FISHERY CHARACTERISTICS, GENETIC STRUCTURE, POPULATION DEMOGRAPHY AND VALUE CHAIN OF SKIPJACK AND KAWAKAWA EXPLOITED IN COASTAL WATERS OF THE WESTERN INDIAN OCEAN

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By
Fatuma Ali Mzingirwa-20M6735

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Supervisors: Prof. Warwick Sauer and Dr Gladys Okemwa

GENERAL ABSTRACT

Tuna represents a highly valuable global fishery, comprising 7.9% of the total 67.9 million metric tons (MT) of marine finfish catch. Among tuna species, *Katsuwonus pelamis,* skipjack and *Euthynnus affinis,* kawakawa are commercially important, particularly for artisanal fisheries. Skipjack is the most dominant tuna species globally, contributing over 60% to total tuna production. In the Indian Ocean (IO), skipjack catches approximately 420,000 MT annually. Kawakawa, the second most abundant neritic tuna in the IO, accounting for roughly 12% of neritic tuna landings, is primarily harvested by artisanal fleets, with annual catches of around 160,000 MT. While current assessments indicate that skipjack and kawakawa stocks in the IO are not overfished, maintaining their long-term health is crucial.

This research addresses three key areas: genetic diversity, population structure, and connectivity of skipjack and kawakawa tuna in the Western Indian Ocean (WIO); size structure and reproductive characteristics of these species within the WIO; and the value chain of the Kenyan artisanal tuna fishery, focusing on skipjack and kawakawa. To achieve these objectives, skipjack and kawakawa samples were collected from Kenya, Tanzania, Mozambique, and South Africa. A non-random sampling approach was employed to obtain specimens and data from artisanal and recreational fisheries. Biological and genetic sampling were conducted concurrently. The economic value chain of the Kenyan artisanal tuna fishery was examined through questionnaires and catch data. This analysis focused on the socio-demographic profiles of key actors, the value chain structure, and associated economic benefits across four Kenyan landing sites.

To investigate stock structure in WIO skipjack and kawakawa tuna, we employed tunable Genotyping-by-Sequencing (tGBS) to generate genome-wide Single Nucleotide Polymorphism (SNP) data. Skipjack analysis revealed 7005 SNPs with an average observed heterozygosity (Ho) of 0.206. While overall genetic differentiation (FST) among samples was low (global FST = 0.003) between samples ($F_{\mathrm{ST}} = 0 - 0.013$), significant genetic differences were observed between skipjack samples taken north of Mtwara in southern Tanzania (i.e., northern Tanzania, Kenya and Sri Lanka) and those to the south (i.e., southern Tanzania, Mozambique and South Africa), with Seychelles falling closer to the southern grouping. Kawakawa analysis, based on 14806 SNPs and an average Ho of 0.2585, indicated a patchy distribution of low but significant genetic differentiation among WIO populations (global

FST = 0.018) between-sample ($F_{ST} = 0.003 – 0.036$) but with no obvious geographically-based pattern. However, unlike skipjack, a clear geographic pattern in genetic structure was not evident for kawakawa.

Skipjack and kawakawa populations in the WIO exhibited seasonal fluctuations in size distribution, potentially influenced by environmental conditions and fishing practices. Landings of both species were male-biased, with sex ratios of 58% and 53% for skipjack and kawakawa, respectively. Female skipjack reached sexual maturity at a fork length (FL) of 42.0 cm, while males matured at 47.0 cm FL. For kawakawa, female and male maturation lengths were 44.0 cm FL and 45.3 cm FL, respectively. Spawning occurred throughout the year, with peak activity coinciding with the Northeast Monsoon (NEM) season.

Our analysis of the artisanal tuna value chain indicates that fishers primarily sell their catch to agents (53%), with the remaining proportions going to traders (20%) and processors (18%). Processors, predominantly women, play a key role in the value chain and realized the highest net profit margin (49.5%). Limited post-harvest infrastructure, inadequate transportation, and poor marketing conditions were identified as key challenges impacting the quality of fish lowering their income. These challenges disproportionately affect fishers with limited access to market information and financial resources. The findings demonstrate the need for multi-level interventions to optimize benefits from the artisanal tuna fishery along the entire value chain taking into consideration the economic, environmental, and social dimensions.

This research provides crucial information for effective tuna management in the IO. Current management practices treat skipjack and kawakawa as a single, homogenous population across the entire IO. However, our genetic findings suggest the presence of distinct population groups (stocks) for both species within the WIO. Moreover, seasonal variations in size structure and reproductive characteristics observed support this hypothesis of multiple stocks. These results emphasize the need for a precautionary approach to tuna management in the region. Collaborative efforts among countries are essential to develop sustainable fisheries management strategies that consider biological, economic, and social factors. By integrating these perspectives, we can ensure the long-term health of tuna populations while supporting the livelihoods of fishing communities.

PREFACE

This thesis comprises three data chapters (Chapters 3, 4 and 5) which are presented as scientific papers, all of them have been submitted to the African Journal of Marine Science. Also included are a general introduction (Chapter 1), a description of the study area and data collection (Chapter 2), and a general discussion and conclusion (Chapter 6). The three chapters are presented as manuscripts hence there is some repetition in the thesis that is unavoidable.

I am the main author of the scientific papers submitted as follows:

a) **Genome-wide genetic marker variation uncovers potential stock structuring of oceanic tuna (skipjack) and coastal tuna (kawakawa) within the Western Indian Ocean (Under review)**

Mzingirwa FA, McKeown NJ, Sauer WHH, Okemwa GM, Halafo JS, Grayson J, Kamau J, Shaw PW

b) Size structure and reproductive biology of skipjack and kawakawa in the Western Indian Ocean (Under view)

Mzingirwa FA, Okemwa GM, Farthing MW, Bova CS, Halafo JS, Grayson J, Athman AA, Sauer WHH

c) Value chain analysis of Kenya's artisanal tuna fishery targeting skipjack and kawakawa (In press)

Mzingirwa FA, Okemwa GM, Marcone O, Viana S, Bova CS, Sauer WHH

DECLARATION

I, Fatuma Ali Mzingirwa, declare that this thesis is entirely my original work under the supervision of Prof. Sauer and Dr Okemwa. This work is being submitted to the Department of Ichthyology and Fisheries Science, Rhodes University, and has not in any form been submitted to any other university.

All research activities were conducted under the Rhodes University Animal Ethics and Standards Council approval number: 2021-4853-6063 and the Human Ethics (RU-HEC) approval number: 2021-2754-5923.

Signature: __________ Date: 16th August 2024

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DEDICATION

I dedicate this thesis to the most influential man in my life, my dad **(Baba)**. “I would never have started this without your encouragement and I would never have finished this without knowing how proud it would make you”.

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LIST OF ABBREVIATIONS AND ACRONYMS

Symbol	Name
AO	Atlantic Ocean
BMU	Beach Management Unit
CCRF	Code of Conduct for Responsible Fisheries
CCSBT	Commission for the Conservation of Southern Bluefin Tuna
cm	Centimetre
CPUE	Catch per Unit Effort
DNA	Deoxyribonucleic Acid
DWFNs	Distant Water Fishing Nations
EACC	East Africa Coastal Current
EEZ	Exclusive Economic Zone
EPO	Eastern Pacific Ocean
EU	European Union
FAO	Food Agriculture Organization
FL	Fork length
GI	Gonad Index
GW	Gonad Weight
H_E	Expected Heterozygosity
HWE	Hardy Weinberg Equilibrium
H_O	Observed Heterozygosity
IAATC	Inter America Tropical Tuna Commission
ICCAT	International Commission for the Conservation of Atlantic Tuna

i.e.	that is
IO	Indian Ocean
IOTC	Indian Ocean Tuna Commission
k	Growth coefficient
KES	Kenya shillings
kg	Kilogram
km	Kilometre
L	Length
$L\infty$	Length at infinity
Lm	Length at first maturity
L50	Length at 50% maturity
m	Meter
MAF	Minimum Allele Frequency
mtDNA	Mitochondrial DNA
MT	Metric tonnes
MSY	Maximum Sustainable Yield
NEM	North East Monsoon
NGS	Next Generation Sequencing
O_2	Oxygen
PCoA	Principal Coordinate Analysis
RAPD	Random Amplified Polymorphic DNA
RFLP	Restriction Fragment Length Polymorphism
RFMO	Regional Fisheries Management Organization

SE	Standard Error
SEC	South Equatorial Current
SEM	South East Monsoon
SNP	Single Nucleotide Polymorphism
SST	Sea Surface Temperature
tBBS	Tunable Genotyping By Sequencing
TL	Total length
UNSFA	United Nations Fish Stocks Agreement
URT	United Republic of Tanzania
USD	United States Dollar
VCA	Value Chain Analysis
WIO	Western Indian Ocean
WCPO	Western Central Pacific Ocean
WCPFC	Western and Central Pacific Fisheries Commission

CHAPTER ONE

GENERAL INTRODUCTION AND LITERATURE REVIEW

Overview of the chapter

This chapter presents the background knowledge and key concepts that underpin the research covered in Chapters 3 to 5. Sections 1.1 to 1.3 offer an overview of the importance of tuna globally and in the WIO region and how they are managed. Sections 1.4 and 1.5 provide detailed descriptions of the taxonomic classification of tuna, biology and ecology of skipjack and kawakawa. The status of the stocks, genetic connectivity and population structure of skipjack and kawakawa and the impact of climate change on these two species in the Indian Ocean is described in sections 1.6-1.8. Section 1.9 discusses the knowledge gaps identified during the literature review and states the purpose of the study, whereas the structure of the thesis is described in section 1.10.

1.1 Global Tuna Fishery

Tuna is a globally significant resource, providing food, income, and employment (FAO 2022). As one of the world's most valuable fisheries (Juan-jordá et al. 2011), tuna comprises 7.9% of the 67.9 million metric tons (MT) marine finfish catch (FAO 2019). The global tuna industry is divided into four major regions: the Western and Central Pacific Ocean (WCPO), Eastern Pacific Ocean (EPO), Indian Ocean (IO), and Atlantic Ocean (AO). The Pacific (WCPO and EPO) dominates production, contributing 70% of the global catch, followed by the IO at 21% (ISSF 2021). Indonesia is the world's leading tuna producer, landing over 620,000 MT primarily in the eastern Indian and western Pacific Oceans (McKinney et al. 2020).

Global tuna landings approximate 4.9 million MT, with tropical species comprising 95% of this total (ISSF 2020). This industry contributes an estimated $40 billion annually to the global economy (McKinney et al. 2020). Key commercial tuna species include skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares),* bigeye (*T. obesus*), albacore (*T. alalunga),* northern bluefin (*T. thynnus),* and southern bluefin (*T. maccoyii*) (Majkowski 2007, Restrepo et al. 2016). Skipjack is the most abundant tuna species, with landings exceeding 3.2 million MT, accounting for over half of the total tuna catch (McKinney et al. 2020). Despite its lower unit price compared to yellowfin, bigeye, and bluefin, skipjack ranks second in overall value after yellowfin (McKinney et al. 2020).

Neritic tuna encompasses seven species: longtail (*Thunnus tonggol),* blackfin (*T. atlanticus*), black skipjack (*Euthynnus lineatus),* kawakawa (*E. affinis*), little tunny (*E. alletteratus*), bullet (*Auxis rochei),* and frigate tuna (*A. thazard*) (Majkowski 2007). Primarily caught by poorly documented domestic fleets from developing countries, these species contribute to local food security and livelihoods (Ahmed et al. 2015, Cohen et al. 2019). The IO neritic tuna has gained commercial prominence, with industrial fleets targeting these species within Exclusive Economic Zones (EEZs), particularly in countries like Iran and Indonesia. Historically, Somali piracy diverted fishing efforts from tropical to neritic tuna (IOT 2013). With piracy reduced, the focus has shifted to data collection and monitoring for effective neritic tuna management and conservation in the WIO to ensure sustainable fisheries (IOTC 2023).

1.2 The Indian Ocean Tuna Fishery

The IO is the world's second-largest tuna fishing ground, producing approximately 920,000 MT annually, representing 21% of the global tuna supply and 16% of the industry revenue (US$2.3 billion) (Lecomte et al. 2017, ISSF 2021). Despite covering less than 5% of the global ocean, the IO generates 10% of global tuna catch and over United States Dollar (USD) 1.6 billion in revenue (Coulter et al. 2020). The IO tuna fishery is divided into the Western Indian Ocean (WIO), Eastern Indian Ocean (EIO), and Central Indian Ocean (CIO). The WIO contributes to 80% of the region’s tropical tuna catch. Skipjack tuna is the dominant species, comprising 53% of the total catch, followed by yellowfin at 38%, bigeye at 9%, and kawakawa at 2% (IOTC 2019).

The IO tuna fishery comprises artisanal, semi-industrial, and industrial sectors. Artisanal fisheries dominate, contributing over half of the total catch. Primarily uses pelagic gillnets, accounting for over 34% of the catch (Walmsley et al. 2006). The semi-industrial sector is emerging, with Seychelles leading in vessel numbers, followed by Mauritius and Madagascar. Industrial fishing is dominated by Distant Water Fishing Nations (DWFNs), particularly the European Union (EU), with Spain as the leading member contributing over

70% of the EU's catch (Macfadyen and Defaux 2019). Other key players include Indonesia, Maldives, Sri Lanka, Seychelles, and Iran. While the EU catches a significant portion of the IO tuna catch, India, Indonesia, and Iran collectively contribute around 44%. Notably, these three countries land over 50% of neritic tuna species (India: 59%, Indonesia: 51%, Iran: 53%) (Macfadyen and Defaux 2019).

A variety of fishing gear are used to catch tuna species in the IO. Skipjack tuna are primarily targeted using purse seines (40%), followed by pole-and-line (20%) and gillnet (20%). Kawakawa, on the other hand, are predominantly caught with gillnets (50%), purse seines (30%), including coastal fleets, and lines (16%) (IOTC 2019). Purse seine fishing, introduced to the WIO in the late 1970s, is employed by distant water fleets. Gillnets are another common gear, utilized by approximately 3,000 vessels in the region (Anderson et al. 2020a). The Maldives operates a domestic pole-and-line skipjack fishery within its waters. While industrial longline fishing has been practised in the IO since the 1950s, its prevalence is lower compared to other ocean basins (Allen 2010).

1.3 Management of Tuna

The involvement of multiple nations and diverse fishing gears in targeting tuna necessitates robust management strategies to safeguard this valuable resource and prevent stock collapse. Tuna fisheries are managed by the Regional Fisheries Management Organizations (RFMOs), which were established by the Food and Agriculture Organization Code of Conduct for Responsible Fisheries (FAO CCRF) and the United Nations Fish Stocks Agreement (UNFSA). These bodies were established to enhance cooperation among member states and ensure sustainable use, conservation and management of fish stocks (Allen 2010). The five tuna RFMOs responsible for tuna fisheries are the Western and Central Pacific Fisheries Commission (WCPFC), the Inter-American Tropical Tuna Commission (IATTC), the International Commission for the Conservation of Atlantic Tuna (ICCAT), the Indian Ocean Tuna Commission (IOTC), and the Commission for the Conservation of Southern Bluefin Tuna (CCSBT) (Figure 1.1).

The IOTC manages tuna fisheries in the IO, spanning from eastern South Africa to eastern Australia and Indonesia. Established under the FAO Constitution in 1996, the IOTC is the sole tuna RFMO under FAO's purview (Allen 2010, Sinan and Bailey 2020). Its primary mandate is conserving and managing straddling and highly migratory fish stocks. The IOTC comprises 31 member states, including 22 coastal nations and nine DWFNs (IOTC 1993). While all members contribute to the commission, DWFNs often exert greater influence and gain a larger share of the region's benefits (Allen 2010). The IOTC manages 16 tuna and tuna-like species, including neritic tuna primarily caught by artisanal fishers (Allen 2010). Despite managing these species (Kolody et al. 2013), overfishing has impacted yellowfin and bigeye tuna populations since 2014 (IOTC 2022). Increased fishing pressure, particularly from EU fleets (Macfadyen and Defaux 2019), coupled with inadequate regulatory control due to the diverse membership and coexistence of artisanal and industrial fisheries, has exacerbated the issue (Juan-jordá et al. 2017, Collette 2017, Murua et al. 2015, McCluney et al. 2019). Effective IOTC management is hindered by insufficient data due to poor coordination among numerous small-scale vessels and limited capacity in developing member states (Pons et al. 2017, Ceo et al. 2012).

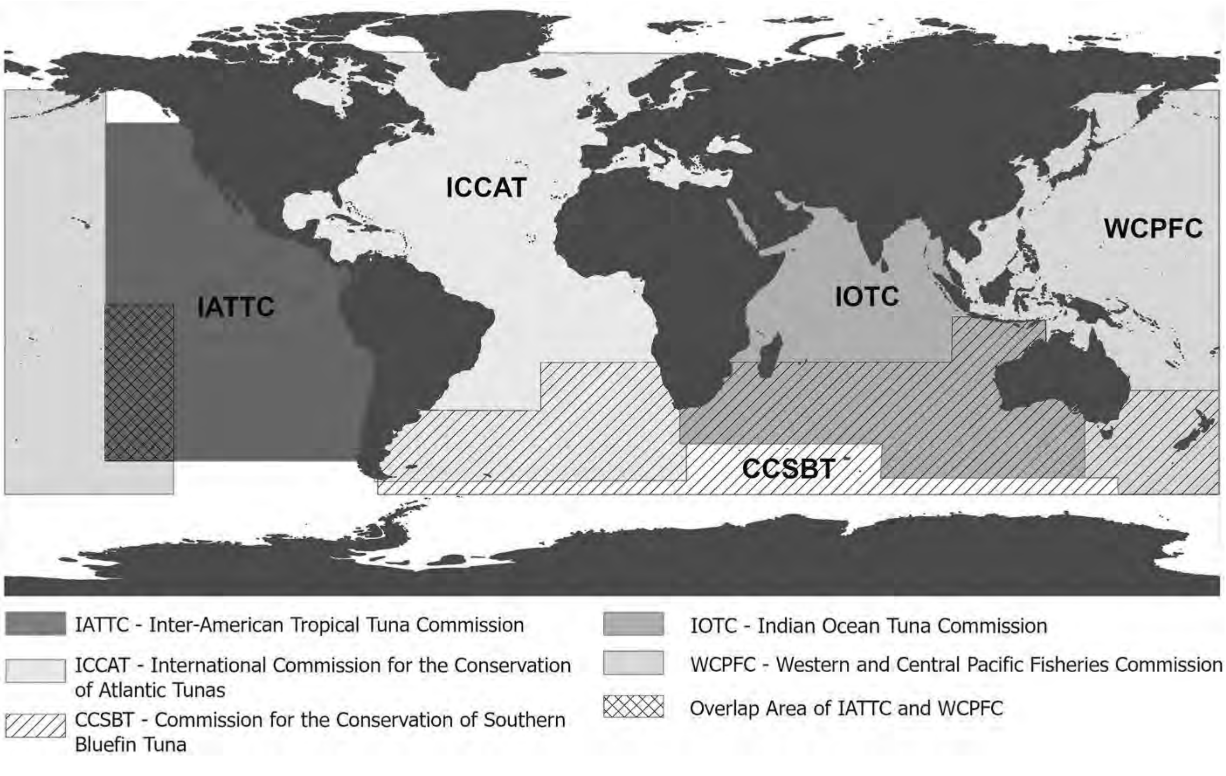


Figure 1.1. Area of jurisdiction (convention area) of the five tuna Regional Fisheries Management Organizations (RFMOs) (source: Heidrich et al. 2022).

1.4 Taxonomic Classification of Tuna

Skipjack, *Katsuwonus pelamis* and kawakawa, *Euthynnus affinis* belong to the Scombridae family, which is divided into two subfamilies: Gasterochismatinae (one species) and Scombrinae (53 species). The Scombrinae further comprises four tribes: Scombrini (10 primitive mackerel species), Scomberomorini (21 Spanish mackerel species), Sardini (seven bonito species), and Thunnini (15 true tuna species) (Figure 1.2). The Thunnini tribe includes five genera: *Thunnus* (eight species: *T. albacares, T. obesus, T. tongol, T. atlanticus, T. maccoyii, T. thynnus, T. orientalis, T. alalunga*), *Euthynnus* (three species: *E. affinis, E. alletteratus, E. lineatus*), *Auxis* (two species: *A. thazard, A. rochei*), *Katsuwonus* (one species*:* *K. pelamis*), and Allothunnus (one species: *A. fallai*) (Collette et al. 2001, Restrepo et al. 2016).

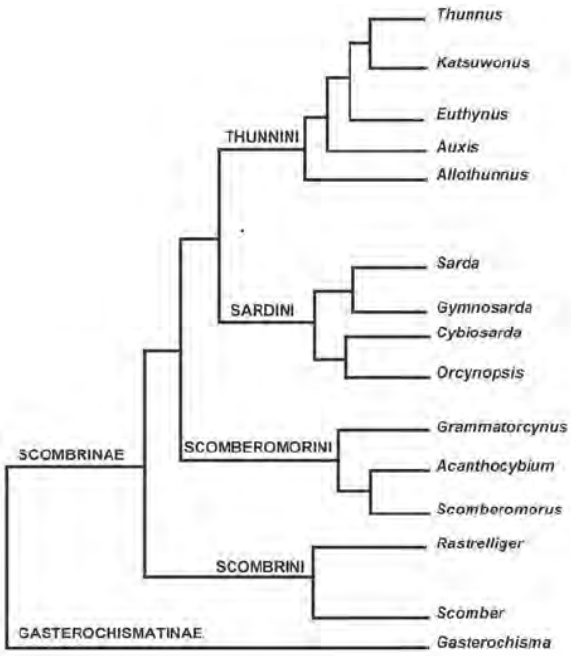


Figure 1.2. Phylogenetic tree of Scombridae family up to genus level (source: Collete et al. 2011).

1.5 Biological characteristics and ecology of skipjack and kawakawa

1.5.1 Morphology and Distinctive Features

Katsuwonus pelamis (Linnaeus 1758) is characterized by four to six distinct, dark longitudinal stripes on its body that appear as discontinuous lines of dark blotches in live specimens (Figure 1.3). It has a streamlined, elongated body with a dark purplish blue dorsal surface and a silvery underside and abdomen. Lacking scales except for a corselet and lateral line, they possess robust keels on either side of the caudal fin base, separated by two smaller keels. Its dentition consists of small, conical teeth arranged in a single row. Gill rakers are numerous ranging from 53 to 63 on the first arch. They have two dorsal fins, separated by a short interspace (a little bigger than an eye). The first frontal dorsal fin has 14 to 16 spines, with the anterior spines notably taller than the central ones, creating a concave profile. A second dorsal fin with seven to nine finlets follows. The pelvic fins are separated by two flaps (inter-pelvic process), and the anal fin is succeeded by seven or eight finlets (Collette et al. 2001).

Euthynnus affinis (Cantor 1849) is distinguished by three to four dark dots between the pelvic and pectoral fins, these spots are not always visible (Figure 1.3). It has a medium-sized, robust, and fusiform body. Its dorsal colouration is dark blue with an intricate striped pattern, and its underside is silvery white. The species lacks vomerine teeth but possesses small, conical teeth in a single row. Two dorsal fins are present, with the first bearing 11 to 14 spines. Notably, the interspace between these fins is smaller than the eye diameter, differentiating it from *Auxis thazard*. Similar to skipjack, the first dorsal fin's anterior spines are elongated, creating a concave profile. The second, shorter dorsal fin is followed by eight to 10 finlets. Pectoral fins are small and do not reach the interspace between dorsal fins. The body is scaleless except for the corselet and lateral line. The caudal peduncle is slender with a pronounced lateral keel flanked by two smaller keels. The fish can retract its first dorsal and anal fins into body grooves and pectoral and pelvic fins into depressions during rapid swimming. They have a very thin caudal peduncle with a noticeable lateral keel sandwiched between two minor keels at the base of the caudal fin (Collette et al. 2001).

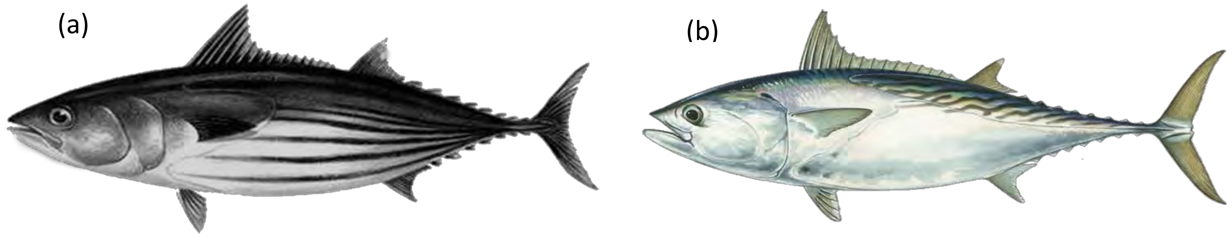


Figure 1.3. Picture images of (a) skipjack and (b) kawakawa.

1.5.2 Anatomical and Physiological characteristics of tuna

True tunas (excluding *Allothunnus*) exhibit unique endothermic capabilities due to a counter-current heat exchange system called the rete mirabilia. This system conserves metabolic heat in muscles, viscera, and the brain, allowing tunas to maintain warmer body temperatures than the surrounding water (Collette et al. 2001). Coupled with elevated metabolism and cardiac efficiency, this adaptation supports sustained, rapid swimming and expands habitat suitability (Graham and Dickson 2004).

Katsuwonus, Euthynnus, and *Auxis* share a common cutaneous artery structure with a short, dendritic ventral branch lacking a vascular plexus. However, skipjack uniquely divides this artery before reaching the ribs, with sparse and irregular arterioles compared to other tunas. Skipjack also has distinct venous drainage, with the dorsal and ventral cutaneous veins emptying directly into the duct of Cuvier rather than the postcardinal vein. *Euthynnus* possesses a dorsal cutaneous artery running the body length, branching into dorsal and ventral segmental arteries without forming plexuses but adhering to segmental veins. A single row of arterioles creates the cutaneous rete's capillary sheet. Notably, the dorsal cutaneous artery in *Euthynnus* consistently follows a dorsal path, adhering to the dorsal cutaneous vein (Stevens and Neill 1978).

1.5.3 Biogeography and Habitat Utilization

Skipjack tuna is classified as a tropical species but exhibits a broader distribution, inhabiting deeper, colder waters of the Atlantic, Indian, and Pacific Oceans (Artetxe-Arrate et al. 2021). Within the IO, skipjack are found between 10°N and 10°S, with temperature and oxygen preferences varying by size. Juveniles occupy the epipelagic zone above the thermocline, in waters with temperatures between 18°C and 31°C (Barkley 1978, Pecoraro et al. 2017). Larvae require even warmer waters (>31°C) and have more restricted habitat ranges (Wexler et al. 2011, Su et al. 2015, Reglero et al. 2014). Adult skipjack also exhibit size-specific habitat preferences. Smaller individuals (<4 kg) avoid waters colder than 18°C or with oxygen levels below 3.5 ml/L, while larger fish (4-9 kg) require cooler waters (<26°C) and higher oxygen levels and thus are spatially confined. The largest skipjack (>9 kg) are further restricted to waters cooler than 22°C making them more spatially confined (Barkley et al. 1978, Gooding et al. 1981, Graham and Dickson 2004).

Kawakawa is classified as a neritic species, along with longtail, frigate, and bullet tunas, inhabiting similar temperature ranges (18-29°C) but remaining closer to shorelines (Collette and Nauen 1983, Poisson 2006, Griffiths et al. 2020a). Their distribution spans the Indo-West Pacific between 35°N and 25°S, and 40°E and 37°W (Froese and Pauly 2019), including the coasts of East Africa, the Arabian Peninsula, the Indian subcontinent, Malaysian Peninsula, the Red Sea, the Persian Gulf, and various IO islands (Williams 1963, Rohit et al. 2012).

While studies on adult skipjack and kawakawa habitat preferences exist (Barkley et al. 1978, Collette and Nauen 1983, Poisson 2006), further research on critical life stages, such as spawning and larval development, is needed. This information will support spatial planning to protect crucial habitats and inform accurate population models for enhanced conservation efforts.

1.5.4 Trophic ecology and feeding

Skipjack and kawakawa exhibit opportunistic feeding behaviours, consuming a diverse diet primarily composed of pelagic fish, cephalopods, and crustaceans (Ménard et al. 2010, Olson et al. 2016, Griffiths et al. 2009, Rohit et al. 2012). Dietary preferences vary with size, time of day, and location. Adult skipjack have broader diets compared to juveniles, which focus on smaller prey near the coast in warmer waters (Smale 1986, Olson et al. 2016, Duffy et al. 2017). Kawakawa demonstrate size-dependent dietary shifts, with larger individuals consuming a wider prey range, including demersal species when surface prey is scarce (Vigneshwaran et al. 2018, Griffiths et al. 2009). Juvenile kawakawa primarily feed on fish and crustacean larvae (Pillai and Gopakumar 2003). Both species exhibit diel feeding patterns, adjusting their foraging activity based on day-night cycles (Roger 1994a).

Understanding the dietary ecology of these species is crucial for ecosystem modelling and sustainable fisheries management. Assessing their trophic roles and potential impacts of removals through fishing requires further research, especially on feeding behaviour within the IO.

1.5.5 Age and Growth

Fish growth is described as the definite change in fish size (length or weight) with time, it is usually quite rapid in early life and slows down with age (von Bertalanffy 1951). Age estimation is crucial for assessing fish stocks through natural mortality rates. Growth is influenced by environmental factors (temperature, oxygen, salinity, photoperiod) and nutritional intake (both quality and quantity) (Morgan et al. 2009). While short-lived species in warm climates exhibit determinate growth, long-lived species in cold regions demonstrate indeterminate growth (Dutta 1994). Growth in tropical tunas is assessed using methods such as age determination from calcified structures (otoliths, spines, vertebrae) and tagging, as well as Length Frequency Analysis (LFA) models like ELEFAN (Campana and Thorrold 2001, Murua et al. 2017).

Skipjack tuna is renowned for its rapid growth (Murua et al. 2017). Von Bertalanffy Growth Function (VBGF) models estimate high growth coefficients ($k > 0.4$) and maximum lengths ($L\infty$) below 82.5 cm FL for Indian Ocean skipjack (Sivasubramaniam 1985). However, estimates vary, with Koya et al. (2012) reporting $L\infty$ of 92.0 cm and k of 0.50 yr-1. Skipjack exhibit two growth phases: rapid initial growth followed by a slower rate (Dortel et al. 2015, Eveson et al. 2015). They reach 45 cm FL in the first year, 50-65 cm FL in the second and subsequent slower growth (Artetxe-Arrate et al. 2021). However, age determination beyond 60 cm is challenging (Kayame et al. 2004). Skipjack mature at 1.3 years (>45 cm FL), have a generation time of 1.9 years, and have a maximum lifespan of 12 years (Froese and Pauly 2023).

Kawakawa also exhibit rapid growth, with $L\infty$ values of 81.7 cm and 81.9 cm FL, and k values of 0.79 and 0.56, respectively (Khan 2004, Rohit 2012). Unlike skipjack, kawakawa show distinct length groups corresponding to age classes. Length groupings of 31 cm, 47 cm, 57 cm, 67 cm, and 70 cm correspond to the first, second, third, fourth and fifth-year age classes (Khan 2004). Maturity occurs at 1.1 years, with a maximum lifespan of 5.1 years and a generation time of 1.8 years (Froese and Pauly 2023). Growth parameter estimates vary across studies due to factors such as sampling design, sampling tools and data analysis (Morrongiello 2015, Blomberg et al. 2011). Therefore, combining multiple methods is essential to minimize bias (Eveson et al. 2015, Dortel et al. 2015).

1.5.6 Reproductive Biology

Fish reproductive success relies on energy availability, life expectancy, and the ability to produce viable eggs (McBride et al. 2015). Understanding reproduction is crucial for sustainable resource management through population dynamics and species modelling (Schaefer 2001, Murua and Motos 2006). Reproduction influences population productivity and resilience to fishing and environmental pressures (Le Bris et al. 2015). For tuna and tuna-like species, reproductive strategies are key to comprehending population dynamics and predicting fishing impacts on reproductive potential (Morgan et al. 2009, Zudaire et al. 2013).

Key reproductive parameters for estimating fish reproductive potential include sex ratios, spawning seasons, length/size at maturity (Lm), spawning frequency, and fecundity (Ashida 2020, Saba et al. 2021). A combined approach to analysing these indicators minimize bias and provides comprehensive insights into species biology and ecology for informed management strategies (Zudaire et al. 2013).

Sex ratio

Fish sex is determined by genetics, environment, or a combination of both. Temperature significantly influences sex determination in some species, with variations in early life stages impacting sex ratios (Geffroy et al. 2020). The sex ratio, defined as the proportion of males to females, is crucial for assessing spawning stock biomass and informing management decisions (Marshall et al. 2006, Armstrong and Witthames 2012). Studies on IO skipjack indicate a female-dominated population (sex ratios of 0.55 and 0.57) (Batts 1972, Bodin et al. 2018). However, sex ratio data for kawakawa in the region is inconsistent, with reports of both female-dominated (0.82) and male-dominated (1.264) populations (Nissar et al. 2015, Chiou et al. 2004).

Accurately estimating sex ratios is challenging due to potential biases introduced by fishing methods, timing, and location. To ensure effective management strategies, robust and reliable sex ratio data for the WIO region is essential.

Spawning season

Understanding a fish species' spawning season is crucial for reproductive success, as environmental conditions and parental characteristics (size, age) significantly influence spawning timing and duration (Hutchings and Myers 1993, Bondarev et al. 2019). Fishing practices that target older, larger fish can disrupt spawning, impacting recruitment (Wright and Trippel 2009). Several studies in the WIO indicate year-round spawning for skipjack tuna, with peaks during the Northeast (NEM) and Southeast (SEM) monsoons (November-March and June-July, respectively) (Stéquert et al. 2001, Grande et al. 2014). While Koya et al. (2012) reported similar year-round spawning with peaks in December-March and June-August. Norungee and Kawol (2011) observed spawning during colder periods, particularly in July.

Mature kawakawa exhibit year-round spawning in most of the IO region, with regional variations in peak spawning periods. Seychelles experience spawning peaks during the NEM (October-November to April-May), while East African waters show peaks from January to July (Collette and Nauen 1983). Similar patterns with two peak spawning seasons (NEM and SEM) have been observed in Tanzanian waters (Johnson and Tamatamah 2013).

Length at first maturity

Fish attain sexual maturity at specific sizes, typically denoted by the length (L50) and age (A50) at which 50% of the population is mature (Chen and Paloheimo 1994). Understanding maturity is crucial for fisheries management as it aids in estimating the proportion of immature and mature individuals (Schaefer 2006). Environmental factors and fishing pressure can influence size at maturity, affecting reproductive traits (Wright et al. 2020). Changes in size at maturity serve as indicators of stock status (Froese et al. 2015, Lappalainen et al. 2016), emphasizing the importance of accurate maturity assessments for effective stock evaluation. Two primary methods determine length at maturity: macroscopic visual examination (Schaefer 1987) and microscopic histological analysis of ovaries (Zudaire et al. 2013). The binomial approach estimates fish lengths and calculates the first length at maturity (Lm) using logistic regression (Zuur et al. 2007).

Studies on WIO skipjack tuna report varying L50 estimates. Grande et al. (2014) found female skipjack reaching first maturity at 39.9 cm FL and full maturity at 49 cm FL. Other studies reported L50 values of 43 cm, 42.9 cm, and 41.01 cm FL (Norungee and Kawol 2011, Tampubolon et al. 2014, Chodrijah et al. 2020) (Table 1.1).

For kawakawa, the lowest estimated Lm in the IO was 37.7 cm FL (Ahmed et al. 2015). Female kawakawa reach L50 at 49 cm FL, while males attain L50 at 49.7 cm FL. Fish smaller than 41 cm FL are considered immature (Khan 2004). Chiou et al. (2004) reported kawakawa maturity at 45-50 cm FL, with full maturity beyond 50 cm FL (Deepti and Sujatha 2012).

Fecundity

Fecundity, or the number of offspring produced per spawning season, is crucial for estimating fish stock reproductive capacity and informing stock assessments (Murua et al. 2003). Larger fish generally produce more eggs, both in absolute and relative terms. Environmental factors like temperature influence fecundity by affecting fish behaviour, metabolism, and food availability (Murua et al. 2003). A trade-off often exists between egg quantity and size, with organisms investing less in offspring number producing larger, more viable eggs (Einum and Fleming 2000). Skipjack tuna in WIO exhibit individual fecundity ranging from 80,000 to 1.25 million oocytes (Stéquert and Ramcharrun 1995, Grande et al. 2014). Kawakawa fecundity varies widely across the IO, with estimates ranging from 200,000 to 2,500,000 oocytes (Rao 1964, Muthiah 1985, Chiou et al. 2004, Nissar et al. 2015).

Studies on skipjack and kawakawa in the WIO reveal inconsistencies in fecundity, spawning season, sex ratio, and length at maturity estimates. These discrepancies may be attributed to factors such as the presence of distinct stocks and changing environmental conditions. Comprehensive data on reproductive characteristics is essential for accurate population dynamics modelling and sustainable fisheries management.

Table 1.1. Some previous estimates on size at maturity (L50) of skipjack (*Katsuwonus pelamis*) and kawakawa (*Euthynnus affinis*) recorded in the Indian Ocean.

Species name	**L50**	**Sex of fish**	**Reference**	**Geographic area**
K.pelamis	39.9 cm (FL)	Female	(Grande et al. 2014)	WIO
	43 cm 44 cm	Female Male	(Norungee and Kawol 2011)	WIO
	42.9 cm	Both	(Tampubolon et al. 2014)	East Indian Ocean
	41.01cm	Both	(Chodrijah et al. 2020)	Indonesia
	43 cm 40 cm	Female Males	Amarasiri and Joseph 1986	Central Indian Ocean (Srilanka)
E.affinis	37.7 (FL)	Both	(Ahmed et al. 2015)	Pakistan
	49 cm (FL) 49.1 cm (FL)	Female Male	(Deepti and Sujatha 2012)	North Andhra Pradesh
	48	Both	Chiou et al. 2004	Taiwan
	47 cm (TL 52 cm FL	Female Male	Johnson and Tamatamah 2013	Tanzania

1.6 Status of tuna in the Indian Ocean

Some tuna stocks in the IO, such as yellowfin and bigeye, are classified as overfished and experiencing overfishing (Juan-Jordá et al. 2022, Heidrich et al. 2023). Overexploitation of these species can impact other tuna species through changes in predator-prey interactions, leading to ecological consequences such as disrupted trophic integrity, reduced ecosystem productivity, and decreased resilience to environmental change (Baum and Worm 2009, Sumaila et al. 2011, Srinivasan et al. 2010, Ortuno-Crespo and Dunn 2017). Long-term overexploitation can result in declining catches, stock collapse, and negative socioeconomic impacts on fishing communities.

In contrast, the skipjack stock is considered healthy, with exploitation rates below target levels and biomass exceeding the reference point (IOTC 2022). Assessments of kawakawa stocks in the IO also indicate a healthy status with optimal fishing levels (IOTC 2015, Zhou et al. 2018, Raza et al. 2022). However, given the increasing fishing pressure from both the industrial and artisanal fleets, regular monitoring of skipjack and kawakawa stocks is essential to maintain their healthy status.

1.7 Genetic connectivity and population structure

Understanding genetic diversity, population structure, and connectivity of commercially important tuna species like skipjack and kawakawa is crucial for effective stock management. Genetic information helps determine whether a species is panmictic (random mating) or comprises distinct subpopulations within its geographic range (Hellberg et al. 2002). Additionally, genetics provides insights into a species' response to fishing pressure, with overharvesting potentially causing population fragmentation, loss of genetic variation, and selective genetic changes (Allendorf et al. 2008). Integrating genetic factors into management strategies aids in identifying distinct populations and predicting stock responses to fishing and climate change.

In the IO, most tuna species have been traditionally managed as single, panmictic populations due to their high migratory behaviour (IOTC 2017a, 2017b, 2017c, Pecoraro et al. 2017). However, the potential for spatial population structure necessitates investigations into relative abundances among different regions (Hoyle 2018, Hoyle and Langley 2020). Misidentification of distinct stocks can occur, emphasizing the need for genetic studies to inform appropriate management strategies (Allendorf et al. 2008).

Population genetics investigates genetic variation within and among populations, examining its origins, distribution, and temporal changes. This field studies genotype and phenotype frequencies in response to natural selection, genetic drift, mutation, and gene flow (Milgroom 2015). Genetic variation within populations can arise from allelic differences at specific loci, chromosomal variations, and cytoplasmic factors. Several genetic markers, including Restriction Fragment Length Polymorphism (RFLP), Random Amplified Polymorphic DNA (RAPD), mitochondrial DNA (mtDNA), and microsatellite markers, have been employed to assess genetic variation in marine fish populations, including skipjack and kawakawa in the IO (Dammannagoda et al. 2011, Kumar and Kocour 2015, Johnson et al. 2016). While all these markers can detect genetic differentiation, microsatellite markers are particularly effective due to their codominant nature and high polymorphism, enabling discrimination even between closely related species. In contrast, maternally inherited mtDNA markers exhibit high mutation rates but lack recombination, limiting their power compared to microsatellite markers. Consequently, microsatellite markers have been widely used in fish population genetics.

Advancements in population genetics have led to the development of Next-Generation Sequencing (NGS) techniques, which have surpassed the effectiveness of traditional genetic markers (Sanz et al. 2009). NGS studies on tuna species have revealed genetic variations and restricted gene flow among regional populations (Pecoraro et al. 2018). For example, NGS analyses of yellowfin tuna (*Thunnus albacares)* detected genetic differentiation between the Atlantic, Pacific, and Indian Oceans but not within the IO (Pecoraro et al. 2018). Mullins et al. (2018) also identified pure yellowfin tuna stocks in South Africa. These findings highlight the potential of NGS for precise population structure assessments and improved fisheries management.

While limited NGS studies exist for skipjack and kawakawa in the IO, previous research using microsatellite and mtDNA markers has provided some insights. For skipjack, studies in the northwestern IO identified significant genetic differentiation and potential population structure using mtDNA and microsatellite loci (Dammannagoda et al. 2011). However, other studies using mtDNA D-loop found evidence of a single panmictic population between the Atlantic and Indian Oceans (Ely et al. 2005). Menezes et al. (2008) reported both single and multiple populations of skipjack in the eastern Indian and Pacific Oceans using mtDNA and RFLP markers, but only a single population using microsatellite markers. For kawakawa, limited genetic studies are available. Johnson et al. (2016) identified a single genetic stock in the northern coastal waters of Tanzania using mtDNA control region analysis. In contrast, Kumar and Kocour (2015) found a single, non-differentiated genetic stock with some phylogeographic structure in Indian waters using the same marker.

The inconsistencies in population structure findings for skipjack and kawakawa highlight the need for more comprehensive genetic studies using NGS techniques to accurately determine population boundaries and inform effective management strategies.

1.8 Impacts of climate change on tuna

Climate change is altering fish population dynamics through accelerated ocean warming, affecting spatial distribution and productivity (Rijnsdorp et al. 2009, Koenigstein et al. 2016). Rising temperatures decrease phytoplankton productivity, impacting tuna larvae and juveniles reliant on this food source (Lehodey et al. 2013). To track preferred temperatures, marine species may shift their ranges to deeper waters (Sunday et al. 2012, López et al. 2014, Poloczanska et al. 2016), influencing fisheries' ecological and socioeconomic conditions (Ramos et al. 2018).

Climate change projections for skipjack indicate initial biomass increases followed by a dramatic decline in the latter half of the century (Senina et al. 2015). While warming oceans may benefit some skipjack habitats (Muhling et al. 2015), the impact on coastal kawakawa remains uncertain, although range shifts to deeper waters are anticipated. Changes in skipjack distribution and abundance can affect coastal economies by altering accessibility EEZs (Sumaila et al. 2011). Shifting catches from tropical waters to higher latitudes over the next 50 years may lead to significant declines in some tropical fisheries (Cheung et al. 2010), impacting dependent communities through fluctuating fish prices and values (Barange et al. 2014). To mitigate climate change impacts, controlling fishing and enhancing fish stock health is crucial for building ecosystem resilience (Sumaila and Tai 2020).

1.9 Knowledge gaps and purpose of the study

Tuna resources are a global asset, providing food and income for nations worldwide. The WIO significantly contributes to global tuna production. However, the region lacks comprehensive data on the tuna value chain and its economic impact. Overcapacity and the prevalence of both artisanal and industrial fleets hinder fishing effort assessment (Moreno and Herrera 2013). Moreover, poor or limited catch data impede accurate stock estimation (IOTC 2016). These challenges, coupled with climate change threats, jeopardize the region's tuna industry and coastal food security.

Each tuna species has unique habitat requirements and is highly sensitive to environmental changes. Climate change-induced oceanographic shifts can alter tuna species' distribution and abundance (Roxy 2014). Skipjack and kawakawa were selected for this study due to their substantial economic and social benefits to WIO artisanal fishers. While both species are currently considered healthy with fishing levels below the maximum sustainable yield (MSY) (IOTC 2022), increasing fishing pressure necessitates robust population dynamics data.

Maintaining healthy skipjack and kawakawa stocks requires a comprehensive understanding of their genetic structure and reproductive biology. While some studies have explored stock structures for these species, existing research using conventional methods has limitations in detecting genetic differentiation. Advanced genomic techniques, such as Genotyping by Sequencing (GBS), have successfully identified population structures in other tuna species, but have yet to be applied to skipjack and kawakawa in the WIO. Moreover, information on the reproductive biology of these species is outdated and requires updating due to changing environmental conditions.

This study aims to assess skipjack and kawakawa populations in the WIO to inform sustainable coastal tuna fisheries management. Specific objectives include examining population connectivity and structure using genomic techniques, investigating regional exploitation and reproductive patterns of these species, and describing associated fishery value chains.

1.10 Thesis Structure

The thesis has been divided into six chapters.

The first chapter introduces the research providing an overview of current literature and the study's significance within international and regional contexts.

Chapter two; describes the study sites, characterizing the Indian Ocean's systems and seasonality. This chapter also establishes the foundational knowledge and methodological framework for data collection.

Chapters three, four and five present manuscript papers with the following titles;

Chapter three; Genome-wide genetic marker variation uncovers potential stock structuring of oceanic tuna (skipjack) and coastal tuna (kawakawa) within the Western Indian Ocean

Chapter four; Size structure and reproductive biology of skipjack and kawakawa in the Western Indian Ocean

Chapter five; Value chain analysis of Kenya's artisanal tuna fishery targeting skipjack and kawakawa

Chapter six concludes the study by synthesizing key findings from the preceding chapters and assessing their collective contribution to advancing knowledge, conservation, and management practices in the WIO for maximizing economic benefits. This chapter also identifies research challenges and proposes recommendations for future studies.

CHAPTER TWO

STUDY SITE AND FIELD SAMPLING

2.1 The Western Indian Ocean systems and currents

The Western Indian Ocean (WIO), also designated as FAO major fishing area 51 (Mbendo and Tsamenyi 2009, Groeneveld 2014), extends from eastern South Africa to the Arabian Gulf (Longhurst 1998). Encompassing the exclusive economic zones (EEZs) of eastern South Africa, Mozambique, Tanzania (including Zanzibar), Kenya, Somalia, Madagascar, Mauritius, Seychelles, Comoros, and France (via Mayotte and Reunion), the region boasts approximately 12,000 kilometres (km) of coastline, including island territories. This extensive coastline is characterized by a diverse mosaic of habitats and substrates, such as estuaries, lagoons, mangroves, coral reefs, seagrass beds, mudflats, algal beds, barrier islands, and sandy and rocky beaches (Ngoile and Lindén 1997). As a tropical/subtropical region, the WIO exhibits high biodiversity and endemism, attributed to the varied habitats along the continental shelf and surrounding isolated islands or subsurface plateaus (van der Elst et al. 2009).

The WIO region is significantly influenced by two predominant wind systems: the Southeast Monsoon (SEM) and Northeast Monsoon (NEM) (McClanahan 1996, Richmond 1997). The SEM, prevailing from April to October, is characterized by lower air temperatures, strong winds, and cooler, less productive waters. Conversely, the NEM, active from November to March, brings higher air temperatures, weaker winds, and warmer waters (McClanahan 1996). These monsoonal shifts induce seasonal variations in rainfall, temperature, phytoplankton concentration, ocean currents, and mixed layer properties, impacting overall oceanographic conditions and tuna species distribution (van der Elst et al. 2005). Between monsoons, inter-monsoonal periods occur, characterized by weakened dynamic conditions, rising sea temperatures, and shallower thermocline depths (Schott and McCreary 2001).

Major ocean currents dominate the WIO's coastal oceanography (Figure 2.1). The East Africa Coastal Current (EACC) along coastal Tanzania and Kenya, intensifies during the SEM and weakens during the NEM, giving rise to the seasonally reversing Somali Current (Schott and McCreary 2001, Schott et al. 2002). In contrast to the oligotrophic waters further south, upwelling and deep-water mixing render the Somali Current region nutrient-rich and productive. The westward-flowing South Equatorial Current (SEC) traverses the Mascarene

Plateau, intersecting with the East Madagascar Current (southern branch) and feeding into the EACC. The Mozambique Channel exhibits a circulation pattern characterized by mesoscale eddies (Lutjeharms 2006). Originating near the southern Mozambique Channel, the Agulhas Current flows south-westward along the shelf edge, before veering offshore and northward, forming the Agulhas Return Current (Lutjeharms, 2006).

Figure 2.1. A part of the WIO region and the complex ocean current systems and monsoon seasons (source: Lutjeharms 2006).

2.2 Description of Country Sampling Sites

This research was conducted in the WIO region, specifically along the coastlines of Kenya, Tanzania, Mozambique, and South Africa. The shared borders among these nations highlight the need for transboundary management strategies. Kenya, situated between longitudes 34° and 42° East and latitudes 5° North and 5° South, boasts approximately 640 kilometres of marine coastline, encompassing 9,700 km^2 of territorial waters and 142,400 km^2

of EEZ (GOK 2016, Rasowo et al. 2020). Kenya's diverse coastal and marine habitats, including estuaries, seagrass beds, coral reefs, and nearshore and offshore waters, serve as critical habitats, breeding grounds, and feeding areas for various marine species and fisheries.

The United Republic of Tanzania (URT) is East Africa's largest country, situated between longitudes 29° and 41° East and latitudes 10° and 12° South. Tanzania possesses a territorial sea spanning 64,000 km^2 and an EEZ of 223,000 km^2, constituting 24% of its total area. The country's continental shelf encompasses approximately 17,900 km^2 and boasts a 1,400 km coastline. Tanzania shares a maritime border with Kenya to the north and Mozambique to the south.

Mozambique, situated in southeastern Africa between latitudes 10°27'S and 26°52'S and longitudes 30°12'E and 40°51'E, boasts approximately 2,700km of coastline. The country's maritime territory encompasses a total continental shelf area of around 104,300 km^2 and an EEZ of approximately 999,000 km^2. Mozambique's coastline is divided into three regions: (i) the northern coast (Cabo Delgado and Nampula provinces) with a 770 km coastline characterized by a rocky, coral-bearing seabed and a narrow continental shelf; (ii) the central coast (parts of Nampula, Zambézia, and Sofala provinces) with a 980 km coastline facing the Sofala Bank; and (iii) the southern coast (Inhambane, Gaza, and Maputo provinces) with a 950 km coastline featuring a mix of coral, rock, and sandy bottom. While fishing activities occur along the entire coast, the Sofala Bank stands out as the most productive fishing ground for the national fleet.

South Africa is situated between latitudes 22°S and 35°S and longitudes 17°E and 33°E, occupying the southern tip of the African continent. The country boasts a coastline extending over 2,850 km stretching from Namibia on the Atlantic coast, around the southern tip, and northward to Mozambique on the IO. South Africa's total land area encompasses 1,220,813 km^2, while its EEZ spans 1,535,538 km^2.

2.3 Data and sample collection

Sampling for skipjack and kawakawa was conducted in Kenya (Kilifi and Vanga), Tanzania (Mtwara, Tanga, and Dar es Salaam), northern Mozambique (Pemba), and South Africa (Eastern Cape) (Figure 2.2, Tables 2.1 and 2.2). Specimens were obtained from commercial fishers targeting these species. Biology, size structure and genetic data were collected concurrently from 2019 to 2022.

A non-randomized sampling approach was employed for genetics, biology and size structure analysis, collecting specimens from commercial artisanal and recreational catches. All gear types employed by these sectors were included in the sampling process. Fishing vessels were randomly selected upon arrival, with priority given to the first vessel returning from a fishing trip. Catches weighing less than 20 kg were sampled entirely, while larger catches underwent a 10-20% subsampling. Sampled fish were sorted by species, and fork length (FL) was measured to the nearest centimetres (cm) using a measuring board. The gear type used at each landing site was documented through observations and fisher interviews.

For reproductive biology, a macroscopic examination of fish gonads was conducted to assess reproductive features (Tomkiewicz et al. 2003). Randomly selected samples underwent dissection, with gonads removed and weighed to the nearest gram. Visual inspection determined sex and maturity stages. Stages I and II were classified as immature, while stages III, IV, V, and VI were considered mature, following Diouf's (1980) classification. Mature females exhibited fully developed ovaries containing yellowish to creamy-yellow eggs or spent ovaries, while mature males displayed enlarged, white testes (Bezerra et al. 2013). For genetic studies, fin clips from pectoral fins were preserved in 70% ethanol for subsequent DNA extraction.

A value chain analysis of the Kenyan artisanal tuna fishery, focusing on kawakawa and skipjack, was conducted using a combination of secondary and primary data. Secondary data included catch assessment survey (CAS) data from April 2020 to March 2021, a subset of Okemwa et al. (2023) data. Catch data for each species were disaggregated by landing site, month, season (NEM and SEM), and gear type. A semi-structured questionnaire survey (see Appendix 1) was conducted to collect primary data. The questionnaire was administered during September 2021 and February 2022. These periods represented the tuna fishery's low and high seasons. Tuna value chain actors were categorized based on their interactions and activities within the Kenyan artisanal tuna fishery. A pilot survey refined the main survey questionnaires. A snowball sampling technique (Huntington 2000, McGoodwin 2001) was employed for data collection at fish landing sites. Interviewees were briefed on the study's objectives and provided with colour-coded photos of Kenyan tuna species to ensure accurate identification.

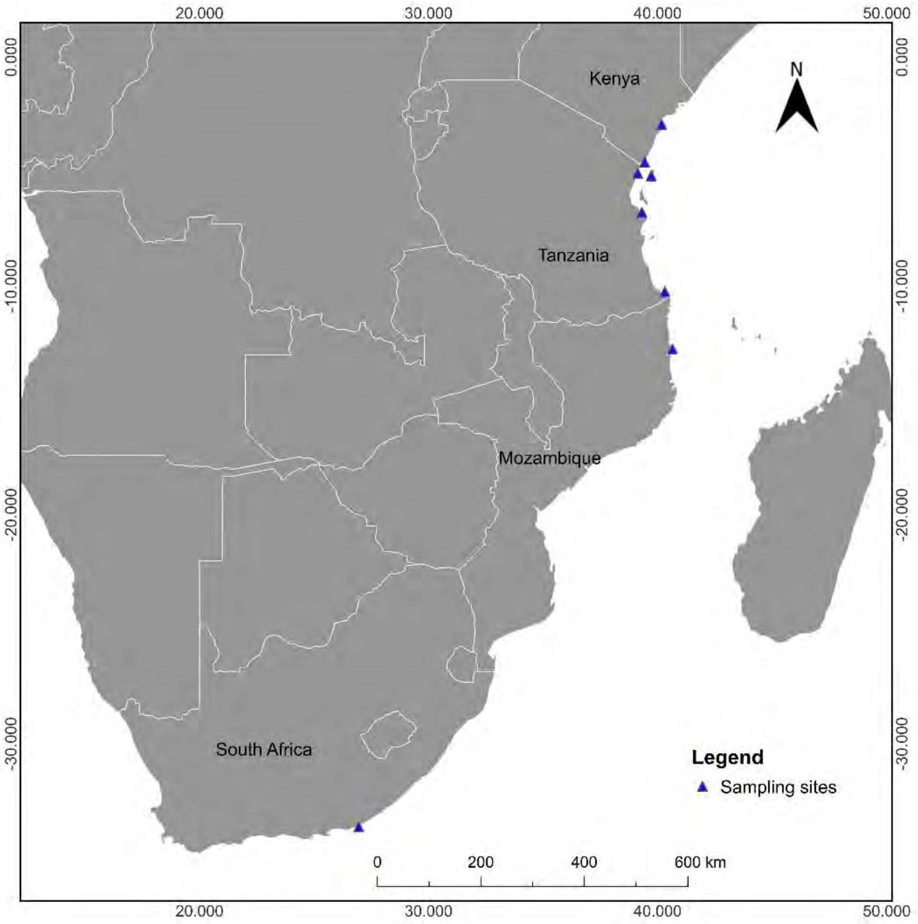


Figure 2.2. A map showing sampling sites of skipjack and kawakawa in WIO during the study period.

Table 2.1. Sample size (n) of size length data, Maturity and Genetics data of kawakawa collected per month in WIO sampling sites during the survey period.

	Kenya			**Tanzania**			**Mozambique**		
Month	Size (FL)	Maturity	Genetics	Size (FL)	Maturity	Genetics	Size (FL)	Maturity	Genetics
Jan	238	126		411	89		7	7	
Feb	149	41		92	92				
Mar	44	24		350	47		10	10	30
Apr	80	19		365			29	28	
May	22	22		120	101		204	24	
Jun	2					33	139	28	
Jul	227	99		32	32				
Aug	13	11		72	72		128		
Sep	79	10	72	129	10	21			
Oct	47	14		103	71		51		
Nov	110	40		48	48		1	1	
Dec	400	118		14	14		36	29	

Table 2.2. Sample size (n) of size length data, Maturity and Genetics data of skipjack collected per month in WIO sampling sites during the survey period.

	Kenya			**Tanzania**			**Mozambique**			**South Africa**		
Month	Size (FL)	Maturity	Genetics	Size (FL)	Maturity	Genetics	Size (FL)	Maturity	Genetics	Size (FL)	Maturity	Genetics
Jan	59	34		9	9		28	28				
Feb	141	48		14	14							
Mar	92	90		165	13		17	17				
Apr				17		66				33	24	
May					8		62	2		21	12	
Jun							54	4	27	5	2	
Jul							20					30
Aug	4	4		8	8					12	6	
Sep	5		30	8			12					
Oct	18	13		9			10					
Nov	16			2	2		9					
Dec	133	111	36	2	2	55	9	1				

2.4 Data collection challenges and mitigation strategies

The study was conducted during the COVID-19 pandemic, resulting in data collection challenges due to restrictions in certain locations and periods. While a standardized protocol guided biological and genetic data collection, inconsistencies arose due to personnel variations across sites. Furthermore, improper genetic sample labelling hindered the correlation of genetic findings with biological data (e.g., size, maturity). For value chain analysis, limited responses on fixed assets (boats, engines, gear) and operational costs hampered the estimation of fishing operation costs.

To address these limitations, biological data was standardized, and DNA quality checks were implemented. Unsuitable data were excluded. Additionally, data pooling from all sites provided a regional overview of skipjack and kawakawa size structure and reproductive biology. Future research is recommended to fill identified data gaps.

CHAPTER THREE

GENOME-WIDE GENETIC MARKER VARIATION UNCOVERS POTENTIAL STOCK STRUCTURING OF OCEANIC TUNA (SKIPJACK) AND COASTAL TUNA (KAWAKAWA) WITHIN THE WESTERN INDIAN OCEAN

Abstract

Tuna and tuna-like species are highly mobile and migratory, assumed to have single highly connected populations over large ocean regions. However, empirical data on the genetic population structure of such species in the Western Indian Ocean (WIO) remains limited. Understanding these structures is crucial for managing stocks across territorial and transnational waters. This study tested the hypothesis of single genetic stocks of skipjack tuna (*Katsuwomis pelamis*) and kawakawa (*Euthynnus affinis*) within the WIO (Kenya, Tanzania, Mozambique, South Africa and Seychelles). Samples were collected from commercial fishers between September 2019 and July 2020. Genome-wide single nucleotide polymorphism (SNP) data for skipjack (7005 loci, average $H_O = 0.206$) revealed low overall genetic differentiation (global $F_{ST} = 0.003$; between-sample $F_{ST} = 0 – 0.013$) but significant genetic differences between skipjack samples taken north of Mtwara in southern Tanzania (i.e., northern Tanzania, Kenya and Sri Lanka) and those to the south (i.e., southern Tanzania, Mozambique and South Africa), with Seychelles falling closer to the southern grouping. SNP data for kawakawa (14806 loci, average $H_O = 0.2585$) indicate a patchy distribution of low but significant genetic differentiation among WIO sites (global $F_{ST} = 0.018$; between-sample $F_{ST} = 0.003 – 0.036$) but with no obvious geographically-based pattern. In comparison with data from previous studies, we conclude that there is evidence for genetically differentiated stocks of skipjack and kawakawa within the WIO and that a precautionary approach should be adopted for future fishery management.

3.1 Introduction

The WIO supports several economically and ecologically important small tuna and tuna-like species, including skipjack tuna (*Katsuwonus pelamis*), kawakawa (*Euthynnus affinis*), narrow-barred Spanish mackerel (*Scomberomorus commerson*), frigate tuna (*Auxis thazard*) and wahoo (*Acanthocybium solandri*). Currently, these species are managed as individual stocks in the WIO, following the Indian Ocean Tuna Commission's (IOTC) recommendations. WIO countries implement these management measures through national fisheries policies, aligned with their international commitments as IOTC members (Chassot et al. 2019).

Tuna constitutes a significant portion of the global seafood market, with an annual value exceeding USD 42 billion (FAO 2022). This high value renders tuna susceptible to overfishing due to increased fishing pressure. Consequently, effective management strategies are imperative for ensuring the long-term health of tuna stocks (IOTC 2023). Similar to other global tuna resources, skipjack and kawakawa in the IO face growing exploitation from multiple nations (IOTC 2022, IOTC 2023). Although currently being considered not overfished within the IOTC area (IOTC 2019, IOTC 2023), sustainable management practices are crucial to prevent future worldwide depletion of marine fish populations (Myers and Worm 2005). Accurate identification of biological stocks is essential for sustainable management, as mismatches between biological stocks and management units pose significant threats to long-term sustainability (Reiss et al. 2009, Kerr et al. 2017). Skipjack and kawakawa are vital to WIO countries, providing income, food security and contributing to wealth creation. Maintaining healthy fish stocks is essential for supporting coastal community development throughout the region.

Skipjack and kawakawa are medium-sized pelagic species inhabiting open waters. While both species are found in the Indo-West Pacific (with skipjack also present in the Atlantic), kawakawa tends to inhabit waters closer to the coastline compared to skipjack, which prefers slightly colder temperatures (18-29°C for skipjack, 14.7-30°C for kawakawa) (Collette and Nauen 1983, Froese and Pauly 2019). Both species are commercially valuable, contributing significantly to WIO catches (IOTC 2016). Skipjack is the most dominant tuna landed globally, accounting for over half of the world's tuna catch (Majkowski, 2007) and more than 50% of IO tuna landings (McKinney et al. 2020). Kawakawa is the second most abundant neritic tuna species in the WIO, comprising approximately 12% of neritic tuna landings (Lecomte et al. 2017). In addition, kawakawa, as a top predator in shallow coastal waters, plays a crucial ecological role. Increased exploitation of kawakawa could disrupt trophic pathways and impact marine ecosystem structure and function (Griffiths et al. 2020b). Despite heavy fishing pressure, both species maintain healthy populations due to high fecundity and rapid growth rates (Froese and Pauly 2023).

Most tuna species in the IO are managed as single stocks, assuming panmictic populations with no evidence of distinct morphological or demographic groups (De Leiva and Majkowski 2005). Skipjack tuna, for instance, exhibits biological and life history traits consistent with large-scale population mixing and interbreeding, including fast swimming, high mobility, and documented large-scale dispersal and seasonal migrations (Adam and Sibert 2002, IOTC 2008, Fonteneau 2014). Several genetic studies align with this assumption, showing no differentiation between skipjack populations across the Atlantic, Indian, and Pacific Oceans, or between western and central Pacific regions (Ely et al. 2005, Anderson et al. 2020b). However, skipjack also exhibits behaviours, such as size-based preferences for specific temperature and oxygen conditions, which may temporarily restrict population mixing on smaller scales (FAO 2004).

More localized genetic studies employing mitochondrial DNA Control Region (mtDNA CR) sequencing and microsatellite DNA markers have revealed significant genetic variation among skipjack populations along the west coast of India (Menezes et al. 2012), between Sri Lanka and the Maldives (Dammannagoda et al. 2011), and within Indonesian waters (Jatmiko et al. 2019). Recent studies utilizing Single Nucleotide Polymorphism (SNP) markers have yielded inconsistent results. While Davies et al. (2020) found no clear genetic differentiation across the northern IO, Rodríguez-Ezpeleta et al. (2020) detected some genetic separation between Atlantic (Gulf of Guinea) and southern Australian samples, but without clear spatial patterns within the IO.

Kawakawa exhibit rapid growth, reaching 30-49 cm FL within their first year and attaining sexual maturity at 37.7 cm FL (Ahmed et al. 2015). Characterized by high fecundity and a relatively short lifespan of a maximum of six years (Mann 2013) and undertakes regular migrations between feeding and spawning grounds (Chiou et al. 2004). These life history traits have led to the assumption of a widely panmictic population, prompting IOTC to manage kawakawa as a single stock. However, a lack of comprehensive population studies introduces uncertainty regarding the number of populations within the IO.

To date, limited information exists on the genetic population structure of kawakawa across the Indo-Pacific region. Previous studies using mitochondrial DNA markers, a limited tool for pelagic fish, have found little evidence of population structuring within restricted localised areas across a small area of northern Tanzania (Johnson et al. 2016), around the coast of India (Kumar et al. 2012), in the Strait of Malacca (Masazurah et al. 2012) and around the Philippines and Malaysia (Santos et al. 2010). The potential for marker limitations to mask true population structure may lead to misinformed fisheries management decisions leading to overfishing and the collapse of stocks. This highlights the need for improved genetic markers (Ying et al. 2011).

The advent of Next-Generation Sequencing (NGS) techniques has significantly enhanced our ability to detect genetic differentiation among populations (Waples 2008, Allendorf et al. 2010, Davey et al. 2011, Narum and Hess 2011, Andrews and Luikart 2014). NGS also enables the identification of "outlier loci" potentially influenced by local adaptation, uncovering genetic differentiation missed by neutral markers (Natasha et al. 2022). Studies on Pacific Ocean yellowfin tuna exemplify this, with allozyme, microsatellite, and mitochondrial DNA markers detecting only two main populations, whereas SNP markers revealed finer-scale genetic structure among local subpopulations (Ward et al. 1997, Díaz-Jaimes and Uribe-Alcocer 2006, Li et al. 2015, Grewe et al. 2015).

SNP markers have been successfully applied to several tuna species, confirming either genetic homogeneity and high gene flow across large geographical areas (Mullins et al. 2018, Natasha et al. 2022) or revealing differentiation and stock structure in previously assumed single mixed populations (Barth et al. 2017, Mullins et al. 2018, Pecoraro et al. 2018, Vaux et al. 2021). This study aimed to develop and apply NGS-based SNP marker approaches to investigate genetic diversity and differentiation in skipjack and kawakawa populations across the WIO. Given the species' biology and life history characteristics, which suggest large-scale movement and mixing, our initial hypothesis was that both species would exhibit genetic homogeneity among WIO sites.

3.2 Material and Methods

3.2.1 Sample collection, DNA extraction and species verification

Samples of skipjack and kawakawa were collected between September 2019 and July 2020 from commercial fishers targeting these species in WIO (Figure 3.1, Table 3.1). Sampling of each species within countries occurred within a single month, except for

Mozambique which required multi-month sampling (December-June) due to logistical constraints (Table 3.1). Fin clips from individual fish were fixed in 95% ethanol and stored at -20°C until genomic DNA extraction. DNA was extracted using a phenol/chloroform/isoamyl alcohol (PCIA) method following Winnepenninckx (1993). A 633 base pair segment of the mitochondrial control region was amplified from each individual with the polymerase chain reaction (PCR) and sequenced in both directions using tuna-specific primers (F:TCCTACCCCTAACTCCCAAAG; R: AAACTGTGGGGATTCTCAC) and standard PCR and sequencing protocols (see Mullins et al. 2018). Resulting sequences were BLAST-searched against the GenBank database to confirm species identity.

Table 3.1. Sampling sites and sample numbers for skipjack and kawakawa collected in the Western Indian Ocean, plus an outgroup site (Sri Lanka).

	Skipjack		**Kawakawa**	
Sampling site	**Sampling period**	**Sample size (n)**	**Sampling period**	**Sample size (n)**
South Africa (E. Cape)	Jul 2020	30	-	-
Mozambique North (Pemba)	Dec 2019 to June 2020	27	Dec 19 Mar 2020	36 30
Tanzania South (Mtwara)	Dec 2019	55	Jun 20	33
Tanzania Central (Dar)	Apr 2020	16	-	-
Tanzania North (Pemba)	Apr 2020	50	-	-
Tanzania North (Tanga)	-	-	Sep 19	21
Kenya South (Vanga/Gazi	Dec 2019	30	Sep 19	36
Kenya North (Kilifi/Watamu)	Dec 2019	36	Sep 19	32
Seychelles	Sep 2019	30	Sep 2019	30
Sri Lanka	Jan 2018	30	-	-

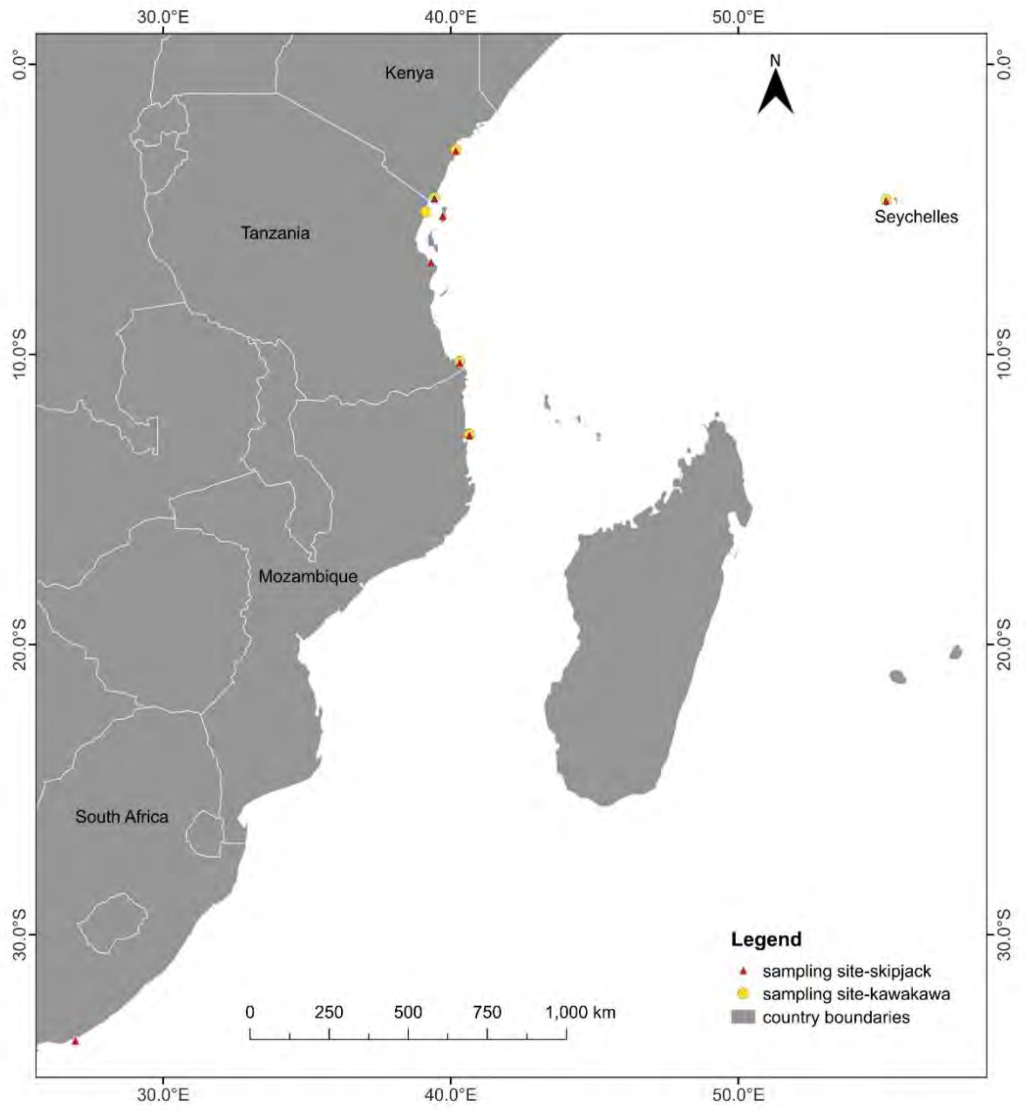


Figure 3.1. A map of WIO showing sampling sites where skipjack and kawakawa samples were collected during the survey period.

3.2.2 SNP genotyping

SNP genotyping employed tunable Genotyping By Sequencing (tGBS), a modified RADSeq technique that incorporates digestion with two enzymes for genome reduction resulting in an increased number of reads per site (Ott et al. 2017). The tGBS libraries were sequenced on a Life Technologies Ion Proton System by a commercial company (Data2Bio, USA). Sequenced reads were analysed using a custom Perl script (available at https://github.com/orgs/schnablelab), which assigned each read to a sample and removed barcode sequences. Seqclean (source forge.net/projects/seqclean) was then used to remove proton adaptor sequences and chimaeric reads harbouring internal restriction enzyme sites.

Retained reads were subjected to quality trimming in two phases using the software Lucy2 (Li and Chou 2004) in which bases with PHRED scores <15 (of 40) were removed. In the first phase, sequences were scanned at each end, whereas in the second phase, sequences were scanned using overlapping 10 bp windows. Quality trimmed sequence reads were aligned to the reference genome of Pacific bluefin tuna, *Thunnus orientalis* (Nakamura et al. 2013), using GSNAP (Wu and Nacu 2010). Sequence alignments were then scanned for polymorphisms. A SNP was called homozygous if at least 15 reads supported the genotype at the site and at least 90% of all reads covering that site shared the same nucleotide. A SNP was considered heterozygous if each of the two nucleotide variants was reported at least 10 times, and each allele was represented in >30% of the total reads. To reduce any bias that may be introduced by retaining low-frequency SNPs (Roesti et al. 2012), the minimum allele frequency (MAF) was set at 10%. SNP loci across the dataset were tested for conformity to Hardy Weinberg compliance (ARLEQUIN 3.4.2.2, Excoffier and Lischer 2010), and loci showing significant departure removed.

3.2.3 Geographical structuring of genetic variation

SNP allele frequencies and observed (H_O) and expected (H_E) heterozygosity within geographical samples in each species were estimated using ARLEQUIN 3.4.2.2 (Excoffier and Lischer 2010). ARLEQUIN was also employed to test for departures from expectations of Hardy–Weinberg equilibrium (HWE) using Exact Tests. To identify loci potentially under selection the hierarchical Bayesian approach implemented in BAYESCAN 2.1 (Foll and Gaggiotti 2008) was used. This method aims to separate locus-specific effects (e.g. selection) from population effects (neutral gene flow and genetic drift) and has been shown to have a low Type I error rate (Narum and Hess 2011, De Mita et al. 2013). All parameters that can be modified in the software were left as default. The false discovery rate was set at 5% meaning that a marker with a q value of < 0.05 was considered an outlier. The BAYESCAN analysis was performed globally (i.e., across all samples) and between all pairs of samples as recommended (Vitalis et al. 2001).

Genetic differentiation among samples was quantified by global and pairwise F_{ST} (Weir and Cockerham 1984) with statistical significance evaluated in ARELQUIN with 10,000 permutations. Principal coordinate analysis of genetic distances (F_{ST}) between samples was performed in GENEALEX (Peakall and Smouse 2006). Genetic structuring was also investigated using an individual-based analysis using the Bayesian clustering method in

STRUCTURE 2.3.4 (Pritchard et al. 2000), which identifies the most probable number of genetically distinct groups (K) represented by the data and estimates assignment probabilities (Q) for each individual to these groups. The analysis was performed with and without the LOCPRIOR model, in both cases assuming admixture. Simulations were run 10 times for each proposed value of K (1–9 for Skipjack, 1-7 for Kawakawa) to assess convergence. Each run had a burn-in of 100 000 MCMC samples followed by 1 000 000 MCMC repetitions, with the best fit for K assessed using DK (Evanno et al. 2005).

3.3 Results

3.3.1 Species identification and quality checks

Genomic DNA was extracted from a total of 300 skipjack individuals, tested for DNA quality and concentration, and then screened for correct species identification by PCR amplification and sequencing of a 633bp fragment of mtDNA Control Region. Most individuals (250) were confirmed as skipjack, but 43 individuals collected from Kenya South and 7 individuals from Tanzania North were identified as Frigate tuna (*Auxis thazard*). After filtering for suitable DNA quality for the SNP discovery and genotyping procedure, 192 skipjack individuals were processed using tGBS.

Genomic DNA was extracted from all 218 kawakawa individuals, tested for DNA quality and concentration, and then screened for correct species identification by PCR amplification and sequencing of a 633bp fragment of mtDNA Control Region. All individuals were confirmed as kawakawa. After filtering for suitable DNA quality for the SNP discovery and genotyping procedure, 192 kawakawa individuals were sent for tGBS.

3.3.2 Genetic diversity and differentiation of skipjack

A total of 2 x 211,532,508 raw sequence reads were obtained from 192 individuals from 9 population samples of skipjack, with an average of 1,468,976 per individual. After the exclusion of individuals with poor-quality extracted DNA or that did not produce enough high-quality reads to fulfil the minimum sequence coverage, and excluding SNPs with a minimum allele frequency across all samples of < 0.1, the final data set comprised 7,005 independent SNP marker loci screened across 144 skipjack individuals. Levels of variation (i.e., polymorphic SNP number, and expected and observed heterozygosity) were similar across all samples, with all samples conforming to Hardy-Weinberg genotype proportions (Table S3.1). Across the whole sample set from the wider WIO, there was a general pattern of low genetic differentiation (global $F_{ST} = 0.003$ and pairwise between-sample $F_{ST} = 0 – 0.013$, i.e., less than or equal to ~1% of total diversity), but with a patchy distribution of significant differences among samples (Table 3.2).

Table 3.2. Pairwise genetic differentiation (FST) values between samples of skipjack tuna, estimated from 7005 SNP loci (below diagonal) and 87 outlier SNP loci (above diagonal). Numbers in bold are significantly above zero ($p < 0.05$; 10000 permutations).

	SA	Mz	Tz-M	Tz-D	Tz-P	K-S	K-N	Sey	SL
South Africa (E. Cape)	-	0.051	**0.143**	0.115	**0.367**	0.006	0.135	-0.060	**0.129**
Mozambique (Pemba)	0.001	-	**0.068**	**0.271**	**0.572**	**0.118**	**0.274**	-0.072	**0.284**
Tanzania (Mtwara)	**0.004**	0.003	-	**0.285**	**0.525**	**0.179**	**0.294**	0.033	**0.301**
Tanzania (Dar es Salaam)	**0.005**	**0.005**	**0.007**	-	-0.001	-0.006	-0.043	**0.164**	-0.041
Tanzania (Pemba)	**0.010**	**0.011**	**0.013**	0.000	-	0.117	0.046	**0.381**	0.021
Kenya (S)	0.003	0.001	0.003	0.000	0.000	-	-0.015	0.045	-0.022
Kenya (N)	**0.003**	0.004	**0.007**	0.000	0.000	0.000	-	**0.153**	-0.026
Seychelles	**0.003**	0.001	0.001	0.002	**0.008**	0.000	0.003	-	**0.157**
Sri Lanka	**0.006**	**0.005**	**0.009**	0.000	0.000	0.000	0.000	0.002	-

Within Tanzanian samples there was moderate ($F_{ST} = 0.007\text{-}0.013, p < 0.05$) and significant differentiation between Mtwara in the south and the other two sites in the north (Dar and Pemba) of the country, but no difference between Dar es Salam and Pemba ($F_{ST} = 0.000, p > 0.05$). The South African Eastern Cape sample displays the most consistently significant differentiation from most other samples ($F_{ST} = 0.003\text{-}0.010, p < 0.05$) except Mozambique and South Kenya ($F_{ST} = 0.001\text{-}0.003, p > 0.05$), whereas the S Kenya sample is not significantly different from any other sample. There is however a geographically based pattern in the significant tests: 12 of the 14 significant tests occur between samples south of Dar es Salam (i.e., Mtwara, Mozambique and Eastern Cape) and the samples north of Mtwara (including the outgroup population in Sri Lanka), with only one significant difference between samples north of Mtwara (Seychelles versus Tz-Pemba $F_{ST} = 0.008, p < 0.05$ - Table 3.2). The divide between the southern and northern samples is evident from the 1st axis of the Principle Coordinate Analysis (PCoA) of genetic relationships among samples (representing 78.6% of total genetic variation among samples), with the 2nd axis separating and showing greater diversity among samples within the southern group (representing 14.9% of total variation in the dataset), although in this case it shows the Seychelles sample to be more closely clustered with the southern than the northern group (Figure 3.2).

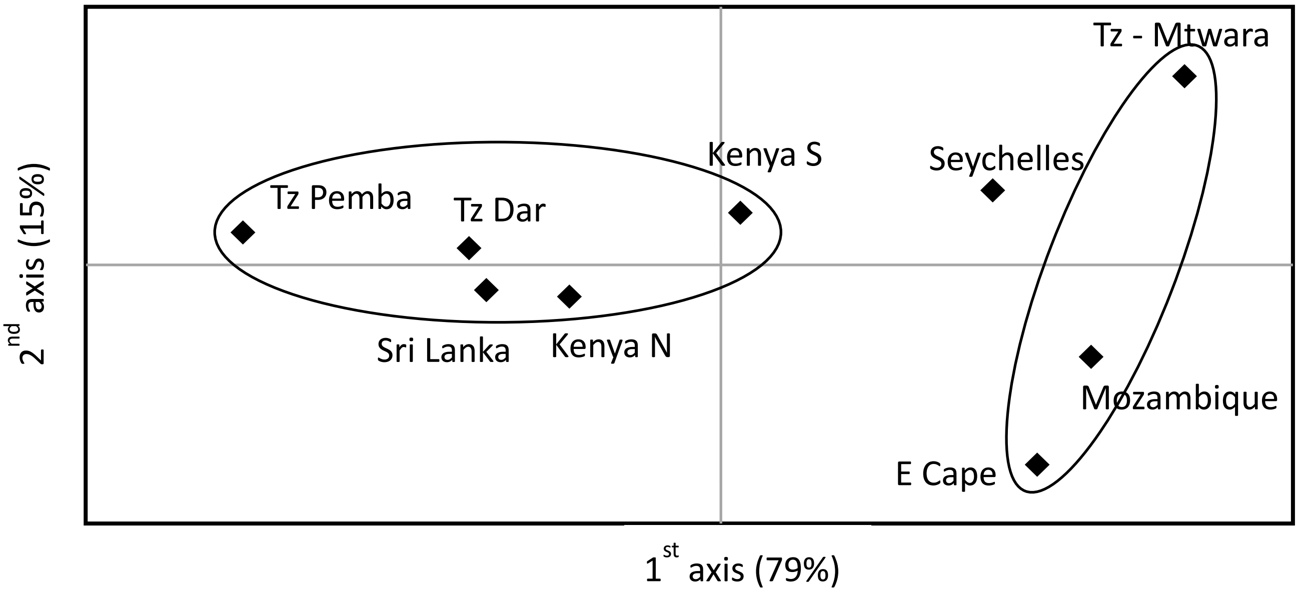


Figure 3.2. PCoA analysis, with a percentage of total dataset variation represented by 1st and 2nd axes, of genetic similarity among skipjack tuna samples, based on genetic differentiation (F_{ST}) estimated from 7005 SNP loci.

The individual-based STRUCTURE analysis showed no clear clustering of individuals to distinct subpopulations, with an indication of a single genetic cluster across the samples (K=1).

The BAYESCAN global analysis identified 87 outlier SNP loci potentially under positive selection among skipjack samples across the WIO. As with the analysis of the full 7,005 SNP loci, analysis of the 87 outlier loci alone resulted in a similar pattern of genetic differentiation among samples with F_{ST} values ranging from 0.000 to 0.525 and most high and significant values associated with the northern (northern Tanzania, Kenya, Sri Lanka) samples versus the southern (southern Tanzania, Mozambique, Eastern Cape – 12 of 15 comparisons) samples and the Seychelles sample (5 of 6 comparisons), with little significant differentiation within groups or between the Seychelles and the southern group (Table 3.2). The PCoA of the pairwise among-sample values of outlier loci F_{ST} (Fig.S3.1) illustrates the separation of the northern and southern groups along the 1st axis (86% of total genetic variation) and separation among samples within the southern group (including Seychelles) on the 2nd axis (6% of total genetic variation).

3.3.3 Genetic diversity and differentiation of kawakawa

A total of 2 x 363,108,373 raw sequenced reads were obtained from 178 individuals from 6 population samples of kawakawa, with an average of 2,814,794 per individual. After the exclusion of individuals with poor-quality extracted DNA or that did not produce enough high-quality reads to fulfil the minimum sequence coverage, and excluding SNPs with a minimum allele frequency across all samples of < 0.1, the final data set comprised 14,806 independent SNP marker loci screened across 129 kawakawa individuals. Levels of variation (i.e., number of polymorphic SNP loci, and expected and observed heterozygosity) were similar across all samples; Table S3.2), with all samples conforming to Hardy-Weinberg genotype proportions.

As found for skipjack, across the whole sample set from the wider WIO there was a general pattern of low genetic differentiation (global F_{ST} = 0.018; between-sample F_{ST} = 0.003 – 0.036), although the values were noticeably higher in kawakawa than in skipjack. Pairwise FST comparisons revealed a patchy distribution of low/non-significant and moderate/significant values, with some geographically distant comparisons showing significant differentiation (Mozambique: Seychelles F_{ST} = 0.009-0.012, $p < 0.05$) but then other similar combinations showing no significant differences (Mozambique: Kenya F_{ST} = 0.003-0.005, $p > 0.05$), whereas some less geographically distant comparisons show highly significant differentiation (Tz-Tanga: Kenya F_{ST} = 0.010, $p < 0.001$, Tz-Mtwara: Mozambique F_{ST} = 0.030-0.035, $p < 0.001$), as presented in Table 3.3. A notable point is that both Tanzanian samples are consistently differentiated from all other sites, with highly significant values for this marker set (1-3.5% divergence), and from each other at the same level of divergence. Likewise, the Seychelles sample is consistently differentiated from the continental coast samples (F_{ST} = 0.009-0.036, $p < 0.001$) except for Kenya (F_{ST} = 0.004, $p > 0.05$).

Table 3.3. Pairwise genetic differentiation (FST) values between samples of kawakawa estimated from 14806 SNP loci (below diagonal) and 29 outlier SNP loci (above diagonal). Numbers in bold are significantly above zero *(p* < 0.05; 10000 permutations).

	Mozambique (Pemba - Dec)	Mozambique (Pemba - Mar)	Tanzanian (Tanga)	Tanzania (Mtwara)	Kenya	Seychelles
Mozambique (Pemba - Dec)	-	**0.029**	**0.165**	**0.190**	**0.025**	**0.144**
Mozambique (Pemba - Mar)	0.003	-	**0.204**	**0.242**	**0.041**	**0.135**
Tanzania (Tanga)	**0.012**	**0.013**	-	**0.172**	**0.129**	**0.368**
Tanzania (Mtwara)	**0.036**	**0.031**	**0.028**	-	**0.143**	**0.432**
Kenya	0.005	0.003	**0.010**	**0.017**	-	**0.215**
Seychelles	**0.012**	**0.009**	**0.022**	**0.036**	0.004	

PCoA analysis of the pairwise among-sample values of F_{ST} (Fig.3.3) illustrates the clear separation of Seychelles and Tanzanian samples along the 1st axis (58% of total genetic variation) and differentiation between the two Tanzanian samples on the 2nd axis

(21% of total genetic variation).

Similar to skipjack, the individual-based STRUCTURE analysis showed no clear clustering of kawakawa individuals to distinct subpopulations, with an indication of a single genetic cluster across the samples (K=1).

The BAYESCAN global analysis identified 29 outlier SNP loci potentially under positive selection among kawakawa samples across the WIO. As with the analysis of the full 14,806 SNP loci, analysis of the outlier loci resulted in a similar pattern of genetic differentiation among samples with F_{ST} values ranging from 0.025 to 0.432, with clear differentiation of the Seychelles and Tanzanian samples and lower but no significant differentiation among the Mozambique and Kenyan samples (Table 3.3). PCoA analysis of the pairwise among-sample values of F_{ST} described a similar pattern to that shown by the full SNP dataset in Fig.3.3, so is not shown.

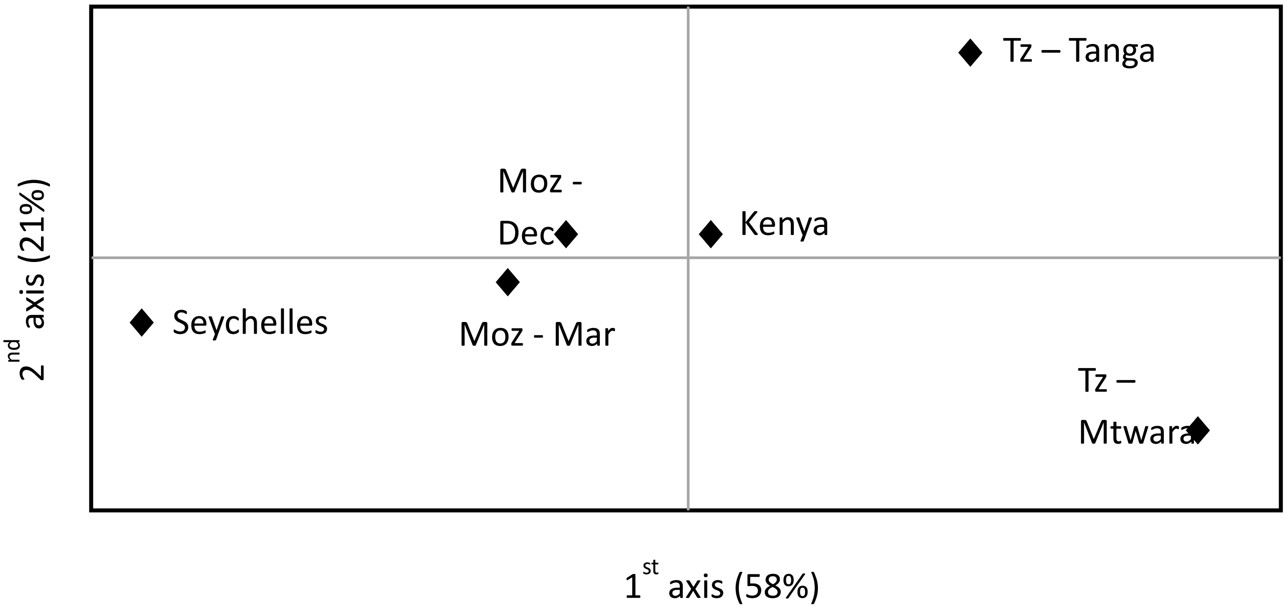


Figure 3.3. PCoA analysis, with the percentage of total dataset variation represented by 1st and 2nd axes, of genetic similarity among kawakawa samples, based on genetic differentiation (F_{ST}) estimated from 14806 SNP loci.

3.4 Discussion

Mismanaging heavily fished species like tuna, particularly when management units do not accurately represent biological subpopulations, poses a double threat. It jeopardizes both the fishery's long-term sustainability and the fish populations' adaptability to environmental changes, such as those induced by climate change. This lack of adaptability can lead to catastrophic population collapse (Reiss et al. 2009). Although skipjack and kawakawa stocks in the IO are currently assessed as healthy and not overfished (IOTC 2019), understanding the number and distribution of biologically independent populations across the WIO is crucial for developing sustainable management strategies.

3.4.1 Large spatial scales of genetic mixing but distinct regional stocks of skipjack across WIO

Skipjack exhibited consistent genetic diversity across the sampled region. Both the extensive 7005-locus neutral SNP dataset and the reduced 87-locus outlier dataset revealed low genetic differentiation among WIO samples, suggesting high levels of population mixing across the region, aligning with the species' biology and life history. However, a patchy distribution of low but significant genetic differences among samples, indicates the presence of completely free genetic exchange and mixing, i.e., indicating the potential presence of multiple genetically divergent and reproductively non-interbreeding skipjack stocks across this region. Notably, samples from south and north of Mtwara, Tanzania, displayed significant differences, suggesting a potential genetic breakpoint between Mtwara and Dar es Salaam.

Our data cannot definitively confirm the presence of multiple, genetically differentiated skipjack stocks within the WIO, however, the observed patterns are consistent with the possibility suggested by Rodríguez-Ezpeleta et al. (2020). Our findings indicate two broad regions of differential mixing of multiple stocks along the continental East African coast with a boundary in the area of southern Tanzania. The coast around Mtwara, where the west-flowing South Equatorial Current splits into the north-flowing East African Coastal Current and the south-flowing Mozambique Current, represents a potential biogeographic breakpoint (Ali and Huber 2010). These divergent current systems may act as partial barriers to transporting early life stages or adult skipjack tuna, hindering free mixing between northern and southern populations.

As found in the present study, previous genetic studies of skipjack tuna indicated little evidence for genetic differentiation of populations across large regions of the Atlantic, Indian and Pacific Oceans using Mt DNA (Ely et al. 2005) and SNP marker (Anderson et al. 2020b) but that significant genetic variation has been observed within more localised regions of the IO (Dammannagoda et al. 2011, Menezes et al. 2012, Jatmiko et al. 2019). Other recent studies using similar genetic techniques (SNP marker) on skipjack tuna in the IO found conflicting results. One study (Davies et al. 2020) observed no clear genetic differences across the northern IO. In contrast, another study by Rodríguez-Ezpeleta et al. (2020) suggested that skipjack tuna in the Atlantic, southern Australia, and the IO are genetically distinct. This latter study also hinted at the possibility of several genetically differentiated stocks across the IO, with differing levels of mixing within (Rodríguez-Ezpeleta et al. 2020).

A precautionary approach to fishery management would suggest considering skipjack tuna stocks to the south and north of southern Tanzania (Mtwara) separately until confirmation of non-interbreeding discrete stocks can be tested fully. To clarify the genetic structure in this region, a more detailed and targeted spatiotemporal sampling of different age groups of skipjack across the Dar es Salam-Mtwara area would be recommended, particularly of young-of-the-year individuals. This will help determine whether populations north and south of Mtwara represent distinct genetic stocks or if observed genetic differences arise from varying compositions of migrating adults originating from other regions, such as South Africa or the northwestern IO.

3.4.2 Possibility for multiple genetic stocks of kawakawa across the WIO

A key finding of our study indicated low but significant levels of genetic differentiation among kawakawa samples, which may suggest the existence of spatially and/or temporally distinct genetic stocks across the WIO. Previous genetic studies on kawakawa in the IO employing the limited discriminatory power of mtDNA control region sequencing found no evidence of population structure (Masazurah et al. 2012, Menezes et al. 2012, Johnson et al. 2016).

However, a concurrent study employing RADseq-based screening of SNP markers, identified clear genetic differentiation of northern (Pakistan to western Indonesia) and eastern (western Indonesia to Andaman Sea) regions (Davies et al. 2020, Feutry et al. 2020) with a small number of samples (6 individuals) included from the WIO (Seychelles) grouped with the northern region (Feutry et al. 2020). These findings with similar studies on other tuna species, such as yellowfin tuna (Mullins et al. 2018, Pecoraro et al. 2018) demonstrate that even abundant, widespread, highly mobile and migratory pelagic species such as kawakawa may exhibit genetic differentiation suggesting restrictions to free movement and interbreeding across the species range due to environmental boundaries or behavioural characteristics.

Our study indicated a patchy distribution of significant values of genetic differentiation (F_{ST}) among kawakawa samples, with geographically distant comparisons significant (Mozambique–Seychelles) but then other similarly distant comparisons showing no significant differences (Mozambique-Kenya). Notably, some less distant comparisons showed highly significant differentiation (Tanzania Tanga-Kenya, Tanzania Mtwara-Mozambique) including the two sites within Tanzania. One consideration with the Tanzanian samples is that they were collected in different periods (Tanga in September 2019, Mtwara in June 2020) and may reflect seasonal differences in species migration or reproductive characteristics, with different stocks along the Tanzanian coast at different times of the year. However, the two Mozambique (Pemba) samples were also collected at different time points (December 2019 and March 2020) but showed no significant differences. This suggests potential temporal stability of gene frequencies in the Mozambique region and a more complex population structure in Tanzania, possibly influenced by factors beyond temporal variation (Natasha et al. 2022).

The observed spatial and temporal (seasonal) patchiness in the genetic differentiation of kawakawa populations may be attributed to the migratory behaviour of moving between distinct feeding and spawning grounds (Chiou and Lee 2004). Migration of kawakawa inshore to the coast is seasonal, reflected by high catch rates by artisanal fishers during the NEM and much lower catches during the SEM (Kimani et al. 2018, Okemwa et al. 2023). Monthly catch statistics indicate that kawakawa appear in large numbers on the coast from September to May and then move offshore to their spawning grounds in July and August. This seasonal movement aligns with temporal genetic variability in other tuna species such as bluefin tuna populations in the western and eastern AO (Puncher et al. 2018), emphasizing the need for multi-year sampling to investigate the population structure of migratory marine fishes. Kawakawa's ability like other tropical tunas to inhabit both cooler (as low as 10°C) and warmer waters, as well as coastal and deeper oceanic environments (Collette and Nauen 1983, Poisson 2006), further supports the potential for ecological structuring of populations in time and space.

The greater discrimination achieved among kawakawa samples by the tests using the 29 outlier loci potentially under positive selection hints at a signal of locally adapted stocks underlying the overall pattern of low differentiation, similar to findings in other tuna species (Vaux et al. 2021). The possibility for locally adapted subpopulations of kawakawa and/or the more localised population dynamics of this species compared to skipjack (more coastal in distribution, i.e., less large-scale migration across offshore oceanic waters, and more spatially limited migration patterns) may explain the higher genetic differentiation observed in this species ($F_{\mathrm{ST}} = 0.003 – 0.036$) compared to skipjack across the same region ($F_{\mathrm{ST}} = 0 – 0.013$). These differing levels of genetic differentiation between skipjack and kawakawa might arise from the widespread mixing of individuals from different populations. Skipjack's extensive migration may result in more homogeneous populations while kawakawa's more limited regional migration movement could lead to greater genetic differentiation among localized groups (so less mixing), resulting in higher F_{ST} values among samples reflective of the identity of individuals in that area at that time. To further investigate these species differences, additional temporal sampling within the same sampling locations is necessary, along with the identification of spawning individuals.

3.4.3 Methodological considerations

This study included two small tuna species to enable cross-species comparisons. However, direct and informative comparisons were limited due to sampling discrepancies (geographical coverage, temporal extent) and differing numbers of generated genetic markers. Kawakawa yielded nearly twice as many SNP loci as skipjack, potentially attributed to the density of sequence reads generated for the two sample sets (more initial reads across fewer individuals in kawakawa than in skipjack, resulting in greater density of reads in kawakawa after the stringent filtering processes used – see Methods), which itself may be a product of lower DNA quality across the skipjack samples and choice of restriction enzymes used. These differences might be equalised in future studies by choosing a more frequent DNA enzyme cutter for skipjack rather than the bp 12861 enzyme used here for both species.

There were also differences in fundamental aspects of the results generated, for example, the prevalence of significant and positive F_{IS} values within samples of skipjack compared to no significant F_{IS} values within samples of kawakawa. The presence of positive F_{IS} values (deficit of heterozygotes, excess of homozygotes) may indicate inbreeding effects, including large differences in individual contributions to recruitment (biased reproductive success), or Wahlund effects resulting from the mixing of genetically different subpopulations. For skipjack the latter (Wahlund effect) explanation is more likely, given that the extremely large population sizes, high fecundity and widespread migration/mixing of skipjack populations should prevent inbreeding effects. As the present skipjack F_{ST} data suggest a regional scale differentiation of two subpopulations (north and south of southern Tanzania), the possibility for Wahlund effects is clear through the mixing of subpopulations over large parts of the region due to large-scale migrations of individual fish or groups of fish. Dammannagoda et al. (2011) also reported such a pattern in Sri Lankan waters. To distinguish between the F_{IS} values being due to stochastic recruitment success within a panmictic population and mixing of individuals from different populations, future work should include individuals sampled from known spawning grounds and/or be restricted to screening individuals from specific age cohorts.

3.4.4 Management recommendations

Emerging evidence from multidisciplinary studies indicates the presence of multiple skipjack and kawakawa stocks in the IO (Pillai and Silas 1979, Wujdi et al. 2017, Jatmiko et al. 2019, Binashikhbubkr et al. 2022) necessitating a shift in management strategies for small tuna and tuna-like species. While the current study did not definitively confirm or refute the existence of spatially or temporally distinct genetic stocks of skipjack and kawakawa within the WIO, it highlights the need for a more comprehensive sampling design. This should involve temporally repeated sampling preferably of all age classes including larvae, juveniles and actively spawning adults captured in or close to spawning areas. This will help capture the reproductive seasons and spatial movements of local populations. The present study has developed the genetic procedures (tGBS genome-wide genotyping) and demonstrated the statistical discriminatory power of a suitable DNA marker set so that a methodology is now in place to examine further sample sets with confidence in the success of the study. If suitable sampling schemes can be put in place, combined with robust methods of sample collection and genetic tissue fixation/storage, then there is the potential to provide detailed, accurate and highly discriminatory assessments of stock structures of tuna and tuna-like species.

CHAPTER FOUR

SIZE STRUCTURE AND REPRODUCTIVE BIOLOGY OF SKIPJACK AND KAWAKAWA IN THE WESTERN INDIAN OCEAN

Abstract

Skipjack (*Katsuwonus pelamis)* and kawakawa (*Euthynnus affinnis*) are economically valuable tuna species targeted by artisanal fisheries in the Western Indian Ocean (WIO). To inform management strategies, knowledge of their reproductive biology, particularly size at maturity and proportion of females to males is crucial. This study investigated size variation, reproductive traits, and spawning seasonality of skipjack and kawakawa in the WIO. Samples were collected from artisanal fishers in Kenya, Tanzania, Mozambique, and recreational fishers in South Africa. The results revealed seasonal variations in the size structure of both species, potentially linked to environmental factors and fishing methods. The sex ratio was male-biased for skipjack (58%) and kawakawa (53%) landings. Size at maturity (L50) was estimated at 42.0 cm (Fork length, FL) for female skipjack and 47.0 cm (FL) for male. Similarly, for kawakawa, female matured at 44.0 cm (FL) and male at 45.3 cm (FL). Spawning activity was observed year-round across the study sites, with peaks coinciding with the Northeast Monsoon (NEM) season. The findings provide updated information on the reproductive demographics of skipjack and kawakawa, which can be valuable for assessing their stock status in the WIO and informing sustainable fishery management practices.

4.1 Introduction

Accurate information on the biology of an exploited species is fundamental for sustainable fisheries management. This knowledge supports stock assessment and calculation of Maximum Sustainable Yield (MSY), a crucial parameter for setting catch quotas that balance resource conservation and fishery viability (Morgan et al. 2009). Tuna resources, valued at USD 40 billion and supplying over 4.9 million MT annually play a significant role in global food security (ISSF 2022, FAO 2022). Understanding tuna reproductive dynamics is critical for accurate stock size estimations. This, in turn, allows for predictions regarding stock response to current and future management strategies (Santos 2023, Cooper and Weir 2006). Overexploitation, often driven by size-selective fishing, can have severe short- and long-term consequences for fish population dynamics and demographics. In the short term, it may lead to declining catches. Over the long term, it can result in stock collapse, jeopardizing the socio-economic well-being of communities dependent on these fisheries.

Reproductive demographic traits, such as sex ratio and size-at-maturity, are key biological indicators for estimating Spawning Stock Biomass (SSB) which is a widely used proxy for reproductive potential and serves as a crucial biological reference point in fisheries management (Ohashi et al. 2019). Accurate determination of size-at-maturity is essential which can be used to set minimum size limits, ensuring fish are harvested only after they have reproduced (Diekert et al. 2010, Sileesh et al. 2020). Similarly, understanding the sex ratio allows for the estimation of the proportion of spawning females within a stock. These demographic traits can also exhibit spatial variation across a species' range due to factors like temperature, food availability, and genetic differences in life history strategies (Sileesh et al. 2020). Therefore, case-by-case studies of reproductive demographics are crucial for effective fish stock management.

Skipjack tuna and kawakawa are two medium-sized tuna species that are significant components of the WIO artisanal fishery (Parks 1991, Tampubolon et al. 2014), yet the biological characteristics in this region are still unclear. These species are smaller than their co-occurring tropical tuna counterparts, yellowfin (*Thunnus albacares)* and bigeye tuna (*Thunnus obesus),* with maximum lengths of 110 cm (FL) for skipjack and 100 cm FL for kawakawa (Froese and Pauly 2019). Their faster growth rates, coupled with smaller body sizes, likely contribute to relatively larger populations compared to the larger tuna species (Kumar and Kocour 2015, Anderson et al. 2020b). Skipjack tuna exhibit a wider oceanic distribution, inhabiting deeper, cooler waters (15-30°C) across the Atlantic, Indian, and Pacific Oceans. Within the IO, they are found between 10°N and 10°S latitudes (Artetxe-Arrate et al. 2021). Kawakawa, in contrast, prefer warmer waters (18-29°C) and are typically found closer to shorelines (Collette and Nauen 1983, Poisson 2006). Their geographic range encompasses the Indo-West Pacific region, spanning latitudes from 35°N to 25°S and longitudes from 40°E to 37°W (Froese and Pauly 2019).

Skipjack tuna is a dominant species in the WIO tuna fishery, accounting for over 60% of global tuna production and roughly 53% of all IO tuna landings (McKinney et al. 2020, Moazzam 2020). Industrial fleets primarily target skipjack using purse seine gear, while artisanal fishers employ gillnets (Moreno and Herrera 2013, Galland et al. 2016). An estimated 450,000 metric tons (MT) of skipjack are landed annually in the IO, with the WIO contributing approximately 80% of this total (ISSF 2021, Coulter et al. 2020). Distant Water Fishing Nations (DWFNs) play a major role in the WIO's industrial skipjack fishery, with the European Union (EU) being a key player. Spain is the dominant force within the EU, contributing over 70% of the EU's catch (Macfadyen and Defaux 2019).

Kawakawa is another significant tuna species in the IO, with catches rising steadily since the early 1970s (Majkowski 2007, Griffiths et al. 2020a, FAO 2020a). It ranks as the second-most important neritic (inhabiting shallow coastal waters) tuna, constituting roughly 12% of the WIO's neritic tuna landings (Lecomte et al. 2017). Kawakawa are targeted by a variety of fishing gears including ring nets, gillnets, purse seines (including coastal fleets) and lines (Rohit et al. 2012, Ahmed et al. 2015, Haputhantri 2016, Okemwa et al. 2023), The IO reports annual landings of approximately 160,000 MT of kawakawa, with the WIO contributing around 128,000 MT (Lecomte et al. 2017). The growing commercial importance of kawakawa in the IO is evident by increased fishing efforts by industrial fleets targeting neritic tuna within EEZs of countries like Iran and Indonesia (Macfadyen and Defaux 2019). With many nations expanding their fleet capacities to exploit these resources further, there is a potential risk of overexploitation in the near future (IOTC 2019, IOTC 2023).

Despite significant fishing pressure, skipjack and kawakawa stocks in the WIO are currently considered sustainably fished (IOTC 2023). Stock assessments of skipjack indicate that it is not overfished and not subject to overfishing. This means the current catch rate is below a predefined limit and the stock biomass is above the target reference point, with fishing mortality lower than the recommended adopted target (IOTC 2019, IOTC 2022, IOTC

2023). Similarly, stock assessments for kawakawa in the IO suggest a healthy stock with fishing at optimal levels (IOTC 2015, Zhou et al. 2018, Raza et al. 2022, IOTC 2023). Tropical tunas, including skipjack and kawakawa, are generally characterized by rapid growth, early maturity, extended spawning seasons, and relatively short lifespans (Fromentin and Fonteneau 2001). These life history traits suggest a high population turnover rate, potentially making them more resilient to fishing pressure (Fromentin and Fonteneau 2001). However, concerns are emerging regarding the sustainability of skipjack and kawakawa stocks due to several factors. Firstly, domestic tuna fishing fleet capacities within the WIO are increasing (IOTC 2022). Secondly, there is a decline in the abundance of other tuna species, such as yellowfin and bigeye, likely due to overfishing (IOTC 2022). These factors could potentially lead to increased fishing pressure on skipjack and kawakawa. Therefore, fisheries managers must have access to the most up-to-date scientific information to make informed decisions regarding the sustainable management of these commercially important tuna species.

While life history characteristics of skipjack tuna and kawakawa in the WIO are assumed to be favourable for resilience to fishing pressure, robust data is essential for informing sustainable management practices (Morgan et al. 2009, Zudaire et al. 2013). Existing research on skipjack reproductive biology in the WIO reveals substantial variation across locations (Raju 1964, Batts 1972, Matsumoto et al. 1984, Cayré and Laloë 1986, Stéquert and Ramcharrun 1996, Norungee and Kawol 2011, Grande et al. 2014). Sex ratio estimates, for example, have been reported as male-biased (Raju 1964), female-biased (Batts 1972, Matsumoto et al. 1984) and even balanced sex proportions (Cayré and Laloë 1986). Similarly, size at maturity (L50) for female skipjack varies between studies, with estimates of 39.9 cm (Grande et al. 2014), 43.0 cm FL (Norungee and Kawol 2011), and 42.0 cm FL (Stéquert and Ramcharrun 1996). For males, Norungee and Kawol (2011) reported an L50 of 44.0 cm FL. Spawning appears to be year-round (Stéquert et al. 2001), with potential seasonal peaks (Grande et al. 2014).

Information on the reproductive demographic traits of kawakawa in WIO is scarce and existing studies also show considerable variation (Johnson and Tamatamah 2013, Nissar et al. 2015). Similarly, size at maturity (L50) for kawakawa females and males in WIO is estimated as 47cm TL and 52 cm TL respectively reporting females attaining maturity earlier than males, while another study has reported size at maturity of unsexed kawakawa to occur at the size of 43.7 cm (TL) (Johnson and Tamatamah 2013, Mehanna 2024). Spawning appears to occur year-round, with potential seasonal peaks during the NEM (October-March) and SEM (April-September) seasons (Johnson and Tamatamah 2013).

The importance of localized studies for understanding the reproductive biology of skipjack and kawakawa in WIO has been highlighted by several investigations (e.g., Norungee and Kawol 2011, Johnson and Tamatamah 2013, Grande et al. 2014, Nissar et al. 2015). Apart from the changing environmental conditions, the selectivity of fish due to gear type could affect estimates of some reproductive characteristics of skipjack and kawakawa in the region (Wright et al. 2021). This study addresses this knowledge gap by documenting the size structure and reproductive biology of skipjack and kawakawa across the WIO. We analysed length distribution, sex ratio, size at maturity (L50), and spawning seasonality for both species for potential temporal variations. This information will contribute to updating crucial parameters for stock assessment and improved management strategies for these commercially vital tuna species in the WIO.

4.2 Material and Methods

4.21 Sampling sites

The study was carried out in the WIO region, which stretches from the Southeast coast of South Africa to the Arabian Gulf, including the islands of Madagascar, Mauritius, Seychelles and Comoros. This study focussed on the territorial waters of Kenya, Tanzania, Mozambique and South Africa (Figure 4.1). The four countries border each other, posing a transboundary fish stock management concern. This part of the WIO is a tropical/subtropical region with diverse habitats along the continental shelf, and around isolated islands or subsurface plateaus (van der Elst et al. 2009, Groeneveld and Koranteng 2017). This region is dominated by western boundary currents: the Agulhas Current to the south and the Somali Current to the north and the East African Coastal Current, along the coast of Tanzania and Kenya. Additionally, the WIO is characterized by two distinct seasons, the SEM between April to September and the NEM between October to March (Schott and McCreary 2001).

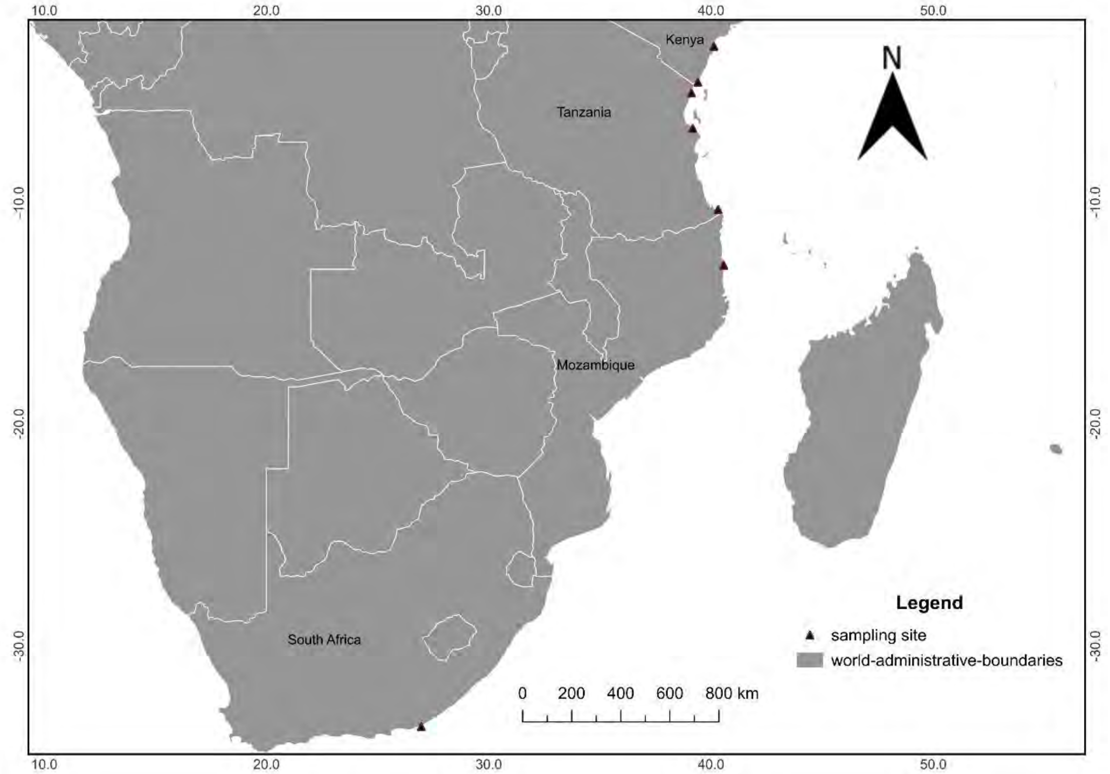


Figure 4.1. Sampling sites of skipjack and kawakawa in WIO during the study period.

4.2.2 Data collection

Skipjack tuna was sampled at fish landing sites across Kenya, Tanzania, Mozambique, and South Africa while kawakawa sampling was conducted at fish landing sites in Kenya, Tanzania, and Mozambique (Figure 4.1). The data collection was conducted between 2019 and 2022. A standardized protocol was developed and implemented by personnel collecting data at each country site. This study employed non-randomized sampling, collecting specimens of both species from commercial catches of artisanal and recreational fisheries. All gear types employed by these sectors were included in the sampling. Fishing vessels were selected for sampling based on convenience, with the first vessel arriving from a fishing trip being prioritized. Catch sampling entailed total sampling of catches that were less than 20kg while for larger catches (greater than 20 kg), a representative subsample (10-20%) was collected. The sampled catch was sorted by species, and the FL of each individual fish was measured in cm using a measuring board. Gear type used to catch tuna at each fish landing site was documented through observation and interviews with fishers.

Macroscopic gonad staging, a well-established method as suggested by Tomkiewicz et al. (2003), was employed to assess fish maturity. This approach offers advantages of speed and cost-effectiveness compared to histological methods, while still providing sufficient accuracy for determining the timing of sexual maturation, length at 50% maturity (L50) and spawning seasonality (Tomkiewicz et al. 2003, Kayaba et al. 2015). Sampling of gonads was also done randomly taking into consideration all size classes. During sample processing, fish were dissected, gonads removed and weighed using a digital weighing balance. Gonad development was classified into the following maturity stages: Immature (I), early developing (II), late developing (III), mature (IV), spawned (V) and Spent (VI) adapted from Diouf (1980). Stage I and II were classified as Immature while stages III, IV, V and VI were classified as mature as summarised in Supplementary Table S4.1.

4.2.3 Data processing and analysis

Sampling of fish sizes and gonads was limited due to low sample sizes recorded in each site hence samples from all study sites were pooled for analysis for a regional overview. Length frequency histograms were used to visualize seasonal differences in size distribution for skipjack and kawakawa across the region. The Kolmogorov-Smirnov (K-S) test was employed to statistically compare the cumulative length frequency distributions between SEM and NEM seasons. The means and size ranges (FL) of both species were analysed by month and gear type used. Standard error (SE) values were included with all reported means. The Kruskal-Wallis H test (Kruskal and Wallis 1952) was used to compare the mean (FL) of each species across months, seasons, and fishing gear types. This non-parametric test is suitable as it does not assume normality in the data distribution.

The monthly sex ratio (proportion of females to males) of the catches was investigated by size class (5 cm FL intervals) for both skipjack and kawakawa. A binomial test (Zar 1984) was employed to statistically assess whether the observed sex ratio in each category (month and size class) deviated significantly from the expected 1:1 ratio. All statistical analyses were performed using R-Studio statistical software version 3.6.3 (Team 2022).

The size at which 50% of the population reaches sexual maturity (L50) was estimated separately for females and males of both skipjack and kawakawa. The ‘sizeMat’ package version 1.1.0 (Torrejon-Magallanes 2019) within R-Studio statistical software version 3.6.3 (Team 2022) was used for analysis using the equation:

$$y = {}^{1}/_{[1 + \mathrm{e} - (a + bx)]}$$

In this logistic model equation, y is the probability of a female being mature at a particular FL, *x.* The intercept (*a*) and the slope (*b*) are estimated parameters. In R, morphologically mature females were organized into 5 cm bins and the data fitted to the aforementioned equation; 'immature' (stage I and II) was denoted by '0' and mature by '1' (stage III, IV, V and VI). The 'sizeMat' analysis package separates individuals into two groups: juveniles and adults. The size (cm; FL) at which 50% of females are mature (L50) was then calculated using the equation $L_{50} = -\frac{\beta_0}{\beta_1}$ where β_0 is intercept and β_1 is slope.

The analysis focused solely on female skipjack and kawakawa to assess trends in the Gonad Index (GI) and proportion of maturity. Monthly GI was calculated for each female fish using the following equation: $\mathrm{GI} = (\mathrm{GW} / \mathrm{FL}^3) \times 10^4$ where GW is the gonad weight and FL is the sample fish's fork length (cm). The percentage of mature females (stages III-VI) within the population was also estimated for each month.

4.3 Results

4.3.1 Variability in size structure

A significant difference (*p*-value = 0.01719 for skipjack; *p*-value = 0.009768 for kawakawa) in the cumulative size frequency distribution was observed between fish caught during NEM and SEM seasons (Figure 4.2). The smallest size class (21-27 cm FL) was caught in both seasons. However, the largest (78 - 96 cm FL) skipjack were caught during NEM. The remaining size classes represent fish caught in both seasons (Figure 4.2). For kawakawa, smaller individuals (24-30 cm FL) were found exclusively in the SEM season, while larger individuals (72-96 cm FL) were caught only during NEM. The intermediate size range (36-66 cm FL) included kawakawa caught in both seasons (Figure 4.2).

Both skipjack and kawakawa exhibited significant seasonal (*p* = 0.0001) and monthly (*p* = 0.0001) variations in mean size (FL). For skipjack, the overall size ranged from 19.5 cm to 97.0 cm FL, with a mean size of 53.93 cm FL ± 0.33 SE (Table 4.1). The largest individual skipjack was caught in March (97.0 cm FL), while the largest mean size (60.89 cm FL ± 1.65 SE) occurred in August (ranging from 45.0 cm to 73.6 cm FL). Conversely, the smallest individual was recorded in January (19.5 cm FL), and the smallest mean size (40.1 cm FL ±

0.78 SE) was observed in May (ranging from 28.0 cm to 65.7 cm FL). The overall mean size for kawakawa was 48.8 cm FL ± 0.22 SE, with a size range of 21.0 cm to 97.0 cm FL (Table 4.1). The largest recorded kawakawa measured 97.0 cm FL (January), while the largest mean size (59.9 cm FL ± 0.63 SE) occurred in November (ranging from 38.5 cm to 78.0 cm FL). The smallest mean sizes were observed in April (33.8 cm FL ± 0.58 SE) and August (37.8 cm FL ± 0.58 SE).

Skipjack and kawakawa are caught by a variety of fishing gear as described in Table S4.2. The type of fishing gear employed significantly influenced the mean FL of both skipjack and kawakawa (*p* = 0.0001) (Figure 4.3). For skipjack, handline gear caught skipjack with the largest mean size (56.9 cm FL ± 0.74 SE), while seine nets caught the smallest individuals (43.6 cm FL ± 1.27 SE). Similar to skipjack, seine nets caught the smallest kawakawa (x̄ = 30.3 cm FL ± 0.29 SE), whereas gillnets caught larger individuals (x̄ = 54.46 cm FL ± 0.46 SE) (Figure 4.3).

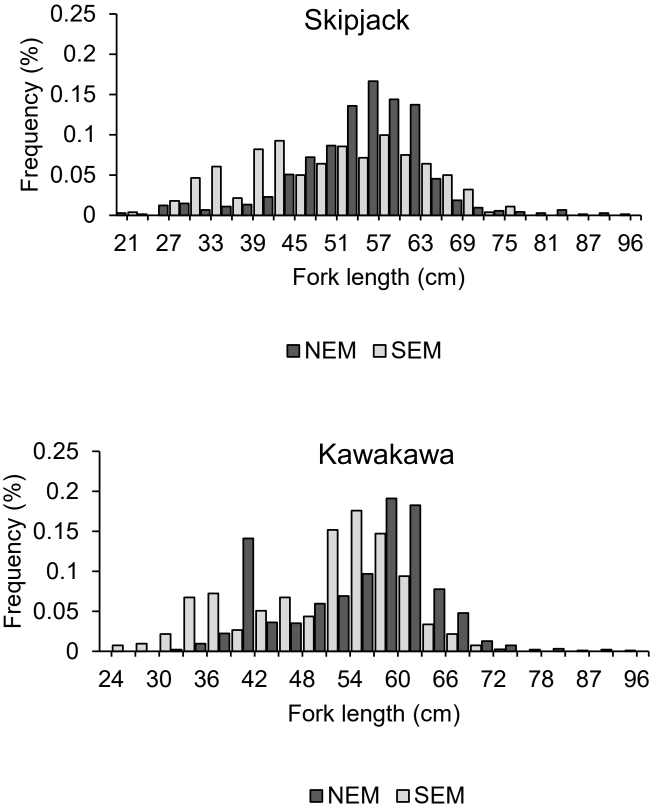
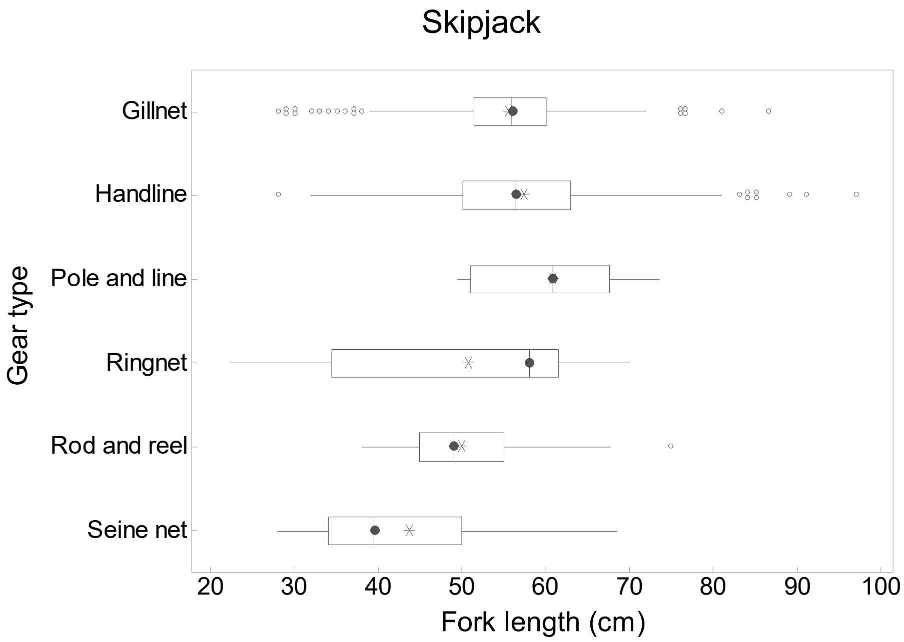


Figure 4.2. frequency distribution of skipjack and kawakawa caught in NEM and SEM season in WIO.

Table 4.1. Monthly variation in mean fork lengths and size range of *Katsuwonus pelamis* (skipjack) and *Euthynnus affinis* (kawakawa) sampled from artisanal landings in WIO during 2019-2022 survey period (n = sample size).

	Skipjack			**Kawakawa**		
Month	**n**	**Mean (cm)**	**Range (cm)**	**n**	**Mean (cm)**	**Range (cm)**
January	96	51.0 ± 0.99	19.5 - 81	644	53.2 ± 0.44	25 - 97
February	155	51.0 ± 0.74	26 - 67	240	53.4 ± 0.83	26 - 85
March	274	60.81 ± 0.50	33 - 97	324	56.1 ± 0.49	30 - 76
April	50	50.5 ± 1.75	22.3 - 74.8	433	45 ± 0.67	21.8 - 68.9
May	83	40.1 ± 0.78	28 - 65.7	202	33.8 ± 0.58	21 - 57.9
June	59	55.1 ± 0.87	30 - 64.1	140	32.6 ± 0.39	24.3 - 46
July	20	60.3 ± 1.99	37.5 - 71	253	54.4 ± 0.32	30 - 67.3
August	24	60.89 ± 1.65	45 - 73.6	213	37.8 ± 0.93	21.8 - 72
September	25	46.2 ± 2.30	26.9 - 68	208	46.6 ± 0.8	27 - 70
October	37	50.3 ± 2.27	25 - 66.9	199	46.2 ± 0.97	24.2 - 91
November	27	59.3 ± 1.19	41 – 67	151	59.9 ± 0.63	38.5 - 78
December	144	53.95 ± 0.47	34 - 68.5	443	50.8 ± 0.53	29.5 - 85.5
Overall	**994**	**53.93 ± 0.33**	**19.5 – 97**	**3450**	**48.8 ± 0.22**	**21 - 97**



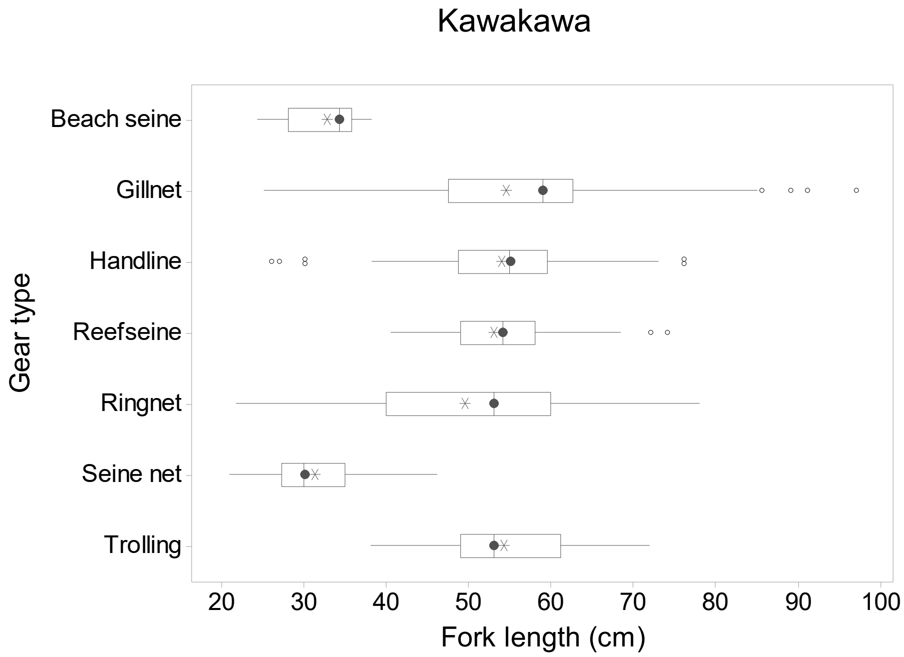


Figure 4.3. Size range and mean sizes of skipjack and kawakawa caught by gear type in WIO during the sampling period; (the symbols ● represent the median while ✳ represent the mean).

4.3.2 Variation in sex ratio

Analysis revealed a dominance of males in the landed catches for both skipjack (58%) and kawakawa (53%) (Table S4.3). Monthly sex ratios for skipjack statistically significantly deviated ($p < 0.05$) from a 1:1 ratio in April and December, where males were dominant (79 and 65% respectively) (Table S4.3 and Figure 4.4). The assessment of size-based sex ratios revealed that skipjack exhibited a significant deviation ($p < 0.05$) from a 1:1 sex ratio only in the 55 cm and 60 cm FL classes, with males dominating at 63% in both instances ($p < 0.05$; Table S4.4 and Figure 4.5). Similarly, kawakawa displayed a male bias in several months, with statistically significant deviations ($p < 0.05$) observed in May (59%), June (64%), August (65%), and December (64%) (Table S4.3 and Figure 4.4). For kawakawa, males dominated the 30, 35, and 40 cm length classes (77%, 79%, and 75%, respectively), while females dominated the 65 cm class (57%) ($p < 0.05$).

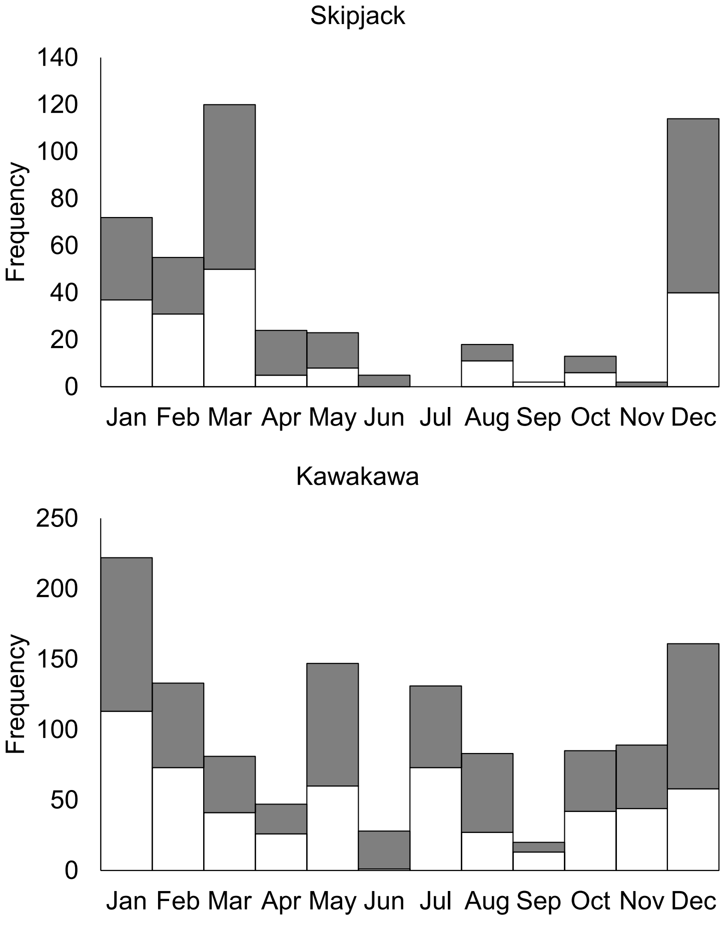


Figure 4.4. Monthly variations in sex ratios skipjack and kawakawa across the WIO during the 2019–2022 survey period.

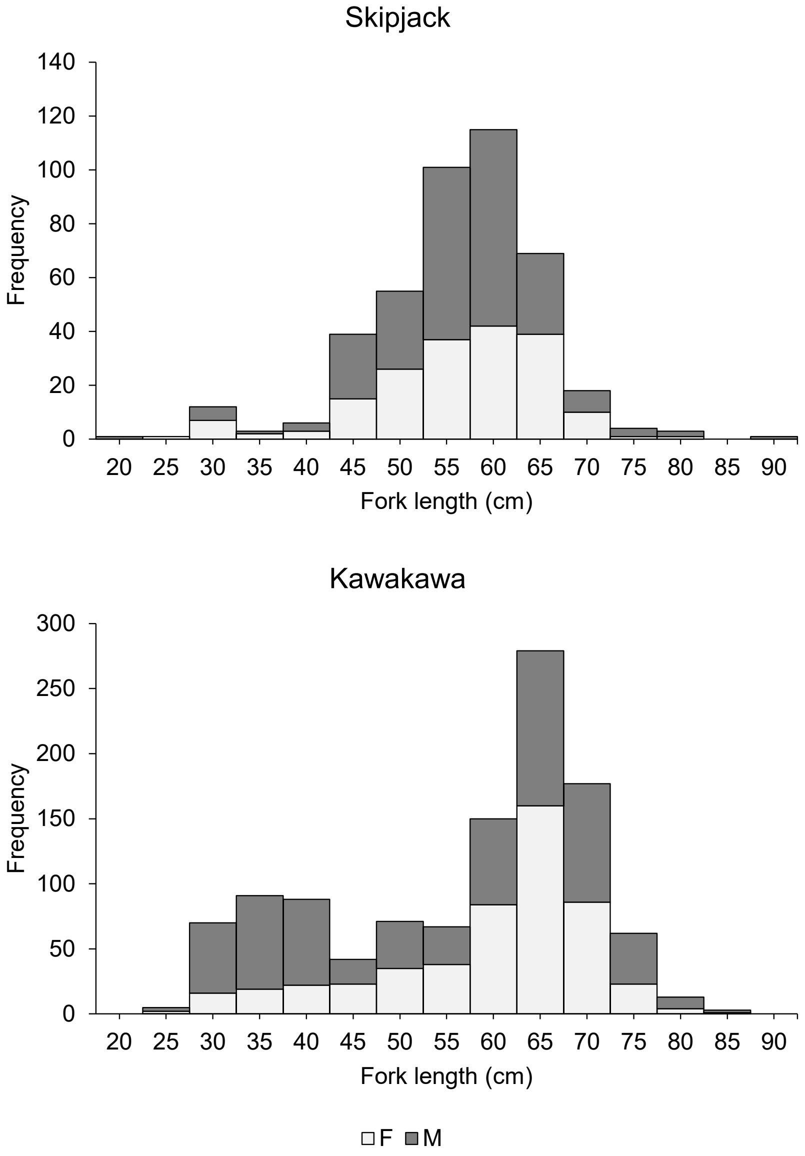


Figure 4.5. Sex ratio of skipjack and kawakawa in fork length (FL) interval (5 cm) from sampling sites in WIO.

4.3.3 Size at maturity (L50) and temporal maturity

The estimated size at maturity (L50) was similar for both skipjack and kawakawa. For female skipjack, the estimated L50 was 42.0 cm FL, with the smallest mature female observed at 32.0 cm FL. Males exhibited a slightly larger L50 of 47.0 cm (Figure 4.6), with the smallest mature male at 40.0 cm FL. For female kawakawa, the estimated length at maturity (L50) was 44.0 cm FL, with the smallest mature female observed at 38.9 cm FL. The estimated L50 for male kawakawa was 45.3 cm FL, with the smallest mature male recorded at 34.0 cm FL (Figure 4.6).

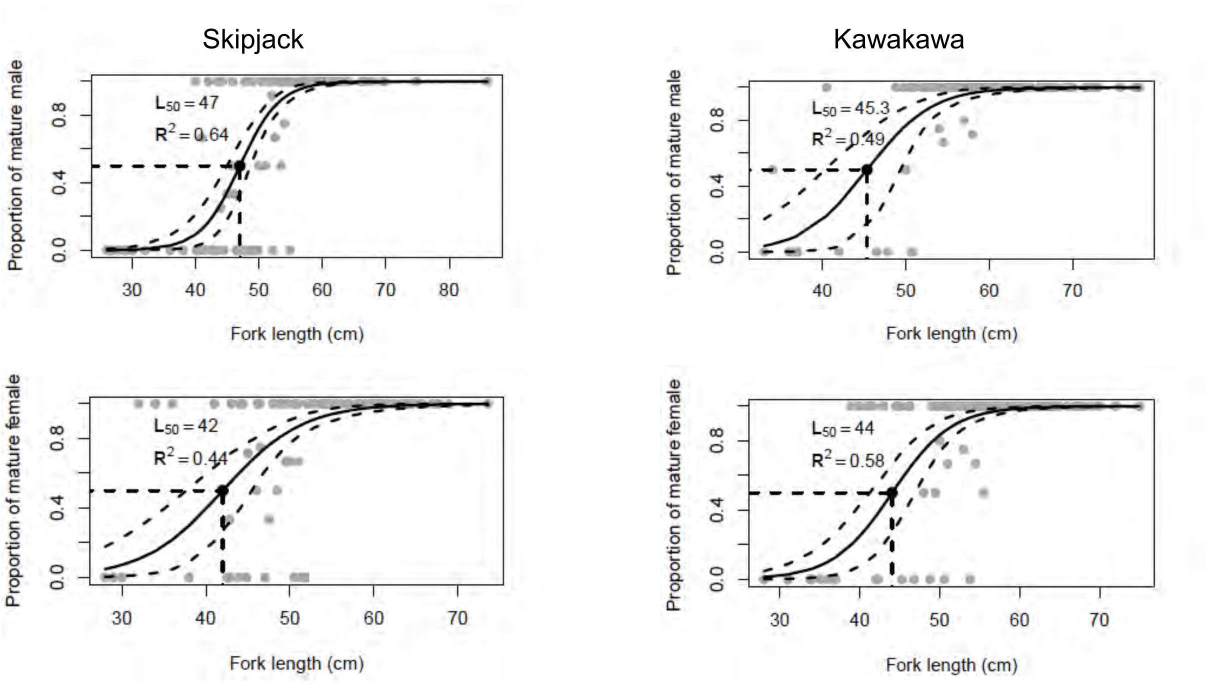


Figure 4.6. Estimated size at maturity of male and female skipjack and kawakawa sampled from sampling sites in WIO during the 2020–2022 survey period.

All mature skipjack (stage III-VI) was recorded in October (100%) and a high proportion of mature skipjack was recorded in all the other months sampled (67% - 93%) except for May which had the highest proportion (60%) of immature individuals (Figure 4.7). This pattern aligns with the GI levels where the highest mean GI (5.6 ± 0.9 SE) coincided with October's peak in mature fish. The lowest mean GI (0.87 ± 0.9 SE) was observed in May, corresponding to the highest proportion of immature individuals (Figure 4.7). For kawakawa, a high proportion (>80%) of mature individuals (stage III-VI) was observed during two periods: September-November and July-December (Figure 4.8). April exhibited the largest proportion of fish in immature stages (I and II; 52%) (Figure 4.8). This trend mirrored the GI levels, with high mean GI values in February (8.0 ± 1.03 SE), November (7.8 ± 0.43 SE), and September (7.5 ± 0.49 SE), coinciding with peaks in mature fish. Conversely, low GI values were observed in April (0.4 ± 0.13 SE) and May (0.08 ± 0.43 SE), corresponding to the high proportion of immature individuals (Figure 4.8).

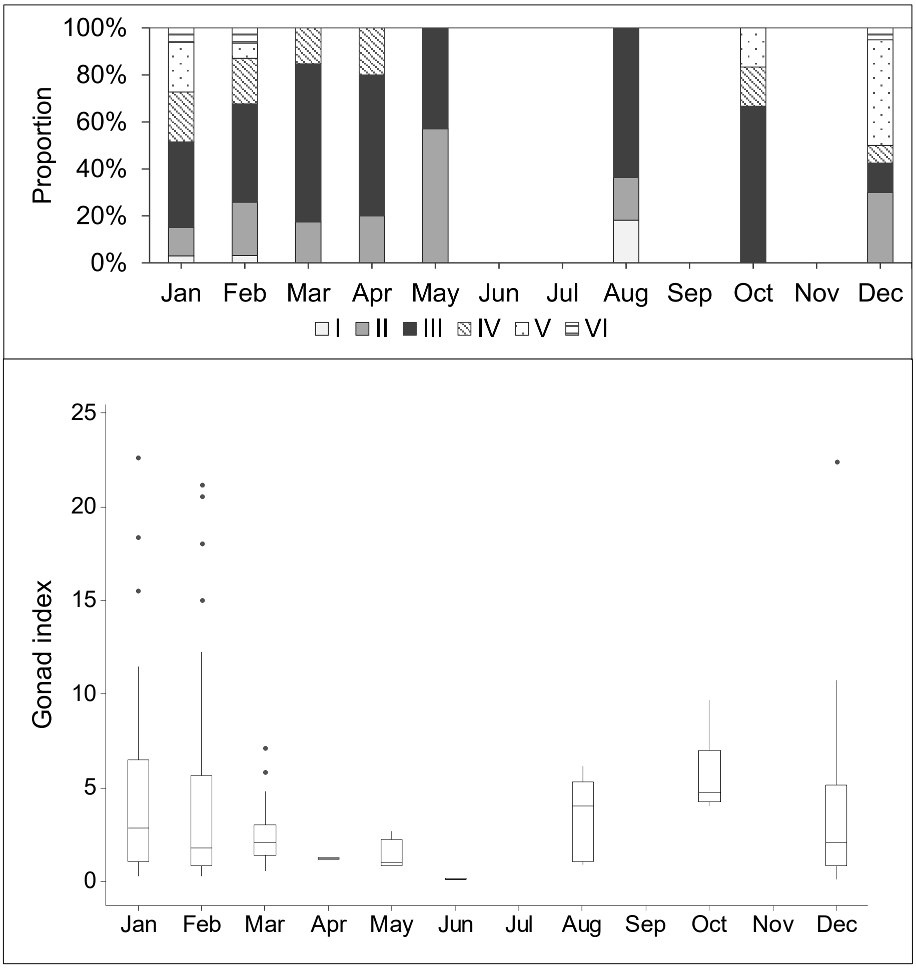


Figure 4.7. Monthly variation in the maturity stages and Gonad Index of female skipjack (*Katsuwonus pelamis)* collected from sampling sites in WIO during the survey period.

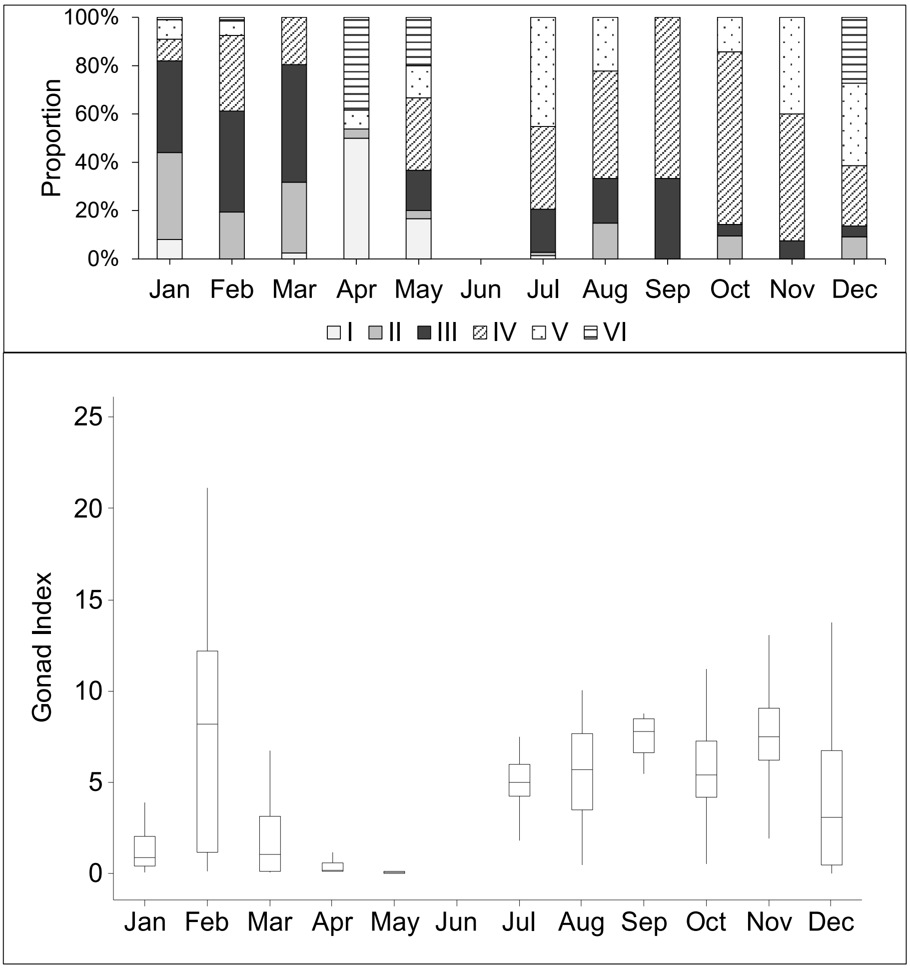


Figure 4.8. Monthly variation in maturity stages and Gonad Index of female kawakawa (*Euthynnus affinis)* collected from sampling sites in WIO during the survey period.

4.4 Discussion

Fish size significantly influences reproductive capacity (Marteinsdottir and Begg 2002), making catch size composition analysis crucial. Our study revealed substantial monthly and seasonal variations in catch length distributions. The prevalence of larger fish in catches potentially indicates sustainable fishing practices, as targeting smaller fish often precedes overfishing (Castagnino et al. 2023, Clovis et al. 2024). Interestingly, the SEM season yielded a higher proportion of smaller fish compared to the NEM season. The NEM's calmer seas and warmer temperatures (Painter 2020) likely improved artisanal fisher access to deeper waters. While vessel size and engine capacity data were unavailable, the use of smaller vessels by artisanal fishers likely limited their access to deeper waters in SEM season. Larger, more powerful vessels typically have greater range, operate in rougher conditions, and access offshore fish stocks (Renfrew 1984). Our study also observed the dominance of larger skipjack catches in March and September, coinciding with inter-monsoon periods known for strong mixing, slow currents, and favourable feeding conditions for tuna (Mayorga-Adame et al. 2017). Larger skipjack tend to inhabit deeper waters, requiring increased fishing effort compared to smaller individuals (Graham and Dickson 2004).

Gear type significantly influenced the size composition of skipjack and kawakawa catches. Handlines consistently caught larger skipjack individuals compared to other fishing methods, while gillnets tended to catch larger kawakawa than other gear types. These findings corroborate previous studies reporting larger skipjack caught by handlines (Tampubolon et al. 2014, Chodrijah et al. 2020) and gillnets (Marsac et al. 2017). Gillnets likely utilize larger mesh sizes compared to ring nets, reef seines, and seine nets. Handlines are more selective, targeting larger fish and reducing juvenile and bycatch species (Wang et al. 2022). Additionally, prevailing environmental and oceanic conditions may influence gear efficiency and size selectivity for skipjack and kawakawa, as demonstrated for yellowfin tuna (Wright et al. 2021).

Selective fishing gear can catch specific size ranges, potentially leading to skewed sex ratios. Male and female individuals of some species exhibit differing size ranges, habitat preferences, migration patterns, or behaviours. Natural selection may favour the less abundant sex, helping to maintain a balanced sex ratio by increasing the rarer sex's reproductive success (Fonteneau 2002). However, differential natural mortality rates can unintentionally target one sex over another, impacting overall sex ratios (Fonteneau 2002). Skewed sex ratios within an ecosystem can have cascading effects, including altered breeding ground competition and potential impacts on population structure and long-term sustainability (Kendal and Quinn 2013).

Selective fishing gear can also bias size at maturity (L50) estimates by disproportionately removing spawning fish or limiting accessible size classes during sampling (Zudaire et al. 2013). This study found that both male and female skipjack reached maturity at larger sizes compared to females. The estimated L50 for skipjack aligns with previous studies (e.g., Norungee and Kawol 2011: females = 43 cm FL, males = 44 cm FL). Conversely, this study estimated a lower L50 for kawakawa than reported in previous research (e.g., Deepti and Sujatha 2012, Chiou et al. 2004, Johnson and Tamatamah 2013). The observed size-based maturity difference between sexes might be attributed to behavioural characteristics. Males may prioritize axial growth (length) over biomass (weight), while females focus on weight gain relative to length (Froese 2006).

High gonad index (GI) values and a high proportion of mature individuals typically indicate a spawning season (Schaefer 2001, Johnson and Tamatamah 2013, Grande et al. 2014, Fakoya et al. 2019). Based on mean GI values exceeding 1.5 and a high proportion of mature fish (>50%) observed monthly, this study suggests year-round spawning for kawakawa in the WIO, with peak activity from July to November and February. Previous IO studies report varying kawakawa peak spawning seasons across regions (Stéquert et al. 2001, Johnson and Tamatamah 2013, Grande et al. 2014). For instance, spawning peaks in the Seychelles occur during October-November and April-May, while East Africa experiences a January-to-July peak (Collette and Nauen 1983). A Tanzanian study documented two distinct spawning peaks associated with the NEM and SEM seasons (Johnson and Tamatamah 2013).

Data limitations prevented a definitive conclusion on the year-round spawning of skipjack in the WIO. However, observed spawning activity during the NEM (October, December-February) aligns with previous studies (Stéquert et al. 2001, Grande et al. 2014). This peak in reproductive activity may correlate with increased primary productivity driven by high oceanographic productivity during the NEM (Schott et al. 2002, Wiggert et al. 2006). Enhanced prey availability associated with increased productivity could subsequently boost skipjack feeding activity (Roger 1994b, Jaquemet et al. 2011), potentially improving reproductive capacity due to their high metabolic rates (Essington 2003).

Fish body size significantly impacts reproductive capacity (Marteinsdottir and Begg 2002). Populations with larger individuals, especially females with larger bodies and presumably larger gonads, exhibit greater reproductive potential. A positive correlation exists between spawning fraction (proportion of mature females spawning) and female size (McPherson 1991, Schaefer 1998). Older, larger fish with superior body condition tend to spawn earlier and for extended periods compared to smaller fish (Kjesbu et al. 1996, Wright and Trippel 2009). Additionally, larger fish generally produce more eggs relative to body weight (Alonso-Fernández and Saborido-Rey 2011). Habitats experiencing high or variable adult mortality, often driven by fishing pressure, can select for traits favouring early maturation and shorter reproductive lifespans, leading to reduced growth, fecundity, and overall survival (Stearns 1992, Wootton 1998, Law 2000, Rochet 2000).

Environmental factors, particularly water temperature, significantly influence gametogenesis and subsequent spawning seasonality (Murua et al. 2003). Additionally, phenotypic characteristics of spawning fish, such as size and age, can substantially impact spawning duration and reproductive potential (Lowerre-Barbieri et al. 2011, Wright and Trippel 2009). Selective removal of larger, presumably older, fish through fishing practices can negatively impact spawning capacity (Wright and Trippel 2009). Understanding tuna spawning seasonality is crucial for effective fisheries management. This knowledge enables the implementation of measures to prevent or control catching spawning individuals, fostering a more sustainable fishery.

4.5. Conclusion

This study provides valuable, recent data on the size structure and reproductive biology of skipjack and kawakawa across a substantial portion of the WIO. Our findings reveal temporal variations in reproductive traits, including sex ratio and spawning capacity, for both species. Additionally, we observed seasonal fluctuations in size distribution. These variations in size structure, sex ratio, and spawning seasonality may be attributed to (1) fishing methods and timing influencing catching specific life stages, affecting observed size distributions; and (2) spatial and temporal variations in environmental conditions influencing fish distribution, behaviour, and reproductive activity. To better understand the relationship between size and reproduction in skipjack and kawakawa, future studies should examine these species across the entire WIO, considering how fish size and maturity vary geographically. Incorporating data on spatial and temporal environmental conditions will provide a more comprehensive understanding of these dynamics.

CHAPTER FIVE

VALUE CHAIN ANALYSIS OF KENYA’S ARTISANAL TUNA FISHERY FOCUSING ON SKIPJACK AND KAWAKAWA

Abstract

This study investigates the value chain of Kenya's artisanal tuna fishery targeting skipjack and kawakawa. The study utilized an integrated approach combining questionnaires and catch data to examine the socio-demographic profiles of the key actors (fishers, agents, traders, processors), the structure and function of the value chain nodes, and associated economic benefits at four landing sites along the Kenya coast. Findings reveal that fishers, the primary actors, sell most of their catch (53%) to agents, with the remainder distributed amongst traders (20%) and processors (18%). Processors, predominantly women, play a key role in the value chain and have the highest net profit margin (49.5%). Limited post-harvest infrastructure, inadequate transportation, and poor marketing conditions were identified as key challenges that impact the quality of fish, and hence income generation. These challenges disproportionately affect fishers who have limited access to market information and financial resources. The findings demonstrate the need for multi-level interventions to optimize benefits from the artisanal tuna fishery along the entire value chain taking into consideration the economic, environmental, and social dimensions.

5.1 Introduction

Marine fisheries play a critical role in the global economy, supplying fish and fish products to local, national, and international markets (Berkes 2001, Thu et al. 2020). Tuna fisheries, in particular, form a significant portion of the global fish landings and value contributing substantially in both developed and developing countries (McCluney et al. 2019). The global tuna catch is estimated at 4.9 million tonnes valued at USD 40 billion providing a source of high-quality food (ISSF 2022). The IO is the world's second largest tuna producer, contributing approximately 1.2 million tonnes accounting for about 20% of the global catch (FAO 2020b, IOTC 2023). The IO tuna catch is estimated at USD 2.3 billion (ISSF 2021). Interestingly, artisanal fishers are responsible for catching more than half of the total tuna landed in the IO (Ardill and Gillett 2011, Christ et al. 2020).

Approximately 37, 000 MT of marine fish is landed annually in Kenya, by approximately 14,500 artisanal fishers with tuna and tuna-like species constituting about 19% (GOK 2024). Like most tropical fisheries, Kenya's artisanal tuna fishery is multi-gear and multi-vessel operating close to the shoreline. Various gear types are used to target tuna, including longlines, multifilament and monofilament gillnets, handlines, and trolling lines (Okemwa et al. 2023). Previously, tuna vessels have been wooden-planked sailboats, although an increasing trend towards motorization is observed (Ndegwa et al. 2020, GOK 2024). Fishing effort exhibits strong seasonality driven by the monsoon cycle, with the primary fishing season occurring during the calm season of the NEM from September to March. However, this may vary by target species (Ndegwa et al. 2020). In 2019, the ex-vessel value of tuna taken by approximately 600 artisanal tuna fishers in Kenya was estimated to be more than three million USD (Ndegwa et al. 2020). Despite generating significant economic value, the Kenya artisanal tuna fishery's value chain and its socio-economic benefits is poorly understood.

This study focuses on two tuna species targeted by artisanal fishers in Kenya: *Katsuwonus pelamis*, skipjack tuna and *Euthynnus affinis,* kawakawa. Skipjack is the most dominant globally, accounting for over half of all landed tuna by volume (IOTC 2023, McKinney et al. 2020). Kawakawa is the second most abundant neritic tuna species in the IO, accounting for about 12% of all neritic tuna in the region (IOTC 2019). Kawakawa is predominantly caught by artisanal fishers, with annual landings reaching approximately 160,000 MT in the IO (Lecomte et al. 2017).

Most of the assessed demersal fish stocks in the IO region are reported to be fully exploited; however, the pelagic stocks including skipjack and kawakawa are generally considered to be in a healthy state (IOTC 2019, IOTC 2022, IOTC 2023). Increasing fishing effort, on both species necessitates robust management strategies to ensure long-term sustainability.

Management of tuna is spearheaded by the Indian Ocean Tuna Commission (IOTC), managing tuna at a regional scale due to the sharing of tuna stocks among nations (IOTC 2023). At a national level, the State Department of Fisheries and Kenya Fisheries Service manages tuna in collaboration with the local communities through the Beach Management Units (BMUs). These co-management systems were established in Kenya to promote sustainable fishing practices and responsible management of fishery resources including tuna and tuna-like species (Tubman et al. 2021). In Kenya, artisanal landings of skipjack are marginal, constituting only 4% of sampled tuna at key landing sites (Okemwa et al. 2023). On the other hand, kawakawa is highly abundant representing approximately 31.5% of sampled artisanal tuna landings in Kenya (Okemwa et al. 2023). Both species are caught by diverse fishing gears across different landing sites with high variations in catch rates (Okemwa et al. 2023). Thus, understanding inputs and outputs during fishing and along the value chain can help identify areas of improvement to maximize fishers' profits.

Value chain analysis (VCA) is the process of identifying the pathways of activities that a product or service goes through, from primary production to final consumption and the activities that add value to the product at each stage (Kaplinsky et al. 2000, Morris 2001). VCA goes beyond simply identifying the sequence of activities; it helps to map the activities that add value at each stage, and evaluate financial performance (i.e. sales, costs, and profits) (Macfadyen et al. 2012). There has been a growing interest in the application of VCA to understand fisheries value chains across the globe (Rosales et al. 2017, Tukana et al. 2023, Leurs et al. 2024). However, limited effort is put towards assessing marine fisheries value chains.

This study maps the value chain actors involved in the skipjack and kawakawa fishery in Kenya and characterizes their roles and socio-demographic profiles. The mapping process also explores product flows and changes in pricing, examining the inputs and outputs alongside profit distribution. Additionally, the study evaluates fishing operations targeting both species and describes the market structure and performance across the various nodes. The study further highlights the challenges and opportunities in the different nodes of the value chain.

5.2 Materials and Methods

5.2.1 Study area

Kenya is endowed with a coastline of approximately 640 km, extending into a 200 nautical mile (nm) Exclusive Economic Zone (EEZ). Except for the northern region, the continental shelf is relatively narrow extending to about 60 nm offshore (Kimani et al. 2018). This coastal zone is rich in natural resources, encompassing marine fish, seagrass beds, mangrove forests, coral reefs, and a diverse cultural heritage. Oceanographic conditions including salinity, Sea Surface Temperature (SST), nutrients and wind patterns are driven by two distinct seasons: the relatively calm northeast monsoon (NEM) prevailing from November to March and the windy and rough southeast monsoon (SEM) dominating from May to September (Jury et al. 2010, Schott and McCreary 2001, Mayorga-Adame et al. 2016).

This study was carried out at four landing sites along the Kenyan coast (Figure 5.1): Vanga and Gazi in the south and Kilifi central and Watamu in the north. These sites were found to be representative due to their prominence as major tuna landing hubs in Kenya, collectively contributing over half of the estimated 6,160 MT of artisanal tuna landings nationwide (GoK 2022).

5.2.2 ***Data collection and analysis***

The study utilized a combination of secondary and primary data to characterize the value chain. The secondary data comprised catch assessment survey (CAS) data collected in April 2020-March 2021, representing a subset of data from Okemwa et al. (2023). Catch data for each species was disaggregated by landing site, month, season (NEM vs SEM) and gear type. For each sampled fishing trip, a raising factor ratio (total weight of the catch / sampled weight of the catch) was estimated and applied as a multiplier to the sampled catch weight to obtain an estimate of the total weight of fish caught for all species. The overall proportion of skipjack and kawakawa caught by different gear types was then calculated. Species-specific catch rates (catch per unit effort, CPUE) were calculated at the vessel level (kg/day) and fisher level (kg/fisher/day). The average landed value of skipjack and kawakawa for each fishing trip was estimated by multiplying the total with the corresponding selling price on the given day. Non-parametric Kruskal–Wallis test (Kruskal and Wallis 1952) was applied to test for significance in catch rates per season. The normality of the data was evaluated using the Shapiro-Wilk test (Shapiro and Wilk 1965) before conducting the statistical test to confirm adherence to assumptions of parametric tests.

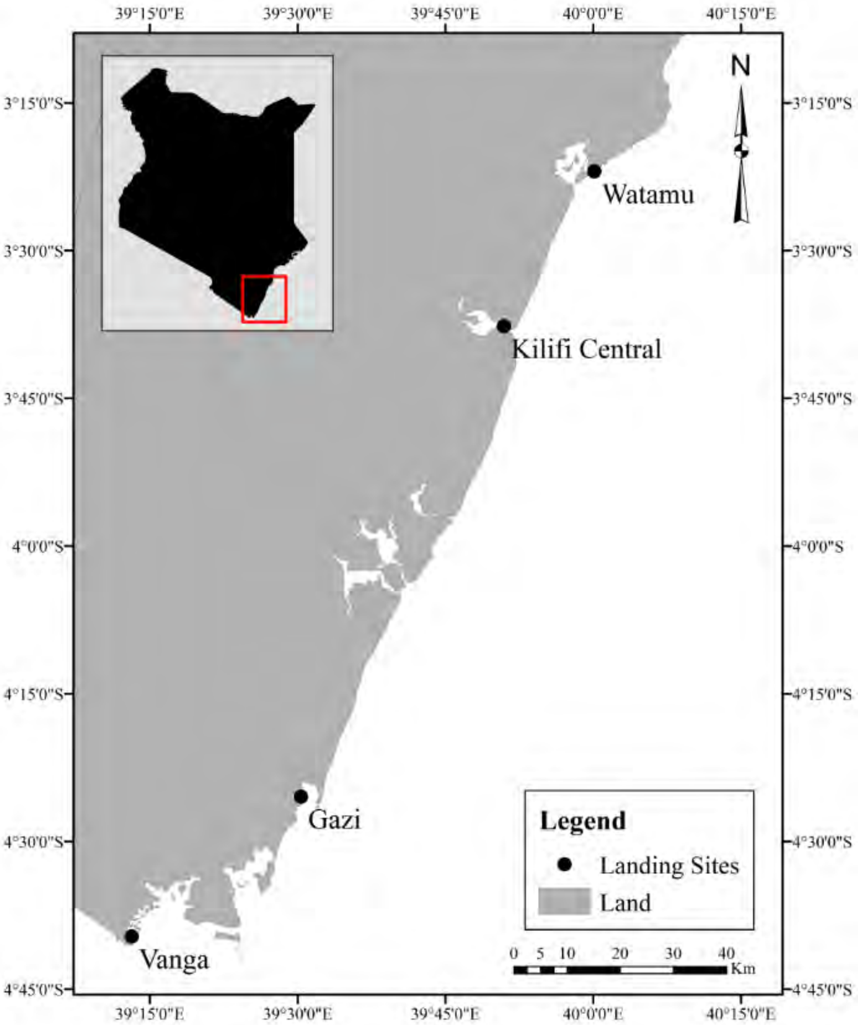


Figure 5.1. A map showing the four sampling sites in Kenya where interviews on the value chain were conducted.

A semi-structured questionnaire survey (see Appendix 1) was conducted to collect primary data. The questionnaire was administered during September 2021 and February 2022. These months corresponded to the low and high tuna fishing seasons respectively. A total of 185 respondents encompassing tuna fishers, traders, processors and agents/investors were interviewed across the study sites (Table 5.1 and 5.2). A reconnaissance survey preceded the actual survey to refine the questionnaires. The "snowball sampling" technique (Biernacki and Waldorf 1981) was used due to the heterogeneity of fisheries and the presence of non-tuna targeting stakeholders at the landing sites. This sampling approach involved requesting officials of BMUs to identify and recommend tuna fishers and other value chain actors willing to participate in the survey. The identified participants were contacted, and consenting individuals were interviewed at the fish landing sites. Before commencing the survey, a briefing informed the participants about the research objectives and their expected role. Participants were also provided with printed colour photos to ensure that they were able to identify the study species. Data processing included coding of questionnaire responses in Microsoft Excel and using descriptive statistics to generate response rates in the form of proportions (%). Variables assessed included socio-demographic characteristics, marketing behaviour, operating costs and returns. These variables are presented as percentages of respondents or mean values. Statistical differences in the socio-demographic characteristics of the actors were assessed using the chi-square test (Pearson 1900) and Fisher's exact test (Fisher 1934). The F-test was used to compare differences in operating costs incurred between the two actors. Additionally, multiple linear regression analysis (Aiken et al. 2003) was conducted to evaluate the influence of socio-demographic characteristics of the key actors on market behaviour (handling practices) and performance (buying and selling prices). All statistical analyses were performed using R statistical software (Team 2022).

Market performance metrics for value chain actors were estimated by adapting methods established by Nguyen and Jolly (2018), derived as follows:

Total gross profit =Selling price-buying price……………………………………………………….. (i)

*Total gross profit margin (%) = (Selling price–buying price)/Selling price) *100…………. (ii)*

Total net profit =Selling price-operating cost………………………………………………………. (iii)

*Total net profit Margin % = (Selling Price–operating Cost)/Selling Price) * 100………… (iv)*

The operating cost (cost of buying the fish and the running costs) was assessed for the processors and traders. Due to difficulty in accurately estimating costs of fixed assets, maintenance expenses and other operational expenditures during fishing, it was not possible to calculate operating costs or derive net profit margins for fishers and agents/investors. A value chain map was generated to visualize product flow, including the proportion of each species at each node and associated price changes.

5.3 Results

5.3.1 Socio-demographic characteristics of the actors

The key actors involved in the skipjack and kawakawa tuna value chain include fishers, agents/investors, traders and processors (Table 5.1, 5.2 and 5.3). Significant gender disparity exists in the fishery (p =0.0001; Table S5.1) with fishers, traders and agents/investors being predominantly men (100%, 85% and 89%, respectively); while the processors are primarily women (95%) (Table 5.3). Over half of the actors have participated in the tuna industry for more than ten years except for processors (Table 5.3). Education level varied significantly across the actors (p =0.0001; Table S5.1). Fishers demonstrated a low level of education compared to traders with 16% having no formal education and only 25% completing secondary education. None of the surveyed fishers held tertiary education. In comparison, 29% of traders had secondary education and 15% possessed tertiary education. Processors also exhibited low education levels with only 3% and 1% achieving secondary and tertiary education respectively (Table 5.3).

Age distribution differed significantly among actors (p =0.0001; Table S5.1). Fishers were the youngest group with 42% falling within the 21-30 years old age bracket. Comparatively, only 12%, 20% and 19% of traders, processors and agents/investors respectively, belonged to this age group (Table 5.3). The primary age range for traders (44%) and agents/investors (38%) was 41-50 years old while processors were predominantly (40%) in the 31-40 years old age bracket (Table 5.3). A significant proportion (p <0.05; Table S5.1) of all value chain actors, except agents/investors (p = 0.23) are registered members of BMUs (Table 5.3). Value chain actors with alternative sources of income were not significant (p > 0.05) except processors (p =0.0001). Approximately, 71% of processors primarily relied on income from the tuna value chain (Table

5.3). High fish consumption within the actor's households was evidenced and significant (*p* =0.0001). Over 70% of fishers, traders and agents/investors consumed more than 20kg of fish per month. Processors, however, exhibited lower fish consumption compared to the other actors (Table 5.3).

Table 5.1. Types and numbers of key actors interviewed in each landing site.

Site/respondents	Fishers	Traders	Processors	Agents/investors	Total
Vanga	12	8	12	4	36
Gazi	20	11	20	9	60
Kilifi	12	8	21	4	45
Watamu	12	9	12	11	44
Total	56	36	65	28	185

Table 5.2. Description of the main actors that participate in the tuna value chain based on the perception and observation in the landing sites sampled.

Actors	**Context, role and activities of value chain actors**
Fishers	Exploit and harvest tuna from the sea and then sell the raw tuna to other actors such as agents/ investors, traders and processors.
Agents/Investors	Provide major inputs to fishers on credit terms when going fishing, they are mainly paid back by the fish catch landed and then sell the catches to other actors and therefore also referred to as traders but commonly known as dealers.
Traders	Traders purchase tuna from agents and sometimes from fishers and sell the raw (sometimes, frozen/iced) tuna to processors, retailers and household consumers, they are also involved in the marketing and distribution of tuna.
Processors	Processors purchase raw tuna from fishers and traders and sell the processed products for final consumption. The majority are women, who process tuna by frying, ready-to-eat products, a few others are men who sometimes process tuna into frozen pieces.

Table 5.3. Demographic characteristics of the artisanal tuna fishery actors based on questionnaire surveys conducted in the selected study sites along the Kenya coast (All numbers are proportions in percentages and have been rounded off).

Item	**Category**	**Value chain actors**			
		Fisher	Traders	Agents/investors	Processors
Gender	Male	100	85	89	5
	Female	0	15	11	95
Age	18-20	7	0	0	0
	21-30	42	12	19	20
	31-40	21	18	15	40
	41-50	18	44	38	26
	51-60	7	23	15	11
	>60	5	3	13	3
Education status	None	16	0	0	47
	Primary	59	56	59	48
	Secondary	25	29	33	3
	Tertiary	0	15	8	1
Experience	<10	44	41	41	58
	10+	56	59	59	42
Alternative source of income	Yes	59	41	48	29
	No	41	59	52	71
Member of BMU	Yes	65	97	56	86
	No	36	3	44	14
Fish consumed per month	<5kg	1	0	0	5
	5-10kg	4	9	0	22
	11-15kg	13	14	11	14
	16-20kg	6	6	0	17
	>20kg	75	71	89	42

5.3.2 Fishing operations

A total of 58, 066 kg of tuna was sampled across the four landing sites during the study period. Vanga displayed the highest proportion (78%) of kawakawa among all landed tuna species, followed by Kilifi central (23%), Watamu (14%), and Gazi (8%) (Table 5.4). Kilifi Central recorded the greatest proportion of skipjack landings (13%). The share of skipjack tuna landed in Watamu and Gazi was considerably lower, at 3% and 2% respectively. Notably, Vanga recorded practically no skipjack landings (<1%) during the sampling period (Table 5.4).

Table 5.4. The proportion of skipjack and kawakawa landed in each sampling site during the catch assessment survey period of 2020-2021.

Sampling site	Total Weight of Tuna landed (kg)	Proportion of kawakawa (%)	Proportion of skipjack (%)
Vanga	12,268.1	78	0
Gazi	13,565.5	8	2
Kilifi central	22,158.7	23	13
Watamu	10,073.8	14	3

This study shows a significant variation of catch rates between the two seasons (NEM and SEM) based on the Kruskal-Wallis test (kawakawa: Kruskal-Wallis $X^2 = 7.82$, $p = 0.005$; skipjack: Kruskal-Wallis $X^2 = 7.59$, $p = 0.006$) (Figure 5.2). Catch rates and value of both skipjack and kawakawa exhibited gear type variation across the landing site as shown in Table 5.5, 5.6 and Figure 5.3. Kawakawa landings employed a diverse range and gear preferences across the landing sites (Table 5.4 and Figure 5.3). For instance, in Vanga, ring net dominated kawakawa catches accounting for 58% of landings. The remaining catches were captured by reef seine (41%), and handline (1%). Similarly, Gazi catches were dominated by ring net (88%) and the remaining catches by gillnet (12%). Conversely, gillnets and trolling lines appeared as the primary gears for catching kawakawa in Kilifi central and Watamu, contributing over 90% of the landings in these regions (Figure 5.3). The highest catch rate of kawakawa was recorded in Vanga by reef seine at a catch per vessel and catch per fisher of 299.82 ± 168.88 kg/trip and 18.91 ± 11.01 kg/fisher/day respectively, followed by ring net fisher at a catch rate of 264.183 ± 58.21 kg/trip and 11.48 ± 2.69 kg/fisher/day. This trend mirrored values obtained as the highest value was obtained by the reef seine fishers at a value of KES 53,967.96/trip and KES 3,404.57/fisher/day. Ring net fishers had a much higher value per vessel (KES 47552.97/trip) compared to gillnet fishers (KES 11035.97/trip) however at an individual value per fisher, gillnet fisher's value was slightly higher than those of ring net fishers at a value of KES 2070.05/fisher/day vs KES 2067.12/fisher/day (Table 5.5).

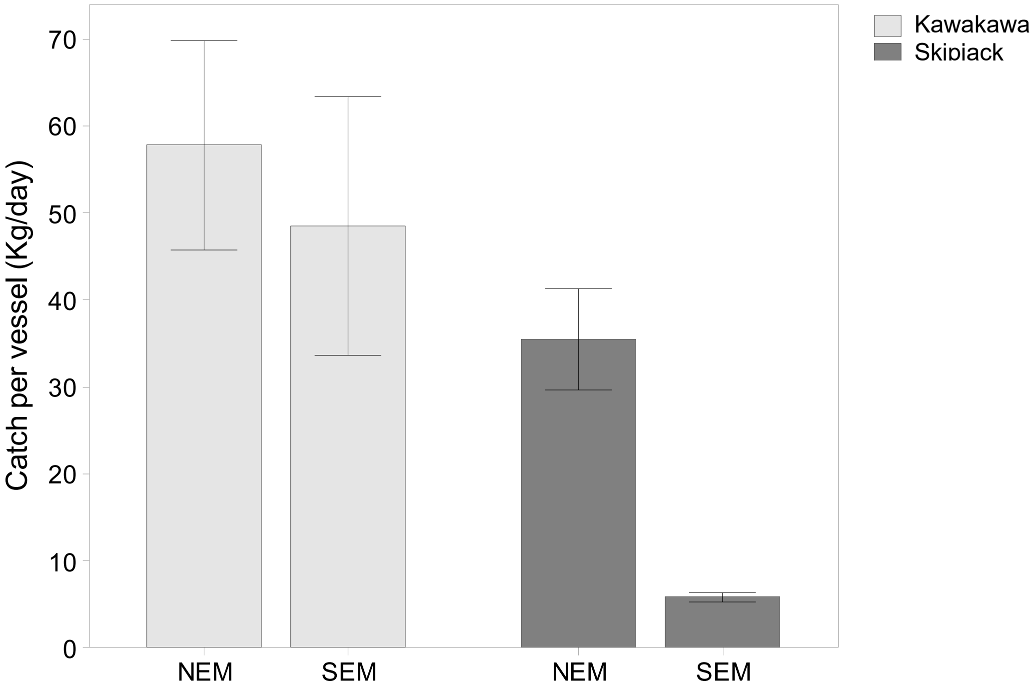


Figure 5.2. Seasonal catch rates of skipjack and kawakawa landed in the sampling sites during the sampling period.

Similar to kawakawa, skipjack landings utilized variation of gear type and preference across the landing sites (Table 5.6 and Figure 5.3). In Kilifi Central and Gazi, gillnets were the primary gear for catching skipjack, contributing to over 99% of landings (Figure 5.3). While skipjack catches in Watamu were predominantly contributed by trolling lines (Figure 5.3). High catch rates of skipjack were recorded by gillnet fishers (Table 5.6). The highest being recorded in Kilifi central at a catch per vessel of 56.19 ± 9.43 Kg/trip and 10.61 ± 1.82/kg/fisher/day which attracted a value of KES 10,114.29/trip and KES 1,909/fisher/day. While gillnet fishers in Gazi had a catch rate of 34.46 ± 9.48 kg/trip and 6.66 ± 1.95 kg/fisher/day at a value of KES 6,203.32/trip and KES 1,198.8/kg/fisher/day respectively (Table 5.6).

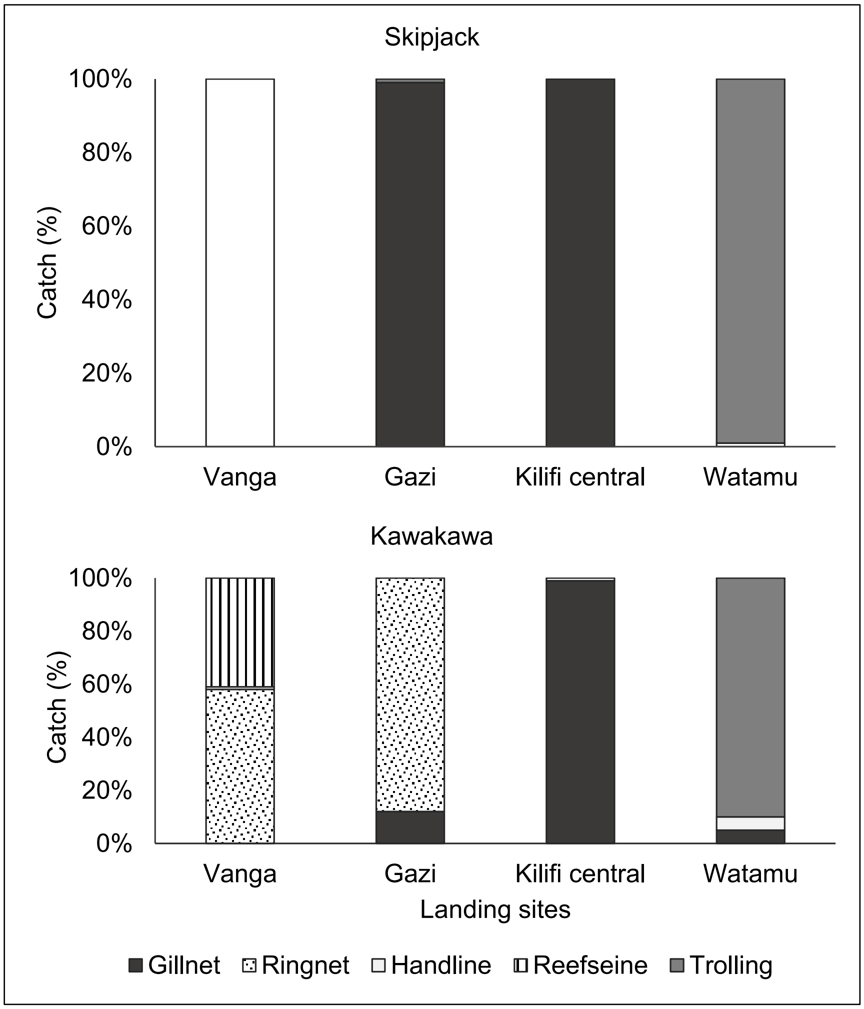


Figure 5.3. Relative contribution of gear types used to catch skipjack and kawakawa in the sampling sites during the survey period.

Table 5.5. Mean catch rates (catch/vessel and catch/fisher) and value of kawakawa attained by fishers in the sampling sites during the sampling period (blank spaces = no data was recorded, highlighted text =only one sample recorded).

	Gear type	**Gazi**	**Kilifi central**	**Vanga**	**Watamu**	**Total**
Average catch per vessel (Kg/trip/day)	Gillnet	32.64 ± 17.70	61.31 ± 6.93	13.92	22.17 ± 6.29	**58.21 ± 6.55**
	Handline		16.27 ± 7.05	54.57 ± 53.43	6.57 ± 1.02	**14.81 ± 7.28**
	Reef seine			299.82 ± 168.88		**299.82 ± 163.88**
	Ring net	457.10 ± 405.89		264.183 ± 58.21		**280.96 ± 59.99**
	Trolling line				7.35 ± 0.37	**7.35 ± 0.37**
Average catch per fisher (Kg/fisher/day)	Gillnet	7.245 ± 4.60	11.50 ± 1.41	0.870125	5.542 ± 1.57	**11 ± 1.31**
	Handline		5.42 ± 0.39	2.89 ± 2.51	1.78 ± 0.27	**2.46 ± 0.48**
	Reef seine			18.91 ± 11.01		**18.91 ± 11.01**
	Ring net	13.64 ± 11.74		11.48 ± 2.69		**11.67 ± 2.56**
	Trolling line				1.82 ± 0.09	**1.82 ± 0.09**
Average value per vessel (KES/trip/day)	Gillnet	5874.35	11035.97	2505.96	3990.24	**10476.93**
	Handline		2927.34	9821.79	1181.91	**2665.53**
	Reef seine			53967.96		**53967.96**
	Ring net	82278.87		47552.97		**50572.61**
	Trolling line				1322.93	**1322.93**
Average value per fisher (KES/fisher/day)	Gillnet	1304.07 ± 826.51	2070.05 ±254.68	156.62	997.56 ± 282.9	**1979.00 ±236.56**
	Handline		975.78 ± 69.45	519.93 ±452.07	320.48 ± 43.4	**442.58 ±86.69**
	Reef seine			3404.57 ±1981.69		**3404.57 ± 1981.69**
	Ring net	2455.11±2113.71		2067.12 ±484.06		**2100.86 ± 461.18**
	Trolling line				327.93 ± 16.89	**327.93 ± 16.89**

Table 5.6. Mean catch rates (catch/vessel and catch/fisher) and value of skipjack attained by the fishers in the sampling sites during 2020-2022 catch assessment survey period (blank spaces = no data was recorded, highlighted text =one sample recorded).

	Gear type	**Gazi**	**Kilifi central**	**Vanga**	**Watamu**	**Total**
Average catch per vessel (Kg/trip/day)	Gillnet	34.46 ± 9.48	56.19 ± 9.43			**53.66 ±8.43**
	Handline			13.18	3.34	**8.26 ± 4.92**
	Trolling line	3.1			5.3 ± 0.31	**5.26 ± 0.32**
Average catch per fisher (Kg/fisher/day)	Gillnet	6.66 ± 1.95	10.61 ± 1.82			**10.15 ± 1.63**
	Handline			4.39	1.114	**2.75 ± 1.64**
	Trolling line	1.55			1.32 ± 0.08	**1.32 ± 0.08**
Average value per vessel (KES/trip/day)	Gillnet	6203.32	10114.29	0	0	**9658.00**
	Handline	0	0	2372.4	601.55	**1486.98**
	Trolling line	558	0	0	953.26	**946.67**
Average value per (KES/fisher/day)	Gillnet	1198.8±350.35	1909.8 ±327.81			**1827 ±293.26**
	Handline			792	199.8	**495 ± 295.146**
	Trolling line	279			237.6 ±14.50	**237.6 ±14.27**

5.3.3 Product marketing and market structure

Significant post-harvest losses were observed due to inadequate fish preservation practices across the tuna value chain. Only 3% of fishers employed cold storage methods at sea or during sale (Figure 5.4). The practice of preservation by fishers was potentially influenced by BMU membership status (details in Table S5.2). Wholesale traders, who also function as agents/investors, purchased unpreserved tuna from fishers and implemented varying preservation techniques (Figure 5.4). Approximately 29.6% used ice, 31.8% employed refrigeration, and 25% opted for freezing. However, a concerning 13.6% did not utilize any preservation method. Processors, in contrast, highly implemented cold storage methods for fish preservation, with 95% employing these methods before or during processing (Figure 5.4).

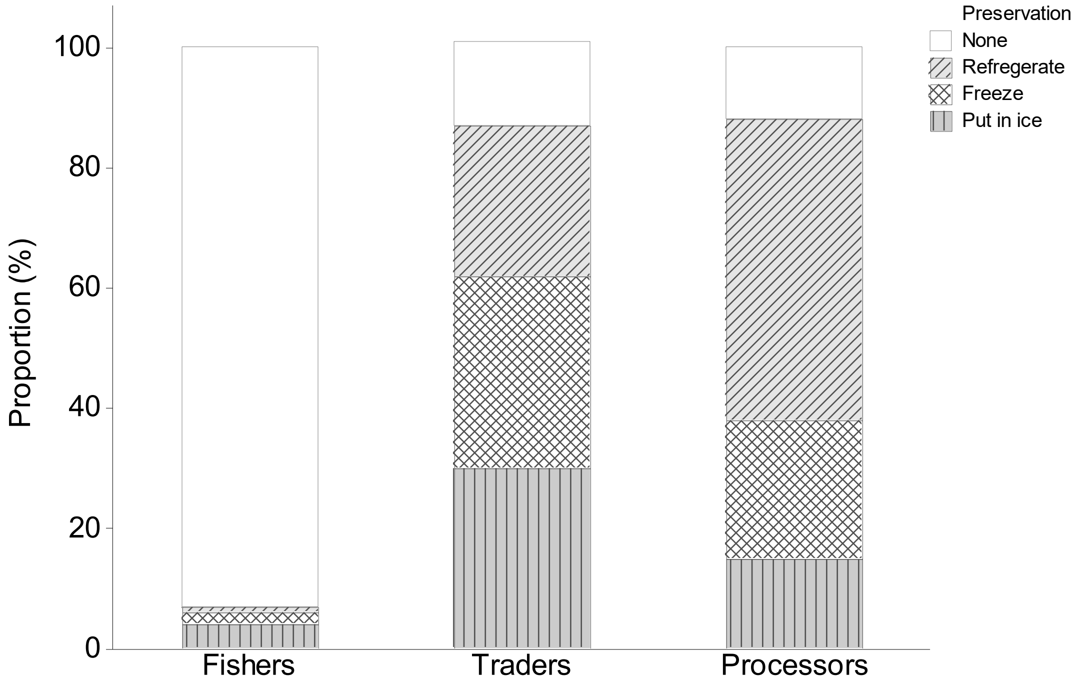


Figure 5.4. The proportion of respondents among artisanal value chain actors regarding methods of handling and preservation in the value chain.

Communication strategies regarding tuna product availability varied among traders (Figure 5.5). A majority (67%) relied on phone calls to notify customers about fish catches. Social media platforms like WhatsApp and Facebook emerged as a growing communication tool, with 13% of traders using these applications to share photos and texts about available products. Open markets, where customers select fish directly, remained a common practice for 15% of traders.

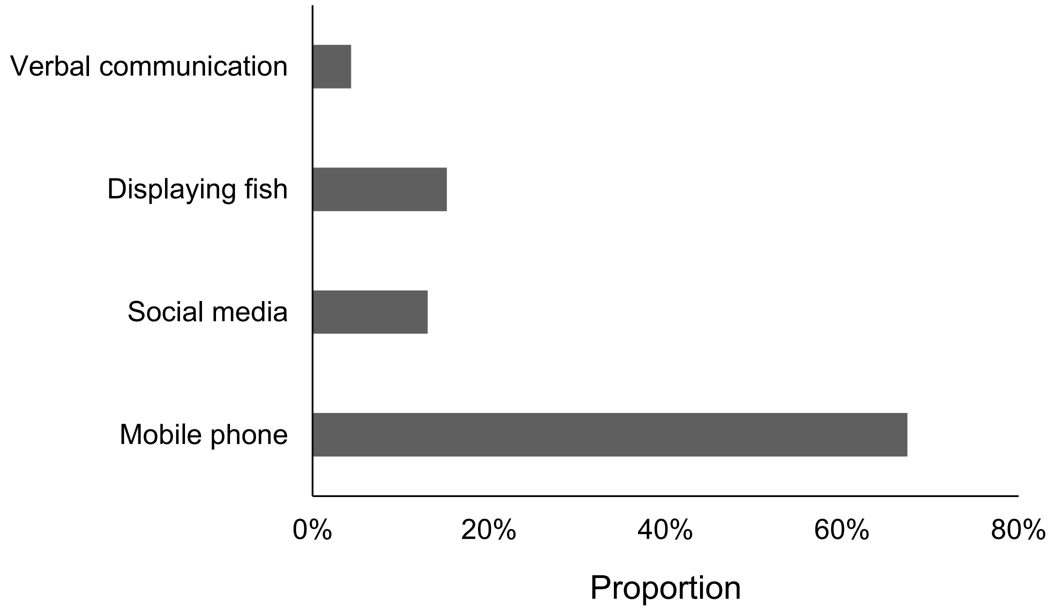


Figure 5.5. The proportion of respondents on the mode of communication being used by traders at the selected landing sites when selling skipjack and kawakawa.

Price determination for tuna at the fisher level occurs through negotiation, primarily with agents/investors. When asked about price setting, 44% of respondents indicated that agents dictate prices, while 11% stated that fishers set the prices. However, the most prevalent response (39%) suggested that prices are negotiated between fishers and agents. Traders employed a variety of transportation methods to reach markets which varied by distance (10-50km) (Figure 5.6). Motorbikes and three-wheeled motor vehicles (commonly known as "tuktuks") were the most popular choices, used by 40% of traders. Public transportation options like buses/matatus were used by 31% of traders. A smaller proportion of traders relied on bicycles (6%) or wheelbarrows (5%) for transport. Interestingly, 11% of traders did not require transportation because they sold fish directly at the landing sites (Figure 5.6).

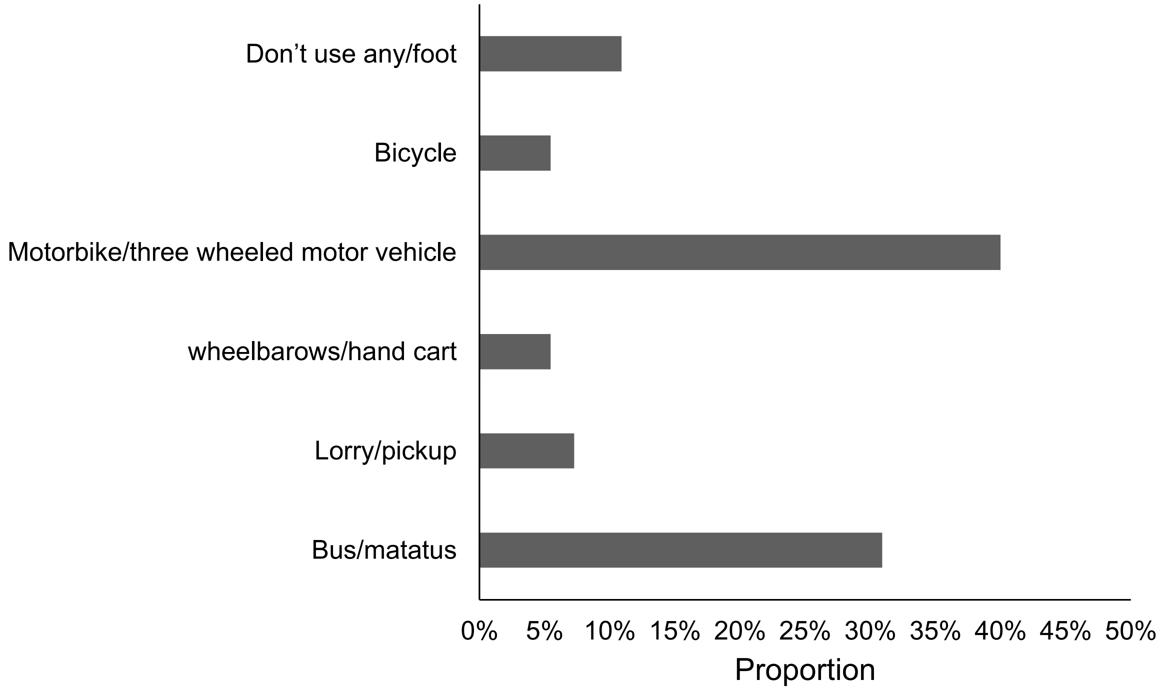


Figure 5.6. The proportion of respondents on the mode of transportation being used by traders at the selected landing sites when selling skipjack and kawakawa.

5.3.4 Flow of tuna and value addition

Skipjack and kawakawa caught by artisanal fishers are entirely consumed by the domestic market. The majority (53%) of their catch is sold to agents/investors, followed by traders (20%) and processors (18%). Approximately 9% of the catch is unaccounted for within the value chain, potentially due to direct consumption or post-harvest losses (Figure 5.7). The value chain is relatively simple (Figure 5.7) with four primary supply chain nodes:

1. Fishers-agents/investors-traders-consumers
2. Fishers-agents/investors-processors-consumers
3. Fishers-traders-consumers
4. Fishers-processors-consumers

Price variation along the value chain were primarily driven by the level of value addition at each node. Fishers, traders, and agents/investors generally offered minimal value addition beyond basic cleaning and occasional preservation. Processors, conversely, significantly increased product value by transforming tuna into ready-to-eat products through gutting, bleeding, and cleaning, and finally cooking by deep frying method. These varying value-added activities resulted in differing operational cost expenditures for processors and traders (Table 5.7). For traders, transportation cost emerged as the leading operational expenditure (30.2%), followed by wages (24.4%), ice for preservation (17.6%), electricity for preservation (9.6%), and packaging (6.9%). In contrast, processors primarily incurred running costs to machinery/ingredients (utensils, fuel, cooking oil, water, spices) at 61.8%, with the remaining expenditure directed towards transportation (24.2%) and packaging (6.6%).

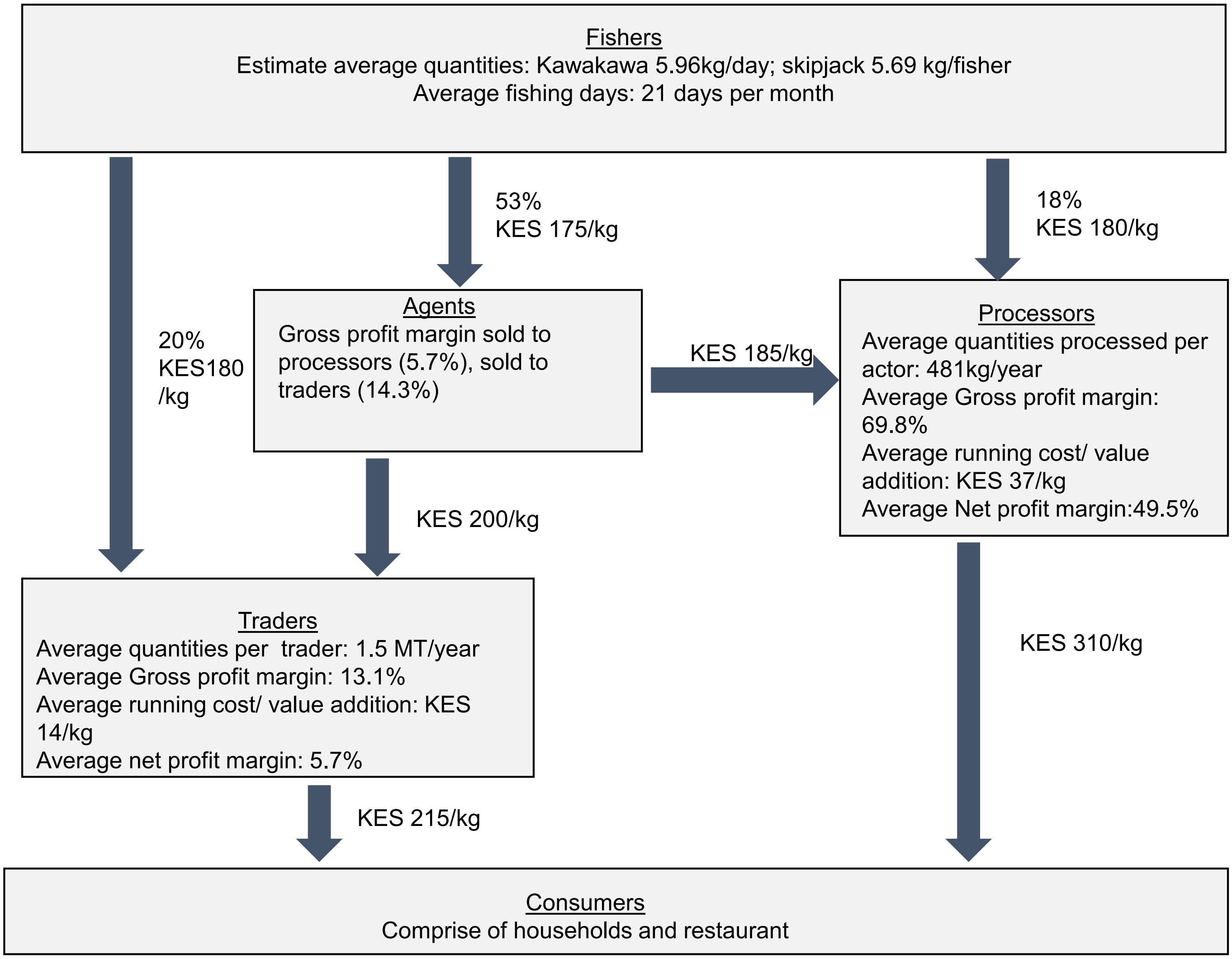


Figure 5.7. The flow of products and value chain of skipjack and kawakawa artisanal tuna fishery in Kenya.

Table 5.7. Types of expenses and average running costs incurred by traders and processors in the artisanal tuna value chain based on the questionnaire surveys conducted in selected sites along the Kenya coast (1 KES = USD 0.009).

Expenses	**Wholesale traders**		**Processors**	
	Cost (KES) per 1 tonne	(%)	Cost (KES) per 1 tonne	(%)
Wages/Salaries	3,420	24.4%	470	1.3%
Fish transportation	4,225	30.2%	8,970	24.2%
Ice	2,470	17.6%	185	0.5%
Electricity	1,340	9.6%	1360	3.7%
Packaging	960	6.9%	2420	6.6%
Marketing	555	4.0%	-	-
Rent	460	3.3%	690	1.9%
Distribution	355	2.5%	-	-
Machinery/ingredients	125	0.9%	22,810	61.8%
Storage	53	0.4%	-	-
Miscellaneous	20	0.2%	-	-
Total	**13,975**	**100**	**36,900**	**100**

5.3.5 *Market performance*

The market value of skipjack and kawakawa is classified as similar by all the value chain actors. Thus, they are typically priced similarly throughout the value chain, although price variation occurs among the value chain nodes. Despite having comparable selling prices by the fishers, kawakawa yielded a slightly higher average daily value per fisher compared to skipjack (KES 1,073 ±122.89 kg/fisher/day vs. KES 1,023.53 ± 160.78 kg/fisher/day), all sites and gears combined; 1KES=USD 0.009) (Table 5.5 and 5.6)). Gillnet fishers in Kilifi Central had the highest average daily value per fisher for skipjack, reaching KES 1,909.8/kg/fisher/day (Table 5.6). Conversely, ring net fishers in Vanga had the highest average daily value per fisher for kawakawa at KES 3,404.57/kg/fisher/day (Table 5.5). These variations potentially reflect site-specific factors influencing catch rates and fishing efficiency for each species.

This study reveals the potential influence of gender and age on selling and buying prices respectively of processors in the value chain (Table S5.2). Agents/investors consistently offered the lowest buying price to fishers for both skipjack and kawakawa (KES 175/kg), while processors and traders paid a slightly higher average price (KES 180/kg) (Figure 5.7). However, agents/investors achieved lower gross profit margins compared to wholesalers and processors**.** An agent/investor's gross profit margin depends on the given supply chain channel. They achieved a higher gross profit (KES 25/kg) when selling to traders compared to processors (KES 10/kg). Processors, in contrast, consistently achieved higher gross profit than traders (KES 125-130/kg vs. KES 15/kg) due to the value addition through processing. Traders' gross profit margins also varied based on their purchase source, reaching 7.5% and 19.4% when buying from agents/investors and fishers, respectively. Conversely, processors made a gross profit margin of 72.2% and 67.6% when buying from fishers and agents/investors respectively. Net profit margins, considering all operational costs, followed similar trends. Processors displayed significantly higher net profit margins (49.9%) compared to traders (5.7%) when buying from fishers and selling directly to consumers.

F-test revealed a significant difference in operational costs incurred by traders and processors ($F = 0.725$, $p = 0.0001$) (Table 5.5). On average, traders' running costs amounted to KES 13.98/kg (rounded to KES 14), while processors' costs averaged KES 36.90/kg (rounded to KES 37; 1KES=USD 0.009). This translates to processors incurring approximately 2.6 times higher running costs compared to traders (Table 5.7).

5.4 Discussion

Previous studies have identified challenges within the tuna value chain, including unfair profit distribution across actors, limited diversification of value-added products, neglect of product quality control, and restricted access to export and better domestic markets (Nguyen and Jolly 2018, Sistani et al. 2021). This study corroborates these findings, highlighting the economic and social disproportions and challenges experienced by various actors in the value chain. Our analysis identified four key actors in the value chain (fishers, agents/investors, traders, and processors) each facing varying benefits and challenges. Fishers are at the heart of the value chain, harvesting, landing and availing it to the next segment, however, they are the least empowered as also reported by Purcell et al. (2017) and Coronado et al. (2020). Understanding the dynamics of their fishing techniques and interaction with other actors across all nodes is crucial as these factors influence economic gains.

This study suggests that socio-demographic characteristics, such as education levels, age, gender, and experience, may influence the marketing and economic performance of actors within the value chain. Fishers displayed high levels of experience in fishing, having more than ten years in the industry. Fishing experience is likely acquired through practice and progressive learning. However, their formal education level was generally low, reflecting a common trend in developing countries (Jimenez et al. 2020, Kimani et al. 2020a, Salas et al. 2011). This may be attributed partly to children frequently accompanying their parents for fishing activities, potentially leading to dropouts from school (Lem 2004). Limited formal education can hinder fishers' access to crucial information, including financial opportunities, economic diversification strategies, and market trends (Jimenez et al. 2020, Wamukota et al. 2014, Garcia Rodrigues and Villasante 2016). This, in turn, weakens their bargaining power within the value chain. Additionally, it can limit their ability to readily adopt new technical advancements and innovative methods for fishing and handling practices (Kimani et al. 2020a). In contrast, agents/investors and traders within the value chain exhibited higher levels of education compared to fishers and processors. This potentially translates to easier access to financing and market information for these actors.

The findings of this study align with other studies which report fish processors are predominantly female (over 90%) (Kimani et al. 2020b and Matsue et al. 2014). They also exhibit low levels of education and experience in the value chain and are the youngest. The high proportion of female processors highlights the importance of women as key stakeholders within the skipjack and kawakawa value chain. Their role potentially provides a linkage between the tuna fishery and low-income consumers (Matsue et al. 2014). The study identified a gender influence on processors' buying prices, although the direction of this influence (advantageous or disadvantageous) remains unclear and warrants further investigation. Interestingly, processors primarily relied on deep-frying as a processing method, mirroring their household cooking practices. This suggests a minimal requirement for professional training, allowing them to gain experience and potentially transition into traders or agents/investors in the future.

Efficient value chain management relies heavily on effective coordination of personnel and resources. This study observed a high proportion of value chain actors as members of BMUs. Membership in a BMU implies direct or indirect participation of these actors in tuna resource management. However, previous research (Tubman et al. 2021, Obiero et al. 2015, Kanyange et al. 2014) highlights the limitations of BMUs in Kenya, including weaknesses in governance, susceptibility to corruption, inadequate funding and equipment, and a lack of necessary knowledge among members to effectively carry out their duties. Ineffective tuna resource management can lead to overfishing and declining catches, ultimately impacting the entire value chain through reduced tuna supply. This scenario poses a significant threat to coastal communities, as many interviewed value chain actors rely heavily on tuna for both income and food as protein sources. The high level of fish consumption within these households was very high. Our findings indicate that most households consume over 20 kg of fish per month, exceeding the recommended global annual individual fish consumption of 20.4 kg per capita (FAO 2022), even for large households with more than 20 people.

The availability of skipjack and kawakawa was demonstrably attributable to selectivity of gear types, seasonality in the abundance of the species and accessibility to fishing grounds. The seasonal variation in the landed volumes of the species therefore resulted in fluctuation of consumer prices. Ring nets, which are unselective, emerged as the most efficient and hence dominant gear used to catch kawakawa in Vanga. On the other hand, skipjack were primarily caught using gillnets and trolling lines. Gear selection is complex as it can be influenced by a multitude of geographical, financial, and sociocultural factors like landing site preference, financial resource availability, social networks, and fisher age (Salas and Gaertner 2004, Omukoto et al. 2018, Tuda et al. 2023).

Market structures and consumer preference for specific species by consumers also influenced the diversity and proportions of fish landed (Salas et al. 2004). This was evident in Watamu where fishers employed trolling lines, known for their selectivity (Eighani et al. 2019) and emerged with the least catch per vessel of skipjack and kawakawa compared to other tuna species. Fishers in Watamu may strategically prioritize targeting other, potentially more valuable, tuna species such as yellowfin tuna, besides skipjack and kawakawa using trolling lines**.** Ring nets in Vanga landed the highest volumes of kawakawa; however, crew size also impacted individual share of the catch, resulting in lower catch per fisher compared to gillnet and handline fishers in Gazi as also noted by Okemwa et al. (2023).

Importantly, catch rates for both skipjack and kawakawa varied between the two seasons, causing inconsistent availability of products within the value chain. The seasonality of skipjack and kawakawa limits the constant and regular supply of products to consumers. As a result, tuna actors are forced to engage with other species during low season. Lack of consistent availability of food is a fundamental driver of failure to achieve food security (Crush and Frayne 2011) which has an impact on the income level of all actors in the value chain. However, due to demand and supply, skipjack and kawakawa caught during the high season fetch lower prices than those caught during the low season (Martinez-Garmendia et al. 2005, Sun et al. 2017). Seasonal fluctuations in tuna supply also affect market destinations, since catches during low season are sold near the landing sites, whilst during peak season they may reach far domestic markets (Huang and Leung 2011).

Unlike tuna value chains in Vietnam, Iran, the United States, and the European Union, which involve exports of raw fish or finished products (Sistani et al. 2021, Nguyen and Jolly 2018, Havice and Campling 2017)**,** the skipjack and kawakawa value chain in Kenya operates entirely within the domestic market. Agents/investors play a crucial role in driving Kenya's tuna value chain by providing financial support for fishing activities and product marketing, both within and outside towns. The chain is characterized by a large number of fishers, an undetermined number of intermediaries (middlemen), and a diverse consumer base, contributing to the generation of economic benefits for many coastal communities.

The identified distribution channels supplying skipjack and kawakawa provide socio-economic benefits to the local communities. The main supply channel (accounting for 53% of product distribution) involves agents/investors acting as intermediaries supplying to traders and processors before reaching the consumers. Agents/investors provide financial assistance and inputs to fishers before fishing trips, with fish catches used to settle debts. While this arrangement offers timely financial support for fishers, it can be disadvantageous as they receive lower prices compared to selling to other actors. This practice may also incentivize overfishing as fishers strive to meet their financial obligations (Walters and Ahrens 2009, Srinivasan et al. 2010). Another channel distributing 20% of products involves direct sales from fishers to traders before reaching final consumers (Figure 5.7). This approach benefits fishers by offering higher selling prices compared to transactions with agents/investors. The final channel (18% of product distribution) utilizes processors to deliver products to consumers (Figure 5.7). Processors typically portion tuna into smaller pieces making it affordable to purchase, enabling accessibility and availability of tuna products to low-income consumers. The absence of intermediaries in this channel benefits both fishers and processors through potentially higher profits compared to other channels. These four channels altogether account for approximately 91% of the skipjack and kawakawa entering the domestic market. The remaining 9% is either consumed directly by fishers and the communities or is lost due to poor post-harvest handling practices (Hasini et al. 2020). The direct sales to consumers streamline the supply chain, potentially resulting in a reduction in consumer prices while enhancing access to fish protein among low-income households.

Previous research studies have suggested a positive correlation between value addition and profitability within a value chain (Saediman et al. 2015, Nguyen and Jolly 2018). Net profit margins reflect market performance and are influenced by the interplay of costs and returns (Nguyen and Jolly 2018). Our analysis confirms this trend. Processors, who add the most value through processing activities, incur higher costs compared to other actors. Consequently, they also achieve the highest net profit margins, aligning with observations by Rosales et al. (2017), Thu et al. (2020) and Kamaylo et al. (2021).

Fishers involved in the skipjack and kawakawa value chain benefited the least, as was evident from the low average daily catch per fisher, translating to lower incomes compared to traders and processors who handle larger volumes and enjoy higher net profit margins (Figure 5.7). This echoes observations from prior research on value chains, where intermediaries like processors often capture a larger share of profits than fishers, as exemplified by the skipjack tuna value chain in Vietnam (Thu et al. 2020) and sea cucumber value chain in Fiji and Kiribati (Purcell et al. 2017). However, small-scale processors are price takers (Fröcklin et al. 2013, Matsue et al. 2014), suggesting limited profit margins. This study was however unable to estimate net profit margins for agents/investors due to limitations in data on capital costs. Nonetheless, some existing literature suggests a positive correlation between capital investment and profitability within a value chain

(Matsue et al. 2014, Kimani et al. 2020a). Actors with greater access to capital tend to handle larger fish volumes and generate higher sales, leading to potentially higher financial gains compared to fishers and processors. It's important to acknowledge that economic benefits within a value chain extend beyond income and profits. Non-market values, such as food security, also play a significant role.

The skipjack and kawakawa value chain demonstrably contributes to global food security by providing a source of animal protein and essential micronutrients. Food security is a multifaceted concept encompassing four key pillars: availability, access, utilization, and stability (Barrett 2010, Coates 2013). The availability of sufficient quantities of high-quality fish within the domestic market is a critical factor when evaluating a value chain's contribution to local food security (Jennings et al. 2016). Skipjack and kawakawa were readily available at affordable prices to the local communities. This is evident from the average fisher selling price of approximately KES 180/kg (1KES= USD 0.009) for skipjack and kawakawa, compared to other tuna and tuna-like species like yellowfin and kingfish, which typically cost over KES 220/kg (GOK, 2022). Furthermore, processors, predominantly women, play a significant role in enhancing food security by offering affordable, ready-to-eat tuna products to the low-income households.

Similar to tuna value chains in other regions (Duggan and Kochen 2016, Jimenez et al. 2020, Sistani et al. 2021) the skipjack and kawakawa value chain in Kenya faces significant infrastructural challenges. These challenges hinder both domestic market performance and potential export opportunities. A key constraint across all nodes of the value chain is the lack of appropriate storage facilities and proper transportation mechanisms. Inadequate cold storage, particularly at the fisher level (the first point of handling), leads to rapid product deterioration and increases the risk of scombroid poisoning for consumers (Mercogliano and Santonicola 2019). This, in turn, undermines domestic market value with lower pricing and restricts access to export markets. Furthermore, inadequate packaging and transportation facilities inhibits the smooth flow of products and limit market performance. Skipjack and kawakawa are often transported on motorbikes in baskets or occasionally cooler boxes, with only a few traders utilizing refrigerated trucks.

Processed products (cooked tuna) are typically sold in rudimentary wooden boxes along roadsides. Overall, poor hygiene and sanitation practices throughout the handling and selling stages further degrade the quality of products within the value chain. Despite these infrastructural limitations observed, mobile phones were identified as a positive communication tool for reaching out to consumers. However, fair trade practices within the value chain are sometimes compromised by specific relationships and conduct among actors. Fishers' dependence on agents for access to capital, infrastructure, and essential fishing inputs creates an unequal power dynamic (Bailey et al. 2016, Jimenez et al. 2020).

In light of the identified challenges, this study proposes several recommendations to enhance sustainable management within the skipjack and kawakawa value chain. Sustainable management, as described by Salas et al. (2011), requires a holistic approach that ensures the well-being of resources, communities, and economies. To maintain healthy resources, continued monitoring efforts are crucial to prevent overexploitation. Socio-economic benefits can be enhanced by empowering value chain actors, particularly fishers who currently benefited the least through the following potential strategies: Collective purchasing by ensuring fishers collaborate to buy essential inputs (e.g., fuel, ice) in bulk at wholesale prices, reducing costs. (ii) Hygiene and sanitation improvements through frequent training programs and financial support directed towards improving hygiene and sanitation practices throughout the handling, storage, and transportation stages. This will enhance product quality and potentially command higher domestic market prices, while also opening doors to export opportunities. (iii) Transparent market access by establishing a tuna auction centre to provide fishers with public and readily accessible market information. This empowers fishers in negotiations and strengthens linkages with other actors in the value chain. (iv) Financial diversification by encouraging fishers to access various financial resources, such as savings plans, credit facilities, and microfinance schemes, which could alleviate their dependence on agents/investors and provide greater financial flexibility. (v) Improved processing methods by enhancing investment in safe and efficient processing techniques so as to minimize post-harvest losses and nutrient degradation, ultimately enhancing product quality and value.

5.5 Conclusion

This study presents the first in-depth analysis of the value chain for skipjack and kawakawa by Kenya's artisanal tuna fishery. Our findings demonstrate significant socio-economic benefits of this value chain, for instance, providing a critical source of food and income for coastal communities. This study also highlights the crucial role women play in the tuna value chain. However, the value chain faces challenges that limit profit maximization. We recommend several strategies to address these limitations, including infrastructure improvement, enhancing marketing strategies, training on new technologies and revision of policies for upscaling. Further research is recommended on estimates of the cost of tuna fishing, market dynamics, traceability of products from fishers to final consumers, quantifying postharvest losses and intervention on minimization of product spoilage and nutrient loss and value addition technologies for maximization of economic benefits.

Sustainable resource management is paramount to the long-term viability of this value chain and this could be achieved by empowering BMUs to strengthen management of people and resources. For instance, empowering BMUs in strengthening accurate reporting within the value chain and compliance enforcement with the established fisheries regulation. These actions can strengthen fisheries governance, secure robust financial returns for stakeholders, and ensure the health of the marine environment.

CHAPTER SIX

GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

Overview of the chapter

The analytical framework of this study demonstrates and affirms the importance of coastal tunas to the local coastal community in the WIO and the necessity for the management and conservation of a healthy stock. This study aimed to advance knowledge and information on the exploitation, biology, genetic connectivity and value chain of skipjack and kawakawa in the WIO. This chapter first considers highlighting the findings and how they relate to one another as identified in chapters 3 to 5 in section 6.1. Drawing from these discussions, section 6.2 outlines the thesis's contribution to the field of science. This chapter concludes by describing the limitations of the study and directions for future research in section 6.3.

6.1 Discussion of Findings

This study aimed to advance the sustainable management of coastal tuna fisheries in the WIO by investigating skipjack and kawakawa genetic connectivity, population and size structure and reproductive characteristics. Additionally, a case-study approach assessed the value chain and economic benefits of the artisanal tuna fishery targeting skipjack and kawakawa in Kenya. By integrating several research methods, such as genomic techniques, catch assessments, biological sampling and interviews, this research offers novel insights into these species. This chapter, synthesizes key findings drawn from chapters three to five, linking them to inform sustainable harvesting and exploitation of skipjack and kawakawa in the WIO.

Information on the population structure of skipjack and kawakawa examined by genomic techniques revealed low but significant genetic differentiation of skipjack between sites, indicating the presence of two distinct genetic groups in the WIO: one encompassing northern Tanzania, Kenya, and Sri Lanka, and another comprising southern Tanzania, Mozambique, South Africa, and Seychelles. The Mtwara region in southern Tanzania may represent a biogeographic breakpoint, with divergent current systems potentially acting as a barrier to the dispersal of early life stages or migration of adult skipjack. Kawakawa exhibited a patchy distribution of significant genetic differentiation across WIO sites, suggesting the presence of genetically distinct stocks. These stocks might be spatially segregated or overlap spatially and temporally in different regions or at varying times of the year. The occurrence of spatial and temporal (seasonal) genetic variation in kawakawa could be attributed to their migratory behaviour between distinct feeding and spawning grounds.

Sustainable harvesting of skipjack and kawakawa in WIO necessitates understanding their biology and size distribution. This study, therefore, examined reproductive characteristics and catch sizes for these species across the WIO. Results indicated significant seasonal variation in catch sizes, with smaller fish prevalent during the SEM and larger fish during the NEM season, potentially contributing to observed temporal genetic divergence. Additionally, gear type influenced the catch size of the two species, suggesting that ocean and environmental dynamics affect gear efficiency and size selectivity for tuna (Wright et al. 2021).

Skipjack and kawakawa are highly migratory species caught by coastal nations within their range. While the socio-economic importance of these species in the WIO region remains largely undocumented, they have significantly benefited artisanal fishers. This study explored the value chain and economic benefits of skipjack and kawakawa in the WIO, using Kenya as a case study. Results indicate that the artisanal tuna fishery provides substantial socio-economic benefits to the Kenyan coastal community through food security and income generation. Fishers serve as primary actors in the tuna value chain, harvesting and distributing tuna to subsequent value chain nodes. Processors, predominantly women, play a crucial role in the tuna value chain and also achieve the highest net profit margins among the value chain actors.

As detailed in Chapter four, skipjack and kawakawa catches exhibited seasonality, prompting fishers to target alternative species during periods of low abundance. Despite substantial catches during peak seasons, the absence of suitable cold storage facilities hindered tuna preservation. Kenya's value chain was impacted by substandard infrastructure, evidenced by inadequate storage, packaging, and transportation, leading to degraded tuna quality (Mercogliano and Santonicola 2019). Consequently, weak domestic markets offered low prices, hindering product flow and limiting export opportunities.

This study has advanced our understanding of skipjack and kawakawa genetic structure, size distribution, and population dynamics (including L50), providing valuable insights for assessing stock status in the WIO. The study also offers information essential for evaluating the species' responses to environmental changes and the socioeconomic implications of sustainable harvesting. Given the transboundary nature of these species, both national and international preventive measures are necessary to combat overfishing. To maximize benefits from the artisanal tuna fishery across the entire value chain, multi-level interventions addressing economic, environmental, and social dimensions are required.

6.2 Contribution of the thesis to literature and management

This thesis has contributed new scientific knowledge on genetics, biology and value-chain of skipjack and kawakawa in the WIO region. As seen in chapters three to five, three manuscripts have been prepared and submitted to journals for publication. Chapter three explores the genetic structure of skipjack and kawakawa, revealing distinct populations and subpopulations within the WIO. This study updated the literature on genetic information previously collected using early genetic methods such as mitochondrial DNA and microsatellites in WIO, highlighting the utility of next-generation sequencing for uncovering genetic differentiation where neutral markers were ineffective. The fourth chapter presents a comprehensive analysis of skipjack and kawakawa reproductive biology, including temporal variations in size structure and reproductive features, as well as the impact of different gear types on catch size composition. This chapter also provides new insights into the size at maturity (L50) for both species estimated from a larger geographical area. Chapter five offers the first in-depth examination of the market structure, value chain, and economic benefits of Kenya's artisanal tuna fishery. This chapter provides baseline information on the primary actors within Kenya's artisanal tuna fishery and the socio-economic benefits at each node of the value chain. It also identifies obstacles hindering the sector's performance and offers suggestions for maximizing value.

Chapter three of this thesis outlines the optimization and development of genetic techniques (tGBS genome-wide genotyping) for skipjack and kawakawa in the WIO. The established methodology can be applied by researchers and students to explore other sample sets within the region. The protocol also supports routine genetic diversity monitoring by local laboratories, facilitating stock identification and fish product traceability.

The findings of this thesis provide an important contribution to the management of tuna resources in the IO. Current management practices assume a single, panmictic stock for tuna and tuna-like species within the region. However, this study suggests the presence of multiple skipjack and kawakawa stocks, necessitating a more stringent management approach. The identified variations in size structure, reproductive characteristics, and catch patterns by season and gear type highlight the need for multinational management plans, including gear regulations. To maximise the economic benefits of the artisanal tuna fishery, this research advocates for policy revisions, infrastructure improvements, enhanced marketing strategies, and training in new harvesting and post-harvest technologies.

6.3 Limitations and direction for future research

The importance of integrating several methodologies to answer a research question is demonstrated in this thesis by how well the results of the various methods complement each other. Nevertheless, the study faced limitations due to the sample size, sampling frequency, and spatial coverage all affecting the quality of the outcomes. Genetic sample collection lacked comprehensive sampling of fish of all sizes simultaneously and year-round, resulting in a lack of spatial and temporal coverage. Reproductive biology sampling inconsistencies across sites limited cross-country site comparison for spatial analysis. In addition, COVID-19 restrictions disrupted data collection in certain months resulting in the maturity data gaps for annual scrutiny. The economic and value chain analysis was constrained by a focus on the Kenyan case study, limiting its regional scope.

Due to the above limitations, this thesis recommends further research on the genetic population structure of skipjack and kawakawa in the WIO. A more intricate sampling plan is recommended, considering various locations and time points necessary to account for spawning seasons and spatial stock dynamics. For reproductive studies, a standardized protocol should be implemented to ensure data consistency across different sites. Combining histological techniques with environmental parameters will provide a more comprehensive understanding of skipjack and kawakawa spawning and reproductive characteristics. To gain a broader perspective on the value chain of skipjack and kawakawa, a comprehensive study encompassing multiple WIO countries is recommended. This study should analyze the costs and returns incurred by fishers, tracing the quantity and quality of products from primary producers (fishers) to final consumers. To optimize benefits, thorough investigations into post-harvest losses and innovative value-added technologies are essential.

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Supplementary Figures

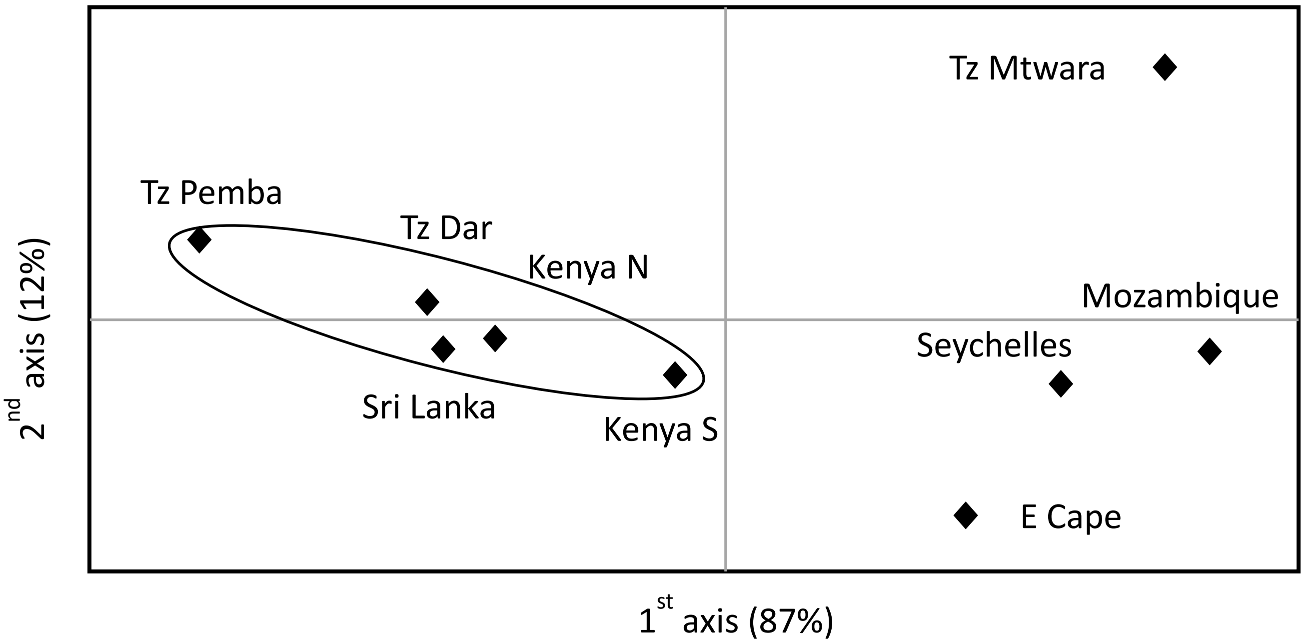

Figure S3.1. PCoA analysis, with percentage of total dataset variation represented by 1st and 2nd axes, of genetic similarity among skipjack tuna samples, based on genetic differentiation (FST) estimated from 87 outlier SNP loci.

Supplementary Tables

Table S3.1. Measures of genetic variation estimated from RADseq genomic screens of nine samples of skipjack tuna from the SW Indian Ocean: N_{poly} = number of polymorphic SNP loci; H_O = observed heterozygosity; H_E = expected heterozygosity; F_{SI} = inbreeding coefficient; Number in bold shows significant differences.

	N_{poly}	H_O	H_E	F_{IS}
South Africa (E. Cape)	6331	0.201	0.224	0.107
Mozambique (Pemba)	6813	0.183	0.208	**0.127**
Tanzania (Mtwara)	5986	0.228	0.255	0.106
Tanzania (Dar es Salaam)	6314	0.217	0.245	0.114
Tanzania (Pemba)	5295	0.232	0.275	**0.167**
Kenya (S)	6503	0.198	0.226	**0.127**
Kenya (N)	6699	0.192	0.216	0.114
Seychelles	6717	0.215	0.231	0.067
Sri Lanka	6399	0.196	0.224	**0.126**

Table S3.2. Measures of genetic variation estimated from RADseq genomic screens of six samples of kawakawa from the SW Indian Ocean: N_{poly} = number of polymorphic SNP loci; H_O = observed heterozygosity; H_E = expected heterozygosity; F_{SI} = inbreeding coefficient.

	N_{poly}	H_O	H_E	F_{IS}
Mozambique (Pemba Dec)	16299	0.244	0.260	0.062
Mozambique (Pemba Mar)	16101	0.241	0.260	0.076
Tanzania (Tanga)	15763	0.253	0.245	0.044
Tanzania (Mtwara)	12938	0.307	0.292	-0.071
Kenya	15663	0.242	0.261	0.075
Seychelles	15017	0.264	0.275	0.041

Table S4.1. Maturity stage classification for visual examination of gonads for large pelagic species.

Stages	**Criteria**	
	Male	**Female**
1	Gonads small ribbon-like, not possible to determine sex by gross examination	Gonads small ribbon-like, not possible to determine sex by gross examination
II	Testes extremely thin, flattened and ribbon-like, but sex determinable by gross examination	Two distinct, transparent visible opaque, orange lobes with well-developed blood vessels.
III	Enlarged testes, triangular in cross section, no milt in central canal	Early maturing; gonads enlarged but individual ova not visible to the naked eye
IV	Maturing; milt flows freely if testes pinched or pressed	Late maturing; gonads enlarged, individual ova visible to the naked eye
V	Ripe; testes large, milt flows freely from testes	Ripe; ovary greatly enlarged, ova translucent, easily dislodged from follicles or loose in lumen of ovary
VI	Spent; testes flabby, bloodshot, surface dull red, little or no milt in central canal	Spawned; includes recently spawned and post-spawning fish, mature ova remnants in various stages of resorption, and mature ova remnants about 1.0mm in diameter

Table S4.2. Description of types of gears commonly used in WIO.

Gear type	Description
Handline	A line made of a single monofilament nylon with steel hooks for attaching bait
Rod and line	A single or more lines made of monofilament nylons with steel double or triple hooks for attaching live bait or artificial baits that is towed through surface waters.
Gillnet	Meshed nets are made of multifilament nylon made of varying thicknesses and mesh sizes. They are suspended by floats at the head rope and held vertically by anchors at the foot rope, they are either drifting or set gillnet
Monofilament	Meshed nets made of monofilament nylon with small floats at the top and small weights at the bottom of the net
Ring net	A multi-filament nylon mesh net suspended with floats at the top and weighted at the bottom, it has a foot rope threaded through metal rings at the bottom which is used to close the net.
Seine net	A multi-filament nylon net with preferably a small mesh size. The net has a float line and a weighted foot rope. The net consists of a conical netting body, two wings, and a bag, there are mainly two types “beach seine” are deployed at the beach and “reefseine” are deployed offshore
Trolling	Same as rod and line, but specifically for fishing done from a moving boat.
Pole and line	Consists of a hooked line attached to a pole, maybe hand-operated or mechanized, with the pole movement being entirely automatic.

Table S4.3. Monthly variations in sex ratios of skipjack and kawakawa across the WIO during the 2019–2022 survey period; Nd = not done; highlighted values were significant different (binomial test, $p < 0.05$).

	Skipjack			**Kawakawa**		
Months	**F**	**M**	**Ration (F-based)**	**F**	**M**	**Ratio (F-based)**
Jan	37	35	0.51	113	109	0.51
Feb	31	24	0.56	73	60	0.55
Mar	50	70	0.42	41	40	0.51
Apr	5	19	0.21	26	21	0.55
May	8	15	0.35	60	87	0.41
Jun	0	5	Nd	1	27	0.36
Jul	-	-	-	73	58	0.56
Aug	11	7	0.61	27	56	0.35
Sep	2	0	Nd	13	7	0.65
Oct	6	7	0.46	42	43	0.49
Nov	0	2	Nd	44	45	0.49
Dec	40	74	0.35	58	103	0.36
All months	**190**	**258**	**0.42**	**571**	**656**	**0.47**

Table S4.4. Sex ratio of skipjack and kawakawa in fork length (FL) interval (5 cm) from sampling sites in WIO; Nd means not done; highlighted values are statistically significantly different (binomial test, $p < 0.05$).

Size class	Skipjack			Kawakawa		
	F	M	F ratio	F	M	F ratio
15-19.9	0	1	Nd	0	0	Nd
20-24.9	1	0	1	2	3	0.4
25-29.9	7	5	0.58	16	54	0.23
30-34.9	2	1	0.6	19	72	0.21
35-39.9	3	3	0.5	22	66	0.25
40-44.9	15	24	0.38	23	19	0.54
45-49.9	26	29	0.47	35	36	0.5
50-54.9	37	64	0.37	38	29	0.57
55-59.9	42	73	0.37	84	66	0.56
60-64.9	39	30	0.57	160	119	0.57
65-69.9	10	8	0.56	86	91	0.49
70-74.9	1	3	0.25	23	39	0.37
75-79.9	1	2	0.33	4	9	0.31
80-84.9	0	0	Nd	1	2	0.33
85-89.9	0	1	Nd	0	0	Nd

Table S5.1. Chi-square test result of the socio-demographic characteristics of the value chain actors.

Socio-demographic characteristics	**Actors**	**chi-squared**	**p-value**
Gender	Fishers	-	-
	Traders	49	0.00001
	Agents/Investors	60.84	0.00001
	Processors	81	0.00001
Age	Fishers	59.2	0.00001
	Traders	47.1	0.00001
	Agents/Investors	21.2	0.00029
	Processors	21.84	0.00001
Education status	Fishers	30.86	0.00001
	Traders	26.06	0.00001
	Agents/Investors	39.02	0.00001
	Processors	81.2	0.00001
Working experience	Fishers	-	-
	Traders	3.24	0.7186
	Agents/Investors	3.24	0.7186
	Processors	2.56	0.1096
BMU membership	Fishers	9	0.002
	Traders	88.36	0.00001
	Agents/Investors	1.44	0.2301
	Processors	51.84	6.021
Fish consumption	Fishers	199.9	0.00001
	Traders	114.16	0.00001
	Agents/Investors	60.84	0.00001
	Processors	37.9	1.175
Alternative source of income	Fishers	3.24	0.07186
	Traders	3.24	0.7186
	Agents/Investors	0.16	0.6892
	Processors	17.64	0.00001

Table S5.2. The p-values of multiple linear regression analysis results of some socio-demographic characteristics of value chain actors against handling, selling price and buying prices (Highlighted text shows significant difference).

	Age	**Experience**	**Education**	**Gender**	**Income**	**BMU**	**Consumption**
Correlation between handling of fish and demographic characteristics							
Fishers	0.2592	0.8537	0.1739		0.3605	0.046	0.4288
Traders	0.425	0.489	0.685	0.633	0.588	0.877	0.184
Processors	0.636	0.816	0.895	0.703	0.216	0.517	0.121
Correlation between selling price of fish and demographic characteristics							
Fishers	0.8538	0.4155	0.5952		0.5475	0.01	0.6484
Traders	0.0479	0.1488	0.6373	0.0613	0.4257	0.8473	0.1348
Processors	0.525	0.08689	0.0934	0.0975	0.6989	0.2154	0.22076
Correlation between buying price and demographic characteristics							
Traders	0.798	0.391	0.664	0.15	0.361	0.672	0.639
Processors	0.6566	0.0742	0.2527	0.0387	0.4706	0.2279	0.764

Appendix

Skipjack/kawakawa value chain interview script

INFORMED CONSENT

This interview is part of a study that aims to characterize and determine the economic contributions of Kawakawa and Skipjack tuna fisheries in the WIO region, to support management and optimization of societal benefits. Your participation is completely voluntary and your answers will be treated with confidentiality. Information obtained will only be used for this study. This interview lasts approximately 20-30 minutes.

Respondent particulars

○ Country ____

○ Town/County ____

○ Landing Site ____

○ Date (DD/MM/YY) ____

○ Starting Time (24-hr format HH:MM)

____

○ Form # ____

By agreeing to participate in this interview, you acknowledge that are at least 18 years old, and that your participation is completely voluntary and you may refuse to answer any questions and end the interview at any time. **Do you agree to participate in the interview?**

○ Yes No

Do you participate in commercially catching tuna, trading tuna, processing tuna, or investing in any of the previously mentioned activities?

○ Yes No

Which of the following do you participate in?

☐ Fishing commercially? (Complete Fishers Section)

☐ Trading or Wholesaling fish? (Complete Traders Section)

☐ Processing seafood ie. gutting, freezing, portioning, salting etc.? (Complete Processor section)

☐ Investing/Agents in fish activities? (Complete Investor Section)

FISHERS SECTION

1. How many days per week do you usually go fishing in the following seasons? (per site)

○ Non-monsoon ________ Northeast Monsoon _______ Southeast Monsoon ______

2. How much time do you usually spend at sea per trip? _________________

3. Which type of vessel(s) do you fish from? (per site)

☐ I am a foot fisher (skip to Q10) Dugout canoe Fibreglass boat

☐ Mashua Outrigger Other

____

4. If your vessel uses a motor, what is the total horsepower? (per site)

____

5. Which fishing methods do you use? (per site)

Gill net Rod/reel Ring net Hand line
Trolling Seine net Traps Spear/Spear gun
Longline Diving Other __________________________

6. Of the methods you use, please rank the top three from most used to least used.

○ Most used ____

○ Second most used ____

○ Third most used ____

7. Please rank the following tuna species in terms of how much you catch from most catch to least catch. (NA = do not catch, 1 = most catch, 8 = least catch) (per site)

______ Yellow fin
______ Long tail
______ Big eye
______ Skipjack
______ Kawakawa
______ Frigate
______ Bullet

8. Which are the three tuna species that you most frequently target? (Please list in the order of most targeted to least targeted). (per site)

○ Most targeted ____
○ Second most targeted ____
○ Third most targeted ____

9. Which tuna do you use as bait, and what are you targeting?

	Which tuna species is used as bait?	**Which species are you targeting with this tuna?**	**I do not use tuna as bait**
	Tuna species	Target species	None

Tuna bait 1			○
Tuna bait 2			○
Tuna bait 3			○
Tuna bait 4			○

10. Over the past five years have your revenues from tuna catches been increasing, decreasing, or staying the same?

○ Extremely increasing Slightly increasing

○ Staying the same Slightly decreasing

○ Extremely decreasing

11. Why do you think this is the case?

____

12. What percentage (%) of your total catch is comprised of tuna species?

○ Non-monsoon season ______ Northeast monsoon ________ Southeast monsoon _______

13. What percentage (%) of your total catch is comprised of skipjack or kawakawa? (skip to Q23 if they did not indicate they catch skipjack or kawakawa)

○ Non-monsoon season ____% Northeast monsoon ______% Southeast monsoon ______%

14. Do you put the fish on ice, refrigerate or freeze them immediately after they are caught?

○ Put them on ice Freeze them

○ Put them in a refrigerator None of these

15. In your experience, over the past five years have catches of kawakawa been increasing, decreasing or staying the same?

○ Extremely increasing Slightly increasing Staying the same

○ Slightly decreasing Extremely decreasing

16. In your experience, over the past five years have catches of skipjack been increasing, decreasing or staying the same?

○ Extremely increasing Slightly increasing Staying the same

○ Slightly decreasing Extremely decreasing

17. Which months of the year do you usually encounter skipjack and kawakawa with eggs

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Skipjack	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Kawakawa	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐

18. How do you utilise the eggs? (use for bait, sell, eat, etc.) **** put NA if they do not make use****

____

19. How many crew members do you fish with on average, including yourself? (per site)

____

20. On average, how many people are engaged with onshore activities relating to your fishing activities, including yourself?

____

21. Who finances the operational costs of fishing? (fuel, food, fishing gear, etc)

☐ Shared contribution from fishers Boat owner Traders
☐ Investors BMU member
☐ Other(s) ____

22. Please indicate ownership details of the following items, and their average annual costs to you.

	Please indicate whether you own, rent, borrow, or have any other arrangement for use of the following items					Average annual costs of items (fees, maintenance, loan repayments,rental, licensing etc.)
	Own	Rent	Borrow	Other (detail)	NA	Cost (indicate currency)

Fishing vessel	○	○	○	○	○
Fishing rods and reels	○	○	○	○	○
Fishing nets	○	○	○	○	○
Boat motor	○	○	○	○	○
Cooler boxes	○	○	○	○	○
Storage containers	○	○	○	○	○
Generators	○	○	○	○	○
Refrigerators/freezers	○	○	○	○	○
Insurance	○	○	○	○	○
Boat storage/mooring	○	○	○	○	○
Licensing	○	○	○	○	○
Fish finders/GPS/Safety equipment/Other boating equipment	○	○	○	○	○

23. What do you do with the fish you catch?

☐ Eat them Sell them Give to friends/family

☐ Other ____

24. Who do you sell your catch to?

☐ Households Other fishers Wholesalers/Traders

☐ Processors Retailers Agent/investors

☐ Export markets Other

____

25. Please rank the following people in terms of whom you sell your catch to from most sales to least sales. (1 = most sales, 8 = least sales) (per site)

______ Households
______ Other fishers
______ Wholesalers/Traders
______ Retailers
______ Processors
______ Agents/Investors
______ Export markets
______ Other

26. How are fishers in your crew paid?

☐ By catch profits By fishing trip By share of catch

☐ Other ____

27. When does the crew get paid?

☐ Per trip Per week Per month Per season

☐ Per year Other (specify)

____

28. Who are the catches shared with before they are sold?

☐ They are not shared with anyone (skip next question) Boat owners

☐ Crew members Agents/Investors Traders

☐ Other (indicate) ____

29. How are the catches shared before sale?

☐ % to boat owners ___________________ % to crew members

____

☐ % to Agents/investors _____________ % to Traders _____________

☐ % to Other _____________

30. How much money do you take home on average per fishing trip during the high and low seasons (specify currency)? (per site)

☐ High Season _________________ Low Season

____

31. Which months of the year do you consider as the High and Low seasons?

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
High Season	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Low Season	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐

32. How is the price of your catches set with the buyer(s)?

____

33. Can you please tell us the price range per kg of whole Kawakawa for each buyer type during different seasons?

	High Season Prices			**Low Season**		
	Lowest	Highest	Average	Lowest	Highest	Average

Household consumers						
Other Fishers						
Wholesalers/Traders						
Retail (hotels/ restaurants/ fish shops)						
Processors						
Agents/Investors						
Export Markets						
Other						

34. Can you please tell us the price range per kg of whole Skipjack for each buyer type during different seasons? (If same as Kawakawa, just fill in table below)

		High Season Prices			**Low Season**		
	Same as Kawakawa	Lowest	Highest	Average	Lowest	Highest	Average
Household consumers							
Other Fishers							
Wholesalers/Traders							
Retail (hotels/ restaurants/ fish shops)							
Processors							
Agents/Investors							
Export Markets							
Other							

35. Do you have any difficulty selling your catches?

○ No (skip next question)

○ Sometimes

○ Yes

36. Why do you think you have difficulty selling your catch?

____

37. On average, approximately how many kg of tuna are wasted before or during the selling process for any reason per year?

____

TRADERS/WHOLESALERS

Make it clear that these questions only pertain to fish that they sell in which they did not add any processing.

38. For how many years have you been selling tuna? _______________

39. Approximately how many kgs or tons (specify) of fish do you sell annually?_____________

40. What proportion of the fish you sell annually do tuna species comprise (%)?___________________

41. What proportion of the total fish you sell is from kawakawa and skipjack?

____

42. If you sell kawakawa or skipjack, how much do you prefer selling kawakawa or skipjack over other tuna species?

○ Much more preferred   Slightly more preferred

○ Neither more less preferred   Slightly less preferred   Much less preferred

43. From where do you obtain the tuna you sell and what form are they obtained in?

	select all that apply	Fresh Whole	Whole Frozen	Fresh Gutted/Dressed	Frozen Gutted/Dressed	Fresh Portioned	Frozen Portioned	(
From fish that I caught	☐	☐	☐	☐	☐	☐	☐	
From Fishers	☐	☐	☐	☐	☐	☐	☐	
From Other Traders/Wholesalers	☐	☐	☐	☐	☐	☐	☐	
From Agents/Investors	☐	☐	☐	☐	☐	☐	☐	
From Processors	☐	☐	☐	☐	☐	☐	☐	
Other	☐	☐	☐	☐	☐	☐	☐	

44. Which forms of tuna do you purchase most (1) to least (7)

______ Fresh Whole
______ Frozen Whole
______ Fresh Gutted/Dressed
______ Frozen Gutted/Dressed
______ Fresh Portioned
______ Frozen Portioned
______ Other

45. Can you please tell us the price range you pay per kg for whole Skipjack during different seasons? (skip if they do not buy fish, fill in if its the same as Kawakawa)

	High Season Prices			**Low Season**		
	Lowest	Highest	Average	Lowest	Highest	Average
Fishers						
Wholesalers/Traders						
Processors						
Agents/Investors						
Import Markets						
Other						

46. Can you please tell us the price range you pay per kg from various providers for whole Kawakawa for type during different seasons? (skip if they do not buy fish)

		High Season Prices			**Low Season**		
	Same as skipjack	Lowest	Highest	Average	Lowest	Highest	Average
Fishers							
Wholesalers/Traders							
Processors							
Agents/Investors							
Import Markets							
Other							

47. When is the supply (supply based on tuna landing) of tuna fish highest and lowest? (Tick all that applies)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Highest Supply	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Lowest Supply	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐

48. Are there any common problems with the tuna you buy? (ex. too small, not well preserved etc.)

____

49. How often do you reject small or undersized tuna when buying?

○ Never Sometimes About half the time

○ Most of the time Always

50. How often do you reject damaged tuna when buying?

○ Never Sometimes About half the time

○ Most of the time Always

51. How do you handle the tuna before selling?

☐ Placed on ice Refrigerate Store in freezer

☐ None Other

____

52. Would you say the size of fish that you sell now is larger or smaller than 5 years ago?

○ Much larger now Slightly larger now

○ Same size Slightly smaller now Much smaller now

53. Which tuna species do you sell and which forms do you sell them in?

					Tuna species sold			forms of tuna sold	
	Species	Fresh whole	Frozen whole	Dressed fresh/frozen	Filleted fresh/frozen	Portioned fresh/frozen	Dried	Cooked	Other (specify)
Skipjack	○	☐	☐	☐	☐	☐	☐	☐	☐
Kawakawa	○	☐	☐	☐	☐	☐	☐	☐	☐
Yellowfin	○	☐	☐	☐	☐	☐	☐	☐	☐
Big Eye	○	☐	☐	☐	☐	☐	☐	☐	☐
Long Tail	○	☐	☐	☐	☐	☐	☐	☐	☐
Frigate	○	☐	☐	☐	☐	☐	☐	☐	☐
Bullet	○	☐	☐	☐	☐	☐	☐	☐	☐

54. On average, approximately how many kg of tuna are wasted before or during the selling process for any reason per year?

____

55. What challenges do you face during selling?

____

56. Who do you sell your fish to?

☐ Households Fishers Wholesalers/Traders

☐ Other processors Retailers Agent/investors Export markets

☐ Other ____

57. Can you please tell us the average price per kg for various forms of kawakawa that you sell for each buyer type?

	Price per kg of various forms of kakawa that you sell							
	Fresh whole	Frozen whole	Dressed fresh/frozen	Filleted fresh/frozen	Portioned fresh/frozen	Dried	Cooked	Other (specify)
Household consumers								
Fishers								
Wholesalers/Traders								
Retail (hotels/ restaurants/ fish shops)								
Other Processors								
Agents/Investors								
Export Markets								
Other								

58. Can you please tell us the average price per kg for various forms of skipjack that you sell for each buyer type? (fill in if same as kawakawa)

	Price per kg of various forms of kakawa that you sell							
	Fresh whole	Frozen whole	Dressed fresh/frozen	Filleted fresh/frozen	Portioned fresh/frozen	Dried	Cooked	Other (specify)
Household consumers								
Fishers								
Wholesalers/Traders								
Retail (hotels/ restaurants/ fish shops)								
Other Processors								
Agents/Investors								
Export Markets								
Other								

59. What factors affect the selling price of your fish?

____

60. When is the demand for tuna fish highest and lowest? (Tick all that applies)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Highest Demand	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Lowest Demand	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐

61. What challenges do you face when selling your fish?

____

62. What proportion of fish are you sometimes unable to sell? (%) ____________

63. What do you do with fish you are unable to sell?

____

64. How many people are employed in your trading/selling operation including yourself?

____

65. How frequently are sales staff paid?

○ Daily Weekly Monthly

○ Seasonally Annually

Other______________________________________

66. Please indicate how much is spent annually on the following items (specify currency)

	Do you use the following items to help sell your fish?		**How much is spent on these items?**
	Yes	No	Cost (indicate currency)

Tuna species for selling	○	○	
Wages/Salaries	○	○	
Distribution	○	○	
Rent	○	○	
Loan repayment	○	○	
Packaging	○	○	
Food	○	○	
Beverages	○	○	
Electricity	○	○	
Fish transportation	○	○	
Ice	○	○	
Storage	○	○	
Marketing	○	○	
Machinery	○	○	
Other (specify)	○	○	
Other (specify)	○	○	

67. What forms of marketing do you use to sell your fish (ie. calling customers, fish display, advertising, packaging etc.)?

____

68. How are fish transported from buying point to selling point?

____

End of Block: TRADERS/WHOLESALERS

PROCESSORS

Make it clear that these questions only pertain to the fish that they process and sell (not just sell or resell)

69. Approximately how many kg or tons of fish do you process per year? ________________

70. What proportion of your total fish processed is comprised of tuna? (%)________________

71. What proportion of fish you process is Skipjack or Kawakawa? _____________________

72. If you process kawakawa or skipjack, how much do you prefer processing kawakawa or skipjack over other tuna species?

○ Much more preferred   Slightly more preferred   Neither more less preferred

○ Slightly less preferred   Much less preferred

73. Why is this your preference?

____

74. From where do you obtain the tuna you process and what form are they obtained in (Skip to "PROCESSING SPECIFIC" section if they already completed trader section)?

	Where are fish obtained for processing	Form of fish before processed by you					
	select all that apply	Fresh Whole	Whole Frozen	Fresh Gutted/Dressed	Frozen Gutted/Dressed	Fresh Portioned	Fro Porti
From fish that I caught	☐	☐	☐	☐	☐	☐	☐
From Fishers	☐	☐	☐	☐	☐	☐	☐
From Traders/Wholesalers	☐	☐	☐	☐	☐	☐	☐
From Other Processors	☐	☐	☐	☐	☐	☐	☐
From Agents/Investors	☐	☐	☐	☐	☐	☐	☐
Other	☐	☐	☐	☐	☐	☐	☐

75. Which forms of tuna do you purchase most (1) to least (7)

______ Fresh Whole
______ Fresh Gutted/Dressed
______ Fresh Portioned
______ Frozen Whole
______ Frozen Gutted/Dressed
______ Frozen Portioned
______ Other

76. Can you please tell us the price range you pay per kg from various providers for whole Kawakawa during different seasons? (skip if they do not buy fish or if they completed trader section)

	High Season Prices			**Low Season**		
	Lowest	Highest	Average	Lowest	Highest	Average
Fishers						
Wholesalers/Traders						
Processors						
Agents/Investors						
Import Markets						
Other						

77. Can you please tell us the price range you pay per kg for whole Skipjack during different seasons? (skip if they do not buy fish,or if they completed trader section)

		High Season Prices			**Low Season**		
	Same as kawakawa	Lowest	Highest	Average	Lowest	Highest	Average
Fishers							
Wholesalers/Traders							
Other Processors							
Agents/Investors							
Import Markets							
Other							

78. When is the supply (supply based on tuna landing) of tuna fish highest and lowest? (Tick all that applies)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Highest Supply	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Lowest Supply	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐

79. Are there any common problems with the tuna you buy? (ex. too small, not well preserved etc.)

____

80. How often do you reject small or undersized tuna when buying?

○ Never Sometimes About half the time

○ Most of the time Always

81. How often do you reject damaged tuna when buying?

○ Never Sometimes About half the time

○ Most of the time Always

82. How do you handle the tuna before processing?

☐ Placed on ice Refrigerate Store in freezer

☐ None Other ____

PROCESSING SPECIFIC

83. Which tuna species do you process, and which types of processing do you use?

				Tuna species processed				Types of processing	
	Species	Dressing	Freezing	Filleting	Portioning	Salting	Drying	Cooking	Other (specify)
Skipjack	○	☐	☐	☐	☐	☐	☐	☐	☐
Kawakawa	○	☐	☐	☐	☐	☐	☐	☐	☐
Yellowfin	○	☐	☐	☐	☐	☐	☐	☐	☐
Big Eye	○	☐	☐	☐	☐	☐	☐	☐	☐
Long Tail	○	☐	☐	☐	☐	☐	☐	☐	☐
Frigate	○	☐	☐	☐	☐	☐	☐	☐	☐
Bullet	○	☐	☐	☐	☐	☐	☐	☐	☐

84. On average, approximately how many kg of tuna are wasted before or during processing for any reason per year?__________________________

85. What challenges do you face during processing?

____

86. Who do you sell your processed fish to?

☐ Households Fishers Wholesalers/Traders

☐ Other processors Retailers Agent/investors

☐ Export markets Other

____

87. Can you please tell us the average price per kg for various forms of processed kawakawa for each buyer type?

	Price/kg for each processing type							
	Dressed	Frozen	Portioned	Filleted	Salted	Dried	Cooked	Other (specify)

Household consumers								
Fishers								
Wholesalers/Traders								
Retail (hotels/ restaurants/ fish shops)								
Other Processors								
Agents/Investors								
Export Markets								
Other								

88. Can you please tell us the average price per kg for various forms of processed Skipjack for each buyer type? (If same as Kawakawa, just fill in table below)

	Price/kg for each processing type							
	Dressed	Frozen	Portioned	Filleted	Salted	Dried	Cooked	Other (specify)
Household consumers								
Fishers								
Wholesalers/Traders								
Retail (hotels/ restaurants/ fish shops)								
Other Processors								
Agents/Investors								
Export Markets								
Other								

89. On average, how much value-added profit do you generate from processing tuna?

____

90. Would you say the size of fish that you process now is larger or smaller than 5 years ago?

○ Much larger now   Slightly larger now   Same size
○ Slightly smaller now   Much smaller now

91. What factors affect the selling price of processed fish?

____

92. What challenges do you face when selling your processed fish?

____

93. What proportion of fish are you sometimes unable to sell after processing? (%)

____

94. What do you do with fish you are unable to sell after processing?

____

95. How many people are employed in your processing operation including yourself?

____

96. How frequently are processing staff paid?

○ Daily Weekly Monthly Seasonally

○ Annually Other ____

97. Please indicate how much is spent annually on the following items (specify currency)

	Do you use the following items during processing?		**How much is spent on these items during processing?**
	Yes	No	Cost (indicate currency)

Tuna species for processing	○	○	
Wages/Salaries	○	○	
Distribution	○	○	
Rent	○	○	
Loan repayment	○	○	
Packaging	○	○	
Food	○	○	
Beverages	○	○	
Electricity	○	○	
Fish transportation	○	○	
Ice	○	○	
Processing machinery	○	○	
Salt for drying	○	○	
Other (specify)	○	○	
Other (specify)	○	○	

End of Block: PROCESSORS

AGENTS/INVESTORS

98. How many years have you been investing in the fishery?

____

99. Which components of the fishery do you invest in?

☐ Fishers Wholesalers/Traders Processors

☐ Retailers Other Agent/investors Import/Export markets

☐ Boat/machinery sales/repair Training/education facilities

☐ Other ____

100. Which proportion of your investments involve the tuna fishery or tuna processing? __________

101. Which proportion of your investments involve the kawakawa or skipjack fishery or processing?_____

102. How do you provide investment?

☐ Cash loans Providing fishing gear Providing fuel

☐ Providing transport Providing boats Providing processing equipment

☐ Providing storage facilities

☐ Other (list all others) ____

103. What determines the price set for your investments?

____

104. Which of the following forms is your investment returned in ?

○ Cash Fish catches Mobile/electronic payment

○ Bankers check Other ____

105. If you are paid in fish catches, what do you do with the fish?

____

106. How much do you prefer investing in tuna fisheries over other fisheries?

○ Much more preferred Slightly more preferred Neither more less preferred
○ Slightly less preferred Much less preferred

107. Why is this your preference?

108. What challenges do you face when offering your investment services to the tuna fishery?

109. Approximately how much money do you invest in tuna related fisheries per year? (specify currency, if they don't know, ask about all fisheries -indicate all fisheries-)

110. Please indicate whether you own any of the following items relating to tuna fishing, when they were acquired, how much was initially spent on them, and how long you expect them to last.

	Quantity of items	**Acquisition date(s)**	**Initial cost of acquisition(s)**	**Expected lifespan**
	#	mm/yy	specify local currency	indicate years or months
Boat				
Fishing gear				
Outboard engine				
Generators				
Storage facilities				
Refrigerators/freezers				
Processing facilities				
Trading/retail outlets				
Transportation vehicles				

111. Please indicate how much is spent annually on the following items specifically related to investment in the tuna industry (specify currency)

	Do you use the following items for investing in the tuna industry?		**How much is spent on these items?**
	Yes	No	Cost (indicate currency)
Wages/Salaries	○	○	
Distribution	○	○	
Rent	○	○	
Loan repayment	○	○	
Packaging	○	○	
Food	○	○	
Beverages	○	○	
Electricity	○	○	
Collections	○	○	
Marketing	○	○	
Other (specify)	○	○	
Other (specify)	○	○	

112. How frequently are you paid/reimbursed for your investment?

☐ Daily Weekly Monthly Seasonally

☐ Annually Other ____

113. When is the demand for your investments highest and lowest? (Tick all that applies)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Highest Supply	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Lowest Supply	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐

114. Roughly how much do you profit from your investment services annually? (specify currency)

____

End of Block: AGENTS/INVESTORS

DEMOGRAPHICS

115. Are you currently employed?

○ No Yes

116. Who is your employer(s)?

☐ Self-employed Boat Owner Trader/Wholesaler

☐ Fellow fisher BMU member Other ________________________

117. What is your age? ____________________________________

118. How many years have you been involved with the tuna fishing industry?

____

119. What is your highest level of education?

____

120. Where is your area of residence? (town/country)

____

121. What is your gender?

○ Male Female Non-binary / third gender Prefer not to say

122. Do you have another source of income besides from tuna related activities?

○ No Yes

123. What else do you do for an income (list all)?

____

124. What proportion of your total income is generated from tuna related activities?

____

125. Do you travel and work in different fishing areas for different fishing seasons (if yes, provide details)?

○ No Yes

126. Are you a member of a BMU (if yes, which one)? No Yes

127. What is your role within the BMU?

○ Member Official
○ Other ____

128. How many people are in your household?

____

129. Does anyone else in your household engage in fishing related activities?

○ Yes
○ No (skip next question)

130. Who in your household is engaged in fishing activities and what do they do?

____

131. How much fish does your household consume per month on average?

- ○ <5kg
- ○ 5-10kg
- ○ 11-15kg
- ○ 16-20kg
- ○ >20kg

132. What proportion of the fish consumed by your household is tuna?

____

End of Block: DEMOGRAPHICS

Thank you very much for cooperating and participating in this survey. Your answers are very important to our study. If you need any further clarification, please feel free to contact us.
End time: _____________HH: MM