Towards new data for neritic tuna stock assessment in the Indian Ocean: a toolbox of genetic and epigenetic approaches

Chevrier Thomas[1,2], Nieblas Anne-Elise[1], Cowart Dominique[1], Chanut Jérémie[1], Imbert Nguyễn Julie[2], Bernard Serge[3] and Bonhommeau Sylvain[2]

[1]Company for Open Ocean Observations and Logging (COOOL), Saint-Leu, La Réunion, France
[2]Ifremer, DOI Délégation Océan Indien, F-97420 Le Port, La Réunion, France
[3] LIRMM-CNRS, university of Montpellier, rue Ada, 34000 Montpellier, France

Neritic tuna and mackerel species managed by the Indian Ocean Tuna Commission (IOTC), including longtail tuna (*Thunnus tonggol*), kawakawa (*Euthynnus affinis*), frigate tuna (*Auxis thazard*), bullet tuna (*Auxis rochei*), narrow-barred Spanish mackerel (*Scomberomorus commerson*), and Indo-Pacific king mackerel (*Scomberomorus guttatus*), support important commercial, artisanal and recreational fisheries throughout the Indian Ocean. These species contribute substantially to food security, livelihoods and local economies in many countries. Despite their socio-economic importance, they remain among the most data-limited taxa assessed by the IOTC, receiving considerably less scientific attention than highly migratory tuna and billfish species.

Current stock assessments and management advice are constrained by several major biological and ecological knowledge gaps. Reliable information on age and growth remains limited for most species and regions, limiting the estimation of key life-history parameters required for population modelling. Similarly, sex-specific biological information is often unavailable, resulting in poorly characterized sex ratios in catches. Species identification can also be problematic in mixed fisheries, particularly for morphologically similar species (e.g. *E.affinis* ; *A. thazard* and *A. rochei*) and processed products, introducing potential biases into catch statistics. Furthermore, the spatial scale at which populations are structured, connected and replenished remains unresolved, despite the fundamental importance of stock structure for defining appropriate management units and assessing stock status (Feutry *et al.* 2025).

Over the last two decades, molecular biology has emerged as a powerful and cost-effective source of fisheries-independent information capable of addressing many of these limitations. Advances in DNA sequencing technologies, coupled with rapidly decreasing analytical costs, have transformed the accessibility of molecular tools for fisheries science. Genetic approaches are now implemented to investigate population

structure (Vaux *et al.* 2021, Chevrier *et al.* 2024, Feutry *et al.* 2025), connectivity (Smith 2025), effective population size (Hillary RM *et al.* 2018), species identification (Chiba *et al.* 2021) and kinship relationships (Bravington MV, Grewe, and Davies 2016, Bravington MV, Skaug, and Anderson 2016, Anderson *et al.* 2019, Chevrier *et al.* 2026). Several of these methods have already demonstrated their value for highly migratory species, including tropical tunas (Chiba *et al.* 2021, Vaux *et al.* 2021), billfishes (Chevrier *et al.* 2024, Smith 2025, Chevrier *et al.* 2026) and sharks (Hillary RM *et al.* 2018).

More recently, epigenetic approaches have emerged as a complementary source of biological information. Epigenetics refers to molecular modifications that influence gene activity without altering the underlying DNA sequence, among which DNA methylation is currently the most extensively studied mechanism in fishes (Anastasiadi and Piferrer 2019, Mayne *et al.* 2020, Weber *et al.* 2024, Chevrier *et al.* 2026). Epigenetic markers have shown considerable promise for addressing fisheries questions that are difficult to resolve using traditional genetic methods. In particular, methylation-based approaches are increasingly being used to estimate individual age (Anastasiadi and Piferrer 2019, Mayne *et al.* 2020, Weber *et al.* 2024, Chevrier *et al.* 2026), reconstruct environmental histories (Carrothers *et al.* 2025, McDonough *et al.* 2026), investigate phenotypic plasticity (Heckwolf *et al.* 2020) and identify biological responses to environmental stressors (Anastasiadi, Díaz, and Piferrer 2017, Carrothers *et al.* 2025). Epigenetic clocks based on DNA methylation patterns have recently achieved remarkable accuracy across a wide range of vertebrate species (Anastasiadi and Piferrer 2019, Lu *et al.* 2023, Bock *et al.* 2026, Chevrier *et al.* 2026), offering a potential alternative to conventional ageing techniques.

The combination of genetic and epigenetic methodologies now constitutes an expanding molecular toolbox capable of generating multiple streams of information directly relevant to fisheries assessment and management from a minimal non-invasive tissue sample. These approaches can contribute to improved species identification, stock delineation, demographic monitoring, age estimation, and sex determination. Importantly, many of these tools can be applied to tissues already routinely collected during fisheries monitoring programmes, making their implementation increasingly feasible within existing sampling frameworks (Chevrier *et al.* 2026).

This review aims to provide an overview of the principal genetic and epigenetic tools currently available and applicable for fisheries science. By synthesizing recent methodological developments and examples from related large pelagic species, we highlight how molecular approaches can help address persistent data gaps and support the

development of more robust, evidence-based management strategies for these economically and ecologically important resources.

1. Species Identification

Accurate species identification is fundamental to fisheries management, as stock assessments, catch statistics and conservation measures all rely on species-specific information. Misidentification can lead to biased estimates of catch, abundance and exploitation rates, particularly when morphologically similar species are landed together or processed before sampling. This issue is especially relevant in multispecies fisheries, where visual identification may be challenging for juveniles, damaged specimens or closely related taxa such as *E.affinis*, *A. thazard* and *A. rochei*.

Genetic approaches are already being used to identify specific species of certain pelagic tunas, particularly through the amplification and DNA sequencing of certain mitochondrial genes (e.g., COI, cytb, etc.) (Herath, Perera, and Hettarachchi 2025). However, this type of approach requires sequencing and bioinformatics analysis steps, such as processing sequencing files and aligning them with databases, which are not necessarily accessible to all laboratories, particularly those without a sequencer.

Other more rapid molecular approaches are available, such as “DNA barcoding”, which provide reliable species identification from small tissue samples using only PCR assays and gel electrophoresis. Using this approach, we have been able to identify specimens of large pelagic species such as billfish, tuna and two neritic tuna (Fig.4).

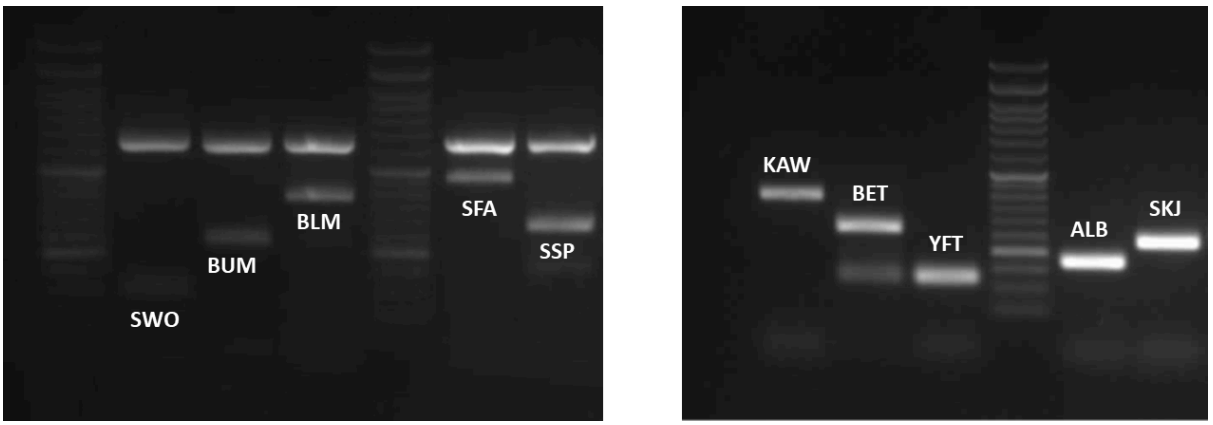

Figure 1: Current authors’ analysis using 2% electrophoresis gel for amplicons obtained species specific primers to discriminate between billfish and tuna species. SWO: Swordfish (*Xiphias gladius*) ; BUM: blue marlin (*Makaira nigricans*); BLM: black marlin (*Makaira indica*); SFA: sailfish (*Istiophorus*

platypterus); SSP: spearfish (*Tetrapturus angustirostris*); KAW: mackerel tuna (*Euthynnus affinis*); BET: bigeye tuna (*Thunnus obesus*); YFT: yellowfin tuna (*Thunnus albacares*); ALB: albacore tuna (*Thunnus alalunga*); SKJ: skipjack tuna (*Katsuwonus pelamis*). The internal PCR control for billfish gels is 16S which corresponds to the top band on the left picture and is used to check whether the PCR runs correctly.

2. Molecular sex determination

Accurate sex determination is an important component of fisheries science, as many demographic and life-history parameters differ between males and females. Sex-specific differences in growth, mortality, age at maturity, reproductive output and migration behaviour can strongly influence population dynamics and stock productivity (Farley *et al.* 2014, 2017, 2021, Corriero *et al.* 2020). Reliable information on sex ratios within catches is therefore essential for assessing spawning potential, monitoring population structure and improving stock assessment models. However, sex determination can be challenging in many fish species, particularly for species without any external sexual dimorphism but also for species gutted onboard for conservation purposes.

Molecular approaches offer a promising and low cost alternative by enabling rapid and accurate sex identification from small tissue samples, thereby providing valuable biological information for fisheries monitoring programmes. For some species of neritic and pelagic tuna, particularly *Thunnus tonggol* and *Katsuwonus pelamis*, genetic tests exist to determine sex (Chiba et al. 2021). However, this PCR-based approach was originally designed for pelagic tunas, for which it works very well (Fig. 3), but much less so for neritic tunas (Chiba et al. 2021). Consequently, sex determination using these primers are not reliable for neritic tuna species, and it would be worthwhile to develop PCR primers specific to neritic tuna.

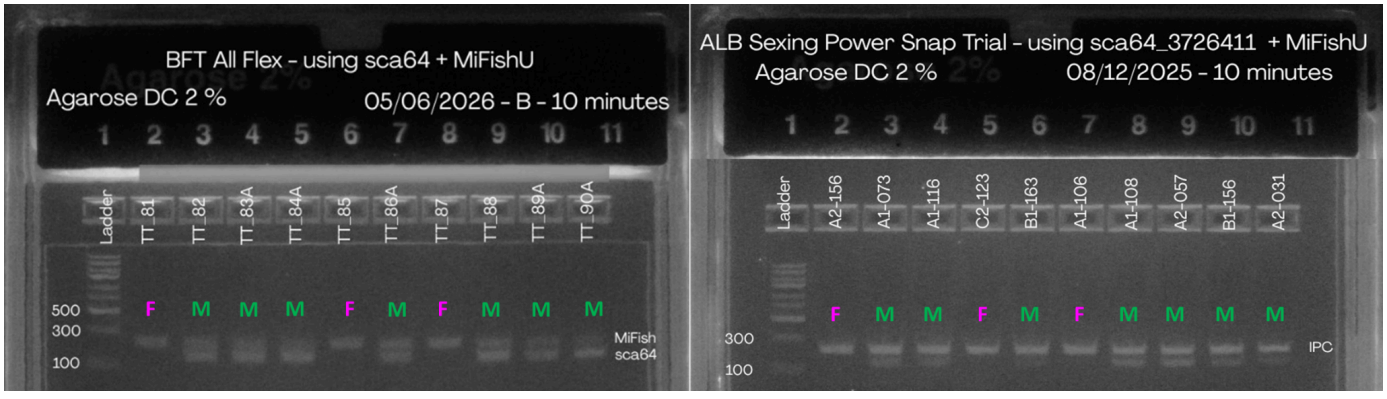

Figure 2: Current authors' analysis using 2% electrophoresis gel for amplicons obtained using the primers III from Chiba et al. (2021) on bluefin (*Thunnus thynnus*, BFT) and albacore (*Thunnus alalunga*, ALB) tuna. "F" stands for female genotypes and "M" for male genotypes. The internal PCR control (IPC) for both gels is MiFishU (Miya et al. 2015). A second band below the IPC band indicates the sample is a male.

3. Epigenetic clock

Accurately determining the age of individuals is a cornerstone of ecological and biological research. Age information underpins a wide range of applications, from assessing population dynamics to evaluating ecosystem health (Ono *et al.* 2015). Reliable age estimates are essential for inferring key life-history traits such as growth rates, age at sexual maturity, and age-specific fecundity (Schaffer 1974, Western 1979, Frisk, Miller, and Fogarty 2001). Consequently, the ability to estimate age enables more robust monitoring of demographic parameters, including population age structure and reproductive potential. Despite its central role, chronological age remains difficult to determine in wild animal populations, particularly in species lacking clear aging markers in hard structures (e.g., vertebrae, otoliths, teeth) or with limited access to long-term observational data (Cailliet *et al.* 2001, Campana 2001). Moreover, such techniques have some shortcomings, they can be costly and time consuming (Helser *et al.* 2019), of low accuracy for some species, require inter-calibration and cross-validation between labs, and are necessarily lethal in the case of otolith and vertebra reading (Campana 2001, Anastasiadi and Piferrer 2019).

Biological aging is a widespread process across animal species and is typically accompanied by molecular modification (Boyd-Kirkup *et al.* 2013, Booth and Brunet 2016). Among the molecular processes associated with aging, DNA methylation at cytosine-phosphate-guanine (CpG) sites has been shown to change with age (Horvath and Raj 2018, Bell et al. 2019, Unnikrishnan et al. 2019, Chen, Ganz, and Sehl 2022, Wang et al. 2022). Methylation profiles have been used to develop biomarkers of age known as epigenetic clocks, which predict chronological age with remarkable accuracy (Horvath 2013, Horvath and Raj 2018, Arneson *et al.* 2022, Lu *et al.* 2023, Teschendorff and Horvath 2025).

The first epigenetic clock on fish was developed by Anastasiadi and Piferrer (2019) on the European sea bass, a marine fish the age of which can be determined with accuracy. Using muscle samples they were able to amplify 48 CpGs from four genes to develop an age predictor in fish that is accurate (r = 0.824) and precise mean average error (MAE = 2.149 years). Since that study, an increasing number of epigenetic clocks have been identified in various fish species, such as zebrafish (Mayne *et al.* 2020), red snapper (*Lutjanus campechanus*) and red grouper (*Epinephelus morio*) (Weber *et al.* 2022), deepwater scorpionfish (*Helicolenus dactylopterus*) (Weber *et al.* 2024), Florida bass (*Micropterus salmoides*) (Weber *et al.* 2025), Atlantic cod (*Gadus morhua)* (Anastasiadi *et al.* 2026) and albacore tuna (*Thunnus alalunga*) (Chevrier *et al.* 2026).

More recently, we applied a targeted bisulfite approach to the yellow-edged lyretail (*Variola louti*), a reef-associated grouper widely distributed throughout the western Indian Ocean, to examine if an epigenetic clock can be developed for this species.

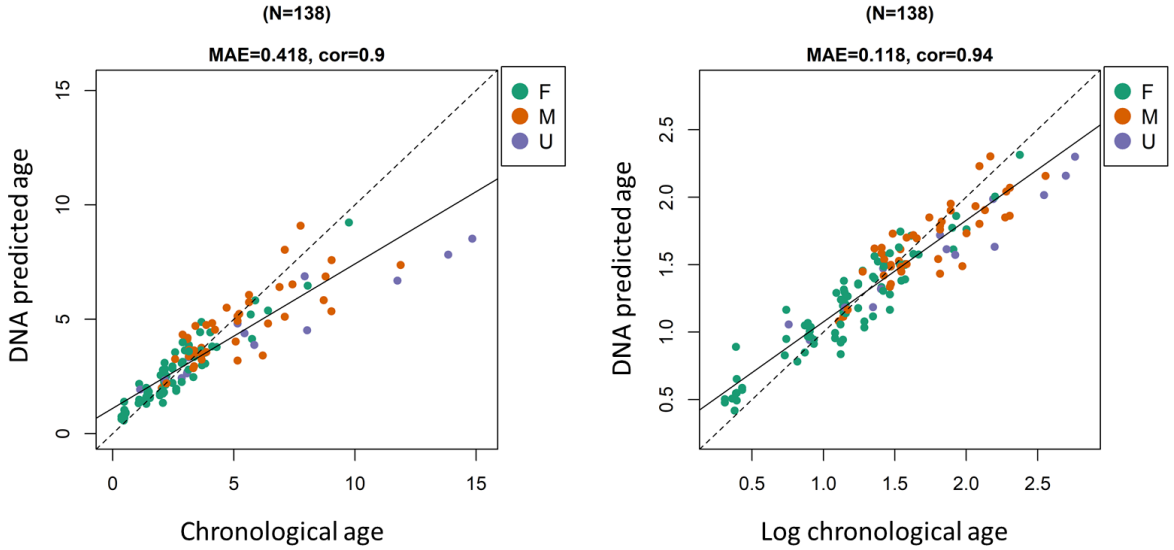

Figure 3: Leave-one-out cross validation (LOOCV) study of the epigenetic clock for Yellow-edged lyretail (*Variola louti*) to estimate the age of individuals from the methylation of specific genome sites. (A) Chronological age (B) log(chronological age). Green colors correspond to females (F), orange males (M) and purple is for undetermined sex (U).

The cross-validation using the Leave-one-out cross validation (LOOCV) for both epigenetic clock based on the otolith age and using a log transform of the otolith age resulted in epigenetic clocks models with a Pearson correlation coefficient (r) of 0.9 and 0.94 respectively and a median absolute residual error (MAE) of 0.418 and 0.125 years after transformation (Fig. 1). In both cases, the accuracy is significantly less than one year, thus confirming the full potential of this approach.

Beyond the age variable, we tested whether epigenetic markers can also accurately predict fish size using the fork length of *Variola louti*. The LOOCV metrics indicate a strong predictive ability of fish size, with a Pearson correlation coefficient of r = 0.97 and a MAE of 2.36 cm (Fig 2). This shows that methylation profiles are a very powerful tool for predicting a fish's size using just a piece of fin.

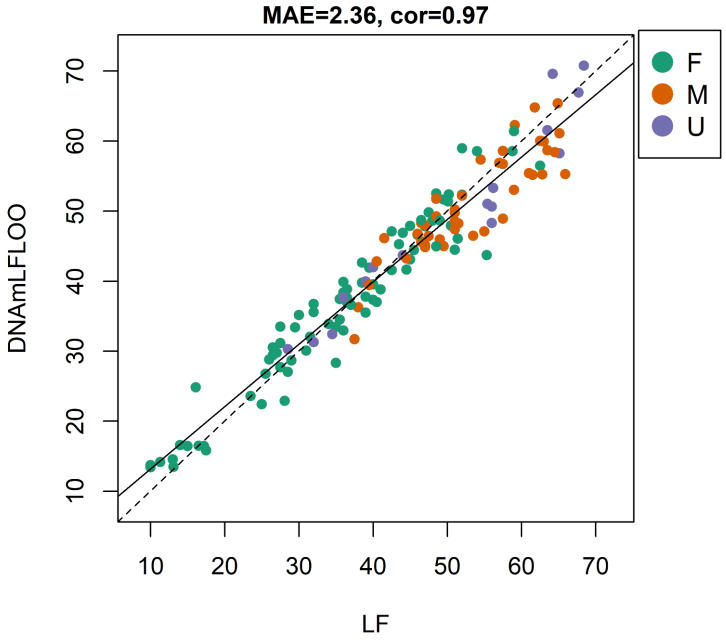

Figure 4: LOOCV study of the epigenetic predictors for yellow-edged lyretail (*Variola louti*) to predict fork length (LF). Green colors correspond to females (F), orange males (M) and purple is for undetermined sex (U).

Similarly, using the total weight of the fish, the LOOCV analysis once again demonstrated strong statistical performance with an r value of 0.95 and a median absolute error of 263 grams (Fig 3).

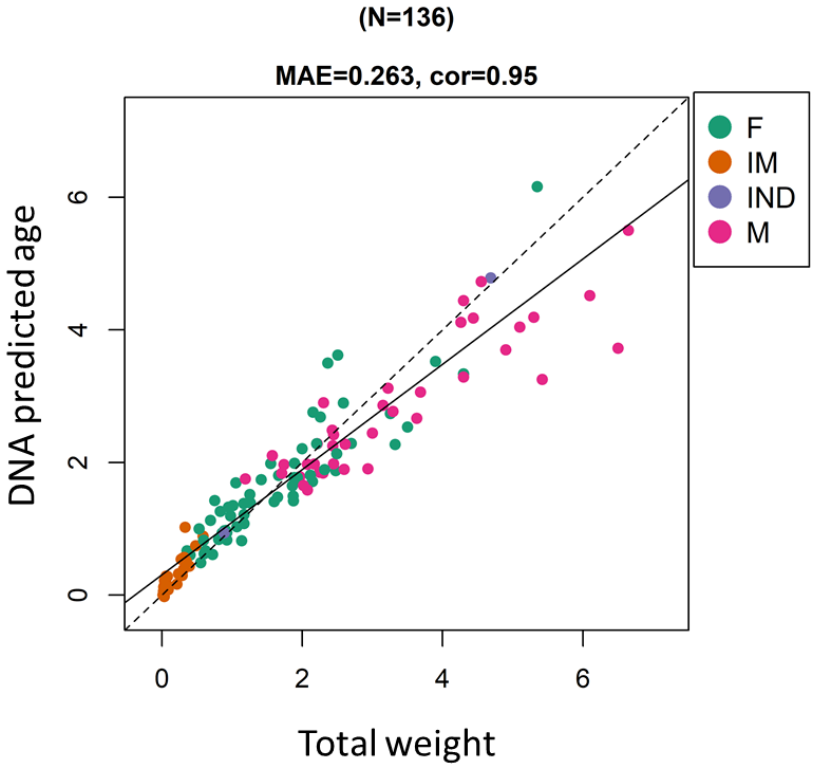

Figure 5: LOOCV study of the epigenetic predictors for yellow-edged lyretail (*Variola louti*) to predict total weight (kg). Green colors correspond to females (F), orange immature (IM), purple is for undetermined sex (IND) and pink is corresponding to the male (M).

To construct an epigenetic clock, it is essential that sampling be conducted uniformly across the entire age range of the target species. A study conducted by Mayne, Berry, and Jarman (2021) showed that a minimum of 70 samples is required, with an optimal number of 134 samples, to obtain the best possible metrics associated with the epigenetic clock.

This work, along with previous studies, demonstrate that methylation-based biomarkers can be developed across a wide range of fish taxa and a wide range of biological parameters. Given the current lack of age data for several neritic tuna species in the Indian Ocean, epigenetic approaches represent a promising avenue for generating key biological information required for fisheries assessment and management. Furthermore, the use of epigenetic markers for size and weight can have important implications for industry, commercial, and research applications.

4. Population structure

Stock assessments require the identification of biological populations that may respond differently to exploitation (Carvalho and Hauser 1994). Within a species, subpopulations can become demographically isolated through behavioural, ecological or geographical processes, resulting in reduced connectivity and, in some cases, local genetic adaptation (Ciftci and Okumus 2002, Reiss *et al.* 2009). Identifying such population structure is therefore a fundamental prerequisite for effective fisheries management (Reiss *et al.* 2009, Neilson *et al.* 2013). When management units do not reflect the underlying biological structure of a species, vulnerable population components may be disproportionately impacted by fishing pressure, potentially leading to local depletion and a reduction in overall stock resilience (Carvalho and Hauser 1994, Righi *et al.* 2020).

The challenge of identifying biologically meaningful population units is particularly pronounced in highly mobile marine species. Pelagic fishes often exhibit low levels of genetic differentiation due to extensive dispersal capabilities, the absence of obvious geographical barriers, and the resulting high levels of gene flow (Ward, Woodwark, and Skibinski 1994). Consequently, detecting subtle population structure has historically been difficult using traditional genetic markers such as microsatellites. However, recent advances in genomic technologies, particularly the use of thousands of single nucleotide polymorphisms (SNPs), have substantially increased the power to detect fine-scale genetic structuring.

A notable example is the swordfish (*Xiphias gladius*) in the Indian Ocean. For many years, available genetic evidence based primarily on microsatellite markers supported the assumption of a single panmictic population throughout the basin (Lu *et al.* 2006, Muths *et al.* 2009, 2013, Grewe *et al.* 2020). More recently Chevrier *et al.* (2024), genome-wide SNP analyses revealed the presence of two genetically differentiated population components distributed along a latitudinal gradient, with this structuring associated with a large chromosomal inversion. These findings demonstrate how genomic approaches can uncover biologically relevant patterns of population structure that remained undetected using earlier methodologies.

Similar approaches have been applied to three neritic tuna and tuna-like species in the Indian Ocean: Longtail Tuna (*Thunnus tonggol*), Kawakawa (*Euthynnus affinis*) and narrow-barred Spanish mackerel (*Scomberomorus commerson*) (Feutry *et al.* 2025). Genome-wide SNP analyses revealed significant population structure in all three species and rejected the assumption of a single homogeneous stock across the sampled regions of the Indian Ocean. Nevertheless, important gaps remain, as sampling coverage is still limited in the western Indian Ocean and does not adequately cover the full distribution range of these species. Expanding genomic sampling should therefore be considered a priority for future research and monitoring programmes coordinated through the IOTC. Particular attention should be given to underrepresented areas of the western Indian Ocean and to regions connecting the Indian and Pacific Oceans, where population connectivity remains poorly understood.

5. *Close-Kin Mark-Recapture (CKMR) for abundance and population structure*

CKMR is an emerging genetic approach that uses kinship relationships identified among sampled individuals to estimate demographic parameters at the population level. By detecting Parent-Offspring Pairs (POPs) or other close relatives such as Half-sibling pairs (HSPs) within a population, CKMR can provide estimates of adult abundance, survival and reproductive output without requiring the physical tagging and recapture of individuals. This approach is particularly valuable for species, for which conventional mark-recapture studies can be logistically challenging, costly or impractical.

In recent years, CKMR has been successfully applied to several commercially important marine species, demonstrating its potential to generate robust population estimates even in data-limited fisheries (Rawding, Sharpe, and Blankenship 2014, Bravington MV, Grewe, and Davies 2016, Hillary RM *et al.* 2018, Bravington M *et al.* 2019, Ruzzante *et al.* 2019, Marcy-Quay *et al.* 2020, Trenkel *et al.* 2022). Because accurate kinship inference relies on large numbers of genetic markers and often benefits from reliable

age, sex and population structure information, CKMR is particularly well suited to integration with modern genomic and epigenetic tools. For neritic tuna species in the Indian Ocean, CKMR could provide a powerful means of estimating adult abundance and improving demographic understanding, thereby reducing key uncertainties in stock assessments and management advice. To this end, it would be useful to conduct simulations on the various species of neritic tuna to assess the feasibility of implementing this approach, following the example of Hillary *et al.* (2022) for Yellowfin tuna and Chevrier *et al.* (2026) for swordfish. This would provide an idea of the sampling effort required in terms of the number of fish, the proportion of juvenile/adult as well as the spatial and temporal scope. Globally, the number of samples required for this type of approach is considerably higher than for the other approaches presented, reaching, for some species, several thousand samples per year.

Conclusion and recommendations

Neritic tuna species managed by the IOTC continue to have a lack of important biological and demographic data. Uncertainties regarding population structure, species identification, age composition, sex ratios and population abundance remain particularly pronounced for several neritic species. Recent advances in molecular biology provide a multiple and rapidly expanding toolbox capable of addressing many of these limitations.

As demonstrated by recent studies on tunas, billfishes and other marine fishes, genetic and epigenetic approaches can give information that is either difficult or impossible to obtain through traditional approaches. Genome-wide SNP datasets can identify biologically meaningful population units and quantify connectivity among regions. DNA barcoding can improve species identification in mixed fisheries and validate catch statistics. Molecular sexing approaches can provide accurate sex-ratio information where external sexual dimorphism is absent. Epigenetic biomarkers offer promising opportunities for individual biological parameters estimation (age, length, sex etc), while close-kin mark-recapture approaches have the potential to provide independent estimates of adult abundance and reproductive population size. Importantly, these methods rely on the same biological material: a piece of tissue sample collected from an individual fish. Consequently, a well-designed sampling programme can generate resources that support multiple current and future applications. The rapidly decreasing costs of genomic analyses further increase the feasibility of integrating these approaches into routine fisheries monitoring programmes.

The implementation of these approaches would progressively build a molecular monitoring framework capable of complementing existing data workflows. Such an approach has the potential to substantially reduce current uncertainties, improve stock assessments

and support more sustainable management of neritic tuna resources throughout the Indian Ocean.

Some recommendations:

1. Establish routine tissue collection programmes within observer programmes, harbor sampling activities and national fisheries monitoring programs for all major neritic tuna species managed by the IOTC.
2. Develop standardized sampling protocols to ensure consistency in tissue collection, preservation, metadata recording and long-term storage.
3. Expand genomic sampling coverage throughout the Indian Ocean, across the Indo-Pacific region and southeast Atlantic region to improve understanding of stock structure and inter-oceanic connectivity.
4. Evaluate the feasibility of integrating genomic and epigenetic data into stock assessment frameworks, particularly for species where conventional biological information remains limited.

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