacknose sharks, the identification of two Atlantic individuals in the Florida Keys across analyses demonstrates that animals are not completely constrained from moving from the Atlantic into the Florida Keys. A total of 47 sharks were sampled from the Florida Straits side of the Keys and 18 from the Florida Bay/Gulf of Mexico side, with both individuals that assigned to the Atlantic captured on the Florida Straits side (Fig. 1b). While the result may reflect uneven sample sizes, it is also possible that greater mixing occurs on the Florida Straits side, where animals from the Gulf and Atlantic co-occur seasonally. The presence of a mixing zone near the Keys has been previously proposed for Atlantic and Gulf stocks of king mackerel, a highly-migratory coastal pelagic that spawns in the summer in northern Gulf and Mid-Atlantic (SEDAR 2014; GMFMC 2017), as well as for common snook (Tringali and Bert 1996). A winter mixing zone of blacknose populations in the Keys would seem plausible since both the Gulf and Atlantic populations migrate southward in the fall and winter after mating (Driggers et al. 2004; Sulikowski et al. 2007). However, only one of the two putative Atlantic individuals, a male, was caught in the fall/winter (November), while the other, a female, was caught in July. Because female blacknose sharks may exhibit biennial reproductive cycles (Driggers et al. 2004), and sexual segregation outside of mating is common in sharks as a means for females to avoid aggressive mating attempts by males (Springer 1967; Klimley 1987), the Keys also may represent a refuge for non-reproductive females. The composition of the Keys samples in this study was 85% female overall (51/60 individuals for which sex information was available) and 89% female during the summer (40/45 individuals for which sex information was available). More extensive catch data also supports sex-skew in the Keys (186:46, females: males, Grubbs unpublished data), while sex ratios near mating grounds to the north are close to 1:1 (Driggers et al. 2007).

Of the twelve individuals sampled in the Keys that were not assigned with confidence to the Gulf or Atlantic with Bayesian clustering, all were female. The saddlepoint method assigned eight of the ambiguous Keys individuals to the Gulf and four to the Atlantic but reclassified five individuals assigned by Bayesian analysis to the Gulf as ambiguous. The efficacy of assignment testing depends on the deployment of an adequate number of polymorphic markers and the degree to which candidate populations have diverged in allele frequencies (Cornuet et al. 1999; Paetkau et al. 2004). While the dataset contained over 2000 putatively orthologous and unlinked markers, the observed divergence between the two reference populations was quite small, likely due to recent co-ancestry of the populations, potential recurrent gene flow, and large effective sizes (Portnoy et al. 2014), and this constrained the ability to confidently assign all individuals to their population of origin. Alternatively, approaches employed here allow for the detection of individuals of mixed ancestry (Pritchard et al. 2000; McMillan and Fewster 2017), and the results could indicate that limited mating occurs between Atlantic and Gulf individuals in or near the Keys, with offspring usually remaining in the area. Consistent with the idea that mating could occur in or near the Keys, one of the females captured for this study in the Keys in July had wounds consistent with recent mating. However, newborns have never been sampled near the Keys (Grubbs unpublished data).

The identification of at least two first-generation migrants in the Atlantic, in the face of significant divergence, raises questions about the biological function of movement between the Gulf and Atlantic because theoretically, few migrants are required every generation to prevent divergence via genetic drift (Lewontin 1974). While the actual number of migrants needed to overwhelm drift in natural populations is likely greater than one-migrant-per-generation (Mills and Allendorf 1996; Vucetich and Waite 2000), the detection of two or three mature migrants, out of 77 individuals sampled in the Atlantic, would suggest that migration should be sufficient to counteract divergence. However, this presumes that movement (potential dispersal) equates directly to gene flow (realized dispersal), an idea that has been challenged in several marine organisms (Weersing and Toonen 2009). The detection of significant differentiation despite the recency of the Gulf-Atlantic split (Portnoy et al. 2014) and the presence of reproductively capable migrants indicates that, for blacknose sharks, individual movement across population boundaries has not led to widespread admixture. Therefore, it is useful to distinguish between individuals moving and breeding with recipient populations (genetic migrants) from individuals moving and not breeding with recipient populations (vagrants).

There are several reasons that vagrant blacknose sharks may move between the Atlantic and Gulf. First, annual sea temperature fluctuations can determine the migratory range for elasmobranchs in a given year, a phenomenon observed in Atlantic bonnethead sharks (*Sphyrna tiburo*). During warm winters, bonnethead sharks caught in South Carolina engage in short migrations to waters off Georgia, but during colder winters, migrate to waters off Cape Canaveral, FL, USA (Keller et al. 2018). It is possible that Atlantic blacknose sharks migrate south to the Florida Keys during cold winters, where they mix with Gulf blacknose sharks, but do not admix genetically. Vagrants may also represent foraging individuals. Gulf females sampled in the Atlantic were caught in November and December, while mating occurs in the summer (Sulikowski et al. 2007), and females on biennial reproductive cycles would be free to move further away from nursery/mating areas during a resting state to search for food. In addition, individuals who move between regions may be unable to identify appropriate breeding or nursery areas in the new region. Female philopatry, fidelity to nursery sites/areas, has been observed in many shark species (Heupel et al. 2004; Chapman et al. 2015) and is thought to occur in blacknose sharks (Hueter and Manire 1994; Hueter et al. 2004). Since breeding takes place in the vicinity of nursery areas for blacknose and other small coastal sharks (Knip et al. 2010), philopatric behavior may be a feature of both sexes (Portnoy et al. 2014). Sharks use multiple cues to govern the timing of migration and to locate nursery/mating habitat, including olfactory information (Gardiner et al. 2015), geomagnetic fields (Klimley 1993), and annual cycles of temperature and light levels (sandbar shark *Carcharhinus plumbeus*, Grubbs et al. 2007; McCandless et al. 2007). If migrants experiencing phenotype-environment mismatch are unable to identify cues necessary to initiate and complete migration due to oceanographic or habitat differences between the Gulf and Atlantic, they may not be able to conform to the migratory cycles of the recipient population and will fail to reproduce, a dynamic that would reinforce divergence (Hendry 2001, Marshall et al. 2010). In addition, migrants may have reduced reproductive success, if localized selection makes them less capable of producing viable offspring (Svensson et al. 2017). No vagrant individuals were detected as far north as the mating areas around South Carolina, further supporting a dissociation between movement and gene flow.

While the overall number of putative migrants between the Atlantic and Gulf (beyond the Keys) observed in this study was small, all were caught in the Atlantic, which may indicate asymmetrical movement. For bony fishes, the east and north-flowing Florida Current (Wang and Mooers 1998; Lynch-Stieglitz et al. 1999) is thought to function as a barrier, restricting movement of smaller fishes and larvae south and west around the Florida Peninsula (Lee et al. 1992). While currents are not often thought to function as barriers to shark movement, moving with a current is more energy efficient. The currents from the Florida Straits may facilitate the movement of blacknose sharks around the eastern Florida Keys and to the north while impeding attempts to move back into the Gulf. Asymmetrical movement with prevailing currents has been documented in migrating sandbar sharks *Carcharhinus plumbeus* (Medved and Marshall 1983; Wetherbee and Rechisky 2000), foraging basking sharks *Cetorhinus maximus* (Sims and Quayle 1998), and in tidal movements of blacktip reef sharks *Carcharhinus melanopterus* (Papastamatiou et al. 2009). Blacknose sharks have high energetic costs associated with locomotion, relative to other carcharhinid sharks (Carlson et al. 1999), and this may reduce the amount of movement against the current and into the Gulf. However, Atlantic individuals were identified in the outer Keys, indicating that while movement against the current may be difficult, it is not impossible.

Overall, the data strongly support the notion that the dividing line between the Atlantic and Gulf occurs off South Florida, and in the vicinity of the Dade/Monroe county line currently used by managers (NMFS 2011a, b). However, the presence of a few Atlantic individuals in the Keys and a few Gulf individuals in the Atlantic indicates mixing with little-to-no gene exchange. This suggests a discrepancy between potential and realized dispersal in this species and that aspects of movement ecology and behavior likely explain the genetic break, rather than a barrier to movement. For exploited species, like sharks, that are very sensitive to overfishing (Musick 1999; Musick et al. 2000), identifying differences between movement and gene flow is vital for identifying critical habitat such as feeding grounds and migratory corridors where stocks may mix and understanding potential spatiotemporal differences in fisheries impacts.

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Data availability Raw sequence data will be hosted online at NCBI under bioproject PRJNA541933. The final SNP dataset that support the findings of this study will be hosted online at https://github.com/pdimens/C.acronotus-data-2019.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. Field sample collections by FSU were approved under FSU IACUC protocols 1111 and 1411.

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