A Spatial Perspective of the Population Structure and Connectivity of Two Small Tuna Species, *Katsuwonus pelamis* (Skipjack Tuna) and *Euthynnus affinis* (Kawakawa), in the Southwest Indian Ocean

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ABSTRACT

Katsuwonus pelamis and *Euthynnus affinis* are two small tuna species of socio-economic and fisheries importance across the Southwest Indian Ocean (SWIO). There is currently a dearth of data and information around various aspects of their biology in the SWIO, including their population structure and connectivity. The availability of such data, including spatially represented biological data, has the potential to address current management discrepancies through the provision of more robust assessments into the stock structure and connectivity of these species and their stocks. This study explored a spatial perspective of the population structure and connectivity of *K. pelamis* and *E. affinis* fisheries in the SWIO to determine the suitability of current Indian Ocean Tuna Commission (IOTC) management measures for the species. It employed two primary data sources: a) Western Indian Ocean Marine Science Association's (WIOMSA) Marine and Coastal Science for Management (MASMA) Project and b) IOTC. WIOMSA MASMA and IOTC data was collected throughout many countries and small island states in the SWIO, and pertained to genetic diversity, catch-weight, length-at-maturity, and morphometrics. Such data were combined and analysed to conduct geospatial analysis. Spatially illustrated genetic divergence, length-at-maturity, catch-weight, and morphometric data supported the presence of three reproductively isolated subpopulations of *K. pelamis* in the SWIO (Dar es Salaam, Tanzania, and Kenya; Mtwara, Tanzania, Mozambique, and Eastern Cape, South Africa; Seychelles). Only spatially depicted genetic divergence data, and morphometrics, supported that *E. affinis* populations were not panmictic in the SWIO, with genetic divergence data supporting the presence of three reproductively isolated subpopulations of *E. affinis* (Northern Mozambique and Kenya; Tanzania; Seychelles). Spatially illustrated length-at-maturity and catch-weight data however did not provide sufficient evidence supporting spatial structuring among *E. affinis* populations in the SWIO. Whilst the present analyses are not definitive to delineate exact stock boundaries, findings supported the contention of current IOTC management policy, indicating spatial population complexity for both species. Future research must increase representation of fishery independent samples and must investigate oceanographic variables driving potential stock separation to further support effective management reform. Until available, a precautionary approach should be adopted for the management of these species across the SWIO, considering the presently proposed distribution of their stocks separate for management.

Key words: marine; fisheries management; Southwest Indian Ocean; geospatial analysis; spatial management; *Katsuwonus pelamis*; *Euthynnus affinis*

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LIST OF ACRONYMS

ANOSIM	Analysis of Similarity
BH	Body Height
CMMs	Conservation Management Measures
CPCs	Collaborating Non-Contracting Parties
ddRADseq	High-throughput Restriction Site-Associated DNA sequencing
DL1	First Dorsal Length
DNA	Deoxyribonucleic Acid
DWFNs	Distant Water Fishing Nations
EH	Eye Height
EPO	Eastern Pacific Ocean
FAO	The Food and Agriculture Organization
FL	Fork Length
FMUs	Fisheries Management Units
GIS	Geographic Information Systems
GPS	Global Positioning System
HCRs	Harvest Control Rules
IATTC	Inter American Tropical Tuna Commission
ICCAT	International Commission for the Conservation of Atlantic Tuna
IDW	Inverse Density Weighting
IO	Indian Ocean
IOTC	Indian Ocean Tuna Commission
IUU	Illegal, Unreported, and Unregulated
KDE	Kernal Density Estimation
MASMA	Marine and Coastal Science for Management
MDS	Multi-dimensional scaling
MH	Mouth Height
MPA	Marine Protected Area
MSY	Maximum Sustainable Yield
MW	Mouth Width
OCKL	Length from Posterior Operculum Margin to the Caudal Keel
PCIA	Phenol/Chloroform/Isoamyl Alcohol
PCoA	Principal Coordinate Analysis
RMFOs	Regional Fisheries Management Organisations
SIMPER	Similarity Percentages Breakdown
SMMs	Spatial Management Measures
SWIO	Southwest Indian Ocean
TAC	Total Allowable Catch
TG	Thorax Girth
UJL	Upper Jaw Length
WCPFC	Western and Central Pacific Fisheries Commission
WCPO	Western Central Pacific Ocean
WIO	Western Indian Ocean
WIOMSA	Western Indian Ocean Marine Science Association
WPO	Western Pacific Ocean

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DECLARATION

I, Christopher John Taylor, hereby declare that the contents reported in the present thesis was conducted at the Department of Ichthyology and Fisheries Science (DIFS), Rhodes University, Makhanda, under the supervision of Christopher Bova, Ian Meiklejohn, and Warwick Sauer. The work presented here is that of the author and has not been submitted to any other university.

Signed: . . . .

Date: 2024/01/18

CHAPTER 1: Literature Review

1.1 Introduction

Tuna fisheries are placed among the most exploited, valued, and essential fishery resources globally (Campling 2012). These fisheries play critical roles towards the development of national social and economic structures through the provision of jobs, income, and food and nutritional security across developed and developing nations (Andriamahefazafy et al. 2019). The effective management of highly migratory fish stocks such as tuna and tuna-like species, is highly complex and challenging, as it involves the selective exploitation of multiple species using various gear types and extends over multiple national jurisdictions as well as the high seas (Azmi and Hanich 2021). Regional fisheries management organisations (RFMOs) are responsible for the implementation of localized management strategies, which are generally undertaken through spatial management measures (SMMs) (McCluney et al. 2019). This involves the establishment of regulations, often in the form of harvest control rules (HCRs) and other conservation management measures (CMMs) that are based on the stock status of target species in relation to preordained reference points, which ensures future sustainable exploitation of the fishery in question (De Bruyn et al. 2013, McCluney et al. 2019). The implementation of successful and effective SMMs is, however, contingent on the availability and accessibility of current data and information that can be synthesised to support decision making at all levels of fisheries management. Spatially represented biological data has the potential to address current management discrepancies through the provision of more robust assessments into the stock structure and connectivity of these species and their stocks. The present thesis therefore emphasizes the importance of collating, synthesizing, and analysing spatial data concerning the important biological and fishery characteristics of exploited fishery stocks such as tuna and tuna-like species. Consolidation of this information is critical toward ensuring well-informed decision making, that will correspond to the implementation of robust and effective management policy. These processes promote sustainable and resilient exploitation practices, which is fundamental toward protecting and conserving the underlying socio-economic and ecological value of these fishery resources in future years.

The Western Indian Ocean (WIO) supports approximately 15% of the total annual tuna species harvested globally, highlighting the scale, productivity, and overall value of the tuna fishing industry across the region (Andriamahefazafy et al. 2019). The Southwest Indian Ocean (SWIO), encompassing the area from South Africa to the northern border of Somalia and extending east to the Seychelles, provides a diversified environment for a variety of highly mobile tuna species, and spans over five continental nations, Somalia, Kenya, Tanzania, Mozambique, and South Africa—and six small island territories, Madagascar, Mauritius, Comoros, the Maldives, Réunion (France), and the Seychelles (Kimani et al. 2009). Commercial tuna exploitation is highly prevalent across the coastal regions and high seas of the SWIO, with numerous Distant Water Fishing Nations (DWFNs) operating across these waters (Andriamahefazafy et al. 2019, Campling 2012). Industrial tuna fisheries primarily target Yellowfin (*Thunnus albacares*), Albacore (*Thunnus alalunga*), Bigeye (*Thunnus obesus*), and Skipjack (*Katsuwonus pelamis*) tuna, which currently form the principal market of this lucrative industry (Andriamahefazafy et al. 2019, Okemwa et al. 2023). These species additionally constitute a small proportion of artisanal and recreational tuna catch across the region; however, limitations in terms of gear capacity and technology (for example: cold storage, vessel capability, Global Positioning System (GPS)) impede optimal access to the fishery (Okemwa et al. 2023). Artisanal tuna fishing operations, however, remain highly established across the region, reportedly accounting for 50% of the total Indian Ocean (IO) tuna catch (Artetxe-Arrate et al. 2021). Neritic tuna species, defined as fish that inhabit oceanic regions situated over the continental shelves, including Bullet tuna (*Auxis rochei*), Kawakawa (*Euthynnus affinis*), Frigate tuna (*Auxis thazard*) and Longtail tuna (*Thunnus tonggol*), form the basis of the artisanal tuna fishery in the SWIO (Okemwa et al. 2023). These species are of paramount importance to the artisanal tuna fishery, as their life history strategies prevent them from undertaking transoceanic migrations, which confines their distribution to the coastal waters of the IO (Andriamahefazafy et al. 2019, Majkowski et al. 2011, Okemwa et al. 2023). Although limited in terms of vessel capacity and gear access, these life history characteristics present artisanal fishers with the opportunity to sustain their livelihoods whilst utilizing traditional fishing practices (Jiddawi and Öhman 2002). The photograph below captures the intricate operations onboard an industrial tuna fishing vessel, illustrating the immense scale on which these vessels operate (Figure 1).

Figure 1. Photograph capturing operations on board a commercial purse seine tuna vessel. The image captures the unloading of tuna caught through purse-seine fishing, which are temporally stored abroad the vessel whilst out at sea. Image credit: Sky News (2018)

Skipjack tuna (*K. pelamis*), and Kawakawa (*E. affinis*), are two small, highly migratory tuna species that are of particular fisheries importance throughout the region (Vayghan 2022, Dan 2020). Belonging to the family Scombridae*,* *K. pelamis* and *E. affinis* inhabit both tropical and subtropical oceanic regions in the Pacific, Atlantic, and Indian Oceans (Collette and Nauen 1983, Artetxe-Arrate et al. 2021, Hazin and da Silva 2022, Zhou and Sharma 2013). *K. pelamis* are found to occupy offshore oceanic environments in water temperature ranges of between 14.7˚C – 30˚C, where they do not exceed depths of approximately 260m (Zainuddin et al. 2023). In contrast, *E. affinis* reside in shallower inshore environments and primarily occupy slightly warmer waters along the coastal regions of the IO, where sea surface temperatures range between 18˚C - 29˚C (Rohit et al. 2012). Both species are considered generalist predators, feeding on a diverse range of marine organisms including teleosts, cephalopods, molluscs, and crustaceans, however, they have been shown to exhibit regional preferences with regards to their feeding behaviour (Vigneshwaran et al. 2018, Druon et al. 2017). Studies investigating the reproductive biology of *K. pelamis* and *E. affinis* have reported variation in the length at maturity between the sexes of both species (Johnson and Tamatamah 2013, Norungee and Kawol 2011). Results from studies across the IO have shown male *K. pelamis* to reach sexual maturity at lengths of 40cm (Timohina and Romanov 1996) and 44cm (Norungee and Kawol 2011) and females at lengths of 39.9cm (Grande et al. 2014) and 43cm (Timohina and

Romanov 1996). In contrast, *E. affinis* are reported to reach sexual maturity at larger sizes, with males reaching sexual maturity at lengths of 49.7cm (Johnson and Tamatamah 2013) and 52cm (Deepti and Sujatha 2012) and females at lengths of 47cm (Johnson and Tamatamah 2013) and 49cm (Deepti and Sujatha 2012). The key morphological features, characteristic to the identification of *K. pelamis* and *E. affinis*, are presented in the figures below (Figure 2, Figure 3).

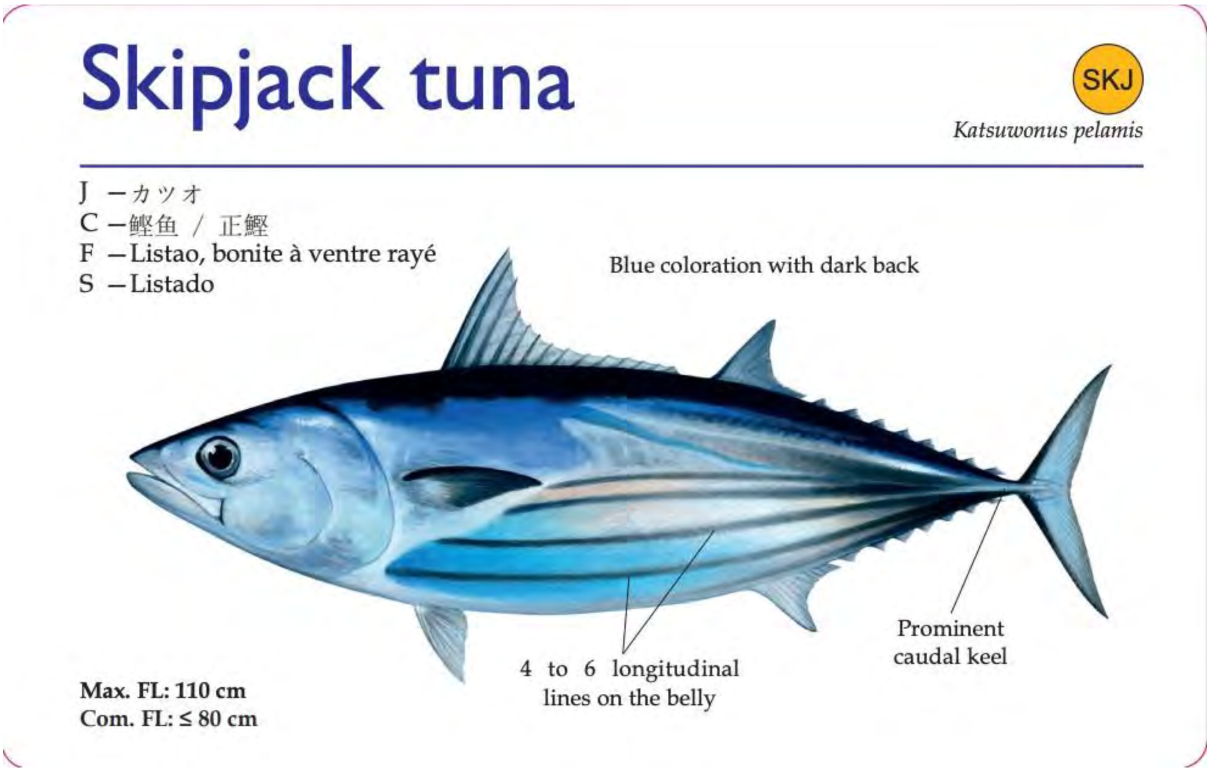

Figure 2. Morphological features of a mature Skipjack tuna (*Katsuwonus pelamis*), illustrating a few of the key features pertinent to it's identification. These include, 4–6 longitudinal lines on the belly, a prominent caudal keel, blue shaded colouration with a characteristic dark back, and a maximum size of 110 cm fork length (FL). Image credit: FAO 2023

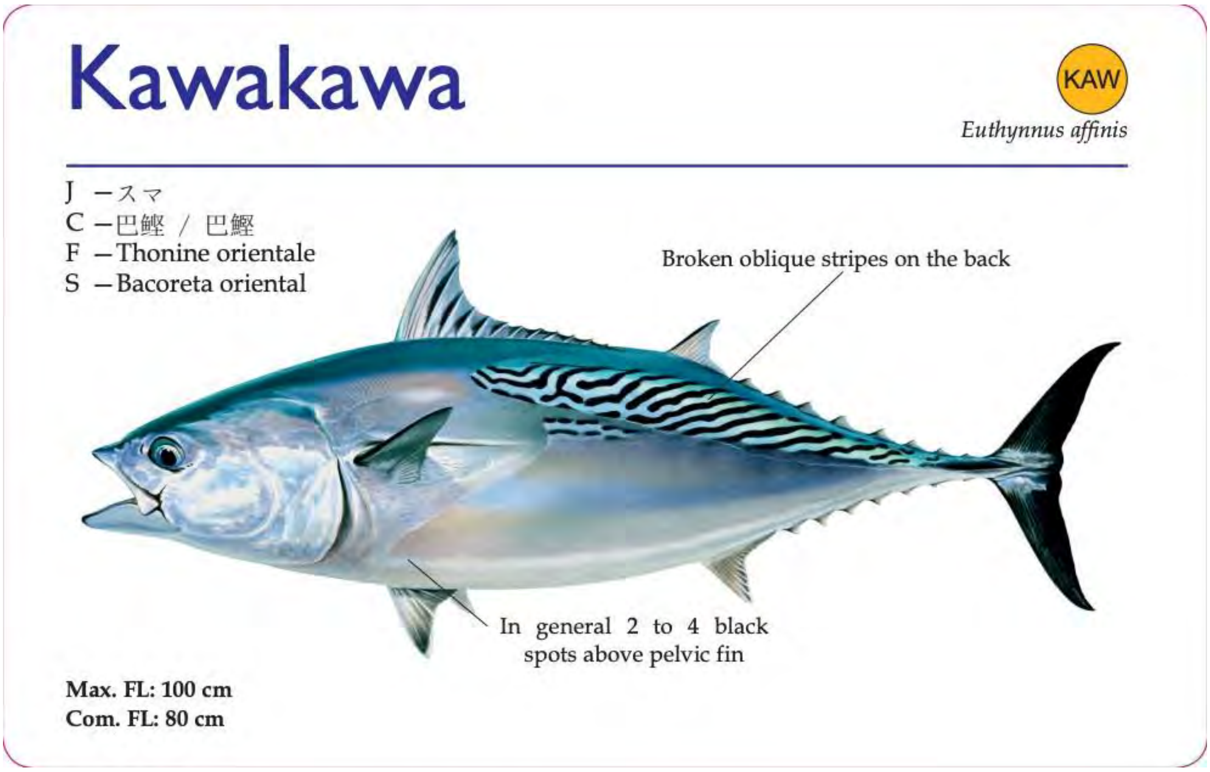

Figure 3. Morphological features of a mature Kawakawa (*Euthynnus affinis*), depicting a few of the key features integral to its identification. These include, 2–4 black spots above the pelvic fin, characteristic broken oblique stripes on the back, and a maximum size of 100 cm fork length (FL). Image credit: FAO 2023

K. pelamis is currently the most exploited tuna species globally, accounting for 60% of all annual tuna catches, and 53% of all tuna catches in the IO (Artetxe-Arrate et al. 2021, Druon et al. 2017). Recent literature has suggested that globally, *K. pelamis* stocks are healthy in terms of both their mortality rates and abundance (Artetxe-Arrate et al. 2021). *E. affinis* on the other hand accounts for 12% of the global annual tuna catches, ranking as the fourth most exploited tuna fishery species (Lecomte et al. 2017). *E. affinis* is currently considered not overfished throughout the WIO, where the stock biomass is currently at the state required to achieve the maximum sustainable yield (MSY) (IOTC 2017). As of the latest available fishery data collected for *K. pelamis* in the IO between 2017-2021, proportions of total annual catch per gear type comprise of purse seine (54.4%), bait boat (19%), gillnet (17.8%), and other harvest methods (8.8%) (IOTC 2022). The commercial tuna sector is dominated by Indonesian, Spanish, and Maldivian flagged fishing vessels, accounting for 18.4%, 17.8%, and 17.4% of the total *K. pelamis* catch in the IO (IOTC 2022). IOTC (2022) also described "other", which constituted the remaining 46.3% of *K. pelamis* catch across the region. IOTC (2022) also reported on *E. affinis* across the IO pertaining to data collected between 2016-2020. The proportions of total annual *E. affinis* catch per gear type used, comprised gillnet (49.1%), purse seine (29.9%), line (16.2%), and other gear types (4.9%) (IOTC 2022). Indonesian, Iranian, and Indian flagged fishing vessels dominated total catches of *E. affinis*, accounting for 30%, 23.1%, and 21% of the total catch respectively (IOTC 2022). IOTC (2022) further described "other", which constituted the remaining 25.7% of total *E. affinis* catch.

The Indian Ocean Tuna Commission (IOTC) is the RFMO which is responsible for coordinating and cooperating with stakeholders surrounding the management of tuna and tuna-like species in the SWIO (Van der Elst et al. 2009). The commission's primary objective is to ensure that stocks of tuna and tuna-like species are maintained at levels that permit MSY (Chassot et al. 2019). Currently, *K. pelamis* and *E. affinis* are managed under the auspices of the IOTC as "singular" panmictic stocks (Artetxe-Arrate et al. 2021, Menezes et al. 2012, IOTC 2016). This implies that populations of both species exist as singular, homogenous units that sustain extensive migration and larval mixing, which causes an even distribution of genes throughout the entire population (Bergh and Getz 1989, Kaplan and Smith 2001). However, if these populations are not panmictic, and there is minimal interaction between population groupings, management policy requires revision to account for spatial structuring among these population groupings (Kaplan and Smith 2001). Emerging genetic analyses have, however, strongly suggested the stock structure of *K. pelamis* may be more complex than previously suggested (Dammannagoda et al. 2011), as has been reported for a variety of other tuna and tuna-like-species in the surrounding regions of the IO (Menezes et al. 2012, Suman et al. 2015). To date, genetic analyses into the stock structure of *E. affinis* is very limited, with only a few studies conducted on the species (Kumar et al. 2012, Kumar and Kocour 2015). Whilst these studies suggest a unified panmictic population structure of *E. affinis* throughout the region, their scope is constrained in terms of spatial sampling extent, sample sizes, and the genetic methodology employed (Kumar et al. 2012, Kumar and Kocour 2015). The lack of knowledge surrounding the connectivity and spatial dynamics of *K. pelamis* and *E. affinis* populations in the SWIO, currently limits their classification as separate stocks (Dammannagoda et al. 2011, Nikolic et al. 2020), and further demonstrates the potentially high likelihood that management institutions are failing to address and account for the spatial complexity associated with these species and their stocks (Kaplan et al. 2014).

Despite emerging genetic evidence suggesting the possibility for spatial heterogeneity among populations of *K. pelamis* and *E. affinis* in the SWIO (Dammannagoda et al. 2011, Kumar and Kocour 2015), there is still a dearth of complementary research and information into the spatial population dynamics of both species across the region (Kaplan et al. 2014). Spatially represented biological information such as morphometrics, catch-and-effort, size frequency, and length-at-maturity have the potential to complement prior genetic research, to provide more robust assessments into the population structure and connectivity of these species and their stocks (Neilson et al. 2007). More importantly, understanding the spatial population dynamics of *K. pelamis* and *E. affinis*, can provide insight into the underlying mechanisms that are driving their observed population structure, which can subsequently aid in the implementation of future management strategies such as HCRs (Neilson et al. 2007).

Morphometric analysis has been widely used for stock identification and separation of fish populations, including a variety of tuna species such as *T. alalunga* (Afzal et al. 2019, Nikolic et al. 2020), and can be applied in the grouping of different stocks in terms of their growth rates and reproductive behaviours (Mojekwu and Anumudu 2015, Rawat et al. 2017). Morphometric variation within a species may indicate existing separate stocks of a species of fisheries importance. These variations are influenced by a combination of environmental factors, selection, and genetics on the development of individuals (Cadrin 2000).

The length at which fishery species reach maturity is another important biological parameter to assess stock status, and subsequent productivity of fish populations (Farley et al. 2014). Understanding the spatial structure of maturity in fish populations can indicate potential differences in the growth rates of individuals, which can provide insight into the stock structure of populations (Farley et al. 2014). Findings from Moore et al. (2020) reported variability in the length-at-maturity of *K. pelamis* in the Eastern Pacific Ocean (EPO) and Western Pacific Ocean (WPO), suggesting the possibility for spatial structuring of *K. pelamis* populations across the region. Schaefer and Fuller (2019) further reported spatially heterogenous distributions in the length-at-maturity of *K. pelamis* in the EPO. Additionally, Longhurst (2006), reported variable growth rates in larval and juvenile *K. pelamis* that were collected between two prominent ecological regions of the Pacific Ocean, which suggests that the fish may have developed within discrete ecological environments.

Lastly, data informative to the relative abundance and distribution of fishery species, such as catch data, provide valuable information that can contribute toward stock assessments of important fishery species (Pawson and Jennings 1996). Assessing the spatial distribution of catch is not only an important parameter in defining fisheries management boundaries but can also be a valuable tool towards stock structure assessments (Begg and Waldman 1999, Neilson et al. 2007). It has been suggested that divisions or gaps in the spatial distribution of fishing, could correspond to gaps in the geographic distribution of fish presence, which may coincide with a segregation of stocks (Gulland 1983, Neilson et al. 2007). Stock identification is seldom the principal focus of research studies that investigate fishery distribution and abundance, and consequently do not provide the fine scale geographic data at the temporal scale needed to support stock delineation (Pawson and Jennings 1996). These data do, however, provide fundamental insight pertinent to the identification and delineation of ecological areas utilized by different stocks, forming the basis to initiate more comprehensive stock structure assessments (Pawson and Jennings 1996). Evidence of such data being used in stock assessment studies has been reported in Bluefin Tuna (*Thunnus thynnus*) (Neilson and Black 2005), where catch-weight distributions were used to define the management boundaries which presently separate East and West Atlantic populations of *T. thynnus* in the International Commission for the Conservation of Atlantic Tunas (ICCAT) forum. These management boundaries were formulated because of observed discontinuities in the spatial distribution of catches in the Atlantic Ocean (Neilson and Black 2005). It is however important to note that these data are more so a reflection of the distribution of the fishery, rather than the distribution of the fishery populations, and therefore should not be the primary source for stock discrimination (Neilson and Black 2005).

While individual datasets such as morphometrics, length-at-maturity, genetics, and catch records might not independently offer conclusive evidence for stock boundaries of *K. pelamis* and *E. affinis*, their combined analysis within a geospatial framework can enhance our understanding. This integrative approach promises a more comprehensive picture of the species' population dynamics. Such enriched insights are invaluable for fisheries managers seeking to develop more effective policies. Future management strategies could benefit from this holistic method of data synthesis, as suggested by Neilson et al. (2007).

The principal challenge toward effective fulfilment of fisheries management objectives for highly migratory species compared to the likes of *K. pelamis* and *E. affinis*, falls in the alignment of the existing spatial population structure with the predetermined fisheries management unit (FMU) (Cadrin 2020). FMUs, under the present context, can be defined as delineated fishery stocks that are considered as separate entities for management under specific geographic jurisdictions (Kerr et al. 2017). These units are acknowledged for management policy to account for the variable ecological complexities that the different population groupings may be subjected to because of their spatial distributions (Kerr et al. 2017). Incorporating FMUs into management policy can contribute to improved fishery productivity through specialized implementation of CMMs and HCRs targeting the unique ecological and behavioural dynamics characteristic of specific population groupings (Kerr et al. 2017). Numerous FMUs are identified according to the spatial extent of jurisdictive boundaries or the grounds over which fishing effort is present, however, conventional models used for the assessment of stocks assumes the resource to exist as a singular panmictic population (Cadrin 2020). Although previous studies have accentuated the importance of aligning predetermined FMUs associated with management policy, with the present biological dynamics of the fishery populations (Reiss et al. 2009), evidence supporting the misidentification of the stock structure of target species is frequently ignored due to the misconception that it is irrelevant, inconvenient, and impractical (Cadrin 2020). These mismatches often occur as fisheries management is highly complex, and involves the consideration and inclusion of multiple social, economic, and ecological factors in the implementation and development of management policy (Reiss et al. 2009). Despite the severe implications that populations are subjected to because of misalignment between biological units and FMUs (Reiss et al. 2009, Berkeley et al. 2004), these management strategies often persist due to the combination of inefficient management and political structures in place (Reiss et al. 2009). Considering the complexity associated with recognizing population structure in fisheries management policy, the use of SMMs has become pervasive throughout marine ecosystems for the conservation, protection, and management of marine resources globally (Boerder et al. 2019). Although their effectiveness toward the management of large, highly migratory fishery species remains inconclusive, emerging evidence has supported the use of SMMs for the management of highly migratory species (Boerder et al. 2019), due their extensive socio-ecological benefits such as habitat restoration, user conflict reduction, stock rehabilitation, and most notably, promotion of sustainable fisheries (Norman et al. 2018).

The effective management of *K. pelamis* and *E. affinis* is further complicated by the complex dynamics associated with the oceanographic characteristics of the SWIO (Crochelet et al. 2016, Lan et al. 2020, Suhermat et al. 2022). The SWIO region, which spans across numerous international boundaries along the East Coast of Africa, also features complex oceanographic dynamics which include the South Equatorial current, the Mozambique channel eddies, the East Madagascar current, the Agulhas current, and climatic systems such as monsoons and upwelling events (Crochelet et al. 2016). These dynamics are illustrated in Figure 4.

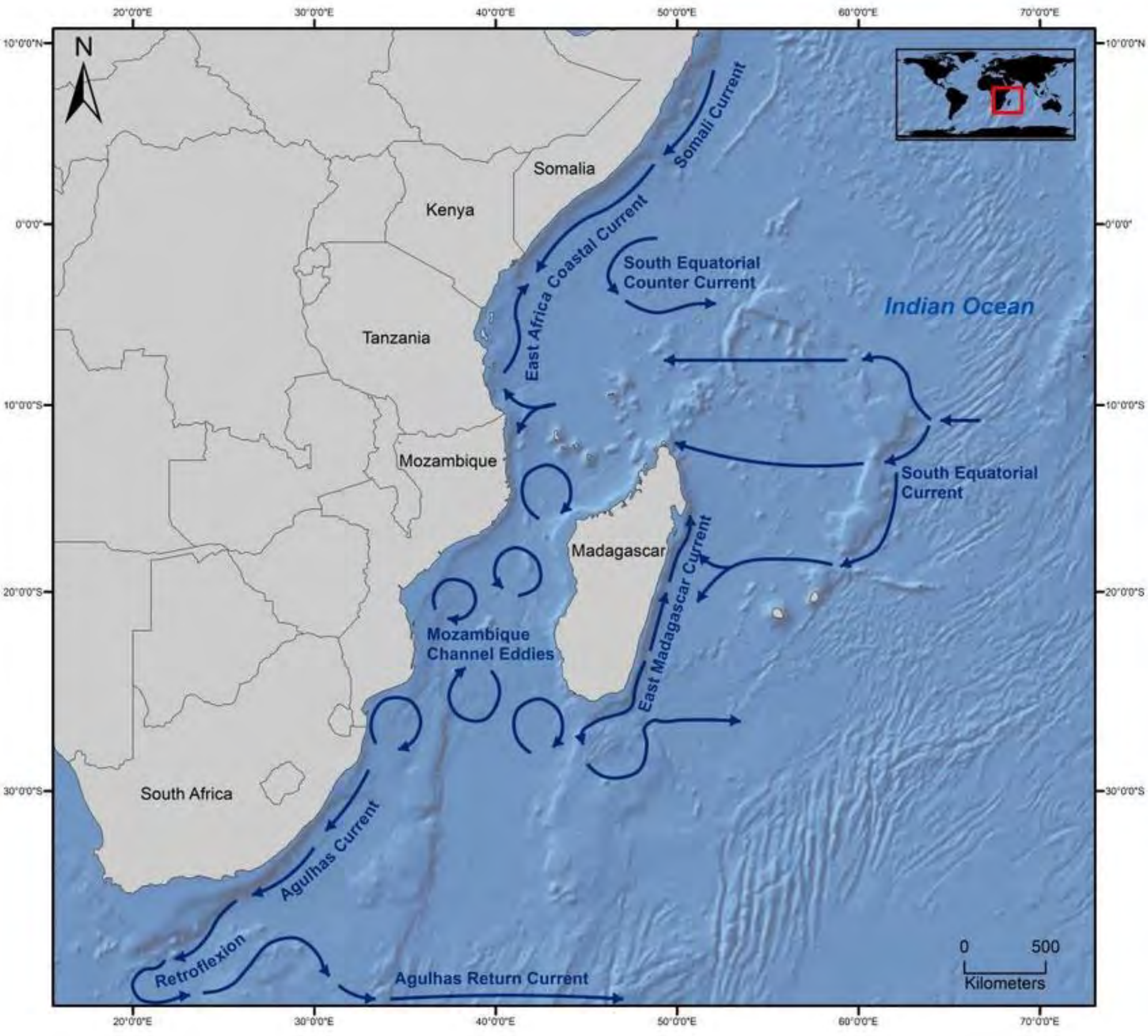

Figure 4. Southwest Indian Ocean (SWIO) depicting the major oceanic current and circulation systems present throughout the region. Image adapted from Crochelet et al. (2016)

These oceanic features, in combination with climatic systems such as monsoons and upwelling events, which are prevalent throughout the region have resulted in the great diversity of habitats and complex ecological dynamics that are prevalent throughout the SWIO (Van der Elst et al. 2005). These unique oceanographic dynamics, encompassing variable sea surface temperatures, primary productivity, and oceanic currents, can alter the distributional ranges and behavioural ecology of highly migratory, pelagic fishery species such as *K. pelamis* and *E. affinis* (Jørgensen et al. 2005). This may lead to the emergence of multiple functional *K. pelamis* and *E. affinis* stocks, which possess specific environmental, ecological, or habitation preferences (Jørgensen et al. 2005, Kerr et al. 2017). These factors complicate the effective management of these species as traditional fisheries management approaches generally rely on singular, panmictic CMMs and HCRs that may not account for the diverse and dynamic nature characteristic of individual functional stocks (Kerr et al. 2017).

It is therefore evident that one of the primary obstacles towards implementing effective management strategies and obtaining concurrence between stakeholders regarding management, lies in the availability and accessibility of current data and information which is currently not in the appropriate format, resolution, and scale to promulgate policy reform. Like many other fisheries, SWIO tuna fisheries are faced with substantial data limitations, which impede the effective management of these important fishery species. These limitations arise primarily from a lack of monitoring, control, and surveillance, combined with insufficient data collection and reporting capacity, which have been attributed partly to funding and enumerator deficiencies (Kimani et al. 2009, FAO 2007). Whilst there is a variety of locale specific data on *K. pelamis* and *E. affinis,* which can be used to inform and support management decisions in the region, they are often fragmented and incomplete, which complicates its utility. Additionally, there is a dearth of research and information into the spatial characteristics of *K. pelamis* and *E. affinis* in the SWIO, which is essentially used as a basis for the setting of management strategies such as HCRs (Kaplan et al. 2014). Due to the immeasurable contributions of these two small tuna species towards food security, livelihoods, and communities throughout the SWIO, insight into the spatial dynamics of *K. pelamis* and *E. affinis* across the region can contribute to their improved management in future years. The present research study therefore provides a comprehensive spatial analysis into the important biological and fishery characteristics of *K. pelamis* and *E. affinis* across the SWIO, which can be used by the IOTC to support future management decisions and policy reform.

1.2 Aims and Objectives

Using all available and openly accessible datasets on *K. pelamis* and *E. affinis* in the SWIO, the present study aimed to determine the suitability of current management measures implemented by the Indian Ocean Tuna Commission for the effective management of *K. pelamis* and *E. affinis* artisanal and industrial fisheries in the Southwest Indian Ocean.

The study objectives are as follows:

1. Spatially depict the genetic diversity of *K. pelamis* and *E. affinis* in the SWIO.

2. Spatially illustrate the size-frequency distributions of *K. pelamis* and *E. affinis* in the SWIO, to assess the spatial extent of mature and juvenile individuals.
3. Map the spatial distribution of *K. pelamis* and *E. affinis* catch-weight throughout the SWIO.
4. Assess the morphometric variability of *K. pelamis* and *E. affinis* between sample countries in the SWIO.
5. Validate the potential multiple stock hypothesis of *K. pelamis* and *E. affinis* in the SWIO through the development of a comprehensive, integrated spatial overview of the important fishery and biological characteristics of these fishery species across the region.
6. Inform future management recommendations to the IOTC concerning the utility of SMMs toward the management, protection, and conservation of *K. pelamis* and *E. affinis* in the SWIO.

1.3 Thesis Framework

The study was conducted from a science for policy perspective. It takes the form of a single manuscript styled research paper, which is divided into four separate chapters. Chapter Two provides a detailed description of the methodology used to conduct the present research, including an introduction into the study area, an outline of the data sources, and lastly a description of the geospatial mapping and analyses. Results are presented in Chapter Three. Chapter Four comprehensively discusses key findings and outlines recommendations for the future management of *K. pelamis* and *E. affinis* throughout the SWIO.

CHAPTER 2: Materials and Methods

2.1 Introduction

This chapter presents information around the study area, the data sources used, and geospatial mapping and analysis, to provide a spatial perspective of the population structure and connectivity of *K. pelamis* and *E. affinis* in the SWIO.

2.2 Study Area

The study was conducted across the geographic boundary of the SWIO, defined by the geographic coordinates 0˚ - 40˚S; 30˚E - 75˚E. Data collection sites spanned five continental nations, Somalia, Kenya, Tanzania, Mozambique, and South Africa—and six small island territories, Madagascar, Mauritius, Comoros, the Maldives, Réunion (France), and the Seychelles.

Two dominant oceanographic features, classified as Western Boundaries currents, prevail along the SWIO (Imawaki et al. 2013, Van der Elst et al. 2009). These are known as the Agulhas current, which flows along the east coast of Africa between 27˚S and 40˚S, and the Somali current, which exhibits seasonal shifts in its directional flow because of the monsoonal cycles that prevail throughout the region (Van der Elst et al. 2009). The Agulhas current is responsible for bringing in warm water from the lower latitudes and is intensified by eddies located on the southern end of the East Madagascar current (Van der Elst et al. 2009). The Somali current is responsible for transporting cold and nutrient rich water Northwards during the winter months, which is observed to have marked impacts toward the local climate and ecology (Wang et al. 2018).

Oceanic circulation and subsequent biological productivity are influenced by monsoonal climate systems that prevail throughout the SWIO (Lopetegui et al. 2022, Orúe et al. 2020). This comprises of the Northeast monsoon which persists throughout the summer months from December to March, and the Southwest monsoon that occurs throughout the winter months between June and September (Lopetegui et al. 2022, Orúe et al. 2020). These primary monsoonal systems are separated by two inter-monsoonal climate systems, which occur over the months of April and May (Autumn intermonsoon) and October and November (Spring intermonsoon) (Lopetegui et al. 2022, Orúe et al. 2020). In conjunction, these monsoonal systems cause a high degree of spatio-temporal variability in oceanic conditions and circulation systems throughout the region (Schott et al. 2009). The Northeast monsoon is accompanied by intense upwelling systems that prevail across the SWIO, resulting in decreased sea surface temperatures, and increased salinity in the upper stretches of the water column (Wiggert et al. 2006, Lopetegui et al. 2022). The result is increasing levels of biological productivity, which is predominantly off the coast of Somalia (Wiggert et al. 2006). Numerous other mesoscale phenomena such as eddies, fronts, and whirls, are also highly influential toward primary biological productivity across the SWIO, and subsequently impact the distributional range of highly migratory fishery species such as tropical tuna (Lopetegui et al. 2022). These oceanographic features alter the biophysical characteristics of the water column, and consequently, can alter the spatial dynamics of pelagic organisms in these waters (Bernal et al. 2017). The study site is presented in the figure below (Figure 5).

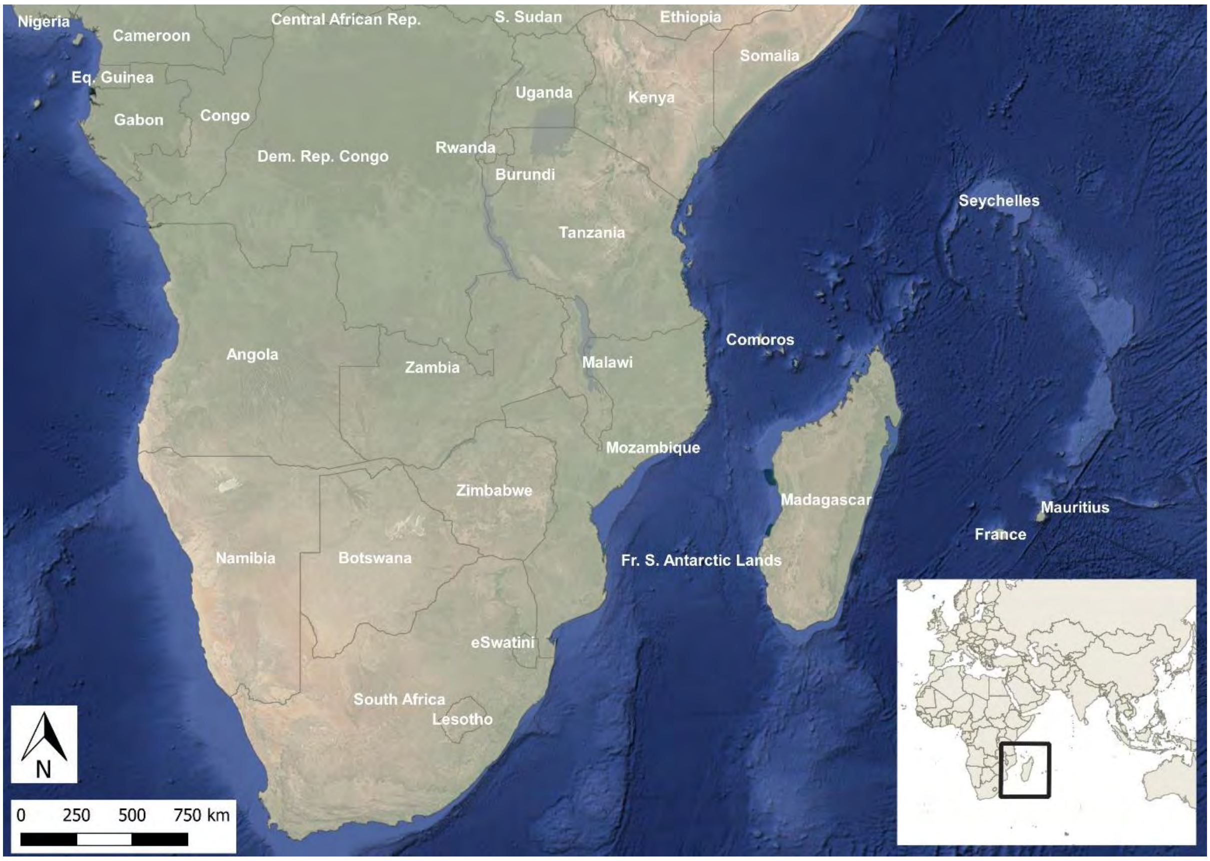

Figure 5. Geographic extent of data collection sites spanning across the Southwest Indian Ocean (SWIO). Data collection sites spanned over five continental nations (Kenya, Mozambique, Somalia, South Africa, Tanzania) and six small island territories (Comoros, Madagascar, the Maldives, Mauritius, Réunion (France), Seychelles)

2.3 Data Sources

Two primary fishery datasets were utilised to conduct the geospatial analysis of *K. pelamis* and *E. affinis* across the SWIO. This included datasets originating from Western Indian Ocean Marine Science Association's (WIOMSA) Marine and Coastal Science for Management (MASMA) project, titled "Enabling Sustainable Exploitation of the Coastal Tuna Species (Kawakawa and Skipjack) in the Western Indian Ocean"; as well as datasets created and stored by the IOTC, which are made publicly available online. Datasets from WIOMSA's MASMA project primarily concerned artisanal fishery data in the SWIO, whereas the publicly available IOTC datasets predominantly involved fishery data derived from industrial fishing practices. The combined analysis of datasets from both sources served to form an integrated spatial perspective on *K. pelamis* and *E. affinis* population dynamics across the SWIO.

2.3.1 WIOMSA MASMA Project

WIOMSA's MASMA project transpired between the years 2018-2021 (Sauer et al. 2022). The research study had three primary aims, which were to a.) Critically assess the population structure, genetic diversity, and connectivity of *K. pelamis* and *E. affinis* across countries in the WIO including South Africa, Mozambique, Tanzania, and Kenya; b.) Assess the drivers and patterns of adaptation of *K. pelamis* and *E. affinis*, and link this to primary ecological processes that occur across the region; and c.) Provide a comprehensive socio-economic analysis of these tuna fisheries across the region (Sauer et al. 2022). In alignment with the aims of the present research study, datasets pertaining to catch-and-effort, genetic diversity, maturity, size-frequency, and morphometrics of *K. pelamis* and *E. affinis* were extracted and utilized for analysis.

Genetic diversity from WIOMSA's MASMA project (Sauer et al. 2022) was investigated using tissue samples of *K. pelamis* (n=274) and *E. affinis* (n=218) collected across various sampling locations in the SWIO (Table 1, Figure 6). Deoxyribonucleic acid (DNA) extraction involved the use of the standard phenol/chloroform/isoamyl alcohol (PCIA) method to extract high molecular weight genomic DNA (Sauer et al. 2022). Genetic analysis involved the use of high-throughput Restriction Site-Associated DNA sequencing (ddRADseq), to provide and account for the high spatial resolution associated with highly migratory species such as *K. pelamis* and *E. affinis* (Sauer et al. 2022). Thereafter genetic differentiation was assessed according to global and pairwise F_{ST}, where results were presented as genetic divergence matrices (Sauer et al. 2022). Lastly, Principal Coordinate Analyses (PCoA's) were performed using genetic divergence data for both species, to assess population separation based on genetic differentiation between sample locations (Sauer et al. 2022).

Table 1. Sample localities and associated sample sizes for *Katsuwonus pelamis* and *Euthynnus affinis* genetic divergence data collected throughout the Western Indian Ocean. Table adapted from Sauer et al. (2022)

Site name	***Katsuwonus pelamis***	***Euthynnus affinis***
Kenya North	36	32
Kenya South	30	36
Tanzania North (Pemba)	50	-
Tanzania North (Tanga)	-	21
Tanzania Central (Dar)	16	-
Tanzania South (Mtwara)	55	33
Mozambique North (Pemba)	27	36+30
South Africa (E. Cape)	30	
Seychelles	30	30

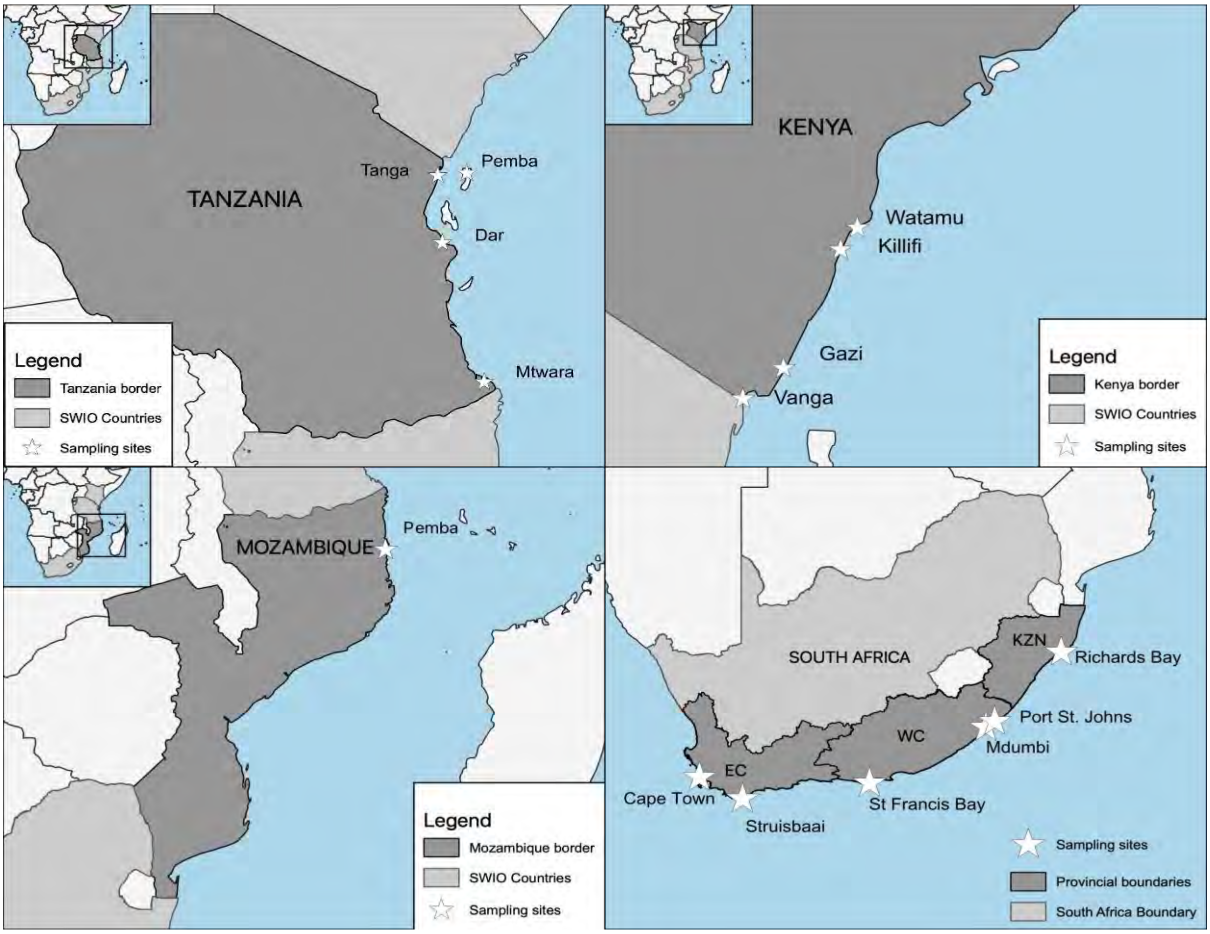

Figure 6. Point localities of genetic sample sites for *Katsuwonus pelamis* and *Euthynnus affinis* across Tanzania, Kenya, Mozambique, and South Africa. Figure credit: Sauer et al. 2022

WIOMSA MASMA data pertaining to catch-effort and size-frequency distribution of *K. pelamis* and *E. affinis* were collected through non-synchronized shore-based catch assessment surveys across Kenya, Mozambique, Tanzania, and South Africa (Sauer et al. 2022). However, for the present research study, size-frequency datasets were not used for analysis due to formatting constraints that did not allow adequate comparison between other datasets. As a result, size-frequency analysis of *K. pelamis* and *E. affinis* were primarily representative of industrial fishing catch preferences.

To complement the genetic data, in order to provide a more comprehensive understanding of the population structure and connectivity of *K. pelamis* and *E. affinis* populations in the SWIO, morphometric analysis was carried out across three countries, including Kenya (n = 187), Mozambique (n= 45), and South Africa (n = 47) for *K. pelamis*, and from two countries, Kenya (n = 141) and Mozambique (n = 71), for *E. affinis*. Sample sizes were based off availability of morphometric data per species and sample country.

Measurements included FL, first dorsal length (DL1), thorax girth (TG), body height (BH), eye height (EH), mouth height (MH), mouth width (MW), upper jaw length (UJL), and the length from the posterior operculum margin to the caudal keel of the fish (OCKL) (Figure 7) (Gonzalez-Martinez et al. 2020).

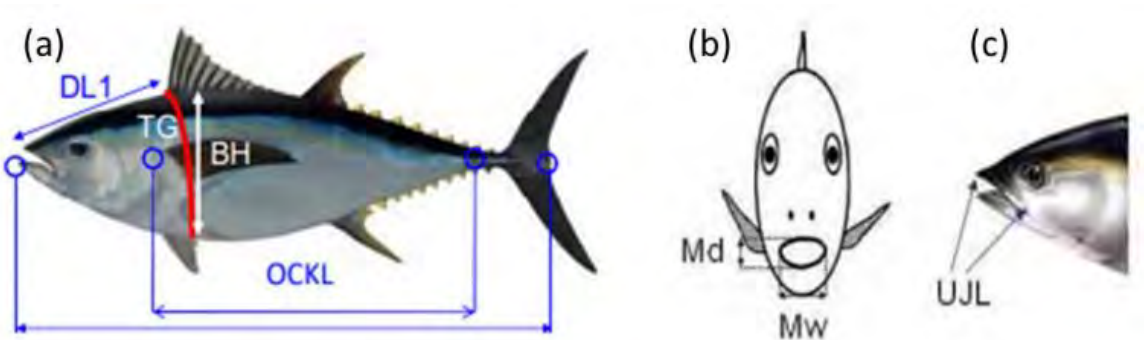

Figure 7. Morphometrics taken for each specimen of *Katsuwonus pelamis* and *Euthynnus affinis*. (a): lateral view; (b): anterior view; (c): close-up of the head. Abbreviations: DL1-first dorsal length; BH-body height; TG-thorax girth; OCKL-posterior operculum margin to caudal keel; Md-mouth dimeter; Mw-mouth width; UJL-upper jaw length. Image adapted from Norman (2013)

2.3.2 IOTC

IOTC datasets pertaining to catch-and-effort, size-frequency, nominal catch, and socioeconomics of tuna and tuna-like-species in the IO is promulgated and readily accessible online (IOTC 2023). The primary source of IOTC data arises from contracting and collaborating non-contracting parties (CPCs) on a flag state basis engaged in tuna and swordfish fisheries in the IO (IOTC 2001). IOTC contracting parties and CPCs engaged within the IOTC area of competence are compelled to supply the IOTC Secretariat with all fishery-related data on an annual basis (IOTC 2001). Through collaboration with local authorities, sampling schemes are further implemented to document illegal, unreported, and unregulated (IUU) catch (IOTC 2001). Additionally, data collected through observer programs also contribute to IOTC datasets (IOTC 2001). For the present research study, datasets pertaining to catch-effort and size-frequency of *K. pelamis* and *E. affinis* in the SWIO were extracted from the IOTC for spatial analysis. Catch-and-effort data are categorized according to gear type, and are presented under the following categories, namely Surface gears, Longline, and Coastal. These datasets, which consist of data collected between the years 1950 - 2021, are accessible under the following sources: Surface gears (https://iotc.org/data/datasets/latest/CE/Surface), Longline (https://iotc.org/data/datasets/latest/CE/Longline), and Coastal (https://iotc.org/data/datasets/latest/CE/Coastal). The combination of catch-effort data across the different gear types (Surface, Longline, Coastal), were used for geospatial analysis. Size-frequency datasets available for *K. pelamis* (https://iotc.org/data/datasets/latest/SF/SKJ) and *E. affinis* (https://iotc.org/data/datasets/latest/SF/KAW), were used to assess the spatial distributions of mature and juvenile individuals across the SWIO. *K. pelamis* were considered mature if their FL ≥ 39cm, and juvenile if their FL < 39cm (Grande et al. 2014). *E. affinis* were considered mature if their FL ≥ 47cm, and juvenile if their FL < 47cm (Johnson and Tamatamah 2013). Both *K. pelamis* and *E. affinis* are reported to exhibit minor variations in length-at-maturity between sexes (Johnson and Tamatamah 2013, Norungee and Kawol 2011), however limitations in the IOTC size-frequency datasets prevented sex discrimination for the present analysis. Consequently, the lowest length-at-maturity results reported in the literature for both *K. pelamis* and *E. affinis* in the WIO were used for the present analysis, for the inclusion of all possible mature specimens.

A grid system format is used by the IOTC to represent data promulgated online, whereby catch-effort and size-frequency data are spatially represented across predetermined geographic quadrants, split by the equator (latitude 0˚) and the Greenwich parallel (longitude 0˚) (Richardson et al. 2022). Where the data permitted, catch-effort and size-frequency data were georeferenced in 1˚ x 1˚ grids to maximise the detail of spatial data that were displayed on the maps. However, where data constraints limited this level of spatial detail, coarser 5˚ x 5˚ grids of latitude and longitude were used to georeference the data.

2.4 Spatial Mapping and Analysis

Spatial mapping and analysis considered the following biological data types: genetic divergence, length-at-maturity, catch-weight, and morphometrics.

2.4.1 Genetics, Length-at-maturity, Catch-weight

Geospatial analysis of genetic divergence, maturity, and catch-weight were performed in ArcGIS Pro 3.1. Genetic divergence of *K. pelamis* and *E. affinis* in the SWIO were mapped according to the Single Species Genetic Divergence Model (Vandergast et al. 2011). Using pairwise genetic divergence values, generated for both species across the SWIO in WIOMSA's MASMA project (Table 2, Table 3) (Sauer et al. 2022), this model constructs a geospatial landscape of genetic divergence across the study region (Vandergast et al. 2011). The model formulates a network, that links sample locations based on closest proximity, with careful consideration to avoid overlapping points (Vandergast et al. 2011). Genetic distance values are then assigned to the mapped midpoints of each connected point (Vandergast et al. 2011). The interpolation method known as inverse distance weighting (IDW) was then used to formulate a picture of the genetic distance values (Vandergast et al. 2011). The model creates a layer with the original genetic distance values, as well as an additional layer that includes values scaled between zero and one to allow equivalent weighting across multiple layers (Vandergast et al. 2011). Similarly, mature, and juvenile *K. pelamis* and *E. affinis* were mapped using IDW as the spatial interpolation method, however Kernal Density Estimation (KDE) proved to be the most effective spatial interpolation method for the spatial analysis of catch-weight data in the SWIO. Bayesian Kriging Analyses were further applied to catch-weight maps of *K. pelamis* and *E. affinis*, where grid cells were scaled according to the Bayesian Kriging value for catch-weight.

Table 2. Genomic diversity values indicating the genetic variation of *Katsuwonus pelamis* sample groups between sampling sites across the Southwest Indian Ocean (SWIO). Bold values indicate significant genetic differentiation between sample groups. Table from Sauer et al. (2022)

	South Africa (Eastern Cape)	**Mozambique (Pemba)**	**Tanzania (Mtwara)**	**Tanzania (Dar es Salaam)**	**Tanzania (Pemba)**	**Kenya (S)**	**Kenya (N)**	**Seychelles**
Eastern Cape	-							
Mozambique	0.0013	-						
Mtwara	**0.0044**	0.003	-					
Dar es Salaam	**0.0045**	**0.0049**	**0.0069**	-				
Pemba	**0.0102**	**0.011**	**0.0129**	0.0000	-			
Kenya (S)	0.0026	0.0013	0.0028	0.0000	0.0001	-		
Kenya (N)	**0.0034**	0.004	**0.0066**	0.0000	0.0000	0.0000	-	
Seychelles	**0.0026**	0.0008	0.001	0.0022	**0.0084**	0.0000	0.0026	-

Table 3. Genomic diversity values indicating the genetic variation of *Euthynnus affinis* sample groups between sampling sites across the Southwest Indian Ocean (SWIO). Bold values indicate significant genetic differentiation between sample groups. Table from Sauer et al. (2022)

	Mozambique (Pemba - Dec)	**Mozambique (Pemba - Mar)**	**Tanzania (Tanga)**	**Tanzania (Mtwara)**	**Kenya**
Mozambique (Pemba Dec)	-				
Mozambique (Pemba Mar)	0.0033	-			
Tanzania (Tanga)	**0.0123**	**0.0131**	-		
Tanzania (Mtwara)	**0.0355**	**0.0305**	**0.0275**	-	
Kenya	0.0051	0.0031	**0.0101**	**0.0167**	-
Seychelles	**0.0122**	**0.0089**	**0.0219**	**0.0363**	0.0035

2.4.2 Morphometrics

To eliminate the common issues associated with allometric growth variation that is experienced in a variety of tuna species, complicating morphometric comparisons, all measurements were size adjusted following the methods of Damora et al. (2021), Agustina and Sulistyaningsih (2022), and Sardenne et al. (2015). The following formula was applied following Gwilliam et al. (2018):

$$y'ij = \log yij - bj(logLFi - logLFoverall)$$

where *y'ij* is the size adjusted value for the measurement of individual *i*, *yij* is the original value for the measurement of individual *i*, *bj* is the pooled regression coefficient value *logY* on *logLF*, *LFi* is the fork length of the individual *i*, and *LFoverall* is the average fork length of all individuals.

To determine if size adjusted data for each range of morphometrics were normally distributed, Shapiro-Wilk tests were applied using statistical analysis in R-studio software. To test if morphometrics differed significantly between countries, non- parametric Kruskal Wallis and Mann-Whitley U tests were applied. To visualize the distribution of significant size adjusted measurements, multi-dimensional scaling (MDS) plots, which incorporated the Bray-Curtis similarity measure, were fitted to the data for each species separately, following Gwilliam et al. (2018). The extent of similarity between data collection sites for each species was then assessed using a one-way analysis of similarity (ANOSIM), where results were considered significant at $P<0.05$. Following this, a similarity percentages breakdown (SIMPER) analysis was performed on each set of morphometrics for each species to assess the contribution of each of the morphometrics to the dissimilarity observed between collection countries. In the case of *K. pelamis*, size adjusted TG, MH, and MW were excluded from analysis due to substantial errors (TG) in the measurement protocol, or deficiencies in sample size (MH, MW) that restricted analysis. Similarly, size adjusted TG was excluded from morphometric analysis of *E. affinis* due to suspected errors in the measurement protocol.

CHAPTER 3: Results

Based on the results of the spatial perspective of *K. pelamis* and *E. affinis* in the SWIO area, two key findings emerged. With regard to *K. pelamis*, spatially illustrated genetic divergence, size-frequency, catch-weight, and morphometrics, provided support for spatial structuring among *K. pelamis* populations. Findings around *E. affinis* were more complex, only spatially depicted genetic divergence data, and morphometrics, supported that populations were not panmictic in the SWIO. Spatially illustrated length-at-maturity and catch-weight data on the other hand supported a homogenous population structure of *E. affinis* in the SWIO. These findings can contribute to a more comprehensive, integrated understanding of the spatial population dynamics and ecology of these two tuna species in the SWIO and lay the foundation for considering a multiple population hypothesis. The results are presented in terms of species and are presented below as genetic divergence analysis, length-at-maturity analysis, catch-weight analysis, morphometric analysis, and integrated spatial perspective.

3.1 *Katsuwonus pelamis*

Genetic divergence analysis

The spatial depiction of genetic divergence of *K. pelamis* in the SWIO indicated the complexity associated with the spatial population structure of the species across the region (Figure 8). The two distinct dark blue shaded areas illustrate zones of considerable genetic discontinuity between sample populations and are suggestive of a prominent genetic break between *K. pelamis* population groups, offset in Central Tanzania. This is indicative of two genetically isolated population groups to the North (Dar es Salaam, Tanzania, and Kenya) and South (Eastern Cape, South Africa, Mozambique, and Mtwara, Tanzania) of this high genetically divergent zone. Although less prominent, an additional genetic discontinuity zone is evident, distinguishing a third potential *K. pelamis* population group in the Seychelles region. As this spatial depiction of *K. pelamis* genetic divergence is affiliated with the genetic diversity matrix values, these results align with locations of significant genetic differentiation (bold values) reported in the matrix (Table 2).

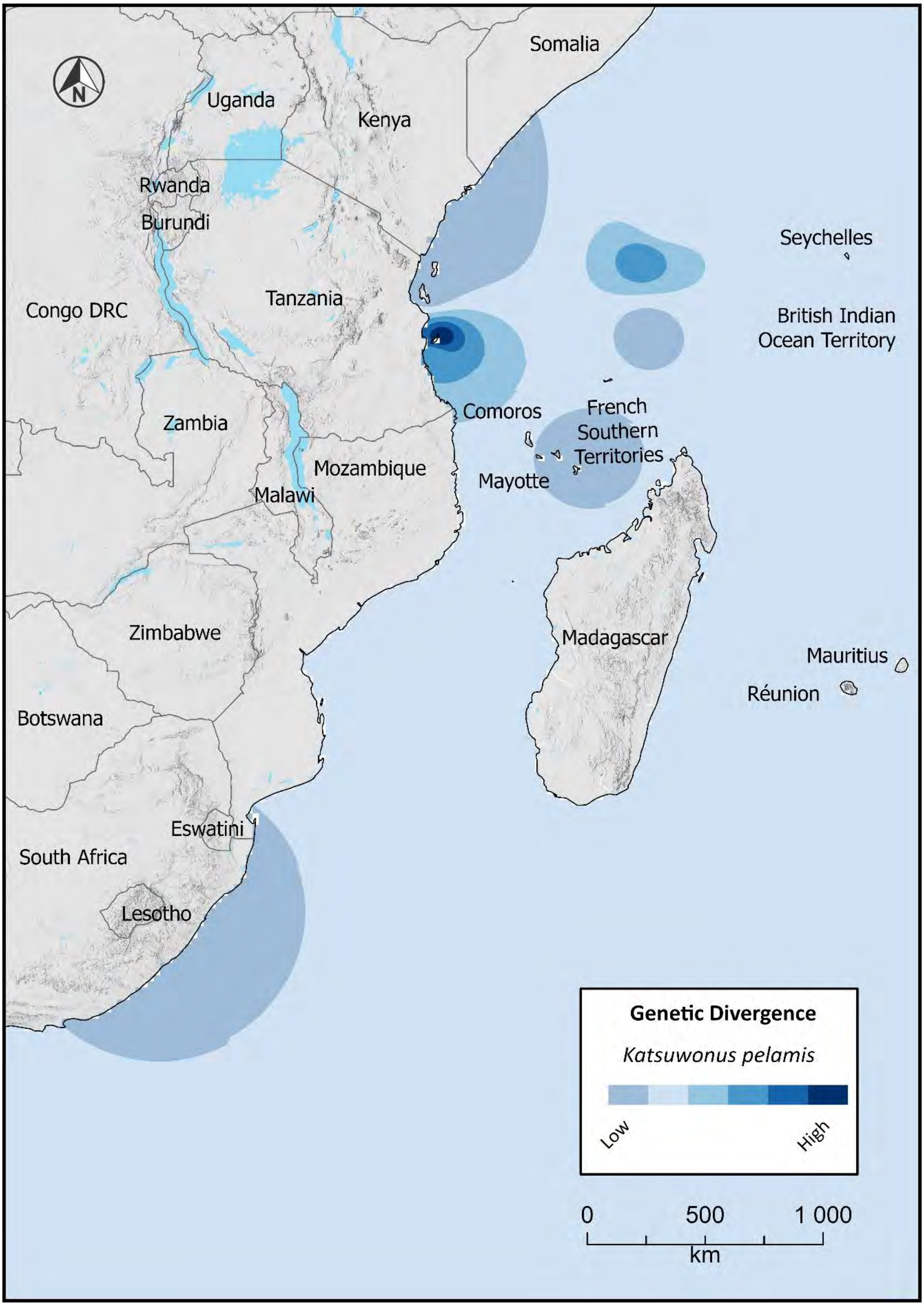

Figure 8. The spatial distribution of genetic divergence of *Katsuwonus pelamis* across sample sites in the Southwest Indian Ocean (SWIO). The degree of genetic divergence between areas was represented with blue shaded areas, where darker shaded zones are representative of greater genetic divergence between sample locations

Length-at-maturity analysis

Distinct dark blue shaded areas on the maps (Figure 9A, Figure 9B) represent geographic hotspots of juvenile and mature *K. pelamis* in the SWIO. The most prominent hotspot of mature *K. pelamis* is prevalent in the Northern region of the SWIO in the coastal and offshore regions of Kenya and Somalia (Figure 9B). South of this zone, off the Tanzanian coastline is a notable gap with a very low density of mature individuals, separating another less prominent hotspot of *K. pelamis* maturity along the Mozambique channel between Mozambique and Madagascar. Although mature and juvenile mapping illustrations cannot be directly compared due to disparate scales resulting from differences in sample sizes, similarities are evident in the geospatial analysis of juvenile *K. pelamis* (Figure 9A). As for mature *K. pelamis* there is a prominent, however less pronounced hotspot of juvenile *K. pelamis* in the Northern region of the SWIO, which covers the region of Somalia. In contrast however, South of this zone are very low densities of juvenile *K. pelamis* with no additional juvenile hotspots.

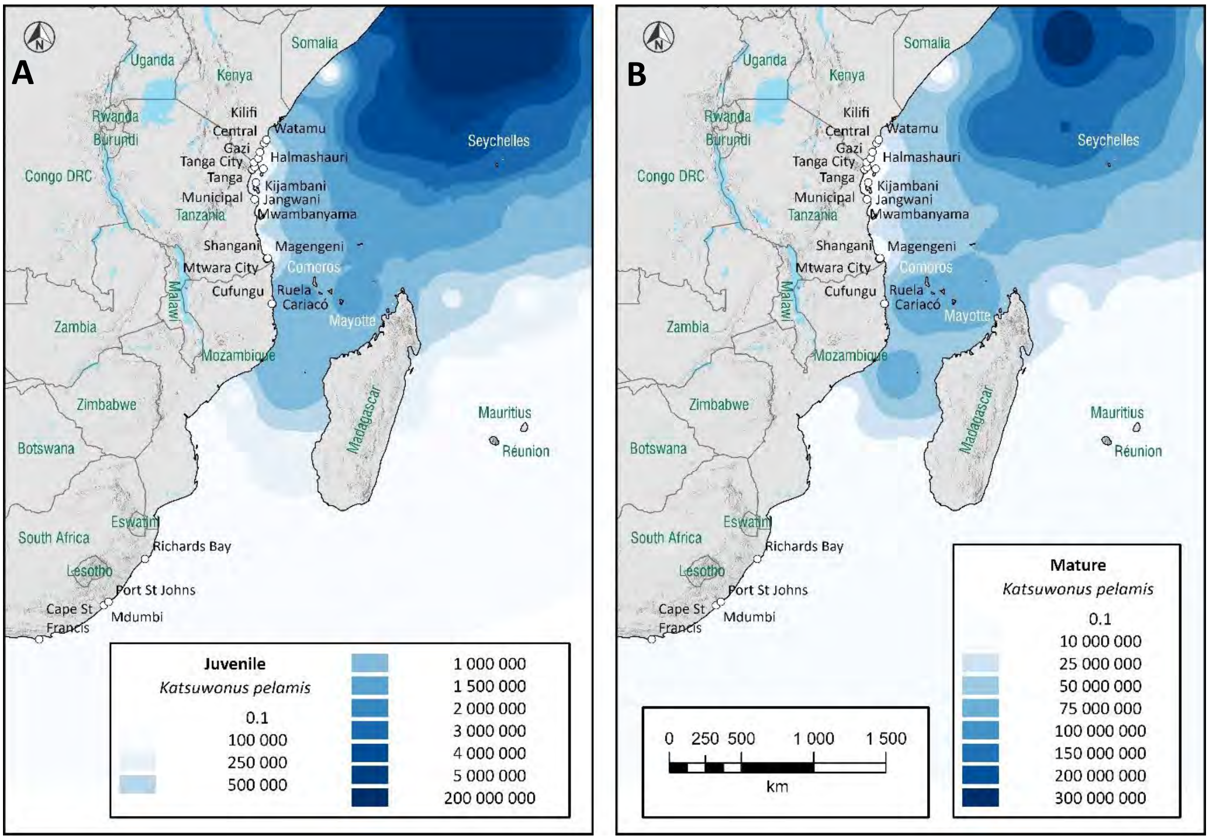

Figure 9. The spatial distribution of *Katsuwonus pelamis* maturity across the Southwest Indian Ocean (SWIO). Darker blue shaded areas represent hotspots of juvenile and mature *K. pelamis* presence. A-Spatial depiction of juvenile individuals (fork length (FL)< 39cm); B-Spatial depiction of mature individuals (FL ≥ 39cm)

Catch-weight analysis

The spatial depiction of *K. pelamis* catch-weight (MT) in the SWIO revealed high volumes and a widely distributed pattern of catches across most parts of the region (Figure 10). In particular, the spatial catch-weight distribution of *K. pelamis* revealed a distinct division in the geographic distribution of *K. pelamis* catch in the SWIO, separating two broad regions of considerably higher catch-weight. This includes an expansive offshore zone extending perpendicular from the borders of Kenya and Somalia and extends offshore covering the area of the Seychelles. Although considerably smaller, the second prominent catch-weight zone extends throughout the Mozambique channel, including the French territories of Mayotte and the Comoros. In contrast, *K. pelamis* catch-weight was lowest along the coastal regions of South Africa, Southern Mozambique, Tanzania, and the high seas regions South of the Mozambique-Tanzania boarder.

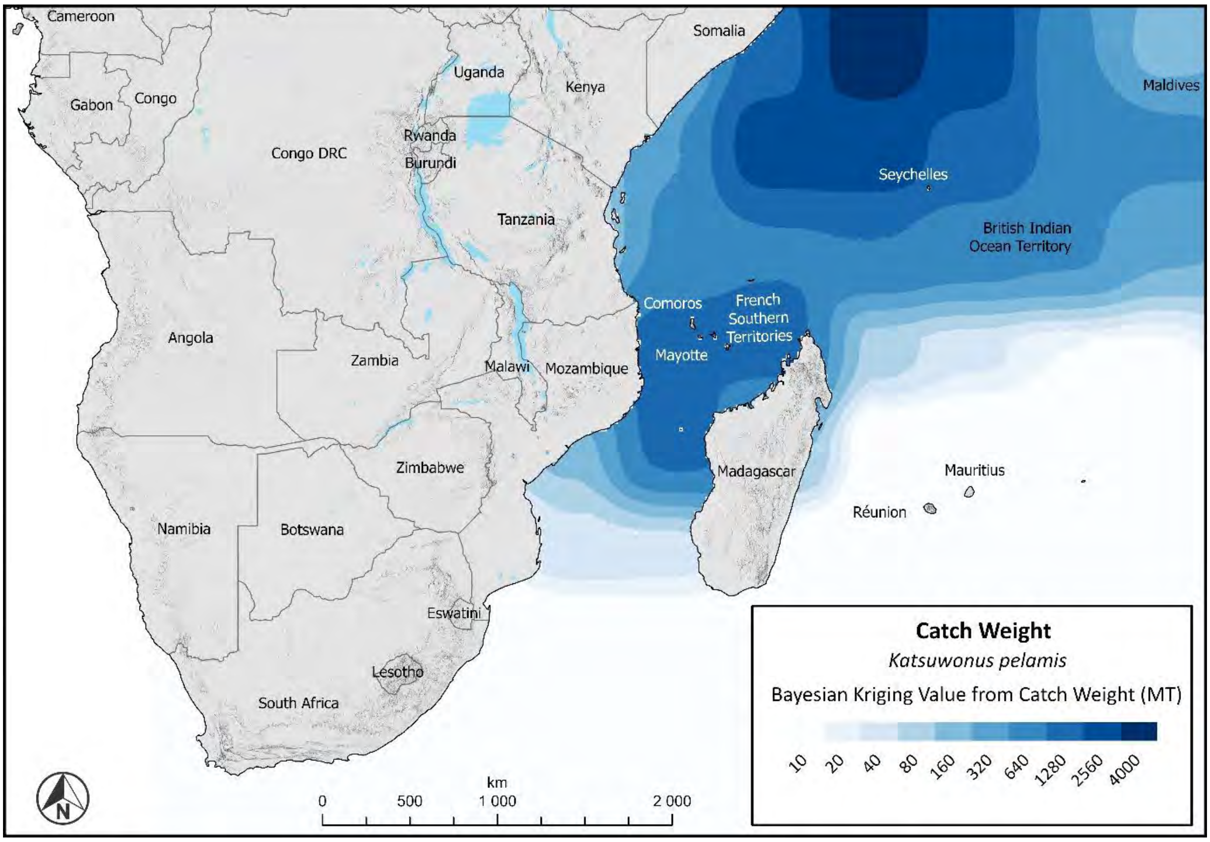

Figure 10. Spatial distribution of *Katsuwonus pelamis* catches across the Southwest Indian Ocean (SWIO), with grid cells scaled according to the Bayesian Kriging value from the weight (MT) of catches across the region. Darker blue shaded areas on the map represent zones of higher catch weight (MT) of *K. pelamis* in the SWIO

Morphometric analysis

Eight of the nine size adjusted morphometric character measurements in *K. pelamis* (DL1, BH, EH, HH, TG, OCKL, MH, UJL) differed significantly (p-value < 0.05) between Kenya, Mozambique, and South Africa (Table 4). MDS plots applied to *K. pelamis* data indicated considerable overlap of significant morphometric characters between Kenya and South Africa, however displayed a high degree of separation when compared to Mozambique, with minimal overlap (Figure 11). Test results from the ANOSIM revealed significant differences in size-adjusted characters between the three countries (Stress: 0.34; R: 0.66; p-value<0.05), thus supporting the trend observed in the MDS plot. According to SIMPER analysis, the most important character traits in explaining the dissimilarity in *K. pelamis* morphometrics between countries were DL1 (38.8% contribution), UJL (34.5% contribution), and BH (12.7% contribution). Cumulatively, these three characters explained 83.9% of the dissimilarity between countries.

Table 4. Size-adjusted measurements of morphometric characters (mean, standard deviation, median, range) for *Katsuwonus pelamis* samples from Kenya (n = 187), Mozambique (n = 45), and South Africa (n= 47). p-values obtained from the Kruskal Wallis H tests are also given. Abbreviations: DL1- First dorsal length; BH- Body height; EH- Eye height; HH- Head height; TG- Thorax girth; OCKL- Posterior operculum margin to caudal keel; MH- Mouth height; MW- Mouth width; UJL- Upper jaw length

	Kenya				**Mozambique**				**South Africa**				
Trait	$\bar{x}$	**SD**	$\tilde{x}$	**range**	$\bar{x}$	**SD**	$\tilde{x}$	**range**	$\bar{x}$	**SD**	$\tilde{x}$	**range**	**p**
DL1	1.19	0.02	1.19	1.10 - 1.24	1.21	0.02	1.21	1.18 - 1.25	1.18	0.03	1.18	1.10 - 1.25	<0.01
BH	1.04	0.03	1.04	0.98 - 1.15	1.17	0.05	1.17	0.91 - 1.22	1.04	0.02	1.04	1.01 - 1.13	<0.01
EH	0.25	0.05	0.25	0.06 - 0.41	0.29	0.03	0.29	0.24 - 0.38	0.28	0.03	0.28	0.21 - 0.35	<0.01
HH	0.76	0.03	0.77	0.58 - 0.85	0.88	0.05	0.88	0.75 - 1.03	0.77	0.04	0.77	0.63 - 0.83	<0.01
TG	1.17	0.02	1.17	1.03 - 1.27	1.49	0.02	1.49	1.43 - 1.54	1.47	0.03	1.47	1.43 - 1.59	<0.01
OCKL	1.52	0.02	1.51	1.47 - 1.64	1.45	0.02	1.45	1.40 - 1.51	1.43	0.03	1.44	1.37 - 1.51	<0.01
MH	0.73	0.08	0.73	0.36 - 0.93	0.56	0.19	0.64	0.08 - 0.85	0.81	0.03	0.81	0.77 - 0.83	<0.01
MW	0.57	0.08	0.59	0.28 - 0.76	0.59	0.06	0.60	0.48 - 0.70	0.58	0.13	0.60	0.43 - 0.69	>0.05
UJL	0.66	0.05	0.67	0.44 - 0.79	0.72	0.03	0.71	0.66 - 0.80	0.70	0.02	0.70	0.62 - 0.73	<0.01

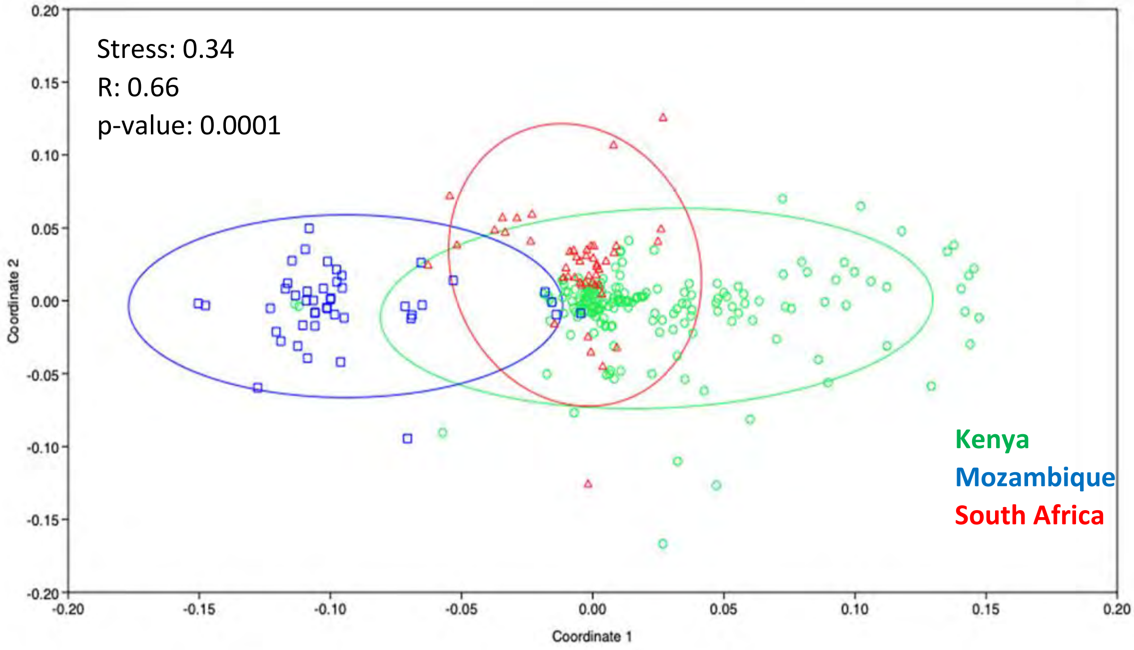

Figure 11. Non-metric multi-dimensional scaling (MDS) plot indicating the distribution of significant morphometric characters of *Katsuwonus pelamis* between Kenya (green, n=187), Mozambique (blue, n=45), and South Africa (red, n=47)

Integrated spatial perspective

The comprehensive synthesis of spatially illustrated genetic divergence, length-at-maturity, catch-weight, and morphometric analyses support the presence of spatially structured *K. pelamis* population groupings across the SWIO. Isolated length-at-maturity and catch-weight abundances, represented through respective mapping illustrations (Figure 9B, Figure 10) aligned with stock structure inferences deduced through spatial genetic divergence analysis (Figure 8), revealing distinct northern and southern population groupings offset in central Tanzania. These hotspots are prominent in the coastal and offshore regions of Kenya, and Somalia, as well in the Mozambique channel, extending throughout the French Territories of Mayotte and the Comoros. A prominent genetic discontinuity zone in central Tanzania corresponds to the separation of two discrete genetic population groupings to the north (Dar es Salaam, Tanzania, and Kenya) and south (Mtwara, Tanzania, Mozambique, and Eastern Cape, South Africa), in alignment with the aforementioned analyses. Spatial catch-weight and length-at-maturity analyses revealed another separate, although less distinct hotspot in the Seychelles region, further aligning with stock structure inferences from an additional genetic discontinuity zone around the Seychelles, represented through genetic divergence analysis. Morphometric analysis also indicated significant differences between sampled countries (Table 4, Figure 11), suggesting population complexity, albeit with limitations in the geographic extent of sampling, which limited direct comparison with the other analyses.

3.2 *Euthynnus affinis*

Genetic divergence analysis

As for *K. pelamis*, the spatial depiction of *E. affinis* genetic divergence in the SWIO reveals the complexity associated with the species spatial population structure across the region (Figure 12). As stated for *K. pelamis*, prominent dark blue shaded areas are illustrative of considerable genetic discontinuity among population groups of *E. affinis* in the SWIO. The map depicts three distinct areas of *E. affinis* genetic divergence, representing regions of potential stock separation. These include a prominent zone between Pemba, Mozambique, and Mtwara, Tanzania, a less pronounced zone in the coastal region of central Tanzania, and finally, a large, definitive zone in the region of the Seychelles. This demonstrates either the scenario of four genetically independent *E. affinis* population groups, or alternatively, indicates the possibility for three genetically discrete stocks, where spatial division has separated two genetically analogous populations that occupied different geographic regions during sampling. As this spatially depicted *E. affinis* genetic data was formulated in accordance with the genetic diversity matrix, significant genetic diversity values (bold values) confirm the latter deduction of three genetically isolated population groups (Table 3). The map therefore illustrates two *E. affinis* population groups along the East African coastline, consisting of one genetically discrete stock in the region of Northern Mozambique and Kenya, which is separated by another genetically isolated population group in the coastal region of Tanzania**.** Lastly, a third genetically distinct *E. affinis* population group is proposed to occupy the region of the Seychelles. Genetic samples of *E. affinis* from South Africa were unavailable, consequently limiting comparison of other population groupings with genetic samples along this stretch of coastline.

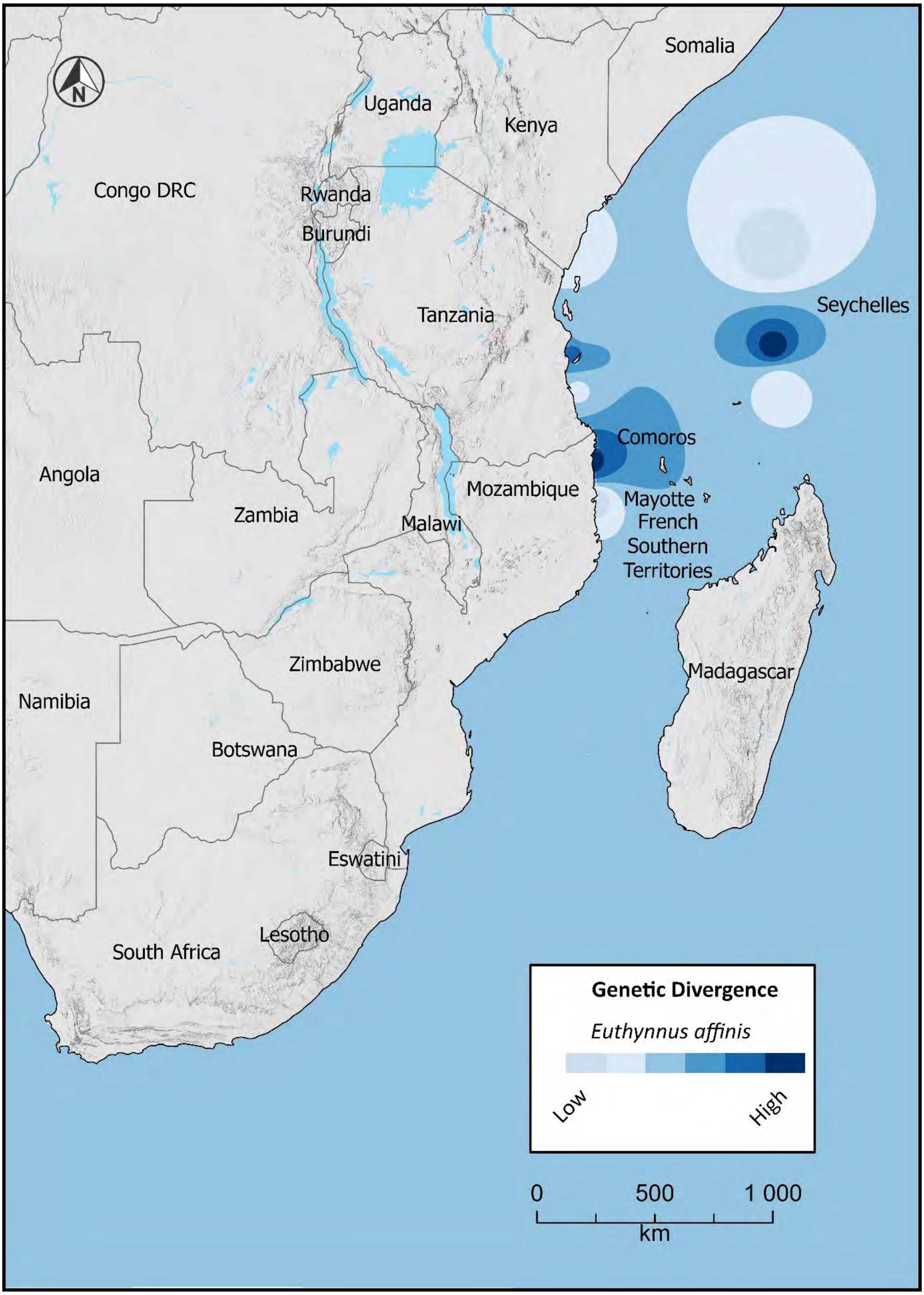

Figure 12. Spatial distribution of genetic divergence of *Euthynnus affinis* across sample sites in the Southwest Indian Ocean (SWIO). The degree of genetic divergence between areas is represented through blue shaded areas, where darker shaded zones are representative of greater genetic divergence between sample locations

Length-at-maturity analysis

Dark shaded areas represent geographic hotspots of juvenile and mature *E. affinis* in the SWIO (Figure 13A, Figure 13B). Spatial analysis revealed one geographic hotspot of mature *E. affinis* in the coastal regions of Northern Tanzania and Kenya (Figure 13B). South of this hotspot is a large, noticeable gap in mature individuals of *E. affinis*, separating a very sparse zone of mature *K. pelamis* in central and Southern Mozambique. Perpendicular to Somalia and Northern Mozambique represent two additional high seas regions of sparse *E. affinis* maturity. Spatial analysis of juvenile *E. affinis* illustrated the same hotspot as portrayed for mature *K. pelamis* in the coastal regions of Northern Tanzania and Kenya (Figure 13A). However, no additional zones of juvenile *E. affinis* presence were reported throughout the SWIO.

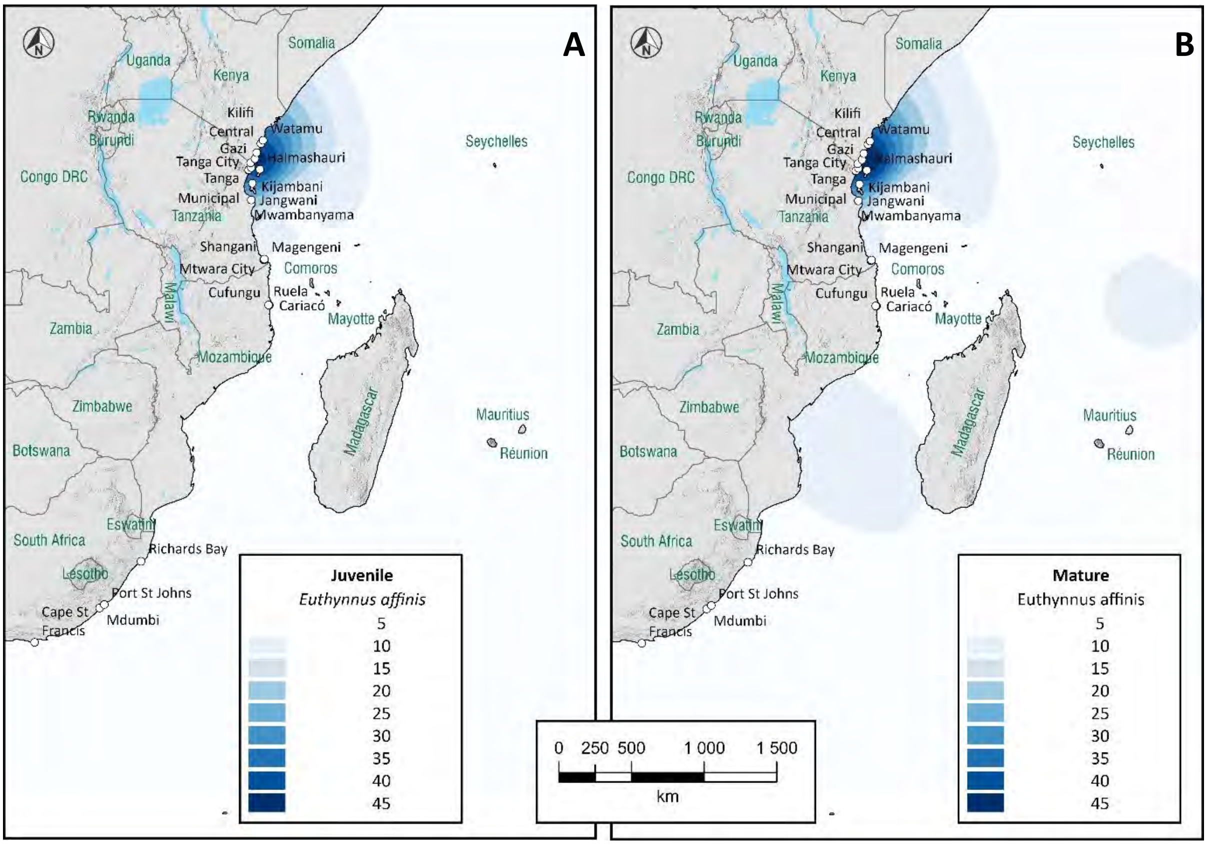

Figure 13. Spatial distribution of *Euthynnus affinis* maturity across the Southwest Indian Ocean (SWIO). Darker blue shaded areas represent hotspots of juvenile and mature *E. affinis* presence. A-Spatial depiction of juvenile individuals (fork length (FL) < 47cm); B-Spatial depiction of mature individuals (FL ≥ 47cm)

Catch-weight analysis

In contrast to the high volume and wide distribution of *K. pelamis* catches across the SWIO, the spatial depiction of *E. affinis* catch-weight (MT) revealed a significantly lower volume and patchy distribution of catches (Figure 14). The catch-weight distribution of *E. affinis* revealed several small zones of high catch-weight across the region. Spatially represented catch-weight data illustrated two distinct areas of considerably higher catch-weight compared to other regions of the SWIO. This included a small zone in the Seychelles, and a larger, more prominent zone throughout the Mozambique channel, including the French territories of Mayotte and the Comoros. Although less abundant in terms of catch-weight, the map illustrated three additional areas of high catch-weight, which included an area surrounding the small island states of Mauritius and Réunion, a small area in the high seas perpendicular to the Mozambique-Tanzania boarder, and lastly, a small area extending throughout the Maldives. In contrast, catch-weight of *E. affinis* were lowest along the coastal regions of South Africa and Southern Mozambique, and Northern Tanzania and Southern Kenya.

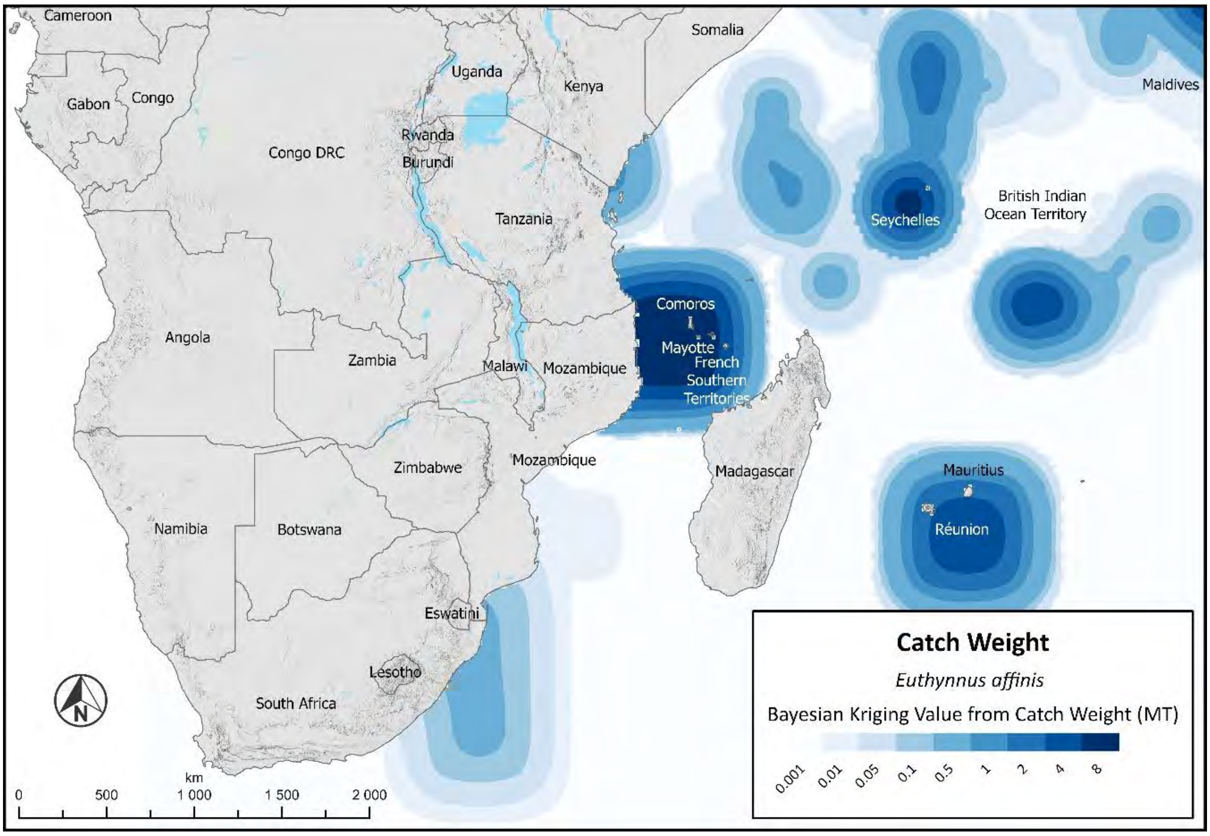

Figure 14. Spatial distribution of *Euthynnus affinis* catches across the Southwest Indian Ocean (SWIO), with grid cells scaled according to the Bayesian Kriging value from the weight (MT) of catches across the region. Darker shaded zones represent areas of higher catch weight of *E. affinis* in the SWIO

Morphometric analysis

All nine of the size adjusted morphometrics (DL1, BH, EH, HH, TG, OCKL, MH, MW, UJL) differed significantly in *E. affinis* between Kenya and Mozambique (Table 5). Non-metric MDS plots applied to *E. affinis* data indicated substantial separation between Kenya and Mozambique (Figure 15). Test results from the ANOSIM indicated that size adjusted morphometric character measurements in *E. affinis* were significantly different between Kenya and Mozambique (Stress: 0.20; R: 0.83; p-value<0.05), which supports the trend observed in the generated MDS plot. According to SIMPER analysis, the most important character traits in explaining dissimilarity in *E. affinis* morphometrics between countries were OCKL (32.6% contribution), HH (19.5% contribution), and EH (19.5% 19 contribution). Cumulatively, these three characters explained 71.6% of the dissimilarity between countries, accounting for 32.64%, 19.49%, and 19.49% of the dissimilarity respectively.

Table 5. Size-adjusted measurements of morphometric characteristics (mean, standard deviation, median, range) for *Euthynnus affinis* samples from Kenya (n = 141) and Mozambique (n = 71). p-values obtained from the Mann-Whitley U tests are also given. Abbreviations: DL1- First dorsal length; BH- Body height; EH- Eye height; HH- Head height; TG- Thorax girth; OCKL- Posterior operculum margin to caudal keel; MH- Mouth height; MW- Mouth width; UJL- Upper jaw length

	Kenya				**Mozambique**				
Trait	$\bar{x}$	**SD**	$\tilde{x}$	**range**	$\bar{x}$	**SD**	$\tilde{x}$	**range**	**p**
DL1	1.17	0.02	1.17	1.06 – 1.23	1.20	0.04	1.19	1.06 – 1.41	<0.01
BH	1.09	0.03	1.08	0.98 – 1.17	1.20	0.03	1.20	1.15 – 1.33	<0.01
EH	0.19	0.07	0.18	0.07 – 0.45	0.49	0.14	0.53	0.21 – 0.84	<0.01
HH	0.75	0.04	0.75	0.54 – 0.85	0.96	0.07	0.95	0.86 – 1.23	<0.01
TG	1.20	0.03	1.20	1.10 – 1.26	1.44	0.10	1.45	0.76 – 1.54	<0.01
OCKL	1.56	0.02	1.57	1.46 – 1.64	1.45	0.04	1.44	1.38 – 1.58	<0.01
MH	0.56	0.10	0.58	0.04 – 0.77	0.60	0.09	0.62	0.30 – 0.80	<0.05
MW	0.54	0.08	0.56	0.13 – 0.68	0.50	0.05	0.50	0.41 – 0.62	<0.01
UJL	0.56	0.10	0.58	0.04 – 0.77	0.75	0.07	0.76	0.61 – 1.00	<0.01

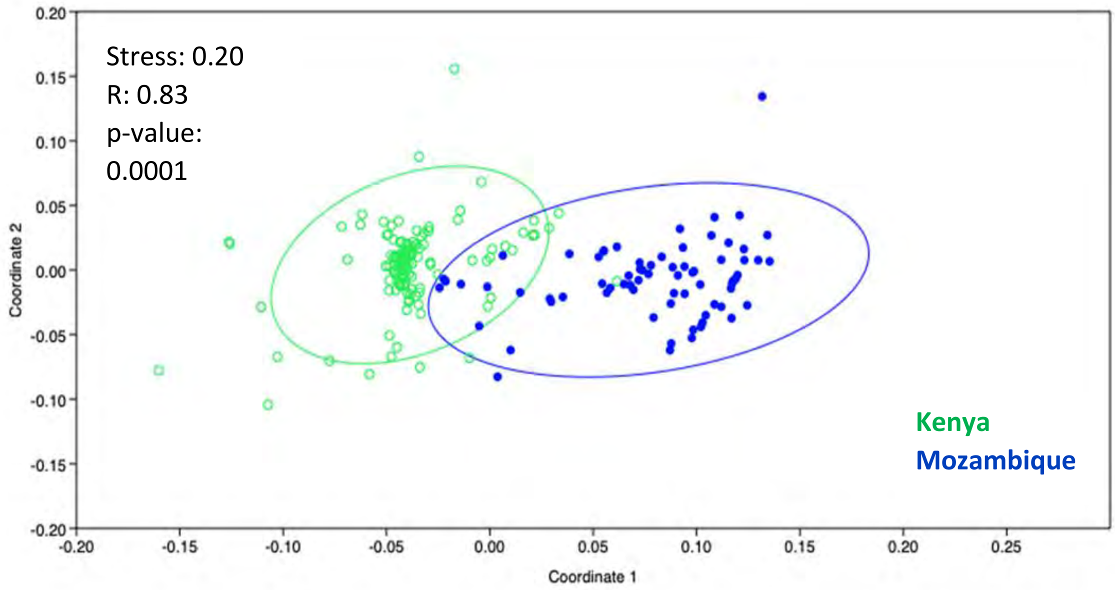

Figure 15. Non-metric multi-dimensional scaling (MDS) plot indicating the distribution of significant morphometric characters of *Euthynnus affinis* between Kenya (green, n=141), and Mozambique (blue, n=71)

Integrated spatial perspective

The comprehensive synthesis of spatially represented genetic divergence, length-at-maturity, catch-weight, and morphometric analyses supports some degree of spatial stratification in *E. affinis* populations. In contrast to *K. pelamis,* findings supported a more nuanced scenario. Genetic discontinuity zones, identified through spatial genetic divergence analysis, elucidated three discreet *E. affinis* population groupings (Northern Mozambique and Kenya; Tanzania; Seychelles) (Figure 12). Mapped length-at-maturity distributions revealed no alignment with proposed genetically isolated population inferred through genetic divergence data, with only one prominent abundance of maturity in the coastal regions of Northern Tanzania and Kenya (Figure 13B). Spatially represented catch-weight analysis, however, revealed a very patchy distribution of catch-weight abundances across the region (Figure 14), which too were not in strong alignment with stock distributions inferred through genetic divergence data. As for *K. pelamis*, limitations in the geographic extent of *E. affinis* morphometric sampling, limited direct comparison of morphometric analysis with other spatially represented analyses. Morphometric analysis did however reveal significant differences between sampled countries, supporting a stratified stock structure of *E. affinis* in the SWIO (Table 5, Figure 15).

CHAPTER 4: DISCUSSION

Integrated spatial analysis of the important biological and fishery characteristics of *K. pelamis* and *E. affinis* in the SWIO provides fundamental baseline information on the population structure and connectivity of these important fishery species. This information is prerequisite to the conduction of adequate stock assessments that will inform effective management strategies for these species (Cadrin and Secor 2009). Findings, based off the spatially structured analyses provide evidence supporting spatial structuring in *K. pelamis* and *E. affinis* populations across the SWIO, indicative that populations of both species comprise of more than singular panmictic stocks. The primary causes of spatial population structuring within *K. pelamis* and *E. affinis* stocks in the SWIO likely pertain to the interplay between the complex biological and ecological dynamics characteristic of the SWIO, such as oceanic currents, biogeographic barriers, and habitat complexity, which is driving variable reproductive isolation that is delineating stocks. The research findings therefore contradict current IOTC management policy, which align CMMs and HCRs within the singular stock hypothesis. Consequently, current management is possibly inadequate for ensuring sustainable exploitation of *K. pelamis* and *E. affinis* fishery resources across the SWIO, and should be subjected to review, given the invaluable socio-economic and ecological contributions of these important fishery resources, as captured by the image below (Figure 16). Failure to adapt IOTC policy to account for these findings can severely affect socio-economic development and ecological health in the region.

Figure 16. Daily catch of *Katsuwonus pelamis* by a local artisanal fisherman in Kiribati, Kenya, depicting the invaluable socio-economic contributions of the species across the region. Image credit: Pala (2021)

4.1 Population structure and Connectivity

Spatially depicted genetic divergence supported the presence of three genetically discrete stock complexes of *K. pelamis* (Dar es Salaam, Tanzania, and Kenya; Mtwara, Tanzania, Mozambique, and Eastern Cape, South Africa; Seychelles) (Figure 8) and *E. affinis* (Northern Mozambique and Kenya; Tanzania; Seychelles) (Figure 12). These proposed groupings of possibly discreet stock complexes of *K. pelamis* and *E. affinis* are supported by the PCoAs (Figure 17, Figure 18) generated from the genetic divergence data in WIOMSA'S MASMA project (Sauer et al. 2022). In the case of *K. pelamis*, the PCoA demonstrates the proposed separation of Northern and Southern population groups in the SWIO (Figure 17). However, contrary to the spatial depiction of *K. pelamis* genetic divergence, PCoA recognized the Seychelles population among the Southern stock of *K. pelamis*, and not as a genetically discrete population group of its own (Figure 17). Similarly, the PCoA applied to *E. affinis* genetic data aligns very closely with the spatial depiction of *E. affinis* genetic divergence, demonstrating the proposed spatial separation of three independent *E. affinis* population groupings in the SWIO (Figure 18) (Sauer et al. 2022).

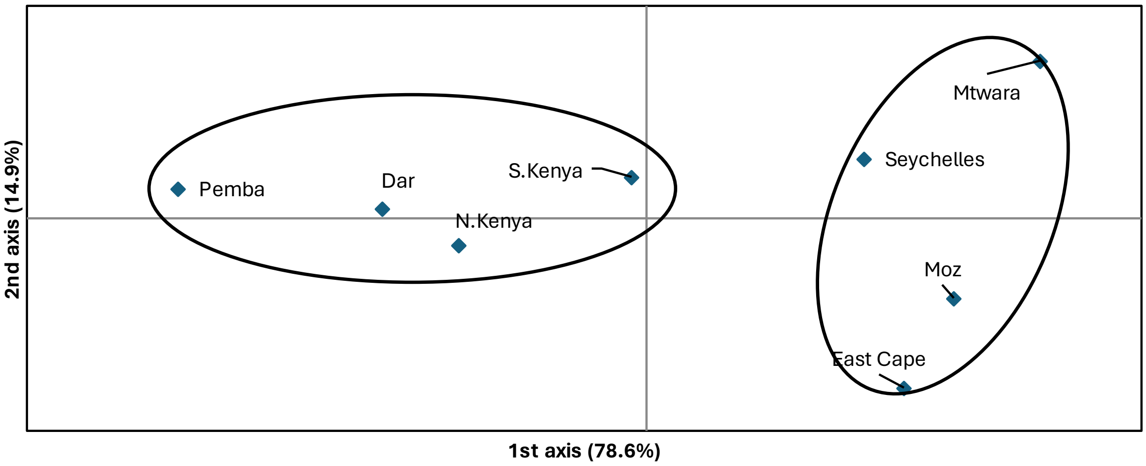

Figure 17. Multidimensional scaling (MDS) plot indicating the separation of *Katsuwonus pelamis* population groups based on genetic differentiation between sampling sites. Ellipses depict where the separation of independent population groups is likely occurring. Image adapted from Sauer et al. (2022)

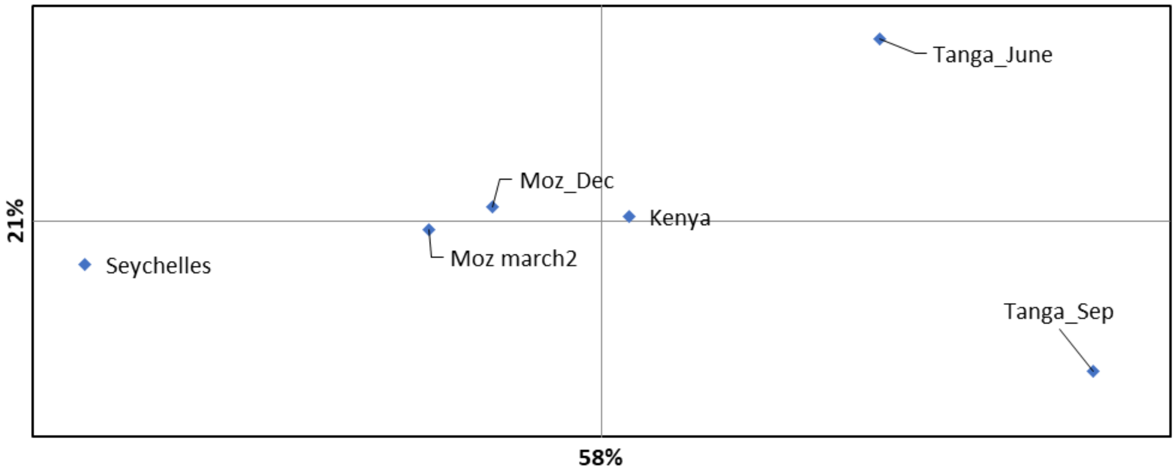

Figure 18. Principal coordinate analysis (PCoA) indicating the separation of *Euthynnus affinis* population groups based on genetic differentiation between sample locations. Image adapted from Sauer et al. (2022)

Evidence supporting spatial population structuring based on within-ocean genetic data are supported by two studies for *K. pelamis*, using mtDNA and nDNA microsatellite data in the wider regions of the IO. Findings from Dammannagoda et al. (2011) strongly supported the likelihood for a spatially heterogenous population structure of *K. pelamis* in the North-western IO, suggesting the presence of two reproductively isolated *K. pelamis* populations across the sampling location. Menezes et al. (2012) further supported these results using mtDNA sequencing data, where findings revealed the presence of four genetically isolated population groupings of *K. pelamis* throughout the coastal waters of India. Despite the respective importance of *E. affinis* toward IO artisanal fisheries, existing research into the population structure and connectivity of the species is very limited, with only a few existing genetic studies on the species (Kumar and Kocour 2015). Prior to the conduction of this study, genetic research on the population structure of *E. affinis* had been confined to the coastal waters of India, and Southern and Western Indonesia, where results aligned with existing management policy, providing no evidence for spatial population structuring in *E. affinis* populations (Kumar et al. 2012, Setyadji et al. 2023). However, over the time of the present research study, Davies (2020) investigated the genetic population structure of *E. affinis*, forming part of the PSTBS-IO Project. Aligning with the present research, these findings supported spatial population structuring of *E. affinis*, providing evidence for two genetically divergent population groupings of *E. affinis* in the Northern and Eastern regions of the IO (Davies 2020).

To date, genetic data offers the most conclusive evidence in support of reproductive isolation in fishery populations (Cadrin 2020). Significant genetic differentiation among fishery population groups suggests that gene flow is limited between discrete stocks, and that there is restricted dispersal of larvae, which combined, prevents the mixing of individuals between spawning areas (Pecoraro et al. 2018). The observed genetic differentiation as reported within *K. pelamis* and *E. affinis* populations throughout the SWIO could be caused by the complex interplay between biological and ecological dynamics, which are driving variable reproductive isolation that is delineating stocks (Pecoraro et al. 2018). These dynamics can include biogeographic barriers, ecological isolation, and adaptation (Pecoraro et al. 2018). A notable pattern in the genetic data for both *K. pelamis* and *E. affinis* is a high degree of genetic divergence in the region of central Tanzania, which is delineating population groupings to the North and South of this region. This region of Tanzania falls near where the prominent South Equatorial Current diverges into the East African Coastal Current, and the Mozambique Current (Sauer et al. 2022). The divergent oceanic circulation in this region forms a biogeographic barrier, which may be responsible for restricting the transport of larval stages, thus preventing free transport among populations of *K. pelamis* and *E. affinis* (Ali and Huber 2010, Sauer et al. 2022). In addition, spatial population structuring among *K. pelamis* and *E. affinis* populations may be attributed to the expansive diversity of habitats and productivity prevalent throughout the SWIO, driving ecological isolation (Hawkins et al. 2016). The combination of high productivity, resource availability, and habitat diversity throughout the SWIO may result in the stratification of *K. pelamis* and *E. affinis* populations, provided that there is limited migration and mixing during recruitment throughout early ontogeny (Hawkins et al. 2016). Ecological isolation may therefore be responsible for the significant genetic differentiation observed for *K. pelamis* and *E. affinis* in the region of the Seychelles. Lastly, isolation by distance, and homing behaviour is another ecological factor that has been reported to cause reproductive isolation among subpopulations of fishery resources (Fujino 1996). However, in the present context this scenario is unlikely, as genetic differentiation values reported between sample locations for *K. pelamis* and *E. affinis* populations were low, which suggests that discreet population groupings sustain relatively high levels of mixing (Sauer et al. 2022). Therefore, owing to the advances of genetic methods toward the detection of reproductive isolation and subsequent stock identification of fishery populations over the past decade (Reiss et al. 2009, Menezes et al. 2012), present genetic analyses combined with broader literature provide substantial support for higher spatial complexity associated with *K. pelamis* and *E. affinis* populations in the SWIO.

The contention of currently imposed IOTC management policy for *K. pelamis* and *E. affinis* is further supported through present spatial length-at-maturity and catch-weight analysis, particularly evident in *K. pelamis*. The research findings based off geospatial maturity analysis closely aligned with the proposed stock boundaries of *K. pelamis*, inferred through genetics, likely illustrating reproductively isolated geographic zones among *K. pelamis* population groupings. However, this is not to say that individuals from discrete stocks are physically isolated, but rather that these suggested functional stocks could overlap spatially but remain functionally distinct due to spatiotemporal separation during periods when spawning takes place (Bacha et al. 2014, Crochelet et al. 2016). The distinct spatial structuring observed in mature *K. pelamis* across the SWIO, may also align with the possible explanations for the reported spatial distribution of genetic differentiation among *K. pelamis* and *E. affinis* populations. The spatial and temporal dynamics of spawning in highly migratory, tropical tuna species generally correspond to favourable oceanographic parameters such as optimal temperatures and resource availability (Reglero et al. 2014). Isolated groupings of mature *K. pelamis*, as reported in the present spatial analysis, may therefore arise due to scattered ecological environments that support oceanographic conditions favourable to spawning. Although variable levels of mixing will still occur among populations, it is likely that individuals will adapt to the ecological niches that they are most exposed to, consequently driving genetic differentiation (Arnegard et al. 2014). Spatially represented *E. affinis* maturity data provided no support for the multiple stock hypothesis, as suggested through spatially illustrated genetic divergence data. Consequently, findings from the spatial maturity analysis either suggest a singular panmictic population structure for *E. affinis* in the SWIO, or could be attributed to sampling limitations, which constrained the present analysis. Considering the findings from *E. affinis* genetic analysis, combined with limited artisanal fishery sample representation, which accounts for majority of *E. affinis* catch across the region, it is likely that the latter scenario is constraining stock structure conclusions for *E. affinis* across the region.

Whilst spatial maturity analysis inferred through size-frequency data may not directly construe stock structure conclusions, it may aid in the identification of geographic zones of reproductive isolation, driving genetic variation between potential stock complexes (Mejuto 2018). Although inferences from size-frequency data may denote potential spawning grounds among *K. pelamis* and *E. affinis* populations, driving reproductive isolation, spatially represented larval distribution, gonad maturation, and ovarian histological data have been the most effective methods in determining reproductive isolation for closely related species such as Swordfish (*Xiphias gladius*) (Neilson et al. 2007). Future research should therefore bolster the present analyses through the inclusion of these data types, to develop more robust conclusions surrounding potential spawning and reproductively isolated geographic zones of *K. pelamis* and *E. affinis* in the SWIO.

Spatially depicted *K. pelamis* catch-weight distributions also aligned with spatial genetic and maturity data, further contending currently imposed IOTC management policy. As for the maturity analysis, spatially represented *E. affinis* catch-weight data provided no correlation in support of the spatial genetic analysis. This too may be the result of inadequate sampling representation of *E. affinis* and should be reinforced with greater sample sizes and representation for the provision of more conclusive results. Examples of these data applied for the assessment of fishery population structure is evident off the coast of Newfoundland for *Hippoglossoides platessoides* (Neilson et al. 2007), off the coast of New England for *Merluccius bilinearis* (Almeida 1987), and off the Scotian Shelf for *Pollachius pollachius* (Neilson et al. 2006). In addition, present spatially represented catch-weight analyses provide insight into the varying levels of exploitation that *K. pelamis* and *E. affinis* are subjected to across the suggested spatial boundaries of their stocks. These present analyses clearly illustrate geographic hotspots of high catch abundance of *K. pelamis* and *E. affinis* in the SWIO, which can subsequently be used by the IOTC to implement more informed stock management strategies. It is, however, also important to acknowledge the limitations of catch-weight data toward the provision of stock structure conclusions surrounding fishery populations (Neilson et al. 2007). Although spatially represented catch-weight data may offer initial indication of geographic stock boundaries, these data are more so a reflection of the distribution of the fishery, rather than the distribution of the fishery populations (Neilson and Black 2005). Therefore, in isolation, spatially represented catch-weight analyses cannot infer definitive stock structure conclusions; however, in the present context, are useful in complementing the concurrent spatially structured analyses.

Morphometric analyses complemented spatially structured genetic divergence, length-at-maturity, and catch-weight data, providing fundamental insight into the stock structure of *K. pelamis* and *E. affinis* in the SWIO (Zischke et al. 2013). Morphometric findings supported increased spatial population complexity, indicating significant morphometric variability between sampled countries for *K. pelamis* (Kenya; Mozambique; South Africa) (Table 4,

Figure 11) and *E. affinis* (Kenya; Mozambique) (Table 5, Figure 15), in contradiction to current management policy. Although the geographic distribution of morphometric sampling effort limited direct comparison with other spatially structured analyses, which were finer scaled and encompassed a larger geographic scope, they were still useful in discerning notable differences and variability among populations of both species. The delineation of fishery stocks inferred through morphometric analysis has been widely documented, with numerous studies acknowledging the application of morphometric techniques toward stock identification of fishery populations (Pawson and Jennings 1996, Afzal et al. 2019, Nikolic et al. 2020). Results from Hajjej et al. (2013) were sufficient to denote four population groupings of little tuna (*Euthynnus alletteratus*) in the coastal waters of Tunisia and the Eastern Atlantic based off morphometric differentiation between sampled locations. The use of morphometric variation has further been documented for the identification of Mediterranean horse mackerel (*Trachurus mediterraneus*) populations in the Black, Aegean, Marmara, and Eastern Mediterranean seas, where Turan (2004) reported the presence of three morphometrically discrete local population groupings among sampled areas.

It is important to recognise that alike to genetic divergence, spatially heterogenous morphometrics observed in *K. pelamis* and *E. affinis* populations may be the result of the interplay between diverse biogeographic and ecological dynamics driving reproductive isolated populations between sample areas, which lead to phenotypic variability (Pecoraro et al. 2018). As is for most tropical tuna species, *K. pelamis* and *E. affinis* do not exhibit consistent temporal spawning dynamics (Grande et al. 2014, Nissar et al. 2010), where their spawning events generally correspond to oceanographic dynamics and resource availability (Grande et al. 2016). Because the timing of sampling events was not aligned between sample countries, significant morphometric differences observed between sampled countries may be attributed to variability in body condition corresponding to a recent spawning event (Zischke et al. 2013). However, findings indicted that DL1 and UJL, for *K. pelamis*, and OCKL, HH, and EH, for *E. affinis* were the highest contributors to the observed dissimilarity among sample countries, all of which are independent of body condition. It is also important to acknowledge that environmental variability, characteristic of the complex SWIO oceanography, may drive the observed morphometric heterogeneity as reported from the present analyses (Tudela 1999). Oceanographic variability can result in spatially structured selection of genetic traits that correspond to favourable phenotypic characteristics toward specific environments (Torrado et al. 2020). Therefore, owing to the highly migratory, pelagic nature of *K. pelamis* and *E. affinis* across the SWIO, it is possible that population groupings may have adapted phenotypically to the specific ecological niches that they most frequently occupy, which could ultimately drive reproductive isolation between phenotypically different population grouping. This is supported through the findings of Milano et al. (2014), which attributed population structuring of European hake (*Merluccius merluccius*), to adaption to local oceanographic conditions.

In contrast, possible methodological errors throughout data collection and analyses may also contribute to the significant morphometric heterogeneity reported between sampled countries. Morphometric data were collected independently throughout each sample country, and consequently, discrepancies in the measurement protocol may be a factor contributing to the reported differences in measurements between sampled countries. This is highlighted by one measurement in particular, TG, which was removed from the present analyses due to implausible reported standardized measurement ranges.

Therefore, although the spatially represented analyses do not definitely delineate or confirm the exact geographic boundaries of reproductively isolated populations of *K. pelamis* and *E. affinis* across the SWIO, the research findings support the presence of spatial structuring among *K. pelamis* and *E. affinis* stocks that experience variable levels of spatio-temporal overlap. The establishment of definitive stock boundaries and dynamics associated with *K. pelamis* and *E. affinis* populations in the SWIO requires a more in-depth sampling protocol, which will need to increase the spatial and temporal scale of data collection. This will ensure that distinct spawning periods, and the movement of discrete populations are incorporated into the analysis, which will ultimately provide more conclusive insight into the mechanisms driving the observed stock separation.

4.2 Management Implications

Over recent years, research centred around stock identification and population delineation of important fishery species has shifted toward a holistic, multi-method approach, in account of the complexities that act across varying biological processes of differing spatio-temporal scales (Papa et al. 2021)**.** Although the present study's integrated spatial analyses do not definitively denote the exact geospatial boundaries of *K. pelamis* and *E. affinis* stock complexes in the SWIO, the analyses combined with wider literature, support a more complex population structure of the study species, particularly in the case of *K. pelamis*. Numerous studies throughout the literature have accentuated the importance of both acknowledging and preserving spatial population dynamics for fishery productivity (Cadrin 2020, Ciannelli et al. 2013, Berkeley et al. 2004), and have highlighted how the failure to acknowledge stock complexities, can lead to overexploitation, and ultimately population collapse (Cadrin 2020, Ciannelli et al. 2013, Berkeley et al. 2004). The case study of Walters and Maguire (1996) is arguably the seminal work on this, outlining how stock assessment failures and subsequent ineffective management led to the collapse of the Northern Cod (*Gadus morhua*) fishery off the coast of Newfoundland, Canada. The overexploitation of one or more reproductively isolated stock complexes can remain undetected if the population complexes are not viewed as disparate units (Berkeley et al. 2004), which is implicated by the present analysis.

Directly associated with the ecological implications of mismanaging artisanal and commercially important fishery species such as *K. pelamis* and *E. affinis*, are the extensive, cascading, and deep-rooted socio-economic repercussions. Classification and acknowledgement of the associated socio-economic impacts of stock mismanagement are paramount to effective restructuring of present management, which will target the mitigation of presently mismanaged *K. pelamis* and *E. affinis* fishery stocks in the SWIO. The WIO generates $1.6 billion through its tuna fisheries annually, where food, and livelihood provision for local communities generated through small scale fisheries is valued at approximately $200 million (Obura 2017). Considering the increasing economic dependence that coastal countries and small island territories throughout the SWIO place on *K. pelamis* and *E. affinis* small scale artisanal and commercial fisheries (Kimani et al. 2018), prolonged mismanagement of these species can have detrimental impacts toward food security, livelihoods, and socio-economic development of these countries (McClanahan et al. 2015). This is highlighted in the case study of Warren and Steenbergen (2021), which indicated how the collapse of the sardine (*Sardinella lemuru*) fishery in Bali, Indonesia had considerable impacts on the livelihoods of commercial and artisanal fishers across the region. The case study found that the government's inability to regulate, monitor, and control overfishing, led to resource declines, which resulted in fishery stakeholders losing up to 50% of their standard income (Warren et al. 2021). Additionally, stock mismanagement of *K. pelamis* and *E. affinis* can create conditions conducive to IUU fishing activity (Petrossian 2015). This is attributed to a host of factors which can include, poor monitoring and enforcement, increased competition within the fishery, inadequate repercussions for illegal fishing activity, and socio-economic pressures such as sustaining livelihoods (Petrossian 2015). Captured below demonstrates the European Commission's inspection delegation's attempts to combat IUU tuna fishing activity (Figure 19). Therefore, considering the far-reaching socio-economic, and ecological adversities associated with the mismanagement of artisanal and commercially important tuna species inclusive of *K. pelamis E. affinis* in the SWIO, it is vitally important that current management policy is reviewed and restructured, to ensure the resilience and sustainability of these invaluable fisheries in future.

Figure 19. Photograph capturing the European Commission's inspection delegation combatting illegal, unreported, and unregulated (IUU) tuna fishing activity. Image credit: FAO (2023)

Globally, the management of large pelagic fishery species such as tuna, subjected to high levels of exploitation, have been managed by RFMOs using unilateral spatial management and spatial fishery closures (Boerder et al. 2019). The implementation of these measures has been reported to target recognized spawning and aggregation sites for species such as *T. thynnus* in the Mediterranean Sea as well as in the Gulf of Mexico (Boerder et al. 2019). Present SMMs implemented by RMFOs generally take the form of gear selective or seasonal closures (Boerder et al. 2019). The Inter American Tropical Tuna Commission (IATTC), Western and Central Pacific Fisheries Commission (WCPFC), and the ICCAT, all currently utilize SMMs for the protection of their target tuna fishery species, including *T. albacares*, *T. obesus*, and *K. pelamis*

(Boerder et al. 2019). The IATTC was the first RMFO to utilize SMMs, implementing a temporary closure on the purse seining of *T. albacares* over the years 1966-1978, and 1999-2001 (Boerder et al. 2019). The IOTC has record of two SMMs that have been implemented for the target tuna species, *T. obesus*, and *T. albacares*, however presently, none of which remain active (Norman et al. 2018). These measures were implemented to reduce the effort placed on these fishery species, however, were unsuccessful in achieving these goals, due to uncertainty around their stock dynamics (IOTC 2010).

Owing to the pervasiveness of RFMO led SMMs for the management of highly mobile, exploited fishery species, combined with present findings contending currently imposed IOTC management policy for *K. pelamis* and *E. affinis* in the SWIO, SMMs could be a valuable tool to improve the current management of these important fishery species (Boerder et al. 2019). Considerable debate has however surrounded the use of SMMs for the management of large and highly pelagic species, characteristic of the study species, due to the lack of research initiatives conducted on these species (Boerder et al. 2019). These measures require implementation across extensive pelagic environments, which are characterized by constant change over spatio-temporal scales, and where effective governance is more challenging to achieve (Kaplan et al. 2014). Emerging evidence has however emphasized the importance of spatial management approaches aimed at specific fish life history stages, such as spawning periods, and juvenile stages, to limit their exposure to the fishery (Boerder et al. 2019). More notably, modelling orientated research initiatives have indicated that highly migratory pelagic species subjected to SMMs, particularly closed areas, display more resilience toward population collapse, and exhibit greater catch yields compared to populations without SMMs (West et al. 2009, Dueri and Maury 2013). These deductions were supported through research on *K. pelamis* in the IO, which modelled the effects of a hypothetical Marine Protected Area (MPA) in the WIO on present *K. pelamis* populations. The findings showed that the MPA reduced fish mortality and proved to be successful in achieving stability within the spawning population (Dueri and Maury 2013). Furthermore, the advantages of SMMs are more evident in scenarios where IUU fishing is highly prevalent, where policies such as Total Allowable Catches (TACs) are difficult to monitor, and most importantly, where there is mismanagement within the fishery, all of which are applicable to SWIO *K. pelamis* and *E. affinis* fisheries (Boerder et al. 2019). Therefore, SMMs, in the form of selective closures, demonstrate immense potential for the improvement of current management of *K. pelamis* and *E. affinis* in the SWIO, however it is vitally important that these measures target critical spawning and potential aggregation sites, and combine these measures with improved effort controls, to achieve the most effective management outcomes.

Although SMMs may appear successful toward the conservation and protection of *K. pelamis* and *E. affinis* population groupings in the SWIO, it is important to acknowledge the socio-economic implications associated in the context of such policy arrangements. The closure of the Western Central Pacific Ocean (WCPO) *T. obesus* fishery off the coast of Hawaii, United States provides a case study outlining how policy changes in the form of closed areas, impacted the livelihoods of stakeholders of the fishery (Richmond et al. 2015). The fishery's closure led to the decline in both the market supply and quality of the product, which ultimately resulted in a substantial increase in price (Richmond et al. 2015). Fishers were additionally required to travel further distances to obtain their catch, which further resulted in increased fishing costs (Richmond et al. 2015). Consequently, owing to the complexities associated with the conservation and protection of artisanal and commercially important fishery resources, it is vitally important that all socio-economic and ecological aspects are factored into management policy. If left unaccounted for, fishers may require alternative income opportunities to sustain their livelihoods (Allison and Ellis 2001).

Therefore, according to existing and accessible data on *K. pelamis* and *E. affinis* in the SWIO, it is highly likely that both species display spatial structuring among their populations, in support of the multiple stock hypothesis. However, these inferences are based off data which are very limited and constrained throughout most parts of Africa, particularly in the case of artisanal, and subsistence fleets, as well as on the impacts of IUU fishing that prevails across the SWIO. Therefore, considering that the present spatial analysis of *K. pelamis* and *E. affinis* in the SWIO was conducted primarily using commercial fishery catch data, it is vitally important for continued research to bolster the present analysis with the inclusion of fishery independent data, which will incorporate spawning and juvenile samples over different spatio-temporal scales, as well as an increased representation of artisanal and subsistence fishery data. Not only will this improve current spatial population analysis, particularly for *E. affinis*, but will contribute to the identification of potential spawning and aggregation sites, which SMMs can aim to target. Future research must also aim to incorporate additional biological characteristics, particularly pertaining to maturity and reproductive dynamics of *K. pelamis* and *E. affinis* in the SWIO. This will provide organizations such as the IOTC with more conclusive results surrounding geographic zones of reproductive isolation, which will improve the present understanding of the stock structure and connectivity of these important fishery species. Finally, future research must investigate oceanographic variables, and link them to present spatial analysis, to provide a more comprehensive understanding of the mechanisms driving the observed spatial separation of these species and their stocks. Addressing the present research gaps will provide more conclusive evidence in contention of currently imposed IOTC management policy and ultimately enable more sustainable exploitation of these important fishery species in future years. Until such research is available, a precautionary approach should be adopted when implementing CMMs for these species across the SWIO, considering the presently proposed distribution of their stocks separate for management.

CONCLUSION

This study provides valuable insight into the spatial population structure and connectivity of two small tuna species, *K. pelamis* and *E. affinis* in the SWIO, which has contributed to addressing the present management discrepancies surrounding these socio-economically important fishery species. The study provides evidence supporting that *K. pelamis* and *E. affinis* do not exist as singular panmictic populations across the SWIO, but rather display varying degrees of spatial structuring, existing as multiple, reproductively isolated subpopulations, which experience variable degrees of mixing between subpopulation units. Spatially illustrated genetic divergence, length-at-maturity, catch-weight, and morphometric analyses provided substantial evidence for spatial structuring among *K. pelamis* populations in the SWIO, supporting the presence of three reproductively isolated subpopulation groupings in the following geographic distributions: Dar es Salaam, Tanzania, and Kenya; Mtwara, Tanzania, Mozambique, and Eastern Cape, South Africa; Seychelles. Findings around *E. affinis* were more complex. Only spatially illustrated genetic divergence, and morphometric data provided evidence for spatial population structuring, with genetic data supporting the presence of three genetically discrete subpopulation groupings in the following geographic distributions: Northern Mozambique and Kenya; Tanzania; Seychelles. Spatially illustrated length-at-maturity and catch-weight data however did not provide sufficient evidence supporting spatial structuring among *E. affinis* populations in the SWIO. Findings from this study's research approach exemplify current management's potential oversimplification of the complexity associated with the spatial distribution of *K. pelamis* and *E. affinis* stocks across the SWIO and emphasize the need to restructure present management policy. In dealing with the management of such spatial population complexity among *K.*

pelamis and *E. affinis* populations in the SWIO, the use of SMMs have been proposed. However, without definitive information available to decern the exact geographic boundaries of *K. pelamis* and *E. affinis* stocks in the SWIO, the implementation of SMMs remains complex, with the potential for unintended socio-economic implications. Until such research is available, a precautionary, participatory approach should be adopted when implementing SMMs for these species across the SWIO, considering the presently proposed distribution of their stocks separate for management. This will ensure the continuation of sustainable harvest and exploitation of these invaluable fishery species in future years.

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