DETERMINANTS OF HABITAT USE BY FISH AND CRUSTACEANS IN MANGROVES: USING HABITAT CHARACTERISTICS TO PREDICT COMMUNITIES.

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DEDICATION

I dedicate this thesis to You Elohim, the One who sees. Thank you for your everlasting love, kindness and mercy. You enabled me to start, continue and finish this journey successfully. I will honour you all the days of my life. To you my dear husband, Gitundu Kairo, our children Kairo Jnr), Wanjiku, Wachira and Wangui, I also dedicate this thesis. You stood with me strongly and lovingly to ensure that I completed my studies, even when sickenss threatened completion of this work. You are a treasure in my heart. Aunt Lucy, this thesis is also dedicated to you for your great sacrifice. Finally, I dedicate this thesis to the memory of my late mum, Eunice Wangui who reminded me and my siblings that a good education was the only meaningful inheritance we were ever going to get from her. Thank you so much for this inhetitance.

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EXECUTIVE SUMMARY

Healthy mangroves are important for the provisioning of ecosystem goods and services that contribute to human wellbeing. Productive fisheries have been associated with healthy mangrove forests which function as nursery habitats for juvenile reef species. The threats facing mangroves and other nearshore habitats like seagrass beds are still high. Despite these threats, the rate of loss for instance for mangroves is on the decline due to increased global awareness. Replanting and reforestation of degraded areas has also been on the increase. Greater attention is now paid on the quality of the remaining forests and of restored areas and how this affects the capacity to provide ecosystem goods and services. The current study sought to explore the role of forest quality in fish and crustacean community structure (biomass, abundance, species diversity) in the Vanga mangrove ecosystem, in south coast Kenya. Further, it aimed to explore the role of the seascape (a mosaic of connected habitats), with a focus on seagrass beds, on the faunal community assemblages sampled in mangrove areas.

Chapter one discusses mangrove goods and services and especially the role they play in supporting healthy fisheries. It explores the definition of ‘nursery habitats’ and the key elements that define them. It also discusses roles of mangroves as refugia and feeding grounds for juvenile fish and the links between mangroves and offshore fisheries.

Chapter two describes fish and crustacean community assemblages in Vanga. Fyke nets were used to sample fish at 14 mangrove sites between September 2015 and September 2017. Fishes were sampled once every three months. A total of 59 fish and 16 crustacean species were encountered with 50% of these species (both fishes and crustaceans) being of commercial importance. Circa 70% of the catch was dominated by six species, as is common with nearshore habitats. Over 95% of the fishes caught were juveniles, further strengthening the argument for mangroves as nursery habitats.

Chapter three addresses the importance of mangrove forest quality on faunal communities. The Complexity Index (C.I.), a product of forest structural features (stem density, mean tree height, basal area and no. of species) was used as a proxy for habitat quality of mangroves. Broad scale and fine scale forest features were regressed against fish and crustacean variables: biomass, abundance and number of species. Fine scale forest features were not important in structuring fish and crustacean communities whilst broad scale features did show significant relationships. Mean fish abundance decreased with increasing C.I. while mean crustacean abundance increased with increasing C.I. There were sites that showed high diversity and corresponding high fish biomass for fishes and high abundance and biomass for crustaceans over time.

Chapter four discusses the diet of six of the most abundant fishes that were sampled. A total of 193 stomachs were analysed using the stomach content analysis method. Nine food categories consisting of 36 different prey items were ingested and crustaceans were the most dominant food category. All six sampled species ingested insects, which they most likely got from the mangrove forests. This indicates that some feeding took place in the mangroves. The diet breadth was narrow and ranged between 0.08 – 0.45 revealing that most fish species fed on a low variety of prey items.

Chapter five explores the influence of seagrass metrics on fish and crustacean assemblages sampled in the mangrove forest sites. The spatial analysis and calculation of seagrass geometry was done using ArcGIS. Seagrass metrics - area, perimeter, perimeter/area ratio, cumulative area and cumulative perimeter - were regressed against fish and crustacean variables. Fish variables were positively correlated with seagrass area and responded negatively to increasing perimeter/area ratio. On the other hand, crustaceans increased with increasing perimeter/area ratio; hence there was a tendency for fishes and crustaceans to respond in opposite ways to seagrass seascape metrics. In this respect, these results mirrored those found when exploring the effects of forest quality metrics. Most fishes and crustaceans responded to seagrass metrics measured within a distance of 3.5km from the catch sites. From this study, seascape features of the seagrass beds are found to be important for some of the fish and crustacean species caught in the mangroves meaning that it is not sufficient to explain faunal assemblages with a focus on a single seascape habitat.

Chapter 6 is a synthesis of all the chapters in this thesis bringing together all the findings and generating general conclusions and their implications on management approaches. Multiple linear regression models that include both forest and seascape variables were tested against fish and crustacean variables. The strongest significant relationship (p=0.001) was between the Indian white prawn *Penaeus indicus* and perimeter/area ratio at 2.5km, and mean tree height, number of tree species and stem density of mangroves. About 87% of the variation was explained by these predictor variables. This study suggests that, given the increasing interest in a holistic approach to seascape management and conservation, seascape habitats can no longer be studied in isolation. In addition, the current work has shown that different faunal groups and even individual species respond differently to forest and seascape features and therefore, the notion of a single ‘nursery habitat ecosystem function’ is simplistic; rather the mangrove/seagrass seascape provides a range of different nursery services for the species present.

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ABSTRACT

There is a broad consensus that mangroves are often important nursery habitats, providing refuge and food for juveniles of offshore fauna. However, despite the large number of studies that investigate the presence, strength and mechanisms responsible for this function, much uncertainty and ignorance remains. For example, it remains generally impossible to predict which forests might be most important for fish and crustaceans and, within individual forests, what areas and types of habitat are most important. The present study sought to identify whether there were consistent differences in the fish and crustacean communities between sites within a mangrove forest. It then investigated whether mangrove forest attributes (complexity index, stem density, no. of species, basal area and tree height) and seascape metrics relating to the position of mangrove sites with relation to seagrass (seagrass perimeter, area and perimeter/area ratio) can predict and explain these differences. The null hypotheses of no relationships between forest characteristics and seagrass metrics (predictor variables) and fish and crustacean community variables (response variables) in the Vanga mangrove system were tested.

Fourteen sites, differing in forest characteristics that were assessed at fine and broad scales and summarised by the Complexity Index (C.I.), were selected in the >4000ha Vanga mangrove site in southern Kenya. Fyke nets deployed at the mangrove creek mouths repeatedly sampled faunal communities leaving these sites during ebb tide. Fishes were identified and measured, stomach contents were used for diet analysis and the influences of forest and environmental variables on community structure were explored using univariate and multivariate statistics.

A total of 59 fish species and 16 crustacean species were recorded (although catches were dominated by only seven species). Stomach contents showed a novel dependence on insects for a large fraction of the fishes. No association existed between faunal characteristics and fine scale forest variables, but some significant relationships were evident with the broad scale characteristics. Linear regressions showed that C.I. was negatively associated with mean fish abundance and positively associated with mean crustacean abundance. Perimeter/area ratio and patch size of seagrass showed strong significant positive relationships with some of the faunal variables at various distances and directions. Linear regression relationships between combined forest and seascape variables (predictor variables) and fish and crustacean variables (response variables) were tested. The Indian whiteprawn, *Penaeus indicus* and the humpbacked cardinalfish, *Yarica hyalosoma* displayed strong and significant relationships with combined forest and seascape features. This study suggests that whilst there are differences between sites within mangroves, which can partially be explained by environmental variables, there are no simple summary characteristics that explain why some sites supported high diversity and biomass of ichthyofauna while others supported low diversity and biomass.

1.0 CHAPTER 1: GENERAL INTRODUCTION

1.1 Mangrove ecosystem services

Ecosystems provide essential services that contribute to human wellbeing throughout the world (Costanza et al., 1997; de Groot et al., 2012); these are generally grouped into regulatory, cultural, supporting and provisioning services (MEA, 2005). Provisioning services have long been recognised, due to their tangible nature and ease of sale in conventional markets. The other services were largely ignored and frequently under-valued until recently. The application of economic valuation techniques to ecosystem services (e.g. Costanza et al., 1997) is one approach taken to communicate the value of these other services.

Whilst mangrove forests have long been recognised as important ecosystems, the scale of their contribution has only become apparent in the past fifteen years. As the most carbon-dense forests, they are globally important carbon sinks sequestering up to five times more carbon compared to productive terrestrial tropical forests (Donato et al., 2011). They are effective coastal buffers and are capable of land building in the face of sea level rise (Mazda et al., 2002; Dahdouh-Guebas et al., 2005; Koch et al., 2009). They also provide a wide range of forest products such as timber and honey (Abuodha & Kairo, 2001). The recognition of these ecological services provides powerful arguments for conservation.

Despite the critical role mangroves play in providing multiple ecosystem services, they continue to be converted, degraded and abused in the face of short term development priorities and chronic harvesting and poaching (Spalding et al., 1997; Valiela et al., 2001; Giri et al., 2011). These pressures are likely to be exacerbated by the effects of climate change, particularly sea level rise (de Groot et al., 2012). Since 1980, about 35% of the world’s mangroves have been lost at an estimated annual rate of 2.1% per annum (Valiela et al., 2001). A more recent study by Giri et al. (2011) revised this figure to 0.7% by area per annum. Fragmentation of mangrove habitats puts these ecosystems under further risk, with Duke et al., (2007) predicting possible extinction of mangrove forests in the coming 100 years. In Kenya, over 18% of mangrove forests have been lost since 1980 due to a combination of human induced factors, ranging from over-exploitation of resources, conversion of mangrove areas to other land uses, and pollution (Abuodha & Kairo, 2001; Kirui et al., 2013).

The Trans - boundary Diagnostic Analysis of land based sources of the Western Indian Ocean Region (WIOMSA, 2009) has cited poor governance along with increased population pressure as two of the leading root causes of mangrove degradation in the WIO region. Some of the consequences of this loss include reduction in fisheries and loss of livelihoods (Barbier, 2006). Established top-down governance approaches to natural resource management in the region have marginalised resource users, partly to avert the tragedy of the commons (Hardin, 1977). However they are often ineffective and have in most cases been blamed for accelerated degradation and loss of natural resources (Ostrom, 1990).

1.2 Mangrove fisheries

Mangroves have for a long time been associated with healthy fisheries (Barbier, 2000). The link between mangroves and coastal fisheries has been widely studied and documented over time (Blaber et al., 1989; Vance et al., 1996; Ikejima et al., 2003; Chong, 2007; Lugendo et al., 2007). Studies on mangrove fisheries have ranged from their role as nurseries for fish (Mumby et al., 2004; Gajdzik et al., 2014) to their connectivity with adjacent seagrass and coral reef ecosystems (Mumby et al., 2004; Crona & Rönnbäck, 2007).

1.2.1 Definition of nursery habitats

Estuarine and inshore habitats, among them mangroves, are important nursery habitats for juveniles (Laegdsgaard & Johnson, 1995; Paillon et al., 2014). The occurrence of high juvenile densities of reef fish species in non - reef habitats like mangrove areas while the adults were largely found in reef habitats suggested ontogenetic shifts and gave rise to the 'nursery concept' (Parrish, 1989). The definition of nursery habitats has evolved from being simply areas where the juveniles of a species occur at high densities (Nagelkerken et al., 2000; De La Morinière et al., 2002), to areas that provide proportionally more recruits into the adult population than comparator sites (Beck et al., 2001), indicating that not all juvenile habitats are nurseries. Juveniles in nursery sites therefore tend to: occur in high densities, increase in biomass, have high survival rates and finally, and crucially, make successful movement from juvenile to adult habitats, necessitating a distinction between juvenile and adult habitats (Beck et al., 2001).

Although this definition makes it easier to prioritise limited conservation funds to real nursery areas, Dahlgren et al. (2006) pointed that it excluded some important habitats e.g. large areas having a lower per unit area density of individuals compared to a smaller area but the former contributing more individuals to the adult populations compared to the latter.

While the above arguments concentrate on the transfer of biomass offshore, the mechanisms that drive these processes, should also be incorporated to make the approach holistic (Kimirei et al., 2013; Sheaves et al., 2014). It should be considered that fish are mobile fauna and in a day could move between several interconnected habitats due to changing resource and service needs (Sheaves, 2005). Therefore, nurseries should be considered as “spatially explicit seascape consisting of multiple mosaics of habitat patches that are functionally connected” (Nagelkerken et al., 2015).

1.2.2 Mangroves as nurseries for fish

Copious studies have reported mangroves of different regions of the world to be important nursery habitats for juvenile fish. In the Caribbean, mangroves are among the most preferred nursery habitats for fish species, greatly influencing fish community structure in adjacent coral reefs (Mumby et al., 2004; Igulu et al., 2013). Compared to protection (a fishery management tool), mangroves have, in some cases, been found to contribute up to 249% increase in biomass in adjacent reefs (Nagelkerken et al., 2012), meaning that healthy mangroves may reduce the need for protection. Likewise the biomass of some commercial fish species, in the same region, is doubled whenever adult habitats are connected to mangroves (Mumby et al., 2004). In Moreton Bay, Australia, mangroves play a greater role as nursery habitats compared to adjacent potential habitats (Laegdsgaard & Johnson, 1995). The main theories that have been advanced to explain why fish are attracted to mangroves suggest that fish enter mangroves for: i) abundant food and ii) predator refuge services for post-larvae and juveniles of most fish species in all or part of their life cycle (Manson et al., 2005; Blaber, 2007).

1.2.3 Mangroves as feeding grounds

Mangrove systems exhibit high primary productivity and food abundance, which has been attributed to the mangrove trees themselves, their associated epiphytes, other larger plants, phytoplankton and benthic microalgae (Robertson & Blaber, 1992). The availability, nutritional value, and digestibility of microphytobenthos and algae makes them very important food sources in mangrove forests (Bouillon et al., 2008). Apart from providing food for the occupants, mangrove litter has, for long time, been hypothesised to contribute extensively to secondary productivity of adjacent waters through outwelled organic matter (Odum & Heald, 1972). However subsequent studies have shown the export to be much less than previously anticipated (Guest & Connolly, 2006; Chong, 2007; Nyunja et al., 2009).

Several studies, using stomach analysis, stable carbon and nitrogen isotopes and visual observations (Verweij et al., 2006; Lugendo et al., 2007; Gajdzik et al., 2014) have documented evidence that fauna do feed in mangrove areas. Mangrove detritus forms part of the diet for different finfish and crustacean species as well food for micro- and macrofauna fed on by fish (Chong & Sasekumar, 1981; Mumby et al., 2004; Chong, 2007). Macrobenthos found in mangrove forests are also consumed by mangrove fish species (Yap et al., 1994; Kiso & Mahyam, 2003). Epiphytic algae on the mangrove roots and stems present rich foraging grounds for several fish species (Laegdsgaard & Johnson, 2001), with similar evidence being deduced from stable isotopes studies on the epiphytic and attached fouling algae (Lugendo et al., 2007). In pristine mangroves in Australia, fish were found to rely on the primary productivity of mangroves, among other sources of food (Abrantes & Sheaves, 2009). Commercially important species have also been observed feeding in mangrove areas (Rooker, 1995; Verweij et al., 2006).

Studies from different regions in the world on the importance of mangroves as feeding grounds for fish have reached divergent conclusions. While they have been found to be very important feeding grounds for juvenile fish in the Indo-Pacific (Robertson & Duke, 1987), in the Caribbean they are less important food sources for most fish species

(Nagelkerken & Velde, 2004). Whereas permanent mangrove residents depend largely on mangroves for food, stable isotope analysis has shown that other fish species may not rely heavily on mangrove derived food, especially when mangroves are adjacent to other food sources like seagrass beds (Marguillier et al., 1997; Nagelkerken & Velde, 2004; Lugendo et al., 2007; Vaslet, 2012).

1.2.4 Roles of forest characteristics in providing refugia

As refugia, mangroves offer hideouts for species escaping from predators. The shallow environments, high turbidity, shade and structural complexity created by prop roots, branches, tree trunks and fallen debris provide ideal escape routes and shelter for fauna seeking refuge (Primavera, 1997; Laegdsgaard & Johnson, 2001; Blaber, 2007; Nagelkerken et al., 2008). Ellis & Bell (2004) noted that small fish in mangrove areas preferred shade to foraging areas when water depth increased.

The structural complexity of mangrove forests is thought to increase the density of finfish and shell fish by reducing predation risk. Primavera (1997) reported an 18.8% reduction in predation risk for shrimp in areas with pneumatophores compared to less complex areas without. The extent of the complexity was also found important as higher fish densities were found in more structurally complex *Rhizophora spp.* prop roots compared to less complex *Sonneratia spp*. pneumatophores (Vance et al., 1996).

The soft substratum in mangrove areas make it easy for prawns to burrow and hide from predators (Rönnbäck, 1999; Macia et al., 2003). Mangrove environments harbour fewer large carnivorous fish, compared to coral reef ecosystems that have clear waters (Vance et al., 1996; Rönnbäck, 1999). Consequently, there is reduced predation risk and increased survival rates of the prey species in mangrove areas (Sheridan & Hays, 2003;

Chong, 2007) promoting faster growth rates and thus increase in biomass in these nurseries.

Laboratory simulations have demonstrated turbidity and presence of pneumatophores to be effective in protecting shrimp against predators (Macia et al., 2003). Other experiments using artificial structures to mimic mangrove roots showed that fish sought shelter from structures in the presence of predators and kept away in their absence, and also when they increased in size and became less vulnerable (Laegdsgaard & Johnson, 2001). Thus, mangrove root structures are deemed to be positively correlated with high juvenile densities. This has also been noted even in replanted mangroves (Primavera, 1997; Bosire et al., 2004; Crona & Rönnbäck, 2007). Shade in mangrove forests is envisaged to provide camouflage for prey from attacking predators (De La Morinière et al., 2002).

1. 2. 5 Seascape

The importance of mangroves as nursery habitats cannot be investigated in isolation from adjacent seascape habitats such as seagrass beds and coral reefs (Dorenbosch et al., 2007). Where connectivity between seascape habitats exist, understanding the temporal and spatial interaction of organisms between them is important in designing sustainable fisheries management approaches (Bostrom et al., 2011; Berkström et al., 2012). Mangrove dependent fishes often use adjacent habitats such as seagrass beds during ebb tides (Jelbart et al., 2007). For example, the home range of approximately half of the fish species in Zanzibar includes more than one seascape habitat (Berkström et al., 2012) whereas in other regions, faunal abundance and densities were found to respond to the structure of habitat mosaics (Nagelkerken et al., 2001; Nagelkerken & Velde, 2002; Jelbart et al., 2007; Grober et al., 2009). Nagelkerken et al. (2001) recorded that in the Caribbean, fish migrated from adjacent mangroves and seagrass beds to mudflats, while seagrass beds near mangroves had higher species diversity and abundance than those in isolation. Jelbart et al. (2007) found low densities of mangrove-utilising fish in seagrass beds far from mangroves, whereas juveniles of the French grunt, *Haemulon flavolineatum* were found to be abundant in mangroves that were less than 100m from seagrass beds that had over 40% cover (Pittman et al., 2007) and vice versa. Therefore, it is increasingly common to adopt and apply landscape ecology principles to coastal seascapes with the purpose of exploring the relationships between these varying habitats and the organisms that depend on them. Seascape ecology is therefore an emerging field of study applied to coastal habitats which adapts landscape ecology methods to understand the causes and outcomes of spatial heterogeneity of the seascape (Pittman et al., 2011).

1.2.6 Contribution of mangroves to offshore fisheries

Various studies globally have pointed to a positive relationship between mangroves, as nurseries, and offshore fisheries productivity (Martosubroto & Naamin, 1977; Sasekumar & Chong, 1989; Mumby et al., 2004). Rönnbäck (1999) estimated that globally, a hectare of mangroves supported capture fisheries worth between US$ 750 - 16,750 annually. National estimates from different countries vary from these estimates. In Mexico, the annual support of mangrove fringe per kilometre to fisheries was estimated at circa US$ 25,000, while in the Gulf of California, mangrove related fish and crabs worth US$32,500 per ha were harvested (Aburto-Oropeza et al., 2008). The Pak Phanang mangroves in Thailand supported a multi species fishery that yielded 442 - 551 tons of fish annually worth US$ 368,038 – 733,973 (Islam & Ikejima, 2010). In Malaysia, mangroves contributed to approximately US\$846ha^{-1}yr^{-1} net worth of fisheries Chong, (2007). In Bangladesh, although mangroves were once found to contribute to 85-95% of the artisanal fisheries, this service was later seriously threatened by conversion of mangroves for aquaculture (Islam & Haque, 2005).

Despite the large literature documenting positive relationships between various species of fauna and the presence and extent of mangroves, this relationship is highly variable and is not always present (Loneragan et al., 2005; Aburto-Oropeza et al., 2008; Ellis & Bell, 2013). Understanding these patterns is further complicated by the different reporting methods used, different kinds of fishery in mangroves and the diversity of fishing gears making it difficult to compare data (Hutchison et al., 2014).

1.2.7 Contribution of mangrove quality to biodiversity/fisheries

Mangrove forests provide habitats for fish, birds, mammals, epifauna and mesofauna among others (Nagelkerken et al., 2008). Since changes in the biological and physical status of mangroves can benefit some organisms whilst disadvantaging others, the term 'mangrove habitat quality' can be ambiguous and may be circular (if, for example, high quality forest is identified by high levels of biodiversity, then by definition a forest is lower quality if it has lower biodiversity). These definitional problems are common to all attempts to define ecological quality or ecosystem health and careful analyses of the issue involve use of reference systems and long term data to show what relatively pristine ecosystem states might look like (Tett et al., 2013). However, in practice it is generally agreed that decreasing habitat quality (implying a degraded forest) can be measured through the diminution of the ability of the system to provide ecosystem services. Carugati et al. (2018) found that the degradation of mangrove forests led to reduced quality which in turn led to 20% biodiversity loss of benthic organisms and other fauna. In India, the reduced quality of mangroves through degradation was found to impact biodiversity including fish in mangrove areas negatively (Sahu et al., 2015).

However, it should be noted that so far, there are no set criteria used to determine mangrove forest quality and different studies use different parameters (e.g. (Koetsu et al., 2009; Gratwicke & Speight, 2005).

1.2.8 Problem statement

Mangrove forests are under great pressure from habitat degradation and transformation, over-exploitation of resources and pollution effects. Short-term gains from forest harvesting and coastal development often override long-term goals of mangrove conservation, including the preservation and enhancement of the fisheries nursery function of mangroves that is important both for local livelihoods and for commercial catches.

Whilst a broad-scale relationship between mangroves and nursery provision is well established, this relationship is not always observed and is highly variable between sites. Some of the mechanisms by which mangroves support survival and growth of juvenile fish and crustaceans are understood; the provision of food for fauna and predator refuges are well documented. However, this work has mostly been conducted at very small scales and sometimes involves artificial conditions. Hence there are significant gaps, particularly at the mesoscale, in our knowledge of how different feature of the forest and of the seascape in which it is situated may influence the presence, growth and behaviour of fish and crustaceans. Few studies (in Kenya or elsewhere) have tried to relate specific mangrove features and conditions within one or a few sites to fisheries production. For example, the relationships between mangrove area, species type and mix, forest quality and fisheries provision are poorly understood. Quantitative relationships between the size and quality of the forest and the number and diversity of fish are missing so informing managers of the costs and risks involved in marginal removal is not possible (Faunce & Serafy, 2006).

Developing a fuller understanding of these relationships will contribute to ecological science as well as having important implications for management; for example, it could highlight what areas of forest to preserve from harvesting and other uses, and allow the refining of economic and management models that incorporate nursery values. The present study, therefore, seeks to understand the relationships between mangrove forest conditions (area, quality, type and location within the broader seascape) and fish as well as crustacean abundance and community structure. Figure 1.1 shows the location of the sampling sites in Vanga mangrove ecosystems.

1.2.9 Overall objective

To study the role of mangroves in supporting fisheries in the Vanga mangrove ecosystem.

1.3 Specific objectives

1) To characterise the fish and crustacean communities in Vanga mangrove ecosystems
2) To investigate fish and crustacean use of different types of mangrove habitat and explore the roles of mangrove forest quality and type in determining fish community structure.
3) To explore the relationships between mangrove forest quality and fish diet
4) To investigate the role of seascape metrics in structuring the fish community and crustacean community structure in the Vanga mangrove ecosystem.

1.4 Null Hypotheses

1. There are no differences in fish and crustacean communities in mangroves of different quality in the Vanga ecosystem.

2. There are no differences in fish diet type and breadth in mangroves of different quality in Vanga.

3. There are no relationships between fish as well as crustacean variables with seagrass metrics

1.5 Scope of study and thesis structure

This aim of this study is to develop a thesis titled "**Determinants of habitat use by fish and crustaceans in mangroves: using habitat characteristics to predict communities"** which will be composed of six chapters in line with the thesis objectives. It is from these chapters that some of the papers the study aims to publish will be derived.

Chapter I: General introduction to mangrove fisheries

This chapter deals with the definition of mangrove nurseries, what is known about mangroves as nurseries. It explores the evidence to support their importance as nurseries and especially the refuge and feed theory. This chapter also seeks to demonstrate the importance of the study, what features of the forest are important for the fisheries and whether they can be used for management decisions and especially sustainable management.

Chapter II: Description of fish and crustacean communities in Vanga

This chapter will concentrate on describing the fish and crustacean communities of the mangroves of Vanga, including spatial and temporal variation and morphological data on key species.

Chapter III: Estimation of the effects of mangrove forest quality and other predictor variables on fish and crustacean communities.

This chapter looks at the effect of habitat quality on fish densities and species across the Vanga mangrove ecosystem. It explores how complexity index and associated factors of mangrove forests are related to the juvenile fish communities and crustaceans in the area.

Chapter IV: Diet analysis of juvenile fish in Vanga mangrove ecosystems

One of the hypotheses postulated to explain mangroves' suitability as nursery areas is the abundance of food available for juveniles. The stomachs of fish caught in these areas were analysed for diet type and breadth and these variables are related to habitat quality i.e. does a good quality habitat ensure more food of greater variety or does that depend on other factors besides habitat quality

Chapter V: The role of seascape metrics in structuring fish and community

This chapter utilises the seascape metrics data generated with the help of ArcGIS software to explore relationships of fish as well as crustacean variables with seagrass metrics.

Chapter VI: Conclusion and synthesis

This chapter summarises the findings on the relationship between mangrove habitat quality and fish communities in Vanga mangrove ecosystems. It also summarises the findings of the other chapters and relates them to the overall objectives of this study.

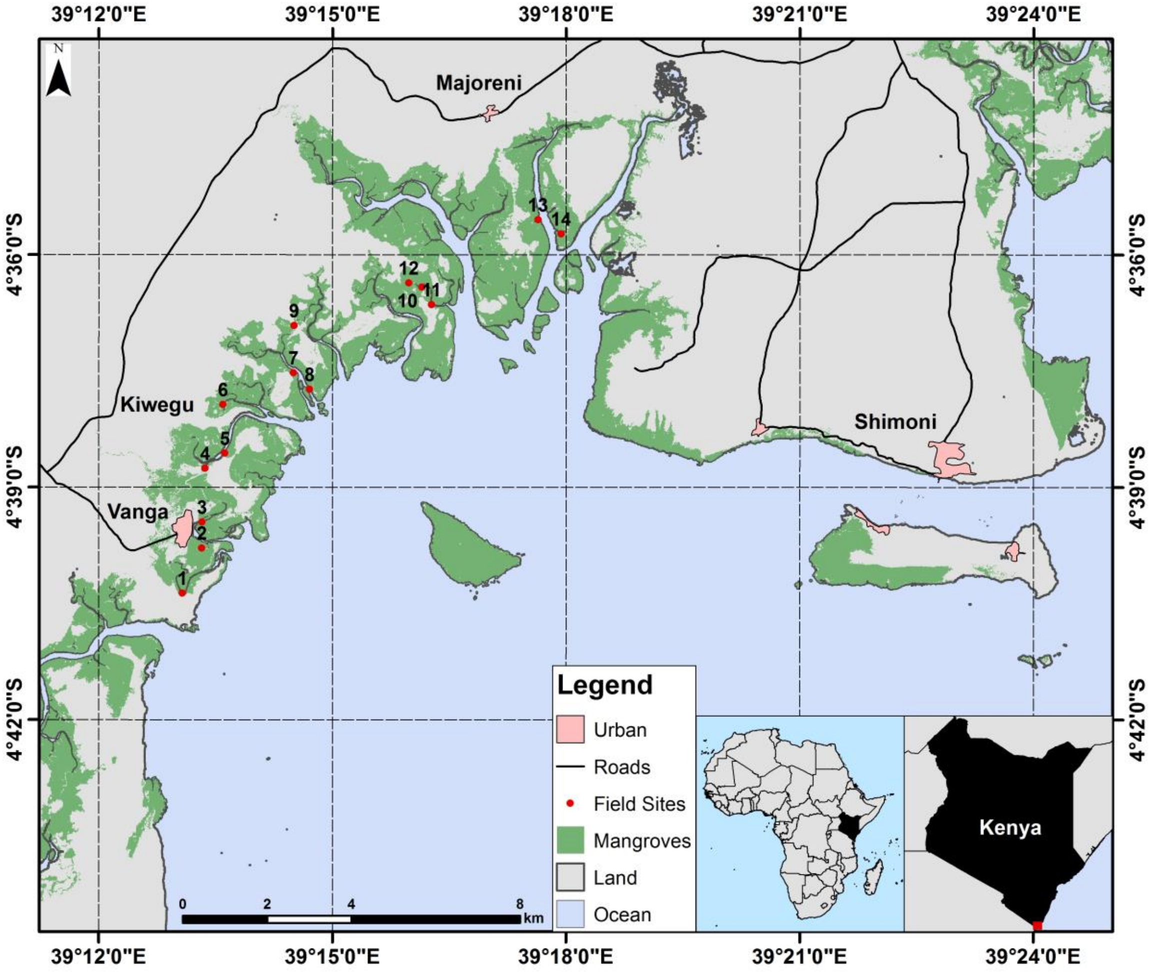


Figure 1.1 Location of Kenya (insets) and the sampling sites across the Vanga mangrove ecosystem (sampling sites shown as red dots and site numbers in black).

2.0 CHAPTER 2: DESCRIPTION OF THE FISH AND CRUSTACEAN COMMUNITY STRUCTURE IN VANGA

Abstract:

A majority of coastal communities in the Western Indian Ocean region depend on fisheries as the major source of livelihood. Mangroves support fisheries due to their role as nurseries for juvenile reef fish. Continued anthropogenic pressure on these habitats has increased threats that include overharvesting, conversion to other uses and general degradation of forests. The threats meted on the organisms that use mangroves result in reduction in abundance, declining species and an overall reduced recruitment into the fishery. This study sought to describe fish and crustacean communities in Vanga mangrove ecosystems for the first time. Sampling was done during spring tides in 14 mangrove sites, once every 3 months using fyke nets. The sampling period covered the north east (NEM) and south east (SEM) monsoon season. A total of 112 samples were collected between September 2015 and September 2017. A total of 1, 879 fish were caught, represented by 28 families and 59 species. Over 95% of the fish caught were juveniles with 50% of both fish and crustacean species being of commercial importance. Similar to other nearshore habitats, 70% of the catch was dominated by six fish species with *Yarica hyalosoma* and *Acropoma japonicum* contributing, 25% and 18.9% of the total abundance respectively. The most species rich family was Serranidae (5 species) followed by Lutjanidae and Haemulidae each with 4 species. Sixteen species of crustaceans were sampled with *Penaeus semisulcatus* and *P. indicus* constituting 82.7% of the total catch. ANOSIM revealed significant differences but weak separation of fish assemblages between NEM and SEM seasons on square root transformed abundance data of 12 of the most abundant fish species (R^2=0.304, p=0.001). Crustaceans did not display any clear seasonality. The findings of this study suggest that mangroves are a habitat for juvenile fish of commercial importance.

2.1 Introduction

Nearshore estuarine habitats are often important nursery areas for juvenile fish and crustaceans (Robertson & Duke, 1987; Laegdsgaard & Johnson, 1995; Rozas & Minello, 1997; Sheridan & Hays, 2003; Barbier, 2011; Lefcheck et al., 2019). Nursery habitats are defined as areas that contribute disproportionately to adult populations of fish, with juveniles occurring in high densities, or achieving better growth or survival, or all of them combined (Beck et al., 2001).

The nursery function of mangroves has been studied in almost all regions of the world where mangroves grow, including South America and the Caribbean, South East Asia, Australia and East Africa (Primavera, 1997; Laegdsgaard & Johnson, 2001; Verweij et al., 2006; Blaber, 2007; Lugendo et al., 2007; Nagelkerken et al., 2008; Abrantes & Sheaves, 2009; Gajdzik et al., 2014). These studies and others have provided evidence that mangroves can provide shelter and food for juvenile fish, but it is still challenging to prove that these juveniles successfully move from mangrove nurseries to adult habitats (Beck et al., 2001; Gillanders et al., 2003). Research is on-going to provide this evidence and methodologies such as telemetry (active and passive), hydroacoustics and otolith microchemistry among others (Lucas & Baras, 2001; Chapman et al., 2012) are being developed to track and prove these migrations (Deegan, 1993; Chong et al., 1990; Gillanders et al., 2003). Work on mangrove fisheries typically reports large spatial and temporal variability, which arises partly through methodological limitations, but could also imply major differences in the value of areas within mangrove sites for individual species or for fish communities as a whole. Explaining this variability remains a major research challenge.

2.1.1 Fish communities in Western Indian Ocean (WIO) mangroves

Mangroves in the WIO face numerous anthropogenic threats including overharvesting, development, conversion to other uses and reduced fresh water influx (Kairo et al., 2002; Huxham et al., 2015). Fisheries is an essential resource for many coastal people in the region, who depend on it for sustenance, livelihood and income (Ochiewo, 2004). Given the broad and frequent association between healthy mangrove ecosystems and fisheries production (Barbier, 2000 and references above), securing a reliable and sustainable supply of fishes and crustaceans will require sound mangrove and coastal management. Management approaches need to be appropriate for the particular socio-economic and political settings and should be based on solid scientific and indigenous knowledge.

A small but growing body of literature from the WIO region is available to inform the understanding of the interaction between fisheries and mangroves and how management might best be conducted. Past studies in Zanzibar, Tanzania, Mozambique and Kenya form the baseline for current and future research. In Tanzania, mangrove fisheries studies have mainly focussed on the function of shallow bay habitats, including mangroves, as nurseries for fish (Lugendo et al., 2007), the influence of spatio-temporal factors on mangrove creek fish assemblages (Mwandya et al., 2010) and ontogenetic habitat shifts of mangrove/seagrass dependent coral reef fishes (Kimirei, et al., 2011).

The mangrove ichthyofauna and related topics have been researched in Kenya in both the North and the South coast. In the North, semi-quantitative studies have been carried out in the Tudor mangrove estuaries using towed nets (Little et al., 1988; Wakwabi & Mees, 1999; Wainaina et al., 2013) with over 72 teleost fish species being recorded in each of the studies. In Mida creek, investigations on mangrove fisheries yielded 27 teleost fish species (Gajdzik et al., 2014). On the Southern coast, mangrove fisheries studies have concentrated on Gazi bay. Kimani et al. (1996) studied nekton communities in Gazi mangrove and seagrass areas and recorded a total of 128 fish species. In addition, quantitative studies (that allow per unit area density estimates) on mangrove fish, using stake nets, have been carried out in forested and unforested sites and also in natural and replanted sites with a maximum 49 fish species being recorded (Huxham et al., 2004; Crona & Rönnbäck, 2007) (Table 2.1). The use of mangroves by penaeid shrimp as nursery habitats has also been studied in Gazi bay (Crona & Rönnbäck, 2005).

Research on mangrove fishes in Mozambique is scant. A few studies have explored the role of mangroves as nursery habitats for penaeid shrimp, which are of great commercial value in the country (Hughes, 1966; Macia, 2004). The most abundant species were *Penaeus indicus*, *Metapenaeus stebbingi* and *Marsupenaeus japonicus* (Macia, 2004).

Some of the dominant fish taxa encountered in the shallow coastal habitats of East Africa include families such as Gerreidae, Clupeidae, Gobiidae and Lutjanidae with *Gerres oyena* being the most commonly occurring species in all these habitats. Other common species in these studies include *Atherinomorus lacunosus*, *Terapon jarbua* and *Lutjanus fulviflamma*. Despite the high species diversity in these habitats, a few common species dominate the catch, as is common with other tropical estuarine systems (Kimani et al., 1996). Studies on shallow water habitats from the WIO region (summarised in Table 2.1) have consistently registered high juvenile densities with a majority of the studies encountering few or no adults, as is typical for tropical nearshore habitats (Wakwabi & Mees, 1999; Lugendo et al., 2007; Crona & Ronnback, 2007;

Kimirei et al., 2011). A few species, like *Ambassis gymnocephalus*, *Sphaeramia orbicularis*, *Leiognathus equulus* and some Gobiids, are permanent mangrove residents (Kimani et al., 1996; Lugendo et al., 2007).

Table 2.1: Summary of studies on mangrove fisheries in the East African region

Country	**Site studies**	**No. of species**	**Dominant taxon**	**Source**
Kenya, Tudor creek	mangrove creeks	83	Clupeidae, Gobiidae	Little et al., 1988
Kenya, Tudor creek	mangrove bordered seasonal estuary	72	Penaeidae, Gobiidae, Lutjanidae, Plotosidae	Wakwabi & Mees, 1999
Kenya, Tudor creek	mangrove tidal creeks	72	*Gerres oyena*, *Terapon jarbua*, *Lutjanus fulviflamma*	Wainaina et al., 2013
Kenya, Gazi bay	mangrove creeks with silty sandy, muddy and seagrass substratum	128	Gerreidae, Atherinidae, Clupeidae	Kimani et al., 1996
Kenya, Gazi bay	paired forested and unforested site	30	*Gerres oyena*, *Chanos chanos*, *Acentrogobius nebulosus*	Huxham et al., 2004
Kenya, Gazi bay	natural, degraded and replanted *Sonneratia alba*	49	*Gerres oyena*, *Atherinomorus lacunosus*	Crona & Rönnbäck, 2007
Kenya. Mida creek	inside mangrove forests incl. sites with permanent pools of water	27	*Spratelloides orbicularis*, *Gerres oyena*	Gajdzik et al., 2014
Tanzania, Chwaka bay	mangrove creek, channels, sand/mud flats, seagrass beds	150	*Gerres oyena*, *Ambassis gymnocephalus*, *Apogon lateralis*, *Leiognathus equulus*	Lugendo et al., 2007
Zanzibar	shallow water habitats	2[a]	*Lutjanus fulviflamma*, *L. ehrenbergii*[a]	Dorenbosch et al., 2004
Tanzania	Coral reefs and nearshore habitats	4[a]	*Lethrinus harak*, *L. lentjan*, *Lutjanus fulviflamma*[a]	Kimirei et al., 2013
Zanzibar	Non - esturarine mangrove creeks	70	*Mugil cephalus*, *Leiognathus equulus*, *Lethrinus harak*, *Gerres oyena*, *Sillago sihama*	Mwandya et al., 2010
Mozambique, Inhanca island	mangrove creek, sandflat, mudflat, seagrass meadow	5	*Penaeus indicus*, *P. japonicus*, *P. semisulcatus*, *Metapenaeus stebbingi*	Macia, 2004

Key: a – species of study interest

The scarcity of permanent residents in these species rich habitats means that most of the species such as Lethrinidae, Lutjanidae and Monodactylidae (Wainaina et al., 2013) are mangrove dependent, but utilise other habitats as well.

2.1.2 Crustacean communities in Western Indian Ocean (WIO) mangroves

Crustacean community assemblages in nursery habitats have not been extensively studied but their use of mangrove habitats at various life stages has been documented (Rönnbäck et al., 1999). The commercially important penaeid shrimp species in these habitats include *Penaeus indicus, Penaeus semisulcatus, Penaeus monodon* and *Metapenaeus monoceros* (Wakwabi & Mees, 1999; Macia, 2004). In Gazi mangroves, penaeid shrimp dominated the catch where *P. indicus* preffered vegetated to bare areas while *Marsupenaeus japonicus* preferred the latter probably due to the ability of the species to burrow and disguise itself from predators (Macia, 2004: Crona & Ronnback, 2005). In North, coast Kenya, (Munga et al., 2013) found *P. indicus* to prefer shallow waters with clear waters and muddy bottoms while *P. semisulcatus* preferred deep less clear waters. Other penaeid species like *P. monodon* and *P. monoceros* were found in both habitats. *Penaeus indicus* was the most abundant species of panaeid shrimp in Malindi Ungwana bay Kenya where generally, penaeid shrimp did not show any seasonality in the two monsoon seasons, south east monsoon and north east monsoon (Ndoro et al., 2014).

2.1.3 Vanga

Vanga has one of the largest contiguous mangrove blocks in the Kenyan coast and is also a rich fishing ground (Obura, 2001; GoK, 2017). The fishery is a transboundary resource that attracts a substantial number of migrant fishers over the fishing seasons. It is also gradually changing from a traditional to modern fishery where motorised fishing vessels and modern gears are in use (Ochiewo, 2004; Fulanda et al., 2009). The mangroves and the fishery resources of Vanga are threatened by anthropogenic pressures and resource use conflicts, among other threats, from within and without the immediate area (Ochiewo, 2004; Fulanda et al., 2009). Despite the importance of mangrove-related resources and the threats to them in Vanga, there is a major gap in knowledge with respect to the ecology of the area. So far, the only peer -reviewed published study on mangrove ecology at Vanga is that of Gress et al. (2016), which documents carbon storage. Therefore, the present study attempts to document for the first time the community structure of mangrove fishes and crustaceans in the Vanga mangrove ecosystem.

2.1.4 Methodological approaches to mangrove fisheries surveys

Effective quantitative sampling of mangrove fish presents a great challenge, because the forest floor is covered by complex root networks that render the use of most types of gear impossible. A review of mangrove fish sampling surveys from 1955 - 2005 concluded that most of the studies had failed to sample inside the mangrove forest due to such limitations and instead concentrated on the creeks (Faunce & Serafy, 2005). In order to overcome this, barrier enclosure samplers (stake nets) and visual methods (whenever water is clear enough) have been used to collect quantitative data on fish species (Thayer et al., 1987; Vance et al., 1996; Rönnbäck et al., 1999; Huxham et al., 2004; Crona & Ronnback, 2005; 2007). Although such approaches can provide thorough quantitative data, they are very labour intensive and cumbersome, are restricted to sampling small (and possibly unrepresentative) areas and tend to be limited to mangrove areas that are easily accessible.

Fyke nets are passive gears mostly used in shallow water in sites with uneven floor or debris and hence suitable for sampling in mangrove areas by deploying them in creeks that drain different mangrove areas. They have been used to explore the nursery function of mangroves to fisheries in various regions (Kuo et al., 1999; Hindell & Jenkins, 2004; Giarrizzo & Krumme, 2007). In Kenya fyke nets have been used in studies in Mida creek (Gajdzik et al., 2014) and Gazi bay (Mees et al., 1999) and have generally been found to target pelagic species (Franco et al., 2012).

2.1.5 Overall aim

To describe the fish and crustacean community structure of the Vanga mangrove ecosystem

2.1.6 Specific objectives

1. To describe the teleost fish and crustacean community structures found in the Vanga ecosystem
2. To investigate the size classes of teleost fishes in the Vanga mangrove ecosystem
3. To investigate the effect of seasonality on fish and crustacean species

2.2 Study approach and methodology

2.2.1 Study sites

The study site is Vanga in the south coast of Kenya, at latitude 4° 39' 38.42"S and longitude 39° 13' 9.71"E. The climate of Vanga is similar to that of the east African coastal areas where the Inter Tropical Convergence zone (ITCZ) partitions the seasons into two distinct seasons i.e. South East Monsoon (SEM) and North East Monsoon (NEM). The SEM season is from March to October and NEM from September to March (McClanahan, 1988). The SEM season is rainy with increased terrestrial runoff into the coastal systems contributing to low water salinities especially in nearshore areas. The high cloud cover in this season leads to reduced solar radiation and low water temperatures. During NEM, there is less rainfall, increased water temperature and salinity and reduced wind energy. Fish catch and reproduction peak during NEM at the

East African coast (McClanahan, 1988). The Kenya coast experiences warm tropical conditions with sea surface temperatures ranging between 24°C and 29°C during the year (McClanahan, 1988). Salinity levels range between 34.5 ‰ and 35.4 ‰ with the lowest salinities occurring during the rainy SEM season and the highest salinities occurring during the dry NEM season (McClanahan, 1988; UNEP, 1998). The tidal regime is semi diurnal and ranges between amplitudes of 1.5m in neap tide and to 4m in spring tides (Obura, 2001).

The Vanga mangrove complex covers a total area of about 4000ha and six species of mangrove trees are found there: *Avicennia marina*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, *Rhizophora mucronata*, *Sonneratia alba* and *Xylocarpus granatum* (Figure 2.1) (GoK, 2017). These mangroves can be classified as either creek or estuarine. The rivers Umba and Mwena drain fresh water into the Vanga mangrove ecosystem, with River Umba, whose source is in Tanzania, discharging circa 16 million m^3 of fresh water into the sea annually, with cyclic flooding every December (UNEP, 1998; GoK, 2017). Fishing is the major economic activity in Vanga with fishing grounds being a complex of mangroves, seagrass and coral reef ecosystems. The fishery in Vanga is mostly artisanal, multi gear and multi species (McClanahan & Mangi, 2004).

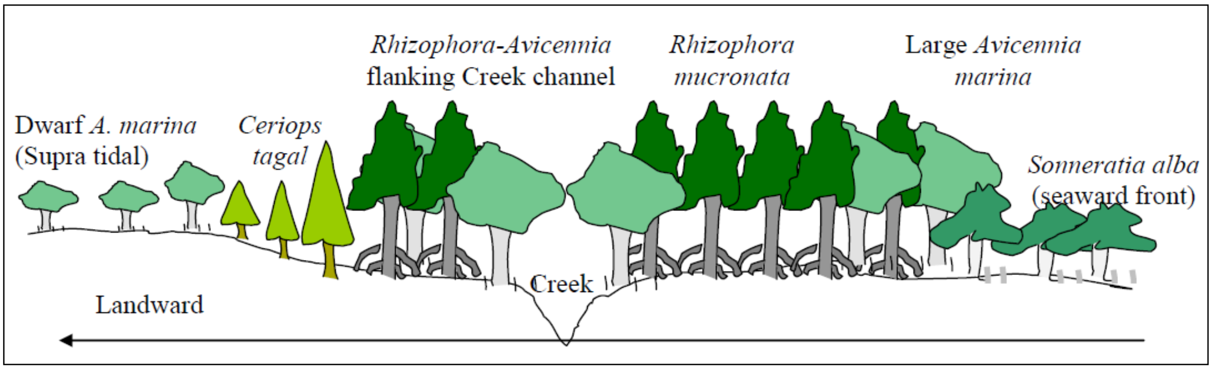


Figure 2.1: Mangrove vegetation profile typical of the Kenyan mangrove forests Source: (Lang'at, 2008)

2.2.2 Sampling design and methodology

Fish and crustaceans were sampled using fyke nets, at 14 mangrove creek sites situated between Jimbo and Majoreni villages in Vanga. The sites were chosen to give a wide geographical coverage of the Vanga mangrove forests, whilst still being accessible enough to allow regular sampling. Fyke nets were deployed at the creek mouths that drain the mangrove forest sites (Plate 2.1a), to sample fish communities leaving these sampling areas during the ebb tide. The fyke nets had two wings each of 9.5m length and a height of 1m. The length of the body frame was 3.6m. The main frame was made of metal measuring 1m x 1m which had three rings of diameter 0.9m, 0.7m, and 0.6m along the body frame and a net of mesh size 1.9cm when stretched (Plate 2.1b). Sampling was carried out from September 2015 to September 2017 during new moon spring tides. Each sampling campaign was carried out over a six day period where each of the 14 sites was sampled once. Hence replicate samples were taken eight times from each of the 14 sites at intervals of three months as shown in Table 2.2. March 2017 was not sampled due to logistical reasons. A total of 112 samples were collected.

Table 2.2: Sampling regime

Sampling time	Season	No. of times sampled	No. of sites sampled	Total samples
September 2015	SEM	1	14	14
December 2015	NEM	1	14	14
March 2016	NEM	1	14	14
June 2016	SEM	1	14	14
September 2016	SEM	1	14	14
December 2016	NEM	1	14	14
June 2017	SEM	1	14	14
September 2017	SEM	1	14	14
Total samples				**112**

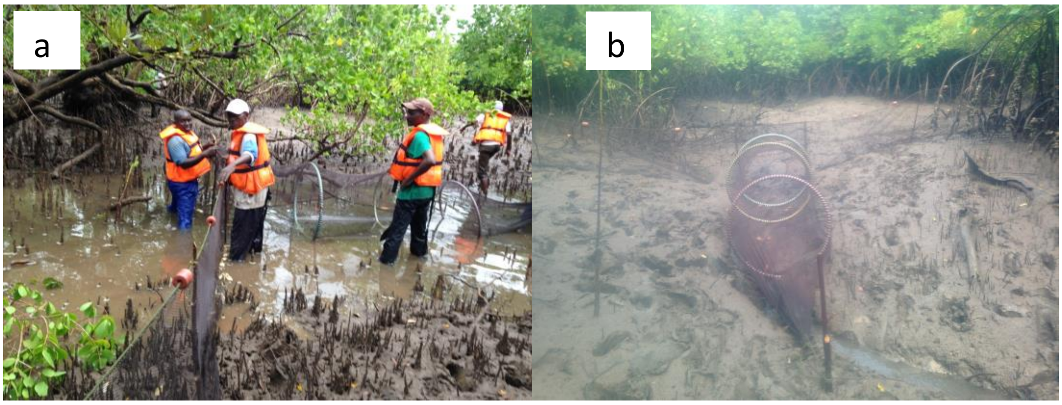


Plate 2.1: (a) Fyke net deployment and (b) Fyke nets

The fish and crustacean samples were collected in the field and placed in a cool box for a few hours, while they were transported to the field laboratory where they were sorted and identified to the lowest taxon possible using Anam & Mostarda (2012) and Richmond, (2011). The fish standard and total lengths were measured (to the nearest 0.1cm) and individual mass recorded (to the nearest 1g). The carapace length of crustaceans was measured to the nearest 0.1cm. Some individuals were partly predated on and in such cases, they were identified whenever possible and their numbers recorded for inclusion in abundance data. To classify the fishes into size classes, the maximum length of each species was sourced from FishBase (Froese & Pauly, 2017). Using guidelines from Nagelkerken & Velde (2002), fishes with total length ≤1/3 maximum length were classified as small juveniles, between >1/3 to ≤ 2/3 maximum length classified as large juveniles/sub adults and those >2/3 maximum length were classified as adults. Fishes were also classified into their trophic groups and importance to fisheries as guided by information on FishBase (Froese & Pauly, 2017).

2.2.3 Statistical analysis

Fish and crustacean data were analysed separately. Fish' in this case stands for all the teleost fish species caught while crustaceans included shrimp and crabs. Data were analysed using R Core Team (2013). Shannon's diversity index (H'), Pielou's evenness index (J') and Margalef's D (see formulae below) were used to compare fish community structure between seasons.

i) Shannon's diversity index (H')

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where: H = the Shannon diversity index, P_i = fraction of the entire population made up of species I, S = number of species encountered, ∑ = sum from species 1 to species S

ii) Pielou's evenness index (J')

$$H = (\sum - (P_i * \ln P_i))/\ln S$$

Where s = species richness

iii) Margalef's D

Margalef's richness index: (S-1)/ln(n),

Where S is the number of taxa, and n is the number of individuals.

Statistical analysis used all the 112 samples as raw data in this analysis. It also considered all fish and crustacean species (59 fish and 16 crustacean species, respectively) as well as the most abundant species; fish species which constituted >1.5% of the total individuals (12 fish species) caught, and crustacean species that had over 5 individuals (7 species). Multivariate, non-metric, multi-dimensional scaling (nMDS) was computed to describe fish and crustacean assemblages in the seasons.

The Bray-Curtis similarity index on square root and fourth root transformed abundance data was used, to look for clusters between species using Plymouth Routines In Multivariate Ecological Research (PRIMER) version 6.0 Clarke & Warwick, (2001). For seasonal data, September and June data were pooled under the season 'South East Monsoon (SEM)' and March and December data for 'North East Monsoon (NEM)'.

Non-metric multidimensional scaling (nMDS) ordination plots were then developed to visualize seasonal differences. One way Analysis of Similarities (ANOSIM) was used to test for significant differences among fish and crustacean community structures between seasons, after which similarity of percentages (SIMPER) was used to establish the fish and crustacean taxa that mainly contributed to the differences found. A null hypothesis that there were no significant difference between mean fish abundance in both SEM and NEM season was tested usind ANOVA. Non parametric Wilcoxon tests were used to compare mean crustacean abundances between seasons after residuals in abundance data failed to meet the conditions for normality even after transformation. *Yarica hyalosoma, Acropoma japonicum* and *Gerres oyena* were sufficiently abundant to allow comparisons of size-frequency distributions between seasons, in order to explore growth patterns at the location. Chi square tests of association were conducted using Minitab 17.

2.3 Results

2.3.1 Fish community structure

A total of 1, 879 individuals were caught, represented by 28 families and 59 species, most were identified to species level. Six species dominated the catch and contributed to about 70% of the total abundance: *Yarica hyalosoma* (25%), *Acropoma japonicum*

(18.9%), *Ambassis natalensis* (11.2%), *Ambassis ambassis* (7.2%), *Leiognathus equulus* (7.2%) and *Gerres oyena* (5.7%) (Table 2.2). The five most dominant families in terms of abundance were Apogonidae, Ambassidae, Acropomatidae, Gerreidae and Leiognathidae. Serranidae was the most diverse family with five species followed by Lutjanidae and Haemulidae, which had four species each. Thirteen of the 28 families were represented by a single species. *Yarica hyalosoma*, the most dominant species, appeared in all but two sites throughout the sampling period. *Gerres filamentosus* and *G. oyena* were each caught at 10 different sites. About 42% of the species had ≤ 2 individuals throughout the sampling season. The species *Lutjanus fulvus*, *Lutjanus bohar*, *Pterois volitans* and *Tylosurus crocodilus* were represented by a single individual throughout the study period and were considered rare. About 50% of the total species caught were of commercial importance, based on information from FishBase (Froese & Pauly, 2017), while the other 50% were of no or of minor commercial importance. Zoobenthivores was the most common trophic group with 27% of the species belonging to the zoobenthivores/piscivores group (Table 2.3).

Table 2.3: Fish abundance (Catch per net), respective families, importance (HC=highly commercial, C=commercial, MC=minor commercial, AQ=Aquarium, Non = no commercial importance) based on Froese & Pauly, (2017). Under functional groups: Z=zoobenthivore, PS=piscivore, Pl=zooplanktivore, O=omnivore, H=herbivore, I= insectivore, *= No information)

Family	**Species**	**Importance**	**Group**	**Sampling sites**													
				1	2	3	4	5	6	7	8	9	10	11	12	13	14
Gobiidae	*Acentrogobius nebulosus*	*	Z/PS	0	0	1	0	1	0	0	0	1	0	0	0	0	0
Acropomatidae	*Acropoma japonicum*	C	Z/PS	29	6	96	49	29	23	4	14	7	5	0	0	0	0
Ambassidae	*Ambassis ambassis*	Non	Z/PS	0	0	70	25	14	26	0	0	0	1	0	0	0	0
Ambassidae	*Ambassis gymnocephalus*	MC	PS	0	0	0	0	8	0	0	0	0	0	0	0	0	0
Ambassidae	*Ambassis natalensis*	C	PS/I	0	2	107	13	28	53	0	0	6	0	0	0	1	0
Apogonidae	*Yarica hyalosoma*	Non	Z	178	45	99	1	7	0	27	40	16	22	9	4	9	21
Tetraodontidae	*Arothron immaculatus*	MC	PS	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Atherinidae	*Atherinomorus lacunosus*	C	PL	2	0	0	0	0	0	20	44	0	11	3	6	0	0
Percophidae	*Bembrops platyrhynchus*	Non	*	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Percophidae	*Bembrops caudimacula*	*	Z/PL	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Gynglymostomatidae	*Blue spotted goby*	*	Z/PS	0	0	0	3	0	0	0	0	0	0	0	0	0	0
Carangidae	*Carangoides ferdau*	C	Z/PS	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Carangidae	*Caranx ignobilis*	C	PS/I	0	0	0	0	0	0	1	0	0	1	0	1	0	0
Chanidae	*Chanos chanos*	HC	O	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Mugilidae	*Crenimugil crenilabis*	C	O	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pomacentridae	*Dascyllus* spp.	*	O	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Serranidae	*Epinephelus coeruleopunctatus*	MC	Z/PS	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Serranidae	*Epinephelus coioides*	C	Z/PS	0	1	0	2	1	0	1	0	0	0	0	0	0	0
Serranidae	*Epinephelus lanceolatus*	C	Z/PS	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Serranidae	*Epinephelus malabaricus*	HC	PS/Z	0	1	0	2	2	0	0	0	0	1	0	0	1	0
Serranidae	*Epinephelus spilotoceps*	C	PS/Z	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Antennariidae	*Frog fish (unidentified)*	*	PS	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Leiognathidae	*Gazza minuta*	C	P	0	0	0	7	0	1	0	0	40	0	0	0	4	0

Gerreidae	*Gerres longirostris*	C	PS	1	0	0	0	0	2	0	0	0	0	0	0	1	1
Gerreidae	*Gerres filamentosus*	MC	Z	20	25	12	1	10	0	1	0	1	0	4	1	13	0
Gerreidae	*Gerres oyena*	C	Z	28	0	1	4	4	1	17	0	0	15	1	8	22	7
Gobiidae	*Goby*	AQ	Z/PS	0	1	0	0	3	0	0	1	1	0	0	0	0	0
Hemiramphidae	*Hyporhamphus gamberur*	Non	*	1	0	2	1	0	0	1	0	0	0	0	0	0	0
Hemiramphidae	*Hyporhamphus affinis*	Non	Z/O	13	0	10	6	2	0	2	4	0	3	1	0	0	0
Leiognathidae	*Leiognathus equulus*	MC	Z	2	0	0	1	0	3	0	0	125	3	0	2	0	0
Lethrinidae	*Lethrinus harak*	C	Z/PS	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lutjanidae	*Lutjanus argentimaculatus*	C	Z/PS	1	2	0	1	3	0	0	0	0	3	0	0	0	0
Lutjanidae	*Lutjanus bohar*	C	ZB	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lutjanidae	*Lutjanus fulviflamma*	C	Z/PS	3	0	1	0	0	0	1	0	0	4	2	1	0	0
Lutjanidae	*Lutjanus fulvus*	C	Z/PS	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Monodactylidae	*Monodactylus argenteus*	MC	O	7	0	0	0	4	4	7	0	0	0	0	0	15	0
Mugilidae	*Moolgarda seheli*	C	PL	0	0	15	4	3	0	0	0	1	0	0	0	0	0
Mugilidae	*Mugil cephalus*	HC	PL	0	10	0	0	5	0	0	0	0	0	0	0	0	0
Gobiidae	*Periopthalamus* spp.	*	PS	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ephippidae	*Platax orbicularis*	MC	O	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Ephippidae	*Platax pinnatus*	MC	O	0	0	0	1	0	0	1	0	0	0	0	0	0	1
Platycephalidae	*Platycephalus indicus*	C	ZB/PS	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Haemulidae	*Plectorhinchus plagiodesmus*	C	Z/PS	0	1	1	0	0	0	0	1	0	0	0	0	0	0
Haemulidae	*Pomadasys argenteus*	C	Z	0	0	1	1	0	1	2	0	0	3	0	0	0	0
Haemulidae	*Pomadasys multimaculatus*	C	ZB	0	1	0	1	1	3	0	3	0	2	0	2	0	0
Haemulidae	*Pomodasys kaakan*	C	P	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Scorpaenidae	*Pterois volitans*	C	Z/PS	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Clupeidae	*Sardinella gibbosa*	HC	PL	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Sillaginidae	*Sillago sihama*	C	Z	0	0	0	5	0	7	0	0	13	2	0	9	0	0
Sphyraenidae	*Sphyraena barracuda*	MC	Z/PS	2	0	1	0	0	0	0	0	0	1	1	1	1	0
Sphyraenidae	*Sphyraena jello*	C	PS	2	2	2	0	0	0	3	0	1	3	1	0	1	0
Sphyraenidae	*Sphyraena putnamae*	C	PS	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Clupiedae	*Spratelloides gracilis*	MC	A	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Engraulidae	*Stolephorus commersonnii*	C	Z	0	0	0	0	1	0	0	0	0	0	0	1	0	0

Terapontidae	*Terapon jarbua*	MC	O	0	0	5	0	0	0	0	0	3	0	0	1	0	0
Engraulidae	*Thrysa setirostris*	MC	PS	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Belonidae	*Tylosurus acus melanotus*	C	PS	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Belonidae	*Tylosurus crocodilus*	C	PS	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hemiramphidae	*Zenarchopterus dispar*	C	H/PL	1	0	2	5	0	0	0	0	0	0	1	0	0	0
Total individuals (N)				293	100	427	135	128	125	102	108	217	81	23	37	69	34
Total species (S)				18	15	18	22	20	12	24	8	13	17	9	12	11	7

2.3.2 Crustacean community structure

The total number of crustaceans recorded in this study was 1,161 individuals and a total of 16 species. They mostly fell within infra order Brachyura for crabs and family Penaeoidea for the shrimp. The most abundant crustacean species were *Penaeus semisulcatus* (46.5%) and *Penaeus indicus* (36.2%) (Table 2.4). *Penaeus indicus, P. semisulcatus* and *Thalamita crenata* were encountered in all fourteen sites sampled. All penaeid species, as well as *Macrobrachium rude, Scylla serrata* and *T. crenata* are species of high commercial value.

Table 2.4: Crustacean abundance, respective families and commercial importance

Family	**Species**	**Percentage (%) of total N**	**Importance**	**Sampling sites**													
				1	2	3	4	5	6	7	8	9	10	11	12	13	14
Caridea	Caridean shrimp	1.5	C	1	0	0	2	6	0	0	1	1	2	1	3	0	0
Matutidae.	*Ashtoret lunaris*	0.2		1	0	0	0	0	1	0	0	0	0	0	0	0	0
Brachyura	Crab 1	0.2	NA	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Brachyura	Crab 2	0.2	NA	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Brachyura	Crab 3	0.2	NA	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Palaemonidae	*Macrobrachium rude*	2.7	HC	1	0	0	16	5	0	0	3	0	3	0	3	0	0
Penaeidae	*Metapenaeus stebbingi*	0.2	HC	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Penaeidae	*Metapeneaus monoceros*	1.7	HC	1	0	0	1	0	1	0	5	0	5	0	7	0	0
Penaeidae	*Penaeus indicus*	36.2	HC	1	42	19	48	77	82	28	24	13	42	2	18	19	5
Penaeidae	*Penaeus monodon*	5.9	HC	1	1	1	2	4	6	4	5	0	12	5	7	8	12
Penaeidae	*Penaeus semisulcatus*	46.5	HC	1	11	4	4	4	15	13	22	15	177	10	75	13	176
Portunidae	*Scylla serrate*	1.7	HC	1	4	0	2	1	4	0	1	1	1	0	0	3	2
	Shrimp 1 (unidentified)	0.2	NA	1	0	0	0	0	0	0	0	0	0	0	0	1	0
	Shrimp 2 (unidentified)	0.2	NA	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Portunidae	*Thalamita crenata*	2.5	HC	1	3	1	1	1	3	0	3	1	2	2	1	7	3
Ocypodidae	*Uca* spp.	0.2	Non	1	0	0	0	0	0	0	0	0	0	1	0	0	0
No. of individuals N				16	61	26	77	98	112	45	64	33	245	21	114	51	198
No. of species				16	5	5	9	7	7	3	8	7	9	6	7	6	5

2.3.3 Fish assemblages

In this analysis, all the 112 samples were used as raw data. The Bray-Curtis cluster analysis of the square root transformed data of 12 of the most abundant species defined three groups of fish assemblages in the sites at 30% similarity. The species in cluster A were *S. sihama*, *L. equulus* and *G. minuta*. Cluster B included *A. ambassis, A. natalensis, A. japonicum* while cluster C was composed of *G. oyena* and *G. filamentosus* and *H. affinis* among others (Figure 2.2).

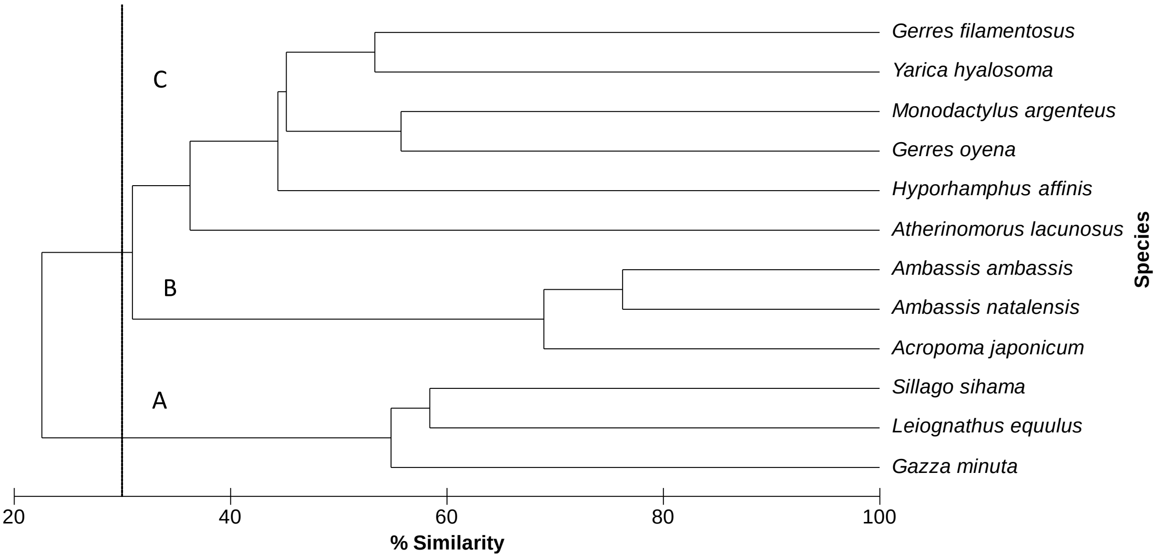


Figure 2.2: Bray Curtis similarities for the square root transformed abundance data of the most abundant fish species in Vanga mangrove ecosystems at 30% similarity as indicated by the vertical line.

2.3.4 Crustacean assemblages

Patterns of crustacean assemblage structure of square root transformed abundance data of seven of the most abundant species among sites were displayed through the Bray-Curtis cluster analysis that showed three clusters. Cluster A comprised of penaeid shrimp *P. indicus* and *P. semisulcatus*, cluster B comprised of *M. rude* and *Caridean* spp. and cluster C was made up of *P. monodon*, *S. serrata* and *T. crenata* (Figure 2.3).

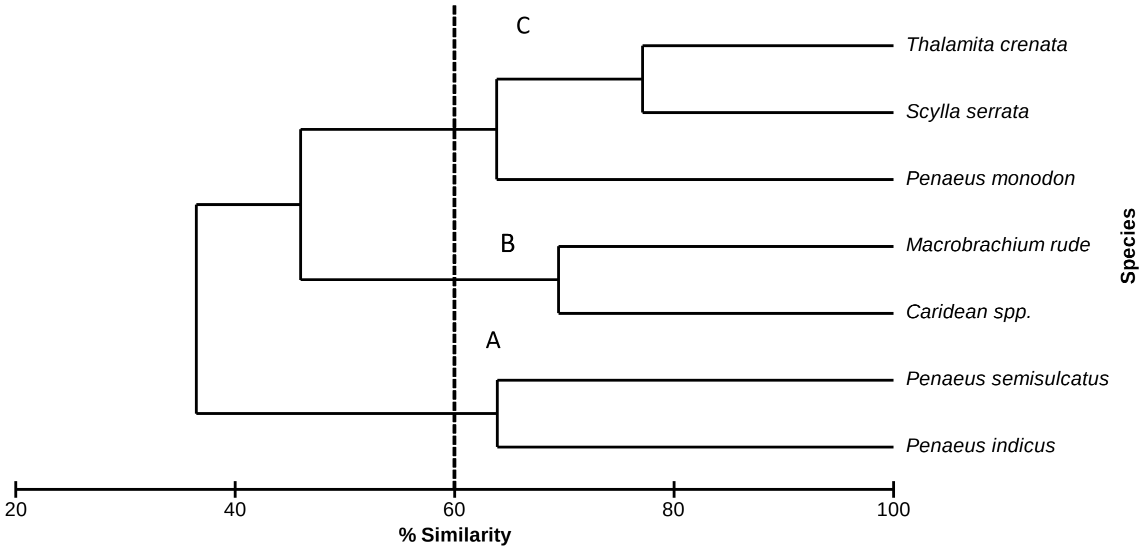


Figure 2.3: Species-based Bray-Curtis similarities for square root transformed abundance data of the most abundant crustacean species in the sites at 60% similarity as indicated by the dotted line.

2.3.5 Length relationships for fish species

In this study, 52% of all individuals caught were small juveniles while 43% were large juveniles/subadults. About 58% of the species were caught as small juveniles only e.g. *Leiognathus equulus, Lutjanus fulviflamma* and *Monodactylus argenteus*. On the other hand, *Ambassis natalensis* and *Ambassis ambassis* had 97.8% and 100% large juveniles/sub adults, respectively. About 97% of *Gerres oyena* were small juveniles. Overall, only two species i.e. *Zenarchopterus dispar* and *Stolephorus commersonnii* were found as adults (9 and 1 individuals respectively). The standard and total lengths were recorded for all the fish samples caught throughout the sampling period. The maximum lengths for the fish samples identified to species level were acquired from Fishbase (Froese & Pauly, 2017). The exception was *Perioptthalamus* spp., frog fish, goby (Gobiidae), *Dascyllus* spp., and the blue spotted goby (Gobiidae) which were not identified to species level. On Fishbase, the maximum length for most species was given as total length (TL), but for some species, as standard length (SL). The life stages of the fishes caught in this study are shown in Table 2.5.

Table 2.5: Maturity stages of fish species caught in Vanga from September 2015 to June 2017. The maturity stage was determined according to Nagelkerken & Velde (2002). Individuals with a third or less of the maximum length were classified as small juveniles, between one third and two thirds of maximum length as big juveniles to sub adults and above two thirds maximum length as adults. Max. length, preferred habitats and environment were sourced from Froese & Pauly (2017), TL = total length and SL = standard length.

Fish species	**Min TL (cm)**	**Max TL (cm)**	**N**	**% Juveniles (Juv)**	**% Sub – adults (Sa)**	**% Adults (Ad)**	**Max length (cm)**	**Preferred habitat**
*Acentrogobius nebulosus**	6.1	9.7	3	0	100		18.0 SL	sandy shorelines, reefs
Acropoma japonicum	1.7	9.3	252	86.9	13.1	0.0	20.0 TL	sand, sandy mud bottoms
*Ambassis ambassis**	3.2	5.7	136	2.2	97.8		15.0 TL	no information
Ambassis gymnocephalus	5.2	5.9	5	20.0	80.0		16.0 TL	no information
Ambassis natalensis	4.6	7.5	178	0.0	100	0.0	9.0 SL	no information
Yarica hyalosoma	1.0	9.3	470	41.9	58.1	0.0	17.0 TL	mangrove estuaries, tidal creeks (Ad)
Arothron immaculatus	5.3	5.4	2	100			30.0 TL	weedy areas, estuaries, seagrass
Atherinomorus lacunosus	3.5	9.2	84	90.5	9.5	0.0	25.0 TL	sandy shorelines, reef margins.
Bembrops caudimacula	8.0	9.0	3		100		24.1 TL	no information
Bembrops platyrhynchus	6.5	6.5	1	100	0.0	0.0	25.0 TL	inhabits offshore trawling grounds
Carangoides ferdau	6.1	6.1	1	100			70.0 TL	sandy beaches; near reefs
Caranx ignobilis	10.6	11.8	3	100			170 TL	Clear lagoons, seawardreefs (Ad))
*Chanos chanos**	14.7	16.5	2	100			180 SL	offshore marine waters, shallow coastal embayments
Crenimugil crenilabis			1	100			60.0 TL	sandy/muddy lagoons, reef flats

Epinephelus caeruleopunctatus	41.8	41.8	1	100	100		76.0 TL	coral-rich areas, deep lagoons,
Epinephelus coioides	15.0	27.8	5	100	0.0	0.0	120 TL	brackish water, mangroves (Juv)
Epinephelus lanceolatus	45.0	45.0	1	100			270 TL	caves, estuaries
Epinephelus malabaricus	12.5	35.0	7	100			234 TL	coral reefs, estuaries, mangroves
Epinephelus spilotoceps	22.3	22.3	1		100		35.0 TL	lagoon, reefs,
Gazza minuta	1.2	7.0	49	100	0.0	0.0	21 TL	young ones enter mangrove estuaries/silty reef areas
Gerres filamentosus	4.7	15.2	88	65.9	34.1		35.0 TL	mangrove (Juv)
Gerres longirostris	5.1	7.0	5	100	0.0	0.0	44.5 TL	adults, coastal waters (Ad), estuaries (Juv)
Gerres oyena	4.9	11.0	106	97.2	2.8	0.0	30.0 TL	saltwater lagoons, estuaries
*Hyporhamphus affinis**	5.0	13.4	40	90.0	10.0		38.0 SL	coral reefs
Hyporhamphus gamberur	12.0	13.7	3	33.3	66.7	0.0	37.0 TL	common around reefs
Leiognathus equulus	2.3	6.4	136	100			28.0 TL	muddy inshore areas, mangroves
Lethrinus harak	6.3	6.3	1	100			50.0 TL	shallow sandy, mangroves, seagrass
Lutjanus argentimaculatus	11.4	19.6	10	100			150 TL	Mangrove (Juv & young adult)
Lutjanus bohar	15.5	15.5	1	100			90.0 TL	coral reefs
Lutjanus fulviflamma	6.5	15.5	36	100	0.0	0.0	35.0 TL	coral reefs (Ad), mangrove (Juv)
Lutjanus fulvus	5.8	5.8	1	100			40.0 TL	lagoons (Ad) , mangroves (Juv)
*Monodactylus argenteus**	3.9	8.2	36	100			27.0 SL	bays, mangroves
Moolgarda seheli	6.7	10.8	23	100			60.0 TL	coastal waters, estuaries
*Mugil cephalus**	5.3	12.9	15	100			100.0 SL	coastal waters
Platax orbicularis	5.5	7.3	2	100			60.0 TL	sandy areas (Ad), mangroves (Juv)
Platax pinnatus	3.1	5.2	3	100			45.0 TL	reef slopes (Ad), mangroves (Juv)
Platycephalus indicus	9.8	9.8	1	100			100.0 TL	sandy and muddy bottoms
Plectorhinchus plagiodesmus	7.1	19.4	3	100			90.0 TL	coastal, coral crevices
Pomadasys argenteus	5.6	10.4	8	100			70.0 TL	coastal waters
Pomadasys kaakan	9.4	9.4	1	100	0.0	0.0	80 TL	inshore waters (sandy to muddy) bottoms , estuaries
Pomadasys	4.9	15.6	13	100	0.0	0.0	76.0 TL	coastal waters,

multimaculatus								tidal estuaries
Pterois volitans	20.0	20.0	1		100		38.0 TL	lagoons, reefs, turbid inshore
*Sardinella gibbosa**	6.1	6.4	2		100		17.0 SL	no information
*Sillago sihama **	9.0	14.7	33	87.9	12.1	0.0	31.0 SL	beaches, sandbars, mangrove
Sphyraena barracuda	11.3	28.7	7	100			200 TL	murky harbors (Ad), mangroves (Juv)
Sphyraena jello	4.0	21.4	15	100	0.0	0.0	150 TL	Reefs, bays, estuaries
Sphyraena putnamae	14.6	17.5	2	100			90.0 TL	lagoons, seaward reefs, bays, turbid lagoons
*Spratelloides gracilis**	3.5	3.5	1		100.0		10.5 SL	coastal, reefs
*Stolephorus commersonnii **	10.0	10.2	2	0.0	0.0	100	10.0 SL	coastal waters, brackish water
Terapon jarbua	4.0	11.3	9	100			36.0 TL	shallow sandy bottoms (Ad) sandy intertidal areas (Juv)
*Thrysa setirostris**	7.5	7.8	2		100.0		18.0 SL	no information
Tylosurus acus melanotus	29.8	29.8	1	100			100.0 TL	offshore, coastal waters
Tylosurus crocodilus	35.8	35.8	1	100			150 TL	lagoons, seaward reefs
Zenarchopterus dispar	8.6	14.5	9		88.9	11.1	19.0 TL	shallow water, mangroves

*species where standard length (SL) (cm) was used as maturity length

2.3.6 Size classes of the most abundant fishes

Size classes for three of the most abundant species *A. japonicum*, *Y. hyalosoma*, and *G. oyena* are as shown on Figure 2 4 – 2.6 and were used to conduct cohort analysis. For *A. japonicum* the mode did not change from September 2015 to March 2016. In June 2016, the number of individuals reduced but they increased in modal size. The mode shifted slightly to the right in June 2017 (Figure 2.4). *Yarica hyalosoma* had a stable mode on most months (Figure 2. 5). *Gerres oyena* had numerous small fish in June 2016 and September 2016, whereas in September 2015 and September 2017, the fish were less in numbers but bigger in size. In June 2016, there were more fish that were smaller (Figure 2.6).

Chi – square tests were performed to test for differences between size class distributions at different times for *Y. hyalosoma*, *A. japonicum* and *G. oyena*. The size class distributions for *Gerres oyena* were significantly different between June and September 2016, X^2=19.288, df=1 and p<0.001. There was also a significant association between size classes and sampling time (December 2015, March 2016 and June 2016) for *Y. hyalosoma* at X^2=52.85, df=4 and p<0.001. A significant association at X^2=9.98, df=1, p=0.041 was also found between the size classes and the sampling seasons (December 2015, March 2016, June 2016, September 2016 and December 2016) for *A. japonicum*.

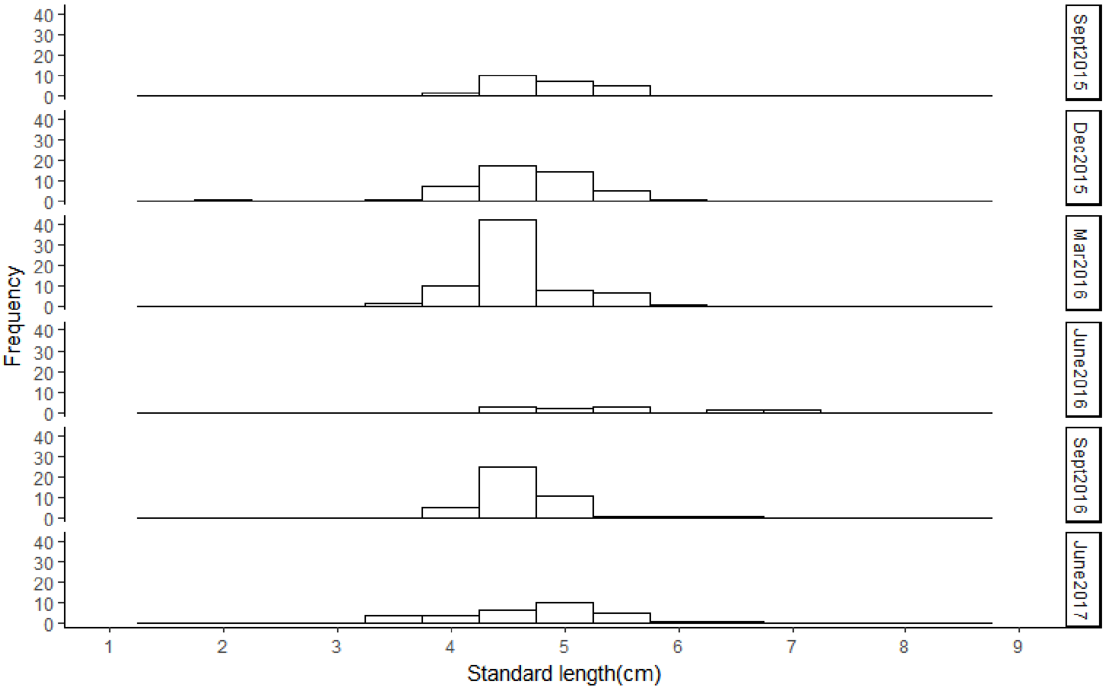


Figure 2.4: Size classes of *Acropoma japonicum* (max. length= 20cm) over the sampling period

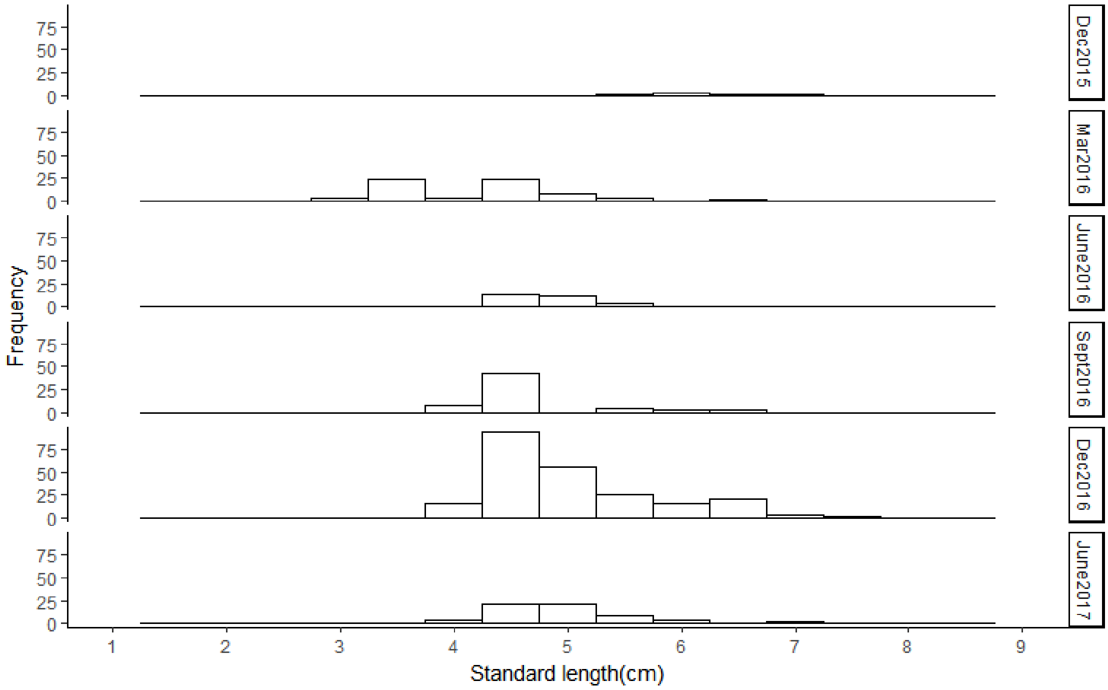


Figure 2.5: Size classes of *Yarica hyalosoma* (max. length=17cm) over the study period

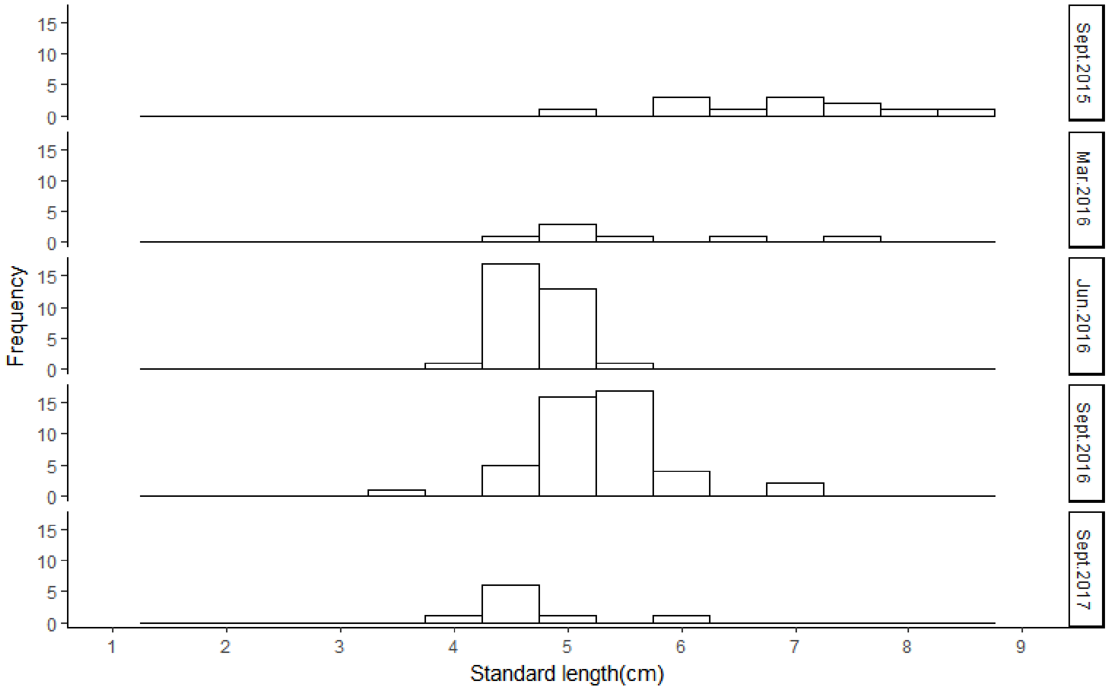


Figure 2.6: Size classes of *Gerres oyena* (max. length= 30cm) over the study period

2.3.7 Seasonal variations for fish and crustaceans (SEM – NEM)

a) **Fish**

Sampling took place in September and June (SEM season) and March and December (NEM season) from September 2015 to September 2017. March 2017 was not sampled due to logistical reasons. The mean catch per net of total fish abundance in SEM was 330 and 294 individuals in September and June, respectively. In comparison NEM had a mean of 80 and 139 individuals in December and March, respectively (Figure 2.7). The number of species encountered in each of the sampling months show September and June (SEM) having the highest number of species compared to December and March (NEM) (Figure. 2.8).

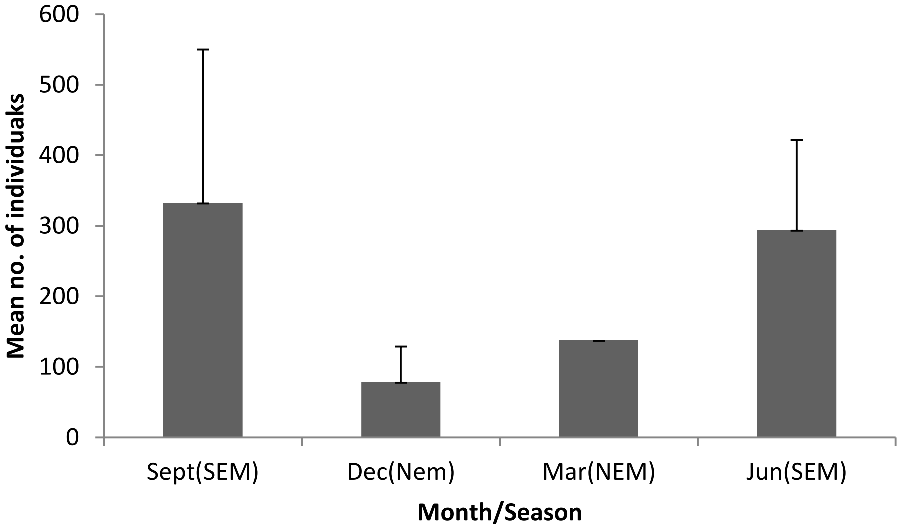


Figure 2.7: Mean number of fish individuals over the sampling season

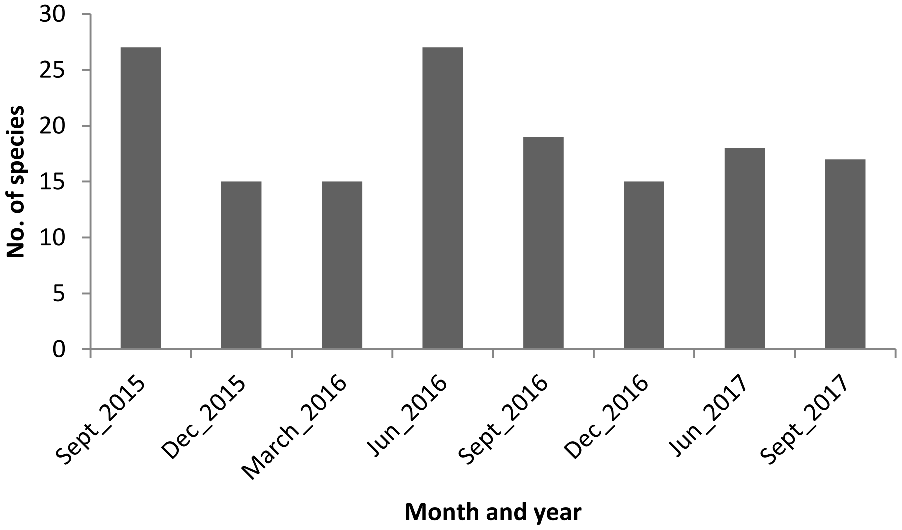


Figure 2.8: Total number of fish species caught in each of the eight sampling periods

The most abundant species in NEM were *A. japonicum*, *Y. hyalosoma*, *L. equulus* and *S. sihama.* In SEM, the most abundant species were *Y. hyalosoma*, *A. ambassis*, *A. natalensis* and *L. equulus*. The family Ambassidae that comprised of *A. ambassis, A. natalensis* and *A. gymnocephalus* showed strong seasonality as it only occurred in SEM. *Acropoma japonicum,* the second most dominant species overall, had a higher mean abundance in NEM than in SEM i.e. 40 and 28 individuals respectively. Other species that showed marked seasonality in terms of abundance include *G. oyena* and *A. lacunosus* (Appendix 2.1). The highest species diversity H' was in June 2016 (H'=2.15) and the lowest was in June 2017 (H'=1.64). The species evenness index (J) was more stable, varying between J=0.58 (June 2017) - 0.72 (Dec 2015) (Table 2.6). A one way ANOVA revealed a significant difference between the fish abundance in the NEM and SEM seasons ($F_{(1,110)}$=8.58, p=0.004). The null hypothesis was thus rejected. A non-metric multi-dimensional (nMDS) ordination plot of square root transformed abundance data of the 12 most abundant fish species in the sites during NEM and SEM seasons showed clustering of the SEM months and some scattering in NEM months (Figure 2.9). ANOSIM revealed significant differences but weak separation of fish assemblages between NEM and SEM seasons on square root transformed abundance data of the most abundant fish species, with Global R=0.304 and p=0.001).

Table 2.6: Diversity indices for fish species in the different sampling months/seasons

Sample	**Sep-15^a**	**Dec-15^b**	**Mar-16^b**	**Jun-16^a**	**Sep-16^a**	**Dec-16^b**	**Jun-17^a**	**Sep-17^a**
No. of species	26	15	15	27	18	15	17	17
No. of individuals (N)	578	48	139	385	183	112	202	230
Margalef's species richness (D)	3.93±0.5	3.62±0.7	2.84±0.6	4.37±0.8	3.26±0.7	2.97±0.5	3.01±0.6	2.94±0.7
Pielou's evenness index (J')	0.59±0.2	0.72±0.1	0.62±0.2	0.65±0.2	0.66±0.2	0.66±0.2	0.58±0.2	0.7±0.2
Shannon diversity index (H')	1.91±0.5	1.96±0.5	1.67±0.5	2.15±0.6	1.92±0.5	1.78±0.4	1.64±0.5	1.99±0.5

*a=SEM, b=NEM seasons

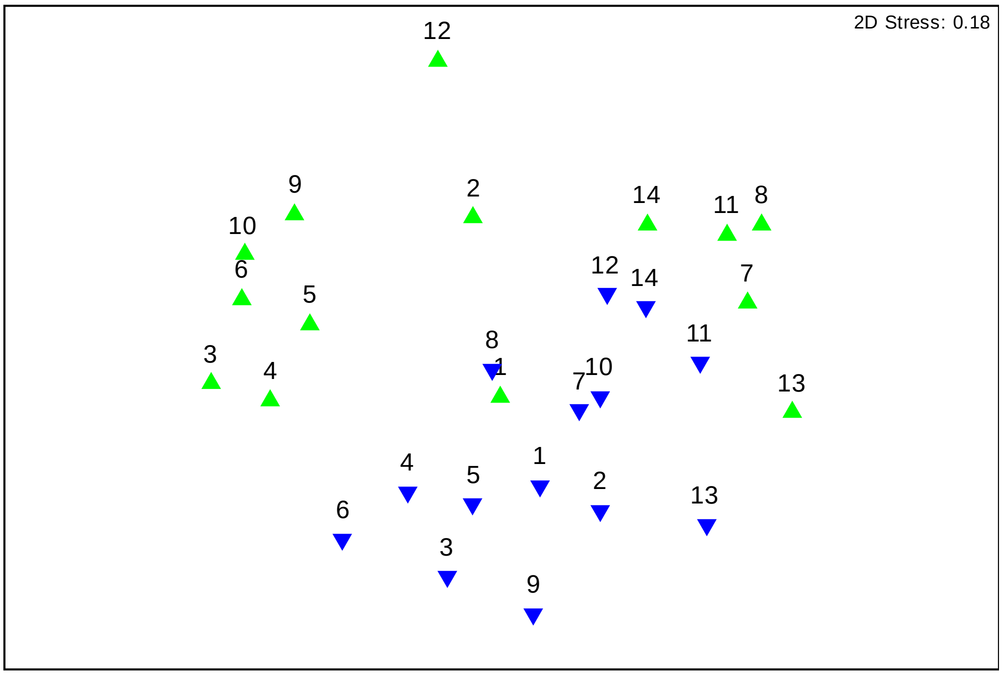


Figure 2.9: Nonmetric multi-dimensional scaling (nMDS) of seasonal fish abundance (pooled number of individuals per season) based on Bray–Curtis using square root transformed data of all sites for each sampling season, blue triangles stand for SEM and green for NEM, numbers refer to separate sampling locations.

Further SIMPER analysis showed several species contributed to an average 77.71% dissimilarity between the seasons. The species that contributed to the differences were: *Y. hyalosoma,* 18.6%, *A. japonicum* 12.6%, *G. oyena* 11.0%, *G. filamentosus* 9.1% and *A. natalensis* 8.9%, *A. lacunosus*, 8.4%, *A. ambassis*, 6.4%, *L. equulus*, 6.3%, *H. affinis*, 5.4% and *S. sihama*, 4.8%.

b) Crustaceans

Penaeus indicus did not show any marked seasonality while *T. crenata* and *M. rude* showed tendencies to seasonality as they mostly occurred in SEM. Generally the highest crustacean abundance was recorded in NEM as opposed to fish where the highest abundances were in SEM. A Kruskal Wallis test was used to test for differences in mean crustacean abundance between NEM and SEM season. There were no significant differences detected (p =0.843). The pattern of crustacean seasonality was visualised in an nMDS ordination plot (Figure 2.10), whereby sampling locations in SEM season were more clustered with adjacent locations being closer as opposed to NEM months. Significant differences were recorded in crustacean assemblages between NEM and SEM seasons (ANOSIM R=0.223, p=0.001) but the separation between the seasons was weak. SIMPER analysis revealed an average dissimilarity of 43.8% for the most abundant species between the two seasons. Further, it showed *P. semisulcatus* (19.8%), *P. indicus* (17.6%), *T. crenata* (16.7%) and *P. monodon* (15.2%) as being the major species contributing to the difference.

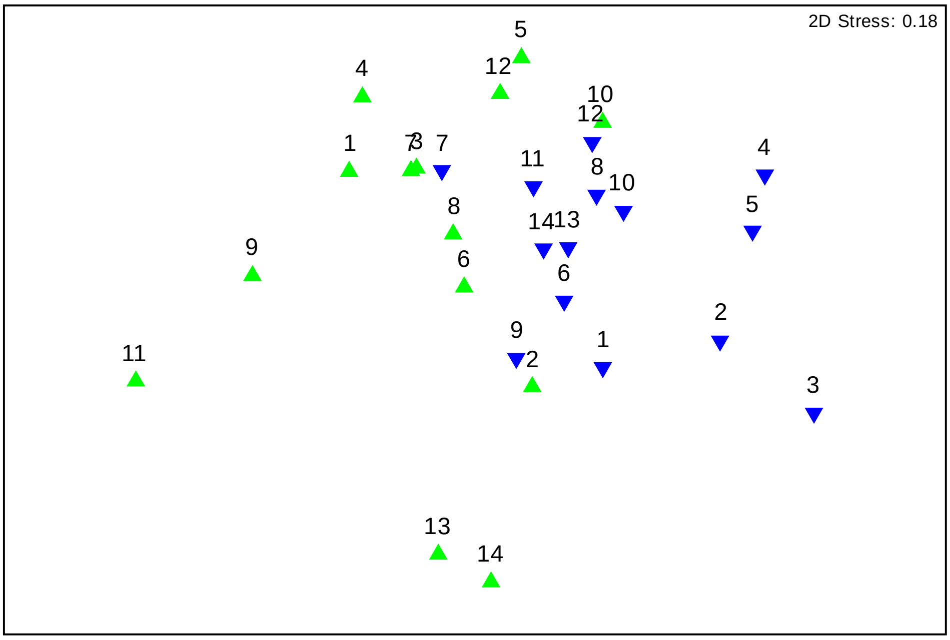


Figure 2.10: nMDS of seasonal abundance of most abundant crustaceans of fourth root transformed data for all sampling site for all the sampling periods. Blue triangle represents SEM and green triangle NEM seasons and numbers refer to sampling sites.

2.4 Discussion

2.4.1 Fish community structure

Mangrove fish communities have been extensively studied in various parts of the world. In Kenya, knowledge is gradually building from studies that have taken place in Gazi in the south coast, and in Tudor and Mida creeks in the north coast (Little et al., 1988; Kimani et al., 1996; Wainaina et al., 2013, Gajdzik et al., 2014). The present study documented 59 fish species while (Kimani et al., 1996) and (Wakwabi & Mees, 1999) recorded 128 and 75 species in Gazi, and Tudor respectively. This reflects potential differences between active and passive sampling effort. Little et al. (1988) and Wainaina et al. (2013) recorded 83 and 84 species in Tudor creek. Recent studies using passive gears inside mangrove forests in Gazi however, recorded lower numbers of fish species than those from the current study i.e. 49 (Crona & Rönnbäck, 2007) and 30 species (Huxham et al., 2004). The notable discrepancies in the number of species between these studies could be due to differences between study sites, for example most studies sample mangrove creeks and not inside the forest like in this study. This determines the kind of gear used i.e. active gears such as seine nets for creeks, which tend to catch more fish compared to passive gears like fyke nets in the forest (Franco et al., 2012; Tietze et al., 2011).

It is generally true that fish, like almost all biological communities from inshore habitats, including mangroves, tend to have highly right skewed and steeply sloped rank abundance curves, with only a few species, typically 3 - 7, contributing over 70% of the total abundance (Bell et al., 1984; Giarrizzo & Krumme, 2007; Shervette et al., 2007). Such a pattern was observed in Vanga, where six species i.e. *Y. hyalosoma* (25%), *A. japonicum* (18.9%), *A. natalensis (11.2%), A. ambassis* (7.2%), *L. equulus* (7.2%) and *G. oyena* (5.7%) contributed to about 70% of the total abundance. This is similar to the pattern found in the bay habitats of Tanzania, where nine species contributed 70% of the total individuals (Lugendo et al., 2007), although less equitable than reported from some mangrove studies, such as Tongnunui et al. (2002), found that 20 fish species contributed to 88.5% of the total abundance in the Sikao creek mangrove estuary in Thailand.

The dominant taxa encountered in coastal estuaries in Kenya include Gerreidae, Atherinidae, Clupeidae and Chanidae families (Kimani et al., 1996; Huxham et al., 2004; Crona & Rönnbäck, 2007). *Gerres oyena,* a dominant species in this study, has been cited in most studies in Kenya (Kimani et al., 1996; Huxham et al., 2004; Crona & Rönnbäck, 2007; Wainaina et al., 2013). This species has also been documented in other studies in the WIO (Lugendo et al., 2007; Mwandya et al., 2010) and beyond (El-Regal

& Ibrahim, 2014). *Gerres oyena* is considered a mangrove resident species and that could explain its dominance in these habitats. In Tanzania, *G. oyena* was the most abundant species in forested mangrove sites (Mwandya et al., 2009) while Huxham et al. (2004) recorded the highest abundances in the cleared sites in Gazi, Kenya. Further, *G.oyena* had the greatest abundance in both seaward and landward sites in the Gazi bay mangroves (Huxham et al., 2008). The variation in the other dominant species caught in mangrove habitats along the coast could be due to site specific differences, seasonality or their diurnal behaviour of migrating into and out of mangrove and other habitats.

Despite the abundance of the Ambassidae family in Vanga, these fishes do not seem to be very common at the South coast. They are mentioned to occur in Tudor creek and Gazi by two studies only (Little et al., 1988; Crona & Rönnbäck, 2007). However, it is important to note that even in Vanga, they were totally absent in the NEM season, appearing only during the SEM sampling seasons (September and June).

Serranidae was the most diverse family in Vanga, but it was rarely encountered in previous studies in coastal estuaries of Kenya. In Mida creek, one *Epinephelus coioides* was recorded (Gajdzik et al., 2014). Despite the family’s diversity in this study, species occurrence was rare with mostly single individuals being caught throughout the sampling period. A study on groupers in Kenya’s south coast reported a total of eight species in the Vanga coral reef and *Epinephelus caeruleopunctatus and E. malabaricus* were the two most common species (Agembe et al., 2010). Thus, more than half of the species in the *Epinephelus* genus encountered in the mangroves of Vanga have been previously encountered on the reef in the same area. In contrast to this study, only two species of the genus *Epinephelus* i.e. *Epinephelus lancelotus* and *E. suillus* have been recorded in mangrove creeks and channels in Tanzania (Lugendo et al., 2007). Most of the *Epinephelus* species encountered in Vanga are known to inhabit estuaries and mangrove areas in their juvenile stage (Froese & Pauly, 2017) and overfishing in inshore habitats at the coast could be the reason for their scarcity.

The number of fish species sampled in this study (59) was in a similar range compared to studies elsewhere that used fyke nets to sample mangrove forests. In Taiwan, Kuo et al. (1999) recorded 79 species, while Giarrizzo & Krumme (2007) recorded 65 species in Brazil. Other studies recorded species numbers that were a lot lower than in the current study (Table 2.7). In terms of abundance, the catch performance between gears can differ considerably. Active gears like seine nets, tend to catch more fish compared to passive gears (e.g. fyke nets), which tend to be biased towards pelagics rather than demersal species (Franco et al., 2012).

Table 2.7: A comparison of studies using Fyke nets in mangrove fish sampling

Location	**Gear**	**No. of spp**	**Dominant spp (≥70%)**	**Source**
Taiwan, Western and Southern mangrove creeks	Fyke nets, fence nets 10 m long; 1.2m high; mesh size: 15 mm) and three hoop nets of mesh size of10 mm	79	5	Kuo et al., 1999
Victorian coastline, Western Port, Australia	Fyke, gill, seine. Fyke nets The main four square rings (70 ·70cm), and a wing (10m long·70cm deep)	28[a]	N/A	Hindell, & Jenkins, 2004
New South Wales, Australia	Fyke nets 4m long wings, 40cm wide, 25cm high entrance, 2mm mesh size.	13	5	Mazumder et al., 2006
Gazi, Kenya	Fyke nets mesh size 18mm, mouth area 0.86m^2, wing length 1.77m	22	1	Mees et al., 1999
Macrotidal Curuçá estuary, Pará, north Brazil	Fyke nets two wings each (20 × 6m, 20 mm stretched mesh size) seven circular stainless steel hoops; total length: 7.5m; 13mm	65	6	Giarrizzo & Krumme, 2007
Mida creek, Kenya	Gill, seine & Fyke nets (3 large and 4 small fyke nets, mesh sizes, 15 & 5mm respectively, outer cone of 30mm & inner cone of 15 mm)	27*	2	Gajdzik et al., 2014
Vanga Kenya	Fyke nets wing length of 9.5m each, height 1m, body length3.6m, frame 1m^2 rings of diameter 0.9m, 0.7m, and 0.6m, mesh size 19mm	59	6	This study

a=only fish caught with fyke nets fish were considered, *includes all fish caught with all gears

Seine nets on the other hand target both pelagic and demersal species (Tietze et al., 2011). However, only passive gears like fyke nets and stake nets sample effectively inside the mangrove forest. In this study, individuals of 34 species (57.6%) were categorized as 100% small juveniles while for 10 species individuals occurred as both ‘small and large’ juveniles. These results are similar to those from Thailand, where 57% of the species caught comprised of juveniles only (Ikejima et al., 2003). Similarly in Tanzania, about 95% of individuals caught in bay habitats were juveniles and no adults were encountered (Lugendo et al., 2007). In the Ambassidae family, 100% of *A. natalensis* (100%) and 97% of *A. ambassis* occurred as ‘large juveniles’ but only during SEM. This could be an indication that they enter the mangroves slightly before this stage and leave before they become adults. The smaller size classes of these species may be utilising other nursery habitats. In this study, *Zenarchopterus dispar* and *Stolephorus commersonnii* were the only fish species for which adult life stages were observed i.e. 11% (n=9) and 100% (n=1), respectively.

a) Size classes

In Vanga, the maximum length of *G. oyena* caught was about 11cm TL compared to large sized individuals (29.2cm TL) of the same species caught in mangrove creeks of Gazi (Kimani et al., 1996). However, *G. oyena* caught inside Gazi mangrove forests were comparable in size to those caught in this study i.e. 10.8cm TL (Crona & Rönnbäck, 2007) and 11cm TL for Gazi and Vanga, respectively. From this comparison, it could be suggested that *G. oyena* juveniles were encountered inside the forests and adults in the creeks. It could also be speculated that size classes are likely to differ even in habitat type use within similar ecosystems such as mangrove forests and mangrove creeks. It was not possible to compare the sizes of *Y. hyalosoma* and *A. japonicum* due to lack of literature.

The Chi square tests showed significant difference between the size class frequency and sampling times (phase) in three species i.e. *G. oyena, Y. hyalosoma* and *A. japonicum.* For the three species, there is an indication of increase in numbers and standard length of the fish. It was difficult to conclusively point to particular times of spawning of these species due to lack of supporting literature. This means that increase in size could indicate that the species were the same cohort that is increasing in size while in the mangroves and are likely to be recruited into the fishery later.

b) Seasonality

The change in environmental variables such as salinity, temperature, biological factors like may influence fish community structures by affecting feed availability, reproduction and ontogenic migrations (McClanahan, 1988). The changes in environmental variables in this study are shown on Table 2.8. The overall mean catch per net and total number of species of juvenile fish in Vanga were higher during SEM (rainy) than NEM (dry) season, and significant differences were found in fish abundance between the two seasons. The findings of this study are consistent with findings of similar studies in the WIO region where the monsoon seasons have been found to influence fish community structure (Lugendo et al., 2005; Crona & Rönnbäck, 2007). Similar to this study, fish densities were higher in SEM than NEM in Tudor creek, but the opposite was true for the number of species (Wainaina et al., 2013). It would also be worth noting that artisanal fishers in Kenya do most of their fishing during the NEM season (Fulanda et al., 2009). Other studies from the East African coast have concluded that seasonality did not influence fish community structure in mangrove sites (Little et al., 1988; Mwandya et al., 2010).

Table 2.8: Evironmental variables during SEM and NEM season in this study

	Sep-16 (SEM)			**Dec-16(NEM)**			**Jun-17 (SEM)**		
Site	DO	Temp. °C	Salinity	DO	Temp. °C	Salinity	DO	Temp. °C	Salinity
1	7.6	26.2	34.8	5.1	29.7	35.0	8.0	29.4	28.3
2	5.6	26.1	34.7	5.6	29.6	35.0	6.7	28.3	27.3
3	7.3	27.2	33.8	5.4	29.4	35.3	6.8	28.7	28.7
4	14.3	27.2	32.7	4.2	29.4	35.0	6.9	29.1	25.3
5	16.2	27.2	33.7	4.3	29.2	35.0	7.0	29.6	13.3
6	11.2	25.9	33.7	4.3	29.3	35.7	6.7	28.9	23.3
7	6.3	26.3	34.3	2.9	29.4	35.0	6.7	28.8	24.7
8	8.2	25.8	34.8	2.2	29.4	35.3	6.4	28.7	25.7
9	8.0	26.3	34.7	2.7	29.6	35.3	6.7	28.2	25.7
10	6.2	26.3	34.7	2.3	20.1	35.3	7.8	28.6	25.3
11	6.5	26.2	34.3	2.6	28.9	35.3	8.1	29.1	24.9
12	5.6	25.0	35.8	2.2	28.4	36.0	7.7	28.7	23.7
13	7.1	27.1	34.7	4.9	29.6	37.0	6.4	28.9	28.3
14	6.1	26.7	33.3	5.3	29.8	37.0	6.5	28.6	28.3

*DO=dissolved oxygen, Temp.= temperature

2.4.2 Crustacean community structure

Penaeus semisulcatus and *P. indicus* were the most abundant species contributing to 82.7% of the crustacean abundance. These two species have previously been recorded as most abundant penaeid shrimp in Malindi – Ungwana bay Kenya (Munga et al., 2013). Crustaceans were grouped into three clusters according to their abundance in the sites during the sampling seasons. This meant that the abundance of penaeid shrimp was similar while that of crabs was also similar to each other at 40% similarity (Figure 2.10). This is an expected trend. The mean abundance of the most abundant crustacean species did not show any significant differences between seasons. In this study, the most abundant species had the highest mean in NEM. This contrasts the findings of (Munga et al., 2013) who recorded the highest shrimp catches in SEM during trawling survey in Tana and Sabaki area in North coast Kenya. This could have been due to use of active gears and fishing in areas outside mangroves. In this study, *P. indicus* exhibited no seasonality as 53% of the total individuals occurred in NEM and 47% in SEM. This pattern was also observed in Ungwana bay where Ndoro et al. (2014) recorded 57.6% abundance of *P. indicus* in NEM and 41.5% in SEM during a bottom trawling survey. This could imply that *P. indicus* is equally distributed in all the monsoon seasons in Kenya, but their habitat use differs over the seasons. *Thalamita crenata* and *M. rude* showed tendencies for seasonality, as they mostly occurred in SEM. Generally, the influence of seasonality on crustacean abundance and assemblages in Vanga was not definite and this concurs with the findings of previous studies in Ungwana bay Kenya (Munga et al., 2013; Ndoro et al., 2014). In contrast, Robertson & Duke, (1987) found small crustaceans in neasrshore habitats in Australia to be seasonal.

2.5 Conclusion

Most of the fish families and species encountered in Vanga are common at the East African coast. The dominance of a few species is commensurate with most findings from tropical mangrove ecosystems where few species occur in high densities. *Gerres oyena* has been cited as a dominant species in several sites at the Kenya coast and it could be an important indicator species in mangrove ecosystems. The species in the family Serranidae were unusual in their diversity and this study has so far recorded the highest number of species encountered in the East African mangroves (five species in the genus *Epinephelus*). Despite their high diversity and their use of mangroves as nursery habitats, the species of Serranidae family appeared in very small numbers (mostly one individual per species). The high diversity of this family in Vanga could be due to the size of the bay, which is much bigger than Gazi bay, Tudor and Mida creeks in Kenya. This difference in bay sizes could mean more chances of encountering this family in Vanga compared to the other coastal areas in Kenya. Generally, the low abundance of this family in the entire East African coast could be due to overfishing.

Almost all the individuals encountered in this study were either small or large juveniles. This is expected of such habitats. Thus, it could be concluded that this study further affirmed the hypothesis that mangroves provide habitats for juvenile fauna, which later migrate to other habitats. The general lack of adults especially for resident species like *G. oyena* could be due to fishing or predation. Future work could be aimed at establishing where the large juveniles migrate to after they leave the mangrove habitats.

Seasonality has been found to be an important factor influencing the fish assemblages in Vanga. SEM and NEM seasons influence the fishing activities of artisanal fishers at the coast and it is possible that it influences the availability of fish in the mangrove forests as well.

Crustaceans had their highest abundances in NEM although the differences between the seasons were not significant. Previous studies with similar findings have been short term, just like this one and it would be therefore recommended to study the effect of seasonality on crustacean and especially penaeid shrimp abundance in mangrove areas.

3.0 CHAPTER 3: EXPLORING THE ROLES OF MANGROVE FOREST QUALITY IN DETERMINING FISH COMMUNITY STRUCTURE IN VANGA, KENYA

Abstract

Mangrove loss rate is declining with recent recorded annual rates being as low as 0.16%. Although the threats to these ecosystems remain high, increased public awareness has resulted in reduced deforestation and increasing reforestation efforts of degraded areas. There is however a growing concern on how the quality of the remaining forests affects the provisioning of ecosystems services. Mangroves provide an array of ecosystem services that include provision of juvenile habitats for fauna. This study sought to investigate whether mangrove forest quality could predict fish and crustacean community structure in Vanga. Complexity Index (C.I.), a composite indicator for forest features, was used as a proxy for mangrove forest quality. The 14 mangrove sampling sites had varying C.I.s across the Vanga seascape. Using fyke nets, deployed at creek mouths, fish and crustaceans were sampled once every three months between September 2015 and September 2017. Broad scale (500m – 1km) and fine scale (100m) forest features were regressed against fish and crustacean variables that included species, abundance and biomass. Large and consistent differences in fish and crustacean communities were recorded among sites with some sites correlated with higher abundances of fish and crustaceans than other sites

There was an inverse correlation between fish and crustacean metrics. The results also showed that broad scale and not fine scale forest features were useful indicators for fish and crustacean structure. Fish and crustaceans responded differently to forest features. Mean fish abundance was negatively associated with C.I. (R^2=0.32, p=0.034) while mean crustacean abundance and species *Penaeus monodon* and *P. semisulcatus* were

positively correlated with C.I. (R^2=0.44, p=0.009); (R^2=0.40, p=0.014) and (R^2=0.41, p=0.013), respectively. Forest features did not influence reef species or individual fish species. It was concluded, within the scope of this study, determinants of habitat quality for fish and crustaceans are different. This means that management options are not straightforward.

3.1 Introduction

Coastal habitats, including mangroves, seagrasses and saltmarshes are amongst the most threatened ecosystems in the world (Mcleod et al., 2011). They have been declining in area and quality for decades, and with human migration continuing into coastal areas (Hugo, 2011) the pressure on these systems is likely to increase. For instance, between 1980 and 2000, about 35% of global mangroves were lost (MEA, 2005) and most of what remains is degraded (UNEP, 2004). Seagrass meadows have been declining at a rate of up to 7% per annum since 1990 (Waycott et al., 2009). The Intergovernmental Panel on Climate Change (IPCC, 2007) predicts that should the current habitat conversion rates remain unchanged, over 30% of seagrass and saltmarsh habitats will be lost in the next 100 years. The degradation and loss of these habitats undermines their ability to provide ecosystem goods and services (Dahdouh-Guebas et al., 2005; Duke et al., 2007).

Encouragingly, the rate of mangrove loss has slowed to less than 1% per annum globally (Valiela et al., 2001; Duke et al., 2007; Alongi, 2008), with a rate of 0.7% being recorded in eastern Africa (Kirui et al., 2013) and Friess et al. (2016) recording a rate of 0.16% annual loss. Global efforts are also in place to restore and re-plant mangrove forests (Ellison, 2000; Lewis, 2005). Whilst forest loss remains a concern, there is an increasing focus on the quality of the remaining and restored forests (Giri et al., 2011). The information is however sparse on how change in forest quality affects the provision of ecosystem services (Huxham et al., 2015).

Coastal fisheries have for long been associated, directly or indirectly, with mangrove ecosystems (Barbier, 2000, Manson et al., 2005; Aburto-Oropeza., 2008). The relationships between mangrove variables and fish have been studied globally, including in East Africa (Laegdsgaard & Johnson, 2001; Nagelkerken & Faunce, 2008; Sheaves et al., 2015). There is a broad consensus that mangroves in general act as nurseries for offshore and resident fish and crustaceans and provide habitat and food for them (Robertson & Duke, 1987; Laegdsgaard & Johnson, 1995; Nagelkerken et al., 2010; Lefcheck et al., 2019). Several mangroves features have been explored as supporting this function. Some of the features studied include root complexity (Laegdsgaard & Johnson, 2001; Sheridan & Hays, 2003; MacDonald & Weis, 2013) and mangrove area and extent (Pauly & Ingles, 1986; Loneragan et al., 2005; Manson et al., 2005).

Positive relationships have been found between mangrove area and fish and crustacean diversity and abundance. For example the productivity of penaeid shrimps in Indonesia and the Philippines was influenced by mangrove area (Pauly & Ingles, 1986; Manson et al., 2005). Estimates of fishery loss following mangrove removal were however not possible because the relationship was non-linear. Mangrove area and prawn catches in Malaysia were significantly linearly related in the 1980s and 1990s (Loneragan et al., 2005).

It is worth noting that despite the generally positive relationships documented between mangrove area and fisheries productivity, not all studies reveal strong or significant effects. Barbier & Strand (1997) found that a 2.3% mangrove loss between 1980 and 1990 led to an insignificant (0.4%) drop in shrimp harvest in Campeches Mexico while Barbier (2006) found that only a small monetary loss (USD$69/ha) in the shrimp fishery in Thailand resulted from mangrove destruction. In some coastal areas in Malaysia, positive relationships between mangroves area and prawn productivity were recorded. However, in adjacent areas, prawn productivity did not respond to loss of mangrove area (Loneragan et al., 2005). In Rookery Bay, Florida, the loss of mangrove canopy cover due to pruning, did not have a significant effect on fish community structure before and after the pruning (Ellis & Bell, 2013). Thus, the positive relationship mentioned above may not always be due to mangrove area only and other factors could be responsible as well (Loneragan et al., 2005; Ellis & Bell, 2013).

On a local scale, habitat and structural complexity in mangrove forests have been found to influence faunal species diversity, with complex structures attracting more species compared to simple structures (Blaber &Milton, 1990; Vance et al., 1996; Taniguchi et al., 2003; De La Morinière et al., 2004). In particular, mangrove roots have been found to attract juvenile fish species (Nagelkerken & Faunce, 2008) as they are deemed to exclude large predators hence reducing predation risk and increasing survivorship (Laegdsgaard & Johnson, 2001; Sheridan & Hays, 2003; MacDonald & Weis, 2013). A number of studies on the effects of mangrove root complexity, their structure and other attributes, on fish communities have been carried out in laboratories and in situ. Macia et al. (2003) explored the effects of pneumatophore density on predation rate of penaeid shrimp by *Terapon jarbua* in the laboratory. They found highly complex structures to be effective deterrents as they reduced the efficiency of predators. In order to explore the importance of root orientation to fish, Artificial Mangrove Units (AMUs) were used and fish preference for standing vertical pipes to hanging ones was observed (Nagelkerken et al., 2010). However, the clear relationships that have been recorded between fish and root structures in some studies have proved elusive in other cases (Kon et al., 2009). In Micronesia, differing root structural complexities supported significantly different nekton assemblages but not nekton abundance (Mackenzie & Cormier, 2012).

Besides food provision and refuge, other factors influence the community structure of fish in nursery habitats like mangroves. Tidal ranges in shallow water habitats have for instance been found to influence the abundance and diversity of fauna (Unsworth et al., 2009). Mangroves within narrow tidal ranges offer continuous habitats for fish as opposed to those found within large tidal ranges (Marcus Sheaves, 2005). In northern Australia, mangroves in deeper rather than shallower waters proved to be better nurseries (Vance et al., 1996) probably because the fish can use them for longer.

Environmental variables such as turbidity, salinity, shade, and temperature have also been found to influence fish community structure within and around mangrove habitats (Rönnbäck et al., 1999; Macia, 2004; Barletta et al., 2005; Verweij et al., 2006). Turbidity is envisaged to reduce predation risk in nursery habitats by reducing visibility under water, negatively affecting predator efficiency (Blaber et al., 1995; Macia, 2004; Verweij et al., 2006). In some estuaries, fry have been known to use differences in turbidity scales to guide them to suitable nursery areas (Blaber & Blaber, 1980). The relationship between nekton abundance and turbidity is however not always obvious (Huxham et al., 2008). Like turbidity, shade also tends to reduce the visibility of some prey species in water thus concealing them from the predator’s vision (De La Morinière et al., 2004; Ellis et al., 2004). In other cases, fish assemblages of some species has been structured by salinity variation in estuaries, due to seasonality and/or influx of fresh water (Barletta et al., 2005; Mwandya et al., 2010; Rezagholinejad et al., 2016). In Marudu Bay, Malaysia, four families (Centriscidae, Engraulidae, Mugilidae, and Sillaginidae) were significantly influenced by abiotic factors. Salinity in particular was found to be the main factor affecting the distribution and abundance of Mugilidae families. Overall, regression analysis tests indicated a weak correlation between larval assemblage and environmental parameters in Marudu Bay estuary (Rezagholinejad et al., 2016).

There is therefore a voluminous literature on the relationships between fisheries and various mangrove factors. Despite this, and perhaps surprisingly, few studies have attempted to relate mangrove condition or quality with fish assemblages. It is thus difficult to predict the consequences of mangrove degradation on fish assemblages in nursery areas and on offshore fisheries; hence management decisions on forest use and conservation, such as deciding on the location of protected or extractive areas, are not well informed about the likely consequences on fisheries. This study, therefore, sought to understand the relationships between mangrove forest attributes (quality and location within the broader seascape) and fish and crustacean community structure in the Vanga mangrove ecosystem.

3.1.1 Aim

To investigate fish and crustacean abundance, biomass and species richness at a range of sites within a single mangrove system and explore the roles of mangrove forest quality and type in determining fish community structure.

3.1.2 Specific objectives

1. To investigate whether there are consistent differences in fish and crustacean communities among the sampling sites in Vanga
2. To investigate whether mangrove forest attributes can predict fish and crustacean community structure
3. To investigate the relationship between mangrove forest attributes and reef associated species

3.2 Study approach and methodology

3.2.1 Study site

The study site is as described in chapter 2. The mangrove fish sampling sites are shown on Figure 3.1.

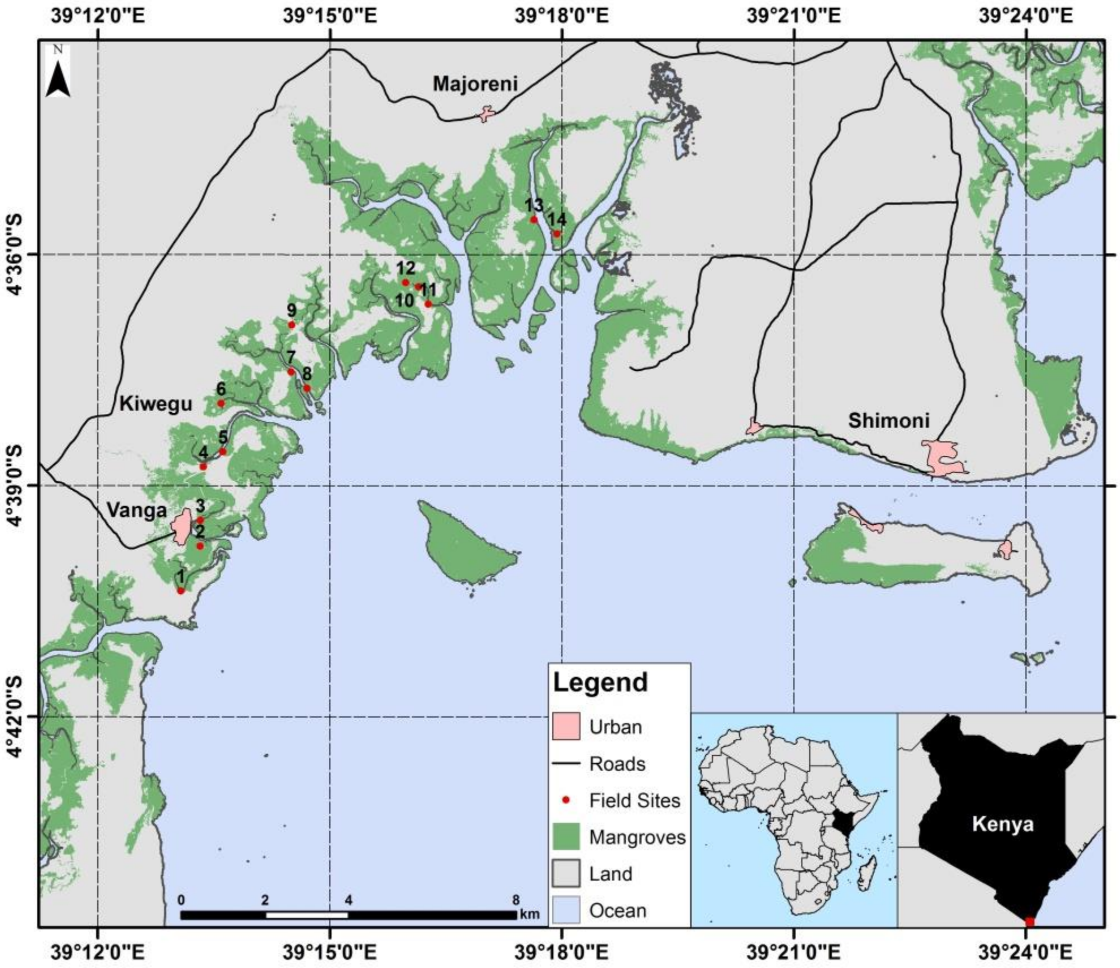


Figure 3.1: Location of sampling sites across the Vanga mangrove ecosystem (sampling sites shown as red dots numbered 1-14)

3.2.2 Methods

3.2.3 Forest quality and fisheries support

Obtaining representative samples of fish from mangrove habitats is difficult because of the structural restrictions on using fishing gears. Sampling sites were chosen to balance logistical tractability (allowing sampling of all the sites within single field campaigns of five days each, to avoid large temporal differences in sampling) and a wide and representative spread of forest variables, in particular of the Complexity Index (C.I.). Since no one parameter can be used to describe the quality of a mangrove forest, C.I. was used to infer quality. C.I. describes the structural complexity of a forest stand (Holdridge, 1967; Amarasinghe & Balasubramaniam, 1992) whereby degraded stands tend to have lower C.I. compared to undisturbed ones (Roth, 2018). The complexity index was calculated according to (Holdridge, 1967). This index combines all floral characteristics (stem density, diameter at breast height (dbh) calculated into basal area, mean tree height and number of a species) to show how complex or structurally developed a stand is:

$\text{C.I.} = 10^{-5}(d)(s)(h)(b)$ where d is the stand density, s is the number of tree species, h is the mean tree height and b is the basal area (Holdridge, 1967).

The calculations are per hectare.

In Kenya, previous studies have found forest stands with low C.I. to be more degraded due to human pressure than those with high C.I. (Kairo et al., 2002; Obade et al., 2004). A high C.I. was taken to mean a more complex forest stand and hence good quality and vice versa.

The lack of standard and effective methods of studying how faunal communities respond to habitat structural complexity has in the past made it difficult to conclusively establish relationships. However, the development of 3D scanning technologies at mesoscale allows such technology to be used to explore relationships between root architecture of different mangrove species and faunal communities (Kamal et al., 2014). On the other hand, restoration of once degraded mangrove, even with monospecific stands, has been found to achieve the functional equivalence of natural forests (Walton et al., 2007). For instance, in Panjay area in the Philippines, replanted monospecific stands functioned nearly as well ecologically as the natural forests in the restoration of mud crab populations (Walton et al., 2007). A socio economic survey in the same area revealed that restored mangroves were important fishing grounds for mangrove fishers (Walton et al., 2006).

3.2.4 Broad scale mangrove forest structure

Originally, sampling sites were selected based on C.I.s calculated from structural data collected by the Kenya Marine and Fisheries Research Institute (KMFRI) in 2015. The forest data were collected according to the protocol developed by Diefenbach & Fritsky (2007). ArcView GIS was used to map the study area and generate the sampling points based on forest cover characteristics. Plot locations were determined prior to going to the field to avoid bias. Due to the heterogeneity of mangroves imposed by the variations of environmental conditions across the intertidal gradient, a combination of systematic and random sampling (within a zone) was deployed. Representative plots were established in the forest to encompass all the different forest and landscape types. Plots measuring 100m^2 and 400m^2 were selected through stratified random sampling, along transects spaced 500m between them and running perpendicular to the shore line across the entire expanse of the mangrove vegetation. The plot size depended on the tree size and density; for large trees, 20 x 20m^2 was used. The number of the plots depended on the size and the different characteristics of the area of interest. Within each plot, the diameter at breast height (dbh) (cm) and height (m) for all the trees with stem (dbh ~1.3m) greater than 2.5cm were measured using a tree calliper and a graduated pole respectively. The number of mangrove species was also established and total tree count recorded. Table 3.1 gives a summary of the broad scale forest attributes. After selecting the sites based on this broad scale sampling, a more intensive forest structure sampling was carried out in all the 14 sites. Thus, the forest sites were selected based on the broad scale forest attributes and afterwards more intensive forest surveys yielded the fine scale forest attributes.

3.2.5 Fine scale mangrove forest structure

A stratified sampling design was used and transects were drawn perpendicular to the mangrove fringe. Three transects were to the right and three to the left of the creek that was fished in each site. There was a 5m allowance from the creek for the first transect to cater for the edge effect. Transects were 10m apart. Along each transect, four 10 x 10m plots were sampled, each 15m away from the other as demonstrated by Figure 3.2. Thus each site had a total of 24 plots.

All the trees in the 10 x 10m plots were measured for diameter at 130cm (D_{130}) and tree height (Cintrón & Novelli., 1984) using a forester's callipers and by using a graduated pole of < 4.5m respectively. Trees with a dbh of <2.5cm were excluded as they were considered saplings. The tree species in the plots were identified and counted so as to estimate the stem density (FAO, 1997; Diefenbach & Fritsky, 2007). The data collected were then used to calculate for each site mean height (m), stem density (stems^{-ha}), no. of species and basal area (m^2 ha^{-1}).

The Complexity Index (C.I.) of the each of the 14 sites, for both broad scale and fine scale attributes, was calculated according the (Holdridge, 1967). A summary of broad scale and fine scale forest attributes of the fourteen sites is given in Table 3.1 and Table 3.2 respectively. The means of the C.I. in finescale and broadscale plots are visualised in Figures 3.3 and 3.4.

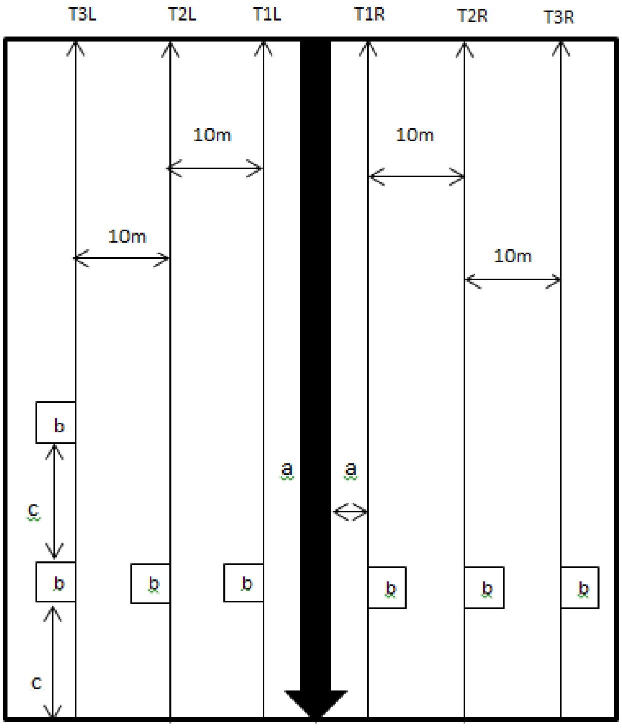


Figure 3.2: Forest structure sampling design for fine scale forest attributes. Key: a is the distance between the creek and the first transect which is 5m from creek edge, b is the 10x10m sampling plot in each transect, c is the distance between one sampling plot to the other along a transect which was 15m, T1L to T3L are the 3 transects on the left side of the creek and T1R to T3R were the transects on the right side of the creek each 10m apart.

Table 3.1: Broad scale forest attributes in Vanga mangrove ecosystem

Site	**Mean height (m)**	**Basal area (m^2 ha^{-1})**	**No. tree spp**	**Stemdensity (individuals ha-1)**	**C.I.**
1	4.82	0.34	4	2925	0.19
2	7.33	1.09	5	1300	0.52
3	6.39	0.37	4	1800	0.17
4	7.61	1.06	2	2200	0.36
5	6.8	2.8	4	1350	1.03
6	4.00	0.19	5	3250	0.12
7	3.18	1.22	5	5258	1.02
8	3.8	0.88	3	4850	0.48
9	4.29	0.66	3	2152	0.18
10	4.62	1.86	6	2676	1.38
11	4.35	1.07	4	2650	0.49
12	5.34	2.11	3	3175	1.07
13	2.8	1.21	3	5175	0.53
14	3.26	1.57	4	4293	0.88

Table 3.2: Site specific (fine scale) forest attributes in Vanga mangroves characteristics

Site no.	**Mean height (m)**	**Basal area (m^2 ha^{-1})**	**No. tree spp.**	**Stem density (individuals ha^{-1})**	**C.I.**
1	3.8	2.2	7	2979.2	1.8
2	4.5	3.2	5	3637.5	2.6
3	5.2	4.5	5	3808.0	4.5
4	4.0	3.1	4	5375.0	2.7
5	3.8	1.6	6	2392.0	0.9
6	4.2	2.1	5	2914.8	1.3
7	4.3	1.9	5	2900.0	1.2
8	5.8	5.3	6	3495.8	6.4
9	2.7	1.9	3	4395.8	0.7
10	3.8	2.6	4	3441.7	1.4
11	2.9	1.6	6	3158.3	0.8
12	4.6	3.7	4	3941.7	2.7
13	3.9	3.1	4	4183.3	2.0
14	5.2	2.4	5	3075.0	1.9

3.2.6 Complexity index

The variability of C.I. between the sites for both broadscale and finescale forest variables is shown in Figures 3.3 and 3.4. A Kruskal Wallis test showed significant differences in C.I. using broad scale forest attributes among the14 sampling sites (df=13, p=0.049). A one-way ANOVA showed significant differences in C.I. using fine scale forest variables among the fourteen sites ($F_{(13,322)} = 10.11$, $p < 0.001$)

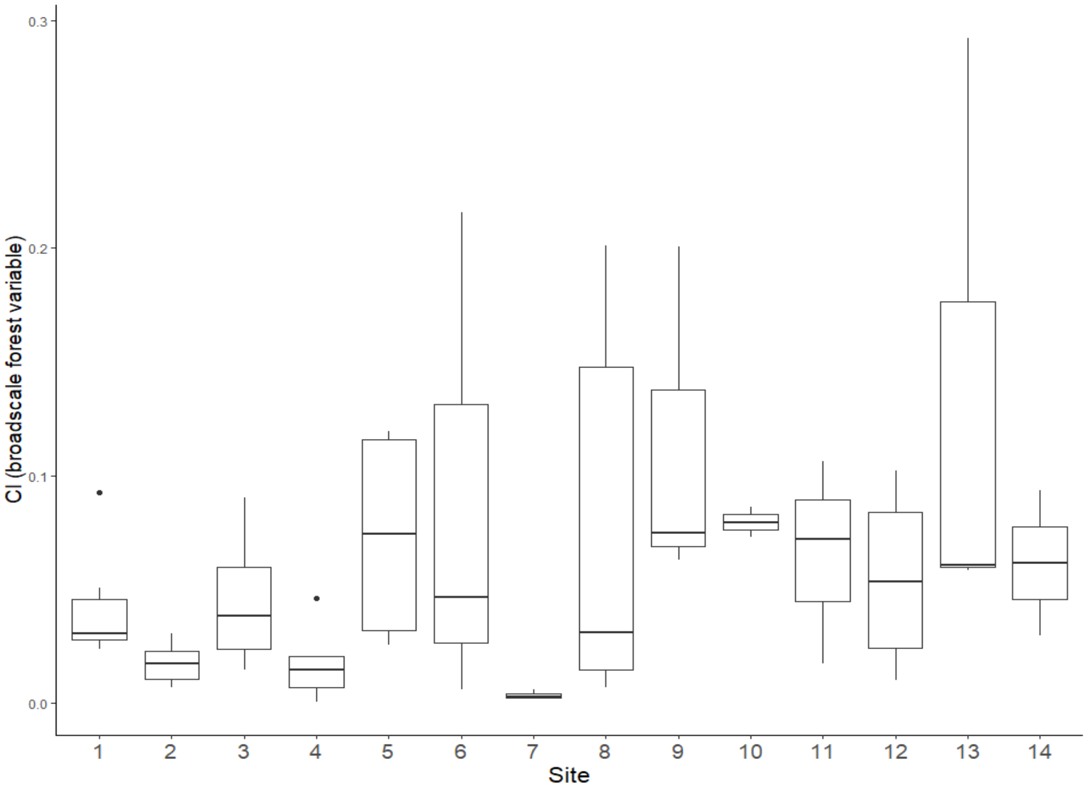


Figure 3.3: The variability in mean C.I of broadscale forest features

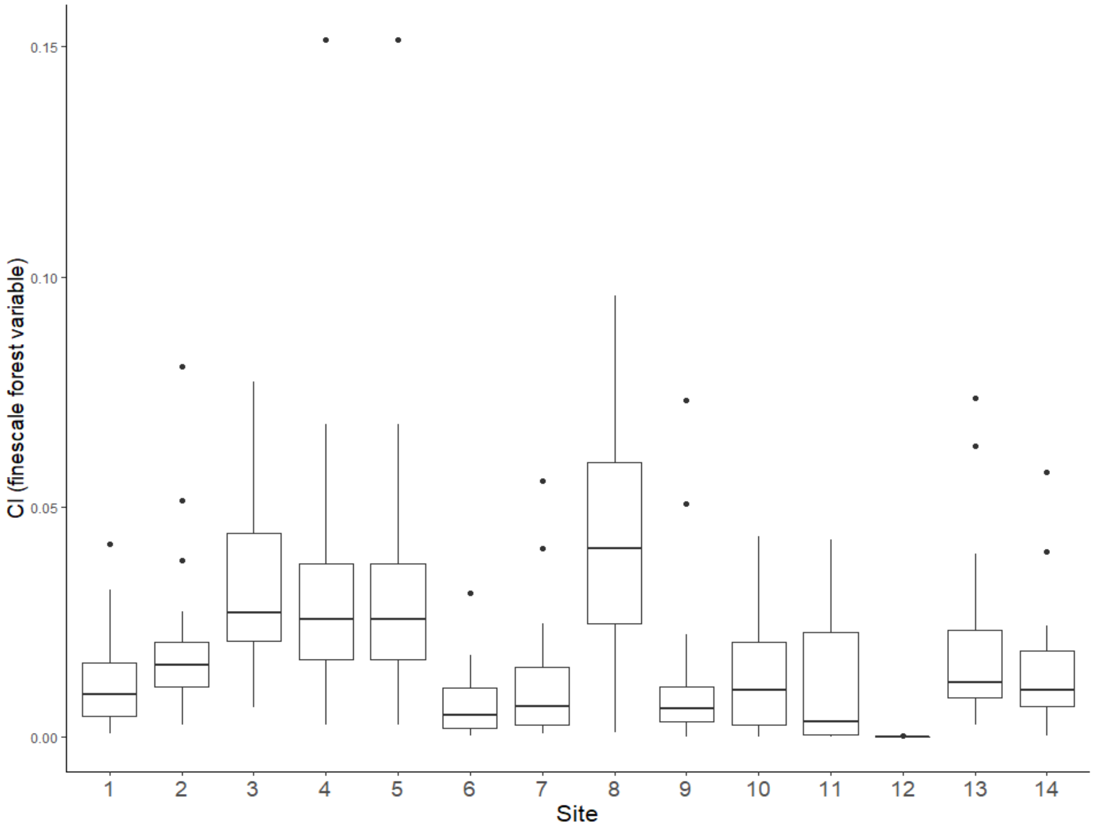


Figure 3.4: The variability in mean C.I of finescale forest features

3.2.7 Sampling design and methodology

Fish and crustaceans were sampled at fourteen mangrove creek sites situated between Jimbo and Majoreni. The sites were chosen to give a wide geographical coverage of the Vanga mangrove forest whilst still being accessible enough to allowing regular sampling. Sampling was done once every three months during spring tides over five consecutive days from September 2015 to September 2017. However, March 2017 was not sampled for logistical reasons. Thus, eight replicate samples were taken from each of the 14 sites making a total of 112 samples. Fyke nets were deployed in the morning during low tide and collected 24 hours later during low tide. They caught fauna leaving these sampling areas during the ebb tide. The fish and crustacean samples collected in the field were placed in a cool box while in the field. They were sorted and identified to the lowest taxon possible using Anam & Mostarda (2012) and Richmond (2011). The fish standard and total lengths were measured (to the nearest 0.1cm) and weighed (to the nearest 1g). The carapace length of crustaceans was measured to the nearest 0.1cm. Some individuals were partly predated on so in such cases, they were identified whenever possible and included in abundance data. Further, fish were also classified into function groups like reef associates and non-reef associates groups guided by information in FishBase (Froese & Pauly, 2017) .

3.2.8 Environmental variables

After deploying the nets, in situ environmental parameters were measured for the months of June 2016, September 2016, December 2017 and June 2017. Salinity was measured using a refractometer, dissolved oxygen (DO) and water temperature were measured with a DO meter (Hanna instruments brand), and a Secchi disk of 40cm diameter was used to measure turbidity. In instances when the equipment failed, water quality parameters were not recorded. Complete data sets for water temperature, salinity and dissolved oxygen were available for the months of September 2016, December 2016 and June 2017.

3.2.9 Fish and crustacean habitat use

Fyke nets were deployed at the creek mouths that drain the mangrove forest sites, to sample fish communities leaving these sampling areas during ebb tide. The fyke nets had two wings each of length of 9.55m, height of 1m, and body frame length of 3.6m. The main frame was made of metal measuring 1m x 1m. There were three rings of diameter 0.9m, 0.7m, and 0.62m along the body frame and a net of mesh size 1.9cm when stretched. Fish and crustacean abundance (number of individuals per net), biomass and number of species per net were obtained along with seasonal variations. These data were used to explore the relationships between forest quality (predictor variables) and the fish and crustacean community variables (response variables) of the Vanga mangrove ecosystem.

3.2.10 Statistical analysis

A Pearson product-moment correlation coefficient was computed in Minitab 17 to assess consistent site differences in terms of fish and crustacean abundance, biomass and diversity.

Since the results were similar for both mean and total fish variables (abundance and biomass), mean variables were used throughout this chapter except for individual species (total abundance was used in this case). The strongest correlations were used to determine the overall good sites and bad sites for both fish and crustaceans (sites that supported high diversity and biomass for fish and high abundance and biomass for crustaceans were good and vice versa).

The multivariate non metric multi-dimensional scaling technique based on Bray Curtis similarity was used to investigate if the abundance (pooled numbers for all dates) of the most abundant fish and crustacean species respectively differed among the fourteen sampling sites. Twelve fish species and seven crustacean species were selected. The software PRIMER vs 6 was used (Clarke & Warwick, 2001).

Regression analyses were used to test the null hypothesis that the finescale and broadscale forest variables had no influence on fish and crustacean variables. In order to establish possible relationships, a correlation matrix between both finescale and broadscale forest variables (mean tree height, basal area, stem density, number of tree species and Complexity Index) and fish as well as crustacean variables (mean fish and mean crustacean abundance and biomass and total number of species was developed).

This gave an indication of possible relationships. There were no correlations between finescale forest variables and fish and crustacean variables and so further anaylsis with finescale variables was abandoned. The null hypotheses that there were no relationships between fish as well as crustaceans with fine scale forest variables were tested using multiple and simple linear regressions.

Regression analyses between broadscale forest variables and fish and crustacean variables were used to test hypotheses. Mean fish and crustacean abundance and biomass were used in the regression anylsis. For individual fish or crustacean species, total abundance (pooled data from all sampling dates) was used. The Akaike Information Criterion, using a stepwise linear regression analysis was used to explore significant regression relationships that could be used to derive multiple linear regression models that could predict fish and crustacean community structures using forest variables. Models with the lowest AIC were selected for regression analyses. For the broadscale forest features and fish and crustacean variables, most of the significant multiple regression models that were generated were abandoned after best sub-sets analysis showed that there was no appreciable increase in R-squared adjusted when an extra variable was added to the model. Mostly, simple linear regressions at 95% confidence interval were preferred. Tests for normality of residuals were carried out before analysis and data were $\log_{10}$ transformed whenever the assumption was violated. Bonferonni test for multiple testing was applied for all the regression analysis. Data analysis was carried out using Minitab 17.

Since some of the sites were on one main creek that further split into smaller side creeks, it was expected that the sites on the same creek would be more similar than those further apart.

To investigate the presence of spatial autocorrelation, the Moran's index 'I' was calculated using GeoDa software. Moran's index 'I' is a correlation coefficient that measures the overall spatial correlation in a data set. The 'I' Values range from -1 to 1, with positive values suggesting a positive spatial autocorrelation and -1 strong negative spatial autocorrelation. Zero indicates a random pattern with no spatial autocorrelation. The null hypothesis was that there was no spatial autocorrelation between the sites. All the mean and total fish and crustacean variables were tested. Generally, Moran's I showed no significant spatial autocorrelation for the crustacean variables but significant spatial autocorrelation was found in the fish biomass and abundance ($p\leq 0.05$). To correct for spatial autocorrelation, the generalised least squares (gls) command in R statistical package that included location data was computed using normal errors, and with other error terms such as spherical corrections. Different models were compared using the Akaike Information Criterion (AIC) whereby the lowest score was considered the best. The results suggested that using spherical error terms gave the best fit. After this correction, the p- value in the regression analysis was still significant and actually not very different from standard regression without the autocorrelation correction. Thus correction for auto correlation was found unnecessary.

Complete data sets for environmental variables (temperature, salinity and dissolved oxygen) were available for Spetember 2016, December 2016 and June 2017. Computation of multiple linear regression models between fish and crustacean variables and broadscale and environmental variables guided by the AIC was carried out. Bonferroni adjustment was used to correct all models with multiple testing.

3.3 Results

3.3.1 Measures of diversity for fish and crustacean

Measures of diversity showed that the highest Shannon's diversity index (H') for fish was in site 7 (H'=1.1±0.7) while the lowest was in site 8 (H'=0.4±0.3). Pielou's evenness index however did not follow a similar trend and although the highest value was found in several sites including 11 and 12 and 14 (J'=0.9±0.1), the lowest was in site 8 (Table 3.3). There was no significant difference in Margalef's D (p=0.182) and Shannon's diversity index (p=0.239) in the sites. However, a significant difference in the sites for Pileous' evenness index (F=2.04, p=0.030) was recorded.

For crustaceans, the highest Shannon diversity index was in site 1 (H'=1±0.2) while the lowest in site 14 (H'=0.3±0.2). Pileous' evenness index followed a similar trend with the highest in site 1 (J'=1±0.04) and the lowest in site 14 (J'=0.4±0.2). Margalef's D ranged between (D=0.5±0.3) in site 14 to (D=1.4±0.3) in site 1 (Table 3.4). There was no significant difference in Shannon diversity index (p=0.185), Margalef's D (p=0.175) and Pileous' evenness index (p=0.294) with crustaceans in the sites.

Table 3.3: Variation of Margalef’s species richness index (D), Pielous’ evenness index (J') and Shannon Weiner Index (H') of fish in the fourteen sampling sites.

Diversity measure	**Site**													
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Margalef’s species richness index D	1.2 ±0.7	1.2 ±0.6	0.8 ±0.4	1.3 ±0.8	1.2 ±0.5	0.9 ±0.5	1.9 ±1.0	0.8 ±0.4	1.1 ±0.4	1.3 ±0.8	1.1 ±0.5	0.9 ±0.7	1.0 ±0.5	1.0 ±0.5
Pielous’ evenness index J'	0.6 ±0.2	0.9 ±0.1	0.6 ±0.2	0.7 ±0.2	0.7 ±0.1	0.6 ±0.2	0.8 ±0.2	0.3 ±0.1	0.7 ±0.2	0.8 ±0.2	0.9 ±0.1	0.9 ±0.1	0.8 ±0.2	0.9 ±0.1
Shannon Weiner Index H'	0.8 ±0.5	0.6 ±05	0.8 ±0.5	1.0 ±0.5	1.0 ±0.4	0.7 ±0.4	1.1 ±0.7	0.4 ±0.3	0.7 ±0.4	0.9 ±0.6	0.6 ±0.3	0.6 ±0.5	0.7 ±0.4	0.6 ±0.3

Table 3.4: Variation of Margalef’s species richness index (D), Pielous’ evenness index (J') and Shannon Weiner Index (H') of crustaceans in the fourteen sampling sites

Diversity measure	**Site**													
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Species richness Margalef (D)	1.4 ±0.3	0.8 ±0.5	0.7 ±0.5	0.8 ±0.5	0.9 ±0.4	0.8 ±0.4	0.6 ±0.4	0.9 ±0.2	0.9 ±0.4	0.9 ±0.1	1.2 ±0.5	0.7 ±0.3	0.9 ±0.3	0.5 ±0.3
Pielou's evenness (J')	1 ±0.04	0.7 ±0.2	0.8 ±0.02	0.8 ±0.3	0.7 ±0.1	0.7 ±0.2	0.7 ±0.2	0.8 ±0.3	0.6 ±0.1	0.7 ±0.02	0.9 ±0.2	0.7 ±0.2	0.7 ±0.2	0.4 ±0.2
Shannon Weiner (H')	1 ±0.2	0.8 ±0.4	0.7 ±0.4	0.7 ±0.4	0.7 ±0.2	0.8 ±0.3	0.5 ±0.3	0.7 ±0.3	0.7 ±0.2	0.8 ±0.2	0.8 ±0.4	0.6 ±0.1	0.6 ±0.2	0.3 ±0.2

3.3.2 Fish and site

The clustering of 12 of the most abundant fish was visualised through non – metric multidimensional ordination plot of Bray Curtis similarity based on the square root transformed abundance data (pooled data for all sampling dates). Sites were displayed to be in two overlapping clusters, where cluster A had sites mostly of low numbers (3, 4, 5, 6 and 9) while most of the sites in cluster B had higher number (7, 8, 10, 11, 12, 13, 14) at 45% similarity (Figure 3.5). Thus, sites that were close together tended to cluster near each other.

A one way ANOSIM showed significant differences but a weak separation of sites R=0.16 and p=0.001. A pairwise one way ANOSIM comparison test showed that most sites were not significantly different from each other. However, significant differences were found between site 9 and several sites like 2, 13 and 14. Site 11 was significantly different from site 4 and 6, site 12 was significantly different from 2 and 3, site 13 was different from 2 and 6, site 14

was different from site 6 and site 2 was different from site 6 and 7. SIMPER analysis showed that *Y. hyalosoma* and *A. japonicum* contributed to the differences between most of the sites.

Figure 3.5: Ordination plot of nonmetric multi-dimensional scaling (nMDS) output based on Bray–Curtis similarities in sites for square root transformed abundance data (pooled data for all the eight sampling dates) of the most abundant fish species at 35% similarity. S stands for site.

3.3.3 Crustaceans and site

A non – metric multidimensional ordination plot based on Bray Curtis similarity of the fourth root transformed abundance data (pooled data for all sampling dates) showed separation of sites into two distinct groups. Cluster A had sites 3 and 7 while cluster B had the rest of the sites (Figure 3.6) (refer to Figure 3.1). Further analysis using one way ANOSIM showed significant differences but weak separation between crustacean abundance (pooled data for all sampling dates) and sites R=0.29 and p=0.016. SIMPER analysis showed that the species that contributed to the similarity in most of the sites were *P. indicus* and *P. semisulcatus*

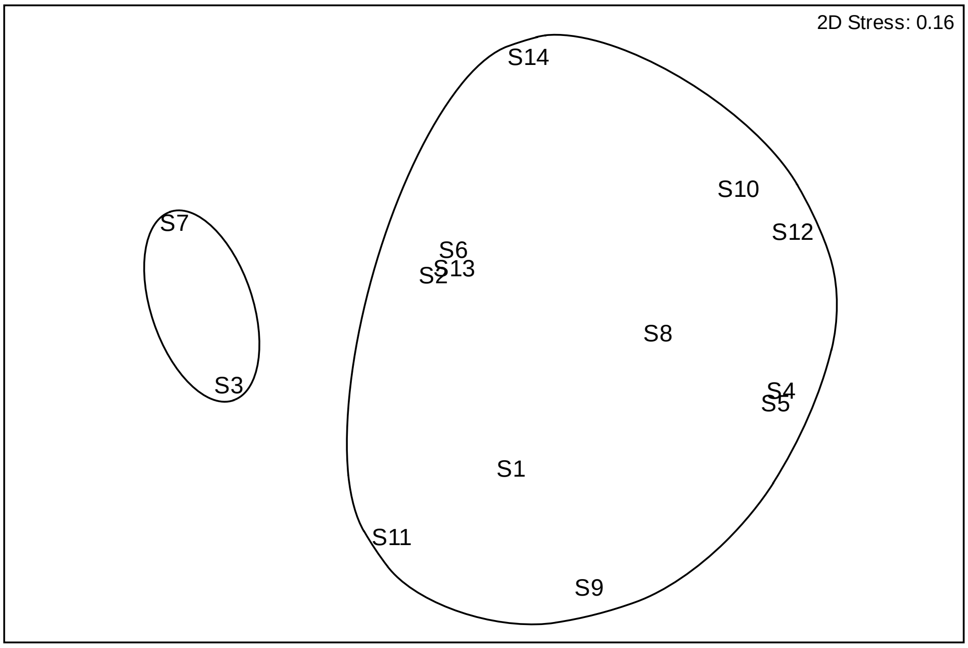


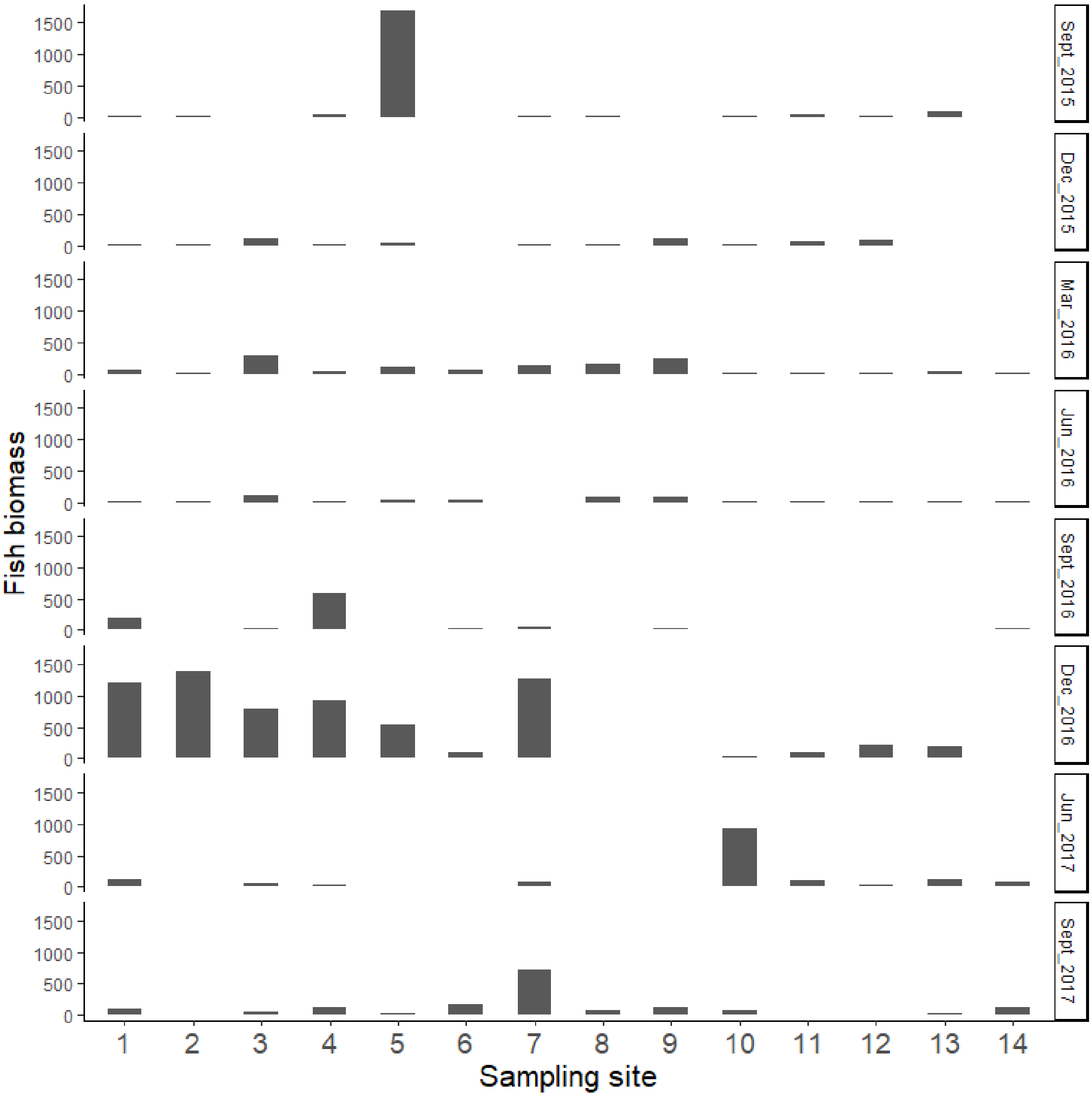
Figure 3.6: Ordination plot of nonmetric multi-dimensional scaling (nMDS) output based on Bray–Curtis similarities in sites for fourth root transformed total abundance data (pooled data for all sampling dates) of the most abundant crustaceans with similarity 70%. S stands for site

3.3.4 Fish

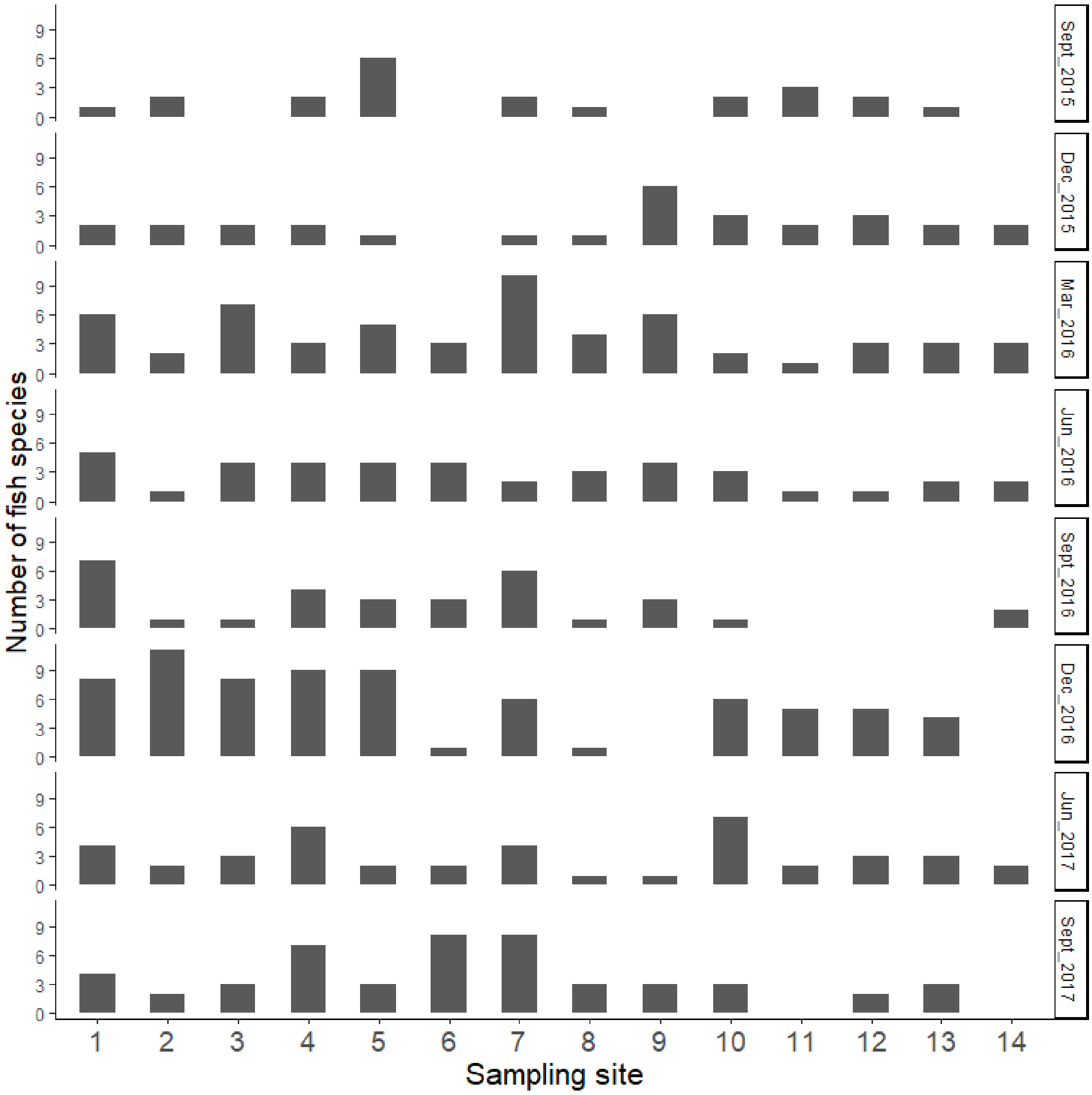
The trend of fish biomas and number of fish species and fish abundance is shown in Figure 3.7a, b and c. High numbers fish variables were mostly recorded in the first seven sites with the low numbers in the last 7.

A very strong positive correlation was revealed between mean fish biomass and cumulative fish species (R=0.93, df=$_{(1,12)}$, p<0.001; Figure 3.8). A correlation analysis between (log) mean fish abundance and total number of species using a Pearson product-moment correlation coefficient revealed a moderate positive and significant correlation (R=0.535, df=$_{(1,12)}$, p=0.049; Figure 3.9). A Pearson correlation was also performed on (log) mean fish abundance and mean fish biomass.

a)


Fish biomass
1500
1000
500
0
Sept_2015
Dec_2015
Mar_2016
Jun_2016
Sept_2016
Dec_2016
Jun_2017
Sept_2017
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Sampling site

b)


Number of fish species
Sampling site
0
3
6
9
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Sept_2015
Dec_2015
Mar_2016
Jun_2016
Sept_2016
Dec_2016
Jun_2017
Sept_2017

c)

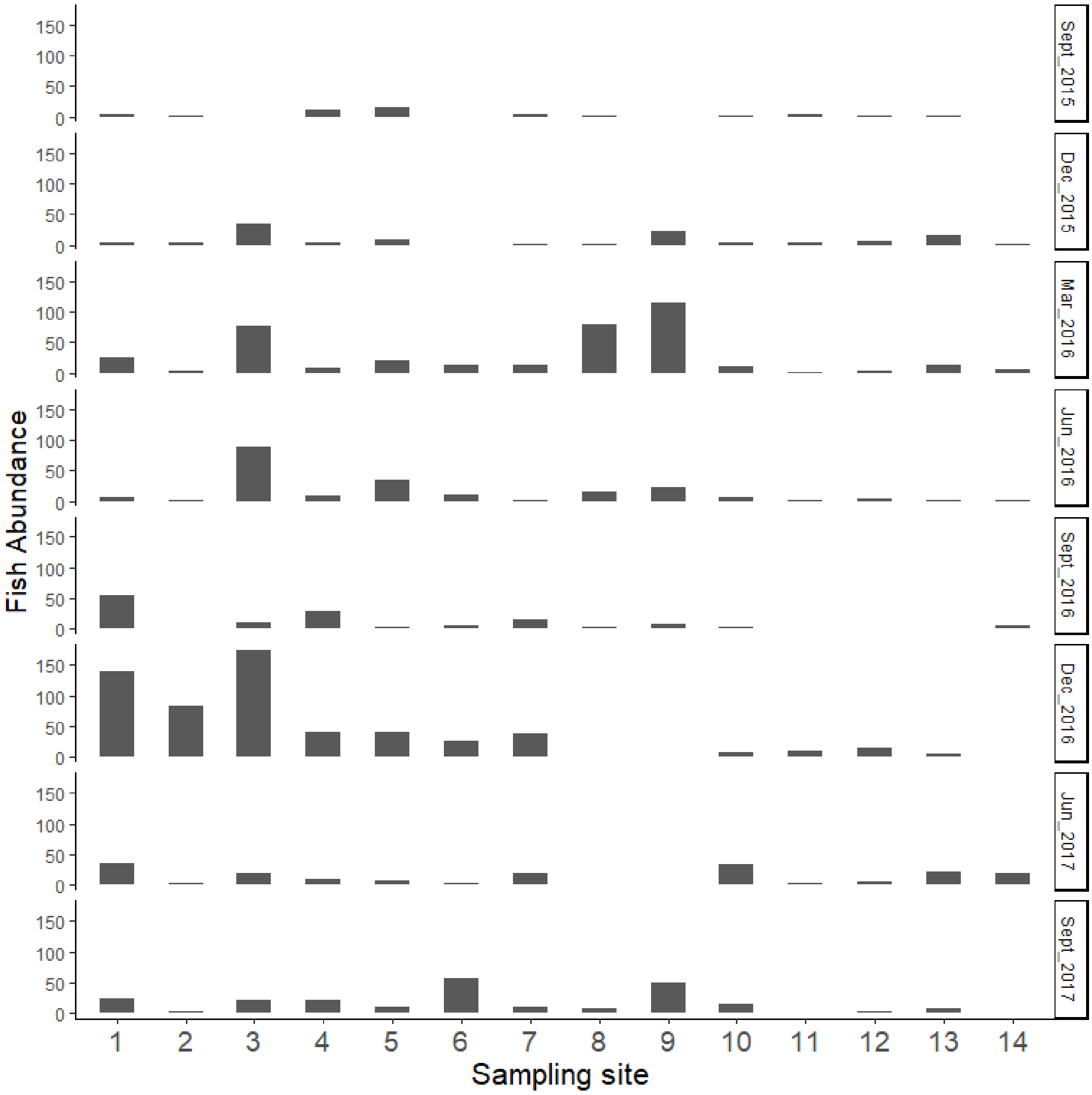


Figure 3.7: Trends of a) Fish biomass, b) Numbers of fish species c) Fish abundance in during the 8 sampling dates.

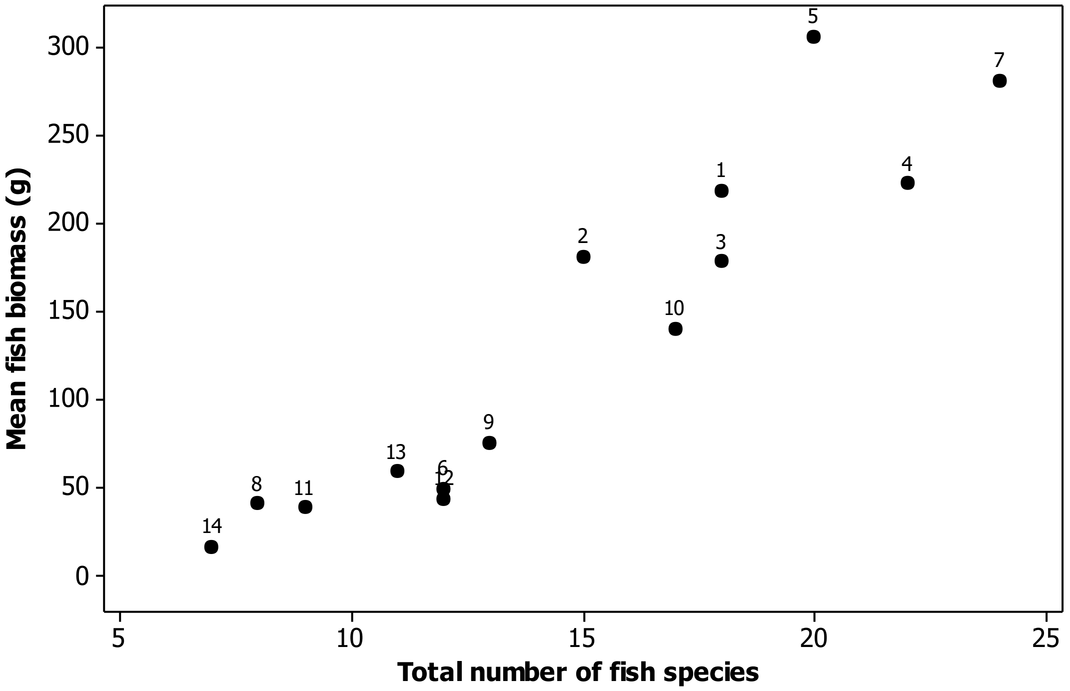


Figure 3.8: Scatter plot of mean fish biomass versus total number of fish species per site

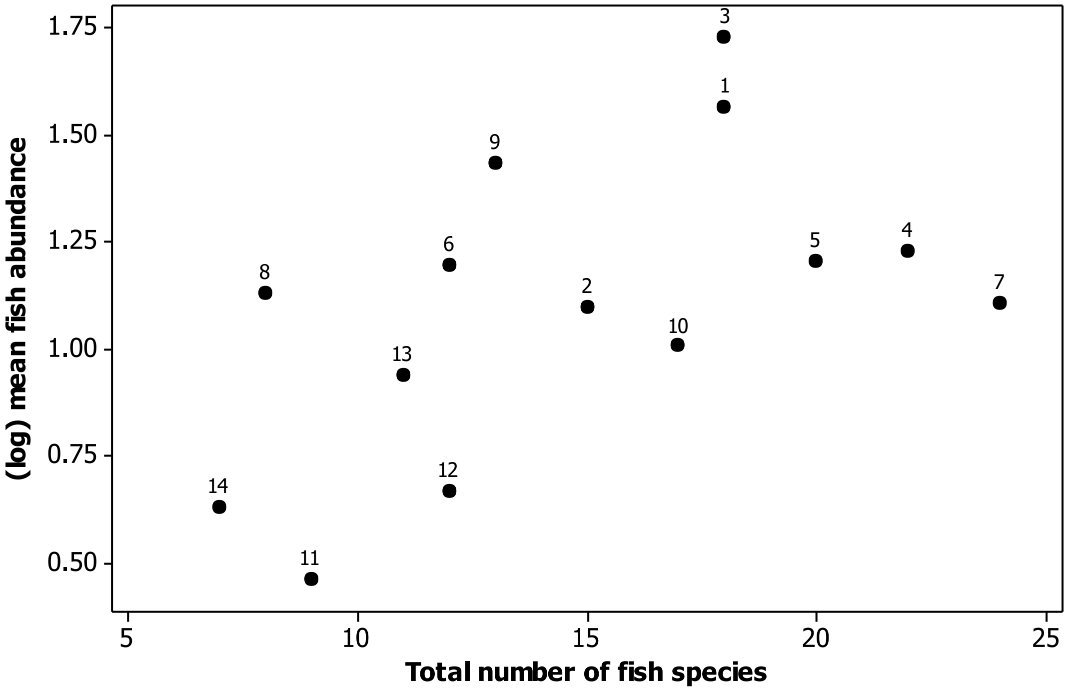
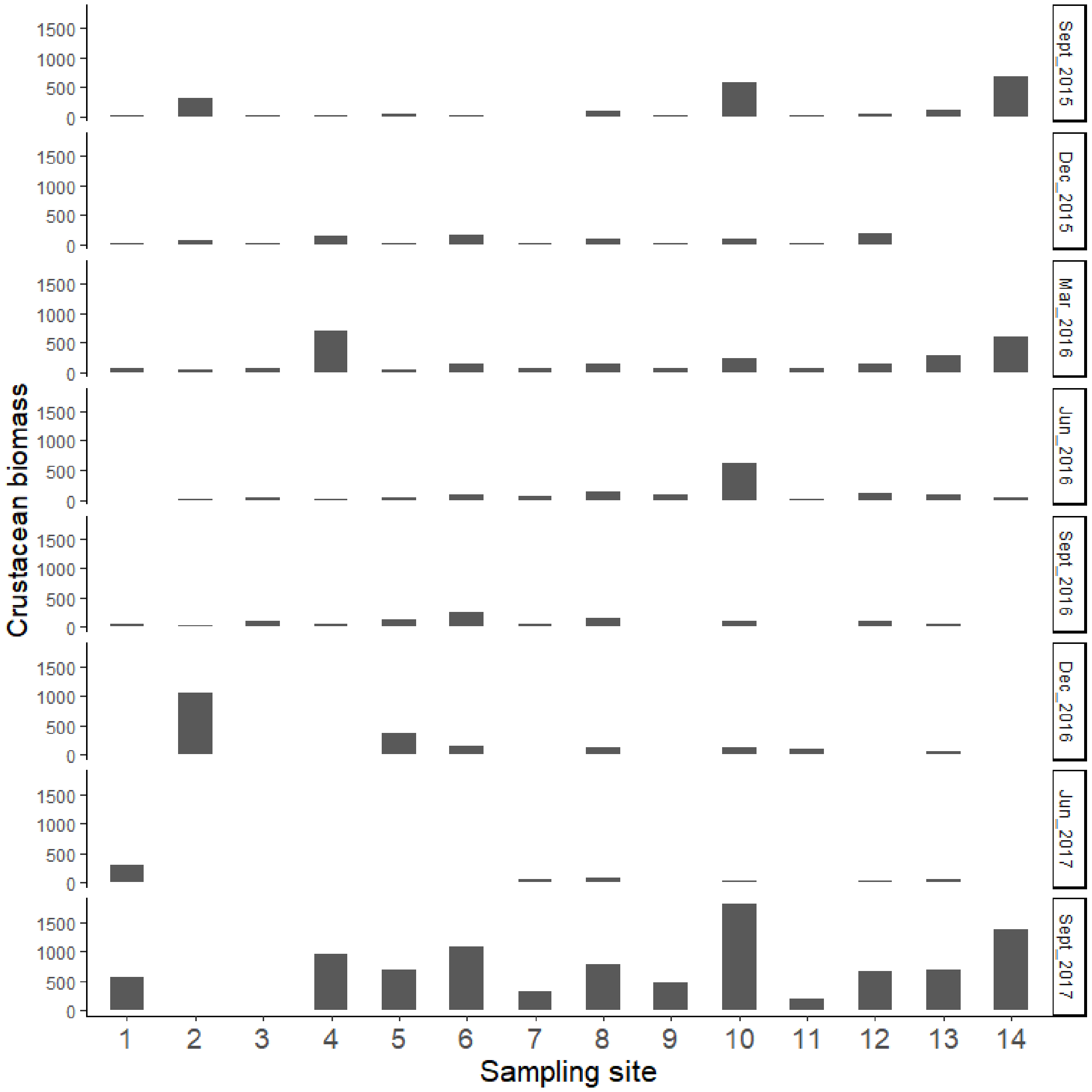


Figure 3.9: Scatter plot of (log) mean fish abundance versus total number of fish species per site

3.3.5 Crustaceans

Trends in crustacean biomass and abundance over the 8 sampling dates is shown in Figure 3.10a and b. High numbers of crustacean biomass and abundance mostly occurred in the last sites (8 -14). A Pearson product-moment correlation coefficient revealed a strong, positive and significant relationship between (log) mean crustacean abundance and log crustacean biomass (R=0.726, df= $_{(1,12)}$, p=0.003) (Figure 3.11). Sites 14, 10, 12, 6 and 5 had higher mean crustacean abundance and high mean crustacean biomass while sites 11, 3, 1 and 9 had low mean crustacean abundance and mean crustacean biomass. Site 14, 7 and 1 had high fish diversity and mean fish biomass but this was not true for crustaceans. Sites 5 and 10 had high diversity and high mean abundance for fish and also high mean abundance and mean biomass for crustaceans.

a)


Crustacean biomass
1500
1000
500
0
Sept_2015
Dec_2015
Mar_2016
Jun_2016
Sept_2016
Dec_2016
Jun_2017
Sept_2017
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Sampling site

b)

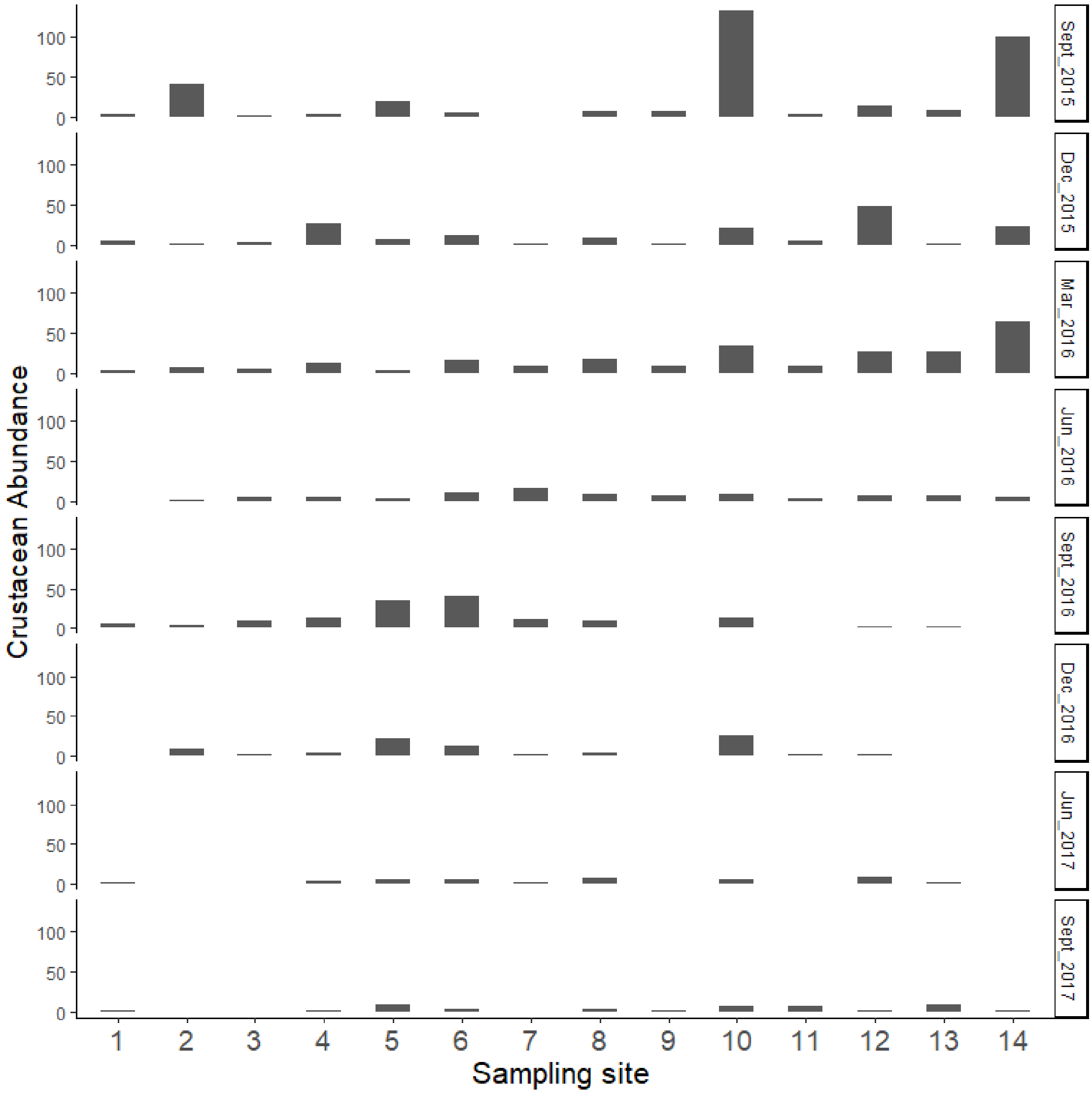


Figure 3.10: Trends of a) crustacean biomass, b) crustacean abundance in during the 8 sampling dates.

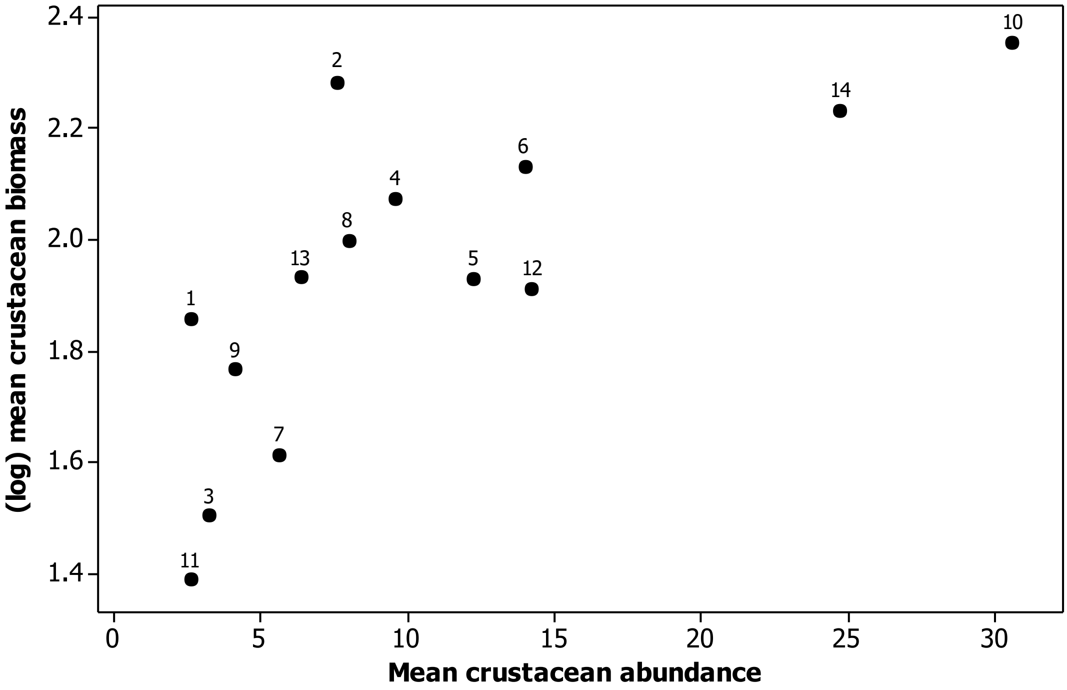


Figure 3.11: Scatter plot of (log) mean crustacean biomass versus mean crustacean abundance

3.3.6 Mangrove habitat and fish variables

The correlation matrix developed to explore relationships between broadscale mangrove forest variables (mean height, basal area, stem density, no of tree species and complexity index) and fish and crustacean variables is shown on Table 3.5.

The output of this matrix showed that some fish and crustacean variables were correlated with the C.I of broadscale forest variables. Simple linear regressions were then developed between the C.I, mean tree height and basal area of broadscale forest variables and fish and fish and crustacean variables identified from the correlation matrix. Important results of simple linear regressions of fish and crustacean variables with C.I. are presented in Table 3.6. Other regression outputs are in Appendix 3.1.

Table 3.5: Correlation matrix between broadscale forest variables and fish and crustacean variables. Signifcant correlations are in bold.

Response	**mnhtR2**	**basalarea**	**no.ofspp**	**stemden**	**C.I**
Mean fish biomass	**0.527**	0.201	0.189	-0.349	0.152
Mean fish abundance	0.312	**-0.536**	-0.05	-0.372	**-0.567**
Mean crustacean abundance	-0.109	0.501	0.404	0.062	**0.668**
Mean crustacean biomass	0.127	0.232	0.425	-0.062	0.367
Cumultive fish species	0.48	0.095	0.159	-0.107	0.133
Yarica hyalosoma abundance	0.096	-0.462	0.116	-0.294	-0.367
Acropoma japonicum abundance	**0.541**	-0.346	-0.154	-0.115	-0.452
Gerres oyena abundance	-0.38	0.034	0.138	-0.431	0.23
Gerrres filamentosus abundance	0.395	-0.149	0.132	0.438	-0.281
Penaeus semisulscatus abundance	-0.287	0.396	0.353	-0.369	**0.637**
Penaeus indicus abundance	0.381	0.224	0.272	0.182	0.1
Penaeus monodon abundance	-0.519	0.441	0.3	-0.31	**0.645**
Reef fish species abundance	-0.258	-0.088	0.06	0.47	0.208

*abundance = pooled data for all sampling dates

A simple regression between mean fish abundance and C.I. showed a negative relationship that was nearing significance (after Bonferroni correction) (R^2=0.32, $F_{(1,12)}$=5.71, p=0.034; Figure 3.11). The regression equation was: mean fish abundance=28.49 - 19.47C.I. (Table 3.6).

Table 3.6: Simple linear regression output for fish and crustacean variables with C.I. of broadscale forest variables.

Response variable	**F**	**R^2 (%)**	**P**	**Bonferroni correction (P<0.01)**
Mean fish abundance	5.71	32.22	0.034	NS
Mean crustacean abundance	9.66	44.60	0.009	S
Penaeus monodon abundance	8.51	41.50	0.013	S
Penaeus semisulcatus abundance	8.21	40.63	0.014	S

*NS= not significant, S=significant

There were no significant relationships between other fish and crustacean variables such as mean fish biomass, cumulative fish species, abundances of *Y. hyalosoma*, *A. japonicum*, *G. oyena*, reef fish species, mean crustacean biomass and *P.indicus* with C.I. of broadscale forest variables.

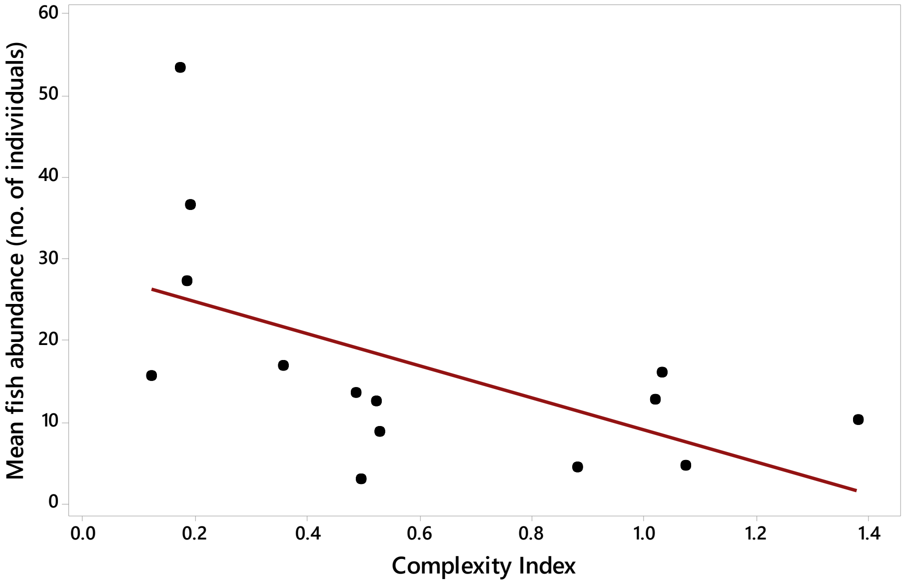


Figure 3.12: Scatter plot for mean fish abundance versus Complexity Index (C.I.)

3.3.7 Forest habitat versus crustacean variables

There were no significant relationships between crustacean variables (mean abundance and mean biomass) and fine scale forest variables. From the correlation matrix there were correlations between mean crustacean abundance, the abundance (pooled data for all sampling dates) of *P.semisulcatus* and the abundance of *P.monodon* (pooled data for all sampling dates) and the C.I. of broad scale forest variables. A simple linear regression between mean crustacean abundance and C.I. was computed and a significant relationship (R^2=0.44, $F_{(1,12)}$=9.66, p=0.009; Figure 3.12) was revealed (Table 3.6). The regression equation was: mean crustacean abundance =2.08 +13.83C.I. The null hypothesis was thus rejected. There was a moderate linear positive relationship between *P. monodon* total abundance and complexity index (R^2=0.41, $F_{(1,12)}$=8.51, p=0.013; Figure 3.13), with a regression equation of: *P. monodon* abundance =1.27 + 6.08C.I. The null hypothesis was rejected for this relationship. A positive linear relationship was recorded between the total abundance (pooled number of individuals from the 8 sampling campaigns) of *P. semisulcatus* and complexity index (R^2=0.40, $F_{(1,12)}$=8.21, p=0.014; Figure 3.14), and the regression equation was *P. semisulcatus*=-18.6 + 96.0C.I. (Table 3.6). The null hypothesis was rejected for this relationship. There was no relationship between C.I of broadscale forest variables and other crustacean variables i.e. mean crustacean biomass, *Penaeus indicus*.

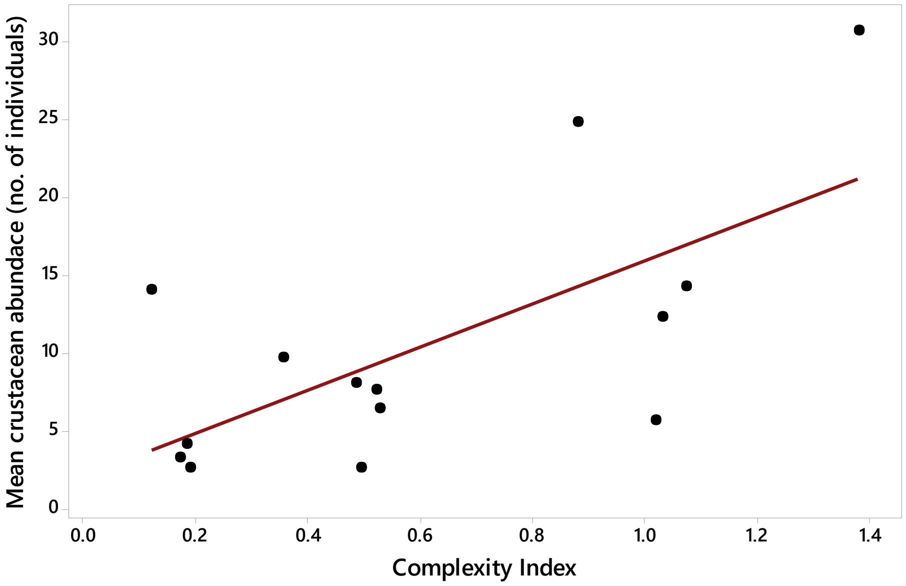


Figure 3.13: Regression analysis for mean crustacean abundance (pooled data for all sampling dates) versus complexity index (C.I.)

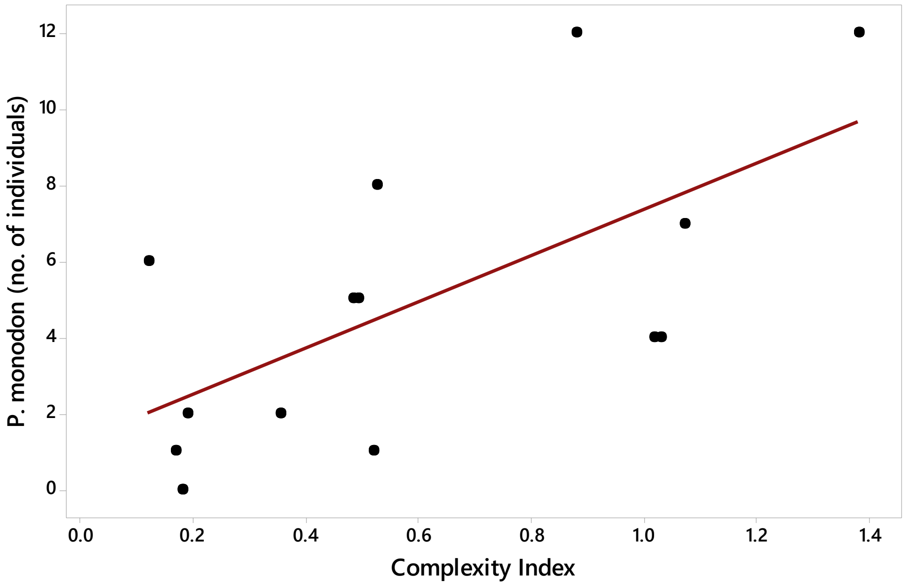


Figure 3.14: Scatter plot of *Penaeus monodon* abundance (pooled data for all sampling dates) and complexity index (C.I.)

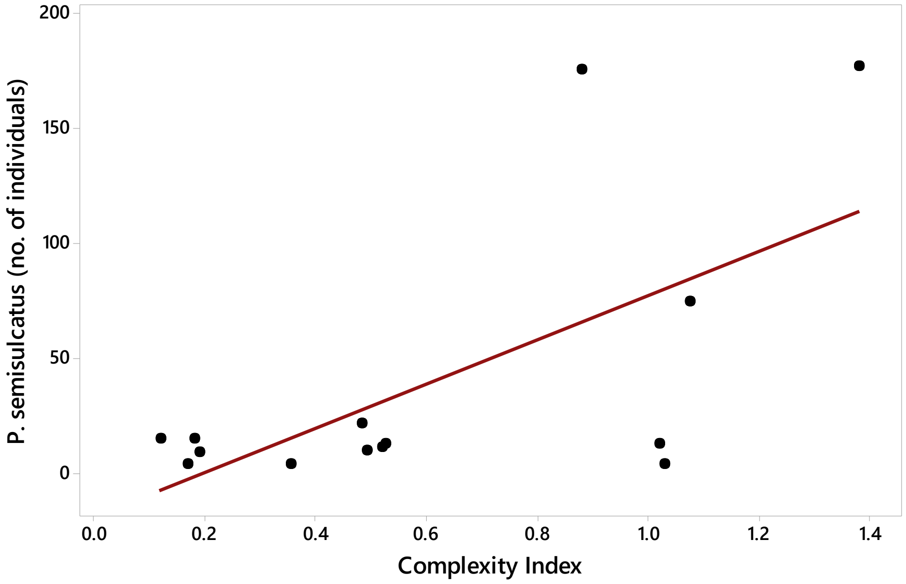


Figure 3.15: Scatter plot of *Penaeus semisulcatus* abundance (pooled data for all sampling dates) versus complexity index (C.I.)

3.3.8 Multiple linear regressions

Most of the models for fish and crustacean variables identified as having low AIC figures had a single predictor variable and could not be further improved. However, for *P.monodon* the model with lowest AIC had both mean tree height and C.I. as the predictor variables. A multiple linear regression analysis found a significant relationship between mean tree height and C.I. of broadscale forest variables and *P.monodon* (R^2=0.62, $F_{(2,13)}$ =9.66, p=0.004) with a regression equation of *P.monodon* = 7.01 + 5.66 C.I - 1.12 mean tree height. The VIF for both response variables was 1.1.

3.3.9 Effect of environmental variables on fish variables and crustacean variables

Environmental variables (temperature, salinity and dissolved oxygen) for September 2016, December 2016 and June 2017, together with overall broadscale forest variables (mean tree height, basal area, stem density, no. of tree species and C.I) were used to develop multiple linear regression models with fish and crustacean variables sampled on those particular months (abundance, biomass and number of fish species). Using the AIC, some models with low AIC were identified where multiple linear regressions were attempted. In September 2016, square root transformed fish abundance data was related to C.I, basal area and water temperature (R^2=0.55, $F_{(3,10)}$=4.05, p=0.040). Mean tree height, salinity and dissolved oxygen explained 53% of the variability of square root transformed crustacean abundance data ($F_{(3,10)}$=3.78, p=0.048). Further in June 2017, stem density, temperature and salinity were significantly related to square root transformed crustacean abundance data (R^2=0.73, $F_{(3,10)}$=8.96, p=0.003; Table 3.13). Further models with other fish and crustacean variables and predictor variables were not possible.

Table 3.7: Multipe linear regression models for response variables: sqrt transformed fish abundance data and square root transformed crustacean abundance and broadscale forest predictor variables (C.I, basal area, mean tree height, stem density) and environmental variables (temperature, salinity and dissolved oxygen). The coefficients for the independent variables indicate whether the relationship is positive or negative.

Response variable	**Predictor variable (Distance)**	**Coefficients**	**Df**	**Model F ratio**	**Model R^2**	**P**	**Bonferroni correction (p<0.006)**	**VIF**
Sqrt fish abundance	Sept 2016		3,10	4.05	0.55	0.040	NS	
	C.I.	5.59						4.17
	basal area	-2.61						4.10
	temperature	1.66						1.13
Sqrt crustacean abundance	Dec. 2016		3,10	3.78	0.53	0.048	NS	
	mean tree height	0.96						1.96
	salinity	2.30						1.86
	dissolved oxygen	-0.94						1.38
Sqrt crustacean abundance	June 2017		3,10	8.96	0.73	0.003	S	
	stem density	0.0005						1.43
	temperature	-1.74						1.41
	salinity	-0.18						1.56

*NS= not significant, S=significant

3.4 Discussion

3.4.1 Habitat complexity

Past studies on mangrove ecosystems have found a range of relationships between various forest attributes e.g. roots, area, and type of forest on one hand and fish and crustacean community structure on the other (Martosubroto & Naamin, 1977; Pauly & Ingles, 1986; Manson et al., 2005; Lugendo et al., 2006; Nagelkerken & Faunce, 2008). Further, structurally complex estuarine habitats are known to support higher faunal abundances and diversity (Attrill et al., 2000; Willis & Anderson, 2003; Gratwicke & Speight, 2005; Lefcheck et al., 2019). Positive correlations have been drawn between faunal community structure and species diversity with various indices of complexity (Willis & Anderson, 2003; Gratwicke & Speight, 2005; Schneider & Winemiller, 2008).

Quantifying the complexity of habitats is however complicated and there is no standard method that has been developed for similar habitats let alone different habitats (Kovalenko et al., 2012). Scholars thus tend to develop different indices for measuring habitat complexity in relation to the faunal species of interest (Gratwicke & Speight, 2005) and habitats such as freshwater systems, seagrass, mangroves, coral reefs and other littoral habitats (Amarasinghe & Balasubramaniam, 1992; Attrill et al., 2000; Willis & Anderson, 2003; Gratwicke & Speight, 2005).

The aim of the current work was to relate mangrove forest attributes (stem density, basal area, number of tree species, mean tree height and C.I.) and the fish and crustacean community structure therein. The C.I. was used to infer quality of the mangrove sites. The broad scale forest attributes in this study had a C.I. range of 0.12 to 1.38 while the fine scale attributes had a C.I. range of 0.7 to 6.4. The C.I.s in this study were within the range of C.I.s reported from mangroves in Kenya but were generally low especially for the broad scale forest attributes. For instance, Bosire et al. (2003) recorded a C.I. of between 12.5 to 35.6 in a natural stand and 0.3 – 2.4 in reforested stands in Gazi Bay Kenya, while another study in Gazi bay, indicated complexity indices ranging between 1.86 to 16.84 and 1.12 to 4.64 in Makongeni and Kinondo respectively (Obade et al., 2004). In Mida creek North coast, mangrove stands were found to have a C.I. range of 0.12 to 6.55 (Kairo et al., 2002). High C.I. values indicate structurally more developed (and often older) mangrove stands (Pool & Lugo, 1977, Amarasinghe & Balasubramaniam, 1992) while a low C.I. in the mangrove forests is an indication of diminishing complexity. In Mida creek and Gazi, the low C.I.s were attributed to high anthropogenic pressure on the forests (Kairo et al., 2002; Obade et al., 2004). The mangroves of Vanga are easily accessible and are a source of livelihood for the local people for the provision of timber and fuel. This could have led to diminished forest complexity and hence quality. In this study, basal area was highly correlated with the C.I. for both broad scale and fine scale forest characteristics. Higher basal area (along with height), which contributes to higher C.I. values, is typically associated with older, larger, less dense stands of forest.

3.4.2 Consistency of sites as habitats for fish and crustaceans

Some sites supported higher diversity and biomass for fish while others supported higher abundance and biomass for crustaceans over the sampling period. Given the large literature showing high variability in catches, differences among sites was to be expected. However such variability could, in principle, reflect random statistical noise. Thus, establishing that some areas registered high number of species and biomass while others had low number of species and biomass over the sampling periods provides important new information. Further, some of the sites that were favoured by fish were not preferred by crustaceans and vice versa. For instance, site 14 which had low biomass and a low number of species for fish was among the sites that had high mean crustacean abundance and mean biomass. This trend was further exhibited when the regression analysis showed fish abundance to be negatively related to complexity index whereas crustacean variables had a positive relationship with C.I. The sites that supported high fish diversirty and biomass were mostly between Vanga and Kiwegu villages whereas most sites near the Majoreni village had low fish diversity and biomass (Figure 3.1). Although there are no clear explanations for kind of the separation of sites, it was speculated that the non discriminative beach seine fishing activities within the seascape around Majoreni, where fish diversity and biomass was lowest, could be affecting the fauna abundances in the mangroves (*Pers. observation*). In this study, fish preferred different sites to crustaceans and this could be due to various factors. A study in the Philippines observed a similar trend whereby the highest densities of shrimp were found in a replanted *Rhizophora apiculata* forest (the most structurally developed) whereas the highest fish densities were realised in the less structurally comple *Avicennia* spp.(Rönnbäck et al., 1999). The conditions that favour fish could be different, and in some cases almost opposite to, those that favour crustaceans. In comparison, sites 1, 2, 3, 4, 5, 7 and 10 had high fish biomass and species diversity for fish while sites 14, 13, 12, 11, 8, 9 and 6 had low fish biomass and less species (Figure 3.7).

Indices of diversity are influenced by the number of species in a site but also of importance is the distribution of the species. In Vanga, the highest Shannon diversity H' (1.1±0.7) and Pielous' evenness index J' (0.9±0.1) were found in site 7 and 11 respectively. However, the lowest values of both indices were found in corresponding sites (site 8). Overall H' and J' values in this study were within the findings of similar studies (Shervette et al., 2007; Wainaina et al., 2013).

3.4.3 Mangrove variables and fish habitat

The (log) mean fish abundance was negatively related to both the C.I. and the basal area which explained 32.2% and 28.07% of the relationship respectively (although note that because the C.I. is a derived index which includes basal area these are not independent findings). The negative relationship (Figure 3.9) between (log) mean fish abundance and C.I. does not seem to support the evidence showing that complex structures attract fish as they provide habitat and refuge from predators therefore improving their survival (Primavera, 1997; Macia et al., 2003). For example positive relationships have been recorded in the British Virgin Islands whereby structure in several littoral habitats was responsible for 22% of the differences in nekton abundance in those habitats (Gratwicke & Speight, 2005). Likewise, fish assemblages in the rocky reefs in New Zealand were positively related to the substratum complexity (Willis & Anderson, 2003). In Indonesia, out of several variables used to measure habitat complexity in 10 mangroves forests, the *Rhizophora* species prop root density within a 1km radius was the most strongly correlated variable with mangrove fish diversity (Green et al., 2012). More generally, a review of the nursery literature shows that structurally complex habitats, such as seagrass beds and mangroves, tend to support higher densities of fish than structurally simple ones such as mudflats. This is because they are considered to offer refuge and food to fauna (especially juveniles) compared to unstructured habitats (Lefcheck et al., 2019). However some other studies have, like in this study, found negative relationships between complex structures and fish. As well, Huxham et al. (2004) found less complex structures in mangrove forests (non - vegetated) to attract more fish compared to the complex ones (vegetated ones) in Gazi. One explanation for the apparent contradiction between the findings of the current study and the literature showing enhanced fish abundance in more complex habitats is that complexity is measured at different scales and with different methods in different studies. Here, C.I. gives a broad scale indication of forest quality. C.I. increases as forests become older, have more species and have larger trees. Such a measure does not capture structural complexity at smaller scales, such as pneumatophore density.

The positive relationship between (log) mean fish biomass and mean tree height (Figure 3.9) has no direct explanation. However, Suwa et al. (2009) suggested the likelihood of a relationship between decreased tree height of *Bruguiera gymnorrhiza* and *Kandelia obovata* and stressors like nitrogen deficiency in soils and high salinity. Thus, high mean tree height could mean less stressor to the trees as well as the fish.

3.4.4 Mangrove variables and crustacean habitat

The crustacean abundance was positively related to the C.I., which was responsible for 44.6% of the variation. The species *P. semisulcatus* and *P. monodon* were also positively related to the C.I. with 40.6% and 41.5% respectively of their variation being explained by the C.I. These results resonate with previous studies where shrimp abundance was strongly associated with high structural complexities (pneumatophores) in mangrove areas (Primavera, 1997; Rönnbäck et al., 1999; Macia et al., 2003). High structural complexity increases habitat quality and provides shelter from predation (Rönnbäck et al., 1999). In simulated laboratory studies, the effect of increased structural complexity (pneumatophores) in reducing predation of *Metapenaeus monoceros* by the predator *Terrapon jarbua* exceeded the effect of turbidity (Macia et al., 2003). In another laboratory experiment, there were lower predation rates for *P. monodon* due to structure but not for *P. merguiensis*. This is because the juveniles of the latter tended not to seek for refuge while escaping from predators (Primavera, 1997). In the Philippines, the high structural complexity of a 5 year old replanted *Rhizophora* mangroves attracted more shrimp than other habitats of less structural complexity (Rönnbäck et al., 1999). Normally, juveniles of *P. semisulcatus* are mostly found in seagrass habitats (Robertson & Duke, 1987; Macia, 2004), but they have also been found to be strongly associated with forested sites such as in Gazi (Crona & Ronnback, 2005). In this study, the reason for the abundance of these species in the mangroves could be due to the adjacent seagrass beds in most of the sites (*Per. observation*). *P. monodon* are shelter seeking and they are mostly found in mangrove forest. In aquaculture, they thrive better in ponds that have structure which they use as shelter from predators (Primavera, 1997; Primavera & Lebata, 2009). They normally shelter in mangrove estuaries and are of great economic value in many countries including Kenya (Mohan et al., 1997). Some shrimp species e.g *Marsupenaeus japonicus* have been found to prefer bare sites to vegetated sites and this could be due to their good camouflage in sandy flats and their habit of burying themselves in the sand (Macia, 2004, Crona & Ronnback, 2005). Apart from structure, other factors such as predators and prey behaviour could also be responsible for provision of refuge for fauna (Primavera, 1997).

3.4.5 Environmental variables (turbidity, dissolved oxygen and salinity)

In estuarine habitats, fauna tend to migrate according to the seasonal fluctuations in abiotic factors (Blaber & Blaber, 1980, Barletta et al., 2003; Macia, 2004; Barletta et al., 2005, Rezagholinejad et al., 2016). In Inhaca Island Mozambique, salinity, temperature and water depth were found to influence (negatively or positively) the abundance and densities of various penaeid shrimp species (Macia, 2004). The effect of abiotic factors can also be species specific as in Marudu bay Malaysia where Rezagholinejad et al. (2016) found that 52% of the larval abundance of the Mugilidae family was determined by abiotic factors. Mangrove habitats tend to be influenced by environmental variables such as salinity and turbidity due to rain water or freshwater influx from the surrounding terrain especially during the rainy season. In Chwaka bay Tanzania, Lugendo et al. (2007) found that visibility, dissolved oxygen and temperature influenced fish density in both mangrove and sand/mud flat areas during the rainy season as opposed to habitats such as seagrass beds that were more buffered from these changes. In this study, two rivers (Umba and Mwena) drained near some of the sites that were fished. In Vanga, River Umba, which originates from the Usambara mountains in Tanzania brings in a lot of sediment load into the system during the rainy season. It was thus expected that this would influence fish and crustacean community structure in nearby sites as opposed to sites away from this influence. The multiple linear regression results from this study indicated that only crustacean abundance was affected by water temperature, dissolved oxygen and salinity ($p<0.05$). Basal area, C.I. and temperature explained 55% of the variation in square root transformed fish abundance data, although after Bonferroni correction, this was not signifiicant. This means that environmental factors accounted for the some of the variance in fish and crustacean abundance.

3.5 Conclusion

Multiple, repeated sampling at different sites within a mangrove forest showed that there were large differences in fish and crustacean communities among sites and that these differences were consistent, with some sites being much better than others for fish and crustacean catches. Surprisingly, these differences were not shared between fish and crustaceans; there was a broad negative correlation between fish and crustacean abundance and species richness, suggesting that the factors that contribute to high habitat quality for fish, at the scales measured in the current work, are different from those for crustaceans. The Complexity Index is used as a composite indicator of forest quality in the mangrove literature and here its utility as a predictor for fish and crustacean habitat was explored. It showed moderately strong, significant correlations with fish and crustacean variables, suggesting that it does capture some of the environmental characteristics of importance to these organisms. However no simple picture – for example of ‘high forest quality’ supporting more fauna – emerges. Rather it is clear that determinants of quality for the two faunal groups (and indeed probably for individual species) are different at the scales at which this study operated. It is likely that understanding these determinants will require species-level research using a wide range of approaches. One implication of the current results for management is that the maintenance of the fisheries ecosystem service of a mangrove forest, that includes both fish and crustacean species, is unlikely to involve a simple selection and protection of ‘high quality’ areas of forest. Rather a range of different environmental settings and characteristics will be required to support a wide range of species.

The emergence sites that had high fish diversity and biomass versus sites that had low fish diversity and biomass in this study is a strong indication that there other factors apart from those explored in this study could be responsible for this kind of structuring. Further investigation is therefore recommended. For instance, it was speculated throughout this study that activities that took place in the seascape might have an influence on the faunal structure in mangrove forests.

4.0 CHAPTER 4: DIET ANALYSIS OF SIX JUVENILE FISH SPECIES IN THE VANGA MANGROVE ECOSYSTEM

Abstract

Mangroves, like other nearshore habitats, provide shelter and food for resident and visiting fauna. The most common food items in these habitats include detritus, macro algae, benthic microalgae, crustaceans, invertebrates among others. The importance of mangroves as feeding sites depends on regions, tidal regimes, proximity to other habitats, and geomorphology. In regions with high tidal range, mangroves are important feeding grounds during inundation. This study aimed to characterise food items used by the six most abundant fish species sampled in fourteen sites in Vanga. Sampling took place in June 2016, 2017 and September 2017 using fyke nets. A total of 193 stomachs were analysed using stomach content analysis method. The species were *Gerres oyena*, *Atherinomorus lacunosus*, *Leiognathus equulus*, *Acropoma japonicum*, *Yarica hyalosoma* and *Ambassis natalensis*. The hypotheses that there were no differences in food items ingested by the species and also between sites were tested. The study identified nine food categories and 36 prey items with crustaceans being the most important prey item. All the six fish species ingested insects at one sampling time or another. In June 2016, *Gerres oyena* mostly fed on Annelids and Insecta. The major diet for *Atherinomorous lacunosus* in September 2017 was Insecta while *Ambassis natalensis* mostly fed on Protozoa. A one way ANOSIM revealed no differences in the diets of fish in the three sampling months (Global R =0.006 and p=0.447). The diet preferences of the six species were not affected by site characteristics (sites with increasing species diversity and increasing fish biomass versus sites with low species diversity and low fish biomass). The diet breadth for the species was low meaning they fed on a narrow diet. The ingestion of insects, which are terrestrial, is a strong indicator that partial feeding took place in the mangroves supporting this hypothesis that fish use mangroves as feeding grounds.

4.1 Introduction

The life cycle of some offshore and reef fish species includes ontogenetic shifts from estuarine habitats such as seagrass beds and mangrove forests (Nagelkerken et al., 2000, Gajdzik et al., 2014). The larvae of these reef fishes migrate to estuarine nursery habitats where they seek food and escape from predators (Laegdsgaard & Johnson, 1995; Sheridan & Hays, 2003; Adams et al., 2006; Grol et al., 2014). The provision of these nursery services by in-shore habitats leads to increased biomass and survivorship for juveniles that later migrate offshore (Beck et al., 2001; De La Morinière et al., 2003).

Mangroves are very productive systems that provide food items through various trophic pathways for resident or visiting fauna (Laegdsgaard & Johnson, 2001). Mangrove litter enhances the forest productivity by increasing detritus and nutrients released through mineralisation of organic matter (Robertson & Daniel, 1989; Laegdsgaard & Johnson, 2001). The accumulated detritus in mangrove areas has been assumed to sustain the high numbers of detritivores, compared to other aquatic systems (Lin et al., 2007). For instance, fish species of the genus *Mugil* in the Sundarban mangrove system in India were found to depend solely on mangrove detritus for their survival (Ray & Straškraba, 2001). However, not all apparently detritivorous species depend on detritus only. The fish species *Planiliza macrolepis* in Taiwan mangrove estuaries, although found to consume over 50% detritus in volume, was found to actually feed on benthic microalgae most of the time as indicated by the stable carbon isotope method (Lin et al., 2007). Apart from detritus, other food items encountered in mangrove habitats and consumed by fauna, either directly or indirectly, include macro-algae, crustaceans, other invertebrates, benthic microalgae and microphytobenthos (Thayer et al., 1987; Sheaves & Molony, 2000; Lin et al., 2007; Bouillon et al., 2008).

One of the ways that mangroves are connected to adjacent estuarine habitats is through export of organic matter (Alongi, 1989, Bouillon et al., 2008). Tides are a key factor in the direct and indirect export of mangrove carbon to adjacent habitats (Day et al., 2012). Initially, outwelled mangrove carbon was postulated to contribute immensely to the diets of fauna in adjacent habitats (Odum & Heald, 1972). However, further research has shown that the impact of outwelled mangrove carbon on food webs of nearby habitats may not be as huge as previously thought. The mangrove carbon signal often diminishes rapidly with increasing distance from mangroves (Robertson et al., 1992; Hemminga et al., 1994; Bouillon et al., 2007; Claudino et al., 2015). Thus, the suggested direct importance of mangrove litter and hence carbon in the food webs of adjacent habitats has been downscaled (Nyunja et al., 2009; Bouillon et al., 2008; Claudino et al., 2015). Mangrove carbon is transferred to nearby habitats indirectly through movement of fauna that have fed directly or indirectly on organic matter from mangroves (Vance et al., 1996; Sheaves & Molony, 2000). In the Indo – Pacific region, Sheaves & Molony, (2000) demonstrated that food chains involving predators provide short carbon export chains. Carnivorous fishes that feed on sesarmid crabs, which ingest mangrove litter directly, export the mangrove carbon when they move offshore (Sheaves & Molony, 2000).

The importance of mangroves as feeding sites for fish varies between regions and geomorphological settings, with accessibility of sites largely dictated by the tidal regimes (Baker et al., 2015). For instance, in the Caribbean, where tidal ranges are small, only two out of 23 juveniles fish species, *Acanthurus chirurgus* and *Haemulon chrysargyreum*, found in mangrove and adjacent seagrass habitats fed substantially from mangroves, while the rest fed from the seagrass beds (Nagelkerken & Velde, 2004). In the Indo Pacific region, mangroves are considered important feeding areas for fishes during inundation (Nagelkerken & Velde, 2004; Lugendo et al., 2007). In the Western Atlantic region, transient fishes preferred seagrass beds as superior feeding grounds to adjacent mangroves, whereas mangroves were more important for resident fishes (Vaslet et al., 2012). Apart from regional differences, other factors such as the setting (mangrove creeks that retain water during ebb tide versus fringing mangroves that retain no water in ebb tides) , geomorphology and tidal ranges influence the importance of mangroves as fish feeding areas (Lugendo et al., 2007; Bouillon et al., 2008). Lugendo et al. (2007) investigated the importance of mangrove-lined habitats and fringing mangroves as feeding areas and found that the mangrove-lined habitats, which remained inundated throughout, were better feeding areas than the latter, which drained at ebb tides. In the mangrove-lined habitats the fishes were able stay longer and feed. Physical and biological factors in the habitats have also been found to affect dominant prey categories ingested by the same species (Nyunja et al., 2002).

Trophic relationships in estuarine areas have continued to draw scholarly attention in most regions of the world (Layman & Silliman, 2002; Corrêa & Uieda, 2007; Lin et al., 2007). In East Africa, the majority of the studies have taken place in Tanzania and Kenya. In Kenya, a number of studies have been carried out in Gazi Bay. Some focused on carbon export between mangroves and adjacent seagrass beds (Hemminga et al., 1994; Bouillon et al., 2008; Nyunja et al., 2009). They concluded that in terms of organic carbon exchange, mangroves and seagrass systems in Gazi were strongly linked (Hemminga et al., 1994; Bouillon et al., 2007). De Troch et al. (1995), used stomach content analysis to establish that the trophic guilds of 14 fish species in the estuarine environment in Gazi Bay were dominated by benthivores alongside planktivores and piscivores. It was recorded that in the interlinked mangrove and seagrass systems in Gazi Bay, seagrass was the main source of food for the fauna while mangroves offered shelter (Marguillier et al., 1997; Nyunja et al., 2009). Most of these studies used stable C and N Isotope analysis. Other studies on fish diets have been carried out in the north coast of Kenya including Mida and Mtwapa creeks (Nyunja et al., 2002; Mavuti et al., 2004; Gajdzik et al., 2014).

Stomach content analysis of animals is a standard procedure to establish their food and feeding habits; it gives an instantaneous impression of what the fish ate before it was caught, but it cannot be used to determine the exact source of food (Hyslop, 1980). Previous studies on diets of estuarine juvenile fishes in the mangroves of Kenya have analysed stomachs of very few species leaving the most common species unstudied. In fact, of the fish species whose stomachs were analysed in this study, only three species have been studied in the past i.e. *Gerres oyena*, *Atherinomorus lacunosus* and *Leiognathus equulus* (Nyunja et al., 2002; Mavuti et al., 2004). However, *Acropoma japonicum*, *Yarica hyalosoma* and *Ambassis natalensis* are being studied for the first time. Diet analysis studies based on stomach contents of fish caught in actual mangrove forests (as in this study) are also rare.

4.1.1 Overall aim,

To investigate the feeding habits of the six most abundant species of fish caught in this study: *Gerres oyena, Acropoma japonicum, Yarica hyalosoma, Leiognathus equulus, Atherinomorus lacunosus* and *Ambassis natalensis*.

4.1.2 Objectives

1. To characterise the food items of six species of juvenile fish in the Vanga mangrove ecosystem
2. To investigate the relationship between food intake and the sampling months

3. To investigate the relationship between food availability and the sites where fish were caught

4.2 Materials and methods

4.2.1 Study site

The study site is in Vanga in the south coast of Kenya at latitude 4° 39' 38.42"S and longitude 39° 13' 9.71"E (see details in chapter two). It is also 71km south Gazi bay. The climate of Vanga is influenced by monsoon winds leading to two main seasons i.e. South Eastern Monsoon (SEM) – May to October and North Eastern Monsoons (NEM) – November to March (McClanahan, 1988). The Vanga mangrove complex covers a total area of about 4000ha and six species of mangrove trees are found there: *Avicennia marina*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, *Rhizophora mucronata*, *Sonneratia alba and Xylocarpus granatum* (see details in chapter 2).

4.2.2 Methods

4.2.3 Fish sampling

Obtaining representative samples of fishes from mangrove habitats is difficult because of the structural restrictions on using fishing gears. Sampling sites were chosen to balance logistical tractability (allowing sampling of all the sites within single field campaigns of five days each, to avoid large temporal differences in sampling) and a wide and representative spread of forest variables, in particular in relation to the Complexity Index (C.I.). The complexity index combines all floral characteristics (stem density, diameter at breast height (dbh) calculated into basal area, mean tree height and number of tree species) to show how complex or structurally developed a forest stand is. Fyke nets were deployed, at the creek mouths that drain the mangrove forest sites, to trap fish left during ebb tide and collected after 24 hours. Sampling was done every three months during spring tides over five consecutive days. Fish samples were collected from fourteen different sampling sites in the Vanga mangrove ecosystem in June 2016, June 2017 and September 2017 (see chapter 2 for further details). The fish samples were preserved on ice in a cool box and later taken to the laboratory where sorting and identification to the lowest taxon possible was done using and Richmond, (2011) and Anam & Mostarda, (2012). The total length was measured (to the nearest 0.1cm) and weighed (to the nearest 1g). Fish species with a total of four individuals at any one sampling season were included in the stomach analysis study. The species that were included in the analysis were: *Gerres oyena*, *Acropoma japonicum*, *Yarica hyalosoma*, *Leiognathus equulus*, *Atherinomorus lacunosus* and *Ambassis natalensis*.

4.2.4 Determination of fish diet type and diet breadth

Diet type

The fish were dissected and the stomach carefully separated from the rest of the gut using a scalpel blade. The foregut was then preserved in 10% formalin – water solution to prevent further digestion. The stomachs were then taken to the laboratory and the formalin was removed under running fresh water and then dissected longitudinally and contents emptied in a graduated Petri dish. The different food items were identified to genera level and where possible to species level under a dissecting microscope. All food items were identified, counted and recorded. Identification remnant body parts such as heads, legs and claws guided by identification keys used to identify such body parts in stomach analysis. Using qualitative numerical and volumetric methods (Hyslop, 1980), the stomach contents were identified to the lowest possible taxon. The number of individuals of each prey item (N) was counted and expressed as a percentage of total items. The number of stomachs in which each food item occurred was recorded as the frequency of occurrence (FO). Volume (V) of the prey items was calculated using the Points method (Hynes, 1950) whereby the prey with the largest volume was assigned 16 points and the other prey items were assigned 8, 4, 2 and 0 points according to the volume they occupied. The Volume of the prey items was documented and expressed as percentages (Hyslop, 1980). The index of relative importance (IRI) (Pinkas et al., 1971) was calculated and then converted into a percentage as shown below:

$$\text{IRI} = (\%\text{N} + \%\text{V}) \times \%\ \text{FO}$$

$$\%\text{IRI} = (\text{IRI}_{\text{prey category}} / \text{IRI}_{\text{total}}) \times 100$$

Diet breadth

The diet breadth of pooled site data of each of the six species was computed using Levin's standardized index (Krebs, 1999).

$$B_i = 1/(n - 1)\ \{(1/\Sigma\ pij^2) - 1)\}$$

Where: B_i is the Levin's index, n is the number of prey categories for predator i, pij is the proportion of predator i's diet made up of prey category j. This number varies between 0 - 1 where zero means that the predator fed on only one prey type whereas a B_i of 1 means the predators ingest available items in equal proportions. A B_i of 0.6 – 1 is considered high and ≤0.4 is low (Novakowski et al., 2008). A trophic diagram was manually constructed to show the prey categories that the predators fed on based on the %IRI of the prey items. The thickness of the lines depicts the contribution of the prey to the %IRI of the predator.

4.2.5 Statistical analysis

The importance of prey items ingested by the six fish species was tested. A Cluster analysis, based on %IRI from pooled site data, was done using Bray Curtis similarity index of square root transformed %IRI of the six species in the three seasons. Group average was used for clustering. Differences between sampling months and also among species were assessed using Analysis of similarities (ANOSIM). The %IRI data were square root transformed in order to reduce the effect of dominant prey items

In order to explore whether there were differences in the prey items at the different sites, a total of six different sites, where a minimum of five fish stomachs were collected were identified. Site 1, 3 and 8, were considered good sites for fish since increasing number of fish species corresponded with increasing fish biomass. Sites 9, 10 and 13 had low number of fish species and corresponding low biomass (Chapter 2). The %FO data used were fourth root transformed and an nMDS analysis based on Bray Curtis similarity conducted and nMDS plots generated. In order to test for the differences in sites, multivariate analysis, specifically ANOSIM was conducted using PRIMER (Clarke & Warwick, 2001).

4.3 Results

4.3.1 Characterization of fish diets

A total of 250 stomachs of six species (*G. oyena, A. japonicum, Y. hyalosoma, L. equulus, A. lacunosus* and *A. natalalensis*) were examined, of which 57 were empty (Table 4.1). Empty stomachs were not included in the analysis. A total of nine different food categories were identified in this study (Protozoa, Mollusca, Nematoda, Annelida, Porifera, Kinorhyncha, Crustacea, Insecta, and Detritus) (Table 4.2).

Table 4.1: Sample size of stomachs for the six fish species used in the analysis

Species	**Number of stomachs**						**Total length**
	June 2016	June 2017	Sept 2017	Empty	Total	Analysed	Fish (cm)
Gerres oyena	25	0	5	5	35	30	5.2 - 6.6
Acropoma japonicum	20	6	4	10	40	30	4.8 - 9.4
Yarica hyalosoma	24	43	0	32	99	67	4.0 - 7.5
Leiognathus equulus	11	0	0	3	14	11	3.2 - 5.8
Atherinomours lacunosus	17	0	7	3	27	24	3.7 - 9.2
Ambassis natalensis	0	0	31	4	35	31	4.5 - 8.0

Crustaceans and insects were important prey items for most of the fish species at all sampling times. All the six fish species fed on crustaceans and insects at one time or another (Table 4.2). A total of 36 prey items were recorded in the nine food categories and most of them belonged to Crustacea (19 prey items) and Insecta (7 prey items) categories. The most commonly ingested crustaceans were amphipods and caridean shrimps (Table 4.3).

4.3.2 Description of diet per fish species

In June 2016, annelids (oligochaetes and polychaetes) and crustaceans were equally important food categories for *G. oyena* (72%N, 44%FO, 38.7%IRI and 22.3%N, 84%FO, 38.5%IRI, respectively). However, crustaceans occurred in more stomachs (84%FO) compared to 44%FO) of stomachs for annelids. In September 2017, insects and annelids were the most important food items for *G. oyena* (50%N, 40%FO, 46.34%IRI and 37.5%N, 40%FO, 36.6%IRI, respectively). Crustaceans were the least important prey category (Table 4.2).

The diet of *A. japonicum* in June 2016 consisted mainly of crustaceans (64.2%N, 41.3%V, and 40.2%IRI) and insects (32.1%N, 56.1%V, and 25.8%IRI). Annelids and Protozoa were the least important prey items. In June and September 2017, *A.*

japonicum fed on crustaceans only (Table 4.2). The most important crustaceans that were ingested included brachyura zoeae, mysids and penaeid shrimp (Table 4.3).

Table 4.2: Diet composition of the six fish species sampled in June 2016 (A), June 2017 (B) and September 2017 (C). Number (N), frequency of occurrence (FO) and Index of relative importance (IRI) are given as percentage (%)

Fish species	**TAXON**	**%N**	**%FO**	**%V**	**%IRI**
June_ 2016					
Gerres oyena (n=25)	Crustacea	22.29	84.00	27.46	38.54
	Annelida	72.14	44.00	23.32	38.74
	Insecta	0.34	12.00	0.78	0.12
	Detritus	0.75	52.00	40.41	19.74
	Nematoda	2.70	36.00	4.15	2.27
	Porifera (Macrostella)	0.06	4.00	0.26	0.01
	Mollusca (Bivalvia)	1.61	12.00	3.37	0.55
	Protozoa	0.11	4.00	0.26	0.01
Acropoma japonicum (n=20)	Crustacea	64.18	65.00	41.32	40.15
	Annelida	2.24	5.00	1.65	17.11
	Insecta	32.09	50.00	56.20	25.85
	Protozoa	1.49	5.00	0.83	16.89
Yarica hyalosoma (n=24)	Crustacea	97.73	95.83	94.74	99.83
	Annelida	1.14	4.17	1.05	0.05
	Detritus	1.14	4.17	4.21	0.12
Leiognathus equulus (n=11)	Crustacea	60.39	81.82	26.20	54.23
	Annelida	2.52	27.27	10.16	2.65
	Insecta	19.26	9.09	8.02	1.90
	Detritus	0.88	72.73	42.78	24.30
	Nematoda	15.97	81.82	10.70	16.70
	Porifera	0.44	9.09	0.53	0.07
	Kinorhyncha	0.22	9.09	0.53	0.05
	Mollusca	0.22	9.09	0.53	0.05
	Protozoa	0.11	9.09	0.53	0.04
Atherinomorus lacunosus (n=17)	Crustacea	71.40	41.20	60.80	71.20
	Insecta	28.60	29.40	39.20	26.80
June_2017					
Acropoma japonicum (n=6)	Crustacea	100.00	100.00	100.00	100.00
Yarica hyalosoma (n=43)	Crustacea	81.15	44.19	36.58	71.88
	Annelida	1.05	4.65	3.89	0.32
	Insecta	12.57	27.91	33.46	17.75
	Detritus	5.24	23.26	26.07	10.06

September_ 2017					
Gerres oyena (n=5)	Crustacea	12.50	20.00	9.38	17.07
	Annelida	37.50	40.00	40.63	36.59
	Insecta	50.00	40.00	50.00	46.34
Acropoma japonicum (n=4)	Crustacea	100.00	100.00	100.00	100.00
Ambassis natalensis (n=31)	Crustacea	1.07	19.35	20.61	12.32
	Annelida	0.20	6.45	5.70	1.12
	Insecta	13.70	29.03	27.63	35.23
	Detritus	0.04	6.45	7.02	1.34
	Protozoa	84.99	38.71	39.04	50.00
Atherinomorus lacunosus (n=7)	Crustacea	2.94	28.57	2.78	5.42
	Insecta	97.06	71.43	97.22	94.58

In June 2016 and 2017 crustaceans were the most important prey items for *Y. hyalosoma* (97.7%N, 95.8%FO, 99.9% IRI and 81.1%N, 44.2%FO, 71.8%IRI), as shown in Table 4.2. Detritus (5.2%N, 10.1% IRI) and insects (12.6%N, 27.9%FO and 17.7%IRI) were also ingested in June 2017. Generally, *Y. hyalosoma* species encountered in this study fed on 12 different types of crustaceans the most common being unidentified crabs, penaeid shrimp, mysids, and caridea shrimp (Table 4.3). *Leiognathus equulus* were only sampled in June 2016 and had the most varied diet composition of nine different taxa. Crustaceans were the most important and most frequently ingested diet category (60.4%N, 81.8%FO and 54.2%IRI). Detritus was the second most important feed category in terms of frequency of uptake (72.7%) and %IRI (24.3) (Table 4.2). The most commonly ingested prey category was Nematoda, while crustaceans such as harpacticoid, oithona and caridean shrimp were also common in many stomachs (Table 4.3). The least important feed item was the category Protozoa, which was also ingested by *G. oyena* in small quantities.

Crustaceans and insects were the only prey categories ingested by *A. lacunosus* in June 2016 and September 2017. Crustaceans were the most important food category (71.4%N, 41.2%FO and 71.2%IRI) in June 2016 for this species, while insects were the important feed category in September 2017 (97.0%N, 71.4%FO and 94.5%IRI). In June 2016, amphipods (Crustacea) were found in 29.4% of the total stomachs (Table 4.3). In both June 2016 and September 2017, *A. lacunosus* ingested insects, but apart from a few specimens from the order Diptera, most others could not be identified (Table 4.3).

Ambassis natalensis mostly fed on Protozoa (85.0%N, 38.7%FO and 50%IRI) with insects being the second most important diet category (13.7%N, 29.0%FO and 35.2%IRI). Annelids and crustaceans were the least important food items (Table 4.2).

Table 4.3: Frequency of occurrence (%FO) of prey items found in the stomachs of the six species Gerres oyena (GA), *Acropoma japonicum* (AJ), *Yarica hyalosoma* (YH), *Leiognathus equulus* (LE), *Atherinomorus lacunosus* (AL) and *Ambassis natalensis* (AN) in June 2016, June 2017 and September 2017

Month	**June 2016**					**June 2017**		**September 2017**			
Taxon	**GO n=25**	**AJ n=20**	**YH n=24**	**LE n=11**	**AL n=17**	**AJ n=6**	**YH n=41**	**GO n=5**	**AJ n=4**	**AN n=31**	**AL n=7**
Crustacea											
Amphipoda (unidentified)	8.0	5.0	4.2		29.4	5.0	4.7				
Brachyura zoea		10.0				10.0					
Calanoida		5.0			5.9	5.0					
Caridea shrimp			8.3	9.1	5.9		14.0		50.0	16.1	14.3
Copepoda (unidentified)	4.0						9.3				
Corycaeus		5.0				5.0					
Crab (unidentified)		5.0	25.0			5.0	4.7		25.0		
Varunidae			4.2								
Gammaridea	12.0		8.3								
Harpacticoida	44.0	5.0		72.7	5.9	5.0					
Isopoda (unidentified)	4.0			9.1	17.6			20.0			
Macrophthalmus spp.			4.2								
Megalopa crab		5.0	8.3			5.0					
Metacirolana mbudya			4.2								
Mysidae (unidentified)		10.0				10.0	9.3		25.0		
Oithona	4.0	5.0		18.2		5.0					
Penaeid shrimp		10.0	25.0		5.9	10.0					
Shrimp (unidentified)			4.2								
Tanaidacea (unidentified)	8.0						2.3				
Insecta											
Ceratopogonidae		10.0				10.0					

Culicoides spp.		5.0			5.9	5.0	4.7				
Halovelia							2.3				
Insect (unidentified)		30.0			11.8	30.0	16.3	40.0		29.0	71.4
Insect nymph(unidentified)	8.0			9.1							
Order Diptera (unidentified)		10.0			11.8	10.0					
Phlebotomus (Sandfly)							4.7				
Mollusca											
Order Gastropoda (unidentifed)	4.0			9.1							
Order Bivalvia (unidentified)	8.0										
Nematoda (uindentified)	32.0			90.9							
Annelida											
Oligochaeta	20.0		4.2	18.2				40.0			
Polychaeta	12.0			9.1			4.7			6.5	
Porifera											
Tectitethya macrostella	4.0			9.1							
Protozoa											
Foraminifera	4.0			9.1							
Protozoa (unidentified)		5.0				5.0				38.7	
Kinorhyncha				9.1						6.5	
Detritus	40.0		4.2	72.7			23.3				14.3

4.3.3 Cluster analysis prey categories

A cluster analysis was carried out on seven major food categories (Crustacea, Nematoda, Annelida, Protozoa, Insecta, detritus and others). The ‘others’ category combined three food categories Kinorhyncha, Porifera and Mollusca) that were rare (not ingested by more than two fish species) (Table 4.3). The Bray Curtis similarity matrix of the fish species’ %IRI in the different months showed two main clusters of species at 45% similarity (Figure 4.1). Cluster 1 consisted of most of the species in September 2017 (*G. oyena, A. lacunosus* and *A. natalensis*). Cluster 2 was composed of all the species in June 2016 and June 2017 and one from September 2017. In Cluster 1, the most important prey item was detritus at 50.51% ±15.28SE, while in cluster 2 crustaceans were the most important with the mean %IRI of 76.81± 13.77 SE (Figure 4.1). The division of sub groups 2(i), 2(ii) and 2(iii) was based on the percentage of crustaceans that the species in the sub group consumed.

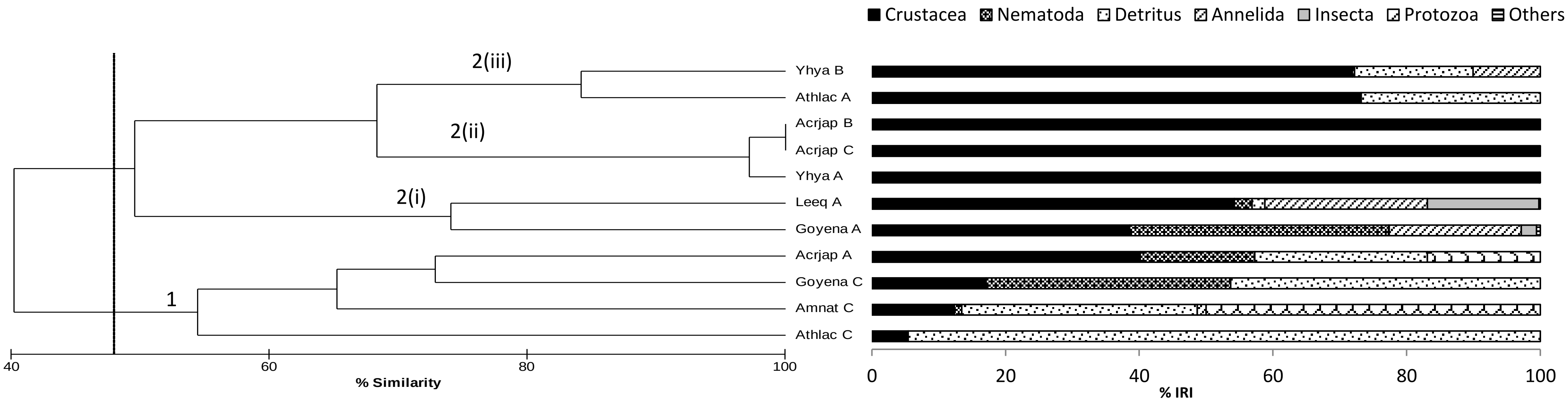


Figure 4.1: Diet similarities based on %IRI, of six fish species: *Gerres oyena* (Goyena), *Atherinomorus lacunosus* (Athlac), *Ambassis natalensis* (Amnat), *Acropoma japonicum* (Acrjap), *Yarica hyalosoma* (Yhya), *Leiognathus equulus* (Leeq) over three different months: June 2016 (A), June 2017(B) and September 2017 (C).

ANOSIM revealed no evidence of differences in the diets of fish in the three sampling periods that they were sampled Global R=0.006 and p=0.447. ANOSIM also showed no significant differences between the prey categories ingested by the species, Global R=0.26, p=0.136. A non-Metric Dimensional Scaling (nMDS) cluster analysis was performed to investigate the %FO of all the prey items in six different sites where the fish were caught. The nMDS plot showed separation into three cluster i, ii and iii (Figure 4.2). Cluster (i) and (ii) consisted of both sites that had high fih diversity and biomass as well as those that had low fish diversity and biomass i.e. sites (1, 9, 10 & 13) and (3, 6, 8, 9, 10) respectively whereas cluster (iii) consisted of sites that had high fish diversity and biomass only (1, 3, 8). Cluster (i) consisted of mainly *G. oyena* species while cluster (ii) was largely made up of *Y. hyalosoma*. This shows that the diet preferences of the six species were not affected by site characteristics where the fishes were sampled. A one way ANOSIM did not detect significant differences between prey items in sites for the different fish species (Global R – statistic value =0.04, p=0.417).

4.3.4 Diet breadth

The diet breadths of the six fish species in this study were: *G. oyena*, $B_i=0.11$, *A. japonicum*, $B_i=0.08$, *Y. hyalosoma*, $B_i=0.09$, *L. equulus*, $B_i=0.17$, *A. lacunosus*, $B_i=0.45$ and *A. natelensis*, $B_i=0.09$ (Figure 4.3). All of these values were below 0.6 of the Levin's niche index. This implies that the diet breadth of these species was quite narrow. *Atherinorous lacunosus* ($B_i=0.45$) had the highest B_i, which is considered moderate (Sá-Oliveira et al., 2014). A simple trophic diagram based on %IRI of the six fish species showed that all predators ingested prey from the crustacean and insect prey categories (Figure 4.4).

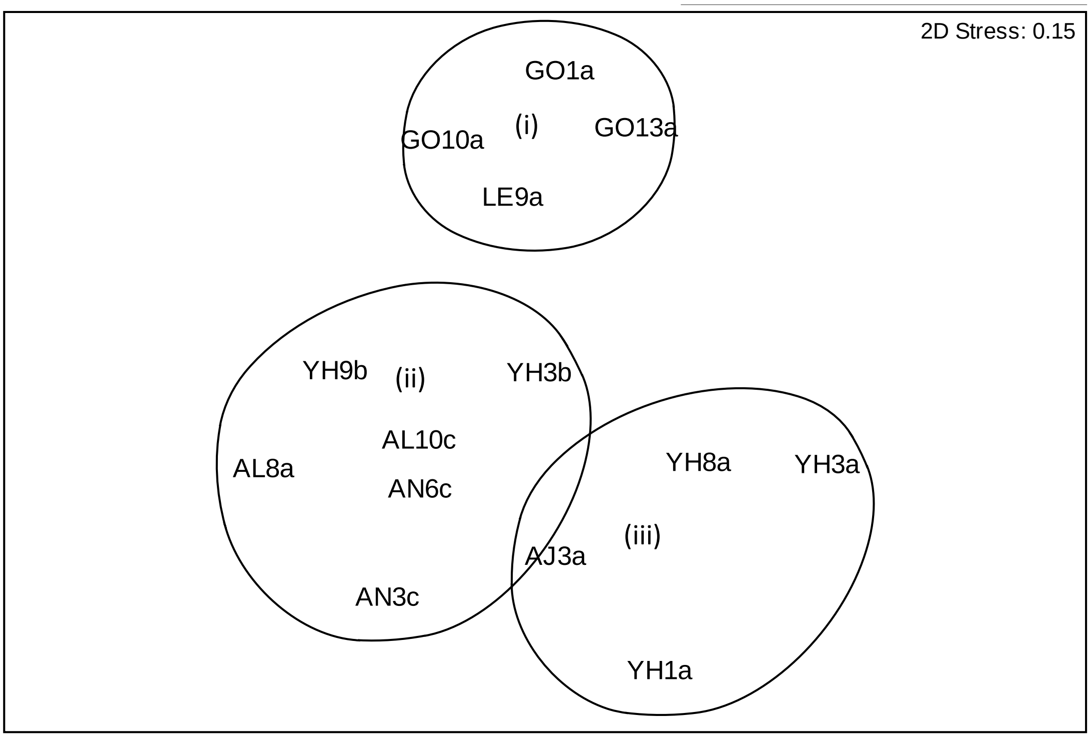


Figure 4.2: Non-metric multidimensional scaling (nMDS) plot of fourth root transformed %FO of prey items in stomach samples of for six species in seven different sites. Species were *Y. hyalosoma* (YH), *A. japonicum* (AJ), *G. oyena* (GO), *L. equulus* (LE), *A. lacunosus* (AL) and *A. natalensis* (AN). The letters a, b and c depict sampling periods i.e. June 2016, June 2017 and September 2017 respectively. Sites 1, 3 and 10 were determined as sites that strongly supported high fish diversity and biomass while sites 11, 12 and 16 supported low fish diversity and biomass.

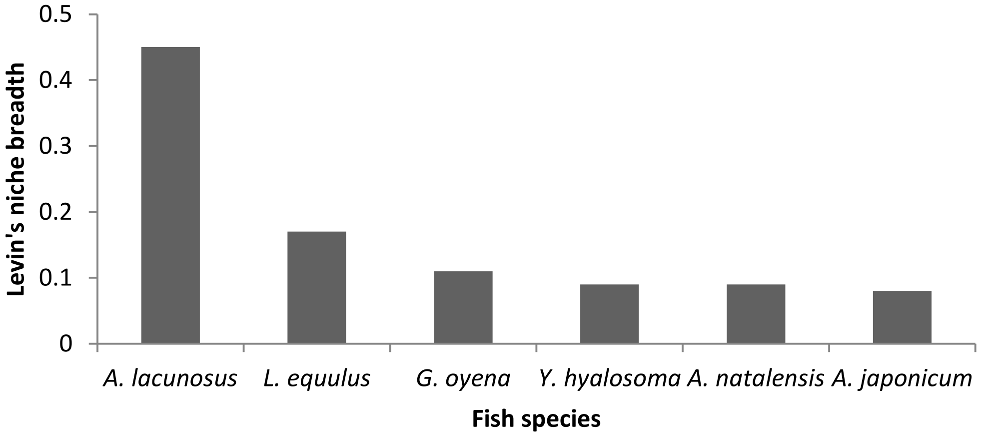


Figure 4.3: Levin's niche breadth (B_i) for the six fish species arranged in order of decreasing B_i

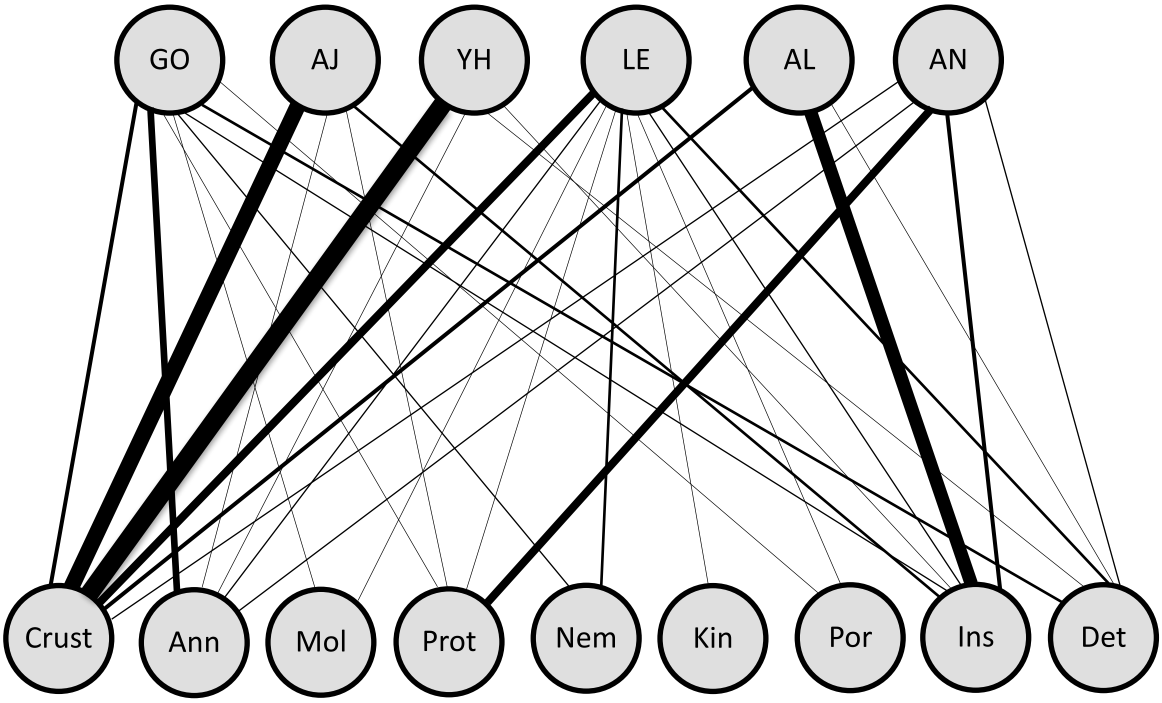


Figure 4.4: Trophic diagram based on the %IRI of the six species in Vanga mangrove system. The species were abbreviated as: *A. japonicum* (AJ), *A. natalensis* (AN), *Y. hyalosoma* (YH), *G. oyena* (GO), *L. equulus* (LE), *A. lacunosus* (AL). The food items were: Crustaceans (Crust), Annelida (Ann), Mollusca (Mol), Protozoa (Prot), Nematoda (Nem), Kinorhyancha (Kin), Porifera (Por), Insecta (Ins) and Detritus (Det). The

thickness of the line depicts the %IRI with thicker lines showing higher IRI and vice versa.

4.4 Discussion

The attraction of nursery areas in mangrove habitats for juvenile fish is in their functions of providing food and shelter (Laegdsgaard & Johnson, 2001). In this study, the diets of six fish species in Vanga mangrove ecosystems were examined using stomach content analysis. The species included *Y. hyalosoma*, *A. lacunosus* and *L. equulus* which are transient species (Lugendo et al., 2006) while *G. oyena* is creek dependent (Wainaina et al., 2013) and spends part of its life in mangrove estuaries. Past studies of stomach analysis of fish species in coastal estuaries in Kenya have encountered trophic guilds like planktivores, benthivores and piscivores (De Troch et al., 1998; Nyunja et al., 2002; Mavuti et al., 2004). In this study, most of the studied species exhibited zoobenthivore behaviour. Since over 95% of the fishes were juveniles (see chapter 2), this could change with ontogenetic transitions (Nanjo et al., 2008). Herbivorous fishes were not encountered in this study as opposed to similar trophic studies on mangrove fishes. Unsworth et al. (2008) found seagrass fish to be distributed in such a way that herbivorous fishes were found nearer mangroves while predators dominated seagrass habitats near the reef. Nanjo et al. (2008) found a few (9.2%) of the mangrove fishes in southern Japan to be herbivores that fed on different types of algae, such as filamentous algae and algal fronds. There is a possibility that some of the fishes in this study fed on plant materials that were probably too digested for identification during analysis.

4.4.1 **Stomach contents**

Based on %IRI, crustaceans were the most important prey category for most of the fish species studied during the three sampling months (June 2016, June 2017 and September 2017). This is in agreement with the findings of several other studies on fish diets in estuarine habitats, whereby zooplanktonic crustaceans have been found to dominate prey items (Martin & Blaber, 1983, Tse et al., 2008, Park & Huh, 2018). Amphipoda and caridean shrimp were the most commonly ingested crustaceans with each being ingested by five out of the six fish species. However, prey for *G. oyena*, *A. natalensis* and *A. lacunosus* (September 2017) was dominated by annelids, Protozoa and insects respectively.

In June 2016 and September 2017, the important prey item for *A. lacunosus* in Vanga mangroves (South coast) were crustaceans (71.2%IRI) and insects (99%IRI), respectively. Contrary to these findings, a similar study carried out in 2001 in Wasini and Mtwapa creeks, Kenya (115km away) found nematodes and copepods to be the most important food items for *A. lacunosus* during SEM and NEM seasons, respectively (Nyunja et al., 2002). The variation in the dominant prey categories ingested by the same fish species in similar habitats could be due to the many factors including physical, and biological variables in the habitats (Nyunja et al., 2002), as well as differences in time of sampling and sampling methods.

Gerres oyena is a common species in mangrove estuaries and has been encountered in several studies that have focussed on their diets (Hajisamae et al., 2003; Mavuti et al., 2004; Tse et al., 2008). In this study, annelids and crustaceans were found to be the most important diet categories (38.7%IRI and 38.5%IRI respectively) for *G. oyena* in June 2016. However, in September 2017, insects and annelids were the main prey items.

Most past studies found crustaceans to be the most important prey category for *G. oyena*. In Hong Kong *G. oyena* mostly fed on crustacean zooplankton in both summer and winter seasons (Tse et al., 2008). In other studies, *G. oyena* from nearshore habitats were found to feed mainly on copepods while those from mudflats fed mostly on detritus (Hajisamae et al., 2003, Lugendo et al., 2006). Though not very common, the dominance of annelids in the diet of *G. oyena* in this study is comparable to results from similar studies elsewhere. In the Kosi estuaries of South Africa, annelids (polychaetes) were the most important prey item (Cyrus & Blaber, 1983). Mavuti et al. (2004) found polychaetes to be important prey items for *G. oyena* and *L. equulus* in North coast Kenya. Other Gerridae like *G. erythrourus* in Johor straight in Singapore and *Eugerres brasilianus*, *Eucinostomus melanopterus* and *Diapterus rhombeus* in Goiana Estuary, north-east Brazil have also been found to feed on annelids (Hajisamae et al., 2003, Ramos et al., 2014). Thus *G. oyena* could be defined as a generalist species that feeds on prey that is available in the habitat.

Crustaceans (54.2%IRI) dominated the diet of *L. equulus,* which also fed on detritus and nematodes (24.3%IRI and 16.7%IRI respectively). Hajisamae et al. (2006) recorded similar findings, whereby this species fed on different crustaceans as well as nematodes. In South China Sea, *L. equulus* mostly fed on calanoid copepods and gammaridean amphipods (Hajisamae et al., 2006).

The most important prey category for *A. japonicum* in all sampling months was crustaceans comprised of calanoid copepods, amphipods, shrimps and crabs. These results concur with its classification as benthopelagic fish that preys on planktonic copepods and caridean shrimp (Park & Huh, 2018). The dominance of crustaceans in the diet of this species has also been found to persist over different size classes (Park & Huh, 2018).

In South Africa, the diet of *A. natalensis* from six different estuaries revealed that the primary prey items were planktonic crustaceans followed by insects. Fishes were also part of their diets. Due to their diverse diet, this fish species is considered euryphagic (Martin & Blaber, 1983). In this study, Protozoa were the most important prey item for *A. natalensis* (50.0%IRI), while insects were the second most important (35.2%IRI). *Ambassis natalensis* is a surface prey feeder, which could explain the importance of insects in this study (Martin & Blaber, 1983). In the Natal estuaries, the diet of Ambassidae species was found to be quite broad and was dictated by the availability of prey (Martin & Blaber, 1983).

The trophic status of a fish is dependent on several factors such as seasonality (Giarrizzo & Krumme, 2007, Varghese & Somvanshi, 2016), ontogenetic changes (De La Morinière et al., 2003), physical conditions (Martin & Blaber, 1983) and water quality (Nyunja et al., 2002) among others. Therefore, a change in any of these factors could lead to a diet shift of the fishes (De La Morinière et al., 2003, Giarrizzo & Krumme, 2007, Park & Huh, 2018). Seasonality determines the availability of prey items, which in turn affect the diet of the predators (Novakowski et al., 2008, Park & Huh, 2018). The feeding activity of *Sardinella gibbosa* in Mtwapa creek and Wasini channel Kenya, decreased during the South East Monsoon (SEM) because of increased water turbidity hampering their ability to locate food (Nyunja et al., 2002). Park & Huh. (2018), noted a dietary change for *A. japonicum* due to seasonal changes in water temperature. Varghese & Somvanshi, (2016) found that the seasonal variation in abundance of two major prey items for yellow fin tuna in the Arabian Sea affected their diet. Martin & Blaber, (1983) concluded that the diet of Ambassidae species in Natal estuaries was quite broad and dictated by the availability of prey. Although ontogenetic shifts have been found to affect the diets of fish, herbivores have been found to remain in the same trophic guild throughout their growth cycle (Giarrizzo & Saint-Paul, 2008;

Park & Huh, 2018). In this study, ANOSIM revealed no significant differences between the prey categories that were ingested in the different sampling months. There were also no significant dietary differences between species. In most studies on fish diets, seasonality has been found to affect the dietary intake of fish (Hajisamae et al., 2003, Park & Huh, 2018). Giarrizzo & Saint-Paul, (2008) found that during the dry season, fish tended towards a generalistic feeding behaviour, probably due to scarcity of food while the dietary intake was more defined during the rainy season. In this study, seasonality did not seem to play an important role in determining the diet of fish.

Planktonic crustaceans were ingested with varying intensity and importance by the six fish species investigated in this study. However, for species like *G. oyena*, *A. lacunosus*, and *A. natalensis*, prey categories like annelids, insects and Protozoa were more important. Since juvenile fish species in mangrove estuaries are considered generalists, it is possible that some of the species ingested other available prey items to avoid competition with other predators. Martin & Blaber (1983) found an obvious differentiation in diet when they were studying three sympatric species of Ambassidae in the Natal estuary. They concluded the ingestion of different types and amounts of prey items by these fish species was aimed at reducing competition among them.

Using the %FO to investigate whether there were significant differences in prey items in the diet of fish species in sites that had high diversity and biomass of fish and those with low fish diversity and biomass, this study found no differences. It was expected the nMDS plots would show separation and clustering of species in sites with high fish diversity and biomass and sites that had low diversity and biomass of fish. Instead, the three clusters showed fish species from both site categories in one cluster. Further, ANOSIM gave non-significant results and a very low global R. This could probably be due to similar food being available in all the different sites and equally, resulting in the ingestion of similar food in both site categories. Some fish families like the Ambassidae have been found to feed on available prey (Martin & Blaber,1983) and this may have been the case in this study. In other cases, the quality of the environment such as salinity variation determine what the fish feed on (Ley et al., 1994). In this study, it is therefore clear that other factors, apart from sites determined the diet of fish.

4.4.2 Diet breadth

The diet breadth (B_i) of the species studied ranged from 0.08 to 0.45 with five of the species having a B_i of below 0.2. This shows that only a few diet items contributed greatly to the diet of these species. The species *G. oyena* and *L. equulus* preyed on eight and nine prey categories respectively but they had a low B_i (0.11 and 0.17 respectively). Thus, although these species fed from a wide variety of prey, the proportions were very low meaning that only a few prey categories contributed substantially to the diet. Hammerschlag et al. (2010) encountered similar trends with the blue stripped grunt, *Haemulon sciurus* and the seabream, *Archosargus rhomboidalis* (Linnaeus, 1758). The former had a higher diet breadth in the dry season (5 food categories) as opposed to the wet season when it consumed more diverse prey items (6 food categories). Similarly, the diet breadth of the seabream was similar in both wet and dry season despite the fish consuming more than twice the number of food categories in the wet season than in the dry season.

Generally, narrow diet breadth values are common in coastal estuaries. Arceo-Carranza & Chiappa-Carrara (2015) classified six fish species from the coastal lagoon in southeastern Mexico, whose diet breadth (B_i) ranged from 0.026 – 0.163, as stenophagus. In the South China Sea, *L. equulus* (B_i=0.40) had the highest diet breadth with the rest of the species such as *Sillago sihama*, *Ambassis kopsii* and *Lethrinus* *lentjan* having much lower B_i values of 0.05, 0.11 and 0.25, respectively (Hajisamae et al., 2006). Yellowfin tuna (*Thunnus albacares*) in the Arabian Sea were found to have very low B_i suggesting that few prey items dominated their diet and they probably maximized feeding efforts on the prey with the highest densities (Varghese & Somvanshi, 2016). A study at the Kenyan coast, considered the feeding strategy for *A. lacunosus*, *G. oyena* and *L. equulus* to be generalistic, with species taking advantage of physical and biological conditions in their habitats to maximise their feeding strategy (Mavuti et al., 2004). This may be explained by the optimal foraging theory (MacArthur & Pianka, 1966), which states that the diet breadth of a predatory species should widen during food scarcity and narrow in times of abundant food (MacArthur, & Pianka 1966; Levins & MacArthur, 1969; Rödel et al., 2004; Tse et al., 2008). This theory has however been contradicted in some studies. For instance, the findings of Hammerschlag et al. (2010) were such that although the diet breadth of three species: *Lutjanus griseus*, *Haemulon sciurus* and *Sphyraena barracuda* changed seasonally, it broadened when food abundance was high. This could have been due to continued abundance of food items for the predators over the different sampling seasons. Due to unavailability of food data in this study, it is difficult to make conclusions as to the cause of the low diet breadth. It could however be guessed that most of the fishes had a narrow choice of prey in Vanga mangrove ecosystems.

4.5 Conclusion

The fish species in this study were juvenile fishes that use the Vanga mangrove ecosystem as nursery habitats. They are typical fish species found in the Western Indian Ocean region. The results suggest to some extent that the Vanga mangroves are feeding grounds for these fishes, since they were caught inside the mangrove forests during ebb tide. Generally, all the species fed on a very narrow diet range and this could be due to unavailability of other prey items in the habitat. Some species like *G. oyena* and *A. natalensis* deviated from the overall crustacean dominated diet and ingested annelids and protozoa in greater quantities than crustaceans. This could mean some specialization in these two species and the reasons could be myriad including avoiding competition with other fish species in the sites. Since there were no significant differences in the prey items for all the species, it could be that most species were more generalist in nature and fed on what was available especially crustaceans and insects.

A striking feature of these results is the importance of insects in the diets of marine fish; all six sampled species fed on insects. Insecta is a generally a terrestrial class so these insects are closely associated with the mangrove forest (flowering plants), probably falling into the water from the mangrove trees. This is direct evidence of feeding within the mangrove system and shows an unusually close link between marine and terrestrial food chains. In this study, it was not possible to get enough samples for species for sampling during the SEM and NEM season. Future studies could focus on a few species available during both seasons and carry out both stomach analysis and stable isotope analysis to ascertain whether the prey actually came from mangroves or elsewhere.

5.0 CHAPTER 5: ANALYSIS OF THE IMPORTANCE OF SEASCAPE FEATURES IN DETERMINING FISH AND CRUSTACEAN COMMUNITIES IN VANGA

Abstract

Seascape ecology is gradually gaining acceptance as a new approach for exploring coastal ecology. The movement of mobile fauna between habitats may be influenced by proximity, tidal water flows and ontogenetic shifts. In the tropics, mangroves, seagrasses and coral reefs are among the most common habitats in the coastal seascape. These habitats are functionally connected and as such, organisms living in them are often dependent upon and influenced by processes and properties that transcend single habitat boundaries. Landscape ecology metrics such as patch area, perimeter, perimeter/area ratio and extent of edge are now used to quantify spatial patterns in seascape studies. In this study, a spatial analysis was conducted in order to assess the influence of seagrass metrics on fish and crustaceans sampled within mangrove forest sites. The distance from each of the 14 mangrove sampling sites to seagrass points was calculated using standard buffer tools in ArcGIS. A set of buffers with intervals of 0.5km and extending up to 9km into the seascape were used. In order to isolate regions immediately in front of the sampling site, directions from each sampling site were calculated at increments of 20 degrees. The oceanic section was further extracted from the directional buffers. The geometry of seagrass patches at each distance and directional buffer were calculated. Null hypotheses were of no relationships between the community level variables of mean biomass, mean abundance and total (cumulative) species counts for fish and crustaceans, as well as abundance and biomass for key individual species, caught within the mangrove sites. Linear regressions revealed a range of moderate to strong models. Fish variables generally increased with increasing seagrass area. Strong correlations were for instance found between mean fish biomass (R^2=0.56, p=0.034) mean fish abundance (R^2=0.61, p=0.020) and the abundance of

individual fish species *Yarica hyalosoma* (R^2=0.75, $p<0.001$) and *Gerres filamentosus* (R^2=0.70, p=0.001) and seagrass area, at distances of 2km and below. In contrast, crustaceans were negatively correlated with seagrass area, for example for *Penaeus indicu*s at between 1-2.5km distances, and positively correlated with perimeter/area ratios at distances of 2km and 9km for *Penaeus indicu*s abundance (R^2=0.52) and *P. monodon* abundance (R^2=0.37) respectively. The results of this study indicate that nearby seagrass structures are important in explaining some of the fish and crustacean community variables sampled at mangrove sites in Vanga, but suggest that key fish and crustacean species may be responding in different and possibly opposite ways to the presence of local seagrass habitat. Putative management interventions aimed at conserving species and stocks would have to consider how fish and crustaceans are affected differently by seagrass metrics at different distances. Simple approaches aiming to enhance only one part of the seascape would be unlikely to promote greater biomass and abundance across all faunal groups.

5.1 Introduction

The last several years have seen a gradual adoption and application of landscape ecology principles to coastal seascapes with the purpose of exploring causes and outcomes of spatial heterogeneity (Pittman et al., 2011). Ecologically, a landscape is a heterogeneous habitat consisting of different types of habitat patches in which a target patch is embedded (Dunning et al., 1992; Turner, 2005). A seascape is conceptually similar but is, of course, in the sea rather than on land; it has been described as 'a mosaic of patches', a spatial gradient, or some other geometric patterning quantified from either benthic or pelagic environments' (Bostrom et al., 2011). Seascape ecology is an emerging field of study in coastal habitats which is adapting landscape ecology methods to marine ecology settings.

In the coastal tropics, mangroves, seagrasses, coral reefs, mudflats and sandflats form an assortment of interconnected patches that cover the seascape and offer habitats for different kinds of organisms (Ogden, 1988). Seascape habitats are interdependent and support each other ecologically and functionally. For instance, mangroves and seagrasses filter out pollutants and sediments that may harm corals reefs, which in turn protect them from strong waves by breaking their energy (Ogden, 1988; Moberg & Folke, 1999).

Different models have been used to study landscape patterns, the most common being the patch–matrix and patch–mosaic models. The patch–matrix model is based on the theory of 'island biogeography'; a binary classification system that categorises landscapes of interest as homogenous high quality patches (habitat islands) embedded in a lower quality matrix e.g. sediment, considered non habitat (MacArthur & Wilson., 1967; Mcneill & Fairweather, 1993; Bostrom et al., 2011). The extent of isolation of these ‘islands’ affects the mobility and survival of organisms. The patch–mosaic model on the other hand views the landscape as heterogeneous, consisting of different interacting patch types, which influence ecological functions of the landscape. Composition and spatial configuration of mosaics are the most important factors in this model (Wiens, 1993).

5.1.1 Connectivity

Connectivity in landscape ecology explains how interactive pathways link species and ecological processes with landscape elements (Crooks & Sanjayan, 2006). In the seascape, connectivity is determined by the extent to which patches allow or deter movement of resources and individuals between or across patches or patch types. Connectivity is key in determining the growth, survival and movement of marine organisms among the seascape habitats (Grober-dunsmore et al., 2009).

Resource managers can use information on the degree to which a seascape permits connectivity to decide what part or aspect of the seascape to prioritise in conservation (Grober-dunsmore et al., 2009). The functional connectivity of a seascape refers to a number of things that include: the interaction of organisms with a seascape, the ecological processes and the movement of materials and energy, across the seascape (Wiens, 2006). The nursery function of mangroves and seagrasses for juvenile reef species underscores the importance of the functional connectivity of seascape habitat patches (Nagelkerken et al., 2015).

The movement of mobile fauna in tidal migrations (Sheaves et al., 2005) and ontogenetic shifts (Dahlgren & Eggleston 2000; Kimirei et al., 2013) connects patches and habitats in the seascape by transferring nutrients, genetic material and biomass between them (Moberg & Folke, 1999; Lundberg & Moberg, 2003).

In the Caribbean and the Indo–Pacific, juvenile fishes have been recorded to use mangroves and seagrasses while adults utilise coral reef habitats (Dorenbosch et al., 2004; Mumby et al., 2004). Due to the episodic inundation of mangrove forests during high tides, mangrove-dependent fish tend to move to seagrass habitats during low tides since they cannot survive in the mangroves (Sheaves, 2005; Jelbart et al., 2007). In addition, fish species have been found to seek refuge in permanently-inundated mangroves during the day and to migrate to adjacent seagrass beds for nocturnal feeding (Nagelkerken et al., 2000; Verweij et al., 2006). Reef species that reside in nursery areas later migrate after attaining sub adult stages, to reside offshore. This further emphases the importance of connectivity of these habitats (Nagelkerken et al., 2001; Jelbart et al., 2007). However, instead of migrating offshore, some species of grunt and snapper families in the Caribbean have been found to expand their home ranges to include adjacent seagrasses and coral reefs (Hitt et al., 2011).

5.1.2 Seascape spatial metrics

Seascape ecology uses landscape-ecology metrics to quantify spatial patterns in the seascape. The metrics are grouped into three categories. Firstly, landscape composition includes the abundance and diversity of patch types. Secondly, spatial configuration metrics include mean patch area, perimeter, perimeter/area ratio and distance to nearest seascape structure (patch). Thirdly, fractal dimension metrics investigate shape complexity of a patch or landscape (Wedding et al., 2011). Aquatic fauna has demonstrated relationships (or lack of) with different seascape metrics such as size, fragmentation, area and perimeter/area ratio of patches. However, the implications of these relationships are largely unknown (Kendall, 2005; Bostrom et al., 2011).

A number of studies have found evidence that patch area and distance between patches may influence reef fish community structure in various ways such as increases or decreases in fish densities or species richness (Kendall, 2005; Dorenbosch et al., 2007; Bostrom et al., 2011). For example, experiments using artificial seagrass units (ASU) concluded that the total area, rather than the edge length, of small patches influenced species richness (Jelbart et al., 2007). In contrast, Mcneill & Fairweather (1993) tested the Single Large or Several Small theory (SLOSS) in a natural aquatic environment and found species diversity was significantly higher in several small seagrass patches than in single large beds. Furthermore, when the effects of edge and bed size of seagrasses in the Pittman estuary in Australia were investigated, edge had no effect on species diversity in smaller beds, but in larger beds, species diversity was lower on the edge than 4m inside the seagrass bed (Jelbart et al., 2007). In other work, mangroves close to continuous seagrass beds were found to attract more fishes than those near patchy beds or with no seagrass at all (Pittman et al., 2007). Connolly & Hindell (2006) reviewed early studies on seascape ecology and concluded that most studied taxa showed no response to seascape metrics like patch size and edge while proximity of habitats had greater influence than the former two. The lack of response to spatial attributes could also signify that other factors such as biological interactions could be more influential than spatial metrics (Connolly & Hindell, 2006). Hence, the limited existing literature suggests seascape features may be important, but that their effects may be complex and poorly understood.

Knowledge of the influence of seascape metrics on faunal assemblages in the Indo-Pacific is gradually growing. Previously, most studies explored relationships between faunal assemblages and isolated seascape structures (Kimani et al., 1996; Gullström et al., 2008; Unsworth et al., 2008; Mwandya et al., 2010; Wainaina et al., 2013). This may have led to the notion that connectivity of seascape structures in the Indo-Pacific was either very weak or non-existent. Recent studies are gradually challenging this belief.

In Zanzibar for instance, Berkström et al. (2012) and Dorenbosch et al. (2005; 2007), have documented that numerous reef fish species utilise more than one seascape habitat, supporting existence of connectivity in the region. Further studies in Zanzibar, on the influence of seascape metrics on fish assemblages by Dorenbosch et al. (2007) found the configuration of seagrass beds to be more important rather than their structural complexity. The effect of edge was also more pronounced on fish densities in seagrass beds near the reef edge than those that were far away, emphasising that the proximity of seascape structures affects fish assemblages (Dorenbosch et al., 2007). Also in Zanzibar, Gullström et al. (2008) found seagrass structure and the proximity of other seascape habitats to be the key drivers of faunal community structure.

The seascape approach is therefore a holistic approach to coastal ecology and management that does not isolate habitats, but addresses their connectivity, interaction and their support for each other ecologically (Pittman et al., 2011; Nagelkerken et al., 2015). The seascape ecology approach is still in its infancy in most regions of the world, but its importance in achieving sustainable coastal management cannot be overemphasised. There is a dearth of information on the spatial configuration of the seascape in Kenya. Studies on mangrove fishes and seascapes are rare and those that exist were performed on permanently inundated mangroves. The novelty in the current study involves testing how seascape metrics of habitats adjacent to mangroves that function as low-tide refuges for mangrove fishes, structure high-tide mangrove fish assemblages. The study seeks to test whether seascape metrics can predict fish and crustacean assemblages sampled in a Kenyan mangrove ecosystem. Specifically, we tested: a) how seagrass seascape metrics influence mangrove fish and crustacean assemblages, and b) whether distance to seagrass seascapes was important in structuring mangrove fish and crustacean communities.

5.2 Materials and methods

5.2.1 Study area

The study site is in Vanga Bay, situated on the south coast of Kenya at latitude 4° 39' 38.42"S and longitude 39° 13' 9.71"E (see details in chapter two). The climate of Vanga Bay is influenced by monsoon winds leading to two main seasons: South Eastern Monsoon (SEM) – May to October and North Eastern Monsoons (NEM) – November to March (McClanahan, 1988). Fishing is the major economic activity across Vanga Bay with fishing grounds being located across the complex seascape including mangroves, seagrass and coral reef ecosystems. The fishery in Vanga Bay is mostly artisanal, multi-gear and multi-species (McClanahan & Mangi, 2004). The field site coordinates were recorded during the fish sampling campaigns in the mangrove areas. The GPS points were collected with a Garmin GPS World Geodetic System (WGS) 1984 and projected onto the Universal Transverse Mercator (UTM) 37S.

5.2.2 Fish sampling

Fish species and crustaceans were sampled at fourteen mangrove creek sites situated between Jimbo and Majoreni villages in the Vanga region (see Fig. 1.1). The sites were chosen to give a wide geographical coverage of the Vanga mangrove forest whilst still being accessible enough to allowing regular sampling. Fyke nets were deployed at the creek mouths that drain the mangrove forest sites, to sample fish and crustacean communities leaving these sampling areas during the ebb tide (see details of fyke net specifications in chapter 2). Over two years (September 2015 – September 2017), I sampled each field site once every three months over five consecutive days during spring tide. Replicate samples were taken eight times from each of the 14 sites making a total of 112 samples. March 2017 was not sampled for logistical reasons. The fish and crustacean samples were collected in the field and placed in a cool box. They were sorted and identified to the lowest taxon possible using Anam & Mostarda (2012) and Richmond (2011). The standard and total lengths of the fishes were measured (to the nearest 0.1cm) and their weight was recorded (to the nearest 1g). The carapace length of crustaceans was measured to the nearest 0.1cm. Some individuals were partly predated on and in such cases, they were identified whenever possible and their numbers recorded for inclusion in abundance data only.

5.2.3 Spatial structure of fish catches

The spatial structure of fish catches was measured using Morans I. Since some of the sites were on one main creek that further split into smaller side creeks, it was expected that the sites on the same creek would be more similar than those further apart. To investigate the presence of spatial autocorrelation and its influence on fish and crustacean assemblages, the Moran's index 'I' was calculated using GeoDa software. Moran's index 'I' is a correlation coefficient that measures the overall spatial correlation in a data set. The 'I' Values range from -1 to 1, with positive values suggesting a positive spatial autocorrelation and -1 strong negative spatial autocorrelation. Zero indicates a random pattern with no spatial autocorrelation. The null hypothesis was that there was no spatial autocorrelation between the sites. All the mean and total fish and crustacean variables (abundance, biomass and cumulative species) were tested. Generally, Moran's I showed no significant spatial autocorrelation for the crustacean variables but significant spatial autocorrelation was found in the fish biomass and abundance ($p \leq 0.005$) (Table 5.1). To correct for spatial autocorrelation, the generalised least squares (gls) command in R statistical package that included location data was computed using normal errors, and with other error terms such as spherical corrections. Different models were compared using the Akaike Information Criterion (AIC) whereby the lowest score was considered the best. The results suggested that using spherical error terms gave the best fit. After this correction, the p - value in the regression analysis was still significant and actually not very different from standard regression without the autocorrelation correction. Thus correction for auto correlation was found unnecessary.

Table 5.1: Spatial autocorrelation test output for mean fish and crustacean variables (abundance, biomass and number of species) using Moran's I.

Indicator	**I**	**pseudo p-value**	**expected**	**mean**	**std**	**z**
Mean fish biomass	0.2847	**0.0285**	-0.0769	-0.0771	0.1515	2.3882
Mean fish abundance	0.2170	**0.0305**	-0.0769	-0.0767	0.1295	2.2678
Mean crustacean biomass	-0.1872	0.2374	-0.0769	-0.0771	0.1458	-0.7554
Mean crustacean abundance	-0.4472	0.3427	-0.0769	-0.0771	0.1360	0.2377
Cumulative fish species	0.1337	0.0965	-0.0769	-0.0770	0.1498	1.4058

5.2.4 Spatial analysis of correlation between the seascape and fish catches

In order to assess the fish catch in the fourteen mangrove sites in relation to seascape features, we used ArcGIS to conduct a spatial analysis. A Sentinel-2 image from 27/03/2017 covering the study area was downloaded and used as a base map for qualitative interpretation. The Sentinel-2 image was taken at low tide. A false colour composite was created using the Near Infrared (NIR), red and green in which land, sea and the intertidal zone were clearly distinguished. The Normalised Difference Water

Index (NDWI) values were used to extract ocean from the Sentinel-2 image scene and converted to a shapefile for subsequent masking. Seagrass data were taken from Harcourt et al. (2018). These differ slightly from the published map, which included only seagrass presence/absence, whereas the map used in this study encompasses only those areas where seagrass is dominant.

For each of the 14 sampling sites, a set of buffers with intervals of 0.5km were used, extending out to a maximum distance of 19km from the sampling point to seagrass areas (Figure 5.1a). The distance between each mangrove field site to various seagrass points was calculated using standard buffer tools in ArcGIS. In order to exclude land from these buffers, the ocean mask was used to extract only those regions covered by water. Further, we calculated the direction from each field point at increments of 20 degrees in order to isolate regions immediately in front of a sampling point (Figure 5.1b). The final step was to extract the oceanic section of these direction buffers. This was computed for each of the fourteen points making a total of 14 directional polygons. In order to compute the final datasets, the far field analysis in the seagrass meadow map was added. The datasets were then combined with the intersect tool so as to obtain patches of seagrasses in each distance and direction buffer and the geometry of these patches was calculated so as to avoid including large seagrass patches that extend across multiple buffer boundaries. The attribute table was then edited for non- seagrass areas.

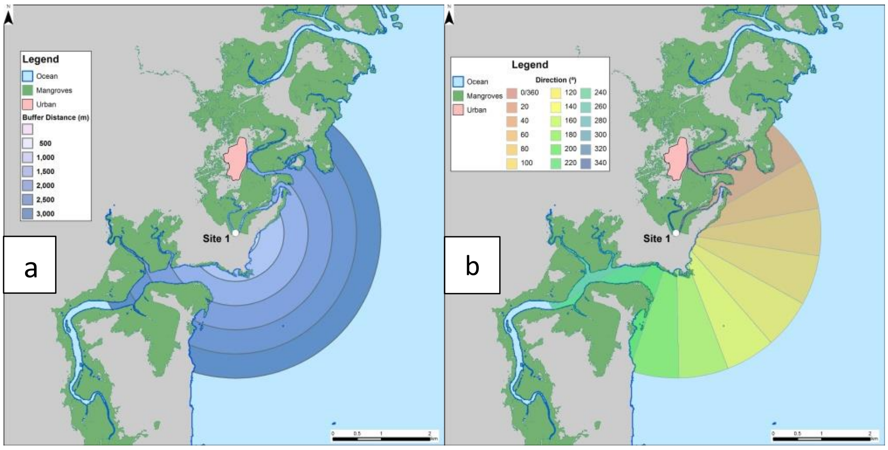


Figure 5.1: A map showing (a) several distance buffers from the site 1 at an interval of 0.5km (b) some directions within each buffer in site 1 at intervals of 20 degrees from a mangrove sampling site

5.2.5 Data analysis

In principle, the analyses of seagrass seascape metrics, moving in concentric circles of increasing diameter away from each sample site, could incorporate all detectable seagrass within tens or hundreds of kilometres of each site. This is neither biologically sensible nor logical, given that the species of interest will be limited in their daily movements and that as the diameter increases eventually data from all the sites will overlap and lose particularity. In the absence of any biological information on the movements of the main species we used a simple empirical approach to obtain a limit. The outer limit of Vanga Bay lies ~22.5km from the most distant site, hence this distance was set as an initial maximum limit. Plotting cumulative curves of the proportions of the total seagrass habitat recorded in the Bay that was covered at each sampled distance for each site showed that after 9km there was only around 50% difference in proportions of cumulative area (Figure 5.2), implying that beyond this distance more than half of the seagrass measured for any given site would be shared with another. Hence, 9km was set as the maximum distance for this analysis.

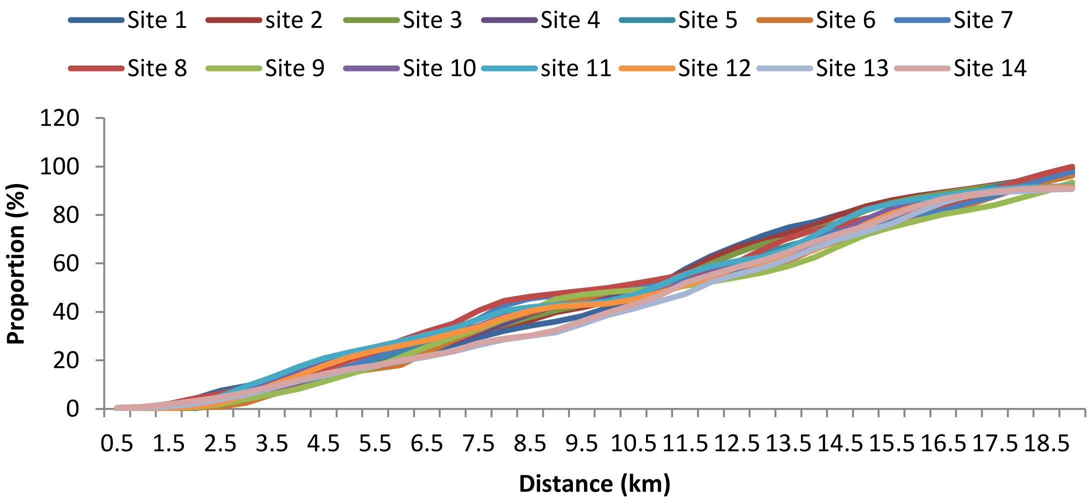


Figure 5.2: Proportion curves of cumulative area of seagrass.

Seascape metrics (i.e. patch area, perimeter, perimeter/area ratio, cumulative seagrass area and cumulative perimeter of seagrass habitat) for all directions within the ocean (landward directions were excluded) were assigned as predictor variables. The predictor and response variables are shown in Table 5.2. Using Minitab 14, each predictor variable was visually examined against each response variable for linearity using scatter plots. In order to explore the relationships between predictor and response variables, correlation matrices were developed at distances of 0.5km – 9km. The next step was to explore whether any robust models could be constructed using multiple regressions of the predictor variables at all the distances against fish and crustacean variables. Initial explorations were performed using stepwise regressions, with both addition and subtraction approaches, to identify distances that consistently showed no or little evidence of effects. Multiple regressions were then computed to test for the best possible models (using the best subsets approach) for each predictor variable, and the assumptions of multiple regressions were tested; the normality of residuals were tested using Anderson Darling normality tests in Minitab 14. Best models were chosen by comparing R^2 values, p - values, the strength of coefficients, and variance inflation factors (VIF) for multicollinearity, with a VIF of >5 deemed unacceptable. Finally, simple linear regressions were performed between those predictors and response variables shown to have the strongest relationships through the multiple regressions and by visual inspection of the plots. Given the collinearity inherent in some of the predictor variables and the dangers of inflated type 1 error following multiple tests, the results are presented in full and examined for key signals rather than interpreted simply as significant or non-significant relationships. The Bonferroni correction factor was used in all the linear regressions to account for multiple testing. Under this factor, some of the p values ($p<0.05$) were found not significant

Table 5.2: Fish and crustacean variables which responded to seagrass metrics

Predictor variables	Response variables (fishes)	Response variables (crustaceans)
Seagrass area	Mean fish abundance	Mean crustacean abundance
Seagrass perimeter	Mean fish biomass	Mean crustacean biomass
Cumulative seagrass area (total seagrass perimeter from the mangrove sampling site to seagrass distance)	Species richness (cumulative fish species)	*Most dominant crustacean species: *Penaeus monodon* and *Penaeus indicus*
Cumulative seagrass perimeter (total perimeter in the distance from the mangrove sampling site)	Most dominant fish species: *Yarica hyalosoma*, *Acropoma japonicum*, *Gerres oyena*, *Gerres filamentosus*, reef associated species	
Perimeter/area ratio of seagrass		

*Most dominant species means species that had the highest number of individuals in the study

5.3 Results

5.3.1 Relationships between seagrass metrics with fish and crustacean variables

A correlation matrix was developed to describe relationships and show strength of effects between predictor variables (seascape metrics) at distances of 05km - 9km and response variables (composite fish and crustacean variables and individual species Table 5.2). Overall, the strongest correlations for fish was between cumulative seagrass perimeter and *Y. hyalosoma* abundance at 0.5km ($R^2=0.80$) (Table 5.6a). *Penaeus* *indicus* strongly correlated with perimeter/area ratio at 1.5km (R^2=0.72) (Table 5.3a). Generally, more fish and crustacean variables responded to the perimeter/area ratio of seagrass compared to the other seascape metrics (Table 5.3a).

a) Perimeter/area ratio (P/A ratio) of seagrass

A correlation matrix was developed between perimeter/area ratio of seagrass and fish variables over a spatial extent that ranged from 1km to 6.5km. Most of the significant relationships were negative. Simple linear regression models were developed for fish variables over a spatial extent that ranged from 3.5km to 5.5km. All the significant relationships were negative except for *Gerres oyena*. Mean fish biomass (R^2=0.38, $F_{(1,12)}$= 7.41; p=0.019), log (x+1) *Acropoma japonicum* total abundance (R^2=0.36, $F_{(1,12)}$=6.97; p=0.023) and *G. filmentosus* mean abundance (R^2=0.47, $F_{(1,12)}$ = 10.72; p=0.007) were negatively related to perimeter/area ratio of seagrass(Table 5.4b). *Gerres oyena* abundance was positively related to perimeter/area ratio of seagrass at 3.5km (R^2=0.3, $F_{(1,12)}$= 5.04; p=0.044). *Penaeus indicus* abundance was strongly related with perimeter/area ratio at 1.5km (R^2=0.52, $F_{(1,12)}$=13.03; p=0.004) while (log) *P. monodon* demonstrated a significant relationship with perimeter/area ratio of seagrass at 9km (R^2=0.43, $F_{(1,12)}$=9.15; p=0.011) (Table 5.4b). The other ouput for linear relationships for some fish and crustacean variables are shown in Appendix 5.1. The R^2 values for the correlations of fish and crustacean variables with perimeter/area ratio of seagrass at various distances is shown in Figure 5.3a and b where the strongest relationship (highest R^2) for fish were at 3.5km for fish and 1.5km for crustaceans. Some relationships are visualised in Appendix 5.3.

.

Table 5.3a: Correlation matrix for fish and crustacean variables and perimeter/area ratio of seagrass at distances of 0.5km – 9km. Significant relationships are in bold. MFB=mean fish biomass, MFA= mean fish abundance, MCA=mean crustacean abundance, MCB=mean crustacean biomass, CFS=cumulative fish species, Yhyal=*Yarica hyalosoma*, Ajap=*Acropoma japonicum*, Goyena=*Gerres oyena, Gfil=Gerres filamentosus, Psemicul=Penaeus semisulcatus,* Pindicus=*Penaeus indicus,* Pmonodon=*Penaeus monodon,* reefspp. =reef fish species.

	Fish and crustacean variables (R^2)												
Distance (km)	**MFB**	**MFA**	**MCA**	**MCB**	**CFS**	**Yhyal.**	**Ajap.**	**Goyena**	**Gfil**	**Psemisul.**	**Pindicus**	**Pmonodon**	**reefspp**
0.5	0.537	0.354	-0.166	-0.144	0.379	0.612	0.2	0.46	0.455	-0.229	0.123	-0.244	-0.307
1	**0.560**	0.032	0.053	-0.092	0.4	-0.169	0.201	-0.104	0.084	-0.216	**0.604**	-0.132	-0.186
1.5	0.454	-0.023	0.103	-0.025	0.4	-0.367	0.201	-0.243	-0.161	-0.225	**0.722**	-0.158	-0.256
2	-0.087	-0.238	0.324	0.114	0.003	**-0.560**	-0.096	-0.219	-0.466	0.01	**0.722**	0.195	-0.32
2.5	-0.212	-0.309	-0.346	0.064	-0.136	**-0.595**	-0.226	-0.075	-0.483	0.096	**0.564**	0.346	-0.286
3	-0.339	-0.489	0.356	-0.08	-0.318	**-0.555**	-0.524	0.11	**-0.595**	0.339	0.019	**0.540**	-0.086
3.5	**-0.551**	-0.533	0.369	-0.03	-0.477	-0.517	**-0.606**	0.148	**-0.687**	0.426	-0.159	**0.613**	0.006
4	-0.251	-0.49	0.297	0.096	-0.302	-0.44	**-0.559**	0.212	-0.442	0.282	0.013	0.511	-0.062
4.5	-0.254	-0.366	0.157	-0.187	-0.324	-0.174	**-0.583**	0.384	-0.274	0.277	-0.297	0.422	0.07
5	-0.395	-0.338	0.173	-0.139	0.444	-0.016	**-0.649**	0.454	-0.248	0.381	-0.463	0.488	0.169
5.5	-0.408	-0.28	0.113	-0.116	-0.445	0.174	**-0.630**	**0.544**	-0.095	0.358	**-0.547**	0.444	0.217
6	-0.401	-0.398	0.154	-0.12	-0.499	0.036	**-0.659**	0.51	-0.11	0.404	**-0.586**	0.512	0.162
6.5	-0.344	-0.35	0.286	-0.023	-0.436	0.083	**-0.568**	0.45	-0.083	0.525	**-0.549**	**0.563**	0.134
7	-0.285	-0.292	0.253	-0.063	-0.409	0.06	-0.476	0.445	-0.002	0.452	-0.465	**0.539**	0.057
7.5	-0.111	-0.331	0.237	-0.021	-0.301	-0.023	-0.378	0.373	0.106	0.375	-0.333	0.495	-0.096
8	-0.21	-0.441	0.305	0.072	-0.363	-0.106	-0.412	0.39	0.062	0.425	-0.317	**0.598**	-0.133
8.5	-0.283	-0.375	0.388	0.094	-0.393	-0.04	-0.332	0.429	-0.013	0.477	-0.362	**0.635**	-0.104
9	-0.308	-0.356	0.3	0.067	-0.42	0.028	-0.316	0.489	0.029	0.42	-0.325	**0.658**	-0.037

Table 5.3b: Simple linear regressions for fish and crustacean variables and perimeter/area ratio of seagrass at distances of 1.5km, 2km, 3.5km, 5.5km and 7km. Only species relationships with the highest R^2 and lowest p values are presented.

Response variable	Distance	F ratio	Model R^2	Model P	Bonferroni correction ($p<0.01$)	Slope
Fish variables						
Mean fish biomass	3.5km	7.41	0.38	0.019	NS	-ve
log 10 (x+1) *Acropoma japonicum*	3.5Km	6.97	0.36	0.023	NS	-ve
Gerres oyena	5.5Km	5.04	0.30	0.044	NS	+ve
Gerres filamentosus	3.5Km	10.72	0.47	0.007	S	-ve
Crustacean variables						
Penaeus indicus	1.5km	13.03	0.52	0.004	S	+ve
(log) *Penaeus monodon*	9km	9.15	0.43	0.011	S	+ve

*NS= not significant, S=significant

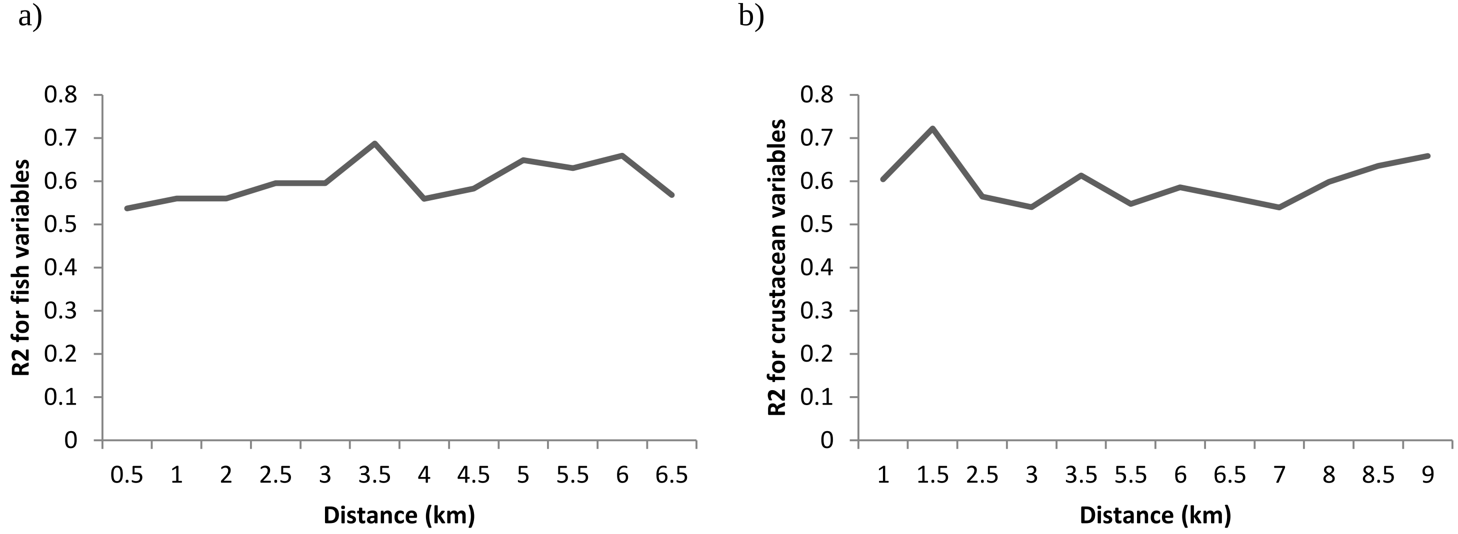


Figure 5.3: The R^2 of the corrrelationships between a) fish variables and b) crustacean variables, with perimeter/area ratio of seagrass at various distances

b) Perimeter of seagrass

A correlation matrix between perimeter of seagrass at various distances and fish and crustacean variables showed some correlations (Table 5.4a). These relationships were further explored using simple linear regressions. There were significant positive relationships between cumulative fish species and perimeter of seagrass at distances of 5 – 8km. Seagrass perimeter at 7.5km was able to predict 29.1% of the variation in (log) cumulative fish species ($F_{(1,12)}$=5.4; p=0.047). Reef fishes were correlated with perimeter of seagrass at 1.5km (R^2= 0.55, $F_{(1,12)}$= 14.61 ; p=0.002. For individual fish species, *G. filamentosus* had the strongest relationship with perimeter of seagrass at 4km

(R^2=0.47, $F_{(1, 12)}$= 10.48, p=0.007). Seagrass perimeter at 6km predicted the variation in *P. monodon* (R^2=0.33, $F_{(1, 12)}$=7.87, p=0.016) (Table 5.4b). These relationships are visualised in graphs in Appendix 5.4. From the correlation matrix, the highest R^2 in fish variables was at spatial extent of 4km fish and crustacean variables (Figure 5.4)

Table 5.4a: Correlation matrix for fish and crustacean variables and seagrass perimeter. Significant relationships are in bold. MFB=mean fish biomass, MFA= mean fish abundance, MCA=mean crustacean abundance, MCB=mean crustacean biomass, CFS=cumulative fish species, Yhyal=*Yarica hyalosoma*, Ajap=*Acropoma japonicum,* Goyena=*Gerres oyena, Gfil=Gerres filamentosus, Psemicul=Penaeus semisulcatus*, Pindicus=*Penaeus indicus*, Pmonodon=*Penaeus monodon*, reefspp.=reef fish species.

Distance (km)p	**Fish and crustacean variables (R^2)**												
	MFB	**MFA**	**MCA**	**MCB**	**CFS**	**Yhyal.**	**Ajap.**	**Goyena**	**Gfil**	**Psemisul.**	**Pindicus.**	**Pmonodon.**	**reef fishes**
0.5	-0.278	-0.116	-0.034	0.056	-0.408	0.064	-0.076	-0.068	0.021	0.143	-0.382	0.209	0.048
1	0.317	-0.126	-0.032	0.208	-0.465	0.373	-0.315	0.005	0.198	0.191	-0.482	0.09	0.268
1.5	0.104	-0.089	-0.082	-0.149	0.001	0.366	-0.22	0.401	-0.009	0.095	-0.043	0.171	**0.741**
2	0.049	-0.235	-0.105	-0.274	0.101	-0.089	0.035	0.242	-0.16	-0.026	-0.33	0.12	0.207
2.5	-0.122	-0.452	0.3	0.265	0.016	-0.484	-0.19	-0.115	-0.255	0.234	0.039	0.209	-0.125
3	-0.037	-0.289	0.265	0.13	0.051	-0.418	0.134	-0.31	-0.283	0.201	0.078	0.206	-0.244
3.5	-0.121	-0.269	0.291	0.099	0.092	-0.418	0.129	-0.092	-0.437	0.223	0.057	0.26	-0.127
4	-0.498	-0.48	0.324	0.145	-0.264	-0.511	-0.316	-0.149	**-0.683**	0.343	-0.141	0.349	0.078
4.5	0.157	-0.172	-0.06	-0.217	0.333	-0.386	-0.003	-0.055	**-0.619**	-0.151	0.099	-0.125	0.351
5	0.496	-0.015	-0.171	-0.128	**0.568**	-0.144	0.188	-0.124	-0.267	-0.287	0.178	-0.383	0.333
5.5	0.388	0.205	-0.34	-0.074	0.436	-0.02	0.389	-0.388	-0.015	-0.419	0.115	**-0.603**	0.131
6	0.263	0.27	-0.348	-0.036	0.41	-0.027	0.404	-0.366	-0.049	-0.496	0.293	**-0.629**	0.018
6.5	0.326	0.247	-0.044	0.127	0.464	-0.112	0.444	-0.435	-0.21	-0.277	0.516	-0.473	-0.023
7	0.243	0.048	-0.15	-0.086	0.292	-0.227	0.374	-0.266	-0.307	-0.343	0.338	-0.272	0.083
7.5	0.453	-0.036	-0.079	-0.048	**0.569**	-0.294	0.289	-0.134	-0.284	-0.289	0.388	-0.274	0.107
8	0.415	0.04	0.051	0.077	**0.543**	-0.284	0.38	-0.16	-0.207	-0.187	0.449	-0.237	-0.033
8.5	0.23	0.196	-0.031	0.094	0.337	-0.176	0.424	-0.285	-0.14	-0.183	0.285	-0.346	-0.23
9	0.146	0.129	-0.028	0.162	0.192	-0.067	0.409	0	0.056	-0.215	0.349	-0.099	-0.134

Table 5.4b: Simple linear regression of fish and crustacean variables with seagrass perimeter at distances of 1.5km,4km, 5km and 6km. Only the strongest relationships with the highest R^2 and the lowest p value are presented.

Response variable	**Distance**	**Df**	**R^2**	**P**	**Bonferroni correction (p<0.01)**	**Slope**
(log) cumulative fish species	7.5km	5.4	29.1	0.047	NS	+ve
Gerres filamentosus	4km	10.48	46.6	0.007	S	-ve
Reef fishes	1.5km	14.61	54.9	0.002	S	+ve
Penaeus monodon	6km	7.87	39.6	0.016	NS	-ve

*NS= not significant, S=significant

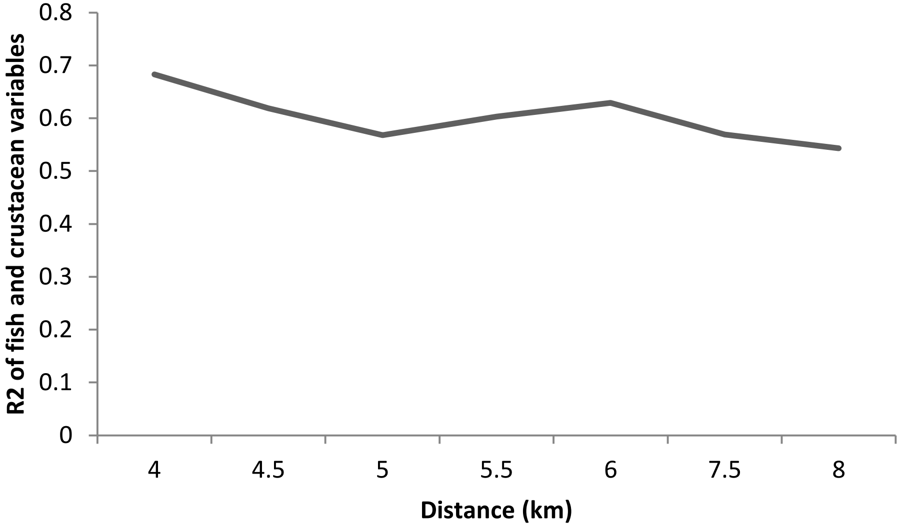


Figure 5.4: The R^2 of correlations between fish variables and crustacean variables with perimeter of seagrass at various distances

c) Cumulative area of seagrass

The results of a correlation matrix between cumulative area of seagrass and fish and crustacean variables are shown in Table 5.5a. A simple linear regression between the predictor variables and response variables showed that cumulative fish species were negatively correlated to cumulative area of seagrass at 0.5km (R^2=0.31, $F_{(1,12)}$=5.41; p=0.038). On the other hand, log(x+1) *Y. hyalosoma* abundance was positively related to cumulative area of seagrass at distances of 1.5km, 2km and 2.5km. The strongest relationship was at spatial extent of 2km of cumulative seagrass area (R^2=0.66, $F_{(1,12)}$=13.32, p=<0.001). (log) *Penaeus indicu*s was negatively related to cumulative seagrass area with the strongest relationship being at 2km (R^2=0.35, $F_{(1,12)}$=6.12, p=0.025) (Table 5.5b). Other relationships are shown in Appendix 5.1. From the correlation matrix, the trend of R^2 of fish and crustacean variables with the predictor variable is visualised in Figure 5.5. The highest R^2 was at 2km. Some of the strong relationships are visualised in Appendix 5.5

Table 5.5a: Correlation matrix for fish and crustacean variables and cumulative seagrass area. Significant relationships are in bold. MFB=mean fish biomass, MFA= mean fish abundance, MCA=mean crustacean abundance, MCB=mean crustacean biomass, CFS=cumulative fish species, Yhyal=*Yarica hyalosoma,* Ajap=*Acropoma japonicum,* Goyena=*Gerres oyena, Gfil=Gerres filamentosus, Psemicul=Penaeus semisulcatus,* Pindicus=*Penaeus indicus,* Pmonodon=*Penaeus monodon,* reefspp.=reef fish species.

	Fish and crustacean variables (R^2)												
Distance (km)	MFB	MFA	MCA	MCB	CFS	Yhyal.	Ajap.	Goyena	Gfil	Psemisul.	Pindicus	Pmonodon	reefspp
0.5	-0.423	-0.237	0.135	0.13	**-0.558**	-0.001	-0.242	-0.002	-0.037	0.35	-0.455	0.399	-0.082
1	-0.332	-0.118	-0.029	0.155	**-0.525**	0.371	-0.268	0.055	0.171	0.197	-0.503	0.162	0.233
1.5	-0.057	0.091	-0.197	0.003	-0.234	**0.649**	-0.137	0.352	0.394	0.047	**-0.547**	0.023	0.482
2	0.11	0.179	-0.325	-0.19	-0.086	**0.719**	-0.013	0.389	0.468	-0.073	**-0.581**	-0.087	0.492
2.5	0.103	-0.037	-0.201	-0.063	-0.087	**0.524**	-0.148	0.258	0.447	0.026	-0.534	-0.027	0.367
3	0.077	-0.047	-0.08	0.059	-0.068	0.389	-0.019	0.08	0.459	0.08	-0.375	0.019	0.169
3.5	-0.011	-0.139	0.052	0.033	-0.099	0.205	-0.033	0.047	0.284	0.194	-0.333	0.18	0.059
4	-0.265	-0.273	0.192	0.075	-0.267	0.041	-0.179	0.002	-0.018	0.374	0.349	-0.383	0.341
4.5	-0.244	-0.375	0.242	0.014	-0.21	-0.146	-0.232	-0.052	-0.268	0.332	-0.241	0.386	0.202
5	-0.05	-0.379	0.155	-0.069	-0.019	-0.238	-0.183	-0.129	-0.334	0.19	-0.133	0.23	0.259
5.5	0.006	-0.297	0.045	-0.137	0.006	-0.206	-0.162	-0.21	-0.323	0.095	-0.157	0.089	0.305
6	0.049	-0.159	-0.077	-0.17	0.052	-0.129	-0.093	-0.324	-0.282	-0.061	-0.046	-0.1	0.302
6.5	0.097	-0.101	-0.143	-0.202	0.104	-0.133	-0.075	-0.378	-0.271	-0.176	0.087	-0.208	0.258
7	0.077	-0.119	-0.149	-0.224	0.067	-0.161	-0.08	-0.401	-0.348	-0.199	0.123	-0.192	0.272
7.5	0.117	-0.122	-0.135	-0.249	0.148	-0.211	-0.082	-0.353	-0.433	-0.213	0.183	-0.189	0.313
8	0.206	-0.049	-0.129	-0.249	0.265	-0.225	0.004	-0.369	-0.444	-0.241	0.265	-0.254	0.297
8.5	0.244	0.034	-0.162	-0.239	0.306	-0.246	0.074	-0.474	-0.419	-0.297	0.326	-0.375	0.184
9	0.272	0.08	-0.179	-0.233	0.328	-0.263	0.134	-0.513	-0.423	-0.347	0.404	-0.418	0.141

Table 5.5b: Simple linear regression of cumulative mangrove fish species, *Yarica hyalosoma* and *Penaeus indicus* and cumulative area of seagrass at 0.5km and 2km. Only the strongest relationships with the highest R^2 and the lowest p value are presented.

Response variable	**Distance**	**F ratio**	**Model R^2**	**Model P**	**Bonferroni correction ($p<0.01$)**	**Slope**
Cumulative fish species	0.5km	5.41	31.1	0.038	NS	-ve
Log(x+1) *Yarica hyalosoma*	1.5km	9.13	58.0	0.001	S	+ve
	2km	13.32	63.2	0.001	S	+ve
(log) *Penaeus indicus*	2km	6.12	35.4	0.025	NS	-ve

*NS= not significant, S=significant

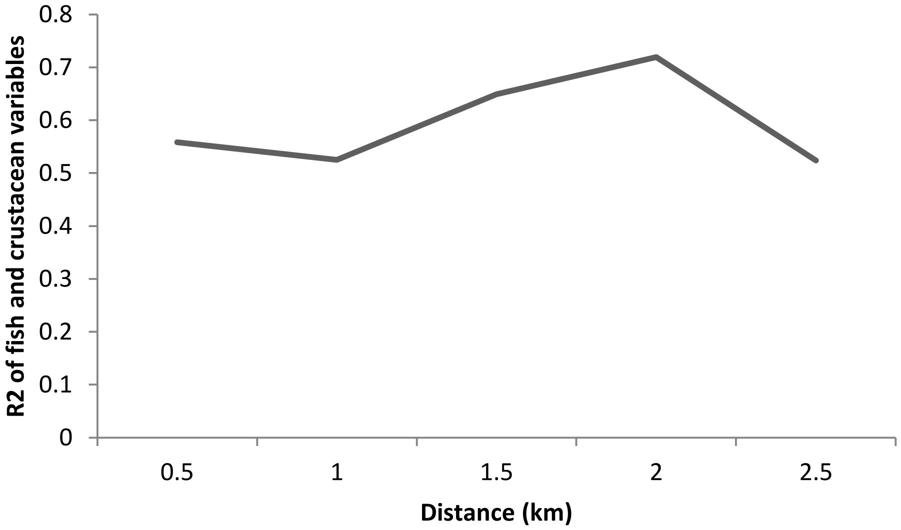


Figure 5.5: R^2 of the relationships between fish as well as crustacean variables with cumulative seagrass area.

d). Cumulative perimeter of seagrass

A correlation matrix between cumulative perimeter of seagrass and fish and crustacean variables demonstrated that *Y. hyalosoma*, *G.filamentosus* and *P.monodon* were correlated with the predictor variables. These relationships were further explored using simple linear regressions. A significant positive relationship between cumulative perimeter of seagrass at 0.5km was found with log(x+1) (*Y. hyalosoma* abundance (R^2 =0.64, $F_{(1,12)}$ =21.6, p=0.001) (Table 5.6a). There was a negative linear relationship between *P. monodon* and cumulative seagrass perimeter with the strongest correlation being at 4km (R^2= 0.33, $F_{(1,12)}$=5.82; p=0.033. Some of the strong relationships are visualised in Appendix 5.6. The peak R^2 ftom the correlation matrix for both fish and crustacean variables with cumulative perimeter of seagrass was at 0.5km (Table 5.6a; Figure 5.6).

Table 5.6a: Correlation matrix for fish and crustacean variables and cumulative perimeter of seagrass. Significant relationships are in bold. MFB=mean fish biomass, MFA= mean fish abundance, MCA=mean crustacean abundance, MCB=mean crustacean biomass, CFS=cumulative fish species, Yhyal=*Yarica hyalosoma,* Ajap=*Acropoma japonicum,* Goyena=*Gerres oyena, Gfil=Gerres filamentosus, Psemicul=Penaeus semisulcatus,* Pindicus=*Penaeus indicus,* Pmonodon=*Penaeus monodon,* reefspp.=reef fish species.

	Fish and crustacean variables (R^2)												
Distance (km)	**MFB**	**MFA**	**MCA**	**MCB**	**CFS**	**Yhyal.**	**Ajap.**	**Goyena**	**Gfil**	**Psemisul.**	**Pindicus**	**Pmonodon**	**reefspp**
0.5	0.132	0.3	-0.248	-0.117	-0.074	**0.802**	0.039	0.526	0.49	0.057	0.43	-0.06	0.422
1	0.111	0.183	-0.181	-0.015	-0.143	**0.741**	-0.09	0.386	0.495	-0.013	-0.365	-0.057	0.392
1.5	0.196	0.083	-0.144	-0.101	-0.046	**0.623**	-0.145	0.426	0.338	0.01	-0.333	0.033	0.554
2	0.145	-0.078	-0.134	-0.223	-0.09	0.457	-0.197	0.437	0.233	0.04	-0.416	0.156	0.506
2.5	0.009	-0.361	0.087	-0.069	-0.184	0.147	-0.401	0.339	0.119	0.225	-0.362	0.345	0.333
3	-0.152	-0.407	0.188	-0.01	-0.274	0.015	-0.36	0.18	0.008	0.341	-0.382	0.439	0.168
3.5	-0.302	-0.453	0.274	0.016	-0.342	-0.091	-0.363	0.147	-0.126	0.437	-0.403	**0.542**	0.092
4	-0.373	-0.502	0.327	0.026	-0.389	-0.179	-0.439	0.111	-0.247	0.465	-0.352	**0.572**	0.091
4.5	-0.33	-0.509	0.284	-0.073	-0.333	-0.216	-0.48	0.135	-0.362	0.414	-0.337	**0.535**	0.2
5	-0.243	-0.496	0.22	-0.126	-0.241	-0.215	-0.482	0.107	-0.405	0.348	-0.332	0.44	0.295
5.5	0.181	-0.4	0.092	-0.174	-0.193	-0.127	-0.425	0.032	-0.341	0.24	-0.37	0.275	0.351
6	-0.144	-0.331	0.004	-0.209	-0.158	-0.111	-0.385	-0.067	-0.313	0.128	-0.299	0.144	0.329
6.5	-0.072	-0.26	0.001	-0.202	-0.104	-0.094	-0.333	-0.145	-0.296	0.079	-0.17	0.068	0.295
7	-0.039	-0.242	-0.04	-0.253	-0.101	-0.138	-0.276	-0.221	-0.349	-0.008	-0.069	0.031	0.287
7.5	0.169	-0.229	-0.029	-0.262	0.171	-0.296	-0.152	0.277	-0.47	-0.115	0.187	-0.066	0.277
8	0.169	-0.229	-0.029	-0.262	0.171	-0.296	-0.152	-0.277	-0.47	-0.115	0.187	-0.066	0.277
8.5	0.196	-0.132	-0.049	-0.265	0.219	-0.329	-0.053	-0.407	**-0.529**	-0.162	0.258	-0.188	0.181
9	0.21	-0.087	-0.073	-0.273	0.219	-0.332	0.017	-0.43	**-0.541**	-0.239	0.38	-0.204	0.164

Table 5.6b: Simple linear regression of cumulative mangrove fish species, *Yarica hyalosoma* and *Penaeus monodon* and cumulative perimeter of seagrass at 0.5km, 1km and 4km. Only the strongest relationships with the highest R^2 and the lowest p value are presented

Response variable	**Distance**	**F ratio**	**Model R^2**	**Model P**	**Bonferroni correction (p<0.01)**	**Slope**
Log(x+1) *Yarica hyalosoma*	0.5km	21.59	44.27	0.009	S	+ve
	1km	14.58	49.85	0.005	S	+ve
Penaeus monodon	4km	5.82	32.67	0.033	NS	-ve

*NS= not significant, S=significant

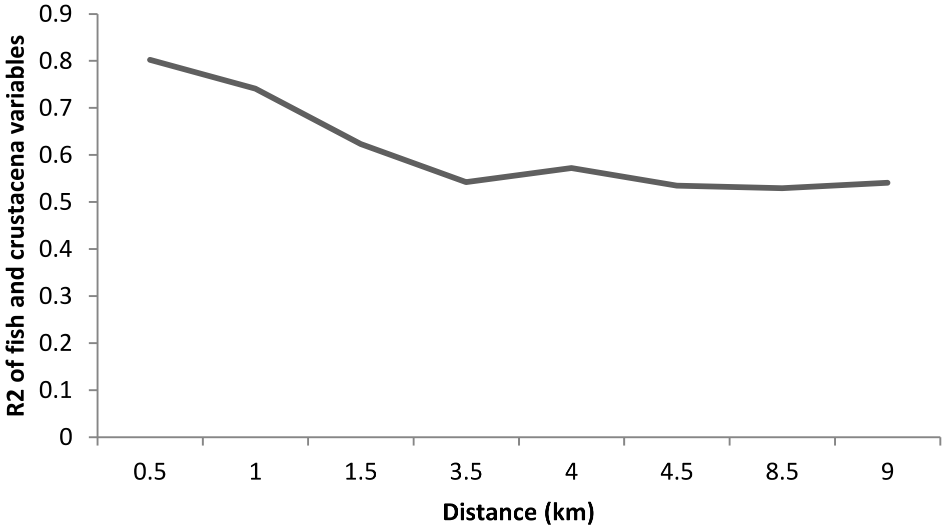


Figure 5.6: R^2 of the relationship between fish as well as crustacean variables and cumulative perimeter of seagrass at various distances

e). Seagrass area

The correlation matrix between seagrass area and fish and crustacean variables showed that only *Y.hyalosoma* was correlated to seagrass area (Table 5.7a). A simple linear regression between seagrass area and log(x+1) *Y.hyalosoma* at 1.5km showed a moderate positive relationship (R^2=0.66, $F_{(1,12)}$=23.44; p<0.001;Table 5.7b). Appendix 5.7 visualises the most significant relationship.

Table 5.7a: Correlation matrix for fish and crustacean variables and seagrass area. Significant relationships are in bold. MFB=mea 5.7 n fish biomass, MFA= mean fish abundance, MCA=mean crustacean abundance, MCB=mean crustacean biomass, CFS=cumulative fish species, Yhyal=*Yarica hyalosoma*, Ajap=*Acropoma japonicum,* Goyena=*Gerres oyena, Gfil=Gerres filamentosus, Psemicul=Penaeus semisulcatus*, Pindicus=*Penaeus indicus*, Pmonodon=*Penaeus monodon*, reefspp. = reef fish species.

Distance (km) a	**Fish and crustacean variables (R^2)**												
	MFB	MFA	MCA	MCB	CFS	Yhyal.	Ajap.	Goyena	Gfil.	Psemisul.	Pindicus	Pmonodon	reefspp
0.5	-0.389	-0.244	0.134	0.149	-0.504	-0.036	-0.191	-0.023	-0.071	0.331	-0.433	0.372	-0.077
1	-0.265	-0.077	-0.075	0.158	-0.451	0.438	-0.233	0.059	0.205	0.128	0.091	0.068	0.309
1.5	0.137	0.217	-0.29	-0.1	-0.009	**0.762**	-0.025	0.507	0.495	-0.061	-0.518	-0.078	0.603
2	0.455	0.281	-0.459	-0.437	0.329	**0.558**	0.314	0.298	0.394	-0.316	-0.398	-0.325	0.37
2.5	0.162	-0.341	0.143	0.236	0.216	-0.328	-0.044	-0.23	-0.063	0.061	0.1	-0.041	-0.11
3	0.173	-0.016	0.133	0.228	0.321	-0.293	0.417	-0.317	-0.08	-0.047	0.331	-0.106	-0.218
3.5	0.158	-0.112	0.116	0.054	0.33	-0.343	0.292	-0.292	0.311	-0.015	0.188	-0.02	0.066
4	-0.011	-0.156	0.126	0.126	0.192	-0.326	0.157	-0.151	-0.443	0.031	0.091	-0.018	0.104
4.5	0.262	-0.082	0.016	0.025	0.415	-0.335	0.26	-0.152	-0.375	-0.169	0.305	-0.169	0.107
5	0.364	-0.016	-0.082	0.001	0.473	-0.241	0.301	-0.16	-0.214	-0.239	0.245	-0.293	0.085
5.5	0.309	0.045	-0.11	0.02	0.419	-0.186	0.334	-0.194	-0.197	-0.235	0.175	-0.326	0.095
6	0.307	0.121	-0.131	0.057	0.447	-0.135	0.397	-0.213	-0.149	-0.303	0.302	-0.386	0.034
6.5	0.317	0.044	-0.09	0.045	0.457	-0.212	0.346	-0.186	-0.194	-0.275	0.322	-0.328	0.018
7	0.251	-0.024	-0.045	0.04	0.368	-0.229	0.309	-0.171	-0.272	-0.2	0.239	-0.223	0.076
7.5	0.296	-0.017	-0.036	0.023	0.456	-0.253	0.296	-0.127	-0.297	-0.198	0.262	-0.235	0.111
8	0.324	0.057	-0.026	0.062	0.471	-0.203	0.369	-0.138	-0.199	-0.188	0.264	-0.268	0.038
8.5	0.277	0.067	-0.051	0.084	0.404	-0.2	0.361	-0.19	-0.152	-0.2	0.238	-0.301	-0.051
9	0.248	0.029	-0.021	0.106	0.367	-0.175	0.347	-0.09	-0.136	-0.163	0.213	-0.203	-0.01

Table 5.7b: Simple linear regression of *Yarica hyalosoma* and *seagrass* area at 1.5km and 2km.

Response variable	**Distance**	**F ratio**	**Model R^2**	**Model P**	**Bonferroni correction (p<0.01)**	**Slope**
log (x+1) *Yarica hyalosoma*	1.5km	23.44	66.11	<0.001	S	+ve
log (x+1) *Yarica hyalosoma*	2 km	5.42	31.12	0.038	NS	+ve

*NS= not significant, S=significant

5.3.2 Fish communities

The multiple linear regression models that best predicted fish variables and seagrass metrics were computed. The composite fish variables i.e. mean fish biomass and mean fish abundance, cumulative fish species and the total abundance of fish species; *G. oyena*, *A. japonicum*, *Y. hyalosoma* and *G. filamentosus* (most abundant fish species) were associated with seagrass metrics at various distances. Only the strongest models for each fish variable are shown in Table 5.8 with other significant relationships shown in Appendix 5.2.

The multiple linear regression models that best predicted mean mangrove fish biomass and mean mangrove fish abundance was at the 2km buffer. Three predictors i.e. seagrass area, cumulative perimeter and perimeter explained 61% of mean mangrove fish abundance at 2km (R^2=0.61, $F_{(3,10)}$=5.24, p=0.020) while seagrass area, cumulative area and perimeter explained 56% of the variation in mean mangrove fish biomass ($F_{(3, 10)}$=4.33, p=0.034). Seagrass area was positively correlated with mean fish biomass while cumulative area and perimeter were negatively correlated (Table 5.8). The abundance of *G. oyena* was influenced by seagrass perimeter, cumulative perimeter and perimeter/area ratio at 1km (R^2=0.55, $F_{(3,10)}$=4.03, p=0.039). The abundance of *A. japonicum* responded to seascape metrics**.** Three multiple linear regression models were developed at distances of 3.5km, 5km and 9km that showed significant relationships with *A. japonicum* abundance and cumulative area, cumulative perimeter and perimeter/area ratio. The strongest multiple linear regression model between *A. japonicum* and cumulative seagrass area and perimeter/area ratio of seagrass was at 3.5km (R^2 =0.81, $F_{(2,11)}$=24.31, p<0.001 (Table 5.8). The strongest multiple linear regression model for *Y. hyalosoma* and seagrass metrics was at spatial extent of 1.5km. The model predicted 75% of the *Y. hyalosoma* abundance ($F_{(2,11)}$=17.19, p<0.001).

Table 5.8.: Multiple linear regression models for response variables: mean fish biomass, mean fish abundance and species, *G. oyena*, *A. japonicum*, *Y. hyalosoma* and *G. filamentosus* and independent variables (area, perimeter, cumulative perimeter and cumulative area and perimeter/area ratio) at distances of:1km, 1.5km, 2km and 3.5km. The coefficients for the independent variables indicate whether the relationship is positive or negative.

Response variable	**Predictor variable (Distance)**	**Coefficients**	**Df**	**Model F ratio**	**Model R^2**	**P**	**Bonferroni correction (p<0.01)**	**VIF**
Mean fish biomass	2km		3,10	4.33	0.56	0.034	NS	
	Area	556						4.22
	Cumulative area	-121.5						2.57
	Perimeter	-6.39						2.27
Mean fish abundance	2km		3,10	5.24	0.61	0.02	NS	
	Area	64.7						2.87
	Cumulative perimeter	-0.34						1.82
	Perimeter	-0.99						1.81
Gerres oyena	1km		3,10	4.03	0.55	0.039	NS	
	Cumulative perimeter	0.823						2.84
	Perimeter	1.691						4.16
	Perimeter/area ratio	0.03						2.16
Acropoma japonicum	3.5km		2,11	24.31	0.81	<0.001	S	
	Cumulative area	-7.04						1.1
	Perimeter/area ratio	-3.57						1.1
Yarica hyalosoma	1.5km		2,11	17.19	0.75	<0.001	S	
	Area	213.7						2.79
	Perimeter	3.03						2.79
Gerres filamentosus	1.5km		2,11	13.06	0.7	0.001	S	
	Area	38.05						2.79
	Perimeter	-0.85						2.79

*NS= not significant, S= significant

Multiple linear regression models for *G. filamentosus* abundance and seagrass metrics were developed at spatial distances 1.5km, 2km and 3.5km. The model with the strongest R^2 and the lowest p was at distance 1.5km (R^2=0.70, $F_{(2, 11)}$=13.06, p=0.001) (Table 5.8). The partial correlations were positive for area and negative for perimeter. Other significant models mentioned in here are shown in Appendix 5.2.

5.3.3 Crustacean Communities

Penaeus monodon was the only crustacean species for which multiple linear regression models were possible at 2km, 3.5km and 5.5km from mangroves. The model that had the strongest R^2 and lowest p value was at 5.5km (R^2=0.66, $F_{(3, 10)}$=6.5, p=0.010). The other modelsat 2km was almost as strong with R^2 of 0.65 (Table 5.9).

Table 5.9: Multiple linear regression models for response variable *P. monodon* and independent variables: area, perimeter, cumulative perimeter, and cumulative area at distances of 2km, and 5.5km. The coefficients for the independent variables indicate whether the relationship is positive or negative.

Response variable	**Predictor variable (Distance)**	**Coefficients**	**Df**	**Model F ratio**	**Model R^2**	**P**	**Bonferronic orrection (p<0.01)**	**VIF**
Penaeus monodon	2km		3,10	5.24	0.65	0.011	S	
	Area	-18.84						
	Cumulative perimeter	0.113						
	Perimeter	0.23						
Penaeus monodon	5.5km		3,10	6.5	0.66	0.010	S	
	Area	2.6						
	Cumulative area	1.42						
	Perimeter	-0.26						

*NS= not significant, S= significant

Seagrass area had a negative coefficient at 2km distance but a positive partial correlation in the other models, while perimeter of seagrass had negative partial correlations. Other models are shown in Appendix 5.1.

5.4 Discussion

Some of the seagrass metrics (area, perimeter and perimeter/area ratio) demonstrated strong relationships with fish and crustaceans sampled in the 14 mangrove sites in the Vanga seascape. Crustaceans were generally positively correlated with perimeter/area ratio of seagrass while fish variables were generally positively correlated with seagrass area and perimeter at various distances. However, no single variable derived from the seagrass metrics proved to be a strong predictor for all the fish and crustacean responses, hence these results do not support any simple message of increased abundance or diversity of all groups with increased seagrass in the vicinity of mangroves.

5.4.1 Perimeter/area ratio of seagrass

Compared to other seagrass metrics, more fish and crustacean variables co varied with the perimeter/area ratio. Generally, crustaceans were positively correlated to perimeter/area ratio of seagrass. For example, perimeter/area ratio exhibited positive moderate relationships with abundance of *P. indicus* (R^2=0.52) and log *P. monodon* (R^2=0.43). In contrast, key fish variables (mean fish biomass, *Y. hyalosoma*, *A. japonicum* abundance and *G. filamentosus* abundance) were negatively correlated to perimeter/area ratio.

Other studies have found perimeter/area ratio to positively influence faunal assemblages in varying habitats. Like the crustaceans in this study that were positively associated with perimeter/area ratio of seagrass, the density of *Lutjanus griseus* in the Gulf of Mexico responded strongly positively to perimeter/area ratio of mangroves (Drew & Eggleston, 2008). Further, in the marsh creeks of Essex and Suffolk, UK, the perimeter/area ratio of the marsh creek was among the factors that explained fish populations and densities in these estuaries (Green et al., 2012). Using artificial seagrass units, Jelbart et al. (2006) found a slight but indirect positive relationship between perimeter/area ratio and fish species diversity. Patch isolation and perimeter/area ratios were important influencers of fish settlement in eastern coast of Australia. In the Phillipines however, (Salita et al., 2003) found perimeter/area ratio ineffective in structuring faunal assemblages in seagrass meadows. The perimeter/area ratio of the patches increases with increased fragmentation (Macreadie et al., 2009) and also with increasing edge (Green et al., 2012). Therefore, it is likely that the fish and crustacean variables were also responding to the fragmentation and edge of the seagrass patches in different ways. In line with this theory, Green et al. (2012) found the perimeter of mangrove patches to negatively affect fish assemblages and suggested that high perimeter implied increased fragmentation, which made the juveniles vulnerable to higher predation risk. Hence one message that emerges is that fish and crustaceans are, in general, responding differently to the geometry of seagrass, with key fish species showing negative responses to greater seagrass perimeter/area ratio whilst crustaceans respond positively.

5.4.2 Seagrass perimeter and area

In this study, seagrass perimeter was correlated to cumulative fish species and the abundance of *Y.hyalosoma* was positively correlated to seagrass perimeter while the abundance of *G. filamentosus* and *P. monodon* were negatively correlated with seagrass perimeter. Seagrass area was positively correlated to the abundances of *Y. hyalosoma* and negatively correlated to abundance of *P. indicus* up to a spatial extent of 2.5km. Other fish and crustacean variables did not show relationships with both perimeter and area. Jelbart et al. (2007) found that smaller seagrass beds had greater densities of small fish compared to beds of medium and large areas. Similarly, in North Carolina, USA, *Palaemonidae* sp., amphipods and isopods had higher densities in smaller patch sizes (0.25m^2) than large (1m^2) patch sizes of artificial seagrass, oyster shells or a mixture of both (Eggleston et al., 1999). Using natural and artificial seagrass units, (Jelbart et al., 2006) found higher species richness in smaller areas as opposed to larger areas.

In this study, less than four fish and crustacean species responded significantly to seagrass area. This could be partly due to small sample sizes of most of the fish and crustaceans caught in mangrove areas. As well, such results are not uncommon in seascape studies. One review on seascape studies found that only 33% of the fauna studied responded either positively or negatively to seascape metrics (Connolly & Hindell, 2006), while a more recent one concluded that about 30% and 25% of the fish and invertebrates respectively responded to the patch size of the habitats under study (Bostrom et al., 2011). Bostrom et al. (2011) further found that invertebrates were more likely to have a positive rather than a negative relationship with patch size of the various seascape structures studied. Similarly to these contradicting results, this study found that the fish and crustacean variables that responded to seagrass patch size in various distances responded in different directions.

5.4.3 Distance

Most seascape data has shown strong evidence that the seascape structures at close proximity tend to influence faunal community assemblages. In this study, we generally found that *P. indicus* abundance and *Y. hyalosoma* abundance co varied with seagrass metrics that were in close proximity to the mangrove sampling sites (0.5 – 2.5km), with the strength of relationships generally declining at greater distances. Studies from Puerto Rico found similar results where the abundance of the juvenile French grunt, *Haemulon flavolineatum,* was found to be significantly higher in mangroves that were <100m from seagrass beds and had >40% cover (Pittman et al., 2007). Seagrass beds near mangroves in southeastern Australia and the Indo Pacific were found to host significantly higher abundances and diversity of mangrove dependent fish species whose numbers dropped with decreasing proximity (Connolly & Hindell, 2006; Jelbart et al., 2007; Unsworth et al., 2007). In Moreton Bay Australia, seagrass adjacent to mangroves harboured high abundances of penaeid shrimp *Penaeus plebejus* and *Metapenaeus bennettae* compared to other habitats (Skilleter et al., 2005). In the Caribbean, coral reefs that were >9km from mangroves and seagrasses, were totally lacking or showed diminished abundances of the species that utilise these habitats as nurseries (Dorenbosch et al., 2007). It is thought that one of the reasons as to why proximity contributes to species richness and diversity could be because adjacent structures tend to be extended areas for refuge and food for the fauna (Unsworth et al., 2007).

Other findings in this study showed that for most of the time. the abundance of *P. monodon* was not correlated to the seagrass metrics in adjacent sampling sites in the mangroves (0.5km - 2.5km) but was strongly correlated to seagrass metrics at further distances (3 - 9km). For instance, perimeter/area ratio was positively correlated to the abundance of *P. monodon* at spatial extent of 9km from the mangrove fish sampling site. In this study, it could be that fragmentation of seagrass (see Macreadie et al., 2009) at further distances could have led to an increase in the abundance of *P. monodon*. Though such responses are not common, a number of studies have recorded instances where faunal diversity and abundance have been found to increase with increasing distance of seagrass from mangroves, especially for non-mangrove species (Connolly & Hindell, 2006). In Moreton Bay Australia, Skilleter et al. (2005) found *Penaeus esculentus* abundance was higher in seagrass beds further away from the mangroves although they could not find a possible explanation due to the scope of the study. In this study, proximal seagrass metrics were more important to both fish and crustacean assemblages than the distal ones. However, it was not clearly understood as to why *P. monodon* abundance responded to seagrass that were at a further distance from sampling sites. Adults of this species are found offshore in waters that are 20 - 40m deep (Motoh, 1985) and hence may be moving over larger distances than other species in this study.

5.5 Conclusions

The current results support the importance of seagrass for faunal species using mangroves, because there were numerous significant and often strong relationships observed. However, there are no simple associations that apply equally to all species. In general, the composite fish variables (along with the single species variables for the dominant species) showed positive relationships with metrics associated with total seagrass area within ≤5km of each mangrove site, whilst the results for crustaceans showed the opposite trend. These findings are consistent with and help to explain those of chapter 3 that show that, in general, sites within Vanga that had high diversity nd biomass generally showed low abundance and biomass for crustaceans and vice versa.

Whilst strong correlations were generally found with metrics from relatively close distances, in some cases significant associations extended up to 9km, genuine causal effects may well be possible up to and beyond such distances. However they may also reflect type 1 errors that are likely in correlational work such as this that explore multiple possible relationships without the opportunity for experimental tests of causality.

In conclusion, this study has found seagrass metrics in Vanga to be important in structuring fish and crustacean variables in the sampled mangrove sites and such metrics should therefore be considered in holisitic coastal management. Penaeid shrimp, (*P. monodon* and *P. indicus)* are important commercial species at the Kenyan coast as well as globally and therefore sustainable conservation efforts should consider what aspects of the seascape should be considered. It is no longer feasible to isolate habitats in the seascape. Also, since different species respond differently to seascape metrics, it is important to take a species-specific approach in identifying and prioritising areas for conservation. The knowledge from this study will form the baseline information upon which future studies on the seascape can be built and expanded.

6.0 CHAPTER 6: SYNTHESIS, CONCLUSIONS AND RECOMMENDATIONS

6.1 Introduction

The contribution of mangroves to human wellbeing through the provision of various ecosystem goods and services is well established (Costanza et al., 1997; MA, 2005). Specifically, their role in coastal fisheries and as nursery habitats for juvenile fish is well documented (Barbier, 2000; Mumby et al., 2004; Paillon et al., 2014). Over the years, the overexploitation of mangrove goods, especially wood (Alongi, 2002), and the conversion of mangroves to alternative uses has led to a severe reduction in their acreage (exceeding 35%); (Naylor et al., 2000; Valiela et al., 2001; Giri et al., 2011), which has negatively affected their nursery function (Mwandya et al., 2009; Blaber, 2013). However, the causal mechanisms underpinning the nursery function remain contested, the strength of the relationship is site dependent and the consequences of less dramatic changes in mangrove ecosystems than total removal – especially partial removal and degradation – remain unknown. Whilst high levels of spatial variability are routinely reported in studies of ichthyofauna in mangroves, explanations for this remain speculative and little is known about the consistency of any local site effects at medium (0.5-5km) scales; for example whether sites routinely hosted high fish diversity and biomass or weakly supported biomass and diversity. The current study sought to explore and understand variation in fish and crustacean community structure among sites within a single large mangrove forest, with the aim of contributing both fundamental understanding and insights of use to fisheries and coastal managers.

6.1.1 Fish and crustacean assemblages in Vanga mangrove ecosystems

A total of 59 finfish and 16 crustacean species were sampled using fyke nets placed within mangrove creeks in this study. These species totals were broadly representative of similar studies in the region (Mwandya et al., 2010; Wainaina et al., 2012). About 50% of the fish catches were of commercial importance (Froese & Pauly, 2017). All catches were dominated by juveniles; 100% of key species such as *Leiognathu equulus, Lutjanus fulviflamma* and *M. argenteus* were made up of small juveniles, with others such as *Gerres oyena* having 97% small juveniles. The fact that over 90% of the fish caught in this study were juveniles is consistent with the nursery hypothesis for mangroves (Beck et al., 2001), although a rigorous test of this would require comparisons of fish densities with other habitats and tracing of fish migration and survival to adult habitats.

Significant differences were observed in the mean fish abundance between SEM and NEM seasons with the highest abundances being recorded in SEM. In the mangroves of Gazi, Kenya, Crona & Rönnbäck (2007) found juvenile fish to have higher abundances in the SEM than in the NEM season. On the contrary, densities of larval assemblages in Marine parks in Kenya were higher in NEM when waters were calm compared to the rougher SEM season (Mwaluma et al., 2011). There could be a possibility then that these fish move into the nursery habitats during the rougher SEM season. An important exception to this pattern was for fishes in the Ambassidae family. Whilst this family is generally uncommon in intertidal areas of Kenya's south and north coast, it was amongst the most abundant in the present study (contributing 18.4% in abundance) and only appeared in the NEM season. Further studies into the life cycles of its species may help shed more light on its ecology.

The Serranidae family was the most diverse, with the genus *Epinephelus* dominating the catch (5 species). However all the species caught were represented by single individuals. *Epinephelus* is a highly commercial genus that has experienced a sharp decline at the Kenya coast over the last three decades (Kaunda-Arara, 1996; Kaunda-arara et al., 2003). A study on the distribution of Serranidae along the south coast of Kenya showed Vanga to have the lowest species diversity (8 species) compared to other locations like Msambweni and Shimoni (Agembe et al., 2010). Its high commercial value and sedentary nature could have exposed this family to high mortality (Kaunda-arara et al., 2003; Sadovy, 2005) . Dynamite fishing in Vanga by fishermen from neighbouring Tanzania has also been suggested as the cause of these low numbers (Samoilys, 1988). The results of the present study – showing low abundance and relatively low diversity - therefore confirm previous findings that this diverse and commercially important genus could be threatened and this creates concern for its future survival.

Penaeid shrimp were the most abundant crustaceans comprising 90% of the crustaceans caught in this study with *P. semisulcatus* and *P. indicus* being the most dominant. About 50% of crustacean species sampled were of commercial importance (based on information from FishBase, Froese & Pauly, 2017). Generally crustaceans did not show any clear seasonality in this study. In Malindi-Ungwana bay, Kenya (a commercial prawn trawling area), gravid prawns of all penaeid species were recorded all year round with their abundance peaking in December, February and March (Mwatha, 2002). Similarly, in the same area, *P. indicus* was among the most abundant of penaeid species (Munga et al., 2013; Ndoro et al., 2014). Munga et al. (2013) found significantly higher prawn densities in SEM compared to NEM while Ndoro et al. (2014) found the biomass of penaeid prawns to be high in NEM with no seasonliaty in abundance. The apparent lack of seasonality for penaeid shrimp means that exploitation can continue throughout the year. The risk of overfishing is real especially for juveniles that use intertidal areas as nurseries. In order to protect the stocks, which use mangroves as nurseries, from overfishing, Mwatha (2002) suggested that the fishery should be closed in February, December and March, the peak months for gravid females. Frequent fishing of juvenile shrimp could also lead to losses as they fetch a poor price in the market (Watson et al., 1993).

The intertidal and shallow subtidal areas of the ocean are very important for artisanal fishers in Kenya’s south coast, who fish using traditional fishing vessels and gears (Ochiewo, 2004). Fishers use gears such as basket traps, fence traps, hand lines and seine nets among others to fish (McClanahan & Mangi, 2004). Continued unregulated fishing, with no control on effort or on damaging gear, in these nursery areas could further increase overfishing of juveniles and thus jeopardizing the future of the fishery.

6.1.2 Effects of forest quality on fish and crustacean assemblages

Enhanced biomass and diversity in coastal fish assemblages are associated with more complex, in comparison with simpler, habitats (Lefcheck et al., 2019). Substantial literature explores what structural features of mangroves might attract fish at very local scales (Laegdsgaard & Johnson, 2001; Loneragan et al., 2005; Manson et al., 2005). The relationship between structural complexity of the forest and faunal abundance has been widely studied (Blaber & Milton, 1990; Taniguchi et al., 2003; De La Morinière et al., 2004). For example field studies and laboratory experiments have shown complex mangrove roots provide refuge for juvenile fish by deterring predators from attacking them (Laegdsgaard & Johnson, 2001; Macia et al., 2003; Sheridan & Hays, 2003). Environmental parameters have also been found to influence juvenile assemblages in mangrove areas (Blaber et al., 1995; De La Morinière et al., 2004; Rezagholinejad et al., 2016). This work, conducted mostly at small (meter) scales, implies that differences in fish and crustacean communities measured among sites at larger (100s m – km) scales should be predictable and relate to forest characteristics. However it should be noted that the role of scale in ecology is rarely simple or predictable. It could also vary between habitats and faunal groups or even species.

Forest structure is related to, and helps to determine, the quality of forests. However ‘quality’ as a characteristic may depend on the ecosystem service in question; in most of the literature it is equated to high standing stocks and/or relatively pristine conditions with little human impact. Comparisons of state managed and community managed forests in the Philippines revealed that community managed forests were of better quality based on higher tree height and bigger basal area (Sudtongkong & Webb, 2008). Likewise, in Mida creek Kenya, mangrove forests that were more difficult to access and therefore less disturbed had trees of higher height and bigger basal area compared to easily accessible ones (Kairo et al., 2002). Across the whole Kenyan coast the highest quality forests, as defined by standing stocks of carbon, are found in the far north in areas with low populations that are difficult for people to access (Huxham et al., 2015). Walters (2004) also recorded that trees in an uncut forest had bigger basal area (higher diameter at breast height) compared to those of a cut forest. The research question that has remained unanswered is how these forest features (tree height, basal area, and stem density), which describe the nature of the forest in terms of quality for standing stock, influence the icthyofauna that use these habitats as nurseries?

In the current study, the Complexity Index (C.I.) was used as a summary measure for forest quality, with a high C.I. denoting good forest quality and vice versa (Chapter 3). C.I. is a composite product of forest features: stem density, number of species, mean tree height and basal area. It was expected that fish and crustacean variables would be positively associated with the C.I. as it is envisaged that a degraded forest (poor quality) would be less attractive to faunal assemblages compared to a good quality one. However simple patterns that were consistent across groups did not emerge. The C.I. explained 44%, 41.5% and 40.6% the variation of mean crustacean abundance and of the key species *P. monodon* and *P. semisulcatus* respectively, which all increased with increasing C.I. Meanwhile mean fish abundance decreased with increasing C.I., a relationship, which explained 32.2% of the variation (Chapter 3). These findings, in which fish and crustaceans responded differently to forest quality as measured by the C.I., were reflected in the ranking of forest sites for faunal quality. An important initial conclusion was that sites showed consistency over time in their relative importance for fauna; the spatial variability was not random. Further, sites that had the lowest diversity and mean fish biomass (sites 14, 7 and 1) recorded some of the highest mean abundance and mean biomass for crustaceans. This is a key finding in this study and it clearly shows that management efforts directed at maintaining nursery areas cannot be general but, as in this case, would need to address fish and crustacean species (and maybe other organisms) separately.

There are no direct explanations as to why crustaceans responded positively to increasing C.I. and fish responded negatively. The C.I. is positively related to basal area, which is positively related to the size of trees – (height). For example on the coasts of Florida, Mexico, Puerto Rica and Costa Rica, Pool et al. (1977) found that mangrove forests with taller trees and thicker girths had higher C.I. than shorter thinner trees. Similarly, the post hurricane Joan mangrove forest structure in Nicaragua had a low C.I. since older tress (taller with bigger diameters) had been destroyed (Roth, 1992). Therefore, high C.I. implies older trees. These are also generally less dense. Younger forests tend to have higher tree density, low basal area and height, and tend to have low C.I.s. The current study therefore suggests that fish may be using dense trees and roots –

possibly in younger stands – whilst shrimp prefer areas of open mud to burrow in (normally found in older forests). For instance, although penaeid shrimp inhabit mangrove areas, most are found in creeks (Vance et al., 2002) and mangrove fringes (Rönnbäck et al., 2002) where structural complexity is low. For example, at Inhanca Island, Mozambique, higher densities of shrimp, especially *P. indicus,* were generally found in the mangrove fringe rather than inside the forest. In Oman, post larvae and pre adults of *P. indicus* preferred muddy bottoms, where they occurred in high densities (Mohan & Siddeek, 1996). *Metapenaeus monoceros* preferred open sandflats to mangrove habitat (Rönnbäck et al., 2002).

In this study, forest characteristics measured at both broad (500m – 1km ambit) and fine (100m ambit) scales were tested against faunal assemblages caught in the creeks. Only the broad scale habitat attributes were found to be useful in predicting fish and crustacean assemblages in mangrove forests. The use of fyke nets in mangrove creeks to sample fish during the ebb tide meant that an area greater than the immediate $100m^2$ was sampled, since captured fauna will have travelled further up creeks and into the forest during the flood tide, possibly hundreds of metres away from the catch site. Since it was not possible to know how far into the forest the fish travelled before they were caught, the area sampled remains unknown. However the relevance of broad, rather than fine, scales of measurement in explaining faunal communities is congruent with an understanding of fauna using the whole forest during high tide (rather than, for example, remaining in the creeks).

Berkström et al. (2012), using scales similar to those of this study to investigate the influence of seascape on fauna in Zanzibar, found both scales to be important in structuring faunal assemblages. To the best of my knowledge, this is the first study that has attempted to link forest attributes at a medium scale (of 10s m – 100s m) and faunal assemblages. The results generated from this study can only be considered preliminary and hopefully more studies to investigate these relationships will be carried out in the future. In particular, better knowledge on how far individual fish and crustaceans move into the mangroves would help to inform the relevant scales for further studies and for management decisions that might impact the quality of the forest as a nursery habitat.

6.1.3 Diet

One of the reasons that nursery areas are postulated to attract fish is their provision of food to juveniles (Laegdsgaard & Johnson, 2001; Grol et al., 2014). The utility of mangroves as feeding areas appears to vary between regions. In the Caribbean (small tidal ranges) most fish species have been found to feed in seagrass beds adjacent to mangroves (Nagelkerken & Velde, 2004). In the Indo – Pacific (wide tidal ranges), mangroves are important feeding areas for fish (Nagelkerken & Velde, 2004; Lugendo et al., 2007).

Using stomach content analysis, this study sought to establish what the fish ate shortly before they were caught. Fyke nets were deployed at mangrove creek mouths to target only fish leaving the forest at ebb tide. Hence some or most of the prey items found inside the stomachs were caught within the mangroves. For instance, the results show that all the six fish species that were dissected had ingested insects. The insects were most likely from a terrestrial origin and meaning that they occurred inside mangrove forests. Finding and identifying insect remains clearly demonstrates feeding by these fish within the mangrove habitat during the preceding high tide period (i.e. 4-6 hours). Some scientists have provided some insight on the time taken to digest prey items in the stomachs of some fish species. Residence times within fish stomachs are generally small. For example, while analysing the stomachs of two predator species, Legler et al. (2010) documented that the newly hatched larvae ingested were all identified in the prey's stomachs under two hours of feeding, while there was a 50% chance of identifying remains, 2 - 4 hours after ingestion. This strongly suggests that these fish species partially fed inside the forest and supports the theory of juvenile fishes seeking mangrove habitats for feeding.

This study also found that a majority of the fish species sampled had narrow diet breadths (B_i=0.08 to 0.17) with only one species having a B_i of 0.45 (Chapter 4). *Gerres oyena* and *L. equulus* preyed on eight and nine prey categories respectively, but both had a low B_i of 0.11 and 0.17 respectively. This means that the proportions of diverse prey ingested were too small to influence the B_i. In a similar study, these two species were classified as 'generalist' meaning they maximised their predation on the available prey items (Mavuti et al., 2004). Narrow diet breadths are not uncommon in nearshore areas. In a coastal lagoon of southeastern Mexico, six fish species had diet breadths (B_i) that ranged from 0.026 – 0.163 (Arceo-Carranza & Chiappa-Carrara., 2015). Apart from the generalistic feeding behaviour, another reason for low B_i could be that prey items appeared in low number or that feeding competition was high making it difficult for the fish species to ingest substantial amounts of the different prey items.

This study did not investigate the food availability in the mangrove sampling sites to determine what prompted the fish to feed on what they fed on. It is known that several factors (apart from food availability) determine the stomach contents of fish. Ley et al. (1994) examined the stomachs of some fish species in north-eastern Florida Bay areas with varying salinity. Fish ingested poor quality diets in upstream areas (high salinity variation) and good quality diet downstream (low salinity variation). The variation in stomach contents in that case was as a result of habitat quality (variation in salinity) and not food availability. There was no evidence that fish in ‘good sites’ (Chapter 3) had greater access to a higher abundance or quality of prey than those in ‘poor sites’ (for example there was no difference in stomach fullness or the types of items consumed among sites). Thus factors other than food availability, such as the provision of predator refuges or ease of safe access from the bay, are more likely to have driven differences in fish communities between sites.

Overall, this study was limited in the number of stomach samples that were studied, since most species were too few to provide appropriate sample numbers; in particular species feeding at higher trophic levels were very rare. The lack of consistent numbers of samples between seasons made it difficult to explore the seasonality of diets because some of the species appeared in very low numbers in some seasons.

6.1.4 Effects of seascape on fish communities in mangrove areas

Studies that consider the influence of single coastal habitats on faunal assemblages have often failed to fully explain the relationships found (Kendall, 2005). There is increasing appreciation of the role played by adjacent habitats and the spatial complexity of the seascape in structuring faunal communities (Kendall, 2005; Dorenbosch et al., 2007; Meynecke et al., 2008; Bostrom et al., 2011). In chapter 3 of this thesis, investigations into the influence of mangrove forest features on fish and crustacean variables showed that, whilst some variables showed significant relationships, most results were of limited strength and much variability remained unexplained. It was thus speculated that the seascape, especially spatial features related to the seagrass beds, could be influencing the faunal assemblages and further investigations were conducted.

In this study, some of the fish and crustacean variables were strongly associated with seagrass metrics. The perimeter/area ratio of seagrass – which will increase with increasing fragmentation and decreasing patch size of seagrass - proved the best predictor. Fish and crustacean variables were generally negatively and positively associated with this metric respectively. The abundance of *P. indicus* gave the strongest association at a distance of 2km (R^2=0.72,) and *P. monodon* abundance was also significantly positively correlated to perimeter/area ratio (R^2=0.66). Generally, fish variables e.g. mean fish biomass, *Y. hyalosoma* abundance and *G. filamentosus* abundance, were negatively correlated with perimeter/area ratio and positively correlated with seagrass area. Hence, fishes and crustaceans responded differently to the seascape metrics, just as they did to forest attributes (with fishes showing a negative relationship and crustaceans a positive relationship with C.I.). It seems that fishes preferred mangrove/seagrass seascapes with large amounts of seagrass and dense juvenile trees with low C.I. The mangrove and seagrass could be providing hiding places for the juveniles from predators. On the other hand, crustaceans (penaeid shrimp) seem to prefer older less dense mangrove sites with fragmented seagrass in the seascape. Older and fragmented patches provide some bare areas with either sand or muddy bottoms where the shrimp could burrow and hide.

The spatial area over which seascape features may exert influence on the structures of communities caught at one particular site is in most cases unknown and is likely to differ between species. Generally, in most ecological studies on mobile aquatic fauna, it is difficult to identify the spatial scale of the study and it is rare for a specific rationale for choosing the scale to be mentioned (Pittman & Mcalpine, 2001). The smallest ambit applied to seagrass metrics in this study was 0.5km from a catch site. Within a spatial extent of up to 9km, most of the faunal variables showed the strongest and the most significant responses to seagrass metrics up to 3km. This was an interesting finding because most seascape studies have looked at spatial extents of tens -100s of meters from the sampling point. For instance, Grober-dunsmore et al. (2007) studied the influence of seagrass within 1km distance from the reef and more seagrass associated species were recorded at reefs that were between 100m to 1km from the seagrass. Also noted was that the community structure of reef fishes significantly varied between reefs with and without adjacent seagrass (Grober-dunsmore et al., 2007). Pittman et al., (2018) found that juvenile *Haemulon flavolineatum* responded to seagrass beds that were <100m away whilst juvenile *Lutjanus griseus* responded to beds 600m away from mangroves. Therefore the spatial scale of an ecological study should be species specific. In view of this, it is possible that ecological features such as the home range of species (Hitt et al., 2011) could offer direction on the choice of spatial scale in ecological studies, although for most species (such as those in this study) this is largely unknown. Stable isotope studies can also be used to generate knowledge of the extent of movement of mobile species across seascape habitats (Gillanders et al., 2003). For instance, Christian, (2004) found that fish from mangrove areas moved great distances to ingest prey from seagrass habitats.

In this study, *P. indicus* abundance was negatively related with cumulative seagrass area at 2km. *Penaeus monodon* abundance on the other hand was strongly associated with more distal seagrass metrics (5 – 9km). *Penaeus monodon* tends to move offshore for spawning, and this could be the reason why it was influenced by remote seagrass metrics (Munga et al., 2013). In chapter 3, *P. monodon* abundance was also found to be significantly positively associated with the C.I. of mangroves (R^2=0.42, p=0.013). This suggests that both seagrass and mangroves are important in structuring *P. monodon* assemblages.

This study has demonstrated that adjacent seascape structure is related to faunal assemblages. Different studies consider different distances ‘near’ according to the study’s scale of interest. In this study, for instance, distances of 0.5 to 2.5km were considered close whereas in other studies, for example Grober-dunsmore et al. (2007), the furthest distance was 1km.The results from this study also suggest that spatial extents of up to 9km were influential for some of the fauna like *P. monodon* abundance and therefore, management efforts and scenarios should consider these extents. Penaeid shrimp species *P. monodon* and *P. indicus* are of very high commercial value globally (Froese & Pauly, 2019). The sustainable management of the seascape is therefore important for continuous flow of benefits from these resources.

It is not surprising that few fish and crustacean variables responded to seagrass metrics in the current study. Low sample sizes limited the power of the analyses for most species. In addition, a review of previous literature on the association of fauna and the seascape found that, overall, 70% of the species studied did not respond to seascape metrics (Connolly & Hindell, 2006; Bostrom et al., 2011). This means that these relationships cannot be generalised but must be considered separately for each species (Connolly & Hindell, 2006). The lack of response to spatial attributes by some of the species could also signify that multiple factors, including biological interactions, are important (Connolly & Hindell, 2006).

6.1.5 Faunal response to combined forest and seascape features

From chapter 3 and chapter 5, some fish and crustacean variables were found to respond to some forest variables and seagrass metrics. Here, the predictor variables are combined and regressed against fish and crustacean variables to explore the effects of both forest and seascape predictors together. Stepwise linear regression was conducted in order to identify predictor variables (forest variables and seascape variables) that could be used to develop multivariate models. The AIC was used to identify strong models which had low AIC numbers. The identified predictor variables were then used to develop multiple linear regression models with fish and crustacean variables. *Penaeus monodon*, *P. indicus* abundance and *Y. hyalosoma* abundance were strongly associated with the combined predictor variables than with individual forest and seascape predictor variables. The perimeter/area ratio of seagrass at 2.5km, and mean tree height, number of tree species and stem density of mangroves explained 86% of the variation for *P. indicus* abundance. *Yarica hyalosoma* abundance was positively correlated with seagrass area at 1km and negatively related cumulative area and basal area of mangroves (R^2=0.80, p=<0.001) (Table 6.1).

Combining both forest variables and seagrass metrics and regressing them against fish and crustacean variables produced strong multiple linear regression models which were more robust than when the predictor variables were regressed with faunal variables separately. Previous studies have pointed to mangroves and seagrass influencing each other's faunal structure and especially when these habitats are proximal (Robertson & Duke, 1987; Jelbart et al., 2007; Unsworth et al., 2009). The results in this study show that combining mangrove and seagrass variables can produce stronger models to explain the abundance of crustaceans and fish such as *P. indicus* and *P. monodon* and *Y. hyalosoma*. This further supports the seascape approach in studying the interaction between organisms and nearshore habitats.;

Table 6.1: Multiple linear regression analysis between faunal variables and forest and seagrass variables

Response variable	**Predictor variable (Distance km)**	**Coefficients**	**df**	**Model F ratio**	**Model R^2**	**P**	**Bonferroni correction (p<0.005**	**VIF**
Penaeus monodon	9km		2,11	11.28	0.67	0.002	S	
	Perimeter/area ratio	0.95						1.1
	C.I.	4.78						1.1
Penaeus indicus	2.5km		4,9	13.48	0.86	0.001	S	
	Perimeter/area ratio	1.69						1.1
	Mean tree height	20.2						4.5
	Tree species	12						1.2
	Stem density	0.01						4.2
Penaeus indicus	1.5km		2,11	11.94	0.68	0.002	S	
	Perimeter/area ratio	0.25						1
	No .of tree species	9.74						1
Yarica hyalosoma	1.5km		2,11	16.42	0.75	<0.001	S	
	Area	146						1.1
	Stem density	-0.02						1.1
Yarica hyalosoma	1km			11.28	0.80	0.001	S	
	cumulative perimeter	3.81						2.4
	cumulative area	-140.3						2.4
	basal area	-28.7						1.1

*NS= not significant, S= significant

6.2 Conclusions

This study has demonstrated that:

a) There are consistent differences in the faunal communities between sites within the Vanga mangrove forest complex.

b) Sites that support the highest abundances and diversity of fishes are different from those best for crustaceans.

c) Forest characteristics, as summarised by the Complexity Index and measured at broad (10m-1km) scales, help explain faunal communities, but show opposite relationships for key fish and crustacean species.

d) Measures of seascape focused on seagrass presence and spatial structure show predictive utility at distances up to and including 9km from catch sites. Similar to forest characteristics, these measures tend to show opposite predictions for fishes and crustaceans.

e) The major fish species in this study not only take refuge in mangroves, but also feed there as demonstrated by the results of the stomach content analyses

f) Combined effects of mangroves and seagrass beds on fauna was in some cases stronger than the effect of individual habitats.

Based on these results, the management approach to the Vanga seascape cannot be simplistic. A complex rather than a simple approach to mangrove management is implied, one that appreciates that the assorted microhabitats in the seascape support an array of ecosystem services. In particular, it is clear that 'the fishery nursery service' of the mangrove seascape is not a single service at Vanga, but potentially a specific one for each species and maybe even for each ontogenic life stage.

6.3 Management recommendations

1. The management and conservation of fisheries resources in Kenya is currently being addressed through Beach Management Units (BMU) whose membership includes all the fisheries stakeholders. One of the objectives of the BMU is to protect nurseries and breeding areas for fish (GoK, 2019). One way to achieve this is through the establishment of Locally Managed Marine Areas (LMMA) by the local communities, with the help of other stakeholders. The design of any

LMMAs in Vanga would greatly benefit from the findings of this study that already has provided baseline information on the productive sites for fish and crustaceans. The recent launch at Vanga of the Vanga Blue Forest project, that aims to establish community-based mangrove management funded through the sale of carbon credits, means that the capacity for local people to manage their marine resources in the area may soon develop. The results of this study will also shed light on the other seascape features like seagrass and the spatial extents that are most important for both fishes and crustaceans. As explained earlier in this chapter, these findings provide good baseline information and hopefully ignite interest for further research in different seascapes where BMUs and LLMAs are operational or plans for establishment exist.

2. Most of the fishing activities in Kenya are artisanal and take place in nearshore areas. Fishery function is the most important ecosystem service that mangroves provide to the community (GoK, 2017). The provision of this ecosystem service is however threatened by illegal harvesting of trees and conversion of mangrove to other uses. Under the fisheries program, the National Mangrove Management Plan (NMMP), 2017 proposes the conservation of fish habitats including fish nursery areas in coastal Kenya (GoK, 2017). The knowledge gained in this study will be important in the implementation of this program. For instance, this study shows that the likely priority conservation areas for fish and crustaceans in Vanga are different. The Vanga Blue Forest carbon project will create opportunities for the protection and enhancement of selected areas of the forest, and these may be chosen using information delivered here.

3. The findings of this study on the importance of assorted seascape structures on faunal assemblages are consistent with other literature that has found seagrass to be a vital linked habitat. Unlike mangrove forests that are managed by the Kenya Forest Service, the conservation and management of seagrass meadows in Kenya are not under the mandate of any specific institution, and this may lead to them being forgotten and ignored. This study has demonstrated that apart from forest quality, fish sampled in mangrove sites are influenced by the seagrass metrics as well. Mangroves and seagrass ecosystems need to be considered together. Future studies, including those focused on management approaches, should look at the synergistic support that these ecosystems give each other, in terms of their functionality as nursery habitats and for other services such as shoreline protection. Other habitats like mud flats and sand flats should be included in future studies.

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8.0 APPENDICES

Appendix 2.1: Seasonal variation of the most abundant species in Vanga mangrove ecosystem

Species	Season	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11	Site 12	Site 13	Site 14	Total
Acropoma japonicum	SEM	21	3	55	10	20	11	4	14	2	0	0	0	0	0	140
	NEM	8	37	7	39	9	12	0	0	5	5	0	0	0	0	122
Ambassis Ambassis	SEM	0	0	70	25	14	26	0	0	0	1	0	0	0	0	136
	NEM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ambassis natalensis	SEM	0	2	107	13	28	53	0	0	6	0	0	0	1	0	210
	NEM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apogon hyalosoma	SEM	140	43	90	1	7	0	22	36	16	22	4	4	4	18	407
	NEM	47	2	0	0	0	0	5	4	0	0	5	0	5	3	71
Atherinerous lacunosus	SEM	2	0	0	0	0	0	17	44	0	11	2	5	0	0	81
	NEM	0	0	0	0	0	0	3	0	0	0	1	1	0	0	5
Gerres filamentosus	SEM	20	25	12	1	10	0	1	0	1	0	4	1	3	0	78
	NEM	0	0	0	0	0	0	0	0	0	0	0	0	10	0	10
Gerres oyena	SEM	27	0	0	3	2	1	17	0	0	15	1	8	22	4	100
	NEM	2	0	0	1	2	0	0	0	0	0	0	0	0	3	8
Hyporamphus affinis	SEM	13	0	8	6	2	0	2	4	0	1	0	3	0	0	39
	NEM	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Leiognathus equulus	SEM	2	0	0	0	0	3	0	0	111	3	0	2	0	0	121
	NEM	0	0	0	1	0	0	0	0	14	0	0	0	0	0	15
Monodactylus argenteus	SEM	6	0	0	0	4	3	2	0	0	0	0	0	15	0	30
	NEM	2	0	0	0	0	0	5	0	0	0	0	0	0	0	7
Moolgarda Seheli	SEM	0	0	12	3	2	0	0	0	0	0	0	0	0	0	17
	NEM	0	0	3	1	1	0	0	0	1	0	0	0	0	0	6
Sillago sihama	SEM	0	0	0	5	0	6	0	0	6	1	0	4	0	0	22
	NEM	0	0	0	0	0	1	0	0	7	1	0	5	0	0	14

Appendix 3.1: Output of simple linear regression models between broad scale forest variables and fish and crustacean variables

Mean fish abundance	**F**	**R^2**	**P**	**Bonferroni correction (p<0.01)**
mean height	1.29	9.70	0.278	NS
basal area	4.83	28.70	0.048	NS
no. of tree species	0.03	0.25	0.864	NS
stem density	1.92	13.82	0.191	NS
Mean fish biomass				
mean height	5.86	32.82	0.032	NS
basal area	0.51	4.05	0.490	NS
no. of tree species	0.45	3.59	0.517	NS
stem density	1.66	12.18	0.221	NS
complexity index	0.23	2.21	0.612	NS
Cumulative fish species				
mean height	3.60	23.06	0.082	NS
basal area	0.11	0.90	0.747	NS
no. of tree species	0.31	2.53	0.587	NS
stem density	1.13	8.63	0.308	NS
complexity index	0.21	1.60	0.658	NS
Mean crustacean abundance				
mean height	0.15	1.2	0.709	NS
basal area	4.02	25.07	0.068	NS
tree species	2.32	16.19	0.154	NS
stem density	0.05	0.38	0.833	NS
Yarica hyalosoma				
mean height	0.11	0.94	0.742	NS
basal area	3.26	21.36	0.096	NS
no. of tree species	3.92	26.27	0.073	NS
stem density	0.16	1.33	0.695	NS
complexity index	1.86	13.41	0.198	NS
Penaeus monodon				
mean height	4.43	26.97	0.057	NS
basal area	2.89	19.41	0.115	NS
no. of tree species	1.19	9.00	0.297	NS
stem density	3.54	22.76	0.085	NS
Penaeus semisulcatus				
mean height	1.07	8.19	0.321	NS
basal area	2.23	15.66	0.161	NS
no. of tree species	1.71	12.46	0.216	NS
stem density	0.41	3.32	0.533	NS

*NS= not significant, S= significant

Appendix 5.1: Simple linear regression of fish and crustacean variables with various seagrass metrics and various distances

Response variable	**Distance**	**F ratio**	**Model R^2**	**Model P**	**Bonferroni correction ($p<0.01$)**	**Slope**
Perimeter/area ratio of seagrass						
Mean fish biomass	3.5km	5.24	0.30	0.041	NS	-ve
Acropoma japonicum	3.5km	6.97	0.36	0.023	NS	-ve
Acropoma japonicum	4km	5.44	0.31	0.038	NS	-ve
Acropoma japonicum	4.5km	6.17	0.30	0.040	NS	-ve
Gerres oyena	5.5km	5.04	0.30	0.044	NS	+ve
Penaeus monodon	7km	6.92	29.07	0.047	NS	+ve
Penaeus monodon	8km	6.68	35.76	0.024	NS	+ve
Penaeus monodon	8.5km	8.12	0.40	0.015	NS	+ve
Perimeter of seagrass						
Cumulative fish species	5km	5.73	0.28	0.050	NS	+ve
Cumulative fish species	8km	5.03	0.29	0.049	NS	+ve
Gerres filamentosus	4.5km	7.47	0.38	0.018	NS	-ve
Penaeus monodon	5.5km	6.85	0.36	0.022	NS	-ve
Cumulative area of seagrass						
Penaeus monodon	1.5km	8.11	0.30	0.043	NS	-ve
Cumulative perimeter of seagrass						
Gerres filamentosus	8.5km	4.66	27.98	0.052	NS	-ve
	9km	4.97	29.27	0.046	NS	-ve
Penaeus monodon	3.5km	4.99	29.37	0.045	NS	-ve
	4.5km	4.81	28.62	0.049	NS	-ve

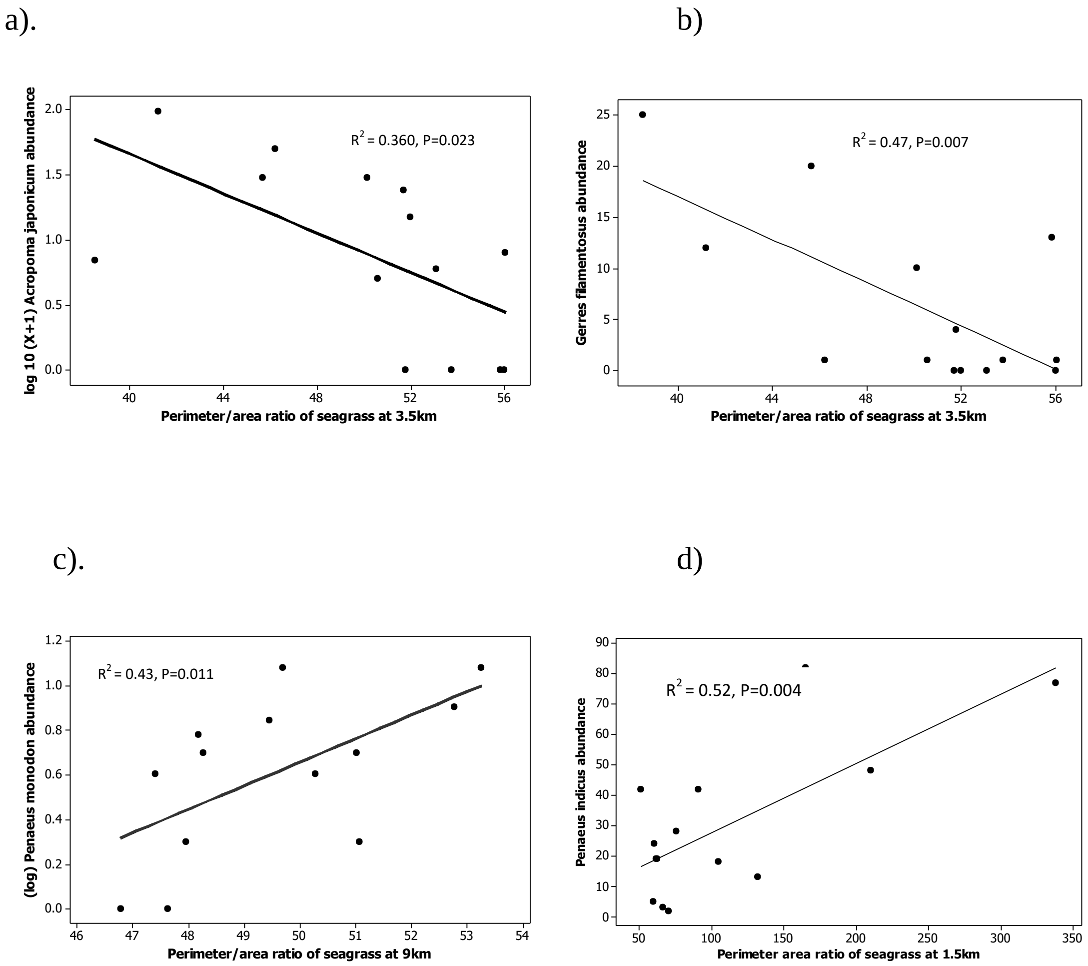
*NS= not significant, S= significant

Appendix 5.2: Multiple linear regression models of fish variables and crustaceans variables and seagrass metrics: perimeter, perimeter/area ratio, cumulative area and cumulative perimeter of seagrass at various distances

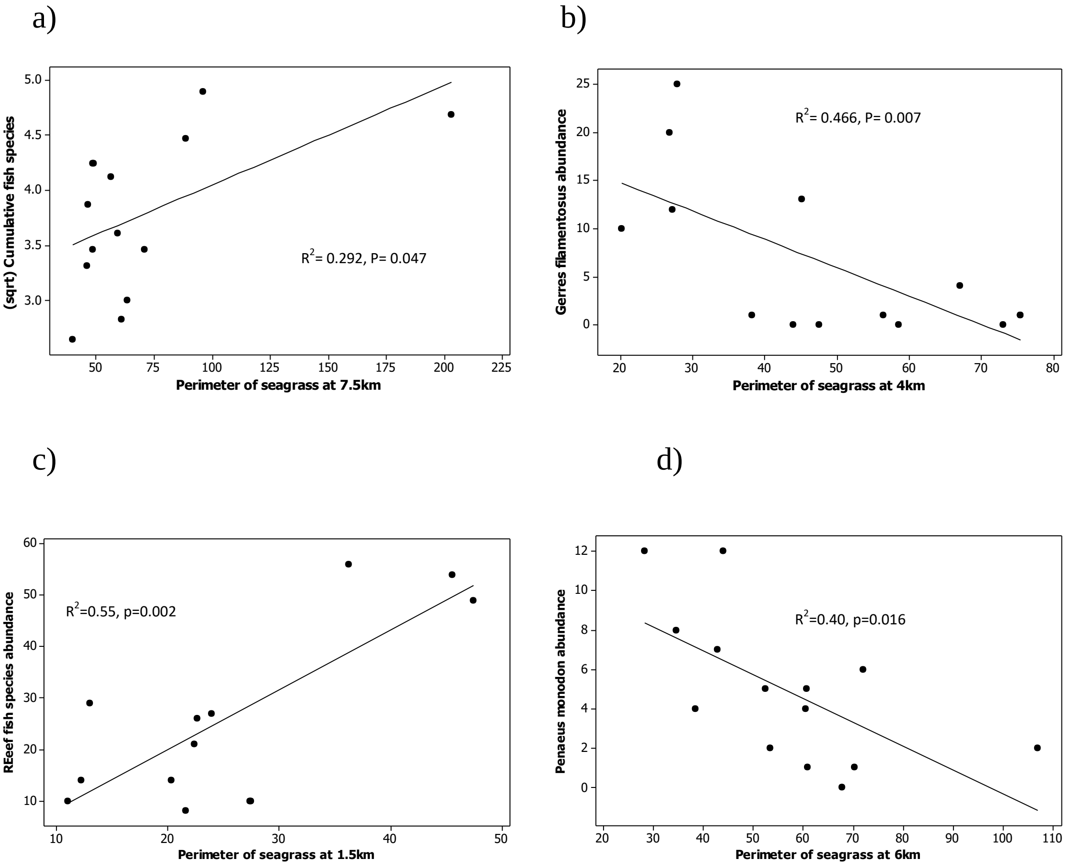
Response variable	**Predictor variable (Distance)**	**Coefficients**	**df**	**Model F ratio**	**Model R^2**	**P**	**Bonferroni correction (p<0.01)**
Mean fish biomass	1.0km		2,11	4.03	0.43	0.049	NS
	Cumulative area	-493					
	Cumulative perimeter	5.99					
Mean fish biomass	2.5km		2,11	4.63	0.46	0.035	NS
	log (area)	779.7					
	(log) perimeter	-794.5					
Mean fish biomass	4km		2,11	5.37	0.49	0.024	NS
	Area	68.8					
	Perimeter	-5.13					
Acropoma japonicum	5km		2,11	21.69	0.76	<0.001	S
	Cumulative area	23.12					
	Cumulative perimeter	-0.54					
Acropoma japonicum	9km		2,11	5.35	0.49	0.024	NS
	Area	0.408					
	Perimeter: area ratio	-4.83					
Yarica hyalosoma	2km		2,11	9.37	0.63	0.004	S
	Area	189.5					
	Perimeter	-2.97					
Yarica hyalosoma	3km		2,11	7.17	0.57	0.01	S
	Area	-51					
	Perimeter: area ratio	-5.06					
Gerres filamentosus	3.5km		2,11	6.17	0.53	0.16	NS
	Cumulative area	12.24					
	Cumulative perimeter	-0.22					
Penaeus monodon	3.5km		2,11	6.7	0.55	0.013	S
	Cumulative area	-3.95					
	Cumulative perimeter	0.11					

*NS= not significant, S= significant

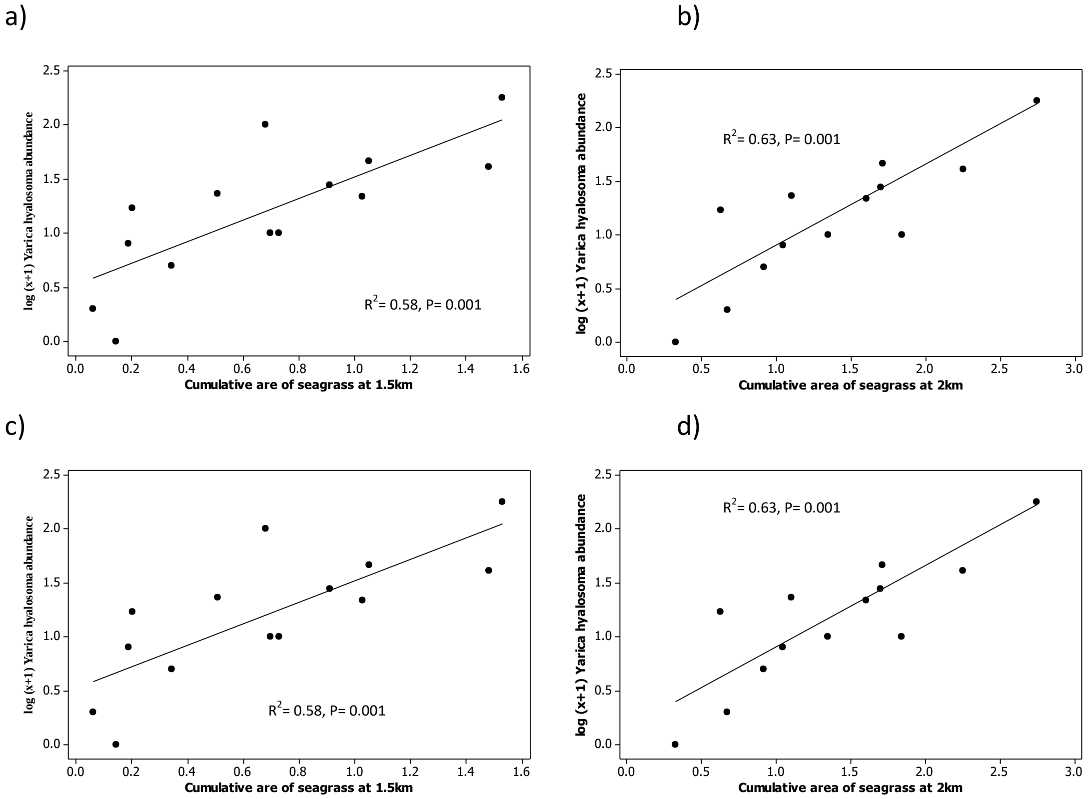
Appendix 5.3: Simple linear relationship between perimeter/area ratio and fish and crustacean: a) log (x+1) *Acropoma japonicum* abundance at 3.5km, b) *Gerres filamentosus* abundance at 3.5km c) (log) *Penaeus monodon* abundance at 9km and *d*) *Penaeus indicus* abundance at 1.5km.



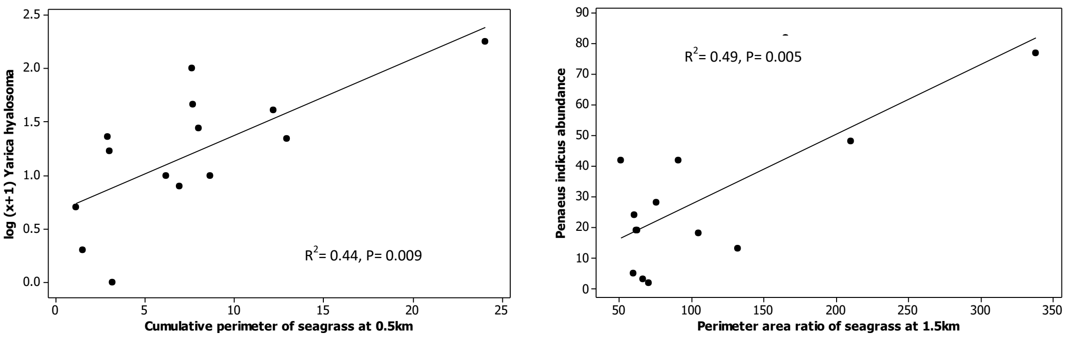
Appendix 5.4: Simple linear relationships between perimeter of seagrass area and fish-crustacean: a) (log) Cumulative fish species at 7.5km, b) *Gerres filamentosus* abundance at 4km, c) Reef fishes abundance at 1.5km d) *P. monodon* abundance at 6km. Only the most significant relationships are presented in graphs.



Appendix 5.5: Simple linear regression between cumulative area of seagrass and fish and crustaceans: a) Cumulative fish species at 0.5km b) (log) *Penaeus indicus* at 2km, c) log(x+1) *Yarica hyalosoma* abundance at 1.5km and d) log(x+1) *Y. hyalosoma* abundance at 2km. Only the most significant relationships were visualised in graphs.



Appendix 5.6: Simple linear regression of cumulative perimeter of seagrass and fish and crustacean: a) log(x+1) *Yarica hyalosoma* abundance at 0.5km b) log (x+1) *Y. hyalosoma* abundance at 1km


a)

b)

Appendix 5.7: Simple linear regression of of seagrass area and log(x+1) *Yarica hyalosoma* abundance at 0.5km