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Global genetic connectivity and phylogeography of a highly migratory, apex predator shark, the shortfin mako

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Global genetic connectivity and phylogeography of a highly migratory, apex predator shark, the shortfin mako

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Abstract

The shortfin mako shark, *Isurus oxyrinchus*, is a large, epipelagic, apex predator with a worldwide oceanic-coastal distribution in tropical and temperate oceans. Overfishing of this species for its meat and fins has created significant declines in population abundance, resulting in shortfin makos now classified by the International Union for Conservation of Nature (IUCN) as Globally Endangered. Given this shark's dire population status globally, knowledge of its genetic population status and history is needed to aid its international management and recovery. In this study, we evaluated the global population genetic structure and genetic diversity of the shortfin mako shark, using the mitochondrial DNA control region (mtCR) sequence as a genetic marker. We assessed 588 partial mtCR sequences from the Atlantic, Indian, and Pacific oceans. The null hypothesis of global panmixia was rejected based on F_{ST} and Φ_{ST} fixation indices, and the shortfin mako exhibited population structure within the Atlantic Ocean and among ocean basins. The collective mtCR sequences revealed 51 haplotypes with haplotypic and nucleotide diversities of 0.864 (±0.010) and 0.004 (±0.002), respectively. Demographic history revealed that the shortfin mako population in the ocean basins experienced a bottleneck event followed by rapid population growth. These findings suggest considering at least two matrilineal populations in the Atlantic, one in the Indian Ocean, and one in the Pacific, which should be managed independently to safeguard their evolutionary potential against current anthropogenic pressures on this species.

Keywords: population structure, elasmobranchs, fisheries management, marine conservation genetics.

Introduction

Population genetic studies enable assessment of whether a species is genetically panmictic across its entire distribution or structured into several metapopulations due to historical and/or ecological processes (Gaggiotti and Foll 2010; Angst et al. 2023). This topic is particularly interesting in the ocean realm, where despite the existence of relatively few physical barriers to dispersal compared to terrestrial environments, genetic panmixia in species is not always present (Bowen et al. 2016). Even highly migratory species, such as some large sharks and rays with their long-distance swimming abilities, often demonstrate population structure due to their occupation of diverse marine ecosystems and sex-biased dispersion associated with reproductive philopatry (Daly-Engel et al. 2012; Chapman et al. 2015; Eustache et al. 2023).

Oceanic sharks, which represent only about 6% of the world's total Chondrichthyes, are among the largest and most wide-ranging predators in the ocean. Despite their high migratory capacity, allowing them to traverse marine environments with contrasting oceanographic conditions, many oceanic sharks repeatedly aggregate in and use predictable habitat hotspots (Queiroz et al. 2016). These preferred habitats are often associated with strong sea surface temperature gradients relative to surrounding areas (Queiroz et al. 2016). Occupying environmentally heterogeneous habitats and repeatedly moving among them require frequent physiological adjustments, potentially exposing populations to strong natural selection (Palumbi et al. 2019).

Ecological methods such as capture–mark–recapture and telemetry have been fundamental for describing shark movements, habitat preferences, and distribution patterns (Edwards et al. 2022; Grusd et al. 2019). Although these methods effectively characterize individual shark movements, they provide limited insight into reproductive connectivity, temporal variation in effective population size, and the evolutionary

consequences of dispersal. Consequently, they cannot reliably identify population boundaries, reconstruct historical demographic changes, or evaluate the maintenance and erosion of genetic diversity under conditions of species exploitation or environmental change; these questions can be better addressed using molecular markers (Ovenden, 2013).

The shortfin mako shark (*Isurus oxyrinchus;* Lamnidae, Lamniformes) is a large, highly migratory species that inhabits tropical and subtropical oceanic and coastal waters worldwide, from the surface to depths of ~ 979 m and typically in waters above 16°C (Santos et al. 2021). Like many elasmobranchs, the shortfin mako is vulnerable to overfishing, primarily due to its life cycle characteristics typical of a K-strategist, including slow growth, late gonadal maturation, high longevity, and low fecundity (Hoenig and Gruber, 1990; Dulvy et al. 2014), and gestation period ranging from 15 to 18 months (Mollet et al. 2000). This species is caught mainly as bycatch by industrial pelagic longline fleets worldwide primarily targeting tunas and swordfish (Stevens, 2008). The main reason for fisheries retention of shortfin makos is the high value of their fins in Asian markets (Ferrette et al. 2019) and their meat. Due to the large volumes of shortfin mako catches, this species is classified as globally 'Endangered' on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Rigby et al. 2019), and has been included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Sellheim, 2020). Despite this shark's precarious conservation status, however, few studies have investigated its population genetic dynamics, including elucidating levels of genetic variability and identifying discrete populations across its global distribution (e.g., Corrigan et al. 2018; Gonzalez et al. 2023; Bernard et al. 2025).

Against this background, this study aimed to assess the global matrilineal population structure, genetic diversity, and demographic history of the shortfin mako using samples spanning much of its worldwide distribution. Specifically, we sought to (i) determine whether the species comprises genetically differentiated matrilineal populations across ocean basins; (ii) quantify genetic diversity within and among geographic regions; and (iii) investigate historical changes in effective population size and identify signatures of demographic expansion, contraction, or stability. By integrating broad geographic sampling with population genetic and demographic approaches, we provide a comprehensive assessment of the evolutionary and demographic history of the shortfin mako, with implications for stock delineation, fisheries management, and the conservation of its evolutionary potential and adaptive capacity.

Material and methods

2.1 Sampling locations

Muscle and/or fin tissues were sampled from shortfin mako sharks captured by Portuguese, American, and Brazilian pelagic longline fleets at various locations in the Atlantic and Indian Oceans between 2015 and 2017 (Figure 1). A total of 286 individuals were sampled for this study from sites in the Atlantic Ocean: Northwestern Atlantic (NWAt, n = 46), Gulf of Mexico (GM, n = 39), Cape Verde (CV, n = 12), Equatorial Atlantic (EqAt, n = 12), Southeastern Atlantic (SEAt, n = 9), Southwest Atlantic (SWAt, n = 32), Central Southern Atlantic (CSAt, n = 29), and South Africa - Atlantic Ocean side (SAAt, n = 15), as well as from the Southern Indian Ocean side (SAIO, n = 92). Furthermore, to supplement sampling in regions where we had limited coverage, partial control region mitochondrial DNA (mtCR) sequences were obtained from Corrigan et al. (2018), from the Atlantic Ocean: Northeastern Atlantic (NEAt, n = 30); Indian Ocean:

Oman (OM, n = 77), Southern Indian Ocean (SIO, n = 30), and Indo-Pacific (IP, n = 21); Pacific Ocean: Northwest Australia (NWAu, n = 9), Southern Australia (Sau, n = 22), Northeast Australia (NEAu, n = 74), and New Zealand (NZ, n = 39) (Genbank accession numbers MH759795 - MH760159; Corrigan et al. 2018) (Figure 1).

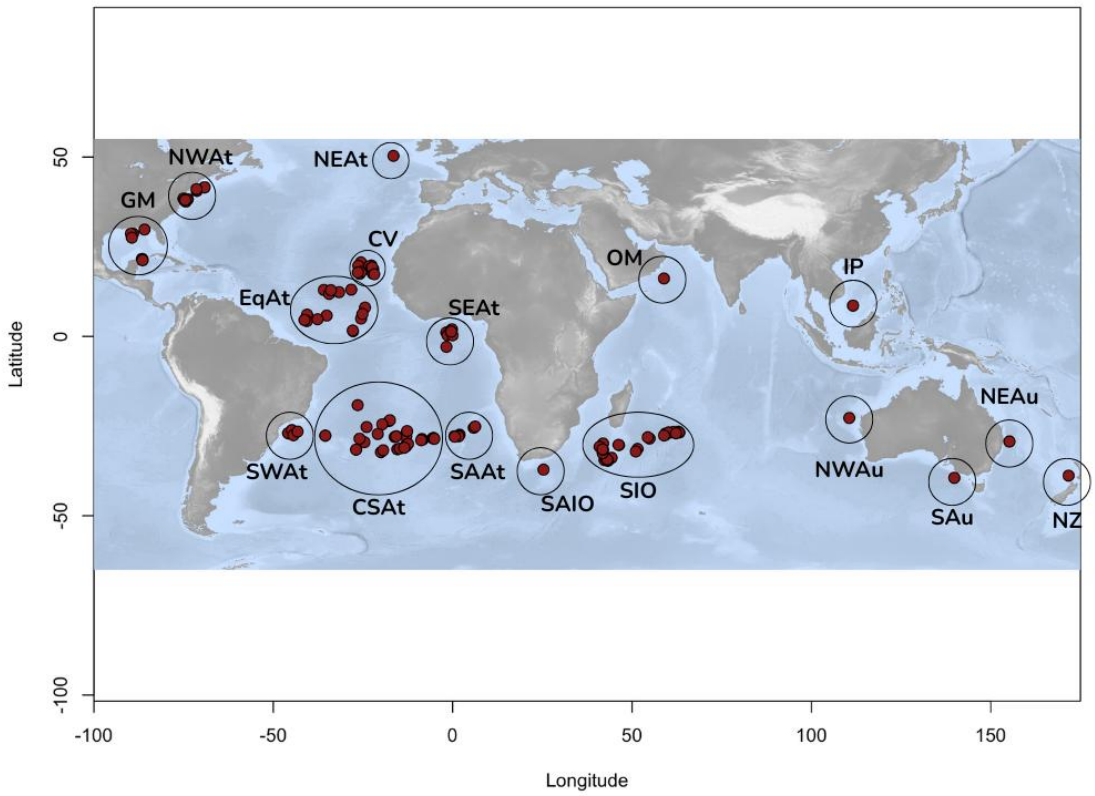


Figure 1. Sampling locations of shortfin mako shark (*Isurus oxyrinchus*) individuals, organized geographically from west to east: Northwestern Atlantic (NWAt, n = 46), Gulf of Mexico (GM, n = 39), Southwestern Atlantic (SWAt, n = 32), Southeastern Atlantic (SEAt, n = 9), South Africa-Atlantic Ocean side (SAAt, n = 15), Central Southern Atlantic (CSAt, n = 29), Equatorial Atlantic (EqAt, n = 12), Cape Verde (CV, n = 12), Northeastern Atlantic (NEAt, n = 30), South Africa-Indian Ocean (SAIO, n = 92), Southern Indian Ocean (SIO, n = 30), Oman (OM, n = 77), Northwestern Australia (NWAu, n = 9), Southern Australia (SAu, n = 22), Northeastern Australia (NEAu, n = 74), Indo-Pacific (IP, n = 21), and New Zealand (NZ, n = 39).

2.2. DNA extraction, amplification, and sequencing

All shortfin mako tissue samples were stored in 95% ethanol at -20°C until genomic DNA extraction. Total genomic DNA was extracted from approximately 20 mg of tissue using the QIAmp DNA extraction kit (Qiagen Inc., Valencia, CA, USA).

The mitochondrial control-region (mtCR) region was amplified by polymerase chain reaction (PCR) using two external primers: Pro-L (5′-AGGGGRAAGGAGGGTCAAACT-′3) (Keeney and Heist 2006) and Prol-Falc2 (5′-CCCGGGGTGATCCTAATAAT-′ 3) developed for this study. The amplification was performed in 25 µL reactions containing 2 µL of the extracted genomic DNA, 10.0 mM of each primer, 1X Buffer, 2.5 mM dNTPs, 2.0 units of Taq polymerase (Fermentas, Life Science), and ultrapure water. The PCR thermal cycling profile consisted of 15 minutes (min) at 95 °C, followed by 35 cycles of: 94 °C for 1 min, 62 °C for 30 seconds (s), and 72 °C for 30 s, with a final extension step at 72 °C for 7 min. The PCR products were purified using the QIAquick PCR Purification Kit (Qiagen Inc., Valencia, CA, USA) following the manufacturer's instructions. Sequencing was performed using the Applied Biosystems Big Dye Terminator v3.1 Kit (Life Technologies, Carlsbad, CA, USA) according to the manufacturer's instructions. The amplicons were sequenced on an Applied Biosystems 3130 Genetic Analyzer, and bases were identified using Applied Biosystems Sequencing Analysis Software version 5.2. Finally, sequences were aligned and manually edited as necessary using Codon Code Aligner software (v. 5.1.5, Codon Code Corporation).

2.3 Genetic Diversity and Population Structure

Genetic diversity parameters such as nucleotide composition, number of transitions and transversions, haplotype diversity (h) and nucleotide diversity (π), number

148 of haplotypes (*H*), variable sites (*S*), and polymorphism distribution were estimated using
149 Arlequin 3.5 software (Excoffier and Lischer, 2010).

150 To test whether genetic diversity in the shortfin mako differs from that of other
151 confamilial (lamnid) and non-lamnid pelagic sharks, we conducted a multilevel random-
152 effects meta-analysis of 15 published mtCR datasets that reported standard errors (SE)
153 for haplotypic diversity (h) and nucleotide diversity (π) (Table S1). For each dataset, we
154 extracted h, π, their SEs, and sequence length (L). Diversity was analyzed on the logit (h)
155 and log (π) scale, and SEs were transformed accordingly (delta method for h; log-normal
156 variance, $\log[1 + (SE/\pi)^2]$, for π). Models were fitted using Restricted Maximum
157 Likelihood (REML) in the metafor package (Viechtbauer 2010) in R, with datasets nested
158 within species as random effects to account for non-independence among datasets of the
159 same species. Pooled estimates were obtained for all datasets and separately for the
160 shortfin mako and other sharks. The difference between the shortfin mako and other
161 sharks was tested by including species group as a fixed-effect moderator, together with
162 log-transformed sequence length (log L) as a covariate to account for variation in the
163 analyzed fragment length. Moderator effects were evaluated using Wald-type tests.
164 Residual heterogeneity was assessed with Cochran's Q_E, the variance components at the
165 species and dataset levels (σ^2), and a multilevel I^2 (Nakagawa et al. 2023).

166 To test the null hypothesis of global panmixia in the shortfin mako, genetic
167 structure among all locations was estimated using Wright's F_{ST} and the sequence-based
168 analogue of Wright's F_{ST} (Φ_{ST}). Statistical significance was determined through 10,000
169 permutations and $\alpha = 0.05$ (Cockerham and Weir, 1993). Estimated *p*-values were
170 corrected using sequential Holm-Bonferroni adjustments for multiple tests (Holm, 1979).
171 In addition, global population structure and the proportion of variance distributed among
172 sampling locations were estimated using a molecular variance analysis – AMOVA

(Arlequin 3.5; Excoffier et al. 1992) in a hierarchical framework to test alternative regional and ocean-basin population scenarios.

2.4 Phylogeography and Demographic History

The relationship between haplotypes and their geographic distributions was assessed using the Median-Joining network in PopART 1.7 (Population Analysis with Reticulate Trees; Leigh et al. 2015). In addition, to test for historical population contraction or expansion, two neutrality tests were performed: Tajima's D (Tajima, 2011) and Fu's Fs (Fu, 1997), with statistical significance assessed via 10,000 permutations in Arlequin 3.5 software (Excoffier and Lischer, 2010).

3. Results

3.1 Genetic Diversity and Population Structure

This study used a DNA alignment of 569 base pairs (bp) of the mtCR from a total of 588 shortfin mako sharks. The nucleotide composition was 27.07% cytosine, 34.47% thymine, 25.47% adenine, and 13.99% guanine. The overall haplotype diversity (h) was 0.864 (±0.011), with a minimum of 0.573 (±0.067) in OM and a maximum of 0.944 (±0.070) in NEAu. The overall nucleotide diversity (π) was 0.004 (±0.003), ranging from 0.002 (±0.002) in OM to 0.005 (±0.003) in NZ. The haplotype and nucleotide diversities across ocean basins showed similar values (Table 1). The final sequence dataset (n = 588) resolved 51 haplotypes and 26 variable sites (Table 1). Considering only the samples generated in this study (n = 224), 34 haplotypes and 569 variable sites were also observed.

198 **Table 1**. Genetic diversity indices and neutrality test results for the shortfin mako shark
199 (*Isurus oxyrinchus*) from different regions and their respective ocean basins. n number of
200 individuals, *S* polymorphic sites; *H* number of haplotypes, *h* haplotype diversity and
201 standard deviation, π nucleotide diversity and standard deviation. Significant values are
202 indicated in bold. The abbreviations are defined in Figure 1.
203

Region	n	S	H	h	π	Tajima' D	Fu´s FS
Regional							
Groups							
SAu	22	9	13	0.931 ± 0.036	0.004 ± 0.003	-0.055	**-7.453**
NEAu	74	15	19	0.893 ± 0.021	0.005 ± 0.003	-0.411	**-7.572**
IP	21	9	11	0.895 ± 0.047	0.005 ± 0.003	0.095	**-4.424**
NZ	39	12	12	0.827 ± 0.051	0.005 ± 0.003	-0.028	-2.644
OM	77	13	15	0.573 ± 0.067	0.002 ± 0.002	-1.325	**-8.471**
SAIO	92	15	21	0.882 ± 0.020	0.004 ± 0.002	-0.627	**-10.480**
NWAu	9	6	7	0.944 ± 0.070	0.004 ± 0.003	0.248	**-3.297**
SWAt	32	10	13	0.843 ± 0.055	0.004 ± 0.002	-0.336	**-5.851**
SEAt	9	6	6	0.889 ± 0.091	0.005 ± 0.003	0.797	-1.496
NWAt	46	11	13	0.841 ± 0.040	0.004 ± 0.002	-0.303	**-4.288**
GM	39	10	12	0.854 ± 0.034	0.005 ± 0.003	0.296	-3.039
SIO	30	13	16	0.883 ± 0.051	0.004 ± 0.002	-1.234	**-11.688**
EqAt	12	8	7	0.879 ± 0.075	0.005 ± 0.003	-0.111	-1.793
CSAt	29	13	14	0.879 ± 0.045	0.004 ± 0.002	-1.081	**-7.768**
SAAt	15	9	7	0.781 ± 0.102	0.004 ± 0.003	-0.576	-1.406
CV	12	9	6	0.864 ± 0.072	0.004 ± 0.003	-0.695	-0.785
NEAt	30	7	8	0.814 ± 0.049	0.003 ± 0.002	0.301	-1.380
Ocean Basins							
Pacific	135	18	24	0.895 ± 0.016	0.005 ± 0.003	-0.485	**-9.889**
Indian	199	20	29	0.801 ± 0.027	0.004 ± 0.002	-0.736	**-16.228**
Indo-Pacific	30	11	13	0.897 ± 0.036	0.004 ± 0.003	-1.107	**-19.188**
Atlantic	224	20	30	0.865 ± 0.014	0.004 ± 0.003	-0.309	**-5.342**
Total	588	26	51	0.864 ± 0.011	0.004 ± 0.003	-0.893	**-26.232**

204
205

The multilevel meta-analysis revealed no significant differences in genetic diversity between the shortfin mako and other pelagic shark species (Figure 2). Estimated h for the shortfin mako was high (h = 0.83, 95% CI: 0.73–0.90) and did not differ significantly from that of other shark species (Q_M = 0.09, p = 0.76). Substantial residual heterogeneity was detected among datasets (Q_E = 619.3, p < 0.0001; I^2 = 99.7%), with a between-dataset variance of σ^2 = 1.87 on the logit scale, and the variance attributable to species was estimated at zero. Similarly, π did not differ significantly between the shortfin mako and other pelagic sharks (Q_M = 0.03, p = 0.86). Estimated π for the shortfin mako was 0.0040 (95% CI: 0.0019–0.0085), compared with 0.0036 (95% CI: 0.0028–0.0046) for the other sharks. Heterogeneity in π was also high (Q_E = 1071.8, p < 0.0001; I^2 = 98.1%; σ^2 = 0.10 on the log scale). Sequence length did not significantly explain variation in either metric (h: p = 0.90; π: p = 0.63).

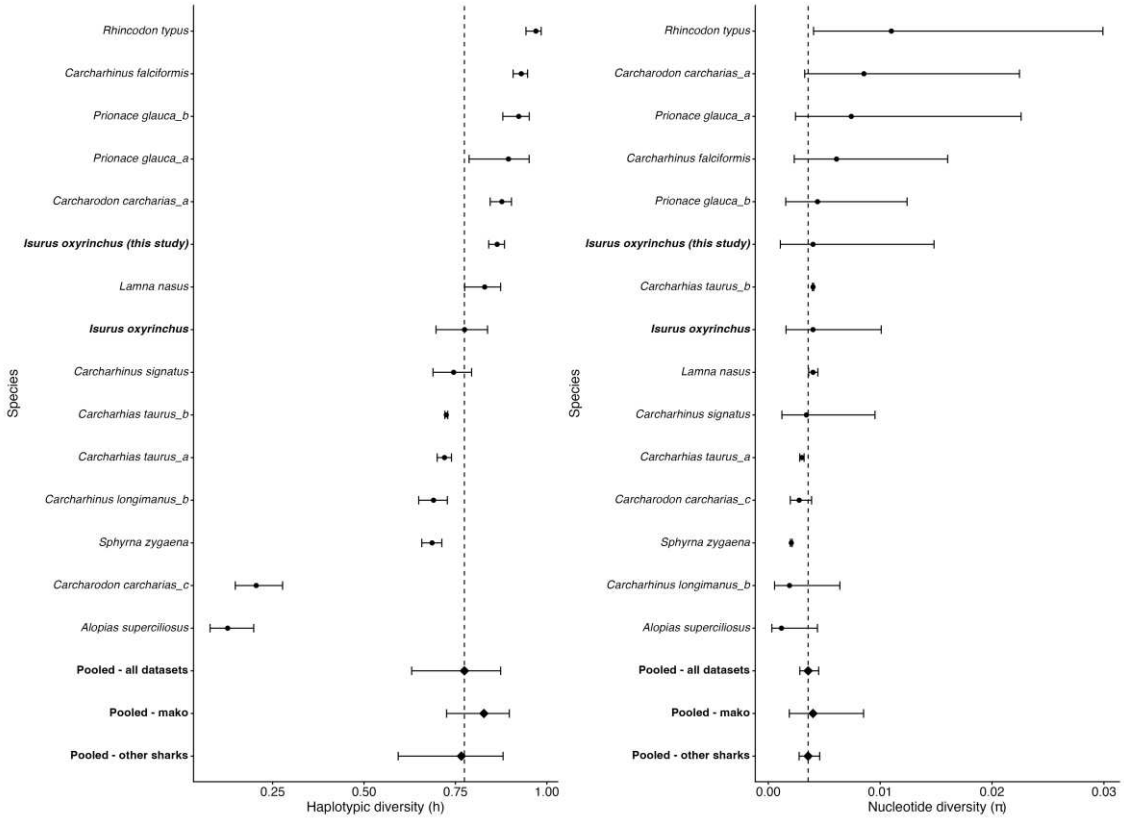


Figure 2. Forest plot of a random-effects model to estimate genetic diversity among Lamnidae and non-lamnid pelagic sharks. Points represent individual study estimates,

and diamonds indicate overall pooled estimates from the random-effects meta-analysis. Horizontal bars show 95% confidence intervals. The dashed vertical line in the left panel indicates the pooled estimate for haplotypic diversity. The dashed vertical line in the right panel marks the unweighted arithmetic mean of π across all studies. Letters after species names (_a, _b, …) distinguish independent datasets for the same species. Bold text highlights *Isurus oxyrinchus* datasets, including data generated in this study (*Isurus oxyrinchus* (this study)). References for all studies are provided in Supplementary Table S1.

The null hypothesis of panmixia in shortfin makos across their global distribution was rejected based on a statistically significant, albeit low, global F_{ST} value ($F_{ST} = 0.072$, $p < 0.05$) and the global Φ_{ST} value ($\Phi_{ST} = 0.045$, $p < 0.05$). For regional groups, the highest F_{ST} value was 0.356 ($p < 0.05$), observed between the EqAt and OM. Significant F_{ST} values were also found between OM and other regions, including the NEAt ($F_{ST} = 0.355$, $p < 0.05$), the NWAt ($F_{ST} = 0.347$, $p < 0.05$), and NEAu ($F_{ST} = 0.243$, $p < 0.05$) (Figure 3A; Table S2). The highest Φ_{ST} value was found between OM and SAu ($\Phi_{ST} = 0.247$, $p < 0.05$), while the lowest was between the tip of Africa (SAIO) and SAu ($\Phi_{ST} = 0.045$, $p < 0.05$) (Table S2). Notably, comparisons involving OM consistently showed the highest levels of differentiation. At the ocean basin level, the highest F_{ST} value was between the Indian and Atlantic Oceans ($F_{ST} = 0.075$, $p < 0.05$), while the lowest was between the Indian and Pacific Oceans ($F_{ST} = 0.019$, $p < 0.05$). Similarly, the Indian and Atlantic Oceans showed the highest value among ocean basins ($\Phi_{ST} = 0.026$, $p < 0.05$) (Figure 3B; Table S3).

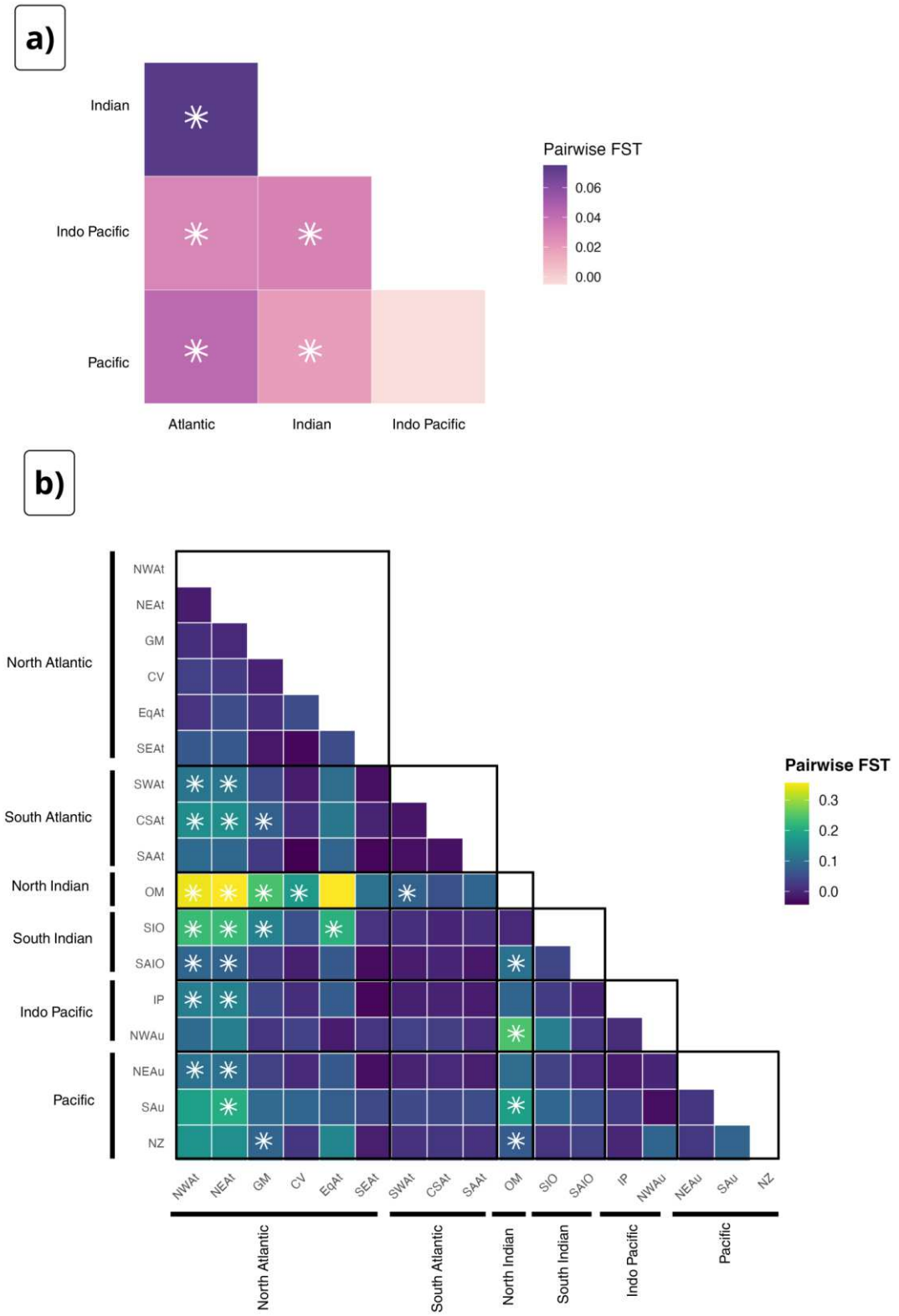


Figure 3. Fst heatmap between sampling locations. A) by ocean basins and B) by sampling sites. The abbreviations are defined in Figure 1. Stars indicate statistically significant values.

Of the 39 AMOVA scenarios analyzed, five showed significant Φ_{CT} values. Four of these five significant scenarios involved samples exclusively from the Atlantic Ocean, indicating that hierarchical genetic structure is primarily detected within this basin (Table S4). In the two-population scenarios, testing the separation between the South (SWAt, CSAt, SAAt) and North (SEAt, NWAt, GM, EqAt, CV, NEAt) Atlantic resulted in the highest differentiation value (Φ_{CT} = 0.085, $p < 0.05$), reflecting low but statistically significant hierarchical differentiation. Although the three population-structure scenarios included different configurations of Atlantic samples, all consistently supported genetic differentiation among populations from the South, Central, and North Atlantic. (Table S4).

3.2 Phylogeography and Demographic History

The haplotypic network did not reveal apparent clustering of haplotypes by ocean basins, as haplotypes were separated by only one mutation step (Figure 4). The network exhibited a star-shaped pattern, with primitive and high-frequency haplotypes more central and derived unique haplotypes on the periphery. Although clear clustering was not observed, the upper clade was dominated by haplotypes from the Atlantic, whereas haplotypes from the Indian Ocean dominated the lower clade. The most frequent haplotypes were H7 (n = 185), H10 (n = 84), H3 (n = 47), and H14 (n = 30), which occur in all ocean basins (Figure 4).

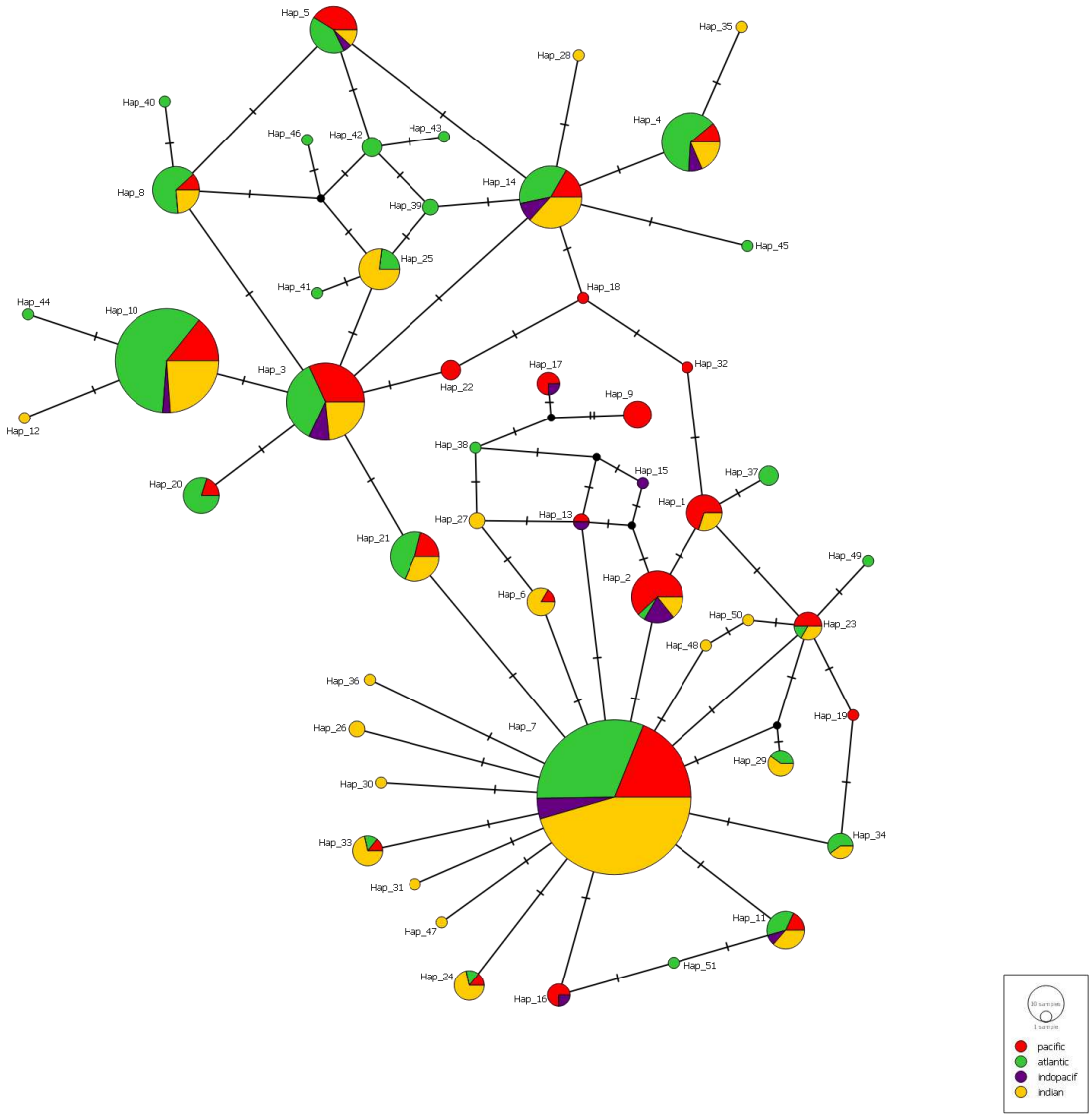


Figure 4. Haplotype network by ocean basins of the shortfin mako shark (*Isurus oxyrinchus*). The size of the circles is proportional to the frequency of each haplotype. The segments represent mutation events, and the red dots represent hypothetical, unsampled haplotypes. Blue: Atlantic Ocean, green: Pacific Ocean, red: Indo-Pacific Ocean, yellow: Indian Ocean.

Tajima's *D* neutrality test showed negative but non-significant values for both regional groups and ocean basins (Table 1), while Fu's F_S test showed negative and

278 significant values (F_S = -26.232, $p < 0.02$) for 59% of the regional groups and for all
279 ocean basins (Table 1).
280
281 **4. Discussion**
282 This study provides the first global scale insight into the patterns of matrilineal
283 population genetic structure, levels of genetic diversity, and aspects of the demographic
284 history of the shortfin mako shark, a critically endangered species. Based on
285 mitochondrial DNA, the shortfin mako exhibits discrete global matrilineal populations,
286 with the strongest signal of population structure occurring between the northern and
287 southern Atlantic, as well as significant differentiation among ocean basins, patterns that
288 may be most appropriately interpreted in the context of defining biologically meaningful
289 management units. This species also shows high mitochondrial genetic diversity and
290 historical population expansion. These results directly affect the conservation of this
291 species in both the short and long term, since fisheries management can utilize these
292 findings to conduct more accurate stock assessments by recognizing the genetically
293 distinct management units. Given the high levels of genetic diversity detected, these
294 results are important for maintaining the species' adaptive capacity and resilience under
295 ongoing environmental and anthropogenic pressures.
296 The overall genetic diversity detected in the mtCR of the shortfin mako shark was
297 high and similar among all collection areas and the discrete populations identified. The
298 meta-analytic synthesis did not detect significant differences in either haplotypic or
299 nucleotide diversity between the shortfin mako shark and other lamnid and non-lamnid
300 wide-ranging pelagic sharks. Despite the lack of significant differences between species
301 groups, substantial residual heterogeneity was detected for both genetic diversity metrics,
302 likely reflecting variation in geographic coverage, sampling design, molecular markers,

and demographic history among datasets. The absence of a significant relationship between sequence length and either haplotypic or nucleotide diversity further indicates that differences in sequence length did not explain the variation in genetic diversity estimates among the datasets analyzed. The lack of a detectable difference between the shortfin mako and other pelagic sharks may be consistent with the broad dispersal potential and extensive migratory behavior characteristic of many pelagic shark species. Such movements can facilitate gene flow among geographically separated populations, potentially contributing to the maintenance of genetic diversity and limiting population differentiation (Karl et al. 2011).

Despite the high levels of genetic diversity observed in the shortfin mako, contemporary anthropogenic pressure may rapidly alter this condition. Overfishing pressures on marine organisms have escalated significantly in recent decades, with the percentage of fish stocks captured sustainably declining from 90% in 1990 to 65.8% in 2017 (FAO, 2020). This scenario impacts the population size of species, which is closely related to the reduction in their genetic diversity, and poses a serious threat to the long-term survival of a species, as the ability to adapt to frequent environmental changes is primarily influenced by the level of genetic variation within a population (Agashe et al. 2023). The overfishing-induced loss of genetic diversity provokes varied outcomes depending on habitat differences, population connectivity, presence of refugia, and species-specific life-history traits that influence exploitation vulnerability (Sadler et al. 2023; D'Aloia et al. 2020). This highlights the importance of genetic studies for characterizing the evolutionary potential of the management units (Domingues et al. 2018). The situation is exacerbated in the case of sharks, which are K-strategists, making these species particularly susceptible to anthropogenic pressures, such as overfishing, environmental changes, and pollution (García et al. 2008; Dulvy et al. 2014, 2021).

328 The null hypothesis of global genetic panmixia in shortfin mako sharks was
329 rejected based on the partial mtCR sequences, with evidence of discrete populations
330 within and between different ocean basins. Based on F_{ST} and Φ_{ST} tests, significant
331 differences were observed within the Atlantic Ocean, suggesting the presence of at least
332 two matrilineal populations (north and south hemispheres), which corroborates the
333 findings for this species in the Atlantic Ocean by Bernard et al. (2025) using 85
334 mitogenomes. The AMOVA revealed weak but significant population structure when
335 testing different scenarios within the Atlantic Ocean. In the Indian Ocean, there were also
336 significant differences between localities from the south and north, suggesting two
337 distinct female populations. In contrast, in the Pacific Ocean, there were low to moderate
338 significant differences between some sampling locations. These results indicate discrete
339 populations of shortfin mako sharks in the north and south of the Atlantic and the Indian
340 Ocean. We lacked samples from the North Pacific to test hemisphere-oriented population
341 structure. These findings are congruent with previous results for shortfin mako sharks
342 (Corrigan et al. 2018) and other pelagic sharks such as the silky shark (*Carcharhinus*
343 *falciformis*; Domingues et al. 2018) and night shark (*C. signatus*; Domingues et al.
344 2018c), in the Atlantic Ocean, and porbeagle shark (*Lamna nasus*; González et al. 2021)
345 and blue shark (*Prionace glauca*; Veríssimo et al. 2017; González et al. 2023) in the
346 Pacific Ocean.
347 Similarly, there was low but significant population differentiation among shortfin
348 mako sharks across all oceanic basins. The high migratory capacity of large, globally
349 distributed pelagic fish, such as the shortfin mako, can result in low population structuring
350 (Bowen et al. 2016; Gaither et al. 2016). However, historical processes such as vicariant
351 events, dispersal, or demographic expansion can contribute to population divergence even
352 at low levels of gene flow (Kelly et al. 2006). Low population structure may result from

353 factors such as soft barriers and historical processes (Avise, 1994; Palumbi, 1994). In
354 sharks, however, one of the primary drivers of gene flow disruption and the consequent
355 formation of discrete populations is reproductive philopatry (Feldheim et al. 2014;
356 Chapman et al. 2015), the tendency of an individual to return to or remain in its natal or
357 adopted locality (Mayr, 1963). This behavior may limit connectivity between different
358 geographic regions and random mating, leading to population distinctiveness over time
359 (Chapman et al. 2015).

360 Mito-nuclear discordance observed in population structure assessments is an
361 indicator of possible philopatric behavior, and is commonly observed in highly migratory
362 shark species (Corrigan et al. 2018). Philopatric behavior underscores the importance of
363 identifying breeding and nursery grounds. The observed regional mitochondrial
364 population structure across the Atlantic Ocean is consistent with female philopatry and
365 suggests sex-based dispersal in the shortfin mako shark, as previously reported by
366 Bernard et al. (2025) using both nuclear and mitochondrial markers.

367 Although evolutionary history and migratory behavior are the primary causes
368 reported for population structure in sharks, other phenomena, such as oceanographic
369 features, also play an important role in restricting dispersal and random mating (Grobler
370 et al. 2024). Satellite tracking studies have consistently shown that shortfin makos exhibit
371 seasonal horizontal movements within their global range, with a preference for warm
372 waters. For example, in the eastern North Pacific Ocean, latitudinal migrations have been
373 observed in response to seasonal changes in water temperature (Block et al. 2011). For
374 the western North Atlantic coast, detailed information on migrations from satellite
375 telemetry indicates temperature-driven horizontal movements (Vaudo et al. 2016; Byrne
376 et al. 2019). Regarding oceanographic conditions, Byrne et al. (2024) revealed that the
377 Oxygen Minimum Zone (OMZ) in the Eastern Pacific Ocean acts as an environmental

barrier, limiting the distribution of shortfin makos. The analysis showed that these sharks consistently avoid areas with low dissolved oxygen levels and high surface temperatures, spending less time in regions where the OMZ compresses the available habitat. This behavior contrasts with that observed in the Atlantic, where the absence of an OMZ allows for greater use of habitats with higher temperatures. These observed patterns offer valuable insights into contemporary shortfin mako migrations and provide clues about possible migratory routes; however, it is important to acknowledge the limitations of mitochondrial DNA, whose evolutionary rate restricts its resolution for detecting more recent processes.

Similar to Bernard et al. (2025), our haplotype tree displayed a star-like topology and did not reveal a phylogeographic break among collection sites and oceanic basins. In contrast, other pelagic shark species, such as the silky shark (Clarke et al. 2015; Domingues et al. 2018) and the blue shark (Veríssimo et al. 2017), both of which exhibit high migratory capacity and a global distribution, showed a clear phylogeographic break between ocean basins. For the shortfin mako, the star-like topology was characterized by the presence of more central primitive haplotypes at high frequencies, from which unique, less frequent haplotypes radiated, suggesting the occurrence of a rapid population expansion process (Kottillil et al. 2023). High haplotypic diversity with low nucleotide diversity further supports the hypothesis of population expansion throughout the shortfin mako's evolutionary history (Grant and Bowen, 1998).

Additionally, the significant negative values from Fu's Fs test suggest that shortfin mako populations could have experienced a bottleneck event followed by rapid population growth. This bottleneck could be likely associated with the species' reproductive dependence on coastal habitats, which serve as essential nursery grounds for the development of young-of-year and juveniles (Conde-Moreno and Galván-Magaña,

2006; Bustamante and Bennett, 2013). This close association with coastal areas may have contributed to the bottleneck effect during past environmental fluctuations, including temperature variations and sea-level changes, which reached up to 130 meters below current levels during the Pleistocene (Ludt and Rocha, 2015). Indeed, bottleneck events followed by expansion have been reported for coastal (Portnoy et al. 2014) and pelagic shark species (e.g., Domingues et al. 2018, 2018c).

Finally, our study provides key insights for the global fisheries management of the shortfin mako by identifying genetically distinct matrilineal populations across ocean basins. The detection of unique genetic variation within each oceanic basin reinforces the need for region-specific fishing regulations by Regional Fisheries Management Organizations to ensure both short and long-term conservation of this shark species. Despite the conservation need for this endangered shark, only one study to date has applied genomic markers in a population-level study (Bernard et al. 2025); while a second study described several molecular markers from DNA and RNA but did not apply them in a population genomics study (Domingues et al. 2022).

Ethics. No ethical approval or permit for animal experimentation was required, as the individuals were not sacrificed specifically for this study.

Data accessibility. The sequences will be deposited in NCBI upon acceptance.

Authors' contributions. FM, MS, and RC coordinated the tissue collection. FM, MS, and RC provided resources. RD, IB, and AB performed labwork and sequencing work. AM, IN, BLSF, RD conducted the data analysis. AM, RD, IN, BLSF wrote the manuscript. All authors reviewed the manuscript and approved the final version.

Competing interests. The authors declare that there are no conflicts of interest.

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