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Feasibility of a Close-Kin Mark-Recapture for Stock Assessment of Indian Ocean Swordfish (*Xiphias gladius*)

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Abstract

The Indian Ocean Tuna Commission (IOTC) manages swordfish, *Xiphias gladius*, a species of high economic importance in the Indian Ocean. Current stock assessments rely on catch per unit effort indices, which can be biased, complicating reliable abundance estimates. We explored alternative approaches by assessing the feasibility of the close-kin mark– recapture (CKMR) method, a powerful genetic-based approach. This pilot study aimed to validate protocols and guide future CKMR implementation at the IOTC scale. CKMR simulations were conducted to estimate the sample sizes required to detect sufficient kin pairs. Kinship analyses assumed a single panmictic population across the Indian Ocean, consistent with current IOTC management. A total of 2068 individuals were genotyped using SNP markers, identifying one parent-offspring pair (POP) and at least two half-sibling pairs (HSPs). As predicted by simulations, this sampling scale precludes robust estimation. However, results indicate that robust CKMR-based estimates could be achieved by sampling at least 18,000 swordfish over three years, representing about 20% of the current sampling effort already undertaken by contracting parties. The annual cost of genomic data generation for CKMR represents less than 0.5% of the first-sale market of swordfish in the Indian Ocean. Overall, this study supports the feasibility of CKMR for swordfish and provides a foundation for scaling up future programs to improve Indian Ocean stock assessments.

Keywords: fisheries management; single nucleotide polymorphism; kinship; fisheries-independent abundance index; feasibility study

Key Contribution: This study demonstrates the feasibility of close-kin mark–recapture (CKMR) to estimate swordfish abundance in the Indian Ocean by combining simulation-based sampling optimization with empirical kinship detection and provides quantitative benchmarks for sampling effort required to detect parent-offspring and half-sibling pairs.

Academic Editor: Ying Xue

Received: 21 January 2026
Revised: 26 February 2026
Accepted: 2 March 2026
Published: 4 March 2026

1. Introduction

Stock assessment is a critical component for fisheries management and conservation efforts as it assists in evaluating the stock status needed to make informed decisions regarding sustainable harvesting [1]. A major source of information used in stock assessments is abundance indices, which provide an estimate of the relative abundance of the populations over time. Abundance indices can be developed using various methods, including scientific surveys [2–4] or fisheries-based indicators like catch per unit effort (CPUE) data. Because

fishery-dependent indices such as CPUE are sensitive to changes in fishing behavior, targeting, and spatial coverage, there is increasing interest in fisheries-independent genetic approaches capable of delivering potentially more reliable abundance estimates.

Continued advances in the fields of genetics and genomics have opened the door to novel research applications aimed at improving understanding of key ecological and population parameters for species under management. The close-kin mark-recapture (CKMR) method is one such contemporary approach that has emerged as a powerful and accurate method for estimating demographic parameters, such as abundance, survival rate and connectivity [5–7]. Unlike recapturing a physically marked and released individual, as is the case with traditional mark-recapture techniques [8,9], CKMR "recaptures" close relatives of an individual. This is done either directly by sampling the individual and its offspring, which corresponds to a parent-offspring pair (POP) [10], or indirectly by sampling at least two offspring, such as a full-sibling pair (FSP) or, more commonly for marine species, a half-sibling pair (HSP) [11]. In contrast with the traditional mark recapture method, CKMR does not need to release individuals; thus, samples can be derived from dead fish, such as those obtained by fishery catches. As an offspring's two parents were by definition alive at its conception, CKMR can supply information about the abundance of reproductively mature individuals in the years of birth of the sampled offspring [6]. Unlike mark-recapture, the use of kinship as an identification mark remains robust to many forms of catch heterogeneity, including variation in fishing gear efficiency and tagging effects such as mortality [12].

Each offspring serves as a genetic marker for both of its parents, and the likelihood of an adult being identified as one of these marked individuals depends on the total number of parents present in the population during the offspring's birth year. The frequency at which parents are encountered is then theoretically used to estimate adult abundance [10,13,14]. Additionally, datasets may reveal second and third-degree kin relationships, such as HSPs. HSPs represent a weaker degree of relatedness than first-order kin, such as a full-sibling pair (FSP), and they can easily be distinguished from this type of kin ($r = 0.5$) [15]. Although more challenging, it is possible to distinguish HSPs from kin pairs such as grandparents (GGPs) based on birth-year differences, as GGPs require an age gap of at least twice the age at sexual maturity. Similarly, for species with short adult lifespans, birth-year differences can help separate HSPs from full-thiatic pairs (FTPs, e.g., full aunt-niece). However, this requires knowledge of the age of the fish sampled, which is not always available, particularly in our case study. In CKMR studies, POPs and HSPs, particularly cross-cohort HSPs (XHSPs), which originate from different reproductive events or "cohorts", provide critical information on adult abundance and survival rates. In contrast, FSPs provide very little independent information on adult abundance and survival rate, and for highly migratory fish, are very often obtained from juveniles of the same cohort, which can lead to bias in estimates due to the "lucky litter" effect [10]. For example, a small number of parents can be overrepresented in the sample population due to a disproportionately large number of surviving offspring within a given cohort, with survival due primarily to chance (e.g., favorable environmental conditions, temporarily reduced predation).

Over the last decade, several studies have highlighted the use of CKMR for estimating the abundance of aquatic species, including adult chinook salmon, *Oncorhynchus tshawytscha* [16], southern bluefin tuna, *Thunnus maccoyii* [13], the endangered Northern River shark, *Glyphis garricki* [17], white shark, *Carcharodon carcharias* [11], brook trout, *Salvelinus fontinalis* [12,18] and the thornback ray, *Raja clavata* [19]. While these studies illustrate the broad applicability of CKMR, implementing this approach in large-scale marine stocks, particularly highly migratory species such as tuna or billfish, presents specific challenges. These include strong assumptions regarding population structure, individual movements

across management boundaries, and heterogeneous spatial and temporal sampling. As shown by simulations, CKMR is sensitive to age structure and age determination, as misclassification of juveniles and adults can bias the expected frequencies of POPs and HSPs and therefore affect abundance estimates [20]. These challenges are especially relevant for species with long lifespans, overlapping generations, and poorly resolved life-history parameters. However, no CKMR studies have yet been conducted on any billfish species, despite them being theoretically well-suited for this approach. Compared with highly abundant tuna stocks, billfish populations have lower estimated abundances, meaning that sufficient numbers of kin pairs could be detected with a more manageable and cost-effective sampling effort. For example, spawning stock biomass for swordfish is estimated at 77,000 t in the Indian Ocean versus more than 1 Mt for yellowfin tuna [21].

The Indian Ocean Tuna Commission (IOTC) is responsible for managing the swordfish (*Xiphias gladius*) fisheries in the Indian Ocean, a species of substantial commercial value. Approximately 30,000 t of swordfish are harvested annually in the Indian Ocean, underlining its significant importance in the region. Although the current assessment classifies the Indian Ocean swordfish stock as neither "overfished" nor "subject to overfishing", the stock assessment remains uncertain. This uncertainty is largely driven by persistent biological data gaps, including limited knowledge of stock structure, age composition, recruitment variability, and spatial mixing. Accordingly, the IOTC has identified the acquisition of key biological information as its primary research priority for swordfish, particularly regarding age and growth dynamics as well as spawning timing and location [22]. Further, IOTC has identified the implementation of a pilot CKMR study for swordfish abundance estimation as the second research priority in the last Working Party on Billfish, highlighting the need to improve the assessment approach [22].

This study evaluates the effectiveness of the sampling design and genetic protocols underlying the CKMR approach for estimating the absolute abundance of *Xiphias gladius* in the Indian Ocean. CKMR has previously been applied to large, highly migratory marine species, such as swordfish, southern bluefin tuna, and, more recently, the western stock of Atlantic bluefin (*Thunnus thynnus*); these feasibility studies have demonstrated that the number of individuals required for effective sampling can be considerable, often exceeding 13,000–25,000 individuals per year [10,23,24]. Given the scale of sampling and investment required, careful preparatory work is essential before embarking on full-scale implementation [23]. This paper contributes to that objective by coupling simulations to a realistic sampling strategy, providing a laboratory workflow, as well as empirical data that can inform future simulations and optimize the CKMR study design. Before starting the empirical analyses, we first performed a series of simulations to inform the study design. These simulations aimed to estimate the sample size required to detect a sufficient number of POPs and HSPs for reliable abundance estimation. Based on previous CKMR studies, at least 50 POPs/HSPs, and ideally around 100 POPs/HSPs, are needed to minimize the coefficient of variation in abundance estimates [10,25]. The simulations also allowed us to predict the expected number of detectable kin pairs given the available sample size. This preliminary step was essential to evaluate the feasibility of the CKMR approach for swordfish and to optimize sampling strategies under realistic logistical constraints. Then, 2068 individuals were genotyped using a single nucleotide polymorphism (SNP) dataset generated via DArTseq technology [26]. Kinship was analyzed using the Weighted Pseudo-Exclusion rate (WPSEX) and predicted pseudo-log-odds-ratio (PLOD) for each candidate kin pair, following the approach described in reference [13]. A single population structure scenario was considered, assuming a panmictic swordfish population across the Indian Ocean, consistent with the current IOTC stock management framework. In this context, this pilot-scale study represents a critical first step to evaluate logistical feasibility, validate

laboratory and analytical workflows, and assess the likelihood of detecting sufficient kin pairs before committing to full-scale implementation. The findings from this pilot study will help refine the design of future CKMR programs for *X. gladius* and support the development of more robust, genetics-based stock assessments to reduce key uncertainties in the management of this fishery.

2. Materials and Methods

2.1. Simulation Design

A simulation framework was developed to estimate the expected number of close-kin pairs under alternative sampling designs, based on the close-kin mark–recapture methodology [25]. Two classes of genetic relationships were considered: (i) parent-offspring pairs between sampled juveniles and adults, and (ii) half-sibling pairs among sampled juveniles, among sampled adults, and between juveniles and adults. Expected kin probabilities were derived from demographic and reproductive parameters using analytical expressions rather than explicit pedigree reconstruction.

In this demographic model, we assumed a stationary, age-structured population with constant recruitment and exponential age-specific survival. Individual growth, weight, and maturity were modeled using standard von Bertalanffy, allometric, and logistic functions, respectively. The parameters and data for the different functions were extracted from the IOTC swordfish stock assessment in 2023. The average recruitment was estimated at 2.9 million individuals over the last five years of the stock assessment. This level of recruitment is similar to that covering the sampling period of this study (2.85 million individuals), which makes the simulations comparable to the results from the kinship analyses. Reproductive output depended on both maturity and body weight for both sexes. Kinship probabilities were computed following standard CKMR formulations as in Hillary et al. [25]. For parent-offspring pairs, kin probabilities accounted for adult survival between offspring birth and sampling, adult reproductive output at the offspring's birth year, and total sex-specific reproductive output. For HSPs, probabilities were derived from cross-year convolutions of reproductive output, accounting for parental survival across birth-year gaps. Maternal and paternal HSP probabilities were computed separately and then summed. The same approach was extended to adult–adult and adult–offspring comparisons using inferred adult birth years (sampling year minus age at capture). Expected counts of POPs and HSPs were obtained by summing probabilities over all pairwise combinations, weighted by the number of individuals sampled in each cohort.

2.2. Sampling Design

Samples were selected from the IOSSS project [27]. Between 2009 and 2011, 3127 *X. gladius* samples were collected, of which 2359 from 24 different surveys (Supplemental Table S2) were identified as having sufficient tissue for DNA extraction, sequencing, and genotyping (Figure 1). For genetic analyses, we selected 2068 samples, prioritizing those collected within the IOTC convention area (Figure 1) between 2009 and 2011, while also including samples from 2006 obtained around the Glorioso Islands to improve the spatial representation of the dataset (Supplemental Table S2). To ensure balanced representation, we maintained equal proportions of samples across different life stages (1:1; juvenile and adult) and between sexes at each sampling site. Samples were classified as 'juvenile' or 'adult' based on their gonad stage using a maturity scale [27], where immature samples were recorded as juvenile, and all other mature samples were considered as adults. Maturity stage was estimated from the individual length compared to the sex specific Lm50 (length at which 50% of the population is mature), for fish that had been gutted or their gonads were not examined by experts.

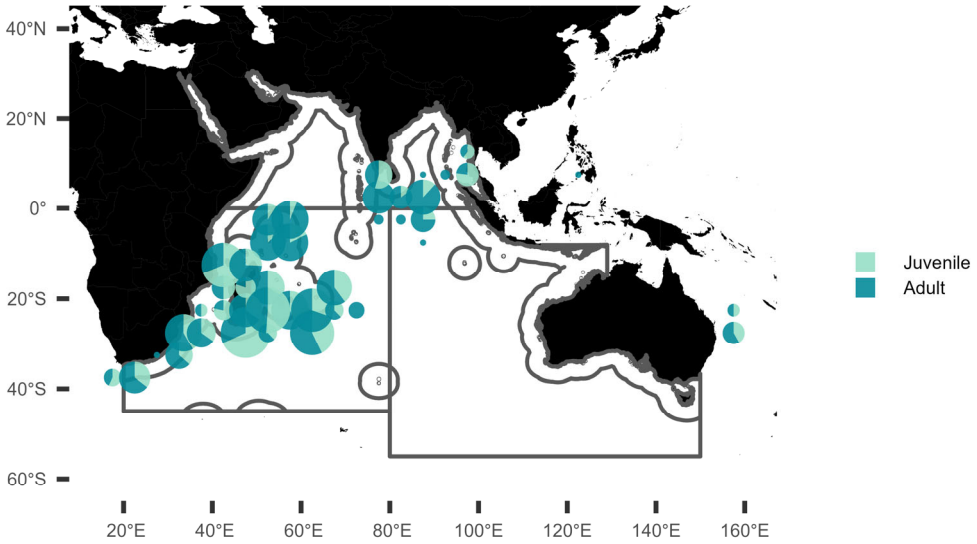

Figure 1. Sample location and log proportion of juveniles (light shaded) vs. adults (dark shaded) for each sampling survey in the IOTC area, indicated as polygons for one panmictic population of swordfish in the Indian Ocean.

2.3. Sample Submission and Processing

SNP genotyping of all selected samples was performed by Diversity Arrays Technology (DArT PL), based in Canberra, Australia. The DArTseq technology combines complexity reduction methods with next-generation sequencing platforms, enabling optimized sequencing of reduced genomic representations that are tailored to different organisms and applications. For *X. gladius*, DArT used the PstI-SphI enzyme combination and processed DNA samples following a modified version of the [28] protocol (Supplementary Information). This method integrates Illumina-compatible adaptors with unique barcodes, enabling efficient sequencing while enhancing the precision and adaptability of genomic assays across diverse species [26,28]. The DArTseq technology was previously applied for genotyping in other large pelagic fishes such as southern bluefin tuna, *Thunnus maccoyii* [13], yellowfin tuna, *Thunnus albacares* [29], Atlantic bluefin tuna, *Thunnus thynnus* [30] and blue skate, *Dipturus batis* [31]. After being applied to all 2068 samples, the DArTseq workflow produced FASTQ files that underwent an initial filtering phase for quality control to remove poor-quality sequences (Supplementary Information). Sequence data were then aligned to the *X. gladius* genome available on the National Center for Biotechnology Information (NCBI) (accession GCF_016859285.1, July 2022) to call SNP loci, followed by additional quality filtering steps detailed in the Supplementary information. Finally, DArT provided a dataset that included all genotyped samples, identified SNPs, call rates, and the co-dominant status of each sample.

Sequencing data were successfully obtained for 2227 individuals, comprising 2038 primary samples and 189 technical replicates, with one sample processed in four replicates instead of the standard two. Additionally, 30 individuals failed to yield sequencing results. Among the failed samples, eight were identified as belonging either to species other than *X. gladius* or interspecific hybrids. These non-swordfish samples were excluded from further analysis, resulting in 2030 samples retained for downstream analyses (Supplementary Table S3).

2.4. Computational Processing

2.4.1. Data Filtering and Conversion

As *X. gladius* is a diploid organism, SNP bases (A, T, C and G) are represented with two states for each individual at each locus. A total of 86,409 binary SNPs were returned

for 2030 individuals. To code the data, the following nomenclature was used: "0" for the homozygous reference allele, "1" for the homozygous SNP, and "2" for heterozygotes. Usually, the most common alleles are defined as the reference alleles to ensure that, regardless of the type of file provided by DArT, the nomenclature will always be the same. SNPs which could not be scored are indicated with "NA" or "-".

The dataset was filtered through multiple steps to retain only SNPs that were reliably scored, near Hardy–Weinberg equilibrium, free from linkage disequilibrium, and with a call frequency of at least 99%. Individuals were included if at least 95% of their SNPs were successfully genotyped. This process resulted in a final dataset consisting of 3479 SNPs across 2028 individuals, prior to kinship analysis. Detailed steps for SNP dataset processing and filtering are provided in the Supplementary Table S4.

2.4.2. Kinship

POPs and HSPs, as well as other second-degree kin, were identified using established statistical methods as outlined by reference [32]. The WPSEX, an exclusion statistic designed to account for null alleles and similar to the empirical exclusion rate when null alleles are negligible, was used to identify POPs [19]. As offspring inherit half of their genes from each of their parents, an excluding locus for a POP occurs when one individual has, e.g., 'AA', whereas the other has 'BB', which is impossible following inheritance rules for a true POP. The offspring should indeed inherit at least one A from its parent, except for rare mutation events and errors in sequencing and genotype assignment. WPSEX is often computed for pairs already identified as kin, helping to distinguish POPs from other kin types. A high WPSEX value indicates a lower probability of the pair being a POP and a higher likelihood of it being unrelated, while HSPs and FSPs generally exhibit lower WPSEX scores than unrelated pairs. WPSEX is particularly important for ensuring the robustness of CKMR analyses by minimizing errors in kinship assignments, which directly influence population size and demographic estimates. The threshold value for WPSEX used to distinguish POPs from other pair types was determined empirically at the level of the highest WPSEX for a POP.

For identifying HSPs, XHSPs, and other second-order kin for studying metapopulation structure and adult survival rate, we calculated the PLOD as described in reference [10], and also used in references [11,19,30]. For each locus, the probability of the observed genotypes for a pair can be computed under two hypotheses. First, a hypothesis where the pair is unrelated, then an alternative hypothesis where the pair is a second-order kin, such as HSP. The PLOD for each pair is the sum of the log-odds ratios across all retained loci for HSP: unrelated pairs (UP), as in Equation (1):

$$\mathrm{PLOD}_{\mathrm{HSP:UP}}(i,j) = \sum_{l \epsilon \mathrm{loci}} \log \frac{P\left[g_{il}, g_{jl} \middle| k_{ij} = \mathrm{HSP}\right]}{P\left[g_{il}, g_{jl} \middle| k_{ij} = \mathrm{UP}\right]} \quad (1)$$

where g_{il} is the genotype of individual i at locus l (AA, AB or BB).

Expected mean PLODs can be predicted for every true kin-pair type (POPs, FSPs, HSPs, etc.) based on allele frequencies. The thresholding and false-negative estimation follow the approach in [10]. These two indicators (WPSEX and PLOD) are complementary and essential for ensuring the robustness of CKMR analyses, particularly when it comes to validating parentage assignments.

3. Results

3.1. Simulation Design

CKMR simulations showed that the number of kin pairs increased significantly with the number of individuals sampled each year over different sampling scenarios (Figure 2). Regardless of the sampling duration (3, 4, or 5 years), the number of detected POPs was maximized when the juvenile: adult ratio was balanced, with an offspring proportion equal to 0.5 (Figure 2A). This reflects that POP detection requires sampling of both reproductive adults and offspring. Balanced age composition, therefore, maximizes the probability that both members of a POP are included in the dataset. In contrast, highly biased age compositions (i.e., dominance of either adults or juveniles) consistently resulted in fewer detected POPs, even under high overall sampling effort (Figure 2A,B). However, this pattern does not hold for HSPs, for which the number of detected kinship increases as sampling becomes increasingly biased toward juveniles. Because HSPs arise from shared parents across different cohorts, their detection primarily depends on sampling multiple offspring from the same reproductive adults rather than directly sampling the adults themselves. For swordfish, the maximum number of HSPs is obtained when the juvenile proportion reaches 0.9 (Figure 2C), highlighting that juvenile-dominated sampling maximizes the likelihood of detecting offspring originating from the same parental pool across cohorts.

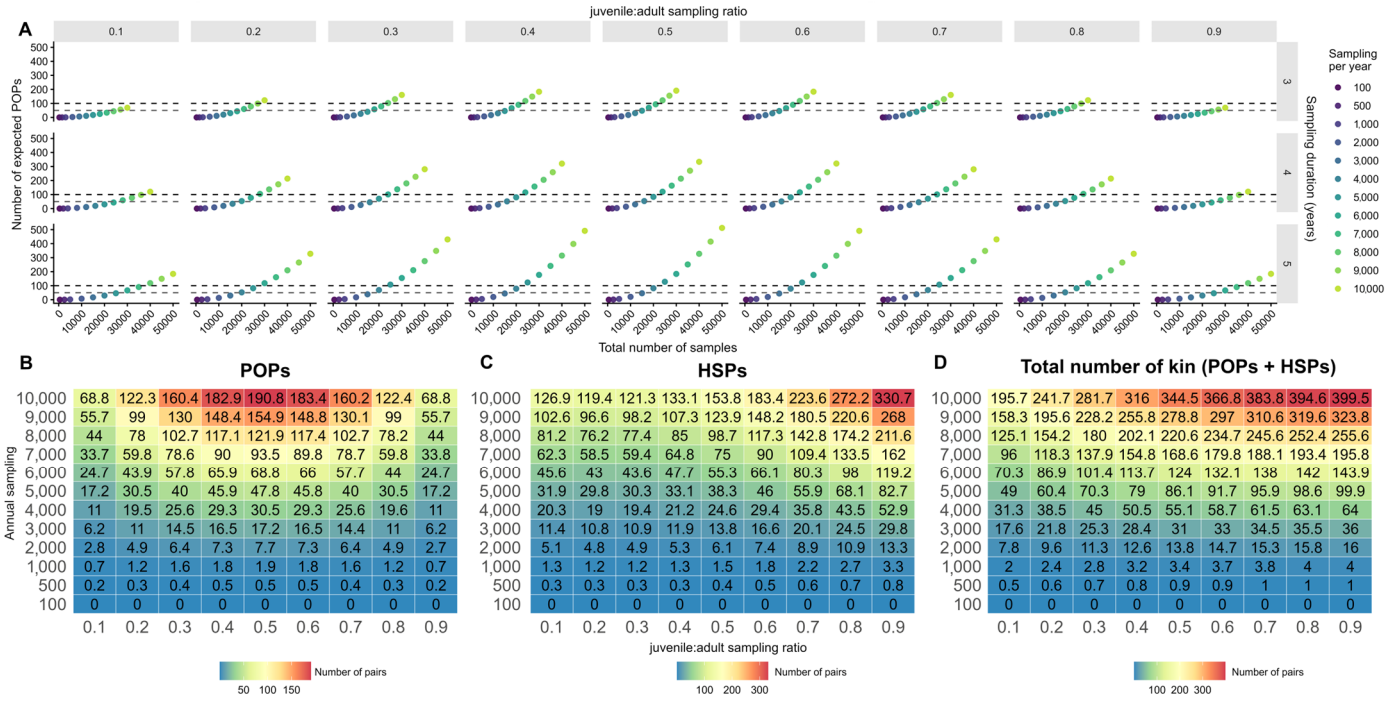

Figure 2. Effects of sampling intensity, age composition, and sampling duration on CKMR kinship detection: (**A**) expected number of parent-offspring pairs (POPs) across adult-juvenile ratios and annual sample sizes for different sampling durations (3, 4, or 5 years in the top, middle and bottom panel, respectively). Horizontal dashed gray and black lines represent reference thresholds of 50 and 100 POPs, respectively. (**B**–**D**) Predicted number of (**B**) parent-offspring pairs (POPs); (**C**) half-sibling pairs (HSPs); and (**D**) POPs + HSPs for different juvenile: adult sampling ratios (*x*-axis) for a range of total samples collected each year over three consecutive years (*y*-axis). The blue end of the color scale indicates fewer predicted numbers of POPs, HSPs or POPs+HSPs, and the red end indicates more predicted numbers.

These results also showed that for an equivalent total sample size, the number of kinship relationships decreases as the sampling period increases. This reflects the dilution of annual sampling intensity when total effort is spread over longer time periods, reducing the probability of detecting close-kin pairs within overlapping cohorts. For a total sample size of 30,000 individuals with a juvenile: adult ratio of 0.5, the number of POPs will be higher in three years, with 10,000 samples per year, than after five years with an annual sample size of 6000 swordfish (Figure S2).

Focusing on a sampling duration of three years, the simulations indicate that a minimum sampling threshold is required to obtain a substantial number of kin pairs. When more than 4000 individuals were sampled annually, including at least 40% juveniles, simulations consistently predicted more than 50 kin pairs (Figure 2D), which represents a practical lower bound beyond which CKMR starts to yield informative numbers of kin pairs. This number exceeded 100 kin pairs when annual sampling reached approximately 6000 individuals, even with a lower proportion of juveniles ($\geq$30%), indicating that increased sampling intensity can partially compensate for a less optimal age structure (Figure 2D).

If restricting the CKMR approach to POPs only, without considering HSPs, our simulations indicate that at least 6000 swordfish must be sampled annually, with a minimum of 30% juveniles or adults, to obtain a sufficient number of POPs for a robust prediction of adult abundance. Under the same age composition, achieving approximately 100 POPs would require a cumulative sampling effort of about 24,000 swordfish over a three-year period.

Simulations using the empirical sampling size and juvenile ratio of the IOSSS project indicated that the expected number of POPs that can be detected was 0.655 and 0.495 for HSPs.

To assess the sensitivity of kin-pair expectations to uncertainty in recruitment, we further quantified the coefficient of variation (CV) of the number of detected kin relationships by allowing annual recruitment to vary between 2,650,000 and 3,350,000 individuals, based on the range of recruitment estimates derived from the stock synthesis (SS3) assessment performed by the IOTC. Across this recruitment range, the CV of the number of kin pairs was homogeneous across the entire sampling matrix and remained low, with an overall value of 6.8%, indicating that moderate fluctuations in recruitment have a limited effect on expected CKMR outcomes under the sampling scenarios considered here.

3.2. Kinship Analysis

After quality filtering, our final dataset used for kinship analyses comprised 3177 SNP loci and 1695 individuals, including 943 adults and 752 juveniles, representing 0.44 of the samples (Supplemental Table S4). This dataset was used for all subsequent relatedness analyses.

Using the WPSEX metric, one POP was detected, corresponding to individuals GE-XA195 and GE-IE060 (Figure 3A). Based on the PLOD metric, at least ten pairs of individuals showed positive PLOD values, ranging from 1 to 220 (Figure 3B). The PLOD value associated with the POP identified by WPSEX was close to the expected value for parent-offspring pairs ($PLOD_{mean}$ POP = 266; Figure 3B), providing strong support for a true parent–offspring relationship between these two individuals.

Two additional pairs (GE-XA233/GE-IC015 and GE-IC031/GE-IC052) exhibited a PLOD value close to the expected value for half-sibling pairs or other second-order kin ($PLOD_{mean}$ HSP = 90; Figure 3B).

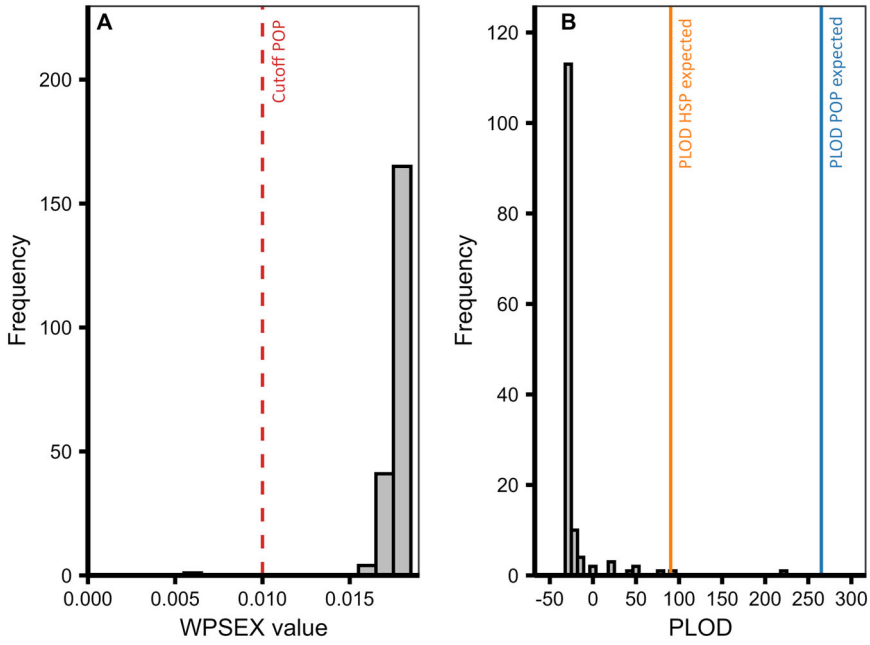

Figure 3. Distribution of (**A**) WPSEX and (**B**) PLOD values for the detection of close-kin relationships. (**A**) The distribution of WPSEX values for tested pairs of individuals is lower than 0.018. The vertical dashed red line indicates the WPSEX cutoff used to identify candidate parent-offspring pairs (POPs). (**B**) Distribution of PLOD values for pairs with positive likelihood support. Vertical solid lines indicate the expected mean PLOD values for parent-offspring pairs (POP; blue line) and for half-sibling pairs or other second-order kin (HSP; orange line).

For seven of the kin pairs with positive PLOD values, the precise kinship category could not be confidently assigned (PLOD > 1 and <52, Figure 3B). This uncertainty is mainly due to the limited number of detected kin pairs, which restricts the ability to define a robust PLOD threshold for second-order kin and to reliably estimate the associated false-negative rate.

Both kin pairs forming the POP and HSP were identified from the southwest Indian Ocean surveys of Reunion Island and south of Madagascar. The POP consists of a mature female (GE-XA195), which measured 233 cm (low jaw–fork length) at the time of collection south of Reunion Island on 18 November 2009.

One year later, a male offspring (GE-IE060) was retrieved approximately 753 km west, and measured 155 cm with stage 2 maturity. The first HSP consisted of two females retrieved 983 km away and several days apart in November 2009: GE-IC015, which was collected west of Reunion Island, measuring 188 cm with an unrecorded maturity stage, and GE-XA233, collected south of Madagascar, measuring 252 cm and classified as an adult. The second HSP involved IC031, sampled in November 2009, of unknown sex, measuring 173 cm, and IC052, sampled in June 2010, measuring 135 cm, and was identified as an immature female. Given the limited number of pairs, observing three pairs that are geographically close cannot be interpreted as evidence for or against a panmictic population, and similarly, an absence of POPs or HSPs between distant locations does not automatically indicate population structuring, which, for example, could be due to individual migration at the moment of capture. Additionally, the timescale at which CKMR detects parentage relationships is much shorter than the timescale over which population genetic structure develops. As a result, kinship patterns and population structure are not directly comparable metrics, with the exception of sufficient and long-term CKMR sampling and a marked absence of kin pairs between regions, which was not the case in our study.

4. Discussion

Since the initial application of the CKMR method [10], this approach has been used in several other species, highlighting its effectiveness at producing reliable abundance estimates. Hillary et al. [11] implemented CKMR to provide the first direct estimate of adult abundance and survival rates of the endangered white shark, *Carcharodon carcharias*, collected from two distinct populations in western Australia and eastern Australia/New Zealand, recovering 20 HSPs to approximate the size of the eastern population. Similarly, Bravington et al. [17] examined the endangered Northern River shark, *Glyphis garricki*, within six rivers, detecting four POPs, 34 FSPs and 130 HSPs to provide estimates of adult abundance, adult survival rate, and percent change per year of adult abundance. More recently, Trenkel et al. [19] examined the adult population size of the thornback ray, *Raja clavata*, in the Bay of Biscay. In addition to detecting two distinct populations within the bay, a total of 99 POPs and 431 FSPs were identified, though only 73 POPs were deemed usable to estimate adult abundance [19]. Each of these studies illustrates that the successful application of CKMR often requires substantial sampling effort to recover a sufficient number of close-kin pairs, particularly for robust estimation of demographic parameters. Consequently, careful study design is essential prior to data collection, including the use of simulation-based approaches to evaluate expected kin-pair recovery under different sampling scenarios and to optimize sampling strategies.

4.1. Sampling Design and Feasibility of CKMR Implementation

Our study on swordfish in the Indian Ocean demonstrated, through simulation analyses based on IOTC data, that implementing a CKMR approach for this species is feasible with a sampling scheme spanning three to five years. Specifically, simulations indicated that annual sampling efforts of approximately 7500 individuals over three years or 4500 individuals over five years, while maintaining comparable proportions of juveniles and adults ($p = 0.5$), would be required to recover 100 POPs. These simulations highlight the importance of balancing sampling duration, sample size, and the juvenile/adult ratio of the sample. When designing a CKMR approach, the choice of these parameters must take into account both the actual availability of resources and the time window for accessing samples. In terms of biological sampling, IOTC resolution 15/02 [33] requires one fish sampled per ton of fish landed. In the case of swordfish, that represents 30,000 fish measured each year by the different IOTC contracting parties. For the purpose of CKMR sampling, 6000 fish should be sampled each year, which represents 20% of the current sampling effort already undertaken by contacting parties. This sampling seems realistic for the Indian Ocean, given the 30,000 tons of swordfish caught annually in the basin. However, implementing such a study would require collaboration with and training of the scientific observers. This sampling program is currently being piloted by IOTC, starting in 2026.

Consistent with our simulations, three kin pairs were identified in the southwest Indian Ocean, including one POP and two HSPs. These results also align with the biological data for the sampled fish, as no immature individuals were identified as parents of adults. For the seven remaining potential kin pairs, characterized by PLOD scores ranging from 1 to 52, classification between second-order (e.g., HSPs) and higher-order relationships remains ambiguous due to substantial overlap in PLOD score distributions [19]. Consequently, increasing sample sizes is necessary to improve the robustness of the CKMR approach. Larger datasets would allow a more comprehensive understanding of PLOD score distributions across relatedness orders and reduce the false-negative rate in kin detection. In addition, integrating identity-by-descent (IBD)-based relatedness estimation could further enhance kin classification in future work. Recent approaches that infer IBD segments shared between individuals have demonstrated the capacity to resolve fine-scaled gradients of relatedness

beyond traditional pedigree or allele-sharing methods, even revealing previously hidden relatives and more continuous relatedness distributions from genomic data [34]. Applying IBD analyses alongside PLOD scoring in CKMR studies could help distinguish second-order from higher-order kinship more accurately, especially where PLOD distributions overlap, and yield deeper insights into the structure and dynamics of fisheries populations. Importantly, validation using samples of known relatedness is currently not feasible for swordfish. The species is not maintained in aquaculture, controlled crosses are unavailable, and spawning areas remain poorly characterized, preventing the collection of individuals with confirmed pedigree relationships (e.g., true POPs or HSPs).

The very limited number of kin pairs detected also has implications for abundance estimations. The effect of insufficient sampling intensity on CKMR estimation has been clearly demonstrated in recent simulation and empirical work, particularly by reference [35]. Through their study, they showed that abundance estimates derived from CKMR can become biased and highly imprecise when the sampled individuals represent only a very small proportion of the total population, regardless of the absolute population size. Importantly, they demonstrated that although the absolute number of samples required increases with population size, the proportion of the population that must be sampled to obtain accurate and reasonably precise estimates decreases as population size increases. These findings are consistent with our simulation results: when sampling intensity is low, the expected number of detected kin pairs (e.g., POPs or HSPs) declines sharply, increasing the uncertainty in abundance estimates. More broadly, empirical CKMR applications have shown that the precision of abundance estimates is strongly driven by the number of detected POPs. For instance, approximately 50–60 POPs have been associated with relatively low coefficients of variation (CV $\approx$ 0.15), whereas substantially lower numbers of POPs result in markedly higher uncertainty [35]. However, the threshold of 50 POPs is not intended to represent a strict requirement for accurate population size estimation. Rather, it is used as a practical reference point based on previous CKMR studies, where several tens of POPs have been shown to provide sufficient statistical power to estimate adult abundance with reasonable precision, assuming realistic levels of recruitment variability and sampling error [10,11,35,36].

4.2. Age and Sex Data Considerations in CKMR Analysis

Age and sex data are essential for CKMR inference; age at sampling determines the inferred year of birth and whether a potential parent was mature at the time of reproduction. In swordfish, age determination is commonly derived from reading aging structures (otoliths or spines); however, in this pilot study, age was approximated from body length due to the absence of systematic and exhaustive collection of aging structures during historical sampling campaigns. As highlighted by previous studies [19,20], uncertainty in age, particularly when inferred from length, can propagate into CKMR abundance estimates through errors in cohort assignment and maturity status. This issue becomes more pronounced in large individuals reaching asymptotic length, where the flattening of the growth curve makes length a poor proxy for age, and small measurement differences may translate into substantial age uncertainty. Such uncertainty may bias the distinction between HSPs and more distant intergenerational categories, such as GGPs, and may also affect the expected number of POPs in the likelihood. In addition, individual variability in growth rates, driven by genetic and environmental factors such as temperature and food availability, further increases uncertainty in age-length conversions. Future CKMR applications for swordfish must benefit from more precise ageing methods, such as validated otolith readings or emerging ageing techniques, such as epigenetic clocks [37], to reduce uncertainty in cohort assignment and maturity stages. Molecular approaches for genetic

sex determination would also improve inference, particularly for estimating sex-specific abundance and survival rates when sufficient XHSPs and POPs are available.

4.3. Implications of Population Structure for CKMR

One of the key assumptions of this study is that swordfish form a well-mixed population, consistent with the current "single stock" hypothesis used in management by the IOTC. Although not yet adopted by the IOTC, a recent study by Chevrier et al. [38] revealed the presence of a latitudinal population structure in Indian Ocean swordfish, linked to a structural variant on one chromosome. However, if this biological population subdivision is confirmed, this could violate the assumption of panmixia inherent to our CKMR model and potentially bias abundance estimates, particularly when sampling is spatially unequal among subpopulations. As we currently lack information on migratory flows between these potential two subpopulations and the proportions of each subpopulation in each fishery, it would be highly valuable to conduct a study similar to Martinez et al. [39] on striped marlin in the North Pacific, who reassessed the stock composition by combining previously generated and new SNP data to verify that the previously proposed second stock was actually an artifact, and in fact, the fishery was mixed with individuals from both the North Pacific and Oceania. Such an approach could assist in informing future management measures for swordfish in the Indian Ocean.

5. Conclusions

In conclusion, this study successfully tested and implemented integrated field and genetic protocols, along with simulation-based sampling strategies, to prepare for potential future CKMR analyses, thereby establishing a solid foundation for subsequent abundance estimation efforts despite the currently limited number of detected kin pairs. Importantly, these results provide a concrete scientific framework to inform the next steps of the IOTC toward the operational implementation of CKMR for swordfish in the Indian Ocean. Current management of swordfish at IOTC includes a management procedure based on the trend of the Japanese longline CPUE. Providing a fishery-independent abundance index would be critical for the harvest control rule based on CPUE, which can be sensitive to fishing pattern changes (e.g., changes in areas, target species).

Looking ahead, studies with substantially larger sample sizes of 18,000 or more individuals sampled over three or more years are expected to yield sufficient kin pairs to support robust abundance estimates. Simulation studies will be essential to guide the design of these future efforts by identifying optimal and feasible sampling strategies. However, simulation-based projections rely on demographic assumptions (e.g., survival, fecundity, age structure, and sampling design) and should therefore be interpreted as strategic guidance rather than precise forecasts. The empirical results presented here provide critical inputs for fine-tuning these simulations and analytical frameworks.

Based on our findings, we recommend several key steps for the implementation of a potential future large-scale CKMR program on swordfish in the Indian Ocean. These recommendations are intended to guide the implementation of a pilot sampling program by IOTC on a basin-wide scale. First, a dedicated study should be conducted to clarify the extent of stock mixing under a two-subpopulation hypothesis, including the incorporation of samples from the eastern Indian Ocean. Second, simulation analyses should be performed to determine the total sample size and the optimal juvenile-to-adult sampling ratio required to generate sufficient kin pairs for robust abundance estimation, while explicitly accounting for the inferred population structure. Third, the implementation of robust age-determination approaches such as otolith reading or epigenetic clock methodologies will be essential to minimize biases associated with size-based age estimation. Finally, sampling

should be conducted as homogeneously as possible across the geographic range of the putative subpopulation(s), in accordance with the identified optimal juvenile-to-adult ratio. Such sampling must rely on a dedicated program with clear and standardized protocols for tissue collection and handling, in line with current genomic standards. Inadequate genetic sampling campaigns can result in the loss of a large proportion of samples, as observed in our study, where only 83% of the sequenced samples were ultimately exploitable. Expanding the CKMR approach in this manner will help reduce major sources of uncertainty in stock assessments, ultimately improving the scientific basis for the management and conservation of this ecologically and economically important species. Nevertheless, the potential sustainability of this kind of project from an economic point of view must be highlighted. Assuming that the operational sampling design requires 18,000 samples over three years, this represents an annual sequencing cost of €240,000, or a total of €720,000 (sampling and bioinformatic costs not estimated). About 30,000 tons of swordfish are caught in the Indian Ocean annually. With an average first-sale price of €5 per kilogram [40], this represents €150 million annually. The annual cost of CKMR sequencing represents less than 0.5% of the first-sale market of swordfish in the Indian Ocean.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes11030149/s1, Figure S1: Specification for the temperature cycle for the PCR; Table S1: Parameters used to filter the raw sequencing data; Table S2: Samples selection from IOSSS project; Table S3: Numbers of samples and loci after each laboratory processing or computational filtering steps. The technical replicates (n = 189) were added by DArT prior to the sequencing and genotyping steps. The final number of samples/files does not include the technical replicates, the samples that failed to sequence, nor the non-swordfish samples; Table S4: CKMR Bioinformatic process; Table S5: Specifications for the metadata file provided by DArT. Each line defines a specific component within the final data report file; Table S6: Demographic and life-history parameters used in CKMR simulation scenarios; Figure S2: Effects of sampling intensity, juvenile/adult composition, and sampling duration on CKMR kinship detection; Figure S3: Map illustrating the spatial range of the three kin-pairs identified, POPs (blue) and HSPs (orange) [26,41–46].

Author Contributions: All authors were thoroughly involved in each step of the workflow; however, S.B. (Sylvain Bonhommeau) and S.B. (Serge Bernard) were responsible for the conceptualization of this study, while S.B. (Sylvain Bonhommeau), S.B. (Serge Bernard), A.-E.N. and D.A.C. were responsible for acquiring funding. A.-E.N. and D.A.C. led the process of sample design and selection. T.C. led the sample handling process with the help of J.C. and T.C. performed the bulk of the sequence data analyses, while T.C. and D.A.C. produced the first draft of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This work has been co-funded by the European Maritime and Fisheries Fund (EMFF, n°PFEA400018DM0980002) for the project FLOPPED. The IOSSS-Espadon project has been co-funded by the European Fund for Fisheries #DAE4/20090164.

Institutional Review Board Statement: Not applicable. The samples come from fish that were already dead, caught by commercial fisheries. No live animals are involved in our experimental design.

Data Availability Statement: For this manuscript, the datasets generated and analyzed can be obtained from the corresponding author upon reasonable request. The code used for the manuscript is available here: https://github.com/ThomasCOOOL/Feasability_Swordfish_CKMR (accessed on 1 March 2026).

Acknowledgments: We extend our thanks to the team at DArT for their work and guidance during the course of this project. Furthermore, we are sincerely grateful to Shane Baylis and Mark Bravington for sharing with us the *kinference* and *gbasics* R packages as well as their valuable feedback and insightful suggestions throughout the course of this project. We thank Laura Babet, Blandine Brisset and Hugues Evano for their assistance during the sample preparation phase of the project. We thank

our colleagues from the U.S. National Marine Fisheries Service (NMFS) of the National Oceanic and Atmospheric Administration (NOAA), Matthew Lauretta and John F. Walter, for helping us to estimate the number of POPs that could potentially be retrieved based on the number of genotyped samples. We are thankful to the partners of the IOSSS-Espadon project (European Fund for Fisheries #DAE4/20090164) for the sample collection over the Indian Ocean.

Conflicts of Interest: Authors Thomas Chevrier, Dominique A. Cowart, Anne-Elise Nieblas and Jérémie Chanut were employed by the Company for Open Ocean Observations and Logging (COOOL). The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Abbreviations

The following abbreviations are used in this manuscript:

CKMR	Close-Kin Mark-Recapture
IOTC	Indian Ocean Tuna Commission
SNP	Single Nucleotide Polymorphism
POP	Parent-offspring pair
HSP	Half-sibling pair
CPUE	Catch per unit effort
FSP	Full-sibling pair
GGP	Grandparent pair
FTP	Full-thiatic pair
XHSP	Cross-cohort Half-sibling pair
WPSEX	Weighted Pseudo-Exclusion rate
PLOD	Pseudo-log-odds-ratio
DNA	Deoxyribonucleic acid
UP	Unrelated pair
IBD	Identity-by-descent
CV	Coefficient of variation

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