BIOTIC INTERACTIONS BETWEEN CATADROMOUS ANGUILLIDS WITH SYMPATRIC RIVERINE ICHTHYOFAUNA ALONG ATHI-GALANA-SABAKI AND RAMISI RIVERS, KENYA

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DECLARATION AND RECOMMENDATION

Declaration

This thesis is my original work and has not been presented in this University or any other for the award of a degree.

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Recommendation

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DEDICATION

I dedicate this work to my mother (Mekinda), dad, and all my siblings for their exemplary moral support, financial and encouragement. The work is also dedicated to my entire family and friends who willingly supported me through this journey, not forgetting my good friend Mr. Gronvik Knut, his wife Brita, and the family for their generous and kind financial support to keep me through and all others who assisted me in achieving this work.

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ABSTRACT

Biotic interactions are among the most powerful ecological drivers influencing fish species occurrence. Biotic interaction especially competition and predation are of particular concern, precipitating population declines especially migratory fish such as eels. Along the Western Indian Ocean (WIO) region, declines of three of the four catadromous Anguillid; *Anguilla bicolor, A. bengalensis,* and *A. mossambica,* have been reported and primarily blamed on anthropogenic activity but the role of biotic interactions among eels and sympatric fish remains poorly studied. This study elucidate the biotic interactions between sympatric fish and eels along two east flowing rivers in Kenya, Athi-Galana-Sabaki and Ramisi. Eels and sympatric fish from Athi and Ramisi were captured monthly using fyke nets from April 2021 to March 2022. Species occurrence data was used to evaluate species composition and habitat utilization. Data on gut-content, evaluated diet breadth and overlap between eels and sympatric fish guilds. One way Analysis of Similarity (ANOSIM) was used to detect differences between sympatric fish assemblage and eels. Data on habitat utilization was analyzed using Permutational Multivariate Analysis of Variance. ANOSIM was employed to demonstrate diet preferences between sympatric fish guild and eels. Results indicated significant differences in both sympatric fish and freshwater eel assemblage along the two rivers (R=0.49, p<0.05). At both rivers, sympatric fish (57%) and eel (84%) were prevalent in pools but also demonstrated an active habitat selectivity on vegetation (0.03±0.002 and 0.26±0.02) respectively which were not significant different (F=0.69, p=0.81). The influence of environmental variables on occurrence of fish species was comparable (p=0.17). Eel primarily consumed assorted fish (43%), shrimps (14%) and prawns (13%). Sympatric fish on the other hand, consumed detritus (27%), shrimps (20%) and fish (14). The most significant dietary overlaps were observed between predatory sympatric carnivorous fish and *A. bicolor* (0.81±0.01) at Athi. At Ramisi, diets of *A. bicolor* (0.74±0.11) overlapped with those of omnivorous guilds. Although significant differences in diet preference occurred among fish types (R=0.09, p=0.0005), eel and carnivorous guilds were comparable (p=0.08), especially for predatory carnivorous (p=0.1). It is apparent that eel co-occur with sympatric fish, share habitats, but mostly importantly compete with exotic carnivorous fish. Therefore, with these observations, the findings imply that these species are at greater risk of previous undescribed competition attesting to their higher IUCN ranking. Further integration of stable isotopes analyses should be given credence to elucidate feeding habits and trophic interactions.

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LIST OF ABBREVIATIONS AND ACRONYMS

ANOSIM	Analysis of Similarity
ANOVA	One way analysis of variance
AOM	Animal organic matter
Athi	Athi-Galana-Sabaki
CCA	Canonical Correspondence Analysis
CPUE	Catch per unit effort
DOM	Dead organic matter
FAO	Food and Agriculture Organization
FTL	Fish total level
GPS	Geographical Position System
HSD	Tukey’s Honest Significant Difference test
IBA	Important Bird Area
IRS	Image Recognition System analysis
IUCN	International Union for Conservation of Nature
LWM	Limnology and Wetland Management
ASL	Meters Above sea level
MSc	Master of Science Degree
NACOSTI	National Commission for Science and Technology & Innovations
NMDS	Non-Metric Multidimensional Scaling
PAST	Paleontological statistics
PCA	Principal Component Analysis
PERMANOVA	Permutational analysis of variance
Ph.D.	Doctor of philosophy
POM	Plant organic matter
QHA	Quality Habitat Assessment score
RCV	Rotary Club of Vienna
SIMPER	One-way Similarity Percentages analysis
SPSS	Statistical Software for Social Sciences
TBW	Fish total body weight
TDS	Total Dissolved Solids
TL	Trophic level
TN	Total Numbers
TW	Total Weight

WIO	Western Indian Ocean

CHAPTER ONE

INTRODUCTION

1.1 Background information

Biotic interactions, acting through intraspecific and interspecific competition, predation, mutualism, and commensalism (Ben-Natan *et al*., 2004), are critical ecological drivers to the distribution, abundance, and community dynamics in terrestrial and aquatic habitats (Abrahams *et al*., 2007; Tadesse, 2018). These interactions are especially critical to vulnerable fauna such as catadromous long-distance migratory eels that are already impacted by multiple stressors along their migratory routes (Lin, 2017) including the Western Indin Ocean (WIO) region. Although impacts of overfishing (Jellyman *et al*., 2000), pollution (Sayce *et al*., 2004), habitat alteration (Revenga, 2003) and climate change (Strayer & Dudgeon, 2010) on eels and other aquatic faunal occurrence have been characterized, the influence of biotic interactions of other species with eels remain largely undescribed, potential impact on ecosystem structure needs description. Furthermore, introduction of exotic fish (Okwiri *et al*., 2019) coupled with variation in predatory pressure, intensify biotic interactions in rivers, limiting resource use to the detriment of endemic and vulnerable taxa (Kotler *et al*., 1994). Similarly, diet and habitat overlap trigger intense niche specialization and species exclusion (Welcomme, 2003) especially when the carrying capacity of interacting species approach critical limits (Hickley *et al*., 2008). Consequently, the biotic interaction between catadromous vulnerable eels, indigenous and exotic ichthyofauna present in rivers require elucidation.

Globally, migratory freshwater fishes have life-history strategies involving long-distance inter-ecosystem migration in a quest for quality breeding and feeding resources (McIntyre *et al*., 2016). These migratory strategies are exemplified by catadromous Anguillid eels of the WIO region and African countries that migrate between marine habitats in the Indian Ocean, and associated freshwater habitats in east flowing rivers of east Africa (Lin *et al*., 2018). Immature eels stages (leptocephali larvae, glass eel and elvers) have a relatively shorter oceanic phase (several months) before they enter estuaries to access freshwater habitats (Arai, 2016), undergo a long freshwater maturation (>10 years) into sub-adult yellow eels and subsequently into adult silver eels (Arai & Kadir, 2017). Globally, the genus *Anguilla* comprises of 16 species (Arai & Kadir, 2017), of which the WIO region harbours four Anguillid species, representing 25% of the highest global biodiversity (Schabetsberger *et al*., 2016). Globally, Anguillid eels are extremely valuable socioeconomically and ecological important and particularly sought after fish (Kuroki *et al*., 2014). They include the most economically value fish today per weight (Zhang *et al*., 2008), and represent an important part of the biodiversity of tropical, sub-tropical and temperate regions of the world's oceans (Arai, 2016). Global declines in wild eel populations have been observed in temperate (Europe, North America) and subtropical (Japan, New Zealand) regions, largely associated with changes in oceanic circulation, habitat degradation, overexploitation and migration stressors (Dekker, 2016). In Kenya, prior to 1960's the larger Kenyan eastward flowing rivers such as Athi-Galana-Sabaki and Tana River, harbored all the four WIO species; *Anguilla bengalensis, Anguilla bicolor, Anguilla marmorata,* and *Anguilla mossambica* (Mann, 1969; Van Someren, 1950; Van Someren & Whitehead, 1959), but surveys subsequent to 1970's proliferation of dam and related river modification, upstream deforestation and pollution are lacking except information on annoted checklist by Seegers *et al*. (2003). Nevertheless, recent review on WIO eels by Hanzen *et al*. (2019) suggested review of IUCN status of 75% (*A. bicolor, A bengalensis,* and *A. mossambica*) of WIO eels cited as nearly threatened coupled with lack of adequate data, highlight the urgent need for monitoring and subsequent management.

During their long freshwater phase, eels encounter and interact through predation, competition and/or facilitation with both indigenous and introduced fish, invertebrates (e.g., macroinvertebrates), amphibian (e.g., frogs), reptiles (e.g., crocodiles, snakes, and alligators), fish-eating birds (e.g., cormorants, kingfishers), mammals (e.g., hippopotamus and waterbucks), (Arai & Kadir, 2017) and man. As reported by Hickley *et al*. (2008) and Okwiri *et al*. (2019) for other freshwater fish such as the black bass (*Micropterus salmoides*), brown trout (*Salmo trutta*), grass and common carp (*Ctenopharyngodon idella* and *Cyprinus carpio* respectively), predation and competition with exotic fauna, as well as local fish, pose potential threats to occurrence and habitat utilization. Outcomes of such intense interspecific interactions include but are not limited to; species disappearance, explosive expansion of previously minor fish populations (Tadesse, 2018) and apparent competition of individual species preying on similar food items (Bhattarai *et al*., 202). Subsequently, these interspecific interactions precipitate changes in habitat and resource partitioning resulting in niche specialization (Kotler *et al*., 1994).

Similarly, the introduction of carnivorous exotic trouts and Bass (*Micropterus spp.*) into Australian aquatic ecosystems for example, resulted in competition for space and food with native fishes (James *et al*., 2003) resulting in collapse of local species. Along Kenyan inland lakes and rivers, there are several cases of introductions of exotic fish species (Hickley *et al*., 2008), either to boost fisheries e.g., Rainbow trout (*Salmo gairdneri*), Grass carp (*Ctenopharyngodon idella),* sharptooth catfish (*Clarias gariepinus*), omnivorous common carp (*Cyprinus carpio*) or accidental escape from ornamental or aquaculture ponds e.g., Nile tilapia (*Oreochromis niloticus*) (Hickley *et al*., 2008). Proliferation of such introduced species, pose severe threats to vulnerable endemic taxa such as catadromous eels, especially when their habitat and/or food requirements overlap.

Intraspecific competition among eel species is rarely described primarily because European, Japanese and American eels are monospecific compared to multiple species in tropical regions (Feunteun *et al*., 2003). In these monospecific eels, competition between stages, with juveniles restricted to downstream reaches are commonly reported (Feunteun *et al*., 2003). However, Gollock *et al*. (2005) partly attributed the collapse and decline of *A. anguilla* populations in Europe to intraspecific competition with the introduced *A. japonica*. Whether the documented *A. bengalensis. A. mossambica*, and *A. bicolor* declines in the WIO region (Hanzen *et al*., 2019) can be linked to interspecific dietary overlap also requires investigation.

Sub-adult and adult anguillids, are predatory on a wide variety of prey, including fish and /or sub-adult eels, aquatic insects, crustaceans (e.g., crabs and shrimps), and mollusks (De Meyer *et al*., 2018) and hence are critical riverine apex predators (Arai, 2016; Jellyman, 2021). Among eels, ontogenic dietary shift results in niche specialization limiting intraspecific competition (Jellyman *et al*., 1999; Laffaille *et al*, 2004). Stage specific dietary niche specialization is manifested since newly hatched eel leptocephali larvae and adult silver stages are non-feeding, juvenile glass eel and elvers are planktivorous, consuming amphipods and insect larvae, while sub-adult yellow eels, are generalists' carnivores, consuming other fish and crustaceans (Arai *et al*., 2020). In comparison, while adult yellow eels are frequently apex ichthyofaunal predators in most rivers, juvenile eels are prey to a variety of sympatric predatory carnivorous fish species (Arai & Kadir, 2017).

Along Kenyan east flowing rivers, co-occurrence between native predatory lungfish (i.e., *Protopterus spp*.) and catfish (i.e., *Clarias spp*.) with eels has been mentioned (Okeyo, 1998; Okeyo & Ojwang, 2015; Seegers *et al*., 2003) but their diets have yet to be compared. In addition, predation on juvenile eels, dietary and habitat overlap has also been reported by Arai (2016) with adult eels may ensue. Diet overlap coupled with interference competition between salmonids and eels have been reported from the Dwyfach River in Gwynedd (Sinha & Jones, 1967; Ward *et al*., 2007). Furthermore, McDowall (2006) demonstrated habitat and diet overlap between exotic rainbow trout and resident cyprinids precipitated resident species displacement from previously trout-free upstream reaches of large east flowing rivers that also host eels. Along the Athi-Galana-Sabaki system, introduced exotic species such as common carp reportedly affect indigenous fish through competition for space and food (Okeyo, 1998; Okwiri *et al.*, 2019) and displacement of dominant native cyprinids and cichlids (Seegers *et al.*, 2003), however similar exotic introduction have not been reported from the smaller east flowing rivers such Ramisi and others, which may also host eels. Whether differences in interactions and their resultant niche overlaps can be demonstrated along Kenyan east flowing rivers with different introduction history require elucidation and hence the current study.

1.2 Statement of the problem

Freshwater anguillids, functioning as catadromous apex predators, hold ecological and socioeconomic significance in global river systems. However, they face vulnerability to various anthropogenic threats, including pollution, habitat alterations, hydrological changes, and climate shifts, across the extensive >10,000 km of ocean and river environments they traverse. Subsequently, these challenges significantly impact their continued survival, but the role of biotic interactions has received less attention to understand its contribution to the threats faced by anguillid eels. Unlike temperate and subtropical monospecific eels, where biotic interactions are limited to stage-specific ontogenic dietary shifts and the exotic introduction of Japanese eels, interactions among tropical multispecies eels may result in more complex but poorly documented outcomes. Biotic interactions between resident and exotic fish with monospecific eels in temperate and subtropical rivers have been observed to induce biotic stress, leading to niche specialization. Considering the recent upgrading of WIO eels, investigating diet and habitat overlap between resident eels and sympatric native fish becomes crucial, as it may add additional stress to vulnerable eel populations during their extended and critical riverine maturation. Given the long history of exotic fish introductions and other anthropogenic disturbances in larger east-flowing rivers in Kenya, such as the Athi-Galana-Sabaki, elucidating the impacts of biotic interaction pressure is important. Consequently, evaluating the contribution of such interactions to the conservation status of eels, in general, and river health, in particular, is critical for identifying hotspots for river management, conservation efforts, and accompanying restoration initiatives.

1.3 Objectives

1.3.1 General objective

The main aim of this study is to elucidate the patterns of biotic interaction between sympatric riverine ichthyofauna with catadromous eels along Kenyan east flowing rivers impacted by different levels of anthropogenic disturbance (Athi, Ramisi) in Kenya. This will be achieved through the following specific objectives:

1.3.2 Specific objectives

i. To characterize and compare the sympatric fish assemblages co-occurring with freshwater eels along disturbed Athi-Galana-Sabaki and relatively undisturbed Ramisi Rivers in Kenya.
ii. To compare patterns of habitat exploitation between sympatric fish and freshwater eel along two rivers under different anthropogenic stressors.
iii. To compare the dietary composition and overlaps between the sympatric fish guilds and freshwater eel along the two rivers.

1.4 Hypotheses

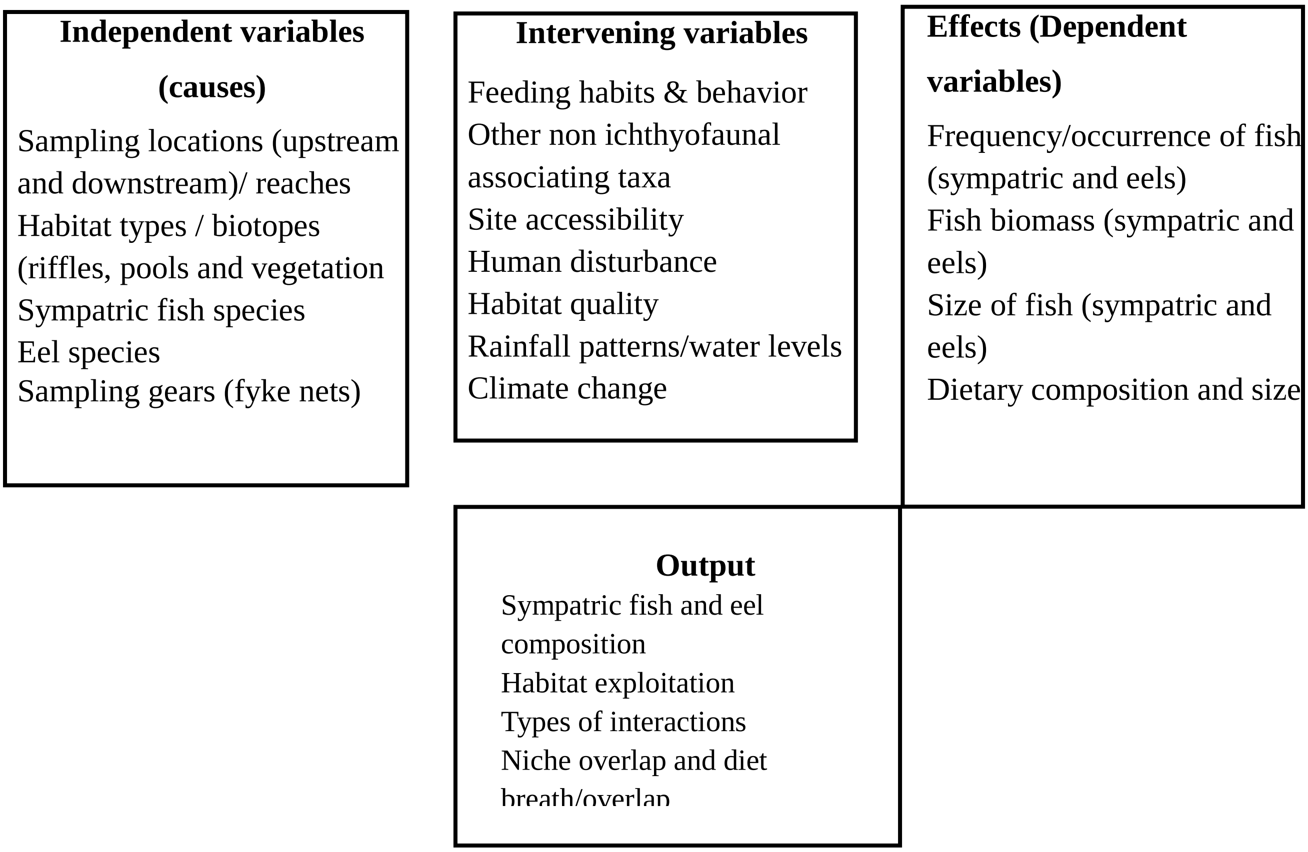
i. There are no significant differences in the sympatric fish assemblage occurring with freshwater eels along the two rivers.
ii. There are no significant variations in patterns of habitat exploitation between sympatric fish and freshwater migratory eel along the two rivers.
iii. There are no significant differences in dietary composition and overlaps among sympatric fish guilds and the freshwater eels along the two rivers.

1.5 Justification

Evaluating biotic interactions between sympatric fish and anguillids is crucial, as these interactions pose an additional, yet undescribed stress on species already vulnerable to various stressors prevalent in Kenyan and global rivers. Describing the variation in fish assemblages among rivers with different levels of human disturbance helps map spatial distribution patterns, while examining diet and habitat overlaps reveals variations in the intensity of interactions among rivers. These biological components are essential for ascertaining interactions that render eel populations vulnerable. Deciphering these interactions is vital for predicting eel occurrence and distribution, contributing to a comprehensive understanding of threats and survival in Kenya and the region. In the absence of such critical information, the occurrence of Anguillids and associated fisheries is at risk, emphasizing the need for their conservation and protection as the last global biodiversity hotspot. Furthermore, understanding the biotic interactions of catadromous eels is crucial for implementing targeted, sustainable management interventions along focal rivers. This information can serve as the foundation for development of evidence-based management strategies to sustainably conserve and protect this elusive resource. The data generated will also contribute to enhancing our knowledge of the IUCN status of tropical multi-eel species and the role of biotic interactions. Additionally, this study aligns with the objectives of the Kenya Biodiversity Strategic Action Plan and the Convention on Biological Diversity (CBD) agenda, aiming to protect migratory species.

1.6 Conceptual framework

Conceptual framework highlighting the main predictor and dependent variables that largely contributed to the expected output.



Independent variables (causes)

Sampling locations (upstream and downstream)/ reaches
Habitat types / biotopes (riffles, pools and vegetation
Sympatric fish species
Eel species
Sampling gears (fyke nets)

Intervening variables

Feeding habits & behavior
Other non ichthyofaunal associating taxa
Site accessibility
Human disturbance
Habitat quality
Rainfall patterns/water levels
Climate change

Effects (Dependent variables)

Frequency/occurrence of fish (sympatric and eels)
Fish biomass (sympatric and eels)
Size of fish (sympatric and eels)
Dietary composition and size

Output

Sympatric fish and eel composition
Habitat exploitation
Types of interactions
Niche overlap and diet breath/overlap

Figure 1: A conceptual framework showing the overall work done in the study highlighting the major variables that influenced the project outcomes

1.7 Definition of terms

Amphidromous	Refers to a type of diadromous of fish species migration where regularly they migrate between freshwater and the sea (in both directions), but not for the purpose of breeding, as in anadromous and catadromous species
Anadromous	Anadromous describes a migratory life cycle where fish live most of their life in saltwater but return to where they hatched to spawn in freshwater
Catadromous	This is a type of migration where fish spend most of their lives in fresh water, then migrate to the sea to breed. This type is exemplified by eels of the genus *Anguilla*
Diet overlaps	Feeding behaviors in trophic interactions where organism share or compete for similar food resources, resulting to food resource portioning
Extralimital species	These are fish species introduced outside their natural geographic range within a geopolitical area which are often not recognized as invasive or potentially invasive
Feeding guilds	These are functional feeding groups where organism such as fish belong to, and exploit the same class of environmental resources in a similar way" regardless of taxonomic affiliation. A guild sets the stage for understanding ecological relationships
Fish assemblage	Refers to the variety and abundance of fish species in a given aquatic ecosystem (rivers, lakes, oceans etc.)
Fish biomass	In a fisheries context, biomass is the total weight of a stock or biological unit of fish or a defined fraction of it.

Fish density	Refers to the quantity of fish individuals per unit area in a system
Introduced species	These are fish species that has been intentionally or inadvertently brought into a region or area. Also called an exotic or non-native species"
Niche	A niche is a subset of a habitat where only a particular fish species lives
Niche breadth	Refers to the diversity of resources used or environments tolerated by an individual, population, species, or clade of fishes.
Native species	These are indigenous fish species to a given region or ecosystem if its presence in that region is the result of local natural evolution
Potamodromous	This is a fish life cycle where fish migrate and complete their life cycle entirely within freshwater.
Sympatric species	Two related fish species or populations that exist in the same geographic area and thus frequently encounter one another. An initially interbreeding population that splits into two or more distinct species sharing a common range exemplifies sympatric speciation.
Stable isotopes	These are non-radioactive forms of atoms. Although they do not emit radiation, their unique properties enable them to be used in a broad variety of applications, including water and soil management, environmental studies, nutrition assessment studies and forensics. Stable isotopes are very powerful to study fish ecology. They can help determine, diet (and changes in diet), habitat use (and changes in habitat use) as

	well as elucidate aspects of the physiological ecology of fish
Trophic levels	These are the positions of organisms in a food chain or food web. The different levels help define the flow of energy within an ecosystem. The lowest trophic level is primary producers, such as algae and phytoplankton, which generate their own energy from the sun via photosynthesis

CHAPTER TWO

LITERATURE REVIEW

2.1 Anguillid eels of the western Indian Ocean region

The Western Indian Ocean (WIO) Anguillid eels (*Anguilla spp*.) are long distance catadromous migratory fishes that use both marine and inland/coastal ecosystems along the WIO region to complete their life cycles (Hanzen *et al*., 2019). In the WIO region, there are four Anguillid eel species as per studies by Schabetsberger *et al*. (2016), representing 25% of the global eel biodiversity of Anguillids. Along the East coast of Africa, all four of the Anguillid eel species (*Anguilla mossambica, A. bengalensis, A. marmorata* and *A. bicolor*) undertake long distance, catadromous migrations from their oceanic breeding sites into estuaries and rivers along the east coast of Africa where they grow and mature, then migrate back into the ocean to breed and die (Miller *et al*., 2018). By straddling marine and freshwater ecosystems at different stages of their life history, they are particularly vulnerable to threats in both freshwater and marine ecosystems, and act as ecological indicators of the ecological wellbeing of riverine and marine ecosystems in the region (Schabetsberger *et al*., 2016). Eels not only contribute to the subsistence fishery, and thereby the livelihoods of local communities, but also contribute to social, recreational activities and spiritual beliefs of communities throughout the WIO region (Crook *et al*., 2014).

2.2 Biology of Anguillids

The freshwater Anguillids of the WIO region have a long and dynamic life cycle including facultative catadromous migrations from the Indian Ocean into estuaries and rivers flowing along mainland states on the east coast of Africa (Robinet *et al*., 2008). The reproductive ecology of tropical anguillids, remains speculative, but are known to aggregate and spawn within oceanic spawning areas (Tsukamoto *et al*., 2011). The freshwater eel are composed of six principal stages: egg, leptocephalus, glass eel, elvers, yellow and silver eel (Arai *et al*., 2020). Newly hatched leptocephalus larvae originating from ocean spawning grounds drift with ocean currents towards island and mainland state (Tzeng, 2003). Subsequently, the eegs, metamorphose into glass eels that enter into estuaries where they become pigmented elvers (Tesch, 2008). Afterwards, they penetrate upstream rivers growing in freshwater habitats as the yellow eel stage (immature stage) (Réveillac *et al*., 2009).

During the upstream migration, elvers become yellow eels and live-in freshwater habitats such as rivers, estuaries, and lakes for between 10 to 25 years and then metamorphose into the adult silver eels (Arai & Chino, 2012). During the silver eel stage, gonadal development commences, and these individuals start downstream migrations back to the spawning oceanic grounds, where they spawn and die (Kurogi *et al.*, 2011).

2.3 Major anthropogenic threats affecting freshwater Anguillids

2.3.1 Impact of River damming and flow regulation on eels

Long-distance migratory fishes, including eels, depend on movement for essential activities such as foraging and avoiding predators (Nathan *et al.*, 2008). Eels, categorized as catadromous fish, undergo two extensive migrations—from their oceanic spawning grounds (Fukuda *et al.*, 2016) to growth habitats in rivers and then back to coastal spawning grounds (Arai & Chino, 2012). However, human activities like damming, channelization, and diversion negatively impact eels by disrupting their migratory routes and altering cues for migration (Lin, 2017). These disruptions lead to restricted movements (Welcomme, 2003), habitat fragmentation (Drouineau *et al.*, 2018), and loss of inter-habitat connectivity (Lin, 2017). In Kenya, damming activities, particularly the seven forks' dams on the Tana River for hydroelectric power, have been reported to hinder eels from reaching their original feeding grounds (Okeyo, 1998). River Sabaki is highlighted as the last remaining system for the conservation of Kenyan eels due to damming in the Tana River Basin (Okeyo, 1998). Nevertheless, dams like Twake on the Athi River, intended for water supply, along with numerous small barriers such as irrigation channels and weirs, pose additional challenges to the movement of eels.

2.3.2 Impact of pollution on eels

The increasing population and the consequent rise in industrial, domestic, and agricultural discharge have considerably transformed global rivers and streams. This has led to escalating concentrations of nutrients, heavy metals, organohalides, hormones, and suspended sediments (Masese & McClain, 2012). In Kenyan streams, pollution stemming from both industrial and agricultural operations as well as untreated human waste (Kitheka & Mavuti, 2016), along with agrochemical discharges, threaten aquatic system health (Horak *et al.*, 2020). These pollutants significantly impact the water nutrients level and its oxygen-carrying capacity, crucial for supporting biological communities, including fish (Brink *et al.*, 2018). The heightened loads of pollutants diminishes the assimilation capacity of fish that undertake extensive journeys in the "world of water" to reproduce at sea, as exemplified by catadromous eels (Jones & Reynolds, 1997).

Heavy metal and toxic organohalides loads bio-accumulate across food chain and hence apex predators such as eels and man may records higher levels (Freese *et al.*, 2017). Furthermore, such toxic chemicals are commonly stored in lipid reserves and metabolized during periods of high energy use (Maes *et al*., 2005). Consequently, freshwater eels are particularly vulnerable to contamination during their silver eel stages when lipid levels are highest to achieve their transoceanic migration to their spawning grounds (Belpaire *et al*., 2009). According to Dutil (1984), there are reported cases of direct eel mortalities as a result of contaminants. Largely, majority of the cases, are at sub lethal level ranging from tissue damage to behavioral alterations (Geeraerts & Belpaire, 2010). Furthermore Byer *et al*. (2013) also recorded contaminants to be supposedly transferred to offspring resulting in larval malformation.

2.3.3 Impacts of catchment degradation and modification

Riparian catchment modification, especially associated with agricultural activities (Basset *et al*., 2013) and other floodplain land uses (Mango *et al*., 2011), have markedly increased in the last decade globally (Basset *et al*., 2013). Catchment modification is blamed for spawning migration failures not only in eels (Berkeley *et al*., 2004), but also in salmon (Jamu *et al*., 2003). Catchment modification such as deforestation alters sediment load (Basset *et al*., 2013) and increase nutrients inputs (Malthus & Mitchell, 1988) coupled with channelization which alters flow speed (Limburg & Waldman, 2009). Haro *et al*. (2000) have reported loss of typical eel habitats, such as estuarine marshes and intertidal zones as a result of agricultural activity along river catchments. Alteration of hydrological regimes results in loss of connectivity for catadromous fish populations such as eels due to impact on flood pulse and change chemical signature (Limburg & Waldman, 2009).

2.3.4 Overfishing and overexploitation

Globally, eel fishery is a well-recognized indigenous source of food in the European countries. Studies are present for other counties such as those of America (MacGregor *et al*., 2009), Europe (Drouineau *et al*., 2018), New Zealand (Jellyman, 2006), Japan and East Asia (Tatsukawa, 2003) indicating overexploitation of eels. In the context of Kenya, no previous studies have indicated the exploitation rate, although eel are vulnerable and nearly threatened. Eels are targeted for both subsistence and commercial use at all stages of their life (Jellyman *et al*., 2000). Among eel species, European, America and Japanese eels are the only widely commercially exploited species but commercial exploitation of Australian eels has also been reported (Jellyman, 2007). In Europe, America and Japan, all eel stages are exploited, but silver stages are preferred in Europe and America, due to higher fat content, while glass eel are an appetizer as well as largely used in stocking grow out aquaculture ponds, reducing eel recruitment (Briones *et al*., 2007). The collapse of Japanese eel population in the 1970’s subsequently led to global expansion of live glass eel export (Engler-Palmer *et al*., 2013).

However, although very little of the commercial value of Anguilla eels along the WIO is known, there are new indications of exploitation of this important resource in Asian markets in particular who import large quantities of elvers (juvenile eel) from Europe, America and recently, from Africa, for stocking fattening ponds (Jacoby & Gollock, 2014).

Some African countries (including Madagascar) have now entered the global trade and sporadically export eels to the South-East Asian markets. Several reports have mentioned the trade of African eels including FAO (2013) which reported regular export from Madagascar, Mozambique, Tanzania and South Africa first observed in 1998 while TRAFFIC (Crook, 2014) showed the export of eel from Madagascar, Mauritius and South Africa in the recent years. Similarly, the Indian Ocean Commission (Yvergniaux *et al*., 2016) reported a production of 10 tonnes of yellow eels through aquaculture in Madagascar, all of which was exported. Between 2011 and 2013, Madagascar exports represented 4% of eel imports into East Asia according to TRAFFIC (Crook, 2014).

2.3.5 Impact of exotic fish introduction on freshwater ecosystems

Biological invasions are widely acknowledged as major threats to biodiversity (Sala *et al*., 2000) but management approaches for dealing with introduced species are generally lacking (Britton *et al.*, 2010). Introduced exotic species have significant impact on native biodiversity (Hickley *et al*., 2008), including migratory eels (Dekker, 2016). Among the impacts confronted by native fish species include; direct predation of sub-adult and displacement (Mboya *et al*., 2004) or indirectly through competition (Hart & Pitcher, 2012), coupled with habitat alteration (Britton *et al*., 2010), through competition for cover and spawning sites (Hickley *et al*., 2008). Subsequently, altering the food webs and trophic structures of aquatic systems as described by Okwiri *et al*. (2019). For example, rainbow trout (*Oncorhynchus mykiss*) being a predator, has been deemed harmful to native fish fauna in many areas where it has been introduced (Crowl *et al*., 1992).

2.4 Fish assemblage structure and occurrence

2.4.1 Sympatric riverine fish assemblages co-occurring with eels

Globally, the precise number of existent fish species remains to be determined but higher occurrences have been reported in tropical and subtropical regions compared with temperate and Polar Regions (Levêque *et al*., 2007). Globally, freshwater fish belongs to 207 families, and 2,513 genera comprising of 44,000 species (Darwall *et al*., 2005). Biogeographically, 4,035 species (705 genera) are in the Neotropical region, 2,938 (390 genera), Afrotropical, 2,345 (440 genera), Oriental, 1,844 (380 genera), Palaearctic, 1,411 (298 genera), Nearctic and 261 (94 genera) in the Australian (Levêque *et al*., 2007). Around

3,360 species of fresh and brackish water fish species have been described for Africa, belonging to 95 families (Paugy, 2010). Of which Cichlids form an important group (Paugy, 2010).

Cyprinids, cichlids, mormyrids, and gobies (*Awaous spp*.) are among the resident freshwater fishes occurring in most of the Kenya's six inland freshwater systems (Okeyo, 1998). Other notable publications including those of Seegers *et al.* (2003), Wanja (2013) and Okeyo and Ojwang (2015) have reported the presence of *Protopterus, Marcusenius, Mormyrus, Petrocephalus, Megalops, Barbus, Labeo, Neobola and Clarias spp.* in Kenyan rivers. The Tana basin is reported to be dominated by *Alestes*, *Tilapias* (e.g *Sarotherodon mossambicus*), *Barbus*, Catfish (*Clarias spp*.), *Protopterus spp* (e.g *Protopterus amphibius*), and labeo species (Seegers *et al*., 2003). On the other hand, the Athi River consists of a diverse family; dominated by Cyprinidae, Mormyridae, Mochokidae, Clariidae and Claroteidae (Wanja, 2013).

2.4.2 Patterns of introduction of exotic sympatric fish species

Globally, fish are among the most introduced non-native aquatic animals mainly through aquaculture (39%), capture fisheries (17%), ornamental trade (8%) and biocontrol (6%) (FAO, 2016; Gozlan, 2008) and most threatened fauna (Hoffmann *et al*., 2008). Globally, over 624 freshwater fishes have been reported to be introduced outside their natural range (Gozlan, 2008), with measurable effects on recipient ecosystems (Gozlan, 2010).

The introduction of exotic fish species into freshwater systems has a long and extensive history in Kenya (Hickley *et al*., 2008). Most of the introductions were deliberate such as carnivorous Nile perch (*Lates niloticus)*, Grass carp (*Ctenopharyngodon idella)*, Nile tilapia (*Oreochromis niloticus*) (Seegers *et al*., 2003), a few accidental introductions from escapes from fish farms such as common carp (*Cyprinus carpio)* and trouts (Hickley *et al*., 2008). In addition to local extralimital intersystem introductions such as *Oreochromis esculentus* translocated from Lake Victoria to Pangani system and *Astatoreochromis alluaudi* from Lake Victoria drainage to upper Athi system, as well as *Oreochromis spilurus* from Athi river system to Rift valley (Seegers *et al*., 2003). In Kenya, over 206 species belonging to 38 families have been described as introduced species originating from Europe, North America, Asia and other parts of the world, including Africa (Seegers *et al*., 2003).

2.5. Habitat use by eel and sympatric fish species

2.5.1 Habitat use by Anguillids

The population of Anguillids are distributed widely across the world from tropical, temperate, and subtropical regions (Jacoby *et al*., 2015). Their habitats along the rivers are classified into upper reaches/mountain streams, middle reaches, and lower reaches/estuaries associated with hydrological conditions (Arai & Kadir, 2017). During their riverine stages, eels inhabit various microhabitats from upstream to downstream reaches of rivers with preferences for midstream to downstream sections. For example, Arai (2016) reported giant mottled eel (*Anguilla marmorata*) and plain snake-eel (*Ophichthus unicolor*) coexisting in comparable habitats in both upstream and downstream. On the other hand, Briones *et al.* (2007) collected samples of *A. bicolor* in the lower reaches close to the estuary and *A. mormorata* on the upper reaches. *A. mossambica* has been reported to spend majority of its life in both quiet and fast-flowing freshwater, brackish and coastal habitats (Réveillac *et al.*, 2009). These observations indicates that microhabitats of eel species evolved differently to avoid interspecific competition for both food and space (Arai & Kadir, 2017). Briones *et al.* (2007) further suggest that, the choice of habitat uses is associated with plasticity response to local river conditions such as salinity, temperature, elevation, river size, and carrying capacity. However, this is still unknown in the tropical region including the Kenyan east flowing rivers.

Several studies, such as those of Shiao *et al.* (2003) reported that, although *A. marmorata* tends to live in freshwater gradients rather than in in brackish and marine habitats, the species can occupy a broad range of habitats from brackish estuaries to upland headwaters (Arai & Chino, 2012). This demonstrate that, eels are flexible in their habitat utilization, provided there are no significant obstacles particularly for large adult eels (Jellyman & Arai, 2016), and if dissolved oxygen requirement are met (Tesch, 2008). This adaptability is exemplified in the case of *A. bicolor*, exhibiting a preference for midstream to downstream areas with tidal influences (Moriarty, 2003). In contrast, *A. bengalensis* has been noted to primarily inhabit freshwater throughout its continental growth, occupying various habitat types such as pools and vegetation (Arai *et al.*, 2020).

2.5.2 Habitat use by native sympatric riverine fish species

Riverine resident fish are distributed in both upstream and downstream habitats of river reaches (Masese *et al.*, 2020). The gilled lungfish (*Protopterus amphibius)* has been found in the lower parts of Ewaso Nyiro and the coastal drainages (Lower Tana and Sabaki) (Seegers *et al.*, 2003). The upper Athi River systems (including Tsavo drainage and Mzima Springs) have been reported to house Bernhard's elephant-snout fish (*Mormyrus bernhardi*) and elephant-snout fish (*Mormyrus hildebrandti*) (Seegers *et al.*, 2003). Other studies, including those of Okeyo and Ojwang (2015) reported common species for Tana River such as Tilapiines, *Barbus,* and Catfish distributed on both upper and lower reaches of the basin, despite the five large hydroelectric power dams constructed along its mid-section (Okwiri *et al*., 2019). The power dams are reported to regulate the upstream and downstream movement of fish assemblages in the drainage (Seegers *et al*., 2003).

Other fish species have been reported to occupy the entire river drainage (Okeyo, 1998). For example, species of *Labeo* (e.g *Labeo victorianus*) and *Barbus spp* have been reported to move up rivers of Lake Victoria (e.g Sondu miriu, Yala and Nzoia) and passing through flood water pools to spawn (Kibaara, 1986). Similar distributions have been recorded for *Labeo cylindricus* in the upper reaches and *L. gregorii* in the lower reaches of Tana River (Okeyo, 1998). Within their range, fish inhabit different habitat types such as demersal, benthos, riverbanks, and muddy pools. The *Mormyrus tenuirostris* and *M. ckannume* for example have been reported in Tana River drainage (Mann, 1969) to inhabit vegetation, brackish and coastal habitat (Wanja, 2013).

2.5.3 Habitat use by introduced sympatric fish species

The established introduced fish species are distributed throughout freshwater drainages (Wanja, 2013). Okeyo (1998) reported Egyptian mouthbrooder (*Pseudocrenilabrus multicolor)* to be spread in both upper and lower reaches of the Athi and Tana drainage. On the other hand, common carp were a successful establishment throughout the entire drainages at multiple points (Roggeri, 1985). The carnivorous Gilled lungfish (*Protopterus amphibius)* accidentally introduced to Tana River was found common "in water-holes, flood-water pools and swamps in the lower reaches of both Athi and Tana (Mann, 1969). The carnivorous Brown trout and rainbow trout were reported common in the upper reaches of Tana drainage (Okeyo & Ojwang, 2015).

2.6 Major biotic interactions affecting eel populations among riverine fish

2.6.1 Competition between eels and other fish

Competition between introduced and native species has been frequently cited as a potential threat to fish community (Hickley *et al*., 2008) threatening aquatic ecosystem health (Gozlan, 2008). Competition occurs as a result of niche and diet overlap among interacting species (Welcomme, 2003) competing for similar resources; such as mates, food resources and space (Tadesse, 2018). Studies by Fausch (1988) in Kenyan inland freshwater ecosystems reported resource competition for food and space interceded by interference and aggression coupled with apparent competition on native species resulted from exotic introduction. Subsequently weakening species performance and extinctions of migratory fishes such as eels (Ward *et al*., 2007) as well as interruption of resource flows used by local resident with far reaching effect in inter-connected ecosystems (Baxter *et al*., 2004).

There have been reports of invasive rainbow trout (*Oncorhynchuc mykiss*) and brown trout (*Salmo trutta*) in rivers and streams of the Mount Kenya region replacing native fish species (Seegers *et al*., 2003). Rainbow trout have been linked to displacements of other fish species as a result of both habitat and diet overlap (McDowall, 2006). Killifish and cyprinids for example are cited to be at risk from guppy fish (*Poecilia reticulata*), while mosquitofish (*Gambusia holbrooki*) feed aggressively on fish eggs, invertebrates, and other fish as a pest, proliferating to reduced native fish (Arthington & Marshall, 1999). The introduction of brown trout and rainbow trout has also been observed to cause alterations in trophic structure and species distribution of the Ewaso Nyiro drainage (Kadye & Magadza, 2008). This is largely attributed to intraspecific rivalry (Mboya *et al*., 2004), resulted from exploitation coupled with scramble competition for limited resources (Ward *et al*., 2007). In the worst situation, such competition could result in species extinction (Arthington, 1991). However, whether similar outcomes may impact eel assemblage along Kenyan east flowing rivers remains undescribed, necessitating examination.

Freshwater eels, especially the longfin eel (*Anguilla mossambica*) (Armstrong *et al*., 2003) within their range, share comparable biotopes with other sympatric fish species during their maturation stages, such as muddy pools, hard-bottom substrates, and flowing rivers. According to Shiao *et al*. (2003), *A. marmorata* were reported to inhabit the upper reach of Taiwan River. On the other hand, *A. japonica* inhabited the lower reaches. Competition as described by Okwiri *et al*. (2019) occasioned from utilization of similar dietary items among sympatric fish species such as salmon, trout and eels have been reported to compete on similar foot items such as aquatic insect larvae, Crustacean, Mollusca, Annelida and fish as the main diets in two Welsh streams of River Dwyfach in Gwynedd, largely blamed on apparent competition during warmer months (Sinha & Jones, 1967). However, according to Drouineau *et al*. (2018) he further suggested that eels choose their habitats for diet as a trade-off between survival (which is typically higher in upstream habitats), growth (which is typically higher in downstream habitats) and competition avoidance (higher in downstream habitats), subsequently proliferating to chances of niche overlap with other fish (Welcomme, 2003). No records are however available, describing such interactions along the Kenyan east flowing rivers, although they are regarded as a threat to eel occurrence (Sinha & Jones, 1967).

Many fish species found within the east-flowing rivers along the Kenyan coast are spread throughout their upper and lower reaches (Okwiri *et al*., 2019). The carnivorous Brown trout (*Salmo trutta*) and Rainbow trout are largely widespread in the upper reaches of the Tana drainage (Okeyo, 1998), as well as common carps (*Cyprinus carpio*) that were introduced in the Athi basin (Okeyo, 1998). Their likelihood of interacting with eels within their range is intensified by the observed patterns of distributions which needs further elucidation of such species had successfully establishments after elaborative introductions (Arai & Kadir, (2017) noted that both sub-adult and adult eels are opportunistic in both their habitat and diet utilization and thus exposing them to interspecific competition.

2.6.2 Predation between freshwater eels and other fish species

Predation for food selection is a fundamental ecological process that supports consumers meet their energy requirements (Sih *et al.*, 1998), in addition to playing an important role in shaping community structure (Tadesse, 2018). Predation pressure has been reported to affects the foraging behavior as well as distribution and habitat selection by both prey and predators (Magurran, 2005). The introduction of piscivorous fish for example has been reported to almost decimate many of the resident species in their new habitats in Sondu-Miriu River of Lake Victoria (Ochumba & Ala, 1992). Subsequently, this has resulted to direct predation and complete disappearance of individuals in inland waters as described by Hickley (1994).

The introduction of predatory Nile perch in inland waters has resulted in a significant decline and extinction of indigenous fish species, along with adverse effects on aquatic ecosystems, as reported by McDowall (2006). Native predator fish play a crucial role in trophic interactions, influencing fish community composition significantly (Ogutu-Ohwayo *et al.*, 2016). Despite the global decline in eel populations and their vulnerability in the Western Indian Ocean (WIO) region, there are no reported records of their status, raising concerns (Hanzen *et al.*, 2019). Although, other factors like damming (reported for Tana River) and pollution are implicated in the decline of migratory fish, including eels, no evidence directly links these factors to reduced eel abundances in the basin. Okeyo (1998) emphasized that the introduction of omnivorous common carp in the 1980s contributed significantly to changes in fish diversity in the Tana River and the Athi-Galana-Sabaki, with native cyprinids, cichlids, mormyrids, and gobies families being replaced by a common carp-dominated reach (Roggeri, 1985). However, it remains unclear whether such introductions are associated with reduced eel populations, and there is no clear evidence of local extinction. Notably, historical records indicate the presence of eels in the drainage before these introductions (Mann, 1969; Van Someren, 1950).

2.7 Feeding habits of Anguillids

The carnivorous eel feeds on dead and/or living prey of aquatic insects, crustaceans (e.g., crabs), mollusks, and fish (Arthington, 1991). Depending on the species, eels can feed in freshwater for ten years or more before returning to the ocean to spawn (Hagihara *et al*., 2018). Eels coexist within their ranges in both tropical and subtropical regions and forage for similar food items to meet their nutritional requirements (Shiao *et al*., 2013). Consequently, resulting to interspecific competition as well as diet overlap (Leander *et al*., 2013).

Minimal intraspecies competition for food among various eel growth stages have been reported in various habitats (Laffaille *et al*., 2004). Intermediate eels prefer feeding in deeper habitats while large eels of more than 360 mm, have a strong preference for large ditches with deep water (Jellyman *et al*., 1999) demonstrating habitat shift along the growth in search for food (Arai & Kadir, 2017). The eel niche breadth undergoes a dramatic shift as a result of inclusion of piscivory in their diets as their size increases (Barak & Mason, 1992). Studies by Cullen and McCarthy (2007) reported eels in riffle habitat types feeding on macroinvertebrates, and subsequently undergoing an ontogenic diet shift to fish at a length of 400 mm (Schulze *et al*., 2004). Similar results were demonstrated by Jellyman and Sykes (2003) on *A. australis* resident yellow eels shifting its diet to exclusively piscivorous at a size greater than 500 mm.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study Rivers

This study was conducted at two east flowing Kenyan rivers; Athi-Galana-Sabaki (Athi) and Ramisi, both draining into the Indian Ocean. The river catchments receive a bimodal rainfall; the long (March–May) and short (October–December) rains interspersed with dry seasons. The daily average temperature at both catchments is about 26°C, with an annual precipitation ranging from 800mm in the highland upstream to 400mm at the downstream coastal reaches (Kiteresi *et al*., 2012; Kitheka & Mavuti, 2016). The two rivers have comparable drainage, but differ in discharge, catchment size and levels of human disturbance, which may have an impact on ichthyofaunal assemblage.

3.1.1 The Athi-Galana-Sabaki River Catchment

The Athi–Galana–Sabaki River basin is the second largest, Kenyan eastward flowing river with a catchment of (~ 46 600 km^2) (Figure 2), after the Tana River (Marwick *et al*., 2018). It has a total length of 390 km, before debouching into the Indian Ocean near Malindi town. The upstream reach of the river is called the Athi River that rises in the Gatamaiyo Forest, on the southern slopes of the Aberdare range at an altitude of 1440m above sea level (asl). The Athi River drains the southern slope of the Aberdare and the eastern slope of Mount Kilimanjaro, draining an area approximately 70 km^2 (Seegers *et al*., 2003) (Figure 2). The major tributaries of the upstream Athi are the Nairobi and Kiboko rivers (Okeyo, 1998). Below Lugard’s Falls, after the confluence of Tsavo and Athi, the river name changes to Galana River. The Tsavo River, which is maintained by the Mzima Springs, is the only permanent flowing affluent feeding the lowest drainage of the river. On leaving the vast Tsavo east national park, the river is named Sabaki River, which is the lowermost reach of the Athi-Galana-Sabaki system, discharging into the Indian Ocean through the Sabaki estuary, 11.3 km North of Malindi town.

The annual rainfall differs spatially within the catchment, ranging from around 500 mm in the mid and lower reaches near the Tanzanian border to 1,200 mm in the mountainous upper reaches (Marwick *et al*., 2018). Land in the upper reaches is extensively developed through urban settlement, agriculture, road infrastructure, and industrial establishments, whereas agricultural production, particularly livestock keeping, dominates in the middle and lower reaches (Kithiia, 2012). The upstream reaches of Athi River, has an annual average precipitation of 810 mm per year in the highly populated central highlands (Marwick *et al*., 2018). The upstream reaches are characterized by a predominance of volcanic rocks (Kithiia, 2012). The land-use changes spatially from a rich agricultural above 4000m asl to a residential cum urban to an industrial system between Nairobi city and Machakos County (Kithiia & Wambua, 2010). The upper reaches flow through Nairobi City (Figure 2) the largest city in East Africa with an average density of 6,247 person.km^{-2} dominated by informal human settlement and over 50 small and large industries especially around Athi River town (Lumbasi, 2003).

The middle (Galana) and lower reaches (Sabaki) of the river traverse vast arid and semi-arid lands (ASALs), characterized by scarce, unpredictable, and erratic rainfall of below 750 mm yr-^{1} and temperature of above 28°C (Marwick *et al*., 2018). The soils in the middle and lower (Galana, Sabaki) reaches of the river are characterized as highly erosive with high sediment fluxes (Van Katwijk *et al*., 1993). The middle and downstream land use is predominated by livestock and small-scale irrigation agricultural initiatives (Kitheka & Mavuti, 2016). Furthermore, the downstream section has a broad floodplain with a meander, 220 km where the Galana River flows through semi-arid savannah plains for 220 km before emptying into the WIO as the Sabaki River, 11.3 km North of Malindi town (Marzadri *et al*., 2014). For this study, two sampling locations were selected on the Athi-Galan-Sabaki River: one on the upper Kiaoni and one on the lower reach Sabaki Bridge.

The Kiaoni upstream location; (1° 13' 53.49" S; 37° 27' 41.706" E), is approximately 45 km North of Masii Town in Machakos County, 220 km North-west of Nairobi city, and 367 km from the headwaters at Aberdare Forest (Figure 2). Administratively, Kiaoni is located in Yatta Sub County, Kithimani ward, with a population density of 205 person.km^{-2}. The major agroeconomic activity around this location, is agriculture through irrigation schemes, such as the Kabaa and Yatta schemes. These schemes were established in 1990^{s} to boost food security and reduce perennial hunger in the region. Additionaly, the riparian community also engages in artisanal fishing using hooks and nets, targetting mainly catfish (*Clarias gariepinus*), *tilapine spp*. and eels (Kihia per commuication). Sand harvesting, to supply insatiable demand for building material to Nairobi is an evident but poorly described livelihood within Machakos and Kitui Counties. The riaprian zone is poorly demarcated and encroached and at several areas eucalyptus trees may be observed. In areas with slow moving waters, the instream is covered with exotic water hyacinth (*Eichhornia crassipes*), with the riparian area accumulated with debris of plastics coupled with smells of sewage and the water is greeninsh in colour.

The downstream Sabaki Bridge location; (3° 9' 10.8972" S‘40° 7' 39.9144" E), lies approximately 11 km North of Malindi Town and 130 km North of Mombasa city (Kimakwa, 2004). It is approximately 676 km South of Nairobi City and 821 km from headwaters at Aberdares forest. The Sabaki estuary occurs in the Northern drier parts of Kilifi County, in Sabaki ward of Magarini Sub County receiving an annual rainfall of about 650mm and temperature of about 32°C (Kitheka & Mavuti, 2016). The Sabaki Bridge established in 1996 traverses the estuary joining, Malindi to Magarini Sub-counties in Kilifi County on the Malindi-Lamu highway. Patches of mangrove forest and sand dunes occur on the seaward side of the bridge. The Sabaki estuary has been designated an important bird area (IBA) due to prevalence of waders including Palearctic migratory gulls and terns, as well as lesser flamingoes (Kung'u & Jackson, 2017). The riparian community with a population density of 718-person km^{-2}, are dominated by Giriama, Chonyi and Kauma, primarily practicing small scale subsistence farming of maize as well as livestock coupled with tourism related income generating activities. The river name Athi-Galana-Sabaki in this thesis will be abbreviated to as Athi and used interchangeably in subsequent sections.

3.1.2 The Ramisi River Catchment

The Ramisi River is located in Kwale County in the Southern Coast of Kenya. The river is situated approximately 58km from Vanga, about 539km north of Kenya-Tanzania border (Figure 2). The river rises from the Shimba hills and flowing eastward of the Duruma sandstone outcrop series at an elevation of 120-450 m als through the Shimba Hill National Reserve located 33 km from Mombasa. The reserve is home for a remaining coastal rainforest, woodland and grassland (Schmidt, 1992). The river flows 60 km, draining a catchment of about 1800 km^2, discharging about 8,190 m^3 yr-^{1} of water into the Indian Ocean, through the Kiwambale mangrove forest at Shimoni (Kiteresi *et al*., 2012). The Ramisi catchment receive an annual rainfall of about 1200 mm and temperature of 26°C. The Ramisi catchment has a relatively lower population density of around 105 person.km^{-2}. Although Kwale has been referred to as the 'mineral' county of Kenya due to its rich mineral deposits, poverty levels remain comparatively high, with majority of the residents depending on small-scale farming, fishing and keeping of livestock to earn their livelihood (GoK, 2008).

The upper reach of the Ramisi River harbours a sparse human population density of 101 persons. Km-^{2}, dominated by Kamba and Digo communities (KNBS, 2019). Subsistence agricultural production is the predominant economic activity in the upper catchment dominated by cash crop of Mango, Bixa and Cashew nut. At the upper catchment, the river flows through the crocodile infested Mkanda dam (4° 23' 38.9184" S; 39° 19' 20.3952" W), which is the only major modification along the river, before traversing about 600 ha Buda Forest. The forest forms part of the few remnants of East African coastal forests that occur as heterogeneous group of isolated evergreen or semi-evergreen closed canopy forests of a tropical dry savanna (Wekesa *et al.*, 2019). The dam established to supply domestic drinking water in 1980, is about 4 km long with a capacity of approximately 1.6 billion liters (Mwikali, 2013).

The lower reaches of the Ramisi River occur between latitude (4° 25' 1.7" S) and longitude (39° 20' 25.82" E), before debouncing at Kiwambale (4° 34' 56.2224" S; 39° 23' 15.6912" W). At the lower reaches, the river passes through the Kwale international sugar plantation and processing factory. The company has 45,000-acre sugar plantations, employing over 3, 000 workers. The factory premises lie about, 2.1 km from Ramisi village, which is a small Swahili town in the western bank of the river. For this study, two sampling locations along the Ramisi River representing the upstream (Eshu) and downstream reach (Taliani-Kanana) of Ramisi River, were selected for sampling.

The upstream Eshu location; (4° 25' 1.7" S; 39° 20' 25.82" E), is about 23 km, west of Msambweni town and 32 km Northwest of Ukunda town and approximately 40 km from the headwaters of the Shimba hill (Figure 2) in Kubo South ward of Matunga Sub County, Kwale County. Smallholder farming pre-dominate land-use with perennial cash crops such as coconut, cashew nuts, Bixa and annual maize as well as a few livestock (goat, cows, and chicken) in addition to artisanal fishing and sand harvesting supplementing household livelihoods. The riparian community is dominated by Digo, Duruma and Kamba ethnicities.

The lower catchment location "Taliani" (4° 32' 31.75" S; 39° 22' 40.44" E), is located about 23km and 32km Southwest of Msambweni and Ukunda Towns, respectively and 45km from the headwaters at Shimba hills (Figure 2) in Ramisi ward of Msambweni Sub County in Kwale County. The location has a relatively higher population of about 245 person.km^{-2} than upper reaches dominated by the Digo, Duruma, Giriama and Kamba community. The riparian community are smallholder subsistence farmers, growing maize and cash crops including Mango as well as ocean fishing.

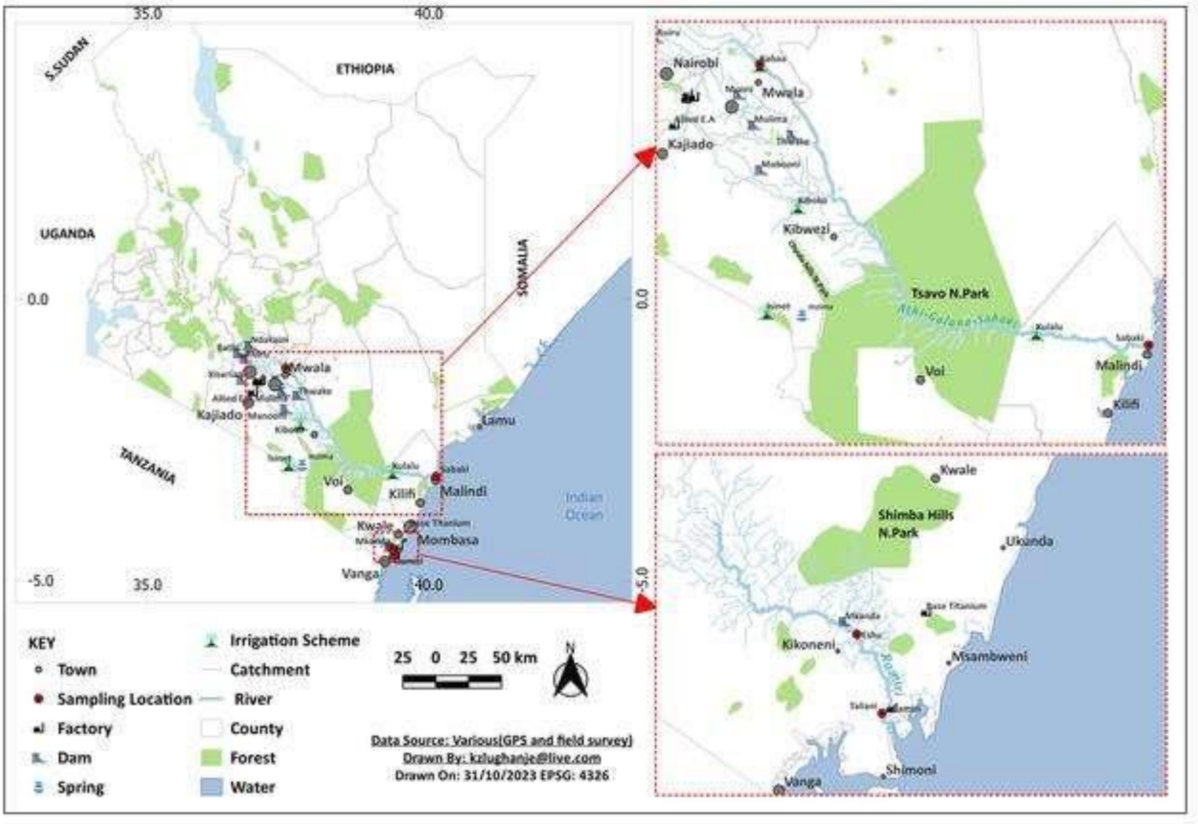


Figure 2: A map of Kenya showing location of Rivers Athi-Galana-Sabaki and Ramisi with upstream and downstream sampling locations highlighted in red and major town in black.

3.2 Study design

The study employed a longitudinal design, where comprehensive assessment and quantitative fish sampling surveys were undertaken. Afterwards, selected sampling locations within dominant biotopes were appropriately selected at the upstream and downstream reaches of the rivers. Periodic monthly samplings were conducted fortnightly from April 2021 to May 2022. Dominant biotopes present in each location along the rivers; pool, riffles or vegetation edges were identified for subsequent periodic sampling. Fish were captured using both commercial double and glass eel fyke nets. The fishing gears (fyke nets), were deployed in the sampling locations in selected sites at both upstream (Kiaoni and Eshu) and downstream (Sabaki and Taliani) (Figure 2) among selected dominate biotopes, left *in situ* and socked overnight for 12 hours. The specific sampling points where nets were deployed, were chosen based on easy accessibility. The nets were reinforced to the substrate with sticks for stability to avoid being carried away by water current, especially at Sabaki estuary due to tidal fluctuations and Hippopotamus movements.

The glass eel fyke nets (plate 1a) were stretched and laid with their wings facing into the downstream direction where water was flowing to from the upstream, and installed with ropes tightened on poles. On the other hand, the tails were anchored in the opposite direction with their cod end secured with poles into the substrate. The double fyke nets were stretched and installed across the channel, with their ropes tightened on poles that were reinforced into the ground substrate (Plate 1b).

Plate 1: Deployment of a) glass eel fyke net and b) Commercial double fyke net at Sabaki Bridge

3.2.1 Sampling site characterization

The study was conducted in two rivers and four sampling locations as shown in (Figure 2) selected from both upstream and downstream locations of the river drainages. At each sampling locations, sampling sites along the longitudinal section of the rivers were demarcated based on; the distribution of river habitats (e.g., river beds, river banks, and floodplains) and, landforms (e.g., base levels, plunge pools, braided rivers and meanders) as proposed by Seegers *et al*. (2003), in addition to ease accessibility and presence of preferred dominant biotopes.

Site characterization through site mapping as described in Kleynhans (1996) habitat quality assessment score (HQA) protocol, were used to assessed both in-stream and riparian conditions at each site. Subsequently, this was used to describe how the ecosystem is either natural or modified by both anthropogenic and natural factors.

Plotless sampling methods as described by Kumarathunge *et al*. (2011) was employed for riparian vegetation assessment (Plate 2). Three transect were established parallel to the edge of the river to the edge of the riparian zone (~12m). Sampling plots were established 0, 6, 12 meters or more from the water edge on relatively undisturbed sites. Plant species occurring within each sampling plot were identified with the assistance of a plant taxonomist. The Diameter at Breast Height (DBH) of the trees was measured at 1.3 m above the ground using a diameter tape, and average height estimated for floristic structure estimate of the riparian areas as described by Wekesa *et al*. (2019).

Plate 2: Sampling riparian vegetation at a) Sabaki and b) Kiaoni, Athi-Galana-Sabaki River

3.2.2 Determination of river morphometry and physico-chemical variables of the river waters

During each sampling occasion and site, river channel morphometry; width (m), depth (m), current velocity (m/s), discharge (m^3/s) and physico-chemical variables were measured. River width and depth were estimated with a measuring tape and weighted graduated rope at a minimum of 5 points across the river at every reach location as described by Masese *et al*. (2014). River means current velocity was estimated in triplicate using timed drift across a known distance at every reach (Plate 3a and b). The data was used to estimate mean discharge following Gordon *et al*. (2004) (Equation 1).

$$Q = \sum VA$$

(1) **a** **b**

Where; Q = Discharge (m^3/s), V = Mean current velocity (m/s) and A = Cross-sectional area of the river channel (m^2)

Selected water variables including; temperature, electrical conductivity (EC), total dissolved solids (TDS), pH, and dissolved oxygen (DO) were measured *in situ* at four selected points and four replicates at each reach using a multi-probe meter (HACH HQ -40d).

Plate 3: Measuring River channel depth and width at a) Sabaki and b) at Taliani along the Athi-Galana-Sabaki and Ramisi Rivers

3.2.3 Fish sampling

Fish samples (both eels and sympatric fishes) were obtained monthly at each sampling location using glass eel and double fyke nets deployed overnight from April 2021 to May 2022 (Plate 4a and b), with the help of experienced local fishermen. After retrieval, each net deployed was examined and all fish captured identified and counted.

3.2.4 Fish sample characterization

During each fish sampling occasion, fish samples in nets were emptied into a white tray, sorted, identified, counted, individual were weighted, total length were measured and selected fish photographed for subsequent use in Image Recognition System analysis (IRS). The fish were initially field identified based on morphological analysis, and subsequently validated using identification keys to the lowest taxonomic level possible. Identification keys used include the FAO species catalogs, standard reference books and field guides such as Wanja (2013), Okeyo and Ojwang (2015) and Froese and Pauly (2019). Photographs taken were also used for identification using an Image Recognition System analysis (IRS) for unidentified fish. Additionally, literature sources and FishBase were used to obtain further details on the species such as exotic, native, endemism, fish migration and IUCN status (Froese & Pauly, 2019). Fish total body weight (TBW) was measured using a digital weighing balance to the nearest (±0.1 g) grams (Plate 4a).

The fish total length (FTL) was measured from snout to end of caudal fin using a flat graduated tape measure to the nearest (±0.1cm) centimeters (Plate 4b). A sample of each fish species were immediately fixed and preserved in 5% formalin and maintained as reference specimen as described by Baker *et al*. (2014) for subsequent species confirmation and further comparison, and the remaining live fish were returned to the river. The fish samples were transported to the laboratory in the department of biological Sciences at Egerton University.

Plate 4: Field measurement of fish weight and length measurement a) *Oreochromis spilurus* and b) *Anguilla bicolor*

3.2.5 Fish assemblage structure determination

Data on fish abundance and weight collected as described 3.2.4 was used to enumerate relative abundance (Equation 2), fish density and catch per unit effort (CPUE). The CPUE was used to estimate fish biomass, which was estimated per gram, day and number of traps deployed (g/trap/day). The number of individuals per species were used to calculate fish density which was quantified per day and number of traps deployed at each sampling location (Individuals/trap/day). Fish abundance and occurrence data were also used to compute diversity (H) (Equation 3), species evenness (J) (Equation 4) and species richness (D) (equation 5). The data on species occurrence (presence-absence) were used to generate the species composition and abundance of fish assemblages co-occurring with eels.

Relative abundance (R.A)

$$\mathrm{RA} = \frac{\text{Number of individuals per species}}{\text{Total number of individuaks of all species recorded}} \mathrm{X100}$$

(2)

Species diversity (H)

$$H = \sum_{i=1}^{n} \left(\frac{ni}{N} \; \lceil \text{Log}^{2} \rceil \; \left(\frac{ni}{N} \right) \right)$$

(3)

Where; H = Shannon-Wiener index of diversity, ni = Total no of individuals of a species and N = Total No of individual of all species

Species Evenness (J)

$$\text{Species evenness} = \frac{H}{LN\ S} \text{x } 100$$

(4)

Where; H = Shannon's diversity index, LN = is natural logarithm of species richness and S = is the total number of species

$$\text{Species richness index (D)} = \frac{S-1}{\text{In } N}$$

(5)

Where; D = species richness index; S = number of species; N = total number of individuals.

3.2.6 Determination of habitat utilization between sympatric fish and freshwater eel

Data on sympatric fish guild and eel relative abundance as well as for sympatric fish in each biotope among the rivers and sampling locations was used to compute habitat breadth index (Equation 6) following Levin's (1968). Resource matrix data used included fish abundance data contributed by each biotope among the sampling locations evaluated.

$$\text{Habitat breadth index (HBI)} = 1/\sum pi^{2}$$

(6)

Where habitat breadth index (HBI), referred to the standardized habitat breadth showing similarity and preference in habitat resource exploitation among fish types, pi^{2}- is the number of fish abundance encountered on each biotope (habitat type).

Fish occurrence and frequency data was used to compute abundance index (AI) (Equation 7) frequency index (FI) (Equation 8) and dominance index (DI) (Equation 9) to describe the most abundant species in each biotope

$$\text{Abundance index} = \frac{\text{Total no. of a perticuler species in a biotope}}{\text{Total no. of all species}} \text{X } 100$$

(7)

$$\text{Frequency index} = \frac{\text{No of sampling biotopes the particuler species was encountred}}{\text{Total number of sampling biotopes}} \text{x } 100$$

(8)

$$\text{Dominance Index} = \text{Abundance Index} + \text{Frequency Index}$$

(9)

Habitat electivity index (E) (Equation 10) was evaluated following Ivlev (1961) index of electivity, used to compare feeding habits of fishes and other aquatic organisms with the availability of potential food resources in natural habitats.

$$\text{Electivity Index} = E = \frac{s-b}{s+b}$$

(10)

Where, s; is the types of habitats present in each reach and b; habitat types utilized by the fish species at each location. The index has a possible range of -1 to +1, with negative unity indicating avoidance or inaccessibility of the habitat, zero (0) indicating random selection of habitat types from the environment, while positive unity, indicating active selection of the habitat type.

3.2.7 Determination of trophic interactions between sympatric fish species and Anguillids

A subsample of each species encountered in the fyke nets, was considered and subjected for gut content analysis. Representative fish samples were dissected at the field (Plate 5a), stomach content removed and preserved in 5% formalin in plastic sampling bottles for subsequent laboratory analysis and diet characterization in the department of biological Sciences at Egerton University (Plate 5b). For removal of the stomach content for preservation, a longitudinal cut was made on the sampled fishes from the ventral side of the fish, behind the isthmus of the gill's posterior to the anal fish (Plate 5a). Two transverse cuts were made at each end of the first cut, to open up the digestive track and separate it from the other visceral organs.

Prior to gut content examination in the laboratory, stomach relative fullness of each gut was examined as in Manko (2016) and scored as empty (0), quarter (5), half (10), three quarter (15) and completely full (20), using the modified point method described by Hynes (1950) and Hyslop (1980). Each preserved fish stomach contents were then emptied into a Petri dish, washed with distilled water and constituent food items sorted, separated and identified to the lowest taxonomic groups possible (Appendix 10) under a dissecting microscope (Plate 5b). Relevant guides for invertebrate (Gerber & Gabriel, 2002) and vertebrate (Keppeler *et al*, 2020), were used in taxonomic identification.

Plate 5: a) Fish dissected at the field for gut content removal and b) laboratory analysis of gut content using a dissecting microscope

The contribution (%) of each identified food item to the stomach was visually estimated on a point scale and assigned a number of points proportional to the estimated contribution related to the total points for each stomach. Each food category was expressed as a percentage by dividing the total points awarded to all food types into the number of points awarded to the food type (Equation 11) (Agembe *et al*., 2019; Hyslop, 1980). The categorized food items were subsequently used to determine the most frequently consumed prey and the relative importance score of each food types to the fish diets.

$$\%\ \text{Contribution} = \frac{\text{Points for each food types}}{\text{Total number of points for all food types}} \text{x } 100$$

(11)

Data on relative abundance of each food items obtained above were used to compute Levin (1968), overlap association indices between eels and co-occurring resident and introduced sympatric fish guilds. Resource matrix data used included the relative diet abundances contributed by each dietary item and categorized in each fish gut content evaluated. Basic data such as the number of records for each species in each category were used for niche and diet breadth following Levin's index (1968). These were then expressed as percentages of each record for each species in each category. Using the relative abundance proportion squared data, niche and diet breadth (B) was calculated following (Equation 12).

$$\text{B (breadth)} = 1/\sum pi^2$$

(12)

Where B- is the Levin’s standardized niche breadth, pi- is the proportion of each food item in the gut.

Pianka dietary overlap (O) was calculated for each food item and fish type (Equation 13) using the product of the proportion for each species pair in each category as used by Pianka's index (1981).

$$\mathrm{Oij} = \sum(\mathrm{pijpik})/\sqrt{\sum(\mathrm{pij})^2\sum(\mathrm{pik})^2}$$

(13)

Where Oij-is the Pianka’s measure of niche overlap between species j and species k, pij is the proportion of the food type i in gut of fish type j, while pik is the proportion food type i in gut of fish type k. The Pianka’s index values range from 0 (total diet separation) to 1 (total overlap).

Trophic interaction was examined through computation of trophic levels (TL) of each fish species examined (Equation 14) as used by Choi *et al.* (2008) and Kihia *et al.* (2015) to compute relative contribution of each food type.

$$TL_f = 1.0 + \left(\sum_i^s FI_{is} \times T_{is}\right)$$

(14)

Where TL_f-trophic level of fish species f, FI_{is} -relative importance of diet item i to s, T_{is}-trophic level of diet item i to s.

The food trophic levels for each dietary items were obtained from Kihia *et al.* (2015) and Keppeler *et al.* (2020). Food trophic level obtained ranged from 0-1 for vegetation, seeds and plant detritus. 1.1-2 was allocated for herbivorous fauna such as detritus (1.2), snails (1.3), plant detritus (POM) (1.4), coleopteran, dipteran, trichopteran, ephemeropterans and basommatophoran (1.5). The trophic levels of animal detritus (AOM), annelids, bivalves and earthworm were assigned an intermediate value of (2). Documented carnivorous invertebrate such as prawns and penaeid shrimps (2.1), crabs (2.2), while carnivorous vertebrates such as birds (2.3) and finfish (3.0). Data on the relative contribution of each food item (FI) calculated and respective food item trophic level (Tis) were subsequently used to compute Fish trophic levels (TL) as in Choi *et al.* (2008) and Kihia *et al.* (2015).

The trophic levels determined were then used to categorize the sympatric fish species into three distinct feeding guilds; Carnivorous (>2.8), omnivorous (2.5-2.8) and herbivorous (<2.5). Carnivorous fish guilds included those whose diets contained more animal than non-animal material, thus obtained higher trophic level (TL>2.8). The generated data on Trophic level was compared among species, reaches and rivers.

3.3 Data analysis

Descriptive statistics were used to present a summary of the percentage contribution of the individual fish species encountered, relative abundance, and spatial variation in physico-chemical water quality parameters, hydrology data and diet proportions consumed by fish types among rivers. Species occurrence (presence–absence) and distribution data were summarized for each sampling locations using the number of species (S), total number of individuals, biomass and relative abundance of each species. The following assemblage structural indices (Shanon-Weinner, Richness, Evenness and Dominance) were calculated and compared using one way analysis of variance (ANOVA).

Analysis of Similarity (ANOSIM) test was used to calculate the variance of fish species assemblage structure occurrence ranging from 0 to 1, with higher values indicating greater differences among sampled species, reaches and rivers. Abundance and presence absence data for fish species was subsequently subjected to One-way Similarity Percentages analysis (SIMPER) using Bray-Curtis dissimilarity index (Southwood & Henderson, 2009) to evaluate dissimilarities as detected by ANOSIM.

The differences and association in fish assemblage composition of both sympatric fish and eel species among the habitat types (biotopes) was analyzed using a non-metric multidimensional scaling (NMDS) analysis. Habitat type fish occurrence data was subjected to Permutational analysis of variance (PERMANOVA) for comparisons between fish assemblages among the habitat types and establish any significant differences. Principal Component Analysis (PCA) was applied to summarize variations in physico-chemical parameters and reduce data dimensionality across the sampling locations. Canonical Correspondence Analysis (CCA) ordination was further used as a direct gradient approach to determine how much variation in fish occurrence (both sympatric and eels) could be explained with the environmental variables among sampling locations. Before the ordination analysis, rare species with occurrence frequency lower than (5%) (Appendix 1) were removed following Li *et al*. (2012).

Characterization of diet preference among the sympatric fish species and eels was performed using ANOSIM test to demonstrate relationship on dietary resource use. Particularly, the test on diet relationship was conducted between eel species and three grouped sympatric feeding guilds (carnivorous, omnivorous and herbivorous). Pianka and Levin's association indices on the diet proportions were used to evaluated diet breadth and overlap among the fish types. All the data collected were entered and stored in Microsoft Excel$^{®}$ (Version 2019) and analyzed using Minitab 18, IBM SPSS Statistics software

(Version 26), and Paleontological Statistics (PAST) software package (Version 4.03) at a significance level of 0.05 ($p<0.05$). All the graphs were drawn using SigmaPlot (Version 14.0).

CHAPTER FOUR

RESULTS

4.1 Habitat characteristics among the sampling locations on the Athi and Ramisi rivers

The mean river width (54.41±5.42m), depth (1.16±0.16m) and cross section area (64.42±12.77m^2) for Athi River were significantly higher ($p<0.05$, t=9.40, 6.14, and 10.29 respectively) than the Ramisi (7.1±0.7, 0.24±0.1m, 0.24±0.1m and 1.69±0.31m^2 respectively). Mean river velocity were however, comparable and ranged from 0.26 m/s for Ramisi to 0.3 m/s for Athi. This corresponded to noticeably higher discharge at Athi (34.28±13.15m^3/s) compared to Ramisi River (0.55±0.16 m^3/s). When river hydrological attributes are compared between upstream and downstream locations, the upstream location of Athi (Kiaoni) recorded a significantly higher width (65.12±4.56m), depth (1.85±0.12m), cross section area (116.97±7.05m^2) (ANOVA, $p<0.05$, F=45, 48, 68 respectively). The discharge (46.30±12.48) at the upstream location of Athi (Kiaoni) was higher compared to either the downstream location of Athi (Sabaki) or both locations at Ramisi River (Table 1). Velocity was comparable across all the sampling locations. In addition, sampling sites at the Ramisi River had comparable hydrological parameters (Table 1).

Table 1: Geographical position, morphometry and hydrological river characteristics (Mean ±SE) along sampling location at the Athi-Galana-Sabaki (Athi) and Ramisi Rivers

Rivers	Athi -Galana-Sabaki (Athi)		Ramisi	
Reaches	Upstream	Downstream	Upstream	Downstream
Parameters	Kiaoni	Sabaki	Eshu	Taliani
Latitude	01° 14' 00" S,	03° 08' 56"	04° 25' 19"S,	04° 32' 32" S
longitude	037° 27' 57" E	S 040° 07' 30" E	039° 20'27" E	039° 22' 40" E
Width (m)	65.12±4.56^a	37.96±4.20^b	6.67±3.67^c	7.44±3.67^c
Depth(m)	1.85±0.12^a	0.58±0.11^b	0.22±0.10^b	0.25±0.10^b
Velocity (m/s)	0.27±0.07^a	0.33±0.06^a	0.197±0.06^a	0.33±0.06^a
Discharge (m^3/s)	46.30±12.48^a	24.1±11.48^{ab}	0.17±10.04^b	0.93±10.04^b
Cross section (m^2)	116.97±7.05^a	20.63±6.43^b	1.04±5.57^b	2.35±5.57^b

Notes: Sampling locations with different letters (a, b, c) in the same row indicate significant differences

Conductivity (EC) (6144.94±529.82µS/cm) and total dissolved solids (TDS) (4326.84±710.3mg/l) were significantly higher ($p<0.05$, t=25 and 20 respectively) at Ramisi

River, compared to Athi River (723.59±54.14µS/cm) and (498.08±49.28mg/l) respectively. Both locations at Ramisi River recorded the highest EC and TDS values compared to Athi River (Table 2). However, the upstream location of Ramisi recorded the lowest values of EC (5878.57±406.79µS/cm) and TDS (3488.14±598.94mg/l) respectively compared to the downstream location (Table 2), which were significantly higher ($p<0.05$, F=59, 13 respectively) compared to both locations at Athi River (Table 2).

pH was higher among upstream locations, which ranged from 7.36 at Ramisi to 7.55 at Athi River. The lowest was recorded at the downstream locations and ranged from 6.78 at Ramisi to 7.02 at Athi River. Conversely, salinity levels were higher among downstream locations, with Ramisi River (3.58±0.34ppt) significantly higher (F=33, $p<0.05$) than Athi River (0.57±0.26ppt). The salinity levels were comparable at both locations of Ramisi River (Table 2). Dissolved oxygen (DO) levels were higher at the upstream locations, particularly at Athi River (7.50±0.24 mg/l), and lowest among downstream locations, especially at Ramisi River (4.44±0.28mg/l). Recorded temperatures were lower at the upstream location of Athi River (24.33±1.05°c) and higher at the upstream location of Ramisi River (31.42±1.02°c) (Table 2).

Table 2: Results of one-way analysis of variance (ANOVA) with Tukey's HSD test for water quality variables (Mean ± SE) among different sampling locations along Athi and Ramisi Rivers

Rivers	Athi -Galana-Sabaki (Athi)		Ramisi	
Reaches	Upstream	Downstream	Upstream	Downstream
Sampling locations	Kiaoni	Sabaki	Eshu	Taliani
Conductivity (µS/cm)	400.04±394.21^{b}	925.98±322.34^{b}	5878.57±406.79^{a}	6624.4±545.76^{a}
TDS (mg/l)	220.63±181.7^{b}	720.03±593.47^{b}	3488.14±598.94^{a}	5836.49±803.56^{a}
Salinity (ppt)	0.19±0.284^{b}	0.57±0.26^{b}	2.92±0.26^{a}	3.58±0.344^{a}
DO (mg/l)	7.50±0.24^{a}	7.10±0.27^{a}	7.12±0.22^{a}	4.44±0.28^{b}
pH	7.55	7.02	7.36	6.78
Temperature (°c)	24.33±1.05^{c}	28.58±1.01^{ab}	31.42±1.02^{a}	26.69±1.35^{bc}

Notes: Water quality variables with different letters (a, b, c) in the same column indicate significant differences

Ramisi river had the highest Quality Habitat Assessment score (QHA) (93%) compared to Athi River (63%). Subsequently, Ramisi River was classified under class (B) of

QHA, largely natural with only minor modifications with Athi River being QHA class (C), largely modified, with loss of both natural habitats and biotas. Both Riparian and Instream Scores contributed comparable scores (92.34%) and (92.64%) to the QHA score at Ramisi. On the other hand, the Riparian score contributed the least (60.12%) compared to the instream score (66.82%) at Athi River, attributed to disturbances along the riparian zone. The upstream location of Ramisi River (92%) and downstream (93%) contributed higher scores to the QHA (Table 3). The upstream location Athi recorded an intermediate QHA score (69%), with the least value obtained at the downstream location (58%). The riparian scores contributed significantly lower at both locations of Athi River; (55%) downstream and (66%) at the upstream compared to Ramisi River (Table 3). As a result, both locations at Athi River were largely modified, with loss of natural habitats and biota, although basic ecosystem functions such as fish survival remain dominant.

Table 3: Habitat quality assessment among the sampling locations along Athi and Ramisi Rivers

Rivers	Athi -Galana-Sabaki (Athi)		Ramisi	
Reaches	Upstream	Downstream	Upstream	Downstream
Parameters	Kiaoni	Sabaki	Eshu	Taliani
Riparian Score (%)	65.68	54.56	93.72	90.96
Instream Score (%)	72.36	61.28	89.60	95.68
*QHA-S (%)	69.02	57.92	91.66	93.32
Class	C	D	B	B

*QHA-Quality Habitat Assessment score (%) ranging from 100 (pristine/natural), 80-99 (natural with few modification), 60-79 (moderately modified), 40-59 (largely modified), 20-39 (loss of natural habitats and basic ecosystem function) and 0-19 (completely modified).

Generally, although the riparian vegetation at the Athi-Galana-Sabaki River had taller and larger trees, density and taxon richness was lower than at Ramisi River sites (Table 4). Species diversity was comparable among the sampling locations. Athi River was largely dominated by *Eucalyptus saligna* and *Sida masaica* (11%) at the upstream location predominated by Myrtaceae (22%) and Malvaceae (11%) families. The lower reach of the river was largely dominated by *Monodora grandidieri* (26%) followed by *Azadirachta indica* (19%) and *Prosopis juliflora* (12%). Annonaceae (26%) followed by Fabaceae (21%) and Meliaceae (19%) recorded the highest relative occurrence among the predominating species. On the other hand, the upstream location of Ramisi River was dominated by *Phyllanthus* *reticulatus* (13%), *Premna chrysoclada* (11%) and *Rothmania sp* (8.7%) from Euphorbiaceae and Rubiaceae (13%).

Table 4: Vegetation structure across the study sampling locations along Athi and Ramisi Rivers

Rivers	Athi-Galana-Sabaki (Athi)		Ramisi	
Reaches	Upstream	Downstream	Upstream	Downstream
Parameters	Kiaoni	Sabaki	Eshu	Taliani
DBH (mm)	0.378±0.1^a	0.198±0.06^a	0.145±0.062^a	0.214±0.12^a
Height (m)	8.633±1.04^b	3.015±0.68^a	3.015±0.68^a	3.218±1.33^a
Taxon richness	28	25	45	14
Diversity (H)	0.308±0.01^a	0.307±0.01^a	0.303±0.01^a	0.315±0.01^a
Density (m^{-2})	9.64	6.72	13.30	14.52

Vegetation structure with different letters (a, b) in the same row indicate significant differences and DBH- Diameter at breast height

4.2 Characterization of the sympatric fish and eel assemblage along the Athi and Ramisi rivers

The data for sympatric fishes and eels' assemblage structure will be presented in the form of species composition, relative abundance, biomass (g/day/trap), density (individuals/day/trap), diversity indices, migration patterns, occurrence and distribution among rivers and sampling locations.

4.2.1 Sympatric fish composition

A total of 6243 sympatric fish representing 32 families and 43 species (Appendix 1) were collected from April 2021 to May 2022. The majority, constituting 77% (4786 individuals) were obtained from Athi River and 23% (1457 individuals) from Ramisi River. *Oreochromis niloticus* emerged as the most prevalent taxon, with over 2454 individuals (39%). The next most common were *Glossogobius giuris* (14%) and *Eleotris fusca* (8%), which together with *O. nilticus* comprised (61%) of the total fish encountered. Notably, double fyke nets and glass eel fyke nets were the primary methods of capture, accounting for 40% (2517) and 55% (3449) of the captured fish, respectively. Fishers predominantly utilized gill nets (4%), hooks (0.1%), ring nets (0.1%), seine nets (0.5%), and traps cage (0.1%) for their landings. When comparing the contributions of different locations, the upstream (27% or 1710 individuals) and downstream (49.3% or 3076 individuals) sections of Athi River yielded more fish (4786 individuals) than both the upstream (13% or 782 individuals) and downstream (11% or 675 individuals) locations of the Ramisi River (Table 5).

Among the sympatric fish species landed, Cichlidae was the most species-rich family, at both Athi (50%) and Ramisi (40%). The next most common family at Athi was Gobiiidae (36%) and at Ramisi Eleotridae (30%), while the least was recorded on Muraenidae (0.07%). Downstream locations commonly featured Gobiiidae (46%), Cichlidae (31%) and Ambassidae (6%), whereas upstream locations were characterized by a prevalence of Cichlidae (74%) and Eleotridae (13%) (Appendix 1). Notably, Cichlidae, constituting 46% of the total, was the most important family across all sampling locations, with the introduced *O. niloticus* contributing over 82%. Of the encountered species, 23 were identified as carnivorous, 11 herbivorous, and 8 omnivorous (Appendix 1). Carnivorous fish, comprising 2478 individuals (65%), were predominantly associated with downstream locations, spanning 21 species. Herbivores accounted for 1266 individuals (33%) from 8 species, while the least prevalent were omnivores, represented by 56 individuals (2%) representing 5 species. The upstream locations were largely characterized by herbivorous species, making up 76% of the total, distributed across 6 species, with Cichlidae being particularly prominent. Carnivorous species, representing 13% and consisting of 4 species, followed in prevalence, while the least common were omnivorous species, contributing 11%, comprised of 6 different species (Appendix 1).

A vast majority, exceeding 98% (6058 individuals), of the sympatric species comprising 43 species were categorized as "least concern" (LC) on the IUCN Red List, with *O. niloticus* dominating at 2454 individuals, representing 41% of the total abundance. The recorded instances of Critically Endangered (CR) species were minimal, with only two individuals (0.05%) identified as *Oreochromis variabililis* and *Neobola fluviatilis* (Athi sardine), exclusively located at a single site (Appendix 1). *Pisodonophis cancrivorus* (longfin snake-eel), listed as "not evaluated" (NE) on the IUCN Red List, was also commonly found in estuarine downstream locations. Evaluation of fish composition among the rivers revealed that both Athi and Ramisi rivers exhibited a predominant prevalence of *O. niloticus* (39% and 40%, respectively). However, the subsequent most common taxa varied between the two rivers. At Athi, *Glossogobius giuris* (19%) and *Oligolepis acutipennis* (18%) were the next most common. In contrast, at Ramisi, *Eleotris fusca* (29%) and *Ambassis gymnocephalua* (15%) were the next most common species (Appendix 1).

The distribution pattern of fish species across the rivers indicated that only two species, *O. niloticus* (39%) and *C. gariepinus* (2.3%), exhibited a cosmopolitan distribution across all the river catchments, both of which are recognized as highly invasive (Table 5). A total of ten sympatric fish species were exclusively confined to the estuarine downstream location, while 27 species displayed a restricted distribution, suggesting a potential for local endemism (Appendix 1). *Bagrus docmak,* a species typically associated with Rift Valley lakes, was documented at Sabaki, potentially considered as extralimital.

The predominant lifestyles of sympatric fish in both rivers were characterized by potamodromous (59%, 46%) and amphidromous (37%, 49%) species in Athi and Ramisi Rivers, respectively. Anadromous fish (1%, and 0.5%) were the least prevalent in both rivers. In terms of the longitudinal gradient along both rivers, the number of fish species decreased from 16 at the upstream location to 36 at the downstream locations. Specifically, upstream of Athi, eleven (11) species were identified, increasing to 27 at the adjacent downstream location. In the case of Ramisi, the number of fish species increased from six (6) to 21, respectively (Table 5).

In assessing fish distribution, composition, and abundance at catchment scales in both the Athi and Ramisi rivers, a One-way Analysis of Similarity (ANOSIM) was conducted, treating sampling locations (upstream: Kiaoni and Eshu, downstream: Sabaki and Taliani) as factors. The analysis revealed a statistically significant dissimilarity (Global R=0.49, p<0.0001). Additionally, a significant dissimilarity between the two rivers was observed (r=0.5, p<0.05) in terms of fish distribution. Notably, three fish species; *O. niloticus* (25%), *E. fusca* (11%), and *G. giuris* (11%), accounted for over 40% of the dissimilarity (Appendix 2). Further examination of dissimilarities among upstream locations using (SIMPER) highlighted the substantial contributions of specific species. For instance, *O. niloticus* (32.45%), *E. fusca* (20%), *O. spilurus niger* (12.2%), and *C. gariepinus* (8.6%) significantly influenced differences in fish distribution. Conversely, *G. giuris* (20.5%), *O. acutipennis* (19.26%), and *O. niloticus* (18%) played crucial roles in the dissimilarities among downstream locations (Appendix 2). Riverine longitudinal dissimilarities along the Athi River, key contributors included *O. niloticus* (25.32%), *G. giuris* (18.51%), *O. acutipennis* (17.36%), and *O. spilurus niger* (8.84%). Similarly, along the Ramisi, *O. niloticus* (26.28%) was responsible for the differences, followed by *E. fusca* (20.89%) and *A. gymnocephalua* (15%).

Notable differences in fish assemblages were apparent when the upstream and downstream locations of each river were examined. At the downstream location of Athi, *Glossogobius giuris* (28%) emerged as the dominant species in terms of abundance, followed by *Oligolepis acutipennis* (27.6%) and *O. niloticus* (22.4%), while *Carangoides fulvoguttatus* (0.03%) was the least common (Table 5). Meanwhile, at the downstream location of the Ramisi River, *Ambassis gymnocephalua* (32%) was the most prevalent, followed by *O. niloticus* (29%) and *Eleotris fusca* (19%) (Table 5).

In terms of catch per unit effort (CPUE) biomass, Athi River recorded the highest value (118±25 g.d^{-1}) compared to Ramisi (36.76±6.90 g.d^{-1}), and this difference was statistically significant (t-test t=2, df=222, P<0.04). Similar variations in composition were observed at upstream locations. In the upstream locations of both Athi and Ramisi Rivers, the introduced *O. niloticus* dominated both abundances (70% and 49%, respectively) and biomass (643±423 g.d^{-1} and 58±15.6 g.d^{-1}, respectively) (Table 5). At Athi, the next most abundant species was the endemic *O. spilurus niger* (16%), followed by the introduced *C. gariepinus* (7%). Conversely, at Ramisi, *Eleotris fusca* (39%) and *C. gariepinus* (1.9%) were the next most abundant taxa (Table 5).

The Athi River exhibited varying catch per unit effort (CPUE) and biomass for different fish species. *Oreochromis niloticus* had a CPUE of 357.41±71 g.d^{-1}, and *Clarias gariepinus* had the highest CPUE (424±88 g.d^{-1}), followed by *O. spilurus niger* (302.05±100 g.d^{-1}). In contrast, the Ramisi River saw *Gymnothorax javanicus* contributing the most biomass (225±291 g.d^{-1}), followed by *C. gariepinus* (119±53 g.d^{-1}), and *Eleotris fusca* (81±21 g.d^{-1}) (Appendix 1). Among the different sampling locations, *C. gariepinus*, with a CPUE of 511±88.8 g.d^{-1}, had a lower density of 0.91±2.8 Ind.sampling^{-1}. *Oreochromis niloticus*, with a CPUE of 643±423 g.d^{-1}, showed a relatively higher density at 14.7±2.8 Ind.sampling^{-1}, while *O. spilurus* niger, with a CPUE of 302±100 g.d^{-1}, recorded a density of 3.2±3.1 Ind.sampling^{-1}, marking the highest CPUE at the upstream location of Athi River, specifically at Kiaoni (Appendix 1). In the downstream location of Athi at Sabaki, *Bagrus docmak* had the highest biomass at 60.6±23.9 g.d^{-1}, followed by *O. spilurus spilurus* at 44.6±16.9 g.d^{-1}, and *G. giuris* at 38±13.2 g.d^{-1}. Notably, higher densities were recorded for *O. acutipennis* (7.06±3.7 Ind.sampling^{-1}), *O. niloticus* (4.34±2.92 Ind.sampling^{-1}), and *G. giuris* (4.18±3.1 Ind.sampling^{-1}) at the downstream location (Appendix 1).

In the Ramisi River, *Clarias gariepinus* unveiled the highest catch per unit effort (CPUE) at both locations, registering at 177.7±95.5 g.d^{-1} at Eshu and 59.1±35.2 g.d^{-1} at Taliani (Table 5). However, these higher CPUE values corresponded to lower fish densities, specifically 1.09±0.60 Ind.sampling^{-1} at Eshu and 0.64±4.80 Ind.sampling^{-1} at Taliani (Appendix 1). *Eleotris fusca* (144±32 g.d^{-1}) and *Oreochromis niloticus* (58±15.6 g.d-1) represented the second-highest CPUE values (Table 5). Analyzing fish density, the most prevalent species, *O. niloticus*, recorded the highest density at 6.31±2.4 $Ind.sampling^{-1}$, followed by *E. fusca* at 4.79±1.0 $Ind.sampling^{-1}$, while the least density was recorded for *Ambassis gymnocephalua* at 0.18±0.06 $Ind.sampling^{-1}$ (Appendix 1). Notably, the lower fish density of *Ambassis gymnocephalua* corresponded to a lower CPUE of 0.57±0.02 g.d-1 (Table 5).

Table 5: Sympatric fish composition, at Athi -Galana-Sabaki (Athi) and Ramisi Rivers

Location	**Family**	**Species**	**Frequency (n and %)**	**CPUE g. d^{-1}**	**IUCN STATUS**
Athi upstream	Amphiliidae	*Amphilius uranoscopus*	2 (0.2)	8.75±0.1	LC
	Clariidae	*Clarias gariepinus*	115 (6.7)	511±88.8	LC
	Clariidae	*Clarias liocephalus*	1 (0.06)	4.25±0.1	LC
	Poeciliidae	*Gambusia affinis*	4 (0.24)	0.12±0.10	LC
	Cyprinidae	*Labeo cylindricus*	17 (1.0)	101±98.2	LC
	Cyprinidae	*Labeobarbus oxyrhynchus*	25 (1.5)	79±11.7	LC
	Cichlidae	*Oreochromis niloticus*	1192 (69.7)	643±423	LC
	Cichlidae	*O. spilurus niger*	265 (15.5)	302±100	LC
	Cichlidae	*Oreochromis variabililis*	2 (0.12)	106±0.1	CR
	Cichlidae	*Oreochromis zillii*	2 (0.12)	106±0.1	LC
	Poeciliidae	*Poecilia reticulata*	86 (5.0)	2.30±2.19	NE
Total	**6**	**11**	**1710 (100)**	**1863.42±725**	**3**
Athi downstream	Ambassidae	*Ambassis gymnocephalua*	5 (0.2)	0.04±0.01	LC
	Ariidae	*Arius africanus*	5 (0.2)	8.31±0.01	DD
	Gobiiidae	*Awaous aeneofuscus*	4 (0.13)	3.90±0.1	LC
	Bagridae	*Bagrus docmak*	154 (5.0)	60.60±23.9	LC
	Carangidae	*Carangoides fulvoguttatus*	1 (0.03)	0.83±0.1	LC

	Chaetodontidae	*Chaetodon vagabundus*	4 (0.13)	0.03±0.1	LC
	Chanidae	*Chanos chanos*	10 (0.3)	0.75±0.33	LC
	Clariidae	*Clarias gariepinus*	3 (0.10)	32±29.2	LC
	Carangidae	*Decapterus russelli*	12 (0.4)	1.86±0.1	LC
	Eleotridae	*Eleotris fusca*	50 (1.6)	5.33±1.58	LC
	Gobiiidae	*Glossogobius giuris*	860 (28.0)	38.0±13.2	LC
	Atherinidae	*Hypoatherina barnesi*	2 (0.06)	0.02±0.1	NE
	Lutjanidae	*Lutjanus argentimaculatus*	19 (0.6)	1.87±1.79	LC
	Lutjanidae	*Lutjanus monostigma*	2 (0.07)	1.92±0.1	LC
	Syngnathidae	*Microphis fluviatilis*	5 (0.16)	0.03±0.01	DD
	Monodactylidae	*Monodactylus falciformis*	3 (0.10)	0.50±0.1	LC
	Mugilidae	*Mugil cephalus*	22 (0.7)	1.31±0.80	LC
	Cyprinidae	*Naziritor chelynoides*	11 (0.4)	1.24±0.19	VU
	Chedrinae	*Neobola fluviatilis*	1 (0.03)	0.19±0.1	CR
	Gobiiidae	*Oligolepis acutipennis*	848 (27.6)	23.21±7.02	LC
	Cichlidae	*Oreochromis niloticus*	688 (22.4)	36.5±13.7	LC
	Cichlidae	*O. spilurus spilurus*	263 (8.6)	44.6±16.9	LC
	Sciaenidae	*Otolithes ruber*	14 (0.5)	2.137±0.41	LC
	Cynoglossidae	*Paraplagusia bilineata*	1 (0.03)	0.01±0.1	LC
	Oxudercidae	*Periophthalmus barbarus*	2 (0.04)	0.74±0.1	LC
	Ophichthidae	*Pisodonophis cancrivorus*	49 (1.6)	33.50±12.1	NE
	Teraponidae	*Terapon jarbua*	35 (1.1)	1.42±0.82	LC
Total	**22**	**27**	**3076 (100)**	**300.85±123**	**5**
Ramisi upstream	Ambassidae	*Ambassis gymnocephalua*	3 (0.4)	0.57±0.02	LC
	Clariidae	*Clarias gariepinus*	15 (1.9)	177.7±95.5	LC
	Eleotridae	*Eleotris fusca*	304 (39.1)	144±32	LC

	Cyprinidae	*Enteromius kersteni*	51 (6.6)	4.21±1.36	LC
	Gobiiidae	*Glossogobius giuris*	26 (3.4)	4.35±2.24	LC
	Cichlidae	*Oreochromis niloticus*	378 (48.6)	58±15.6	LC
Total	**5**	**6**	**777 (100)**	**388.83±147**	**1**
Ramisi downstream	Ambassidae	*Ambassis gymnocephalua*	216 (32.1)	8.7±2.5	LC
	Carangidae	*Carangoides chrysophrys*	5 (0.74)	0.54±0.32	LC
	Clariidae	*Clarias gariepinus*	8 (1.2)	59.1±35.2	LC
	Carangidae	*Decapterus russelli*	15 (2.2)	11.9±10.1	LC
	Eleotridae	*Eleotris fusca*	125 (18.5)	29.6±16.4	LC
	Cyprinidae	*Enteromius kersteni*	3 (0.4)	1.83±1.1	LC
	Gobiiidae	*Glossogobius giuris*	6 (1.0)	9±2.0	LC
	Atherinidae	*Hypoatherina barnesi*	6 (1.0)	0.18±0.02	NE
	Lutjanidae	*L. argentimaculatus*	3 (0.4)	5.3±5.3	LC
	Monodactylidae	*Monodactylus falciformis*	36 (5.3)	11.28±7.8	LC
	Mugilidae	*Mugil cephalus*	6 (1.0)	8.06±6.7	LC
	Gobiiidae	*Oligolepis acutipennis*	23 (3.4)	25.8±15.8	LC
	Cichlidae	*Oreochromis niloticus*	196 (29.0)	41.9±27.6	LC
	Cichlidae	*Oreochromis zillii*	3 (0.4)	19.75±8.20	LC
	Ophichthidae	*Pisodonophis cancrivorus*	2 (0.3)	35.4±25.4	NE
	Teraponidae	*Terapon jarbua*	6 (0.9)	4.14±4.03	LC
	Tetraodontidae	*Tetraodon pustulatus*	13 (1.9)	0.203±0.1	EN
	Muraenidae	*Gymnothorax javanicus*	1 (0.15)	225±35	LC
	Haemulidae	*Plectorhinchus schotaf*	2 (0.30)	1.53±0.1	LC
	Gerreidae	*Gerres oyena*	3 (0.44)	1.54±0.46	LC
	Acanthuridae	*Acanthurus nigrofuscus*	1 (0.15)	0.07±0.1	LC
Total	**14**	**21**	**675 (100)**	**500.82±204.2**	**3**

Note: The number outside the bracket on frequency is (n) and inside bracket in relative abundance (%) and CPUE – catch per unit effort in terms of fish species biomass. LC-least concern, CR-Critically Endangered, NE-Not Evaluated, DD-Data Deficient, VU- Vulnerable and EN- Endangered.

4.2.2 Eel occurrence

A total of 304 eels were captured, with 23% (70) landed from the Athi River and the remaining 76% (234) from the Ramisi River. The majority of the landed eels, over 75%, belonged to the species *Anguilla bengalensis*, followed by *A. bicolor* (12%) and *A. mossambica* (8%) endemic to the WIO region, with *A. marmorata* representing the least at 5%. The primary capture methods were commercial double fyke nets (112) and glass eel fyke nets (172), while hooks (12) and seine nets (8) contributed to less than 3% of the captures. Although *A. bengalensis* dominated in abundance at both Athi (47%) and Ramisi (84%) rivers, *A. marmorata* was the least prevalent in both rivers, accounting for 13% at Athi and 3% at Ramisi. In terms of biomass, Athi River recorded a lower eel biomass at 67.50±26.6 g.d-1 compared to Ramisi River at 151±51.8 g.d-1. However, this difference was not statistically significant (Mann–Whitney U-test U=381, P>0.05).*Anguilla bengalensis* emerged as the most widely distributed species, present at all locations, with particularly high abundance at the upstream sites of both Athi (72.4%) and Ramisi (87.8%) rivers. The Ramisi upstream location recorded the highest biomass for *A. bengalensis* at 322±65 g.d^{-1}, whereas *A. marmorata* had the highest catch per unit effort (CPUE) at Athi (229±97.65) (Table 6). The dominance patterns at downstream locations also varied across sampling sites. At the downstream location of Athi, *A. bicolor* dominated abundance (41.46%), while *A. marmorata* had the highest biomass (46±0.67 g.d^{-1}). In contrast, at the downstream location of Ramisi, *A. mossambica* dominated in abundance (75%), while *A. bicolor* had the highest biomass recorded (193±1.23 g.d^{-1}) (Table 6).

Table 6: Eel species composition, relative abundance, biomass assemblage structure and their conservation status within the IUCN Red List along Athi-Galana-Sabaki (Athi) and Ramisi Rivers

Rivers	**Reaches**	**Species**	**Frequency**	**CPUE g.d-^{1}**	**EUCN STATUS**
Athi	Upstream	*A. bengalensis*	21 (72.4)	71.4±109.8	NT
		A. bicolor	2 (6.9)	30±190.23	NT
		A. marmorata	5 (17.2)	229± 97.65	LC

		A. mossambica	1 (3.5)	35.94±26.9	NT
	Total	**4**	**29 (100)**	**366.34±424.28**	**2**
	Downstream	*A. bengalensis*	12 (29.3)	27±135	NT
		A. bicolor	17 (41.5)	32±110	NT
		A. marmorata	4 (9.8)	46±0.67	LC
		A. mossambica	8(19.5)	34±12	NT
	Total	**4**	**41 (100)**	**139±257.67**	**2**
Ramisi	Upstream	*A. bengalensis*	195 (87.8)	322±65	NT
		A. bicolor	14 (6.3)	53.3±155	NT
		A. marmorata	6 (2.7)	8.76±135	LC
		A. mossambica	7 (3.2)	12.64±1.5	NT
	Total	**4**	**222 (100)**	**396.70±356.5**	**2**
	Downstream	*A. bengalensis*	1 (8.3)	4.22±260	NT
		A. bicolor	2 (17)	193±1.23	NT
		A. mossambica	9(75.0)	48.41±19	NT
	Total	**3**	**12 (100)**	**245.63±280.23**	**1**

The number outside the bracket on frequency is (n) and inside bracket in relative abundance (%) and CPUE – catch per unit effort in terms of eel species biomass. NT-Near threatened and LC-Least Concern.

Comparison of sympatric and eel biomass among locations revealed a significant difference (F=3.0, $p<0.05$). Specifically, the upstream location of Athi recorded significantly higher sympatric biomass (331±41.8 g.d^{-1}) at Kiaoni compared to eels (111±73.30 g.d^{-1}). Conversely, at the upstream location of Ramisi at Eshu, eel biomass (164.91±40 g.d-1) surpassed sympatric biomass (67.62±16 g.d^{-1}) significantly ($p<0.05$). In comparison to downstream locations, sympatric biomass for Sabaki and Taliani (22.58±4.04 g.d^{-1} and 21.81±5.95 g.d^{-1}, respectively) was lower than eels (32.19±10 g.d^{-1} and 97.57±50 g.d^{-1}, respectively) (Figure 3). Notably, the sympatric CPUE at the upstream location of Athi River was nearly fivefold higher than the corresponding site on the Ramisi River (Figure 3). Comparing eel CPUE with sympatric, it is evident that although sympatric fish dominate in abundance, eels have a higher biomass (105.25±38.82 g.d^{-1}) than sympatric fishes (83.57±18.88 g.d^{-1}) (Figure 3).

Furthermore, eel biomass varied significantly among sampling locations (ANOVA; F=2.89, p=0.04). The upstream location of the Ramisi River at Eshu recorded significantly higher ($p<0.05$) biomass (165±40.0 g.d^{-1}) compared to the corresponding upstream location of the Athi River at Kiaoni (110.9±35.0 g.d^{-1}) and its corresponding downstream location at Sabaki (32.2±10 g.d^{-1}) (Figure 3). The prevalent *A. bengalensis* (88%) contributed the highest biomass at Eshu compared to other eel species (Table 5). Additionally, CPUE was comparable across Ramisi River locations, but the estuarine downstream location at Taliani (97.6±50 g.d^{-1}) had a higher CPUE than the corresponding downstream location of Athi at Sabaki (Figure 3).

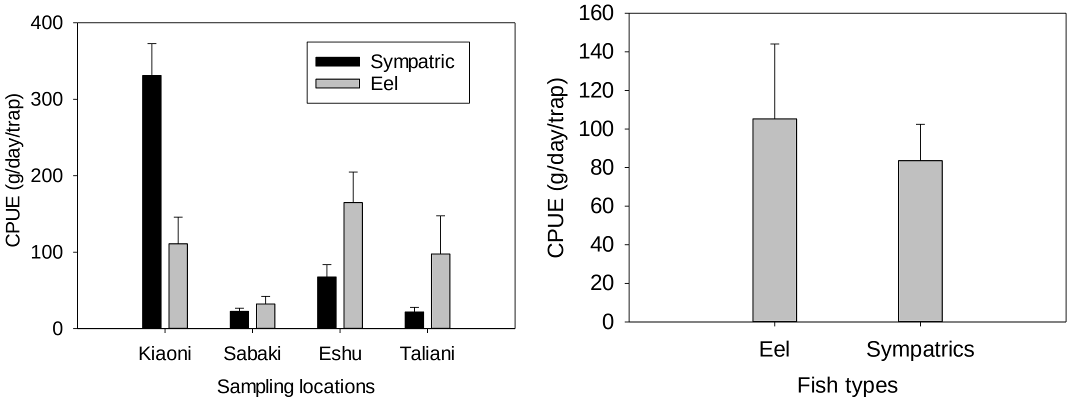


Figure 3: a) Sympatric fish and eel biomass with Standard Errors (SE) bars at upstream (Kiaoni, Eshu) and downstream (Sabaki, Taliani) sampling locations along Athi and Ramisi rivers, Kenya and b) biomass among fish types with Standard Errors (SE) bars

A one-way analysis of similarity (ANOSIM) examining the distribution, composition, and abundance of sympatric fish and eels, with rivers and sampling locations as factors, revealed a statistically significant dissimilarity (Global R-statistic value=0.49, $p<0.05$). The SIMPER analysis further identified two eel species, *A. bengalensis* and *A. bicolor*, as key contributors to the significant differences observed among the evaluated catchments (Table 7). Specifically, *A. bengalensis* (6%) played a major role in generating differences among the rivers, while *A. marmorata* contributed the least (> 0.45%). Downstream variations in *A. bengalensis* decline was notable responsible for the differences among the rivers. Similarly, at upstream locations, *A. bengalensis* (11%) contributed significantly to the dissimilarities, while *A. bicolor* (1%) accounted for the differences among downstream locations. Notably, among the reaches, changes in *A. marmorata* and *A. mossambica* at downstream locations were driving factors in the observed differences (Table 7).

Table 7: One-way SIMPER analysis of fish abundance among the sampled locations in Athi and Ramisi Rivers, Kenya. Significant contributions to dissimilarities are in bold with an asterick.

	Reaches	Upstream		Downstream		Focal rivers	
	Locations	Kiaoni vs Eshu		Sabaki vs Taliani		Athi vs Ramisi	
Common name	Species	Av. dissim	Contrib. %	Av. dissim	Contrib. %	Av. dissim	Contrib. %
African Mottled Eel	*A. bengalensis*	9.27	**11.20***	0.30	0.32	5.13	**5.89***
Shortfin Eel	*A. bicolor*	1.06	1.28	1.11	**1.20***	0.97	1.12
Giant mottled Eel	*A. marmorata*	0.53	0.64	0.12	**0.12***	0.40	0.45
Longfin eel	*A. mossambica*	0.52	0.63	0.94	1.02	0.84	0.96

4.2.3 Sympatric fish and eel biodiversity indices at Athi and Ramisi rivers

Sympatric fish diversity was higher in the Athi River (1.17±0.1) compared to the Ramisi River (1.05±0.1), although this difference was not statistically significant (Df=34, t=0.91, p=0.37). Downstream locations (1.29±0.1) harbored significantly higher taxon richness (1.68±0.13) and diversity (1.57±0.13) than upstream locations (ANOVA; F=15.4, p<0.05, respectively) (Table 8). Among the upstream locations, Eshu in the Ramisi River (0.82±0.12) had the lowest diversity compared to Kiaoni (1.04±0.12) in Athi River. Despite lower diversity in the upstream locations, they corresponded to higher dominance (0.43±0.06 and 0.53±0.06, respectively), which differed significantly (ANOVA; F=4, p<0.05) compared to other locations.

Athi River (0.91±0.13) showed higher eel diversity values than the Ramisi River (0.38±0.17), although the difference was not significant (t-test, t=0.48, p=0.63). However, when comparing river reaches, estuarine downstream locations (Sabaki and Taliani) demonstrated significantly higher eel diversity (F=15.63, p<0.05) (0.67±0.13 and 0.42±0.21) and richness (0.75±0.16 and 0.72±0.25) than corresponding upstream locations, Kiaoni

(0.46±0.19) and Eshu (0.41±0.15) (Table 8). The diversity at both locations in the Ramisi River was comparable, unlike that observed in the Athi River (Table 8). Additionally, eel dominance was significantly higher ($p<0.05$) at the upstream locations, similar to the pattern observed in sympatric fish (Table 8).

Table 8: Diversity indices of fish communities along Athi -Galana-Sabaki (Athi) and Ramisi Rivers, Kenya

Fish types	Location	Reaches	Richness (S)	Frequency (n)	Dominance _D	Richness index (D)	Diversity (H)
Eel	Kiaoni	Upstream	4	29	0.85 ± 0.1^{ab}	0.46 ± 0.19^{a}	0.24 ± 0.13^{ab}
	Sabaki	Downstream	4	41	0.58 ± 0.1^{a}	0.75 ± 0.16^{b}	0.67 ± 0.13^{b}
Sympatric fish	Kiaoni	Upstream	11	1710	0.43 ± 0.1^{ab}	0.86 ± 0.14^{a}	1.04 ± 0.12^{ab}
	Sabaki	Downstream	27	3076	0.40 ± 0.06^{a}	1.68 ± 0.14^{b}	1.29 ± 0.12^{b}
Eel	Eshu	Upstream	4	222	0.82 ± 0.06^{b}	0.41 ± 0.15^{a}	0.35 ± 0.12^{a}
	Taliani	Downstream	3	12	0.71 ± 0.11^{a}	0.72 ± 0.25^{b}	0.42 ± 0.21^{b}
Sympatric fish	Eshu	Upstream	6	778	0.53 ± 0.06^{b}	0.62 ± 0.15^{a}	0.82 ± 0.12^{a}
	Taliani	Downstream	21	679	0.38 ± 0.07^{a}	1.57 ± 0.14^{b}	1.29 ± 0.12^{b}

Diversity indices with different letters (a, b) in the same column indicate significant differences

4.3 Patterns of habitat utilization among sympatric fishes and freshwater eels along Athi-Galana-Sabaki and Ramisi Rivers, Kenya.

4.3.1 Fish Assemblage composition among habitat types

The dominant species varied among the habitat types. *Oreochromis niloticus,* for example, was a generalist and commonly encountered in pools (39%), vegetation (38%), and rifles (36%). On the other hand, *Oligolepis acutipennis* was more common in pool (18%) and riffles (10%), while *G. giuris* (14%) occurred in vegetation (14%) and riffles (8%). *Ambassis gymnocephalua* (11%) was dominant among vegetation, while *Eleotris fusca* (8.35%) dominated riffles (Appendix 3). Among the eels, *A. bengalensis* was common at all biotopes, pools (6%), riffles (1.0%) and vegetation (0.8%), while *A. bicolor* (0.7%) dominated pools (Appendix 3). Among the rivers studied, sympatric fish dominated pools (57%) followed by riffles (24%), and vegetation (16%) at Athi River (Figure 4a). Similarly, at Ramisi River, fish were dominant in pools (52%) but lower in vegetation (9%). Eels as well preferred pools (46, 95%) at Athi and Ramisi Rivers respectively followed by riffle (37, 5%) (Figure 4b).

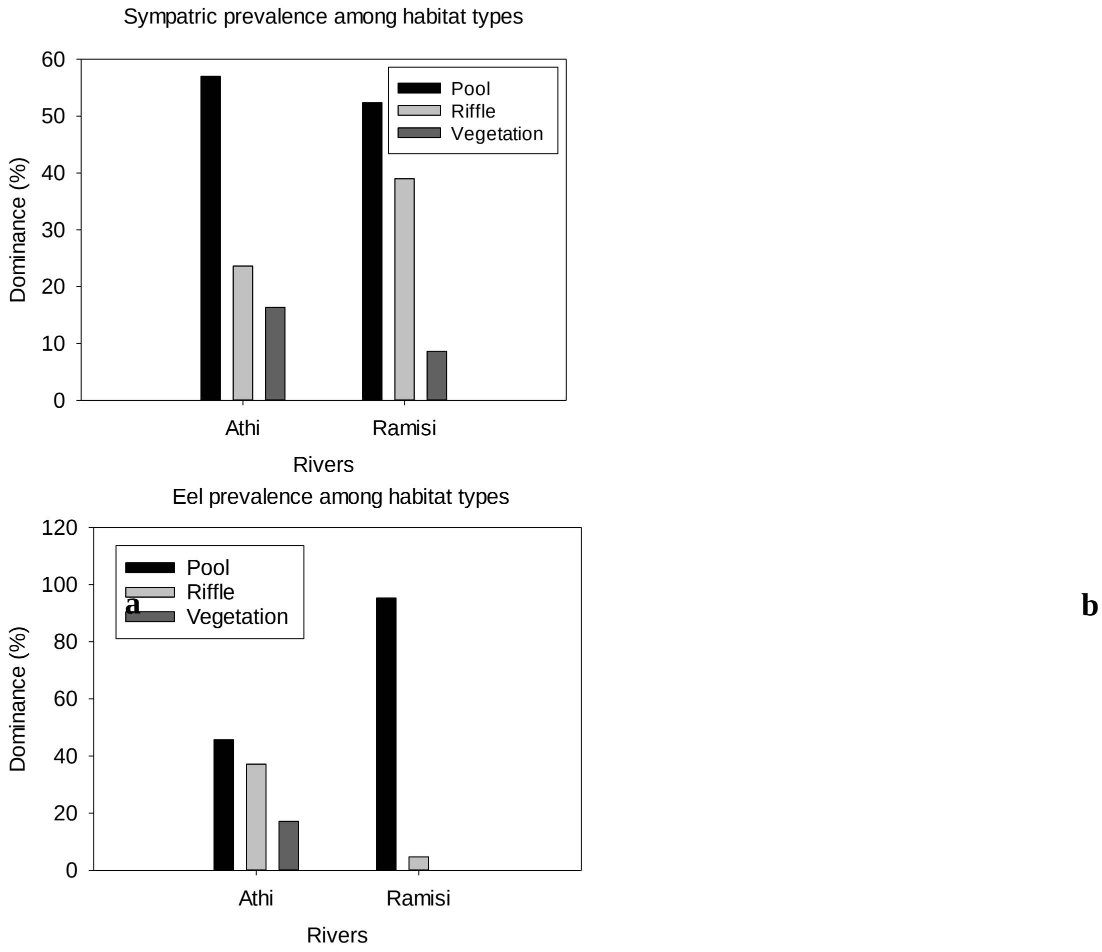


Figure 4: a) Prevalence of sympatric fish and b) eel among habitat types along Athi-Galana-Sabaki (Athi) and Ramisi Rivers

Among the reaches, fish at the upstream location of Athi River largely preferred pools (42%) followed by vegetation (32%). Fish at the downstream location similarly preferred pool (67%), with the second most preferred biotope being riffles (23%). At the upstream location of Ramisi River, fish were common in pools (89%) with riffles (71%) being more preferred at the downstream location (Appendix 4). Among the fish types evaluated, sympatric fishes dominated pools (57%) and overlapped with eels (84%), demonstrating habitat type sharing (Table 9). Species diversity among the fish types (sympatric and eels) on habitat type utilization showed no significant differences (ANOVA; F=3, p=0.07). Besides, sympatric fish recorded a significantly higher ($p<0.05$) density among riffles (0.1±0.001) followed by vegetation (0.09±0.002). Eels were prevalent in pools (0.11±0.003) compared to the other habitat types (Table 9). No significant differences were observed among the fish types on habitat type selection (F=0.02, p=0.99), demonstrating a degree of similarity in habitat utilization by the populations. Although both eels and sympatric fish predominated pools at all sites (as shown in Figure 4 above), they also portrayed an active habitat selection on vegetation (0.26±0.02 and 0.03±0.002) respectively (Table 9). Furthermore, habitat breadth overlapped as well among the habitat types but did not differ significantly (F=0.02, p=0.99) (Table 9).

Table 9: Results of one-way ANOVA of fish type assemblage structure indices (Mean ±SE) among different habitats along Athi -Galana-Sabaki (A-G-S) and Ramisi Rivers. Most preferred habitat types with higher dominance are in bold with an asterick.

Fish types	Habitat types	N	Dominance index (%)	Shannon Index (H')	Fish Density (ind/trap/day)	Selectivity Evlev index (E)	Habitat breadth (B)
Sympatric fish	Pool	3491	**57.25***	0.10±0.01	0.08±0.001	0.014±0.001	0.53±0.01
	Riffle	1699	27.86	0.13±0.01	0.10±0.001	0.026±0.001	0.67±0.01
	Vegetation	908	14.89	0.12±0.01	0.09±0.002	0.029±0.002	0.65±0.01
Eels	Pool	255	**83.88***	0.21±0.01	0.11±0.003	0.069±0.004	0.76±0.03
	Riffle	37	12.17	0.24±0.02	0.10±0.01	0.214±0.01	0.89±0.06
	Vegetation	12	3.95	0.17±0.03	0.09±0.02	0.257±0.018	0.88±0.10

Permutational Analysis of variance revealed no effect on habitat types association with fish type assemblages (PERMANOVA, pseudo-F=0.69, p=0.81) (Appendix 5). Axis 1 (33%) and Axis 2 (20%) of NMDS analysis accounted for over (53%) of the variations on fish occurrence among the habitats (Figure 5). The third axis of NMDS, was only responsible for (18%) of the differences. Three of the four eel species (*A. bicolor*, *A. mossambica* and *A. marmorata*) occurred in pools together with *G. giuris*, *Chanos chanos* and *O. niloticus*. While

A. bengalensis also used vegetation and riffles with *C. gariepinus*, *O. spilurus* and *E. fusca* (Figure 5).

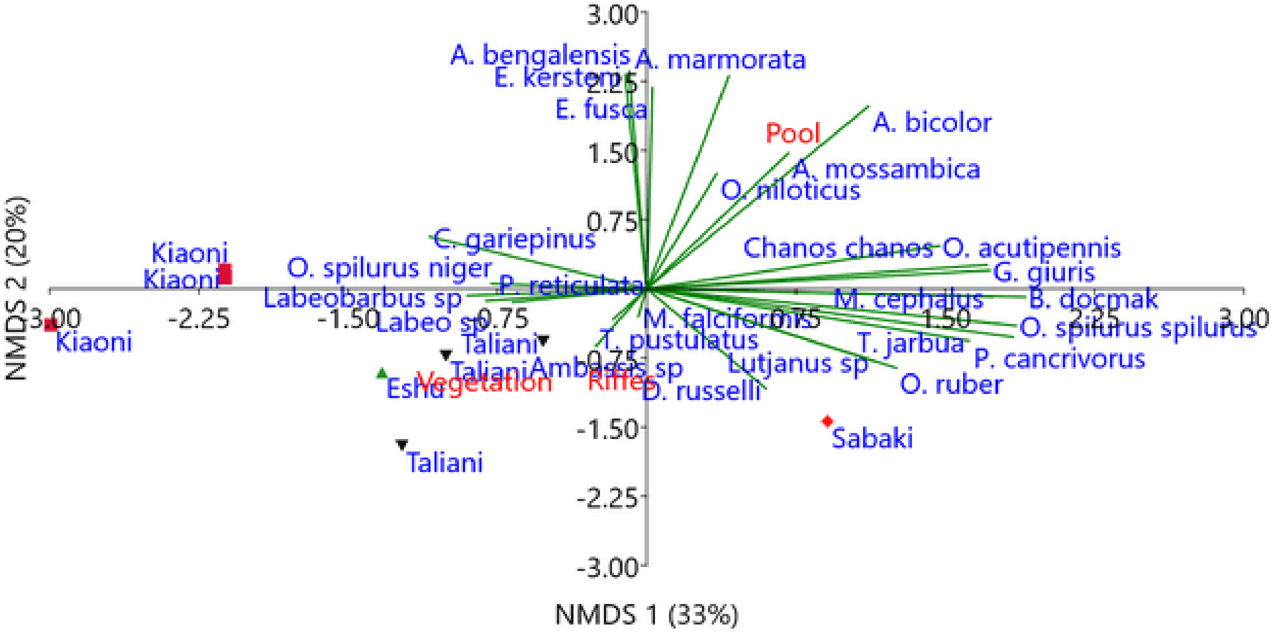


Figure 5: Non-metric Multidimensional Scaling (NMDS) ordination of fish assemblage in different habitat types among sampling locations along Athi -Galana-Sabaki (Athi) and Ramisi Rivers, indicating axis 1 (33%) and Axis 2 (20%) explaining majoring of variations

4.3.2 Relationship between Fish Assemblage and Environmental Variables

After removing rare species with a relative abundance of less than 5% (Appendix 1) from the sympatric fish species, only 28 sympatric fish and four eel species were chosen and considered for ordination analysis (Li *et al.*, 2012). Seven environmental variables were selected after first subjected to Principal Component Analysis (PCA) for multidimensional scaling and stepwise selection of the most important variables, which included conductivity (EC), total dissolved solids (TDS) (mg/l), discharge (m^3/s), temperature (°c), pH, salinity (ppt), and dissolved oxygen (mg/L), with PCA 1 (64.97%) and PCA 2 (24.95%) explaining most of the variations (Figure 6 and Appendix 6). Temperature, velocity, conductivity, TDS, were most important in Ramisi River compared with depth, pH, and dissolved oxygen at Athi River (Figure 6). The upstream location of Ramisi is characterized by higher temperature, while downstream by higher velocity. The locations at Athi River are separated mainly by discharge and water depth (Figure 6).

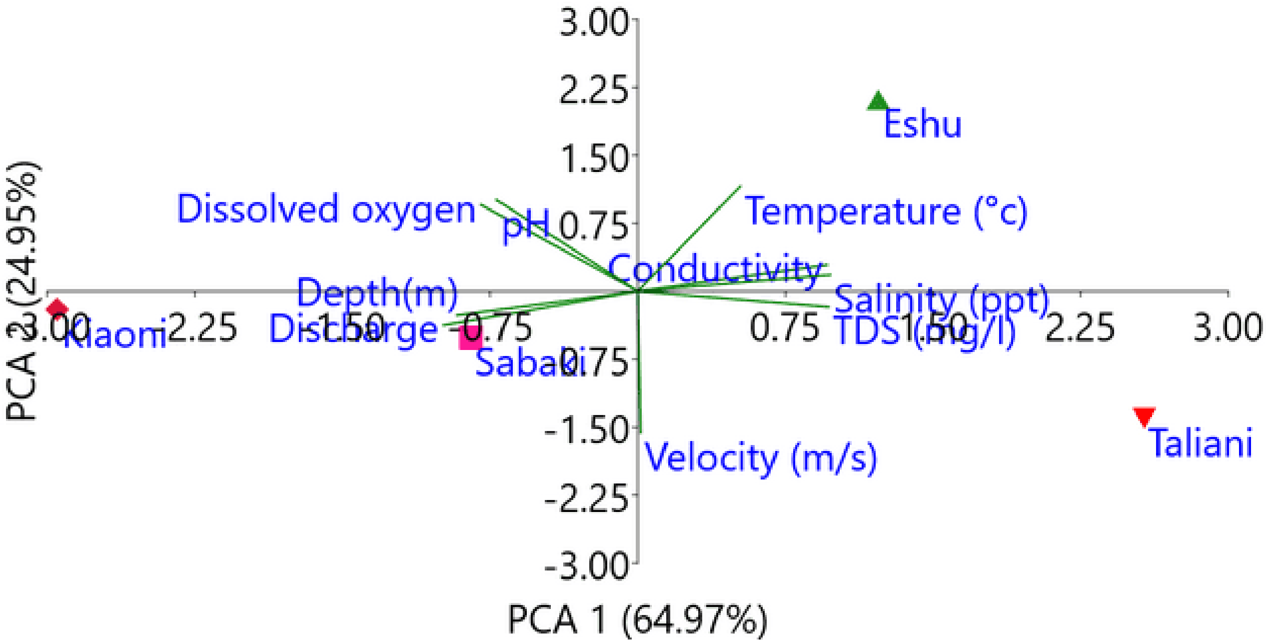


Figure 6: Principal component analysis (PCA) for multidimensional scaling of environmental variables PCA 1 (65%) and PCA 2 (25%) influencing occurrence of fish species among the sampling locations Athi-Galana-Sabaki (Athi) (Kiaoni and Sabaki) and Ramisi Rivers

Furthermore, the identified environmental variables were subjected to Canonical Correspondence Analysis (CCA). The results of CCA revealed the first two axes CCA 1 (45%) and CCA 2 (32%) accounted for over 77% of the variations in the occurrence of the 32 fish species (28 sympatric fish and 4 eel species) (Figure 7). The third axis (CCA 3) was responsible for (24%) of the variations. CCA 1 demonstrated that different fish species preferred different environmental variables among the sampling locations (Eigen value=0.60, p=0.04) (Appendix 7).

Anguilla mossambica was negatively influenced by temperature, *A. bicolor* and *A. bengalensis* positively correlated by salinity, TDS and conductivity, while *A. marmorata* by pH, especially at the upstream location of Athi River at Kiaoni. Estuarine species such as *Eleotris fusca* and *Ambassis gymnocephalua* had similar environmental sensitivity as *A. bicolor* and *A. bengalensis*. *Oreochromis spilurus spilurus*, estuarine species such as *Terapon jarbua*, *Mugil cephalus*, and *Glossogobius giuris* had similar response as *A. mossambica* which were also negatively correlated with both dissolved oxygen and discharge except *G.*

giuris which was positively correlated. *Clarias gariepinus*, *P. reticulata*, *O. spilurus* and *O. niloticus* had similar response with *A. marmorata*, which were in addition negatively influenced by dissolved oxygen and discharge (Figure 7). Although axis 1 of the Canonical Correspondence analysis showed that fish species preferred different environmental gradients (Figure 7), no significant differences were observed among the fish species (Eigen Trace value=1.34, p=0.17) (Appendix 7).

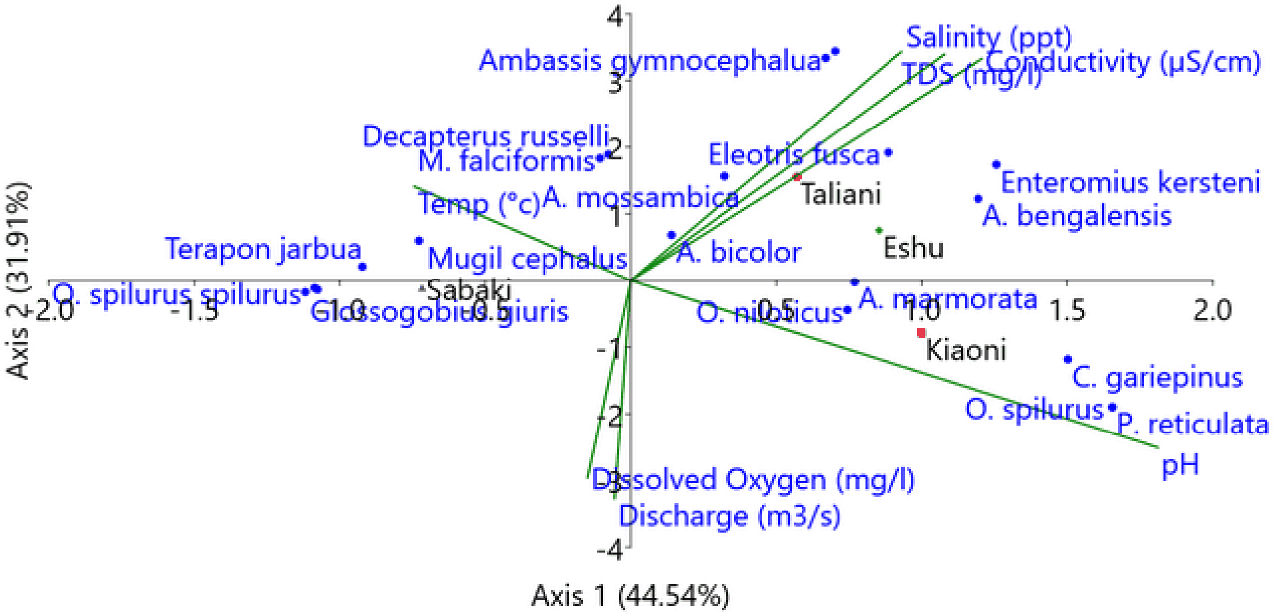


Figure 7: Canonical Correspondence Analysis (CCA) ordination between fish assemblage, sampling locations and environmental variables along Athi-Galana-Sabaki (Athi) and Ramisi Rivers

4.4 Diet preference, niche overlap and trophic interactions between sympatric fish and eels along the Athi-Galana-Sabaki and Ramisi rivers, Kenya

4.4.1 Diet composition and preference

Stomachs contents of 350 (283, 51) sympatric fish and 75 (31, 44) eels, from upstream and downstream locations of Athi and Ramisi Rivers were examined. 38 fish specimens for eels and sympatric fish (5, 33) at Athi and Ramisi Rivers respectively had empty stomachs and were excluded from subsequent evaluations. At Athi River, 30 (13, 17) eels and 254 (83, 171) sympatric fish were evaluated at the upstream and downstream locations respectively, while at Ramisi, 40(36, 4) eels and 63 (38, 25) sympatric fish were evaluated, respectively.

A total of 22 food types were identified among which; Penaeid shrimps (19%) and fish (18%) were most common (Table 10). Vegetation (9%), Caddisflies, crabs, detritus and prawn were consumed between 5 to 10% of the fish. Beetles, unidentified insect and mayflies were consumed between 2 and 5% of fish, while birds, annelid worms, bivalves, seeds, flies and stoneflies were the least consumed (Table 10). Similarly, penaeid shrimps (19.0%) followed by fish (18.34%) were most importance to stomach fullness contribution (Table 10).

The diet contribution among the rivers differed significantly (χ^2 test=46.10, df=18, p<0.05). Fish at Athi River consumed 20 food items, dominated by penaeid shrimps (22%), fish (16%) and vegetation (10%), while detritus (7.8%) mainly dominated by plant detritus (12%), caddisflies (7%) and crabs (6%) were of intermediate importance (Table 10). Fish in the Ramisi River consumed 12 food items dominated by fish (30%), prawns (29%) and unidentified detritus (11%) while crabs (8%) and penaeid shrimps (6%) were of intermediately importance (Table 10). Fish at Athi consumed more variety of invertebrate (13) than at Ramisi (4) (Table 10).

Table 10: Diet importance in stomach of fish at Athi-Galana-Sabaki (Athi) and Ramisi Rivers, Kenya. Most important food items are in bold with two asterick and intermediate with an asterick.

Food items	Occurrence (n)	Relative abundance (RA) (%)	Relative importance of diet items to stomach fullness (%)	Athi (%)	Ramisi (%)
Annelid worm	1	0.2	0.15	0.2	0.0
Earthworm	2	0.3	0.30	0.4	0.0
Beetle	16	2.4	2.41	2.6	1.6
Bugs	5	0.8	0.75	0.9	0.0
Bivalve	1	0.2	0.15	0.0	0.8
Pond snails	4	0.6	0.60	0.7	0.0
Caddisflies	37	5.6	5.56	**6.8***	0.0
Damselfly	3	0.5	0.45	0.6	0.0
Mayflies	11	1.7	1.65	2.0	0.0
Stoneflies	1	0.2	0.15	0.2	0.0
Chironomidae	5	0.8	0.75	0.9	0.0
Unidentified Insect	22	3.3	3.31	3.5	2.5

Animal detritus (AOM)	60	9.0	9.02	10.5	2.5
Plant organic matter	66	9.9	9.92	11.8	1.6
Unidentified detritus	32	4.8	4.81	3.5	**10.7***
Vegetation	62	10.3	9.17	**9.8****	7.4
Plant seeds	1	0.2	0.15	0.0	0.8
Crab	43	6.5	6.47	**6.1***	8.0*
Penaeid Shrimps	126	**19.0****	**19.0****	**22.0****	6.0*
Prawns	36	5.4	5.41	0.2	**28.7****
Fish	122	**18.4****	**18.0****	**16.0****	**30.0****
Birds	2	0.3	0.30	0.4	8.2

AOM-Animal organic matter

Fish at Athi consumed 20 items compared to 12 at Ramisi Rivers. Fish at the upstream location of Athi River consumed 15 dietary items dominated by unidentified detritus (36%), mainly composed of plant detritus (19%), caddisflies (19%) and vegetation (13%), while fish (8%) beetle (7.0%) and mayflies (5%) were of intermediate importance. In contrast, at the downstream location fish similarly consumed 15 items but dominated by penaeid shrimps (35%) and fish (21%), while crabs (10%) and vegetation (8%) were of intermediate importance (Table 11). Although fish at both locations of Athi consumed similar number of items (15), beetles, caddisflies, bugs, chironomids and prawn were only encountered at upstream whereas penaeid, crab, damselfly and stoneflies were encountered at the downstream location. Exotic fish at both reaches consumed the highest number of food items (14) at the upstream location largely dominated by Caddisflies (22%) and (15) at downstream dominated by penaeid shrimps (33 %).

Table 11: Dietary resource and their importance at upstream and downstream reaches of Athi River among eels and sympatric native/residents and exotic/introduced fish

Focal river	Athi-Galana-Sabaki (Athi)							
Reaches	Upstream/Kiaoni (%)				Downstream/Sabaki (%)			
Food items	Eels	Native	Exotic	All	Eels	Native	Exotic	All
Annelid worms	-	-	0.63	0.5	-	-	-	-
Earthworms	-	-		-	2.5	-	0.61	0.6
Beetles	-	-	8.86	7.0	-	-	-	-
Bugs	-	-	2.0	1.5	-	0.72	0.61	0.6
Pond snails	7.14	3.57	0.63	2.0	-	-	0.61	0.3
Caddisflies	-	10.71	**21.52***	**19***	-	-	-	-
Damselflies	-	-	-	-	-	0.72	1.22	0.9
Mayflies	-	14.29	3.80	5.0	-	-	0.61	0.3
Stoneflies	-	-		-	-	-	0.61	0.3
Chironomidae	-	-	3.16	2.5	-	-	-	-
Insects	-	-	5.1	4.0	2.5	2.88	3.66	3.2
Animal detritus	-	21.43	13.30	13.5	7.5	10.1	7.93	8.75
Plant detritus	-	28.57	18.35	**19***	-	8.0	9.76	7.87
DOM	-	10.71	2.53	3.5	2.5	5.76	1.83	3.4
Vegetation	7.14	10.71	14.0	**13***	7.5	5.76	9.76	8.0
Crabs	-	-	-	-	20	10.80	6.10	**10***
Penaeid shrimps	-	-	-	-	35	37.0	**33.0***	**35***
Prawns	-	-	0.63	1.0	-	-	-	-
Fish	**78.57***	-	2.53	8.0	22.5	18.71	22.0	**21***
Bird	7.14	-	-	0.5	-	-	0.61	0.3

At the upstream location of the Ramisi River, fish consumed twelve (12) food items dominated by prawns (37%) and fish (35%) while crabs (7.3%), DOM and vegetation (6.3%) were of intermediate importance. In contrast, at the downstream location, fish consumed seven (7) items dominated by detritus and penaeid shrimps (27%), and fish and crabs (12%). Insect, prawn, bivalve and seeds were only consumed at the upstream location of Ramisi, while penaeid shrimp were encountered at the downstream location (Table 12). Similarly, exotic fish consumed the highest number of food items at both upstream (8) dominated by prawns (27%) followed by fish (23%) and downstream (6) largely composed of penaeid shrimps (33%) and plant detritus (22%) (Table 12).

Table 12: Dietary resource and their importance at upstream and downstream reaches of Ramisi River among eels and sympatric native and exotic fish. Most important food items are bolded with an asterick

Focal river	Ramisi							
Reaches	Upstream/Eshu (%)				Downstream/Taliani (%)			
Food items	Eels	Native	Exotic	All	Eels	Native	Exotic	All
Beetles	-	-	4.55	1.0	-	-	11.11	4.0
Bivalves	2.13	-	-	1.1	-	-	-	-
Insects	4.26	-	4.45	3.1	-	-	-	-
Animal detritus	-	7.41	4.55	3.13	-	-	-	-
Plant detritus	-	-	-	-	-	-	22.22	7.69
DOM	-	3.70	22.73	6.3	33.33	45.46	-	**27.0***
Vegetation	6.40	7.41	4.55	6.3	17.00	9.10	11.11	**12.0***
Plant seeds	2.13	-	-	1.1	-	-	-	-
Crabs	4.25	11.0	9.1	7.3	-	18.18	11.11	**12.0***
Penaeid Shrimps	-	-	-	-	17.00	27.27	**33.33***	**27.0***
Prawns	**30.0***	55.56	**27.3***	**37***	-	-	-	-
Fish	**51.1***	14.82	23.0	**35***	33.33	-	11.11	12.0

DOM- Dead organic matter and is composed of unidentified detritus

One-way analysis of similarity (ANOSIM) revealed a significant dissimilarity in food compositions in fish among the rivers (Global R=0.46, p<0.05), as well as the location (R=0.403, p<0.05) (Appendix 8). Among rivers, detritus (25.7%), penaeid shrimp (25%), fish (14%) and prawns (10.4%) contributed the most to the dissimilarities (Appendix 9). Among locations, detritus (17% and 19%) and fish (30% and 13%) were responsible for 47% and 32% of dissimilarity at both upstream and downstream of Ramisi and Athi and also upstream of Athi and Ramisi (detritus, 27%) and (fish, 18.45%) respectively (Appendix 9). Prawns (28%) were most important for dissimilarity between both locations of Ramisi. Penaeid shrimp contributed to dissimilarity between both locations of Athi (upstream and downstream) as well as between downstream locations of Athi and Ramisi. Crabs were important for dissimilarity between downstream locations of Athi and Ramisi (Appendix 9).

The anguillids encountered primarily consumed 12 food items dominated by fish (43%), and crustaceans (36%); Penaeid shrimp (14%) and prawns (13%), while crab (9%) were of intermediate importance. Pond snails, birds, bivalves, earthworms, and seeds (0.94%) were the least consumed (Figure 8). Among the eels*; A. bengalensis* was purely carnivorous feeding on fish (55%), prawn (23%), crab (5%), and even birds (2%). *A. mossambica* was mainly carnivores on fish (32%), penaeid shrimp (21%), and crabs (16%), but also consumed detritus (11%), particularly in Athi River. Both *A. bicolor and A. marmorata* were omnivorous consuming fish, prawns, penaeid shrimps, insects, vegetation and detritus.

The sympatric fish consumed 21 dietary items dominated by detritus (27%), penaeid shrimps (20%) and fish (14%). Vegetation (10%) was intermediately important while caddisflies (7%) and crab (6%) were less often consumed (Figure 8). Both eels and sympatric fish shared crabs, detritus, fish, penaeid shrimps, prawns and vegetation.

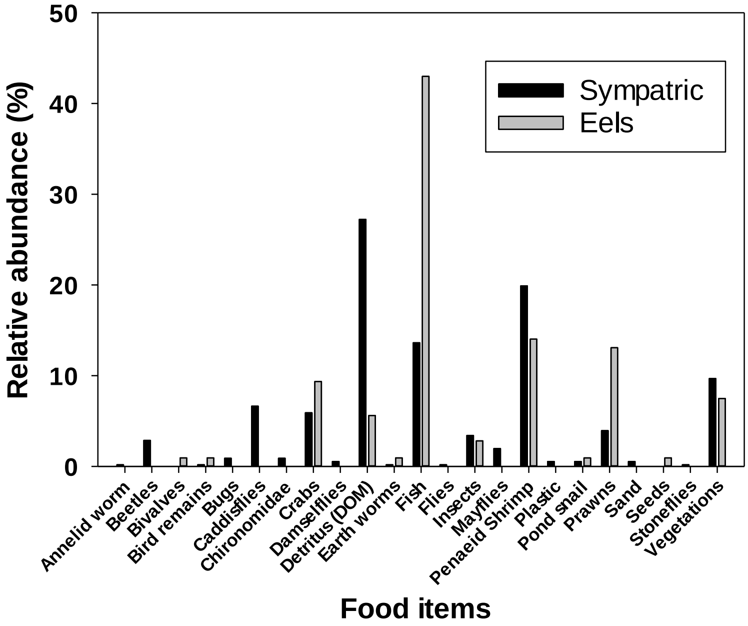


Figure 8: Diet preferences between sympatric fish and eels along the two east flowing rivers, Kenya

Diet preferences of the fish types evaluated differed significantly (ANOSIM; $p<0.05$) among the sampling locations. Sympatric fish at the upstream location of Athi River primarily consumed detritus (38%) composed of POM (23%) and AOM (15%), followed by caddisflies (20%) and vegetation (13%). At downstream, penaeid shrimps (35%), detritus (21.5%), fish (21%) were most important, with crab and vegetation (8%) being least important. The eels at the upstream primarily consumed fish (79%) while penaeid shrimps

(35%), followed by fish (23%) and crabs (20%), were more consumed at the downstream, which were comparable to those of sympatric fish diets (Table 13). At the upstream of Ramisi River, sympatric fish mainly consumed prawns (43%), fish (18%), detritus (18%) and crabs (10%), while at the downstream, sympatric fish consumed detritus (35%), penaeid shrimps (30%), crabs (15%) and vegetation (10%). Fish and beetles (5%) were least consumed (Table 13). Eels at the upstream of Ramisi consumed fish (51%) and prawns (30%) whereas at the downstream detritus, fish, penaeid shrimps and vegetation were comparable consumed by both eels and sympatric fish (Table 13).

At the upstream locations of both rivers, eels mainly consumed fish, while at downstream locations detritus, fish and vegetation were commonly encountered. Prawns were only consumed at upstream of Ramisi with penaeid at downstream locations.

Table 13: Diet preferences between sympatric and eel fish along Athi-Galana-Sabaki (Athi) and Ramisi rivers. Most important food items are bolded with an asterick.

Rivers	Athi-Galana-Sabaki (Athi)				Ramisi			
Reaches	Upstream		Downstream		Upstream		Downstream	
Locations	Kiaoni		Sabaki		Eshu		Taliani	
Food items	Sympatric	Eel	Sympatric	Eel	Sympatric	Eel	Sympatric	Eel
Annelid worms	0.5	-	-	-	-	-	-	-
Earth worms	-	-	0.3	2.5	-	-	-	-
Beetles	7.5	-	-	-	2.0	-	5.0	-
Bugs	1.6	-	0.7	-	-	-	-	-
Bivalves	-	-	-	-	-	2.1	-	-
Pond snails	1.1	7.1	0.3	-		-	-	-
Caddisflies	**20.0***	-	-	-	-	-	-	-
Damselflies	-	-	1.0	-	-	-	-	-
Mayflies	5.4	-	0.3	-	-	-	-	-
Chironomidae	2.7	-	-	-	-	-	-	-
Unidentified insects	4.3	-	3.3	2.5	2.0	4.3	-	-
Plastic	1.6	-	-	-	-	-	-	-
Detritus (DOM)	**38.2***	-	**21.5***	10	**18.4***	-	**35.0***	33.3

Vegetation	**13.4**	7.1	7.9	7.5	6.1	6.4	**10.0***	16.7
Plant seeds	-	-	-	-	-	2.1	-	-
Crabs	-	-	8.3	**20***	**10.2***	4.3	**15.0***	-
Penaeid shrimps	-	-	**34.7***	**35.0***	-	-	**30.0***	16.7
Prawns	0.5	-	-	-	**42.9***	**29.8***	-	-
Fish	2.2	**78.6***	**20.5***	**22.5***	**18.4***	**51.1***	5.0	33.3
Bird	-	7.2	0.3	-	-	-	-	-

Exotic sympatric predatory carnivorous fish, particularly Bagrus docmak, exhibited a preference for 15 different food items, with penaeid shrimps (35%), fish (24%), and vegetation (10%) dominating their consumption, while crabs (8%) were less frequently consumed. In comparison, native carnivorous fish such as Glossogobius giuris, Eleotris fusca, Oligolepis acutipennis, and Pisodonophis cancrivorus consumed a total of 9 food items. Their diet was led by penaeid shrimps (35%), fish (19%), and crabs (14%), with an intermediate consumption level of detritus (10.8%) and vegetation (7.9%) (Appendix 10). Among the native predatory carnivorous fish, a significant proportion of Oligolepis acutipennis (70%), Glossogobius giuris (47%), and Pisodonophis cancrivorus (39%) primarily consumed penaeid shrimps, while Eleotris fusca (56%) showed a preference for prawns. Additionally, Otolithes ruber (50%), O. acutipennis (30%), and G. giuris (29%) were observed to consume fish.

Exotic omnivorous fish, such as *Clarias gariepinus*, were found to ingest a total of 17 different food items. Among these, caddisflies (17%) and vegetation (15%) were the preferred choices, while fish (8%) held intermediate importance. On the contrary, native omnivorous fish such as *Terapon jarbua* and *Naziritor chelynoides* consumed a total of seven (7) items, with penaeid shrimps (33%), fish (27%), and detritus (10%) dominating their dietary preferences (refer to Appendix 10). Sympatric herbivorous exotic fish, including *O. niloticus*, *O. variabililis*, and *O. zillii*, demonstrated a preference for plant detritus (42%) and caddisflies (15%) among their 10 consumed food items, while beetles (8%) were of intermediate importance (Appendix 10).

The analysis of variance indicated a significant difference between eels and sympatric fish guilds (Global R=0.09, p<0.05). Despite this, there was an observed similarity in diet preference between the predatory sympatric carnivorous guild and eels (p=0.08) (Table 14), particularly notable in exotic predatory carnivorous species, which exhibited higher feeding similarities with eels (ANOSIM; p=0.1) (Appendix 11). This similarity was attributed to the consumption of fish (32%) and penaeid shrimps (23%). Conversely, dissimilarity was noted between eels and omnivores (36%) and between eels and sympatric predatory carnivorous fish (32%), which was primarily due to variations in fish consumption.

Table 14: Summary statistics of One-way ANOSIM pairwise correlation between fish types and food items preferences (P values in bold are significant at p<0.05)

Fish types	Eel	Carnivorous	Herbivorous	Omnivorous	Native	Introduced
Eel	1					
Carnivorous	**0.0827**	1				
Herbivorous	0.0001	0.0082	1			
Omnivorous	0.0074	**0.185**	**0.0817**	1		
Native	0.0082	0.1131	0.0448	0.0335	1	
Introduced	**0.0107**	0.1094	0.0915	0.0983	0.7675	1

4.4.2 Sympatric fish species feeding guilds and diet overlaps along Athi and Ramisi Rivers

The sympatric fish population in the Ramisi River belonged to higher trophic level (3.01±0.1) than at the Athi River (2.88±0.03), although this difference was not significant (Mann-Whitney U=39392, p=0.38). The fish species examined for gut content at Ramisi were composed of 7 species, dominated by *Eleotris fusca* and *Clarias gariepinus* while at Athi there were 19 species dominated by *Bagrus docmak* and *Clarias gariepinus*. Among the examined fish, a total of 17 sympatric resident/native fish species were identified at both locations, with Pisodonophis cancrivorus, Glossogobius giuris, and Eleotris fusca being dominant. Exotic fish species were represented by Bagrus docmak, Clarias gariepinus, and O. niloticus, found in both catchments (Table 5). Notably, Oligolepis acutipennis recorded the highest trophic level (TL) (3.66±0.18).

At the Athi River, among the 14 resident/native fish species, 6 species (*Glossogobius giuris, Oligolepis acutipennis*, *Otolithes ruber, Terapon jarbua, Chanos chanos* and

Pisodonophis cancrivorus) had the highest trophic level (TL) of above 3.0, while *Mugil cephalus* and *Macolor niger* had less than 2.4. Among the 5 exotic species at Athi River, two were (*Bagrus docmak*, and *Clarias gariepinus*) which had the highest TL, while *O. zillii* and *O. spilurus* had the lowest (>2.3). At the Ramisi River, among the 5 resident/native species, *Ambassis gymnocephalua, Eleotris fusca* and *Pisodonophis cancrivorus* had the highest TL with *Terapon jarbua* having the lowest (Table 15).

Mean diet breadth of sympatric fish examined was (1.49±0.08) for both Athi and Ramisi Rivers, but there were significant differences among rivers (t=3.4, df=85, p=0.01) and residency (t=6, df=292, p<0.05). The diet breadth of sympatric fish from Athi River was higher (1.65±0.05) than Ramisi (1.32±0.1) (Table 15). Among all sympatric fish species, the widest diet breadth was recorded on exotic omnivorous *Clarias gariepinus* at both catchments (Table 15). Among the resident fish from Athi River, the widest diet breadth was recorded for the carnivorous *Arius africanus* and herbivorous *Labeobarbus oxyrhynchus* and *O. spilurus spilurus*, while the lowest for the herbivorous was *Labeo cylindricus, Macolor niger* and *Mugil cephalus*. Among the exotic sympatric fish species at Athi River, the widest was omnivorous *Clarias gariepinus* and carnivorous *Bagrus docmak* while the lowest for the herbivorous *O. zillii* (Table 15).

At Ramisi among the resident fish examined, predatory carnivorous *Eleotris fusca* (2.80±0.14) and *Pisodonophis cancrivorus* (2.25±0.47) had the widest diet breadth while omnivorous *Terapon jarbua* (1.60± 0.67) and carnivorous *A. gymnocephalua* (1.00±0.67) had the narrowest. Among the exotic species at Ramisi, the omnivorous *Clarias gariepinus* (4.37±0.20) had wider breadth than *O. niloticus* (2.20±0.25), which was higher compared to all the species.

Table 15: Trophic levels (TL) and diet breadth of sympatric fish species at Athi-Galana-Sabaki (Athi) and Ramisi Rivers. The values in bold with an asterick represent higher species TL and diet breadth (B)

Rivers	Species	Residency status	Feeding guilds	N	Trophic level (TL)	Diet breadth (B)
Athi	*Arius africanus*	Resident	Carnivores	5	**2.95±0.21***	3.34±0.3
	Glossogobius giuris	Resident	Carnivore	23	**3.30±0.10***	2.47±0.14

		s			
Oligolepis acutipennis	Resident	Carnivores	8	3.66±0.18	1.697±0.22
Otolithes ruber	Resident	Carnivores	3	3.46±0.27	1.92 ±0.39
Pisodonophis cancrivorus	Resident	Carnivores	24	3.13±0.10	2.53±0.14
Terapon jarbua	Resident	Omnivores	4	3.06±0.24	2.56±0.34
Bagrus docmak	exotic	Carnivores	77	**3.12±0.05***	3.65±0.08
Chanos chanos	Resident	Omnivores	1	3.19±0.47	2.53±0.67
Naziritor chelynoides	Resident	Omnivores	2	2.5±0.33	2.00±0.47
Clarias gariepinus	Exotic	Omnivores	39	2.60±0.08	**6.65±0.11***
Labeo cylindricus	Resident	Herbivores	1	2.4±0.47	1.00±0.67
Labeobarbus oxyrhynchus	Resident	Herbivores	7	2.49±0.18	4.90±0.25
Macolor niger	Resident	Herbivores	1	2.2±0.47	1.00±0.67
Mugil cephalus	Resident	Herbivores	3	2.27±0.27	1.00±0.39
O. spilurus niger	Resident	Herbivores	11	2.49±0.14	3.03±0.20
O. spilurus spilurus	Resident	Herbivores	13	2.44±0.13	2.98±0.19
O. niloticus	Exotic	Herbivores	35	2.44±0.08	2.48±0.12
O. variabililis	Exotic	Herbivores	1	2.53±0.47	2.60±0.67

	O. zillii	Exotic	Herbivores	1	2.4±0.47	1.00±0.67
	Average				2.88±0.03	1.65±0.05
Ramisi	*Ambassis gymnocephalua*	Resident	Carnivores	1	3.1±0.47	1.00±0.67
	Eleotris fusca	Resident	Carnivores	22	3.24±0.1	2.80±0.14
	Pisodonophis cancrivorus	Resident	Carnivores	2	3.0±0.33	2.25±0.47
	Terapon jarbua	Resident	Omnivores	1	2.43±0.47	1.60± 0.67
	Clarias gariepinus	Exotic	Omnivores	11	**3.36±0.14***	**4.37± 0.20***
	O. niloticus	Exotic	Herbivores	7	2.29±0.18	2.20±0.25
	Average				3.01±0.1	1.32±0.1

4.4.3 Diet diversity and selectivity among sympatric fishes and eels

Mean diet diversity was (0.19±0.02) but differed significantly with river (2-tailed test; Df=168, t=5.1, p<0.05) and locations (F=16.4, p<0.05). Diet diversity at the Athi River (0.23±0.01) was higher than at the Ramisi River (0.15±0.02), with the upstream location harboring the highest diet diversity (0.26±0.01) compared to the downstream location (0.21±0.01). In contrast, the downstream location of Ramisi River had the highest diet diversity (0.17±0.03), compared to the upstream location (0.14±0.14), which were lower compared to Athi River locations.

The 13 food items consumed by eels were dominated by fish and crustaceans (as shown in Figure 8 above), corresponded to a diet diversity of (0.16±0.02) and a mean trophic level of (3.47±0.69). Eel diet diversity and trophic level were dependent on rivers (F=5.0, p<0.05; F=2.4, p=0.1), locations (F=8.0, p<0.05; F=11.0, p<0.05) and species (F=6.1, p<0.05; F=5.0, p<0.05) for diversity and trophic level respectively. *Anguilla marmorata* (0.30±0.07) had the highest diet diversity, *A. mossambica* and *A. bicolor* demonstrated an intermediate diversity which were comparable, while *A. bengalensis* (0.12±0.02) recorded the least diet diversity (Figure 9).

Sympatric fish (0.22±0.01) had significantly (2-tailed test; Df=146, t=3.6, p<0.05) higher diet diversity compared to eels (0.16±0.02) (Figure 9). The eel diet diversity was lower than that of exotic sympatric fish (0.25±0.01) but comparable to resident fish (0.17±0.01). Among the sympatric fish feeding guilds evaluated, omnivores (0.29±0.01) such as resident *Chanos chanos* followed by exotic *C. gariepinus* (as shown in Table 15 above), had the highest diet diversity with lowest being on carnivores (0.21±0.01) as a result of diet specialization similar to eel (Figure 9). Predatory resident species such as *P. cancrivorus* (0.24±0.02) contributed the highest diversity, with the least recorded on *A. gymnocephalua* (0.001±0.1).

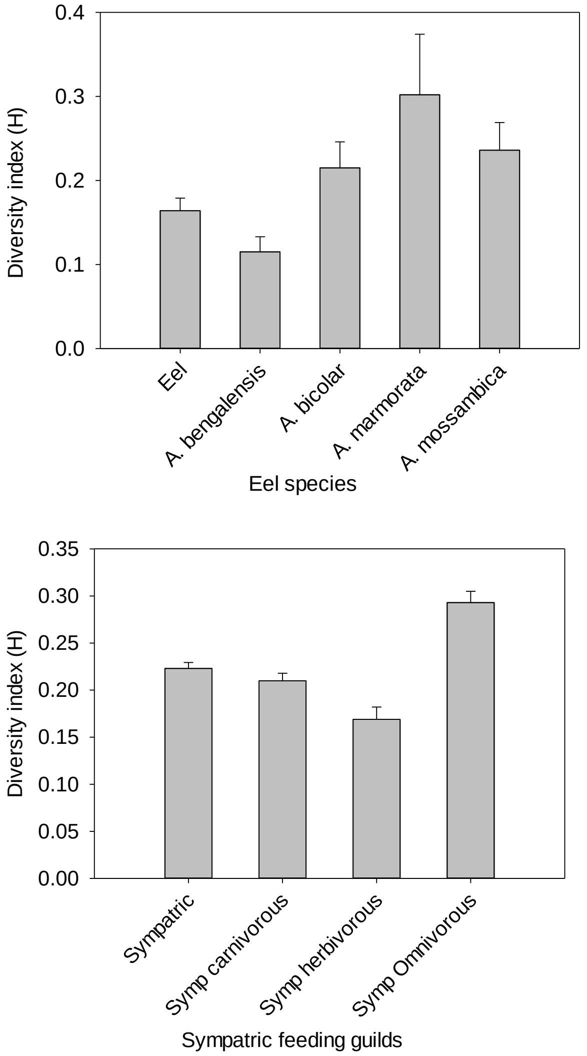


Figure 9: a) Diet diversity among eel and b) sympatric fish feeding guilds with Standard Error (SE) bars

Diet selectivity along the rivers was (0.39±0.02), which did not differ among the rivers (Mann-Whitney U=29910, p=0.09), but subsequently differed among; locations

(F=12.22, p<0.05), fish type (Mann-Whitney U=26042, p<0.05), feeding guilds (F=23.22, p<0.05) and residency (F=20.3,**a**p<0.05). Eels**b** had a higher diet selectivity (0.44±0.03) compared sympatric fishes (0.35±0.01). Eel diet selectivity was however comparable to resident fish (0.43±0.02) but higher than that of exotic fish (0.30±0.01). Among the eel, *A. marmorata* corresponded to the least selectivity (0), while *A. bengalensis* (0.55±0.03) and *A. mossambica* (0.32±0.06) displayed an active diet selection from the environment. (Figure 10).

Sympatric resident (0.43±0.02) and exotic (0.30±0.01) fish had comparable diet selectivity with sympatric herbivores (0.46±0.02), while resident and exotic omnivores (0.22±0.02) (for resident and exotic respectively) and carnivorous (0.37±0.02) (for resident and exotic respectively) were significantly (F=18.09, p<0.05) lower than eels (0.44±0.03) (Figure 10), demonstrating a higher diet specialization for eel feeding habits. In the contrary, sympatric herbivorous fish diet selectively (0.46±0.02) was higher compared to the other sympatric fish feeding guilds.

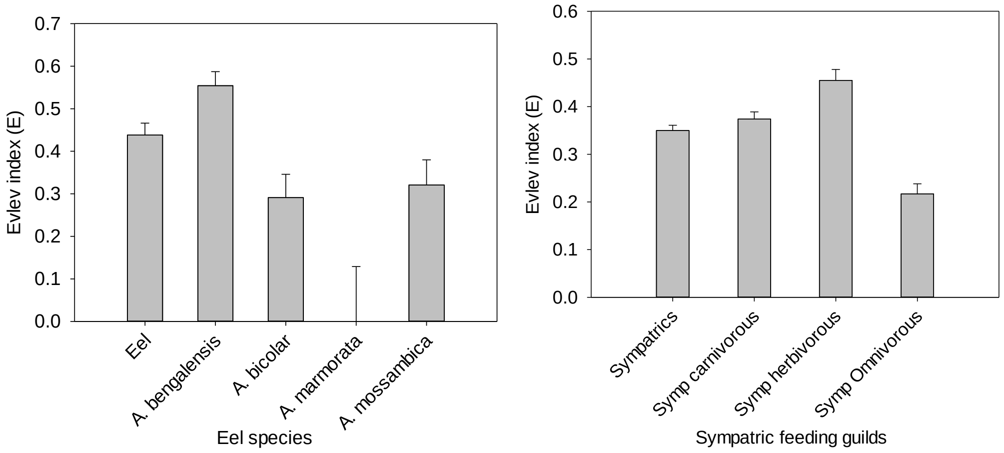


Figure 10: a) Diet selectivity among eel and b) sympatric fish feeding guilds with Standard Error (SE) bars

4.4.4 Diet and niche breadth (B) and trophic levels between eel species, feeding guilds and residency

Eel belonged to significantly (F=113, p<0.05) higher trophic levels (TL) (3.47±0.69), especially for *A. bengalensis* (3.61±0.07) at all sites followed by *A. bicolor* (3.20±0.15) compared to (2.90±0.03) for either resident (2.98±0.6) or exotic/introduced (2.8±0.04) sympatric fish. The trophic level of *A. bicolor* (3.67± 0.34**)** increased at Ramisi compared to Athi (3.09±0.16). *Anguilla marmorata* had the lowest TL (2.45±0.49) at all sites (Table 16). The sympatric resident fish (3.00±0.02) had a higher trophic level compared to exotic fish (2.88±0.02) but did not differ significantly (Mann-Whitney U=24987, p>0.05). The TL recorded for Athi River was higher for resident (3.0±0.02) than exotic fish (2.86±0.02) though significantly (F=146, p<0.05) lower compared to Ramisi River for either exotic fish (3.01±0.06) or resident (2.99±0.05). Sympatric carnivorous fishes recorded a higher trophic level (3.19±0.04) at Athi River but at Ramisi the TL was comparable between omnivorous and exotic fishes (Table 16).

The lower TL recorded for sympatric fishes, subsequently corresponded to a wider diet breadth compared to eel. The narrow diet breadth for eel accounts for their active diet selection, unlike sympatric fishes associated with an unselective feeding habit to wider dietary options. The sympatric herbivorous had the least TL (2.40±0.05), at all sites especially in Ramisi River. Resident sympatric fish at Athi had a higher trophic level (3.0±0.02) while exotic (3.01±0.05) recorded the highest at Ramisi (Table 16) although significantly lower (F=4.0, p=0.03) than eel at all sites. Sympatric fish diet breadth (B) (0.27±0.05) was always significantly higher (t=3.15, df=132, p<0.05) compared to eels (0.20±0.1) in both rivers. Resident sympatric fish had lower diet breadth (0.43±0.04) than exotic fish (0.57±0.06), attributed to expansive diet specialization. Similarly, at both location residents (0.23±0.15, 0.20±0.30 for Athi and Ramisi respectively) had lower diet breadth than corresponding exotic fishes (0.32±0.13, 0.26±0.43 for Athi and Ramisi respectively).

Omnivorous fish recorded a higher diet breadth (0.43±0.3) followed by carnivorous (0.30±0.4) which corresponded to an intermediate diet breadth at all sites, particularly among the estuaries. The least diet breadth was encountered among herbivores (0.27±0.3) at all sites largely due to their specialization feeding habit on dead organic matter (DOM). Among the rivers, omnivorous fish at both Athi (0.53±0.1) and Ramisi (0.33±0.2) corresponded to the widest breadth significantly higher (p<0.05) compared to eels except for exotic fish at Ramisi River (Table 16). Introduced sympatric fish always recorded the widest diet breadth at Athi (0.40±0.2) and Ramisi (0.39±0.4) compared to resident sympatric fish and eel, which did not differ significantly (F=0.1, p=0.91). Among the eels, highest breadth was encountered on *A. mossambica* (0.27±0.3) at Athi and *A. marmorata* (0.19±0.69) at Ramisi demonstrating unselective feeding habits.

Table 16: Levin's diet breadth indices and trophic levels among sympatric fish species feeding guilds and eels at Athi-Galana-Sabaki (Athi) and Ramisi Rivers. The values in bold with an asterick represent higher TL and diet breadth (B) for eel species and sympatric fish feeding guilds

Rivers	Fish	Fish type	N	Trophic level	Diet breadth

	categories			(TL)	(B)
Athi	Eels	*A. bengalensis*	14	**3.79±0.12***	0.10±0.18
		A. bicolor	9	3.09±0.16	0.16±0.23
		A. mossambica	6	3.34±0.18	**0.27±0.26***
		A. marmorata	0	-	-
	Sympatric fish	Carnivorous	243	**3.19±0.04***	0.22±0.06
		Omnivorous fish	115	2.65± 0.07	**0.53±0.10***
		Herbivorous fish	106	2.44±0.06	0.22±0.08
		Introduced	322	2.86±0.02	0.40±0.2
		Native	167	3.0±0.02	0.30±0.3
		Eel	31	3.42±0.04	0.31±0.5
Ramisi	Eels	*A. bengalensis*	34	**3.53± 0.08***	0.17±0.12
		A. bicolor	2	**3.67± 0.34***	0.11±0.49
		A. marmorata	1	2.45±0.47	**0.19±0.69***
		A. mossambica	3	2.8±0.27	0.12±0.40
	Sympatric fish	Carnivorous fish	29	**3.21± 0.10***	0.23±0.14
		Omnivorous fish	23	**3.28±0.14***	**0.33± 0.20***
		Herbivorous fish	14	2.26±0.14	0.11±0.21
		Introduced	31	3.01±0.06	**0.39±0.4***
		Native	38	2.99±0.05	0.30±0.3
		Eel	40	3.36±0.04	0.31±0.3

4.4.5 Diet overlap between eels and sympatric fish

Among the sympatric fish evaluated at Athi, greatest overlap was observed between omnivores and herbivores (0.50±0.1) but also carnivores (0.24±0.1). At Ramisi greatest overlap was between carnivores and omnivores (0.35±0.2) (Table 17).

Table 17: Dietary overlap among sympatric fish feeding guilds along Athi -Galana-Sabaki (Athi) and Ramisi Rivers. The values in bold with an asterick represent higher diet overlaps between sympatric fish feeding guilds.

Rivers	Fish type	Carnivores	Omnivores	Herbivores
A-G-S	Carnivores	-		

	Omnivores	**0.24±0.1***	-	
	Herbivore	0.17±0.6	**0.50±0.1***	-
Ramisi	Carnivores	-		
	Omnivores	**0.35±0.2***	-	
	Herbivores	0.08±0.1	0.26±0.2	-

Among the eel species evaluated in Athi, the greatest overlap was between *A. bengalensis and A. mossambica* (0.65±0.1), especially on fish diet items. The least overlap was encountered between *A. bicolor* and *A. mossambica* (0.29±0.1). Highest diet overlap was observed between *A. bengalensis* and *A. bicolor* (0.92±0.6) at Ramisi, while the lowest was observed between *A. marmorata* and *A. mossambica* (0.08±0.1) (Table 18).

Table 18: Pianka symmetrical niche overlaps among eel taxa at Athi -Galana-Sabaki (Athi) and Ramisi Rivers. The values in bold with an asterick represent higher diet overlaps between eel species

Rivers	Fish type	*A. bengalensis*	*A. bicolor*	*A. marmorata*	*A. mossambica*
Athi	*A. bengalensis*	-			
	A. bicolor	0.43±0.4	-		
	A. marmorata			-	
	A. mossambica	**0.65±0.1***	0.29±0.1		-
Ramisi	*A. bengalensis*	-			
	A. bicolor	**0.92±0.6***	-		
	A. marmorata	0.20±0.01	0.20±0.01	-	
	A. mossambica	0.41±0.2	0.45±0.16	0.08±0.1	-

The greatest dietary overlap for resource portioning were observed between predatory sympatric carnivorous and *A. bicolor* (0.81±0.01) at Athi, followed by *A. bengalensis* (0.48±0.1) and lower on *A. mossambica* (0.18±0.1) respectively (Table 19). The sympatric carnivorous fishes responsible for the overlaps included *G. giuris*, *Arius africanus* and *Oligolepis acutipennis*, particularly along the estuarine. *Anguilla bicolor* had a higher overlap with sympatric omnivorous fish (0.33±0.06) followed by *A. mossambica* (0.29±0.2) (Table 19) contributed by *Clarias gariepinus*. *Anguilla bicolor* (0.07±0.1) recorded the least diet overlap with sympatric herbivorous fish. At Ramisi River, diets of *A. bicolar* (0.74±0.11) overlapped with those of omnivorous fish such as *C. gariepinus,* while *A. bengalensis* (0.52±0.1) overlapped with those of carnivorous fish (Table 19) such as *Ambassis gymnocephalua* and *Eleotris fusca*. The diet of *A. mossambica* occasionally overlapped with those of herbivorous (0.89±0.3) and omnivorous (0.46±0.4). Subsequently, Athi River recorded the highest overlap (0.33±0.18) compared to Ramisi river (0.31±0.15), demonstrating greater relative amounts of inter and intraspecific competition on consumer-resource interaction between eel and sympatric fishes. No significant differences (p>0.05), were however observed on both niche and dietary overlap among the fish taxa and rivers.

Table 19: Overlap between sympatric fish and eels along Athi -Galana-Sabaki (Athi) and Ramisi Rivers. The values in bold with an asterick represent higher diet overlaps between sympatric fish feeding guilds and eel species.

Rivers	Fish type	*A. bengalensis*	*A. bicolor*	*A. marmorata*	*A. mossambica*
Athi	Carnivores	**0.48±0.1***	**0.81±0.01***	-	0.18±0.1
	Omnivores	0.10±0.13	**0.33±0.06***	-	0.29±0.2
	Herbivores	0.04±0.3	0.07±0.07	-	0.17±0.2
Ramisi	Carnivores	**0.52±0.1***	0.22±0.01	0.08±0.01	0.29±0.1
	Omnivores	0.45±0.1	**0.74±0.11***	0.13±0.01	0.46±0.4
	Herbivores	0.01±0.4	0.005±0.1	0.03±0.01	**0.89±0.3***

CHAPTER FIVE

DISCUSSION

5.1 Characterization of sympatric fish assemblage co-occurring with freshwater eels

5.1.1 Sympatric fish assemblage composition and endemicity

The 43 species and 32 families (Appendix 1) recorded for both Athi and Ramisi Rivers falls short of the 62 species described by Okeyo (1998) and the 58 species reported by Wanja (2013) for the Athi River, which included at least 39 endemic species. This study reported only 27 endemic species with a limited distribution between the two rivers, indicating a notable decline in endemicity. Other studies, such as Barnosky *et al*. (2011), have also reported global species extinction among freshwater ecosystems, resulting in a change in freshwater biodiversity metrics at a faster rate than terrestrial ecosystems (Sala *et al.*, 2000). Only *O. spilurus spilurus* (Sabaki tilapia) and *O. spilurus niger* (Athi river Tilapia), are considered truly riverine tilapiines (Seegers *et al.*, 2003; Wanja, 2013). Despite the low endemism reported in this study among the rivers, it's crucial to recognize that there is no substitutability among the river systems, as no single river supports the entire fish diversity in healthy and sustainable populations.

Furthermore, previous studies by Okeyo (1998) identified Cyprinidae as the most common family with 14 species, followed by Cichlidae with 6 species. However, the current study reveals a decline in both Cyprinidae (4 species) and Cichlidae (5 species). The study identifies Cichlidae, particularly dominated by the introduced species *Oreochromis niloticus*, as the most species-rich family across all sites. Besides, the highlighted lower relative abundances for certain fish species in both rivers (Table 1), along with restricted distributions, pose a risk of local extinctions due to increasing anthropogenic threats coupled with lack of long-term monitoring (Sayer *et al.*, 2018). The greater prevalence of species categorized as "least concern" on the IUCN Red List in this study can be mainly ascribed to insufficient data. Furthermore, the true riverine cichlids recorded are rare, and their conservation status remains uncertain, potentially indicating local extinctions.

Although Seeger *et al.* (2003) reported at least 18 exotic fish species introduced into Kenyan rivers, this study found only six (6) and three (3) exotic species for the Athi and Ramisi rivers, both dominated by *O. niloticus* (84% and 96%) respectively followed by *Bagrus docmak* (7%) and *C. gariepinus* (5%), particularly at Athi river. Among these, *O. niloticus* and *C. gariepinus* were highly invasive in both rivers. Similarly, *O. niloticus* have been reported in other studies, including those of Masese *et al.* (2020), to be highly invasive throughout the range of Lake Victoria Basin Rivers (LVB). Only *O. spilurus* is considered truly riverine among the tilapiines (Wanja, 2013), while the other three taxa were introduced from other lakes and aquaria (Hickley *et al*., 2008; Seegers *et al*., 2003). Similarly, while *C. gariepinus* may be a resident riverine fish, widespread introductions may have rendered it invasive.

The majority of exotic species identified in this study were landed in substantial numbers, exhibiting various size classes larger than native species. This observation suggests the establishment of populations, posing a significant threat to indigenous riverine populations (Masese *et al*., 2020; Okwiri *et al*., 2019). In contrast to previous studies Okeyo (1998), Seegers *et al*. (2003) and Wanja (2013), certain introduced species like *Ctenopharyngodon idella* (Valenciennes, 1844), *Cyprinus carpio* (Linnaeus 1758), *Oncorhynchus mykiss* (Walbaum, 1792) and *Salmon trutta* (Linnaeus 1758), introduced for sport fishing (Kenya Gov, 1970) and aquaculture revitalization, were not encountered in this study. Their current absence suggests changes in fish communities over time, prompting the need for further investigation.

5.1.2 Longitudinal patterns in fish distribution and migration

As the rivers flow into the Indian Ocean, there was a general increase in both fish species and abundance (Table 5). Although only two species exhibit a cosmopolitan longitudinal distribution, some fishes are exclusive to either the upper or lower reaches of the rivers. For instance, *Enteromius kersteni* is found only in the upper reach of the Ramisi River, while species like *Amphilius uranoscopus*, *Clarias liocephalus*, *Gambusia affinis*, *Labeo cylindricus*, *Labeobarbus oxyrhynchus*, *Oreochromis spilurus niger* and *Poecilia reticulata* are exclusively reported in the upper reach of the Athi River. Estuarine locations between the rivers exhibit higher species communities, with similarities attributed to the diverse habitat in estuaries despite stressful environmental conditions (Able, 2005). In the lower reaches, Gobiiidae and Cichlidae become prominent, though no family stands out as particularly dominant.

Only two species, *O. niloticus* and *C. gariepinus*, demonstrate a widespread distribution across all reaches. Fish migrations between the two rivers are largely dominated by potamodromous and amphidromous species, particularly in the lower reaches, highlighting a distinctive feature of estuarine fish communities. The documented lifestyles of these fish, such as amphidromous species, are not as well-known as those of their marine counterparts. Amphidromous species, known as estuarine spawners, either spend their entire life in the estuary or migrate in to spawn (Naiman *et al*., 2002). The presence of three species (*O.*

niloticus, Glossogobius giuris, and *B. docmak)* is attributed to differences in fish assemblages detected by ANOSIM as revealed by SIMPER (Appendix 2). The invasive *O. niloticus* is among the most widespread species across all sampling reaches, while *G. giuris* and *B. docmak* dominate the estuarine location, particularly at Sabaki.

5.1.3 Eel occurrence and distribution patterns

Eel fish species have different ecological preference, influencing their distribution patterns in the two rivers. *A. bengalensis* displayed a broad distribution, exploiting both estuarine and upper reaches, indicating adaptability across different habitats. This versatility, particularly demonstrated by *A. bengalensis*, makes them susceptible to various environmental stressors (Lin, 2017). Conversely, *A. bicolor* is constrained to lower reaches characterized by elevated salinity gradients (Shiao *et al*., 2003). The predominance of *A. marmorata* in upper reaches suggests a preference for predominantly freshwater environments. These findings align with prior studies by Shiao *et al*. (2003), Arai *et al*. (2020) and Briones *et al*. (2007), which categorize *A. bengalensis* and *A. marmorata* as freshwater-contingent species. However, this contradicts the suggestion by McCosker *et al*. (2003) that *A. marmorata* has an extensive geographical range from the east coast of Africa to the Galapagos Islands.

The results obtained in this study further differs with previous findings of Copley (1958) and Okeyo (1998) that reported *A. mossambica* to occur in both reaches of Athi River. This study reports *A. mossambica* as an estuarine-favoring contingent species, owing to its higher prevalence in estuaries (Table 6). This is the first current study of its kind to demonstrate that tropical eels in East flowing rivers and their associated streams inhabiting estuarine, brackish, and freshwater habitats during their growth stages, unlike those of Okeyo (1998) only highlighting the presence eels along Athi River.

5.1. 4 Sympatric fish and eel biomass contribution on riverine fishery

Although all fish in east-flowing rivers are edible, only a select few species are capable of sustaining a commercial fishery along the Athi River. Notable species in the upper catchment include *O. niloticus*, *C. gariepinus*, *O. spilurus niger*, *Labeo cylindricus* and *O. variabililis*, while the lower catchment sees *Bagrus docmak*, *C. gariepinus*, *O. spilurus spilurus*, *G. giuris*, *O. niloticus* and *P. cancrivorus* as commercially viable. Despite the potential of endemic species to support the fishery, invasive species overshadow them, recording the highest biomass among catches. In the Athi River, eel species like *A. marmorata* and *A. bengalensis* exhibit the highest biomass compared to other sampled species. In the Ramisi River, key fishery species include *C. gariepinus*, *Eleotris fusca* and *O. niloticus* in the upper catchment, and *G. javanicus*, *C. gariepinus*, *O. niloticus*, and *P. cancrivorus* in the lower catchment (Table 5).

Eel species at the Ramisi River, particularly *A. bengalensis* and *A. bicolor*, have the highest biomass compared to sympatric fish species, aligning with previous findings by Rowe *et al*. (1999) highlighting the dominance of eels in fish biomass. The study underscores that the contribution of fish to the fishery is determined by biomass in catches, translating to economic gains measured in tons. While some similarities exist across reaches in terms of species value to the fishery, there are nuances, such as the case of *P. cancrivorus* (snake eel) in the lower reaches, which, despite being a high biomass species, lacks cultural acceptance as a delicacy, requiring further validation.

The upper reaches of the sampled locations demonstrated the highest biomass contribution for both sympatric fishes and eels in comparison to the lower reaches, pointing to a more commercially viable fishery in the upper reaches. This is attributed to the prevalence of large individual fish proliferated with a higher fish density. The study supports previous studies noting a decline in riverine fisheries in Kenyan rivers over the past 70 years, (Cadwalladr, 1965; Ochumba & Manyala, 1992; Owiti *et al*., 2013) reflected in the lower commercial fish species recorded in the lower reaches of this study. Despite higher density and abundance, the lower reaches demonstrate lower commercial value, with the once lucrative riverine commercial fishery in the lower reaches of Lake Victoria Basin Rivers having collapsed and been replaced by a subsistence fishery (Masese *et al*., 2020).

In the Ramisi River, eels contribute more biomass than sympatric fish, especially in the upper reach, primarily due to the dominance of a single species, *A. bengalensis*, compared to other eel species. These findings are consistence with those of Kuroki *et al*. (2014), emphasizing that eels have the highest economic value per weight. This underscores the economic significance of *A. bengalensis*, positioning it as a valuable species and a potential candidate for commercial fishery and international trade (Monticini, 2014).

5.1.5 Sympatric fish and eel biodiversity

The diversity of both eels and sympatric fish varies across rivers and reaches, ranging from 32 species (27 sympatric and 4 eels) in the lower Athi River at Sabaki to 15 species (11 sympatric and 4 eels) in the upper reach. In the lower reach of the Ramisi River, there are 25 species (21 sympatric and 3 eels), while the upper reach has 10 species (6 sympatric and 4 eels) (Table 8). Unlike the lower catchments, the upper river catchment exhibits low species richness (4-15 species), with a high abundance of one or two species reported. These findings agree with previous studies by Okeyo (1998) and Wanja (2013), indicating higher species richness in the lower reach compared to the upper reach of the Athi River. Similarly, Vinagre and Costa (2014) reported higher species richness and abundance in estuarine habitats, emphasizing the significance of habitat heterogeneity for organism distribution (Diop *et al*., 2016). The prevalence of a specific species, *A. bengalensis* (Table 6), leads to a higher eel dominance index in the Ramisi River compared to sympatric fish species across reaches. This, combined with fewer disturbances and favorable river hydrological conditions, suggests that protected areas within river catchments support large fish populations (Saunders *et al*., 2002). The biological diversity indices used in the study consistently highlight differences in fish diversity and richness between rivers and reaches (Table 8).

The heightened diversity of both eel and sympatric fish species observed at estuarine locations (Table 8) is primarily attributed to increased interconnectivity, the influx of riverine species from upstream, the presence of oceanic origin and estuarine species (Seegers *et al*., 2003; Kimakwa, 2004), and the coexistence of all ecological categories (Albaret *et al*., 2004). The estuarine diversity encompasses both riverine and estuarine species, including Anguillid eels, *C. gariepinus*, *Tilapiine spp*., *G. giuris, P. cancrivorus* and *Periophthalmus barbarus*. Additionally, commonly found marine species include *Terapon jarbua*, *Mugil cephalus*, *Otolithes ruber*, *Lutjanus monostigma*, *Ambassis gymnocephalua*, *Chanos chanos* and *Monodactylus falciformis*. The incursion of marine-based species into estuarine diversity is linked to temporal changes in estuarine conditions (Kimakwa, 2004).

The species rich families, included Gobiiidae and Eleotridae (Appendix 1) attributed to their ability to withstand the higher salinity regimes of the estuaries and freshwater conditions from upstream (Okeyo, 1999; Whitfield, 2015). According to Tornabene (2014), gobies can be found in nearly every aquatic habitat on earth, constituting the most diverse and numerically abundant fish in tropical and subtropical habitats. According to Masese *et al*. (2020), lower Shannon diversity index indicates widespread degradation affecting fish communities, similar to results obtained for sympatric fish (<1.044±0.12) and eel (<0.346±0.12) among the upper reaches in this study (Table 8). In comparison to Ramisi, Athi River had the highest diversity of sympatric fish species and eels, owing to its larger river size and wider channel. Despite the high pollution levels reported by Kitheka and Mavuti (2016), the higher eel species diversity for Athi River perhaps demonstrates their resilient to anthropogenic stressors (van Ginneken *et al*., 2001), that collectively have enabled them to become a successful and widespread genus (Jellyman, 2021), demonstrating remarkable adaptability during their freshwater residence (Tsukamoto & Arai 2001).

5.2 Habitat utilization between sympatric fishes and freshwater eels

5.2.1 Environmental variables of the river sampling locations among habitats

Majority of the environmental gradients varied (Table 2), with an exception of pH, which was relatively higher, especially at Sabaki. This demonstrates that land use changes along the two catchments, impact the river systems in significantly different ways (Giri & Qiu, 2016). The higher velocity among the downstream estuarine locations, particularly at Sabaki, was largely attributed to the wide channel, which subsequently allowed tidal waves to penetrate much deeper into the estuary (Kitheka & Mavuti, 2016). In contrary, the shallow depth at Ramisi River downstream location (Table 1), resulted in a reduced penetration of semi-diurnal tidal waves into the estuary. However, the upstream location of Athi river was much deeper compared to the other sampling locations (Table 1). The higher discharge at the upstream location of Athi River was due to intrusions of high-water runoffs from the upstream catchment compounded with land use change (Kithiia, 1997), as well as water intrusions from nearby tributaries draining into the mains river channel (Wanja, 2013). As a result of its large and wider charnel, Athi River recorded thirty threefold discharge higher than Ramisi River, similar to previous studies by Kitheka and Mavuti (2016), which proliferated to higher sediment loads to the downstream reach (Kithiia & Wambua, 2010).

Conductivity (EC), Total Dissolved Solids (TDS), and salinity were significantly higher at Ramisi River compared to Athi River, owing to the high salinity levels recorded at both locations (Table 2). Similarly, the inflows of brackish geothermal waters from the Mwananyamala hot springs are also blamed to play a significant role (GoK, 2017). Furthermore, previous pre-historical geological studies, such as those of Soper (1967) and Gregory (1926), noted that Ramisi River sits on the Duruma Sandstone crops, with Shimba Hills, being the river's source, also forming part of the Duruma Sandstone Series in its upper catchment (Caswell, 1953). In addition, this geological reference, largely explains the higher values recoded regardless of land use change from the catchment scale, considering the catchment is intact compared to Athi River (Kitheka & Mavuti, 2016; Muriithi, 2016). According to this study, the high levels of EC and TDS are linked to characterizations of highly saline rivers. However, the higher salinity gradients recorded at both downstream locations, could be attributed to sea water intrusion into the estuaries (Vinagre & Costa, 2014).

The higher conductivity and TDS recorded at the downstream location of Athi River are linked to land use change and high sediment inputs from the upstream catchment (Kithiia & Wambua, 2010) and within the basin (Fleitmann *et al.*, 2007; Kithiia, 1997). Kithiia and

Wambua (2010) recorded similar results, demonstrating an increased trend downstream along the Athi River associated with increased sediment loads downstream. Besides, the upstream location of Athi River recorded higher values compared to previous studies (Kithiia, 2012) in some Nairobi River sites draining into the Athi River. The findings of this study contends that the upper part of Athi River should have much higher values due to its proximity to and draining of Nairobi city, characterized by a dynamic land use change (Kithiia, 2006).

The lower pH value >7.02) (Table 2) recorded at the downstream locations of both rivers were attributed to sea water intrusions coupled with an increased salinity which curtained water buffering (Kimakwa, 2004), compared to the upstream locations which were much higher (<7.36), especially for Athi River. In contrast, lower temperature levels were recorded at the upstream reach of Athi, linked to higher altitudinal climatic conditions associated with upstream rivers (Hellawell *et al.,* 1994).

5.2.2 Fish assemblage composition among habitat types

Fish communities in riverine ecosystems require various habitat types for their assemblages (Huang *et al*., 2019). In this study, *O. niloticus* emerged as the predominant fish species among sympatric fish across all sampling locations, showcasing dominance in all evaluated habitat types, notably pools and vegetation recognized as favorable habitats for aquatic organism refuge (Seegers *et al*., 2003). Other studies suggests that individuals of the same species may utilize different habitats depending on their ontogeny stage (Pennock *et al*., 2018), emphasizing the influence of feeding patterns on fish habitat selection (Stergiou & Karpouzi, 2002). Additionally, carnivorous sympatric fishes like *Oligolepis acutipennis*, *G. giuris*, and *Eleotris fusca*, belonging to the Gobiiidae family associated with a relatively higher trophic level, also exhibited a preference for pools, vegetation, and riffles with high velocity, particularly evident at the Sabaki estuary, as described by Huang *et al.* (2019) elsewhere.

Fish within the rivers demonstrated a preference for pools, which are associated with an abundance of food refuge, followed by riffles characterized by highly oxygenated waters (Armantrout, 1998; Bain & Jia, 2012). Huang *et al.* (2019) emphasize the significance of pools and step pools in fish community breeding and growth, serving as crucial refuges during dry seasons. Upstream in the Athi River, fish, particularly *C. gariepinus, O. niloticus,* and eels, were observed to prefer vegetation as a key habitat type (Figure 5). Conversely, downstream in the Ramisi River, fish, including eels, predominantly occupied fast-flowing habitats with fine substrate due to its shallow depth (Jellyman *et al*., 2003).

Among the four evaluated eel species, *A. bengalensis* and *A. bicolor*, the most dominant, exhibited a strong preference for pools (Jellyman, 2021). Although eel species were found to dominate both pools and riffles, they were widely distributed and often overlapped with vegetation, including debris clusters, particularly around invasive water hyacinth. This overlap served to provide cover and shade, contributing to their broader habitat breadth (Johnson & Nack, 2013). The four eel species were occasionally encountered in all other habitat types as well (Appendix 3). These findings are consistent with these of Arai (2016), which demonstrated that eels inhabit various microhabitats throughout the river, increasing their chances of overlapping habitats with sympatric fishes. Their adaptability allows them to utilize a wider range of environments and habitats than other freshwater genera (Piper *et al*., 2013). Arai and Kadir (2017) proposed that the microhabitats of these species evolved differently to mitigate inter and interspecific competition for food and space, a notion supported by the observed habitat overlaps with impactful sympatric fish species in this study.

Habitat homogenization can reduce species richness and fish diversity (Walrath *et al*., 2016). Consequently, this study revealed that habitat types had a significant impact on fish diversity for both sympatric fish and eels (Huang *et al*., 2019). However, the habitat types had no effect on the fish type habitat selection, indicating a degree of similarity in the frequency of distribution and utilization of habitats by fish population. Furthermore, all of the fish types displayed a random selection of habitat from the environment, linked to lower selectivity index values that were close to zero (Table 9). Similar feeding behavior were reported by Jellyman *et al*. (2003) and Laffaille *et al*. (2003), who proposed that eels have an ontogenetic difference in preferred habitats occupied, although they might inhabit the same general area for several years (Jessop *et al*., 2008).

5.2.3 Relationship between fish assemblage and environmental variables

Only seven of the nine measured environmental gradients had a significant impact on fish assemblage along the two rivers. These included both river morphometry and physico-chemical water quality variables (Figure 6). However, different fish species preferred different environmental variables characterizing habitat quality across the sampling locations (Figure 7) based on their tolerance levels. As such, this indicates that, the adaptability of fish communities is based on presence of habitat heterogeneity (Vinagre & Costa, 2014), coupled with quality, which are measures of water quality (Giri & Qiu, 2016). The fish composition which included both eels and sympatric fishes, was heavily influenced by salinity, TDS, and conductivity, which were significantly higher in both reaches of Ramisi River compared to the other locations. Additionally, the results of this study further revealed that, the fish and eel compositions in both estuaries were adapted to significant habitat heterogeneity in terms of salinity and temperature variables, which are important for organism distribution (McLusky & Elliott, 2004). As a result, eels' resilience allowed them to tolerate harsh water quality conditions such as warm temperatures and low dissolved oxygen, as described by Luo *et al*. (2013). For resistance the temperate eels, were observed to survive and grow better at water temperatures ranging from 28 to 33 (°c). Other studies, however, have reported that they can survive in low temperatures of 1-3 (°C) but enter into a torpor state (Sadler, 1979), demonstrating their adaptability evolution (Jellyman, 2021).

Furthermore, the fish encountered at the estuarine location of Athi River, Sabaki were positively correlated with moderate temperatures, similar to previous result by Kimakwa (2004), and largely negatively influenced by both dissolved oxygen and discharge, which were relatively moderate compared to the other sampling locations. The moderate dissolved oxygen reported for the Sabaki estuary is attributed to sea water intrusion, supporting the estuary's self-replenishment. Despite variations in abiotic variables that make estuaries stressful environments, estuaries continue to house diverse species, spawning grounds, refuge from predators, and migratory routes for many species (Elliott & Hemingway, 2002), as evidenced by this study.

pH, dissolved oxygen, and discharge had a positive influence on the occurrence of sympatric fish and eels at the upstream locations of Athi River. The high discharge recorded in the upper reach is largely due to river habitat modifications and morphometry characterized by gobbles, which enhanced continuous water flow, proliferated with the river slope elevation. The findings of this study agree with those of Briones *et al*. (2007), who proposed that eel choice of habitat use is influenced by plasticity in response to local conditions such as salinity, temperature, and elevation. Furthermore, the results of this study confirm that, as shown by the Canonical Correspondence Analysis, species distribution, abundance, and composition at the reaches were a response to different environmental gradient.

5.3 Diet preference, characterization, trophic interactions, Diet and Niche overlaps

5.3.1 Diet composition and preference among eels and sympatric fish

Among the food items evaluated, penaeid shrimps and fish were the most important food items for fish (Table 10), indicating that, majority of the fish species encountered along the two rivers largely preferred high protein-rich food resources. Subsequently, this demonstrates a prevalence of high trophic level fishes among the rivers, particularly for Ramisi. The upstream locations had a higher diet composition, especially for Athi River, indicating unselective feeding habits among upstream river fishes (Gerking, 2014) largely from a diverse range of prey items, especially for sympatric fishes.

The upstream location of Athi River harbored unique food item strictly associated with freshwater taxas (Itakura *et al*., 2015), and of lower trophic level such as vegetation, detritus and macroinvertebrates (Keppeler *et al.,* 2020; Kihia *et al*., 2015) considered as indicators of high pollution (Kobingi *et al*., 2009). Supposedly, this suggest that pollution may not only reduce the variety of prey items for eels in rivers, but also compromise growth conditions (Drouineau *et al*., 2018). Additionally, majority of the fishes encountered belonged to lower trophic levels, such as tilapiines and *Clarias sp*, which are primarily herbivores and omnivorous respectively (Abdel-Tawwab, 2005; Kadye & Booth, 2012). These findings are consistent with those of Tófoli *et al.* (2013) who reported *Clarias sp* to primarily feed on Chironomidae and trichopteran, known to be highly resistant to extreme pollution conditions (Walsh *et al*., 2005), suggesting that these groups are undoubtedly associated with polluted urban rivers.

The downstream estuarine locations on the other hand, displayed a lower diet composition attributed to higher diet specialization, dominated by food items found only in brackish waters such as shrimps and crabs (Itakura *et al*., 2015). These findings agree with those of Maitra *et al*. (2018), who reported higher specialization among estuarine fishes, attributed to greater food availability in brackish environments than freshwater (Kaifu *et al*., 2013). The downstream location of Athi River was mainly dominated by high pretentious diets than the corresponding upstream location, attributed to the presence of higher trophic level fish (Pasquaud *et al*., 2010) with an interplay of oceanic fish species (Kimakwa, 2004).

In contrast to the Athi River (Table 10), fish in the Ramisi River predominantly consumed protein rich diets associated with higher trophic levels, a pattern attributed to the prevalence of high trophic level fishes in the upstream location of the river. The inclination towards higher trophic level diets among fish, particularly in the upstream area of the Ramisi, can be largely linked to the prevalence of resident carnivorous eels. Elsewhere, this phenomenon, has been reported by Jellyman (2021), associated with increased competition for common resources (Mylius *et al*., 2001). The current study findings align with the work of Cutwa and Turingana (2000) and Navia *et al*. (2010), who proposed using knowledge of natural diets to infer information about fish nutritional requirements within species across diverse habitats. This approach aids in comprehending trophic levels, energy dynamics, and modeling outcomes related to the utilization of food resources among ecosystems.

In the upstream location of the Athi River, eels demonstrated a preference for novel diets with higher trophic levels compared to sympatric fish (Arthington, 1991; Jellyman & Sykes, 2003). However, at the downstream location, both eels and sympatric fish consumed similar high-protein rich diets, suggesting increased interspecific interaction at the estuary (Manko, 2016) and potential competitive trophic interactions in aquatic food webs (Chipps & Garvey, 2007). Similarly, in the Ramisi River, eels demonstrated a preference for high-protein diets, including fish and crustaceans. This aligns with previous studies by Sinha and Jones (1967) and Irakura *et al*. (2015), whereas sympatric fish were reported for the first time in this study, highlighting incidents of inter- and intra-specific interactions among species (Zacharia, 2017). Consequently, feeding patterns varied across rivers for both sympatric fish and eels. Understanding such variations in feeding patterns is crucial for conservation efforts, particularly for endangered species and exploited populations like eels, which have been reported to continuously decline (Hanzen *et al*., 2019; Jellyman, 2021). Information about trophic interactions and dietary preferences, as presented in this study, can play a vital role in guiding preservation and management strategies.

The present study further revealed that eels occupy higher trophic levels by exclusively consuming fish, crustaceans, and bivalves (Irakura *et al*., 2015). Moreover, there was a notable correlation in feeding habits between eels and sympatric carnivorous fishes, indicating potential diet overlaps (Guzzo *et al*., 2015). Additionally, omnivorous fish displayed a diet similar to that of eels. This echoes findings observed in salmon and trout, where they consumed diets preferred by eels (Moorhouse-Gann *et al*., 2020; Sinha & Jones, 1967).

Moreover, among the encountered eel species, some exhibited unselective feeding behavior, including the consumption of detritus and vegetation. This behavior aligns with ontogenic feeding patterns (Sagar *et al*., 2005), portraying them as opportunistic predators and scavengers with a diverse diet (Itakura *et al*., 2020; Jellyman, 2021). This partly suggests that eels may serve as indicator species for freshwater biodiversity conservation due to their feeding habits (Itakura *et al*., 2020). The study's results also uncovered that, in addition to preying on sympatric fishes, eels were predators of birds, particularly in the upstream area of the Athi River (Table 11). Although other studies have documented eels as a significant dietary component for various predators, including birds, impacting eel populations (Leukona, 2002), the predatory exotic fish also demonstrated a preference for birds in their diet, especially at Sabaki, recognized as one of the key Important Bird Areas (IBA) (Okuku *et al*., 2022). This points to potential competition between eels and predatory exotic fish for avian prey.

5.3.2 Sympatric fish species feeding guilds, trophic levels (TL) and diet breadth

The highest trophic level observed among sympatric fish species in the Ramisi River (Table 15) is linked to the prevalence of high trophic guilds found across various sampling locations, primarily contributed by resident sympatric fishes. Species like the omnivorous *C. gariepinus*, predatory carnivorous *E. fusca*, *P. cancrivorus*, and *A. gymnocephalua* were among the fish occupying higher trophic levels. In contrast to the Athi River, the omnivorous *C. gariepinus* claimed the highest trophic level in the Ramisi River due to its active diet selection, leading to a broader diet breadth. Consequently, the Ramisi River holds significance for both hedonistic human values (Tsikliras & Polymeros, 2014) and intrinsic ecosystem values (Duffy, 2002), underscoring its higher importance for conservation efforts (Barbier *et al*., 2009).

Conversely, the lower trophic level observed in the Athi River was primarily attributed to the presence of fish species occupying lower trophic levels. It's noteworthy that the estuarine location contributed significantly to the trophic level due to the high trophic level diets found in the stomach contents of fish species with elevated trophic levels (Keppeler *et al*., 2020). The results of this study align with those of Romanuk *et al*. (2006), illustrating changes in the structures of food webs across river systems, transitioning from mountainous to lowland areas, as evidenced in this study.

5.3.3 Diet diversity and selectivity among sympatric fish and eels

The Athi River displayed a more diverse diet, particularly in the upstream location, compared to the Ramisi River, although consisting of lower trophic levels. Fish in the Athi River demonstrated a broad range of diets in contrast to the Ramisi River, but these diets were of lower nutritional value, mainly attributed to the prevalence of herbivorous and omnivorous species throughout the ecosystem (Wanja, 2013). The result of this study indicated that sympatric fishes had higher diet diversity, indicative of lower diet selectivity compared to eels. Eels, being specialists with a highly active diet selection (Sagar *et al*., 2005), stood in contrast to the generalist nature of sympatric fish, as reported by Omondi *et al*. (2017). The generalist behavior of sympatric fish increases the likelihood of niche overlaps and competition among interacting species, driven by diet sharing (Welcomme, 2003), thereby influencing ecological niches (Kotler *et al*., 1994).

Anguilla marmorata exhibited the greatest generalist feeding pattern among the eel species evaluated, as a result of its unselective feeding on a wide range of prey items, accounting to the high diet diversity in the gut content. On the other hand, *A. bengalensis* portrayed the highest diet specialization. These findings are consistent with those of Schulze *et al*. (2004), who demonstrated eels' feeding patterns to undergoing dramatic ontogenic shifts. Additionally, majority of the diet diversity among the sympatric fish was largely contributed by introduced sympatric species, providing them with profound weights on diet competition with eels. Sympatric predatory carnivorous fish such as *N. chelynoides, O. acutipennis, O. ruber, A. africanus*, and *G. giuris* showed a prominent diet selectivity with eels. The results of this study, show that an unchecked upsurge in exotic and highly injurious sympatric species can negatively compound resource sharing (Vitule *et al*., 2009), contributing to the dwindling of eel populations particularly along the WIO region (Hanzen *et al*., 2019).

5.3.4 Diet and niche breadth (B) trophic interactions

Eel belonged to significantly higher trophic levels than sympatric fish attributed to their feeding habits on high trophic level diets and active diet selection (Belpaire *et al*., 2009). As such, this subsequently corresponded to a lower diet breadth. Afterward, among the eel species encountered, *A. bengalensis* had the highest trophic level, placed higher on the food web pyramid, with *A. marmorata* recording the lowest TL and with a wider breadth (Table 16), attributed to unselective feeding habits. The unselective feeding habits of *A. marmorata*, supposedly give credence to its least concern classification by IUCN. Sympatric fishes on the other hand, had a wider diet breadth, indicating the presence of diverse dietary options and unselective feeding habits from the environment. Predominantly, this feeding behavior was most noticeable in exotic fishes. Although, sympatric fish had the lowest trophic level, carnivorous fish recorded the highest trophic level indicating quantified trophic overlaps with eels (González-Bergonzoni *et al*., 2020; Hecnar & M'Closkey, 1997) with lower diet breadth indicating diet specialization. In the contrary, omnivorous fish recorded a wider diet breadth attributed to a wider range of dietary items from the environment (Gerking, 2014). As such, both feeding guilds may be harmful to eels as they compete on similar diets, revealing overlaying niche breadth. Similar findings on European catfish (*Silurus glanis*) have been reported to potentially compete with freshwater eels as a result of niche breadth and overlaps (Bevacqua *et al*., 2011).

5.3.5 Niche and diet overlap

Carnivorous and omnivorous diets at Athi River overlapped with those of eels, particularly *A. bicolor* and *A. bengalensis*, which were more prominent on carnivorous guilds. This is directly linked to their comparable trophic level and diet specialization. On the other hand, omnivorous guilds partially overlapped with *A. mossambica* diets, indicating a likelihood of unselective feeding behavior, classifying it as Near Threatened (NT) by the IUCN classification (Jellyman, 2021). Furthermore, the recorded food resource partitioning between carnivorous and *A. bicolor* and *A. bengalensis* render them vulnerable to competition pressure (Bevacqua *et al*., 2011), possibly contributing to their NT status on the IUCN red list. As a result of the needs to meet energy and nutritional requirements (Sih *et al*., 1998), the diets of eels overlapped, particularly between *A. bengalensis* and *A. mossambica* (Table 17), resulting in interspecific competition (Arai, 2016) demonstrating coexistence throughout their range (Leander *et al*., 2013). These findings are consistent with those of Laffaille *et al*. (2004), who resported minimal intraspecies competition for food among various eel growth stages.

Conversely, at Ramisi River, omnivorous diets largely overlapped with those of *A. bicolor*, while carnivorous diets overlapped with those of *A. bengalensis* (Table 19), demonstrating that omnivorous fishes share their diets habitually with eels. However, *A. mossambica* diets mostly overlapped with those of herbivorous followed by omnivorous, indicating that eels, in addition to being generalists (Jellyman, 2021), can undergo ontogenic diet shifts (Schulze *et al*., 2004). *Anguilla bengalensis* had the highest food resource portioning with *A. bicolor* among the eel diets studied. Supposedly, under selection pressure, eels may evolve both morphological and physiological characteristics to reduce interspecific competition, maximize sustainability, and achieve maximum benefit for each species (Briones *et al*., 2007) to meet their diet needs for nutritional value (Shiao *et al*., 2003). Following that, Athi River had the higher relative amounts of inter and intraspecific competition for consumer-resource interaction between eels and sympatric fish species than Ramisi River mainly ascribed to higher diet overlaps.

CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

There were several conclusions to be derived from this study. From the first (1) specific objective, this study demonstrated that, the sympatric fish co-occurring with freshwater eel assemblage differed along the two rivers. Although exotic *O. niloticus* was most prevalence at both rivers, it was mostly encountered at the upstream location of Athi River. The predatory *Glossogobius giuris* and *Oligolepis acutipennis* were prevalent at Athi River with *Eleotris fusca* dominating at Ramisi River. These species were responsible for the significant dissimilarities observed among the rivers which occurred with eel species. *Anguilla bengalensis* and *A. bicolor* were responsible for the significant differences observed on eel assemblage between the river catchments, in addition eels demonstrated a specialty with reaches. Besides, only two sympatric fish species including *O. niloticus* and *C. gariepinus* demonstrated a cosmopolitan distribution across all the rivers which are considered highly invasive although they were prevalent at the upstream location of Athi River. Athi River had the highest diversity of sympatric fish and eel species compared to Ramisi River. The downstream locations of both rivers recorded the highest species diversity, composed of local inter-basin migratory species from both marine, estuarine, and freshwater residents which differed among the rivers. Subsequently, the local catadromous freshwater eels recorded the highest biomass when compared to sympatric fish species. Thus, the null hypothesis that there are no significant differences in the sympatric fish assemblage occurring with freshwater eels along two east flowing rivers is rejected.

From specific objective 2, this study concluded that different fish types and species preferred different environmental variables, as a result of differences in ecological requirements. However, the patterns of habitat exploitation for both sympatric fish and freshwater eel assemblage did not differ at both rivers as they both largely preferred pools and hence habitat heterogeneity was important for both eel and sympatric fish diversity. Although both eels and sympatric fish predominated pools at all sites, they also portrayed an active habitat selection on vegetation demonstrating a degree of similarity in habitat utilization. Therefore, the null hypothesis that there are no significant variations in patterns of habitat exploitation between sympatric fish and freshwater migratory eel along two east flowing rivers is accepted.

From specific objective 3, this study concludes that both eel and sympatric fish guilds primarily shared penaeid shrimps and fish, regarded as the most protein-rich and high trophic level dietary items among the focal rivers in addition to prawns, crabs, detritus and vegetation and hence the diet composition between eel and sympatric fish was comparable. Ramisi River was subsequently, predominated with the highest trophic level diets. The most significant dietary overlaps were observed between predatory sympatric carnivorous fish with *A. bicolor* and *A. bengalensis* at Athi, while at Ramisi, diets of *A. bicolor* overlapped with those of omnivorous guilds, especially for exotic *C. gariepinus* and *A. mossambica* overlapping with herbivores guilds particularly the exotic *O. niloticus*. The biotic interactions between sympatric fish species and eels were largely influenced by competition, and it is clear that the diets not only overlapped but also shared food items. As such, the diet overlaps between eel taxa and predatory carnivorous occurring at Athi suggest that eel communities are more susceptible to competition from previously undescribed competition from carnivorous fish coupled with river modification, recruitment failures, overfishing and pollution. Based on these results, the null hypothesis that there were no significant differences in dietary composition and overlaps among sympatric fish guilds and the freshwater eels along two east flowing rivers is rejected except for predatory carnivorous.

6.2 Recommendations

i. The estuarine downstream locations of east flowing rivers should be given more credence and attention for the conservation of freshwater fish biodiversity. The upper reaches of the rivers, particularly the Athi River, require special attention for effective removal of introduced species. Furthermore, transboundary species, particularly long-distance local catadromous freshwater eels, which are panmictic species contributes to ecosystem conservation status and play an important role as major global ecosystem connectors. Consequently, conserving eels protects both marine and freshwater ecosystems. Conservation of both local intra-habitat fish species and highly migratory eels, call for river connectivity and conservation approaches should be river specific.

ii. The preservation and restoration of diverse river habitats is critical for vulnerable fish conservation and long-term river management for sustainability as fish communities will always co-exist within their range for a self-sustainable ecosystem.

iii. Selective fishing strategies by fishermen for high trophic level fish can be adopted to reduce possible competition on eels. Further trophic interaction studies using integration of stable isotope analysis should be considered to elucidate feeding habits and validate data generated from gut content analysis as currently used in this study. Besides, Ramisi River should be given special attention for conservation measures to maintain the rich eel biodiversity. Additionally, the estuarine location of Athi River harbours higher trophic level fish as well, proliferated with high trophic level diets, meriting conservation attention.

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APPENDICES

Appendix A: Species composition, relative abundance, biomass and density assemblage structure and their conservation status within the IUCN Red List along Athi-Galana-Sabaki and Ramisi rivers, Kenya

Locations	**Family**	**Species**	**N**	**Relative Abundance %**	**Biomass (g/trap/day)**	**Density (ind/trap/day)**	**Feeding Guild**	**Trophic levels**	**EUCN STATUS**
Upstream	Amphiliidae	*Amphilius uranoscopus*	2	0.2	8.75±0.1	0.25±8.3	Carnv	2.9	LC
Kiaoni	Clariidae	*Clarias gariepinus*	115	6.7	511±88.8	0.91±2.8	Omnv	3.8	LC
	Clariidae	*Clarias liocephalus*	1	0.06	4.25±0.1	0.13±8.3	Omnv	3.3	LC
	Poeciliidae	*Gambusia affinis*	4	0.24	0.12±0.10	0.13±5.9	Omnv	3.1	LC
	Cyprinidae	*Labeo cylindricus*	17	1.0	101±98.2	0.50±5.8	Herb	2	LC
	Cyprinidae	*Labeobarbus oxyrhynchus*	25	1.5	79±11.7	0.49±4.2	Herb	3.2	LC
	Cichlidae	*Oreochromis niloticus*	1192	69.7	643±423	14.7±2.8	Herb	2	LC
	Cichlidae	*O. spilurus niger*	265	15.50	302±100	3.2±3.1	Herb	2.6	LC
	Cichlidae	*Oreochromis variabililis*	2	0.12	106±0.1	0.5±8.3	Herb	2	CR
	Cichlidae	*Oreochromis zillii*	2	0.12	80±0.1	0.5±8.3	Herb	2.5	LC
	Poeciliidae	*Poecilia reticulata*	86	5.0	2.3±2.19	2.3±4.8	Omnv	3.2	NE

Total	**6**	**11**	**1710**	**100**	**1863.42±725**	**23.61±5.69**	**3**		3
Downstream Sabaki	Ambassidae	*Ambassis gymnocephalua*	5	0.16	0.034±0.01	0.15±5.86	Carnv	3.9	LC
	Ariidae	*Arius africanus*	5	0.16	8.31±0.01	0.12±8.31	Carnv	3.8	DD
	Gobiiidae	*Awaous aeneofuscus*	4	0.13	3.90±0.1	0.27±8.31	Herb	2.1	LC
	Bagridae	*Bagrus docmak*	154	5.0	60.6±23.9	0.89±2.77	Carnv	4.1	LC
	Carangidae	*Carangoides fulvoguttatus*	1	0.033	0.83±0.1	0.06±8.31	Carnv	4.4	LC
	Chaetodontidae	*Chaetodon vagabundus*	4	0.13	0.028±0.1	0.11±8.31	Omnv	2.9	LC
	Chanidae	*Chanos chanos*	10	0.33	0.75±0.33	0.07±4.80	Herb	2.4	LC
	Clariidae	*Clarias gariepinus*	3	0.10	32±29.2	0.08±5.9	Omnv	3.8	LC
	Carangidae	*Decapterus russelli*	12	0.40	1.86±0.1	0.67±8.31	Carnv	3.7	LC
	Eleotridae	*Eleotris fusca*	50	1.63	5.33±1.58	1.01±4.81	Carnv	3.8	LC
	Gobiiidae	*Glossogobius giuris*	860	27.96	38±13.2	4.18±3.1	Carnv	3.7	LC
	Atherinidae	*Hypoatherina barnesi*	2	0.06	0.023±0.1	0.11±8.31	Carnv	3.3	NE
	Lutjanidae	*Lutjanus argentimaculatus*	19	0.62	1.87±1.79	0.51±5.90	Carnv	3.6	LC
	Lutjanidae	*Lutjanus monostigma*	2	0.07	1.92±0.1	0.17±8.31	Carnv	4.3	LC
	Syngnathidae	*Microphis fluviatilis*	5	0.16	0.03±0.01	0.17±5.88	Carnv	3.4	DD
	Monodactylid	*Monodactylus*	3	0.10	0.5±0.1	0.17±8.31	Herb	3.5	LC

	ae	*falciformis*							
	Mugilidae	*Mugil cephalus*	22	0.72	1.31±0.80	0.28±3.72	Herb	2.5	LC
	Cyprinidae	*Naziritor chelynoides*	11	0.36	1.24±0.19	0.17±5.88	Carnv	3	VU
	Chedrinae	*Neobola fluviatilis*	1	0.03	0.19±0.1	0.06±8.31	Carnv	3.2	CR
	Gobiiidae	*Oligolepis acutipennis*	848	27.57	23.21±7.02	7.06±3.7	Carnv	4	LC
	Cichlidae	*Oreochromis niloticus*	688	22.37	36.5±13.7	4.34±2.92	Herb	2	LC
	Cichlidae	*O. spilurus spilurus*	263	8.6	44.6±16.9	1.73±2.94	Herb	2.6	LC
	Sciaenidae	*Otolithes ruber*	14	0.46	2.137±0.41	0.12±3.72	Carnv	3.6	LC
	Cynoglossidae	*Paraplagusia bilineata*	1	0.03	0.01±0.1	0.06±8.31	Carnv	3.5	LC
	Oxudercidae	*Periophthalmus barbarus*	2	0.04	0.74±0.1	0.09±5.88	Carnv	3.2	LC
	Ophichthidae	*Pisodonophis cancrivorus*	49	1.60	33.5±12.1	0.41±2.87	Carnv	3.8	NE
	Teraponidae	*Terapon jarbua*	35	1.14	1.42±0.82	0.48±4.12	Omnv	3.9	LC
Total	**22**	**27**	**3076**	**100**	**300.85±123**		**3**		**5**
Eshu	Ambassidae	*Ambassis gymnocephalua*	3	0.39	0.57±0.02	0.18±0.06	Carnv	3.9	LC
Upstream	Clariidae	*Clarias gariepinus*	15	1.93	177.7±95.5	1.09±0.60	Omnv	3.8	LC
	Eleotridae	*Eleotris fusca*	304	39.07	144±32	4.79±1.0	Carnv	3.8	LC
	Cyprinidae	*Enteromius kersteni*	51	7.0	4.21±1.36	0.77±0.28	Omnv	3	LC

	Gobiiidae	*Glossogobius giuris*	26	3.4	4.35±2.24	1.44±0.67	Carnv	3.7	LC
	Cichlidae	*Oreochromis niloticus*	378	49	58±15.6	6.31±2.4	Herb	2	LC
Total	**5**	**6**	**777**	**100**	**388.83±147**		**3**		**1**
Taliani Downstream	Ambassidae	*Ambassis gymnocephalua*	216	32	8.7±2.5	5.15±2.92	Carnv	3.9	LC
	Carangidae	*Carangoides chrysophrys*	5	0.74	0.54±0.32	0.25±4.8	Carnv	4.3	LC
	Clariidae	*Clarias gariepinus*	8	1.2	59.1±35.2	0.64±4.8	Omnv	3.8	LC
	Carangidae	*Decapterus russelli*	15	2.2	11.9±10.1	0.67±4.8	Carnv	3.7	LC
	Eleotridae	*Eleotris fusca*	125	18.52	29.6±16.4	2.77±3.0	Carnv	3.8	LC
	Cyprinidae	*Enteromius kersteni*	3	0.44	1.83±269	0.5±8.31	Omnv	3	LC
	Gobiiidae	*Glossogobius giuris*	6	1.0	9±269	1.0±8.31	Carnv	3.7	LC
	Atherinidae	*Hypoatherina barnesi*	6	1.0	0.18±0.02	0.46±5.88	Carnv	3.3	NE
	Lutjanidae	*L. argentimaculatus*	3	0.44	5.3±5.3	0.25±5.88	Carnv	3.6	LC
	Monodactylidae	*Monodactylus falciformis*	36	5.33	11.28±7.8	0.92±3.1	Herb	3.5	LC
	Mugilidae	*Mugil cephalus*	6	1.0	8.06±6.7	0.5±5.88	Herb	2.5	LC
	Gobiiidae	*Oligolepis acutipennis*	23	3.41	25.8±15.8	1.5±5.88	Carnv	4	LC
	Cichlidae	*Oreochromis niloticus*	196	29.02	41.9±27.6	3.03±2.77	Herb	2	LC
	Cichlidae	*Oreochromis zillii*	3	0.44	19.75±269	0.75±8.31	Herb	2.5	LC
	Ophichthidae	*Pisodonophis cancrivorus*	2	0.30	35.4±25.4	0.17±5.88	Carnv	3.8	NE

	Teraponidae	*Terapon jarbua*	6	0.88	4.14±4.03	0.39±5.88	Omnv	3.9	LC
	Tetraodontidae	*Tetraodon pustulatus*	13	1.93	0.203±0.1	0.71±4.8	Carnv	3.5	EN
	Muraenidae	*Gymnothorax javanicus*	1	0.15	225±35	0.25±8.31	Carnv	3.9	LC
	Haemulidae	*Plectorhinchus schotaf*	2	0.30	1.53±0.1	0.25±8.31	Carnv	3.9	LC
	Gerreidae	*Gerres oyena*	3	0.44	1.54±0.46	0.25±5.9	Herb	2.7	LC
	Acanthuridae	*Acanthurus nigrofuscus*	1	0.15	0.07±0.1	0.17±8.31	Herb	2	LC
Total	**18**	**21**	**675**	**100**	**500.82±204.23**		**3**		**3**

LC- Least Concern, NE- Not Evaluated, VU-Vulnerable, DD-data deficient; Carnv – carnivorous, Herb- herbivorous and Omnv- omnivorous and ind-individuals

Appendix B: One-way SIMPER analysis of sympatric fish abundance among the sampled locations in Athi-Galana-Sabaki and Ramisi rivers, Kenya. Significant contributions to dissimilarities are in bold.

	Reaches	Upstream		Downstream		Focal rivers	
	Locations/Rivers	Kiaoni vs Eshu		Sabaki vs Taliani		Athi vs Ramisi	
Common name	Taxon	Av. dissim	Contrib. %	Av. dissim	Contrib. %	Av. dissim	Contrib. %
Nile tilapia	*Oreochromis niloticus*	26.85	**32.45**	16.54	**18.01**	21.91	**25.14**
Dusky sleeper	*Eleotris fusca*	16.38	**19.79**	5.61	6.11	9.78	**11.21**
Tank goby	*Glossogobius giuris*	1.35	1.63	18.84	**20.51**	9.35	**10.73**
Sharptail goby	*Oligolepis acutipennis*	0.00	0.00	17.69	**19.26**	8.82	**10.12**
Dark mahseer	*Naziritor chelynoides*	0.00	0.00	0.18	0.20	0.09	0.10
Flat fish/sole	*Paraplagusia bilineata*	0.00	0.00	0.03	0.03	0.01	0.02
Bald glassy	*Ambassis gymnocephalua*	0.12	0.14	8.11	**8.83**	5.56	6.37
Athi river Tilapia	*Oreochromis spilurus niger*	**10.09**	**12.20**	2.31	2.51	5.75	6.60
Sudan catfish	*Bagrus docmak*	0.00	0.00	5.50	5.98	2.52	2.90
Sharptooth catfish	*Clarias gariepinus*	7.11	**8.59**	0.65	0.71	3.85	4.42
Sabaki Tilapia	*O. spilurus spilurus*	0.00	0.00	3.03	3.30	1.42	1.62
Redspot barb	*Enteromius kersteni*	2.83	3.42	0.14	0.16	1.39	1.59
Redbelly tilapia	*Oreochromis zillii*	0.36	0.44	0.33	0.36	0.37	0.43
Pangani barb	*Labeobarbus oxyrhynchus*	1.21	1.46	0.00	0.00	0.58	0.66
longfin snake-eel	*Pisodonophis cancrivorus*	0.00	0.00	2.19	2.38	1.04	1.20

Full moony	*Monodactylus falciformis*	0.00	0.00	1.81	1.97	1.28	1.47
Thornfish	*Terapon jarbua*	0.00	0.00	1.20	1.31	0.66	0.76
Puffer fish	*Tetraodon pustulatus*	0.00	0.00	0.69	0.75	0.48	0.55
Indian scad	*Decapterus russelli*	0.00	0.00	0.85	0.92	0.55	0.63
Flathead grey mullet	*Mugil cephalus*	0.00	0.00	0.99	1.08	0.57	0.65
Mangrove red snapper	*Lutjanus argentimaculatus*	0.00	0.00	0.62	0.67	0.33	0.38
Redeye labeo	*Labeo cylindricus*	0.83	1.00	0.00	0.00	0.39	0.45
Tigertooth croaker	*Otolithes ruber*	0.00	0.00	0.54	0.58	0.25	0.28
Victoria tilapia	*Oreochromis variabililis*	0.36	0.44	0.00	0.00	0.18	0.21
Mosquitofish	*Gambusia affinis*	0.28	0.34	0.00	0.00	0.13	0.15
Barnes' silverside	*Hypoatherina barnesi*	0.00	0.00	0.22	0.24	0.14	0.16
Common silver-biddy	*Gerres oyena*	0.00	0.00	0.14	0.15	0.10	0.11
Longnose trevally	*Carangoides chrysophrys*	0.00	0.00	0.16	0.17	0.10	0.12
Giant moray	*Gymnothorax javanicus*	0.00	0.00	0.11	0.12	0.08	0.09
Brown surgeonfish	*Acanthurus nigrofuscus*	0.00	0.00	0.03	0.04	0.02	0.03
Minstrel sweetlips	*Plectorhinchus schotaf*	0.00	0.00	0.05	0.05	0.030	0.03
Guppy	*Poecilia reticulata*	3.58	0.44	0.00	0.00	1.69	1.94
Milkfish	*Chanos chanos*	0.00	0.00	0.22	0.24	0.10	0.12
Freshwater pipefish	*Microphis fluviatilis*	0.00	0.00	0.13	0.14	0.06	0.07
Freshwater goby	*Awaous aeneofuscus*	0.00	0.00	0.10	0.11	0.05	0.05
African sea catfish	*Arius africanus*	0.00	0.00	0.07	0.07	0.03	0.04
Vagabond butterflyfish	*Chaetodon vagabundus*	0.00	0.00	0.05	0.05	0.02	0.03

Yellow spotted trevally	*Carangoides fulvoguttatus*	0.00	0.00	0.03	0.03	0.01	0.02
Stargazer mountain catfish	*Amphilius uranoscopus*	0.02	0.02	0.00	0.00	0.01	0.01
White snapper	*Lutjanus monostigma*	0.00	0.00	0.16	0.17	0.07	0.08
Athi sardine	*Neobola fluviatilis*	0.00	0.00	0.03	0.03	0.01	0.02
Smoothhead catfish	*Clarias liocephalus*	0.01	0.01	0.00	0.00	0.01	0.01
Atlantic mudskipper	*Periophthalmus barbarus*	0.00	0.00	0.10	0.11	0.05	0.05

Appendix C: Habitat use dominance among Fish species along Athi -Galana-Sabaki and Ramisi River, Kenya. The values in brackets represent percentages, outside bracket (n values)

		Relative abundance on habitat types		
Fish types	Species	Pool (%)	Riffle (%)	Vegetation (%)
Eels	*A. bengalensis*	205 (6)	17 (1.0)	7 (0.8)
	A. bicolor	25 (0.7)	9 (0.5)	1 (0.1)
	A. marmorata	12 (0.3)	0 (0.0)	3 (0.3)
	A. mossambica	13 (0.4)	11 (0.6)	1 (0.1)
Sympatric fish	*Acanthurus nigrofuscus*	0 (0.0)	0 (0.0)	1 (0.1)
	Ambassis gymnocephalua	6 (0.16)	115 (6.6)	103 (1)
	Amphilius uranoscopus	0 (0.0)	0 (0.0)	2 (0.2)
	Arius africanus	0 (0.0)	0 (0.0)	5 (0.5)
	Awaous aeneofuscus	4 (0.11)	0 (0.0)	0 (0.0)
	Bagrus docmak	81 (2.16)	47 (2.7)	18 (2)
	Carangoides chrysophrys	0 (0.00)	4 (0.2)	1 (0.1)
	Carangoides fulvoguttatus	1 (0.03)	0 (0.0)	0 (0.0)
	Chaetodon vagabundus	4 (0.11)	0 (0.0)	0 (0.0)
	Chanos chanos	10 (0.27)	0 (0.0)	0 (0.0)
	Clarias gariepinus	41 (1.09)	50 (2.9)	38 (4)
	Clarias liocephalus	1 (0.03)	0 (0.0)	0 (0.0)
	Decapterus russelli	0 (0.00)	19 (1.09)	8 (0.9)
	Eleotris fusca	332 (9)	145 (8.4)	2 (0.2)
	Enteromius kersteni	51 (1.36)	3 (0.2)	0 (0.0)
	Gambusia affinis	0 (0.0)	4 (0.2)	0 (0.0)
	Gerres oyena	0 (0.0)	3 (0.2)	0 (0.0)
	Glossogobius giuris	610 (16.3)	146 (8.4)	131 (14)
	Gymnothorax javanicus	0 (0.00)	1 (0.06)	0 (0.0)
	Hypoatherina barnesi	2 (0.05)	2 (0.12)	4 (0.43)
	Labeo cylindricus	4 (0.11)	13 (0.75)	0 (0.0)
	Labeobarbus oxyrhynchus	10 (0.27)	10 (0.6)	1 (0.1)
	Lutjanus argentimaculatus	2 (0.05)	19 (1.09)	1 (0.1)

Lutjanus monostigma	0 (0.0)	2 (0.12)	1 (0.0)
Microphis fluviatilis	0 (0.0)	5 (0.29)	0 (0.0)
Monodactylus falciformis	0 (0.0)	38 (2.19)	1 (0.1)
Mugil cephalus	13 (0.35)	11 (0.6)	4 (0.43)
Naziritor chelynoides	7 (0.19)	3 (0.17)	1 (0.1)
Neobola fluviatilis	0 (0.0)	1 (0.06)	0 (0.0)
Oligolepis acutipennis	684 (18)	174 (10)	13 (1.4)
Oreochromis niloticus	1449 (39)	621 (36)	347 (38)
Oreochromis spilurus niger	29 (0.77)	19 (1.09)	138 (15)
Oreochromis spilurus spilurus	106 (2.8)	91 (5.3)	66 (7)
Oreochromis variabililis	2 (0.05)	0 (0.0)	0 (0.0)
Oreochromis zillii	2 (0.05)	3 (0.2)	0 (0.0)
Otolithes ruber	2 (0.05)	6 (0.4)	6 (0.7)
Paraplagusia bilineata	1 (0.03)	0 (0.0)	0 (0.0)
Periophthalmus barbarus	1 (0.03)	0 (0.0)	1 (0.11)
Pisodonophis cancrivorus	18 (0.48)	23 (1.2)	10 (1.09)
Plectorhinchus schotaf	0 (0.0)	2 (0.12)	0 (0.0)
Poecilia reticulata	0 (0.0)	85 (5)	0 (0.0)
Terapon jarbua	17 (0.5)	23 (1.3)	1 (0.11)
Tetraodon pustulatus	0 (0.00)	11 (0.6)	2 (0.22)

Appendix D: Prevalence of sympatric fish and eel among habitat types along Athi -Galana-Sabaki and Ramisi rivers. The values in brackets represent percentages, outside bracket (n values)

				Habitat types (%)		
Fish types	Rivers	Locations	Reaches	Pools	Riffles	Vegetation
Sympatric	Athi	Kiaoni	Upstream	661(42)	418 (26)	509 (32)
		Sabaki	Downstream	2073 (67)	713 (23)	273 (9)
	Ramisi	Eshu	Upstream	695 (89)	83 (11)	0
		Taliani	Downstream	68 (10)	485	126 (19)

					(71)	
Eels	Athi	Kiaoni	Upstream	6 (21)	13 (45)	10 (34)
		Sabaki	Downstream	26 (63)	13 (32)	2 (5)
	Ramisi	Eshu	Upstream	220 (99)	2 (1)	0
		Taliani	Downstream	3 (25)	9 (75)	0

Appendix E: Permutational analysis of variance on fish type habitat utilization. The value in bold represent p> 0.05

PERMANOVA			
Permutation N:	9999		
Total sum of squares:	3.174		
Within-group sum of squares:	2.708		
F:	0.6869		
p (same):	**0.8086**		
Habitat types	Pool	Riffles	Vegetation
Pool	1	0.6619	0.7184
Riffles	0.6619	1	0.8256
Vegetation	0.7184	0.8256	1

Appendix F: Principal component analysis (PCA) for multidimensional scaling reduction of environmental variables. The values in bold represent variables that influence major variations.

Variables	PC 1	PC 2	PC 3
Depth(m)	-0.90345	-0.16082	0.3974
Velocity (m/s)	0.015011	-0.94927	-0.31412
Discharge (m3/s)	**-0.96896**	-0.22848	0.094372
Conductivity (EC) (µS/cm)	**0.94545**	0.17729	0.2733
Dissolved Oxygen (mg/L)	**-0.78185**	0.58122	-0.22559
pH	**-0.70513**	0.61397	0.35472
Temperature (°c)	0.51179	**0.70505**	-0.49089
Salinity (ppt)	**0.96006**	0.10971	0.2574
TDS (mg/l)	**0.95181**	-0.10386	0.28856
Eigenvalue	5.84728	2.2453	0.907411

% Variance	**64.97**	24.948	10.082

Appendix G: Canonical Correspondence Analysis (CCA) on significant contributions of the different axes on environmental variable influence on fish occurrence. Significant contribution from the CCA is indicated in bold.

Axis	Eigen values	CCA %	P values
1	**0.6012**	**44.54**	**0.04**
2	0.4267	31.91	0.40
3	0.3131	23.55	0.42
Trace	1.341		0.17

Appendix H: One-way ANOSIM Pairwise on diet composition among sampling locations along Athi-Galana-Sabaki and Ramisi rivers. Significant differences are indicated in bold.

Sampling locations	Eshu	Kiaoni	Sabaki	Taliani	Athi	Ramisi
Eshu	1					
Kiaoni	0.003	1				
Sabaki	0.0007	0.002	1			
Taliani	0.004	0.006	0.003	1		
Athi	0.001	0.026	**0.70**	0.001	1	
Ramisi	**0.92**	0.004	0.006	0.005	**0.006**	1

Appendix I: One-way SIMPER analysis of diet contribution and composition among the sampled locations in Athi-Galana-Sabaki and Ramisi rivers, Kenya. Significant contributions to dissimilarities are in bold.

Reaches	Upstream		Downstream		Upstream vs Downstream				Focal rivers	
Sampling locations	Kiaoni vs Eshu		Sabaki vs Taliani		Kiaoni vs Sabaki		Eshu vs Taliani		Athi Vs Ramisi	
Taxon	Av. dissim	Contrib. %	Av. dissim	Contrib. %	Av. dissim	Contrib. %	Av. dissim	Contrib. %	Av. dissim	Contrib. %
Penaeid Shrimp	0.00	0.00	33.95	**40.09**	26.66	**36.61**	5.90	6.43	19.16	**25.40**
Detritus	21.30	**27.28**	19.25	**22.73**	14.01	**19.25**	15.41	**16.79**	19.45	**25.79**
Fish	14.40	**18.45**	12.67	**14.96**	9.64	**13.24**	27.46	**29.91**	10.18	**13.49**
Prawns	15.34	**19.65**	0.00	0.00	0.04	0.05	26.11	**28.43**	7.84	10.40
Crabs	2.61	3.35	9.86	11.64	6.68	9.17	4.52	4.92	4.44	5.89
Vegetations	7.28	9.33	4.19	4.95	3.13	4.30	4.29	4.68	5.01	6.64
Insects	2.49	3.19	3.28	3.87	2.72	3.73	4.96	5.41	2.76	3.65
Damselflies	0.00	0.00	0.41	0.48	0.35	0.47	0.00	0.00	0.23	0.31
Bugs	0.37	0.47	0.32	0.38	0.43	0.60	0.00	0.00	0.31	0.41
Mayflies	1.09	1.39	0.23	0.28	0.89	1.22	0.00	0.00	0.57	0.75
Earth worms	0.00	0.00	0.18	0.22	0.12	0.17	0.00	0.00	0.10	0.14
Pond snails	0.53	0.68	0.13	0.16	0.33	0.46	0.00	0.00	0.28	0.37
Beetles	2.83	3.63	0.10	0.11	1.83	2.51	0.34	0.37	1.06	1.40
Stoneflies	0.00	0.00	0.07	0.08	0.06	0.08	0.00	0.00	0.04	0.06

Bird	0.84	1.08	0.04	0.05	0.52	0.71	0.00	0.00	0.35	0.46
Annelid worms	0.08	0.11	0.00	0	0.05	0.07	0.00	0.00	0.03	0.04
Bivalves	0.47	0.60	0.00	0.00	0.00	0.00	0.65	0.71	0.26	0.34
Caddisflies	6.61	8.47	0.00	0.00	4.53	6.23	0.00	0.00	2.69	3.57
Chironomidae	1.11	1.42	0.00	0.00	0.68	0.93	0.00	0.00	0.37	0.48
Flies	0.26	0.33	0.00	0.00	0.14	0.19	0.00	0.00	0.16	0.22
Plant seeds	0.45	0.57	0.00	0.00	0.00	0.00	2.17	2.37	0.14	0.18

Appendix J: Diet composition and preferences among eel species and feeding guild residency along Athi and Ramisi Rivers. The values in brackets represent percentages and outside bracket (n values)

Food items	Eel	Introduced carnivorous	Introduced herbivorous	Introduced Omnivorous	Resident carnivorous	Resident herbivorous	Resident omnivorous
Animal detritus	3 (2.8)	12 (8.1)	3 (4.2)	20 (15.0)	14 (10.1)	7 (13.7)	1 (6.7)
Bird	1 (0.9)	1 (0.7)	-	-	-	-	-
Annelid worms	-	-	-	1 (0.8)	-	-	-
Bivalves	1 (0.9)	-	-	-	-	-	-
Bugs	-	1 (0.7)	-	3 (2.3)	-	-	1 (6.7)
Beetles	-	-	6 (8.3)	10 (7.5)	-	-	-
Crabs	10 (9.4)	10 (6.8)	-	3 (2.3)	20 (14.4)	-	-
Caddisflies	-	-	11 (15.3)	23 (17.3)	-	3 (5.9)	-
Chironomidae	-	-	2 (2.8)	3 (2.3)	-	-	-
unidentified detritus	3 (2.8)	3 (2.0)	8 (11.1)	1 (0.8)	1 (0.7)	14 (27.5)	2 (13.3)
Damselflies	-	2 (1.4)	-	-	-	-	1 (6.7)
Earth worms	1 (0.9)	1 (0.7)	-	-	-	-	-
Fish	46 (43)	35 (23.7)	-	11 (8.3)	26 (18.7)	-	4 (26.7)
Unidentified insects	3 (2.8)	6 (4.05)	4 (5.6)	5 (3.8)	1 (0.7)	2 (3.9)	1 (6.7)
Penaeid Shrimps	15 (14.0)	52 (35.1)	1 (1.4)	4 (3.0)	48 (34.5)	1 (2.0)	5 (33.3)
Mayflies	-	1 (0.7)	-	6 (4.5)	-	4 (7.8)	-
Pond snails	1 (0.9)	1 (0.7)	-	1 (0.8)	-	1 (2.0)	-

Prawns	14 (13.1)	0.0	1 (1.4)	6 (4.5)	15 (10.8)	-	-
Plant detritus	-	5 (3.4)	31 (43.1)	11 (8.3)	3 (2.2)	16 (31.4)	-
Vegetation	8 (7.5)	15 (10.1)	5 (6.9)	20 (15.0)	11 (7.9)	3 (5.8)	-
Plant seeds	1 (0.9)	-	-	-	-	-	-
Stoneflies	-	1 (0.7)	-	-	-	-	-
Plastic	-	-	-	3 (2.3)	-	-	-

Appendix K: One-way ANOSIM pairwise correlation between eel and different sympatric fish feeding guilds belonging to different residency and food items preferences. P values in bold are significant at $p<0.05$

	Eel	Introduced carnivorous	Introduced Omnivorous	Introduced herbivorous	Resident carnivorous	Resident omnivorous	Resident herbivorous
Eel	1						
Introduced carnivorous	**0.095**	1					
Introduced Omnivorous	0.016	**0.193**	1				
Introduced herbivorous	0.001	0.011	0.072	1			
Resident carnivorous	0.003	0.025	0.070	0.007	1		
Resident omnivorous	0.001	0.220	0.018	0.001	0.0003	1	
Resident herbivorous	0.003	0.030	**0.120**	**0.973**	0.01	0.003	1

Appendix L: National Commission for Science, Technology & Innovation (NACOSTI) research permit

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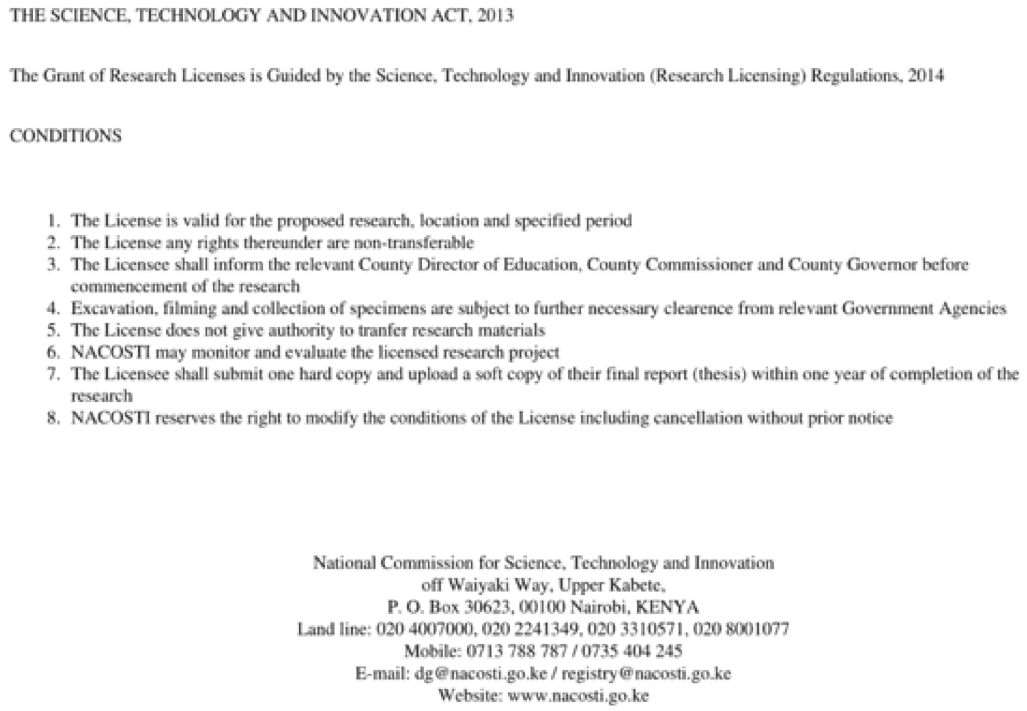

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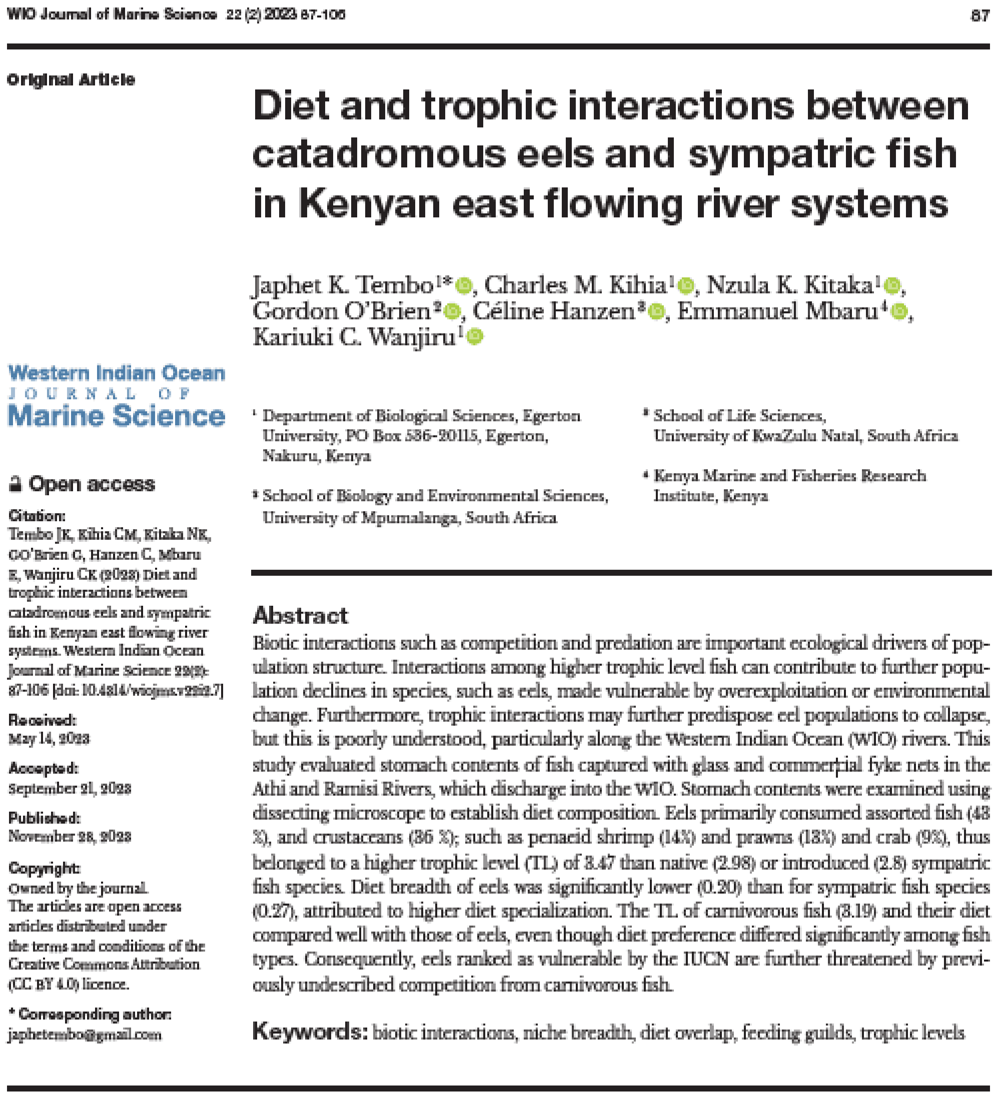
Appendix M: An abstract of a paper that has been published from the thesis



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Original Article

Diet and trophic interactions between catadromous eels and sympatric fish in Kenyan east flowing river systems

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Abstract

Biotic interactions such as competition and predation are important ecological drivers of population structure. Interactions among higher trophic level fish can contribute to further population declines in species, such as eels, made vulnerable by overexploitation or environmental change. Furthermore, trophic interactions may further predispose eel populations to collapse, but this is poorly understood, particularly along the Western Indian Ocean (WIO) rivers. This study evaluated stomach contents of fish captured with glass and commercial fyke nets in the Athi and Ramisi Rivers, which discharge into the WIO. Stomach contents were examined using dissecting microscope to establish diet composition. Eels primarily consumed assorted fish (43 %), and crustaceans (36 %); such as penaeid shrimp (14%) and prawns (13%) and crab (9%), thus belonged to a higher trophic level (TL) of 3.47 than native (2.98) or introduced (2.8) sympatric fish species. Diet breadth of eels was significantly lower (0.20) than for sympatric fish species (0.27), attributed to higher diet specialization. The TL of carnivorous fish (3.19) and their diet compared well with those of eels, even though diet preference differed significantly among fish types. Consequently, eels ranked as vulnerable by the IUCN are further threatened by previously undescribed competition from carnivorous fish.

Keywords: biotic interactions, niche breadth, diet overlap, feeding guilds, trophic levels