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Genomic population structure of great hammerhead sharks (*Sphyrna mokarran*) across the Indo-Pacific

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ABSTRACT

Context. Currently, little information exists describing the population structure of great hammerhead sharks (*Sphyrna mokarran*) in Australian waters. **Aims.** This study used single nucleotide polymorphisms to investigate fine-scale population structure in *S. mokarran* across the Indo-Pacific. **Methods.** DNA was extracted from 235 individuals across six Australian locations and a Red Sea outgroup. Population parameters were calculated and visualised to test structuring across locations. **Key results.** No fine-scale population structuring was observed for *S. mokarran* across the Indo-Pacific. However, population structuring occurred for all Australian locations when compared to the Red Sea outgroup. **Conclusions.** Findings suggest a single stock is most likely for *S. mokarran* found in Australian waters. Results provide key information for understanding the broad range movements of *S. mokarran* and help to define the scale of management required to preserve genetic diversity in this species. The structuring between Australia and the Red Sea indicates limited gene flow and movement. **Implications.** Results indicate that large-scale movements of *S. mokarran* could be occurring to facilitate genetic mixing. Future research focusing on individual tagging to corroborate movements would be highly beneficial to determine how far (and often) individuals are dispersing, and to note where cross-jurisdictional management, including from neighbouring regions in the Indo-West Pacific–Oceania region, are most critical.

Keywords: Australia, gene flow, management scale, panmixia, population genomics, Red Sea, shark fisheries, single nucleotide polymorphisms.

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Introduction

More than one-third of the world's shark and ray species are threatened with extinction, mainly due to overfishing (Dulvy *et al.* 2021; Pacoureau *et al.* 2021). With a global listing as Critically Endangered, the great hammerhead shark (*Sphyrna mokarran*) is among those species of most concern (Rigby *et al.* 2019). Throughout its distribution across inshore and oceanic tropical and temperate waters, *S. mokarran* is targeted and bycaught in various commercial, recreational and artisanal fisheries (Compagno 1984; Stevens and Lyle 1989; Compagno *et al.* 2005). Global declines of *S. mokarran* (and hammerhead sharks more broadly) have been widespread and swift, approaching 99% in some regions, including off South Africa and in the Mediterranean Sea (Gallagher *et al.* 2014; Miller *et al.* 2014; Roff *et al.* 2018; Raoult *et al.* 2019). Shark finning and meat or cartilage trade are major drivers of global population declines, with the largest hammerhead species (including *S. mokarran*, smooth hammerheads, *S. zygaena* and scalloped hammerheads, *S. lewini*) often sought for their large fins and supposed medicinal benefits (Clarke *et al.* 2006; Cardeñosa *et al.* 2022).

Across its Australian range, *S. mokarran* is caught in several commercial and recreational fisheries, and often managed collectively within the Sphyrnidae family. Approximately 90% of catches originate from five regulated fishery groups, with the remaining 10% as bycatch (Department of Agriculture Water and the Environment 2021). However, overall

the catches of *S. mokarran* within Australian waters is considered to be low, and key fishery groups are managed by precautionary jurisdictional measures that aim to limit catches and prevent overfishing. Australia's 2014 non-detriment finding (NDF) reported that if the relevant regional fisheries remained within annual quota limits, the harvest of *S. mokarran* would not be detrimental to populations (Department of Agriculture, Water and the Environment 2014). Nevertheless, if hammerheads leave Australian waters, they can be exposed to other commercial and artisanal fisheries, often with fewer regulations or low monitoring and enforcement capacity (Clarke *et al.* 2006; Dudley and Simpfendorfer 2006).

There have been various attempts to document the migration (and connectivity) of *S. mokarran*, with most studies employing tagging methods. In the western North Atlantic Ocean off Florida and The Bahamas, Guttridge *et al.* (2017) reported the first evidence of philopatric behaviour for *S. mokarran*, with observations for both sexes of large-scale migrations, seasonal residency and site fidelity. In addition, Boube *et al.* (2023) reported sexual segregation, seasonal residency or long-term site fidelity for *S. mokarran* off French Polynesia, noting aggregations and the possibility of natal grounds nearby. Similarly, Queiroz *et al.* (2016) found that when *S. mokarran* were not making long distance movements, they remained in localised preferential habitats. Other recent tracking off northern Australia by Heupel *et al.* (2020) found localised movements but was limited to small specimens (200–240-cm total length). Although it is less precise due to rely on chemical tracers, Raoult *et al.* (2020) noted that adult *S. mokarran* captured in New South Wales (NSW) waters are likely residents further north in Queensland (Qld) and possibly as far north as Papua New Guinea. It is these challenges in obtaining local tracking data across an appropriate size and sex range that requires alternative assessment techniques to decipher stock structures and connectivity, among which genetic applications are uniquely relevant.

Identifying genetic stock structure is an integral component of fisheries management, so that the spatial scale required for the assessment and management of stocks is based on the appropriate management 'units'; that is, the number of stocks within a given management jurisdiction (Begg *et al.* 1999). Over recent decades, genetic analysis has evolved into an invaluable tool for fisheries management (Benestan 2020), and nowadays complimentary to fish tagging, parasite and isotope methods. Although tagging efforts reflect individual movement and are often stochastic, genetic signatures are relevant at the population level, allowing inferences of historical connectivity or isolation (Kraft *et al.* 2020). Few studies have investigated genetic population structure to determine the scale of genetic structuring for *S. mokarran*. Previous work by Testerman *et al.* (2008) using mitochondrial DNA (mtDNA) found genetic differences between North Atlantic and Indo-Pacific conspecifics, with little spatial exchange of haplotypes (i.e. across ocean basins). This study further revealed significant population structuring with both microsatellites (msats) and mtDNA between samples collected in waters of the western North Atlantic, Australia, and the northern Indian Ocean (Testerman 2014). Similarly, using mtDNA, Naylor *et al.* (2012) reported two distinct populations of *S. mokarran*: one from the North Atlantic, and the second from Australia and Borneo.

Evaluation of within-basin population structure for the Atlantic and Indian oceans by Gonzalez *et al.* (2017), Testerman *et al.* (2008) and Testerman (2014) failed to note any genetic structuring. Currently, only one technical report by Heupel *et al.* (2020) has undertaken single nucleotide polymorphism (SNP) analysis for northern Australian specimens, revealing no evidence of structuring and a relatively homogenous panmictic population extending to Papua New Guinea. It should be noted, however, that this study had only five Australian samples. The report of Heupel *et al.* (2020) recommends further studies using SNPs due to their power to resolve fine-scale population structure and applications in similar species (Green *et al.* 2019; Green *et al.* 2022). Additionally, previous studies emphasise that an appropriate sample size is needed for sufficient testing, so that appropriate conclusions can be made. Considering the above limitation, we aim to evaluate: (1) the population structure or connectivity using SNPs across a number of sampled locations throughout the Australian range of *S. mokarran*; and (2) test for any population structuring between individuals from Australia and the Red Sea (a spatially separated outgroup).

Methodology

Sampling design and collection

Tissue samples of *S. mokarran* (n = 235 individuals) were sourced from various collections across Australia (Fig. 1, Supplementary Table S1). Red Sea samples were opportunistically obtained through collaboration with Dr Julia Spaet, in order to include an outgroup. For specific collection processes see associated papers (Red Sea, Spaet and Berumen 2015; NSW, Broadhurst and Cullis 2020). Samples were either small fin clips or muscle pieces from captured specimens, stored in 99% ethanol that were provided along with data on individuals total length (TL), sex and sampling location. Samples within this study contain individuals of both sexes at varying life stages (see size distribution in Fig. S1). In addition to the Red Sea outgroup, sampling locations were arranged into Australia's predefined current commercial fishing management zonings of Western Australia (WA), Northern Territory (NT), Queensland (Qld), Qld Gulf of Carpentaria (Gulf), north-east Qld, south-east Qld and NSW (Fig. 1 and 2).

This work was authorised under the University of the Sunshine Coast's risk assessment number 210095 and ethics approval number ANA21180 from the University's Animal

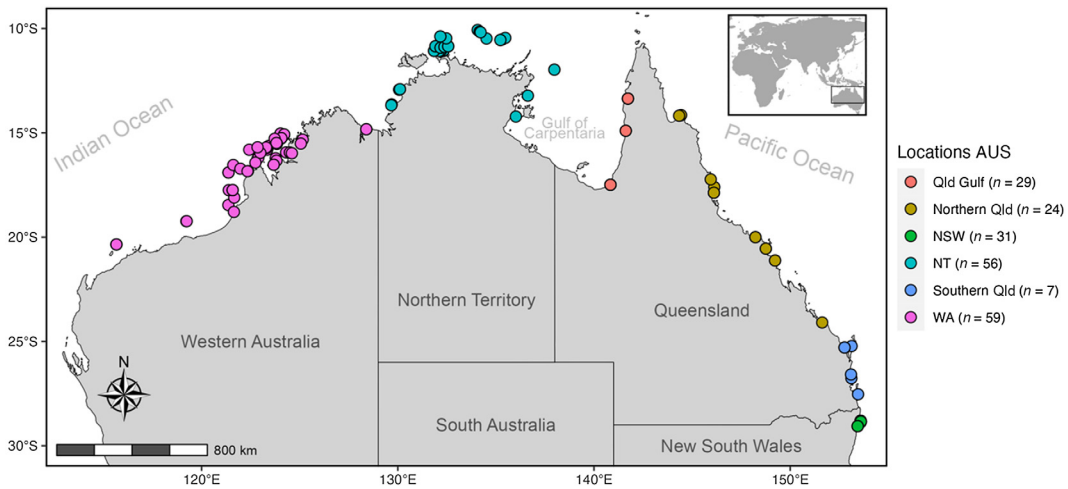

Fig. 1. Sampling locations for great hammerhead (*Sphyrna mokarran*) tissue samples across northern Australia.

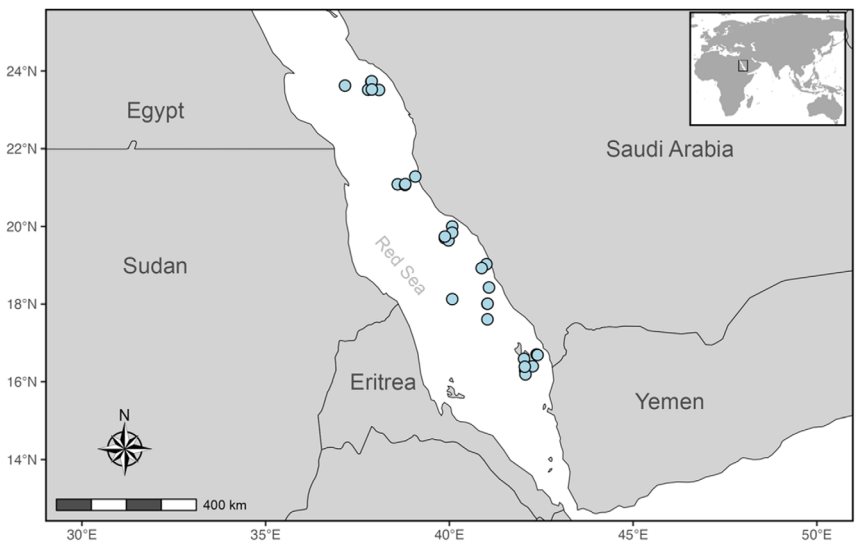

Fig. 2. Sampling locations for great hammerhead (*Sphyrna mokarran*) tissue samples in the Red Sea.

Ethics Committee. Samples used in this analysis collected from within the North-west Marine Parks Network were obtained under permit numbers AU-COM2020-485, AU-COM2020-488, AU-COM2020-494, issued by the Director of National Parks, Australia. Additional samples sourced elsewhere were collected under the corresponding researchers permits and ethics.

DNA extraction, sequencing and genotyping

DNA was extracted using QIAGEN DNeasy blood and tissue kits following their outlined standard protocol (Qiagen, Valencia, CA, USA). The DNA concentrations were tested using a Nanodrop 2000 spectrophotometer machine (ThermoFisher Scientific, Waltham, MA, USA), where samples were diluted or further concentrated to obtain a concentration of between 50 and 100 ng μL^{-1}. The DNA isolates within this range were transferred to a 96-well plate and sent to Diversity Arrays Technology for sequencing (DArT Pty Ltd, Canberra, ACT, Australia). Sequencing involved using the DArTseq (DArT Pty Ltd) protocol to uncover SNPs (variations in the DNA sequence) within the species (Kilian *et al.* 2012; International Society of Genetic Genealogy 2020). The DArTseq was used to significantly reduce the complexity using four restriction enzymes. Sequences were processed using DArT Pty Ltd analytical pipelines producing high-quality SNP markers and metadata. In-depth protocols for such procedures can be reviewed in Georges *et al.* (2018).

Single nucleotide polymorphism filtering

Of the 235 tissues sampled across the seven locations, the DArTseqTM pipeline yielded 83,579 SNP markers for 233 *S. mokarran*. Quantitative analyses were undertaken using the statistical package R (ver. 4.2.1, R Foundation for Statistical

Computing, Vienna, Austria, see https://www.R-project.org/). The SNP data and metadata produced by DArT Pty Ltd was converted into a genlight object for further filtering using the package *dartR* (ver. 2.7.2, see https://cran.r-project.org/package=dartR; Gruber *et al.* 2018). Filtering for repeatability, loci call-rate and minor allele frequencies removed 9409, 2783 and 19,508 loci respectively (Table S2). With all populations pooled, 403 loci were removed for Hardy–Weinberg disequilibrium (Table S2). Using the *gl.outflank* function nested within *dartR*, 69 loci were identified as outliers and removed. South-east and north-east Qld were combined to form a single 'Qld' grouping due to a small regional sample size, similar genetic distance and non-significant F_{ST} and *P*-values. Following quality control procedures, 3846 putatively neutral SNPs were retained for 211 individuals, whereas 69 outlier SNPs were identified (Table S2). These individuals comprised 29 from the Gulf, 29 from east Qld, 23 from NSW, 52 from the NT, 22 from the Red Sea and 56 from WA.

An additional dataset was constructed from the filtered dataset above to support a fine-scale population structure analysis among Australian locations using high pairwise fixation indexes (F_{ST}) loci. The approach was undertaken in which outlier loci were firstly identified and removed as they are assumed to be putitively under selection that can lead to biased population differentiation estimates (Luikart *et al.* 2003; Maduna *et al.* 2024). To identify potential SNPs under selection, both pcadapt and OUTFLANK methods were used. OUTFLANK identified zero outliers whereas pcadapt observed 249, which were subsequently removed, creating a neutral dataset. To characterise fine-scale population genetic structure, the remaining loci in the neutral were ordered to high to low F_{ST}, and a subset panel was constructed by selecting the 300 neutral diagnostic SNPs with the highest locus-specific F_{ST}.

Population structure analyses

Genetic differentiation between populations was quantified through F_{ST} following Weir and Cockerham's methods, with Bonferroni adjusted conservative alpha significance and 99% confidence intervals (CIs) through bootstrapping 2000 times (Weir and Cockerham 1984; Pembleton *et al.* 2013). The *dartR* package was used to estimate the number of alleles (*n*), inbreeding coefficients (F_{IS}), observed (H_O) and expected (H_E) heterozygosity (Gruber *et al.* 2018). The function *snmf()*, embedded in the R package *LEA* (ver. 3.8.0, see https://bioconductor.org/packages/release/bioc/html/LEA.html; Frichot and Francois 2015), estimated individual admixture coefficients from the genotypic matrix, assuming *K* ancestral populations (Frichot and Francois 2015). The package is similar to the Bayesian clustering program STRUCTURE, but it provides a cross-entropy criterion from least-squares estimates testing 10 repetitions of scenarios $K = 1$–7 for the number of ancestral populations (*K*) that best explain a dataset (Frichot and Francois 2015).

Population differentiation was visualised through three different approaches. To identify locations, individuals were plotted with their original location (e.g. south-east and north-east Qld) and not with groupings assigned for analyses. First, a principal components analysis (PCoA) was performed to visualise population patterns and genetic similarity between individuals and locations using *dartR* (Gruber *et al.* 2018). A discriminate analysis of principal components (DAPC) without priors was conducted through the package *adegenet* (ver. 2.1.7, see https://cran.r-project.org/package=adegenet) to establish optimal clusters based on the Bayesian Information Criterion (BIC) (Jombart 2008). A final admixture plot was produced to visualise a geographic map of ancestry coefficients for different *K* scenarios using the *tess3r* package (ver. 1.1.0, see https://rdrr.io/github/cayek/TESS3_encho_sen/man/tess3r.html; Caye *et al.* 2016). Additional methods of genetic distance and isolation by distance (IBD) tests were conducted to determine if there was a correlation between gene flow and geographical distance (Gruber *et al.* 2018).

Results

No significant deviations in heterozygosity were found at any location ($P > 0.05$, $H_E = 0.129$–0.140; $H_O = 0.126$–0.142, Table 1). The Red Sea outgroup had greater heterozygosity than all Australian samples ($H_E = 0.140$; $H_O = 0.142$, Table 1). Gene flow between Australian locations was high, indicated by the inbreeding coefficient (F_{IS}) observations being similar ($F_{IS} = 0.037$–0.052, Table 1). The F_{IS} value for the Red Sea outgroup (0.010) was closer to HWE and varied to the Australian locations (Table 1). A Euclidean distance matrix revealed non-significant population differentiation between the Australian locations and the Red Sea outgroup (Table S3).

The estimates of genetic pairwise differentiation (F_{ST}) from samples collected between all locations were small (mean $F_{ST} = 0.006$). Significant gene differences were observed

Table 1. Population parameters for great hammerhead (*Sphyrna mokarran*).

Location	*n*	H_O	H_E	F_{IS}
Gulf	29	0.132	0.135	0.040
Qld	29	0.134	0.138	0.052
NSW	23	0.126	0.129	0.041
NT	52	0.130	0.134	0.037
Red Sea	22	0.142	0.140	0.010
WA	56	0.133	0.137	0.037

n, number of individuals; H_O, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient; Gulf, Queensland Gulf of Carpentaria; Qld, Queensland; NSW, New South Wales; NT, Northern Territory; RS, Red Sea; WA, Western Australia.

Table 2. Pairwise genetic differentiation (F_{ST}) values collected for great hammerhead (*Sphyrna mokarran*) samples below the diagonal and *P*-values above the diagonal.

	NSW	WA	Qld	NT	Gulf	RS
NSW		0.2525	0.7345	0.4960	0.0340	**0.0000**
WA	0.0004		0.0325	0.0135	0.0500	**0.0000**
Qld	−0.0004	0.0008		0.025	**0.001**	**0.0000**
NT	−0.000003	0.0007	0.0009		**0.001**	**0.0000**
Gulf	0.0014	0.0008	0.0020	0.0015		**0.0000**
RS	0.0163	0.0148	0.0144	0.0157	0.0175	

Significant *P*-values ($P < 0.01$) shown in bold. Gulf, Queensland Gulf of Carpentaria; Qld, Queensland; NSW, New South Wales; NT, Northern Territory; RS, Red Sea; WA, Western Australia.

between samples from all Australian locations and the Red Sea outgroup ($P < 0.01$, Table 2), with the highest differences ($F_{ST} = 0.0175$) being observed between the Red Sea and Qld Gulf samples (Fig. 3 and S5). A lack of significant genetic differentiation was detected between Australian regions using the neutral dataset, with the exception of comparisons between the Qld Gulf and each of the NT, and east Qld, which showed low but significant differentiation ($P < 0.01$, Table 2). However, significant genetic differentiation was detected for all Australian locations when testing with the 300 diagnostic SNPs ($P > 0.01$, Table 3).

Based on the cross-entropy criterion, the optimal number of ancestral populations (K) was two (Fig. S2). Population structuring was visible from the DAPC plot with all

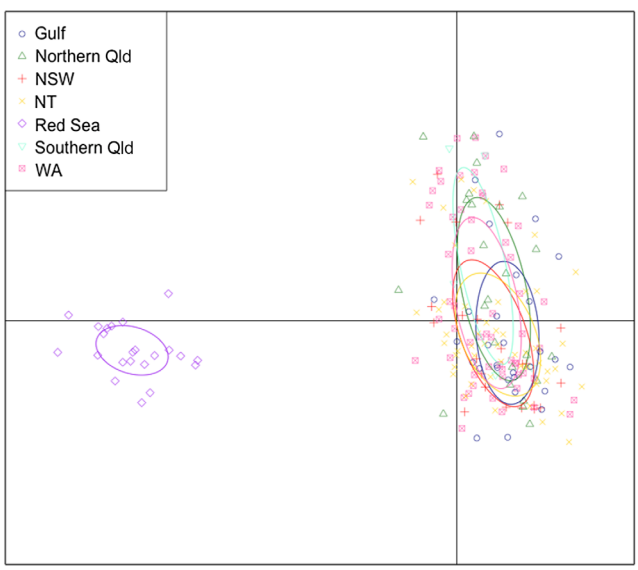

Fig. 3. DAPC using neutral SNP genotypes, visualising Indo-Pacific structuring of great hammerhead (*Sphyrna mokarran*) along the first two axes. Locations ($n = 7$) were used as priors for clustering calculated with Bayesian Information Criterion.

Table 3. Pairwise genetic differentiation (F_{ST}) values collected for great hammerhead (*Sphyrna mokarran*) samples below the diagonal and *P*-values above the diagonal.

	East Coast	WA	NT	Gulf
East Coast		**0**	**0**	**0**
WA	0.0228		**0**	**0**
NT	0.0194	0.0203		**0**
Gulf	0.0322	0.0298	0.0294	

Significant *P*-values ($P < 0.01$) shown in bold. Gulf, Queensland Gulf of Carpentaria; East Coast, Queensland and New South Wales combined; NT, Northern Territory; WA, Western Australia.

Australian locations clustered together, whereas the Red Sea outgroup sat independently (Fig. 3). This outcome was further supported by a PCoA output which showed seperation of the Red Sea outgroup and Australian locations into two separate clusters (Fig. S5). When undertaking a hirachical investigation with the Red Sea outgroup removed, no population structuring was detected in the PCoA plot among Australian locations (Fig. 4*a*). Additional investigation using the diagnostic dataset of 300 of the most informative SNPs showed marginal overlap of Australian locations (Fig. 4*b*). With all locations connected through a central cluster, location-based variance was observed between WA, the Gulf of Carpentaria, NT and the East Coast, with overlap visualised between the latter two.

Population and location admixture plots showed the admixture ancestry coefficients for scenarios $K = 2$ and $K = 3$ (Fig. S3 and S4). The Red Sea outgroup showed strong differentiation and population structuring for all admixture scenarios when compared against Australian locations (Fig. S3 and S4).

Both the PCoA and DAPC were visualised for datasets against sex and maturity or immaturity. This was done for the purpose of identifying any signatures driven by various life events (i.e. pupping, residency, philopatry) from biases in size, sex or both. Nevertheless, no structuring was evident (Fig. S6 and S7).

Discussion

Here, we present the first comprehensive study assessing the fine-scale genetic population structure of selected *S. mokarran* populations in the Indo-Pacific, complimenting earlier efforts for conspecifics between the Atlantic and Indian oceans (Testerman *et al.* 2008; Testerman 2014; Gonzalez *et al.* 2017). Further, by analysing samples from various regional locations throughout *S. mokarran*'s Australian range, we have highlighted high genetic connectivity and facilitated comparisons against previous work. These results contribute to the limited genetic knowledge employing more recent

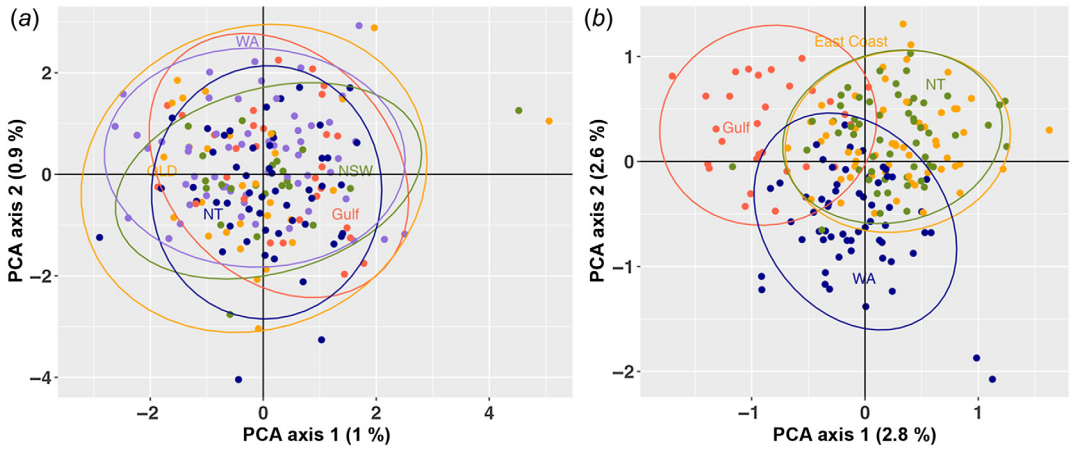

Fig. 4. (*a*) Scatterplot of great hammerhead (*Sphyrna mokarran*) structuring for Australian only locations using PCoA modelling. The first two principal coordinate axes are shown with the amount of variance explained by each axis in parentheses. (*b*) PCoA modelling of great hammerhead (*S. mokarran*) structuring for Australian only locations using the most informative 300 diagnostic SNPs.

next-generation sequencing techniques with the use of SNPs for greater detection of structure. The results can be discussed with respect to key life-history parameters and ultimately used to support the regional and international management of *S. mokarran* populations.

Australian structuring

Both the DAPC and PCoA results indicated a lack of genetic structure among *S. mokarran* from all sampled Australian locations. Further, the F_{ST} values (a measure of population differentiation due to genetic structure, Frankham *et al.* 2002) for all Australian locations (mean = 0.006) were low, indicating little genetic differentiation and high gene flow between the sampled locations, although there were some significant pairwise differences. Additionally, the diagnostic SNPs indicate low, but significant, differentiation between all Australian locations (F_{ST} mean = 0.026). This result is supported by the PCoA plot indicating marginal overlap, but not complete panmixia. Ovenden (2013) notes that elasmobranchs are likely to experience phenomena termed 'crinkled connectivity', whereby 'connectivity is large enough to make the populations genetically similar, but not large enough to make them demographically linked'. This crinkled connectivity is similar to what has been observed in this study. It infers that a number of migrants are successfully exchanging genetic material across locations to comprise of a single stock, yet the proportion of migrants is not significant enough to infer complete demographic connectedness and panmixa. Waples (1998) noted that some departures from complete panmixia are expected when comparing geographic samples. It is suggested that the complete dispersal throughout northern Australia is unlikely and instead *S. mokarran* populations (relevant to location) are remaining connected through this crinkled connectivity method. Admixture plots also show the mixing of ancestry across all locations and so there does not appear to be fine-scale genetic population structuring for *S. mokarran* off Australia.

Our results suggest that broad-scale population connectivity (i.e. across the Australian coastlines) is being maintained, despite movement of tagged *S. mokarran* not having been recorded at this spatial scale to date (3030 km largest return trip reported in Florida, Guttridge *et al.* 2017). This potential for population admixture aligns with conclusions from Raoult *et al.* (2020) that suggest *S. mokarran* forage across large parts of the eastern Australian coastline. Further, *S. mokarran* reportedly use shallow coastal environments to target prey (Chapman and Gruber 2002; Doan and Kajiura 2020) and extend across both pelagic and oceanic shelf waters (Queiroz *et al.* 2016; Raoult *et al.* 2019). Guttridge *et al.* (2022) also studied the thermal and vertical range of the species, noting they primarily use shallow depths (75% at <30 m) and occupy warm waters (89% between 23 and 28°C). This range reflects the possibility for significant connectivity due to the <100 m of water connecting the Gulf of Carpentaria to the Timor Sea, Arafura Sea, Torres Strait and Gulf of Papua (National Oceanic and Atmospheric Administration 2022) as well as the continuous shallow continental shelf along Qld's Great Barrier Reef (Dudgeon *et al.* 2009). This preferential habitat, to a degree, may facilitate the connectivity seen in this study around the Australian coastline. Although it is unknown what level of influence the direct long-distance movement of individuals has on the genetic homogeneity found herein, we theorise that it may be substantial and likely remains understudied. Specifically, additional tracking of *S. mokarran* to further understand contemporary movements, along with consideration to the spatiotemporal segregations among *S. mokarran* based on life-stage and sex

(Harry *et al.* 2011; Chin *et al.* 2017), will be critical for understanding the species demography.

Indo-Pacific structuring

Inclusion of the Red Sea outgroup provided an important genetic comparison, revealing structuring against all Australian locations, and therefore implying no regular movement and interbreeding of individuals across the Indian Ocean. This conclusion is reinforced by within-basin structuring in the Indian Ocean (i.e. comparing the Red Sea individuals to only those in WA). The distance between the Red Sea and Australia, combined with the deep waters of the Timor Trench (2–3 km) and Wallace's Line in Indonesia, are both regarded as potential geographical barriers between WA, northern Australia and Indonesia, preventing movement and gene flow among various species, which might explain the clear separated population structures between these regions (Ovenden *et al.* 2009; Chin *et al.* 2017). Similar restriction of genetic mixing is seen between the Atlantic and Indian oceans and often explained by the Benguela Barrier, a cold-water current flowing around the southern tip of Africa that limits transfer. This phenomenon likely reflects the genetic differences found in Atlantic and Indo-Pacific *S. mokarran* (Briggs 1995; Dudgeon *et al.* 2012; Testerman 2014). Despite such environmental barriers limiting mixing, it is possible some Red Sea and Australian specimens have nevertheless exchanged genetic material off Indonesia, or instead, the slight shared genetic signals seen in the admixture plots are a result of shared histories.

The challenge of this study was that the variance is driven only by what has been sampled. Although testing of specific groupings (i.e. immature or mature and male or female) failed to reveal any trends, the sample sizes of these specific groups was limited. Additional sampling of neonates warrants testing in future studies. Also, coupling SNPs with mtDNA would be an interesting and beneficial way to investigate if both males and females are dispersing (e.g. occurring in the blue shark, *Prionace glauca*; Veríssimo *et al.* 2017), if movement is solely male (e.g. *S. lewini*; Marie *et al.* 2019) or female mediated, or driven by natal philopatry like in other species (e.g. lemon sharks, *Negaprion brevirostris;* Feldheim *et al.* 2001). The observed trends seen in the Australian *S. mokarran* here could reflect broad movements of a select number of individuals resulting in the spreading of alleles across their population range. Initially, mtDNA literature noted that large movements of *S. lewini* were male-mediated with females exhibiting philopatry (Daly-Engel *et al.* 2012). However, using SNPs, large-scale movement has been shown in both sexes (Green *et al.* 2022). Philopatric behaviours exhibited by *S. mokarran* over large spatial scales have previously been discussed in the literature, yet it is unclear if these instances relate to natal philopatry, mating opportunities or functional residency behaviours like feeding events (Chapman *et al.* 2015; Guttridge *et al.* 2017; Boube *et al.* 2023).

Management implications and conclusions

Defining genetic connectivity and structuring of species like *S. mokarran* provides valuable information which can help to define populations used in stock assessment and development of biologically relevant management units (Green *et al.* 2022). Our study describes a genetically mixed stock of *S. mokarran* within Australian waters. Until more is known about the contemporary movements of *S. mokarran* (using tagging or telemetry), we suggest that the species is managed as a single Australian genetic population. To support this, continued research into the reproductive biology, natal or nursery areas and tagged movement for the species will be valuable.

To more effectively manage the *S. mokarran* population, fisheries' harvest strategies should clearly encompass cross-jurisdictional biological assessments to determine if efforts are affording enough protection against harvest levels. Jurisdictional approaches to managing this species may have limited success in isolation if this species regularly crosses Australian jurisdictional boundaries, as implied by this study. Recent management changes within Qld have led to *S. mokarran* becoming a no-take species within Qld waters. These changes are likely to lead to a complete loss of data from the fishery, and will undoubtably make cross jurisdictional assessment and management for this species throughout northern Australia a more challenging process.

It is also evident that, although stringent restrictions and limits apply under Australian law for *S. mokarran*, this only extends to the limit of the Australian Exclusive Economic Zone (EEZ). International waters and neighbouring countries are less regulated, with high illegal, unreported and unregulated (IUU) fishing activity (Vince *et al.* 2021). Fishing efforts in these areas are likely to have ongoing impacts on this migratory species, which may affect Australian populations. Through further efforts of population assessments and modelling, especially in adjacent regions to the Australian EEZ, understanding of the species can be better managed with consideration of cross-jurisdictional movement and exchange.

Supplementary material

Supplementary material is available online.

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Data availability. The datasets generated during or analysed during the current study are available from the corresponding author on reasonable request.

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