Selection and sex-biased dispersal: the influence of philopatry on adaptive variation

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Abstract

Sex-biased dispersal is expected to homogenize nuclear genetic variation relative to variation in genetic material inherited through the philopatric sex. When site fidelity occurs across a heterogeneous environment, local selective regimes may alter this pattern. We assessed spatial patterns of variation in nuclear-encoded, single nucleotide polymorphisms (SNPs) and sequences of the mitochondrial control region in bonnethead sharks (*Sphyrna tiburo*) collected, a species thought to exhibit female philopatry, from summer habitat used for gestation. Geographic patterns of mtDNA haplotypes and putatively neutral SNPs confirmed female philopatry and male-mediated gene flow along the northeastern coast of the Gulf of Mexico. A total of 30 outlier SNP loci were identified; alleles at over half of these loci exhibited signatures of latitude-associated selection. Our results indicate that in species with sex-biased dispersal, philopatry can facilitate sorting of locally adaptive variation, with the dispersing sex facilitating movement of potentially adaptive variation among locations and environments.

Introduction

Sex-biased dispersal arises when individuals of one sex exhibit site fidelity (philopatry), while individuals of the opposite sex are prone to disperse (Pusey 1987). This occurs in a wide variety of vertebrate taxa (Karl *et al.* 1992; Clark *et al.* 1997; Hutchings & Gerber 2002; Möller & Beheregaray 2004) and is thought to result from fitness differences between the sexes associated with local competition for resources (including mates), inbreeding avoidance, and/or parental investment (Gandon 1999; Perrin & Mazalov 2000). There also is a relationship between mating system and which sex is dispersive; monogamous species feature territorial males and dispersive females, while polygamous species feature female philopatry and male dispersal (Greenwood 1980). Sex-biased dispersal tends to have a homogenizing effect on bi-parentally inherited nuclear variation via gene flow through the dispersive sex; uniparentally inherited markers (e.g., heterologous sex chromosomes, mtDNA), however, sort through the philopatric sex and may diverge at a greater rate through time (Avise 1994). If habitats of a philopatric species vary spatially, genetic patterns potentially can become more complex as the homogenizing effects of sex-mediated gene flow may be counteracted by localized selection operating on specific genomic regions (Garant *et al.* 2007).

Studies in several species of live-bearing sharks have revealed spatial genetic patterns (homogeneity in nuclear-encoded microsatellites and heterogeneity in maternally-inherited mtDNA) consistent with female philopatry and male-mediated gene flow (Portnoy and Heist 2012). Females in these species exhibit considerable parental investment, giving birth after long gestation periods to small litters of fully developed offspring, suggesting that return to a favourable habitat could enhance embryonic growth during gestation (Economakis & Lobel 1998, Driggers *et al.* 2014) as well as provide predictable access to food and shelter from predators (Heupel *et al.* 2007). It also is known that habitats used by the same species for gestation and/or parturition may differ substantially, even at small spatial scales (DiBattista *et al.* 2007; Feldheim *et al.* 2014). Based on the above, philopatric sharks represent a good model system to assess possible effects that localized adaptation may have on genome-wide patterns of variation in the context of sex-asymmetric gene flow.

We assessed spatial patterns of variation in nuclear-encoded single nucleotide polymorphisms (SNPs) and sequences of the mitochondrial control region in bonnethead sharks (*Sphyrna tiburo*), a species thought to exhibit female-biased philopatry (Driggers *et al.* 2014). Bonnetheads are common seasonal residents in coastal and estuarine waters of the western Atlantic Ocean (Atlantic), including the Gulf of Mexico (Gulf), and are known to use nearshore habitat for gestation and parturition (Compagno 1984; Driggers *et al.* 2014) We sampled adult and sub-adult animals from three localities along the west coast of Florida (Gulf of Mexico) and one locality off the coast of North Carolina (western Atlantic Ocean). Sample localities in the Gulf were selected because of identified latitudinal differences in life-history parameters among bonnetheads in the region (Lombardi-Carlson *et al.* 2003); the sample from the Atlantic was included to have a sample outside the Gulf and because of identified differences in life history between bonnetheads in the Gulf and Atlantic (Frazier *et al.* 2014). We used a ddRAD approach [20] to genotype individuals at thousands of nuclear-encoded SNPs, permitting a search for spatial differences in genomic regions putatively under selection; inclusion of putatively neutral SNPs and mtDNA sequences allowed us to assess further whether dispersal in bonnetheads is sex-biased.

Material and Methods

Tissues (fin clips) from 134 bonnetheads sampled between 1998 and 2000 from four near-shore localities (Fig. 1) were used in the study. Fish were obtained during the summer months (May to September) when mature individuals are in areas used for gestation, parturition, and mating. Individuals sampled were mostly a mix of mature females and males.

Double-digest RAD (ddRAD) libraries were prepared following Peterson *et al.* (2012); details of the protocol may be found in the electronic supplementary material (Supplemental Methods). Libraries were sequenced on two lanes of an Illumina HiSeq 2000 DNA sequencer. The first library was sequenced as a paired-end run for reference contig assembly and to facilitate downstream bioinformatic inference. The second library was sequenced as a single-end run, as a cost-effective manner to genotype SNPs. The *dDocent* pipeline (Puritz *et al.* 2014) was used for reference contig assembly, read mapping, and SNP genotyping. Default parameters were used for each step, with the exception of contig assembly, where a customized script was used to mitigate the high levels of repeats and duplications expected in large genomes. The initial set of data consisted of 648,035 variant SNP loci across 147,920 fragments.

The entire mitochondrial control region (1,134 bp) was amplified using primers Pro-L and 282H (Keeney *et al.* 2003); details of the protocol may be found in the electronic supplementary material (Supplemental Methods). Electrophoretograms were examined by eye, aided by GENEIOUS v.7.1 (Biomatters Ltd.); all sequences were trimmed to 1,064 bp due to occasional non-specific amplification on the 3’ end that made accurate base calling difficult.

SNPs were extensively filtered before further analysis. The initial raw data set was filtered to remove all genotypes with <5 reads per individual and loci called in <75% of all individuals. Consequently, only the top 90% of individuals in genotype call rate were retained. The resulting data set contained 121 individuals. SNPs were then filtered to meet the following criteria:

presence in 97.5% of individuals across the data set, minor allele frequency greater than 5% across the data set, and conformance to expectations of Hardy-Weinberg equilibrium (HWE). Additional parameters considered during filtering included allele balance within heterozygous individuals, SNP quality to depth ratio, percentage of contribution from forward and reverse reads, maximum mean read depth across individuals, and removal of possible paralogs (Details on SNP filtering described in Supplemental Methods). The final, filtered data set, consisting of 5,914 SNPs spread across 3,967 fragments.

Genetic diversity (nuclear genome) within each locality was assessed as the mean nucleotide diversity (π) across all SNPs, using VCFTOOLS (Danecek *et al.* 2011). Homogeneity of π across localities was assessed using analysis of variance (ANOVA) and Tukey-Kramer HSD independent contrasts as implemented in JMP® v.11 (SAS Institute Inc.). Genetic diversity (mtDNA) was assessed as mean nucleon (h) and nucleotide diversity (π) within each locality, using ARLEQUIN v.3.5.1.2 (Excoffier and Lischer 2010).

Relatedness of individuals within each locality was assessed in VCFTOOLS, using the statistic developed by Yang *et al.* (2010). Two individuals in the sample from Florida Bay (FB) possessed high relatedness to each other (0.61) relative to the average relatedness (-0.045) across all individuals, suggesting these two individuals share parents. The individual with more missing data was removed from subsequent SNP-based analyses to avoid possible issues with consanguinity. SNPs were then organized into haplotypes (loci), using a custom Perl script that produces output in GENEPOP format. During haplotyping, a total of 23 loci were excluded from further analysis; 11 were identified as possible paralogs and 10 could not be haplotyped in more than 90% of individuals assayed. GENEPOP files were converted to BAYESCAN format, using PGDSPIDER v.2.0.7 (Lischer and Excoffier 2012), and BAYESCAN (Foll and Gaggiotti 2008) was used to identify individual outlier loci by assessing fit to different models of selection. The program was run with all default values, with the exception of 30 pilot runs and a thinning interval of 50; significance of outlier loci was determined using a *q*-value which directly corresponded to a false discovery rate of 0.05. Loci were then divided into two sets: one that contained putatively neutral SNPs (N-SNP loci) and one that contained outlier SNPs (O-SNP loci) putatively under selection.

Geographic homogeneity among localities in N-SNP and O-SNP loci was tested using single-level analysis of molecular variance (AMOVA), as implemented in GENODIVE V.2.0 (Meirmans & Van Tienderen 2004). Pairwise F_{ST} values (both nuclear data sets) were estimated using GENODIVE; significance of pairwise F_{ST} values was assessed by permuting individuals between samples 10,000 times. Homogeneity of mtDNA haplotypes among localities was tested using single-level AMOVA, as implemented in ARLEQUIN. Distances were calculated using a Kimura 2-parameter model (Kimura 1980), as selected by jMODELTEST v. 2.1.4 (Guindon and Gascuel 2003; Darriba *et al.* 2012). Pairwise Φ_{ST} values were estimated using ARLEQUIN, with significance determined by permuting individuals between samples 10,000 times. Correction for multiple testing was implemented using the false discovery rate (FDR) procedure (Benjamini and Hochberg 1995).

Discriminant Analysis of Principle Components (DAPC: Jonmbart *et al.* 2010) was carried out on both N-SNP and O-SNP loci, using the ADEGENET package (Jombart and Ahmed 2011) in R v.3.0.2 (R Development Core Team 2013), with prior group membership defined by locality. DAPC also was carried out on O-SNP loci, with prior group membership inferred using *k*-means clustering (MacQueen 1967); contribution of O-SNP loci to genetic clustering was then inferred from loading variables used in each discriminant function. For all O-SNP loci, the reference contig, assembled from paired-end reads, was screened against the NCBI nucleotide-read database, using the BLASTN algorithm (Altschul *et al.* 1990). The top three hits with E-values less than 0.01 were recorded.

Results

Summary statistics for SNPs and mtDNA are given in Table S1 (electronic supplementary material); GENBANK accession numbers and geographic distribution of mtDNA haplotypes are given in Table S2. Estimated mean nucleotide diversity (π) across all SNP loci per sample (± SE) varied from 0.296 (± 0.002) in the sample from North Carolina (NC) to 0.319 (± 0.002) in the sample from FB. Mean estimates of π differed significantly across samples ($F_{[3]}$=21.483, $P <$ 0.001), with mean π in NC being significantly lower than in the other samples (Tukey-Kramer HSD – $P < 0.001$). The same pattern was observed in haplotype diversity of mtDNA sequences; estimated diversity was lower in NC (h=0.719 ± 0.077), while h values did not differ among the other three samples.

A total of 30 haplotypes, containing 49 O-SNPs, were identified as candidate loci under selection ($q < 0.05$); the remaining SNPs (5,865 scattered across 3,910 haplotypes) were consistent with a neutral model. A total of 72 alleles were identified among the 30 O-SNP loci; 21 loci were bi-allelic, while nine were multi-allelic (Table S3). Significant heterogeneity among all four localities in all three marker types was detected by AMOVA (Table S4); the proportion of the total genetic variance explained by geography (locality) was 0.79% (N-SNP loci), 7.77% (mtDNA haplotypes), and 27.07% (O-SNP loci). Pairwise estimates of F_{ST} and Φ_{ST} (Table 1) revealed differences among the three marker types. For N-SNP loci, allele frequencies in NC differed significantly from those in FB, TB (Tampa Bay), and PC (Panama City); allele frequencies in the latter three were homogeneous. For mtDNA, the haplotype distribution in NC differed significantly from those in FB, TB, and PC; estimates of Φ_{ST} between FB and PC differed significantly from one another, while those between FB and TB and TB and PC were homogeneous. Allele frequencies of O-SNP loci in both NC and PC differed significantly from one another and from those in FB and TB, while allele frequencies in FB and TB were homogeneous. Significant heterogeneity among the three localities in the Gulf also was detected by AMOVA for mtDNA haplotypes ($F_{ST} = 0.027$, $P = 0.033$) and O-SNP loci ($F_{ST} = 0.157$, $P = 0.000$), but not for N-SNP loci ($F_{ST} = 0.0003$, $P = 0.151$); the proportion of the total genetic variance explained by geography (locality) was 0.03% (N-SNP loci), 2.68% (mtDNA haplotypes), and 15.70% (O-SNP loci).

Analysis of N-SNP loci, using DAPC and with prior group membership defined by locality, revealed two distinct clusters along the primary (X) axis (Fig. 1A); one was comprised of individuals from NC, while the other contained individuals from the three localities in the Gulf. Analysis of O-SNP loci, with prior group membership defined by locality, revealed a different pattern along the primary axis (Fig. 1B). Twelve individuals from PC clustered with individuals in the sample from NC, while the remaining individuals formed a second cluster; both clusters were more diffuse than in the analysis of N-SNP loci. When prior group membership of O-SNP loci was inferred using *k*-means clustering, three distinct clusters were revealed in DAPC analysis (Fig. 1C). One cluster contained primarily individuals from NC and PC and one individual from TB; one cluster contained individuals from the Gulf, primarily from PC; and one cluster contained mostly individuals from FB and TB and one individual from PC. The primary (X) axis described 99.6% of the variance. Allele frequencies at three representative O-SNP loci (Fig. 1D) clearly reveal a clinal, north-south (latitudinal) pattern in allele frequencies. The correlation between allele (haplotype) frequencies at each O-SNP locus and latitude was then evaluated using standard least squares regression as implemented in JMP v.11. Alleles at 17 O-SNP loci were correlated ($P \leq 0.05$) with latitude and explained 56.9% of the variation along the primary axis, while 18 O-SNP loci had r^2 values ≥ 0.90 and explained 75.6% of the variation along the X.

Eight of the 30 O-SNP loci had no sequence counterpart in GENBANK; the remaining 22 were highly similar (E-value <0.01) to several DNA sequences (Table S5). Frequent 'hits' included sequence similarities to clones or contigs in other species, and to annotated genomic regions of known immune response proteins (e.g., cytokines MIP-3 and interleukin-1β and a T cell receptor), putative regulatory elements (e.g., zinc-finger proteins, Hox genes), and SINE-type sequences.

Discussion

The significant difference in N-SNP loci between bonnetheads from the Atlantic and Gulf indicates genetically distinct populations with little to no gene flow between the two regions. This geographic pattern has been observed in other marine taxa (Avise 1992; Gold & Richardson 1998; Gold *et al.* 2009) including coastal sharks (Portnoy *et al.* 2014), and is hypothesized to stem from biogeographic processes associated with the Florida Current and/or narrowing of the continental shelf in south-eastern Florida (Portnoy *et al.* 2014). The absence of significant divergence in N-SNP loci among the three localities in the Gulf is consistent with gene flow occurring between the Florida Keys (FB) and north-central Florida (PC).

Asymmetry in geographic patterns of variation between N-SNP loci (homogeneous) and mtDNA haplotypes (heterogeneous) among bonnetheads from the Gulf is consistent with female

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philopatry and male-mediated dispersal (Melnick & Hoelzer 1992). Similar patterns have been documented in several shark species (Portnoy & Heist 2012; Chapman *et al.* 2015) and inter-annual tag-and-recapture studies of bonnetheads (Driggers *et al.* 2014) demonstrate strong site fidelity of females to specific estuaries. The pattern of mtDNA haplotype variation among bonnetheads in the Gulf indicates an isolation-by-distance effect rather than complete isolation as mtDNA haplotypes in the intermediate sample locality (TB) did not differ significantly from those in sample localities (PC and FB) at the geographic extremes. This also suggests that female bonnetheads may stray from preferred localities but most likely to neighbouring ones.

The largest proportion of the genetic variance explained by locality (geography) was due to O-SNP loci. In theory, outlier loci can reflect genomic regions associated with local adaptive differences (Nielsen *et al.* 2009; Allendorf *et al.* 2010) or genomic regions that have diverged more than expected over time via a non-adaptive process such as genetic drift (Hedrick 2011). However, genetic drift is a genome-wide effect (Luikart *et al.* 2003) and the significant correlations between allele frequencies at O-SNP loci and latitude and the complete absence of any clinal pattern in N-SNP loci indicate that the observed geographic pattern of O-SNP loci stems from localized divergent selection. The greater similarity in allele frequencies at outlier O-SNP loci between PC and NC also supports divergent selection associated with latitude as the two localities are situated at more northerly latitudes yet are at the geographic extreme of possible (homogenizing) gene flow among the localities studied.

Signatures of latitude-driven selection are common given that natural phenomena (e.g., climate, diurnal cycle) impact distributions of biological organisms, and that selection is imposed by the local biotic environment and interactions between a focal population and other organisms (Kawecki and Ebert 2004). Examples of well-known latitude-specific effects on marine fish include demographic traits such as growth rate (Conover and Present 1990) and host-parasite/pathogen systems (Poulin and Morand 2000). A few of the O-SNP loci found in this study did have sequence similarities to regions of genes putatively involved in regulation and development, and there are significant latitudinal differences in growth rate and size at age among bonnetheads in the region of the Gulf sampled (Lombardi-Carlson *et al.* 2003). A larger proportion of the O-SNP loci had sequence similarities to regions of genes involved in immune response. This result might reflect latitudinal variation in parasite infectivity (Poulin and Morand 2000) and increased infectivity of parasites to sympatric hosts rather than allopatric hosts of the same species (Mourand *et al.* 1996). Some caution in interpreting these data, however, is advisable, in part because the O-SNP loci sequences were small in size, and in part because the majority of SNPs recovered using a ddRAD approach are not within protein-coding-genes (Baxter *et al.* 2011)

Occurrence of philopatry in association with a non-random pattern of geographic variation in small genomic regions was reported recently (Stiedens *et al.* 2013) in a study of variation in MHC alleles among philopatric loggerhead turtles in the Cape Verde Archipelago. Both mtDNA haplotypes and MHC alleles were genetically structured among nesting islands, but only nuclear-encoded microsatellites followed a geographic pattern, in this case one of isolation by distance indicative of restricted male dispersal. In our study, only females appeared structured geographically. This and tagging data (Driggers *et al.* 2014) where >95% of inter-annual bonnethead returns to the same estuary were female, indicate that bonnethead males are not philopatric, and moreover, that maintenance of localized adaptive alleles in the species may occur through female matrilines. Thus, selection and sex-specific philopatry can interact to sort adaptive nuclear alleles across geographic space.

Association of spatially discrete matrilines and localized genomic regions under selection suggest that female genotype and philopatry to gestational areas may increase offspring fitness as a maternal effect (Mousseau and Fox 1998; Badyaev and Uller 2009). This is consistent with a review of parental effects in species with sex-asymmetric dispersal and a model which showed that selective pressure to develop locally adaptive parental effects is high when dispersal is sex-biased (Revardel *et al.* 2010). Unfortunately, studies of parental effects in sharks are limited (Hussey *et al.* 2010) despite a female reproductive biology (long gestation, live birth) in several species that suggests occurrence of important maternal effects.

Sex-specific philopatry reduces overall gene flow and consequently may redistribute genetic diversity among rather than within subpopulations or demes. In bonnethead sharks, homogeneity of N-SNP loci across geographic localities within the Gulf demonstrates that genetic diversity was equally partitioned within and among demes, indicating that extensive male dispersal was enough to overcome drift-processes. In contrast, strong differentiation at a small subset of nuclear genes among samples collected at gestational areas indicates that localized selection was sufficiently strong to outweigh the homogenizing force of migration. Thus, while female bonnethead philopatry may promote maintenance of adaptive alleles in specific localities, gene flow mediated by males could serve an important function for long-term population persistence by moving potentially adaptive variation among environments (Garant *et al.* 2007; Bowen & Roman 2005) which may vary on larger temporal scales.

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Data Accessibility: GENBANK accession numbers for mtDNA sequences may be found in Table S2 (online supplementary information). Demultiplexed, raw sequencing reads: Short Read Archive (Bioproject accession #PRJNA286089). The final SNP dataset, in VCF format, the neutral and outlier haplotype datasets, in GENEPOP format, and a script to reproduce bioinformatic filtering: Dryad doi:XXXXXX.

Authors' Contributions: DSP, JBP, and JRG had responsibility for data collection and analysis, and primary responsibility for writing of the manuscript. All other authors have reviewed and contributed to the current version of the manuscript. CMH participated in data collection and analysis and JG and DC obtained samples.

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Table 1. Below diagonal: pairwise F_{ST} values for putatively neutral SNP loci (N-SNP) and for outlier SNP loci putatively under selection (O-SNP), and pairwise Φ_{ST} values for mtDNA haplotypes (mtDNA), between samples of bonnetheads obtained off North Carolina (NC), Florida Bay (FB), Tampa Bay (TB), and Panama City (PC). Above diagonal: probability (*P*) values; those significant after correction for multiple comparisons are italicized and bolded.

	N-SNP					**O-SNP**					**mtDNA**			
	NC	**FB**	**TB**	**PC**		**NC**	**FB**	**TB**	**PC**		**NC**	**FB**	**TB**	**PC**
NC	-	***<0.001***	***<0.001***	***<0.001***	**NC**	-	***<0.001***	***<0.001***	***<0.001***	**NC**	-	***<0.001***	***0.001***	***0.014***
FB	***0.019***	-	0.317	0.038	**FB**	***0.543***	-	0.382	***<0.001***	**FB**	***0.2335***	-	0.158	***0.011***
TB	***0.021***	0.000	-	0.344	**TB**	***0.462***	0.000	-	***<0.001***	**TB**	***0.1605***	0.0138	-	0.406
PC	***0.021***	0.001	0.000	-	**PC**	***0.180***	***0.244***	***0.177***	-	**PC**	***0.0637***	***0.0545***	0.000	-

Figure 1. Sampling of bonnethead sharks obtained off North Carolina (NC, blue), Florida Bay (FB, red), Tampa Bay (TB, orange) and Panama City (PC, yellow); with number of individuals sampled at each locality indicated, results of discriminant analysis of principle components for (A) putatively neutral N-SNP loci, (B) outlier O-SNP loci putatively under selection, with prior group membership defined by sample locality, and (C) outlier O-SNP loci putatively under selection, with prior group membership based on *k*-means clustering. D: Representative allele frequencies of three O-SNP loci (left to right, E66074, E109425, E106435) that contributed ~24% to the distribution of individuals along the X axis. Colours represent sample locations for all figures.