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Cover image: Ngalawa (traditional dugout, outrigger canoe) being readied for a boat race in the 2018-2019 Kraken cup, Kilwa, Tanzania. © Rahim Saggaf

The trophic structure of fish in seaweed farms, and adjacent seagrass and coral habitats in Zanzibar, Tanzania

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Abstract

Coral reefs, seagrasses and seaweed farms (*Eucheuma denticulatum*) are characteristic habitats in many parts of the coast of Zanzibar, Tanzania. However, information on trophic interactions, movements of fish, and variation in fish diet specialization between these habitats are scarce. The present study determined the trophic structure and the variation in diet composition of fish caught in (floating) seaweed farms, and in adjacent seagrass and coral reef habitats in Pongwe, Zanzibar. Fish were caught using traditional basket traps (*dema*) and gut contents of 392 fish were analyzed. A one-way Analysis of Similarities (ANOSIM) showed that there was a significant difference in the composition of prey items eaten by invertivores in different habitats (Global R = 0.109, $p = 0.002$). There was no significant difference in the composition of prey items eaten by herbivores, invertivore-piscivores and omnivores ($p > 0.05$), likely due to movement of fish between these habitats for foraging. There was no significant difference in the relative proportion of trophic groups between the habitats ($p > 0.05$) except for herbivores ($p < 0.05$). Floating seaweed farms attract invertebrates and smaller fish, thus providing feeding grounds for predatory fish, and should be considered as ecologically important habitats as are coral reefs and seagrass beds.

Keywords: trophic structure, seaweed farm, seagrass, coral, habitats

Introduction

Determining the ecosystem state and connectivity of biomass between ecological groups or trophic levels is vital to understanding ecosystem function (Christensen and Pauly, 2004). The understanding of fish trophic networks is important in establishing ecologically based management programmes (Kulbicki *et al*., 2005). Gut content analyses are used in studies related to fish composition and abundance of wild fish assemblages (Arechavala-Lopez *et al*., 2011; Fernandez-Jover *et al*., 2011). They provide information of the most recent meal and can be used to track changes in feeding habits of captured fish (Fernandez-Jover *et al*., 2008), and trophic relationships (Berkstrom *et al*., 2012).

Connectivity of organisms is known to occur between seagrass beds and coral reefs (Berkstrom *et al*., 2013). Fish belonging to trophic groups such as planktivores, piscivores and motile invertebrate feeders that eat high protein and energy-rich food with high assimilation rates (Bowen *et al*., 1995) form the most diverse trophic groups worldwide (Jones *et al*., 1991; Ferreira *et al*., 2004). In many tropical regions, shallow water habitats are strongly connected through ontogenetic or foraging migration of fish (Krumme, 2009). Large piscivores and invertebrate feeders are known to migrate from coral reefs to feed in adjacent seagrass and sandy areas (Appeldoorn *et al*., 2009). Meyer *et al*. (1983) reported at least 15 fish families that leave coral reefs to forage in neighboring areas. Seagrass beds provide high abundance of food and suitable refuge, thus functioning as a complementary or supplementary resource for many multi-habitat species (Pittman *et al*., 2004; 2007). Furthermore, studies from tropical and subtropical marine waters have shown that seasonal changes in resource availability and environmental conditions influence fish feeding patterns and variation in food composition (Harrigan *et al.,* 1989; Layman and Silliman, 2002). Dietary ecology and

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feeding habits can be explored by quantifying variations in resource use and feeding intensity. Individual species are predicted to shift resource use in response to food availability in the environment (Stephens and Krebs, 1986). Therefore, studying how the diet of species from different trophic groups varies within a multihabitat may help to provide knowledge about the nature of interactions that exist between individuals and habitats (Heng *et al*., 2018).

Seaweed farming is being practiced in a number of coastal villages in Zanzibar (Eklund and Pettersson, 1992). While the seaweeds provide income and livelihood to thousands of artisanal farmers, it has been suggested that macroalgal habitats like seaweed farms provide benefits in terms of recruitment, provision of food, shelter and refuge for fish (Bergman *et al*., 2001; Eklöf *et al*., 2006). Seaweeds are used as a source of food for herbivorous reef fish such as the Siganidae as well as foraging sites for invertebrate feeders and omnivores which predate on the associated epifauna (Bergman *et al*., 2001).

There is little information on trophic regimes of fish in seagrass and coral reefs in the Western Indian Ocean (WIO) region (de Troch *et al*., 1998; Almeida *et al*., 2001; de Boer *et al*., 2001; de la Torre-Castro *et al*., 2008). Foraging fish that migrate daily are known to move between a few hundred meters to a few kilometers, often between coral reefs and seagrass beds (Nagelkerken *et al*., 2000; Berkstrom *et al*., 2013), yet information on trophic interactions and movements of fish between seaweed farms, seagrass and coral reefs is scarce and variation in fish diet specialization has not yet been well reported (de Carvalho *et al*., 2015). Thus, the aim of this study was to determine the trophic structure and variation in dietary composition of fish caught in seaweed (*Eucheuma denticulatum*) farms, and adjacent seagrass and coral reef areas.

Methodology

Study area

The study was conducted in Pongwe Village on the mid-eastern coast of Unguja Island, Zanzibar (Fig. 1) from April 2018 to April 2019. The area is located in the equatorial belt of the WIO and experiences two types of seasonal wind patterns annually; the South East Monsoon, which lasts from April to September, and the North East Monsoon, lasting from November to February. The average rainfall is 1,560 mm and the average atmospheric temperature is about 26°C. Pongwe beach is protected by an offshore reef which keeps the inner waters calm and safe. It has a large intertidal area covered by seagrass. The substratum consists of coral rubble and sand. Agriculture, fisheries and seaweed farming form the basic occupations for livelihood sustenance and food security in the area. In this study the seaweed stations were located on deep-water floating farms either over sand or seagrass.

Sampling and data collection

Sampling of fish was carried out during neap tides at intervals of 15 days from planting to harvesting for every seaweed cultivation period (45 days) in each habitat. A fixed basket trap known as "*dema*" was set to capture fish in each seaweed, seagrass, coral reef and sand site. The "*dema*" traps are traditional hexagonal traps measuring 1.04×1.32×0.24 m^3, with a mesh size of 3 cm. Two traps were placed in each station. Each trap was anchored by two stones attached to its sides and fish were lured into a narrow funnel by bait comprising of macroalgae, seagrass leaves, sea stars and brittle stars (after Jiddawi and Öhman, 2002). The respective position of the traps was marked by buoys to allow retrieval and removal of the caught fish. After retrieval the traps were re-baited and re-deployed in a different location within the same habitat.

Processing of fish samples

Fish catch from the traps was harvested and stored in an ice box immediately after capture and preserved to reduce post-capture digestion that could result in loss of dietary information (Bowen, 1996). The samples were transported to the Institute of Marine Sciences (IMS) laboratory in Zanzibar town for sorting into species and analysis of gut contents. Fish were sorted and identified using standard taxonomic keys and guides (Bianchi, 1985; Allen and Steene, 1987; Lieske and Myers, 1994; Richmond, 2011). Fish guts were removed from each individual and food items in each stomach were visually identified to the lowest taxonomic group possible using a stereo microscope. The number of stomach samples including those with and without food items and the types of food categories were recorded. The schemes used by Froese and Pauly (2019) and Berkstrom *et al*. (2012) were adopted to determine the trophic groups of fish according to the types of food categories contained in their stomachs. Fish were classified as (i) herbivores (feeding mainly on seagrass, detritus and algae), (ii) invertivores-piscivores (preying on bivalves, crabs, shrimps, detritus and fishes), (iii) omnivores which had mixed contents of plant material, animal (except fish) and detritus, (iv) invertivores (feeding specifically on bivalves, crabs and shrimps), and (v) piscivores that fed on fishes. However, in this study only one piscivorous fish (*Conger cinereus*) was caught during sampling and therefore this category was not considered for further analysis.

root transformed to reduce the weight of dominant values. Data on trophic groups was analyzed in the SPSS software package. All data were checked for normality and homogeneity of variance. Since much of the data on biological parameters did not meet the criteria for normality and homogeneity of variances,

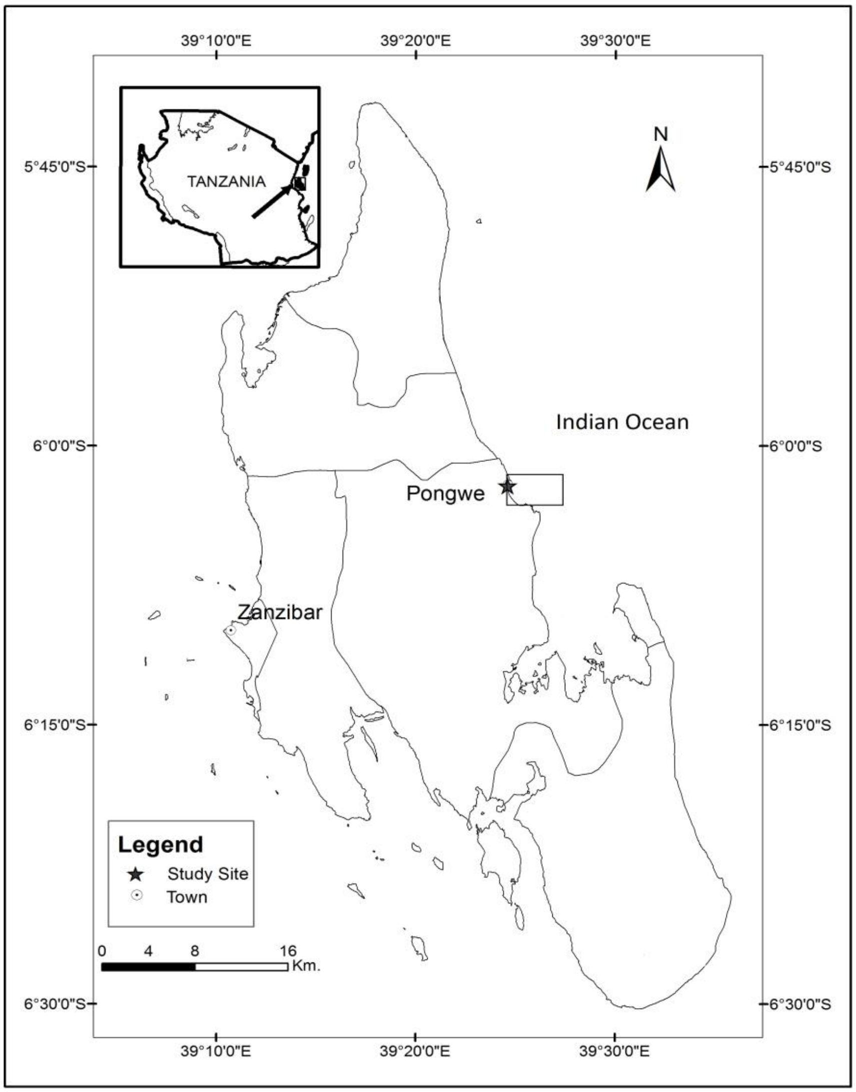

Figure 1. Map of Unguja Island showing the study site.

Data analysis

Comparisons of fish diet composition were tested by one-way Analysis of Similarities (ANOSIM) with 999 permutations (Clarke and Warwick, 1994). Similarity percentage analysis (SIMPER) was used to identify the proportional contribution of individual species to average similarity/dissimilarity (Warwick *et al.*, 1990). Prior to the multivariate analysis, the data were square

a non-parametric Kruskal-Wallis test was used to test for differences in proportion of trophic groups between habitats.

Gut content analysis

Data for gut content composition was obtained from specimens caught by traps at all sampling stations and used for the determination of the feeding trophic level.

Stomach content indices were calculated as:

i. SCIs (%) = (Number of fish stomachs with specific food type per habitat/Number of fish stomachs with variety of food per habitat) x 100

Relative Trophic Composition (RTC) of fish species per site was calculated as:

ii. RTC (%) = (Number of fish specimens belonging to one trophic group per habitat/ Number of fish specimens belonging to all trophic groups per habitat) x 100

Results

Stomach content indices

Gut contents of 392 fish caught by basket traps were analyzed; 159 from coral reefs, 98 from seagrass beds, 69 from sandy habitat, 44 from a floating seaweed farm placed over sand, and 22 from a floating seaweed farm placed over seagrass.

Herbivores

For herbivorous fish caught in coral reefs, results indicated a higher percentage contribution of brown algae (42 %), followed by seagrass, while green and red algae were found only in a few stomachs and in lower percentages. For those caught in seagrasses, the dominant prey item was seagrass with a percentage contribution of 48 %, followed by brown algae, green algae and animals. In the sand area, brown algae had the highest percentage contribution (43 %), followed by seagrass, whereas green and red algae were rarely found. In seaweed farms, both over sand and seagrass, the dominant food item was brown algae (60 % and 50 % respectively) followed by red algae, while seagrass and green algae were rarely observed (Fig. 2). Animals like annelids, nematodes and sipunculids were only observed in stomach contents of fish caught in coral reef, seagrass and sand habitats. A one-way Analysis of Similarities (ANOSIM) showed that there was no significant difference in prey items eaten by herbivorous fish in different habitats (Global R= 0.017, p = 0.191). Similarity percentages (SIMPER) analysis showed that the main contributors for the observed similarities were seagrass ranging from 50-59 % and brown algae (31-100 %).

Invertivore-piscivores

The diet of invertivore-piscivores caught in both coral reefs and seagrasses was dominated by crabs with percentage contribution of 41 % and 33 % respectively, followed by shrimps. Fish, gastropods and bivalves contributed the least. In the sand area bivalves had the highest contribution (36 %) followed by shrimps, gastropods and crabs. Crabs were the dominant prey for fish caught in seaweed farms over sand, with a percentage contribution of 44 % followed by shrimps, while in seaweed farms over seagrass, gastropods contributed highest (43 %), followed by crabs. Sea urchin remains were only observed in samples caught in coral reef habitat and the seaweed farm over seagrasses (Fig. 3). The ANOSIM test showed that there was no significant difference in prey items eaten by invertivore-piscivores in different habitats (Global R= 0.008, p = 0.316.). The SIMPER analysis showed that the prey items contributing most to similarities between habitats were crabs (46-75 %) and shrimps (11-37 %).

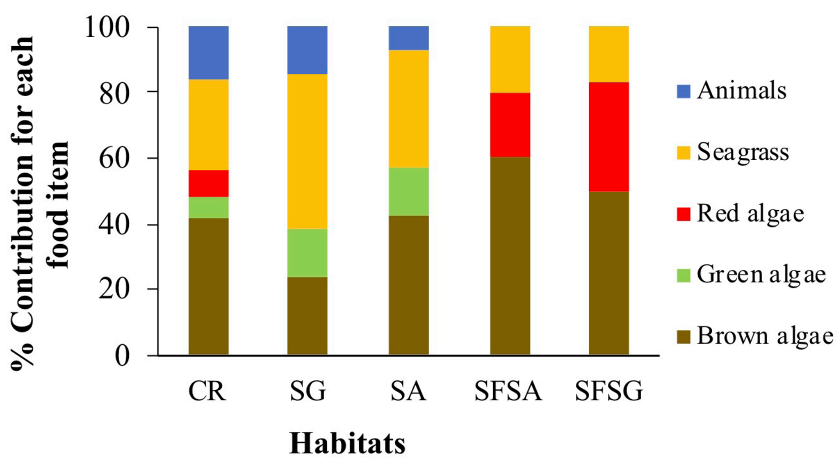

Figure 2. Stomach Content Indices for herbivorous fishes in all habitats. CR = Coral reef, SG = Seagrass, SA = Sand, SFSA = Seaweed farm over sand and SFSG = Seaweed farm over seagrass.

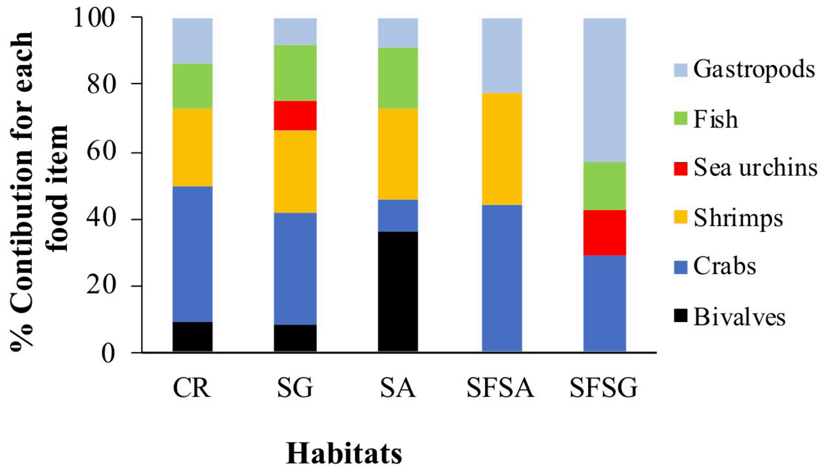

Figure 3. Stomach Content Indices for invertivore-piscivores in all habitats. CR = Coral reef, SG = Seagrass, SA = Sand, SFSA = Seaweed farm over sand and SFSG = Seaweed farm over seagrass.

Invertivores

For invertivores, results indicated a highest percentage contribution of crabs in the diet of fish caught in coral reefs (53 %), seagrasses (50%) and sand (42%), followed by shrimps with a contribution of 30 %, 29 % and 25 % respectively. Gastropods, brittle stars and calcareous algae also contributed to the diet of fishes in each habitat. For fish samples from the seaweed farm over sand, the dominant prey was crabs (50 %), followed by gastropods (33 %), while the diet of invertivores in the seaweed farm over seagrass was composed of only crabs (Fig. 4). ANOSIM showed a significant difference in the composition of prey items eaten by invertivores in different habitats (Global R = 0.109, p = 0.002). Pairwise comparison showed a significant difference in prey item composition between fish caught in coral reefs and the seaweed farm over seagrass (R = 0.252, p = 0.003), and between those in seagrass and the floating farm over sand (R = 0.356, p = 0.001). SIMPER analysis showed that the highest contributors to dissimilarities were crabs (52 %), shrimps (33 %) and gastropods (10 %).

Omnivores

The diet of omnivores was dominated by gastropods for coral reef (42 %) and seagrass (47 %) fish. The dominant prey on samples from sand was gastropods (50 %), followed by polychaetes (21 %) while bivalves

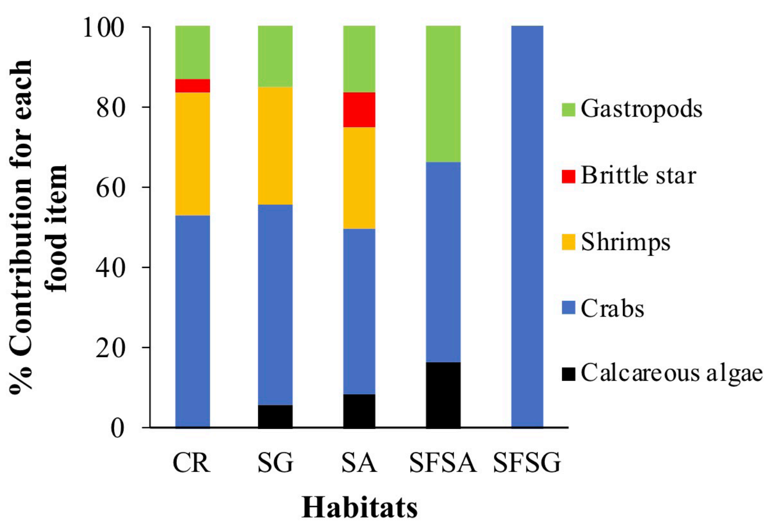

Figure 4. Stomach Content Indices for invertivores in all habitats. CR = Coral reef, SG = Seagrass, SA = Sand, SFSA = Seaweed farm over sand and SFSG = Seaweed farm over seagrass.

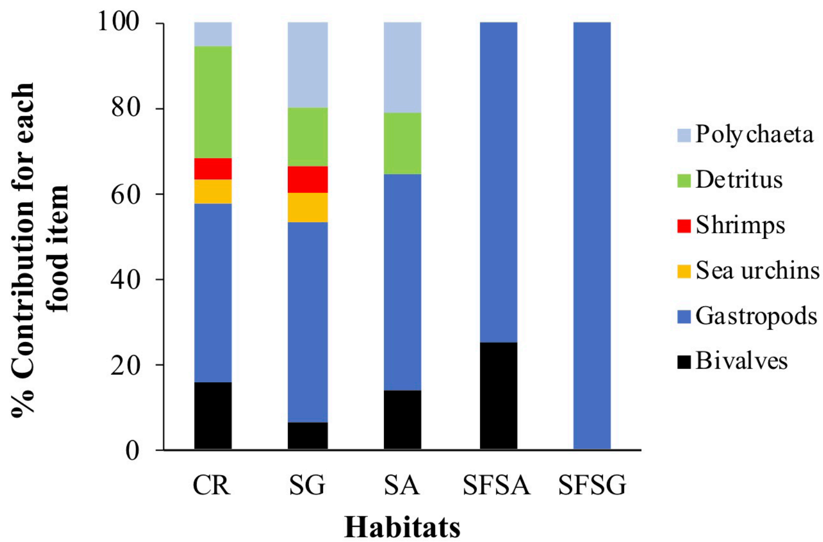

Figure 5. Stomach Content Indices for omnivores in all habitats. CR = Coral reef, SG = Seagrass, SA = Sand, SFSA = Seaweed farm over sand and SFSG = Seaweed farm over seagrass.

featured least in samples from these habitats. For fish caught in the seaweed farm over sand, gastropods contributed 75 % followed by bivalves (25%), while samples from the seaweed farm over seagrass had gastropods only in their stomachs (Fig. 5). The ANOSIM test showed a weak difference in prey items eaten by omnivores between the habitats (Global R =0.020, p=0.011). Similarity percentages (SIMPER) analysis showed that the food item contributing most to dissimilarities were gastropods (40 %), polychaetes (36 %) and detritus (11 %).

Trophic groups and relative trophic composition

In terms of trophic groups, coral reef habitat had the highest numbers of herbivores (66), invertivore-piscivores (28) and omnivores (23). Seagrasses had the highest number of invertivores (46), while the seaweed farm over seagrass had the lowest number of individuals from all four trophic groups (Table 1).

The Relative Trophic Composition (RTC %) indicated that all trophic groups identified were present in all the sites. Fish species belonging to all trophic groups were caught on coral reefs, where unexpectedly, herbivores (represented mostly by Siganids) had the highest RTC % (Table 1). Invertivores had the highest RTC % on seagrass, invertivores and omnivores on sand and invertivore-piscivores on seaweed farms (both over sand and seagrass) (Table 1). Differences in the relative proportion of trophic groups between the habitats were not significant ($\chi^2 = 5.76$, df = 4, $p > 0.05$). A significant difference was observed in the proportions of herbivores between habitats ($p<0.05$), while there was no significant

Table 1. Number of individuals from four trophic groups and Relative Trophic Composition (RTC %) of fish caught at different habitats.

	Herbivores		Invertivore-piscivores		Invertivores		Omnivores	
Sites	**Number**	**RTC%**	**Number**	**RTC%**	**Number**	**RTC %**	**Number**	**RTC %**
Coral reef	66	41.5	28	17.61	42	26.41	23	14.46
Seagrass	26	26.53	15	15.3	46	46.93	11	11.22
Sand	17	24.63	13	18.84	20	28.98	19	27.53
Seaweed farm over sand	8	18.18	15	34.88	11	25.58	10	23.25
Seaweed farm over seagrass	7	31.81	12	54.54	2	9.09	1	4.54

difference for invertivore-piscivores, invertivores and omnivores (p > 0.05).

Discussion

Analysis of stomach content indices (SCIs) showed that herbivorous fish preferred a variety of macroalgae. The higher abundance of brown algae and seagrass in the diet of herbivorous fish caught in these habitats is likely due to the availability of these food groups locally all year round. Furthermore, various species of the brown algae *Sargassum* were the dominant food item and were mainly ingested by herbivorous fish. Similarly, a study by Yatsuya *et al.* (2015) on seasonal changes of diet of *Kyphosus bigibbus*, found that brown algae was the dominant dietary component in all seasons. Contrary to expectations, the red algae *Eucheuma* sp. and green algae *Ulva* and *Enteromorpha* spp. were found in insignificant amounts in most herbivorous fish stomachs except for those caught in seaweed farms, even though *Eucheuma* sp., was available year round and is reported to be a potential food source for herbivores like Siganids. The higher ocurrence of *Eucheuma* sp. in the diet of fish caught in seaweed farms suggests that the farms act as both shelter and a source of food. Comparatively, Anyango *et al.* (2017) also found significant amounts of red algae in the stomachs of herbivorous fish caught in seaweed farms in the coastal waters of Kibuyuni, Kenya. However, Ojeda *et al*. (1999) concluded that green macroalgae were better food items than red macroalgae, and red macroalgae were better than brown macroalgae in terms of their greater protein, calories and digestibility values. Stomach content indices also showed a high occurrence of undigested annelids, nematodes and sipunculids in the stomachs of herbivorous fishes, although it was difficult to determine if these burrowing animals were ingested intentionally or incidentally. There are a few studies which suggest that juveniles of several species of herbivorous fishes consume significant amounts of animal items (Horn, 1989), or in small amounts as adults (Noda *et al*., 2002). The lack of a significant difference in the type of food eaten by herbivores in different habitats could be due to availability of these resources in the area. Macroalgae and seagrasses occur year round in the region, with peaks during the monsoon period (McClanahan, 1988).

For invertivore-piscivores and invertivores, there was a high percentage contribution of *Portunus* crabs and penaeid shrimps in their diet, which was observed in almost all stomachs of the fishes caught in the coral reef, seagrass habitats and seaweed farms throughout the year. This study showed that crustaceans are a potential food source and are mainly ingested by invertivore-piscivores and invertivores in the area. This could be due to their availability in habitats like segrass beds (Unsworth *et al*., 2007) and in seaweed farms as observed in the present study. Kulbicki *et al*. (2005) also reported that crustaceans are a major food items in nearshore, soft bottom and reef habitats and are among the most important item in pelagic fish stomachs. The high pecentages of crabs and shrimps was moslty observed from fish samples caught between December and July, probably due to an increase in abundance after spawning, which is reported to occur between late October to November (Svane and Hooper, 2004). In addition it has been reported that the onset of the wet season (March to May) triggers an offshore migration of juvenile shrimps (Teikwa and Mgaya, 2003). Bivalves were found mostly in the diet of invertivore-piscivore fishes caught in the sandy area, possibly due to the preference of bivalves to such habitats. There are often a very large number of bivalves and other invertebrates living beneath the surface of the sand (Christian, 2007). Gastropods also featured highly in the diet of invertivores caught in seaweed farms. These invertebrates are usually found attached on seaweed fronds.

The presence of crabs and shrimps at higher percentages in fish stomachs contributed to the lack of significant difference in type of food eaten by invertivore-piscivores in these habitats. The observed differences in the type of prey item consumed by invertivores between coral reefs, seagrasses and seaweed farms could be due to higher abundance of epifauna on seaweeds. Moreover, changes in seasonal assemblage, abundance and composition of epifaunal communities associated with seaweeds frequently occurs in tropical areas (Ateweberhan *et al*., 2005), which may contribute to variation in diet composition of fish.

Omnivorous fish were found to prefer a variety of gastropods in their diet. Specifically, the Littorinidae, Trochidae and Strombidae dominated stomach contents of fish collected between October and November. This is a period when they are commonly found attached to seagrasses, coral reef and seaweeds (B. Yahya, pers. obs.). This inter-tropical monsoon period is also a time when spawning activity is typically high in the WIO region (Robinson *et al*., 2008). Polychaetes and detritus were observed in high percentages in most fishes, contributing to the lack of significant difference in type of food eaten by omnivores in these habitats.

Analysis of stomach contents showed four main trophic groups in different habitats. Piscivores were relatively scarce in the samples as were planktivores such as the Pomacentridae, the latter likely due to gear type limitations. The herbivores dominated catch caught in all habitats, with highest RTC % in coral reefs followed by seagrasses, and the lowest in seaweed farms. This could be due to the fact that fish use coral reefs and seagrass beds either as feeding, breeding, nursery or hiding grounds (Beck *et al*., 2001). These habitats also play an important role in the regulation of foraging patterns (Erlandsson *et al*., 1999). Studies indicate that the evolution and development of modern reefs has been dependent on the presence of herbivores, controlling growth of algae and thus creating the space for development and evolution of corals (Bellwood and Wainwright, 2002; Arosemena, 2005). The herbivores may greatly depend on the physical structure of the coral reef and the distribution of the associated benthic organisms (Ferreira *et al*., 1998). An important part of the diet of some herbivores (e.g. Scaridae) is detritus and/or calcified materials (Arosemena, 2005). The lower RTC % of herbivores in seaweed farms could be because they avoid the areas of macroalgal dominance and prefer coral reef areas. According to Hehre *et al*. (2016), Siganidae tend to avoid areas of high macroalgal biomass even though seaweed farms potentially provide them with food subsidies.

The high RTCs % of invertivores and invertivore-piscivores in the coral reef area was likely because most species that belong to these trophic groups use coral reefs as their main habitats, thus making up a substantial proportion of the coral reef fish population (Berkstrom *et al*., 2012), although in this study they were also recorded in seagrasses, seaweed farms and on sand. These results are consistent with earlier findings (Dorenbosch *et al*., 2005; Berkstrom *et al*., 2012) where it was found that although these trophic groups use coral reefs as their main habitats, they are also recorded in other habitats like seagrass and sandy areas where they migrate for feeding. Invertivores dominated on seagrass because seagrass habitats generally produce an abundant invertebrate fauna (Randall *et al*., 2009) and offer important feeding sites for fish (Nakamura and Sano, 2005). The higher RTC % of invertivores and omnivores in sand areas may be due to their food requirements. Omnivores feed on a variety of organisms, including animals (such as small fish and invertebrates common in sand areas), plants and detritus materials and, for example, have been found to be more abundant in zones of rubble and sand (Arosemena, 2005). Seaweed habitats (both over sand and seagrass) were dominated by invertivore-piscivores. Floating seaweed farms may act as fish aggregating devices, whereby they attract smaller fish and invertebrates, thus providing feeding grounds for predatory fish. Further studies are recommended on the cross-boundary movement of fish between seaweed farms and adjacent seagrass and coral reef habitats.

Conclusion

The findings of this study show that fish used food resources variably depending on availability in their environment and also feeding preference. It was unclear why annelids, nematodes and sipunculids were also observed in the stomachs of herbivorous fishes during the period March to October. Further studies are needed to confirm if these animals are eaten accidentally or intentionally and their importance in the herbivores' diet. Studies on trophic structure where seaweed farming occurs may further reveal the importance of this artificial habitat in tropical waters.

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