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ORIGINAL RESEARCH

Evidence of historical isolation and genetic structuring among broadnose sevengill sharks (*Notorynchus cepedianus*) from the world's major oceanic regions

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Abstract Cosmopolitan marine pelagic species display variable patterns of population connectivity among the world's major oceans. While this information is crucial for informing management, information is lacking for many ecologically important species, including apex predators. In this study we examine patterns of genetic structure in the broadnose sevengill shark, *Notorynchus cepedianus* across its global distribution. We estimate patterns of connectivity among broadnose sevengill shark populations from three major oceanic regions (South Atlantic, Oceania and Eastern Pacific) by contrasting mitochondrial and nuclear DNA haplotype frequencies. We also produced time calibrated Bayesian Inference phylogenetic reconstructions to analyses global phylogeographic patterns and estimate divergence times among distinctive shark lineages. Our results demonstrate significant genetic differentiation among oceanic regions (Φ_{ST} = 0.9789, $P < 0.0001$)

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and a lack of genetic structuring within regions ($\Phi_{ST} = -0.007$; $P = 0.479$). Time calibrated Bayesian Inference phylogenetic reconstructions indicate that the observed patterns of genetic structure among oceanic regions are historical, with regional populations estimated to have diverged from a common ancestor during the early to mid-Pleistocene. Our results indicate significant genetic structuring and a lack of gene flow among broadnose sevengill shark populations from the South Atlantic, Oceania and Eastern Pacific regions. Evidence of deep lineage divergences coinciding with the early to mid-Pleistocene suggests historical glacial cycling has contributed to the vicariant divergence of broadnose sevengill shark populations from different ocean basins. These finding will help inform global management of broadnose sevengill shark populations, and provides new insights into historical and contemporary evolutionary processes shaping populations of this ecologically important apex predator.

Keywords Global distribution · Phylogeography · Pleistocene · Population structure patterns · Sharks · Species management

Introduction

The dispersal of marine species and the connectivity among their populations is often influenced by a variety of biotic and abiotic factors, such as life history traits, habitat continuity and availability, ocean currents, and environmental gradients (Bowen et al. 2016; Costello et al. 2017; Kumar and Kumar 2018; Palumbi 1994; Sherman et al. 2008). Complex interactions between these factors shape not only species distributions, but also the spatial extent and strength of migration between habitats, and the overall metapopulation structure across species ranges (Domingues et al. 2017; Miller et al. 2013). Knowledge of these patterns can inform management efforts geared toward preserving patterns of endemism and evolutionary potential, which is pertinent in light of continuing and rapid environmental change (Harrison and Hastings 1996; Kenchington et al. 2003).

Genetic markers are used widely to gain direct estimates of population genetic structure, information on demographic and phylogeographic histories, and genetic factors underpinning species fitness and environmental resilience (Avise 2000; Avise et al. 2016; Larson et al. 2017; Palsbøll et al. 2006; Städele and Vigilant 2016; Thompson et al. 2016). While genetic studies have played pivotal roles in issues such as marine wildlife conservation, fisheries management

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and biosecurity, genetic data remains limited for many marine species (McClenachan et al. 2012). One group of marine species in need of improved genetic information are the elasmobranchs, with only approximately 10% having been investigated in terms of population genetics (Domingues et al. 2018; Dulvy et al. 2014; McClenachan et al. 2012). Sharks are some of the most widely distributed and ecologically important marine organisms occupying the world's oceans, many of which are in a state of decline and in need of improved conservation management (Ferretti et al. 2010; Heithaus et al. 2008; Heupel et al. 2014; Queiroz et al. 2019).

To date, genetic studies on widely distributed shark species have demonstrated patterns of genetic differentiation between major ocean basins; between the Atlantic and Indo-Pacific oceans (scalloped hammerhead (*Sphyrna lewini*), (Duncan et al. 2006); blacktip shark (*Carcharhinus limbatus*), (Keeney and Heist 2006); silky shark (*Carcharhinus falciformis*), (Clarke et al. 2015); tiger shark (*Galeocerdo cuvier*), (Bernard et al. 2016)), between the northern and southern hemispheres (great white shark (*Carcharodon carcharias*), (O'Leary et al. 2015)), and eastern and western Atlantic ocean (oceanic whitetip shark (*Carcharhinus longimanus*), (Camargo et al. 2016)). Yet the degree of genetic structuring and population connectivity is variable across taxonomic groups and has been primarily attributed to adult vagility and habitat use (Giles et al. 2016; Schultz et al. 2008). For example, demersal sharks and species with a preference for coastal habitats show greater genetic structuring and reduced population connectivity (Corrigan et al. 2016; Dudgeon et al. 2009; Geraghty et al. 2014; Karl et al. 2011; Keeney and Heist 2006; Schultz et al. 2008), compared to pelagic species which tend to have shallow genetic structuring and greater connectivity across oceanic regions (Castro et al. 2007; Heist et al. 1996; Schmidt et al. 2009; Veríssimo et al. 2017). Life history and dispersal traits, and habitat affinities seem to play a key role in determining patterns of population and phylogeographic structure in sharks across the world's oceans (Kriwet et al. 2009).

The six- and sevengill sharks (family Hexanchidae, order Hexanchiformes) are a highly distinctive group of elasmobranchs, recognized as one of the most basal lineages of modern sharks, with fossils dating back to the Lower Jurassic ($\sim$ 190 mya) (Maisey 2012; Rus Hoelzel et al. 2006). The genus *Notorynchus* (Ayres, 1855) is considered to be monotypic and consists of the broadnose sevengill shark, *Notorynchus cepedianus* (Péron 1807), common to temperate water inshore bays and estuaries circumglobally (Anderson et al. 1998; Barnett et al. 2012). Tagging studies indicate seasonal, sex specific, and long distance ($\sim$ 1800 km) dispersal patterns within their oceanic regions (Barnett et al. 2011, 2012; Ebert 1996; Stehfest et al. 2014; Williams et al. 2012), however, evidence of transoceanic movement has not been reported. To date only a single population genetic study with a limited geographic focus has been conducted on this species (Larson et al. 2015), reporting significant genetic structuring between two coastal bays separated by approximately 1000 km on the west coast of the United States. Further research is needed to test the degree of population genetic structure across the species distribution to identify isolated populations requiring independent management consideration, and to gain insights into the evolutionary history of this ancient shark lineage.

In this study, we use DNA sequence data from the mitochondrial control region (mtCR) and the nuclear ITS2 locus to explore patterns of population genetic structure in the broadnose sevengill shark sampled across three oceanic regions, Eastern Pacific Ocean (EPO), South Atlantic Ocean (SAO) and Oceania. We also use time calibrated phylogenetic reconstructions to investigate the phylogeographic history of the species, and gain insights into historical factors that

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have shaped contemporary patterns of genetic diversity. Findings from this study enhance our understanding of the population structure and evolutionary history of broadnose sevengill sharks globally, and are expected to assist the management of this ecologically important but under studied apex-predator.

Materials and methods

Tissue collection

Tissue biopsies from 249 individual sharks were provided from six countries in three oceanic basins; Eastern Pacific Ocean (EPO), (United States, n = 33 and Peru, n = 22); South Atlantic Ocean (SAO), (Argentina, n = 47 and South Africa, n = 42); and Oceania, (Australia, n = 65, and New Zealand, n = 40) (Fig. 1). Tissue samples were obtained as fin clips or muscle punches and preserved in 95% ethanol. Biological and collection information such as sex, fork length (FL) or total length (TL), and location were recorded, where possible, for each sample (see Supplementary Information, ESM 1).

DNA extraction and sequencing

Genomic DNA was isolated from tissue samples using QIAGEN DNeasy Tissue kits following the manufacturer's instructions (QIAGEN, Inc., Valencia, CA). An 812 base pair (bp) fragment spanning the entire mitochondrial control region (mtCR) and flanking DNA sequences from the tRNA-thr and 12S rRNA genes were amplified by polymerase chain reaction (PCR) for all tissue specimens using primers CRF6 (C. Bruels, unpublished, 5′ AAGCGTCGACCTTGT AAGTC 3′) and DasR2 (V. Richards, unpublished, 5′ GCTGAAACTTGCATGTGTAA 3′) respectively, for all samples. In addition a 620 bp fragment of the nuclear intergenic spacer subunit 2 region (ITS2) was also amplified using previously published primers (Shivji et al. 2002) for a subset of the samples (United States: n = 8, Peru: n = 9, Argentina: n = 10, South Africa: n = 10, Australia: n = 15, and New Zealand: n = 3). PCR reactions were performed following the protocol outlined in Clarke et al. 2015. Amplified products were purified using the QIAquick PCR Purification Kit (QIAGEN, Inc.) following the manufacturer's instructions prior to direct cycle sequencing of both DNA strands using the respective PCR primers on an Applied Biosystems 3130 genetic analyser (Applied Biosystems, Inc., Foster City,

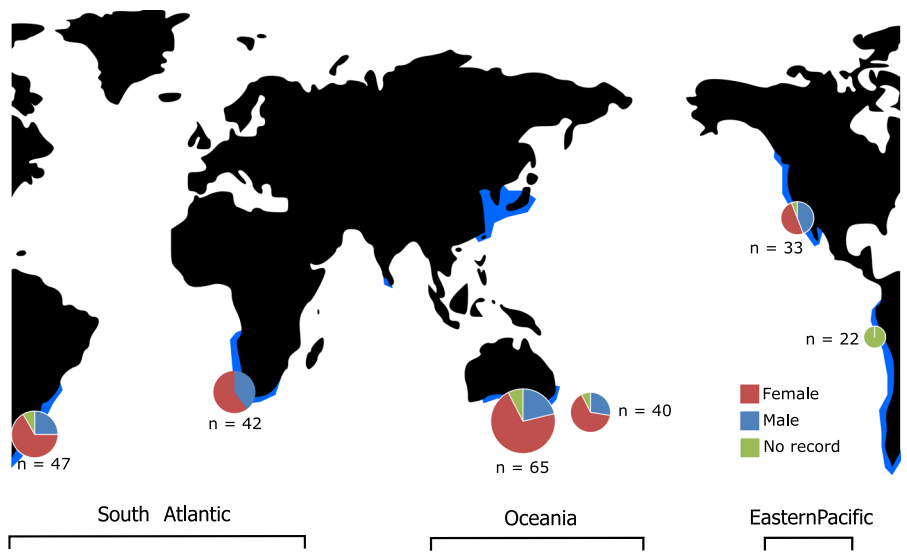

Fig. 1 Map showing distribution (blue) and collection locations (pie charts) for broadnose sevengill sharks (*N. cepedianus*). Collection locations include South Africa, Argentina, New Zealand, Australia, United States and Peru with n values representing the number of mtCR samples per location. The pie chart size represents the proportion of mtCR sequences samples per location and depicts the sex ratios

CA). DNA sequences were aligned and edited using the software Geneious version 4.04 (Drummond et al. 2008) prior to analysis.

Population genetic analysis

The total number of mtCR and ITS2 haplotypes for each sample location was identified using DnaSP v5 (Labrado and Rozas 2009). Diversity indexes such as haplotypic (h) and nucleotide (π) diversity, as well as the number of polymorphic sites (S) were calculated for each region, again using DnaSP v5. To visualize the relationships among haplotypes a median-joining (MJ) haplotype network was constructed (Bandelt et al. 1999) using the program PopART (http://popart.otago.ac.nz). In addition a statistical parsimony network analysis was conducted using TCS (version 1.21:3) software (Clement et al. 2000) using mtDNA sequences for all samples only as ITS2 data showed little divergence. This program joins haplotypes into a network after calculating the 95% probability of a parsimonious connection between haplotypes.

An analysis of molecular variance (AMOVA) was performed on the mtDNA dataset to assess genetic population structure in Arlequin 3.5. The HKY model (Hasegawa et al. 1985) was selected as the best fit model of evolution based on Bayesian Information Criteria (BIC) (Schwarz 1978) implemented in JMODELTEST v.0.1.1 (Posada 2008). However, as HKY model is not included in Arlequin 3.5, the Tamura and Nei model (Tamura and Nei 1993) was used which had a similar BIC score. Global estimates of Φ_{ST} and population pairwise measures of Φ_{ST} were calculated using Arlequin 3.5 with significance determined using 1000 permutations. Demographic history was explored using neutrality tests based on Fu's FS (Fu 1997) and R_2 test (Ramos-Onsins and Rozas 2002) implemented in DnaSP v5. Both Fu's FS and R_2 test were calculated as a deviation from neutrality possibly attributed to selection and/or population size changes, with significance level tested at $P < 0.05$ using 1000 permutations. The sequential Bonferroni procedure (Rice 1989) was used to adjust significance levels when performing multiple simultaneous comparisons. Negative (significant) Fu's FS values and a low R_2 test can be interpreted as a signal of purifying selection or demographic expansion. Evidence of recent population expansions or contractions were further explored via mismatch distribution analysis using Arlequin 3.5.

Exploring phylogeographic patterns and divergence times

Phylogenetic relationships among mitochondrial haplotypes were explored using Bayesian Inference (BI) methods using the HKY model implemented in BEAST 2.3.0 (Bouckaert et al. 2014). Operators were auto-optimized, and five independent Markov Chain Monte Carlo (MCMC) runs were performed using a constant population size coalescent as the tree prior, each running for 5×10^6 generations, sampling every 10,000 states. Log files were examined with TRACER v.1.5 (Drummond and Rambaut 2007) to ensure that runs were sampling from the same posterior distribution, to determine appropriate burn-in, and to ensure that effective sample sizes (ESSs) of parameters of interest were greater than 1000. Tree files of independent runs were then combined with LOGCOMBINER v.2.1.3 (Drummond et al. 2012), discarding the first 20% of trees as burn-in. The maximum clade credibility (MCC) tree was recovered from a sample of 10,000 posterior trees, and branch support was annotated, using TREEANNOTATOR v.2.1.3 (Drummond et al. 2012). All analyses started with a random starting tree and seed with no root specified. Sequence data from *Hexanchus* (Genbank accessions: AB560490 and AB560491) and *Heptranchias* (Genbank accession AB560488) species were used as an outgroup to estimate the root of the mitochondrial gene tree. However, ITS data was not available from an appropriate outgroup taxon, and the ITS BI reconstruction is presented as an unrooted tree topology.

To test the timing of divergence between broadnose sevengill shark mitochondrial lineages, the gene tree was time calibrated with divergence times of nodes being inferred from 95% highest posterior density (HPD) intervals. The time dimension of the analyses was calibrated by fixing the mean substitution rate to 0.4% per million years (clock rate 0.004), calculated as the mean rate per lineage based on previous estimates for MtCR from a variety of shark species (Chevolot et al. 2006; Duncan et al. 2006; Ferrari et al. 2018; Karl et al. 2012; Keeney et al. 2003; Schultz et al. 2008). Substitution rates were set in BEAUti 1.7.3 (Drummond et al. 2012), and TRACER was then used to obtain parameter estimates for time to the most recent common ancestor (tMRCAs) for nodes within the gene tree.

Results

Patterns of genetic diversity and genetic differentiation

DNA sequence data from an 812 bp of the mtCR and flanking regions were successfully obtained from all 249 broadnose sevengill sharks (Fig. 1). Across regions a total of seven mitochondrial haplotypes (referred to as Hap_1–7) were observed, differing by up to 15 polymorphic sites (Tables 1, 2). Haplotype diversity (h) and nucleotide diversity (π) was 0 in the EPO, 0.1496 and 0.0002 respectively in SAO, and 0.236 and 0.0003 respectively in Oceania (Tables 1, 3, 4).

Our median joining haplotype network (Fig. 2) indicated two highly divergent clades (EPO and SAO / Oceania). Individual sharks sampled from the United States and Peru in the EPO shared a single haplotype (Hap_1) that was separated from all the other haplotypes by 11 mutational steps. The remaining haplotypes (Hap_2 – 7) segregated geographically between the SAO (Argentina and South Africa) and Oceania (Australia and New Zealand), however haplotypes between these two regions were only separated by a single base mutation suggesting more recent shared ancestry. The statistical parsimony network analysis indicated similar stratifications of regions, with a decisive separation between the EPO and other regions (Fig. 3). The haplotype frequency for each group is shown in Table 2.

AMOVA indicates strong and significant genetic differentiation between oceanic regions (global Φ_{ST} = 0.9789, $P < 0.0001$), with pairwise Φ_{ST} indicating high levels of significant differentiation between all oceanic regions (EPO, SAO, and Oceania) (Φ_{ST} = 0.8989 to 0.99228; $P < 0.0001$). In contrast AMOVA indicated no significant differences among collection locations within regions ($\Phi_{ST} = -0.007$; $P = 0.479 \pm 0.01$).

Fu's FS calculations for each oceanic region were negative but not significant ($P < 0.001$) for the SAO

Table 1 Population genetics statistics for regions and collection locations

Region	Collection location	Genetic diversity indicies					Neutrality tests		Mismatch analysis	
		N	*H*	*S*	*h*	π	R_2	Fu's *FS*	Harpending's raggedness index	SSD
Eastern Pacific ocean (EPO)	United States	33	1	0	0	0	0	0	0	0
	Peru	22	1	0						
	Pooled EPO	55								
South Atlantic ocean (SAO)	Argentina	47	2, 3, 4	2	0.150 ± 0.05	0.0002 ± 0.000296	0.09527	− 1.609	0.51591	0.00057
	South Africa	42	2, 3, 4	2						
	Pooled SAO	89								
Oceania	Australia	65	5, 6, 7	2	0.236 ± 0.05	0.0003 ± 0.00038	0.08916	− 0.727	0.33526	0.00427
	New Zealand	40	5, 6	1						
	Pooled Oceania	105								
Total samples		249	1–7	15	0.709 ± 0.012	0.00591 ± 0.00038	0.07877	10.145	–	–

Number of samples (N), haplotype number (H), number of polymorphic sites (S), haplotype diversity (h), nucleotide diversity (π), Harpending's raggedness Index, SSD and test of neutrality (R_2 and Fu's Fs) for the broadnose sevengill shark (*N. cepedianus*) mitochondrial DNA control region

Table 2 Frequency of haplotype in the collection locations, haplotype name (Hap_1–7), number of samples (N), for the broadnose sevengill shark (*N. cepedianus*) mitochondrial DNA control region

Haplotype *(N)*	Collection location					
	United States (33)	Peru (22)	Argentina (47)	South Africa (42)	Australia (65)	New Zealand (40)
Hap_1 *(55)*	1.000	1.000	–	–	–	–
Hap_2 *(82)*	–	–	0.915	0.929	–	–
Hap_3 *(3)*	–	–	0.0426	0.0238	–	–
Hap_4 *(4)*	–	–	0.0426	0.0476	–	–
Hap_5 *(91)*	–	–	–	–	0.831	0.925
Hap_6 *(13)*	–	–	–	–	0.154	0.075
Hap_7 *(1)*	–	–	–	–	0.0154	–

Table 3 Pairwise Φ_{ST} values (below diagonal) and *P*-values (above diagonal, + represents statistical significance with *P*-value < 0.05) for broadnose sevengill shark (*N. cepedianus*) across three regions

	Eastern Pacific	South Atlantic	Oceania
Eastern Pacific	0	+	+
South Atlantic	**0.992**	0	+
Oceania	**0.987**	**0.899**	0

Significant results denoted in bold

and Oceania regions (Table 1), but could not be calculated for the EPO region due to a lack of haplotype diversity. Similarly, R_2 test values were low overall, with the exception of EPO, which could not be calculated due to a lack of diversity (Table 1). These findings indicate that populations within the respective oceanic regions may have undergone recent population expansions. The notion of expanding population size is further supported by mismatch analyses which indicates a stochastic and multimodal pattern, with the Sum of Squared Deviation (SSD) and Harpending's Raggedness Index (HRI) not differing significantly ($P > 0.05$) from that which is expected under a population expansion model for the SAO (p(Sim > = Obs) = 0.395 and 0.647, respectively), and Oceania (p(Sim > = Obs) = 0.348 and 0.630, respectively).

In contrast to the MtCR datasets, the ITS2 sequences were highly conserved. The sole difference was a variation in the number of repeats present in a dinucleotide repeat motif (bp 276 to 297 of the 776 bp alignment), separating the dataset into three haplotypes. All individuals from the Californian region had 6–8 repeats, while 10 repeats were present in the Peruvian sequence and the SAO/Oceania regions. As a consequence of this lack of locus specific variation,

Table 4 Pairwise Φ_{ST} values (below diagonal) and *P*-values (above diagonal, + represents statistical significance with *P*-value < 0.05) for broadnose sevengill shark (*N. cepedianus*) within the three regions

	Eastern Pacific		South Atlantic		Oceania	
	California	Peru	Argentina	South Africa	Australia	New Zealand
California	0	–	+	+	+	+
Peru	0	0	+	+	+	+
Argentina	**0.99199**	**0.99069**	0	–	+	+
South Africa	**0.99355**	**0.99242**	− 0.02051	0	+	+
Australia	**0.98362**	**0.98153**	**0.87664**	**0.87953**	0	–
New Zealand	**0.99352**	**0.99234**	**0.92274**	**0.92918**	0.00696	0

Significant results denoted in bold

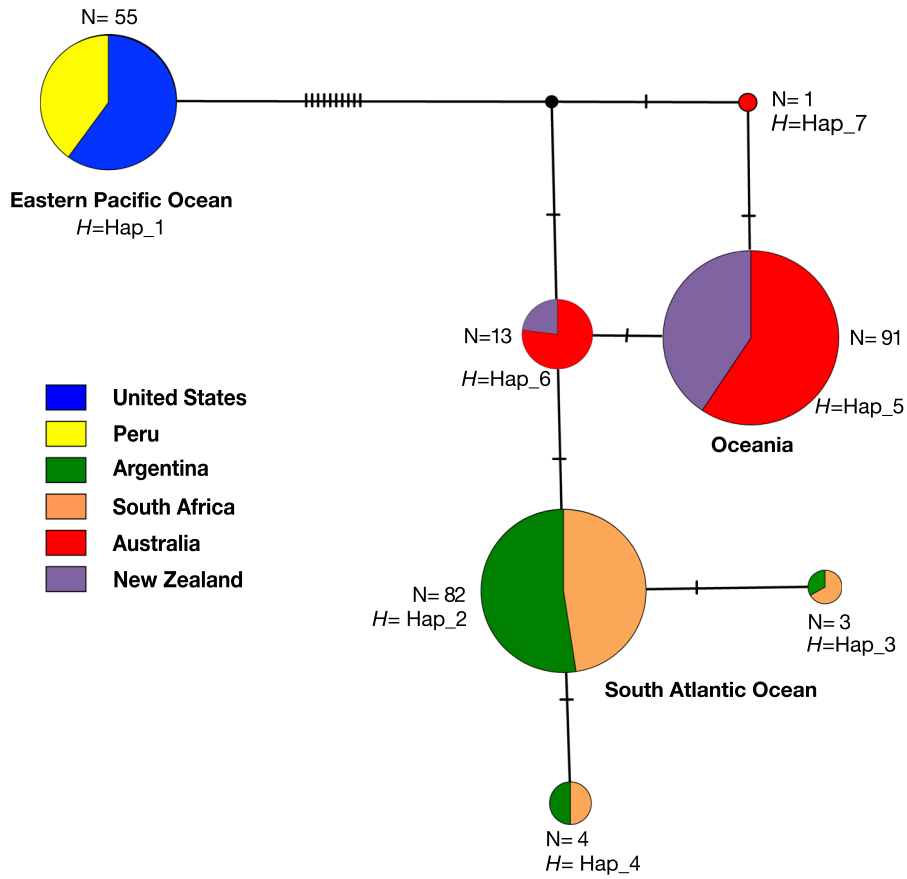

Fig. 2 Median-joining network of mtCR haplotypes for broadnose sevengill sharks. Circles represent individual haplotypes with circle size proportional to haplotype frequency, connection lines indicate one base pair difference and breaks indicate inferred unsampled haplotypes. Collection locations are as follows: United States (Blue), Peru (Yellow), Argentina (Green), South Africa (Orange), Australia (Red), and New Zealand South (Purple). Numbers of samples per circle size (N), haplotype designation (*H*)

the ITS2 data was not used for population genetic or phylogenetic analyses.

Phylogenetics and divergence

Bayesian Inference phylogenetic reconstruction indicated a pattern of paraphyly and strong support for three distinctive monophyletic clades representing the EPO, SAO, and Oceania regions (Posterior Probability (PP $>$ 0.9). A fourth moderately supported (PP = 0.8) clade consisting of haplotypes from the Oceania region was also revealed, indicating potential paraphyly and genetic structuring of the Oceania population. A sister relationship between the SAO and Oceania clades gained strong statistical support (PP = 1.0), while the relationships among the three clades were not fully resolved. A basal position of the EPO clade was also highly supported (PP = 1.0). Time calibrated branch divergences indicate that all four clades diverged from a common ancestor approximately 1.95 Mya (95% HPDs = 1.22 – 2.812), with the SAO and Oceania clades diverging from a more recent common ancestor approximately 0.69 Mya (95% HPDs = 0.39 – 1.08) before the present day. The timing of these events coincides with the early to mid-Pleistocene (Fig. 4).

Discussion

Our study revealed high levels of genetic structuring and a lack of connectivity between broadnose sevengill shark populations from three of the world's major ocean basins; the SAO, EPO and Oceania regions. Time calibrated phylogenetic reconstructions suggest the observed patterns of genetic structure are historical, estimating the EPO population to have been isolated from the SAO and Oceania populations for approximately 1.95 Mya years. In contrast, divergence between SAO and Oceania regions appears to be more recent, diverging from shared common ancestor approximately 0.69 Mya years ago. The sharing of

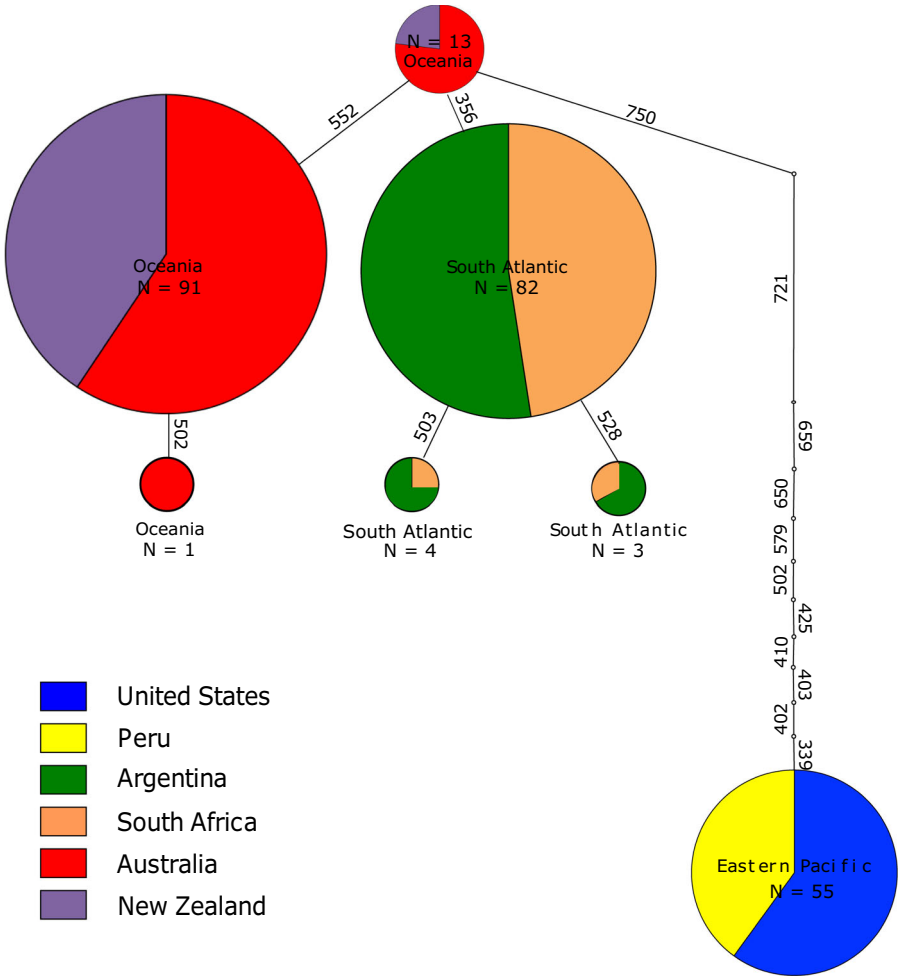

Fig. 3 Broadnose sevengill shark 95% parsimony network. Circles, ovals and square represent haplotypes of the respective regions. Size of the circles and ovals correspond to haplotype frequency and nodes indicate inferred un-sampled haplotypes. The number of samples is represented by "N"

haplotypes among locations within ocean basins suggests a lack of genetic structure and potential connectivity in broadnose sevengill sharks over spatial scales of several hundreds to thousands of kilometers. However, more sensitive marker systems (e.g. single nucleotide polymorphisms or microsatellites) are needed to provide sufficient resolution of contemporary patterns of gene flow within regions.

Our findings indicate deep lineage diversification between broadnose sevengill sharks from different ocean basins, consistent with patterns of genetic structuring reported for several cosmopolitan sharks species, e.g. the tiger shark (*Galeocerdo cuvier*) (Holmes et al. 2017), the tope shark (*Galeorhinus galeus*) (Bester-van der Merwe et al. 2017), and the scalloped hammerhead shark (*Sphyrna lewini*) (Quattro et al. 2006). In particular, several coastal associated shark species, like broadnose sevengill sharks, exhibit similar population structuring across the globe, with distinct grouping between oceanic gradients. Copper sharks (*Carcharhinus brachyurus*), showed phylogeographic delineations between Oceania (Australia and New Zealand) and the south Atlantic/Indian ocean (Namibia and South Africa) and the south Pacific (Peru) (Benavides et al. 2011). Clear genetic divergences were observed for sandbar sharks (*Carcharhinus plumbeus*), with delineations between the Atlantic and Pacific ocean basins (Portnoy et al. 2010). These coastal associated sharks tend to show some form of female fidelity to coastal nursery areas, which may

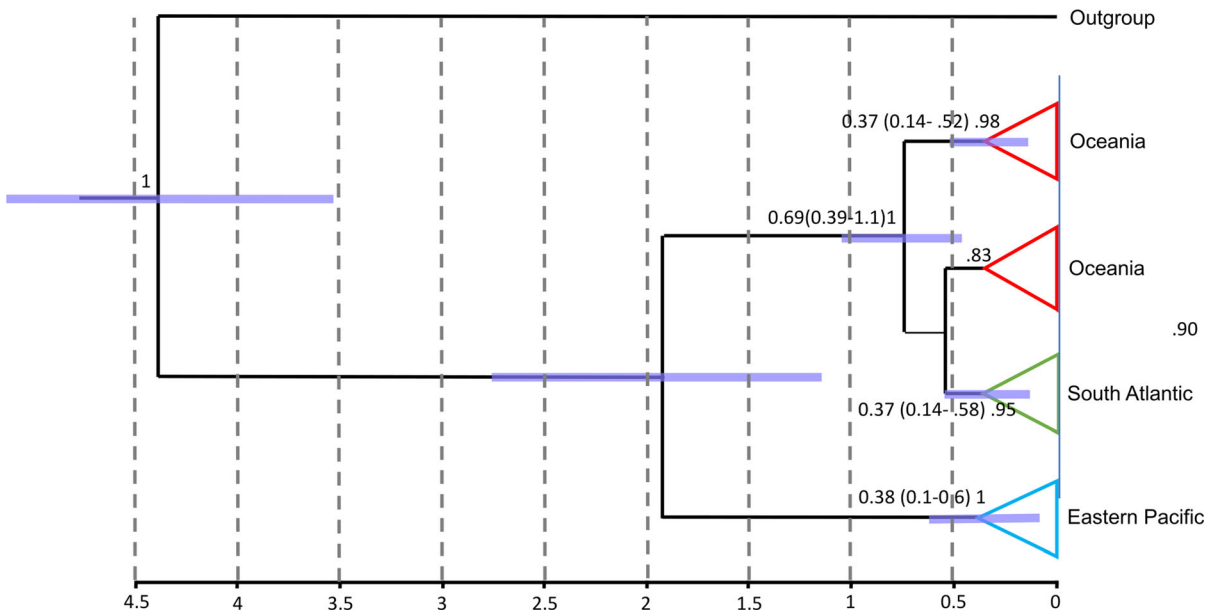

Fig. 4 Time calibrated Bayesin Inference phylogenetic reconstruction of relationships among broadnose sevengill shark mitochondrial control region haplotypes. Nodal support values provided represent Bayesian posterior probabilities (> 0.8), and estimated tMRCAs with 95% highest posterior density intervals (illustrated by purple bars at branch nodes) are provided, with the scale provided in millions of years. The "Outgroup" consists of sister taxa *Heptranchias_perlo* (sharpness sevengill), *Hexanchus_nakamurai* (bigeyed sixgill), *Hexanchus_griseus* (Bluntnose sixgill)

account for the lack of dispersal among regions, promoting delineations between oceanic basins. However, males of these species show limited fidelity to these areas and tend to travel over larger coastal ranges, thus male-mediated gene flow may persist over wider geographical ranges and may provide some connectivity between regions (Benavides et al. 2011; Daly-Engel et al. 2012; Portnoy et al. 2010). Broadnose sevengill sharks have been shown to exhibit fidelity behavior toward feeding grounds in coastal bays, (Barnett et al. 2012, 2010; Ebert 1996; Williams et al. 2012), and only a few studies have discussed anecdotal evidence of nursery/pupping areas within coastal bays (Ebert 1989; Lucifora et al. 2005). Many other marine taxa such as teleosts, cetaceans and marine turtles also display similar phylogeographic patterns (Bermingham et al. 1997; Bowen et al. 1998, 2016; Kraft et al. 2020).

Patterns of genetic structure in marine species from different ocean basins have been attributed to a range of geological and climatic factors, such as of the closure of the Tethys Sea ∼ 13Mya, the uplift Isthmus of Panama ∼ 3.5 Mya, glacial cycles, and the Indo-Pacific Barrier (IPB) (Bermingham et al. 1997; Bowen et al. 2016; Kumar and Kumar 2018). Our time calibrated phylogenies suggest broadnose sevengill shark lineages from the different ocean basins diverged between 0.69 and 1.95 Mya which coincides with the early to mid-Pleistocene epoch (Avise 2000). Silky sharks, *Carcharhinus falciformis* from the Atlantic and Indo-Pacific oceans are estimated to have diverged from a common ancestor during the Pleistocene epoch (Domingues et al. 2017). Glacial cycles throughout the Pleistocene are known to have affected temperate marine habitats primarily through changes in sea level, influencing patterns of habitat continuity and disrupting coastal habitats (Bowen et al. 2016; Cheng et al. 2019) which are key feeding and breeding areas for broadnose sevengill sharks (Barnett et al. 2012). Therefore, it is possible that glacial cycling throughout the Pleistocene epoch has contributed to contemporary patterns of phylogeographic structuring observed in broadnose sevengill and other shark species.

Large expanses of water (e.g. entire oceanic basis) are prominent factors affecting species vagility and biogeographic structuring in marine ecosystems (Bowen et al. 2016; Lessios et al. 1998). Species

abilities to overcome such barriers depend largely on dispersal traits, physiological limitations, and availability of resources such as prey (Bowen et al. 2016). Many marine species, including some sharks, appear incapable of crossing large expanses of temperate water, leading to strong biogeographic structuring of marine communities and genetic differentiation of species populations both between and within oceanic basins (Bowen et al. 2016; Luiz et al. 2012). Temperate oceanic regions tend to have fewer "stepping stone areas" compared to tropical regions, which can restrict an organism's ability to cross large expanses of water. Atolls and islands, including the Hawaiian archipelago, act as a bridge between the east and west tropical Pacific, allowing some species to maintain population connectivity (Duncan et al. 2006; Lara-Lizardi et al. 2020). For example, the scalloped hammerhead sharks, *Sphyrna lewini*, displays gene flow among populations from the east, central and western tropical Pacific, while populations from the Pacific and Atlantic oceans are highly differentiated (Daly-Engel et al. 2012). Consequently, it is possible that contemporary genetic structuring across ocean basins in many temperate marine species is driven purely by geographical distance and the sheer expanse of water that separates temperate habitats.

In contrast to the stark genetic differentiation between broadnose sevengill sharks among ocean basins, we provide evidence of little genetic structuring within oceanic basins, indicating gene flow and connectivity over 100 s to 1000 s of kilometers. Our findings differ from those of (Larson et al. 2015) who demonstrated genetic structuring among populations separated by approximately 1000 km on the west coast of the United States. However, Larson et al. (2015) used microsatellite markers, suggesting genetic differentiation (with some genetic mixing) between populations frequenting certain bays along the west coast of the United States. Larson et al. (2015) also suggested possible separate breeding grounds being used by the two distinct populations. More fine scale analyses within each oceanic region using more sensitive genetic markers, such as SNPs or microsatellites, is needed in the future to fully understand the genetic structure of this species across its distribution. Interestingly, our results suggest historical connectivity across the equator between northern and southern American populations in the EPO, between sites from California and Peru separated by $>$ 2000 km. This is unexpected considering the thermal preferences of broadnose sevengill sharks. As broadnose sevengill sharks have been shown to travel large distances, up to 1800 km (Barnett et al. 2012; Stehfest et al. 2014; Williams et al. 2012) and occur to depths of 360–550 m (Anderson et al. 1998), it is possible that deep cold-water environments may act as a conduit for gene flow between northern and southern EPO populations. Again more sensitive genetic markers along with tagging studies will help to confirm if contemporary gene flow is occurring across the equator.

Conclusion

Across the broadnose sevengill shark's global distribution there are many data deficiencies and knowledge gaps in ecology, biology, as well as fisheries information, such as stock structure, catch data and population status/trajectories. Given that broadnose sevengill sharks are a common bycatch species in multiple fisheries around the world, and targeted in some locations, there is a need for updated information in almost all areas. Indeed, in most countries where they are exploited (bycatch or targeted), there are no species-specific management strategies, yet their life-history and coastal associations suggest that this species may be vulnerable to fishing pressure and coastal habitat disturbances in some locations (Barnett et al. 2012; da Silva et al. 2015; Smith et al. 1999). Results from our study provide a resource for managing populations and stocks of broadnose sevengill sharks across the globe. The findings of this study suggest management of broadnose sevengill sharks needs to give consideration to the isolated and genetically diverse nature of the different lineages from the world's major ocean basins. At this broad level, it would require coordinated approaches by neighboring countries within oceanic regions to manage shared/straddling stocks. Additionally, country-based management strategies are also required and should be based on current available information on broadnose sevengill shark movements (Barnett et al. 2012). However, while our findings suggest little structuring within ocean basins those of Larson et al. (2015) indicate that further studies investigating genetic diversity and stock structure within countries are required.

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Author contributions AB and MSS conceived the project. CCB conducted lab work while ACJS-R and ADM analysed the data. The first draft of the manuscript was written by ACJS-R with assistance from AB, ADM, CDHS, MSS and CCB. All authors commented on previous versions of the manuscript. SS-R assisted with data analysis and figure presentation. Samples were provided by CS, DAE, CGW, CT, JCM, JME, AI, AJJ, MB, JA-S and CD. All authors read and approved the final manuscript.

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Compliance with ethical standards

Conflicts of interest The authors declare, that they have no conflict of interest.

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