TROPHIC ECOLOGY AND EXPLOITATION STATUS OF SHARK SPECIES (PISCES: ELASMOBRANCHII) IN THE NORTH COAST OF KENYA

BY

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DECLARATION

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To my father David Omondi Oddenyo, my mother Florence Aseyo Oddenyo, my beloved grandmothers, family and friends.

ABSTRACT

Sharks are apex predators in marine ecosystems whose trophic ecology is likely to influence community structure and function in their distribution range. Despite this role, data on the trophic ecology and exploitation status of most shark species is lacking especially from the Western Indian Ocean (WIO) region. This study gives information on the trophic ecology and exploitation of shark species from coastal Kenya in an effort to bridge this gap. Six shark species (*Sphyrna lewini*, *Carcharhinus amblyrhynchos*, *Carcharhinus falciformis*, *Carcharhinus melanopterus*, *Carcharhinus leucas* and *Carcharhinus brachyurus*) were collected from Kipini and Ziwayu on the north coast of Kenya from October, 2014 to November, 2015. The species were sampled from the landings and sexed, measured for total length, weighed and the stomachs examined for diet composition. Data were analyzed for size-frequency distributions and exploitation status, trophic positions, diet overlaps, feeding strategy, and niche breadths. A majority of the specimens landed were immature and below the size at maximum possible yield per recruit (L_{opt}). The results indicated the sharks fed mostly on fishes supporting a piscivorous habit found in many studies. However, in this study two species (*C. amblyrhynchos* and *C. falciformis*) appeared to supplement their diet with crustaceans. Interspecies overlaps in diet were high for all species (C_H>0.6), indicative of competition for food resources. The shark species recorded high trophic levels ranging from 3.90-4.238 supporting their position as apex predators. Trophic level–body size relationships showed a high positive correlation for two species, *C. melanopterus*, R^2=97.7% and *C. falciformis*, R^2=96.0% and a negative but poor relationship for one species (*C. amblyrhynchos*, R^2=37.9%) and for all species combined (R^2= 28.3 %). The biomass of prey items consumed by the shark species for the period 2014/2015 was highest for fish at 1.2 MT suggesting potential interaction with the local fishery. It is recommended amongst others, to apply the precautionary approach in conserving the shark populations at Kipini on the north coast of Kenya by restricting the harvests by fishers through gear and seasonal control of fishing effort.

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LIST OF ACRONYMS AND SYMBOLS

BPC	Between Phenotype component of variation
BMU	Beach Management Unit
CITES	Convention on International Trade in Endangered Species
FAO	Food and Agricultural Organization of the United Nations
FO	Frequency of Occurrence
IOTC	Indian Ocean Tuna Commission
IRI	Index of Relative Importance
IUCN	International Union for Conservation of Nature
KMFRI	Kenya Marine and Fisheries Research Institution
L_∞	asymptotic length
L_m	mean length at first maturity
L_{max}	maximum observed length
L_{opt}	length corresponding to the mean age in years at maximum possible
yield	per recruit
NEM	Northeast monsoon season
PCL	Pre Caudal Length
SPC	Secretariat of the Pacific Community
SEM	Southeast monsoon season
SSG	Shark Specialist Group
WIO	Western Indian Ocean
WPC	Within Phenotype component of variation

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CHAPTER ONE

INTRODUCTION

1.1 Background information

Sharks, skates, rays and chimaeras together comprise the chondrichthyan fishes, a group of about 1000 species that has persisted for at least 400 million years, rendering them one of the oldest extant vertebrate groups on the planet (Worm & Branch, 2012). Most elasmobranchs have slow rates of growth, late age-at-maturity and low fecundity compared to bony fishes (Cortés, 2004; Musick, 2005a). These life history traits result in low intrinsic rates of population growth and a limited ability to withstand fishing pressure (Smith *et al.,* 1998). Sharks are harvested primarily for their meat, fins, skin, cartilage and liver (Musick, 2005b). The history of most directed shark fisheries around the world has been one of overharvest, rapid stock decline, and collapse, followed by limited recovery rates (Bonfil, 1994). Examples of such overharvested fisheries include: the porbeagle (*Lamna nasus*) in the North Atlantic (Campana *et al.*, 2008); the soupfin or school shark (*Galeorhinus galeus*) off California and Australia (Ripley, 1946; Olson, 1959; Stevens, 1999); various basking shark (*Cetorhinus maximus*) fisheries (Parker & Scott, 1965; CITES, 2002; McFarlane *et al.,* 2008); and several spiny dogfish (*Squalus acanthias*) fisheries (Bargmann, 2009; Pawson *et al.,* 2009; Rago & Sosebee, 2009; Wallace *et al.*, 2009).

There are no population estimates for shark species in Kenya and most of the Western Indian Ocean (WIO) region. Recent analysis indicate that elasmobranch (sharks and rays) landings in Kenya have declined by about 85% in the last decade (Kiilu, 2016), while fishing for shark fins has significantly reduced populations in most of the WIO region (van der Elst *et al*., 2009; Henderson *et al*., 2009) and globally (Burgess *et al*., 2005). Sharks are apex predators (Myers *et al*., 2007) and have a fundamental influence in prey community structure and in maintaining ecosystem stability through top-down effects (Estes & Duggins, 1995; Myers *et al*., 2007). However, this functional role as apex predators cannot be fully appreciated without establishing the position of different species in food webs and understanding interspecies relationships within a given system (Barnett *et al*., 2013). At its most basic level, the ecological role of a species is defined by its position in the food web with an initial step of identifying its dietary composition (Barnett *et al*., 2013).

Knowledge on foraging ecology, habitat use, and predator-prey interactions of top predators like sharks is important for fisheries management and conservation. Although sharks are apex predators there are surprisingly few studies describing species specific trophic levels (e.g Cortés, 1999). However, such studies are important in understanding the trophodynamics of populations and for formulating ecosystem approaches to fisheries management (Swaleh *et al*., 2015). This study therefore aimed to provide information on the trophic ecology including, trophic levels and exploitation status of the common shark species landed in coastal Kenya for purposes of management and conservation of stocks.

1.2 Problem Statement

Ecological impacts of eliminating top predators can be far-reaching and include the release of mesopredator prey populations from predatory control and induction of trophic cascades (Ward, 2005). Sharks as top predators are exploited for their fins, skin and liver both as a targeted stock and as bycatch species. This has resulted into species such as the scalloped hammerhead (*Sphyrna lewini*) attaining the endangered status as well as being listed in Appendix II of the Convention on International Trade in Endangered Species (CITES) (IUCN.org). The CITES lists species that are 'not necessarily now threatened with extinction but may become so unless trade is closely controlled' (CITES.org). Data reported by FAO represent only some proportion of shark catch (Lack & Sant, 2009). Further, there are significant discrepancies between the exports of sharks by some countries and their reported catch which suggest that catches may be under-reported (Lack & Sant, 2006). This situation gives great impetus to determine exploitation status of species for conservation and management purposes as done in this study. Dietary studies have enabled the complex role of sharks to be modelled in some systems (Kitchell *et al*., 2002), as well as predictions about the effects of their removal on the ecosystem (Stevens *et al*., 2000). Data on the trophic ecology as well as exploitation status of sharks which is vital for their conservation and management are lacking off the Kenyan coast as well as the Western Indian Ocean (WIO) region. This study aimed to fill the gap by providing data on the trophic ecology of the common species of sharks landed on the Kenyan coast.

1.3 Justification

Trophodynamics (temporal-spatial variability in diet) is an important aspect of the ecology of fishes, particularly for those fishes thought to be vulnerable to exploitation such as chondrichthyans (Barnett *et al*., 2013). Fish with highly selective diets are likely to be susceptible to changes in food availability due to fishing mortality or other environmental variations such as climate change effects. In addition, feeding by top predators is a significant factor that shapes fish community structures; often a single or several top predators regulate the lower levels of the food web (Pauly *et al*., 1998a). Shark habitats comprise of open ocean environments occurring over broad geographic ranges, and large-scale impacts such as global climate change that affect ocean temperatures, currents, and potentially food chain dynamics, pose a great threat to these species (Rosa *et al*., 2014). Trends in fisheries management indicate a shift toward an 'ecosystem-based approach' to management (Swaleh *et al*., 2015) that requires data on trophic interactions for purposes of management of the fisheries resources and for theoretical applications. Sharks being apex predators play an influential role in structuring fish communities, but there is virtually no information on their trophic ecology especially in the WIO region. Likewise, information on their exploitation status and hence fisheries sustainability are lacking but are important for setting regulatory frameworks. This study therefore aimed at providing data on their feeding ecology and exploitation levels for purposes of management and conservation of stocks.

1.4 Objectives

Overall Objective

The overall objective of the study was to assess the trophic ecology and exploitation status of the common shark species on the north coast of Kenya.

Specific objectives

The specific objectives of the study were:

1. To determine the species composition and length frequency distribution of the common shark species on the north coast of Kenya

2. To determine the diet of the common shark species landed on the north coast of Kenya in order to evaluate the food web relationships among the landed species.

3. To describe dietary overlaps between the shark species landed on the north coast of Kenya as a means to evaluate levels of competition between the species.

4. To determine the trophic levels of the shark species landed on the north coast of Kenya in order to assess the food web relationships between species.

5. To determine the exploitation status of the shark species landed on the north coast of Kenya for purposes of understanding sustainability of the fishery and conservation status of the populations.

1.5. Hypotheses

This study was guided by the following hypotheses;

H_{o1}: There is no dietary overlap and hence competition for food items between the common shark species on the north coast of Kenya.

H_{o2}: All the common shark species landed on the Kenyan north coast are of the same trophic level.

H_{o3}: The exploitation levels of the shark species on the Kenya north coast are optimum and sustainable.

CHAPTER TWO

LITERATURE REVIEW

2.1 Exploitation status of sharks

Development of advanced fishing technologies in the 1920s lead to the harvesting of chondrichthyans on an industrial scale resulting in reported high global catches of 270,000 t by the 1950s (FAO, 2005). Global shark catches tripled between 1950 and the end of the century, with 893,000 t caught in 2000 (FAO, 2005). Ever since, a downward trend has been observed with catches 15% lower at 766,000t in 2011 (FAO, 2014). The global status of shark and ray populations is therefore poor despite the rather modest recent decline seen in the catch statistics (Musick & Musick, 2011).

Species-specific catch statistics are lacking from most shark fishing countries, although data may be available for aggregations of species in some higher groups (orders or families) (Lack & Sant, 2009). Nominal catches of sharks and rays by species in the Food and Agriculture Organization of the United Nations (FAO) FISHSTAT database (FAO, 2010) are difficult to interpret due to the uneven categorization of catches among landing countries, some countries provide species-specific catch data, whereas some of the most important countries with the highest catches, such as India, simply report “sharks, rays, skates, etc.” (Musick & Musick, 2011). In 2007, only 20 percent of the reported catch was identified to species, while the remaining 80 percent was comprised of several general groupings (Lack & Sant, 2009).

Reported elasmobranch landings in Africa and the Middle East are low and no country ranks in the top twenty worldwide for capture production in 1985–2000 (Clarke *et al.*, 2005). As of 2000, the largest shark and ray fisheries in the Africa were from Nigeria (13,238t) and Senegal (10,757t) (Clarke *et al*., 2005). South Africa reported only 1,665t of elasmobranch catches in 2000 (FAO, 2002). However, given the lack of reporting in artisanal fisheries and the large number of nations fishing in African waters, actual South African landings are believed to be double those in reported catch data (Kroese & Sauer, 1998).

A recent analysis conducted by IUCN Shark Specialist Group (SSG) outlined the conservation status of all recognized chondrichthyans (1,041 species) (IUCN, 2014). Based on species status assessments by 300+ experts using the IUCN Red List Criteria, the SSG classified 181 shark and ray species (17.4% of all species assessed) as threatened with extinction (that is, categorized as Critically Endangerd, Endangered or Vulnerable on the IUCN redlist); 25 species (2.4%) as Critically Endangered; 43 species (4.1%) as Endangered; 113 species (10.9%) as vulnerable; 132 species (12.7%) as near threatened. Only 241 species (23.2%) were assessed as of Least Concern and nearly half (46.8% or 487 species) as data deficient, meaning that information is insufficient to assess their status. By applying the findings for the data sufficient species to those deemed Data Deficient, the experts estimate that one-quarter of all shark, ray, and chimaera species are actually threatened (249 species, 24%) (IUCN, 2014).

2.2 Prey diversity

The presence of specimens of reef and pelagic fish in the diet of the scalloped hammerhead shark, *S. lewini*, (a common species on the Kenyan north coast) off the coast of northeastern Brazil has shown that this species searches for its prey close to the reefs as much as in the adjacent pelagic environment, suggesting that there is a constant displacement between shallow and deep waters (Junior *et al*., 2009). Nevertheless, all the cephalopods preyed upon in the study conducted by Junior *et al*., (2009) were oceanic species, particularly *Histioteuthis* sp., which is a common species in shelf break and oceanic waters (Roper & Young, 1975). Cephalopods like *Chiroteuthis* sp. and *Vampyroteuthis infernalis,* and the shrimp *Heterocarpus ensifer* inhabit deep waters, beyond 300 m, which means that *S. lewini* make incursions into deep waters, descending to the bed to feed upon deep-dwelling prey (Junior *et al*., 2009). Smale and Cliff (1998) observed that adults of *S. lewini* from South Africa consumed more oceanic than neritic cephalopods.

Analysis of the diet of small and coastal specimens of *S. lewini* from Hawaii showed that the most common prey items were alpheid shrimps and two species of goby, the most abundant benthic local megafauna (Bush, 2003). In the Gulf of California (Mexico), dark squid (*Loliolopsis diomedeae*) and the bony fish of the families Carangidae and Gerreidae were the main prey items among the 87 identified (Torres-Rojas *et al*., 2006). In South Africa, 60 teleost species were found in the stomachs of *S. lewini*, with Trichiuridae, Pomadasydae and Sparidae being the most representative fish, but coastal cephalopods, and sharks of the family Scyliorhinidae were also found (Bruyn *et al*., 2005).

Wetherbee *et al*. (1997) investigated the diet of grey reef sharks (*C. amblyrhynchos*) at the Hawaiian islands. In this study, of the 153 stomachs examined, 61 (39.9%) contained food. The diet of sharks of all size classes was dominated by teleost fishes (85.2%), but stomachs also contained cephalopods (29.5%) and crustaceans (4.9%). In terms of frequency of occurrence, there was a decrease for teleosts and an increase for cephalopods for sharks in the largest 2 size classes. Only stomachs of sharks in the largest size class contained undigestible items. The majority of prey items found in stomachs were reef-associated and benthic organisms, indicating that sharks primarily fed near the bottom (Wetherbee *et al.*, 1997). Ontogenetic changes in the type and diversity of prey consumed by the grey reef shark is consistent with reports for a number of other species of sharks (Wetherbee *et al.*, 1990, 1996; Lowe *et al.*, 1996).

The diet of bull sharks (*Carcharhinus leucas*) typically includes a wide variety of prey items (Cliff & Dudley, 1991) but the spatial and temporal scales over which individuals forage is unclear (Daly *et al.*, 2013). Bull sharks are known to exhibit periods of extended site fidelity (Cliff & Dudley, 1991; Brunnschweiler & Barnett, 2013) that may be linked with resource availability but individual home ranges may vary over broad spatial and temporal scales (Daly *et al.*, 2013;Brunnschweiler *et al.*, 2010; Carlson *et al.*, 2010). Bull sharks are capable of ranging over wide geographical areas (Brunnschweiler *et al.*, 2010; Carlson, 2010) and undertake seasonal migrations (Bass *et al.*, 1973; Compagno, 1984; Hammerschlag *et al.*, 2012) but little is known about how bull shark foraging behavior links with these processes (Daly *et al.*, 2013). A recent study suggest that juvenile bull sharks exhibit some level of individual dietary specialization (Matich *et al.*, 2011), however there is little knowledge regarding individual dietary specialization of larger sharks and how factors such as ontogeny, gender or habitat use affect the trophic dynamics of individuals or populations (Daly *et al.*, 2013).

Fish species (*Lutjanus gibbus*, *Plectorhinchus playfairi*, *Umbrina robinsoni*, *Balistapus undulates*, *Rhabdosargus sarba*, *Chrysoblephus puniceus* and *Oplegnathus robinsoni*) made up the largest proportion of potential bull shark diet in the South Western Indian Ocean (Daly *et al*., 2013). The relatively high contribution of similar mesopredatory fish species to the diet of large bull sharks is consistent with previous studies (Cliff & Dudley, 1991; Werry, 2011) but the relatively small contribution of elasmobranchs in the diet of adult sharks contrasts those sampled on the east coast of South Africa (Cliff & Dudley, 1991). This was due to the fact that there is a steep biogeographical gradient along this coast resulting in substantial habitat differences between the study site and the lower east coast of South Africa (Daly *et al*., 2013). Although stable isotope analysis may not provide the taxonomic resolution of stomach content analysis, it does suggest that mesopredatory fish species do constitute a consistently important portion of bull sharks diet over time (Daly *et al*., 2013).

2.3 Ontogenetic shifts in diet

Body size is a life-history trait that affects individual characteristics determining food acquisition (Lucifora *et al*., 2009). In gape-limited predators, the effect of body size on the foraging capacity is especially important (Forsman, 1991). Gape limitation precludes a predator from eating prey larger than its mouth, setting the upper limit to its trophic position (Hairston & Hairston, 1993; Arim *et al*., 2007). This limitation increases the likelihood for the occurrence of an ontogenetic dietary shift since the upper limit of prey size increases with predator's size (Arnold, 1993).

Studies have shown the importance of variable resource use among individuals, which may have important ecological and conservation implications (Bolnick *et al*., 2007, 2011). Individual specialization, defined as a significantly smaller dietary niche of an individual than the population niche for reasons other than sex, body size, or age class, has been measured in diverse taxa including elasmobranchs (Bolnick *et al*., 2003; Matich *et al*., 2011). Determining whether ontogenetic diet shifts occur is vital to creating effective ecosystem-based fisheries management plans (Lucifora *et al*., 2009). *S. lewini* has been described to feed on different proportions of cephalopods, fishes and crustaceans in different places including, Kaneohe, Oahu, Hawaii (Clarke, 1971), Kwazulu-Natal, South Africa (Smale & Cliff, 1988) and Gulf of California (Klimley, 1983).

The presence of mesopelagic and neritic prey in the diet of *S. lewini* may be related to forays these sharks make to depths of 50-450 m (Torres-Rojas *et al*., 2006) and, frequently at night (Klimley *et al*., 1993). Torres-Rojas *et al*. (2006) found that juveniles of *S. lewini* consumed more neritic (Loliginidae) than oceanic cephalopods, but in South Africa, adults of *S. lewini* consumed more oceanic than neritic cephalopods (Smale & Cliff, 1988) indicating spatial and ontogenetic variations in feeding habits. Crustaceans such as shrimps have been found to be more important to the diets of smaller sharks than to larger sharks (Ellis & Musick, 2007), however, more cephalopods have been found in the diet of larger sandbar sharks in Hawaii (McElroy *et al*., 2006) suggesting species specific ontogenetic variations in diet.

2.4 Feeding strategy, niche breadth and dietary overlaps

Analyzing trophic interactions between species helps population ecologists assess the impact of different species traits (e.g., sex, size class) on the relationship between resource use and interactions between organisms (Sutherland *et al*., 2013). A central aspect of feeding strategy, the generalist-specialist dichotomy, is of major importance to niche theory (Pianka, 1988). A generalist predator has a broad dietary niche width, whereas the food niche of a specialist is narrow (Amundsen *et al.*, 1996). Predator species may incorporate prey taxa from multiple food webs into their diets at a population level, but individual-level dietary specialization may serve to keep energy pathways from discrete food webs separate (Matich *et al.*, 2011). For example, Eurasian perch (*Perca fluviatilis*), which have a wide niche width at the population level, segregate into littoral and pelagic specialists, and consequently individuals do not couple these two components of freshwater food webs (Matich *et al.*, 2011;Quevedo *et al.*, 2009).

Individual specialization within populations may be more likely under conditions of; (i) resource scarcity in terms of shark prey, (ii) inter habitat differences in shark prey availability, (iii) fitness trade-offs that result in individual-specific behaviour, (iv) cultural transmission of foraging traditions and ⁄ or (v) cognitive constraints that limit the use of diverse sets of prey (Rendell & Whitehead, 2001; Estes, *et al.*, 2003; Svanback & Persson, 2004; Araujo & Gonzaga, 2007; Darimont, *et al.*, 2009).

For example bull sharks in coastal ecosystems have a relatively wide dietary niche at the population level, preying on teleosts, mollusks, crustaceans, cephalopods and other elasmobranchs (Snelson & Williams, 1981; Snelson *et al.*, 1984; O’Connell *et al.*, 2007). In a study by Wetherbee *et al*. (1997) on grey reef sharks (*C. amblyrhynchos*), the simplified Morisita Index of dietary overlap (C_H) revealed a low degree of overlap between small and medium size sharks, and between small and large sharks. For the medium and large size classes, C_H was high (0.66) indicating perhaps higher competition among large sized sharks. This index is also derived for shark species in this study.

A low niche breadth index value classified juvenile scalloped hammerhead sharks as specialists because they consume more on few prey types (Torres-Rojas, 2006). Klimley *et al*., (1983) classified the scalloped hammerhead as an opportunistic-generalist predator in the Gulf of California; however they found more adults than juveniles, and the feeding behavior in adults is different than that of juveniles, because adults of *S. lewini* consume more on epipelagic and mesopelagic cephalopods (Galván *et al*., 1989). Klimley (1983), mentioned sex segregation in this shark species throughout the year in the Gulf of California, with a high percentage of adult and juvenile females feeding offshore on pelagic prey, while males were caught in coastal areas, where the incidence of benthic prey was higher. Klimley (1983) suggested that differences in proportion of prey do not cause overlapping in diet, this result could be explained by a greater home range of larger sharks. Smale and Cliff (1988) also found that the juveniles of *S. lewini* stay in coastal waters (mainly in bays) for some time, and that, with growth, they move toward oceanic areas during the night to feed, and return to the coast during the day which may result in a broader niche breadth for adults. The niche breadth of the scalloped hammerhead is described and contrasted in this study.

2.5 Trophic ecology of sharks

Baum and Worm (2009) highlight the role of oceanic predators in marine ecosystems with changes in their abundance being linked to cascading top-down effects such as mesopredator release (Myers *et al*., 2007), invertebrate release (Worm & Myers, 2003), mesopredator and invertebrate declines (Hjermann *et al*., 2004; Coyle *et al*., 2007) and trophic cascades (Estes *et al*., 1998; Springer *et al*., 2003).

Findings in Cortés (1999) support the common view that sharks are top predators. The mean trophic level for sharks was identical to that calculated for marine mammals, although the latter did not include sirenians, which are herbivores (TL=2); freshwater dolphins, which are not marine; and polar bears (Hobson & Welch, 1992; Pauly *et al*., 1998b). However, Cortés (1999) indicates that trophic levels of sharks are somewhat higher than those of seabirds obtained from literature, calculated using both dietary and stable-isotope analyses. Results generally suggest that sharks utilize similar resources to these other high-level marine consumers (Cortés, 1999).

Trophic levels estimated by Cortés (1999) agree well with several values reported by Opitz (1996) for sharks and rays of Caribbean coral reef ecosystems, which ranged from 3.9 to 4.1. These values, calculated using Ecopath II, were based on food consumption estimates for 13 species of sharks (9 carcharhinids, 1 ginglymostomid, 2 sphyrnids, and 1 triakid) and two species of rays (1 dasyatid and 1 myliobatid) (Cortés, 1999).

Daly *et al*. (2013) used a range of δ15N values to calculate the trophic position for Bull sharks in the coastal waters of the Southwest Indian Ocean. Their results were similar to other studies that investigated large shark species (Hussey *et al*., 2011; Werry, 2011). The lack of an ontogenetic relationship between the size of bull sharks and δ15N was, however, in contrast to some of these studies (Hussey *et al*., 2011; Abrantes, 2011). The mean trophic position for bull sharks in their study (4.5) based on stomach content analysis alone was slightly higher than the value of 4.3 reported by Cortés (1999). Calculated trophic position, however, can vary considerably depending on the assigned trophic position of the base consumer, the chosen fractionation rate and the type of tissue sampled (McNeil, 2006; Hussey *et al*., 2012). Daly *et al*., (2013) found that bull sharks occupied a high trophic position within the sampled community consistent with the trophic positions of other large shark species calculated from stable isotope analysis (Hussey *et al*., 2011).

Empirically based exploratory analyses suggest that trophic level–body size relationships are highly idiosyncratic (Romanuk *et al*., 2010). Some studies report strong positive correlations (France *et al*., 1998), some weakly positive relations (Fry & Quiñones, 1994) and others no relationship at all (Layman *et al*., 2005). France *et al*. (1998), for example, documented strong, positive correlations between body size and trophic position in benthic food webs that included both invertebrates and fish in four proximally located lakes and two proximally located seagrass meadows. Fry and Quiñones (1994) also found a small positive correlation between trophic position and body mass when comparing across size classes for zooplankton from the north-west Atlantic. In contrast, Layman *et al*. (2005) reported no association between body size and trophic position for predatory fishes in Venezuela. Trophic position-body size relations have also been shown to vary with geographic area (Jennings *et al*., 2001) and functional group identity (Deudero *et al*., 2004). For example, Jennings *et al*. (2001) showed that body size was unrelated to trophic position at the species level for fishes in the North Sea but was positively related for fishes in the Celtic Sea.

Body length and trophic level were moderately correlated by Cortés (1999) who suggested that body mass could have been a better predictor. Even in the case of carcharhinid sharks, which showed the highest correlation, only 30% of the variance was explained by trophic level and body length (Cortés, 1999). The positive trend between body length and trophic level contradicts the view that trophic levels of aquatic organisms are inversely related to size (Pauly *et al*., 1998a). In this study, the relationship between trophic position and body size was investigated for the commonly landed shark species on the north coast of Kenya.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study Area

The study was conducted at two fish landing sites namely, Kipini (2°31'S, 40°31'E), located at the Tana River mouth, and Ziwayu Island (2°37'S, 40°36'E) about 11 km from the shore at Kipini (Fig 3.1). The landing sites are located in Tana River County on the Kenyan north coast. These sites are located in the larger Malindi-Ungwana Bay area, situated between latitudes 2°30'S and 3°30'S, and longitudes 40° 00'E and 41° 00 'E (Fig. 3.1).

The Malindi-Ungwana Bay, that encloses the two landing sites, receives an estimated 6,000 million m^3 of freshwater and 3 million tonnes of sediment annually from rivers Athi and Tana (Tychsen, 2006). The bay and the entire Kenyan coast is affected by the monsoon seasonality namely, the northeast monsoon season (NEM) which occurs between the months of November–March and the southeast monsoon (SEM) occurring between the months of April–October (McClanahan, 1988). The NEM is a period of calm seas, elevated sea surface temperatures and higher salinities, while SEM is characterized by rough seas, cool weather, lower salinities and higher plankton productivity (Kaunda-Arara *et al*., 2009; Ndoro *et al*., 2015). The huge volume of nutrient-laden freshwater from the Athi and Tana Rivers, combined with the associated mangrove systems of the Tana Delta make the Malindi-Ungwana Bay one of the richest and most productive fishery grounds along the Kenyan coast (Fulanda *et al*., 2011).

The fishery based at Kipini and Ziwayu (Fig. 3.1) is composed of artisanal fishers utilizing canoes, outriggers or wooden boats powered either by oars, long sticks, sail or engines (Fulanda *et al*., 2009, 2011; Munga, 2014). Fishers at the site utilize various types of gear such as seine nets, gillnets and handlines targeting both nearshore and offshore fish stocks. The targeted nearshore stocks include prawns, crabs, catfish, tilapia and sharks. Hand lines are utilized offshore on the Kenyan North Bank and target mainly snappers (Lutjanidae), while sharks are caught as by-catch of this fishery. Shark samples used in this study were obtained at the landing site at Kipini from fishers who had caught the sharks either at the nearshore grounds or from near the reef platform at Ziwayu (Fig. 3.1).

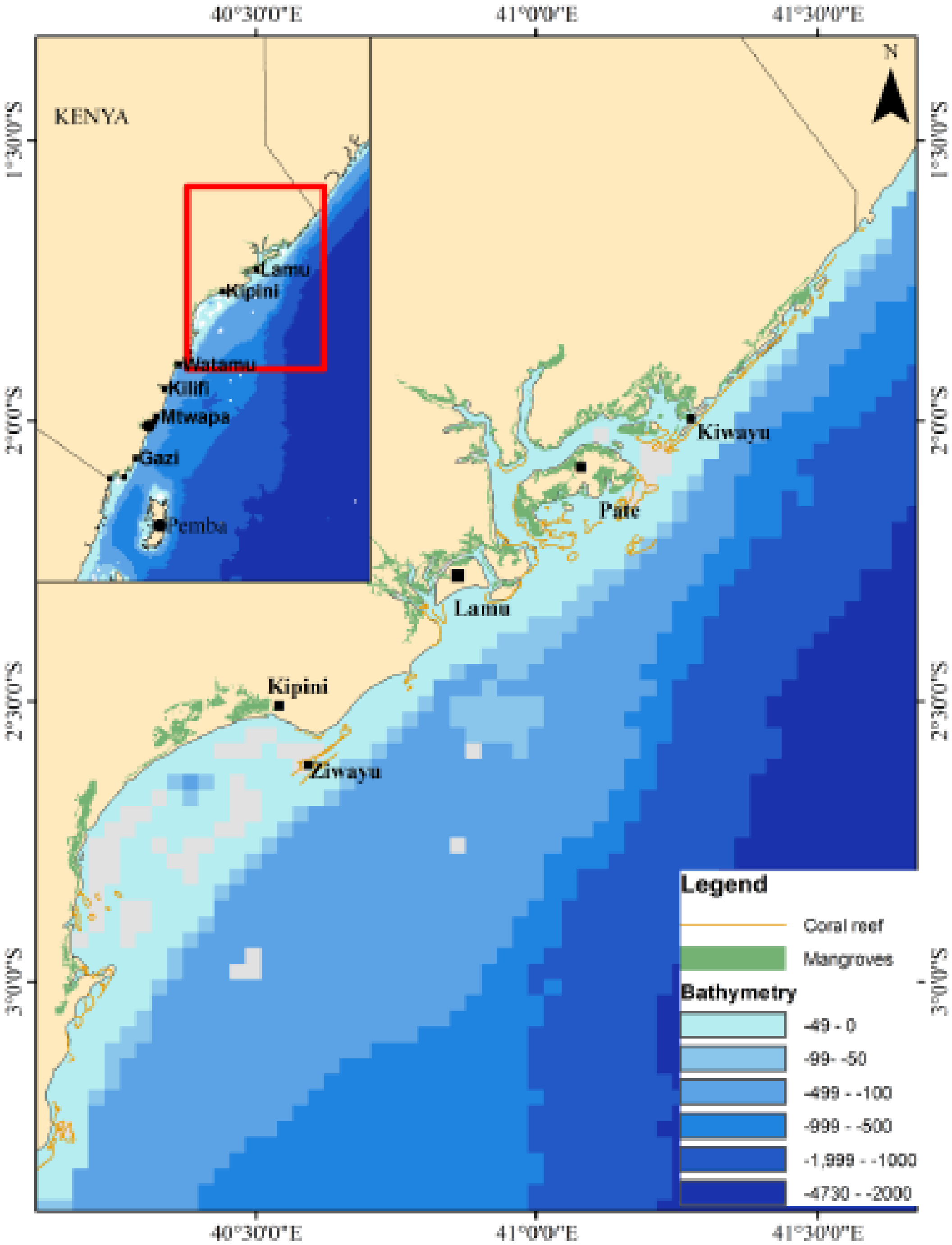

Figure 3.1. Shark landing sites of Kipini and Ziwayu on the Kenyan north coast from where samples were obtained. (Source: Kaunda-Arara, 2014)

3.2 Field sampling of shark species

Field sampling extended from October, 2014 to November, 2015. Artisanal fishers landed their catch at Kipini landing site (Fig. 3.1) on a daily basis throughout the period of study except for religious days and festivals. Shark specimens originating from nearshore Kipini and from Ziwayu Island were obtained from fishers at Kipini landing beach with assistance from the Beach Management Unit (BMU). Samples were obtained at near daily frequency because of the unpredictability of the landings. All sharks landed were examined because of the low daily sample sizes.

3.2.1 Species identification and measurement of morphometrics

The landed sharks were identified to species according to guides by IOTC and SPC (2012), Anam and Mostrada (2012) and Bass *et al*. (1973, 1975). The species of shark identified in the landings are shown in the Appendix. Sex was determined from the presence of claspers attached to each pelvic fin in males and the absence of claspers as a characteristic of females. The weight of each landed specimen was taken to the nearest gram on an automatic self-loading balance for smaller sharks and on a spring balance for larger sharks of more than 5 kg (hanging by the caudal peduncle allowing for water to drain) (Kiilu, 2016). Total length (TL) was measured as the distance from the snout to a point on the horizontal axis intersecting a vertical line extending down-ward from the tip of the upper caudal lobe to form a right angle as in Ebert (2013).

Each shark were dissected to remove the stomachs which was tied at either end with a fishing line wire. The stomachs were then preserved in zip-lock bags filled with 70% ethanol. The zip-lock bags were labeled using a tracing paper and catalogued according to species, sex and date of sampling. The bags were then transported

to the Kenya Marine and Fisheries Research Institute (KMFRI) for gut content analysis.

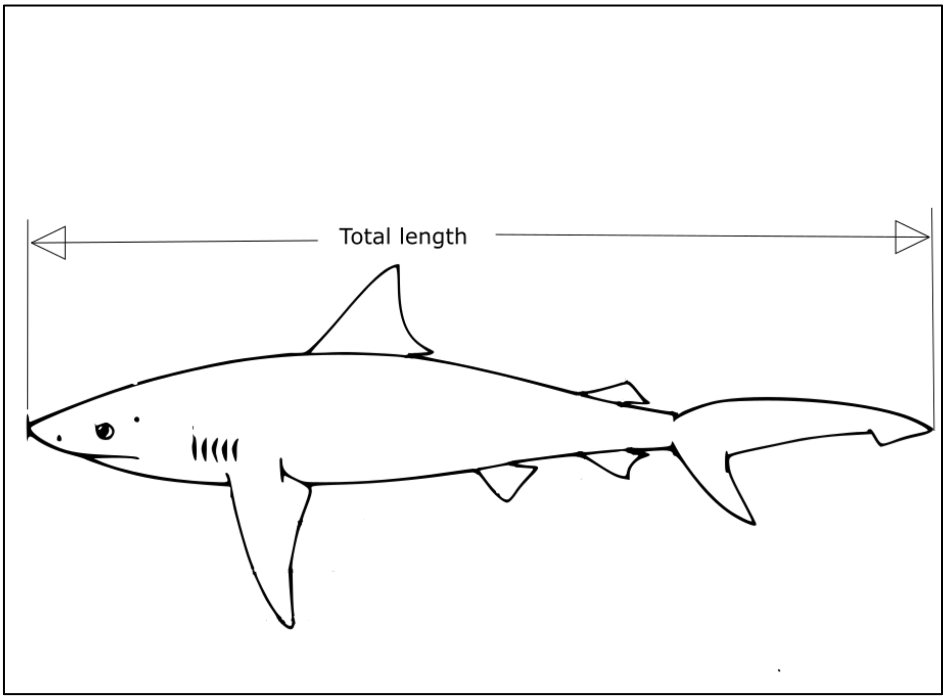

Figure 3.2. Total length measurement in sharks. Source: Ebert, 2013.

3.2.2 Determination of diet composition

Diet composition of the sharks examined in this study was determined by means of the wet weight method described in Hyslop (1980). The zip-lock bags were opened in the laboratory and the field details recorded. Stomachs preserved in ethanol were then split open and rinsed with water over a sieve. Prey items from each stomach retained on the sieve were emptied into a petri dish. These items were then sorted and identified to the lowest taxonomic level possible and counted per stomach. The fish items in the stomachs were identified following keys by Fisher *et al*. (1995) and Thomson *et al*. (2000). Cephalopods were identified from the beaks according to Iverson and Pinkas (1971) and Wolff (1984), while crustaceans were identified using the keys in Fisher *et al*. (1995). Molluscs were identified using Anam and Mostrada (2012) whereas plants were identified using Oliveira *et al*. (2004).

After sorting and identification of prey items in a stomach, the surface water was removed from the prey by blotting them on tissue paper. The bulk weights of the prey items were then taken for each species or taxonomic group to the nearest gram on an electric weighing scale.

3.3 Data Analysis

Following the data generated as above, the following data analysis methods were applied in order to test the advanced hypotheses and to evaluate the set objectives.

3.3.1 Length-Frequency distributions and Exploitation status of species

The exploitation status of each of the landed shark species was established from a simple framework for evaluation of the length-frequency data (Froese & Binohlan, 2000). The framework uses the asymptotic length (L_∞, cm), mean length at first maturity (L_m, cm) and the length corresponding to the mean age in years at maximum possible yield per recruit (L_{opt}, cm) (Froese & Binohlan, 2000).

Empirical relationships adopted from Froese and Binohlan (2000) were used to estimate L_∞, L_m and L_{opt} as follows:

Asymptotic length (L_∞) was estimated from maximum observed length (L_{max}) with the equation;

$$\log L_\infty = 0.044 + 0.9841 * \log(L_{max})$$

Length at first maturity (L_m) was estimated from L_∞ with the equations;

Unsexed: $\log L_m = 0.8979 * \log L_\infty - 0.0782$ (s.e. = 0.127)

Female: $\log L_m = 0.9469 * \log L_\infty - 0.1162$ (s.e. = 0.122)

Male: $\log L_m = 0.8915 * \log L_\infty - 0.1032$ (s.e. = 0.147) and, length at maximum possible yield per recruit (L_{opt}) was estimated from L_m with the equation;

$$\log L_{opt} = 1.053 * \log L_m - 0.0565 \text{ (s.e. = 0.139)}$$

3.3.2 Cumulative trophic diversity curves

The adequacy of the stomach sample size in studying the feeding habits of the species was determined using cumulative trophic diversity curves (Hurtubia, 1973). The diversity of stomach contents was measured with the modified Shannon index (Brillouin, 1956);

$$H = (\frac{1}{N})(\log_2 N! - \Sigma \log_2 N_i!)$$

where;

H = the diversity of the stomach contents per individual shark,

N = the total number of stomach contents per individual shark,

and Ni = the number of the ith prey item per individual shark.

Stomachs were pooled daily for $k = 1,2,3,\ldots$ up to $k = z$ stomachs, with the accumulated trophic diversity (H_k) derived until it reaches an asymptote at a time t- in days of sampling.

3.3.3 Dietary importance of prey categories

The frequency of occurrence (FO) is often used in the description of diet based on stomach contents (Hyslop, 1980). Frequency of occurrence of a given prey type is defined as the number of stomachs in which that prey occurs, expressed as a frequency of the total number of stomachs in which prey are present. It is described as (Hyslop, 1980);

$$\%FO_i = (N_i/N) \times 100$$

where;

$\%FO_i$ = Percentage frequency of occurrence of prey item i

N_i = the number of stomachs with prey item i,

and, N = the total number of stomachs examined with prey items.

The 'index of relative importance' (IRI) (Pinkas *et al*., 1971) which incorporates percentage by number (N), Weight (W) and frequency of occurrence (FO) was used to determine the relative importance of prey items in the diet of the shark species. The IRI was calculated following Pinkas *et al*. (1971) as:

$$IRI_j = (\%N_j + \%W_j) \times \%FO_j$$

where;

IRI_j = Index of relative Importance for the j-th prey category

$\%N_j$ = Percentage number for the j-th prey category

$\%W_j$ = Percentage weight for the j-th prey category

$\%FO_j$ = Percentage frequency of occurence for the j-th prey category

In order to facilitate comparison among species, the IRI values were converted to percentages from the summation of indices of relative importance of all the prey categories (Σ IRI_j) (Cortés, 1997).

3.3.4 Rates of feeding intensity

The feeding intensity of shark species landed in Kipini and Ziwayu was evaluated by calculating the percentage vacuity index which reflects the frequency of feeding, giving the fraction of the population having food in the digestive tract (Euzen, 1987);

$$\% V = (N_e / N_s) \times 100$$

where;

$\% V$ = percentage vacuity

N_e = the number of empty stomachs,

and, N_s = the total number of stomachs examined.

3.3.5 Niche Breadth

The niche breadth is a measurement of how organisms utilize their environment in terms of resources like food and habitat (Krebs, 1989). In this study it was used in determining whether shark species examined were either specialist or generalist feeders by examining their diets. The niche breadth of species was calculated using Levin’s standardized index (Krebs, 1989):

$$B_i = \frac{1}{n-1}\left(\frac{1}{\sum_j P_{ij}^2} - 1\right)$$

where;

B_i = the Levin’s standardized index for predator i,

P_{ij} = the proportion of diet of predator i that is made up of prey j biomass,

n = number of prey items in the diet of predator i.

B_i ranges from 0 to 1 with low values indicative of diets dominated by few prey items (specialist predators) and high values indicative of generalist diets (Krebs, 1989).

3.3.8 Diet overlaps

Krebs (1989) discussed the advantages and disadvantages of the most widely used indices of overlap and similarity (e.g. percentage overlap, Horn's index of overlap) and recommended using Morisita's index as the best measure of resource overlap to minimize bias. The Morisita index varies from 0 (no similarity or diet overlap) to 1 (complete similarity or diet overlap). The simplified Morisita-Horn index (Horn, 1966) was therefore used in the estimation of niche or diet overlaps between shark species and is given by the formula:

$$C_H = \frac{2\sum_I^n P_{ij}P_{ik}}{\sum_I^n P_{ij}^2 + \sum_I^n P_{ik}^2}$$

where;

C_H = Simplified Morisita-Horn Index of overlap diet between species j and species k

P_{ij} = Proportion resource i is of the total resources used by species j

P_{ik} = Proportion resource i is of the total resources used by species k

n = Total number of resource states (I = 1, 2, 3, ...n)

Values of this index vary from 0 to 1, where values >0.6 indicate high overlap, 0.3-0.6 medium overlap and <0.3 low overlap in diet between species (Krebs, 1989).

3.3.9 Feeding strategy

A modified Costello graphical method (Costello, 1990; Amundsen *et al.*, 1996) was applied to the data set of prey taxa in order to assess the feeding behaviour of the shark species. In this method, the prey-specific abundance, defined as the percentage weight or number of a prey taxon consumed by a species is plotted against the frequency of occurrence of the prey in the predator, providing a two-dimensional graph (Fig. 3.3) (Amundsen *et al*., 1996). The prey-specific abundance is summarized as follows:

$$P_i = \left(\sum S_i / S_{ti}\right) 100$$

where;

P_i = prey-specific abundance of prey *i*,

S_i = stomach content (as weight or number) comprised of prey *i*,

S_{ti} = total stomach content weight or numbers in only those fish or predators with prey *i* in their stomachs.

According to Amundsen *et al*. (1996), information on prey importance, feeding strategy and niche width contribution can be inferred through the position of prey types in the two-dimensional plot of prey-specific abundance vs. frequency of prey occurrence (Fig. 3.3).

Information about prey importance and feeding strategy of the predator can be obtained by examination of distributions of points along the diagonals and axes of the diagram (Fig. 3.3). The percent abundance, increasing along the diagonal from the lower left to the upper right corner, provides a measure of prey importance, with dominant prey at the upper, and rare or unimportant prey at the lower end (Amundsen *et al*., 1996).

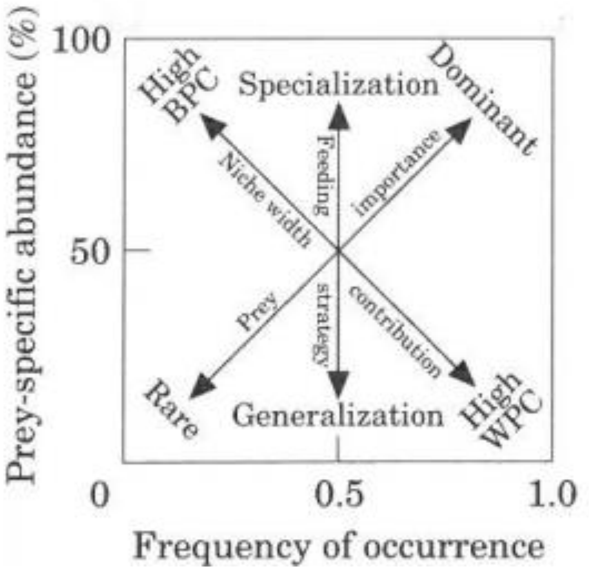

Figure 3.3. Explanatory diagram for interpretation of feeding strategy, prey importance and niche width contribution (adopted from Amundsen *et al*., 1996; BPC = Between Phenotype Component, WPC = Within Phenotype Component).

The vertical axis represents the feeding strategy of the predator in terms of specialization or generalization (Fig. 3.3). The predators that have specialized on prey types are positioned in the upper part of the graph, whereas prey positioned in the lower part have been eaten more occasionally (generalization) (Amundsen *et al*., 1996). Prey points located at the upper left of the diagram would be indicative of specialization of individual predators, and those in the upper right would represent specialization of the predator population (Amundsen *et al*., 1996).

3.3.10 Prey biomass consumption by sharks during the period 2014/15

Estimates of consumption of prey by each species of shark were based on the landings data obtained in this study and assuming there is no variation in the feeding habits of the species through time.

The biomass of prey items consumed by each species of shark between the years 2014-2015 was estimated according to Rosas-Luis *et al.* (2016) as follows:

$$Q_i = \sum_{i=1}^{n} F_j \times \left(\frac{Q}{B}\right)_j \times DC_{ij}$$

where;

Q_i = consumption of a prey item in kg/yr,

F_j = total annual catch in kg of each shark species,

$(Q/B)_j$ = consumption-biomass relationship in the species,

DC_{ij} = composition of the prey (i) in the stomach contents of the predator (j) ($\%IRI_j$ used instead in this work).

3.3.11 Trophic levels

An organism's trophic level (ranging from 1 - 5) is its position in the food chain within an ecosystem food web (Cortés, 1999). The trophic levels of the shark species landed were calculated from; (i) The trophic level of the prey items, and (ii) The standardized proportion of a prey category in the diet of the shark species (Cortés, 1999). The potential range of food categories expected in shark diet and their trophic levels are shown in Table 3.1. An index of standardized diet composition adopted from Cortés (1999) is based on a weighted average that takes into account the sample size (number of stomachs examined) in each species. The formula used to calculate the standardized proportion that each prey category P_j makes up the diet of a species is:

$$P_j = \frac{\sum_{i=1}^{n} P_{ij} N_i}{\sum_{j=1}^{5}\left(\sum_{i=1}^{n} P_{ij} N_i\right)}$$

where,

P_{ij} = the proportion of prey category j in species i (%IRI_j was utilized in this study rather than proportions, as recommended by Cortés (1999))

N_i = the number of stomachs with food used to calculate IRI_j

n = the number of stomachs examined for all food items, and $\Sigma P_j=1$.

The trophic level (TL) of each shark species was then estimated based on a model by Cortés (1999):

$$\mathrm{TL} = 1 + \left(\sum_{j=1}^{n} \mathrm{P_j} \times \mathrm{TL_j} \right)$$

where;

P_j = the standardized proportion of each prey category j in the diet of the predator,

TL_j = the trophic level of the prey category j (From Table 3.1)

n = the total number of prey species in the diet.

Table 3.1. The potential range of food categories expected in a shark's diet and their trophic levels (Cortes, 1999)

Code	Species group	Trophic level*
FISH	Teleost fishes	3.24
CEPH	Cephalopods (squids, octopuses)	3.2
MOL	Molluscs (excluding cephalopods)	2.1
CR	Decapod crustaceans (shrimps, crabs, prawns, lobsters)	2.52
INV	Other invertebrates (all invertebrates except molluscs, crustaceans, and zooplankton)	2.5

ZOO	Zooplankton (mainly euphausids ‘‘krill’’)	2.2
BIR	Seabirds	3.87
REP	Marine reptiles (sea turtles and sea snakes)	2.4
MAM	Marine mammals (cetaceans, pinnipeds, mustelids)	4.02
CHON	Chondrichthyan fishes (sharks, skates, rays, and chimaerids)	3.65
PL	Plants (marine plants and algae)	1

*The trophic levels were taken or calculated from Sanger (1987), Hobson and Welch (1992), Hobson (1993), Hobson *et al.* (1994), Pauly and Christensen (1995), and Pauly *et al.* (1998a).

CHAPTER FOUR

RESULTS

4.1 Species composition, Length-Frequency distribution and Exploitation Status

4.1.1 Species Composition

The composition and abundance of shark species landed at Kipini, on the north coast of Kenya, varied temporally (Table 4.1). The scalloped hammerhead shark, *Sphyrna lewini* was the most abundant species caught between November, 2014 and November 2015 except for a period between January to March, 2015 when they were not in the landings. The grey reef shark, *Carcharhinus amblyrhynchos* and the blacktip reef shark, *Carcharhinus melanopterus* were caught between October, 2014 and April, 2015 resembling most of the distribution of the scalloped hammerhead shark. The silky shark, *Carcharhinus falciformis*, appeared in the landings during the narrow period between February and March, 2015. The copper shark, *Carcharhinus brachyurus*, appeared in the samples only in the month of January and February, 2015, while the bull shark, *Carcharhinus leucas*, was caught between November, 2014 and April, 2015. Except for the *S. lewini*, the other species had zero to few landings during April to November, 2015 (Table 4.1).

Of the six species landed, the silky shark, *C. falciformis* was the largest (mean ± SD) in size (110.6 ± 8.76 cm) and the blacktip reef shark, *C. melanopterus* was the smallest in the samples (57.4 ± 18.80 cm) (Table 4.2). The landed biomass was dominated by *S. lewini* and *C. amblyrhynchos* at 1486 kg and 778 kg, respectively. The mean (± SD) landed biomass ranged between 1.044 ± 1.23 kg for *C. melanopterus* to 5.439 ± 3.701

kg for *C. leucas* (Table 4.2). The total biomass of sharks landed at Kipini was 3.2 metric tons (Table 4.2).

Table 4.1. Monthly distribution of number of shark species landed at Kipini, coastal Kenya from October 2014 to November 2015

Month	*Sphyrna lewini*	*Carcharhinus amblyrhynchos*	*Carcharhinus falciformis*	*Carcharhinus melanopterus*	*Carcharhinus brachyurus*	*Carcharhinus leucas*
2014						
October	-	17	-	8	-	-
November	4	23	-	35	-	8
December	1	53	-	39	-	4
2015						
January	-	113	-	10	24	9
February	-	3	89	4	1	3
March	-	1	14	-	-	-
April	2	13		5	-	8
May	40	-	-	-	-	-
June	55	-	-	-	-	-
July	43	-	-	-	-	-
August	42	-	-	-	-	-
September	74	-	-	-	-	-
October	60	-	-	-	-	-
November	76	-	-	-	-	-
Total	397	223	103	101	32	25

Table 4.2. Statistics of shark species landed in Kipini, coastal Kenya from October 2014 to November 2015

Species	Common name	N	Total landed biomass (kg)	Mean size (TL) (cm ± SD)	Size range (cm)	Mean landed biomass (kg ± SD)
Sphyrna lewini	Scalloped hammerhead shark	397	1486	69.41±34.03	28-254	3.74±11.92
Carcharhinus amblyrhynchos	Grey reef shark	223	778	88.06±31.56	26-135	3.49±3.76
Carcharhinus falciformis	Silky shark	103	533	110.6±8.76	90 – 132.5	5.17±5.81
Carcharhinus melanopterus	Blacktip reef shark	101	105	57.4±18.80	25.4 – 127.5	1.04±1.23
Carcharhinus leucas	Bull shark	32	174	94.29±27.09	39.6 – 150	5.43±3.701
Carcharhinus brachyurus	Copper shark	25	119	109.2± 8.65	82 – 120	4.74±1.11

4.1.2 Sex ratios

Sex ratios were skewed in favor of females for four of the six species of sharks landed at Kipini (Table 4.3). These included *C. falciformis*, with a significantly skewed M:F ratio of 0.02:1, followed by *C. brachyurus* (0.25:1), *C. amblyrhynchos* (0.56:1) and *C. melanopterus* with a M:F ratio of 0.66:1 (Table 4.3). The two species with a M:F ratio skewed in favor of males but not deviating significantly from unity, were *C. leucas* with a M:F ratio of 1.46:1 and *S. lewini* with a ratio of 1.17:1 (Table 4.3).

Table 4.3. Sex ratios (M:F) of shark species landed at Kipini between October, 2014 to November, 2015. *Significantly different from unity at $\alpha=0.05$

Species	N	Males	Females	Sex ratio (M:F)	χ^2	P-value
Sphyrna lewini	397	214	183	1.17:1	2.4207	0.12
Carcharhinus amblyrhynchos	223	80	143	0.56:1 *	17.798	<0.0001

Carcharhinus falciformis	103	2	101	0.02:1*	95.155	<0.0001
Carcharhinus melanopterus	101	40	61	0.66:1*	4.3663	0.037
Carcharhinus leucas	32	19	13	1.46:1	1.125	0.289
Carcharhinus brachyurus	25	5	20	0.25:1*	9	0.003

4.1.3 Length-Frequency distribution

Males and females of shark species with n > 100 were tested for similarity of length-frequency distribution and similar distributions pooled together following the Kolmogorov-Smirnov test (Table 4.4). *Carcharhinus amblyrhynchos* males and females had asymmetric distribution of length-frequencies (Kolmogorov-Smirnov, D = 0.261, p = 0.001) hence their length-frequency (L-F) data were plotted separately (Figs. 4.1a and b). *Carcharhinus amblyrhynchos* females had a bimodal L-F distribution with one modal peak at 40-60 cm and a second mode at 110 cm (Fig. 4.1a). The males also had a bimodal distribution with one modal peak at 40-60 cm and a second mode at 130 cm (Fig. 4.1b). Males and females of *S. lewini* had symetric distribution of length-frequencies (D = 0.076, p = 0.596) hence length data for both sexes were pooled together and one L-F distribution plotted having one modal peak at 60cm (Fig. 4.2a). Similar symmetric distribution between the sexes was found for *C. melanopterus* which had a unimodal L-F distribution with a modal peak at 40-60cm (D = 0.235, p = 0.119, Fig. 4.2b), and *C. falciformis*, with a unimodal peak at 100-120 cm (D = 0.426, p = 0.743, Fig. 4.2c).

Table 4.4. Two-sample Kolmogorov-Smirnov (K-S) tests on the length frequency distributions of males and females of shark species landed in Kipini, coastal Kenya. *D* is a K-S test statistic and P its probability at α = 0.05

Species	Females (n)	Males (n)	*D*	P
Sphyrna lewini	183	214	0.076	0.596
Carcharhinus amblyrhynchos	143	80	0.261	0.001
Carcharhinus falciformis	101	2	0.426	0.743
Carcharhinus melanopterus	61	40	0.235	0.119

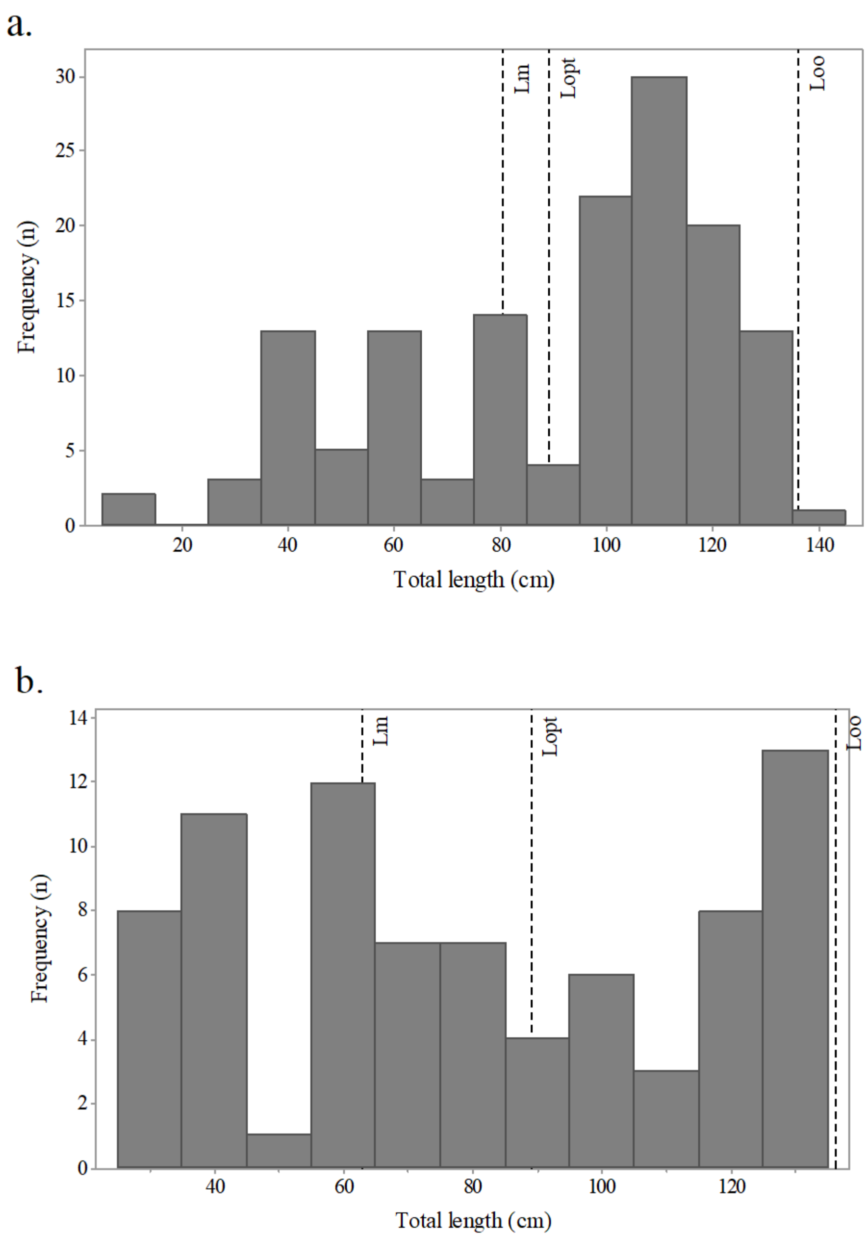

Figure 4.1. Length-Frequency distribution of (a) female and (b) male grey reef shark, *Carcharhinus amblyrhynchos*, landed in Kipini between October, 2014 to November, 2015 with transposed growth parameters L_∞, L_m and L_{opt}. n = 143 and 80, for females and males, respectively.

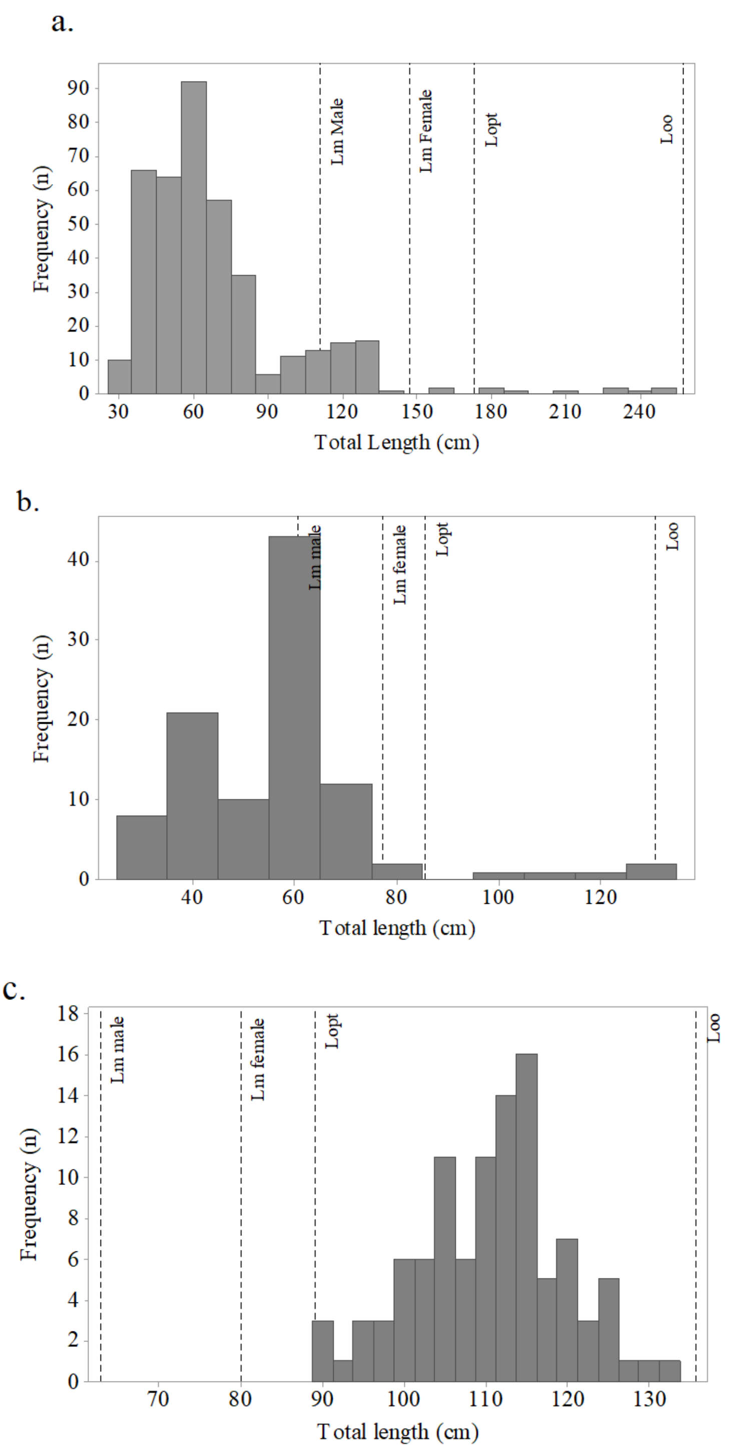

Figure 4.2. Length-Frequency distribution of sharks landed in Kipini between October, 2014 to November, 2015 with transposed growth parameters L_∞, L_m and L_{opt}. (a) *Sphyrna lewini*, n = 397, (b) *Carcharinus melanopterus*, n = 101, (c) *Carcharhinus falciformis*, n = 103

4.1.4 Exploitation status

Empirical relationships adopted from Froese and Binohlan (2000) were used to estimate various growth parameters of sharks landed at Kipini during the study period. These included asymptotic length (L_∞, cm), mean length at first maturity (L_m, cm) and the length corresponding to the mean age in years at maximum possible yield per recruit (L_{opt}, cm). The values derived from the empirical relationships (see section 3.3.1) are shown in Table 4.5.

The derived growth parameters (Table 4.5) were then transposed on the length-frequency distributions of each species of shark (see Figs. 4.1 - 4.2) for purposes of describing their exploitation status in the fishery. A number of sharks caught in the artisanal fishery at Kipini were smaller than the size of maximum possible yield per recruit ($< L_{opt}$) (Table 4.5). These included: 36% of female and 63% of male *C. amblyrhynchos* caught at sizes less than L_{opt} (see dotted lines on Figs. 4.1a and b, respectively). Ninety eight percent (98%) of *S. lewini* landed were smaller than L_{opt} (dotted line on Fig. 4.2a). For *C. melanopterus*, 95% of the specimens landed were less than L_{opt} (Fig. 4.2b). However, *C. falciformis* (silky shark) had lengths larger than L_{opt} (Fig. 4.2c).

The grey reef sharks landed had L_m of 80.3 cm and 63 cm for females and males, respectively, with 31% of females and 40% of males being below L_m (Fig. 4.1 a and b). The scalloped hammerhead shark had the largest mean length at first maturity (L_m) for females and males at 146 cm and 111cm, respectively, with 98 % of females and 87% of males landed being below L_m (Table 4.5 and Fig. 4.2a). The length at first maturity (L_m) for silky shark (*C. falciformis*) were 80 cm and 62.8 cm for females and males, respectively, with no specimens being below L_m (Fig. 4.2c). The shark with the lowest length at maturity (L_m) was the blacktip reef shark (*C. melanopterus*) at 77.2 cm and 60.7 cm for females and males, respectively, with 92% of females and 50% of males being below L_m (Table 4.5 and Fig. 4.2b). Asymptotic length (L_∞) was largest for the scalloped hammerhead shark at 257.4 cm and lowest for the blacktip reef shark at 130.6 cm (Table 4.5).

Table 4.5. Growth parameters of sharks landed at Kipini following Froese and Binholan (2000) empirical equations. (L_{max}, maximum observed length; L_∞, asymptotic length; L_m, mean length at first maturity; L_{opt}, length at maximum possible yield per recruit and < L_{opt}, proportion less than length at maximum possible yield per recruit)

SPECIES	L_{max} (cm)	L_∞ (S.E. range) (cm)	$L_m$female (S.E. range)(cm)	$L_m$male (S.E. range) (cm)	L_{opt} (S.E. range) (cm)	< L_{opt} (%)
Sphyrna lewini (Scalloped hammerhead shark)	254	257.4 (217.1-305.2)	146.7 (110.6-194)	111 (79.2-155.9)	172.9 (146.2-204.6)	98
Carcharhinus amblyrhynchos (Grey reef shark)	133	136.2 (114.8-161.5)	80.3 (60.6-106.3)	63 (44.9-88.4)	89.1 (75.3-105.4)	46
Carcharhinus falciformis (Silky shark)	132.5	135.7 (114.4-160.9)	80 (60.4-106)	62.8 (44.8-88.1)	88.7 (75-105)	0
Carcharhinus melanopterus (Blacktip reef shark)	127.5	130.6 (110.2-154.9)	77.2 (58.3-102.2)	60.7 (43.3-85.1)	85.5 (72.1-100.9)	95

4.2 Trophic interactions

4.2.1 Cumulative trophic diversity curves

Cummulative trophic diversity curves (Fig. 4.3) were used to determine the sufficiency of the sample sizes for diet analysis. The curves of *S. lewini*, *C. melanopterus* and *C. falciformis* (Fig. 4.3 a,b,c) approached an asymptote indicating sufficiency of samples for gut content analysis, while that of *C. leucas* and *C. amblyrhynchos* (Fig. 4.3 e,d) appeared to be far from an asymptotic point indicating insufficient samples. The highest total accumulated trophic diversity (H_k) was that of *C. amblyrhynchos* at 4.12 and *S. lewini* at 4.02 (Table 4.6 and Fig. 4.3 d,a). *Carcharhinus leucas* had the lowest total accumulated trophic diversity of 1, while *C. melanopterus* had an intermediate asymptotic diversity of 2.52 (Table 4.6 and Fig. 4.3b).

The range of trophic diversity (bits per individual) of the food items was highest for the *S. lewini* (0.71 ± 0.23) and nearly equal for *C. melanopterus*, *C. falciformis* and *C. leucas* at about 0.5 (Table 4.6).

Table 4.6. Values of trophic diversity (bits per individual) in each stomach (*H*) and total accumulated trophic diversity (H_k) for shark species landed at Kipini, north coast of Kenya

	H		
	Range	mean *H* ± SD	H_k
Sphyrna lewini	0.35 - 1.27	0.71±0.23	4.02
Carcharhinus melanopterus	0.50 - 0.53	0.50±0.01	2.52
Carcharhinus falciformis	0.50 - 0.65	0.52±0.04	3.68
Carcharhinus amblyrhynchos	0.46 - 0.68	0.60±0.16	4.12
Carcharhinus leucas	0.50	0.50±0.00	1

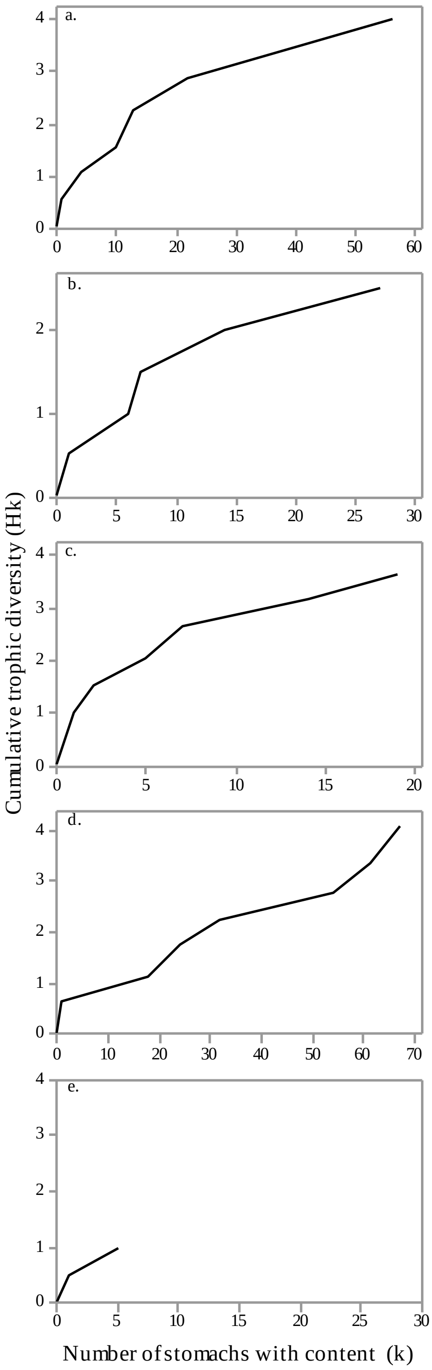

Figure 4.3. Cumulative trophic diversity curves of (a) *Sphyrna lewini*, (b) *Carcharhinus melanopterus*, (c) *Carcharhinus falciformis*, (d) *Carcharhinus amblyrhynchos*, (e) *Carcharhinus leucas*.

4.2.2 Composition of diet of the shark species

Gut content analysis (GCA) indicated that fish are the most important prey items for five shark species (Table 4.7). Fish prey occurred the highest in stomachs of *C.*

melanopterus and *C. leucas* with frequency of occurrence (FO) of 76 and 75%, respectively. *Carcharhinus falciformis* and *C. amblyrhynchos*, had the lowest FO of fish in their stomachs at 46 and 47%, respectively. Fish prey had also the highest importance value in the diet of the sharks as measured by the index of relative importance (%IRI) in *C. leucas* (97.6%), *C. melanopterus* (92.8%) and *S. lewini* (84.6%). Relatively lower importance of fish as prey was found in *C. falciformis* (58.2%) and *C. amblyrhynchos* (45.9%) (Table 4.7). Crustaceans had the second highest importance values as prey recording %IRIs of 43.2 and 41.8% for *C. amblyrhynchos* and *C. falciformis*, respectively. They had lower IRI values in *S. lewini*, *C. melanopterus* and *C. leucas* at 11.49, 3.6 and 1.2%, respectively (Table 4.7). Cephalopods were the third most important prey as indicated by IRI values of 10.9% in *C. amblyrhynchos*, with relatively lower importance values in *S. lewini* (3.8%), *C. melanopterus* (3.6%) and *C. leucas* (1.2%), with *C. falciformis* lacking cephalopods in its diet. The remaining prey items including molluscs and plant materials were only present in the diet of *S. lewini* with very low IRI values of 0.09% and 0.04%, respectively (Table 4.7).

Table 4.7. Percent number (N), weight (W), frequency of occurrence (FO) and index of relative importance (IRI) of prey items found in the stomachs of 5 species of sharks landed at Kipini, north coast of Kenya

Species	Prey item	Number	%N	Weight (g)	%W	FO	%FO	IRI	%IRI
Sphyrna Lewini	Fish	329	74.26	369.028	65.85	48	51.61	7231.0771	84.58
With prey =56 , Empty = 2	Cephalopod	25	5.64	74.325	13.26	16	17.2	325.08	3.8
	Crustacean	76	17.15	108.773	19.41	25	26.88	982.7328	11.49
	Mollusc	11	2.48	7.851	1.4	2	2.16	8.3808	0.09
	Plants	2	0.47	0.415	0.08	2	2.15	1.1825	0.04
Carcharhinus leucas	Fish	6	75	159.127	99.59	6	75	13094.25	97.63
With prey = 6, Empty = 7	Cephalopod	1	12.5	1	0.01	1	12.5	156.375	1.17
	Crustaceans	1	12.5	0.661	0.4	1	12.5	161.25	1.2
Carcharhinus melanopterus	Fish	33	73.33	106	46.04	23	76.47	9128.2239	92.79
With prey = 32 , Empty = 30	Cephalopod	6	13.335	15.212	6.61	6	17.65	352.02925	3.58
	Crustaceans	6	13.335	109	47.35	5	5.88	356.8278	3.63
Carcharhinus falciformis	Fish	31	51.67	724.68	73.05	21	45.65	5693.468	58.19
With prey = 27, Empty = 4	Cephalopod	0	0	0	0	0	0	0	0
	Crustaceans	29	48.33	267.4	26.95	25	54.35	4091.468	41.81
Carcharhinus amblyrhynchos	Fish	59	45.38	393.966	23.28	46	47.42	3255.8572	45.92
With prey = 67 , Empty = 31	Cephalopod	20	15.38	483.221	28.55	17	17.53	770.0929	10.86
	Crustaceans	51	39.24	815.347	48.17	34	35.05	3063.7205	43.22

4.2.3 Rates of feeding intensity and niche breadths

Sphyrna lewini, had the highest feeding intensity as measured by a vacuity index of 3.5% with only 2 out of 60 stomachs completely empty (Table 4.8), *C. falciformis*, had a vacuity index of 12.9%, *C. amblyrhynchos* (31.6%), *C. melanopterus* (48.4%), while *C. leucas* had the lowest feeding intensity at a vacuity index of 53.9% with 7 out of 20 stomachs empty (Table 4.8).

The niche breadth of shark species landed in Kipini determined using Levin's standardized index (B_i) (see 3.3.5) are shown on Table 4.9. *Carcharhinus amblyrhynchos*, had the broadest niche breadth ($B_i = 0.283$), followed by *C. falciformis* ($B_i = 0.247$) indicating a wide range of food items in their diet. The remaining species had narrower niche breadths ranging from 0.043 in *S. lewini* to 0.002 in *C. leucas* (Table 4.9). There were insignificant seasonal differences (t = 5.0, p = 1.0) in the niche breadth of *S. lewini* during NEM (0.101 ± 0.137) and SEM (0.0225 ± 0.011) seasons. Data were not available in both seasons for the other species.

Table 4.8. Rates of stomach vacuity (V%) calculated for five shark species landed at Kipini in coastal Kenya. Ne = number of empty stomachs, Ns = total number of stomachs examined

Species	Ne	Ns	V (%)
Sphyrna lewini	2	58	3.45
Carcharhinus leucas	7	13	53.85
Carcharhinus melanopterus	30	62	48.39
Carcharhinus falciformis	4	31	12.90
Carcharhinus amblyrhynchos	31	98	31.63

Table 4.9. Niche breadth (*Bi*) derived for five shark species landed in Kipini, coastal Kenya

Species	Levin's standardized index (*Bi*)
Carcharhinus amblyrhynchos	0.283
Carcharhinus melanopterus	0.009
Sphyrna lewini	0.043
Carcharhinus leucas	0.002
Carcharhinus falciformis	0.247

4.2.4 Diet overlaps between species

Significant overlap in diet existed between shark species as analyzed using the Morisita-Horn index (Table 4.10). The highest level of dietary overlap was between *C. leucas*, and *C. melanopterus* ($C_H = 0.99$) which both had the highest IRI values for fish (Table 4.7). *Carcharhinus falciformis* recorded relatively lower level of overlap in diet with a C_H of 0.72. *Sphyrna lewini* had the highest dietary overlap with *C. melanopterus* ($C_H = 0.99$) and the lowest dietary overlap with *C. falciformis* ($C_H = 0.77$) (Table 4.10).

Table 4.10. Overlap in the diet of five shark species landed at Kipini on the Kenyan coast as measured by the Morisita-Horn index (C_H). High dietary overlap is indicated by C_H values >0.6

	Carcharhinus leucas	*Carcharhinus melanopterus*	*Sphyrna lewini*	*Carcharhinus amblyrhynchos*	*Carcharhinus falciformis*
Carcharhinus leucas	1	0.9998	0.9947	0.7658	0.7194

Carcharhinus melanopterus	1	0.9962	0.7851	0.7266
Sphyrna lewini		1	0.8209	0.7766
Carcharhinus amblyrhynchos			1	0.9919
Carcharhinus falciformis				1

4.2.5 Feeding strategy

The feeding strategy of the species is evaluated from the two-dimensional space of a plot of prey-specific abundance (P_i) against the frequency of occurrence (%*FO*) of the preys (Fig. 4.4). The percent abundance of prey, increasing along the diagonal from the lower left to the upper right corner, provides a measure of prey importance, with dominant prey at the upper, and rare or unimportant prey at the lower end (see also Fig. 3.3). The predators that have specialized on prey types are positioned in the upper part of the plot, whereas prey positioned in the lower part are eaten more occasionally (generalization).

Fish prey were located in the upper right corner of the plot for all shark species examined except in *C. amblyrhynchos* (Fig. 4.4), indicating its dominance as well as importance, mainly due to the high %*FO* in stomachs as well as demonstrating specialization towards this prey item. Crustaceans were located in the central area of the plots and can be considered as the second most important prey item except in *C. leucas* (Fig. 4.4b) where they were absent and *C. melanopterus* where cephalopods came after teleost fishes in terms of dietary importance (Fig. 4.4c). Cephalopods, molluscs and plants were located in the left areas of the plots in all species examined indicative of their low importance as food items in the sharks examined.

A specialized feeding strategy was adapted towards consumption of molluscs in *S. lewini* as seen from the location of the prey at the top left of the plot, suggesting low *FO* combined with high abundance in the species (Fig. 4.4a). A more generalized feeding strategy was adopted towards cephalopods in all species examined with a low frequency of occurrence and a medium prey-specific abundance except in *C. falciformis* where cephalopods were absent (Fig. 4.4d). Plant materials were present only in the diet of *S. lewini*, which adopted a generalized feeding strategy towards this item (Fig. 4.4a). The low *FO* and prey-specific abundance of plants suggests ingestion perhaps by accident.

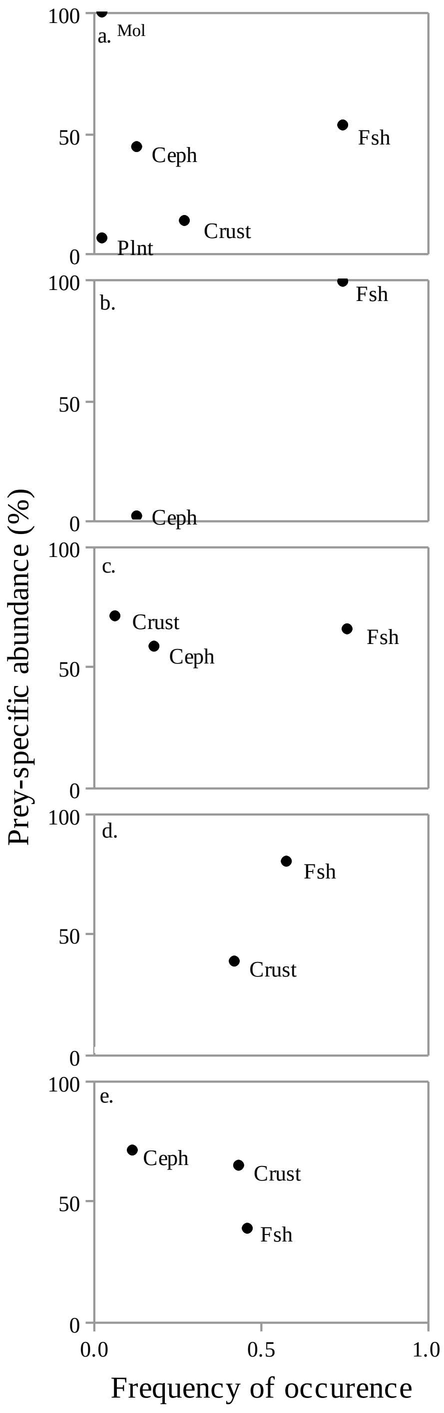

Figure 4.4. Relationship between prey-specific abundance and their frequency of occurrence in the diet used to determine feeding strategy in (a) *Sphyrna lewini*, (b) *Carcharhinus leucas*, (c) *Carcharhinus melanopterus*, (d) *Carcharhinus falciformis*, (e) *Carcharhinus amblyrhynchos*

4.2.6 Annual biomass consumption of sharks during the period 2014/15

The biomass of prey items (kg) consumed by *S. lewini*, during the period 2014/2015 was highest for teleost fish at 333.6 kg, while cephalopods and crustaceans were consumed at 26.6 and 9.7 kg, respectively by the species (Fig. 4.5a). Consumption of molluscs and plants by the species was low at 6.1 and 0.08 kg, respectively (Fig. 4.5a). *Carcharhinus leucas*, consumed 71.9 kg of fish, which was its highest consumed prey (Fig. 4.5b), while crustaceans and cephalopods were consumed at 0.9 kg each (Fig. 4.5b). *Carcharhinus melanopterus*, consumed the highest weight of fish prey at 380.2 kg during the 2014/2015 period, while cephalopods and crustaceans were consumed at 27.1 and 14.9 kg, respectively (Fig. 4.5c). Fish and crustaceans were the only prey items consumed by *C. falciformis* at 276.5 and 198.6 kg, respectively (Fig. 4.5d). *Carcharhinus amblyrhynchos*, consumed crustaceans and fish at 172.1 and 164.1 kg, respectively, while 38.8 kg of cephalopods were consumed by this species (Fig. 4.5e).

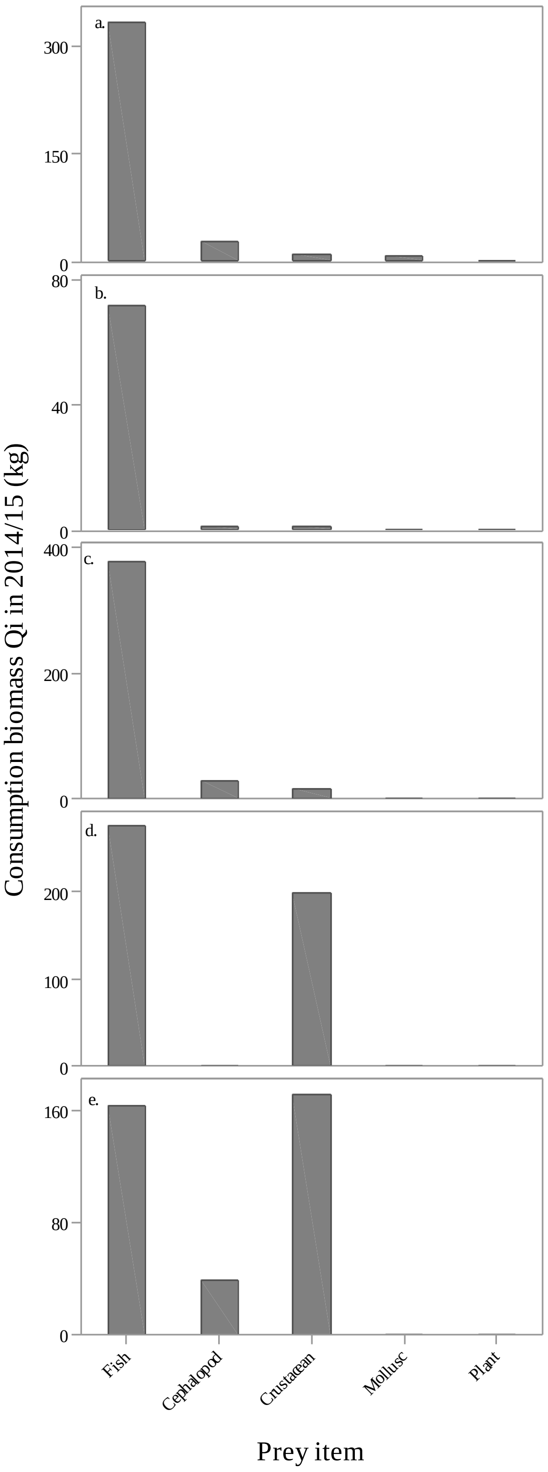

Figure 4.5. Biomass of prey items consumed by sharks landed at Kipini for the period 2014/15. (a) *Sphyrna lewini*, (b) *Carcharhinus leucas*, (c) *Carcharhinus melanopterus*, (d) *Carcharhinus falciformis*, (e) *Carcharhinus amblyrhynchos*.

4.2.7 Trophic Levels

The standardized diet compositions and trophic levels of *C. melanopterus*, *C. amblyrhynchos*, *C. leucas*, *C. falciformis* and *S. lewini* landed at Kipini are shown in Table 4.11. Fishes occurred in the highest dietary proportions in *C. leucas* (99.6%) and the lowest in *C. falciformis* (53.9%). Although crustaceans and cephalopods constituted relatively lower dietary proportions of the sharks, crustaceans occurred in significant proportions in *C. falciformis* (46.1%) and *C. amblyrhynchos* (39%). Molluscs and plants had a standardized proportional contribution of 0.03% and 0.01%, respectively, in the diet of *S. lewini* and were absent in the diet of other shark species examined in the study (Table 4.11).

The Trophic level (*TL*) of sharks landed ranged from 3.90-4.238. *Carcharhinus leucas*, recorded the highest trophic position of 4.238 that was close to that of *C. melanopterus* and *S. lewini* at 4.233 and 4.192, respectively. *Carcharhinus amblyrhynchos* and *C. falciformis* had relatively lower trophic levels at 3.956 and 3.90, respectively (Table 4.11).

The relationship between *TL* and body size was examined by fitting second order polynomial regression lines to the plots of the species with n > 25 as well as for all the species combined (Figs. 4.6a-d). *Carcharhinus amblyrhynchos* indicated a poor negative relationship between *TL* and size with R^2=37.9% (Fig. 4.6a). However, good fits between *TL* and body size were found for *C. melanopterus* and *C. falciformis*, with 97% of the variability in *TL* being explained by body size in *C. melanopterus* (Fig. 4.6b). The relationship between *TL* and body size was also positive and strong for *C. falciformis* with R^2=96% (Fig. 4.6c). At the community level (all sharks combined), results indicated a poor negative relationship between *TL* and body size with R^2=28.30% (Fig. 4.6d).

Table 4.11. Standardized diet compositions (%) and estimated trophic levels (*TL*) of shark species on the Kenyan coast. See Table 3.1 for definitions of prey categories; N is the total number of stomachs analyzed per species, shark species names are as per Table 4.2

		PREY CATEGORY												
Species	N	FISH	CEPH	MOL	CR	INV	ZOO	BIR	REP	MAM	CHON	PL	*TL*	*TL**
C. leucas	13	99.60	0.19	0.0	0.21	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**4.238**	4.3[a] 4.5[b] 4.3[c]
C. melanopterus	62	98.18	0.99	0.0	0.83	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**4.233**	3.9[a] 3.9[c]
S. lewini	58	92.09	1.37	0.03	6.5	0.0	0.0	0.0	0.0	0.0	0.0	0.01	**4.192**	4.1[a] 4.1[c]
C. amblyrhynchos	98	56.08	4.90	0.0	39.02	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**3.956**	4.2[a]
C. falciformis	31	53.90	0.00	0.0	46.10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**3.90**	4.2[a]

*TL****** Estimated Trophic Levels from other studies. Estimates obtained from [a.] Cortés (1999) [b.] Daly *et al*. (2013) [c.] Munga *et al*. (2014).

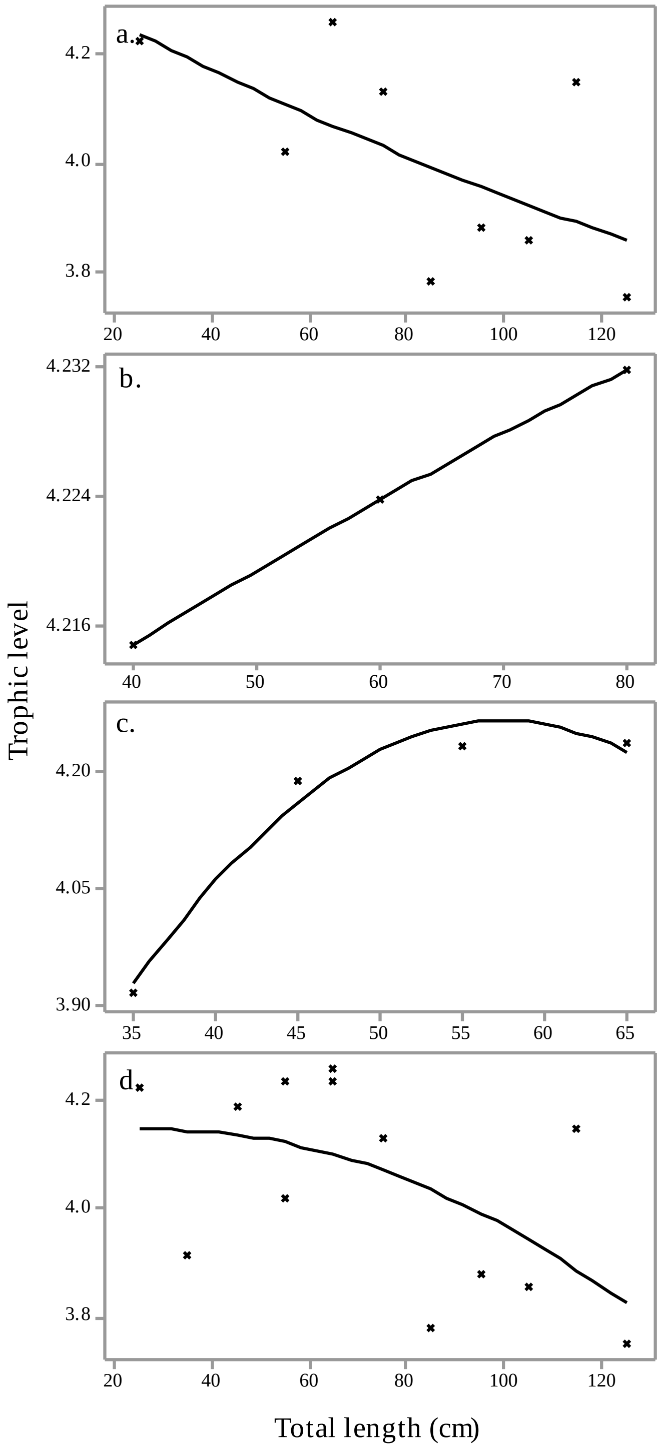

Figure 4.6. Relationship between trophic level and total length in shark species landed at Kipini, north coast of Kenya. Crosses indicate actual data while lines are fitted second order polynomial regression lines. (a) *Carcharhinus amblyrhynchos*, (b) *Carcharhinus melanopterus*, (c) *Carcharhinus falciformis*, and (d) all species combined

CHAPTER FIVE

DISCUSSION

5.1 Shark species composition, size distribution and exploitation status

Sharks landed at Kipini comprised mostly the genus *Carcharhinus*, with the scalloped hammerhead, *S. lewini* (n=397), forming the bulk of the catch. The Carcharhinidae have also been found to dominate landings in other topical areas (White & Sommerville, 2010) that may be largely due to their annual movement patterns to coastal waters (Garla *et al*., 2006). The asymmetrical size-frequency distribution of some of the shark species in this study together with the skewed sex ratios in the landings suggest a need for management regulations that recognizes mixed populations in the landings (Pikitch *et al*., 2005,Hazin *et al*., 2001) and sex biased exploitation (Klimley, 1987; Economakis & Lobel, 1998). Sex skewed exploitation may result into recruitment failure if females are continuously fished out (Camhi *et al*., 1998).

An analysis of length frequency distribution indicates that a number of sharks caught in the artisanal fishery were smaller than the size of maximum possible yield per recruit (L_{opt}). There were also large proportions of sharks caught below length at first maturity (L_m) (eg. in *C. melanopterus* and *C. amblyrhynchos*). This scenario suggests that these species are exploited at less than optimum body mass which may result into reduced recruitment and growth overfishing in the long term (Froese & Binohlan, 2000). The scalloped hammerhead shark which is currently listed as endangered in the IUCN redlist (IUCN.org) is the most vulnerable to stock collapse on the Kenyan coast with 98% of females and 87% of males landed being below L_m. However, the silky shark, *C. falciformis* sizes were larger than L_m as well as L_{opt} indicating that they are being exploited at optimum levels. This study provides preliminary data on the exploitation status of the species, other methods of determining growth parameters such as skeletal analysis (Goldman & Musick, 2006), will be required to validate the reference parameters determined in this study. Nonetheless, the analysis indicates that management measures are required to mitigate the seemingly overexploitation status of the species.

5.2 Diet composition and relative importance of prey items

The results of this study indicate that the shark species are highly piscivorous confirming similar conclusions from elsewhere (Wetherbee & Cortés, 2004; Bruyn *et al*., 2005; Daly *et al*., 2013). The relatively high contribution of fish to the diet of bull sharks is consistent with findings of previous studies (Cliff & Dudley, 1991; Werry *et al*., 2011; Daly *et al*., 2013). Recent studies suggest that juvenile bull sharks exhibit some level of individual dietary specialization (Matich *et al*., 2011), however, there is little knowledge regarding individual dietary specialization of larger sharks and how factors such as ontogeny, sex or habitat use affect the trophodynamics of individuals or populations (Daly *et al*., 2013). All bull sharks landed in this study were juveniles suggesting an influence of river Tana (which enters the sea at Kipini) on their ecology. Juveniles of bull sharks are known to migrate up rivers that discharge into the ocean (McCord & Lamberth, 2009) such as river Tana. The blacktip reef shark, *C. melanopterus* also exhibited high preference for teleost fishes as food. Other studies (e.g. Last & Stevens 1994; Janse, 2003) have reported a piscivorous diet of this species as found in this study. It is likely that the high preference of fish as food by the sharks relates to the bioenergetic value of fish as food for most predators (Duncan, 2006) since most sharks are in constant motion and require energy for movements and buoyancy maintenance. .

The species of fish consumed by the sharks could not be determined in this study due to levels of digestion, however, the presence of specimens of reef and pelagic fish in the diet of *S. lewini* off the coast of northeastern Brazil (Junior *et al*., 2009) indicates that this species searches for prey close to the reefs as much as in the adjacent pelagic environment. In this study *S. lewini*, was found to feed on teleost fishes, crustaceans, cephalopods, molluscs and plants indicating feeding at various depth ranges. Similar diets (cephalopods and fishes) were described previously for scalloped hammerhead sharks from Kaneohe, Oahu, Hawaii (Clarke-Thomas, 1971), Kwazulu-Natal, South Africa (Smale & Cliff, 1988) and Gulf of California (Klimley, 1983). Analysis of the diet of small and coastal specimens of *S. lewini* from Hawaii showed that the most common prey items were alpheid shrimps and two species of goby (Bush, 2003). The results indicate consumption based on local prey resources and not necessarily fidelity to particular prey items.

5.3 Feeding strategy, consumption biomass and trophic levels

The niche breadth of sharks was highest for the *C. amblyrhynchos* and *C. falciformis* that also had high frequencies of occurrence of crustaceans and fish in their diet suggesting generalist feeding strategies in benthic and pelagic environments. Narrow niche breadth in the *S. lewini*, *C. melanopterus* and *C. leucas* are suggestive of specialized feeding strategies adopted by these species.

Significant interspecies overlaps (C_H>0.6) in diet existed between all the shark species examined in this study indicating potential competition for food resources. The high dietary overlap observed in this study could be perhaps due to overlaps in home ranges of the species (Klimley, 1983) or to similarity in resource requirements. Smale and Cliff (1988) found that the juveniles of *S. lewini* stay in coastal waters (mainly in bays) for some time, and that, with growth, they move toward oceanic areas during the night to feed, and return to the coast during the day. Similar behaviour has been observed in the bull shark, *C. leucas* (Brunnschweiler *et al*., 2010) which could be a factor contributing to the overlaps in diet between these and other species that migrate in search of food. Overlaps in diet may lead to reduced growth rates if food is limiting with resultant effect on reproductive outputs (Cortés, 1999).

Trophic levels (*TL*) of sharks landed ranged from 3.90-4.238. These values support the common view that sharks are apex predators (Cortés, 1999; Worm & Branch, 2012). The bull shark recorded the highest trophic position of about 4.24 indicating it is an apex-most predator among the studied sharks. This is similar to the results of Cortés (1999) and Munga *et al*. (2014) for this species. Daly *et al*. (2013) estimated a *TL* of 4.5 for the bull shark in the coastal waters of southern Mozambique. These results are similar to those estimated for the species in this study. The *TL* for the blacktip reef shark, *C. melanopterus* was derived as 4.23 in this study higher than 3.9 estimated by Cortés (1999) and Munga *et al*. (2014) indicating spatial and perhaps temporal variability in *TL* of species. Differences in trophic levels between studies may be due to varying habitat quality as well as variations in the diversity of prey items within certain geographical ranges. Nonetheless, the results of this study indicate that blanket categorization of sharks as apex predators is inaccurate due to the observed species specific differentiation.

Empirically based exploratory analyses suggest that trophic level–body size relationships are highly idiosyncratic (Romanuk *et al*., 2010). This is evident in this study with trophic levels indicating strong positive relationships with size for two species (*C. melanopterus* and *C. falciformis*) and a poor negative relationship for one species (*C. amblyrhynchos*) as well as for all species combined. Strong positive relationships may be attributed to ontogenic shifts in diet (Hairston & Hairston, 1993; Arim *et al*., 2007; Lucifora *et al*., 2009) and indicates more piscivorous diet with increased size. In gape-limited predators, the effect of body size on the foraging capacity is especially important and may obscure the relationship between size and *TL* (Forsman, 1991). At the community level, species specific patterns may obscure the relationship as observed in this study and in Cortés (1999).

Cortés (1999) the highest correlation between *TL* and the size of carcharhinid sharks whereby 30% of the variance in trophic level were explained by the body length. This trend is also evident in this study with a higher explained variance (97% in *C. melanopterus* and 96% in *C. falciformis*) contradicting the view that trophic levels of aquatic organisms are inversely related to size (Pauly *et al*., 1998a) and supporting the view that trophic level scales positively with body size in fishes (Romanuk *et al*., 2010).

CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

The six shark species recorded in the study all belong to the family Carcharhinidae and mostly in the genus *Carcharhinus*. The asymmetry in size-frequency distribution in *C. amblyrhynchos* indicates that males and females of some species may be from different populations or may simply be a reflection of differences in growth rate of the sexes.

There is likely sex-specific movement of some species to the fishing grounds as reflected by differences in sex ratios in the landings. This may result into recruitment failure if females are continuously fished out. In some species the size of specimens were smaller than the size of maximum possible yield per recruit (L_{opt}) and length at first maturity (L_m) which suggests that these species are exploited at less than optimum body mass and may result into reduced recruitment and growth overfishing in the long term. The hypothesis that the exploitation levels of the shark species on the Kenya north coast are optimum and sustainable is therefore accepted for *C. falciformis* but not for *S. lewini*, *C. melanopterus* and *C. amblyrhynchos*.

The generally high %IRIs for fishes in the diet of species are indicative of the highly piscivorous nature of sharks confirmed by the numerous studies on shark diet. The large contribution of crustaceans in the diets of the grey reef shark and the silky shark suggest that teleost fishes may be supplemented by invertebrates as prey in some species.

Narrow niche breadth in the scalloped hammerhead, blacktip reef and bull sharks are suggestive of specialized feeding strategies adopted by these species. Significant interspecies overlaps in diet existed between all the shark species indicating likely high competition for food resources. In this regard, the hypothesis that there is no competition for food items between the common shark species on the north coast of Kenya is not accepted. Narrow niche breadths and diet overlaps may restrict growth rates if food items become scarce in the environment or if climate induced variability in abundance occurs. This notion is reinforced by the specialist nature of some of the species studied. The generalist species (i.e. the grey reef shark and the silky shark) may suffer less from prey variations in the environment.

Trophic levels (*TL*) of sharks landed ranged from 3.90-4.238 indicating them as apex predators and that there is differentiation in *TL* between the species, hence the hypothesis that all the common shark species landed on the Kenyan coast are of the same trophic level is not accepted. Trophic level–body size relationships suggest strong positive relationships for two species of sharks (the blacktip reef shark and the silky shark) and a poor negative relationship for one species (the grey reef shark) as well as for all species combined. Strong positive relationships between *TL*s and size may be attributed to ontogenic shifts to more piscivorous diets as the species mature.

6.2 Recommendations

The following recommendations are made, as per the results of this study:

1. The scalloped hammerhead shark, (*S. lewini*) and the blacktip reef shark, (*C. melanopterus*) face a risk of growth and recruitment overfishing if the current exploitation pattern continues. It is recommended to apply the precautionary approach for the management of the stocks by limiting off take rates or by seasonal limitation in fishing. The use of illegal fishing gear like the monofilament nets should be restricted in the area, due to their high selectivity towards juvenile sharks. Circle hooks rather than j- hooks are recommended because they are known to reduce the efficiency of shark capture.

2. The prey items were categorized according to large taxonomic groups. It is recommended that future studies identify prey items in sharks up to species level in order to narrow down on finer levels of competition between these species. These will require sampling of a wider size range of the species and taking steps to reduce post-capture digestion.

3. All the shark species fed a total of 1.23 MT of fish for the year 2014/15. This may indicate a level of competition with the artisanal fishers especially if the prey species are also fished. Future studies should focus on evaluating the fish species involved and the potential interaction between fishers and sharks in terms of competition for prey.

4. Trophic level models that determine the effect of fishing on ecosystems should consider the fine scale differentiation in trophic levels as determined in this study when modeling effects such as trophic cascades or in the application of trophic-level based ecosystem models.

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APPENDIX

Shark species landed in Kipini, coastal Kenya

Plate 1. Scalloped hammerhead shark, ***S. lewini***

Plate 2. Bull shark, ***Carcharhinus falciformis***

Plate 3. Copper shark, ***Carcharhinus brachyurus***

Plate 4. Silky shark, ***Carcharhinus falciformis***

Plate 5. Blacktip reef shark, ***Carcharhinus melanopterus*** **(Above) and grey reef shark,** ***Carcharhinus amblyrhynchos*** **(Below)**

(Source:Author 2015)