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Composition and structure of the mangrove fish and crustacean communities of Vanga Bay, Kenya

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Abstract

Mangroves support coastal fisheries, particularly by providing nurseries for juvenile fish. However, much remains unknown about the fish and crustacean communities in mangroves and about the lifecycles and behaviours of individual species. This study is the first to describe the fish and crustacean communities in the Vanga mangrove ecosystem, the largest mangrove forest and the most important marine fisheries landing site in southern Kenya. Using fyke nets, 14 mangrove creek sites were sampled once every 3 months during spring tides, between September 2015 and September 2017. The sampling period covered the north east (NEM) and south east (SEM) monsoon seasons. A total of 1,879 fishes and 1,132 crustaceans were caught, represented by 59 and 16 species, respectively. Over 95 % of the fishes caught were juveniles with 50 % of both fish and crustacean species being of commercial importance. About 70 % of the catch was dominated by only 6 fish species with *Yarica hyalosoma* and *Acropoma japonicum* contributing 44 % of the total abundance. *Penaeus semisulcatus* and *Penaeus indicus* dominated the crustaceans. Fish abundances differed significantly between seasons, with the SEM catches almost three times higher than those in the NEM, while crustaceans displayed no clear seasonality. The study documents for the first time the fish and crustacean communities in Vanga mangroves and confirms their importance as juvenile habitat for commercial species. The importance of mangrove and near mangrove habitat as nursery habitat for both fish and crustaceans emphasizes the need for conservation particularly of seaward edges

Keywords: nursery habitat, juvenile, size distribution, intertidal, seasons

Introduction

Estuarine habitats are often important nursery areas for juvenile fishes and crustaceans (Laegdsgaard and Johnson, 1995; Rozas and Minello, 1997; Sheridan and 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 these combined (Beck *et al.*, 2001). The nursery function of mangroves has been studied in most mangrove regions of the world, including South America and the Caribbean, South East Asia, Australia and East Africa (Primavera, 1997; Laegdsgaard and Johnson, 2001; Lugendo *et al.*, 2007; Nagelkerken *et al.*, 2008; Abrantes and Sheaves, 2009;

Gajdzik *et al.*, 2014). These studies and others give 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). The scarcity of permanent residents in intertidal mangrove habitats means that fish within commonly found families such as Lethrinidae, Lutjanidae and Monodactylidae (Kimani *et al.*, 1996; Wainaina *et al.*, 2013), which may be heavily reliant on mangroves at a given site, must utilise other habitats as well.

Penaeid shrimp contribute to artisanal and commercial fisheries in the Western Indian Ocean (WIO) which includes mainland continental states of Kenya,

Tanzania, Mozambique and the small island states of Madagascar, Mauritius, Seychelles, Comoros and Reunion. The commercially important penaeid shrimp species in WIO nearshore habitats include: *Penaeus indicus*, *Penaeus semisulcatus*, *Penaeus monodon* and *Metapenaeus monoceros* (Wakwabi and Mees, 1999; Macia, 2004) and have been shown to use mangrove habitats at various life stages (Rönnbäck *et al.*, 1999; Crona and Rönnbäck, 2005). *P. indicus* has been found to prefer vegetated, muddy bottoms, and other species found in mangrove areas such as *Penaeus japonicus* prefer bare areas (due to its ability to burrow and hide from predators) while *P. semisulcatus* prefers deep, less clear waters (Macia, 2004; Crona and Rönnbäck, 2005; Munga *et al.*, 2013). In Kenya, penaeid shrimp generally exhibit no seasonality (Ndoro *et al.*, 2014).

Given the broad association between healthy mangrove ecosystems and fisheries production (e.g. Barbier, 2000), it is unfortunate that mangroves in the WIO region continue to face a wide range of anthropogenic pressures, such as overharvesting and conversion to other uses, which have resulted in long-term declines in extent and quality (Kairo *et al.*, 2002; Ochiewo, 2004; Fulanda *et al.*, 2009; Huxham *et al.*, 2015). Securing a reliable and sustainable occurrence of fishes and crustaceans, for food and as well as for biodiversity, will require sound mangrove and coastal management, which ideally should be informed by a better understanding of how fishes and other fauna are using the habitat. However, conducting the research that would allow this is difficult; sampling mobile fishes and crustaceans within mangrove forests is challenging. The complex root network in mangroves makes it difficult to use most conventional fish sampling gear to carry out effective and quantitative sampling. Faunce and Serafy (2005) highlighted that most mangrove fish sampling surveys conducted between 1955 - 2005 had failed to sample inside the mangrove forest due to such limitations. Instead, many studies on mangrove fishes restricted sampling to adjacent bays or large, permanently inundated creeks. Whilst this literature provides important insights into the range of species present, doubts remain over whether, and to what extent, individual fish captured adjacent to mangroves venture into the forest at high tide. It is possible that some or many of these species that use permanent open water habitats never enter the inter-tidal areas. To overcome this problem, barrier enclosure samplers (stake nets) and visual methods (whenever water is clear enough) have been used to collect data on fish species within

forests (Vance *et al.*, 1996; Rönnbäck *et al.*, 1999; Huxham *et al.*, 2004; Crona and Rönnbäck, 2005; 2007). Although such approaches provide thorough quantitative data, they are very labour intensive, cumbersome, and restricted to sampling small (and possibly unrepresentative) areas and therefore limited to mangrove areas that are easily accessible or (in the case of visual surveys) low in turbidity.

Work on mangrove fish communities typically features large spatial and temporal variability, which may arise through these methodological limitations; fine-grained approaches at small sites within a forest may sample statistical noise that would disappear in larger data sets. However, this variability may be more than noise; it could imply major differences in the value of sampled areas within mangrove sites for individual fish species or communities as a whole. Explaining this variability remains a major research challenge with important management implications, since identifying forest characteristics that are of importance for the utilization of mangroves by fishes, crustaceans and other fauna would allow managers to target conservation efforts at such areas and features.

The Vanga mangrove ecosystem is one of the largest contiguous mangrove blocks in Kenya and supports rich fishing grounds (Obura, 2001; GoK, 2017). The fishery resource is transboundary and attracts a substantial number of migrant fishers from Tanzania over the fishing seasons. There is evidence that the fishery is under pressure and declining; a recent analysis suggests total officially recorded catches have declined by ~40% over the past ten years (Fortnam *et al.*, 2020). The causes of this decline are unknown; whilst they may be related to changes in mangrove extent and quality (in common with other Kenyan mangroves, the forest here has suffered declines in total area and increasing evidence of human impact such as cutting over the past four decades), there is a major gap in knowledge with respect to the Vanga mangroves; the only peer-reviewed study published on mangrove ecology from the site is Gress *et al.* (2016), which documents carbon storage. The present study therefore is a first step in filling this gap by assessing the community structure of fishes and crustaceans (based on species composition, abundance and size) in the Vanga mangrove ecosystem. In addition, seasonal and spatial variations of these variables for the dominant species were assessed. This will help to understand ontogenetic changes in habitat use in fish, and seasonality effects on fish and crustacean species.

Study sites

The study site is Vanga on the south coast of Kenya ($4^{\circ} 39' 38.42''\text{S}$, $39^{\circ} 13' 9.71''\text{E}$; Fig. 1). The climate of Vanga is typical for east African coastal areas where the Inter Tropical Convergence Zone (ITCZ) partitions the year into two distinct seasons i.e. the South East Monsoon (SEM) and North East Monsoon (NEM). The rainy SEM season is from March to October and the dry NEM season from September to March (McClanahan, 1988). Fish catch and reproduction typically peak during NEM at the east African coast when the waters are more stable and nutrition avail-

Sampling design and methodology

Fishes and crustaceans were sampled at 14 mangrove sites, situated between Jimbo and Majoreni villages in the Vanga Bay along around 11 km of coastline. Sites were chosen to cover a wide geographical area of the Vanga mangrove forest, whilst still being accessible enough to allow regular sampling. Fyke nets were deployed and retrieved after 24 hours within small creeks that drained the 14 mangrove sites, in order to sample fish communities leaving these areas during the ebb tide. The nets had two wings each of 9.5 m length and a height of 1m. The length of the

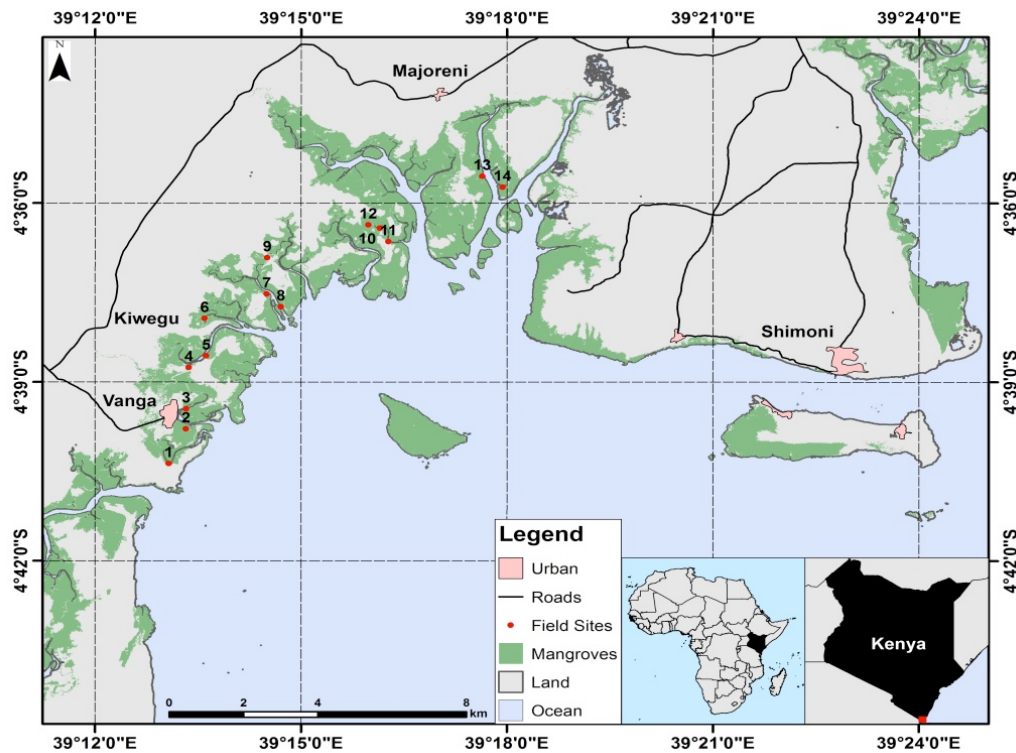


Figure 1: Location of Kenya (inset) and the sampling sites across the Vanga mangrove ecosystem (sampling sites shown as red dots and site numbers in black).

able (McClanahan, 1988). The tidal regime is semi diurnal and ranges between amplitudes of 1.5m at neap tide and up to 4 m at spring tides (Obura, 2001). The Vanga mangrove complex covers a total area of > 4000 ha, and comprises 7 species of mangrove trees, although forests are dominated by 5 common species: *Avicennia marina*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, *Rhizophora mucronata*, and *Sonneratia alba* (GoK, 2017). The rivers Umba and Mwena drain fresh water into the Vanga mangrove ecosystem, with the River Umba, (source in Tanzania), discharging circa 16 million m^3 of fresh water into the sea annually (UNEP, 1998; GoK, 2017).

body frame was 3.6 m. The main frame was made of metal measuring 1 m x 1 m with three rings (0.9 m, 0.7 m, and 0.6 m in diameter) distributed along the body frame. The net had a mesh size of 1.9 cm when stretched. Sites were sampled once every three months between September 2015 and September 2017. Each sampling campaign was spread over a six-day period during new moon spring tides. Hence replicate samples were taken eight times from each of the 14 sites giving a total of 112 samples. March 2017 was not sampled due to logistical reasons. Fish and crustacean samples collected in the field were placed in a cool box and later sorted and identified

in the laboratory to the lowest possible taxonomic level using Anam and Mostarda (2012) and Richmond (2011). Fish standard length and total length were measured (to the nearest 0.1 cm) and individual mass recorded (to the nearest 1 g). Crustaceans were counted and weighed to the nearest 0.1 g. To classify the fishes into size classes, the maximum length of each species was sourced from FishBase (Froese and Pauly, 2017). Using guidelines from Nagelkerken and Velde (2002), fishes with total length $\leq 1/3$ maximum length were classified as small juveniles, between $>1/3$ to $\leq 2/3$ 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 and Pauly, 2017).

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) and Plymouth Routines In Multivariate Ecological Research (PRIMER) version 6.0 Clarke and Warwick (2001). Shannon's diversity index (H'), Margalef's (D) and Pielou's evenness index (J') were used to compare fish and crustacean community structure between seasons. Statistical analysis used all 112 samples as raw data in this analysis.

To test for differences between seasons, September and June abundance data were pooled under the season 'South East Monsoon (SEM)' and March and December data under 'North East Monsoon (NEM)'; separate analyses were performed for fishes and crustaceans.

Non-metric multidimensional scaling (nMDS) ordination plots based on the Bray Curtis similarity index were then developed to visualize seasonal differences (Clarke and Warwick, 2001). One-way Analysis of Similarities (ANOSIM) was used to test for significant differences among fish and crustacean community structure between seasons, after which similarity of percentages (SIMPER) was used to establish the fish and crustacean taxa that mainly contributed to the differences found.

ANOVA was used to test for differences between mean fish abundance in NEM and SEM seasons and a significance level of $p < 0.05$ was used. A Kruskal -Wallis H test was used to test the differences between

mean crustacean abundance in both seasons since the datasets could not meet the assumptions of normality. A significance level of ($p < 0.05$) was used. *Yarica hyalosoma*, *Acropoma japonicum* and *Gerres oyena* were sufficiently abundant (both overall and between dates) to allow comparisons of size-frequency distributions among some of the sampling dates, in order to explore growth patterns. Chi - square tests of association ($p < 0.05$) were performed to test for differences between size classes distributions at different sampling times for *Y. hyalosoma*, *A. japonicum* and *G. oyena*.

Results

Fish and crustacean community structure

A total of 1,879 fishes were caught, represented by 28 families and 59 species. Six species dominated the catch and contributed about 70 % of the total abundance: *Y. hyalosoma* (25 %), *A. japonicum* (18.9 %), *Ambassis natalensis* (11.2 %), *Ambassis ambassis* (7.2 %), *Leiognathus equulus* (7.2 %) and *G. oyena* (5.7 %) (Table 1). The 5 most common families were Apogonidae, Ambassidae, Acropomatidae, Gerreidae and Leiognathidae. Serranidae was the most diverse family (5 species) followed by Lutjanidae and Haemulidae, which had 4 species each. *Gerres filamentosus* and *G. oyena* were the most widely spatially distributed with each being caught at 10 different sites. The species *Lutjanus fulvus*, *L. bohar*, *Pterois volitans* and *Tylosurus crocodilus* (single individuals each) were considered rare. Circa 50 % of the total species caught were of commercial importance, based on information from FishBase (Froese and Pauly, 2017) (Table 1).

A total of 1,161 crustaceans were recorded, distributed between 16 species. Most of them belonged to infra-order Brachyura for crabs and family Penaeoidea for the shrimp. The most abundant crustacean species were *P. semisulcatus* (46.5 %) and *P. indicus* (36.2 %) (Table 2). *P. indicus*, *P. semisulcatus* and *Thalamita crenata* were encountered in all 14 sites sampled. The penaeid species *Macrobrachium rude*, *Scylla serrata* and *T. crenata* are of high commercial value.

Seasonal variations in fish assemblages (SEM – NEM)

The mean catches of fish (pooled across all sites) during the SEM months were 330 and 294 in September and June, respectively. By comparison, the NEM months of December and March had much lower means of 80 and 139, respectively (Fig. 2), a difference which was highly statistically significant (one-way ANOVA $F_{(1,110)} = 8.58$, $p = 0.004$). September and June (SEM) also

Table 1. Summary information on fish communities including fish abundance (catch per net), respective families, associated fish species in the families (fish that were not identified to species level are shown as unidentified), total abundance and total species per site. The commercial importance of the fish abbreviated: HC=highly commercial, C=commercial, MC=minor commercial, AQ=Aquarium, NCI = no commercial importance; based on Froese and Pauly (2017) at the 14 sampling sites in Vanga, Kenya. The symbol (*) was used to indicate fish whose importance has not been documented.

Family	Species	Importance														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Acropomatidae	<i>Acropoma japonicum</i>	C	29	6	96	49	29	23	4	14	7	5	0	0	0	0
	<i>Ambassis ambassis</i>	Non	0	0	70	25	14	26	0	0	0	1	0	0	0	0
Ambassidae	<i>Ambassis gymnocephalus</i>	MC	0	0	0	0	8	0	0	0	0	0	0	0	0	0
	<i>Ambassis natalensis</i>	C	0	2	107	13	28	53	0	0	6	0	0	0	1	0
Antennariidae	Frog fish (unidentified)	*	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Apogonidae	<i>Yarica hyalosoma</i>	Non	178	45	99	1	7	0	27	40	16	22	9	4	9	21
Atherinidae	<i>Atherinomorus lacunosus</i>	C	2	0	0	0	0	0	20	44	0	11	3	6	0	0
	<i>Tylosurus acus melanotus</i>	C	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Belonidae	<i>Tylosurus crocodilus</i>	C	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	<i>Carangoides ferdau</i>	C	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Carangidae	<i>Caranx ignobilis</i>	C	0	0	0	0	0	0	1	0	0	1	0	1	0	0
	<i>Chanos chanos</i>	HC	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Clupeidae	<i>Sardinella gibbosa</i>	HC	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Spratelloides gracilis</i>	MC	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Engraulidae	<i>Stolephorus commersonii</i>	C	0	0	0	0	1	0	0	0	0	0	0	1	0	0
	<i>Thrysa setirostris</i>	MC	0	0	0	0	0	1	1	0	0	0	0	0	0	0
	<i>Platax orbicularis</i>	MC	0	0	0	0	0	0	1	0	0	0	0	0	1	0
	<i>Platax pinnatus</i>	MC	0	0	0	1	0	0	1	0	0	0	0	0	0	1
Gerreidae	<i>Gerres longirostris</i>	C	1	0	0	0	0	2	0	0	0	0	0	0	1	1
	<i>Gerres filamentosus</i>	MC	20	25	12	1	10	0	1	0	1	0	4	1	13	0
	<i>Gerres oyena</i>	C	28	0	1	4	4	1	17	0	0	15	1	8	22	7
	<i>Acentrogobius nebulosus</i>	*	0	0	1	0	1	0	0	0	1	0	0	0	0	0
Gobiidae	Goby	AQ	0	1	0	0	3	0	0	1	1	0	0	0	0	0
	<i>Periophthalmus</i> spp.	*	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Gynglymostomatidae	Blue spotted goby	*	0	0	0	3	0	0	0	0	0	0	0	0	0	0
	<i>Plectorhinchus plagiodesmus</i>	C	0	1	1	0	0	0	0	1	0	0	0	0	0	0
Haemulidae	<i>Pomadasys argenteus</i>	C	0	0	1	1	0	1	2	0	0	3	0	0	0	0
	<i>Pomadasys multimaculatus</i>	C	0	1	0	1	1	3	0	3	0	2	0	2	0	0
	<i>Pomadasys kaakan</i>	C	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Family	Species	Importance														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Hemiramphidae	<i>Hyporhamphus gamberur</i>	Non	1	0	2	1	0	0	1	0	0	0	0	0	0	0
	<i>Hyporhamphus affinis</i>	Non	13	0	10	6	2	0	2	4	0	3	1	0	0	0
	<i>Zenarchopterus dispar</i>	C	1	0	2	5	0	0	0	0	0	0	1	0	0	0
Leiognathidae	<i>Gazza minuta</i>	C	0	0	0	7	0	1	0	0	40	0	0	0	4	0
	<i>Leiognathus equulus</i>	MC	2	0	0	1	0	3	0	0	125	3	0	2	0	0
Lethrinidae	<i>Lethrinus harak</i>	C	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lutjanidae	<i>Lutjanus argentimaculatus</i>	C	1	2	0	1	3	0	0	0	0	3	0	0	0	0
Lutjanidae	<i>Lutjanus bohar</i>	C	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	<i>Lutjanus fulviflamma</i>	C	3	0	1	0	0	0	1	0	0	4	2	1	0	0
	<i>Lutjanus fulvus</i>	C	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Monodactylidae	<i>Monodactylus argenteus</i>	MC	7	0	0	0	4	4	7	0	0	0	0	0	15	0
	<i>Crenimugil crenilabis</i>	C	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Mugilidae	<i>Moolgarda seheli</i>	C	0	0	15	4	3	0	0	0	1	0	0	0	0	0
	<i>Mugil cephalus</i>	HC	0	10	0	0	5	0	0	0	0	0	0	0	0	0
Percophidae	<i>Bembrops platyrhynchus</i>	Non	1	0	0	0	0	0	1	0	0	0	0	0	0	0
	<i>Bembrops caudimacula</i>	*	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Platycephalidae	<i>Platycephalus indicus</i>	C	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pomacentridae	<i>Dascyllus</i> spp.	*	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Scorpaenidae	<i>Pterois volitans</i>	C	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Epinephelus coeruleopunctatus</i>	MC	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	<i>Epinephelus coioides</i>	C	0	1	0	2	1	0	1	0	0	0	0	0	0	0
Serranidae	<i>Epinephelus lanceolatus</i>	C	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>Epinephelus malabaricus</i>	HC	0	1	0	2	2	0	0	0	0	1	0	0	1	0
	<i>Epinephelus spilotoceps</i>	C	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Sillaginidae	<i>Sillago sihama</i>	C	0	0	0	5	0	7	0	0	13	2	0	9	0	0
	<i>Sphyraena barracuda</i>	MC	2	0	1	0	0	0	0	0	0	1	1	1	1	0
Sphyraenidae	<i>Sphyraena jello</i>	C	2	2	2	0	0	0	3	0	1	3	1	0	1	0
	<i>Sphyraena putnamae</i>	C	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Terapontidae	<i>Terapon jarbua</i>	MC	0	0	5	0	0	0	0	0	3	0	0	1	0	0
Tetraodontidae	<i>Arothron immaculatus</i>	MC	0	0	0	1	0	0	1	0	0	0	0	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

Table 2. Summary of crustacean community structure at the 14 sampling sites, including crustacean abundance (catch per net), respective families, number of species and the total abundance and species per sites. The importance of species is abbreviated: NAI=No available information, C=commercial, HC=highly commercial, NCI= no commercial importance.

Family/ infaorder	Species	Percentage (%) of total N	Importance	Sampling sites														
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Brachyura	Crab 1	0.2	NAI	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Brachyura	Crab 2	0.2	NAI	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Brachyura	Crab 3	0.2	NAI	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Caridea	Caridean shrimp	1.5	C	1	0	0	2	6	0	0	1	1	2	1	3	0	0	0
Matutidae	<i>Ashtoret lunaris</i>	0.2		1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ocypodidae	<i>Uca</i> spp.	0.2	NIC	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Palaemonidae	<i>Macrobrachium rude</i>	2.7	HC	1	0	0	16	5	0	0	3	0	3	0	3	0	0	0
	<i>Metapenaeus stebbingi</i>	0.2	HC	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	<i>Metapenaeus monoceros</i>	1.7	HC	1	0	0	1	0	1	0	5	0	5	0	7	0	0	0
Penaeidae	<i>Penaeus indicus</i>	36.2	HC	1	42	19	48	77	82	28	24	13	42	2	18	19	5	5
	<i>Penaeus monodon</i>	5.9	HC	1	1	1	2	4	6	4	5	0	12	5	7	8	12	12
	<i>Penaeus semisulcatus</i>	46.5	HC	1	11	4	4	4	15	13	22	15	177	10	75	13	176	176
Portunidae	<i>Scylla serrata</i>	1.7	HC	1	4	0	2	1	4	0	1	1	1	0	0	3	2	2
Portunidae	<i>Thalamita crenata</i>	2.5	HC	1	3	1	1	1	3	0	3	1	2	2	1	7	3	3
	Shrimp 1 (unidentified)	0.2	NAI	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	Shrimp 2 (unidentified)	0.2	NAI	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Total individuals N				16	61	26	77	98	112	45	64	33	245	21	114	51	198	198
Total species				16	5	5	9	7	7	3	8	7	9	6	7	6	5	5

Table 3. Margalef's species richness (D), Pielou's evenness index (J') and Shannon diversity index (H') (±sd) 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	578	48	139	385	183	112	202	230
Margalef's species richness (D)	3.9±0.5	3.6±0.7	2.8±0.6	4.4±0.8	3.3±0.7	3.0±0.5	3.01±0.6	2.9±0.7
Pielou's evenness index (J')	0.6±0.2	0.7±0.1	0.6±0.2	0.7±0.2	0.7±0.2	0.7±0.2	0.6±0.2	0.7±0.2
Shannon Weiner index (H')	1.9±0.5	2.0±0.5	1.7±0.5	2±0.6	1.9±0.5	1.8±0.4	1.6±0.5	2.0±0.5

^a=SEM, ^b=NEM seasons

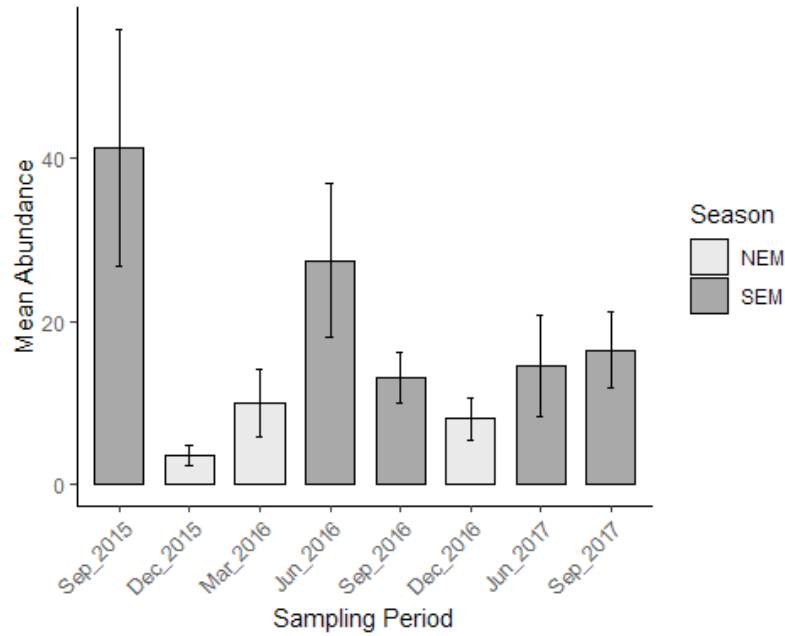


Figure 2. Mean abundance (\pm 95 % CI) of individuals caught at each of the sampling dates. Data are means for all 14 nets at each sampling date.

showed higher diversity compared to December and March (NEM) (Fig. 3). The most abundant species in SEM were *Y. hyalosoma*, *A. ambassis*, *A. natalensis* and *L. equulus*. In NEM the most abundant species were *A. japonicum*, *Y. hyalosoma*, *L. equulus* and *S. sihama*. The family Ambassidae, that comprised of *A. ambassis*, *A. natalensis* and *A. gymnocephalus*, showed strong seasonality as it only occurred in SEM. *Acropoma japonicum* had a higher mean abundance in NEM than in SEM i.e. 40 and 28 individuals respectively. Other species that showed marked seasonality included *G. oyena* and *A. lacunosus*. The highest species diversity H' was in June 2016 ($H'=2.15\pm0.6$) and the lowest was in June

2017 ($H'=1.64\pm0.5$). The species evenness index (J) was more stable, varying between 0.58 ± 0.2 (June 2017) and 0.72 ± 0.2 (Dec 2015) (Table 3). ANOVA revealed no significant differences in Margalef (D) and Pielou's evenness (J') indices of fishes for the 8 sampling dates, $p=0.111$ and $p=0.170$ respectively. However, there was a significant difference in Shannon's diversity index (H') $p=0.036$. A non-metric multi-dimensional (nMDS) ordination plot of square root transformed abundance data of all fish species in the sites during NEM and SEM seasons showed separation between SEM and NEM seasons (Fig. 4). ANOSIM revealed significant differences of fish assemblages between NEM and SEM

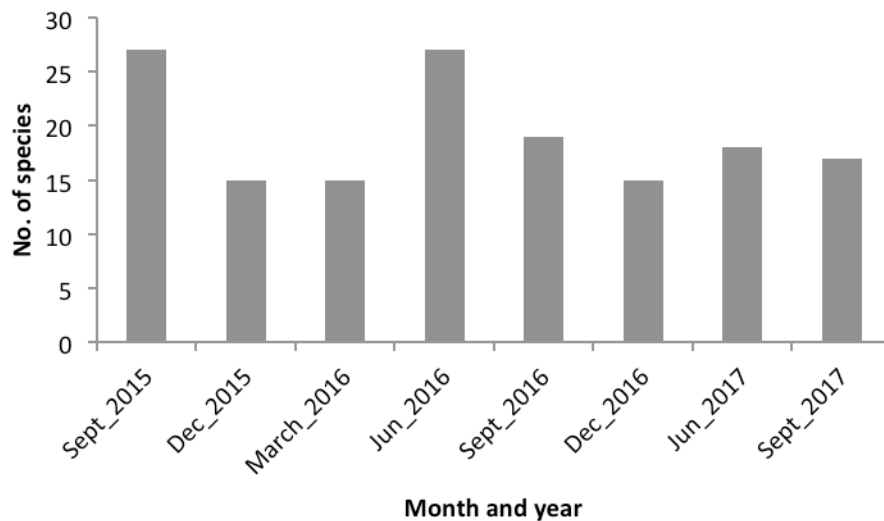


Figure 3. Total number of fish species caught in each of the 8 sampling periods.

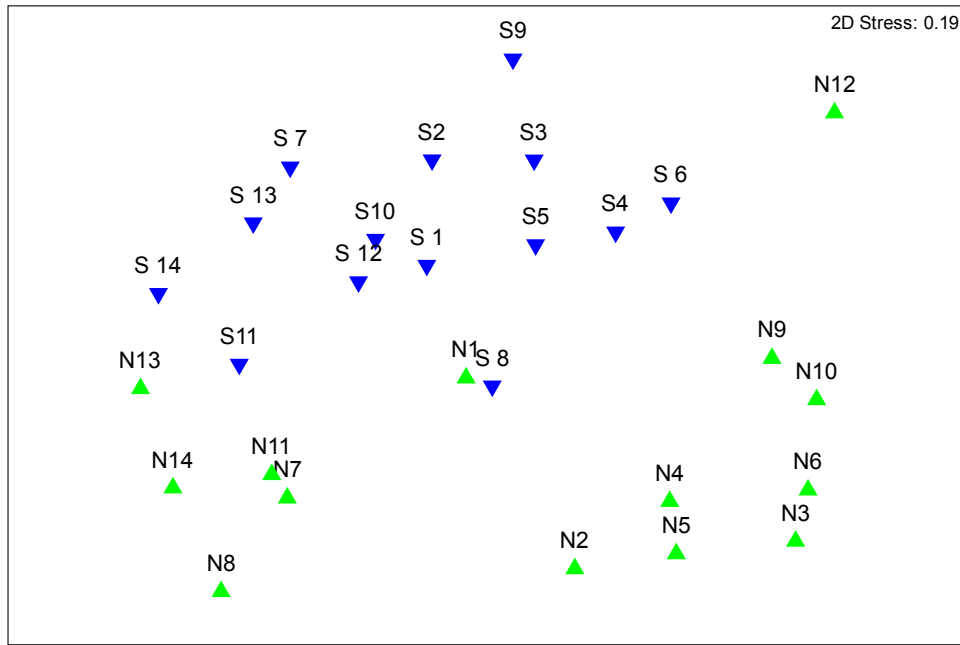


Figure 4. Nonmetric multi-dimensional scaling (nMDS) of seasonal fish abundance (pooled number of individuals per season) based on Bray–Curtis similarity using square root transformed data of crustaceans in all sampling locations for both NEM and SEM seasons. Blue triangles and letter S stand for SEM and green triangles and letter N for NEM. Numbers refer to separate sampling locations.

seasons on square root transformed abundance data, with $R=0.263$ and $p=0.004$. SIMPER analysis showed an average dissimilarity of 82.62 % between the NEM and SEM seasons and the species *A. hyalosoma*, *A. japonicum*, *G. oyena*, *A. natalensis*, *G. filamentosus* and *A. lacunosus* contributing to over 40 % of this dissimilarity.

Seasonal variations in crustacean assemblages (SEM – NEM)

Penaeus indicus did not show any marked seasonality while *T. crenata* and *M. rude* showed tendencies to seasonality as they mostly occurred in SEM (Fig. 5).

Generally, the highest crustacean abundance was recorded in the NEM as opposed to fish where the highest abundances were in the SEM. The highest species diversity H' was found in March 2016 ($H'=0.9\pm0.3$) and the lowest in December 2015 ($H'=0.5\pm0.3$). The species evenness index (J) varied between 0.6 ± 0.3 (December 2015) and 0.9 ± 0.1 (September 2016) (Table 4). ANOVA revealed no significant differences in Margalef’s species richness (D), Pielou’s evenness index (J') and Shannon diversity index (H') in crustaceans in the 8 sampling seasons with $p=0.634$; $p=0.149$ and $p=0.419$ for D , J' and H' respectively. A Kruskal Wallis

Table 4. Margalef’s species richness (D), Pielou’s evenness index (J') and Shannon diversity index (H') (\pm sd) for crustacean 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	6	5	7	11	7	9	7	54
No. of individuals	45	341	151	125	49	164	79	5
Margalef’s species richness (D)	0.9 ± 0.4	0.5 ± 0.3	1.0 ± 0.3	0.9 ± 0.5	0.9 ± 0.4	0.9 ± 0.5	1.0 ± 0.5	0.9 ± 0.4
Pielou’s evenness index (J')	0.8 ± 0.2	0.6 ± 0.3	0.8 ± 0.2	0.7 ± 0.2	0.9 ± 0.1	0.6 ± 0.7	0.8 ± 0.2	0.8 ± 0.2
Shannon Weiner index (H')	0.8 ± 0.2	0.5 ± 0.3	0.9 ± 0.3	0.8 ± 0.3	0.7 ± 0.2	0.7 ± 0.4	0.7 ± 0.4	0.7 ± 0.2

^a=SEM, ^b=NEM seasons

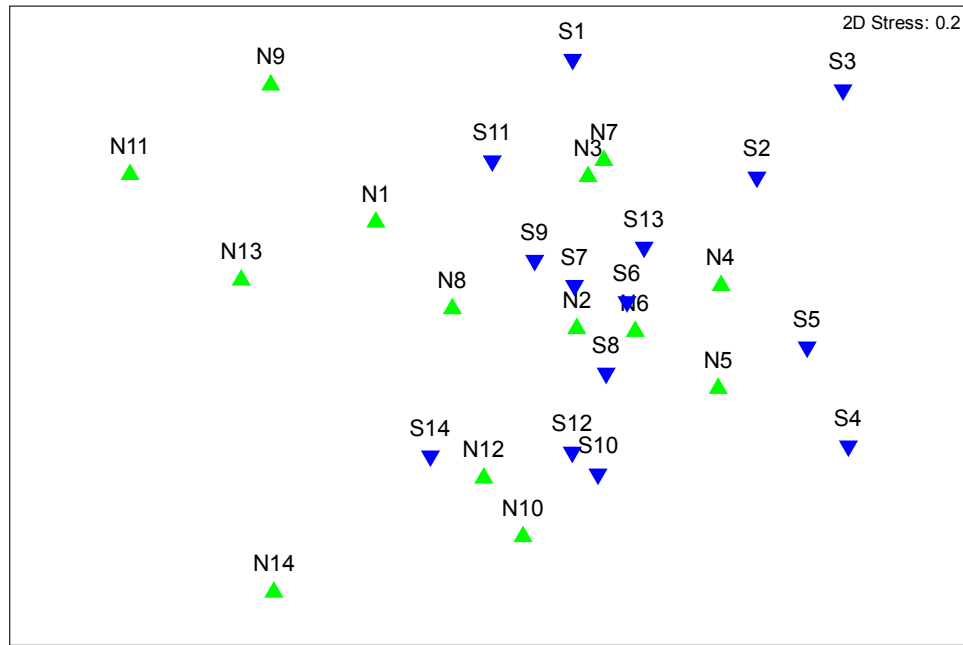


Figure 5. Nonmetric multi-dimensional scaling (nMDS) of seasonal fish abundance (pooled number of individuals per season) based on Bray–Curtis similarity using square root transformed data of fish in all sampling locations for both NEM and SEM seasons. Blue triangles and letter S stand for SEM and green triangles and letter N for NEM. Numbers refer to separate sampling locations.

test was used to test for differences in mean crustacean abundance between NEM and SEM season and no significant differences were detected ($p = 0.843$). The pattern of crustacean seasonality was visualised in an nMDS ordination plot (Fig. 5). The nMDS plots (Fig. 5) revealed differences in the crustacean assemblages between the seasons. One-way ANOSIM showed significant differences in crustacean assemblages on square root transformed abundance data between NEM and SEM seasons ($R=0.158$, $p=0.003$). SIMPER analysis revealed an average dissimilarity of 52.9 % in the assemblages between the two seasons, with *P. semisulcatus* (26.16 %), *P. indicus* (22.92%), *P. monodon* (11.32%) and *T. crenata* (9.97 %) contributing to 70.37 % of the difference between the seasons.

Size classes of the most abundant fishes

Circa 60 % of all individuals caught were classified as small juveniles while 37 % appeared as large juveniles/sub adults. A total of 32 species appeared as small juveniles only while 8 species appeared as 100 % large juveniles/sub adults. Of the 6ix most abundant species, *L. equulus* and *A. natalensis* appeared as 100 % small juveniles and 100 % large juveniles/sub adults, respectively. Ninety seven per cent (97 %) of *G. oyena* were small juveniles (Table 5).

Size classes for 3 of the most abundant species *A. japonicum*, *Y. hyalosoma*, and *G. oyena*, as shown in Figure 6

– 8, were used to conduct cohort analyses to investigate evidence for spawning periods and growth rates. For *A. japonicum* there were significant differences between size frequency distributions ($X^2=9.98$, $df=1$, $p=0.041$).

A fairly stable mode was demonstrated by *Y. hyalosoma* over most sampling months, although the large dispersion was reflected in the significant difference among frequency distributions ($X^2=52.85$, $df=4$, $p<0.001$) (Fig. 7). In contrast with *A. japonicum* the largest individuals were found in December with the smallest in June and September, suggesting a later spawning date during the NEM. For *G. oyena*, the greatest variation was found between size frequency distributions ($X^2=19.288$, $df=1$ and $p<0.001$) with most smaller fish found in September and most larger ones in June, suggesting a late NEM or early SEM spawning time.

Discussion

Fish communities in intertidal areas have been studied using varying sampling techniques and gears. Here, an approach intermediate to sampling large areas adjacent to the forest (such as seine netting in bays) and sampling very small, possibly unrepresentative plots (such as stake netting quadrats) was taken; in order to capture forest variability, fishes were sampled at multiple discrete sites within a forest canopy using repeat samples. Using passive gear (fyke nets) situated in small mangrove creeks, the present study documented 59 fish

Table 5. Maturity stages of fish species caught in Vanga from September 2015 to June 2017. The maturity stage was determined according to Nagelkerken and Velde (2002). Individuals with a third or less of the max 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, standard length, preferred habitats and environment were sourced from Froese and 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 and environment
<i>Acentrogobius nebulosus</i> *	6.1	9.7	3	0	100		18.0 SL	sandy shorelines, reefs
<i>Acropoma japonicum</i>	1.7	9.3	252	86.9	13.1	0.0	20.0 TL	sand, sandy mud bottoms
<i>Ambassis ambassis</i> *	3.2	5.7	136	2.2	97.8		15.0 TL	no information
<i>Ambassis gymnocephalus</i>	5.2	5.9	5	20.0	80.0		16.0 TL	no information
<i>Ambassis natalensis</i>	4.6	7.5	178	0.0	100	0.0	9.0 SL	no information
<i>Yarica hyalosoma</i>	1.0	9.3	470	41.9	58.1	0.0	17.0 TL	mangrove estuaries, tidal creeks (Adults)
<i>Arothron immaculatus</i>	5.3	5.4	2	100			30.0 TL	weedy areas, estuaries, seagrass
<i>Atherinomorus lacunosus</i>	3.5	9.2	84	90.5	9.5	0.0	25.0 TL	sandy shorelines, reef margins
<i>Bembrops caudimacula</i>	8.0	9.0	3		100		24.1 TL	no information
<i>Bembrops platyrhynchus</i>	6.5	6.5	1	100	0.0	0.0	25.0 TL	inhabits offshore trawling grounds
<i>Carangoides ferdau</i>	6.1	6.1	1	100			70.0 TL	sandy beaches; near reefs
<i>Caranx ignobilis</i>	10.6	11.8	3	100			170 TL	Clear lagoons, seaward reefs (Adults)
<i>Chanos chanos</i> *	14.7	16.5	2	100			180 SL	offshore marine waters, shallow coastal embayments
<i>Crenimugil crenilabis</i>			1	100			60.0 TL	sandy/muddy lagoons, reef flats
<i>Epinephelus caeruleopunctatus</i>	41.8	41.8	1	100	100		76.0 TL	coral-rich areas, deep lagoons,
<i>Epinephelus coioides</i>	15.0	27.8	5	100	0.0	0.0	120 TL	brackish water, mangroves (Juveniles)
<i>Epinephelus lanceolatus</i>	45.0	45.0	1	100			270 TL	caves, estuaries
<i>Epinephelus malabaricus</i>	12.5	35.0	7	100			234 TL	coral reefs, estuaries, mangroves
<i>Epinephelus spilotoceps</i>	22.3	22.3	1		100		35.0 TL	lagoon, reefs,
<i>Gazza minuta</i>	1.2	7.0	49	100	0.0	0.0	21 TL	young ones enter mangrove estuaries/silty reef areas
<i>Gerres filamentosus</i>	4.7	15.2	88	65.9	34.1		35.0 TL	mangrove (Juveniles)

Fish species	Min TL (cm)	Max TL (cm)	N	% Juveniles (Juv)	% Sub – adults (Sa)	% Adults (Ad)	Max length (cm)	Preferred habitat and environment
<i>Gerres longirostris</i>	5.1	7.0	5	100	0.0	0.0	44.5 TL	adults, coastal waters (Adults), estuaries (Juveniles)
<i>Gerres oyena</i>	4.9	11.0	106	97.2	2.8	0.0	30.0 TL	saltwater lagoons, estuaries
<i>Hyporhamphus affinis</i> *	5.0	13.4	40	90.0	10.0		38.0 SL	coral reefs
<i>Hyporhamphus gamberur</i>	12.0	13.7	3	33.3	66.7		37.0TL	common around reefs
<i>Leiognathus equulus</i>	2.3	6.4	136	100			28.0 TL	muddy inshore areas, mangroves
<i>Lethrinus harak</i>	6.3	6.3	1	100			50.0 TL	shallow sandy, mangroves, seagrass
<i>Lutjanus argentimaculatus</i>	11.4	19.6	10	100			150 TL	Mangrove (Juveniles and young adults)
<i>Lutjanus bohar</i>	15.5	15.5	1	100			90.0 TL	coral reefs
<i>Lutjanus fulviflamma</i>	6.5	15.5	36	100	0.0	0.0	35.0 TL	coral reefs (Adults), mangrove (Juveniles)
<i>Lutjanus fulvus</i>	5.8	5.8	1	100			40.0 TL	lagoons (Adults), mangroves (Juveniles)
<i>Monodactylus argenteus</i> *	3.9	8.2	36	100			27.0 SL	bays, mangroves
<i>Moolgarda seheli</i>	6.7	10.8	23	100			60.0 TL	coastal waters, estuaries
<i>Mugil cephalus</i> *	5.3	12.9	15	100			100.0 SL	coastal waters
<i>Platax orbicularis</i>	5.5	7.3	2	100			60.0 TL	sandy areas (Adults), mangroves (Juveniles)
<i>Platax pinnatus</i>	3.1	5.2	3	100			45.0 TL	reef slopes (Adults), mangroves (Juveniles)
<i>Platycephalus indicus</i>	9.8	9.8	1	100			100.0 TL	sandy and muddy bottoms
<i>Plectorhinchus plagiodesmus</i>	7.1	19.4	3	100			90.0 TL	coastal, coral crevices
<i>Pomadasys argenteus</i>	5.6	10.4	8	100			70.0 TL	coastal waters
<i>Pomadasys kaakan</i>	9.4	9.4	1	100	0.0	0.0	80 TL	inshore waters (sandy to muddy bottoms), estuaries
<i>Pomadasys multimaculatus</i>	4.9	15.6	13	100	0.0	0.0	76.0 TL	coastal waters, tidal estuaries
<i>Pterois volitans</i>	20.0	20.0	1		100		38.0 TL	lagoons, reefs, turbid inshore
<i>Sardinella gibbosa</i> *	6.1	6.4	2		100		17.0 SL	no information

Fish species	Min TL (cm)	Max TL (cm)	N	% Juveniles (Juv)	% Sub – adults (Sa)	% Adults (Ad)	Max length (cm)	Preferred habitat and environment
<i>Sillago sihama</i> *	9.0	14.7	33	87.9	12.1	0.0	31.0 SL	beaches, sandbars, mangrove
<i>Sphyraena barracuda</i>	11.3	28.7	7	100			200 TL	murky harbours (Adults), mangroves (Juveniles)
<i>Sphyraena jello</i>	4.0	21.4	15	100	0.0	0.0	150 TL	Reefs, bays, estuaries
<i>Sphyraena putnamae</i>	14.6	17.5	2	100			90.0 TL	lagoons, seaward reefs, bays, turbid lagoons
<i>Spratelloides gracilis</i> *	3.5	3.5	1		100.0		10.5 SL	coastal, reefs
<i>Stolephorus commersonnii</i> *	10.0	10.2	2	0.0	0.0	100	10.0 SL	coastal waters, brackish water
<i>Terapon jarbua</i>	4.0	11.3	9	100			36.0 TL	shallow sandy bottoms (Adults) sandy intertidal areas (Juveniles)
<i>Thrysa setirostris</i> *	7.5	7.8	2		100.0		18.0 SL	no information
<i>Tylosurus acus melanotus</i>	29.8	29.8	1	100			100.0 TL	offshore, coastal waters
<i>Tylosurus crocodilus</i>	35.8	35.8	1	100			150 TL	lagoons, seaward reefs
<i>Zenarchopterus dispar</i>	8.6	14.5	9		88.9	11.1	19.0 TL	shallow water, mangroves

*indicates standard and not total length was used

species in the Vanga mangrove system. This is higher than the species numbers recorded from nearby Gazi forest in studies using block nets (another passive gear), which found 30 (Huxham *et al.*, 2004) and 49 species (Crona and Rönnbäck, 2007). Studies in Kenyan mangroves that use active gears, such as seine nets and beam trawls, report higher numbers, for example 128 fish species were recorded in Gazi (Kimani *et al.*, 1996) while at Tudor Creek, 83, 84 and 75 species were recorded by Little *et al.* (1988), Wainaina *et al.* (2013) and Wakwabi and Mees, (1999) respectively. Hence the choice of gear clearly has a large influence on the numbers and diversity of fish caught. Netting in bays and large permanent creeks produces bigger samples (and is logistically more straightforward) than placing passive gear under the canopy (Franco *et al.*, 2012; Tietze *et al.*, 2011). However such sampling is less able to discriminate between forest areas of different quality and may include fauna that are not using mangrove habitats at all.

It is generally true that fish communities, like almost all biological communities from inshore habitats, 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 and Krumme, 2007; Shervette *et al.*, 2007). Such a pattern was observed in the present study in Vanga, where 6 species contributed around 70 % of the total abundance. A similar pattern was found in the bay habitats of neighbouring Tanzania, where 9 species contributed 70 % of the total individuals (Lugendo *et al.*, 2007). In Thailand, Tongnunui *et al.* (2002) found that 20 fish species contributed 88.5 % of the total abundance in the Sikao creek mangrove estuary.

Studies of mangrove fish communities consistently show that juveniles dominate. Ninety nine per cent of the fish reported by Tongnunui *et al.* (2002) were not adults; 71 % were small juveniles and 28 % were large juveniles/sub adults. Out of the 54 encountered species in this study 34 occurred only as small juveniles, while 9 species occurred only as large juveniles. These results conform to research findings in other mangrove systems. In Tudor creek Kenya, 90 % of the

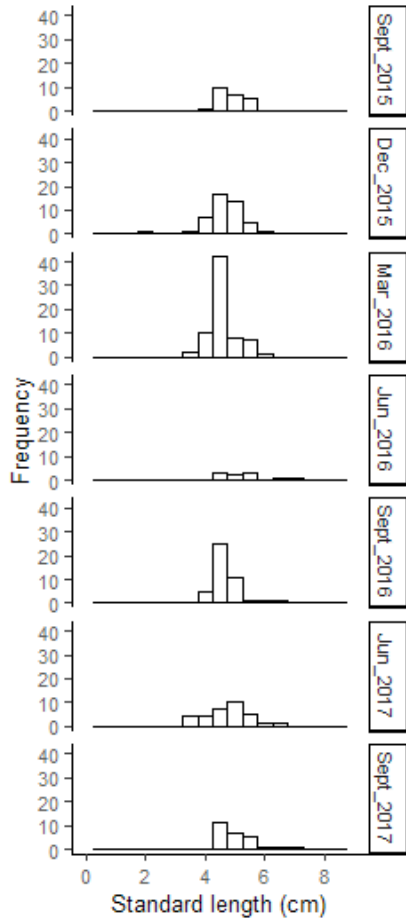


Figure 6. Size classes of *Acropoma japonicum* (max. length= 20 cm) over the study period (Individuals with a third or less of the max length were classified as small juveniles, between one third and two thirds of maximum length as big juveniles to sub adults and above two thirds maximum length as adults).

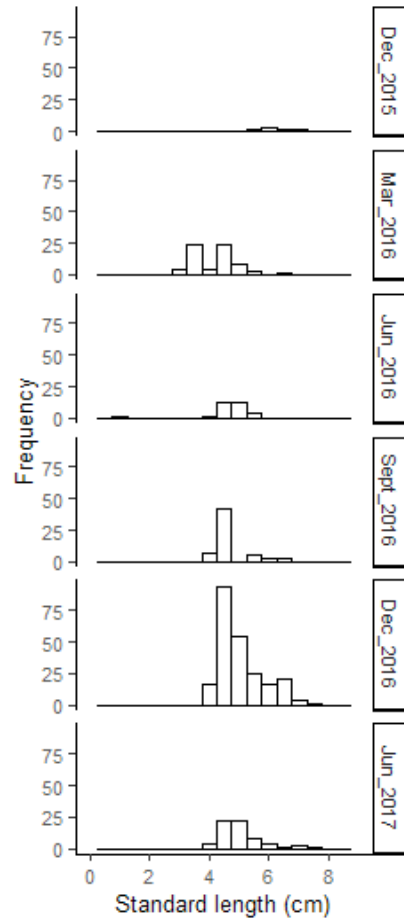


Figure 7. Size classes of *Yarica hyalosoma* (max. length=17 cm) over the study period (Individuals with a third or less of the max length were classified as small juveniles, between one third and two thirds of maximum length as big juveniles to sub adults and above two thirds maximum length as adults).

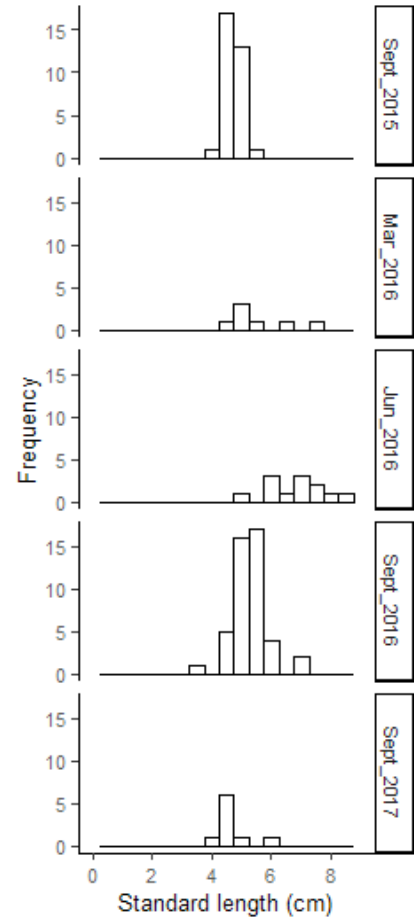


Figure 8. Size classes of *Gerres oyena* (max. length=30 cm) over the study period (Individuals with a third or less of the max length were classified as small juveniles, between one third and two thirds of maximum length as big juveniles to sub adults and above two thirds maximum length as adults).

fishes caught were juveniles (Little *et al.*, 1988) while in Gazi bay, 63 % of the species caught included juveniles with 29 % caught as juveniles only (Kimani *et al.*, 1996). Crona and Rönnbäck (2007) recorded juveniles in almost all fish taxa encountered in Gazi bay. Over 70 % of the fishes caught in bay habitats of Tanzania were juveniles (Lugendo *et al.*, 2007), whilst in Thailand 57 % of the species were caught as juveniles only (Ikejima *et al.*, 2003). In the current work, only 2 % of individuals caught were classified as adults. Hence the findings of this and other studies are 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.

The most abundant species in this study – *Y. hyalosoma*, (previously known as *Apogon hyalosoma*), *A. japonicum*,

A. natalensis, *A. ambassis*, *L. equulus* and *G. oyena* – are reported in most relevant studies in the WIO and also in the Mediterranean (Kimani *et al.*, 1996; Huxham *et al.*, 2004; Crona and Rönnbäck, 2007; Wainaina *et al.*, 2013; Lugendo *et al.*, 2007; Mwandya *et al.*, 2010; El-Regal and Ibrahim, 2014). They have been reported in other regions such as in the intertidal mangrove areas of Thailand where *Y. hyalosoma* was found to contribute up to 7 % of the total catch (Krumme *et al.*, 2015). In Gazi bay, *A. japonicum* was strongly associated with mangrove plantations (Crona and Rönnbäck, 2005). *Leiognathus equulus* is a widely distributed species in inshore areas of the Indo – Pacific region (Blaber and Milton, 1990). Though present in Tudor and Mida creeks in Kenya, it contributed <2% of the total catch in these mangrove systems (Wakwabi and Mees, 1999, Wainaina *et al.*, 2013; Gajdzik *et al.*, 2014). The current study recorded a higher percentage (7.4

%), close to what was recorded (5.4 %) in mangrove habitats of Tanzania (Lugendo *et al.*, 2007). In subtidal seagrass areas of Peninsular Malaysia, *L. equulus* accounted for circa 19 % of fishes sampled in the seagrass beds (Aziz *et al.*, 2005). High percentages (92 %) of *L. equulus* were also encountered in subtidal areas compared to intertidal areas in Thailand (Ikejima *et al.*, 2003). It could therefore be concluded that this species is found in both intertidal and subtidal inshore areas but prefers the latter over the former. Fishes of the Ambassidae family have been found to contribute up to 10 % of the total catch on the north coast (Little *et al.*, 1988; Gajdzik *et al.*, 2014) but are scarcely reported on the south coast of Kenya (Kimani *et al.*, 1996; Crona and Rönnbäck, 2005). In the current study at Vanga (south coast) Ambassidae, which contributed to 18.4 % of total fish abundance, were found in the NEM season only with over 80 % of the individuals being subadults. This concurs with the findings from Mida creek (Gajdzik *et al.*, 2014) and Tanzania (Mwandya *et al.*, 2009) where subadults and adults of this species dominated the catch (Mwandya *et al.*, 2010). In Tanzania Ambassidae were among the dominant families in mangrove areas (Lugendo *et al.*, 2007). *Gerres oyena*, the sixth most abundant species in this study (contributing 5.7 % of total abundance), is considered a mangrove resident and that could explain its abundance 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 species as the most abundant in the small 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 nature of migrating into and out of mangrove and other habitats.

Serranidae was the most diverse family, with 5 species found, all from the genus *Epinephelus*. The Vanga reefs have 8 species of *Epinephelus*, which is lower than other Kenyan reefs such as Msambweni (14 species) and Shimoni (36 species) (Agembe *et al.*, 2010). *Epinephelus* sp. have suffered sharp declines at the Kenya coast over the last three decades (Kaunda-Arara, 1996; Kaunda-Arara *et al.*, 2003). The high commercial value and sedentary nature of the species in this genus have exposed them to threats leading to high mortality (Kaunda-Arara *et al.*, 2003; Sadovy, 2005). Dynamite fishing in reef areas of Vanga by fishermen from neighbouring Tanzania has also been suggested as the cause

of these low numbers (Ochiewo, 2004; Samoilys and Kanyange, 2008). The low abundance (<1 % of total abundance) and relatively low diversity recorded in this study are consistent with other findings, including that of declines in most *Epinephelus* species at Vanga (Fortnam *et al.*, 2020) indicating that this diverse and commercially important genus could be threatened, creating concern for its future survival.

Size classes

The maximum length of *G. oyena*, a common fish species caught in Vanga mangroves, was 11 cm TL compared to large sized individuals (29.2 cm TL) of the same species caught in Gazi bay (Kimani *et al.*, 1996). However, *G. oyena* caught using passive gear inside Gazi mangrove forests were comparable in size to those caught in the current study i.e. 10.8cm TL for Gazi (Crona and Rönnbäck, 2007). From this comparison, it could be suggested that *G. oyena* juveniles are likely to be encountered inside the forests and adults in the creeks and nearshore waters. It could also be speculated that size classes are likely to differ between habitat types within similar ecosystems such as mangrove forests and mangrove creeks. It was not possible to compare the sizes of *Y. hyalosoma* and *A. japonicum* with other sites due to a lack of relevant literature; it seems that very little is known about the growth and possible ontogenetic shifts in these species.

The size frequency distributions compared over time for 3 species i.e. *G. oyena*, *Y. hyalosoma* and *A. japonicum* gave an indication of decreases in numbers as the standard length of the fish increased. It was difficult to conclusively point to particular times of spawning for these species due to a lack of supporting literature and insufficient detail in the current cohort analyses. For *A. japonicum* for instance, the significant differences between size frequency distributions, did not provide an unambiguous indication of likely spawning times and growth rates since the mode remained fairly constant; the smallest individuals were found during December and the largest in September, consistent with spawning in the early NEM season. Increases in size between sampling dates could indicate a single cohort that grows whilst in the mangroves and then leaves to be recruited into the coastal fishery later, however much more information would be needed to confirm such a pattern.

Seasonality

Environmental variables such as salinity and temperature are influenced by seasonality and in turn these

may influence fish community structures by affecting feed availability, reproduction and ontogenic migrations (McClanahan, 1988). In Vanga, like the rest of the Kenyan coast, sea surface temperatures may range between 24 °C and 29 °C during the year with salinity levels ranging between 34.5 ‰ and 23.8 ‰. (McClanahan, 1988; Mwashote, 2003).

The overall mean catch per net (abundance) of juvenile fishes and the number of fish species in Vanga was significantly higher during the SEM (rainy) than NEM (dry) seasons. Fish community structures (abundance and diversity) in the WIO region have been found to vary with monsoon seasons (Lugendo *et al.*, 2005; Crona and Rönnbäck, 2007). While juvenile fishes occupying mangrove habitats have been found to be more abundant in SEM than in NEM, in the current and previous work (Crona and Rönnbäck, 2007), densities of planktonic fish 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). McClanahan (1988) also recorded fish spawning in the East African region to peak during the NEM season (McClanahan, 1988). It is possible that fishes spawned offshore in the NEM season move into the mangrove nursery habitats during the rougher SEM season. Fishes in the Ambassidae family, which constituted a large proportion of the catch in the current study, were only found during the NEM season. Most individuals caught were relatively large sub-adults, and hence may not be showing this pattern since they were not using the Vanga mangroves as habitat during the small juvenile stages. Further studies into the life cycles of these species may help shed more light on their ecology.

Crustacean community structure

Penaeid shrimps comprised over 80% of the crustaceans caught with *P. semisulcatus* and *P. indicus* dominating the catch. These two species have previously been recorded as the most abundant penaeid shrimp in Malindi – Ungwana bay in Kenya (Munga *et al.*, 2013). Similarly, in the same area, *P. indicus* was among the dominant 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 seasonality in abundance. Generally, crustaceans did not show any clear seasonality in the present study. This contrasts strongly with the fish catches reported here and with commercial and artisanal catches of

fish in Vanga waters. 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). The apparent lack of seasonality for penaeid shrimp means that exploitation can continue throughout the year. There is a real risk of overfishing, 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. Uncontrolled fishing especially of juveniles is likely to lead to low returns. This work supports the idea of mangrove and near mangrove habitat as nursery habitat for both fish and crustaceans so emphasising the need for conservation particularly of seaward edges. Future studies should focus on size classes of penaeid shrimp species in nearshore habitats in both the NEM and SEM seasons and this could guide management options such as closed seasons.

Conclusion

Most of the fish families and species encountered in Vanga are common on the East African coast. The dominance of a few species is commensurate with most findings from tropical mangrove ecosystems where a few species occur in high densities. *Gerres oyena* has been reported as a common species in several other mangrove sites on the Kenya coast; it is strongly associated with and possibly dependent upon mangroves. Close to 50 % of the species caught at mangrove sites in Vanga are exploited for commercial fisheries while 32 of the total 59 species were reef associated. Most of these species however occurred in very low numbers. This could mean that they prefer other nursery habitats such as seagrass. If that is not the case, then it can be speculated that their recruitment into the fishery could also be low.

Almost all the individuals encountered in this study were juveniles. This is expected in mangrove habitats. Thus, this study further affirmed the hypothesis that mangroves provide habitats for juvenile fauna, which later migrate offshore.

The strong seasonality in fish catches, with much greater abundance and diversity being found during the SEM season, supports the hypothesis that many species are spawning offshore during the NEM season and then moving into mangroves as juveniles, before

migrating offshore again as sub-adults. In contrast there was no clear seasonality for penaeid shrimp suggesting they show a different lifecycle with more rapid reproduction and more consistent affinity with inshore habitats.

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