RELATIVE IMPORTANCE OF MANGROVES AS FEEDING HABITATS FOR FISHES: A COMPARISON BETWEEN MANGROVE HABITATS WITH DIFFERENT SETTINGS

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ABSTRACT

The importance of mangroves as feeding grounds for fish and other macrozoobenthos in the Indian Ocean and elsewhere has been a subject of debate. This could partly be due to the fact that studies describing this role have been conducted in mangrove systems that differed in their settings. By using stable isotope analysis of carbon and nitrogen, we investigated two different settings of mangroves along the Tanzanian coast, to establish if mangrove setting influences the extent to which this habitat is utilized as a potential feeding ground by fish. The two mangrove settings were: mangrove-lined creeks which retain water during low tides and fringing mangroves that drain completely during low tides. The $\delta^{13}C$ signatures of most fishes from the mangrove-lined creeks were similar to those of food items from the mangrove habitat, which suggests that these fishes feed from the mangrove habitats. In contrast, the overlap in $\delta^{13}C$ of some food items from the fringing mangroves with those from adjacent habitats, and the more enriched $\delta^{13}C$ signatures of fishes from the fringing mangroves with respect to most typical food items from the mangrove habitat could be an indication that these fishes feed from both habitats but to a lower extent from the fringing mangroves. The results suggest that fishes feed more from the mangrove-lined creeks as compared to fringing mangroves which is probably related to differences in the degree of mangrove inundation. The more or less continuous access provided more time for fishes to stay and feed in the mangrove-lined creeks compared to fishes from the fringing mangroves, which have access to these mangroves only during high tide and have to migrate to adjacent habitats with the ebbing tide.

Mangrove ecosystems are widely recognized as potential nursery grounds for juvenile fishes of exploited populations (Blaber et al., 1989; Parrish, 1989; Lugendo et al., 2005). Although most mangrove studies have found a limited role for mangrove detritus in estuarine food webs (Fry and Ewel, 2003), mangrove habitats are assumed to provide abundant food sources, such as algae, crustaceans, and other macrofauna, to resident and transient animals. However, the importance of food from the mangrove habitats is not limited to the potential contribution to fisheries production, rather, to functioning of the whole system that supports fish populations (Fry and Ewel, 2003; Layman, 2007). The importance of mangrove habitats as feeding grounds for fish and other macrozoobenthos is a subject of debate. While some mangrove habitats are reported to form a major feeding habitat for fish and macrozoobenthos in some parts of the Indo-Pacific (e.g., Rodelli et al., 1984; Marguillier et al., 1997; Sheaves and Molony, 2000; Chong et al., 2001; Guest and Connolly, 2004) this importance is refuted in other parts of the Indo-Pacific (e.g., Bouillon et al., 2002a,b) and elsewhere (e.g., Philippines: Primavera, 1996; and the Caribbean: Nagelkerken and van der Velde, 2004a).

The reason for this discrepancy could be due to the fact that these studies have been conducted in mangrove systems that differed in their settings. Lee (1995, 1999)

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pointed out that the degree of "outwelling" of mangrove carbon to adjacent aquatic environments depends to a large degree on the geomorphology and tidal characteristics of the ecosystem. Large tidal ranges that characterize most mangrove ecosystems of the Indo-Pacific influence their functioning as major feeding habitats for fish due to movement of large quantities of seawater and fishes between neighboring habitats showing connectivity by tidally migrating fish (Nagelkerken and van der Velde, 2004b). However, mangrove swamps of the Caribbean, a region characterized in contrast by low tidal differences and slow tidal currents, have also been reported to be major feeding grounds for fish which reside permanently there or always have access to them (Odum and Heald, 1975; Thayer et al., 1987; Ley et al., 1994). More factors than tidal difference alone are involved with respect to the functioning of mangrove habitats as feeding grounds for fish.

Recently, Nagelkerken and van der Velde (2004b) found that fringing mangroves (as opposed to large mangrove forests) in the Caribbean are not an important feeding habitat for most fish species occurring in adjacent habitats. We propose here that the mangrove setting could be one of the important factors influencing the functioning of mangrove habitats as an important feeding area. We investigated two different settings of mangrove habitats along the Tanzanian coast, to determine whether the mangrove setting influences the use of this habitat as a feeding ground by fish. These two mangrove settings were: mangrove-lined creeks which retain water during low spring tides and fringing mangroves which drain completely during low spring tides.

We used stable isotope analysis of carbon and nitrogen since the use of conventional methods such as gut content analysis alone may provide inadequate results because of the following reasons: (1) differences in digestion rates of ingested material, (2) gut contents may be hard to identify, (3) not all contents are digested, (4) gut content analyses provide just a snap-shot of the true diet, and (5) gut content does not reveal from where the food originates (MacDonald et al., 1982; Gearing, 1991; Polis and Strong, 1996). Analysis of the stable carbon and nitrogen isotopes can provide a clearer understanding of diets because they reflect the actual assimilation of organic matter into consumer tissue rather than merely its consumption (Gearing, 1991). The power of stable isotope analysis as a tool in the investigation of aquatic food web structures and dietary patterns is based on the significant and consistent differences in isotopic composition of different types of primary producers due to different photosynthetic pathways or different inorganic carbon sources (Fry and Sherr, 1984; Deegan and Garritt, 1997). The stable isotopic composition of an animal reflects that of its diet with up to 1.0‰ enrichment of ^{13}C and an average of 3.5‰ enrichment of ^{15}N occurring between consumer and its food source (DeNiro and Epstein, 1978; Fry and Sherr, 1984; Minagawa and Wada, 1984) due to the discrimination against lighter isotopes during assimilatory and excretory functions within consumers (Minagawa and Wada, 1984). However, the actual degree of fractionation varies as a function of taxonomy, food quality, type of analyzed tissue, sample treatment, and environmental factors (Vander Zanden and Rasmussen, 2001; McCutchan et al., 2003; Vanderklift and Ponsard, 2003).

The following questions were asked in the present study: (1) is it possible to discriminate potential food items for fishes from the mangrove habitats with those from adjacent habitats in both mangrove settings? and (2) To what degree do fishes present in the mangrove and adjacent habitats utilize food items associated with mangrove habitats?

Materials and Methods

Study Area.—The study was carried out in Tanzanian coastal waters for two different mangrove settings which differ in their degree/duration of inundation (Table 1):

1. Mangrove-lined creeks which retain water during low spring tides. These include the Mapopwe mangrove creek in Chwaka Bay, Zanzibar, and Mbegani mangrove creek in Bagamoyo, Tanzania mainland coast (Fig. 1). Chwaka Bay is a shallow marine bay located on the east coast of Unguja Island, Zanzibar. The bay consists of a large intertidal flat partly covered with mixed assemblages of algae and seagrass beds. On the landward side, the bay is fringed by a dense mangrove forest dominated by *Rhizophora mucronata* Lamarck, 1804 and *Avicennia marina* (Forsskål) Vierh., 1907 with an approximate area of 3000 ha (Mohammed et al., 1995). The mangrove forest has a number of tidal creeks, with Mapopwe Creek (approximately 2 m deep) being the largest and the main water exchange route between the forest and the bay. The mangrove creeks are intertidal in nature with water remaining during low spring tide, and none have any significant freshwater input other than rain. Mbegani mangroves are characterised by a band of mangroves (about 420 m wide) of mainly *Sonneratia alba* J. E. Smith, 1819, but mixed with *R. mucronata*, *A. marina*, and *Bruguiera gymnorhiza* (Linnaeus) Lamarck, 1797. The mangrove forest has a big tidal creek which never falls dry, even during low spring tide. The channel ends into a landward stream (Nyanza river) which can be a potential source of freshwater into the mangrove forest during the rainy season (data were collected here during the dry season). The mudflats adjacent to the mangroves are dominated by heaps of the small bivalve *Arcuatula arcuatula* (Hanley, 1844) imbedded within the mud. There are patches of seagrasses on the mudflat area and a more or less continuous seagrass bed at the mouth of the channel. On the landward side, these mangroves are partly sheltered from the open ocean by the small island Mapopo.

2. Fringing mangroves which drain completely during low spring tides. These are represented by Kaole and Nunge mangroves in Bagamoyo, and Mtoni estuary located south of Dar es Salaam, Tanzanian mainland coast (Fig. 1). Kaole mangroves are characterized by a band of mangroves of about 450 m wide with small intertidal creeks which fall dry during low tide. The mangroves (mainly *S. alba*) are bordered by intertidal seagrass beds that consist of sparse, but mixed (about 8) seagrass species. The Nunge area is characterized by a narrow band (approximately 160 m wide) of mainly *S. alba*. It is also located close to two reefs (Mwamba Pwani and Mwamba Mjini). Between the mangrove fringe and the reefs lies a seagrass bed that contains almost all species of seagrasses found in Tanzania. Topographically, the area is flat and shallow but behind the reef there is a drastic change in slope where the depth increases abruptly. No channels or creeks are found in this area and the mangroves fall completely dry during low tide. Covering an area of 378.4 ha, Mtoni estuary is located south of Dar es Salaam (Fig. 1).

Table 1. Location, setting, characteristics, and type of adjacent habitats of the studied mangrove habitats along the Tanzanian coast.

Location	Site	Mangrove setting	Estuarine vs non-estuarine	Nature of the adjacent habitats
Chwaka Bay, Zanzibar	Mapopwe	Mangrove-lined creek	Non-estuarine	Mud/sand flats and seagrass beds
Bagamoyo	Mbegani	Mangrove-lined creek	Non-estuarine	Mudflats, seagrass beds, and reef habitats
Bagamoyo	Kaole	Fringing mangrove	Non-estuarine	Seagrass beds
Bagamoyo	Nunge	Fringing mangrove	Non-estuarine	Seagrass beds and reef habitats
Dar es Salaam	Mtoni estuary	Fringing mangrove	Estuarine	Mudflats with sparse seagrasses

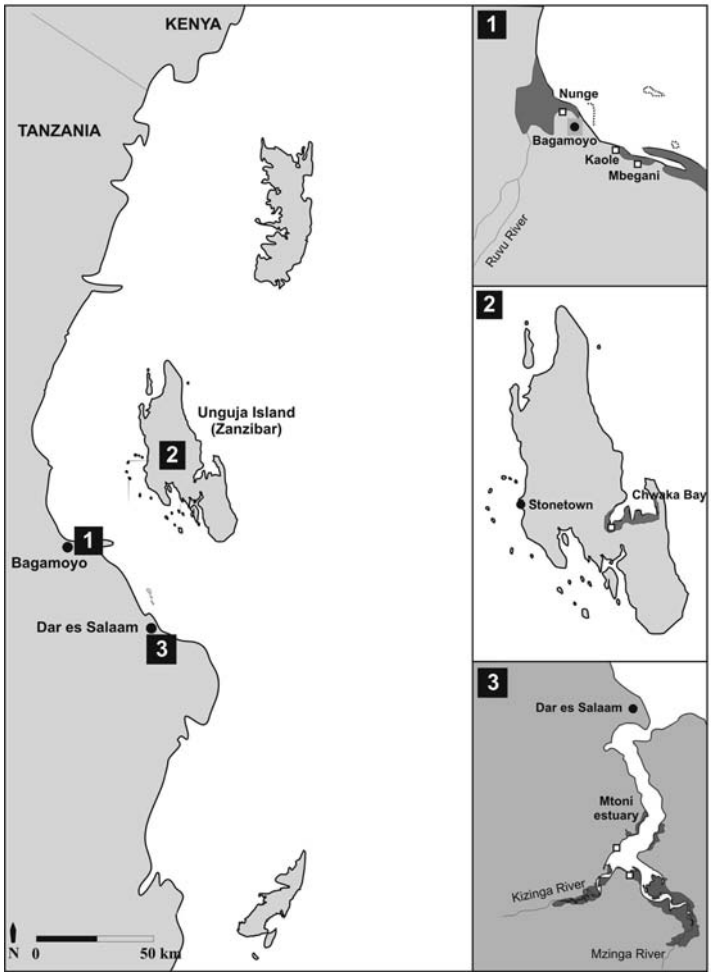


Figure 1. Map of the coast of Tanzania showing the location of Chwaka Bay on Unguja Island (Zanzibar), Kaole, Mbegani and Nunge in Bagamoyo, and Mtoni estuary in Dar es Salaam. Dark grey areas in Bagamoyo, Chwaka Bay and Mtoni indicate mangrove forests, open squares indicate the study sites.

The estuary receives freshwater from two creeks: the Mzinga creek and the Kizinga creek. The estuary is fringed by various species of mangroves with two dominating species, viz. *S. alba* and *A. marina*. Adjacent to the mangroves a large mudflat area with sparse seagrass cover is located. Despite the two creeks that pour freshwater into the estuary, Mtoni mangroves fall completely dry during low tide.

Sampling Design.—Sample collection was carried out between November 2001 and October 2002 in Chwaka Bay, between January and February 2004 in the Mtoni estuary, and between August 2004 and January 2005 in the Bagamoyo area. Fish samples were collected in the mangroves and in the adjacent habitats using a seine net, while a range of benthic macro-invertebrates, seagrasses and algae were collected at the fishing sites by hand. In the continuously inundated mangrove creeks, fish were collected at low tide, whereas in the fringing mangroves the fishes were collected at high tide (when inundated). In all habitats adjacent to the mangroves, fish were collected at low tide. Particulate organic matter was sampled only from Mtoni estuary and was sampled by filtering several liters of seawater over a Whatman GF/C glass fiber filter. In the field, samples were put in a cool box and later frozen at –20 °C

pending analysis. All collected fishes were identified, counted, and their fork length measured to the nearest 0.1 cm. In the majority of the cases, a minimum of three samples were used to include a species in the analysis.

Stable Isotope Analysis.—Muscle tissue was removed from the fish, while molluscs (gastropods and bivalves) and crustaceans (crabs and shrimps) were dissected from their exoskeleton and shell prior to drying. Samples were dried at 70 °C for 48 hrs and ground to powder (homogeneous mixture). For samples rich in carbonates such as whole individuals of small hermit crabs and detritus, sub-samples were acid-washed and oven-dried. These sub-samples were used for stable carbon isotope analysis while the remaining untreated sub-samples were used for stable nitrogen isotope analysis since acid could interfere with stable nitrogen isotopes (Pinnegar and Polunin, 1999). A pre-determined sample of known weight was placed in ultra-pure tin capsules and combusted in a CHN Elemental Analyser from Carlo Erba® (Thermo group), interfaced with a continuous flow isotope ratio mass-spectrometer, the DeltaPlus from Thermo Finnigan, Bremen, Germany. The reference gasses used were calibrated with the IAEA reference standards, IAEA-N-2 and IAEA-CH-6. The potential feeding habitats and food items for fish were estimated in view of the average enrichment in isotope signatures between animals and their potential food items of 1‰ and 3.5‰, for carbon and nitrogen, respectively (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 2001; McCutchan et al., 2003).

Statistical Analysis.—A Levene's test was used to check the data for homogeneity of variances (Field, 2000). In cases where variances were homogeneous, a one-way ANOVA or Student's t-test was done to test for differences in stable isotope signatures of carbon for fish among different habitats. Since sample sizes were very different, a Hochberg's GT2 was used as a post-hoc test due to its greater statistical power in such data compared to other tests (Field, 2000). Either a Kruskal-Wallis test or a Mann-Whitney U-test was used as a non-parametric test equivalent when variances were not homogeneous even after log-transformation. A Games-Howell post-hoc test was used following the Kruskal-Wallis tests because it is more powerful and specifically designed for lack of homogeneity of variances (Field, 2000). A significance level of $P = 0.05$ was used in all tests. All analyses were performed using the programme SPSS 11.5 for Windows (Field, 2000).

Results

Mangrove-lined Creeks.—A clear distinction in $\delta^{13}C$ could be discerned for macrofauna/flora and fishes from the mangrove creeks (Mapopwe and Mbegani) and from the adjacent habitats (Fig. 2). In Mapopwe, the average $\delta^{13}C$ values of macrofauna/flora from the mangrove creeks ranged between –28.4‰ and –20.4‰ (except seagrass leaves) while those from the mud/sand flats ranged between –17.1‰ and –13.8‰ (except detritus; Fig. 2A). Considering the fishes, those from the mangrove habitats were more $\delta^{13}C$ depleted than those from the mud/sand flats (Fig. 2B). The highest enrichment in mean $\delta^{13}C$ values between fish from the mangrove creeks and mud/sand flats was 6.3‰ for individuals of *Lutjanus fulviflamma* (Forsskål, 1775). Three fish species showed deviating values (Fig. 2B). *Siganus sutor* (Valenciennes, 1835) from the mud/sand flats had a highly depleted $\delta^{13}C$ value compared to the other species from the mud/sand flats. *Gerres oyena* (Forsskål, 1775) and *Lutjanus ehrenbergi* (Peters, 1869) from the large mangrove creek showed enriched $\delta^{13}C$ values compared to other species from the mangrove creeks. However, since $\delta^{13}C$ values of *G. oyena* from the mud/sand flats were much more enriched than those from the mangrove creek, we consider that this species also showed the separation in $\delta^{13}C$ between the mangrove creeks and the mud/sand flats. The $\delta^{13}C$ of individuals of *Gerres filamentosus* (Cuvier, 1829), *G. oyena*, *Lethrinus lentjan* (Lacépède, 1802), *L.*

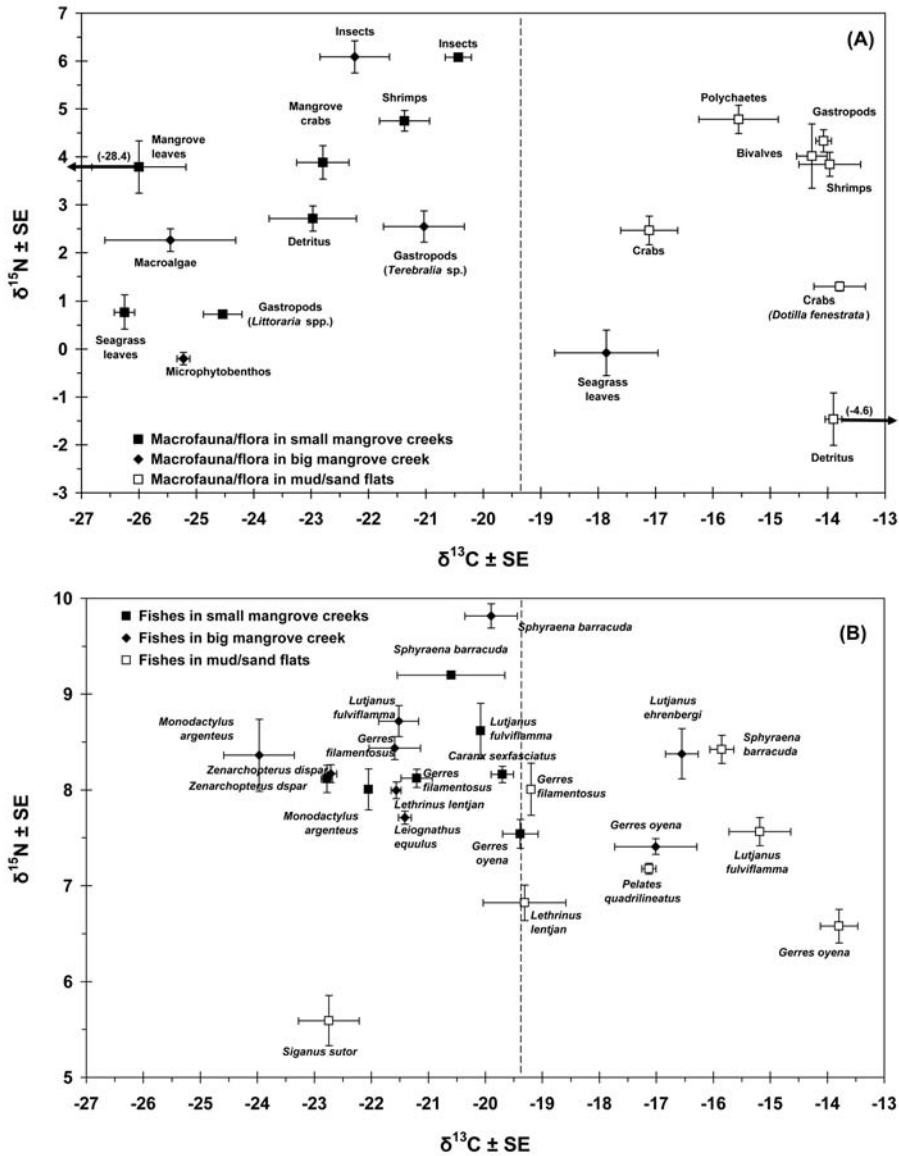
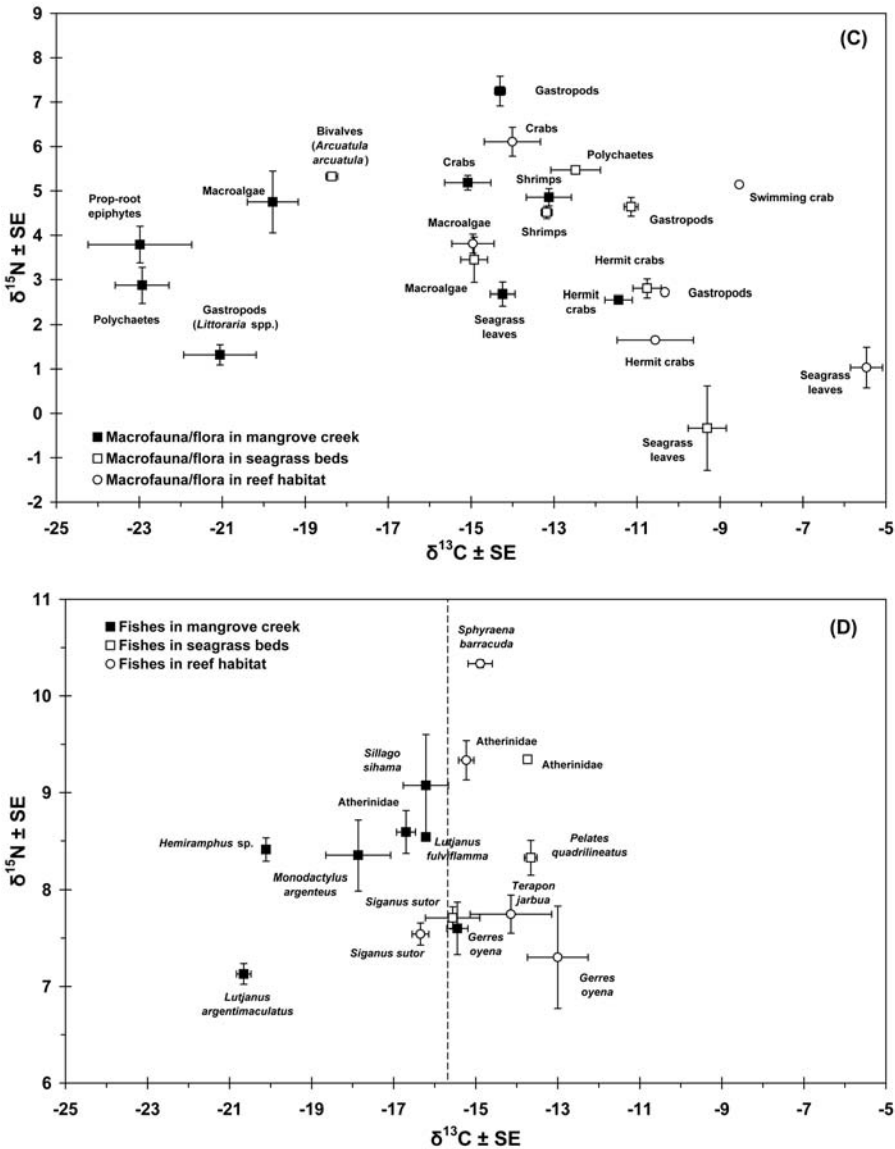


Figure 2. Mean $\delta^{13}C$ and $\delta^{15}N$ values of macrofauna/flora and fishes from mangrove habitats and from adjacent habitats in continuously inundated Mapopwe creek (A–B) and Mbegani creek (C–D) *(opposite page)*. The dotted lines indicate the main separation in $\delta^{13}C$ values between the mangrove and adjacent habitats.

fulviflamma, and *Sphyraena barracuda* (Walbaum, 1792) differed significantly ($P < 0.01$) between the mangrove creeks and the mud/sand flats. The $\delta^{13}C$ values of the other species were not tested because these species occurred in one habitat only. The $\delta^{15}N$ values of food items from Mapopwe ranged from –1.5‰ (detritus) to 6.1‰ (insects) while those of fishes ranged from 5.6‰ (*S. sutor*) to 9.8‰ (*S. barracuda*). These $\delta^{15}N$ values clearly show the trophic position of fishes belonging to different feeding guilds, with lowest values for herbivores, intermediate values for zoobenthivores, and highest values for piscivores.



In Mbegani, average $\delta^{13}C$ values of macrofauna/flora from the mangrove creek ranged between –23.0‰ and –11.4‰ (Fig. 2C). Average $\delta^{13}C$ values of macrofauna/flora from the seagrass bed overlapped in several cases with those from the mangrove and reef habitats and they ranged between –18.4‰ and –9.3‰ for seagrass beds and between –15.0‰ and –5.5‰ for the reef habitat. Considering specific groups of macrofauna/flora, however, there were clear differences in mean $\delta^{13}C$ values for polychaetes, gastropods, macroalgae, and seagrass leaves between mangrove and seagrass/reef habitats (Fig. 2C). With respect to the fish, a very clear separation $\delta^{13}C$ was present between specimens from the mangrove creek and those from the adjacent seagrass beds/reef habitats (Fig. 2D). Fish from the seagrass beds and reef habitats were similar in $\delta^{13}C$ but more enriched (by on average 3.1‰) than those from the

mangrove creek (Fig. 2D). A species of Atherinidae and *G. oyena* from the mangrove creek were significantly depleted (t-test: P = 0.005 and P = 0.013, for Atherinidae and *G. oyena*, respectively) as compared to those from the reef habitat. Statistical tests could not be performed for the other species as they occurred in only a single habitat. For the whole Mbegani area, the $\delta^{15}N$ values of food items ranged between –0.3‰ (seagrass leaves) and 7.2‰ (gastropods) while those of fishes ranged between 7.1‰ (*Lutjanus argentimaculatus* (Forsskål, 1775)) and 10.3‰ (*S. barracuda*), reflecting the trophic positions of the studied fish species (Fig. 2C, D).

Fringing Mangroves.—Although a clear difference in $\delta^{13}C$ values could be discerned for macrofauna/flora between the mangrove habitats and the adjacent habitats in Kaole, Nunge, and Mtoni, this could not be discerned for the fishes in these habitats (Fig. 3). In Kaole, the mean $\delta^{13}C$ values of macrofauna/flora from the mangrove creek ranged between –19.4‰ and –16.0‰ (except shrimps; Fig. 3A). Those from the intertidal seagrass beds ranged between –15.2‰ and –11.3‰, while those from the subtidal seagrass beds overlapped partly with those from the intertidal seagrass beds and ranged between –13.4‰ and –7.5‰. The $\delta^{13}C$ values of fishes from the mangrove habitat of Kaole (mean ± SE = 14.9 ± 0.7‰) overlapped with those from the intertidal seagrass beds (14.9 ± 0.4‰; Fig. 3B). However, fishes from the subtidal seagrass beds were much more enriched in $\delta^{13}C$ (10.9 ± 0.1‰). At species level, *G. oyena*, *Pelates quadrilineatus* (Bloch, 1790), and *L. fulviflamma* from the subtidal seagrass beds all differed significantly (t-test: P < 0.013) from those from the mangrove habitat or intertidal seagrass bed. The $\delta^{15}N$ values of food items ranged between 0.6‰ (*Littoraria* sp.) and 5.4‰ (insects) while those of fishes ranged from 4.9‰ *Leptoscarus vaigiensis* (Quoy and Gaimard, 1824) to 9.4‰ (Atherinidae).

In Nunge, the mean $\delta^{13}C$ values of macrofauna/flora from the mangrove habitat ranged between –21.0‰ and –15.2‰ (except shrimps), those from the seagrass beds ranged between –15.7‰ and –13.2‰, and those from the reef habitat ranged between –15.1‰ and –10.0‰ (except for the gastropod *Terebralia* sp.; Fig. 3C). The $\delta^{13}C$ values of fishes in Nunge did not show a clear distinction between the different habitats, rather their mean $\delta^{13}C$ values were clustered between –16.0‰ and –10.3‰ and overlapped between habitats at species level (Fig. 3D). The $\delta^{15}N$ values of food items ranged from 1.9‰ (*Littoraria* sp.) to 8.3‰ (crabs) while those of fishes ranged from 6.8‰ (*G. oyena*) to 11.7‰ (*P. quadrilineatus*) indicating that different fish species belong to different trophic positions.

In Mtoni, the average $\delta^{13}C$ values of mangrove macrofauna/flora ranged between –25.9‰ and –17.8‰, with the exception of shrimps, swimming crabs, and barnacles (Fig. 3E). Those from the estuary basin ranged between –17.7‰ and –13.5‰, except particulate organic matter, polychaetes, and macroalgae. The $\delta^{13}C$ values of fishes from Mtoni did not show a clear distinction in $\delta^{13}C$ signature between the mangrove habitat and the estuary basin, and did not show a large variation within species (Fig. 3F). Only the herbivore *S. sutor* and one species of Carangidae deviated considerably in their $\delta^{13}C$ and/or $\delta^{15}N$ values from the cluster of other species (Fig. 3F). No significant difference was found between the $\delta^{13}C$ values of fishes from the mangrove habitat and the estuary basin for *Albula glossodonta* (Forsskål, 1775), Carangidae, *G. filamentosus*, *G. oyena*, *Sillago sihama* (Forsskål, 1775), and *Terapon jarbua* (Forsskål, 1775) (t-test: P > 0.144). The remaining species could not be tested statistically as they occurred in only a single habitat. In the whole estuary, the $\delta^{15}N$ values of food items ranged between 3.4‰ (detritus) to 12.6‰ (shrimps) while those

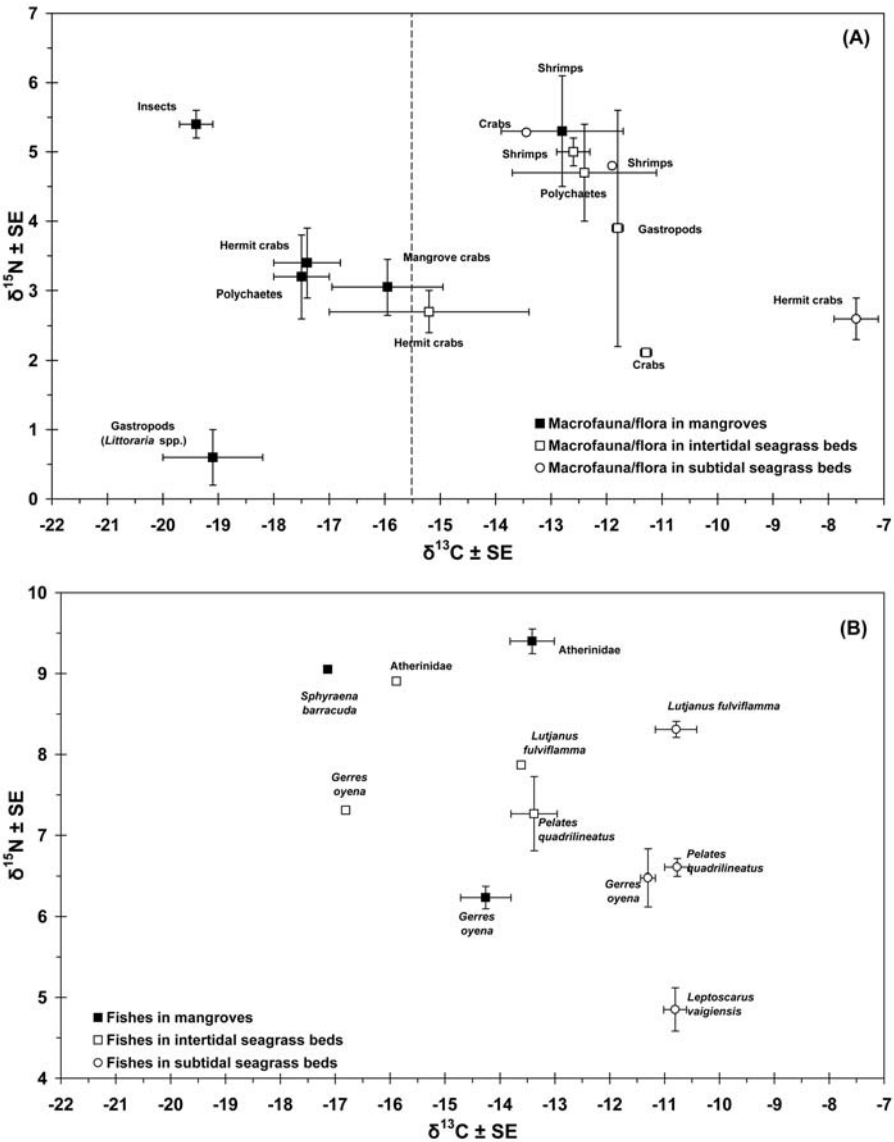


Figure 3. Mean $\delta^{13}C$ and $\delta^{15}N$ values of macrofauna/flora and fishes from the mangrove habitats and from adjacent habitats, in Kaole (A–B), Nunge (C–D) *(on page 506)* and Mtoni (E–F) *(on page 507).* The fish species of Mtoni are represented by the following numbers, 1: *Leiognathus equulus*, 2: Gobiidae sp. 1, 3: *Terapon jarbua*, 4: *Gerres acinaces* (Bleeker, 1854), 5: *Gerres oyena*, 6: *Gerres filamentosus*, 7: *Sillago sihama*, 8: *Albula glossodonta*, 9: *Gerres oyena*, 10: *Albula glossodonta*, 11: *Arothron hispidus* (Linnaeus, 1758), 12: *Scarus russelii* (Valenciennes, 1840), 13: *Lethrinus lentjan*, 14: *Arothron immaculatus* (Bloch and Schneider, 1801), 15: *Sardinella albella*, 16: *Leiognathus equulus*, 17: *Apogon* sp. 1, 18: *Apogon* sp. 2, 19: *Apogon* sp. 3, 20: *Terapon jarbua* (Forsskål, 1775), 21: *Atherinomorus duodecimalis* (Valenciennes, 1835), 22: *Gerres filamentosus*, 23: Atherinidae, 24: *Lutjanus fulviflamma*, 25: Gobiidae sp. 2, 26: *Sillago sihama*, 27: *Gerres acinaces*, 28: Gobiidae sp. 3, 29: *Platycephalus indicus* (Linnaeus, 1758), 30: Mugilidae sp. 1, 31: *Saurida gracilis* (Quoy and Gaimard, 1824), 32: Mugilidae sp. 2, 33: *Callionymus* sp., 34: *Pelates quadrilineatus*, 35: Gobiidae sp. 4, 36: *Siganus sutor,* 37: Carangidae, 38: Carangidae. The dotted lines indicate the main separation in $\delta^{13}C$ values of food items between the mangroves and adjacent habitats.

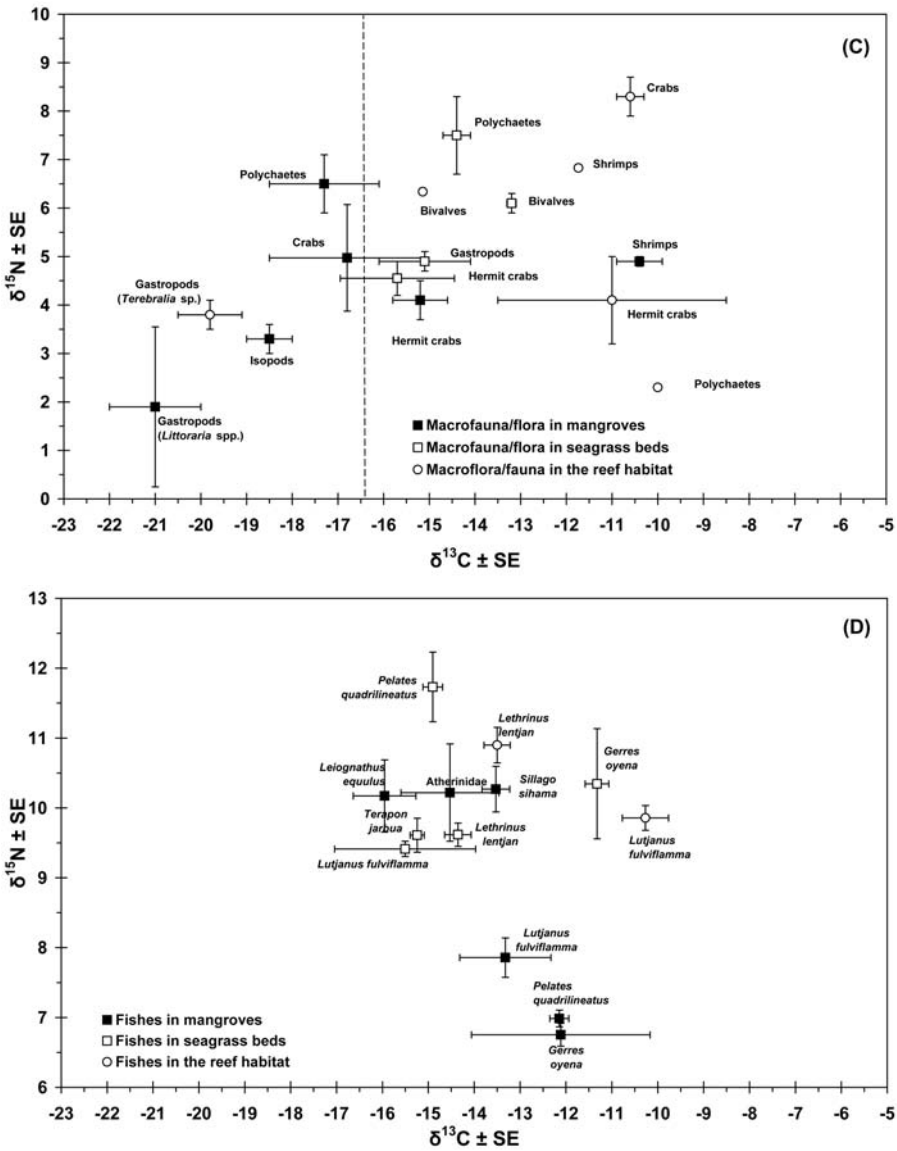


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of fishes ranged from 8.2‰ (Carangidae) to 15.2‰ (*Apogon* sp.). These $\delta^{15}N$ values are relatively higher compared to $\delta^{15}N$ values of the food items and fishes from the other four studied sites, probably due to the inflow of Karibu textile effluents into the area (eutrophication).

Discussion

On the basis of the differences in $\delta^{13}C$ signatures of most of the potential food items in the various habitats, the most likely feeding habitats of the fish can be deduced. The food items (macrofauna/flora) from the mangrove habitats of both man-

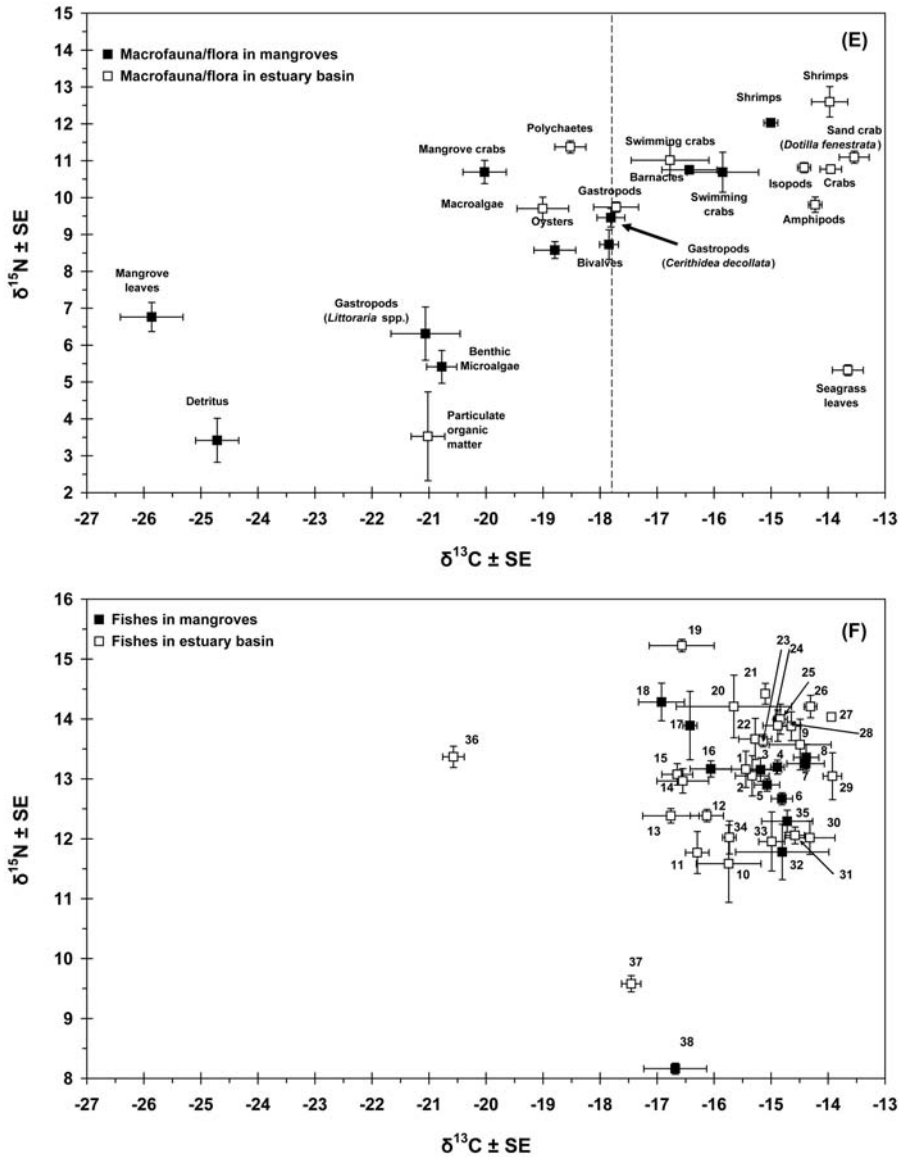


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grove settings were generally more $\delta^{13}C$ depleted compared to similar food items from their respective adjacent habitats. While the stable isotope values of fishes from the mangrove-lined creeks followed a similar trend, those from the fringing mangrove habitats did not. Fishes from the mangrove-lined creeks displayed a $\delta^{13}C$ signature similar or close to food items from the mangrove creeks, which could be an indication that they feed mostly on food items from the mangrove habitats. Another possibility is that the fishes caught from the mangrove creeks feed elsewhere (possibly during high tide), but on food items with a similar $\delta^{13}C$ signature as those of food items from the mangrove habitats; especially those food items which were not covered in the sampling for the present study. However, this is unlikely since food

items from other habitats were always more enriched than those from the mangrove habitats, a situation which has widely been observed in other studies (e.g., Rodelli et al., 1984; Bouillon et al., 2002b; Kieckbusch et al., 2004; Nagelkerken and van der Velde 2004a). In contrast, the much more enriched $\delta^{13}C$ signature of the fishes from the fringing mangrove habitats as compared to those of food items from the mangrove habitats suggests that these fishes obtained most of their food from the adjacent habitats. On the other hand, the overlap in the $\delta^{13}C$ signatures of some of the food items (e.g., motile crabs, shrimps, and hermit crabs) between the fringing mangrove habitats and the adjacent habitats, suggest that possibly those fishes may feed from all the studied habitats.

The above observations suggest that the utilization of mangrove habitats as feeding grounds for fishes is different in the two mangrove settings. Both settings of mangroves are flooded completely only during high tide. However, fishes from the mangrove-lined creeks can remain in the water held within the creeks during low tide, and hence have a more or less permanent access to the mangrove habitat, where they apparently also feed and hence acquire more depleted $\delta^{13}C$ signatures similar to those of food items from the mangrove habitat. In contrast, fishes from the fringing mangroves have access to the mangrove habitats only during high tide, and have to migrate to adjacent habitats (seagrasses, reef or mud/sand flats) with the ebbing tide where they probably also feed. Although these fish could feed in the fringing mangroves at high tide, their more enriched $\delta^{13}C$ signatures (similar to those of food items from the adjacent habitats) suggest that they probably obtained more food from the adjacent habitats than from the mangrove habitats. Since these fringing mangrove habitats are not continuously accessible, this suggests that fishes may partly use these mangrove habitats for feeding at high tide, but largely use adjacent habitats as feeding habitats at low tide. As pointed out by Fry and Ewel (2003), the access and residency (time) of animals within the mangrove ecosystems could influence the utilization of mangrove resources.

Additionally, the fact that fishes caught in the mangrove-lined creeks at low tide did not include fishes with a more enriched $\delta^{13}C$ signature (except possibly *L. ehrenbergi* from the mud/sand flats of Chwaka Bay) suggests that fishes from the mangrove-lined creeks (with a depleted $\delta^{13}C$ signature) and those from adjacent habitats (with an enriched $\delta^{13}C$ signature) form two different feeding populations. This was also observed for permanently inundated fringing mangroves in the Caribbean (Nagelkerken and van der Velde, 2004b).

The species that appeared to feed primarily from the mangrove-lined creeks in the present study have mostly been reported to be mangrove residents, especially at juvenile and young adult stages (i.e., *Caranx sexfasciatus* Quoy and Gaimard, 1825, *G. filamentosus*, *G. oyena*, *Leiognathus equulus* (Forsskål, 1775), *Lutjanus argentimaculatus* (Forsskål, 1775), *L. fulviflamma*, *L. lentjan*, *S. barracuda*, and *Zenarchopterus dispar* (Valenciennes, 1847); Froese and Pauly, 2005; Lugendo et al., 2005). Again, the $\delta^{13}C$ signatures of their respective species in the fringing mangroves were far more enriched, consistent with the fact that fishes from the fringing mangroves probably obtained their food largely from the adjacent habitats. This is another indication that the degree of mangrove inundation is important in determining the extent to which a mangrove habitat is utilized as a feeding ground by fishes.

The size of the mangrove forest itself is believed to be another critical factor that determines the importance of mangroves as major feeding grounds for fishes. Stud-

ies from the Caribbean report large mangrove swamps to be major feeding grounds for fishes (Odum and Heald, 1975; Thayer et al., 1987; Ley et al., 1994) as opposed to small fringing mangroves (Nagelkerken and van der Velde, 2004b). This is applicable to the Chwaka Bay mangrove forest (where the Mapopwe creek is found) due to its large size, but not to the Mbegani mangrove creek which is lined by a narrow mangrove forest. We do not rule out the possible influence of mangrove forest size in selection of feeding habitats by fishes in our study. However, the smaller sizes of the studied mangroves of Bagamoyo (e.g., Mbegani and Kaole mangrove forests together cover 179.1 ha; Semesi, 1991) and the differences in the way they were utilized by fishes, as we observed, is consistent with our hypothesis that degree of mangrove inundation is a more important factor influencing the extent to which mangrove habitats are utilized as feeding grounds by fishes.

Although most fishes did not seem to use the fringing mangroves during low tide as major feeding habitats, some macrofauna did. Some macrofauna species were restricted to the mangrove habitats as suggested by their highly depleted $\delta^{13}C$ signatures (< –19.0‰). This was the case for mangrove crabs (mostly Sesarminae and *Uca* spp.), gastropods (mostly *Littoraria* spp. and *Terebralia* sp.) and insects, which are all known to feed on either mangrove leaves, detritus, micro-epiphytes, diatoms, or mud from the mangrove habitats (Slim et al., 1997; Bouillon et al., 2002a; Ólafsson et al., 2002; Skov and Hartnoll, 2002; Fratini et al., 2004). These species that likely feed solely from the mangrove habitat remained in the mangroves during low tide even when all water drained away. Mangrove crabs and gastropods are adapted to living in intertidal areas for extended periods by retreating in their burrows (crabs) and in their shells (gastropods) during low tide. In contrast, fishes depend solely on the presence of water and must move with the ebbing tide; therefore, degree of mangrove inundation is a crucial determinant of the extent to which fishes can use a mangrove habitat as a feeding ground.

Motile macrofauna (e.g., shrimps, swimming crabs, and hermit crabs) from the fringing mangroves, on the other hand, showed enriched $\delta^{13}C$ values (> 16.8‰) typical for macrofauna from the adjacent habitats, indicating an interaction or connectivity between mangroves and their adjacent habitats. These species probably use the mangrove only as a refuge and feed on food items from the adjacent habitats. The same trend was also evident for sessile filter-feeding barnacles within the mangroves at Mtoni estuary. Since the mangroves drain completely during low tide the barnacles depend on suspended food sources brought in with the incoming tide from the estuary. Furthermore, the $\delta^{13}C$ values of particulate organic matter from the estuary were in-between those of seagrass and mangrove leaves, indicating that it consisted of a mixture of plant material from the terrestrial mangrove habitat and from the estuary basin (e.g., seagrass leaves).

In contrast to the above, in continuously inundated mangroves of Mapopwe Creek (Chwaka Bay) all macrofauna ($\delta^{13}C$ values < –20.3‰) appeared to feed largely from the mangrove habitats. However, in the case of the continuously inundated Mbegani mangrove creek, the mangrove gastropods *Littoraria* spp. and polychaetes ($\delta^{13}C$ values < –21.1‰) appeared to feed largely from the mangrove habitats, whereas the more motile fauna (crabs, shrimps, and hermit crabs) appear to feed largely from adjacent habitats. Interestingly, the $\delta^{13}C$ value of the bivalve *A. arcuatula* from the seagrass habitat of Mbegani (mean $\delta^{13}C$ value of –18.4‰) suggests incorporation of a mixture of material from both the mangrove and seagrass habitats.

In summary, in almost all cases, food items from both mangroves settings could be discriminated by $\delta^{13}C$ from those of adjacent habitats. Exceptions were always found for the motile swimming and hermit crabs and shrimps, and for sessile filter-feeding organisms. Fishes from all habitats adjacent to mangroves, and those from the fringing mangroves showed a more enriched $\delta^{13}C$ signature, indicating that they probably obtained their food largely from the adjacent habitats. In contrast, mangroves that allowed a more or less continuous utilization of the mangrove habitats by fishes appeared to contribute to a larger degree to the food of fishes as compared to fringing mangroves that drain completely during low tide. This study revealed that the potential of a mangrove habitat in functioning as a feeding area for fish can to be influenced by its configuration or setting. Fringing mangrove habitats seem to contribute less to the food items of fishes as compared to continuously accessible mangrove-lined creeks. Ecosystems showing more similarity in configuration may function in a similar way despite geographical differences.

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