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Consideration of sampling requirements and logistics for close-kin mark recapture and a reappraisal of potential for stock structure in Indian Ocean shortfin mako shark

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IOTC Working Party on Ecosystems and Bycatch

September 2025

IOTC-2025-WPEB21(AS)-41

Citation

Patterson TA, Feutry P, Gunasekera R, Burns C, Bessell-Browne P, Baylis S (2025) Consideration of sampling requirements and logistics for close-kin mark recapture and a reappraisal of potential for stock structure in Indian Ocean shortfin mako shark. Working paper, IOTC Working Party on Ecosystems and Bycatch, September 2025, IOTC-2025-WPEB21(AS)-41

Acknowledgement of Country

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Summary

Concerns about population declines, combined with a lack of informative data on shortfin mako shark (*Isurus oxyrinchus*, SMA), have created a need for new assessment aproaches. Close-Kin Mark Recapture (CKMR) is a powerful method for obtaining fisheries independent estimates of spawning stock abundance. It has been applied to both target and bycatch species and for several shark species. The statistical design results given in Patterson and Bessell-Browne (2025) indicates that collection of ~2000 tissue samples annually would provide sufficiently precise abundance estimates to estimate absolute population abundance for shortfin mako in the Indian Ocean (IO). This paper presents an appraisal of potential sampling and data collection opportunities by examining catch records by fleet. Based on recent IOTC catch records, we found that this number of samples could in principle be collected from fisheries operating in the IOTC area and that the target sample range is approximately 4-7% of the recent average annual catch reported by the top 10 SMA catching fleets. We also present an updated appraisal of likelihood of genetic stock structure to be present in IO SMA. This used a mix of previously collected and new samples taken from locations in the Indian Ocean (Sri Lanka, Reunion, Northwest Western Australia), as well as "out group" locations (southern Tasmania, New South Wales and the Atlantic).

The analysis of the ND4 mitochondrial DNA gene confirmed previous results by others suggesting non-random mixing of females across the shortfin mako's geographic range. The mechanisms driving this are not entirely clear; sampling locations share many haplotypes, which could be due to a persistent low level gene flow, incomplete lineage sorting, or non-reproductive migrations before the individuals were caught. The results indicate a need to sample across the Indian Ocean in any future CKMR study. However, CKMR data in addition to supporting abundance estimation would also refine understanding of demographic connectivity. To provide context, we outline requirements for CKMR sampling and discuss challenges and potential next steps required for moving toward obtaining a CKMR estimate for SMA in the Indian Ocean. While some of the information we present is specific to SMA, much of the material would apply equally to sampling for other pelagic shark species.

1 Introduction

1.1 Difficulties in assessing pelagic shark stocks

The key data source for most current stock assessments for shark species in the jurisdictions of Regional Fisheries Management Organizations (RFMOs) is catch per unit effort (CPUE) data, which has been shown to be problematic for use in assessment in many cases (Polacheck 2012; Maunder and Piner 2015). For bycatch species, CPUE can often be a poor representation of actual patterns in catch and effort and therefore unlikely to be useful for constructing reliable abundance indices. Concern about apparent declines in several widely distributed elasmobranchs frequently captured by tuna fleets creates an urgent need to identify alternative data sources to underpin management decisions.

This working paper examines two components which are informative in deciding on the feasibility of a CKMR study: the genetic population structure of the species within the geographic area of interest and the likelihood of obtaining sufficient samples for Close-Kin Mark-Recapture estimates to be produced. This is considered for shortfin mako shark (*Isurus oxyrinchus*; SMA), a pelagic shark species which has a worldwide distribution (Stevens 2008). The species is often captured as bycatch in high-seas fisheries (Murua et al. 2018) and is also targeted in various recreational fisheries (Babcock 2008).

There is concern that the species is vulnerable to declines (Sims, Mucientes, and Queiroz 2021; Kai 2021; Sellheim 2020) due to its susceptibility to capture by longline fishing gear (Murua et al. 2018) and its low population productivity (Coelho, Rosa, and Mourato 2024). This is due to a long lifespan (Liu et al. 2018) with associated late female maturity onset, a relatively low litter size and pupping occurring every 2–3 years (Groeneveld et al. 2014; Mollet et al. 2000).

The species is widespread in the Indian Ocean (IO) and analysis of longline observer data (Wu et al. 2021) suggest that there may be spatial patterns in the size of SMA captured, with smaller sharks caught at higher latitudes and larger SMA caught at lower latitudes.

The summary report of the IOTC scientific committee 2024 (Anon. 2024) states that annual catches of SMA were 846 t in 2022, but combined catches of SMA, mackerel sharks and porbeagle used in the last IOTC assessment are in excess of 2000 tonnes (Anon. 2024). Reconstructed catch estimates have estimated significantly higher recent catches (>12000 t) (Coelho, Rosa, and Mourato 2024) (Figure 1.1).

The most recent assessment of Coelho, Rosa, and Mourato (2024) resulted in a stock status determination that the stock in the IO is currently overfished and subject to overfishing (49.7%) (Anon. 2024). (Coelho, Rosa, and Mourato 2024) concluded that due to high levels of fishing mortality and the species estimated stock status that significant catch reductions are required. A TAC of 40% of current catch levels was recommended (Coelho, Rosa, and Mourato 2024).

Despite the progress toward better understanding demonstrated in the 2024 assessment, the status of the species is still very difficult to characterize. This assessment (like other SMA assessments in ICCAT) used a data-limited Bayesian surplus production framework (Winker et al.

2020). These are driven by CPUE which vary considerably between fisheries and fleets (Coelho, Rosa, and Mourato 2024).

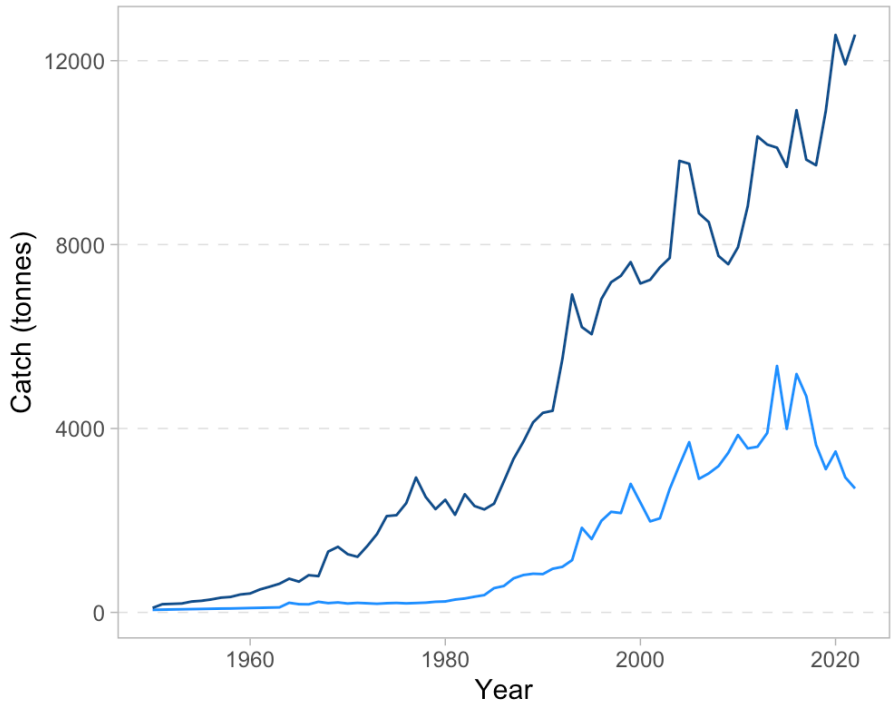

Figure 1.1: Reported (light blue) and reconstructed (dark blue) catch series used in the Coelho et al. (2024) JABBA assessment of SMA.

1.2 Potential for CKMR to address uncertainty

Close-Kin Mark-Recapture (CKMR) is a technique for estimating absolute adult population abundance (Bravington, Skaug, and Anderson 2016) which bypasses the majority of challenges for conventional catch and effort data. A key advantage of CKMR is that it allows for a fishery independent estimate of the breeding stock size. It also allows for estimation of total mortality rates and other key population parameters (Bravington, Skaug, and Anderson 2016; Tremblay-Boyer, Bravington, and Davies 2024), which we detail for SMA in Patterson and Bessell-Browne (2025). The method has been used to assess elasmobranchs; including both commercially targeted species (Thomson et al. 2020; Trenkel et al. 2022) and species which are the focus of conservation efforts (Bruce et al. 2018; Bradford et al. 2018; Patterson et al. 2022). While it produces estimates of spawning population abundance, CKMR can be incorporated into integrated assessment models along with various fishery derived data sources (Hillary et al. 2023; Punt et al. 2024) to provide whole-of-population assessments.

At its core, CKMR relies on application of modern genetic sequencing approaches to a representative number of tissue samples taken from the population of interest. Pairwise comparisons are made between sampled individuals' sequencing data to identify closely related individuals ("kin"). The prevalence of these kin pairs is directly related to the adult abundance.

The “close” kin types used in CKMR are show in Figure 1.2. The method works on the basis that samples from smaller populations will have a higher prevalence of Half-Sibling Pairs (HSPs) / Parent-Offspring-Pairs (POPs) kin-types relative to unrelated pairs (UPs), than would be found in a larger population (Bravington, Skaug, and Anderson 2016). Technical details of estimation of CKMR models is given in Patterson and Bessell-Browne (2025).

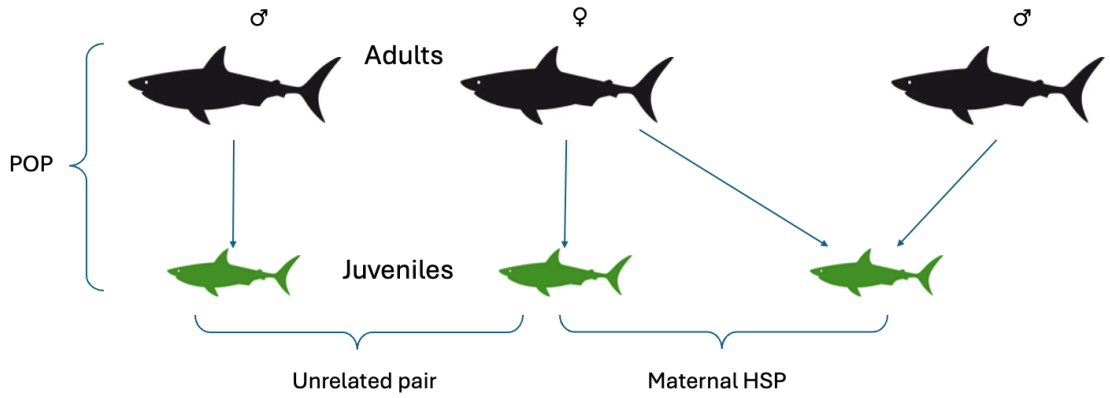

Figure 1.2: The main kin types used in CKMR. POPs - parent offspring pairs; HSP- half sibling pairs and unrelated pairs (UP- neither POP nor HSP). Note that with addition of mtDNA (inherited only through the mother) HSPs can be either paternal (shared father) or maternal (shared mother – as depicted). Note that the other kin-type which could arise are Full sibling Pairs (FSPs), these are not useful for CKMR in most situations.

CKMR projects have 5 main components:

1. A statistical design phase based on current population knowldge (see Patterson and Bessell-Browne (2025) for SMA in the Indian Ocean, Bravington (2019) for Atlantic SMA and also Tremblay-Boyer, Bravington, and Davies (2024) and Hillary et al. (2022) for examples for target tuna species). This phase also encompasses consideration of logistical requirements (as detailed in this paper).

2. Collection of tissue samples from the population - potentially following some type of sex/space/age stratified sampling design.

3. Discovery of a set of genetic markers (typically SNPs - single nucleotide polymorphisims) that are informative on kinship relationships (Figure 1.2), followed by genotyping of all samples.

4. Kin-finding; this is the statistical analysis of genotyping data which involves pairwise comparison of all samples to identify kin-types. The result of this is a data set of the number of kin pairs resulting from a stratified comparisons over combinations of sampled animal cohorts.

5. Population modelling to find abundance, mortality rates and other parameters. As in stock assessment, this involves searching for population model parameters that lead to

the best fit to the kin-pair data. See details of the model in Patterson and Bessell-Browne (2025).

1.3 Biological requirements and sampling considerations for CKMR

Close-Kin Mark-Recapture may be the only currently viable technique for providing reasonably accurate estimates of population status for pelagic sharks. Prior to embarking on a CKMR study, along with considering how many samples are required, it is however necessary to consider likely data sources that might provide those samples. In this case, that requires identifying fishery sectors and fishing nations likely to encounter the species in relatively high numbers so that they are a source of potential samples. It also requires understanding of genetic population structure to know how many genetically distinct populations might actually be being sampled during field collection.

In this paper, we provide practical advice on sampling requirements for CKMR of application to SMA in the IO and comment on biological data inputs required for CKMR modelling and why understanding of stock structure is desirable despite CKMR being able to provide information on spatial connectivity.

Accordingly this paper considers the following questions:

- Does up-to-date sequencing alter the current understanding of a single IO stock for SMA?
- What are the potential sample sources among IOTC contracting parties?
- What ranges of ages and sizes are available?
- Given the results of Patterson and Bessell-Browne (2025), what proportion of the catch would need to be sampled to provide abundance estimates and support an assessment?

In considering these questions, we consider sampling potential for CKMR based on catches reported to IOTC and provide an update on stock structure using nuclear and mitochondrial markers provide complementary insights in population genetic analyses. Mitochondrial DNA (mtDNA) is haploid, maternally inherited, and non-recombining, making it useful for tracing maternal lineages, historical demography, and phylogeographic patterns (Avise et al 1987). However, it represents only a single locus and may not reflect genome-wide diversity. Nuclear markers such as SNPs are biparentally inherited and recombine, offering higher resolution for population structure. Combining both allows researchers to detect sex-biased dispersal, a common phenomenon in elasmobranchs (Ovenden et al 2018), and obtain a more comprehensive view of evolutionary and demographic processes shaping populations (Toews et al 2012).

Over the last decade SNPs have increasingly replaced microsatellites for genetic population structure analyses. SNPs are ubiquitous and evenly distributed across the genome, enabling studies to leverage thousands or even millions of loci thanks to the rise of high-throughput genotyping platforms for SNPs. This abundance of markers substantially boosts statistical power, despite lower per-locus variability compared to microsatellites. SNP genotyping platforms are

also highly automated and reproducible, making large-scale standardised comparison feasible across studies and laboratories. In this study we used DArTseq (Sansaloni et al 2011), Diversity Arrays Technology's (DArT) proprietary high performance restriction site associated DNA genotyping approach to generate tens of thousands of SNP markers for our samples. In addition to these nuclear markers, we used Oxford Nanopore long read technology to sequence the ND4 mitochondrial genes.

1.3.1 Spatial structure and CKMR

CKMR obtains an estimate of adult numbers from the population being sampled. However, populations can be structured in complex ways determined by how individuals breed in space and time. In some populations, the spatial distribution of related pairs is informative about how individuals allocate reproductive output between spatial units (Patterson et al. 2022). So CKMR can provide important information that population genetics typically cannot. Nevertheless, population genetics methods are helpful understand in advance whether any population under consideration is split into genetically distinct units, each having a separate stock of breeding individuals (M. V. Bravington, Skaug, and Anderson 2016).

Genetic divisions as detected through standard population genetics are formed by very limited gene flow over many generations (Graves 1998; Heist 2008; Reiss et al. 2009). In contrast, since kinship data observes relatedness over a few generations, CKMR can inform on genetic drivers of population structure on shorter timescales (Patterson et al. 2022). Population genetics methods therefore compliment CKMR in allowing for detection of distinct stock boundaries. Additionally, CKMR can sometimes identify signatures of female philopatry that are not so easily visible to population genetics.

In the Indian Ocean, SMA have been considered a single stock (Corrigan et al. 2018). However, this was based on relatively imprecise micro-satellite methods. More up-to-date SNP based methods are more powerful for characterising genetic variability and therefore reliably detecting population structure. For this reason the current study re-examines available SMA tissue samples using updated sequencing methods (Nikolic et al. 2023) to look at potential for stock structure in the Indian Ocean.

1.3.2 Practical sampling and metadata requirements

Collection of tissue samples requires both the retention of the tissue for DNA extraction and subsequent sequencing, along with recording of "meta-data" detailing other covariates describing the individual animal being sampled. Therefore, CKMR sampling requires

- A tissue sample stored in an appropriate fixative agent so that DNA will be preserved. Fixative agents such as ethanol or RNAlater are typically used. Each of these has advantages and disadvantages; for example, RNAlater has the advantage of being safe for transportation.
- The date of sampling.

- Meta data detailing age or a quantity that will allow the sampled individual's age to be estimated. Lengths are typically recorded and age-at-length models are used to provide an estimated age. Age is required because assigning a birth year to a sampled animal is a fundamental component of CKMR models, although uncertainty in age can be incorporated into CKMR models (Bravington, Skaug, and Anderson 2016).

- Life status: CKMR will work on either live-released samples or lethally sampled animals. It is important to know whether animals were sampled dead as that rules them out as having offspring after the point of sampling (Bravington, Skaug, and Anderson 2016).

While CKMR estimates can be produced with the information above, it is recommended that information on the following

- Location of sampling – this provides the spatial basis for determining if detected kin pairs display evidence of spatial population structuring.

- Sex of the sampled animal if available. For elasmobranchs, this can usually be easily verified by visual examination for the presence of claspers in males (Natanson et al. 2020).

- Maturity status can be visually obtained for male elasmobranchs via inspection of whether claspers are calcified (Natanson et al. 2020). This is not directly used in CKMR models but can useful in verifying age at first reproduction/maturity schedules.

1.3.3 Background biological knowledge inputs required for CKMR

From the points above, embedding CKMR in an assessment model such as outlined in Patterson and Bessell-Browne (2025) require several pieces of background biology:

(1) An ageing method - this can be a growth model of length-at-age. Ageing elasmobranchs can be challenging. For this reason, uncertainty in age estimates is often incorporated into models (e.g. Bradford et al. 2018). This is because ageing error effects the assignment of individuals to a birth year, complicating both estimation of survival rates and abundance.

(2) Understanding of a maturity schedules are important for a few reasons. Firstly, because CKMR deals in the currency of per capita reproductive output - which often varies by sex, size and age. Often this needs to be captured in model structure and sex-specific reproductive output at age is a fundamental input into CKMR models. This is less of a problem for many sharks where there is often a weaker size/reproductive output relationship compared to fish. Animals where both adults and juveniles can be sampled are likely to yield POPs - this certainly applies to fish, but less so to sharks where often only juveniles are regularly encountered. If adults and juveniles are being sampled, then obviously being able to understand whether an individual is an adult or juvenile at the time of sampling is required.

(3) SNP panel design / marker selection - this is the process of picking a set of SNPs that are particularly informative about parentage when comparing loci from pairs of sampled individuals.

(4) CKMR studies (Patterson et al. 2022) can use mtDNA to determine whether HSPs are maternal or paternal (see Figure 1.2). The distribution of mtDNA haplotypes informs on the adult sex ratio and can therefore be used to estimate sex-specific abundance as demonstrated in Patterson et al. (2022).

2 Materials and Methods

2.1 Sampling intensity as indicated by IOTC size frequency data.

Size frequency data is informative in the CKMR context for three reasons:

Firstly, clearly fleets reporting large numbers of measurements are useful as a source of samples for an CKMR project. For pelagic sharks with relatively large populations and wide spatial distributions, large scale fishery operations are the only feasible way to access enough sharks for realistically informative sample sizes. In our consideration of sampling potential we assume that any viable sampling of SMA would be reliant on tissue collection occurring at some point through the fishing process.

Second, the size and thus age, typically selected by these fisheries will determine whether it is likely that juveniles or adults are captured which has ramifications for the types of kin pairs that would inform an abundance estimate. If adults and juveniles can be sampled as was the case for CKMR on southern bluefin tuna (M. Bravington, Grewe, and Davies 2016), then there is potential to look for POPs. In practice, this requires determining if large/old sharks make up an appreciable proportion of the animals available to be sampled. If high numbers of adults and juveniles are captured it is possible that some POP matches might be found. These inform on abundance in the birth year of juveniles in the sample.

However, the typical situation with sharks is that most frequently, pre-breeding adults are captured by fisheries operations. This may be due to selectivity differences, distributional/habitat differences between juveniles and adults, or simply because breeding adults are much more scarce. The expectation with sharks is that juveniles are routinely encountered and HSP-based CKMR will be the only viable approach.

Third, in order for a full statistical design it is desirable to have a series of catch at age data (Bravington 2019; Hillary et al. 2022) which is not available for Indian Ocean SMA. Age distributions can be estimated from an age-length model, and therefore used to compile a rough estimate of catch-at-age.

In this paper we examined size frequency differences in space by using IOTC grid references to locate the size frequency data in space. We then compared the size distribution regionally to examine

2.2 Data sources

2.2.1 Samples for stock structure

Tissue and genetic samples were collected from various sources globally. A large propoprtion of tissues from Corrigan et al. (2018) were extracted from archived storage and re-extracted. Additionally, new samples were collected from Australia (Tasmania, New South Wales, and Western Australia), Sri Lanka and Reunion Island.

DNA was extracted from tissue samples at CSIRO Marine Laboratories, Hobart, Australia and sent to Diversity Arrays Technology (DArT), Pty. Ltd. in Canberra, Australia for sequencing.

2.3 Analysis for stock structure

DNA extractions were done using the DNeasy Blood and Tissue kit from Qiagen and genotyping was performed following the protocol described in Grewe et al. (2015). Briefly, DNA libraries were prepared using a digestion/ligation approach with two restriction enzymes, PstI and SphI. The PstI site was ligated to a forward adapter containing an Illumina flow cell attachment sequence and a sequencing primer with a variable-length barcode region. The SphI site was ligated to a reverse adapter carrying a flow cell attachment region and reverse priming sequence. Only fragments containing both PstI and SphI overhangs were efficiently amplified by PCR. PCR products from all samples in each 96-well plate were normalized to equimolar concentrations, pooled, and sequenced on an Illumina Novaseq.

Sequence clustering conducted using DArT's proprietary DArT-Soft14 analytical pipeline and allele counts were fed into the R package radiator for SNP calling and data quality control (QC). Radiator uses a stepwise workflow to filter out both low-quality DNA markers (SNP loci) and individual samples of insufficient quality (e.g., low DNA concentration, degraded DNA, or contamination).

For SNP loci, the following parameters were assessed: i) Reproducibility: proportion of consistent genotype calls, estimated using technical replicates (some samples were prepared and sequenced twice); ii) Minor allele count (MAC): frequency of the less common allele; iii) Coverage: average read depth per locus across all individuals; iv) Call rate: proportion of successfully genotyped samples; v) SNP position: location of the SNP within the sequenced fragment; vi) Short linkage disequilibrium: for multiple SNPs on the same fragment, only the SNP with the highest MAC (most informative) was retained; vii) Hardy–Weinberg equilibrium (HWE): evaluated within each sampling location. For individual samples, QC included: i) Missingness: proportion of missing genotype data per individual; ii) Heterozygosity: proportion of loci with two different alleles; iii) Duplicate: pairwise measure of genetic similarity among individuals. Thresholds applied for each parameter during filtering are detailed in Table 2.1

Table 2.1: radiator filtering steps for shortfin mako Isurus oxyrinchus, including threshold values and the number of individuals, locus and markers at the start of each step and the final filtered dataset.

Filters	Values	Individuals	Locus	Markers
Filter DArT reproducibility	0.95	227	45421	57241
Filter markers in common		227	45411	57225
Filter individuals based on missingness	0.060993	227	45250	57060
Filter monomorphic markers		199	45250	57060
Filter MAC	8	199	22136	27638
Filter coverage min / max	16 / 100	199	14921	17986
Filter call rate	0.2	199	14416	17431
Filter SNPs position on the read	all	199	12979	15640
Filter markers snp number	3	199	12979	15640
Filter short ld	mac	199	12944	15494
detect mixed genomes	0 0.228	199	12944	12944
detect duplicate genomes	0.25	195	12944	12944
Filter HWE	3, 0.001	156	12944	12944
Filtered dataset		156	12914	12914

The mitochondrial ND4 gene was sequenced by DArT on an Oxford Nanopore MinION and used for downstream analyses without any further processing.

2.3.1 Data analyses

The number of genetic clusters present in the dataset was evaluated without a priori assumptions using the K-means clustering algorithm implemented in the adegenet package (Jombart, 2008) with the find.cluster() function. The Bayesian Information Criterion was used to assess the best-supported number of clusters as recommended by others (Lee et al. 2009). Once the genetic group assigned, a discriminant analysis of principal components (DAPC, Jombart, 2010) was applied to evaluate the effectiveness of the markers at discriminating the individuals from each genetic group. DAPC is particularly advantageous for analysing complex datasets characterized by overlapping or closely related genetic groups, as it maximizes between-group variance while minimizing within-group variance, thereby enhancing the resolution of group discrimination. DAPC also provides insights into which markers are most discriminatory between groups. A Manhattan plot was generated in order to visualise the marker's DAPC loadings against their position on the shortfin mako genome. In order to avoid over-fitting, we used the K-1 criterion proposed by Thia (2023) and restricted our DAPC analyses to a maximum of eight PCs (nine putative populations, one per sampling locations).

The software Admixture was also run as a complementary clustering approach. 1-10 K clusters were evaluated using a 20,000 burn-in and a 100-fold cross-validation approach.Finally, the package StAMPP was used to calculate the Weir and Cockerham (1984) pairwise population

differentiation index (FST) and the statistical significance was evaluated by calculated P-values over 1,000 bootstraps and the p-values were adjusted for multiple comparison using the false discovery rate approach (Benjamini & Hocherg 1995). Sequences of the mitochondrial ND4 gene were aligned in Geneious prior to building a haplotype network with the pegas package and calculating pairwise PhiST using the haplotypes package. Statistical significance was assessed by calculating p-values over 10,000 permutations and the p-values were adjusted for multiple comparison using the false discovery rate approach (Benjamini & Hocherg 1995).

2.4 Catch and length frequency to inform CKMR designs

To inform on potential for samples to be collected, we examined catch records and size frequency data was obtained from the IOTC portal (https://iotc.org/data/browser). Following Coelho, Rosa, and Mourato (2024) we considered data with species codes SMA (shortfin mako), MAK (all mako sharks) and POR (porbeagle) as these are likely to contain records of shortfin mako.

To determine potential sampling fleets we looked at averages of reported catches from 2015 onwards. The assumption here being that these are likely to be representative of catch levels that are likely to continue over the next 5-10 years in the IOTC and that could therefore form the basis of a targeted sampling program To obtain an approximate idea of age distributions in the catch we applied a conversion of length frequency measurements to ages using a Von Bertallanfy growth function and using values from Liu et al. (2018) and Romanov and Romanova (2009) shown in Table 2.2.

Table 2.2: Von Bertallanfy growth and Length/Weight model parameters used. See text for sources.

Length Parameters	Value	Weight Parameters	Value
L_∞	407.65	a	0.0000349
k	0.04	b	2.7654400
t_0	-7.08		

As a starting point to understand potential for tissue and length collection, we looked at approximate numbers of sharks being measured for length frequency reporting. To get an idea of numbers being caught (not just tonnage) tonnage of SMA reported by fleet was converted into approximate numbers of sharks by first using the weight at length $W = aL^b$ formula with parameters given in Table 2.2 and calculating mean weight of animals captured and estimating numbers as $N_{caught} \approx \left(C_y \times 1000\right)/\bar{W}$.

To examine potential for sample provision we looked at the number of length-frequency samples collected by various fleets and the consistency of sampling through time.

3 Results and Discussion

In the results section we first consider the results from genetic analysis for potential stock structure and then look at sampling potential from catch data.

3.1 Genetics sampling locations

A total of 227 samples were genotyped. The numbers from each sample location are given in Table 3.1. Due to missing meta-data, no location was provided for samples labelled “Corasao”. The assumption was that this was a North Atlantic sample set potentially collected from vessels around Curacao in the Caribbean. This cannot be verified, but given the results detailed below, it is very unlikely that any mis-specification of sampling/collection location is influential on the outcomes reported. The approximate spatial locations of samples in Table 3.1 are shown in Figure 3.1.

Table 3.1: Number of samples (Left column) sequenced and numbers retained with viable mtDNA and SNP data after QC processes

Location	N(sample)	N(mtDNA)	N(SNPs)
Corasao	27	21	20
Indonesia	14	4	14
New Zealand	34	20	19
North Atlantic	21	20	20
NSW	23	21	22
Reunion Is.	42	20	22
Sri Lanka	27	15	25
TAS	18	17	18
WA	21	18	20

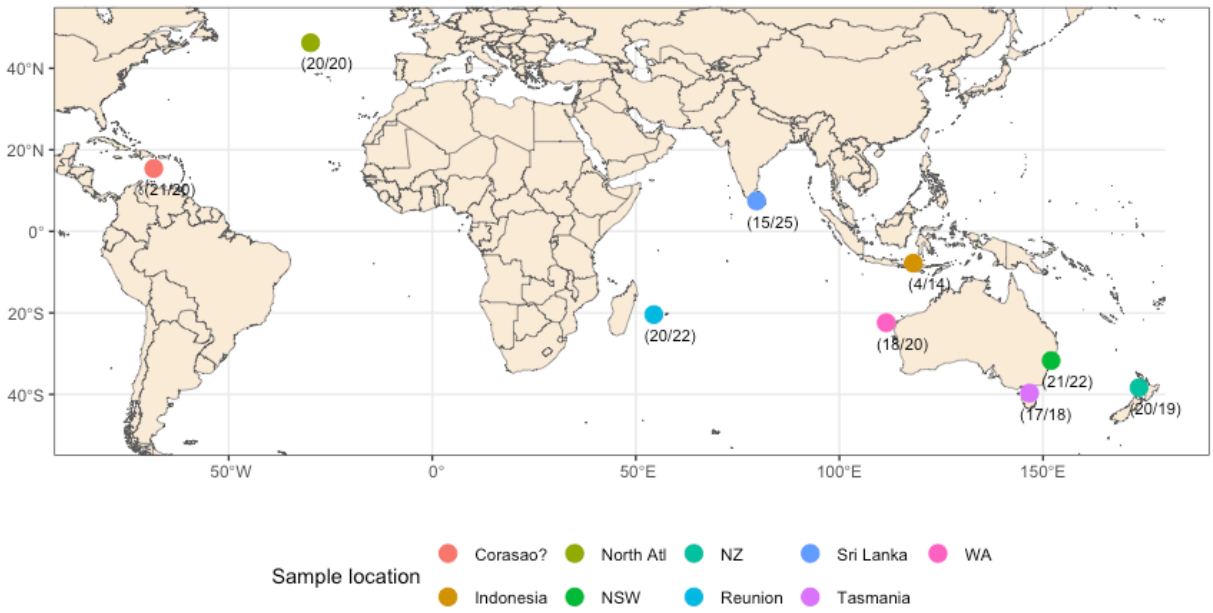

Figure 3.1: Locations of sampling for genetic tissue samples. The numbers in parentheses give n(mtDNA)/n(SNPs) samples from each location. Note that the location of Corosao samples was unclear – see text.

Both the K-means (Figure 3.2 A) and Admixture (Figure (Figure 3.2 B) clustering analyses showed K=2 as the best supported number of clusters. The first group included all the individuals from New Zealand and Reunion Island as well as all the individuals but one or two from Corasao, Tasmania and North Atlantic. It also included three individuals from NSW and seven from WA. The second group included all the individuals from Indonesia and Sri Lanka as well as the remaining individuals from the other locations.

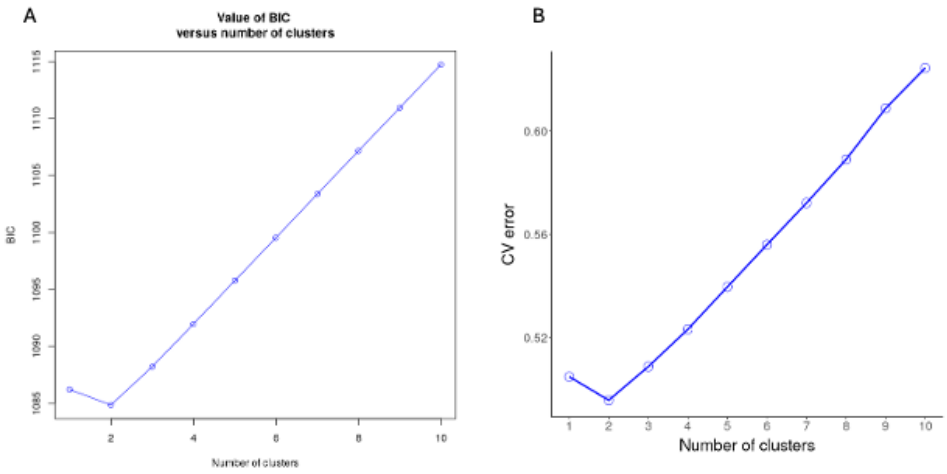

Figure 3.2: Clustering analyses in the shortfin mako Isurus oxyrinchus. A) Bayesian Information Criterion for the evaluation of best supported number of clusters K; B) Cross-validation error for the evaluation of best supported number of clusters K.

Interestingly, some of the individuals, despite being assigned to the second group, had an intermediate position between the two main clusters on the DAPC scatter plot and intermediate membership in the Admixture analyses (Figure 3.3). The Manhattan plot of the DAPC loadings for the discrimination between these two groups showed all the markers with loadings higher than background baseline were located chromosome 1, spanning a region ~142 mb long, i.e. more than half the length of that chromosome (Figure 3.4). This likely indicates the presence of a very large chromosomal inversion.

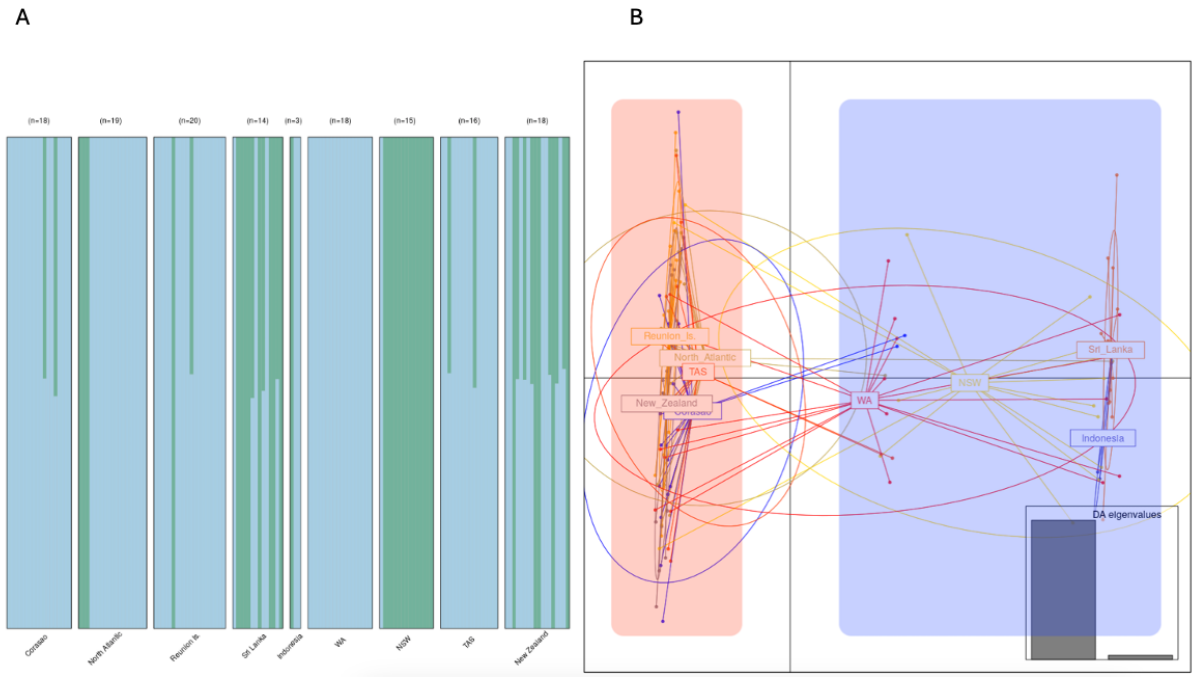

Figure 3.3: Clustering analyses in the shortfin mako Isurus oxyrinchus. A) DACP scatter plot, red and blue areas include all the individuals identified as belonging to the first and second group respectively by the K-means analyses; B) Admixture individual membership probabilities to K1-2

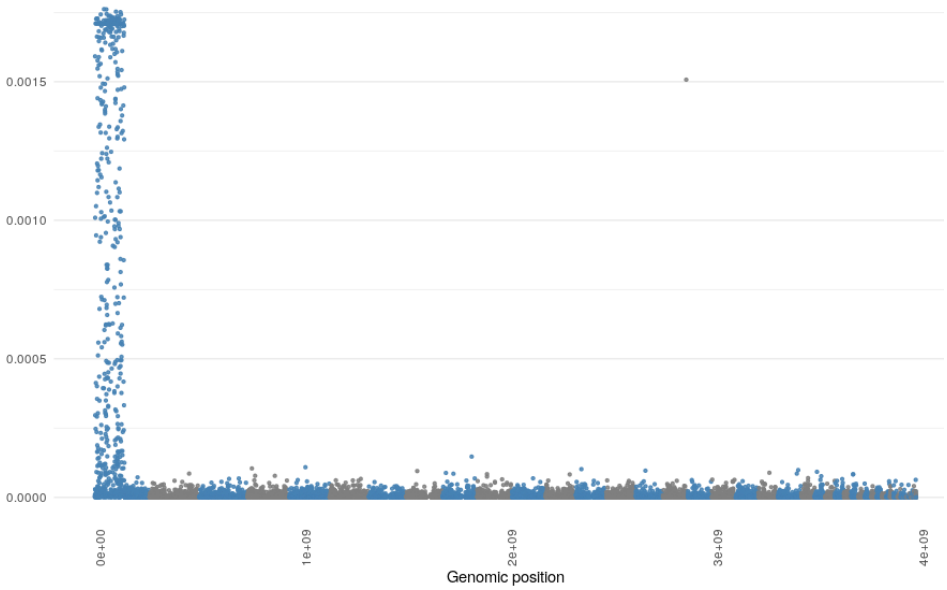

Figure 3.4: Manhattan plot of the DAPC loadings along their chromosomal position. Blue and grey colours alternate at each new chromosome.

Given this large chromosomal inversion on chromosome one was potentially over-riding any other population structure signal in the rest of the genome, we decided to run a second round of clustering analyses after removing any markers located on that chromosome. This time both the K-means and Admixture analyses agreed on K=1 as the best supported number of clusters

The analysis of the mitochondrial gene ND4 revealed non-random mixing between all sampling locations. The non-random distribution of haplotypes across sampling locations (Figure 3.5) is confirmed bit the high PhiST values for all sampling locations pairwise comparisons except between Corasao and North Atlantic (Table 3.2).

Table 3.2: Pairwise FST (above) and associated FDR adjusted p-values (below) based on all nuclear SNPs past QC in shortfin mako Isurus oxyrinchus.

Locations	Corasao	North Atlantic	Reunion Is.	Sri Lanka	Indonesia	WA	NSW	TAS	New Zealand
Corasao	-	-0.0001	0.001	0.0608	0.0596	0.0105	0.0284	0.0005	0.0014
North Atlantic	0.581	-	0.0004	0.0578	0.0552	0.0082	0.026	0	0.001
Reunion Is.	0.0223	0.225	-	0.0673	0.0661	0.0128	0.0328	0.0004	0.0003
Sri Lanka	<0.001	<0.001	<0.001	-	0.0051	0.0212	0.0109	0.0605	0.0685
Indonesia	<0.001	<0.001	<0.001	0.0027	-	0.0185	0.011	0.06	0.0663
WA	<0.001	<0.001	<0.001	<0.001	<0.001	-	0.004	0.0089	0.0135
NSW	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-	0.0261	0.0334
TAS	0.1626	0.503	0.2389	<0.001	<0.001	<0.001	<0.001	-	0.0007
New Zealand	0.0014	0.0206	0.2711	<0.001	<0.001	<0.001	<0.001	0.108	-

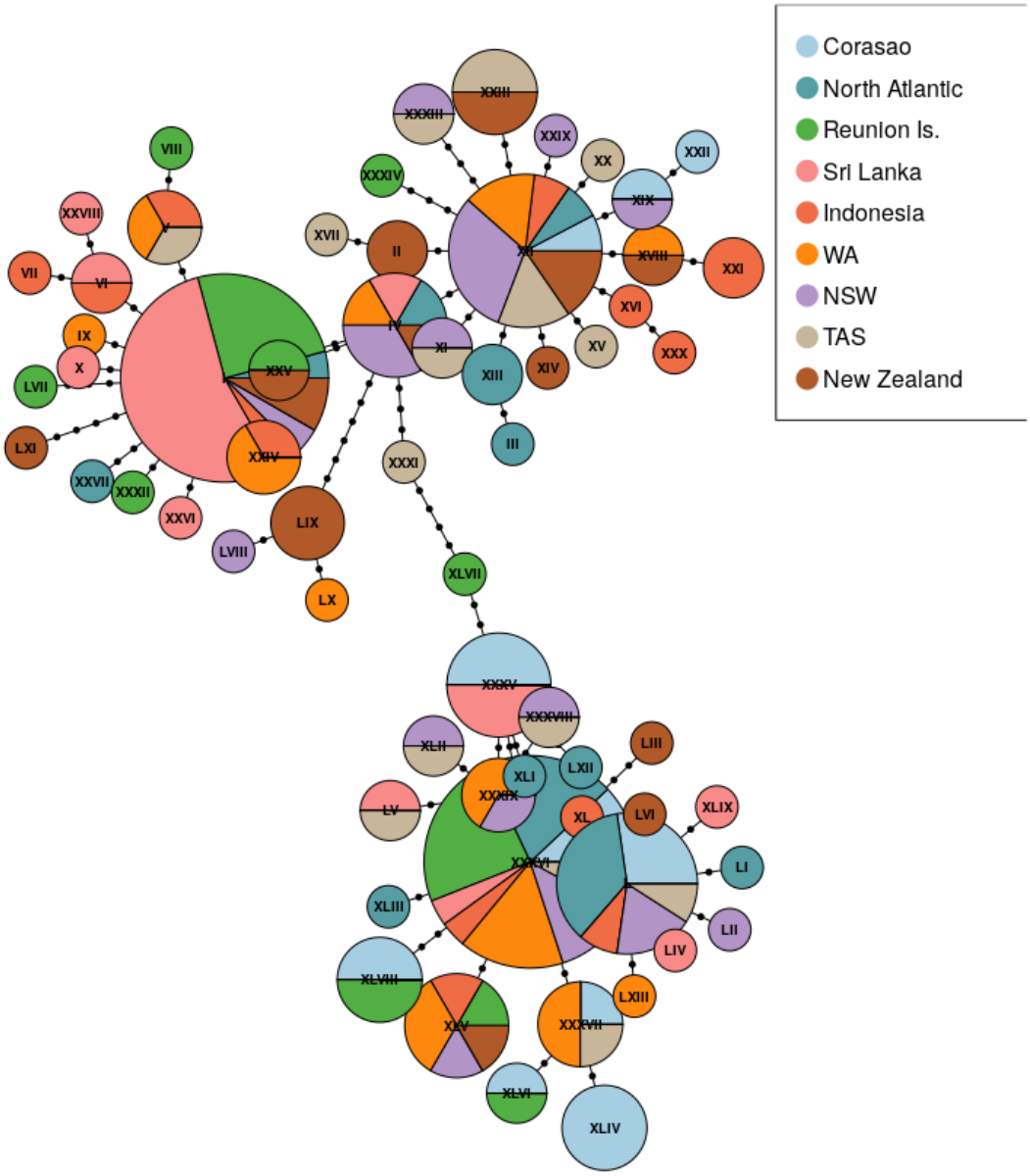

Figure 3.5: ND4 haplotype network for the shortfin mako Isurus oxyrinchus. The size of the pie charts are proportional to the square roots of the number of individuals harbouring each haplotype. Each black dot on the lines linking the haplotype indicates a mutation.

Table 3.3: Pairwise PhiST (above) and associated FDR adjusted p-values (below) based on the mitochondrial gene ND4 in shortfin mako Isurus oxyrinchus.

Locations	Corasao	North Atlantic	Reunion Is.	Sri Lanka	Indonesia	WA	NSW	TAS	New Zealand
Corasao	-	0.053	0.5855	0.183	0.8509	0.9435	0.8309	0.8485	0.3939
North Atlantic	0.0519	-	0.5908	0.2145	0.8292	0.9232	0.8174	0.8335	0.4001
Reunion Is.	<0.0001	<0.0001	-	0.1348	0.862	0.947	0.8442	0.8599	0.452
Sri Lanka	<0.0001	<0.0001	0.0001	-	0.6967	0.8026	0.7258	0.7381	0.3399
Indonesia	<0.0001	<0.0001	<0.0001	<0.0001	-	0.1242	0.0701	0.3729	0.231
WA	<0.0001	<0.0001	<0.0001	<0.0001	0.002	-	0.1584	0.5653	0.4022
NSW	<0.0001	<0.0001	<0.0001	<0.0001	0.0231	0.0003	-	0.3201	0.2985
TAS	<0.0001	<0.0001	<0.0001	<0.0001	0.0001	<0.0001	0.0001	-	0.3097
New Zealand	<0.0001	<0.0001	<0.0001	<0.0001	0.0026	<0.0001	<0.0001	0.0004	-

3.2 Size frequency by fleet

The number of size frequency measurements varied considerable but was exceeded 500 for most years after 2011 (Figure 3.6 A). The series peaked in 2014 at N=1858 samples. The median age predicted in the samples was generally around 6-7 years (Figure 3.6 B) and this did not seem to vary substantially between the sexes (Figure 3.6 C), although for the vast majority of samples, sex was recorded as “UNCL” (92.8 % of N=16463 entries).

Across all the length frequency data, 50% of samples were less than 168 cm fork length (FL) and 75% were less than 196 cm FL. The distribution of estimated ages suggested that 75% of animals measured were less than 10 years old and 50% were younger than 6.5 years old. Only 1.3% of animals were older than 20 y.

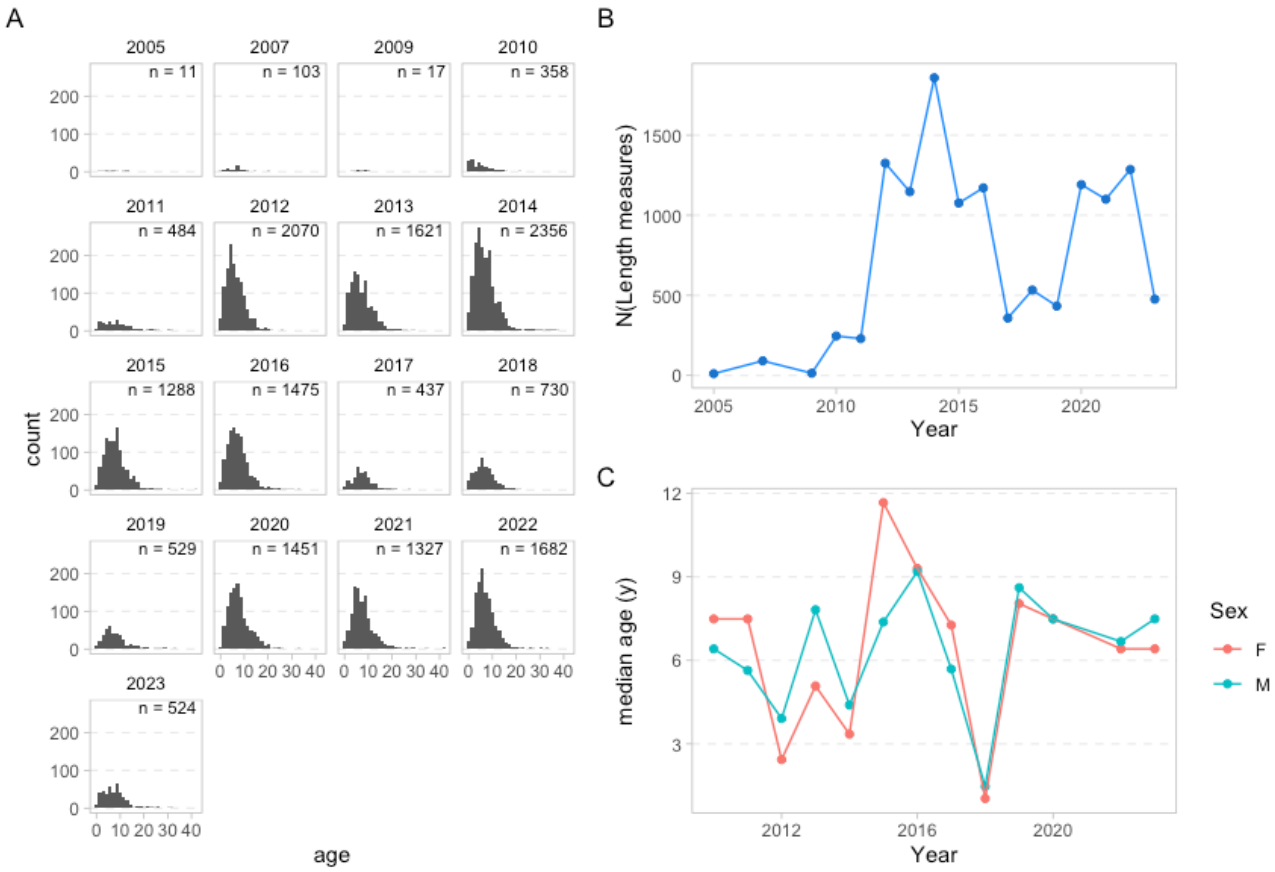

Figure 3.6: A. Estimated age frequency distributions by year from IOTC length frequency measurements. B. Number of length measurements recorded in the IOTC database for SMA. C. Median age by sex (where recorded).

Length frequency data mostly derives from a few fleets - TWN, EUPRT and KOR account for 91% of the data, with TWN providing 69% on its own (Table 3.4).

Table 3.4: Number of measurements by FLEET code from IOTC length frequency data. The bottom row gives percentages of all measurements collected by that particular FLEET over the years tabulated.

Year	CHN	EUESP	EUPRT	EUREU	GBR	IDN	IND	KOR	MOZ	MUS	TWN	ZAF
2005												11
2007								91				
2009		14										
2010		48						198				
2011		8	222									
2012	3	5	374					172			771	
2013	4	5	185					138			815	
2014	8	9	54	11				184			1592	
2015		23	343					11	28.0		671	
2016	13	31	150	9							968	
2017	22	10	109	5	126		2	21			63	
2018		16	225	27	29	9.0		32		10.0	185	
2019		24	168		47				2.0	6.0	186	
2020		68		2							1121	
2021	3			11							1086	
2022	19	60		5							1202	
2023	12	352	54	3								55
% total	**0.7**	**5.4**	**15**	**0.6**	**1.6**	**0.1**	**0**	**6.8**	**0.2**	**0.1**	**69**	**0.5**

3.3 Reported catch variation by fleet

Conversions from length to weight resulted in a median weight of 49.7 kg, which was used to estimate numbers caught from catch tonnage figures. Again, we stress this is a crude measure of the probable numbers of sharks caught but is nevertheless useful for determining whether sampling targets are vastly unlikely given catch figures.

Table 3.5 shows the average annual SMA catches reported to IOTC in years later than 2015 by fleet. Across all of these the mean catch was 122.985174. Fleets TWN and MDG reported the largest catches, but the top 7 fleets in terms of average annual catch since 2015, were all over 150 tonnes. This would equate to ≈ 3000 sharks per year for each fleet, at the median shark weight.

Table 3.5: Mean annual shortfin mako (SMA) catches reported to IOTC > 2015 for the top 10 fleets in terms of average catch

Fleet	Catch (tonnes)
TWN	648
MDG	505
IDN	491
EUESP	408
PAK	325
ZAF	248
EUPRT	154
SYC	83
NEIFR	68
JPN	57

3.4 SMA catch series by fleet

The tonnages and estimated numbers (at the median weight) are shown in Figure 3.7. The total numbers landed (Figure 3.7) show numbers in excess of 40k individual sharks being estimated by our crude measure of numbers captured. The design for CKMR indicates that Patterson and Bessell-Browne (2025) indicates that 2000-3000 samples would likely provide accurate estimates of population status for SMA in the Indian Ocean. The rough conversion of catch to numbers indicates that the this would represent sampling about 4-7% of an average number of individuals captured annually since 2015, by the 10 highest catching fleets.

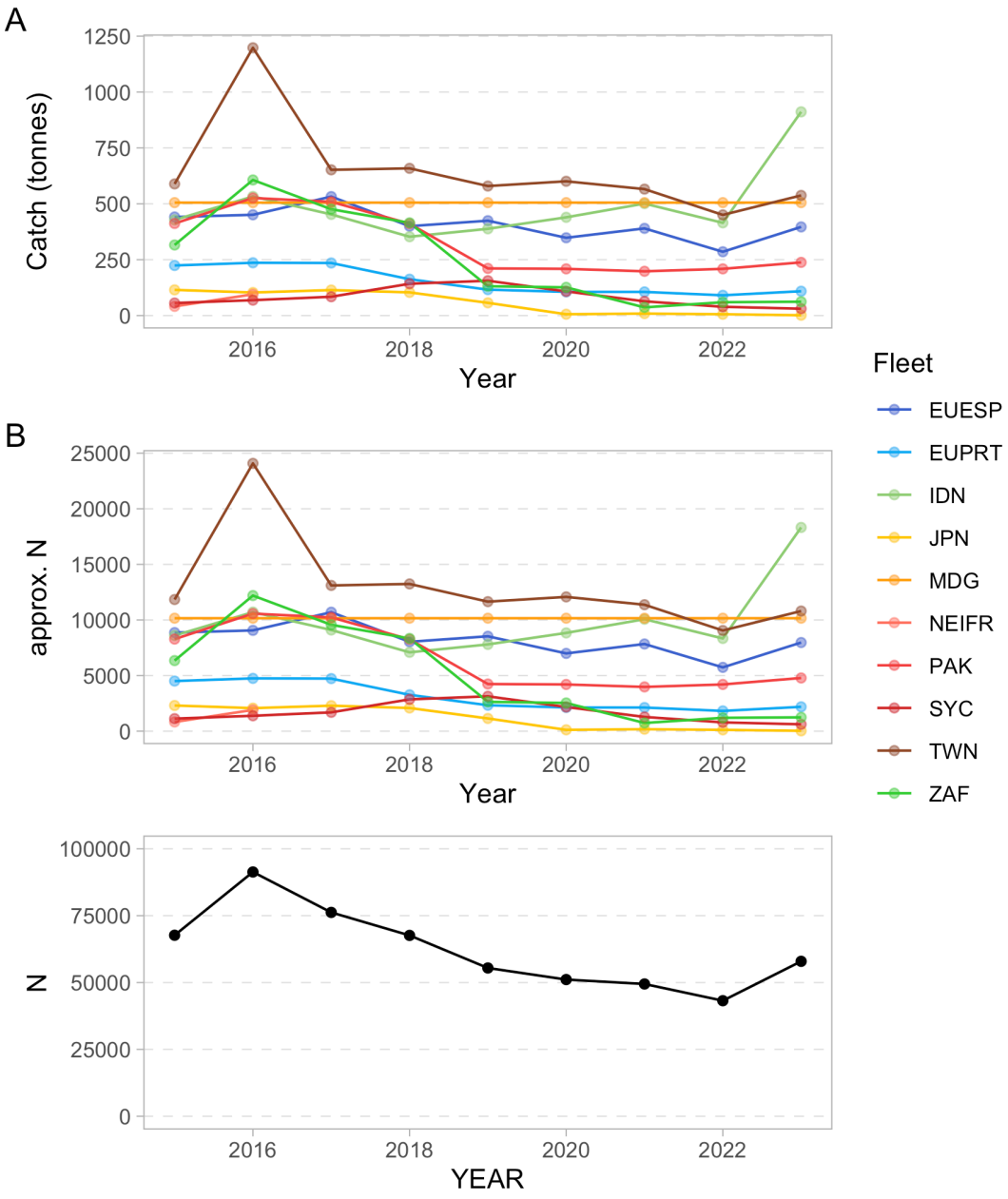

Figure 3.7: A - Reported tonnage of catch by FLEET, of mako sharks in IOTC catch data from 2015 onwards. B- Conversion of tonnes in number of individuals caught by FLEET. C- Total estimated numbers caught per year.

4 Conclusions

The study conducted here did not find evidence of genetic structure in SMA populations that would need to be considered at this stage of CKMR design work.

The analysis of the ND4 mitochondrial DNA gene confirmed previous results by others suggested non-random mixing of females across the shortfin mako's geographic range (Bernard et al. 2025, Corrigan et al. 2018). Despite the statistical significance of these results, sampling locations share many haplotypes, which could be due to low level gene flow, incomplete lineage sorting, or non-reproductive migrations before the individuals were caught. This provide additional support for the need to sample from different part of the Indian Ocean if one wanted to provide a CKMR estimate. In the process, CKMR would allow to refine our understanding of the demographic connectivity of shortfin mako in the Indian Ocean.

The genetic analyses here noted likelihood of a chromosomal inversion in the shortfin mako genome. Chromosomal inversions can reduce fertility because heterozygotes may produce unbalanced gametes (Anton et al. 2005, Kirkpatrick 2010), and while they may affect mating recognition indirectly through phenotypic effects, they are not believed to stop individuals recognising each other as mates (Butlin et al. 1982). As such we believe the structure detected in this study with the SNP data does not necessarily reflect reproductive isolation. It is possible however that some genes located on that inversion are environmentally selected, which could explain the non-random spatial distribution observed in the group assignment from both clustering methods. To what extent demographic processes are affected remains unclear.

This paper has considered catch data from the IOTC against the likely requirement to collect 2000-3000 tissue samples per year of SMA in the Indian Ocean (Patterson and Bessell-Browne 2025). The data indicates that to meet the sampling target outlined in Patterson and Bessell-Browne (2025) would require roughly twice the recent sampling effort by particular individual fleets (e.g. TWN) operating in the IOTC jurisdiction. Potentially less sampling might be sufficient, but it is better to collect a large number of samples early in a sampling program and potentially reduce sample collection if required. While the stock structure work conducted here agreed with previous studies (Corrigan et al, 2018), in finding evidence of structure but without a strong spatial signal, it would be sensible to spatially distribute sampling effort to allow for further information to accrue that would confirm a mixed population.

Our analysis of length frequency data indicates that most animals encountered are immature. The design work in Patterson and Bessell-Browne (2025) was based on the assumption that only immature animals would be sampled and demonstrates that accurate estimates of population abundance are likely. There are obviously several caveats regarding estimating age from length data, which in some cases may be made under less-than-ideal circumstances for maintaining accuracy. This will not influence the likelihood of detecting kin pairs and may mean for instance that POPs would be detected which would only assist abundance estimation.

While these targets are larger than current sampling rates, other multinational tissue collections programs for pelagic species collections have larger targets. E.g. Farley, Eveson, and Gunasekera (2024) and large-scale tissue collection is underway at the moment for a South Pacific tuna species (Tremblay-Boyer, Bravington, and Davies 2024).

Further data from within the Indian ocean would solidify understanding of potential structure. The spatial distribution of detected kin-pairs may help resolve generational spatial patterns. However, with a wide ranging species like SMA, any signals of discrete breeding populations may be lost with juvenile dispersal.

Large scale sampling programs have been discussed in the IOTC realm, with much larger sampling targets than the 2000+ currently recommended for SMA. Williams et al. (2023) mention broadly the sampling requirements for a yellowfin tuna CKMR project. This was mentioned in a research priority for the WPTT work plan back in 2015 to 'Design and develop a plan for a biological sampling program' (see page 202 in

https://iotc.org/sites/default/files/documents/2025/04/IOTC-2024-SC27-RE_0.pdf).

The idea is for the design and development of a plan for a biological sampling program to support research on tropical tuna biology.

> "The plan would consider the need for the sampling program to provide representative coverage of the distribution of the different tropical tuna species within the Indian Ocean and make use of samples and data collected through observer programs, port sampling and/or other research programs. The plan would also consider the types of biological samples that could be collected (e.g. otoliths, spines, gonads, stomachs, muscle and liver tissue, fin clips, etc.), the sample sizes required for estimating biological parameters, and the logistics involved in collecting, transporting and processing biological samples. The specific biological parameters that could be estimated include, but are not limited to, estimates of growth, age at maturity, fecundity, sex ratio, spawning season, spawning fraction and stock structure."

Sampling of sharks would fit within this schema. In fact, by only requiring much more modest sample numbers, the shark sampling should be much more achievable. One of the barriers to using CKMR for robust monitoring is to find mechanisms that allow sampling to occur at scale that accomodates the restrictions of CITES Appendix II listings and in the case of non-retention measures. How best to address these challenges will likely require coordination amongst IOTC CPCs and beyond. Howver, this paper and the results in Patterson and Bessell-Browne (2025) present evidence that solutions to resolve uncertainty surrounding shortfin mako, and other pelagic shark, stocks are available and tractable.

5 Acknowledgements:

This project was supported by funding from the European Union. This document has been produced with the financial assistance of the European Union. The views expressed herein can in no way be taken to reflect the official opinion of the European Union.

We thank Shannon Corrigan (Minderoo Foundation), Michael Drew (South Australian Research and Development Institute), Mike Travers and Matias Braccini (Western Australian Department of Primary Industries and Regional Development), Emily Hunt and Vic Peddemors (New South Wales Department of Primary Industries and Regional Development) for their assistance in sourcing samples from Australian-held collections, during surveys and sampling at recreational fishing competitions.

For Sri Lanka sampling would like to acknowledge all BRT researchers and volunteers for their time and effort in collecting samples at the landing sites. Sample collection in Sri Lanka was supported by the Tokyo Cement Group (TCG) and the Marine Conservation Action Fund (MCAF) of the New England Aquarium.

We gratefully acknowledge input and assistance from Brad Moore, Floriaan Delvoo Devla, Ash Williams and Denham Parker from CSIRO. Laura Tremblay-Boyer and Campbell Davies from CSIRO were instrumental in developing this project. We also thank Lauren Nelson, Paul de Bruyn and Dan Fu of the IOTC for their assistance.

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